

BRIDGERIAN AND UINTAN (EOCENE) MAMMALS FROM SAGE CREEK AREA OF SOUTHWEST MONTANA

Donald Lofgren¹, Debra Hanneman², Bailey Jorgensen¹, Shuwen Zhang³, Laura Li³, Xander Kong³, Jonathan Yu³, Liam Gerkin³, Frank Hu³, Aspen Helgeson³, Yvonne Kan³, Jonathan Becker³, Emily Li³, Sihan Li³, Nick Lee³, Anthony Runkel⁴.

¹Raymond M. Alf Museum of Paleontology, Claremont, California, 91711

²Whitehall GeoGroup Inc., Whitehall, Montana, 59759

³The Webb Schools, Claremont, California, 91711

⁴Minnesota Geological Survey, St. Paul, Minnesota, 55114

ABSTRACT

The oldest vertebrate bearing Tertiary strata in southwestern Montana are the Sage Creek Formation which yielded a limited mammalian assemblage that includes *Eotitanops borealis* and *Palaeosyops paludosus*, index taxa for the Br1a and Br2 biochrons of the Bridgerian North America Land Mammal Age. An ashfall lapilli tuff associated with Br1a mammals in the lower part of the formation yielded a sanidine 40Ar/39Ar age of 49.84 $\pm$ 0.04 Ma consistent with the hypothesis that the Wasatchian-Bridgerian boundary is approximately 50 Ma. A Br2 assemblage was recovered from the upper part of the formation and an ashfall lapilli tuff just below the top yielded a sanidine 40Ar/39Ar age of 48.74 $\pm$ 0.08 Ma indicating that deposition of the formation spanned about 1 Ma. All mammalian taxa from the Sage Creek Formation are known from early Bridgerian strata in Wyoming and Colorado indicating dispersal between southwest Montana and areas to the south. The Sage Creek Formation is overlain disconformably by the Dell beds whose western and eastern exposures were thought to differ in age but new faunal data suggest that they are temporally equivalent. The Dell beds mammalian assemblage correlates with late Uintan Ui3 biochron assemblages and includes the only record of *Pentacemylus* outside of the Uinta Basin, the only known specimen of *Schizotheroides parvus*, and the unique co-occurrence of *Colodon kayi* and *C. woodi*. The presence of *Ischyromys* and the new species *Dolocylindrodon farkei* constitute generic range extensions from Duchesnean into late Uintan strata. The Dell beds mammalian assemblage shares five of the seven known species from Uintan strata in the Gravelly Range 60 km to the east. Otherwise it is most similar to late Uintan assemblages from Wyoming, Utah, and Saskatchewan based on shared species. This indicates that significant dispersal of mammals was occurring within the northern Rocky Mountain States and the Saskatchewan part of the Great Plains during the late Uintan.

INTRODUCTION

The earliest collection of vertebrate fossils from the Sage Creek area in southwest Montana (Figure 1) was made by Earl Douglass (1903), who reported the recovery of four specimens from strata of apparent Eocene age that he called the Sage Creek beds which also contained calcified tree trunks and twigs. These mammals, now housed at the Carnegie Museum of Natural History (CM) were identified by Douglass (1903) as *Heptodon?* (CM 717), *Hyrachyus “priscus”* (CM 784), *Hyrachyus?* (CM 603), and *Metamynodon?* (CM 734). This small collection garnered the attention of Horace Wood, who was revising the Hyrachyidae and subsequently proposed a new species, *Hyrachyus douglassi* (named in honor of its collector) based on CM 784 (Wood 1934). At that time, strata in the Sage Creek area appeared to be “the only Eocene in Montana” (Wood 1934, 253) and Wood hoped to collect additional fossils to determine the age of the beds. A visit in 1933 resulted in the discovery of a series of greenish gray sandstones containing calcified logs, strata referred to as the Sage Creek Formation by Wood (1934) and later considered the type locality of

the formation by Tabrum et al. (1996). Wood (1934) assumed that CM 784 and CM 717 were collected from the greenish-gray sandstones and that buff-colored rocks above the green sandstones yielded CM 603 and CM 734.

Jean Hough from the United States National Museum (USNM) visited the Sage Creek area in 1950–1953 and described specimens representing seven Uintan taxa from buff-colored beds in an area now called Hough Draw, located about 1.5 km east of the type locality of the Sage Creek Formation (Hough 1955). But after an intensive search where no fossils were found in the greenish beds, Hough (1955) argued incorrectly that the four specimens described by Douglass (1903) were all collected from buff-colored strata above the Sage Creek Formation. These buff-colored sediments were informally termed the Dell beds by Fields et al. (1985) and assigned an Uintan age based on unpublished data provided by Alan Tabrum who began a PhD dissertation titled “Stratigraphy, sedimentation, and age relationships of Eocene and Oligocene sediments of a part of the Red Rock Hills and Sage Creek Basin” in 1977 at the University of Montana (not completed). Tabrum’s collecting efforts

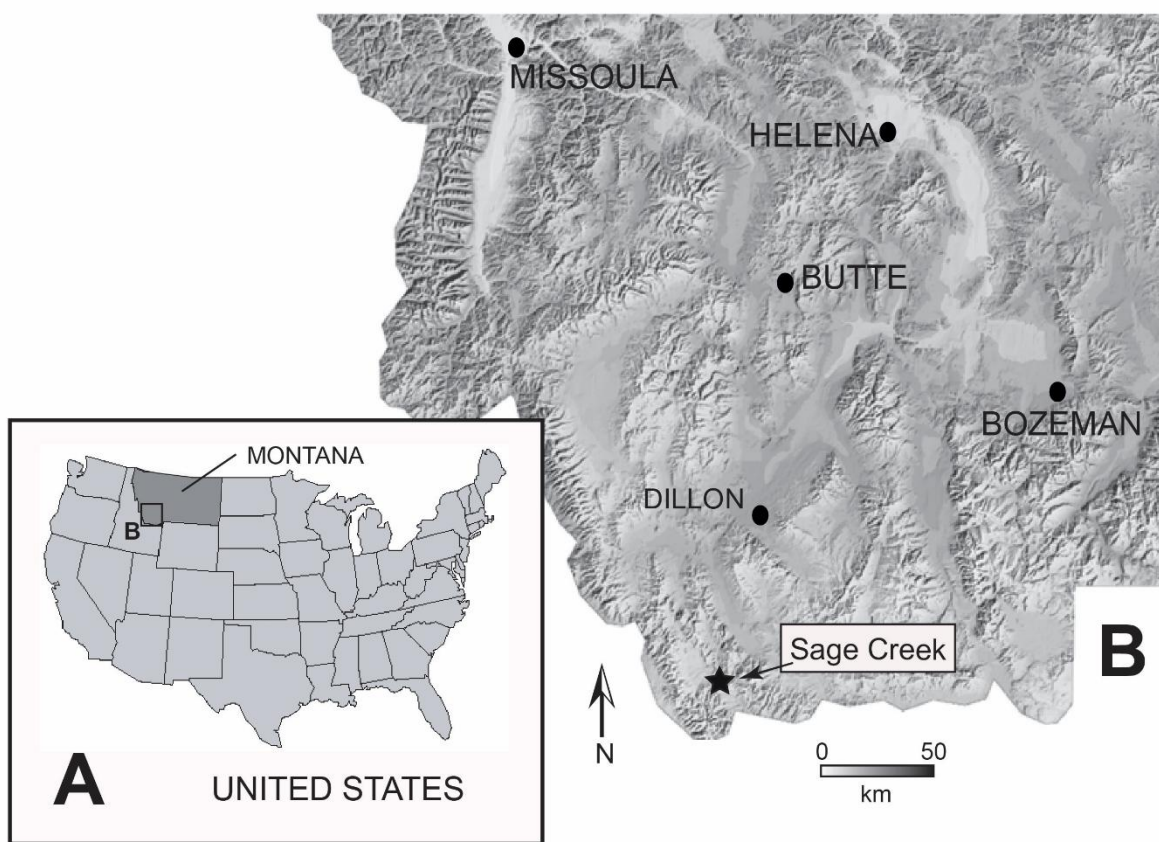


FIGURE 1. Location of the Sage Creek study area on digital relief map of southwest Montana that includes five major cities (sourced from the Montana State Library, Natural Resources Information System 2001 data bank).

confirmed there were two vertebrate fossil bearing Eocene units, the Sage Creek Formation of Bridgerian age and the overlying Dell beds of Uintan age, and that outcrops of the Sage Creek Formation also occurred at Fields Draw and Dunlap Draw in addition to the type locality (Tabrum et al. 1996, 2001). Updated mammalian faunal lists for the Sage Creek Formation and Dell beds were provided by Tabrum et al. (1996, 2001) who noted that CM 717 and CM 784 were from the Sage Creek Formation and CM 603 and CM 734 were from the Dell beds. Until his death in 2017, Tabrum continued to collect in the Sage Creek area while working at the CM but very few of these specimens were described.

Between 2017 and 2023, crews from the Raymond Alf Museum of Paleontology and Whitehall GeoGroup visited the Sage Creek area to collect additional vertebrate fossils from the Sage Creek Formation and the Dell beds. These collections and those housed at the University of Montana Paleontology Center (UMPC/MV), CM, and USNM provide a basis for taxonomic analyses of Eocene

squamates (Lofgren et al. 2023) and mammals (this paper) which include the oldest known mammalian assemblages from Tertiary strata in southwest Montana (Hanneman and Wideman 1991; Tabrum et al. 1996, 2001). Combined with recently dated ashfall tuffs from the Sage Creek Formation, reassessments of the geochronology and biostratigraphy of the Sage Creek Formation and the Dell beds are also provided. Also, mammalian assemblages from these strata are compared to regional biochronologic and biogeographic frameworks for Eocene terrestrial strata in North America, particularly to mammalian assemblages from sites in Wyoming, Utah, California, and Saskatchewan.

MATERIALS AND METHODS

Mammalian teeth and dentigerous elements from the Sage Creek Formation and Dell beds were studied at the CM, UMPC, RAM, and USNM between 2018-2025 and loans were provided by the CM and UMPC for detailed analysis and photography. A

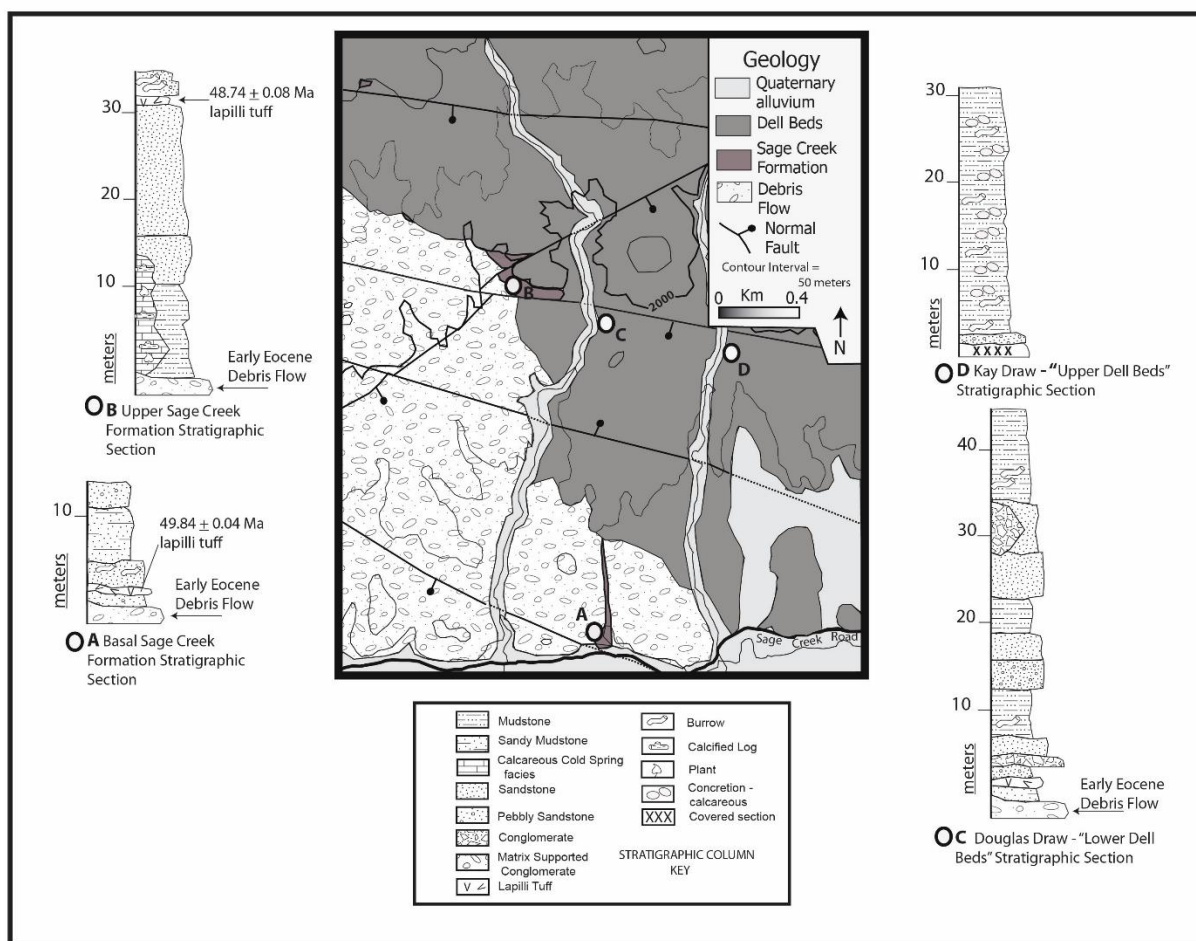


FIGURE 2. Geologic map of study area showing the location of major stratigraphic units and normal faults. A-B represent measured sections of the early Bridgerian Sage Creek Formation, and C-D represent measured sections of the late Uintan Dell beds.

specific site number is provided for each specimen listed in the two Systematic Paleontology sections. Dimensions of mammalian teeth were recorded in mm using a Carrera Precision digital caliper and were photographed using a high-resolution Canon camera system. Specimens from the Sage Creek Formation were recovered from the outcrop surface as were over 80% of those from the Dell beds, screenwashing efforts account for the rest of the Dell beds sample.

Institutional Abbreviations — AMNH: American Museum of Natural History, New York, New York; CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; PU: Princeton University, Princeton, New Jersey (collections now housed at the YPM); RAM: Raymond M. Alf Museum of Paleontology, Claremont, California; SDSNH: San Diego Society of Natural History, San Diego, California; UM: University of Michigan Museum of

Paleontology, Ann Arbor, Michigan; UMPC and MV: University of Montana Paleontology Center, Missoula, Montana; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC; YPM: Yale Peabody Museum of Natural History, New Haven, Connecticut.

SAGE CREEK FORMATION

We recognize the Sage Creek Formation as part of the informal Cenozoic Sequence 1 of Hanneman and Wideman (1991, 2006) which contains largely calc-alkaline flows, ash flow tuffs, and ashfall tuffs that are interbedded with volcanoclastic-rich sedimentary rocks and conglomerate. However, because of historical usage of the "Sage Creek Formation" in lithostratigraphic terminology (e.g. Wood 1934; Hough 1955; Fields et al. 1985; Tabrum

et al. 1996, 2001; Fritz et al. 2007; Schwartz and Graham 2017), we retain this terminology because it facilitates discussion of both strata and vertebrates.

Sage Creek Formation volcanoclastic debris flows and ashfall tuffs accumulated on a pre-existing topography developed on early Eocene volcanics and debris flows. The volcanic units range in composition from rhyolite to basalt and are part of the informal “lower Dillon volcanics” (Fritz et al. 2007; McDonald and Mosolf 2023). Because of the pre-existing topography and as a result of cut and fill, strata are variable in thickness, discontinuous, and areas of outcrop can be geographically separated by more than 2 km (Figure 2). The discontinuous nature and limited aspect of strata indicate that the Sage Creek Formation is an erosional remnant (Wood 1934, this paper). Relationships of isolated patches of outcrops are further obscured by northwest-southeast and northeast-southwest trending normal faults that offset both the Sage Creek Formation and the overlying Dell beds (Figure 2), with offsets ranging from less than a meter to several tens of meters.

The basal part of the Sage Creek Formation lies about 1.8 km south of the type locality and consequently the formation is geographically separated into an older basal stratigraphic section (Figure 2A) and a younger upper stratigraphic section (type locality section) (Figure 2B) based on mammalian biochronology (Tabrum et al. 1996, 2001). These sections were well described by Schwartz and Graham (2017) and we have a few additional observations. The lower section unconformably overlies an early Eocene debris flow and consists primarily of 14.5 m of greenish-gray to light olive, medium to massive-bedded volcanoclastic sandstone and siltstone. An ashfall lapilli tuff 1.5 m from the section’s base (Figure 2A) yielded a Sanidine $^{40}\text{Ar}/^{39}\text{Ar}$ age of 49.84 ± 0.04 Ma. A burrowed horizon is present at about 7 m above the base of the section, indicating at least a temporary hiatus in sediment deposition.

The upper part of the Sage Creek Formation (e.g. type locality of Wood 1934; Tabrum et al. 1996) is approximately 35 m thick and contains strata lithologically similar to the basal Sage Creek Formation with the addition of minor pebble conglomerate beds (Figure 2B) and the presence of locally abundant fossil wood (from twigs to logs). The base of the section is covered but most likely rests unconformably on an early Eocene debris flow as indicated in a nearby water lithology log (Montana Well Log Report 1971). An ashfall lapilli tuff approximately 2 m from the top of the section (Figure 2B) yielded a sanidine $^{40}\text{Ar}/^{39}\text{Ar}$ age of 48.74 ± 0.08 Ma. In contrast to the basal part of the Sage Creek Formation, a lithofacies dominated by cold spring

features occurs at the base of the type section and interfingers eastward into volcanoclastic sandstone. (Figure 2b). A prominent channel fill occurs near the top of the section and a 1.7 m thick composite alfisol that is extensively bioturbated (predominated by dung beetle burrows) and cut by numerous calcified fault zones demarcates the top of the formation (Figure 2B). This alfisol is equivalent to the Sage Creek breccia that earlier authors (Wood 1934; Hough 1955; Tabrum et al. 1996; Schwartz and Graham 2017) described as defining the Sage Creek Formation/Dell Beds contact. Additionally, that the Sage Creek Formation is capped by a composite paleosol contrasts with Fritz et al. (2007, 101) and Schwartz and Graham (2017, fig. 2) who state or imply that the Hall Spring Basalt caps the Sage Creek Formation. The Hall Springs Basalt occurs as erosional remnants at a maximum of 2.1 km northwest of the Sage Creek Formation type locality and has a detrital zircon reported age of 46.2 ± 0.2 Ma (Kent-Corson et al. 2006); a nearby tuff has an age of 45.55 ± 0.14 Ma (McGonigle and Dalrymple 1993). The Hall Springs Basalt does not cap or overlie Sage Creek Formation strata, a relationship illustrated by Fields et al. (1985, fig. 4) and confirmed by our mapping. However, the Hall Spring Basalt is clearly younger than the Sage Creek Formation and older than the Dell beds based on biochronology and geochronology.

