

ARTICLE

DESCRIPTION OF AN EARLIEST ORELLAN FAUNA FROM BADLANDS NATIONAL
PARK, INTERIOR, SOUTH DAKOTA AND IMPLICATIONS FOR THE STRATIGRAPHIC
POSITION OF THE BLOOM BASIN LIMESTONE BED

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ABSTRACT—Three new vertebrate localities are reported from within the Bloom Basin of the North Unit of Badlands National Park, Interior, South Dakota. These sites were discovered during paleontological surveys and monitoring of the park's boundary fence construction activities. This report focuses on a new fauna recovered from one of these localities (BADL-LOC-0293) that is designated the Bloom Basin local fauna. This locality is situated approximately three meters below the Bloom Basin limestone bed, a geographically restricted stratigraphic unit only present within the Bloom Basin. Previous researchers have placed the Bloom Basin limestone bed at the contact between the Chadron and Brule formations. Given the unconformity known to occur between these formations in South Dakota, the recovery of a Chadronian (Late Eocene) fauna was expected from this locality. However, detailed collection and examination of fossils from BADL-LOC-0293 reveals an abundance of specimens referable to the characteristic Orellan taxa *Hypertragulus calcaratus* and *Leptomeryx evansi*. This fauna also includes new records for the taxa *Adjidaumo lophatus* and *Brachygaulus*, a biostratigraphic verification for the biochronologically ambiguous taxon *Megaleptictis*, and the possible presence of new leporid and hypertragulid taxa. The Bloom Basin local fauna represents the earliest Orellan local fauna described from the Big Badlands of South Dakota and provides crucial insights into the age and stratigraphic position of the Bloom Basin limestone bed. The results of this study emphasize the vital importance of paleontological monitoring of high impact activities as a tool for discovering significant new localities and faunas and protecting crucial natural resources.

INTRODUCTION

One of the founding principles behind the establishment of the National Park System (NPS) is the protection and preservation of those natural resources contained within the boundaries of all designated land management units. One crucial component of resource management on NPS lands, with regards to paleontological resources, is the combined use of paleontological surveys prior to high impact activities (e.g., road construction, fencing) and paleontological monitoring during those activities. Together, these practices facilitate the identification, documentation, and preservation of significant paleontological specimens and localities that would otherwise be adversely affected. They also provide opportunities to survey infrequently visited areas, expanding knowledge of a management unit's paleontological resources and providing critical information that can be used to evaluate the impacts of future proposed activities, develop resource protection protocols, and guide scientific research by both park employees and external research partners.

For almost a decade, an extensive fencing project has been ongoing at Badlands National Park to upgrade portions of the boundary fence. Physical science technicians directly monitored construction activities in areas of bedrock outcrop and spot checked the sediments excavated during the drilling of postholes in sod-covered areas as part of the plan to mitigate the impact of these activities on the park's paleontological resources. Three new paleontological localities were identified, documented, and added

to the park's expansive paleontological locality database since 2012 as a consequence of these monitoring activities. One of these localities (BADL-LOC-0292) is a subsurface locality that produced material from an unidentified species of fish that would not have been discovered by traditional paleontological surveying methods. A second is an extensive vertebrate locality (BADL-LOC-0298) that straddles the fence line and would have been directly impacted by the fencing activities without the use of proper paleontological monitoring.

The third locality (BADL-LOC-0293), which is contained entirely within the park immediately adjacent to the fence line, is situated within the southern edge of the Bloom Basin along the park's northern boundary. This locality preserves a unique and diverse fauna (Table 1), here identified as the Bloom Basin local fauna. Sediments at this locality are exposed in an area eroded below the surface of the surrounding prairie. The top of the local stratigraphic section, which is about three meters above the fossil-bearing layer, is capped by a continuous carbonate layer several centimeters in thickness here identified as the Bloom Basin limestone bed (BBLB *sensu* Evans and Welzenbach, 1998; Benton and Reardon, 2006), based on comparisons to the type locality situated to the northeast (see Welzenbach, 1992). The thickness of the BBLB varies throughout the Bloom Basin, being thicker in the center of the basin (~1 meter) and thinning towards the margins before the exposures are lost entirely (Welzenbach, 1992; Evans and Welzenbach, 1998). The BBLB is restricted to the Bloom Basin of south-central South Dakota (Wel-

zenbach, 1992; Evans and Welzenbach, 1998); however, similar limestones appear near the contact between the Chadron and Brule formations within South Dakota (Evans and Welzenbach, 1998). The presence of this marker bed at the top of the local section with no overlying strata present ensures that all fossils collected both in situ and on the surface at this locality were preserved in the strata situated immediately below the BBLB and are not displaced from overlying sediments of the Brule Formation.

The BBLB was deposited within a perennial, stratified, freshwater lake (Welzenbach, 1992; Evans and Welzenbach, 1998) and is traditionally positioned by various authors either at the contact between the Chadron Formation and the overlying Brule Formation (e.g., Welzenbach, 1992; Benton and Reardon, 2006), or slightly below this contact within the Chadron Formation (e.g., Evans and Welzenbach, 1998). However, little prior stratigraphic work has been conducted in the Bloom Basin region of the park, with prior authors basing the stratigraphic position and age of the BBLB largely on correlations with carbonate layers observed in other areas of South Dakota and Nebraska (Welzenbach, 1992). Additionally, little paleontological work has been conducted within the Bloom Basin area, making it impossible to assess the age of the BBLB based on its position relative to biochronologically dated faunas. Here we describe the newly discovered Bloom Basin local fauna, assess the biochronologic age of that fauna, and discuss the implications this study has for the age, stratigraphic position, and regional correlation of the BBLB.

Institutional Abbreviations—BADL, Badlands National Park, Interior, South Dakota U.S.A.; CSC, Chadron State College, Chadron, Nebraska U.S.A.; SDSM, South Dakota School of Mines and Technology, Rapid City, South Dakota U.S.A.; UNSM, University of Nebraska State Museum, Lincoln, Nebraska.

Anatomical Abbreviations—Dental characters are designated with uppercase letters for upper dentition and lowercase letters for lower dentition: I/i, incisors; C/c, canines; P/p, premolars; M/m, molars.

MATERIALS AND METHODS

Fossil Collection and Preparation Methods

Most fossils collected from BADL-LOC-0293 were collected as float specimens after being subaerially eroded, though a few specimens (i.e., BADL 63554) were only partially exposed and remained in situ. No quarrying took place at this locality; therefore, all specimens collected were in some way exposed prior to discovery. Float specimens were not prepared, cleaned, or stabilized in the field. Preparation of specimens was conducted at the seasonal fossil preparation lab at Badlands National Park and further work was conducted in the preparation lab in the James E. Martin Paleontology Research Laboratory at South Dakota School of Mines and Technology. Matrix was removed from specimens using two different

mechanical preparation methods. A pneumatic airscribe (Paleo Tools© Microjack #1) was used to remove relatively soft matrix in easily accessed areas, while air abrasion was used in more delicate areas and in places where the matrix was well-cemented. Two different powder compounds were used during air abrasion: sodium bicarbonate was used to remove softer matrix, while crushed pumice was used on areas where the matrix was well-cemented and difficult to remove. When needed, specimens were stabilized using two different solutions of Paraloid® B-72 (ethyl methacrylate co-polymer), one dissolved in ethanol (5% weight by weight mixture) and the other dissolved in acetone (10% weight by weight mixture).

Screen Washing of Bulk Sediment for Microfossils

Bulk matrix removed during the excavation of a rhinocerotid skull (BADL 63554) during this study was retained and processed for microvertebrate fossils. These sediments were first soaked in warm water for at least twenty-four hours, then placed in a 0.5 mm mesh sieve and placed under running water to remove the silt and mud fraction of the sediment. The sediment was then placed in a drying rack for another twenty-four hours. Once dry, the sediment was dry sieved on a 0.5 mm mesh sieve, and the remaining matrix was retained and examined under a dissecting microscope. All fossil material noted was removed from the sediment sample and retained for identification. Though processing of this sediment is still ongoing, several important specimens of small rodents and reptiles were recovered (see below).

Dental Terminology

In regards to ruminant dental anatomy, we have elected to use the dental terminology proposed by Bärmann and Rössner (2011). That study standardized ruminant dental terminology in order to circumvent previously proposed, but unsupported homology statements.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA Laurenti, 1768

Order TESTUDINES Batsch, 1788

Family TRIONYCHIDAE Gray, 1825

APALONE Rafinesque, 1832

Trionyx Wagler, 1830 (original description)

Apalone Rafinesque, 1832 (original description)

Platypeltis Fitzinger, 1835 (original description)

Trionyx Cope, 1891:5, plate I, figs. 8-9 (revised diagnosis)

Aspideretes Hay, 1904 (in part) (original description)

Platypeltis Hay, 1908:546, plate 113, figs. 1-3 (revised diagnosis)

Amyda Clark et al., 1967:26 (revised diagnosis)

Aspideretes Harksen and Macdonald, 1969:15 (revised diagnosis)

Apalone Meylan, 1987 (new combination)

Apalone Hutchison, 1996:339, fig. 3 (new combination)

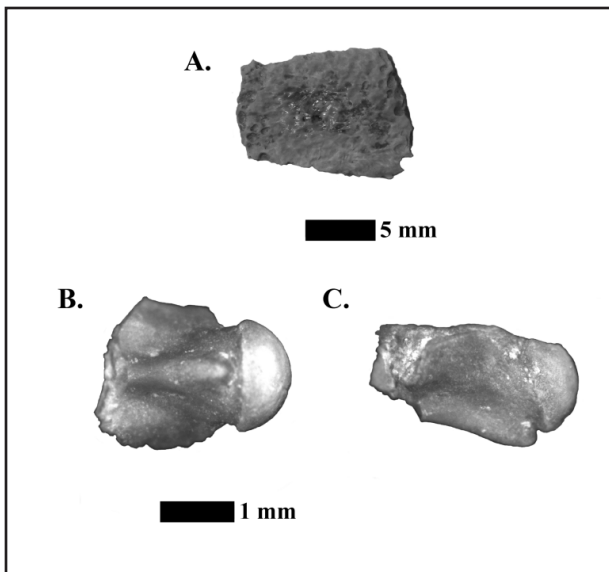


FIGURE 1. Photographs of selected reptiles identified from the Bloom Basin local fauna. **A**, BADL 63556, *Apalone* sp. carapace fragment in dorsal view; **B**, SDSM 63454, *Calamagras angulatus* vertebra in ventral view; **C**, right lateral view of the same. Photo by Ed Welsh.

APALONE sp.
(Fig. 1)

Referred Specimens—BADL 63556, partial costal plate fragment.

Known Occurrences—Cypress Hills Formation, Canada; Chadron Formation, Nebraska, North Dakota, and South Dakota; Brule Formation, North Dakota and South Dakota.

