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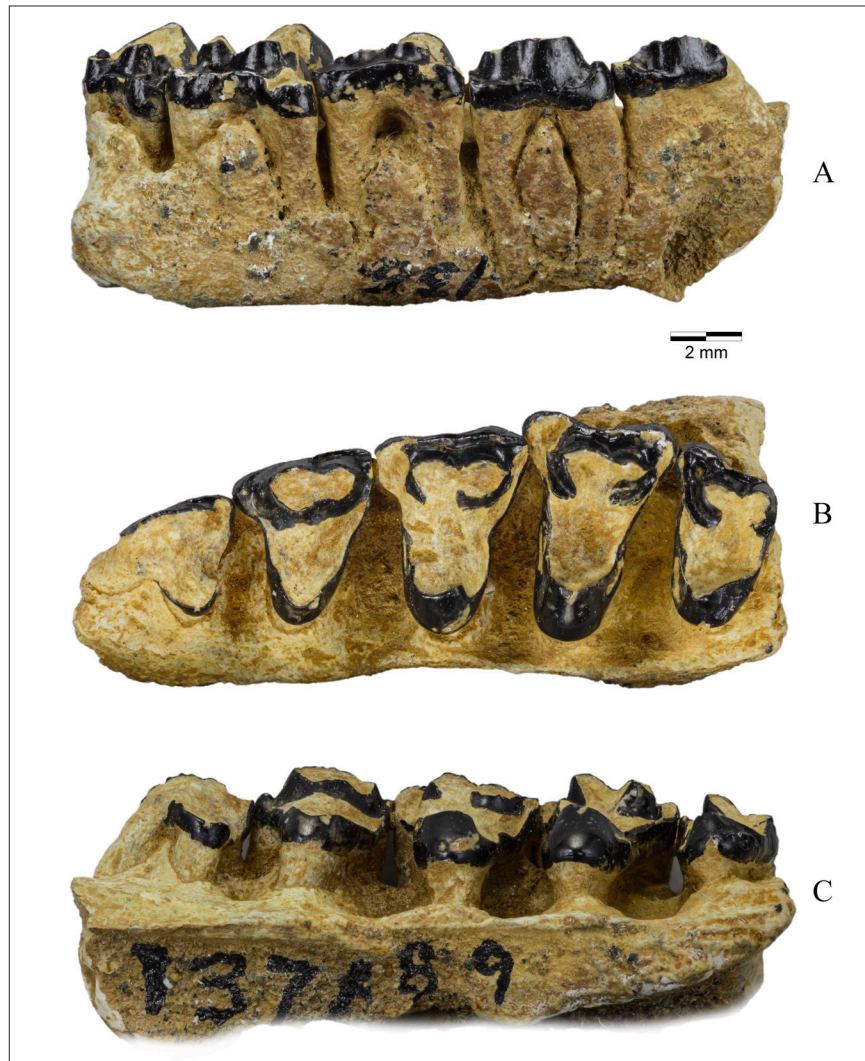
William A. Clemens (2017). *Procerberus* **(Cimolestidae, Mammalia) from the Latest Cretaceous and Earliest Paleocene of the Northern Western Interior, USA.**

Procerberus (Cimolestidae, Mammalia) from the Latest Cretaceous and Earliest Paleocene of the Northern Western Interior, USA

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Three species of the cimolestid *Procerberus* are currently recognized in the northern North American Western Interior in latest Cretaceous and earliest Paleocene (Puercan North American Land Mammal Age) faunas: *P. formicarum*, *P. andesiticus,* and *P. grandis*. Analysis of a new topotypic sample of *P. formicarum* from the Bug Creek Anthills locality provides an estimate of the range of variation of its postcanine dentition. The three currently recognized species occur in Puercan 1 (Pu1) interval zone faunas, but two other occurrences indicate that the genus originated and initially diversified prior to the Cretaceous/Paleogene boundary. Rare occurrences at several localities and entries in faunal lists suggest even greater taxonomic diversity. Limited evidence suggests continued diversification in the later Puercan and possible survival of the genus into the Torrejonian. *Procerberus grandis* or a closely related species may be a sister group of primitive taeniodonts.

Keywords: *Procerberus*, Cimolestidae, Mammalia, Tullock Member, Fort Union Formation, Puercan, Montana

INTRODUCTION

Evolution of the Cimolestidae Marsh, 1889 across the Cretaceous/Paleocene boundary (K/Pg) is documented primarily through the limited perspective of local faunas in the northern Western Interior of North America (Fig. 1). Here the rare, oldest records of the cimolestid *Procerberus* Sloan and Van Valen, 1965 have been found in chronostratigraphically anomalous local faunas interpreted as being referable to the Puercan North American Land Mammal Age (NALMA), but on lithostratigraphic or magnetostratigraphic grounds are considered to be of latest Cretaceous age. The majority of the available fossil record of *Procerberus* is derived from Paleocene local faunas referable to the Puercan 1 Interval Zone (Pu1). In northeastern Montana radioisotopic (Ar^{40}/Ar^{39}) age determinations indicate that Pu1 local faunas occur in strata deposited during approximately the first 70 ka of the Paleocene (Renne et al. 2013, Sprain et al. 2015, Ickert et al. 2015).

The goals of this study include a review of and additions to the Pu1 record of *Procerberus* in northeastern Montana. Specifically, a new, more extensive description of the postcanine dentition of *P. formicarum* Sloan and Van Valen, 1965

is provided and occurrences of *P.* sp. cf. *P. grandis* Middleton and Dewar, 2004 from the Tullock Member of the Fort Union Formation are recorded. The occurrence of two species of *Procerberus* in the Pu1 Mantua Lentil local fauna, Bighorn Basin, Wyoming, has been alluded to in several publications (e.g., Lillegraven 1969, McKenna 1969, Middleton and Dewar 2004). The material on which these observations were based is described below. The biogeographic distribution of the species of *Procerberus* and possible phylogenetic relationships of *P. grandis* Middleton and Dewar (2004) to primitive taeniodonts are explored. Finally, occurrences in two chronostratigraphically anomalous local faunas suggest two species of *Procerberus* were present in the latest Cretaceous of the northern Western Interior.

MATERIALS AND METHODS

The fossil records of cimolestids are based mostly on isolated teeth, which are rare in comparison to the more numerous isolated teeth and more completely preserved fossils representing many species of contemporaneous multituberculates and archaic ungulates ("condylarths"). As a result there has been a lack of agreement on the phylogenetic relationships and classification of the cimolestids. For example, comparisons of the classifications presented by McKenna
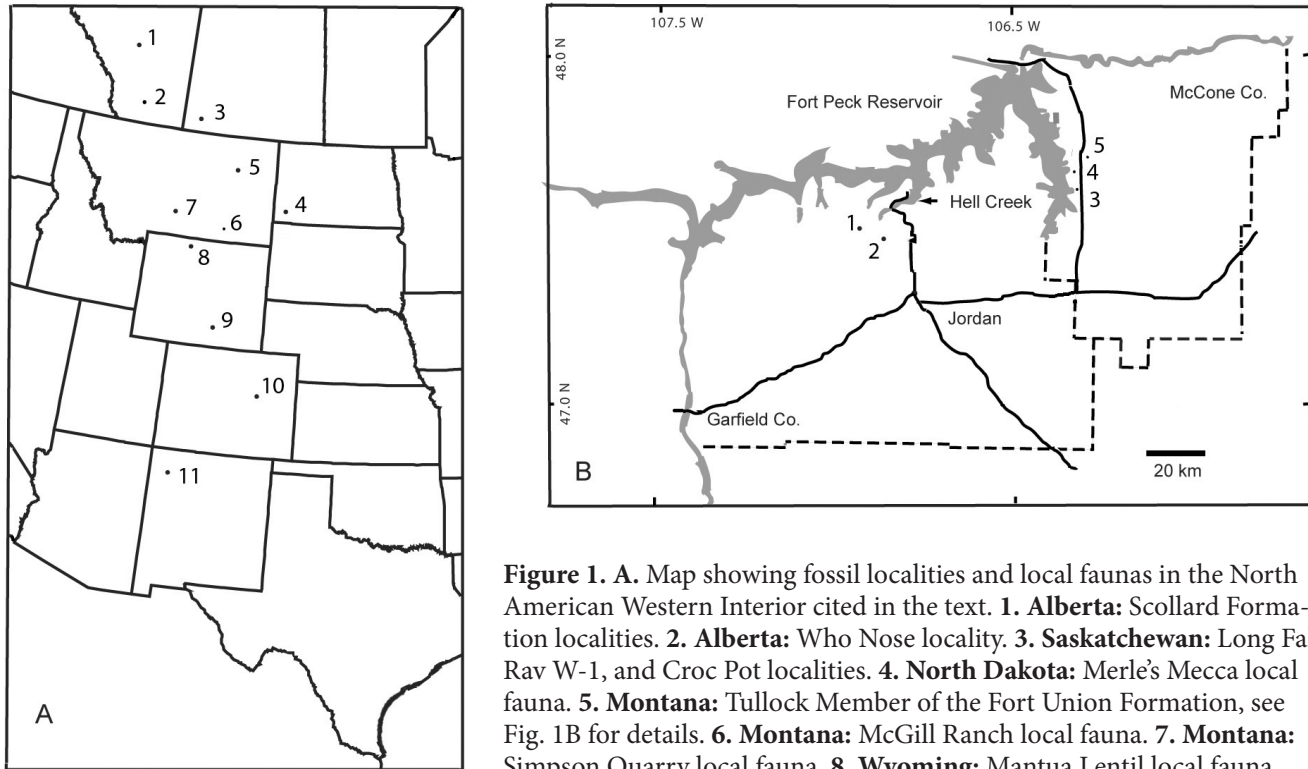
Figure 1. A. Map showing fossil localities and local faunas in the North American Western Interior cited in the text. **1. Alberta:** Scollard Formation localities. **2. Alberta:** Who Nose locality. **3. Saskatchewan:** Long Fall, Rav W-1, and Croc Pot localities. **4. North Dakota:** Merle's Mecca local fauna. **5. Montana:** Tullock Member of the Fort Union Formation, see Fig. 1B for details. **6. Montana:** McGill Ranch local fauna. **7. Montana:** Simpson Quarry local fauna. **8. Wyoming:** Mantua Lentil local fauna. **9. Wyoming:** Ferris Formation localities. **10. Colorado:** Denver Formation localities. **11. New Mexico:** San Juan Basin, Nacimiento Formation localities. **B**. Map showing fossil localities and local faunas in Garfield and McCone counties, Montana, which are cited in the text. **1.** Worm Coulee 1, McKeever Ranch 1, and Harley's Palate localities. **2.** Garbani Channel localities. **3.** McGuire Creek localities. **4.** Bug Creek Anthills. **5.** Purgatory Hill locality.

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and Bell (1997), Gunnell et al. (2008), and Williamson et al. (2011) illustrate the lack of agreement particularly at the family and higher taxonomic levels. For the purposes of this study, which does not include a new phylogenetic analysis of the members of the Cimolesta, McKenna 1975, the classification presented by Williamson et al. (2011) is adopted. *Procerberus* is included in the Cimolestidae.

Upper premolars and molars are designated with an upper case P and M, respectively. A lower case p or m identifies lower premolars or molars, respectively. O'Leary et al. (2013) and some earlier workers (e.g., Novacek 1986) noted the presence of five premolariform teeth in the dentitions of primitive non-placental eutherians. It was hypothesized that the premolars of most later eutherians traditionally designated P3, p3, P4, and p4 are homologous with the P4, p4, P5, and p5 of primitive non-placental eutherians. Simply to facilitate comparisons with previous studies of *Procerberus* and other cimolestids, here their premolars are designated P1, p1, P2, p2, P3, p3, P4, and p4.

Open nomenclature, e.g., *Procerberus* sp. cf. *P. grandis,* is used to indicate uncertainty in reference of material of *Procerberus* to a particular species (see Bengtson 1988). In all cases, use of open nomenclature reflects the small number of available specimens, their heavily worn and/or poorly preserved dentitions, and limited knowledge of ranges of dental variation. These references are simply the most probable interpretations given the paucity of pertinent information.

Length and width of upper molars were measured parallel or at right angles to an axis drawn through the apices or, if worn, the midpoints of the wear facets of the paracone and metacone. Measurements of lower molars were taken either parallel or at right angles to a mesiodistal axis drawn from the lowest point of the protocristid to the most distal point on the crown. All dental dimensions are given in millimeters. Terminology for morphological characters of the postcanines follows Williamson et al. (2011, fig. 3).

University of California Museum of Paleontology locality numbers are given in the format V65127. Precise locality data are available at the museum for research purposes.

Institutional abbreviations—**SPSM**, St. Paul Science Museum, St. Paul, Minnesota, USA; **UCM**, University of Colorado, Museum of Natural History, Boulder, Colorado, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **UF**, Florida Museum of Natural

History, University of Florida, Gainesville, Florida, USA; **UMVP**, University of Minnesota, Bell Museum of Natural History, Minneapolis, Minnesota, USA; **YPM-VPPU**, former Princeton University collections now part of the Yale Peabody Museum's holdings, New Haven, Connecticut, USA.

Other abbreviations—**BCA**, Bug Creek Anthills sandstone; **ka**, thousand years; **K/Pg**, Cretaceous/Paleocene boundary; **NALMA**, North American Land Mammal Age; **Pu**, Puercan.

SYSTEMATIC PALEONTOLOGY

Eutheria Huxley, 1880
Cimolesta McKenna, 1975
Cimolestidae Marsh, 1889
Procerberus Sloan and Van Valen, 1965

Included species

Procerberus formicarum Sloan and Van Valen, 1965
Procerberus andesiticus Middleton and Dewar, 2004
Procerberus grandis Middleton and Dewar, 2004
Procerberus sp. cf. *P. formicarum* Sloan and Van Valen, 1965
Procerberus sp. cf. *P. grandis* Middleton and Dewar, 2004

Records from Northeastern Montana

Procerberus formicarum Sloan and Van Valen, 1965
Figs. 2–4

Holotype—UMVP 1460, fragment of a dentary with p3, p4, and m1. The holotype was not figured by Sloan and Van Valen (1965). Instead, they published figures (Sloan and Van Valen 1965, fig. 6) of isolated teeth, p4 through m3 (SPSM 62-2071, 62-2072, 62-2073, 62-2074) and P3 through M3 (SPSM 62-2066, 62-2067, 62-2068, 62-2069, 62-2070).

Type locality—The type locality of *Procerberus formicarum* is the Bug Creek Anthills locality in western McCone County, northeastern Montana (Section 9, T 22 N, R 43 E). Here a large, cross-stratified sandstone channel filling is exposed over approximately 35 meters along the irregular margin of a grass covered bluff. This channel filling is extraordinarily fossiliferous. Describing their field work, Sloan and Van Valen (1965, p. 220) noted, "In the first 10 weeks about 26,000 mammal teeth, some 1,000 mammal jaw fragments…" and a multitude of other vertebrate fossils were collected. Probably the bulk of their collection came from the outcrops shown in Geological Section 3a described by Fastovsky and Dott (1986, see figs. 1 and 3a) and adjacent anthills. The

UCMP specimens analyzed here were collected from this and other areas of exposure of the Bug Creek Anthills sandstone channel filling (UCMP locs. V65127, V70199, and V70201).