The three locations where the Sage Creek Formation crops out (type locality, Fields Draw, Dunlap Draw) are sparsely fossiliferous. The area of exposures at the type locality is extensive and occurs as discontinuous outcrops of varying thickness for about a kilometer, but less than ten mammalian specimens identified to genus have been found in those exposures in over 120 years. The total area of exposures at the type locality exceeds those at Fields Draw by a factor of 10, but over 20 specimens from Fields Draw are identified to genus in the CM and UMPC collections. Outcrops at Dunlap Draw are exposed laterally for only 50 m but they yielded a brontothere maxilla (UMPC 19800). As testament to the difficulty of recovering identifiable specimens from the Sage Creek Formation, intensive prospecting at all three areas by RAM crews yielded only a brontothere molar from Fields Draw #1 (RAM 28086; *Palaeosyops fontinatis*). Corresponding UMPC/MV, CM, and RAM locality numbers used for the three areas are: **Type Locality**: UMPC/MV 7914, CM 3556. **Fields Draw** (composed of three sites): Fields Draw #1: UMPC/MV 7811, CM 3553, RAM 2017043; Fields Draw #2: UMPC/MV 7812; and Fields Draw #3: CM 3555. Fields Draw #1 and #3 are separated by 50 m with Fields Draw #2 located about 400 meters from the other two. **Dunlap Draw**: UMPC/MV 8115.

SAGE CREEK FORMATION SYSTEMATIC PALEONTOLOGY

Order Tillodontia Marsh 1875
Family Esthonychidae Cope 1883
Trogosus Leidy 1871
Trogosus sp. indeterminate
Figure 3A, Table 1

Referred Specimens—UMPC 9462 right i2 fragment, UMPC 9469 right i2 fragment from UMPC locality MV 7811.

Description—UMPC 9462 and UMPC 9469 have blunt worn tips and a complete labial enamel band that extends to half of the distal and a quarter of the mesial sides of the i2s (Figure 3A), with no evidence of a lingual longitudinal groove. The anteroposterior diameters of these teeth and the labial-lingual diameter of UMPC 9462 are provided in Table 1.

Discussion—Tillodonts are comprised of two subfamilies, Trogosinae and Esthonychinae, with the latter represented only by *Esthonyx* (Lucas and Schoch 1998), which have much smaller incisors than the two Sage Creek Formation specimens. Within Trogosinae, the enamel of i2 of *Megalestonyx* extends over most of the mesial and distal side of the incisor (Rose 1972) and the i2 of *Tillodon* is cylindrical labially and flattened lingually (Gazin 1953), both unlike UMPC 9462 and UMPC 9469. A lingual longitudinal groove in i2 is absent in *Trogosus* (Miyata 2007) and UMPC 9462 and UMPC 9469 align with *Trogosus* in this regard. Bridgerian species of *Trogosus* include *T. minor*, *T. castoridens*, *T. latidens*, *T. hillsii*, and *T. gazini* (Gazin 1953; Miyata 2007; Lucas and Schoch 1998). Specific diagnostic characters of these taxa are features of the skull and cheek teeth (Gazin 1953) and the few known i2s of these species lack defining characteristics. Based on size, UMPC 9462 and UMPC 9469 are slightly larger than the i2 of *T. castoridens* and significantly larger than the i2 of *T. gazini* (Table 1). However, i2s are not known for all species of *Trogosus* (Gazin 1953) so UMPC 9462 and UMPC 9469 cannot be referred to a specific species.

Order Condylarthra Cope 1881
Family Hyopsodontidae Trouessart 1879
Hyopsodus Leidy 1870
Hyopsodus sp. cf. *H. minusculus* Leidy 1873
Figure 3B

Referred Specimen—UMPC 9461 left dentary fragment with p4-m2 from UMPC locality MV 7812.

Description—Although the p4 of UMPC 9461 is moderately worn, all three trigonid cusps are distinct and the talonid basin is small and has a distinct

hypoconid (Figure 3B). The m1-2 of UMPC 9461 have moderate to heavy wear with a distinct metaconid and protoconid and the talonid has a large hypoconid and a smaller entoconid and hypoconulid that are subequal in size. Measurements of the p4-m2 of UMPC 9461 in mm are: p4 length 3.0, width 2.3; m1 length 3.5, width 2.7; m2 length 3.9, width 3.0.

TABLE 1. Measurement in mm of the i2 of *Trogosus castoridens* (USNM 17886 from Gazin, 1953) and *T. gazini* (USNM 364762 from Miyata, 2007) compared with UMPC 9462 and UMPC 9469 from the Sage Creek Formation (*approximate; AP, anteroposterior diameter, LL, labial-lingual diameter).

	<i>Trogosus</i> <i>castoridens</i>	<i>Trogosus</i> <i>gazini</i>	UMPC 9462	UMPC 9469
AP	13.0	14.2	14.4	14.8
LL	20.0	15.3*	23.4	—

Discussion. Specimens of *Hyopsodus paulus* and *H. minusculus* recovered from the Bridger Formation in the southern Green River Basin of Wyoming are almost exclusively differentiated by size (Gazin 1968; West 1979). *Hyopsodus minusculus* is generally 15–20% smaller than *H. paulus* at the same stratigraphic level and the average length of the m1 of *H. paulus* from low in the Bridger Formation is 3.9 mm and increases to 4.3 mm higher in the formation (West 1979). The m1 length of UMPC 9461 is 3.5 mm and the dimensions of the p4 and m2 of UMPC 9461 are within the size range of larger specimens of *H. minusculus* from Bridger A (Gunnell 1998, table 5). Thus, the size of UMPC 9461 compares more closely with *H. minusculus* and we tentatively refer UMPC 9461 to that species.

Order Perissodactyla Owen 1848
Family Brontotheriidae Marsh 1873
Eotitanops Osborn 1907
Eotitanops borealis Cope (1880)
Figure 3C-D, Table 2

Holotype—AMNH 4892, right maxilla, P4-M3 (M2-3 broken), Wind River Basin (precise locality unknown), Wyoming (Gunnell and Yarborough 2000).

Referred Specimens—UMPC 9463 left m2 or m3 fragment, UMPC 9464 left M1 or DP4 from UMPC locality MV 7811; CM 78375 right p4, CM 78378 damaged right M3 from CM locality 3553.

Discussion—These isolated and/or damaged brontothere teeth (Figure 3C-D) are too small to represent *Palaeosyops* and are similar in size to *Eotitanops* (Tables 2-4), which is represented by two species, *E. borealis* and *E. minimus* that differ in size (Gunnell and Yarborough 2000, table 6; Mhlbachler

2008). CM 78375 and CM 78378 are most similar in size to *E. borealis* (Table 2). The molar area of the damaged M3 (CM 78378) is approximately 580 mm which is similar to the mean molar area of M3s of *E. borealis* from the Green River Basin of Wyoming and smaller than M3s of *Palaeosyops* (Gunnell and Yarborough 2000, fig. 11).

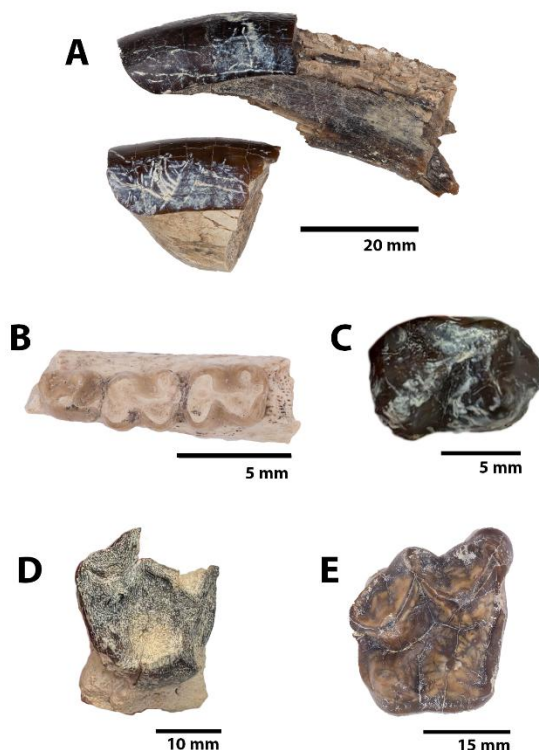


FIGURE 3. Sage Creek Formation mammals. A) Mesial view of UMPC 9469 (top) and UMPC 9462 (bottom) right i2s of *Trogosus* sp. from UMPC locality MV 7811; B) Occlusal view of UMPC 9461 left dentary with p4-m2 of *Hyopsodus* sp. cf. *H. minusculus* from UMPC locality MV 7812. C) Occlusal view of CM 78375 right p4 of *Eotitanops borealis* and D) Occlusal view of CM 78378 damaged right M3 of *Eotitanops borealis* both from CM locality 3553; E) Occlusal view of RAM 28086 right M2 of *Palaeosyops fontinalis* from RAM locality V2017043.

Palaeosyops fontinalis Cope 1873a
Figure 3E, Tables 3-4

Holotype—AMNH 5107 right maxilla with dP4-M1 and erupting M2, bluff on the Green River, Sweetwater County, Wyoming (Gunnell and Yarborough 2000).

Referred Specimens—UMPC 9465 right dentary with p4-m2, UMPC 9466 right M2 missing

part of paracone from UMPC locality MV 7811; CM 78376 left dentary with c, p2, broken m1-2, right dentary with m2-3 and broken p4, CM 78377 broken left MX from CM locality 3553; UMPC 9460 right dentary with p2-m3 and left dentary with p2 and m3 from UMPC locality MV 7812; RAM 28086 right M2 from RAM locality 2017043.

TABLE 2. Measurements in mm of CM 78378 and CM 78375 of *Eotitanops borealis* from the Sage Creek Formation compared with the dentition of *E. borealis* and *E. minimus* from the Green River Basin of Wyoming (Gunnell and Yarborough, 2000:table 6).

		<i>Eotitanops borealis</i>	<i>Eotitanops minimus</i>	CM 78375	CM 78378
p4	L	12.0-13.3	—	12.4	—
	W	7.9-8.8	—	8.7	—
m2	L	16.1-21.5	14.9	—	—
	W	10.4-14.0	10.4	—	—
m3	L	19.0-25.1	16.6	—	—
	W	10.2-13.3	10.2	—	—
P2	L	10.8-11.2	9.7	—	—
	W	8.1-11.0	6.8	—	—
P3	L	11.6-13.0	9.2-9.8	—	—
	W	11.9-14.9	10.8-11.7	—	—
P4	L	9.7-13.5	11.5	—	—
	W	12.3-16.5	13.6	—	—
M 1	L	17.1-23.6	13.7-14.8	—	—
	W	18.6-24.5	17.3-17.7	—	—
M 2	L	15.4-21.3	16.8	—	—
	W	16.4-23.9	18.7	—	—
M 3	L	15.2-21.3	16.0	—	23.2
	W	17.0-24.3	16.6	—	25.1

Discussion—Using Bridgerian specimens from the Green River Basin of Wyoming, Gunnell and Yarborough (2000) demonstrated that species of *Palaeosyops* can be distinguished based on tooth size and the morphology of the upper dentition. If the result of this taxonomic analysis can be applied to brontotheres from the Sage Creek area, two Bridgerian species of *Palaeosyops* (*P. paludosus* and *P. fontinalis*) are present. Lower dentitions from the Sage Creek Formation (CM 78376, UMPC 9465) are similar in size to *Palaeosyops fontinalis* and are smaller than *P. paludosus* (Table 3). Also, UMPC 9466 and RAM

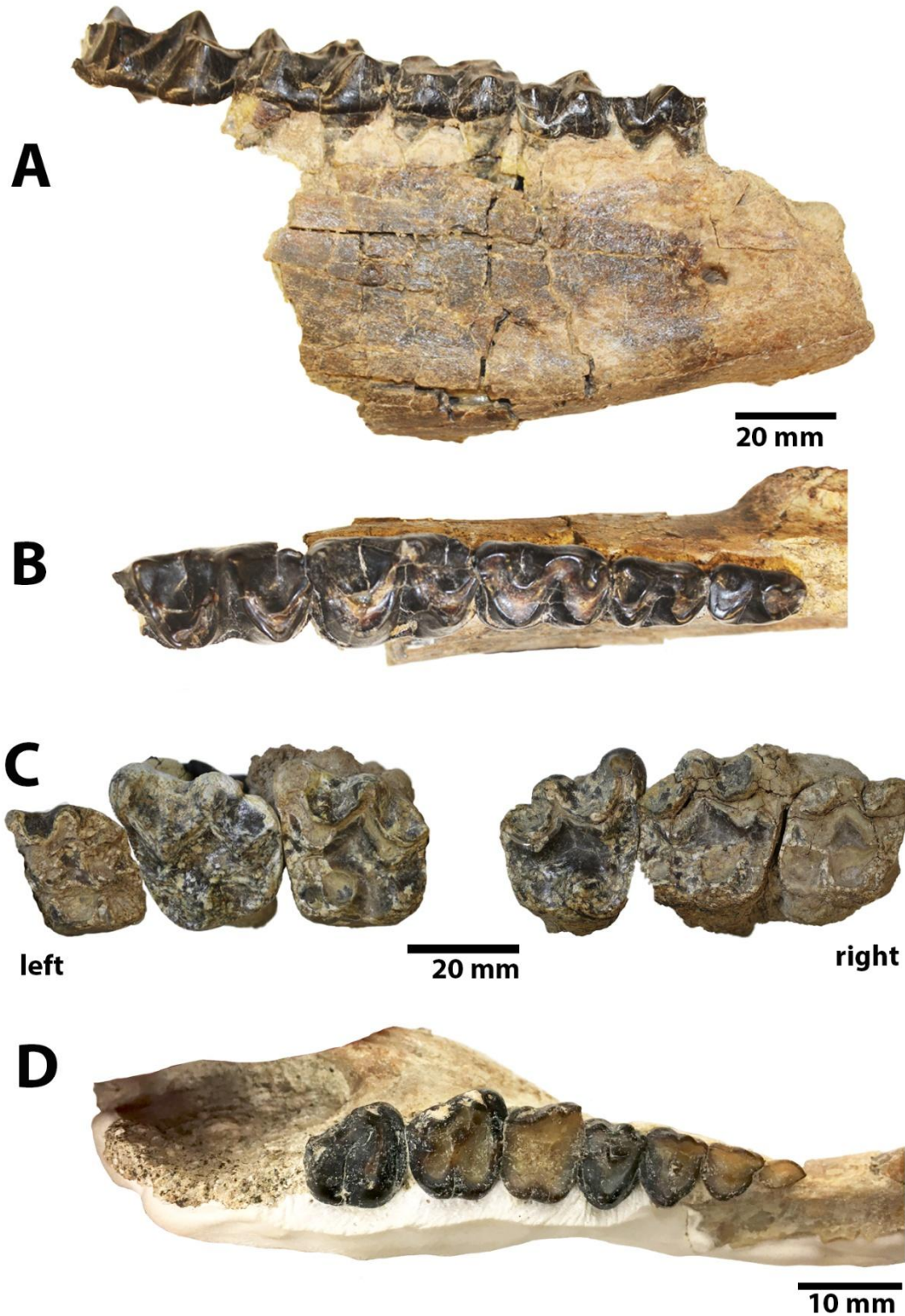


FIGURE 4. Sage Creek Formation mammals. A-B) Labial (A) and occlusal (B) views of UCMP 16736 right dentary with p3-m3 of *Palaeosyops paludosus* from UMPC locality MV 7914. C) Occlusal view of UMPC 19800 left and right M1-3 of *Palaeosyops paludosus* from UMPC locality MV 8115; D) Occlusal view of CM 78371 right maxilla with P1-M3 of *Heleletes nanus* from CM locality 3556.

TABLE 3. Measurements in mm of UMPC 16736 and CM 78372 of *Palaeosynops paludosus* and CM 78376 and UMPC 8465 of *P. fontinalis* from the Sage Creek Formation compared with the lower dentition of *P. paludosus* and *P. fontinalis* from the Green River Basin of Wyoming (Gunnell and Yarborough, 2000:tables 1, 4).

Tooth site		<i>Palaeosynops paludosus</i>	<i>Palaeosynops fontinalis</i>	CM 78382	UCMP 16736	UMPC 9465	CM 78376
p2	L	17.0-20.3	15.6-16.2	18.6-18.7	—	—	15.3
	W	9.4-11.8	8.9	9.6-9.7	—	—	8.8
p3	L	15.6-19.7	14.6-16.3	17.6-17.7	20.1	—	—
	W	10.5-13.3	9.2-10.7	11.3	15.3	—	—
p4	L	18.2-22.2	15.5	18.5-19.0	20.5	15.9	—
	W	13.0-16.0	11.4	13.9-14.3	13.0	11.5	—
m1	L	23.4-29.8	20.2-23.0	25.0-25.2	28.4	21.1	22.6
	W	16.0-20.2	13.6-15.4	16.6-17.0	19.2	15.5	15.0
m2	L	29.8-36.2	25.2-28.4	29.3-29.4	34.2	28.3	26.8-27.9
	W	20.4-25.5	17.3-18.6	19.5-19.8	23.9	17.6	17.2-17.6
m3	L	40.1-51.4	38.0	43.2-44.6	41.3	—	37.7
	W	21.0-27.4	19.3	21.3-23.4	23.7	—	19.3

28086 (Figure 3E) are more similar in size to the M2 of *P. fontinalis* (Table 4) and the molar area of RAM 28086 (985 mm) and UMPC 9466 (763 mm) are more consistent with the mean M2 molar area of *P. fontinalis* (see Gunnell and Yarborough 2000, fig. 11).

Palaeosynops paludosus Leidy 1870

Figure 4A-C, Tables 3-4

Neotype—UM 98890 skull, left and right dentaries, skeletal elements, University of Michigan locality BB-83, lower Bridger Formation, Biochronologic Zone Br2, Uinta County, Wyoming (Gunnell and Yarborough 2000, fig. 1).