Comments—Recent North American trionychids were traditionally attributed to the genus *Trionyx*, until revisions by Meylan (1987) resurrected the genus *Apalone*. Two subgenera, *Apalone* and *Platypeltis*, were also recognized, but those taxa cannot be distinguished from each other based on the morphology of the carapace (Hutchison, 1996). The only species of trionychid turtle previously reported from the White River Group is *A. leucopotamica* (Cope, 1891). Though the type material of *A. leucopotamica* is highly fragmentary, Hay (1908) and Hutchison (1996) were able to confirm the validity of this species based on comparisons with more complete referred specimens from Nebraska. While BADL 63556 is too incomplete and weathered to allow referral to the species level, the dorsal sculpturing on the carapace is clear enough to confidently refer this specimen to the taxon *Apalone*.

Order SQUAMATA Oppel, 1881
Family BOOIDAE Gray, 1825
CALAMAGRAS Cope, 1873c

Calamagras Cope, 1873c:15 (original description)

Aphelophis Cope, 1873c:16 (original description)
Calamagras Sullivan and Holman, 1996:364 (new combination)
Calamagras Holman, 2000:59 (revised diagnosis)

CALAMAGRAS ANGULATUS Cope, 1873c
(Fig. 1)

Calamagras angulatus Cope, 1873c:16 (original description)
Ogmophis angulatus Cope, 1874:783 (new combination)
Calamagras angulatus Sullivan and Holman, 1996:364 (new combination)
Calamagras angulatus Holman, 2000:62, fig. 30 (revised diagnosis)

Referred Specimens—BADL 63454, partial trunk vertebra.

Known Occurrences—White River Formation, Colorado; Brule Formation, South Dakota; Gering Formation, Nebraska; Harrison Formation, Nebraska; Monroe Creek Formation, Wyoming.

Comments—BADL 63454 consists of a partial vertebra, only lacking the neural arch, or accessory processes. The morphology of this specimen corresponds with description of the holotype provided by Holman (2000). Specifically, the vertebra is longer than wide in ventral view and a moderately well-developed hemal keel is present on the ventral surface of the centrum that ends slightly anterior to the border of the posterior condyle. The only other record of this species from South Dakota is based on the referral of two trunk vertebrae (SDSM 20189 and 20197) from the Brule Formation at Reva Gap, Harding County, South Dakota (Sullivan and Holman, 1996).

Class AVES Linnaeus, 1758
Order indet.

Referred Specimens—BADL 61905 and 63559, eggshell fragments.

Comments—There has been no study, as of yet, that can determine the taxonomic or parataxonomic status of this specimen without undertaking destructive sampling to examine the microcrystalline structure of the eggshell. Therefore, referral of these specimens is restricted to the clade Aves.

Class MAMMALIA
Order LEPTICTIDA McKenna, 1975
Family LEPTICTIDAE Gill, 1872
MEGALEPTICTIS Meehan and Martin, 2012
MEGALEPTICTIS ALTIDENS Meehan and Martin, 2012
(Fig. 2)

Referred Specimens—BADL 61907, a left maxillary fragment with P4-M2

REPTILIA Laurenti, 1768	RODENTIA Bowdich, 1821
TESTUDINES Batsch, 1788	ISCHYROMYIDAE Alston, 1876
?TESTUDINIDAE Batsch, 1788	<i>Ischyromys</i> sp.
TRIONYCHIDAE Gray, 1825	APLODONTIDAE Brandt, 1855
<i>Apalone</i> sp.	<i>cf. Brachygaulus</i> sp.
SQUAMATA Oppel, 1881	EUTYPOMYIDAE Miller and Gidley, 1918
<i>Lacertilia</i> indet.	<i>Eutypomys cf. thomsoni</i> Matthew, 1905
BOIDAE Gray, 1825	EOMYIDAE Winge, 1887
<i>Calamagras angulatus</i> Cope, 1873c	<i>Adjidaumo lophatus</i> Korth, 2012
AVES Linnaeus, 1758	HELISCOMYIDAE Korth, Wahlert, and Emry, 1991
Aves indet.	Heliscomyidae indet.
MAMMALIA Linnaeus, 1758	PERISSODACTYLA Owen, 1848
LEPTICTIDA McKenna, 1975	RHINOCEROTIDAE Gray, 1821
LEPTICTIDAE Gill, 1872	<i>Subhyracodon</i> sp.
<i>Megaleptictis altidens</i> Meehan and Martin, 2012	EQUIDAE Gray, 1821
CREODONTA Cope, 1875	<i>Mesohippus</i> sp.
HYAENODONTIDAE Leidy, 1869	ARTIODACTYLA Owen, 1848
<i>Hyaenodon</i> sp. indet.	ENTELODONTIDAE Lydekker, 1883
CARNIVORA Bowdich, 1821	<i>Archaeotherium</i> sp.
CANIDAE Flower, 1869	MERYCOIDODONTIDAE Thorpe, 1923
<i>Hesperocyon gregarius</i> (Cope, 1873c)	<i>Merycoidodon culbertsoni</i> Leidy, 1848
AMPHYCYONIDAE Haeckel, 1866	HYPERTRAGULIDAE Cope, 1879
<i>Daphoenus</i> sp.	<i>Hypertragulus calcaratus</i> (Cope, 1873b)
NIMRAVIDAE Cope, 1880	Hypertragulidae gen. et sp. indet.
<i>Dinictis</i> sp.	LEPTOMERYCIDAE Zittel, 1893
CARNIVORA incertae sedis	<i>Leptomeryx evansi</i> Leidy, 1853
<i>Palaeogale sectoria</i> (Gervais, 1848)	<i>Leptomeryx</i> sp.
LAGOMORPHA Brandt, 1855	
LEPORIDAE Gray, 1821	
<i>Megalagus</i> sp.	
<i>Palaeolagus haydeni</i> Leidy, 1856	
Leporidae indet.	

TABLE 1. Preliminary faunal list for the Bloom Basin local fauna based on specimens collected from locality BADL-LOC-0293.

Known Occurrences—Brule Formation, South Dakota.

Comments—Several diagnostic features of *M. altidens* are noted in BADL 61907. The P4 through M2 display the following features: presence of well-developed, centrally positioned precingula that bear small cuspules; presence of moderate labial cingula; absence of lingual cingula; and, presence of well-developed postcingula with tall hypocones. The holotype of *M. altidens* was collected in the tan silt-stones of the White River Group in Custer County, South Dakota during an 1894 Kansas University field expedition (Meehan and Martin, 2012). This locality description likely refers to high-altitude White River Group deposits situated in the eastern Black Hills. However, the lack of detailed geographic and stratigraphic data recorded with this specimen prevents confident referral of this specimen to either the Chadron or Brule Formation. Based on the fauna collected in association with the

holotype, Meehan and Martin (2012) inferred that the biochronological age of this species was likely Chadronian, but could not completely rule out the possibility that it was Orellan. This uncertainty is the result of a lack of biostratigraphic resolution for these high-altitude faunas preserved in South Dakota. Thus, BADL 61907 serves as the only stratigraphically and biochronologically verified occurrence of this taxon.

Also collected from BADL-LOC-0293 is a moderately preserved leptictid skull and dentaries (BADL 61618). However, the upper and lower dentition on this specimen remain in occlusion and further preparatory work is needed to reveal the taxonomic affinities of that specimen.

Order CREODONTA Cope, 1875
 Family HYAENODONTIDAE Leidy, 1869
HYAENODON Laizer and Pariello, 1838

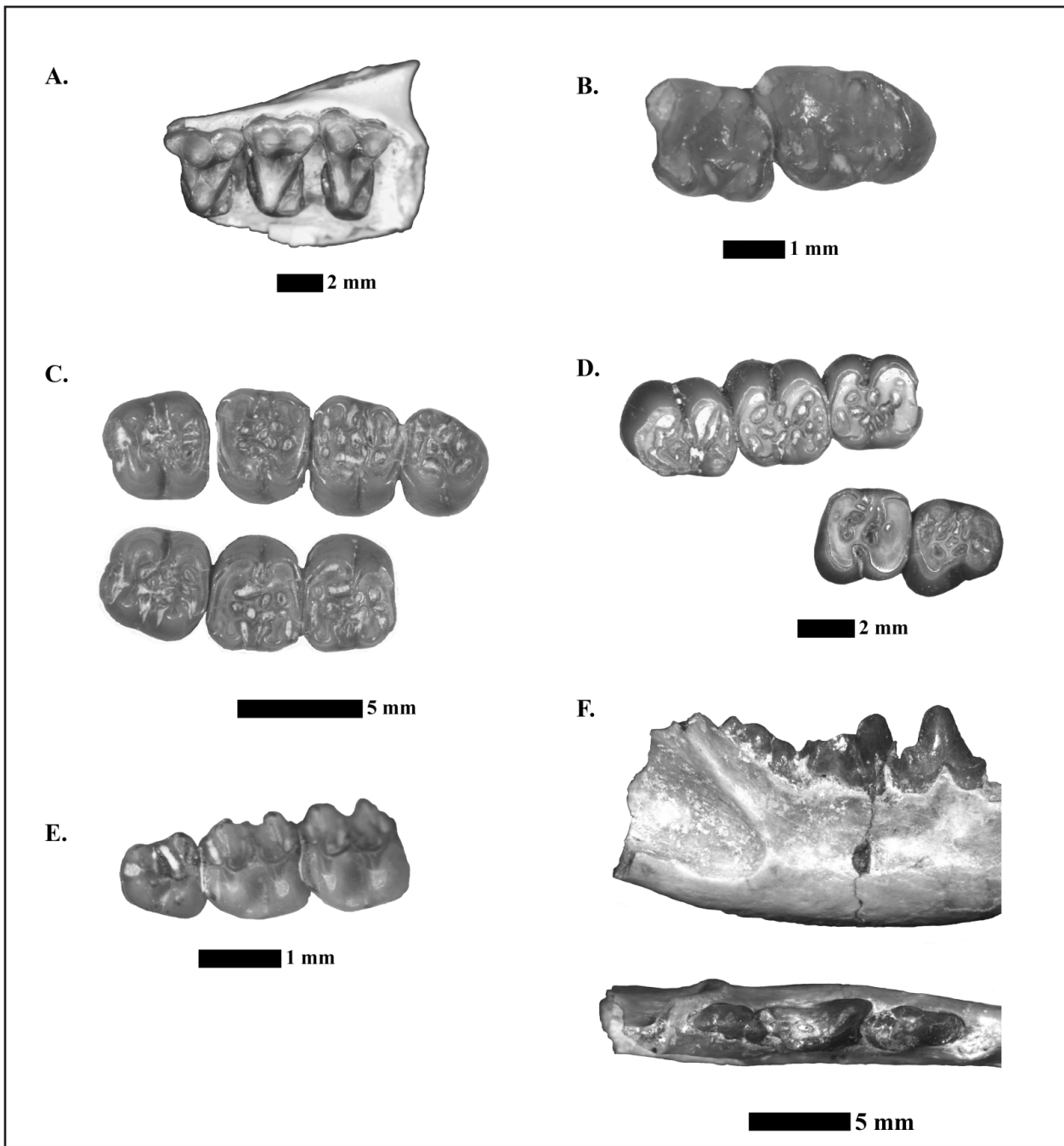


FIGURE 2. Photographs of some significant mammalian fossils from the Bloom Basin local fauna. **A**, BADL 61907, *Megaleptictis altidens* left maxilla fragment with P2 through M2 in ventral view; **B**, crown view of BADL 63453, *cf. Brachygaulus* sp. m2 through m3; **C** crown view of BADL 63460, *Eutypomys cf. thomsoni* maxilla fragments with LM1 through M3 and RP4 through M1; **D**, crown view of BADL 61621, *Eutypomys cf. thomsoni* left m1 through m3 and BADL 61621 right p4 through m1; **E**, crown view of BADL 61615, *Adjidaumo lophatus* p4 through m2; **F**, BADL 63558, *Palaeogale sectoria* dentary fragment with p4 through m2 in labial and dorsal views (edentulous anterior portion cropped from image). Photo by Ed Welsh.