In their detailed study of the geology of the Bug Creek Anthills sandstone (BCA) and other lithostratigraphic units in the area, Fastovsky and Dott (1986, p. 282) concluded, "… the BCA fauna cannot be shown to be either a Cretaceous biota or a Paleocene taphonomic artifact." Lofgren (1995) addressed this uncertainty, "The Bug Creek Problem", in his geological and paleontological studies of a region extending from the southern margin of the area considered by Fastovsky and Dott (1986) approximately seven kilometers south to include exposures in the valley of McGuire Creek. Taking advantage of much more extensive outcrops as well as vertebrate paleontological and paleobotanical evidence, he was able to demonstrate that other Bug Creek Anthills-like assemblages were of Paleocene (Pu1) age. Radioisotopic age determinations (Sprain et al. 2015) also strengthen the working hypothesis that the vertebrate fossils from the Bug

Figure 2 A–C. *Procerberus formicarum,* right maxillary with P3–M3, UCMP 218900. **A.** Buccal view. **B.** Occlusal view. **C.** Lingual view. To highlight the dentition the maxillary bone has been decolorized.
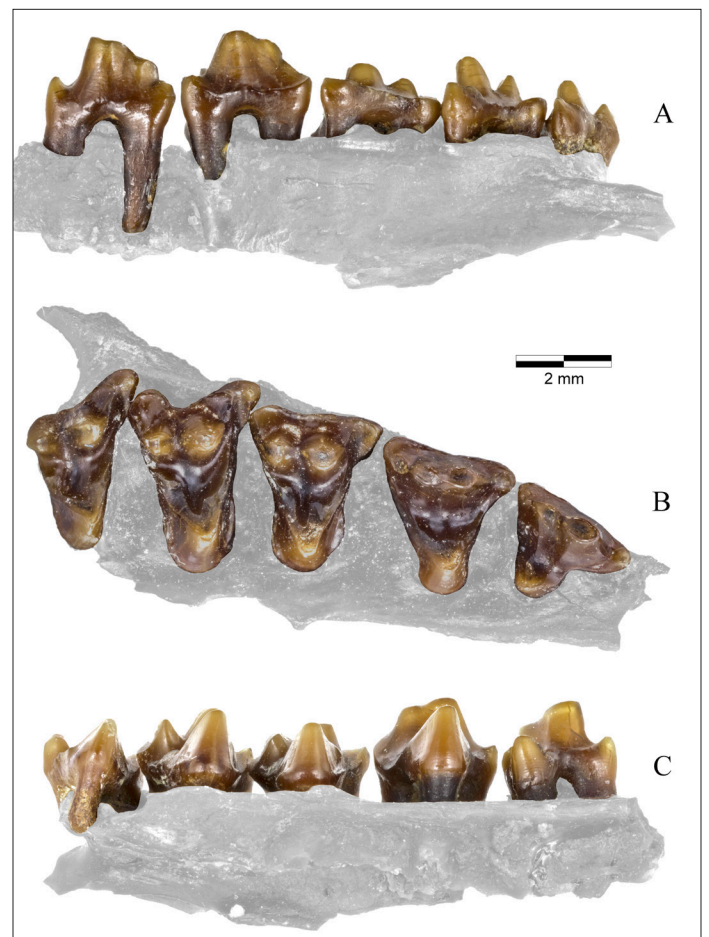
Figure 3 A–C. *Procerberus formicarum,* right dentary of p3-m3, UCMP 171389. **A.** Buccal view. **B.** Occlusal view. **C.** Lingual view.

Creek Anthills locality are a time averaged assemblage containing the remains of earliest Paleocene (Pu1) vertebrates and reworked latest Cretaceous (Lancian NALMA) vertebrate fossils.

Referred specimens consulted for this study—Referred specimens in the UCMP and UMVP collections from the Bug Creek Anthills localities are listed in Appendix 1.

Revised diagnosis— *Procerberus formicarum* differs from *P. andesiticus* in the slightly larger size of its postcanine dentition. P4 tends to have a broader ectocingulum and smaller metacone. M1 and M2 of *P. formicarum* have broader stylar shelves. On these molars the stylocones are either miniscule or usually lacking. Their conules are smaller and lack postparaconule and premetaconule cristae. When present, lingual

cingula are variable in development but tend to be larger. The lower molars have a deeper hypoflexid and the hypoconid is more buccal in position. P4 through M3 of *P. formicarum* are approximately half the size of their counterparts in the dentition of *P. grandis.* The protocone and lingual portion of P4 are narrower and more transverse, and the upper molars (especially M2 and M3) have broader stylar shelves. The apex of the protocone of M1 is more lingual in position.

Description

Published descriptions of the dentition of *Procerberus formicarum* are limited in scope and scattered in the literature. In establishing the genus and species Sloan and Van Valen's (1965) description is unfortunately brief and largely
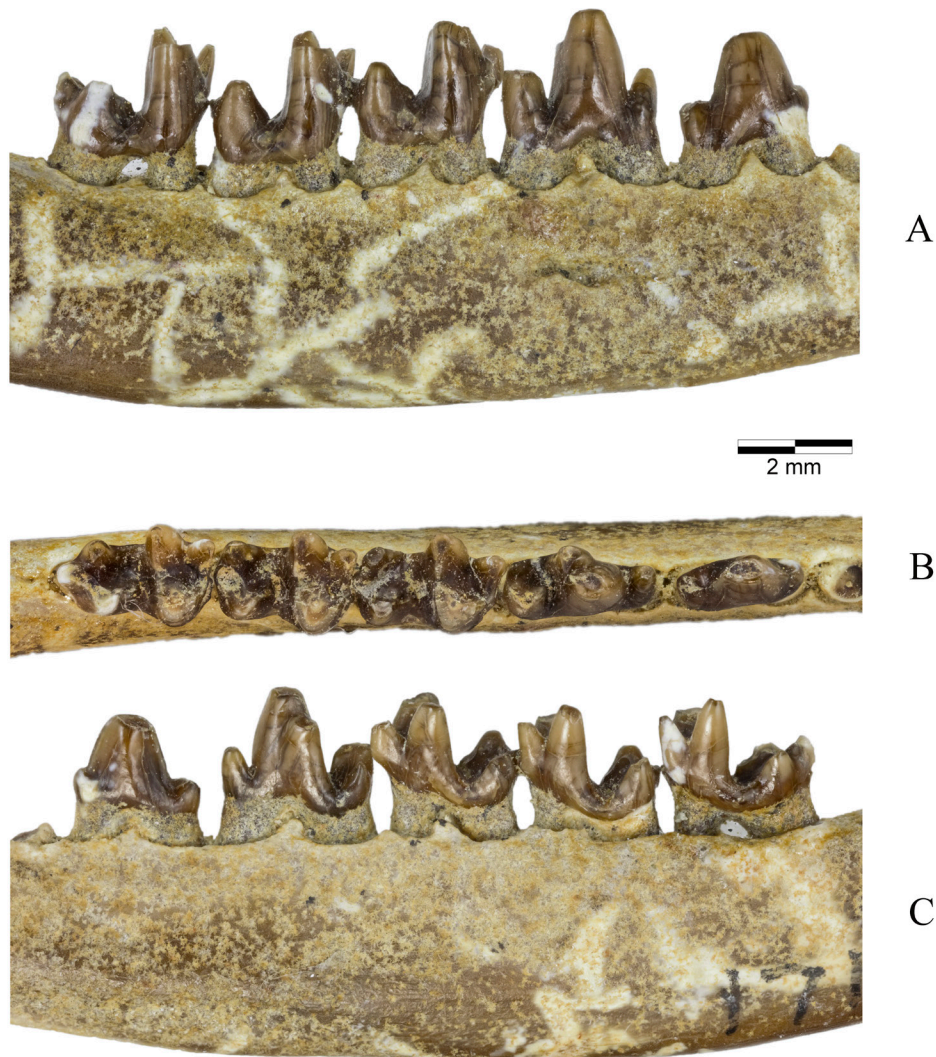
Figure 4 A–C. *Procerberus formicarum,* enlarged views of p3-m3, UCMP 171389. **A.** Buccal. **B.** Occlusal. **C.** Lingual.

qualitative. They provided line drawings of specimens other than the holotype of the species. Van Valen (1967, tables 4 and 5) presented lists of some dental characters. The first thorough description of the dentition of *P. formicarum* was provided by Lillegraven (1969, p. 61-69). In his description of what was then dubbed *Cimolestes cerberoides* Lillegraven, 1969, he presented a detailed qualitative comparison of the dentition of this species with those of *P. formicarum*, *Gypsonictops* Simpson, 1927, and *Leptictis* Leidy, 1868. In addition to adding a few details to the qualitative descriptions, Archibald (1982) provided the first compilation of quantitative data on dimensions of the dentition of *P. formicarum* based on samples from two Pu1 localities in Garfield County, Montana, (UCMP V74110 and V74111). Lofgren (1995, table 39) published the first summary of dental dimensions based on material of *P. formicarum* from the type locality, Bug Creek Anthills, and other localities in McCone County. His topotypic samples were small, two to eight specimens for each measurement. Here, a larger sample from the Bug Creek Anthills locality has been analyzed in order to better document patterns of variation.

Maxillary—The UCMP sample includes two fragmentary maxillaries preserving P3–M3 (UCMP 218900 and 218937). Another preserves M1-M2 (UCMP 102011). Also available for study was a cast of UMVP 2310 that includes P4–M3. (Dimensions of the teeth preserved in these specimens are included in the summary statistics presented in Table 1 and listed individually in Appendix 2.)

UCMP 218900 (Fig. 2) preserves the anterior base of

the zygomatic arch dorsal to M2-3 and part of the rim of the infraorbital foramen above and between the roots of P3 and P4. The crowns of P3, P4, and all the upper molars are supported by three roots.

P3—Narrow ectocingula or swellings of the enamel are present above the salient parastyle and the bases of the metacone and metastylar cusp. Apices of the paracone, metacone, and metastylar cusp are differentiated. The bodies of these cusps are not clearly delimited and form a crest decreasing in height distally. The protocone is a low, mesiodistally narrow cusp, approximately the same height as the parastyle. It is separated from the paracone by a broad, open groove, not a basin. Unlike the more distal postcanines, the width of the crown of P3 is less than its length (71–88%, n=7). Pre- and postcingula are not present.

P4—The crowns of P4 are larger than those of P3, particularly in their greater widths. Other than their larger size and presence of a narrow but usually continuous ectocingulum, P4s are similar to P3s in morphology of the parastyle, paracone, metacone, and metastylar cusp. In contrast, the protocones of P4s are much larger in both length and width. Low cristae demark the mesial and distal edges of the very shallow trigon basin. Rarely, minor irregularities in the width or height of these cristae are present in the paraconular and metaconular regions. Pre- and postcingula are not present.

M1—Its buccal margin is essentially straight or has a shallow ectoflexus. The stylar shelf is broader than the ectocingula of P4s, its buccal margin is slightly crenulated, and the shelf extends from the parastyle to the metastyle. A large parastylar lobe, which is salient mesially, is the site of early development of a transversely oriented wear facet and frequently is heavily worn or broken away. Where preserved, the occlusal surface of a little worn parastylar lobe has one or two small cusps. When two are present the distal cusp can be the buccal terminus of a very low preparacrista, suggesting it is a greatly reduced stylocone. Bases of the paracone and smaller metacone are confluent.

The trigon basin is well defined on M1. Mesially the preprotocrista, paraconule, and preparaconule crista are confluent and form the higher wall of the trigon basin. The preparaconule crista extends buccally to reach the parastylar lobe. Distally, the metaconule, which is larger than the paraconule and more distant from the protocone, and its lingual and buccal cristae form the lower wall of the trigon basin. The postmetaconule crista flares out distally and ends dorsal to the metacone. Cristae extending from the paraconule and metaconule toward the bases of the paracone and metacone are not developed on the floor of the trigon basin.

Morphology of pre- and postcingula is variable. In the sample of M1s (n=15) distinct precingula are present on all teeth. Distinct postcingula are present on six M1s, five have slight rugosities in this area, and four lack postcingula. On teeth where both are present, the precingulum is usually longer and better developed than the postcingulum, which tends to extend closer to the lingual side of the crown. Early wear on M1 and the other molars involved flattening of the protocone and conules as well as blunting the apices of the paracone and metacone.

M2—This molar differs from M1 in its deep ectoflexus, which produces distinct parastylar and metastylar lobes. The ectocingulum is very low and often interrupted at the base of the ectoflexus. Resembling M1, one or two small cusps can be present on the parastylar lobe. Where two are present the distal cusp can be linked to the paracone by a low preparacrista. The paracone is higher than the metacone. The lower halves of their bases are merged. Similar to M1, the paraconule is a minor elevation on the crest forming the mesial side of the trigon basin and the metaconule is lower but more distinct. All but one of the M2s in the sample (n =13) have a precingulum. On most it is a simple set of rugosities on the surface of the enamel and not a continuous shelf. Only about half of the M2s in the sample have either a short postcingulum or, usually, a series of isolated enamel rugosities in this region.

M3—The large parastylar lobe usually bears a small cuspule. The ectocingulum ends at the base of the paracone. A distinct metastylar lobe and associated ectocingulum are not present. Resembling the other molars, the lower halves of the bases of the higher paracone and metacone are merged. Similarly the paraconule is a minor irregularity on the high mesial margin of the talon basin. The metaconule is lower but more distinct, and the postmetaconule crista flares distally forming a basin dorsal to the metacone. Most M3s have a poorly developed precingulum and lack a postcingulum.

Dentary—Three alveoli mesial to the p3 are preserved in the most complete dentary in the UCMP sample (UCMP 171389, Fig. 3). The circumference and width of the most mesial alveolus is greater than either of the following two alveoli. Based on comparisons with dentaries of *Cimolestes incisus* Marsh, 1889 (Clemens 1973, fig. 13) and *Ambilestes cerberoides* Fox, 2015 (Lillegraven 1969, fig. 33) these alveoli are interpreted as holding the roots of a single-rooted p1 and a p2 supported by two roots. All the more distal postcanines were two-rooted with the distal root larger than the mesial. One or two mental foramina are present below p4. Parts of the coronoid and angular processes are preserved on UCMP 171389 as well as UF 22896, which was described by Archibald (1982, fig. 51). Their morphologies suggest that the angular process was slightly inflected.

p3—The three cusps of p3 are positioned linearly with the high central cusp flanked by a lower distal accessory cusp and a smaller mesial accessory cusp (Figs. 3, 4).

p4—Of the cusps of the trigonid, the protoconid is the highest. The metaconid is consistently slightly lower and positioned distolingually to the protoconid. The paraconid is salient mesially, distinctly separated from the protoconid, and the lowest cusp of the trigonid. A deep division separates the distal slope of the merged bases of the protoconid and metaconid from the talonid. In this sample there is no evidence of a ridge on the distal slope of the trigonid connecting the protoconid and the cristid obliqua (*contra* Lillegraven 1969, table 15). The talonid is transversely narrower than the trigonid and is shorter mesiodistally—approximately one-third of the length of the crown—than those of the molars. Consistently the cristid obliqua extends from below the lowest point on the protocristid to the hypoconid. Together the twinned hypoconid and slightly higher hypoconulid are higher than the entoconid. The occlusal surface of the talonid encircled by these structures is variable in size and configuration. On some teeth it is simply an inclined concave surface facing mesiolingually and ending at the distal side of the trigonid. At the other extreme, the concave surface is deeper and ends ventrally in a small depression. Initial wear involved development of a distally sloping wear facet blunting the apices of the protoconid and metaconid. Soon thereafter wear facets developed on the apex of the paraconid and the mesial slopes of the hypoconid and hypoconulid.