Referred Specimens—CM 78382 right dentary with p2-m3 and left dentary with c, p2-m3 from CM locality 3555; UMPC 19800 right and left M1-M3 and left P3 from UMPC locality MV 8115; UMPC 16736, right dentary with p3-m3 from UMPC locality MV 7914.

Discussion—A dentary with p4-m3 (UMPC 16736, Figure 4A-B) was identified by Tabrum et al. (2001) as representing *Telmatherium manteoceras*. Identification of brontotheres is based mainly on the skull and upper dentition (Osborn 1929; Mader 1989, 2008; Muhlbachler 2008) and *Telmatherium* is now considered monospecific with *T. validus* having priority (Mader 2008, Muhlbachler 2008). Lower molars of *T. validus* are similar in size to those of *Palaeosynops* and the m1-3 length for *Telmatherium validus* is 110.0-132.4 mm (Muhlbachler 2008, table 7)

and the m1-3 length for UMPC 16736 is 112.9 mm. But lower molars of *T. validus* are narrower than those of *Palaeosynops* (Muhlbachler 2008) and UMPC 16736 compares more closely with *P. paludosus* in this regard (Table 3).

CM 78382 is represented by associated dentaries whose teeth (particularly the premolars) are similar in size to *Palaeosynops paludosus* and significantly larger than the lower dentition of *P. fontinalis* (Table 3). UMPC 19800, a partial upper dentition (Figure 4C) appears to also represent *P. paludosus* based on size (Table 4). Also, M2s of UMPC 19800 have a molar area of approximately 1200 mm, indicating that UMPC 19800 is too large to represent *P. fontinalis* (see Gunnell and Yarborough 2000, fig. 11).

Family Helaletidae Osborn and Wortman 1892

Helaletes Marsh, 1872

Helaletes nanus Marsh (1871)

Figure 4D, Table 5

Heptodon? Douglass 1903

Holotype—YPM 11080 fragmentary maxillae with right P2-M3 and left P3-M2 (Marsh 1871, fig. x).

Referred Specimens—CM 78380 right m1 or m2, CM 78381 right M3, CM 90745, left M3 from CM locality 3553; CM 78371 right maxilla with C and P1-M3, CM 717 left maxilla with damaged P4-M3 from CM locality 3556.

TABLE 4. Measurement in mm of RAM 28086 and UMPC 9466 of *Palaeosyops fontinalis* and UMPC 19800 of *P. paludosus* from the Sage Creek Formation compared with the upper dentition of *P. paludosus* and *P. fontinalis* from the Green River Basin of Wyoming (Gunnell and Yarbrough, 2000:tables 1, 4).

		<i>Palaeosyops paludosus</i>	<i>Palaeosyops fontinalis</i>	RAM 28086	UMPC 9466	UMPC 19800
P1	L	11.6-14.0	13.0-16.9	—	—	—
	W	7.5-9.5	7.7-8.7	—	—	—
P2	L	15.6-18.3	14.6-15.2	—	—	—
	W	15.3-19.0	13.7-17.1	—	—	—
P3	L	16.4-19.8	14.9-16.9	—	—	18.2
	W	19.4-23.8	17.3-18.7	—	—	24.3
P4	L	17.7-22.4	16.5-19.4	—	—	—
	W	23.0-26.8	20.3-22.5	—	—	—
M1	L	25.4-31.6	23.7-27.3	—	—	27.7-27.5
	W	26.9-32.0	22.8-25.5	—	—	28.5-28.6
M2	L	34.2-40.3	28.7-32.9	30.7	24.6	34.1-34.5
	W	35.2-40.8	27.2-30.4	32.1	31.0	36.0-36.4
M3	L	33.0-41.7	29.5-36.4	—	—	34.2-34.7
	W	35.6-45.8	28.5-34.3	—	—	38.0-38.5

TABLE 5. Measurements in mm of CM 78371, CM 717, CM 78381 and CM 90745 from the Sage Creek Formation compared with the upper dentition of *Heleates nanus* and *H. intermedius* provided by Radinsky (1963:tables 6,7).

Tooth Site		<i>H. nanus</i>	<i>H. intermedius</i>	CM 78371	CM 717	CM 78381	CM 90745
P1	L	5.2-6.5	—	4.6	—	—	—
	W	3.2-4.2	—	3.8	—	—	—
P2	L	6.2-7.3	9.0	5.7	—	—	—
	W	6.4-8.2	9.0	5.7	—	—	—
P3	L	7.0-8.0	9.4-11.0	6.2	—	—	—
	W	8.4-10.3	11.6-12.2	7.7	—	—	—
P4	L	7.7-8.8	10.6-11.2	6.6	5.9	—	—
	W	8.7-11.0	13.3-14.1	9.1	10.2	—	—
M1	L	8.3-10.6	12.7-13.8	8.6	8.7	—	—
	W	10.0-12.0	15.0-15.6	9.7	10.6	—	—
M2	L	10.4-11.6	14.5-15.8	10.6	9.9	—	—
	W	10.8-13.4	16.4-16.8	11.2	10.8	—	—
M3	L	10.1-12.3	15.4-15.6	9.9	10.7	12.1	12.9
	W	10.7-13.3	16.7-17.0	10.5	12.3	13.2	14.1

Description and Discussion—The M1-M3 in CM 717 and CM 78371 have a slightly convex and lingually depressed metacone and a well-developed posterolabial cingulum, with M3 having a slightly shorter metaloph than M1-2 (Figure 4D), features that match those of *Helalestes* (Colbert and Schoch 1998). The degree of molarization of the premolars of *Helalestes nanus* varies as the P3-4 of the holotype (YPM 11080) have hypocones but the P2 does not, while other specimens referred to *Helalestes nanus* lack a hypocone on P3-4 but have a hypocone on P2 (Radinsky 1963). The P2-4 in CM 78371 (Figure 4D) and the P4 of CM 717 are triangular in outline but are heavily worn so it could not be determined if any of these premolars had a hypocone. Specimens of *Helalestes* from the Sage Creek Formation are similar in size to *H. nanus* and significantly smaller than those of *H. intermedius* (Table 5) and thus are referred to the smaller species.

Family Hyrachyidae Osborn and Wortman 1892
Hyrachyus Leidy 1871

Hyrachyus douglassi Wood 1934
Hyrachyus? priscus Douglass 1903

Holotype—CM 784 right maxilla, partial left and right dentaries, and atlas from CM locality 3556 (Douglass 1903, fig. 2; Wood 1934, fig. 23-24).

Description and Discussion—CM 784 was referred to *Hyrachyus? priscus* (Douglass 1903) and later designated as the holotype of *Hyrachyus douglassi* (Wood 1934). *Hyrachyus douglassi* was thoroughly described and figured by Wood (1934, fig. 23-24), who noted that CM 784 differs from all other specimens of *Hyrachyus* in having a hypocone on P2 that with the metaconule forms a metaloph. Although various specimens from the Uinta Basin in Utah might also represent this species (Wood 1934, 209), CM 784 remains the only confirmed specimen.

SAGE CREEK FORMATION BIOCHRONOLOGY AND GEOCHRONOLOGY

The mammalian assemblage from the Sage Creek Formation consists of seven taxa:

TILLODONTIA

Esthonychidae

Trogosus sp. indeterminate

CONDYLARTHRA

Hyopsodontidae

Hyopsodus sp. cf. *H. minusculus*

PERISSODACTYLA

Brontotheriidae

Eotitanops borealis

Palaeosyops fontinalis

Palaeosyops paludosus

Helaletidae

Helalestes nanus

Hyrachyidae

Hyrachyus douglassi

Helalestes nanus, *Hyrachyus douglassi*, *Palaeosyops paludosus*, *P. fontinalis*, *Eotitanops borealis*, *Trogosus*, and *Hyopsodus* sp. cf. *H. minusculus* are all known from Bridgerian strata in Colorado and Wyoming (Robinson et al. 2004; Gunnell et al. 2009). Biochronology of the Bridgerian NALMA is based on vertebrate assemblages from strata in west-central and southern Wyoming (Wind River, Green River, Wasatch, and Bridger formations) and south-central Colorado (Upper Huerfano Formation) and consists of four biochrons (in ascending order), Br1a, Br1b, Br2, and Br3 (Gunnell et al. 2009). Two of the Sage Creek Formation brontotheres are index species of Bridgerian biochrons Br1a (*Eotitanops borealis*) and Br2 (*Palaeosyops paludosus*) (see Gunnell et al. 2009 tables 1-4). Other Sage Creek taxa have these Bridgerian ranges; *Palaeosyops fontinalis* Br1a-Br1b, *Trogosus* Br1a-Br2, *Helalestes nanus* Br1a-Br3, *Hyopsodus* cf. *H. minusculus* Br1a-Br3; *Hyrachyus douglassi* is known from only the holotype but *Hyrachyus* occurs in all four Bridgerian biochrons (Gunnell et al. 2009). Thus, the Sage Creek Formation mammalian assemblage is early Bridgerian and the biochronologic age of strata at the three collecting areas is:

Type Locality: *Helalestes nanus*, *Hyrachyus douglassi*, *Palaeosyops paludosus* Br2

Dunlap Draw: *Palaeosyops paludosus* Br2

Fields Draw #1: *Palaeosyops fontinalis*, *Eotitanops borealis*, *Trogosus*, *Helalestes nanus* Br1a; #2: *Hyopsodus* sp. cf. *H. minusculus* Br1a-Br1b? #3: *Palaeosyops paludosus* Br2

Thus, strata representing Br1a and Br2 are identifiable in the Sage Creek Formation and if strata representing biochron Br1b are present, it is not demonstrable because none of the seven index species listed for the Br1b biochron (Gunnell et al. 2009, table 3) have been recovered. Tabrum et al. (2001) noted the occurrence of Br3 strata at the type locality of the formation based on the presence of the Br3 index taxon *Telmatherium "manteoceras"* (*T. validus*), a specimen (UMPC 16736) we identify as *Palaeosyops paludosus*, a Br2 index taxon.

The two dated ashfall lapilli tuffs, Fields Draw

#1 (49.84 $\pm$ 0.04 Ma) and the type locality (48.74 $\pm$ 0.08 Ma), provide geochronologic age control for Sage Creek Formation strata. The age of 49.84 $\pm$ 0.04 Ma from the lower part of the formation may aid in delineating the geochronologic age of the Wasatchian-Bridgerian NALMA boundary which has proved to be elusive (Robinson et al. 2004). In the greater Green River depositional basin, paleomagnetic reversals were correlated to the Geomagnetic Polarity Time Scale using radioisotopic age constraints and this correlation placed the Wasatchian-Bridgerian boundary in Chron 23r at about 52 Ma (Clyde et al. 2001). In the Green River Formation in southern Wyoming, the Wasatchian-Bridgerian boundary was estimated to be 50.55 $\pm$ 0.43 Ma and the Br1a and Br1b boundary to be 49.83 $\pm$ 0.39 Ma based on interpolations of sanidine $^{40}\text{Ar}/^{39}\text{Ar}$ age determinations (Smith et al. 2003). At Fields Draw #1, the ashfall lapilli tuff about 11 meters below the Br1a mammalian assemblage yielded an $^{40}\text{Ar}/^{39}\text{Ar}$ age of 49.84 $\pm$ 0.04 Ma confirming the presence of early Bridgerian strata in southwest Montana. This age is similar to the interpolated $^{40}\text{Ar}/^{39}\text{Ar}$ age of the Br1a/Br1b boundary (49.83 $\pm$ 0.39 Ma) from the Green River Formation in Wyoming (Smith et al. 2003). Thus, the Fields Draw tuff provides more support for the Wasatchian-Bridgerian boundary age of 50.55 $\pm$ 0.43 Ma of Smith et al. (2003) than the 52 Ma age proposed by Clyde et al. (2001).

The detrital ashfall lapilli tuff (sanidine $^{40}\text{Ar}/^{39}\text{Ar}$ age of 48.74 $\pm$ 0.08 Ma) in the upper part of the section at the type locality is just below a thick paleosol that defines the disconformity between the Sage Creek Formation and overlying the Dell beds. *Palaeosyops paludosus*, (index species for Br2 biochron) was recovered below this tuff (distance below unknown) and the Church Butte Tuff in Br2 strata of the Bridger Formation (Wyoming) yielded ages of 48.27 Ma (Murphey et al. 2011 fig. 4, 2017 fig. 4) and 48.62 $\pm$ 0.31 (Smith et al. 2008, table 3). The age of 48.74 $\pm$ 0.08 Ma from the type locality section of the Sage Creek Formation is similar in age to Church Butte Tuff as dated by Smith et al. (2008) in Br2 strata in Wyoming. Thus, the dated tuff from the upper part of the formation supports its correlation with the Br2 biochron and also indicates that deposition of Sage Creek Formation strata in southwest Montana appears to have spanned approximately one million years.

DELL BEDS

The Dell beds are an informal unit that overlies the Sage Creek Formation (Fields and others 1985, fig. 4) and is Late Uintan in age (Tabrum et al. 1996). Similar to the Sage Creek Formation discussed above,

the Dell beds are part of the informal Cenozoic Sequence 1 of Hanneman and Wideman (1991, 2006), but we will continue the usage of the informal “Dell beds” for this discourse. These strata are more continuous than the underlying Sage Creek Formation, but their deposition on a pre-existing topographic surface and complex faulting in the Sage Creek area limit the accuracy of constructing a composite stratigraphic section. The Dell beds disconformably overlie Sage Creek Formation strata in some areas, and unconformably overlie an early Eocene debris flow elsewhere. The more common lithologic characteristics of the Dell beds are the overall light tan color and the apparent transition from more conglomeratic sediments in the west (Douglass Draw) to primarily mudstone units to the east (Kay Draw) (Figure 2). Thickness of the Dell beds has been estimated to be 100 to 150 m (Tabrum et al. 1996; Schwartz and Graham 2017) and our work suggests that 100 m is closer to a true stratigraphic thickness.

We measured two stratigraphic columns in order to characterize the Dell beds that are geographically separated by approximately 0.70 km (Figure 2). The western stratigraphic section (measured in Douglass Draw, Figure 2C) has a thickness of approximately 50 m and contains mudstone, pebbly mudstone, volcanoclastic sandstone, lenticular cobble-pebble conglomerate, and minor occurrences of ashfall lapilli tuff. Finer-grained units contain numerous burrowed horizons and cobble-pebble channels. A massive 10.5 m thick mudstone occurs at the top of the section and the base is covered but probably overlies an early Eocene debris flow (Figure 2C).

The eastern stratigraphic section (measured in Kay Draw, Figure 2D) is approximately 31 m thick and the basal 1.5 m contains cobble-pebble conglomerate and pebbly sandstone with lenses of mudstone rip-ups. The remaining section consists of medium-bedded to massive mudstone that includes concretions and burrowed horizons (Figure 2D) with dung beetle burrows predominating. Approximately 0.35 km northeast of Kay Draw, a 1.5 m thick calcic paleosol that caps the Dell beds is overlain by strata containing Chadronian vertebrates. This calcic paleosol is structurally truncated within about 0.01 km, but its occurrence does mark the unconformity between the informal Sequence 1 and Sequence 2 of Hanneman and Wideman (1991, 2006) and Hanneman and others (1994).

The outcrop area of the Dell beds is an order of magnitude greater than that of the Sage Creek Formation and outcrops yielding fossils occur on the flanks of north-south to northeast-southwest trending ridges. Strata in the main western area (Douglass Draw) were termed the lower and older part of the Dell beds and outcrops in areas further east (Kay Draw,

Hough Draw) were called the upper and younger part of the Dell beds (Fields et al. 1985; Tabrum et al. 1996, 2001). Fossils recovered from western outcrops were referred to as the Douglass Draw local fauna and those from Kay and Hough draws as the Hough Draw local fauna (Tabrum et al. 1996, 2001). Recently recovered specimens and our biostratigraphic reassessment of the Dell beds (see Biochronology and Chronology section below) indicate that these two mammalian assemblages are too similar to provide support for any age difference. Also, it is possible that the western and eastern sections represent different facies of the same depositional system. Douglass Draw localities are: CM 3557, CM 3558, CM 4006, MV8112, MV 8115, RAM V2019039, RAM V2021035. Hough Draw and Kay Draw localities are: CM 601, CM 603, CM 613, CM 2558, CM 2568, CM 3560, CM 3561, CM 3562, CM 4024, CM 5074, MV 6803, MV 7629, MV 7729, MV 7730, MV8011, RAM V2018033, RAM V2018034, RAM V2020006, RAM V2023005, USNM Hough Draw site.

DELL BEDS SYSTEMATIC PALEONTOLOGY

Didelphimorphia Gill 1872
 Didelphidae Gray 1821
Herpetotherium Cope 1873b
Herpetotherium knighti McGrew 1959
 Figure 5A, Table 6

Holotype—AMNH 55684 right maxilla with M1-3, Locality 5, Tabernacle Butte, upper part of Bridger Formation, Wyoming (McGrew 1959, fig. 3).

Referred Specimens—UMPC 8358 right maxilla fragment with a slightly damaged M3 from UMPC locality MV 7729; RAM 28096 talonid of left m2 or m3 from RAM locality V2018034.

Description—The slightly damaged M3 (UMPC 8358) is moderately worn and the metacone is slightly larger and taller than the paracone and a V-shaped centrocrista is well developed (Figure 5A). The stylar shelf is wide and although the central part of its labial rim is missing due to breakage, a small parastyle, a low but distinct stylar cusp B, and a weakly defined stylar cusp D (smaller than B) are evident. If a stylar cusp C was present, it was lost due to breakage. RAM 28086 is a talonid with a large hypoconid and a posterolingual and closely spaced entoconid and hypoconulid (twinned).

Discussion—*Herpetotherium* (“*Peratherium*”) *knighti* was erected by McGrew (1959) based on the holotype (AMNH 55684), a right maxilla with M1-3 from the Bridger Formation of Wyoming. McGrew (1959) distinguished *H. knighti* from similar species based on the arrangement and relative prominence of the stylar cusps which on M3 are low and positioned

on the extreme labial edge of the stylar shelf. Although the stylar shelf of UMPC 8358 is moderately damaged, prominent and relatively low A and D cusps are positioned on the labial edge of the stylar shelf (Figure 5A). Also, measurements of UMPC 8358 are similar to the M3 of the holotype of *H. knighti* (Table 6). RAM 28086 was recovered from the same site as UMPC 8358 and probably represents the same taxon based on size.