Hyaenodon Laizer and Pariello, 1838 (original description)

Taxotherium Blainville, 1841 (original description)

Hyaenodon Leidy, 1853 (revised diagnosis)

Pseudopteroodon Schlosser, 1887 (original description)

Neohyaenodon Thorpe, 1922b:278, Figs. 1-2 (original description)

Hyaenodon (Protohyaenodon) Stock, 1933:435 (original description)

Hyaenodon Scott and Jepsen, 1936 (new combination)

Hyaenodon Van Valen, 1967:268 (new combination)
Hyaenodon (*Neohyaenodon*) Mellett, 1977 (new combination)
Hyaenodon (*Protohyaenodon*) Mellett, 1977 (new combination)
Hyaenodon Gunnell, 1998:98 (revised diagnosis)

HYAENODON sp.

Referred Specimens—BADL 61619, edentulous skull and mandible.

Known Occurrences—*Hyaenodon* is one of the most cosmopolitan carnivorous mammals with Middle Eocene to Oligocene occurrences in North America and Eurasia, along with a few occurrences in Africa.

Comments—This specimen is represented by the edentulous skull and mandible of a very young individual. The alveoli in this specimen are not mediolaterally angled, as would be expressed by the carnassial set of a carnivoran; rather, the alveoli are anteroposteriorly oriented, which is typical of the posterior-most carnassial teeth in creodonts. This specimen was found in close association with scattered cranial and dental remains of a larger, presumably adult specimen of *Hyaenodon*, but that specimen was considered too fragmentary and weathered to collect.

Order CARNIVORA Bowdich, 1821

Family CANIDAE Flower, 1869

HESPEROCYON Scott, 1890

Amphicyon Leidy, 1856:90
Canis Cope, 1873b:3
Galecynus Cope, 1881:177
Cynodictis Scott and Osborn, 1887:152
Hesperocyon Scott, 1890:37
 “*Pseudocynodictis*” Schlosser, 1902:164
Nothocyon Matthew, 1924:fig. 28
Hesperocyon Green, 1952:124
Nanodelphys? Russell, 1972:7
cf. Hyaenodon? Russell, 1972:47
Hesperocyon Wang, 1994:24. Wang and Tedford, 1996:435 (new combination)

HESPEROCYON GREGARIUS (Cope, 1873b)

Amphicyon? *gracilis* Leidy, 1856:90 nom. preoc. (original description)
Canis gregarius Cope, 1873b:3 (original description)
Canis lippincottianus Cope, 1873c:9 (referred specimen only)
Galecynus gregarius Cope, 1881:177 (new combination)
Cynodictis gracilis Scott and Osborn, 1887:152 (new combination)
Hesperocyon gregarius Scott, 1890:37. Green, 1952:124. Russell, 1972:53 (in part) (new combination)
Cynodictis gregarius Scott, 1898:400 (new combination)
Nothocyon gregarius Matthew, 1924:fig. 28 (new com-

ination)
Pseudocynodictis gregarius Schlosser, 1902:50. Scott and Jepsen, 1936:101. Galbreath, 1953:75. (new combination)
Cynodictis paterculus Matthew, 1903:209 (new combination)
Cynodictis lippincottianus Lambe, 1908:61 (new combination)
Amphicyon angustidens Thorpe, 1922c:425 Fig. 1 (new combination)
Cynodictis paterculus Thorpe, 1922c:428 (new combination)
Pseudocynodictis angustidens (= *lippincottianus*) Hough, 1948:590 (new combination)
Pseudocynodictis nr. paterculus Galbreath, 1953:75 (new combination)
Hesperocyon paterculus White, 1954:416 (new combination)
Pseudocynodictis nr. paterculus Hough and Alf 1956:136 (new combination)
Nanodelphys? *mcgrewi* Russell, 1972:7
cf. Hyaenodon? *minutus* Russell, 1972:47 (NMC 9353 only)
Hesperocyon gregarius Wang, 1994:26, figs. 9-10. Wang and Tedford, 1996:436, figs. 1-2 (new combination)

Referred Specimens—BADL 61614, partial dentary with left m1; BADL 63455, left P4; BADL 63456, left M1.

Known Occurrences—*Hesperocyon gregarius* is one of the most common carnivores in Chadronian through Whitneyan localities and correlative stratigraphic units in Colorado, Montana, South Dakota, Nebraska, North Dakota, and Wyoming, United States and Saskatchewan, Canada.

Comments—The P4 of BADL 63455 has a protocone that is fairly well developed and slightly anterior to the paracone. In *Archaeocyon pavidus* (“*Hesperocyon*” *pavidus*), the protocone is closely appressed to the paracone. BADL 63455 also has a small anterior cingulum that persists to the paracone, in contrast to *H. coloradensis* where the anterior cingulum disappears laterally. In BADL 63456 the labial cingulum is relatively prominent anterior and lateral to the paracone, as opposed to the reduced labial cingulum seen in *A. pavidus*.

The only Chadronian occurrence of Canidae besides *H. gregarius* is *Prohesperocyon wilsoni*, which is restricted to a single locality in Texas representing the early-middle Chadronian (Gustafson, 1986). We chose to leave *Prohesperocyon* out of this discussion owing to significant morphological differences between that taxon and these specimens, regardless of the combined biogeographic and biochronologic removal (see Wang, 1994). Canid specimens recovered from the Scenic Member of the Brule Formation are predominantly referable to *H. gregarius*. *Hesperocyon coloradensis* has yet to be identified from outside of the White River Group in northeast Colorado, and a few specimens of “*Hesperocyon*” *pavidus* are known from the same location (Wang, 1994). Though

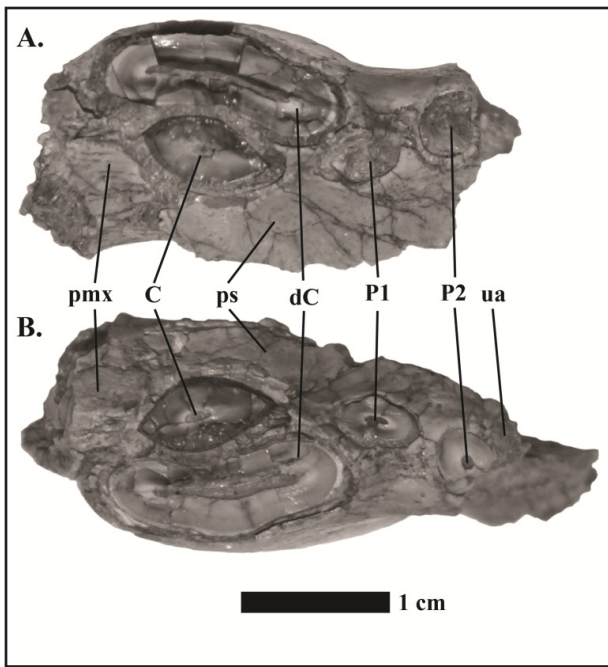


FIGURE 3. Photographs of BADL 61617 (*Dinictis* sp. indet.): **A**, left premaxilla and maxilla in ventral view; **B**, right premaxilla and maxilla in ventral view. Abbreviations: pmx, premaxilla; C, canine; dC, deciduous canine; ps, palatal shelf; ua, unidentified alveolus. Photo by Ed Welsh.

“Hesperocyon” pavidus has been synonymized with the borophagine *Archaeocyon* (in part), none of the Orellan occurrences, all in Colorado, were included (Wang et al., 1999). Wang et al. (1999) did not give any specific assignment to the Colorado material, but suggested that the material might represent a distinct species that could potentially bridge the Hesperocyoninae to the Borophaginae. The only other canid taxa known to occur in the Orellan are *“Meoscyon” temnodon* and *Osbornodon renjei*, both hesperocyonines (Wang, 1994). Both taxa are significantly larger than *Hesperocyon*. Only a single Orellan specimen of *“Mesocyon” temnodon* known from South Dakota and the only specimens of *O. renjei* are restricted to the late Orellan of North Dakota (Wang, 1994).

Family AMPHICYONIDAE Haeckel, 1866
DAPHOENUS Leidy, 1853

Daphoenus Leidy, 1853 (original description)
Galecynus Cope, 1874 (original description)
Canis Cope, 1883 (new combination)
Proamphicyon Hatcher, 1902:95 (original description)
Pseudocynodictis Schlosser, 1902 (new combination)
Cynodictis Thorpe, 1922c:427 (in part) (new combination)
Pericyon Thorpe, 1922a:172, Fig. 3 (original description)
Pseudocynodictis Galbreath, 1953:75 (in part) (new combination)
Daphoenus Hunt, 1998:204 (revised diagnosis)

DAPHOENUS sp.

Referred Specimens—BADL 63451, an unidentified premolar; BADL 63452, left maxillary fragment with M1-2.

Comments—The molars of *Daphoenus* are nearly indistinguishable between species, and there are no current studies distinguishing species of *Daphoenus* based on the morphology of the upper molars (Hough, 1948; Hunt, 1998). In BADL 63452 the M2 is not reduced relative to the size of the M1, supporting the referral of this specimen to *Daphoenus* as opposed to the similar-sized *Brachyrhynchocyon* that displays a reduced M2 (Hunt, 1998).

