STRATIGRAPHIC AND TAXONOMIC REVISION OF A NORTH AMERICAN FALSE SABER-TOOTHED CAT CUB

Ed Welsh[1,*], Clint A. Boyd[2], Kurt Spearing[3], and Paul Z. Barrett[4]
[1]Badlands National Park
Interior, SD 57750
[2]North Dakota Geological Survey
Bismarck, ND 58505
[3]Morningside College
Sioux City, IA 51106
[4]South Dakota School of Mines and Technology
Rapid City, SD 57701
*Corresponding author email: edtwelsh@hotmail.com

ABSTRACT

Specimen F:AM 99259, a well-preserved skull with articulated dentaries representing the earliest ontogenetic stage of development yet observed for a North American nimravid, is occasionally mentioned in the scientific literature. Conflicting reports refer that specimen to either *Eusmilus* or *Nimravus*, with no evidence provided to support those referrals. Examination of specimen F:AM 99259 supports its referral to *Nimravus brachyops* based on the absence of a metaconid on the unerupted m1. The stratigraphic position of specimen F:AM 99259 was reported as the Chadron Formation of Niobrara County, Wyoming, which would represent the earliest North American occurrence of *Nimravus.* However, the geographic position is reported as the first draw east of Robertson Draw, which corresponds with the location of the Little Muddy Creek fossil locality. At least 182 specimens within the collections of the American Museum of Natural History were recovered from that locality, including specimens of *Palaeocastor*, *Diceratherium*, *Mesoreodon*, *Sespia*, and *Pseudolabis*. Additionally, matrix affixed to F:AM 99259 does not match the typically volcanic-rich, uranium-bearing sediments of the Chadron Formation; rather, those sediments are more consistent with the sandstones of the stratigraphically higher Gering Formation, which is reported at Little Muddy Creek. These two lines of evidence support an aarly to middle Arikareean "age" for F:AM 99259, well within the previously reported range of that taxon. Given the basal position of *N. brachyops* within Nimravidae, this specimen provides important insights into the early evolution of saber-toothed features within this clade.

Keywords

Arikareean, Chadron, Gering, *Eusmilus*, Monroe Creek, Nimravidae, *Nimravus*

INTRODUCTION

The Nimravidae comprise a well-studied family of feliform carnivores that existed from the late Eocene through the Oligocene, spanning a wide biogeographical range throughout Eurasia and North America. Despite the numerous specimens curated in museum collections, there is a distinct paucity of known material from specimens representing the earliest ontogenetic stages. Only a handful of very young individuals are described (Bryant 1988; Peigné and de Bonis 2003), making the discovery of new, immature specimens significant.

One of the youngest nimravid specimens yet discovered from North America is F:AM 99259. Previous studies referred that specimen to either *Eusmilus* (Holliday and Steppan 2004; Holliday 2010) or *Nimravus* (Peigné and de Bonis 2003), though no study provides character evidence for these referrals. All of those studies reported the provenance of F:AM 99259 as the Chadron Formation, but the significance of that proposed stratigraphic position was never discussed (Holiday 2010; Holiday and Steppan 2004; Peigné and de Bonis 2003). *Nimravus* is represented in the late Eocene of Eurasia with *Nimravus intermedius*, but the taxon does not appear in North America until the early Oligocene; *Nimravus brachyops* has its first appearance sometime during the Whitneyan North American Land Mammal Age (NALMA) (Prothero and Whittlesey 1998). Thus, the discovery of a specimen of *Nimravus* from the late Eocene of North America would be significant, making the North American and Eurasian first appearances of this taxon synchronous.

This study has two primary goals. The first is to clarify the taxonomic affinities of F:AM 99259. The second is to resolve the stratigraphic position and approximate age of F:AM 99259. The former goal was addressed via extensive examination of the specimen to identify diagnostic characters and comparison to the results of a recent taxonomic revision of the clade (i.e., Barrett 2015). The latter goal was approached in two ways. The lithology of the matrix preserved on the specimen was examined and compared to samples and published descriptions of sediments from the White River Group and the younger Arikaree Group. A biochronologic study was also conducted by compiling a list of taxa reported from the same geographic area as F:AM 99259 and comparing their known stratigraphic ranges to determine a set of NALMAs to which this specimen could possibly be referred. Answering these questions is key to clarifying the scientific importance of this specimen and its role in understanding nimravid ontogeny and the timing and pattern of biogeographic dispersal within the clade.