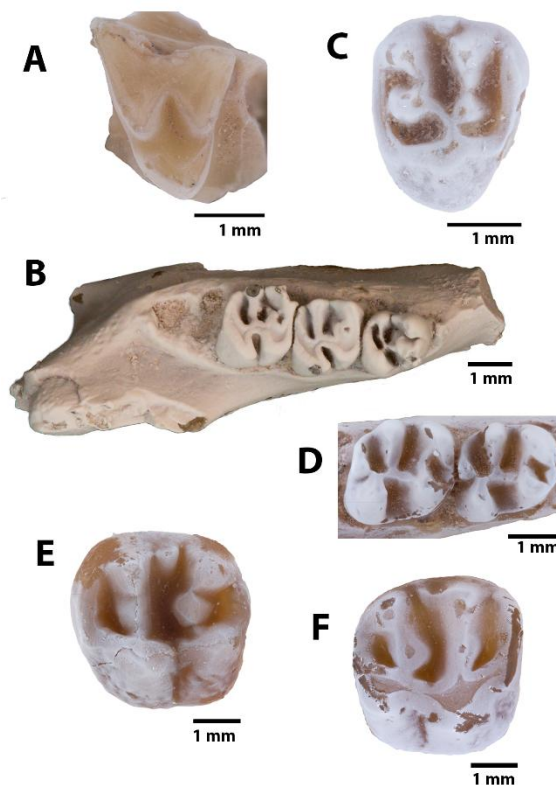


FIGURE 5. *Herpetotherium* and Rodentia from the Dell beds. A) Occlusal view of UMPC 8358 right maxilla fragment with M3 of *Herpetotherium knighti* from UMPC locality MV 7729; B) Occlusal view of UMPC 15956 right dentary with p4-m2 holotype of *Dolocylindrodon farkei* from UMPC locality MV 7629; C) Occlusal view of RAM 28545 right M1 or M2 of *Dolocylindrodon farkei* from RAM locality V2018034; D) Occlusal view of UMPC 15954 right dentary with m1-2 of *Pareumys* sp. cf. *P. mufferi* from UMPC locality MV 7629; E) Occlusal view of UMPC 9558 left M1 or M2 of *Ischyromys* sp. cf. *I. douglassi* and F) Occlusal view of UMPC 9559 right M1 or M2 of *Ischyromys* sp. cf. *I. douglassi* both from UMPC locality MV 7629.

Order Lagomorpha Brandt 1885
 Family Leporidae Fischer de Waldheim 1817
Mytonolagus Burke 1934
Mytonolagus sp. cf. *M. wyomingensis* Wood 1949

Holotype—Amherst College 10022 right P3, Tourtelot locality 15, Badwater Creek, Wagon Bed Formation, Wind River Basin, Wyoming (Wood 1949, figs. 15-24).

Referred Specimens—CM 78959 left m1, CM 78960 left upper tooth, CM 78961 left M2, CM 78962 left M1-M2, CM 78963 left p4, CM 84702 right m1 from CM locality 3560; CM 84489 left P3 from CM locality 7730; UMPC 19529 left mx from UMPC locality MV 8011; RAM 28546 mx from RAM locality V2018034; RAM 28574 mx from RAM locality V2020006; RAM 31230 dentary with m1-2 from RAM locality V2019039.

TABLE 6. Measurement in mm of M3 of UMPC 8358 and RAM 28096 (m2 or m3) from the Dell beds compared with the M1-3 of the holotype of *Herpetotherium knighti* (AMNH 55684) from McGrew (1959:table 1) and the m2-m3 of *H. knighti* from the Bridger Formation provided by Murphey, et al. (2017:table 3) (TW: talonid width).

Tooth Site		AMNH 55684	<i>H. knighti</i>	UMPC 8358	RAM 28096
M1	L	2.0	—	—	—
	W	1.7	—	—	—
M2	L	2.1	—	—	—
	W	2.0	—	—	—
M3	L	2.1	—	2.3	—
	W	2.2	—	2.2	—
m2-3	TW	—	1.2-1.4	—	1.2

Description and Discussion—*Mytonolagus* is commonly found in Uintan deposits in Wyoming and Utah (Dawson 2008). Isolated leporid teeth were recovered from outcrops in Hough Draw and were first identified as *Mytonolagus* sp. cf. *M. petersoni* by Tabrum et al. (1996, table 8) and later *Mytonolagus*? sp. (Tabrum et al. 2001, table 4). These specimens are more hypsodont than those of *M. petersoni* and are comparable in crown height to *M. wyomingensis* and *M. ashcrafti*, and some upper molars from Hough Draw have persistent hypostriae that resemble two specimens of *M. wyomingensis* from Uintan strata at Badwater, Wyoming (Fostowicz-Frelik and Tabrum 2009). Thus, we tentatively refer Dell beds leporid specimens to *Mytonolagus* sp. cf. *M. wyomingensis* until more diagnostic material is available.

Order Rodentia Bowdich 1821
Family Cylindrodontidae Miller and Gidley 1918
Dolocyndrodon Korth and Tabrum 2016

Dolocyndrodon farkei new species
Figure 5B-C, Table 7

Holotype—UMPC 15956 right dentary with p4-m2 from UMPC locality MV 7629, Dell Beds, Montana (Figure 5B).

Referred Specimens—RAM 28545 right M1 or M2 from RAM locality V2018034; UMPC 15963 left M1 or M2 from UMPC locality MV 7729; UMPC 15951 left M1 or M2, UMPC 15959 left m1 from UMPC locality MV 7629; UMPC 15995 right dentary with m1-m2 from UMPC locality MV 6803.

Etymology—Named in honor of Andrew Farke for his leadership of the student research program at the Raymond M. Alf Museum of Paleontology.

Diagnosis—Lower crowned p4 than all other *Dolocyndrodon* species except *D. tobeyi*; dentition larger than *D. vukae* and smaller than *D. texanus*; M1-M2 longer and lower molars larger and squarer in occlusal outline compared to *D. medius*; M1-M2 more rectangular in occlusal outline and lower molars squarer compared to *D. tobeyi*; lower molars slightly longer compared to *D. rahnensis*; paraloph and metaloph of M1 or M2 unite lingually before extending to protocone in two of three specimens, a feature not shared with any other species of *Dolocyndrodon*.

Description—*Dolocyndrodon* was erected based on specimens from Rahn Ranch and Rattlesnake Creek in southwest Montana and the genus also included specimens previously referred to *Pseudocyndrodon* from Texas, Wyoming, and the McCarty's Mountain site in Montana (Korth and Tabrum 2016). *Dolocyndrodon* has four complete transverse lophs in both the uppers and lowers, unlike *Pseudocyndrodon* which lacks a p4 hypolophid and has a weak or absent metalophid II (Korth and Tabrum 2016). The p4 of the holotype of *D. farkei* (UMPC 15956) has a distinct hypolophid and metalophid II (Figure 5B) which confirms its affinity to the genus. The p4-m2 of UMPC 15956 resembles those of the holotypes of *D. rahnensis* and *D. vukae* (Korth and Tabrum 2016, fig. 3B, fig. 4D), *D. medius* (Burke 1938, fig. 4), and *D. tobeyi* (Black 1970, fig. 14) except the m1-2 of *D. farkei* are larger and/or distinctly squarer in occlusal outline (Figure 5B, Table 7). Based solely on the holotype, the p4 of *D. farkei* has a crown height to width ratio of .52, which is lower than other species except for *D. tobeyi* (Table 7). Other than size and crown height to width ratio of the p4, no features of the lower dentition are noted in the diagnosis of *D. vukae*, *D. rahnensis*, or *D. medius* (Korth and Tabrum 2016). The morphology of the lower dentition of *D. farkei* is based on the holotype and two other specimens (UMPC 15959, UMPC 15995) and these teeth lack diagnostic features as well.

TABLE 7. Measurements in mm of the M1-2 and p4-m2 of *Dolocyliodron farkei* from the Dell beds compared with those of *D. vukae*, *D. rahnsis*, *D. medius* provided by Korth and Tabrum (2016:tables 2, 5, 6) and *D. Tobeyi* provided by Black (1970:table 1), all rounded to tenths of a mm. Mean crown-height to width ratios of p4s are 1.0 for *D. vukae*, 0.69 for *D. rahnsis*, 0.62 for *D. medius*, 0.44 for *D. tobeyi* (Korth and Tabrum, 2006:table 1) and 0.52 for *D. farkei*. Measurement of the M1-2 of *D. vukae* are unworn to moderately worn specimens.

Taxon		M1-2	p4	m1	m2
<i>D. farkei</i>	L	1.9–2.2	2.0	2.1–2.2	2.3–2.4
	W	2.5–2.6	2.1	2.4	2.3–2.5
<i>D. vukae</i>	L	1.8–2.0	1.8–2.0	1.9–2.0	1.8–2.0
	W	1.7–1.9	1.5–1.9	1.6–1.9	1.6–1.9
<i>D. tobeyi</i>	L	1.8–2.1	1.6–1.7	1.7	1.8–1.9
	W	1.8–2.4	1.8	2.2–2.3	2.0–2.3
<i>D. rahnsis</i>	L	1.6–1.8	1.9–2.4	1.7–2.0	1.8–2.1
	W	2.3–2.8	1.9–2.3	1.8–2.8	1.9–2.3
<i>D. medius</i>	L	1.4–1.9	1.6–2.3	1.4–2.0	1.6–1.9
	W	1.9–2.5	1.9–2.1	1.7–2.3	1.7–2.2

The upper dentition of *D. farkei* is represented by three isolated teeth (RAM 28545, UMPC 15963, UMPC 15951) which are M1s or M2s that are wider than long and have a rectangular outline in occlusal view. RAM 28545 (Figure 5C) has slight to moderate wear and exhibits four transverse lophs (anterior cingulum, paraloph, metaloph, posterior cingulum) and three transverse valleys (anterior, central, posterior). The paraloph has a large anteroposteriorly compressed paracone and a much smaller protocone and the metaloph has a large anteroposteriorly compressed metacone and a smaller transversely compressed metaconule. In RAM 28545 (Figure 5C) and UMPC 15963, the paraloph and metaloph merge just before they connect lingually to the protocone which is large and crescentic. In UMPC 15951 the metaloph does not connect to the paraloph or protocone and would only connect to the latter after heavy wear. All three upper teeth lack a distinct hypocone. In RAM 28545 the anterior and central valley open labially and a small mesostyle is positioned centrally on the labial cingulum in relation to the central valley but does not block it (Figure 5C) (mesostyle positioned similarly in UMPC 15963 but absent in UMPC 15951). In all three upper teeth, a large metacone blocks the posterior transverse valley from opening labially and the transversely compressed

metaconule almost constricts the posterior transverse valley or effectively divides it.

Few dental features of the upper molars distinguish species of *Dolocyliodron* (other than size) but the diagnosis of both *D. vukae* and *D. rahnsis* note a connection of the transversely compressed metaconule with the posterior cingulum that centrally blocks the posterior transverse valley (Korth and Tabrum 2016). In RAM 28545 (Figure 5C) the metaconule and posterior are almost completely connected, while in UMPC 15963 the metaconule does impede the posterior transverse valley and in UMPC 15951 a small loph connects the metaconule with the posterior cingulum, effectively bifurcating the posterior transverse valley. A character only noted in the diagnosis of *D. vukae* is that the central valley in the upper molars remains open until advanced wear (Korth and Tabrum 2006). For RAM 28545, UMPC 15963, and UMPC 15951 the central transverse valley would also remain open until heavy wear.

Discussion—The only feature that is apparently unique to *D. farkei* is that the paraloph and metaloph merge just before they connect lingually to the protocone in M1 and/or M2. Both RAM 28545 and UMPC 15963 have this feature but UMPC 15951 does not. The descriptions and illustrations for *D. vukae* and *D. rahnsis* (Korth and Tabrum 2016), *D. medius* (Burke 1938), *D. tobeyi* (Black 1970), and *D. texanus* (Wood 1974) make no reference to this feature. Otherwise, *D. farkei* is distinguished from other species by size and the crown height to width ratio of the p4. *Dolocyliodron farkei* is smaller than *D. texanus* because the M1 of the latter is 3.3 mm in width (Wood 1974, table 8), much wider than any other species (Table 7). The dentition of *D. farkei* is larger than *D. vukae* (Table 7) which was noted as being the smallest species of the genus (Korth and Tabrum 2016). The M1-M2 of *D. farkei* are similar in size to those of *D. tobeyi* (Table 7), but *D. farkei* is rectangular in occlusal outline while *D. tobeyi* is square (Black 1970). Also, lower molars of *D. farkei* are square in occlusal outline, while the lower molars of *D. tobeyi* are wider than long (Table 7). The M1-M2 of *D. farkei* are longer than those of *D. medius* and the lower molars of *D. farkei* are larger and squarer in occlusal outline than those of *D. medius* (Table 7). The lower and upper teeth of *Dolocyliodron farkei* are most similar in size and shape to *Dolocyliodron rahnsis*, although the lower molars of *D. farkei* are slightly longer than the lower molars of *D. rahnsis* (Table 7).

The p4 crown height to width ratio of *D. farkei* is .52, less than the mean of any other species except *D. tobeyi* (.44) which is known from the Wood and Rodent localities of the Teepee Trail Formation (Black 1970), sites that are Duchesnean in age (Robinson et

al. 2004). *Dolocyndrododon rahnensis* and *D. medius* are from early Chadronian sites and *D. vukae* is from medial Chadronian strata (Korth and Tabrum 2016), while *Dolocyndrododon farkei* is from the Dells beds which are late Uintan (Tabrum et al. 1996, 2001; this paper). When p4 ratios of *Dolocyndrododon* species are ordered by geologic age (oldest to youngest), these ratios suggest a general progression towards hypsodonty, *D. farkei* .52, *D. tobeyi* .44, *D. medius* .62, *D. rahnensis* .69, *D. vukae* 1.0, with youngest known species the most hypsodont and the smallest.

Pareumys Peterson 1919

Pareumys sp. cf. *P. mufferli* Lofgren et al. 2020

Figure 5D, Table 8

Holotype—AMNH 145526 left dentary fragment with p4-m3 from AMNH *Rapamys* Site, Renova Formation, Madison County, Montana (Lofgren et al. 2020; fig. 7a).

Referred Specimens—UMPC 15954 right dentary with m1-2, UMPC 15962 right m1 from UMPC locality MV 7629; RAM 28557 left dentary with m1-2 from RAM locality V2020006; CM 78261 right M1 or M2 from CM locality 3561, CM 84490 right dentary with m3 from CM locality 4024, CM 84486 right dentary with heavily damaged p4-m2 from CM locality 3562.

Description-Discussion—The m1-2 of UMPC 15954 and RAM 28557 and the m1 of UMPC 15962 have a relatively high metalophid that does not quite extend to the metaconid, and the gap between the anterolophid and metalophid forms a small enamel lake (Figure 5D). The hypolophids of these m1s and m2s extend lingually to distinct entoconids and there is a large gap between the hypoconids and the protoconids, resulting in well-developed ectolophids, characters all shared with the m1-2 of the holotype of *Pareumys mufferli* (AMNH 145526). Also, posterolophids of these m1-2s are short and do not extend to the posterolingual tooth margin (Figure 5D), a diagnostic character of *Pareumys mufferli* (Lofgren et al. 2020). The other diagnostic character of *Pareumys mufferli* is that the p4 is strongly molariform and slightly larger than the m1 (Lofgren et al. 2020). The damaged teeth of CM 84486 (p4-m2) do not provide morphologic details so a well preserved p4 of *Pareumys* from the Dell beds awaits discovery. The dentition of RAM 28557, UMPC 15954, and UMPC 15962 are 10-20% larger than the m1 and m2 of specimens of *Pareumys mufferli* from the Gravelly Range (Table 8, see Lofgren et al. 2020, table 6). Thus, our referral of the six *Pareumys* specimens from the Dell beds to *Pareumys mufferli* is tentative.

TABLE 8. Measurements in mm of the m1-m2 of RAM 28557 and UMPC 15954 and the m1 of UMPC 15962 from the Dell beds. Compared with the m1-2 of RAM 28515 and the holotype of *Pareumys mufferli* (AMNH 145526) from the Gravelly Range. Measurement of AMNH 145526 and RAM 28515 from Lofgren, et al. (2020:table 6).

		RAM 28557	UMPC 15954	UMPC 15962	RAM 28515	AMNH 145526
m1	L	2.5	2.2	2.3	1.7	1.9
	W	2.0	2.0	2.1	1.7	1.7
m2	L	2.5	2.2	—	1.9	2.2
	W	2.1	2.1	—	1.9	1.9

Family Ischyromyidae Alston 1876

Ischyromys Leidy 1856

Ischyromys sp. cf. *I. douglassi* Black 1968

Figure 5E-F, Table 9

Holotype—CM 1122 partial skull lacking parietals, left bulla, occiput, left P2 and M3, McCarty's Mountain, Montana (Black 1968, fig. 7-9, 16).

Referred Specimens—UMPC 9558 left M1 or M2, UMPC 9559 right M1 or M2 from UMPC locality MV 7629.

Description and Discussion: These two M1s or M2s have four transverse crests and are clearly affiliated with ischyromyids, particularly *Ischyromys*. UMPC 9558 is less worn than UMPC 9559 and has a large hypocone and protocone separated by a shallow lingual notch with a well-developed transverse paraloph, a less complete metaloph and small mesostyle, and a paraloph that is weakly connected to the protocone with the protoconule indistinct (Figure 5E). Also, the metaconule is not connected to the hypocone and is weakly connected to the metacone. In UMPC 9559, a mesostyle is absent, a lingual notch is less developed between the protocone and hypocone, the protoconule is distinct, and the metaconule is connected to the hypocone (Figure 5F).

With only two isolated teeth, a comparison to existing taxa is limited, but UMPC 9558 and UMPC 9559 most closely resemble *Ischyromys douglassi*. Distinguishing features of the upper molars of *I. douglassi* are a distinct metaconule, a shallow lingual notch between the protocone and hypocone, and the constriction of the metaloph at the hypocone (Black 1968). The last feature appears to be partially dependent on wear as in CM 1122 (holotype of *I. douglassi*), the metaloph is connected to the hypocone in M1 and M2 (Black 1968, fig. 16), similar to UMPC 9558. But in CM 10966 the metaloph is less worn and

is separated from the hypocone (Black 1968, fig. 17), similar to UMPC 9559. However, the protocone of the P4-M2 of *I. douglassi* is complete and there is no distinguishable protoconule (Black 1968, figs. 16-17) and UMPC 9559 has a distinct protoconule. Two upper molars (CM 16020 and CM 15354) identified as *?Ischyromys* sp. from Badwater Creek, Wyoming (Black 1971, figs. 42-43), also resemble *I. douglassi* but their metalophs are more distinctly separated from the hypocone than UMPC 9558 and UMPC 9559. These Dell beds and Badwater specimens (CM 16020, CM 15354) are similar in size to the sample of *I. douglassi* from McCarty's Mountain (Table 9). Black (1971) notes that the Badwater species of *Ischyromys* (Uintan) may have given rise to *I. douglassi* (Duchesnean-Chadronian), which could be equally argued for the Dell beds species. We refer UMPC 9558 and UMPC 9559 to *Ischyromys* sp. cf. *I. douglassi* until a larger sample of this Dell beds taxon is available.