Family NIMRAVIDAE Cope, 1880
DINICTIS Leidy, 1854

Dinictis, Leidy, 1854:127 (original description)
Daptophilus Cope, 1873b:2 (original description)
Dinictis Bryant, 1996:456 (new combination)

DINICTIS sp.
(Fig. 3)

Referred Specimens—BADL 61617

Comments—BADL 61617 consists of left and right partial premax-maxillary fragments with broken dC1's, erupting C1's, and alveoli with broken P1 through P2. Among North American nimravines, the presence of the P1 is typically indicative of the taxon *Nimravus brachyops* (Martin, 1998), though this feature is also present in the European taxon *Eofelis edwardsi* (Peigne, 2003). Within those taxa, the presence of P1 varies between specimens (present in 63% of *N. brachyops* specimens and 50% of *E. edwardsi* specimens examined by Peigne [2003]). This characteristic can also vary within individual specimens, with the P1 absent on the right side of a specimen of *Nimravus brachyops* (SDSM 348), but present on the left side. Examination of nimravid specimens during the course of this study resulted in the identification of well-preserved specimens referred to the taxa *Hoplophoneus* (CSC-41-42) and *Dinictis* (UNSM 25524) that also retain the P1. Referral of specimens to a given taxon cannot be based solely on the number of upper premolars because this feature is variable across all nimravines, despite the known probability of the P1 being present among nimravids at the generic level.

General statements have been made regarding variation in the size and spacing of the serrations on the upper canines across nimravines (e.g., Martin, 1980), but these differences have yet to be quantified. Current studies are beginning to test the taxonomic utility of nimravine canine serration morphology and density along with the overall dimensions of the tooth (Boyd and Welsh, 2013). Those preliminary inquiries are based on a similar study conducted by Currie and Rigby (1990) that examined in

situ theropod dinosaur teeth to assess the identify criteria that could be used refer isolated and/or fragmentary specimens to specific taxa. The erupting adult canines of BADL 61617 display a serration density count that falls within the range recently reported for *Dinictis* (3–3.5 serrations per millimeter). Based on that evidence, we tentatively refer BADL 61617 to *Dinictis* sp., contingent the publication of additional research into the taxonomic utility of canine serrations in nimravines.

CARNIVORA incertae sedis
PALAEOGALE von Meyer, 1846

Palaeogale von Meyer, 1846 (original description)
Bunaelurus Cope, 1873e:8 (original description)
Palaeogale Flynn and Galiano, 1982:47 (new combination)
Palaeogale Baskin, 1998:165 (new combination)

PALAEOGALE SECTORIA (Gervais, 1848)
(Fig. 2)

Mustela sectoria Gervais, 1848:plate 28 (original description)
Bunaelurus lagophagus Cope, 1874:8 (original description)
Canis osorum Cope, 1873e:8 (original description)
Palaeogale sectoria Schlosser, 1887 (new combination)
Bunaelurus infelix Matthew, 1903:210 (original description)
Bunaelurus parvulus Matthew and Granger, 1924:8 (original description)
Bunaelurus ulysses Matthew and Granger, 1924:8 (original description)
Palaeogale infelix Simpson, 1946:4 (new combination)
Palaeogale lagophaga Simpson, 1946:12 (new combination)
Palaeogale lagophaga Galbreath, 1953:77
Palaeogale sectoria de Bonis 1981:50 (new combination)
Palaeogale sectoria Baskin and Tedford, 1996:495 (new combination)
Palaeogale sectoria Morlo, 1996:200 (new combination)
Palaeogale sectoria Baskin, 1998:165 (new combination)

Referred Specimens—BADL 63558, a right dentary fragment with p4, m1 (broken), and m2.

Known Occurrences—Early Oligocene of Eurasia and North America, with Late Eocene occurrences in Montana.

Comments—BADL 63558 is one of a very few specimens of *Palaeogale* held in the BADL collections. The protoconid on the m1 is broken off, and there is no trace of the metaconid, making the trigonid wide and open. The m1 talonid is labiolingually trenched with the hypoconid positioned posteromedially. The m2 paraconid, protoconid, and entoconid are in a linear position with no development of a trigonid or talonid. The m1 and m2 are tightly com-

pressed to where the m1 hypoconid is situated buccally from the m2 paraconid.

Palaeogale sectoria is the only species of *Palaeogale* known in the Chadronian and Orellan in North America, with the next occurring species, *P. dorothiae*, occurring in the Arikareean (Baskin, 1998). The differences demonstrated between BADL 63558 and the holotype of *P. dorothiae* (SDSM 53326) is a distinct ridge extending anteriorly from the hypoconid, removing the talonid trench as seen previously, and a slightly more reduced m2. Original interpretations of *Palaeogale* place the taxon within the Mustelidae, but more recent assessments demonstrate a closer relationship to Vivverridae (Hunt, 1974; Flynn and Galiano, 1982; Baskin and Tedford, 1996). Despite *Palaeogale* being removed from the Mustelidae, there are no well-defined affinities of this taxon to either Caniformia or Feliformia (Flynn et al., 1988; Baskin and Tedford, 1996).

Order LAGOMORPHA Brandt, 1855
Family LEPORIDAE Gray, 1821
MEGALAGUS Walker, 1931

Megalagus Walker, 1931:234 (original description)
Megalagus Dawson, 1958:10 (revised diagnosis)

MEGALAGUS sp.

Referred Specimens—BADL 63473, right dentary fragment with p3 through m1; BADL 63474, right dentary fragment with p4 (broken) through m3.

Comments—BADL 63473 is referred to the taxon *Megalagus* based on the combined presence of a hypoflexid and absence of a mesoflexid on p3, the almost complete lack of cement on the teeth, and the large size of the specimen (Dawson, 1958). BADL 63474 is referred to the taxon *Megalagus* based on the almost complete lack of cement on the teeth and the large size of the specimen (Dawson, 1958). Dawson (1958) noted the difficulty in distinguishing *Megalagus* from *Palaeolagus intermedius*, stating that the lower cheek-teeth are slightly smaller and more hypsodont in the latter taxon. Based on those differences and comparison to other specimens of *Megalagus*, we support referral to this taxon over *P. intermedius*. However, all of the morphologies used to differentiate species of *Megalagus* are situated in the skull or upper dentition, making the referral of these partial dentaries to a given species impossible (Dawson, 1958).

PALAEOLAGUS Leidy, 1856

Palaeolagus Leidy, 1856:89 (original description)
Tricium Cope, 1873b:4 (original description)
Protolagus Walker, 1931:230 (original description)
Palaeolagus Dawson, 1958:19 (new combination)
Palaeolagus Dawson, 2008:298 (new combination)

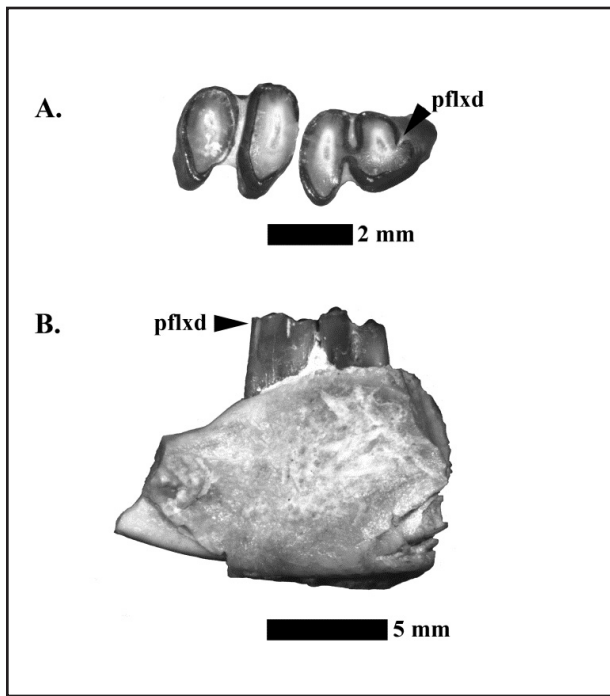


FIGURE 4. Photographs of BADL 63472, Leporidae gen. et sp. indet., right dentary fragment with P3 through P4. **A**, crown view of P3 through P4; **B**, dentary fragment with P3 through P4 in lingual view. Abbreviation: pflxd, paraflexid. Photo by Ed Welsh.

PALAEOLAGUS HAYDENI Leidy, 1856

Palaeolagus haydeni Leidy, 1856:89 (original description)
Palaeolagus agapetillus Cope, 1873a:1 (original description)

Tricium avunculus Cope, 1873b:5 (original description)

Tricium leporinum Cope, 1873b:5 (original description)

Tricium annae Cope, 1873e:4 (original description)

Protolagus affinus Walker, 1931:231 (original description)

Archaeolagus striatus Walker, 1931:236 (original description)

Palaeolagus haydeni Dawson, 1958:20 (new combination)

Palaeolagus hemirhizis Korth and Hageman, 1988:144 (in part) (new combination)

Palaeolagus haydeni Prothero and Whittlesey, 1998:50 (new combination)

Referred Specimens—BADL 63475, left dentary fragment with p3 through p4; BADL 63476, left dentary fragment with p3 through p4; BADL 63477, right dentary fragment with p4 through m1; BADL 63478, left dentary fragment with p4 through m1; BADL 63479, left dentary fragment with m1 through m2; BADL 63480, right dentary fragment with m1 through m2; BADL 63481, right dentary fragment with p4 through m1; 63482, right dentary fragment with p3 through p4; BADL 63483, left dentary fragment with p3 through p4; BADL 63484, left dentary

fragment with m1 through m3; BADL 63485, left dentary fragment with p3 through m1; BADL 63486 left dentary fragment with p3 through p4; BADL 63487, left dentary fragment with p4 through m1; BADL 63488, right dentary fragment with p3 through m2; BADL 63489, left dentary fragment with p3 through p4 and two associated lower cheek teeth.

Comments—When evaluating the taxonomic status of these specimens, the recommendation of Prothero and Whittlesey (1998) was followed in that *Palaeolagus hemirhizis* was considered to be an invalid species that was based on a mixed sample of specimens referable to the species *Palaeolagus temnodon* and *Palaeolagus haydeni*. The specimens listed above are here referred to *P. haydeni* based on the presence of an internal reentrant (mesoflexid) between the trigonid and talonid on p3, long axis of mesoflexid and trigonid oriented roughly mediolaterally on p3 (as opposed to angled from anterointernal to posterolateral), and the presence of a lingual bridge composed of enamel and dentine between the trigonids and talonids of p4 through m2 (Dawson, 1958). In these specimens the mesoflexid is retained longer during wear (based on the extent of the mesostriid on the lingual surface of p3), but would have eventually become enclosed into an isolated enamel lake late in wear. Alternatively, in the morphologically similar taxon *Palaeolagus temnodon* the mesoflexid closes relatively early in wear (Dawson, 1958). These specimens also fall within the size range reported for *P. haydeni*, which is smaller than *P. temnodon* (Korth and Hageman, 1988:fig. 6).

Several leporid maxillae were also recovered from the locality. The morphology of those specimens is consistent with *P. haydeni*, but we have yet to determine if any may represent the morphologically similar taxon *P. temnodon*. Those maxillae are here referred to *Palaeolagus* sp. until further refinement of their taxonomic identities is completed.

LEPORIDAE gen. et. sp. indet.

(Fig. 4)

Referred Specimens—BADL 63472, right dentary fragment with p3 through p4.