Abbreviations—BADL, Badlands National Park, South Dakota, U.S.A.; F:AM, Frick collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York, U.S.A.; FSP, collections of palaeontology, Faculté des Sciences Fondamentales et Appliquées, Université de Poitiers, Poitiers, France; SDSM, South Dakota School of Mines and Technology Museum of Geology, South Dakota, U.S.A.

Stratigraphic position of F:AM 99259—The exact geographic location where F:AM 99259 was collected is unclear, but data recorded with the specimen indicate that it was collected in the general vicinity of the previously well-known and heavily collected Little Muddy Creek area in Niobrara County, Wyoming (Figure

1). Previous publications report that F:AM 99259 was collected from the Chadron Formation (Holiday 2010; Holiday and Steppan 2004; Peigné and de Bonis 2003). The matrix encasing F:AM 99259 consists of a brown, medium-grained sandstone, which is not consistent with the typical clays and sand channels of the Chadron Formation in the Great Plains region. White River Group sandstones are typically greenish in color. The lowest sandstones in the White River Badlands, situated above the Interior Paleosol, are the greenish-white sediments of the "blazing white" sandstone of the Ahearn Member of the Chadron Formation (Clark et al. 1967; Terry 1998). The remaining sandstones of the Chadron Formation are greenish-gray and are found in the type area of the "*Titanotherium* Sandstone" (Osborn 1929; Harksen and Macdonald 1969). However, the brown or brownish-gray sandstone preserved on F:AM 99259 is more consistent with the Gering, Monroe Creek, and Harrison formations (Schultz and Stout 1955; Swinehart et al. 1985). Schultz and Falkenbach (1968) provided a generalized overview of the stratigraphy at Little Muddy Creek, identifying the presence of the upper portion of the Gering Formation and the lower portion of the Monroe Creek Formation. The difficulty of differentiating these beds outside of a few localized sections resulted in the current designation of these formations in the northern Nebraska Panhandle and Wyoming as undifferentiated Arikaree Group