Lower molars—Two dentaries in the UCMP sample preserve both m1 and m2 (UCMP 150017 and 171389). On both, the length of the crown of m1 is greater than that of m2. In contrast, the width of the trigonid of m2 is greater than that of m1 (Appendix 2). The paraconid of m1 is not as closely approximated to the metaconid as these cusps are on m2. This is reflected in a slight bowing, convex mesiobuccally, of the paracristid. Isolated m1s and m2s have been distinguished on the basis of the degree of separation of their paraconids and metaconids. Although there is considerable overlap in observed ranges of variation, the mean values of the length of crown and width of trigonid agree with the proportions of those molars preserved in UCMP 150017 and 171389. The m3s are clearly distinguishable by their larger and more salient hypoconulids.

m1—On m1s the paraconid is the smallest, lowest trigonid cusp. It is positioned mesially and slightly buccal to the metaconid. A precingulid usually is present on the mesiobuccal side of the trigonid below the paracristid. The protoconid and metaconid are of essentially equal height and the lingual face of the protoconid is flat or slightly concave.

The protocristid is sharply notched with a small carnassial notch. The angle formed by the paracristid and protocristid is approximately 45° to 50°.

When viewed laterally, the maximum height of the talonid cusps is approximately half the height of the cusps of the trigonid. The three main cusps of the talonid are of approximately the same height with the entoconid slightly lower than the hypoconulid, which is slightly lower than the hypoconid. The cristid obliqua extends to the base of the distal face of the trigonid below the carnassial notch in the protocristid. A mesoconid usually is present. The lingual side of the talonid basin lacks a continuous rim although on a few teeth a minute entoconulid is present.

m2—As noted above, the most obvious difference between an m1 and m2 is the degree of separation of the paraconid and metaconid. On m2s these cusps are closely approximated, and there is essentially no trigonid basin. Also, there are slight differences in the length of the crown relative to width of the trigonid. The observed range of variation in this ratio on isolated molars, identified on the basis of degree of separation of the paraconid and metaconid, does not show a distinct bimodality. In other characters, the crowns of m1s and m2s are very similar.

m3—The trigonid of m3 resembles the trigonid of m2 in most morphological respects. On a few teeth the precingulid is longer and wider than is typical of m1 and m2. Although the observed ranges of variation overlap slightly, the major difference distinguishing m3 from the other lower molars is the greater total length of its crown reflecting the larger and more distally salient hypoconulid. The hypoconulid is the highest cusp of the talonid exceeding half the height of the protoconid and metaconid. The apex of the entoconid is lower than that of the hypoconulid. The hypoconid is the lowest cusp of the talonid. A mesoconid is present on the cristid obliqua. In contrast to the preceding molars, a small entoconulid or minor rugosities are usually present along the lingual margin of the talonid basin. The mesiodistal diameter of the distal root is noticeably greater than that of the mesial root.

Comments

The holotype of *Procerberus andesiticus* (UCM 43138) is a fragmentary palate preserving parts of the left and right dentitions (Fig. 5). A fragmentary dentary (UCM 39544, Fig. 6) preserves m1–m3. Both specimens are from the Alexander locality. Another fragment of a maxillary records the presence of *P. andesiticus* at the South Table Mountain locality. Both localities are in the Denver Formation, and the taxon is included in the Littleton fauna. This fauna has been correlated with the younger part of the Pu1 interval zone or possibly the early part of the Pu2 interval zone (Eberle 2003,
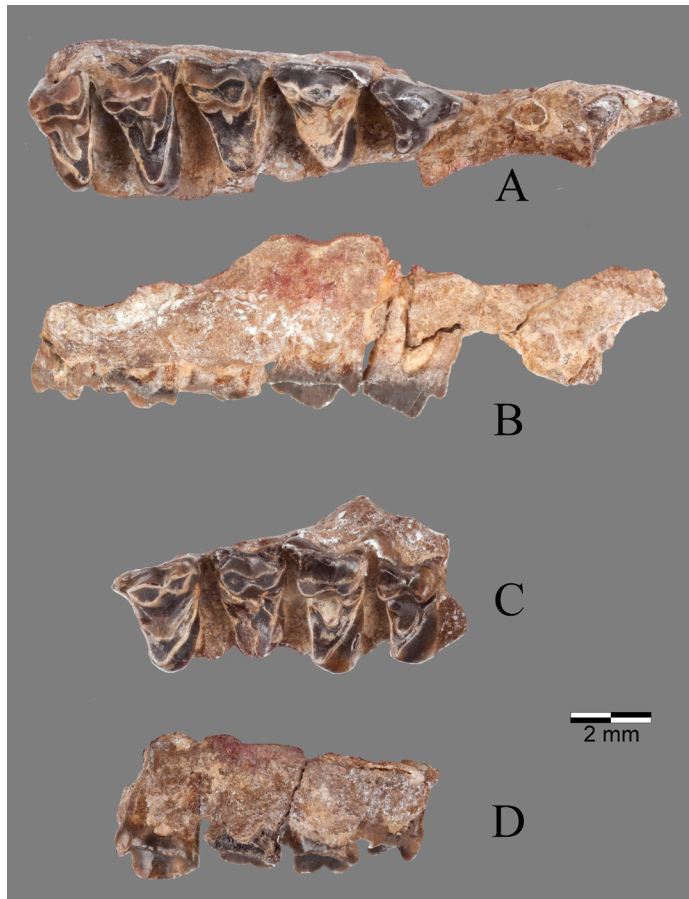
Figure 5 A–D. *Procerberus andesiticus,* holotype, fragments of a palate preserving parts of the left and right dentitions, UCM 43138. **A.** Occlusal view of right P3-M3. **B.** Buccal view of right P3-M3. **C.** Occlusal view of left P4-M3. **D.** Buccal view of left P4-M3.

Figure 6 A, B. *Procerberus andesiticus*, left dentary with fragment of m1 and m2-3, UCM 39544. **A.** Lingual view. **B.** Buccal view.

Middleton and Dewar 2004, Dahlberg et al. 2016).

The morphological differences distinguishing the dentitions of *P. andesiticus* and *P. formicarum* are slight. They include differences in width of the ectocingulum and morphology of the metacone on P4 and width of the stylar shelf, presence of a stylocone, relative sizes of the conules, and development of lingual cingula on the upper molars. Depth of the hypoflexid and position of the hypoconid on the lowers differ as well as the positions of the paraconid and metaconid on m2 and relative size of the hypoconulid on m3. In comparison to the ranges of variation found in the topotypic sample of *P. formicarum,* the dimensions of the teeth of *P. andesiticus* (Appendix 3) usually fall below or, in a few instances, at the low end of the observed ranges for *P. formicarum* (Table 1).

The dental characters distinguishing *P. andesiticus* and *P. formicarum*, particularly the difference in their size, warrant provisional recognition of two distinct but probably closely relat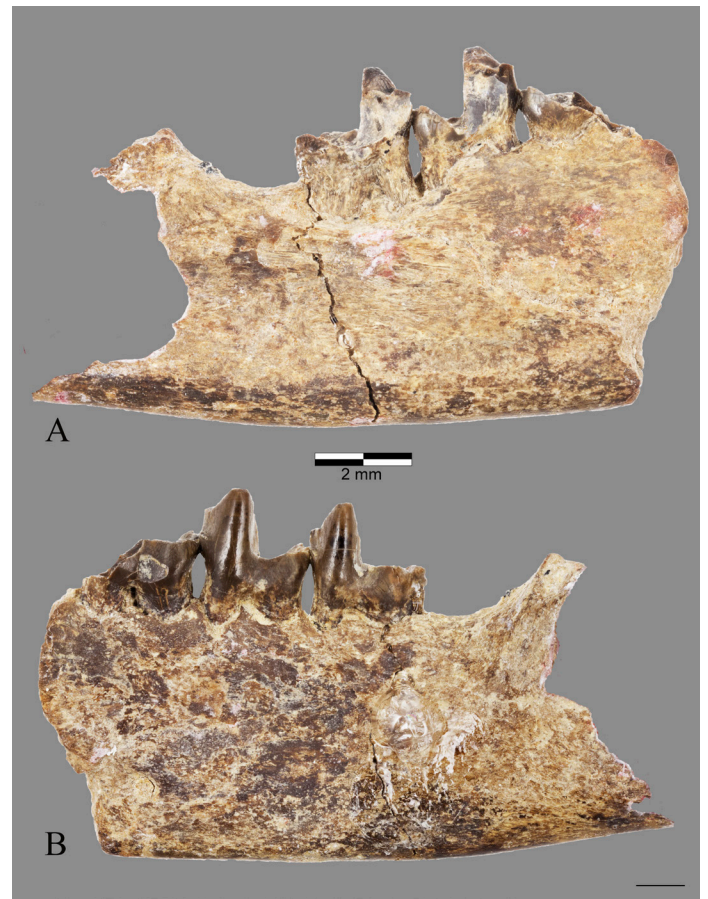ed species. This working hypothesis is supported by the probable older age of the Bug Creek Anthills sample of *P. formicarum* and the possibility of biogeographic heterogeneity of Puercan faunas of the Western Interior.

Procerberus sp. cf. *P. grandis* Middleton and Dewar 2004
Figs. 7, 8

Referred specimens—UCMP 137189, fragment of a maxillary with P3-M3. UCMP 150024, a fragment of a lower molar, is provisionally referred.

Localities—UCMP 137189 was found at UCMP V77136 (Harley's Palate locality), an isolated exposure of the lower part of the Tullock Member, Fort Union Formation, in the valley of Snow Creek approximately 3.4 km south of Worm Coulee 1 (UCMP V74111, see Archibald 1982). UCMP 137189, discovered by the late Harley Garbani, is the only fossil recovered from this locality. The fossil has been informally referred to as "Harley's Palate" (e.g., Middleton and Dewar 2004).

Erosion has removed strata capping this isolated exposure,

Table 1. Dental dimensions of topotypic sample of *Procerberus formicarum.* All dimensions in millimeters. N=number, OR=observed range.

		N	Length	Width	
P3	OR	7	2.34–2.66	1.71–2.24	
	Mean	7	2.52	2.06	
				Mesial Width	**Distal Width**
P4	OR	13	2.43–2.90	2.33–2.93	2.60–3.28
	Mean	13	2.60	2.65	2.92
M1	OR	15	2.43–3.04	2.55–3.59	3.05–3.83
	Mean	15	2.73	3.26	3.46
M2	OR	13	2.47–2.92	3.42–3.91	3.56–4.08
	Mean	13	2.63	3.66	3.83
M3	OR	16	1.92–2.44	2.90–3.90	2.41–3.11
	Mean	16	2.22	3.51	2.87
				Width	
p3	OR	3	2.26–2.64	0.95–1.09	
	Mean	3	2.44	1.04	
				Width trigonid	**Width talonid**
p4	OR	17	2.59–3.12	1.21–1.48	1.03–1.36
	Mean	17	2.82	1.34	1.19
m1	OR	21	2.62–2.95	1.67–2.10	1.33–1.68
	Mean	21	2.81	1.86	1.54
m2	OR	21	2.52–2.84	1.77–2.14	1.34–1.71
	Mean	21	2.66	1.95	1.54
m3	OR	24	2.74–3.34	1.69–2.06	1.31–1.64
	Mean	24	3.02	1.84	1.45

so its stratigraphic position cannot be directly determined. A series of fossiliferous channel deposits in the basal strata of the Tullock Member are present nearby. Two of them (V77128 and V77129) have yielded fossil mammals indicative of their deposition during the Pu1 interval zone. Currently the working hypothesis is that the strata exposed at UCMP V77136 were deposited during the Pu1 interval zone. On the basis of the stage of evolution of its dentition, Middleton and Dewar (2004) suggested that UCMP 137189 might be slightly younger than the hypodigm of *P. grandis* from the Denver Formation.

UCMP 150024, an isolated lower molar, is part of the collection from UCMP V72210 (McKeever Ranch 1, see Archibald 1985). The locality is in the lower part of the Tullock Member and this local fauna is also assigned to the Pu1 interval zone.

Description

A fragment of maxillary, UCMP 137189, contains P3-M3 (Fig. 7). The infraorbital foramen is dorsal to P3. The posterior end of the infraorbital canal appears to have been at the level of the lingual root of M2. The extensive areas of exposed dentine on the teeth are modified, probably by chemical alteration, and lack clearly preserved wear surfaces. On P4 and the molars the general configurations of the preserved surfaces of the dentine relative to the remaining fragments of enamel suggest they approximate the worn surfaces at time of death. The mesial end of P3 might have suffered more extensive damage. The crowns of P3-M3 are supported by three roots. Dental dimensions are given in Table 2.

P3—Enamel is preserved only on the lingual and buccal sides of the crown, which allows measurement of its width. The mesial end of its crown is heavily damaged. What
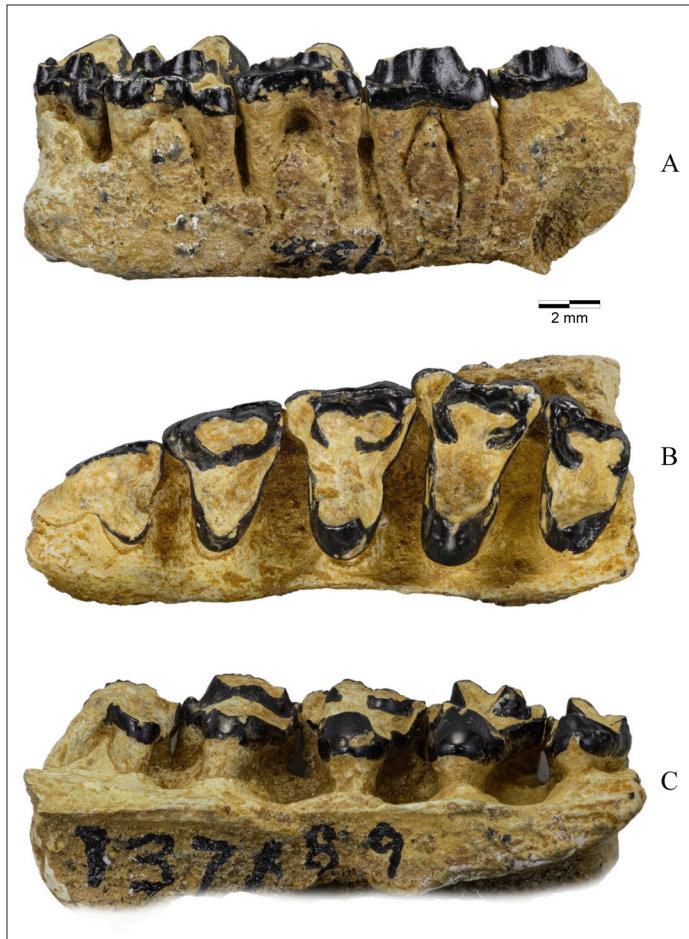
Figure 7 A–C. *Procerberus* sp. cf. *P. grandis,* left maxillary with P3-M3, UCMP 137189. **A.** Buccal view. **B.** Occlusal view. **C.** Lingual view.