Comments—The morphology of this specimen is consistent with that of *P. haydeni* with the exception of a single feature of the p3. The crown of the p3 displays a relatively early stage of wear based on the presence of a narrow bridge composed of dentine and enamel between the mesoflexid and the hypoflexid that connects the talonid and trigonid. Based on the extent of the mesostriid on the lateral surface, the mesoflexid will eventually become enclosed with increased wear, as in *P. haydeni*. However, this specimen differs from all species of *Palaeolagus* in the presence of an anterointernal reentrant (paraflexid) on the p3. In lingual view, a slight parastriid is present that extends further ventrally than the mesostriid, indicating that the paraflexid will persist slightly longer during wear

than the mesoflexid, ruling out the presence of a paraflexid in this specimen being the result of the early wear stage represented by this tooth. A paraflexid is unknown from any palaeolagine leporid (though an anteroexternal reentrant can be variably present in *Palaeolagus burkei* and is present in *Palaeolagus hypsodus*) and is only known from the archaeolagines *Hypolagus apachensis* (Barstovian?–Clarendonian of California) and *Notolagus velox* (late Hemphillian of Mexico) (Dawson, 1958). However, these taxa also display a corresponding anteroexternal reentrant (Dawson, 1958), a feature that is clearly lacking in BADL 63472. The Asian leporid *Gobiolagus tolmachovi* from the Late Eocene of Mongolia displays a similar paraflexid and lack of an anteroexternal reentrant, but it lacks a mesoflexid and the hypoflexid is positioned further posteriorly on the crown (Meng et al., 2005:fig. 2). Additional study of BADL 63472 is necessary to determine if the presence of a paraflexid (and the associated parastrid) in this specimen is the result of individual variation within *P. haydeni*, or if this specimen represents a new leporid species, perhaps one that emigrated from Asia.

Order RODENTIA Bowdich, 1821

Family ISCHYROMYIDAE Alston, 1876

ISCHYROMYS Leidy, 1856

Ischyromys Leidy, 1856 (original description)

Ischyromys Leidy, 1869 (revised diagnosis)

Colotaxis Cope, 1873a (original description)

Gymnoptychus Cope, 1873b (original description)

Ischyromys Miller and Gidley, 1920 (new combination)

Titanotheriomys Miller and Gidley, 1920 (original description)

Ischyromys Troxell, 1922 (new combination)

Titanotheriomys Wood, 1976 (new combination)

Ischyromys Wood, 1980 (new combination)

Ischyromys Heaton, 1993

Ischyromys Korth, 1994 (original description)

Ischyromys Heaton, 1996:373 (new combination)

ISCHYROMYS sp.

Referred Specimens—BADL 61909, nearly complete dentary with p4 through m2; BADL 63470, left dentary with m1 through m3; BADL 63471, right dentary with m2 and left dentary with m1 through m2.

Known Occurrences—Cypress

Comments—The lower cheek teeth of the above listed specimens do not display the sinusoidal trench of the anterior lingual valley, precluding referral to the *Ischyromys* (*Titanotheriomys*) subgenus (Heaton, 1996). However, the most detailed study of the taxon *Ischyromys* yet conducted demonstrated the difficulty of distinguishing individual species of *Ischyromys* within the Plains region (Heaton, 1996). As a result, we refrain from identifying these specimens to the species level at this time.

Family APLDONTIDAE Miller and Gidley, 1918

BRACHYGAULUS Korth and Tabrum, 2011

Brachygaulus Korth and Tabrum, 2011:69 (original description)

cf. *BRACHYGAULUS* sp.

(Fig. 2)

Referred Specimens—BADL 63453, left dentary fragment with m2-3.

Diagnosis—The main character difference between *Brachygaulus* and other prosciurine apodontids is the lophid that develops from the mesostylid to the posterior arm of the protoconid, enclosing the trigonid (Korth and Tabrum, 2011). BADL 63453 contains a rudimentary lophid from the mesostylid on the m2 (see Fig. 4). However, there are slight differences between BADL 63453 and the known species of *Brachygaulus*, including lower lophids and a relatively wider m3. This specimen might be referable to the referred, but undesigned *Brachygaulus* sp. specimen in Korth and Tabrum (2011; see fig. 4 D.), where this lophid is more reduced and the mesostylid to paraconid lophid form a zig-zag pattern. Korth and Tabrum (2011) referred to *Brachygaulus* as the possible prosciurine origin towards the promylagauline mylagaulids, all being found in the Late Orellan. BADL 63453 might be a more primitive form preceding the material from Montana. With the exception of the mesostylid loph, BADL 63433 closely resembles *Prosciurus* (see also Korth, 1989).

Family EUTYPOMYIDAE Miller and Gidley, 1918

EUTYPOMYS Matthew, 1905

EUTYPOMYS cf. *THOMSONI* Matthew, 1905

(Fig. 2)

Eutypomys thomsoni Matthew 1905:21 Fig. 2 (original description)

Referred Specimens—BADL 61621, partial maxilla with P4 through M1, right dentary with p4 through m1, left dentary with m1 through m3; BADL 63459, right dentary fragment with m1 through m2; BADL 63460, left maxilla fragment with M1 through M3 and right maxilla fragment with P4 through M1.

Comments—*Eutypomys* is characterized by complicated enamel lake and reentrant patterns. *Eutypomys thomsoni* is the typical species that occurs throughout the Scenic Member of the Brule Formation. These specimens are similar in size to *E. thomsoni*, but have a less complicated crown pattern, similar to a description of an indeterminate species of *Eutypomys* from Montana described by Wood (1937). The arrangement of enamel lakes and reentrants is somewhat similar to what has been previously described in the Chadronian taxon *E. parvus* (Lambe, 1908; Worley-Georg and Eberle, 2006; Kihm, 2011); however, specimens of *E. parvus* are noticeably smaller than both

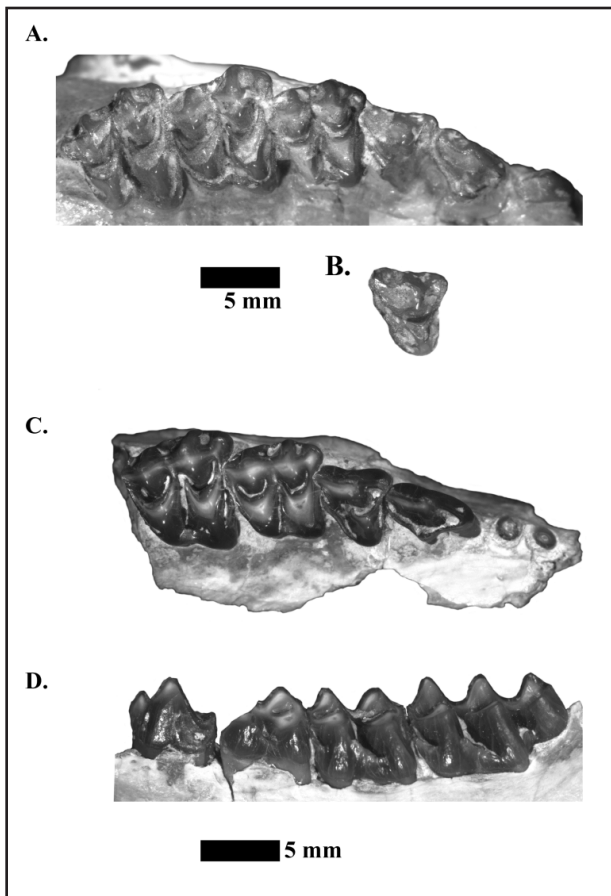


FIGURE 5. Comparative photographs of Hypertragulidae gen. et sp. indet. (BADL 61620) and *Hypertragulus calcaratus* (SDSM 32102). **A**, right P2 through M3 of *H. calcaratus* (SDSM 32102); **B**, horizontally reversed image of left P4 of SDSM 32102; **C**, crown view of P3 through M2 from Hypertragulidae gen. et sp. indet. (BADL 61620); **D**, labial view of p4 through m3 of Hypertragulidae gen. et sp. indet. (BADL 61620). Photo by Ed Welsh.

E. thomsoni and the specimens mentioned herein. We refer these specimens to *Eutypomys cf. thomsoni* because while that taxon is the closest match, the morphology of the referred specimens does differ slightly from that reported in *E. thomsoni*.

Family EOMYIDAE Winge, 1887
ADJIDAUMO Hay, 1899
ADJIDAUMO LOPHATUS Korth, 2012
 (Fig. 2)

Adjidaumo lophatus Korth, 2012:7 Fig. 1 (original description)

Referred Specimens—BADL 61615, coprolite with a left dentary with a broken incisor and p4 through m2 either attached with sediment or incorporated into the coprolite.

Known Occurrences—Dunbar Creek Formation, Montana.

Comments—The crown morphology of this specimen matches that reported for *Adjidaumo* and possesses the lophate brachydont cheek teeth diagnostic of *Adjidaumo lophatus* (Korth, 2012). This species was previously only known from the Chadronian of Montana, representing a temporal and geographic range extension for this taxon (see Discussion).

This specimen was found attached to a piece of carnivorous mammal coprolite; however, it appears that the jaw was secondarily attached to the coprolite with matrix and was not originally part of the coprolite. However, some uncertainty remains regarding the relationship between this dentary and the coprolite, so the two remain affixed together, making photography of this specimen difficult.

Family HELISCOMYIDAE Korth,
 Wahlert, and Emry, 1991
 HELISCOMYIDAE indet.

Referred Specimens—BADL 63461, isolated right M3.

Comments—The M3 of BADL 63461 has a subcircular crown with the only visible cusps being a paracone and large, centrally placed protocone with a faint protoloph. This is the only representative material of this taxon at this site. It is likely that this specimen is referable to the taxon *Heliscomys*, but the contemporaneous presence of additional taxa lacking comparable material (i.e., *Apletotomeus* and *Akmaiomys*) and the fragmentary nature of this specimen prevent the confident referral of this specimen to that taxon.

Order PERISSODACTYLA Owen, 1848
 Family RHINOCERATODAE Gray, 1821
SUBHYRACODON Wood, 1927

Rhinoceros Leidy, 1850b (in part) (original description)
Aceratherium Leidy, 1851a (in part) (original description)
Aceratherium (Subhyracodon) Brandt, 1878 (new combination)
Anchisodon Cope, 1879 (original description)
Caenopus Cope, 1880 (in part) (original description)
Leptacatherium Osborn, 1898 (original description)
Subhyracodon Wood, 1927 (new combination)
Subhyracodon Prothero, 1998:599. (new combination)
Subhyracodon Prothero, 2005:40, figs. 4.10-4.14. (new combination)

SUBHYRACODON sp.

Referred Specimens—BADL 63554, nearly complete skull with right P1 through M3 and left I1 through M3.