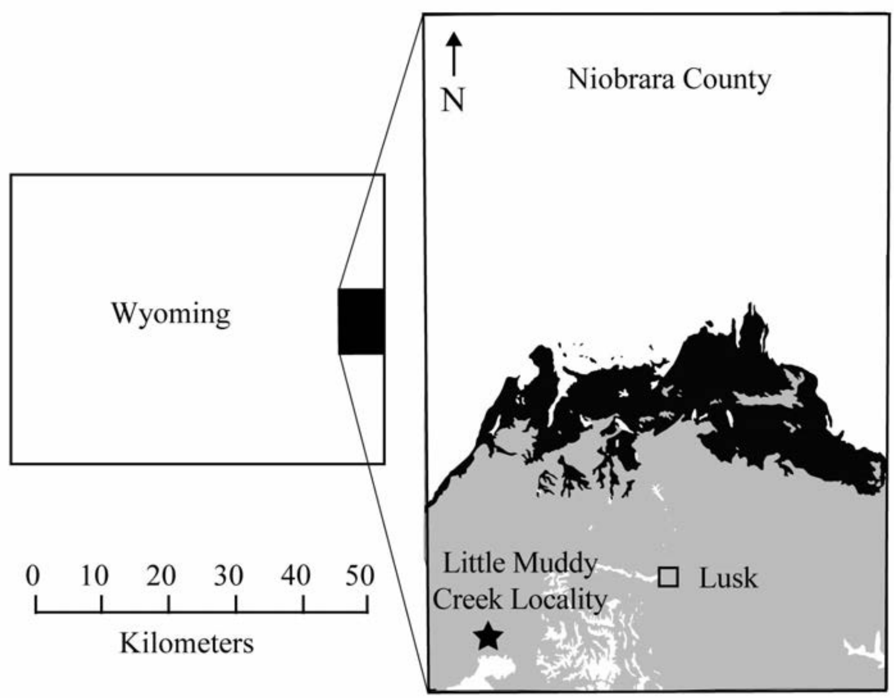

Figure 1. Map showing the location of the Little Muddy Creek area (black star) in relation to exposures of the White River (black) and Arikaree (grey) groups in Niobrara County, Wyoming. All other geologic units in Niobrara County shaded white. Scale bar is for Niobrara County.

(LaGarry 1998). Alternatively, the uppermost Brule Formation of northwestern Nebraska consists of pinkish-tan claystones and siltstones (LaGarry 1998). Given these differences, the sediment preserved on F:AM 99259 is consistent with referral to the Arikaree Group and not the White River Group.

Little Muddy Creek Local Fauna—The fauna recovered from the Little Muddy Creek area of Wyoming has been described in numerous studies, and portions of the fauna have been re-examined and synonymized over the years. For this study, a comprehensive faunal list was assembled for the Little Muddy Creek area, and the stratigraphic ranges of those taxa were compiled based on reports in the published literature in correlation with NALMA biochronologic divisions under the conventions of Woodburne (2004) and Janis et al. (2008). Those results are presented in Figures 2 and 3 and are summarized below.

The rodents of the Little Muddy Creek area are almost entirely Arikareean forms. Wahlert (1983) described the presence of the florentiamyids *Sanctimus stouti*, *Sanctimus simonsi*, *Florentiamys kennethi* (a synonym of *S. stuartae*; Korth 1992), *Florentiamys kingi* (a synonym of *F. loomisi*; Korth 1992), and *Florentiamys kinseyi*. *Sanctimus stouti* and *S. simonsi* are restricted to biochron Ar2, while *S. stuartae* and *F. kinseyi* are restricted to biochron Ar1 (Flynn et al. 2008). Xu (1996) also reported the presence of *Capacikala parvus* and *Capacikala gradatus*, both of which are known from the Arikareean.

The morphologic trends of oreodonts (Merycoidodontidae) have proven to be useful in understanding middle Cenozoic biochronology (Stevens and Stevens 1996, 2007). Though Schultz and Falkenbach (1954, 1968) described numerous merycoidodontids from the Little Muddy Creek area, many of those taxa were eventually restudied and reclassified (Lander 1998; Hoffman and Prothero 2004; Prothero and Sanchez 2008; Stevens and Stevens 1996, 2007). Most of the Little Muddy Creek oreodonts, which are largely represented by members of the Desmatochoerinae and Leptaucheniinae, are characteristically Arikareean taxa, including *Mesoreodon minor*, *Desmatochoerus megalodon*, *Promerycochoerus superbus*, *Sespia nitida*, and *Sespia ultima*. *Leptauchenia decora*, *Leptauchenia major*, and *Leptauchenia lullianus* are also present at Little Muddy Creek, but only *L. lullianus* has a strictly Arikareean record (Schultz and Falkenbach 1968; Prothero and Sanchez 2008).

The only carnivoramorphs previously described from Little Muddy Creek are canids. Wang's (1994) study of the Hesperocyoninae included specimens of *Ectopocynus antiquus*, *Ectopocynus intermedius*, *Enhydrocyon pahinsintewakpa*, and *Philotrox condoni* from the area. Wang et al. (1999) reported the presence of the borophagines *Archaeocyon leptodus*, *Phlaocyon minor*, and *Otarocyon cooki* from the Little Muddy Creek area. Only *E. antiquus* and *A. leptodus* are also reported elsewhere from Whitneyan faunas, while the remaining taxa are restricted to the Arikareean (Figure 2). Specimen F:AM 99259 represents a new addition to the carnivoran component of the Little Muddy Creek local fauna.