Table 2. Dental dimensions of UCMP 137189, *Procerberus* sp. cf. *P. grandis,* Harley's Palate Locality, Tullock Member, Fort Union Formation, northeastern Montana. All dimensions in millimeters.

	Length	Mesial Width	Distal Width
P3	>4.4	3.60	
P4	4.59	5.08	5.28
M1	4.87	5.70	5.86
M2	4.93	6.50	6.97
M3	3.73	5.15	5.02

remains of the crown indicates presence of a small protocone and either a paracone or relatively closely approximated paracone and metacone. A narrow ectocingulum is present on the distal end of the crown.

P4—Enamel completely encircles the base of the crown. The parastylar region carries a small, separate cusp. Cusps are lacking on the essentially straight ectocingulum, which narrows across the buccal side of the paracone and, distally, expands in width across the metacone to end at the metastyle. The apices of the closely approximated paracone and smaller metacone are worn exposing dentine, but their bases are encircled by enamel. The trigon basin lacks enamel. A slight inflection of its mesial enamel margin suggests that a paraconule was present. A deep dorsal deflection of the worn distal enamel margin would have removed the metaconule, if one was present.

M1—Enamel has been removed from the surface of the broad parastylar region, which is mesial to the paracone. Distally, the essentially straight ectocingulum expands in width and carries a few minor crenulations. The bases of the paracone and metacone are not fully separated. A short narrow precingulum is present dorsal to the worn trigon basin. The distal side of the trigon basin is deeply worn leaving only a narrow band of enamel across the base of the crown. A band of exposed dentine extends buccally from the trigon basin distal to the metacone to reach the metastylar region.

M2—In occlusal view, the crown of M2 is slightly longer than that of M1 but is distinctly wider. Unlike M1, the parastylar region is oriented mesiobuccally from the paracone, and a shallow ectoflexus is present. The ectocingulum is preserved from the distal side of the paracone to the metastylar region and carries a few minor crenulations. Grooves in the enamel on the mesiolingual side of the paracone and the distolingual side of the metacone suggest the presence of a distinct paraconule and metaconule prior to wear. A short precingulum and slightly shorter postcingulum are present.

M3—The distal part of the crown is reduced, and it is smaller than those of the preceding molars. A small cusp is present on the surface of the large, mesiobuccally directed parastyle. A distinct ridge encircles the mesial and buccal sides of the parastyle. It is continuous with the ectocingulum that extends distally along the buccal side of the crown to the metacone and bears a few minor crenulations. The apices of the paracone and distinctly smaller metacone are worn. A grove in the enamel mesiolingual to the paracone suggests that a paraconule was present prior to wear. The precingulum is slightly longer and extends more lingually than those of the preceding molars. In contrast, the postcingulum consists of two ridge-like bumps positioned distolingually.

Comments

The teeth preserved in UCMP 137189 are distinctly larger than those in the topotypic samples of upper postcanines of *Procerberus formicarum* and *P. andesiticus*. The difference warrants reference of UCMP 137189 to a separate species. In establishing the species *Procerberus grandis,* Middleton and Dewar (2004) highlighted the significant difference in size of its postcanine dentition, about twice as large as that of
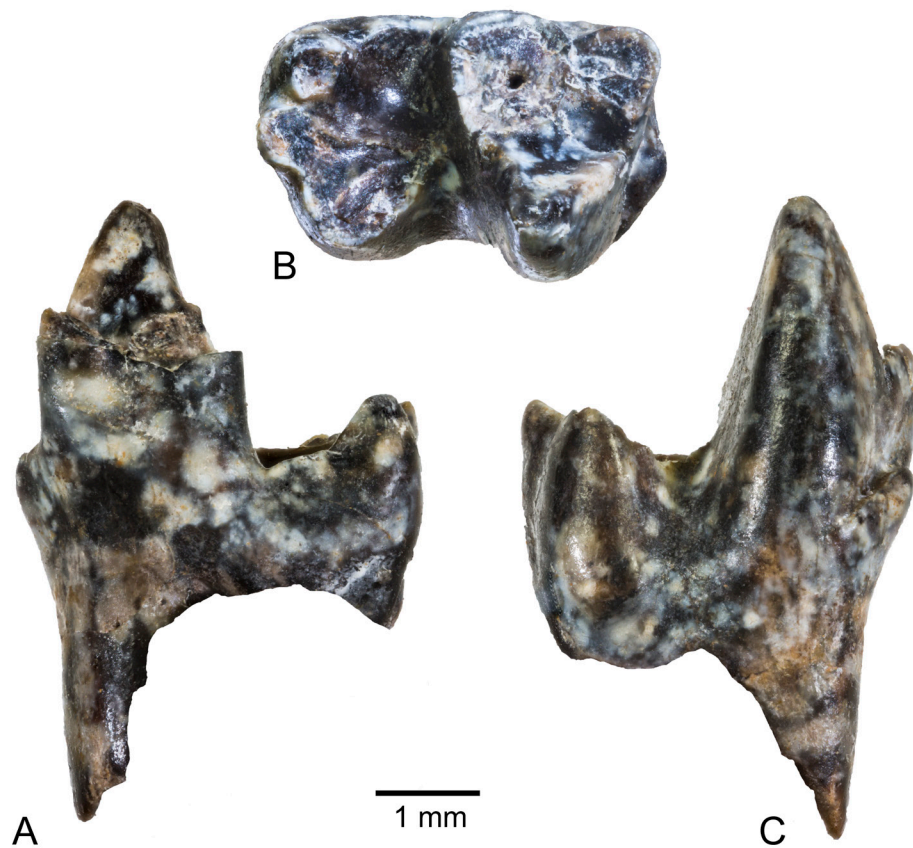
Figure 8 A–C. *Procerberus* sp. cf. *P. grandis,* right lower molar, probably an m2, UCMP 150024. **A.** Lincual view. **B.** Occlusal view. **C.** Buccal view.

P. andesiticus. Precise comparisons of the dental dimensions of UCMP 137189 with *P. grandis* cannot be made because all but one of the reported dimensions of the small hypodigm of *P. grandis* —the holotype preserving P4, M2 and M3, and isolated M1, M2, and m1—are estimates (Middleton 1983, table 15, and see Appendix 4). Recognizing this limitation, in the nine dental dimensions available for the P4, M2, and M3 of the holotype of *P. grandis* (UCM 34970) UCMP 137189 is smaller in seven. Only in the mesial and distal widths of P4 are the dimensions of UCMP 137189 greater than the estimates for the holotype of *P. grandis.* The estimated length and mesial width of the isolated M1 referred to *P. grandis* are smaller than those of the M1 in UCMP 137189; the estimated distal width is only slightly larger. Only the length of the isolated M2 referred to *P. grandis*, which is not an estimate, was reported. It is smaller than that of the M2 of UCMP 137189. This irregular pattern of differences in dental dimensions might fall within the range of variation of *P. grandis.* Given the lack of precision in comparison of dental dimensions of the heavily worn teeth it is best to only identify UCMP 137189 as *P.* sp. cf. *P. grandis.* Discovery of larger samples,

including unworn or only slightly worn teeth, is needed to make a more specific identification.

Wilson (2004, 2014) reported the occurrence of *Cimolestes* sp. A. in the Pu1 interval zone in Garfield County. This record was based on a fragmentary right lower molar, UCMP 150024 (Fig. 8), from UCMP V72210 (McKeever Ranch 1). Its buccally sloping precingulid extends across essentially the entire mesial face of the trigonid. Only the outlines of the bases of the broken paraconid and metaconid remain. The apex of the protoconid is slightly worn. Together the morphology of what remains of the cusps of the trigonid suggests it is an m2. The rim of the talonid basin is worn, but the hypoconulid appears to have been slightly closer to the entoconid than the hypoconid. The heavily worn cristid obliqua ends at base of trigonid below the central notch in the protocristid. Presence or absence of a mesoconid cannot be determined.

UCMP 150024 is a relatively large tooth (length of crown = 3.84 mm, width trigonid = 2.63 mm, width talonid = 2.42 mm). The width of the talonid is only slightly less than that of the trigonid. It is relatively wider than would be expected

in a species of *Cimolestes* (*sensu* Lillegraven 1969). The current difference in height of talonid and trigonid, measured from base of enamel to highest remaining parts of talonid and trigonid, suggests the trigonid was less than twice the height of the talonid. These characters suggest that UCMP 150024 is referable to a species of *Procerberus* rather than *Cimolestes*. Its dimensions are outside the range of variation of *P. formicarum* and smaller than the single known lower molar of *P. grandis*. Provisionally UCMP 150024 is identified as the second Pu1 record of *P.* sp. cf. *P. grandis* in Garfield County but recognizing that additional material might document greater taxonomic diversity.

Records from Northwestern Wyoming

Several authors (e.g., Lillegraven 1969, McKenna 1969, Middleton and Dewar 2004) have mentioned the co-occurrence of two species of *Procerberus* distinguished by differences in dental dimensions in a local fauna found in the Mantua Lentil, Bighorn Basin, Park County, Wyoming. The Mantua Lentil was described by G. L. Jepsen (1930) and later named as a unit of the Polecat Bench Formation (Jepsen 1940), which is now recognized as part of the Fort Union Formation. Fossils from the Mantua Lentil Quarry and the nearby Leidy Quarry are recognized as documenting Pu1 local faunas (Lofgren et al. 2004). The fossils mentioned by earlier authors and other specimens described below are from the Mantua Lentil Quarry.

Procerberus sp. cf. P. formicarum SLOAN AND VAN VALEN, 1965
FIGS. 9, 10

Referred material—YPM-VPPU 17808, fragment of a maxilla with P3-M3; YPM-VPPU 21027, fragment of a maxilla with damaged P3-M2; and YPM-VPPU 21026, a dentary with heavily worn p3-m3.

Description

Of the three fossils from the Mantua Lentil Quarry referred to *Procerberus* sp. cf. *P. formicarum,* YPM-VPPU 17808 (Fig. 9) preserves the least damaged upper postcanine dentition. Comparisons were made with the topotypic sample of *P. formicarum*, particularly UCMP 218900 (Fig. 2), and *P. andesiticus* (Fig. 5). In most morphological characters they are similar, but there are a few differences. The paracone-metacone ridges of P3 and P4 of YPM-VPPU 17808 are slightly lower, and these cusps are not as distinctly separated as those of *P. formicarum* and *P. andesiticus.* Widths of the stylar shelves of M1-M2 of YPM-VPPU 17808 are comparable to those of *P. formicarum*. Their parastylar
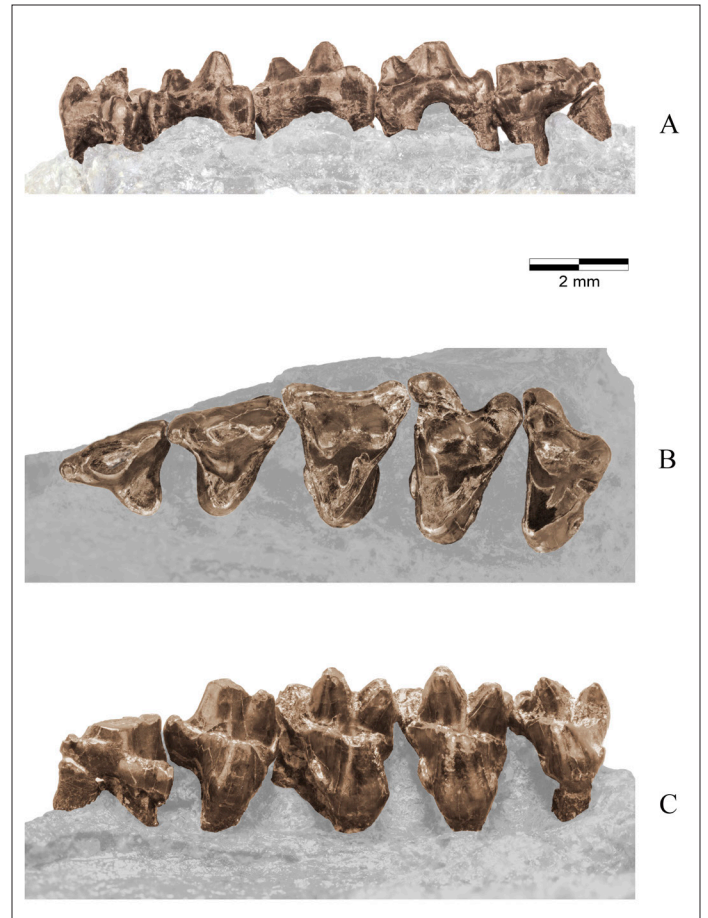

Figure 9 A–C. *Procerberus* sp. cf. *P. formicarum*, left maxillary with P3-M3, YPM-VPPU 17808. **A.** Buccal view. **B.** Occlusal view. **C.** Lingual view. To highlight the dentition the maxillary bone has been decolorized.

lobes are damaged, but, differing from *P. andesiticus,* there is no evidence of the presence of distinct stylocones or preparastylar cristae. The rims but not the floors of their trigon basins are worn. As indicated in Fig. 9, the mesial and lingual margins of the trigon basin of M3 are damaged. If present, the postparaconule and premetaconule cristae were low and short. M1 and M2 have precingula and slight indications of postcingula. On M3 there is a slight indication of a precingulum, and the postcingulum is simply a distinct bulge on the distal side of the crown. Dimensions of the postcanine dentition of YPM-VPPU 17808 (Table 3) are either within the observed ranges of variation of the topotypic sample of *P. formicarum* or, in the case of length of P3, width of P4, and both dimensions of M2, are just below the observed ranges of variation.