Comments—Several of the diagnostic dental features of *Subhyracodon* are difficult to examine in this specimen owing to the advance wear of the premolars. According to

Prothero (2005), the molarization of the P2 distinguishes *Subhyracodon* from the much larger genus *Amphicaenopus*. The size of the molars in BADL 63554 falls well within the size range of *S. occidentalis* (Prothero, 2005) and the skull does not appear to be broad enough or to possess the flared lamboid crest. *Amphicaenopus* is known to sporadically occur in the Chadronian and Whitneyan in South Dakota and questionably in the Arikareean of North Dakota (Prothero 2005). Though the general features of BADL 63554 allow confident referral of this specimen to *Subhyracodon*, we prefer not to refer this specimen to a species based on size alone.

Family EQUIDAE Gray, 1821
MESOHIPPUS Marsh, 1875

Palaeotherium Leidy, 1850c (original description)
Anchitherium Leidy, 1852 (original description)
Miohippus, Marsh, 1874 (in part) (original description)
Mesohippus Marsh, 1875 (original description)
Miohippus Hay, 1902 (in part) (new combination)
Pediohippus Schlaikjer, 1935:141 (in part) (original description)
Mesohippus Prothero and Shubin, 1989:143 (new combination)
Mesohippus MacFadden, 1998:544 (new combination)

MESOHIPPUS sp.

Referred Specimens—BADL 63458, right maxilla fragment with P4 through M3 and associated fragments.

Comments—It is difficult to discern the taxonomic identification of this specimen owing to the advanced wear of the upper dentition. One of the more useful characters for identifying equids from the White River Group is the structure of the hypostyle (Prothero and Shubin, 1989). This specimen lacks the ovate hypostyle described in *M. exoletus* and *Miohippus* (Prothero and Shubin, 1989), supporting referral to the taxon *Mesohippus*. However, referral of this specimen to a specific species of *Mesohippus* is not possible given the highly worn state of the dentition.

Order ARTIODACTYLA Owen, 1848
Family ENTELODONTIDAE Lydekker, 1883
ARCHAEOTHERIUM Leidy, 1850a

Entelodon Aymard, 1846:307 (in part) (original description)
Archaeotherium, Leidy, 1850a:92 (original description)
Arctodon, Leidy, 1851c:275 (original description)
Entelodon Leidy, 1853:392 (original description)
Elotherium Leidy, 1857:175 (new combination)
Pelonax Cope, 1874:504 (original description)
Ammodon Marsh, 1893:409 (in part) (original description)
Archaeotherium Peterson, 1909:47 (new combination)
Megachoerus Troxell, 1920:431 (original description)
Scaptohyus Sinclair, 1921:480 (original description)

Archaeotherium Scott, 1940:379 (new combination)
Archaeotherium Russell, 1980:5 (new combination)
Archaeotherium Effinger, 1998:378 (new combination)
Archaeotherium Foss, 2007:126 Figs.9.5-9.7 (new combination)

ARCHAEOTHERIUM sp.

Referred Specimens—BADL 61622, fragmentary mandible with c1 and p2, partial crown of p3, and additional mandible fragment with dp4; BADL 63457, left maxilla with M1 through M3, associated P3 and other fragments.

Comments—BADL 63457 preserves the molar row in situ, demonstrating the typical quadrate, bunodont, and cusped dentition. The only entelodontid known from the Chadronian–Orellan of the White River Group is *Archaeotherium*. Specimens previously attributed to the taxa *Megachoerus* and *Pelonax* are known from deposits containing Whitneyan taxa, but those taxa were synonymized with *Archaeotherium* by Foss (2007). The referred material is too complete to permit further taxonomic resolution.

Family MERYCOIDODONTIDAE Thorpe, 1923
MERYCOIDODON Leidy, 1848

Merycoidodon Leidy, 1848 (original description)
Oreodon Leidy, 1851a (original description)
Cotylops Leidy, 1851a (original description)
Oreodon Cope, 1884:505 (new combination)
Merycoidodon Thorpe, 1937:45 (new combination)
Prodesmatochoerus Schultz and Falkenbach, 1954:225 (original description)
Otionohyus Schultz and Falkenbach, 1968:106 (original description)
Genetochoerus Schultz and Falkenbach, 1968:134 (original description)
Merycoidodon (*Merycoidodon*) Stevens and Stevens, 1996:514 (new combination)
Prodesmatochoerus Lander, 1998:411 (new combination)
Merycoidodon Stevens and Stevens, 2007:160 (new combination)

MERYCOIDODON CULBERTSONI Leidy, 1848

Merycoidodon culbertsonii Leidy, 1848:48 (original description)
Oreodon priscum Leidy, 1851a:237 (original description)
Cotylops speciosa Leidy, 1851a:239 (original description)
Oreodon robustum Leidy, 1851b:276 (original description)
Oreodon culbertsonii Leidy, 1852:548 (new combination)
Oreodon culbertsonii periculorum Cope, 1884:512 (new combination)
Oreodon macrorhinus Douglass, 1903:163 (original description)
Merycoidodon macrorhinus Douglass, 1907:821 (new combination)

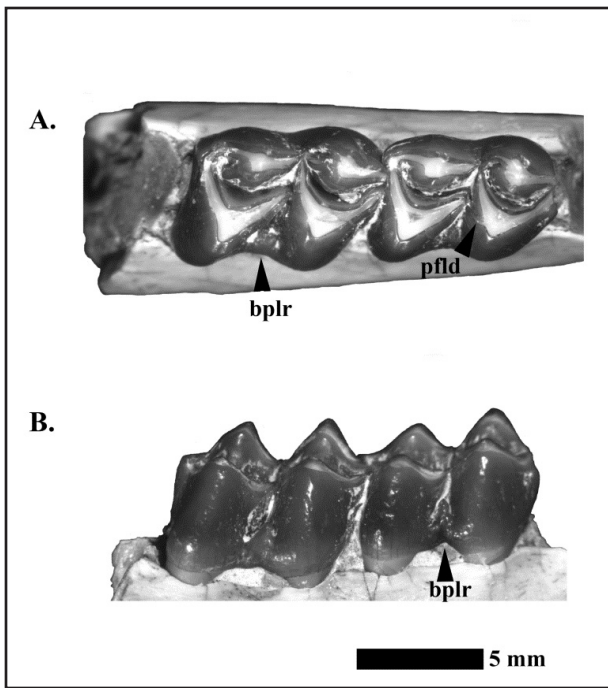


FIGURE 6. Photographs of BADL 63550, *Leptomeryx* sp. indet. right dentary fragment with m1 through m2. **A**, crown view; **B**, labial view. Abbreviations: bplr, buccal pillar (character of *L. speciosus*); pflf, *Palaeomeryx* fold (character of *L. evansi*). Photo by Ed Welsh.

Merycoidodon culbertsonii Thorpe, 1937:47 (new combination)
Merycoidodon culbertsonii periculatorum Thorpe, 1937:55 (new combination)
Merycoidodon lewisi Clark et al., 1967:53 (original description)
Merycoidodon culbertsonii Schultz and Falkenbach, 1968:38 (new combination)
Merycoidodon culbertsonii browni Schultz and Falkenbach, 1968:55 (original description)
Merycoidodon culbertsonii osborni Schultz and Falkenbach, 1968:57 (original description)
Merycoidodon macrorhinus Schultz and Falkenbach, 1968:72 (new combination)
Prodesmatochoerus meekae Schultz and Falkenbach, 1954:226 (original description)
Merycoidodon georgei Schultz and Falkenbach, 1968:86 (original description)
Otionohyus wardi Schultz and Falkenbach, 1968:107 (original description)
Otionohyus vanderpooli Schultz and Falkenbach, 1968:115 (original description)
Otionohyus (Otarohyus) bullatus Schultz and Falkenbach, 1968:118 (in part) (original description)
Genetochoerus (Osbornohyus) norbeckensis Schultz and Falkenbach, 1968:143 (in part) (original description)
Genetochoerus periculatorum Schultz and Falkenbach, 1968:136 (original description)

Merycoidodon Harris 1967:3.

Merycoidodontidae genus and species indeterminate, no. 2 Wilson, 1971:46.

Merycoidodon culbertsonii Prothero 1982:406 (in part).

Merycoidodon culbertsonii Evanoff et al., 1992:123.

Merycoidodon (Merycoidodon) culbertsonii Stevens and Stevens 1996:518, figs. 2-3 (new combination)

Prodesmatochoerus periculatorum periculatorum Lander, 1998:411 (new combination)

Merycoidodon culbertsonii Stevens and Stevens, 2007:160.

Referred Specimens—BADL 63553, nearly complete skull with right and left P1 through M3.

Comments—This skull represents the species *Merycoidodon culbertsonii* as described by Stevens and Stevens (1996). The major feature distinguishing *M. culbertsonii* is the presence of relatively small auditory bullae. Other species of *Merycoidodon* found in the plains (e.g., *M. bullatus* and *M. major*) have significantly inflated auditory bullae, which appear to increase in size in cline with biochronologic time. *M. culbertsonii* differs from the early to middle Chadronian taxon *M. presidioensis* in number of features, including the position of the infraorbital foramen above P3 instead of P2, the lack of a diastema between the P1 and P2, and the relatively small size of M3 (Stevens and Stevens, 1996). The oreodont zonation recognized by previous authors (e.g., Schultz and Falkenbach, 1968; Stevens and Stevens, 1996) may serve as biochronologic indicators in their own right, but do not serve as significant biostratigraphic first appearance or index taxon, since each successive species crosses between the NALMAs recognized within the White River Group.

Family HYPERTAGULIDAE Cope, 1879
HYPERTRAGULUS Cope, 1873d

Leptauchenia Cope, 1873b:7 (original description)

Hypertragulus Cope, 1873d:419 (new combination)

Hypertragulus Scott, 1940:509 (new diagnosis)

Hypertragulus Webb, 1998:470 (new diagnosis)

HYPERTRAGULUS CALCARATUS (Cope, 1873b)

Leptauchenia calcarata Cope, 1873b:7 (original description)

Hypertragulus calcaratus Cope, 1873d:419 (new combination)

Hypertragulus tricostatus Cope, 1873d:419 (original description)

Hypertragulus calcaratus Scott, 1940:521 (new combination)

Referred Specimens—BADL 61903, fragmentary dentary with left m3; BADL 63469, fragmentary right dentary with m3.