TABLE 9. Measurements in mm of UMPC 9558 and UMPC 9559 (which are either an M1 or M2) from the Dell beds compared with the M1 and M2 of *Ischyromys douglassi* from McCarty's Mountain (Black, 1968:table 1) and the M1 or M2 of *?Ischyromys* sp. (CM 15354, CM 16020) from Badwater Creek (Black, 1971:203).

Tooth site	<i>Ischyromys douglassi</i>	CM 15354	CM 16020	UMPC 9558	UMPC 9559
M1/2 L	—	3.4	3.4	3.9	3.7
W	—	3.9	3.9	3.8	4.0
M1 L	3.1-3.8	—	—	—	—
W	3.6-4.5	—	—	—	—
M2 L	2.6-3.8	—	—	—	—
W	3.3-4.1	—	—	—	—

Order Carnivora Bowdich 1821
 Family Miacidae Cope 1880
Tapocyon Stock 1934
Tapocyon robustus (Peterson 1919)
 Figure 6A-B, Table 10

Holotype—CM 3023 partial skeleton with dentary fragments with p4, m1, and m2, vertebrae fragments, partial right humerus and head of femur, Uinta Basin, Utah (Peterson 1919, figs. 1-2, 4-7).

Referred Specimens—CM 72500, left dentary with c, p3-m2 from CM locality 3561; UMPC 6678, right dentary with broken c, p3-4, m1-2 with damaged crowns from UMPC locality MV 7730. These dentaries represent the same individual (noted by A. Tabrum on specimen label for UMPC 6678); UMPC 6678 was found in late 1970s and CM 72500 in 1987.

Description—The p3-m2 of CM 72500 are undamaged and exhibit little wear (Figure 6A-B), while the dentition of UMPC 6678 is damaged and only the p3-4 are well preserved. In both dentaries, p3 is smaller than p4, and both p3-4 have a large central cusp and an anterior basal and posterior accessory cusp (former smaller than latter). The anterior basal cusp of the p4 is deflected lingually and has a well-developed labial cingulum. Based on CM 72500, the m1 trigonid is tall and massive compared to the low and diminutive talonid, and the antero-posteriorly broad protoconid is the largest and tallest trigonid cusp (Figure 6A-B). The m1 paraconid is larger than the metaconid and the paracristid and metacristid are deeply notched, with the paracristid longer than the metacristid. The m1 talonid is relatively small and has a broad, shallow, and antero-posteriorly compressed basin, a small hypoconid, and a cristid obliqua that intersects the trigonid lingual to the protoconid. The m2 trigonid is low and is slightly taller and narrower than the talonid. The protoconid is the largest trigonid cusp, and the paraconid is slightly smaller than the metaconid. The m2 talonid has a small entoconid and hypoconid and a cristid obliqua that intersects the trigonid lingual to the protoconid.

Discussion: Peterson (1919) noted that the m1 of "*Prodaphaenus*" *robustus* has a high and broad trigonid and the smaller m2 has a relatively small heel and a low trigonid, features seen in CM 72500. Stock (1934) described a new genus and species (*Tapocyon occidentalis*) from southern California and considered "*Prodaphaenus*" *robustus* likely to be cogenetic, noting that *Tapocyon* closely resembled "*Prodaphaenus*" but differed in being slightly smaller and having a lingual ledge on the posterior part of the p4. Dawson (1980) referred five specimens of *Tapocyon* from Badwater, Wyoming, to *Tapocyon* cf. *T. robustus* noting their close resemblance to the Uinta Basin sample described by Peterson (1919) and the lack of morphological differences between the California, Utah, and Wyoming specimens. Later, Wesley and Flynn (2003) described the new species *Tapocyon dawsonae*, noting that it is generally smaller than *T. robustus* and has an m2 cristid obliqua running anteriomedially from the hypoconid that terminates between the protoconid and metaconid. Wesley and Flynn (2003) also synonymized *T. occidentalis* into *T. robustus* arguing that distinctions between the two reflected intraspecific differences. More recently, Friscia and Rassmussen (2010) described CM 71198 (m1-2) from the Uinta Basin of Utah and referred it to *Tapocyon robustus* noting that it is larger than *T. dawsonae* and that the m2 cristid obliqua intersects the trigonid just lingual to the protoconid.

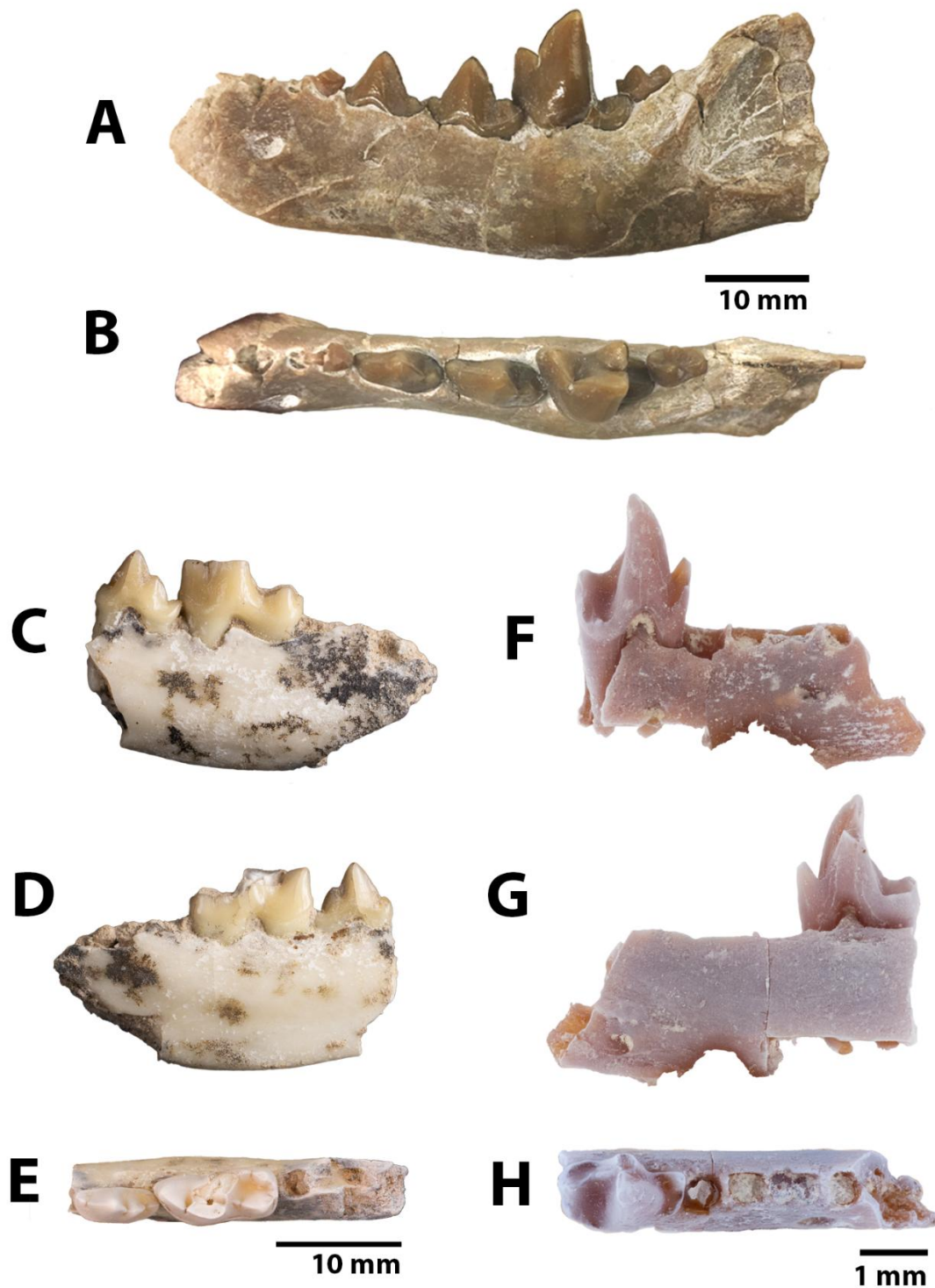


FIGURE 6. Carnivora and Lipotyphla from the Dell beds. A) Labial and B) Occlusal views of CM 72500 left dentary with p3-m2 of *Tapocyon robustus* from CM locality 3561; C) Labial, D) Lingual, and E) Occlusal views of RAM 31228 left dentary with p4-m1 and alveolus of m2 of *Lycophocyon tabrumi* from RAM locality V2019039; F) Labial, G) Lingual, and H) Occlusal views of RAM 28095 right dentary with p4 of *Centetodon* sp. cf. *C. magnus* from RAM locality V2018034.

We follow the synonymy of *T. occidentalis* and *T. robustus* proposed by Wesley and Flynn (2003) and the m2 crista obliqua of CM 72500 terminates just lingual to the protoconid unlike *T. dawsonae*. Also, CM 72500 is more similar in size to *T. robustus* than the slightly smaller holotype of *T. dawsonae* (Table 10).

TABLE 10. Measurements in mm of the p3-m2 of CM 72500 from the Dell lbeds compared with the measurements of the p3-m2 of *Tapocyon robustus* and the holotype of *T. dawsonae* (SDSNH 35221) provided by Wesley and Flynn (2003:table 2).

Tooth Site		<i>T. robustus</i>	SDSNH 35221	CM 72500
p3	L	8.62-9.40	—	8.5
	W	4.14-5.19	3.70	4.1
p4	L	10.50-11.83	10.35	10.1
	W	4.85-5.52	4.55	5.4
m1	L	12.00-13.89	10.87	12.8
	W	7.50-7.97	7.17	7.9
m2	L	5.46-6.71	5.41	6.3
	W	3.84-4.68	3.88	4.0

Caniforma sensu Bryant 1996
Lycophocyon Tomiya 2011
Lycophocyon tabrumi Lofgren et al. 2020
 Figure 6C-E, Table 11

Holotype—RAM 18619 partial skull with right I1-3, P2-M3 and left I1, P2, P4-M2 from RAM locality V2016012, Renova Formation, Montana (Lofgren et al. 2020, fig. 8A-C).

Referred Specimen—RAM 31228 left dentary with p4, damaged m1, and alveoli of m2 from RAM locality V2019039.

Description and Discussion—The p4 of RAM 31228 is undamaged and has well-developed anterior basal and posterior basal cusps and both cusps have strong cingula. The single main cusp has steep anterior and posterior slopes and a well-developed and distinctive posterior cuspule, and a distinctive notch demarcating its apex is positioned about midway on the posterior slope (Figure 6C-E). The m1 has an intact talonid and paraconid but the apices of both the protoconid and metaconid are missing due to breakage. As evident from the width and length of its base, the protoconid was massive and was taller than

the metaconid and paraconid. The broken protoconid is equal in height to the undamaged paraconid in labial view and the height of paraconid and broken metaconid were apparently subequal. Based on the location of exposed nerve cavities in occlusal view, it appears that the apex of the protoconid was slightly transversely anterior to the apex of the metaconid (Figure 6E). A notch is preserved between the paraconid and protoconid and the angle between the paralophid and protolophid is more than 50 degrees. The talonid basin is rectangular and opens labially and the talonid is a little more than half as long as the trigonid. The hypoconid is larger and taller than the entoconid and a narrow ridge connects the two cusps posteriorly which could be termed a diminutive hypoconulid (Figure 6E). A narrow, elongate cuspule/entoconulid is separated from the entoconid by a slight but distinct cleft. The m2 is absent but its position is represented by two antero-posteriorly elongated alveoli.

TABLE 11. Measurements in mm of RAM 31228 from the Dell beds compared with the p4-m1 of *Lycophocyon hutchisoni* provided by Tomiya (2011:table 1).

Tooth Site		<i>L. hutchisoni</i>	RAM 31228
p4	L	8.1-8.9	6.5
	W	3.8-4.3	3.2
m1	L	9.5-10.7	9.7
	W	5.7-6.5	4.2

The cusp morphology of RAM 31228 is very similar to the p4-m1 of *Lycophocyon hutchisoni* described and illustrated by Tomiya (2011, figure 2c, 4 a-c) but the width and length of the p4 and width of the m1 of RAM 31228 are about 20% smaller (Table 11). Similarly, the P4 and M1 of the holotype and only known specimen of *L. tabrumi* (RAM 18619) from Uintan strata in the Gravelly Range (Montana), are about 8% smaller than the P4 and M1 of *L. hutchisoni* (Lofgren et al 2020, table 10). RAM 31228 appears to represent the lower dentition of *L. tabrumi* and is the second record of the species in Montana.

Order Lipotyphla Haeckel 1866
 Family Geolabididae McKenna 1960
Centetodon Marsh 1872
Centetodon sp. cf. *C. magnus* Clark 1936
 Figure 6F-H, Table 12

TABLE 12. Measurements in mm of the p4 of various species of *Centetodon* provided by Lillegraven, et al. (1981:tables 1,2,6,7) and by Lillegraven and Tabrum (1983:table 1) compared with RAM 28095 from the Dell beds.

Tooth Site		<i>C. kuenzii</i>	<i>C. chadronensis</i>	<i>C. pulcher</i>	<i>C. marginalis</i>	<i>C. magnus</i>	RAM 28095
p4	L	1.30-1.64	1.43-1.61	1.60-1.94	1.48-1.90	1.50-2.05	1.70
	W	0.90-0.94	0.79-0.91	0.82-1.03	0.78-1.01	0.90-1.01	0.92

Holotype—PU 13835 right dentary with p4-m3, Flagstaff Rim, Wyoming (Clark 1936, in Scott and Jepsen 1936, plate II, figs 5, 5a).

Referred Specimen—RAM 28095 right dentary with p4 from RAM locality V2018034.

Description—The molariform features of the p4 of RAM 28095 align it with *Centetodon* (Figure 6 F-H). The p4 is unworn but is missing the apex of the metaconid due to breakage. The protoconid is the largest and highest cusp and is transversely adjacent and united throughout a large part of its height with a smaller metaconid whose apex would have been distinctly lower than the protoconid. A small paraconid is positioned low and anterior to the united base of the metaconid and protoconid, and a small and narrow talonid basin with a well-developed hypoconid is present (Figure 6F-H).

Discussion—Seven species of *Centetodon* were recognized by Lillegraven et al. (1981) and soon thereafter, *Centetodon kuenzii* was described from Duchesnean to Orellan strata in southwest Montana (Lillegraven and Tabrum 1983). The p4 of *Centetodon* is not very diagnostic for identification of species (Lillegraven et al. 1981) and it is unclear what species RAM 28095 represents. Based on size, the p4 of RAM 28095 is slightly larger than the p4 of *C. chadronensis* and *C. kuenzii* but is within the size range of p4s of *C. magnus*, *C. pulcher*, and *C. marginalis* (Table 12). Of the latter three species, only *C. magnus* is known from Uintan strata (Lillegraven et al. 1981). RAM 28085 was recovered from late Uintan strata in Hough Draw (Tabrum et al. 1996, 2001; this paper) and is tentatively identified as *Centetodon* sp. cf. *C. magnus* on this basis.

Order Artiodactyla Owen 1848

Family Agriochoeridae Leidy 1869

Diplobunops Peterson 1919

Diplobunops matthewi Peterson 1919

Figure 7A, Table 13

Mesagriochoerus cf. *M. primus* Hough 1955

Holotype—CM 2974 numerous fragments of the skeleton, Uinta Formation, Horizon C, six miles east

of Myton, Utah (Peterson 1919: pl. XXXVIII, figs 1-23).

Referred Specimens—UMPC 3051 left dentary fragment with m2, UMPC 3052 left maxillary fragment with DP3-DP4 and M1-M2, UMPC 8335 left dentary fragment with p2-p4 from UMPC locality MV 6803; UMPC 8233 left dentary fragment with m2 from UMPC locality MV7629; UMPC 8230, right dentary fragment with p3-p4, anterior part of m1, and m2-m3 from UMPC locality MV 7730; CM 8927 maxillary fragment with right and left P3-M3 from CM locality 601; CM 84463 left M2 from CM locality 4006; RAM 28581 left p4 from RAM locality V2021035.

Description and Discussion—CM 8927 (Figure 7A) was identified as *Mesagriochoerus* cf. *M. primus* (Hough 1955) and seven additional specimens from the Dell beds represent a large agriochoerid that closely resembles “*Protoreodon pearcei*” and *Diplobunops matthewi*. Golz (1976) noted that “*Protoreodon pearcei*” and *Diplobunops matthewi* often are difficult to distinguish because of the number of shared characteristics, such as large size and distinct separation of the paracone and metacone in the P4 (Figure 7A). Black (1978) argued that differences between “*Protoreodon pearcei*” and *Diplobunops matthewi* were probably attributable to sexual dimorphism and that “*Protoreodon pearcei*” was a junior synonym of *Diplobunops matthewi*. In a brief review of Oreodontoidea, Lander (1998) placed *Diplobunops* within *Agriochoerus*, but later Emery et al. (2016) argued that *Diplobunops* and *Agriochoerus* were distinct genera. We retain *Diplobunops* and assign the larger agriochoerid specimens from the Dell beds to *Diplobunops matthewi*. The size of these specimens is distinct from the smaller agriochoerid *Protoreodon pumilius* from the Dell beds (Tables 13-14). The relatively complete dentition of *Diplobunops matthewi* exhibited by USNM 20305 from Badwater Creek, Wyoming, is similar in size to specimens from the Dell beds (Table 13). Also, the M1-M3 of USNM 20305 is 39.1-40.0 in length (Black 1978) and the length of the M1-M3 of CM 8927 is 40.0 mm. Also, Dell beds specimens are similar in size to the dentition of *D. matthewi* from the Gravelly Range of Montana (see Lofgren et al. 2020, table 14).