YPM-VPPU 21027 is a maxillary fragment preserving the damaged P3-M2. P3, the least damaged tooth, is heavily worn. It has a distinct protocone that was supported by a separate root. It is the only tooth in YPM-VPPU 21027
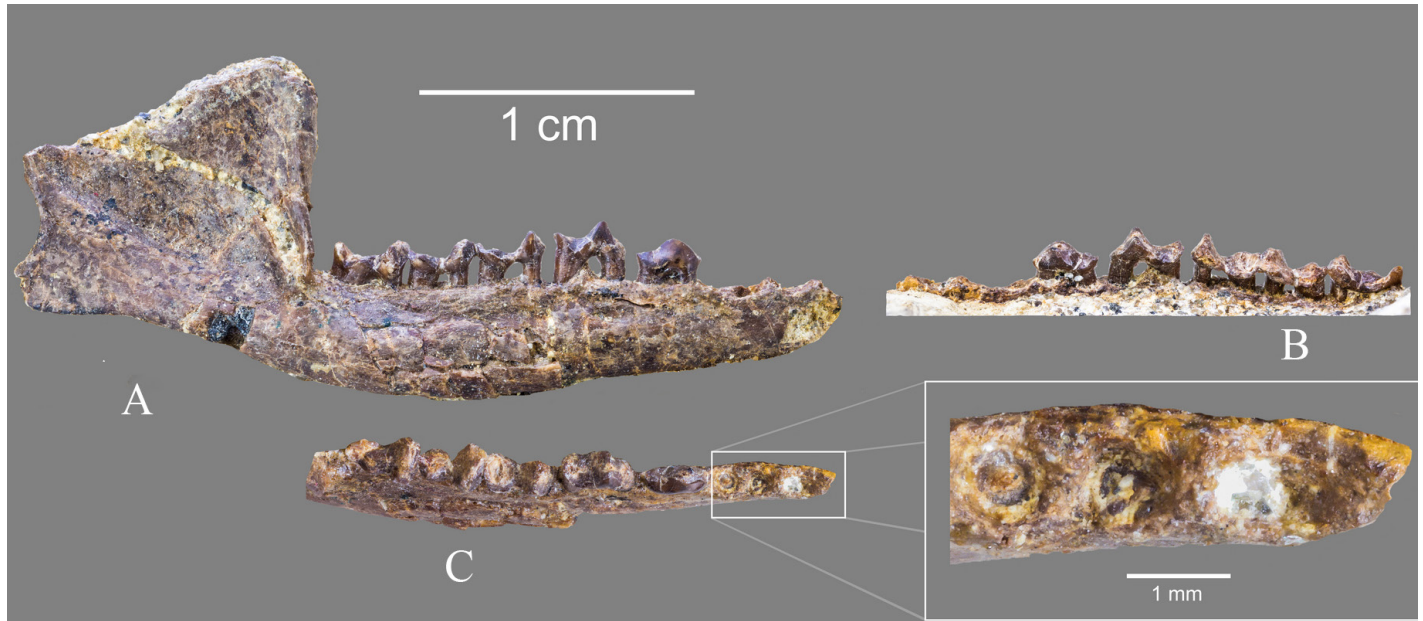
Figure 10 A–C. *Procerberus* sp. cf. *P. formicarum,* right dentary with p3-m3, YPM-VPPU 21026. **A.** Buccal view. **B.** Lingual view. **C.** Occlusal view with mesial end enlarged to show what are interpreted to be alveoli for a single-rooted p1 and a two-rooted p2.

complete enough to preserve the length and width dimensions of its crown (Table 3). These are within the ranges of variation of the topotypic sample of *P. formicarum.* P4 is worn on the paracone, metacone, trigon basin, and protocone. Its distal width is also within the observed range of variation of the topotypic sample of *P. formicarum.* Lingual cingula are not present. On M1 the parastylar surface and buccal side of paracone are missing. Most of the occlusal surface of the tooth is cracked and damaged. A precingulum and longer postcingulum are present. Only the buccal half of the crown of M2 remains. Enough is preserved to show that the paracone was only slightly higher than the metacone.

YPM-VPPU 21026 (Fig. 10) is a right dentary with p3-m3. Of these postcanines p4-m3 are particularly heavily worn. In their size and positions the damaged alveoli mesial to p3 resemble those of the topotypic dentary of *P. formicarum,* UCMP 171389 (Fig. 3) and can be interpreted as housing the roots of a single-rooted p1 and a two-rooted p2. What remains of the crown of p3 resembles p3s of *P. formicarum.* The dental dimensions given for YPM-VPPU 21026 (Table 3) are within the observed ranges of variation of the topotypic sample of *P. formicarum,* but they are best regarded as underestimates of the dimensions of the unworn crowns. A mental foramen is present below and between the roots of p4. If not distorted by postmortem crushing, the angular process of the mandible was only slightly inflected.

Comments

The small dimensions of the dentition of YPM-VPPU 17808 can be interpreted as supporting either its identification

Table 3. Dental dimensions of species of *Procerberus* from the Mantua Lentil Quarry, Polecat Bench Member, Fort Union Formation,Wyoming. All dimensions in millimeters. *=estimated value

Procerberus sp. cf. *P. formicarum*

	Length	Mesial Width	Distal Width
YPM-VPPU 17808			
P3	2.30	1.84	
P4	2.39	2.31	2.45
M1	2.49	3.01	3.24
M2	2.37	3.35	3.44
M3	1.97	3.10	2.64
YPM-VPPU 21027			
P3	2.40	1.89	
P4	2.65*	2.64*	3.00
YPM-VPPU 21026			
		Width	
p3	2.43	1.06	
p4	2.62*		
m1	2.55*		
m2	2.46*		
m3	2.79*		

Procerberus sp. cf. *P. grandis*

	Length	Mesial Width	Distal Width
YPM-VPPU 14213			
P3	3.15	2.41	
P4	3.81	3.68	3.95
M1	3.78*	4.67*	4.79
M2	3.58*	4.68	5.46
M3	3.12	4.83	4.03

as a small individual of *P. formicarum* or a representative of *P. andesiticus*. In contrast, the absence of stylocones and well developed postparaconule and premetaconule cristae on the molars are characters differentiating *P. formicarum* from *P. andesiticus*. On the basis of the latter characters YPM-VPPU 17808 is tentatively identified as *P.* sp. cf. *P. formicarum*.

What remains of the dentition of YPM-VPPU 21027 resembles the dentition of YPM-VPPU 17808. Only P3 is complete enough to provide dimensions of both the length and width of the crown, and they are in the observed range of *P. formicarum* as is the distal width of P4. Identification as *P.* cf. *P. formicarum* is reasonable but based largely on co-occurrence.

The body of the dentary of YPM-VPPU 21026 is slightly more complete than that of UCMP 171389 and morphologically indistinguishable. The alveoli in the mesial end of YPM-VPPU 21026 are similar to those of UCMP 171389 and suggest the presence of a single-rooted p1 and two-rooted p2. The preserved premolars and molars of YPM-VPPU 21026 are heavily worn. Isolated postcanine teeth showing comparable heavy wear are present in the topotypic sample of *P. formicarum*. As with YPM-VPPU 17808 and 21027, reference of YPM-VPPU 21026 to *Procerberus* cf. *P. formicarum* must be regarded as tentative.

Procerberus sp. cf. P. grandis Middleton and Dewar 2004
Fig. 11

Referred specimen—YPM-VPPU 14213, fragment of a maxillary with P3-M3.

Description

In the maxillary, parts of the ventral and posterior margins of the infraorbital foramen are preserved dorsal to the distal end of P3. The posterior end of the maxillary is damaged. What remains suggests the anterior end of the zygomatic arch was dorsal to M3.

P3—This premolar is worn, but it is not as heavily worn as the more distal postcanines. There is no indication of a parastyle or an ectocingulum. The distal slope of the paracone is worn, and the presence or absence of a metacone cannot be determined. A small metastylar cusp is present. Lingually, a small expansion of the crown carrying a very small, worn protocone was supported by what appears to be a separate root.

P4—The paracone, metacone, and protocone are deeply worn exposing the dentine. The original morphology of most of this area of the crown is obliterated. Buccally, what enamel remains preserves a small parastyle, a short and
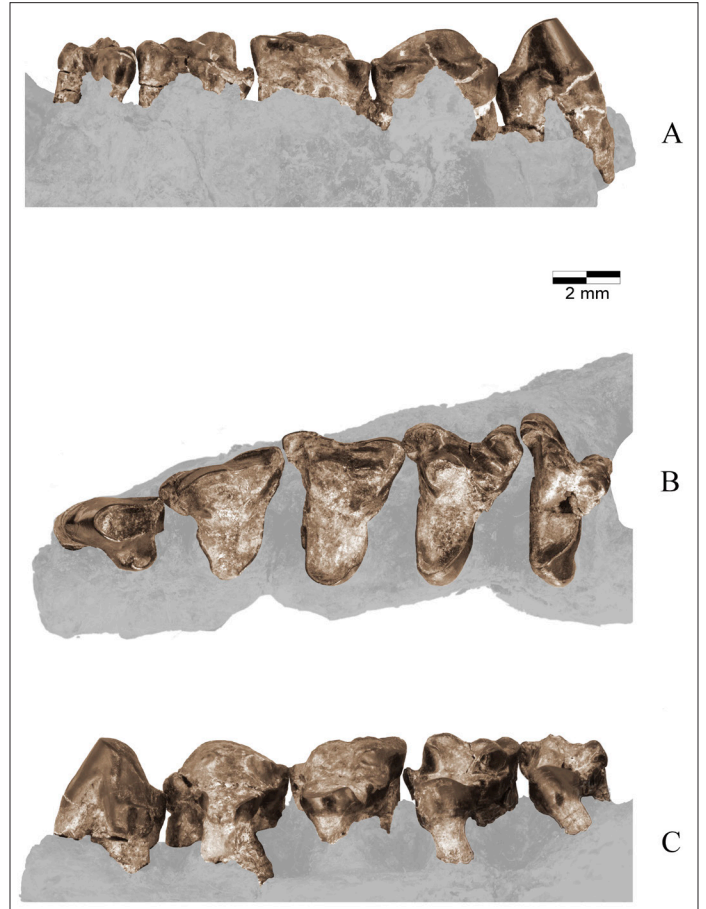

Figure 11 A–C. *Procerberus* sp.cf. *grandis*¸ left maxillary with P3-M3, YPM-VPPU 14213. **A.** Buccal view. **B.** Occlusal view. **C.** Lingual view. To highlight the dentition the maxillary bone has been decolorized.

narrow ectocingulum buccal to the metacone, and a small metastylar cusp. There are no traces of lingual cingula on the deeply worn mesial and distal slopes of the protocone. P4 and the molars were supported by three roots.

M1—The surface of the parastylar region is broken away, and the presence or absence of a stylocone cannot be determined. The buccal margin of the ectocingulum is slightly indented producing a shallow ectoflexus. A wear facet on the crest of the ectocingulum extends to the distal end of the metastylar lobe and converges with the wear facet on the postmetacrista. The apices of the paracone, metacone, and protocone as well as the intervening area of the trigon are heavily worn exposing dentine. A short precingulum is present. Enamel in the area where a postcingulum would be expected has been worn away.

M2—The surface of the parastylar lobe is broken, and there is no evidence of a stylocone on what remains. The metastylar lobe is large. Its mesial edge projects buccally at almost a right angle to the more mesial part of the ectocingulum and

produces a pronounced ectoflexus. The principal cusps and intervening trigon basin are not as heavily worn as on M1, but probably not deep enough to remove pre- and postcingulae. Absence of these cingulae and the mesiodistal narrowness of the trigon basin make the occlusal outline of the lingual half of M2 noticeably slimmer than the occlusal outline of M1.

M3—The parastylar lobe is distinctly elongated and is deeply entrenched lingually by a wear facet. This facet extends lingually to the protocone. The ectocingulum extends distolingually ending at the mesial face of the metacone. Enamel preserved on their buccal sides shows that the bases of the paracone and metacone were confluent. A wear facet exposing the dentine extends from the apices and lingual sides of the paracone and metacone across the trigon basin and blunts the apex of the protocone. A broad band of enamel extends around the base of the protocone, and there is no evidence of the presence of pre- or postcingula. Also, resembling M2 but differing from M1, the mesiodistal width of the trigon is relatively small.

Comments

The dental dimensions of YPM-VPPU 14213 are distinctly larger than those of the postcanine dentition preserved in YPM-VPPU 17808, which is tentatively identified as *Procerberus* cf. *P. formicarum.* In contrast, they are somewhat smaller than those of the postcanine dentition of UCMP 137189 from the Hell Creek region, Montana, and the possibly larger postcanine dentition of the holotype of *P. grandis* from the Denver Basin, Colorado. The P3 of YPM-VPPU 14213 differs from the heavily damaged P3 of UCMP 137189 in the lack of an ectocingulum, and possibly lesser development or absence of a metacone and a smaller protocone. The ectoflexus of M1 and, particularly, M2 are deeper on YPM-VPPU 14213. M2 and M3 of YPM-VPPU 14213 are noticeably different in their narrower protoconal regions and absence of pre- and postcingula. Finally, the mesial width of M3 is greater than that of M2, which is not the case in UCMP 137189 or the holotype of *P. grandis.* In order to highlight its larger postcanine dentition relative to YPM-VPPU 137189, provisionally YPM-VPPU 14213 is identified as *P.* sp. cf. *P. grandis.* The few morphological differences that are preserved in the heavily worn material at hand suggest that with more, better preserved specimens of the taxon represented by YPM-VPPU 14213 recognition of a new species of *Procerberus* will be warranted.

BIOGEOGRAPHY

Each of the Pu1 faunas considered here (the Littleton fauna in the Denver Basin, Colorado; the Mantua Lentil fauna in the Bighorn Basin, Wyoming; and the Pu1 fauna of the Hell Creek region, Montana) have two forms of *Procerberus* with dentitions of distinctly different sizes. The smaller forms in these three faunas are identified as *P. formicarum, P.* sp. cf. *P. formicarum,* or the closely related *P. andesiticus.* The samples of the larger forms are rarer, each essentially consisting of a single maxillary fragment preserving most of the postcanine dentition. In this study, the larger forms from the Mantua Lentil and Hell Creek region have been tentatively identified as *P.* sp. cf. *P. grandis* to call attention to their larger dental dimensions relative to *P. formicarum* and *P. andesiticus.* Given the differences in the dental dimensions of these larger forms, it is unlikely they represent the same species. Larger samples are needed to establish ranges of dental variation before going beyond these preliminary identifications.

In addition to these three Pu1 occurrences of *Procerberus,* a few rare specimens from other parts of the Western Interior indicate broader biogeographic and stratigraphic distributions of the genus. These are reviewed in geographic order starting with occurrences in southern Canada.

Saskatchewan—At different times during excavation of the Medicine Hat Tile and Brick Company quarry two fossiliferous levels were exposed and later destroyed. Both the stratigraphically lower locality, Long Fall and the stratigraphically higher locality Rav W-1 yielded significant samples of microvertebrates. Focusing on the occurrence of isolated teeth of non-avian dinosaurs and marsupials, Johnston and Fox (1984) interpreted the age of the Long Fall local fauna as latest Cretaceous (Lancian). Lerbekmo (1985) questioned the composition of its vertebrate record, and suggested that the Cretaceous vertebrates were reworked from older formations. Because of the apparent absence of vertebrate fossils in the underlying Battle and Whitemud formations, this possibility has been deemed unlikely. In a revised faunal list for the Long Fall locality, Fox (1997) recorded the presence of a variety of archaic ungulates including *Protungulatum* sp., cf. *P. donnae.* On the scale of North American Land Mammal Ages, the boundary between the Lancian and Puercan NALMAs is set at the first occurrence of *Protungulatum donnae* or, in another interpretation, any species of *Protungulatum* (Lofgren et al. 2004, Archibald et al. 2011). Here, on the basis of the occurrence of *Protungulatum,* the Long Fall local fauna is recognized as a Pu1 local fauna of latest Cretaceous age. This and other chronostratigraphically anomalous Canadian local faunas were aptly designated transitional assemblages by Fox (1997).