Comments—These two specimens display the strong lateral cingulum, conical cusps on the metaconids, and

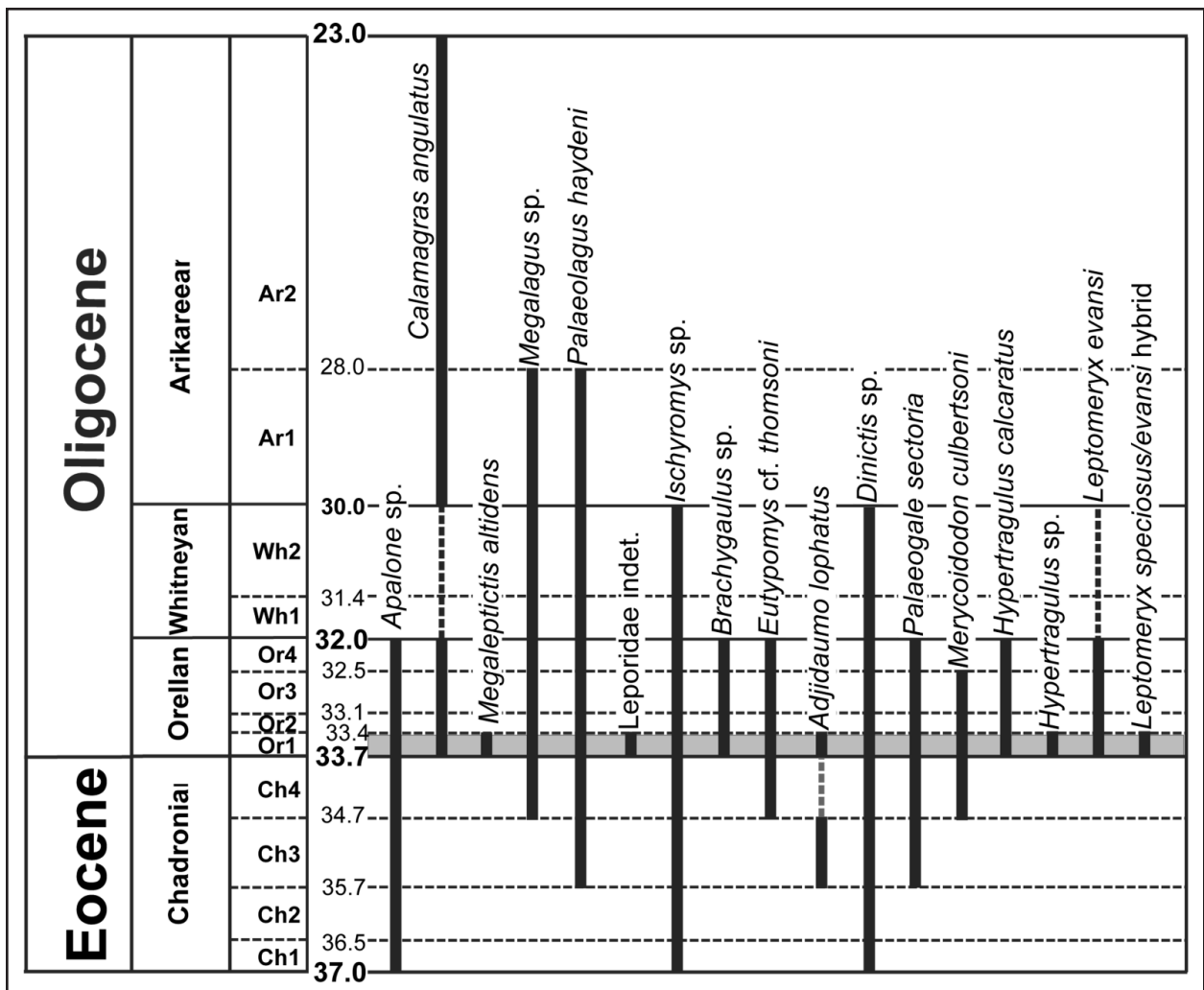


FIGURE 7. Overview of the biostratigraphic distributions of all taxa currently identified from the Bloom Basin local fauna (BADL-LOC-0293). The inferred age of the Bloom Basin local fauna (early Orellan: Or1) is indicated by the horizontal gray bar. The reported age of the Chadronian–Orellan boundary is based on the type section for the *Hypertragulus calcaratus* (Cope, 1873b) Interval Zone in Converse County, Wyoming (Prothero and Whittlesey, 1998) and may not represent the age of this biostratigraphic boundary in the Bloom Basin of South Dakota if the first appearance of *H. calcaratus* is diachronous across different White River locations as suggested by some studies (e.g., Zanazzi et al., 2009). The vertical segmented bars represent gaps in the fossil record.

deep valley between the entoconid and metaconid on the lower molars that diagnose *H. calcaratus* (Zanazzi et al., 2009). Additional specimens recovered from this locality (i.e., BADL 63492 through 63469) are also likely referable to this species, but as they are less complete and given the presence of a second hypertragulid at this locality (see below) we choose to refer those specimens to *Hypertragulidae* indet. at this time.

HYPERTRAGULIDAE gen. et sp. indet.
(Fig. 5)

Referred Specimens—BADL 61620, right partial maxilla fragment with P3-M2 and left dentary fragment with p4-m3.

Diagnosis—BADL 61620 is morphologically similar to *H. calcaratus*, but differs in several key morphologies. The P3 displays a lingual cone reduced to appear more like a small cuspule on the lingual cingulum and the prelabial crista extends farther anteriorly in this specimen. The labial surface of the P3 has a weaker contour in comparison to *Hypertragulus*. The anterior-posterior orientation of the P3 is also angled more labially, where *Hypertragulus* has a more lingually angled P3. In general, the cingula on the upper molars are less pronounced. The M2 of BADL 61620 bears an anterior cingulum, a lingual cingulum situated between the protocone and metaconule, and a reduced posterior cingulum, with no lingual continuations at the protocone or metaconule. *Hypertragulus* has a more complete cingulum that borders the entire lingual area of the

M2 (see Fig. 5 for comparison). The cingula on the lower molars are more pronounced in BADL 61620 in comparison to *H. calcaratus*.

Currently, *H. calcaratus* is the only species of *Hypertragulus* known to occur in the Great Plains region (Webb, 1998; Métais and Vislobokova, 2007). However, confusion exists concerning several species named by Cook (1934) and Frick (1937). Cook (1934) named two additional species of *Hypertragulus*, *H. chadronensis* and *H. crawfordensis*, with both species representing the only known occurrences of the genus from the Chadron Formation at that time. Frick (1937) tentatively named *H. minor* from Nebraska and *H. dakotensis* from the 'Protoceras channels' in South Dakota, but did not describe their variation from *H. calcaratus*. The issue with these taxa is that they are not discussed beyond their holotypical publications, and any recent evaluations of the Hypertragulidae were either unaware of these specimens, or simply inferred synonymy. Therefore, the taxonomic status of these species remains ambiguous until the holotypes are re-examined and their affinities are assessed. On an additional note, the morphology of the upper premolars, with the apparent reduction of the cingula, is approaching the condition seen in the Arikareean hypertragulid *Nanotragulus*. Overall, the morphology of the P3 bears the closest resemblance to *Nanotragulus*, but the cingula on this specimen are not lost entirely, as occurs in *Nanotragulus* (see Lull, 1922:116 Fig. 1). Thus, confident referral of this specimen to a specific hypertragulid taxon is not possible at this time.

Family LEPTOMERYCIDAE Zittel, 1893
LEPTOMERYX Leidy 1853

Leptomeryx Leidy, 1853:394 (original description)
Trimerodus Cope, 1873b:8 (original description)
Leptomeryx Scott, 1940:537 (new combination)

LEPTOMERYX EVANSI Leidy, 1853

Leptomeryx evansi Leidy, 1853:394 (original description)
Trimerodus cedrensis Cope, 1873b:8 (original description)
Leptomeryx lenis Cook, 1934:154 (original description)
Leptomeryx evasni Scott, 1940:553 (new combination)
Leptomeryx evansi Heaton and Emry, 1996 (new combination)
Leptomeryx evansi Korth and Diamond, 2002 (new combination)

Referred Specimens—BADL61901, nine dentary fragments including a right p4 through m2, right m1 through m3, right m1 through m2, right m2, right m2, right unidentified lower molar, left m1 through m2, and left m1 (broken) through m2; BADL 63526, left dentary fragment with erupting m3; BADL 63527, fragmentary, unidentified left lower molar; BADL 63528, right dentary fragment with m1 through m2; BADL 63529, left dentary fragment with m3; BADL 63530, left dentary fragment with m1

through m3 (m1 broken); BADL 63531, right dentary fragment with unidentified molar; BADL 63532, left dentary fragment with p4 through m2 (m2 broken); BADL 63533, unidentified left lower molar; BADL 63534, unidentified left lower molar; BADL 63535, left dentary with unidentified molar; BADL 63536, right dentary fragment with unidentified molar; BADL 63537, left dentary fragment with unidentified molar; BADL 63538, left dentary fragment with unidentified molar; BADL 63539, right dentary fragment with unidentified molar; BADL 63540, right dentary fragment with unidentified molar; BADL 63541, left dentary fragment with m2 through m3; BADL 63542, right dentary fragment with p4 through m1; BADL 63543, right dentary fragment with m2 through m3; BADL 63544, right dentary fragment with dp4 (broken); BADL 63545, right dentary fragment with m1 through m2 (broken); BADL 63546, right dentary fragment with m3 (broken).

Comments—All specimens here attributed to *L. evansi* display the longitudinal crenulations on the metaconid and entoconid, and the distinctive 'Palaeomeryx fold' extending from the protoconid towards the hypoconid that are diagnostic of this taxon (Zanazzi et al., 2009). Numerous other leptomerycid specimens were collected that cannot be referred to the species level given the presence of two different leptomerycid morphs at this locality (see below).

LEPTOMERYX sp.
(Fig. 6)

Referred Specimens—BADL61902, right dentary fragment with m3 and left dentary fragment with m1-3; BADL 63552, right dentary fragments with p2 and p4 through m2; BADL 63550, right dentary fragment with m1 through m2; BADL 63549, right dentary fragment with broken m3; BADL 63551, right dentary fragment with unidentified molar.

Comments—The taxonomic affinities of these specimens remain enigmatic. All specimens display the 'Palaeomeryx fold' diagnostic of *Leptomeryx evansi*, but they also display the buccal pillar (ectostylid) between the protoconid and hypoconid that typifies *Leptomeryx speciosus*, though these features are developed to varying degrees in each specimen. *L. speciosus* is typically only found in late Chadronian faunas; however, only five of the *Leptomeryx* specimens collected from this locality that are identifiable to the specific level display an ectostylid, with the rest all clearly referable to *L. evansi*, which is a characteristic component of Orellan faunas. The significance of presence of this morphologic hybrid at BADL-LOC-0293 is detailed in the Discussion section.