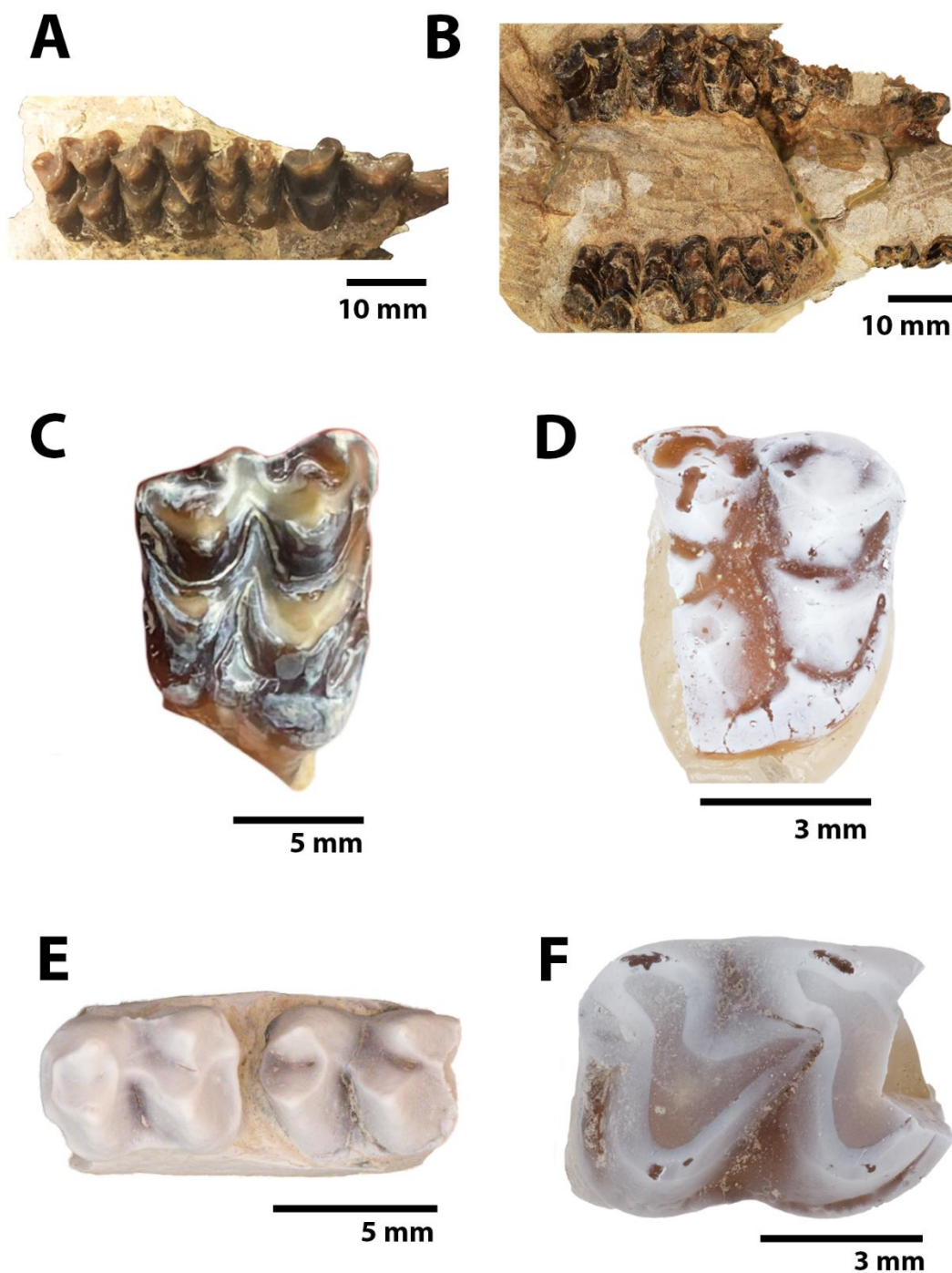


FIGURE 7. Artiodactyla and *Epihippus* from the Dell beds. A) occlusal view of CM 8927, right maxilla with PP3-M3 of *Diplobunops matthewi* from CM locality 601; B) occlusal view of RAM 28587, partial skull with left P1-2, M1-3 and right P1-2, damaged P4, M1-3 of *Protoreodon pumilus* from RAM locality V2018033; C) occlusal view of CM 84460, right M2 of *Leptoreodon marshi* from CM locality 3557; D) occlusal view of UMPC 15958, partial left M1 of *entacemylus leoteensis* from UMPC locality MV 7629; E) occlusal view of RAM 28564, left dentary with m1-2 of *Pentacemylus leotensis* from locality V20220006; F) occlusal view of UMPC 15960 partial right m1 of *Epihippus uintensis* from UMPC locality MV 7629.

TABLE 13. Measurements in mm of the P3-M3 of *Diplobunops matthewi* from the Dell beds compared with USNM 20305, a skull with dentaries of *D. matthewi* from Badwater Creek Wyoming, provided by Gazin (1956).

Tooth Site		USNM 20305	MV 8335	MV 8230	MV 3052	CM 8927
P3	L	11.1	—	—	9.4	9.8-10.2
	W	9.5	—	—	7.9	9.6
P4	L	10.2	—	—	9.8	8.8
	W	12.5	—	—	11.2	11.4-11.6
M1	L	12.5	—	—	12.1	10.5-10.9
	W	13.5	—	—	13.6	12.4-12.5
M2	L	13.7	—	—	14.6	13.9-14.2
	W	16.6	—	—	16.5	14.7-14.8
M3	L	15.0	—	—	—	14.9
	W	18.3	—	—	—	15.3-15.4
p3	L	10.8	10.4	8.5	—	—
	W	6.2	5.8	5.4	—	—
p4	L	11.5	10.3	10.3	—	—
	W	7.2	7.3	6.4	—	—
m1	L	10.9	—	—	—	—
	W	8.1	—	—	—	—
m2	L	13.0	—	12.0	—	—
	W	9.3	—	9.5	—	—
m3	L	20.3	—	19.9	—	—
	W	10.4	—	9.5	—	—

Protoreodon Scott and Osborn 1887
Protoreodon pumilus (Marsh 1875)
 Figure 7B, Table 14

Protoreodon tardus Hough 1955

Holotype—YPM 11890 dentary fragments with right m1 and partial m2-3, left m2, and skeletal fragments, White River, Uinta Basin, Utah, probably Uinta C (Thorpe 1937; not figured by Marsh 1875; see Gazin 1955, pl. 6, fig. 2).

Referred Specimens—UMPC 5618 right maxilla with DP4-M3, UMPC 7467 articulated skull and dentaries with separated left maxilla with M1-M2 and left dentary with m1-m3 from UMPC locality MV6803; UMPC 8231 left dentary with p4, m2-m3, UMPC 8333 left m1-2 with numerous skeletal elements, UMPC 8236 maxilla fragment with P3-4

and broken M1-2, UMPC 8232 right maxilla fragment with DP2-4, UMPC 8239 right maxilla with DP3-4 from UMPC locality MV 7629; UMPC 8334 right dentary with p3-m2, UMPC 8337 right dentary with right m1-m3 and left dentary with m2-m3, UMPC 8237 right maxilla with DP3-4 and right dentary fragment with dp4, UMPC 8234 right maxilla fragment with M1, UMPC 8229 left m1 from UMPC locality MV 7729; CM 9559, partial skull with right P2-M3 and fragmentary left M1-2 and left and right dentaries with p3-m3 from CM locality 2558; CM 84477 left maxilla with M1-2, right dentary with dp4-m3, left dentary with m1-2, CM 84478 left dentary with p3, CM 84465 left maxilla with DP2-4, M1-2, right maxilla with DP4, M1-2 from CM locality 3560; CM 78260 right maxilla with DP2-4, CM 78259 left dentary with dp2-4, m1 from CM locality 3561; CM 84488 partial skull with right M1-2 and left M1-2 from CM locality 3562; CM 93799 left maxilla with DP4-M2, right maxilla with M1-2, left dentary with m1-2, left dentary with dp4-m2 from CM locality 5074; RAM 28591 partial skull with M1-2 from V2019034; RAM 28124 right dentary with m1-3 from RAM locality V2020006; RAM 28090 MX fragment from RAM locality V2018034; RAM 23766 left mx fragment, RAM 28587 partial skull with left C, P1-2, M1-3, right P1-2, P4-M3 from RAM locality V2018033; USNM 19117 left dentary with p3-m3, USNM 19116 left dentary with p3-m3 and right and left dentaries of another individual with left C-m3 and right p3-m3, USNM 20209 right m2 and left m1-2, USNM 205393 broken upper and lower teeth, USNM 205391 right p4, USNM 205394 maxilla fragment with P4-M2, all from Hough Draw area.

Description—Three specimens of *Protoreodon* “*tardus*” (CM 9559, USNM 19116, USNM 19117) were described by Hough (1955) from the Dell beds and these specimens and others collected later (e.g. Figure 7B) are comparable in size to USNM 20352 of *Protoreodon pumilus* (Table 14) and other measurements provided by Gazin (1955, 52), Golz (1976, table 7), and Theodor (1999, table 1). *Diplobunops matthewi* is also present in the Dell beds and the cheek teeth of *D. matthewi* are distinctly wider (Tables 13-14). Also, Dell beds specimens of *Protoreodon* closely resemble those referred to *P. pumilus* from Uintan strata in the Gravelly Range based on size and the development of the P4.

The number of agriochoerid specimens identified as *Protoreodon pumilus* and *Diplobunops matthewi* far exceed those referred to any other taxon from the Gravelly Range or the Sage Creek area and occur in

TABLE 14. Measurement in mm of the P2-M3 and p3-m3 of *Protoreodon pumilus* from the Dell beds compared with the dentition of *P. pumilus* (CM 20352) provided by Gazin (1955).

Tooth Site	USNM 20352	RAM 28587	RAM 28591	MV 8231	USNM 19116	CM 9559
P2 L	9.4	—	—	—	—	8.2
P2 W	5.0	—	—	—	—	4.3
P3 L	9.7	—	—	—	—	8.6
P3 W	8.5	—	—	—	—	8.3
P4 L	8.2	—	—	—	—	7.8
P4 W	11.0	—	—	—	—	10.2
M1 L	10.7	10.1-10.2	9.9	—	—	10.7
M1 W	—	10.7-10.8	11.4	—	—	11.6
M2 L	13.0	11.6-11.7	10.4	—	—	11.8
M2 W	14.2	12.4-12.8	12.7	—	—	13.6
M3 L	13.7	11.2-11.5	—	—	—	13.5
M3 W	16.0	12.9-13.0	—	—	—	13.5
p3 L	9.9	—	—	—	7.9-8.3	9.1-9.4
p3 W	4.9	—	—	—	4.1-4.5	4.2-4.6
p4 L	10.0	—	—	10.0	8.2-9.6	9.7-9.8
p4 W	6.9	—	—	6.5	4.9-5.3	5.8-6.1
m1 L	9.7	—	—	—	8.1-9.2	10.1
m1 W	7.5	—	—	—	6.1-7.4	7.5
m2 L	11.4	—	—	11.7	10.1-10.8	11.4-11.6
m2 W	8.1	—	—	7.8	7.9-8.5	7.9-8.2
m3 L	17.8	—	—	16.7	16.5-16.8	15.9-16.3
m3 W	7.8	—	—	7.9	7.5-8.0	7.6-8.3

different proportions. In the Gravelly Range, the sample of *Diplobunops matthewi* is three times as large as that of *Protoreodon pumilus* (17 versus 5; Lofgren et al. 2020), while in the Dell beds *Protoreodon pumilus* is almost four times as common as *Diplobunops matthewi* (31 versus 8). Sampling bias is apparently not a major factor because both taxa are often recovered from the same sites in both areas. Uintan strata in the Gravelly Range are presently about 900 meters higher in elevation compared to the Dell beds, but whether that was the case in the late Eocene is unknown.

Family Protoceratidae Marsh 1891

Leptoreodon Wortman 1898

Leptoreodon marshi Wortman 1898

Figure 7C, Table 15

Holotype—AMNH 2064 skull, rami, vertebrae,

and limb fragments, from the White River Pocket, Uinta “B” member, Uinta Basin, Utah (Wortman 1898).

Referred Specimens—CM 84457 right maxilla with M1-M2 from CM locality 3558; CM 84460 right M2 and left and right p4, CM 84458 left mx fragment from CM locality 3557.

Description and Discussion—The M2 of CM 84460 is well-preserved and is transversely elongate and has a prominent parastyle and mesostyle and a smaller but distinct metastyle (Figure 7C). The paracone, metacone, protocone and hypocone are large and subequal in size and the labial cingulum is well developed, with smaller but distinct cingula present on the antero-posterolingual tooth margins. *Leptoreodon major* and *L. marshi* are the largest species of *Leptoreodon* (Goltz 1976; Kelly 1990; Ludtke and Prothero 2004) and the molars of CM 84457 and CM 84460 are similar in size to *L. marshi* but smaller than

L. major (Table 15). *Leptoreodon major* has stronger upper molar styles and cingula than *L. marshi* (Ludtke and Prothero 2004). In the M2 of CM 84460 the metastyle is small and only the labial cingulum is well developed (Figure 7C), so the Dell beds specimens are referred to *L. marshi*.

TABLE 15. Measurements in mm of the M1-M2 of the holotype of *Leptoreodon marshi* (AMNH 2064) and M1-M2s of *L. marshi* and *L. major* provided by Ludtke and Prothero (2004:tables 1, 4) compared with CM 84460 and CM 84457 from the Dell beds.

Tooth Site		AMNH 2064	<i>L. marshi</i>	<i>L. major</i>	CM 84460	CM 84457
M1	L	7.3	6.2-7.0	7.3-8.2	—	6.7
	W	9.0	7.7-8.9	9.0-9.6	—	8.3
M2	L	9.0	7.3-8.4	9.0-9.3	7.3	7.6
	W	10.3	10-10.5	10.3-11.9	10.2	9.6

Family Dichobunidae Gill 1872
Pentacemylus Peterson 1931
Pentacemylus leotensis Gazin 1955
 Figure 7D-E, Table 16

Holotype—PU 16310 partial skull and left mandible from Uinta C, Leota Ranch Quarry, Uinta County, Utah (Gazin 1955).

Referred Specimens—UMPC 15958 partial left M1 from UMPC locality MV 7629; RAM 28564 left dentary with m1-2 from RAM locality V2020006.

Description—UMPC 15958 is a moderately worn M1 missing the anterior 1/3 of the paracone, half of the protocone, and nearly the entire paraconule. The paracone, metacone and metaconule are crescentic and a distinct hypocone is absent but its position is represented by a thickening of enamel on a well-developed lingual cingulum (Figure 7D). RAM 28564 is a dentary with m1 and an erupting m2 with the crown mostly exposed. Both molars have two pairs of crescentic cusps, metaconid and protoconid in the trigonid, and hypoconid and entoconid in the talonid (Figure 7E). The apices of the protoconid and hypoconid are slightly lower but their bases are much broader than those of the metaconid and entoconid. In both molars, the protoconid and the hypoconid are transversely anterior to the metaconid and entoconid (respectively) and the transverse valley between the metaconid and entoconid is shallow and broad, but narrow and steep between the protoconid and hypoconid.

Discussion—*Pentacemylus* closely resembles *Bunomeryx* but the upper and lower molars of

Pentacemylus have more crescentic cusps and the M1 lacks a hypocone (Gazin 1955; Stucky 1998). UMPC 15958 lacks a hypocone and has crescentic cusps (Figure 7D) and the principal cusps of the m1-2 of RAM 28564 are crescentic (Figure 7E). *Pentacemylus progressus* and *P. leotensis* are the only known species of *Pentacemylus* (Stucky 1998), but *P. progressus* is larger than *P. leotensis* (Gazin 1955). UMPC 15958 and RAM 28564 are closer in size to *P. leotensis* (Table 16) and are referred to that species.

TABLE 16. Measurement in mm of the M1 and m1-2 of *Pentacemylus progressus* and *P. leotensis* provided by Gazin (1955:33-34) compared with UMPC 15958 and RAM 28564 from the Dell beds.

Tooth Site		<i>P. progressus</i>	<i>P. leotensis</i>	UMPC 15958	RAM 28564
M1	L	6.3	5.3-5.4	5.8	—
	W	7.7	6.9	6.5	—
m1	L	6.2-6.3	5.3-6.0	—	5.7
	W	4.4-4.9	3.7-3.8	—	4.3
m2	L	6.2-6.9	5.7-6.3	—	5.9
	W	4.7-5.0	4.3-4.6	—	4.3

Order Perissodactyla Owen 1848
 Family Equidae Gray 1821
Epihippus Marsh 1877
Epihippus uintensis (Marsh 1875)
 Figure 7F, Table 17

Holotype—YPM 11300 left dentary with p2-m1, Teepee Trail Formation, Wyoming (Marsh, 1875, not figured).

Referred Specimen—UMPC 15960 partial right m1 from UMPC locality MV 7629.

Description and Discussion—UMPC 15960 is a partial right m1 of *Epihippus* that is missing half of the trigonid basin (metastylid to paracristid) due to breakage (Figure 7F). *Epihippus* is one of the poorest known equids and the most common species are *E. uintensis* and *E. gracilis*, which differ in size (MacFadden 1980, 1998). However, Hanson (1996) argued that *E. uintensis* and *E. gracilis* cannot be separated by size and represent the same species with *E. gracilis* having priority. Kelly and Murphey (2016) reviewed the issue of whether the two species were synonymous and determined that if samples of *E. uintensis* and *E. gracilis* from various Uintan localities in San Diego County (California) were combined, the range in size of the dentition of *E. gracilis* would exceed what is normally expected for a species. The

length of UMPC 15960 is within the range of variation of both species but its width exceeds that of *E. gracilis* (Table 17).

Family Hyracodontidae Cope 1879
Triplopus Cope 1880
Triplopus sp. cf. *T. rhinocerinus* Wood 1927
 Figure 8A-B, Tables 18-19

Eotrionias rhinocerinus Wood 1927

Holotype—YPM 13331 left and right maxillae and jaws of one individual (upper dentition figured by Wood 1927, plate 4 figures 17-19; upper and lower dentitions (see Radinsky 1967, figure 4B-C) and the lower molars of a second individual, near mouth of Lake Fork, Uinta Basin, Utah, (Wood 1927; Radinsky 1967).

Referred Specimens—UMPC 8436 left dentary with p2, broken p3 (crown absent), p4 missing anterolingual half of trigonid, and m1-m3 from UMPC locality MV 8115; RAM 27790 right P4 from RAM locality V2023005.