Johnston and Fox (1984) reported the occurrence of *Procerberus* cf. *P. formicarum* in the Long Fall local fauna on the basis of two fragmentary upper molars. The distal width of one (3.8 mm), UA 16075, a presumed M2, is near the mean value for distal widths of the topotypic sample of *P. formicarum.* The second specimen, an M3, was described as,

"…larger than all M3's of *P. formicarum* at hand (UA 6706-9 [total: 4])…" (Johnston and Fox, 1984, p. 210), which suggests the presence of another species of *Procerberus* with a noticeably larger dentition.

The stratigraphically higher Rav W-1 local fauna found in the Medicine Hat Tile and Brick Company quarry (Fox 1990, 1997) currently is correlated with the Pu2 interval zone (Redman et al. 2015). *Procerberus* n. sp. is included in a Rav W-1 faunal list (Fox 1997), but this material has yet to be described. The presence of *Procerberus* sp. also has been reported in the Croc Pot local fauna (Fox 1997) found at a locality approximately 1.5 km southwest of the Medicine Hat Tile and Brick Company quarry. Acknowledging that the fossils representing this local fauna have yet to be thoroughly analyzed, Redman et al. (2015) tentatively included this local fauna within the Pu2 interval zone.

Alberta—Scott (2003) reported the occurrence of cf. *Procerberus* sp. in the Who Nose local fauna, found in the Paskapoo Formation. This local fauna is now thought to be of middle Torrejonian (To2) age (Fox et al. 2010, Scott et al. 2013). This occurrence was based on an isolated m3. The morphology of the trigonid of this m3 is reported to closely resemble that of *P. formicarum*. In contrast, unlike the m3s in the topotypic sample, the breadth of the talonid is only slightly narrower than the breath of the trigonid. Agreeing with Scott, more material is needed to support this tentative identification.

Montana, northeastern—In addition to the Pu1 occurrences of *Procerberus formicarum* and *P.* sp. cf. *P. grandis* discussed above, the record from northeastern Montana includes *Procerberus plutonis* Van Valen, 1978, established on isolated teeth from the Pu3 interval zone Purgatory Hill local fauna, Tullock Member of the Fort Union Formation. The type specimen, UMVP 1464, was identified as a "right M1 or M2". In the diagnosis, measurements of a tooth identified as an "M?2", presumably the type specimen, fall within the observed ranges of variation of m1s and m2s of *P. formicarum* in the Bug Creek Anthills sample. Van Valen (1978, p. 66) briefly characterized the postcanine dentition of *P. plutonis* noting, "Upper and lower molars a little lower crowned and more transverse than in *P. formicarum* and protocone longer proximodistally." Future studies of material from the Purgatory Hill and other Pu3 localities, particularly the Garbani Channel localities in northeastern Montana, might validate this species, but, for the moment, *P. plutonis* is best considered a *nomen dubium*. Wilson (2014) recorded the Pu3 occurrences of the genus in northeastern Montana as *Procerberus* A.

Montana, south-central—Buckley (1994) allocated isolated teeth representing cimolestids from the Simpson Quarry

(Pu2/3, see Fox et al. 2014), Bear Formation, Crazy Mountains Basin, to two indeterminate species of *Cimolestes* and three indeterminate species of *Procerberus*. Of the latter, Buckley's *Procerberus* A is based on the largest number of referred teeth, an M2 and five lower molars. In comparison to Pu1 species of *Procerberus* these teeth are smaller than those of members of the topotypic sample of *P. formicarum* and approximately the same size as the topotypic sample of *P. andesiticus*. Other characters, for example the small size of the para- and metaconules and the weak, rounded postparaconule and premetaconule cristae, resemble the upper molars of *P. formicarum*. Buckley (1994) concluded that *Procerberus* A from Simpson Quarry could not be referred to any of the then known species of *Procerberus*.

Procerberus B was based on a p4 and an m2. The main criterion for recognition of this indeterminate species was the small size of these teeth. Buckley (1994) reported 1.8 mm as the lengths of their crowns, which is distinctly smaller than the lower postcanines of *P. formicarum* or *P. andesiticus*.

Procerberus C was based on a p4 and two m1?s. Again size was the primary character in distinguishing this indeterminate species. Buckley (1994) noted the length of the crown of p4 is 3.5 mm and the lengths of the crowns of the m1?s are 3.2 and 3.6 mm. Judging from the one lower molar in the hypodigm of *P. grandis*, Buckley concluded the dentition of *Procerberus* C was significantly smaller. The lower molars of *Procerberus* C are approximately the same length as the lower molar tentatively referred to *Procerberus* sp. cf. *P. grandis* from the Pu1 McKeever Ranch 1 local fauna, Garfield County, Montana.

Montana, southeastern—Kelly (2014) presented a preliminary report on the McGill Ranch local fauna found in the upper part of the Hell Creek Formation exposed in Powder River County, Montana. A taxonomically diverse assemblage of fossil mammals was obtained from Lane's Little Jaw Site Quarry. Most of the mammals represented are characteristic Lancian species, and the stratigraphy of the site supports the interpretation of its latest Cretaceous age. In addition to *Procerberus* (probably two species), *Baioconodon* cf. *B. nordicus* Jepsen, 1930 and a possible periptychid, *Paleoungulatum hooleyi* Kelly, 2014 are members of this local fauna. Although *Protungulatum* is not present, its phylogenetic relationships to the more derived *Baioconodon* and *Paleoungulatum* suggest the McGill Ranch local fauna might be another chronostratigraphically anomalous local fauna of latest Cretaceous but Puercan age broadly correlative with the Long Fall local fauna in Saskatchewan.

The two species of *Procerberus* in the McGill Ranch local fauna were simply differentiated as "large" and "small" by Kelly (2014). The larger form was based on two fragmentary

dentaries preserving p3-m2 and m2-m3 respectively. These postcanines are distinctly larger than the observed ranges of variation of the topotypic sample of *P. formicarum* and dimensions of the heavily worn lower dentition of *P.* sp. cf. *formicarum* from the Mantua Lentil local fauna but smaller than the single lower molar in the hypodigm of *P. grandis.* The smaller form questionably referred to *Procerberus* was based on an isolated premolar, either a p4 or possibly a dp4. If a p4, the dimensions of its crown are slightly smaller than those of the topotypic sample of *P. formicarum*.

Wyoming—Eberle and Lillegraven (1998) described three fossils representing cimolestids found in the Ferris Formation, exposed in the Hanna Basin. One is an isolated P4, UW 26573, from a Pu3 interval zone locality. They identified it as *Procerberus* sp. on the basis of its close morphological similarity to topotypic P4s of *P. formicarum*. It is slightly smaller than the observed range of variation of dimensions of these P4s. Also, the smaller width of the crown relative to its length sets it apart.

New Mexico—Local faunas representing the Pu1 interval zone have yet to be discovered in the San Juan Basin and records of mammals from its Lancian NALMA sites are rare. In contrast, large samples of local faunas in the basin have served as the bases for characterization of the Pu2 and Pu3 interval zones (Lofgren et al. 2004). In her master's thesis, Standhardt (1980) reported the presence of *Procerberus* sp. in the Pu2 interval zone. With some annotations, this record was cited by later workers (e.g., Williamson 1996). Describing additional material collected since Standhardt's study, Williamson et al. (2011) thoroughly revised the record of cimolestids in the San Juan Basin. Some of the isolated teeth identified as *Procerberus* sp. by Standhardt were referred to *Puercolestes simpsoni* Reynolds, 1937, others to *Chacopterygus minutus* Williamson et al., 2011. In this revision no material was referred to *Procerberus*.

Comments

The available fossil record indicates that species of *Procerberus* ranged from southern Canada south at least to the Denver Basin in Colorado. The oldest records of the genus are in two chronostratigraphically anomalous latest Cretaceous Puercan local faunas in Saskatchewan and Montana. The Canadian record, represented by a few isolated teeth from the Long Fall locality, suggests the presence of two forms with dentitions of distinctly different sizes (Johnston and Fox 1984). Similarly the McGill Ranch local fauna, southeastern Montana, includes two forms of *Procerberus* distinguishable on the basis of differences in the sizes of their dentitions (Kelly 2014). These records indicate that not only the origin but initial speciation of *Procerberus* occurred prior to the Cretaceous/Paleogene boundary.

 The largest samples of *Procerberus* have been collected from Pu1 localities in Garfield and McCone counties, northeastern Montana; the Mantua Lentil, northwestern Wyoming; and the Denver Basin, Colorado. In all three areas, at least two lineages of *Procerberus* are present. The members of the group characterized by a smaller postcanine dentition have been identified as *P. formicarum, P.* sp. cf. *P. formicarum,* or the closely related *P. andesiticus.* The species differ only in a few morphological characters of their postcanine dentitions and dental dimensions. In contrast, only a very few specimens represent the group characterized by larger dental dimensions. Most of the morphological data was drawn from three maxillary fragments preserving heavily worn postcanines. These include the holotype of *P. grandis* and fragments from other localities tentatively identified as *P.* sp. cf. *P. grandis.* Given the differences in dental dimensions and morphology this group might include more than one species.

Procerberus is no longer recognized as a member of the Pu2 fauna of the San Juan Basin, New Mexico (Williamson et al. 2011). The number of Pu2 local faunas north of the San Juan Basin is small. Faunal lists contain records of *Procerberus* n. sp. at Rav W-1 and *Procerberus* sp. at Croc Pot in Saskatchewan (Fox 1997). This material has yet to be described and fully analyzed. *Procerberus* has not been reported in any other Pu2 local faunas in the northern Western Interior.

Pu2/3 local faunas, particularly the Simpson Quarry local fauna with three indeterminate species, give hints of increased species diversity of *Procerberus* late in the Puercan (Buckley 1994). The cimolestids probably referable to *Procerberus* in the Garbani Channel and Purgatory Hill Pu3 local faunas remain to be fully studied. An isolated P4 found in the Hanna Basin, Wyoming, extends the biogeographic range of *Procerberus* during the Pu3 interval zone (Eberle and Lillegraven 1998). Finally, an isolated m3 from the Who Nose local fauna in Alberta suggests *Procerberus* might have survived into the Torrejonian (Scott 2003).

PHYLOGENETIC RELATIONSHIPS

Higher Taxonomic Classification of *Procerberus*

Hypotheses concerning the phylogenetic relationships of *Procerberus* have a complex history. Sloan and Van Valen (1965) classified *Procerberus* as a leptictid and proposed a new subfamily, Procerberinae, for its reception. This classification was based on the overall similarity of the dentition of *Procerberus* to those of taxa then recognized as leptictids. The presence of semimolariform P4s and p4s shared by these taxa was an important consideration. Van Valen (1967, e.g. p. 233) continued to refer the genus to the Leptictidae Gill, 1872.

Supported by a detailed comparison of the dental

morphology of *Procerberus formicarum, Cimolestes cerberoides* (now *Ambilestes cerberoides* Fox, 2015), *Gypsonictops,* and *Leptictis,* Lillegraven (1969) argued that *Procerberus* was not a leptictid but should be classified in the Family Palaeoryctidae Winge, 1917. At this time Palaeoryctidae was used as a very inclusive taxon including *Procerberus* and *Cimolestes*. In subsequent family level classifications (e.g,, McKenna and Bell 1997) two families were recognized. The North American membership of the Palaeoryctidae is now restricted to six genera with distinctly derived dental morphologies (Gunnell et al. 2008, Rankin and Holroyd 2014).

Gunnell et al. (2008) recognized *Procerberus* and *Cimolestes* as the only Puercan members of the Cimolestidae. These authors followed Clemens (1973) and treated the Puercan genus *Puercolestes* Reynolds, 1936 as a synonym of *Cimolestes*. On the basis of subsequently discovered isolated premolars from Pu2-3 localities in the San Juan Basin that probably are referable to this taxon, Williamson et al. (2011) argued that *Puercolestes* warranted recognition as a distinct genus of cimolestid.

The taxonomy of the species of *Cimolestes* stems from the work of Lillegraven (1969). He (Lillegraven 1969, p. 81) clearly expressed his approach, "The use of a common generic name serves a definite function in pointing out a phylogenetic unity, especially to students who are nonspecialists. The specific name indicates satisfactorily that significant differences between species exist." He noted that several colleagues had suggested he should recognize new genera to highlight the significant differences between species (e.g., *Cimolestes magnus* and *C. propalaeoryctes*). Since 1969, the techniques for analyzing phylogenetic relationships have evolved, and phylogenetic analyses based on characterizations of genera have come to dominate. As a result, the significant differences highlighted at the species level by Lillegraven (1969) have been masked in many subsequent phylogenetic analyses. In meeting abstracts, Strauss (2006, 2007) outlined results of his analysis of the species of cimolestids with particular emphasis on *Procerberus* and called attention to this problem.

With recognition of the generic status of *Puercolestes*, Williamson et al. (2011) questioned the coding of characters of *Cimolestes* in previous phylogenetic analyses. To what extent had the holotype of *Puercolestes*, a fragmentary skull preserving most of the upper dentition, been used to characterize *Cimolestes*? Deferring to Strauss' otherwise unpublished study for an analysis of this genus, Williamson et al. (2011) simply recoded the dental characters of *Cimolestes* as a composite taxon drawing data from then recognized species of the genus. With these modifications, they carried out a phylogenetic analysis of selected members of the Cimolestidae. *Maelestes gobiensis* Wible et al., 2007, from the Late Cretaceous of Mongolia was included. This analysis showed *Puercolestes* and the composite taxon *Cimolestes* as a sister group and *Maelestes* and *Batodon* Marsh, 1892 as a second sister group. These two sister groups were united in a polytomy with *Chacopterygus* Williamson et al., 2011, *Betonnia* Williamson et al. 2011, and Cimolestidae gen. et sp. from the San Juan Basin and *Procerberus*. *Alveugena* Eberle, 1999 was not included in this analysis.

Recently Fox (2015) proposed allocation of the species of *Cimolestes* recognized by Lillegraven and later workers among four genera, three of them new: *Cimolestes incisus* Marsh, 1889, *C. stirtoni* Clemens, 1973, *Altacreodus magnus* Fox, 2015, *Ambilestes cerberoides* Fox, 2015, and *Scollardius propalaeoryctes* Fox, 2015. In addition to providing revised or new diagnoses, Fox evaluated hypotheses concerning their phylogenetic relationships. He did not code their morphological characters for phylogenetic analysis. A complete reanalysis of the phylogenetic relationships of the currently recognized genera of cimolestids is well beyond the scope of this study. Such an analysis recognizing the morphological diversity masked under the older interpretation of the genus *Cimolestes* must be undertaken to clarify the phylogenetic relationships of *Procerberus* to other cimolestids.