DISCUSSION

Biostratigraphy in the Northern Great Plains

Fossil vertebrates have been frequently documented within the deposits of the Big Badlands of South Dakota since the Hayden expeditions in the mid-1800's. There are

several classic monographs thoroughly documenting the horizons and specimens of the White River Group (e.g. Leidy, 1869; Cope 1883; Osborn and Wortman, 1894; Scott, 1940) due to the massive collections derived from the highly productive beds in the area that is now situated in and around Badlands National Park. The information compiled from these collections aided in establishing the North American Land Mammal Age (NALMA) system proposed by Wood et al. (1941). This biochronologic schema was founded on collections and literature-based information. However, there were no comprehensive local faunas established at that time, because older collections were not locality-based. These systems were horizon-based, following the conventions of Wortman (1893), Matthew (1899), Wanless (1923), and other published works. The problem was that these faunal divisions were based on lithostratigraphic divisions, which makes the assumption that lithologic facies and paleofaunas are biochronologically and biogeographically conformable. This assumption is exemplified by the use of classic faunal terminology based on geographically restricted lithologic facies such as the “*Protoceras* Channels” and “*Metamynodon* Channels” (e.g., Wanless, 1923). The namesake taxa for these zones are rarely found outside their respective and exclusive river channel facies, making them poor biostratigraphic index taxa unless they are associated with extensive, well-described local faunas that facilitate broader correlations.

The issues regarding lithologic disconformities were addressed by the work of Schultz and Stout (1955), who subdivided the White River formations in Nebraska while correlating local units from Toadstool to Scottsbluff. Shortly afterwards, Bump (1956) established different classifications of similar subdivisions in South Dakota based on the geographic disparity and lithologic dissimilarities. Schultz and Stout (1955) stated that these disconformities would likely be resolved by correlating the oreodonts zones that would later be established by Schultz and Falkenbach (1968). Again, this work did not correct, but perpetuated earlier difficulties because of the continued endorsement of fauna-defined stratigraphy. Extensive lithostratigraphic revisions by Terry (1998), Terry and LaGarry (1998), and LaGarry (1998) replaced the antiquated fauna-defined stratigraphy from Schultz and Stout’s (1955) classic “Roundtop to Adelia” section.

The foundation of biochronologic units was facilitated after researchers began assessing lithology independent of biochronology. Formerly, the Chadron–Brule lithostratigraphic contact and the Chadronian–Orellan biochronological transition were defined by the last appearance of brontotheriids, as categorized by Wood et al. (1941). However, brontotheriids were discovered above the Purplish White Layer in Wyoming (PWL: Prothero and Whittlesey, 1998), which were above the Chadron–Brule/Chadronian–Orellan boundaries of Schultz and Stout (1955). Terry’s (1998) lithostratigraphic revision removed any conflict with those formerly defined boundaries. The disappearance, or last appearance datum (LAD: Walsh, 1998), of a single taxon

is inadequate by itself for biochronologic orientation, so Prothero and Whittlesey (1998) recognized the need for revision of the existing biostratigraphic schema, redefining the Chadronian Orellan boundary at the first appearance datum (FAD: Walsh, 1998) of the hornless ruminant *Hypertragulus calcaratus*. Additionally, that transition is also characterized by the first appearance datum (FAD: Walsh, 1998) of other abundant taxa, including the hornless ruminant *Leptomeryx evansi* and the leporid *Palaeolagus intermedius*, as well as the LADs of several taxa, including brontotheriids (Prothero and Whittlesey, 1998). Subsequent revisions of those biochronologic intervals have also occurred to improve their accuracy and resolution (e.g., Prothero and Emry, 2004). Refined biostratigraphic zones have improved our understanding of faunal succession throughout the North American Cenozoic.

Biostratigraphic Age of the Bloom Basin Local Fauna

Vertebrate fossils are relatively abundant at BADL-LOC-0293 and specimens representing a diverse faunal assemblage have been recovered. Though research focused on elucidating the entirety of the vertebrate fauna at this locality is ongoing, the preliminary faunal list (Table 1) includes taxa previously reported from disparate biochronologic ages (Fig. 7). The rodent *Adjidaumo lophatus* was previously only reported from the Chadronian of Montana (Korth, 2012). The FAD of *Merycoidodon culbertsoni* characterizes the late Chadronian (Prothero and Emry, 2004) and this taxon persists into the late Orellan before being replaced by *M. bullatus* in that taxon’s corresponding zone (Prothero and Emry, 2004; Stevens and Stevens, 1996). Clarity is provided via the identification of specimens of *L. evansi* and *H. calcaratus* at this locality, which are characteristic of the Orellan NALMA. The presence of those latter two taxa confirms that the Bloom Basin local fauna is from the Orellan, not the previously expected Chadronian NALMA, given its position relative to the Bloom Basin limestone bed, which was thought to be at the top of the Chadron Formation, and the recognized unconformity between the Chadron and Brule formations in this area (Prothero and Whittlesey, 1998).

The Orellan biostratigraphic age was subdivided into four parts by Prothero and Whittlesey (1998; see also Prothero and Emry, 2004), which characteristic taxa denoted for each subdivision. These zones are characterized by the FADs of *Hypertragulus calcaratus* (Or1), *Miniochoerus affinis* (Or2), *Miniochoerus gracilis* (Or3), and *Merycoidodon bullatus* (Or4) (Prothero and Whittlesey, 1998; Prothero and Emry, 2004; see also fig. 7). At this time, none of the taxa that characterize the latter three subdivisions are recognized in the Bloom Basin local fauna, indicating that this fauna may correlate with the earliest Orellan biostratigraphic age. This biostratigraphic interval, also referred to as the *Hypertragulus calcaratus* Interval Zone (Prothero and Whittlesey, 1998), is currently unrecognized within South Dakota owing to the unconformity present in most areas between the Chadron and Brule formations

which is estimated to span at least 400,000 years (Prothero and Whittlesey, 1998). That unconformity results in a sudden transition between the Chadronian and Orellan faunas precisely at the contact between the Chadron and Brule Formations within much of South Dakota (Prothero and Emry, 2004). While basing a biostratigraphic assignment on the absence of taxa can be problematic, the pattern of morphological variation observed within *Leptomeryx* specimens collected from BADL-LOC-0293 lends some support to an earliest Orellan age.

The specimens above referred to *Leptomeryx* sp. display a combination of the characters used to differentiate the Chadronian taxon *L. speciosus* and the Orellan taxon *L. evansi*. The dual presence of the ‘*Palaeomeryx* fold’ and an ectostylid on the lower molar is also observed within the Chadron and Brule sections in Douglass, Wyoming (Heaton and Emry, 1996). Similarly, gradual development and increased prominence of the ‘*Palaeomeryx* fold’ in stratigraphically controlled specimens of *Leptomeryx* across the Chadronian–Orellan transition in Toadstool Park, Nebraska (Zanazzi et al., 2009). These observations support the hypothesis proposed by Heaton and Emry (1996) that *L. speciosus* and *L. evansi* represent a chronospecies that demonstrates anagenesis across the Chadronian–Orellan transition. The presence of this transitional form supports the conclusion that the Bloom Basin local fauna is an earliest Orellan fauna situated very close, but subsequent to the termination of the Chadronian–Orellan transition.

Implications for the Age and Stratigraphic Position of the Bloom Basin Limestone Bed

The Bloom Basin limestone bed is traditionally placed either at the Chadron–Brule contact, or within the uppermost Chadron Formation (Welzenbach, 1992; Benton and Reardon, 2006). Between South Dakota and Nebraska collectively, the Chadron Formation is subdivided into four members that are positioned from oldest to youngest as follows: Ahern, Crazy Johnson, Peanut Peak, and Big Cottonwood Creek (Terry, 1998; Terry and LaGarry, 1998). Within South Dakota, an unconformity is recognized between the Chadron and Brule formations (Terry, 1998; Prothero and Whittlesey, 1998), and sediments correlative with the Big Cottonwood Creek Member are considered to be absent (Terry, 1998; Terry and LaGarry, 1998; Prothero and Emry, 2004). This observation is based largely on surveys conducted in the South Unit of Badlands National Park and within the Kudrna Basin and Sage Creek Wilderness Area within the North Unit of the park (e.g., Terry, 1998; Evanoff et al., 2010). However, Terry (1998) suggested that the Big Cottonwood Creek Member in northwestern Nebraska may be temporally equivalent with the BBLB and other lacustrine limestones near the top of the Chadron Formation within South Dakota. Little work has been done on the stratigraphy within the more northerly positioned Bloom Basin aside from studies directly dealing with the BBLB (e.g., Welzenbach, 1992; Evans and Welzenbach, 1998), and much of that work was completed

prior to the formal recognition and description of the Big Cottonwood Creek Member by Terry and LaGarry (1998).

In northwest Nebraska, the closest geographic region with a relatively complete record of this time span, the Chadronian–Orellan boundary is set at two ± five meters above the “upper purplish white layer” (UPW; Zanazzi et al., 2009). The upper boundary of the Big Cottonwood Creek Member in northwest Nebraska is placed nine to ten meters above the UPW (Terry and LaGarry, 1998), meaning that in Nebraska the transition between the Chadronian and Orellan NALMAs occurs within that member of the Chadron Formation and not at the boundary between the Chadron and Brule Formations. These data suggest that the Chadronian–Orellan boundary may be located within the upper Chadron Formation in South Dakota if a complete stratigraphic section were preserved. Therefore, recognition of an earliest Orellan fauna situated below the BBLB would not necessarily contradict prior placement of the BBLB within the uppermost Chadron Formation or at the Chadron–Brule contact. However, that placement would require the sediments containing the Bloom Basin local fauna to be correlative with the Big Cottonwood Creek Member of Nebraska. Alternatively, the age of the Bloom Basin local fauna may indicate that the BBLB is positioned stratigraphically higher than previously proposed, within the Scenic Member of the Brule Formation. At the moment, the detailed sedimentological and stratigraphic data required to evaluate these conflicting hypotheses is lacking, though this work is currently in progress.

The position of an earliest Orellan fauna below the BBLB is also in agreement with prior faunal studies of the BBLB itself. In the original description of the BBLB, Welzenbach (1992) reported that the ostracod fauna was indicative of the early Oligocene and noted the presence of the gastropod taxon *Planorbis*, which is known from the Oligocene to the Recent. No definitively Eocene taxa were reported. Thus, the inferred ages of both the Bloom Basin local fauna and that of the Bloom Basin limestone bed itself are perfectly compatible.

CONCLUSION

Erosion is a powerful force that is constantly transforming the landscape and changing the distribution and density of exposed paleontological resources. In large management units, it is not feasible for resource managers to maintain perfectly up-to-date inventories of paleontological resources under these ever-changing conditions, regardless of how often those resources are surveyed. Thus, paleontological monitoring of high-impact activities is an irreplaceable tool for maintaining the integrity of the resource and ensuring significant scientific data and irreplaceable aspects of our national heritage are protected and conserved. This report highlights the scientific benefits of such programs. Had it not been for paleontological monitoring of fencing work at Badlands National Park, this significant fauna would remain unreported, our understanding of the age and stratigraphic position of the Bloom

Basin limestone bed would be diminished, and important paleontological resources could have been damaged or lost. While maintaining the integral assets of a park (e.g., roads and fences) is a significant priority, it cannot come at the expense of the resources that the park was originally designated to protect. The implementation of paleontological monitoring activities bridges the gap between the need to construct and maintain park assets and the duty to follow the park's primary mission: protection of the natural resources.

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