Description and Discussion—UMPC 8436 is moderately worn dentary (Figure 8A) whose m1-m3 have a small but distinct paralophid that is similar in morphology to molars of *Triplopus* and *Epitriplopus*. These two hyracodontid genera are distinguished by features of their upper dentition, particularly the more molariform premolars in *Epitriplopus* and the small M3 metacone in *Triplopus* that is absent in *Epitriplopus* (Radinsky 1967; Prothero 1998). Tabrum et al. (1996, 2001) identified UMPC 8436 as *Triplopus* sp. cf. *T. rhinocerinus* in the absence of an upper dentition. The molars of UMPC 8436 are similar in size to the holotype of *Triplopus rhinocerinus* and lower dentitions of *T. obliquidens* and *T. implicatus* (Table 18).

The unworn P4 (RAM 27790) of *Triplopus* recovered in 2023 lacks the large hypocone seen in the holotype of *Epitriplopus uintensis* (Radinsky 1967, fig. 14). RAM 27790 is rectangular in occlusal view and has a well-developed ectoloph and protoloph, a distinct paracone, metacone and protocone, and nearly continuous anterior, lingual, and posterior cingula (Figure 8B). The metaloph is short and lacks a hypocone and the protoloph extends posteriorly past the metaloph. The protoloph is separated from the terminus of the metaloph by a deep, narrow valley and only after moderate wear would the lophs converge. The development of the metaloph and protoloph in the P4 in *T. obliquidens*, *T. implicatus*, and *T. rhinocerinus* (Radinsky 1967, fig. 3D, 2A, 4B, respectively) is similar to that of RAM 27790 (Figure 8B). But the Dell beds specimen is larger than any P4 referred by Radinsky (1967) to *Triplopus* and is about 12% larger

than the holotype of *T. rhinocerinus* (Table 19). Thus, RAM 27790 is tentatively identified as *Triplopus* sp. cf. *T. rhinocerinus*.

RAM 23756 (maxilla with P2-M3) from Uintan strata in the Gravelly Range is about 25% larger than the holotype of *T. rhinocerinus* and its P4 is about 15% larger than RAM 27790 from the Dell beds (Table 19). RAM 23756 was referred to *Triplopus* sp. cf. *T. rhinocerinus* but the size of the teeth and the lack of a hypocone in P2 may indicate a new species of *Triplopus* (Lofgren et al. 2020). The size of RAM 27790 suggests it probably represents the same species as the one recovered from the Gravelly Range. The lower dentition (UMPC 8436) from the Dell beds has smaller teeth than RAM 27790 and RAM 23756 and may represent a smaller variant of that species. For now, UMPC 8436 is tentatively considered the same taxon as RAM 27790 and RAM 23756 until additional specimens of *Triplopus* are recovered.

TABLE 18. Measurements in mm of the p2-m3 (*estimate) of UMPC 8436 from the Dell beds compared with the dentition of *T. implicatus*, *T. obliquidens* and the holotype of *T. rhinocerinus* (YPM 13331) provided by Radinsky (1967:tables 2, 3) and Wood (1927:table 2).

Tooth Site		<i>P. progressus</i>	<i>P. leotensis</i>	UMPC 15958	RAM 28564
M1	L	6.3	5.3-5.4	5.8	—
	W	7.7	6.9	6.5	—
m1	L	6.2-6.3	5.3-6.0	—	5.7
	W	4.4-4.9	3.7-3.8	—	4.3
m2	L	6.2-6.9	5.7-6.3	—	5.9
	W	4.7-5.0	4.3-4.6	—	4.3

Family Tapiridae Gray 1821
Heteralestes Peterson 1931
Heteralestes leotanus Peterson 1931
 Figure 8C, Table 20

Dilophodon leotanus Hough 1955

Holotype—CM 11849 left and right adolescent dentaries, from Uinta C horizon, Uinta County, Utah (Peterson 1931, fig. 5).

Referred Specimens—CM 9560 left dentary with p2-m3, right dentary with p2-3, m1-3 from CM locality 2568; CM 78964 left maxilla with M1 from CM locality 3560; CM 78256 partial skull with right C and P2 and left M1-2, CM 78257 right P4, CM

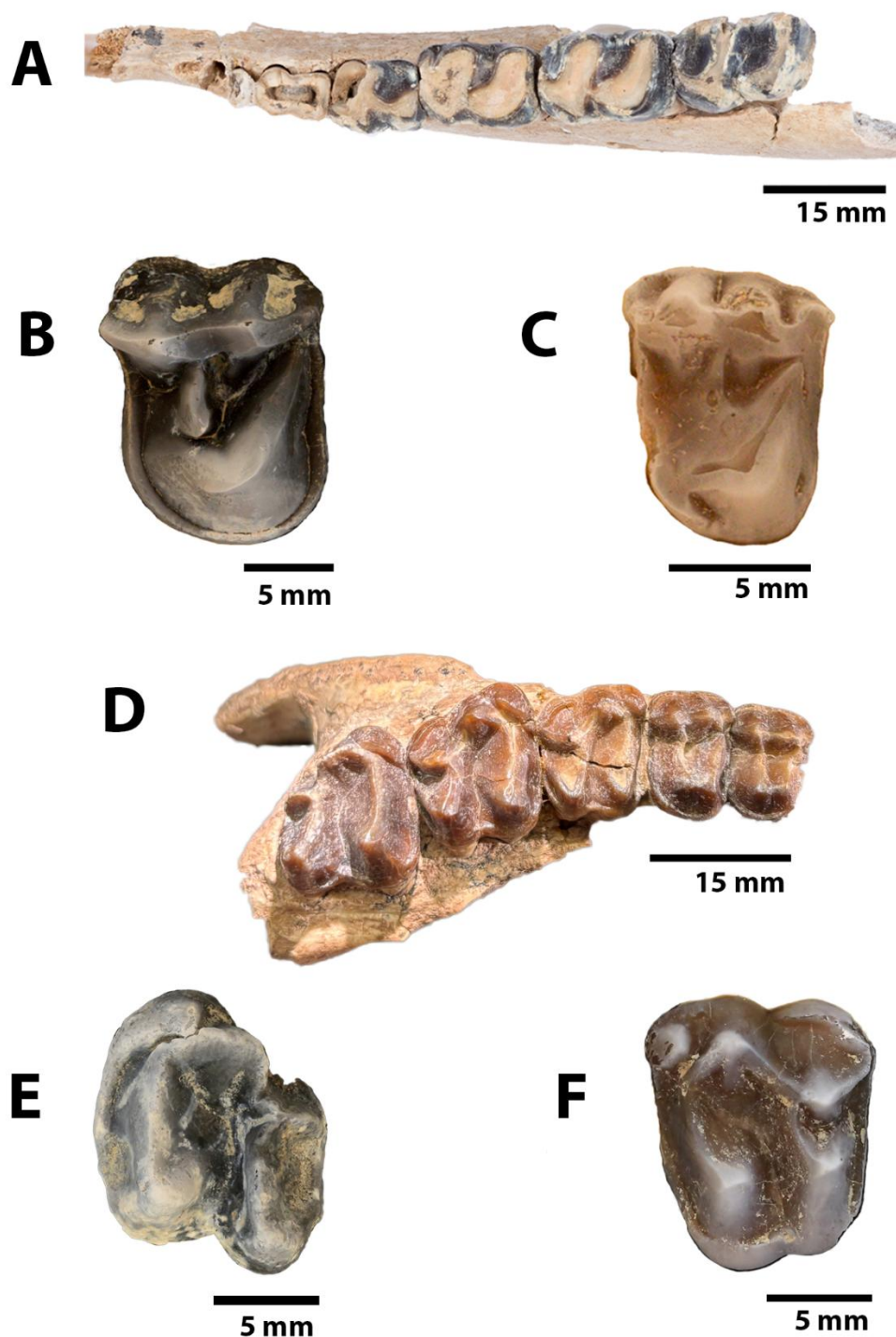


FIGURE 8. Perissodactyla from the Dell beds. A) Occlusal view of UMPC 8436 left dentary with p2, broken p3, partial p4, and m1-3 of *Triplopus* sp. cf. *T. rhinocerinus* from UMPC locality MV 8115; B) Occlusal view of RAM 27790 right P4 of *Triplopus* sp. cf. *T. rhinocerinus* from RAM locality V2023005; C) Occlusal view of CM 78257 right P4 of *Heteralestes leotanus* from CM locality 3561; D) Occlusal view of CM 9561 right maxilla with P3-M3 holotype of *Colodon kayi* from CM locality 2568; E) Occlusal view of RAM 28580 of *Colodon kayi* from RAM locality V2021035; F) Occlusal view of RAM 27258 left M1 of *Colodon woodi* from RAM locality V2020006.

78258 right DP4 from CM locality 3561; UMPC 8352 left maxilla with DP4, UMPC 8349 left dentary with m1, m3, broken m2 from UMPC locality MV 7729; CM 37490 right dentary with m1-m3 and left dentary with p2-p3, m1, broken p4 from CM locality 601; UMPC 8341 right maxilla with M2-M3, UMPC 8347 left M3, UMPC 8345 right P2 from UMPC locality MV 7629; UMPC 8317 partial right and left juvenile dentaries from UMPC locality MV 8112.

Description and Discussion—*Heteralestes leotanus* was erected by Peterson (1931) and distinguished from *Dilophodon* by its smaller size and molarization of the dp4. Hough (1955) referred CM 9560 from the Dell beds and specimens of *Heteralestes leotanus* from Uinta County, Utah (USNM 20207-20208) to *Dilophodon leotanus*, noting that the two genera were similar and that the holotype of *Heteralestes leotanus* (CM 11849) represented a juvenile which negated its small size as a diagnostic character. Colbert and Schoch (1998) resurrected *Heteralestes* but retained *Dilophodon*, distinguishing the genera by the lack of a hypocone in the P3-4 of *Dilophodon* and that the metaloph bypasses the hypocone in P3-4 of *Heteralestes*.

The Dell beds sample of this small tapiroid was first referred to *Dilophodon leotanus* (Tabrum et al. 1996) and later to *Heteralestes leotanus* (Tabrum et al. 2001). Only CM 78257 has a P4 and it has an incipient hypocone denoted on the posterior cingula by a wear facet and the postprotocrista extends towards it (Figure 8C). In CM 16060 (maxilla with P4-M3 of *Dilophodon*, Wagon Bed Formation, Hendry Ranch Member, loc 9) from Badwater, Wyoming, the protocone wear facet is crescentic and the postprotocrista extends towards the metacone and a hypocone is not developed. Thus, the Dell beds sample appears to represent *Heteralestes* and the size of these specimens is slightly smaller or within the size range of specimens referred to *Dilophodon leotanus* from Utah and Wyoming (Table 20).

Family Helaeletidae Osborn and Wortman 1892

Colodon Marsh 1890

Colodon kayi Hough 1955

Figure 8D-E, Table 21

Desmathotherium kayi Hough 1955 in part

Holotype—CM 9561 right maxilla with P3-M3 from CM locality 2568, Dell beds, Sage Creek Basin, Montana (Hough 1955, pl. 7, fig. 8). A maxilla fragment with left P1-P3 and CM 12088 right dentary with p2-m3, left dentary with p4, m2-3 apparently represent the same individual as CM 9561 (Tabrum 2012).

TABLE 19. Measurements in mm of the upper dentition of the holotype of *T. rhinocerinus* (YPM 13331; Wood, 1927:table 2) and *T. implicatus* and *T. obliquidens* (Radinsky, 1967:tables 2, 3) compared with RAM 23756 from the Gravelly Range of Montana (Lofgren, et al, 2020:table 19). Dell beds P4 (RAM 27790) is 13.7 mm in length and 18.0 mm in width.

Tooth Site		YPM 13331	<i>T. implicatus</i>	<i>T. obliquidens</i>	RAM 23756
P2	L	10.0	—	7.4-7.9	12.5
	W	11.0	—	8.9-10.2	17.5
P3	L	10.5	9.3-9.6	8.2-10.2	14.1
	W	14.0	12.0-12.5	9.3-12.8	19.8
P4	L	11.7	10.0-11.7	8.8-10.8	14.7
	W	16.4	14.0-17.2	11.2-14.7	22.7
M1	L	16.0	13.1-14.8	12.2-13.1	19.1
	W	17.6	15.9-17.5	14.3-16.0	22.5
M2	L	16.6	15.5-16.9	14.0-14.8	21.5
	W	19.3	17.2-18.7	14.2-16.9	25.8
M3	L	17.2	14.8-17.2	13.0-15.1	17.2
	W	19.6	16.2-19.3	14.9-18.3	24.5

Referred Specimens—CM 8930 left dentary with p3-m3, right dentary with p3-m3 from CM locality 613; CM 12003 right dentary with p2-m3, left dentary with m2-3 from CM locality 601; UMPC 8340 right maxilla with P3, UMPC 8348 left dentary with roots of m2-3, UMPC 8353 right maxilla with P3 and partial P4, UMPC 8357 right dentary with partial m3 from UMPC locality MV 7629; CM 78965 right maxilla with M2-3 from CM locality 3560; USNM 20203 M3, USNM 20199 M3 from CM locality 2568; RAM 28580 left M3 from RAM locality V2021035.

Description and Discussion—USNM 20203, USNM 20199, and the holotype of *Colodon kayi* (CM 9561) from the Dell beds and three specimens from Badwater Creek, Wyoming (including USNM 20200), were originally referred to “*Desmathotherium*” *kayi* (Hough 1955). Later, Gazin (1956) described “*Desmathotherium*” *woodi* from Badwater Creek noting it was smaller than “*D.*” *kayi* and referred the three specimens from Badwater Creek of “*D.*” *kayi* described by Hough (1955) to “*D.*” *woodi* (USNM 20200 designated as holotype). These specimens were reexamined by Radinsky (1963) who determined that “*Desmathotherium*” was not valid, so specimens from the Dell beds became *Colodon kayi* and those from

TABLE 20. Measurements in mm of the M1-M3 and p2-m3 of *Heteralestes leotanus* from the Dell beds compared with the dentition of “*Dilophodon leotanus*” from Uintanstrata in Utah and Wyoming (Radinsky, 1963:table 8; Black, 1979:table 3).

Tooth Site		<i>D. leotanus</i>	CM 9560	CM 78256	CM 37490	UMPC 8349	UMPC 8341
M1	L	6.6-7.7	—	6.3	—	—	—
	W	8.2-9.5	—	8.7	—	—	—
M2	L	8.2-8.3	—	8.0	—	—	7.7
	W	9.2-9.5	—	9.6	—	—	9.4
M3	L	8.6-9.5	—	—	—	—	8.9
	W	9.3-10.5	—	—	—	—	9.2
p2	L	4.1-4.8	4.2	—	—	—	—
	W	3.1-3.6	3.1-3.2	—	—	—	—
p3	L	5.1-6.1	4.8-4.9	—	5.0	—	—
	W	4.1-4.7	3.9-4.1	—	3.9	—	—
p4	L	5.7-6.5	5.4	—	5.4	—	—
	W	4.7-5.5	4.4	—	4.2	—	—
m1	L	6.9-8.5	6.8	—	6.6	6.8	—
	W	4.8-6.4	4.6-4.7	—	4.7	4.8	—
m2	L	7.4-9.2	7.9	—	7.4-7.6	-	—
	W	5.1-6.5	5.4	—	5.1-5.3	5.5	—
m3	L	9.6-10.6	9.6-9.7	—	9.3	9.2	—
	W	6.1-6.7	5.8-5.9	—	5.9	5.2	—

Badwater Creek *C. woodi*; an assertion advocated earlier by Gazin (1956) and later followed by Colbert and Schoch (1998). The maxilla of the holotype of *Colodon kayi* was illustrated by Hough (1955, pl. 7, fig. 8) and our color photo provides additional clarity of its features (Figure 8D). Both *C. kayi* and *C. woodi* were reported from the Dell beds (Tabrum et al. 1996, 2001) and recent collecting efforts have further delineated the size difference between *C. kayi* and *C. woodi* (Tables 21-22). RAM 28580 (Figure 8E), a recently collected M3 (length:15.5 mm, width:18.0 mm) is almost identical to the M3 of the holotype in morphology and size (holotype M3 length:15.9 mm, width:17.9 mm).

Colodon woodi Gazin 1956
Figure 8F, Table 22

Type specimen—USNM 20200 right maxilla with P3-M3, Teepee Trail Formation, Badwater Creek, Wyoming (Gazin 1956, pl. 2, fig. 4).

Referred specimens—CM 718 left M3 from CM locality 603; RAM 23767 damaged right M3 from V2018034; RAM 27258 left M1 from RAM locality V2020006.

Description and Discussion—CM 718, RAM 23767, and RAM 27258 (Figure 8F) have lingually deflected metacones, a feature indicative of *Colodon* (Radinsky 1963; Colbert and Schoch 1998). As previously noted, *Colodon woodi* and *C. kayi* differ in size (Radinsky 1963, table 9; Black 1979, table 4) and the Dell beds specimens are within the observed range

of M1s and M3s of *C. woodi* (Table 22).

Moropomorpha incertae sedis
Schizotheroides Hough 1955
Schizotheroides parvus Hough 1955
Figure 9A

Holotype—USNM 20205 left M2-3 from Hough Draw, Dell beds, Montana (Hough 1955, plate 8, fig. 1).

Description and Discussion—USNM 20205, recovered in the early 1950s, was described by Hough (1955) and remains the only known specimen of the genus. The M3 is undamaged and exhibits little wear, while the M2 lophs are slightly worn and the parastyle is missing because the anterior labial portion of the tooth is broken. A photo of USNM 20205 is presented here (Figure 9A) because details of the dentition are difficult to discern in the original illustration (Hough 1955, pl. 8, fig. 1). The M3 has a large parastyle, a distinct protocone and hypocone, a weak/absent paracone and metacone, and lacks a protoconule. The M2 has a distinct paracone and metacone, a well-developed hypocone and protocone, a mesostyle positioned on the labial border between the paracone and metacone, and lacks a paraconule; measurements of USNM 20205 (mm) are M2 length 11.0, width 12.4; M3 length 10.6, width 14.0.

USNM 20205 was questionably referred to the Chalicotheriidae based on its resemblance to *Eomoropus “annectens”* (now *E. amarorum* Radinsky 1964) by Hough (1955). The features of the dentition

of USNM 20205 are not aligned with Rhinoceroidea (Skinner and Gooris 1966) and the absence of a protoconule and the transverse orientation of the parastyle precludes its placement in the Chalicotheroidea (Radinsky 1964). However, Radinsky (1964) did note features suggestive of chalicother affinity; sharp, cingular cuspule between paracone-metacone (abnormal variation or incipient mesostyle?) and slight swelling on posterior side of middle of protoloph (incipient protoconule?) (Figure 9A). USNM 20205 is currently referred to *Moropomorpha incertae sedis* (Colbert and Schoch 1998) and additional specimens are required to determine its taxonomic affinity. A second species of *Schizotheriodes*, *S. jackwilsoni* was proposed by Schiebout (1977) based on two specimens from West Texas but this taxon was synonymized with *Toxotherium hunteri* (Emry 1979; Schoch 1989; Colbert and Schoch 1998).