Phylogenetic relationship of *Procerberus* to the Taeniodonta

The current fossil record of the Taeniodonts is principally from Early Paleocene through Middle Eocene deposits in North America. After the K/Pg extinctions, taeniodonts included some of the first lineages to evolve large body size. By the end of the Puercan taeniodonts were broadly divisible into two groups. The conoryctids appear to have been terrestrial quadrupeds. Their skeletons were robust, and the digits were tipped with small claws, which suggest some climbing ability. Estimated body masses of conoryctids range between 5 to 15 kg (Lucas et al. 2008). Their dentitions are distinctly modified. The postcanines are bundont, exhibit the beginnings of hypsodonty, and characterized by heavy wear. The other group, the stylinodontids, evolved even larger body masses ranging from 10 kg to 110 kg in later forms (Lucas et al. 2008). The dentitions of stylinodontids are distinguishable from contemporaneous conoryctids by the enlargement of the canines and mesial premolars and advanced evolution of hypsodonty. Their skeletons were heavily built, particularly the long forelimbs that were tipped with large claws. Initial speculations on the phylogenetic relationships of the Taeniodonta focused on morphological resemblances to Edentates, particularly ground sloths, and Tillodonts, an extinct group of Paleogene eutherians. These resemblances are now considered the results of convergent evolution.

The hypothesis that fossils from the Mantua Lentil documented a close phylogenetic relationship between *Procerberus* and primitive taeniodonts can be traced back to a suggestion made by Lillegraven (1969). Commenting on undescribed specimens of *Procerberus* made available for study by G.L. Jepson, he observed, "One of the probably two species present in this deposit is about one third larger than *P. formicarum*. The nearly equal length-width proportions of the molars of this larger species and its increased grinding function would make it a likely candidate for the origin of the stylinodontine taeniodonts (Patterson, 1949), a possibility suggested to me by both Malcolm C. McKenna and Leigh Van Valen (Lillegraven 1969, p. 69)". In a paper published the same year, McKenna (1969, p. 234), noted that taeniodonts "…arose from *Procerberus* or similar palaeoryctoid insectivore stock at the close of the Cretaceous." Later, in his doctoral dissertation, Middleton (1983, p. 173) was more specific. He identified the specimen from the Mantua Lentil in question as "PU 14213" (now YPM-VPPU 14213).

The hypothesis that "*Procerberus*-like forms" constituted a closely related sister group of the taeniodonts was favored by Schoch (1986) in his monographic analysis of taeniodonts. His group of "*Procerberus*-like forms" included the discussed, but then unpublished, large forms of *Procerberus* from the Denver Basin, Mantua Lentil, and Hell Creek region. Subsequently, Eberle (1999) described the cimolestid *Alveugena carbonensis* from a Pu2 locality in the Ferris Formation, Wyoming. On the basis of a cladistic analysis, she suggested (see Eberle 1999, figs. 3 and 4), two possible hypotheses of its phylogenetic relationships. One that *Alveugena* held a phylogenetically intermediate position between *Procerberus*, particularly *P. grandis*, and the conoryctid taeniodont *Onychodectes* Cope, 1888. Her alternative hypothesis was that *P. formicarum* and *P. grandis* formed a clade that shared a common ancestor with *Alveugena*, *Onychodectes*, and more derived taeniodonts.

Fox and Naylor (2003) described and named *Schowalteria clemensi* based on associated fragments of a skull and lower jaws from a Lancian NALMA locality in the Scollard Formation, Alberta. Citing cranial and dental characters, they argued that *Schowalteria* was a primitive member of the Stylinodontidae, the most derived family of taeniodonts, and disagreed with Eberle's (1999) interpretations of the phylogenetic interrelationships of species of *Procerberus, Alveugena*, and *Onychodectes*. The occurrence of *Schowalteria* in the Lancian well before the first appearance of *Procerberus* and *Alveugena*, genera presumed to be involved in the ancestry of taeniodonts, was noted in support of their challenge. Similarities in dental and cranial morphology between conoryctid taeniodonts and cimolestids such as *Procerberus* were evaluated as convergences. Fox and Naylor (2003) and Fox (2015) concluded that the origin and initial familial diversification of taeniodonts occurred in the Lancian or earlier in the Cretaceous, and that the phylogenetic relationships of taeniodonts to other eutherians remained unresolved.

Research concerning the phylogenetic relationships of taeniodonts continued with description of some new material and a series of phylogenetic analyses. Rook et al. (2010) described a lower jaw attributed to *Alveugena* from the Merle's Mecca local fauna, North Dakota. It provided information on the morphology of the lower dentition of *Alveugena* and extended its range into the Pu1 interval zone. The phylogenetic analysis presented in this paper was revised in two subsequent papers (Rook and Hunter 2011, 2013). In their most recent phylogenetic analysis (Rook and Hunter 2013), *Procerberus formicarum* and *P. grandis* form a sister group to a group including *Cimolestes* (species undesignated), *Alveugena*, and the monophyletic Taeniodonta including *Schowalteria*.

Williamson and Brussette (2013) described new material of the taeniodont *Wortmania* and commented on previous interpretations of the phylogeny of the taeniodonts. They revised the character matrix used by Rook and Hunter (2011) and tested the consequences of treating multistate characters as ordered or unordered in their phylogenetic analyses. Differing from Rook and Hunter (2013) they interpret the species of *Procerberus* as more closely related to *Alveugena* and the Taeniodonta than to *Cimolestes*.

In summary, on the basis of current studies reference of *Schowalteria* to the Taeniodonta seems well supported. The occurrence of *Schowalteria* in a Lancian local fauna indicates the origin of the Taeniodonta occurred prior to the K/Pg boundary extinctions. In contrast, the phylogenetic relationships of *Cimolestes*, *Procerberus*, and *Alveugena* to the Taeniodonta remain to be clarified. In part no doubt, this reflects the small sample sizes of many of these species involved and the limitation to use of their dental characters in these studies. Also, probably the choice of characters attributed to the genus *Cimolestes* has contributed to the lack of resolution.

CONCLUSIONS

As recognized here, *Procerberus* includes three valid species, *P. formicarum, P. andesiticus,* and *P. grandis.* Although first assigned to the Leptictidae, Lillegraven (1969) and subsequent workers have assigned *Procerberus* to the Cimolestidae. On the basis of their similar dental morphologies *P. formicarum* and *P. andesiticus* appear to be very closely related species. The rare topotypic specimens of *P. grandis* from the Denver Basin preserve teeth that are distinctly

larger than those of *P. andesiticus*, which is known only from the Denver Basin, and *P. formicarum*, which is known from occurrences in the Hanna Basin, Wyoming, and a series of localities extending its range into southern Canada.

Two fragments of maxillaries preserving most of the postcanine dentition described here, YPM-PU 14213 and UCMP 137189, have been alluded to in previous publications (e.g., Lillegraven 1969, Middleton and Dewar 2004). The dentition preserved in YPM-PU 14213, from the Mantua Lentil, Wyoming, is distinctly larger than comparable material from this locality tentatively referred to *Procerberus* sp. cf. *P. formicarum*. The dentition preserved in UCMP 137189, from the Hell Creek region, Montana, is larger than the upper teeth in a topotypic sample of *P. formicarum*. The difference in size is even greater than that of the fossils from the Mantua Lentil, but the dentition of UCMP 137189 is smaller than that of *P. grandis*. Given the small size of the available samples, essentially three maxillary fragments preserving heavily worn postcanines, YPM-PU 14213 and UCMP 137189 have been tentatively identified as *P.* cf. *P. grandis*. More material is needed to determine if the differences in size and a few morphological characters are within the bounds of individual or biogeographic variation or signal rapid evolution of these large forms.

Presence of two forms of *Procerberus* with dentitions of different sizes in two chronostratigraphically anomalous local faunas of Cretaceous and Puercan age indicates origin of the genus and initiation of its taxonomic differentiation prior to the Cretaceous/Paleogene (K/Pg) boundary. Pu1 local faunas clearly document the presence of two lineages characterized by differences in size of their dentitions; the smaller *P. formicarum - P. andesiticus* lineage and the larger *P. grandis* complex. The presence of *Procerberus* in the large, recently restudied Pu2 local faunas in the San Juan Basin, New Mexico, is no longer recognized in these or Pu3 local faunas of the area. To the north, Pu2/3 occurrences of *Procerberus* are largely limited to records in faunal lists and the material has yet to be fully described and analyzed. The taxonomic diversity of *Procerberus* in the Pu3 Simpson Quarry local fauna suggests diversification of species in the late Puercan. Cimolestids probably referable to *Procerberus* in the Garbani Channel and Purgatory Hill local faunas remain to be fully analyzed. An isolated lower molar from a site in Alberta suggests the genus survived into the Torrejonian.

Taeniodonts were one of the Paleogene mammalian experiments in evolution of large body size and probably an omnivorous to herbivorous diet. Recent phylogenetic analyses indicate that *Schowalteria* is a taeniodont in the Lancian NALMA of Alberta. Although differing in detail, these analyses indicate that the Pu1 cimolestid *Alveugena* and

contemporaneous species of *Procerberus* have sister group relationships with primitive taeniodonts. This relationship and the occurrence of *Procerberus* in chronostratigraphically anomalous local faunas of Cretaceous and Puercan age indicates origin of the genus and the beginning of its taxonomic diversification in the latest Cretaceous.

ACKNOWLEGEMENTS

LITERATURE CITED

Archibald, J.D. 1982. A study of Mammalia and geology across the Cretaceous-Tertiary Boundary in Garfield County, Montana. *University of California Publications in Geological Sciences* 122:1–286.

Archibald, J.D., Y. Zang, T. Harper, and R.L. Cifelli. 2011. *Protungulatum*,

confirmed Cretaceous occurrence of an otherwise Paleocene Eutherian (Placental?) mammal. *Journal of Mammalian Evolution* 18:153–161.

Bengston, P. 1988. Open Nomenclature. *Palaeontology* 31:223–227.

Buckley, G.A. 1994. Paleontology, Geology and Chronostratigraphy of Simpson Quarry (Early Paleocene), Bear Formation, Crazy Mountains Basin, South-Central Montana. Ph. D. diss. Rutgers, The State University of New Jersey, New Jersey.

Clemens, W.A. 1973. Fossil mammals of the type Lance Formation, Wyoming. Part III. Eutheria and summary. *University of California Publications in Geological Sciences* 94:1–102.

Cope, E.D. 1888. Synopsis of the vertebrate fauna of the Puerco series. *Transactions of the American Philosophical Society, new series* 16:298–361.

Dahlberg, E.L., J.J. Eberle, J.J.W. Sertich, and I.M. Miller. 2016. A new earliest Paleocene (Puercan) mammalian fauna from Colorado's Denver Basin, U.S.A. *Rocky Mountain Geology* 51:1–22.

Eberle, J.J. 1999. Bridging the transition between didelphodonts and taeniodonts. *Journal of Paleontology* 73:936–944.

Eberle, J.J. 2003. Puercan mammalian systematics and biostratigraphy in the Denver Formation, Denver Basin. *Rocky Mountain Geology* 38: 143–169.

Eberle, J.J., and J.A. Lillegraven. 1998. A new and important record of earliest Cenozoic mammalian history: Eutheria and paleogeographic/biostratigraphic summaries. *Rocky Mountain Geology* 33: 49–117.

Fastovsky, D.E., and Dott, R.H., Jr. 1986. Sedimentology, stratigraphy, and extinctions during the Cretaceous-Paleogene transition at Bug Creek, Montana. *Geology* 14: 279–282.

Fox, R.C. 1990. The succession of Paleocene mammals in western Canada. Pp. 51–70 *in* T.M. Bown and K.D. Rose (eds.). Dawn of the Age of Mammals in the northern part of the Rocky Mountain interior. *Geological Society of America, Special Paper* 243.

Fox, R.C. 1997. Late Cretaceous and Paleocene mammals, Cypress Hills region, Saskatchewan, and mammalian evolution across the Cretaceous-Tertiary boundary. Pp. 70–85 *in* L. McKenzie-McAnally (ed.). Upper Cretaceous and Tertiary Stratigraphy and Paleontology of Southern Saskatchewan. *Canadian Paleontology Conference, Field Trip Guidebook 6*, Geological Association of Canada. St. John's, Newfoundland.

Fox, R.C. 2015. A revision of the Late Cretaceous-Paleocene eutherian mammal Cimolestes Marsh, 1889. *Canadian Journal of Earth Sciences* 52:1137–1149.

Fox, R.C. and B.G. Naylor. 2003. A Late Cretaceous taeniodonts (Eutheria, Mammalia) from Alberta, Canada. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 229: 393–420.

Fox, R.C., C.S. Scott, and G.A. Buckley. 2014. A 'giant' purgatoriid (Plesiadapiformes) from the Paleocene of Montana, USA: mosaic evolution in the earliest primates. *Palaeontology* 58:277–291.

Fox, R.C, C.S. Scott, and B.D. Rankin. 2010. New early carnivoran specimens from the Puercan (Earliest Paleocene) of Saskatchewan, Canada. *Journal of Paleontology* 84:1035–1039.

Gill, T. 1872. Arrangement of the families of mammals and synoptical table of characters of the subdivisions of mammals. *Smithsonian Miscellaneous Collections* 11:1–98.

Gunnell, G.F., T.M. Bown, and J.L. Bloch. 2008. "Proteutheria". Pp. 62–81 *in* C.M. Janis, G.F. Gunnell, and M.D. Uhen (eds.). Evolution of Tertiary Mammals of North America, Volume 2, Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 43:649–662.

Ickert, R.B., S.R. Mulcahy, C.J. Sprain, J.F Banaszak, and P.R. Renne. 2015. Chemical and Pb isotope composition of phenocrysts from bentonites constrains the chronostratigraphy around the Cretaceous-Paleogene boundary in the Hell Creek region, Montana. *Geochemistry, Geophysics, Geosystems* 16:2743–2761.

Jepsen, G.L. 1930. Stratigraphy and Paleontology of the Paleocene of Northeastern Park County, Wyoming. *Proceedings of the American Philosophical Society* 69:463–528.

Jepsen, G.L. 1940. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. *Proceedings of the American Philosophical Society* 83:217-341.

Johnston, P.A., and R.C. Fox. 1984. Paleocene and Late Cretaceous mammals from Saskatchewan, Canada. *Palaeontographica, Abt. A* 186:163–222.

Kelly, T.S. 2014. Preliminary report on the mammals from Lane's Little Jaw site quarry: A latest Cretaceous (Earliest Puercan?) local fauna, Hell Creek Formation, southeastern Montana. *Paludicola* 10:50–91.

Leidy, J. 1868. Notice of some remains of extinct *Insectivora* from Dakota. *Proceedings of the Academy of Natural Sciences, Philadelphia* 1868:315–316.

Lerbekmo, J.F. 1985. Magnetostratigraphic and biostratigraphic correlations of Maastrichtian to early Paleocene strata between south-central Alberta and southwestern Saskatchewan. *Bulletin of Canadian Petroleum Geology* 33:213–226.

Lillegraven, J.A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *University of Kansas Paleontological Contributions* 50(Vertebrata 12):1–122.

Lofgren, D.L. 1995. The Bug Creek Problem and the Cretaceous-Tertiary Transition at McGuire Creek, Montana. *University of California Publications in Geological Sciences* 140:1–185.

Lofgren, D.L., P.D. Gingerich, J.A. Lillegraven, W.A. Clemens, and T.E. Williamson. 2004. The first North American Land Mammal Ages of the Cenozoic Era. Pp. 43–105 *in* M.O. Woodburne (ed.). Late Cretaceous and Cenozoic Mammals of North America. University of Columbia Press, New York, New York.

Lucas, S.G,, R.M. Schoch, and T.E. Williamson. 2008. Taeniodonta. Pp. 260–267 *in* C.M. Janis, G.F. Gunnell, and M.D. Uhen (eds.). Evolution of Tertiary Mammals of North America, Volume 2, Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge.

Marsh, O.C. 1889. Discovery of Cretaceous *Mammalia. American Journal of Science, Series 3* 38:81–92.

Marsh, O.C. 1892. Discovery of Cretaceous Mammalia, part iii. American Journal of Science, Series 3 48:249–262.

McKenna, M.C. 1969. The origin and early differentiation of therian mammals. *Annals of the New York Academy of Sciences* 167:217–240.

McKenna, M.C. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21–46 in W.P. Luckett and F.S. Szalay (eds.). Phylogeny of the Primates: a multidisciplinary approach. Proceedings of the Wenner Gren Symposium no. 61.

McKenna, M.C., and S.K. Bell. 1997. Classification of Mammals above the species level. Columbia University Press, New York, New York, 631 pp.

Middleton, M.D. 1983. Early Paleocene vertebrates of the Denver Basin, Colorado. Ph.D. diss. University of Colorado, Boulder, CO.

Middleton, M.D., and E.W. Dewar. 2004. New Mammals from the Early Paleocene Littleton fauna (Denver Formation, Colorado). Pp. 59–80 *in* S.G. Lucas, K.E. Zeigler, and P.E. Kondrashov (eds.). Paleogene Mammals. *Bulletin, New Mexico Museum of Natural History and Science* 26.

Novacek, M.J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bulletin, American Museum of Natural History* 183:1–112.

O'Leary, M.A., J.I. Bloch, J.J. Flynn, T.J. Gaudin, A. Giallombardo, N.P. Giannini, S.L. Goldberg, B.P. Kraatz, Zhe-Xi Luo, J. Meng, X. Ni, M.J. Novacek, F.A. Perini, Z.S. Randall, G.W. Rougier, E.J. Sargis, M.T. Silcox, N.B. Simmons, M. Spaulding, P.M. Velazco, M. Weksler, J.R. Wible, A.L. Cirranello. 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339:662–667.

Patterson, B. 1949. Rates of evolution in taeniodonts. Pp. 243–278 *in* G.L. Jepsen, G.G. Simpson, and E. Mayer (eds.). Genetics, paleontology, and evolution. Princeton University Press, Princeton, New Jersey.

Rankin, B.D. and P.A. Holroyd. 2014. *Aceroryctes dulcis*, a new palaeoryctid (Mammalia, Eutheria) from the early Eocene of the Wasatch Formation of southwestern Wyoming, USA. *Canadian Journal of Earth Sciences* 51:919–926.

Redman, C.M., J.D. Gardner, C.S. Scott, and D.R. Bramen. 2015. Geological setting of vertebrate microfossil localities across the Cretaceous-Paleogene boundary in southwestern Saskatchewan, Canada. *Canadian Journal of Earth Sciences* 52:846–862.

Renne, P.R., A.L. Deino, F.J. Hilgen, K.F. Kuiper, D.F. Mark, W.S. Mitchell, L.E. Morgan, R. Mundil, and J.Smit. 2013. Time scales of critical events around the Cretaceous-Paleocene boundary. *Science* 339:684–687.

Reynolds, T.E. 1936. Two new insectivores from the lower Paleocene of New Mexico. Journal of Paleontology 10:202–209.

Reynolds, T.E. 1937. Two new insectivores from the Lower Paleocene of New Mexico. *Journal of Paleontology* 10:202–209.

Rook, D.L. and J.P. Hunter. 2011. Phylogeny of the Taeniodonta: evidence from dental characters and stratigraphy. *Journal of Vertebrate Paleontology* 31:422–427.

Rook, D.L. and J.P. Hunter. 2013. Rooting around the eutherian family tree: the origin and relations of the Taeniodonta. *Journal of Mammalian Evolution* 21:75–91

Rook, D.L., J.P. Hunter, D.A. Pearson, and A. Bercovici. 2010. Lower jaw of the Early Paleocene mammal *Alveugena* and its interpretation as a transitional fossil. *Journal of Paleontology* 84:2117–1225.

Schoch, R.M. 1986. Systematics, functional morphology and macroevolution of the extinct mammalian order Taeniodonta. *Bulletin, Peabody Museum of Natural History* 42:1–307.

Scott, C.S. 2003. Late Torrejonian (Middle Paleocene) mammals from south central Alberta, Canada. *Journal of Paleontology* 77:745–768.

Scott, C.S., D.N. Spivak, and A.R. Sweet. 2013. First mammals from the Paleocene Porcupine Hills Formation of southwestern Alberta, Canada. *Canadian Journal of Earth Sciences* 50:355–378.

Simpson, G.G. 1927. Mammalian fauna of the Hell Creek Formation of Montana. *American Museum Novitates* 267:1–7.

Sloan, R.E., and L. Van Valen. 1965. Cretaceous mammals from Montana. *Science* 148:220–227.

Sprain, C.J., P.R. Renne, G.P. Wilson, and W.A. Clemens. 2015. High-resolution chronostratigraphy of the terrestrial Cretaceous-Paleogene transition and recovery interval in the Hell Creek region, Montana. *Geological Society of America Bulletin* 127:393–409.

Standhardt, B.R. 1980. Early Paleocene mammals of the Black Toe local fauna, Nacimiento Formation, New Mexico, M.S. thesis, University of Arizona, Tucson, AZ.

Strauss, J. 2006. A preliminary review of cimolestid systematics with comments on the genus *Procerberus. Journal of Vertebrate Paleontology* 26(3):129A.

Strauss, J. 2007. A taxonomic review of Late Cretaceous cimolestids. *Journal of Vertebrate Paleontology* 27(3):153A.

Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. *Bulletin of the American Museum of Natural History* 135 (art. 5):221–284.

Van Valen, L. 1978. The beginning of the Age of Mammals. *Evolutionary Theory* 4:45–80.

Wible, J.R., G.W. Rougier, M.J. Novacek, and R.J. Asher. 2007. Cretaceous eutherians and laurasian origin for placental mammals near the K/T boundary. *Nature* 447:1003–1006.

Williamson, T.E. 1996. The Beginning of the Age of Mammals in the San Juan Basin, New Mexico: Biostratigraphy and Evolution of Paleocene Mammals of the Nacimiento Formation. *New Mexico Museum of Natural History and Science, Bulletin* 8:i-iii, 1–141.

Williamson, T.E. and S.L. Brussette. 2013. New specimens of the rare taeniodont *Wortmania* (Mammalia; Eutheria) from the San Juan Basin of New Mexico and comments on the phylogeny and functional morphology of "archaic" mammals. *PLOS ONE* 8(9):1–35.

Williamson, T.E., A.Weil, and B. Standhardt, B. 2011. Cimolestids (Mammalia) from the Early Paleocene (Puercan) of Colorado. *Journal of Vertebrate Paleontology* 31:162–181.

Wilson, G.P. 2004. A quantitative assessment of evolutionary and ecological change in mammalian faunas leading up to and across the Cretaceous-Tertiary boundary in northeastern Montana. Ph.D. diss. University of California, Berkeley.

Wilson, G.P. 2014. Mammalian extinction, survival, and recovery dynamics across the Cretaceous-Paleogene boundary in northeastern Montana, USA. Pp. 356–392 *in* G.P. Wilson, W.A. Clemens, J.R. Horner, J.H. Hartman (eds.). Through the end of the Cretaceous in the type locality of the Hell Creek Formation in Montana and adjacent areas. *Geological Society of America, Special Paper* 503.

Winge, H. 1917. Udsigt over Insectaedernes inbrydes Slaegtskab *Meddelesler fra Dansk naturhistorisk Forening. Copenhagen* 68:83–203.

Appendix 1. Topotypic sample of the postcanine dentition of *Procerberus formicarum* consulted in this study. Most of the specimens are isolated teeth except those marked with * that are associated with one or more teeth in a fragment of maxillary or dentary (see Appendix 2).
Locality numbers are shown in parentheses after the group of specimens from that locality. Except where noted all specimens are in the collections of UCMP.

P3	71901 (V70201)	218900*	218937*	(V65127)	92617	92619	92620	100526
P4	71932 100498	71933 100525	218900* 102258	218937* 103111	UMVP 2310* 103121	(V65127) 103136	92615 (V70201)	98614
M1	71914 100527 (V70201)	71919 102011*	71923 102236	218900* 102790	UMVP 2310* 103125	(V65127) 103129	100513 103135	100524 103141
M2	71916 100716 (V70201)	71924 102011*	218900* 102234	218937* 102239	UMVP 2310* 102244	(V65127) 102245	98941 102250	100509 103127
M3	71925 (V65127) 103131	71926 98136 (V70201)	71927 28827	71930 100521	71936 100985	218900* 102107	218937* 102246	UMVP 2310* 103119
p3	150017*	171389*	(V65127)	197406*	(V70199)			
p4	71944 92601 102252	72181 99084 102256	150017* 99085 102792	171389* 100497 (V70201)	(V65127) 100505	197406* 100530	(V70199) 102232	92600 102233
m1	71939 150017* 100500	71943 171389* 100504	71946 (V65127) 100507	71948 92592 100514	71960 92594 102105	71961 92596 102247	71962 92597 (V70201)	72171 97854
m2	71938 (V70199) 100516	72172 92591 100518	72176 92593 100522	72179 92595 102142	150017* 92609 102143	171389* 98140 103130	(V65127) 100502 111718	197406* 100515 (V70201)
m3	71941 (V70199) 100743 111715	71942 92598 102231 218938	71949 97855 103104 (V70201)	72174 97915 103113	72175 97896 103115	171389* 98138 103118	(V65127) 100529 103140	197406* 100740 111714

Appendix 2. Dental dimensions of postcanines of *Procerberus formicarum* preserved in association in a maxillary or dentary. Estimated values marked with *.

Upper dentitions			
UCMP 102011. V70201			
	Length	**Mesial Width**	**Distal Width**
M1	2.75	3.19	3.34
M2	2.92	3.61	3.90
UCMP 218900, V65127			
	Length	**Width**	
P3	2.58	2.24	
		Mesial Width	**Distal Width**
P4	2.73	2.84	3.11
M1	2.73	3.15	3.30
M2	3.64	3.85	3.70
M3	2.25	3.66	2.76
UCMP 218937, V65127			
	Length	**Width**	
P3	2.61	2.11	
		Mesial Width	**Distal Width**
P4	2.65	2.71	2.93
M1	2.42*	3.16*	3.16
M2	2.47	3.47	3.56
M3	2.17	3.51	2.91
UMVP 2310, cast, V65127			
	Length	**Mesial Width**	**Distal Width**
P4	2.58	2.64	3.01
M1	2.72	3.29	3.45
M2	2.65	3.91	3.78
M3	2.29	3.74	3.02

Lower dentitions		
UCMP 150017, V65127		
	Length	**Width**
p3	2.64	1.09
p4	3.16	1.42
	Width Trigonid	**Width Talonid**
m1	2.88 / 2.10	1.58
m2	2.67 / 2.14	1.55
UCMP 171389, V65127		
	Length	**Width**
p3	2.26	0.95
p4	2.73	1.30
	Width Trigonid	**Width Talonid**
m1	2.66 / 1.78	1.41
m2	2.52 / 1.85	1.41
m3	2.74 / 1.80	1.35
UCMP 197406, V65127		
	Length	**Width**
p3	2.41	1.08
p4	2.59	1.31
	Width Trigonid	**Width Talonid**
m2	2.59 / 2.01	1.62
m3	2.90 / 2.79	1.44

Appendix 3. Dental dimensions of *Procerberus andesiticus* from the Denver Basin, Colorado. Data are quoted from Middleton 1983 (table 14). **Abbreviations: CV**=Coefficient of variation; **OR**=Observed range of variation; **SD**=Standard deviation, *****=Estimated value.

Specimen number		Length	Width	
P2				
UCM 43138 (right)		1.37	0.65	
P3				
UCM 43138 (right)		2.11	1.76	
UCM 43748		2.05	1.48	
	Mean	2.08	1.62	

			Mesial Width	Distal Width
P4				
UCM 43138 (left)		2.25	2.54	2.58
UCM 43138 (right)		2.18	2.55	2.69
UCM 43748		2.15	2.45	2.55
	OR	2.15-2.25	2.45-2.55	2.55-2.69
	Mean	2.19	2.51	2.61
	SD	0.05	0.06	0.07
	CV	2.3	2.2	2.8
M1				
UCM 43138 (left)		1.90*	2.72*	
UCM 43138 (right)		1.90	2.71	2.90
UCM 43748		2.36	2.90	3.06
	OR	1.90-2.36	2.71-2.90	
	Mean	2.05	2.78	2.98
	SD	0.27	0.11	
	CV	12.9	3.8	
M2				
UCM 38202		2.35*	3.05*	3.12*
UCM 43138 (left)		2.05	3.16	3.16
UCM 43138 (right)		2.02	3.29	3.33
UCM 43748		2.29	3.20	3.15
UCM 47641		2.35	3.20	3.19
	OR	2.02-2.35	3.05*-3.29	3.12*-3.33
	Mean	2.21	3.18	3.19
	SD	0.16	0.09	0.08
	CV	7.4	2.7	2.6

Appendix 3 (continued)

	Length	Mesial Width	Distal Width
M3			
UCM 43138 (left)	1.70*	3.30	2.69
UCM 43138 (right)	1.90	3.15	2.66
UCM 47641	1.90	2.91	2.40
OR	1.70*-1.90	2.91-3.30	2.40-2.69
Mean	1.83	3.12	2.58
SD	0.12	0.20	0.16
CV	6.30	6.30	6.20

		Width trigonid	Width talonid
UCM 39544			
m1	2.48	1.50	1.38
m2	2.35	1.57*	1.36
m3	2.45	1.32*	1.12

Appendix 4. Dental dimensions of *Procerberus grandis* from the Denver Basin, Colorado. Data are quoted from Middleton 1983 (table 15).*=Estimated value.

Specimen number	Length	Mesial Width	Distal Width
P4			
UCM 34970 (left)	5.1*	4.9*	5.1*
M1			
UCM 34574	4.3*	5.3*	5.9*
M2			
UCM 34333	4.80		
UCM 34970 (left)	5.5*	7.0*	7.5*
UCM 34970 (right)	5.1*	7.2*	7.2*
M3			
UCM 34970 (left)	4.1*	6.5*	5.8*
UCM 34970 (right)…	4.3*		

		Width trigonid	Width talonid
m1			
UCM 34955	5.60	3.5*	3.6*