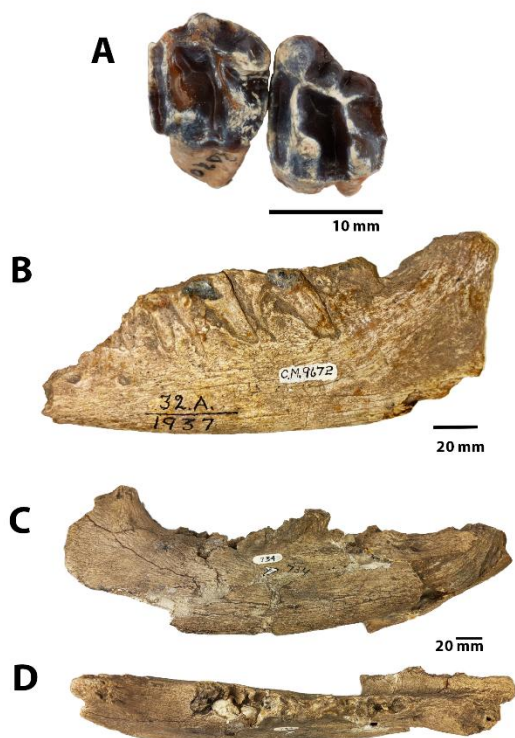


FIGURE 9. *Schizotheriodes parvus* and amynodonts from the Dell beds. A) Occlusal view of USNM 20205 left M1-2 holotype of *Schizotheriodes parvus* from Hough Draw; B) Labial view of CM 9672 left dentary with damaged p4 and worn M1-3 of amynodont genus indeterminate from CM locality 601; C) Labial and D) Occlusal views of CM 734 damaged right dentary with alveoli of incisors to m3 and small part of crown of m1 of amynodont genus indeterminate from CM locality 603.

Family Amynodontidae Scott and Osborn 1883
Amynodont genus indeterminate
Figure 9B-D

Metamynodon? Douglass 1903

Amynodontopsis cf. *A. bodei* Hough 1955

Referred Specimens—CM 734 heavily damaged right dentary with alveoli of incisors to m3 (part of m1 crown present) from CM locality 603; CM 9672 left dentary with worn m1-3 and damaged p4 from CM locality 601.

Description and Discussion—CM 734 is one of the four original specimens from the Sage Creek area and was referred to *Metamynodon* (?) in spite of its almost total lack of teeth, based on the reduction in number of the incisors and premolars, enlargement of the canine, and great lengthening of the symphysis (Douglass 1903). Shortly thereafter, CM 734 was listed as *Metamynodon?* = ?*Amynodon* in Faunal Lists of Tertiary Mammalia from the West (Osborn and Matthew 1909). Hough (1955) redescribed CM 734 and referred it to *Amynodontopsis* cf. *A. bodei*. By that time, a second amynodont specimen, a left dentary (CM 9672) found by Kay in 1937 was available for study, but apparently Hough was not aware of it. Wood (1934), Bjork (1967), and Wilson and Schiebout (1981) commented on earlier identifications of CM 734 and later it was identified as *Amynodon* sp. cf. *A. adventus* (Tabrum et al. 1996, 2001). However, CM 734 is currently cataloged as *Metamynodon?* sp. and CM 9672 as *Amynodon* sp. cf. *A. adventus*.

We have these observations concerning CM 734 and CM 9672 which are illustrated here for the first time (Figure 9B-D). The poor condition of CM 734 makes identification difficult because only a part of the crown of the m1 is preserved and premolar alveoli damage makes it difficult to confirm if p2 was present (Figure 9C-D). CM 9672 is a left dentary with a small fragment of the symphysis, heavily worn molars, and a damaged two rooted p4 missing the anterior half of the crown (Figure 9B). The roots of the molars in labial view are at an oblique angle in relation to the orientation of the dentary. Also, the molars are relatively small (length, width in mm, m1 21.4, 16.7, m2 31.0, 20.7, m3 31.5, 16.6) compared to those of *Amynodon advenus* and *Amynodontopsis bodei* (Wilson and Schiebout 1981, see table 15). When CM 734 and CM 9672 are placed side by side in occlusal view, the distance from the posterior edge of the symphysis to the posterior edge of m3 for each is approximately equivalent, which suggests they might represent the same taxon. Until more complete material is recovered from the Dell beds, CM 734 and CM 9672 are not referred to a specific genus.

BIOCHRONOLOGY AND GEOCHRONOLOGY OF THE DELL BEDS

The proposal to divide the Dell beds mammalian assemblage into two local faunas (Douglass Draw and Hough Draw) based on geographic location and biostratigraphy (Tabrum et al. 1996, tables 6-7) is questionable. As noted previously, the westerly located “lower Dell beds” (Douglass Draw) and easterly located “upper Dell beds” (Hough and Kay draws) could represent lateral facies of a dynamic depositional environment. Dell beds stratification at both draws is horizontal and these outcrops are currently at the same elevation, but normal faults limit any attempt to correlate strata or facies. Also, the mammalian assemblages from Douglass Draw and Hough Draw are very similar and do not support the assertion they differ in age. Excluding *Triplopus* which is from Dunlap Draw, the sparse Douglass Draw assemblage included three taxa (*Leptoreodon marshi*, *Colodon* sp. cf. *C. woodi*, *Triplopus*) not found in the Hough Draw area (Tabrum et al. 1996, tables 6-7) and the presence of *Colodon woodi* in the Douglass Draw assemblage suggested “that more than one level was present” in the Dell beds (Tabrum et al. 1996, 301). However, *Colodon woodi* and *Triplopus* were recently recovered from Dell beds strata in the Hough Draw area (this paper). Also, strata at Douglass Draw (“lower Dell beds”) and Hough Draw (“upper Dell beds”) were sampled for paleomagnetic analysis and both sections were mostly of reversed polarity (Tabrum et al. 1996, fig. 6a). The “lower Dell beds” were interpreted to correlate with the early part of Chron C18r and the “upper Dell beds” to the latter part of Chron C18r (Tabrum et al. 1996), but without definitive evidence for an age difference. Thus, we use Douglass Draw area and Hough and Kay Draw areas to describe major western and eastern exposures of the Dell beds and consider the Dell beds mammalian assemblage as one entity for biochronologic analysis.

The assemblage is:

DIDELPHIMORPHA

Didelphidae

Herpetotherium knighti

LAGOMORPHA

Leporidae

Mytonolagus sp. cf. *M. wyomingensis*

RODENTIA

Cylindrodontidae

Dolocyndrododon farkei new sp.

Pareumys sp. cf. *P. mufferi*

Ischyromyidae

Ischyromys sp. cf. *I. douglassi*

CARNIVORA

Miacidae

Tapocyon robustus

Lycophocyon tabrumi

LIPOTYPHILA

Geolabididae

Centetodon sp. cf. *C. magnus*

ARTIODACTYLA

Agriochoeridae

Diplobunops matthewi

Protoreodon pumilus

Protoceratidae

Leptoreodon marshi

Dichobunidae

Pentacemylus leotensis

PERISSODACTYLA

Equidae

Epihippus uintensis

Hyracodontidae

Triplopus sp. cf. *T. rhinocerinus*

Tapiridae

Heteralestes leotanus

Helaletidae

Colodon kayi

Colodon woodi

Moropomorpha

Schizotheroides parvus

Amynodontidae

Amynodont genus indeterminate

The Dell beds mammalian assemblage is late Uintan and correlates with biochron Ui3, the youngest Uintan biochron. Based on the biostratigraphy and biochronology of the Uintan NALMA provided by Gunnell et al. (2009, tables 6-9, appendix), the range of numerous Dell beds taxa overlap in the Ui3 biochron; *Herpetotherium knighti* (Ui1-3), *Mytonolagus* sp. cf. *M. wyomingensis* (genus Ui2-3), *Tapocyon robustus* (Ui2-3), *Pareumys* sp. cf. *P. mufferi* (genus Ui1-3), *Diplobunops matthewi* (Ui3), *Protoreodon pumilus* (Ui3), *Leptoreodon marshi* (Ui2-3), *Pentacemylus leotensis* (Ui3), *Epihippus uintensis* (Ui2-3), *Heteralestes leotanus* (Ui3), and *Triplopus* (Ui1b-Ui3). Also, *Epihippus*, *Protoreodon*, *Mytonolagus*, and *Triplopus* are characteristic Uintan genera and *Epihippus* is restricted to Uintan strata (Robinson et al. 2004). Furthermore, the last record of *Tapocyon* and the first occurrence of *Colodon* and *Diplobunops matthewi* is biochron Ui3 (Gunnell et al. 2009, Robinson et al. 2004) and *Pentacemylus leotensis* is only known from Leota Quarry, a Ui3 site in Utah (Prothero 1996). Thus, correlation of the Dell beds mammalian assemblage with biochron Ui3 is robust. *Dolocyndrododon* and *Ischyromys* are known from Duchesnean strata in the Western Interior (Black 1970; Tabrum et al. 1996, 2001; Korth and Tabrum 2016) and range extensions of these genera into the late Uintan are proposed here.

PALEOBIOGEOGRAPHY OF SAGE CREEK MAMMALIAN ASSEMBLAGES

The small Bridgerian Sage Creek Formation mammalian assemblage includes *Helalestes nanus*, *Hyrachyus douglassi*, *Palaeosyops paludosus*, *P. fontinalis*, *Eotitanops borealis*, *Trogosus*, and *Hyopsodus* sp. cf. *H. minusculus* and is very similar to Bridgerian assemblages from Wyoming and Colorado as noted earlier. *Palaeosyops paludosus*, *P. fontinalis*, *Eotitanops borealis*, *Trogosus*, *Helalestes nanus* are all present in the Huerfano Formation of the Raton Basin in southern Colorado (Robinson 1966) and one or more of the Bridgerian basins of southern and western Wyoming (Wind River, Green River, Bridger) (Bown 1982; Stucky and Krishtalka 1983; McGrew and Sullivant 1971; Stucky 1984; Gunnell et al. 1992; Gunnell 1998; many others). *Trogosus* and *Helalestes nanus* are also known from northern Utah (Krishtalka and Stucky 1984) and *Trogosus* from the Delmar Formation in San Diego County California (Walsh 1996). *Hyopsodus* sp. cf. *H. minusculus* is difficult to distinguish from *H. paulus* and they both commonly occur in the Huerfano Formation of Colorado and the Wind River, Green River, and Bridger basins of Wyoming (West, 1979, Gunnell 1998). *Hyrachyus douglassi* is limited to the holotype and this species is the only endemic taxon in the Sage Creek Formation mammalian assemblage, although the genus has a cosmopolitan distribution in western North America (Schoch 1989). In any case, the Sage Creek Formation mammalian assemblage, although presently limited to seven taxa, is strikingly similar to Bridgerian assemblages from Colorado and Wyoming. This indicates that dispersal between these areas was not hampered by climatic or geographic barriers during the Early Eocene.

The late Uintan Dell beds mammalian assemblage has two endemic taxa, *Schizotheroides parvus* and the new species *Dolocylindrodon farkei*. However, *Schizotheroides parvus* is known from only a single specimen and *Dolocylindrodon farkei* has generic representatives in southwest Montana based on three species that are Chadronian in age (Korth and Tabrum 2016). Thus, endemism of the Dell beds mammalian assemblage is relatively minor but its paleobiogeography is more complex compared with the Bridgerian Sage Creek Formation assemblage because many Dell beds taxa are not known from similar aged strata in adjacent states and or Uintan strata elsewhere in southwest Montana.

Only 60 km to the east is the late Uintan or early Duchesnean *Rapamys* Site/Black Butte Low mammalian assemblage from the Gravelly Range where five of the seven mammalian taxa recovered

there are also present in the Dell beds (Table 23). Prior to initiation of our collecting efforts, only three of the seven Gravelly Range taxa were known from the Dell beds, but with the addition of *Lycophocyon tabrumi* and confirmation of the presence of *Triplopus* sp. cf. *T. rhinocerinus* in the Dell beds, similarity of the two assemblages increased. When working with very small (Gravelly Range, N= 7) and moderate sized samples (Dell beds, N= 18), new records can greatly affect the percentage of similarity. The sparse *Rapamys* Site/Black Butte Low mammalian assemblage was surprisingly more similar to late Uintan assemblages from southern California rather than Wyoming and Utah, but this result was likely skewed by the presence of a single specimen each of two rare California taxa, *Lycophocyon* and *Hesperalestes borineyi* (Lofgren et al. 2020). Thus, the impending description of the more diverse Dell beds assemblage (this paper) would test whether the southwest Montana to southern California affinity would remain most robust (Lofgren et al. 2020).

Based on shared species, mammalian assemblages from Wyoming and Utah appear to have the strongest affinity with the Dell beds assemblage (Table 23). Southern California shares 10 taxa with the Dell beds but only three are species. Six of the 11 shared taxa with Wyoming are species and *Colodon woodi* is uniquely shared between the Dell beds and strata in Wyoming. Seven of the 10 shared taxa with Utah are species and all four species of artiodactyls from the Dell beds occur in the Uinta Basin of Utah (Table 23), including *Pentacemylus* which was known only from northern Utah. The Saskatchewan comparison appears to be strong as well because five of seven shared taxa are species (Table 23). Swift Current Local Fauna of Saskatchewan is the only known Uintan mammalian assemblage from the Great Plains (Storer 1996), and it includes *Colodon kayi* which is only known elsewhere from southwest Montana (Dell beds and Pipestone Springs Main Pocket); co-occurrence of *C. kayi* and *C. woodi* is unique to the Dell beds. The Diamond O Ranch mammalian assemblage (late Duchesnean-early Chadronian) also shares a number of genera with the Dell beds but only one species (Table 23), a reflection of its younger age. Thus, the Dell beds assemblage does not have the closest affinity to southern California based on species, but its generic affinity with southern California is still significant. The relatively high number of shared taxa between the Dell beds and sites in Wyoming, Utah and Saskatchewan indicate that barriers to dispersal were not greatly restrictive in the northern Rocky Mountains and Great Plains in the late Uintan. Also, based on generic similarity, there was considerable dispersal between southern California and southwest Montana as well.

SUMMARY

The oldest vertebrate bearing Tertiary strata of southwest Montana are contained within the sparsely fossiliferous Bridgerian Sage Creek Formation which crops out in three areas (type locality, Fields Draw, Dunlap Draw) near Dell, Montana. The formation contains pyroclastic and volcanoclastic sedimentary deposits and is exposed as erosional remnants in faulted terrain. These strata have yielded a small mammalian assemblage composed of *Trogosus*, *Hyopsodus* sp. cf. *H. minusculus*, *Eotitanops borealis*, *Palaeosyops fontinalis*, *Palaeosyops paludosus*, *Hyrachyus douglassi* and *Helaletes nanus*. *Eotitanops borealis* and *Palaeosyops paludosus* are index taxa for the Bridgerian North America Land Mammal Age and indicate the presence of strata that represent the Br1a and Br2 biochrons. Fields Draw strata represent the oldest part of the formation and are Br1a and Br2. An ashfall lapilli tuff associated with the Br1a assemblage (*Palaeosyops fontinalis*, *Eotitanops borealis*, *Trogosus*, *Helaletes nanus*) yielded a sanidine $40\text{Ar}/39\text{Ar}$ age of 49.84 ± 0.04 Ma which provides support for the hypothesis that the Wasatchian-Bridgerian boundary is approximately 50 Ma. The type locality and Dunlap Draw yielded a fauna (*Helaletes nanus*, *Hyrachyus douglassi*, *Palaeosyops paludosus*) that correlates to the Br2 biochron and an ashfall lapilli tuff at the top of the section at the type locality yielded a sanidine $40\text{Ar}/39\text{Ar}$ age of 48.74 ± 0.08 Ma indicating that deposition of the formation spanned about 1 Ma. The top of the formation is exposed at the type locality and is marked by a thick extensively burrowed composite alfisol paleosol overlain disconformably by strata informally named the Dell beds. All taxa from the small Sage Creek Formation mammalian assemblage are known from early Bridgerian strata (Wind River, Bridger, Green River formations) in the Bridger/Wind River/Green River basins of west-central and southwestern Wyoming and the Raton Basin (Huerfano Formation) of southern Colorado. Thus, mid-Eocene dispersal between Montana and Wyoming/Colorado was not limited by climatic or geographic barriers.

Buff colored Dell beds disconformably overlie the Sage Creek Formation and are roughly 100 m thick and more conglomeratic in the western Douglass Draw area relative to finer grained strata in the eastern Kay and Hough draw area. These western and eastern outcrop areas were tentatively considered to differ in age but cannot be differentiated temporally based on faunal or paleomagnetic data. Thus, we consider the Dell beds mammalian assemblage as a single entity. Also, the two areas may represent lateral facies of the same depositional system, but normal faulting, discontinuous exposures, and the lack of lateral

marker beds limits this determination. The Dell beds are overlain disconformably by the Cook Ranch Formation (Chadronian and Orellan) and this relationship is represented by a thick calcic paleosol exposed in Hough Draw.

Dominated by surface-collected agriochoerids, the Dell beds mammalian assemblage correlates closely to late Uintan Ui3 biochron assemblages from western North America and includes the only record of *Pentacemylus* outside of Utah, the holotype and only specimen of *Schizotheroides parvus*, and the only known co-occurrence of *Colodon kayi* and *C. woodi*. The Dell beds assemblage also includes *Ischyromys* sp. cf. *I. douglassi* and the new species *Dolocylindrodon farkei* which are early range extensions of genera from Duchesnean into late Uintan strata. The Dell beds mammalian assemblage shares five of the seven known species from the sparse *Rapamys* Site/Black Butte Low fauna in the Gravelly Range. Compared with other late Uintan assemblages from the northern Rocky Mountains, Saskatchewan, and southern California, the Dell beds mammalian fauna from southwest Montana is most similar to those from Wyoming, Utah, and Saskatchewan based on shared species but also has a significant generic affinity to southern California. These shared taxa indicate that dispersal of mammals during the late Uintan was occurring between southwest Montana and other northern Rocky Mountain States and the Great Plains in Saskatchewan, but less so with southern California.

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