Overall, the majority of the taxa reported from the Little Muddy Creek area are elsewhere reported only from early Arikareean faunas, although a handful of those taxa are also reported from the late Whitneyan (Figures 2 and 3). The only taxon reported from this area that has a reported distribution restricted to the Whitneyan is *Merycoidodon major* (Stevens and Stevens 2007). Assuming this identification is correct, it suggests that some upper Brule Formation sediments may be exposed in the Little Muddy Creek area. Alternatively, if Chadron Formation sediments were exposed in that area, the presence of typical Chadronian-Orellan taxa would be expected from the collection area (e.g., *Agnotocastor*, *Trigonias*, *Subhyracodon*, *Poebrotherium*, *Hesperocyon gregarius*, *Merycoidodon culbertsoni*, etc.).

Given the evidence presented above, F:AM 99259 is likely part of an Arikareean age fauna. This conclusion is supported by prior reports that specimens collected in the Little Muddy Creek area were recovered from the Monroe Creek Formation (e.g., Schultz and Falkenbach 1968).

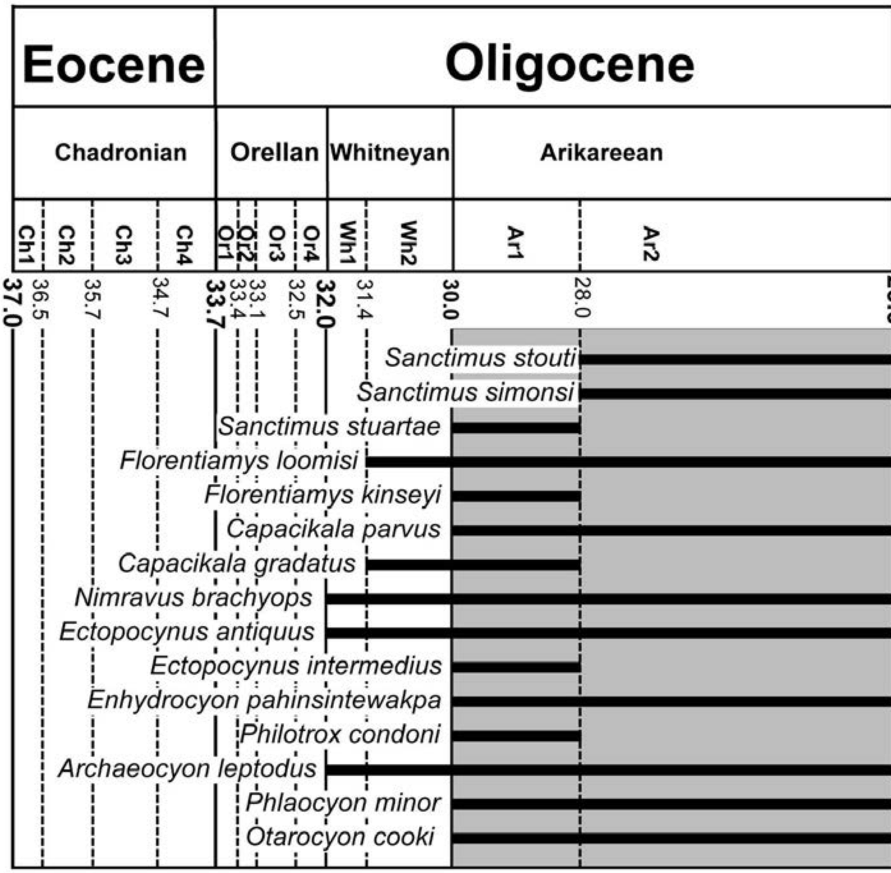

Figure 2. Little Muddy Creek local fauna, Part 1. Diagram displaying known biochronologic ranges of rodent and carnivore taxa previously described from the Little Muddy Creek site and the ranges of each known taxa (Bryant 1996; Flynn et al. 2008; Flynn and Jacobs 2008; Korth 1992; Martin 1998; Wahlert 1983; Wang 1994; Wang et al. 1999; Xu 1996). Gray area represents the biostratigraphic zones previously recognized in the area.

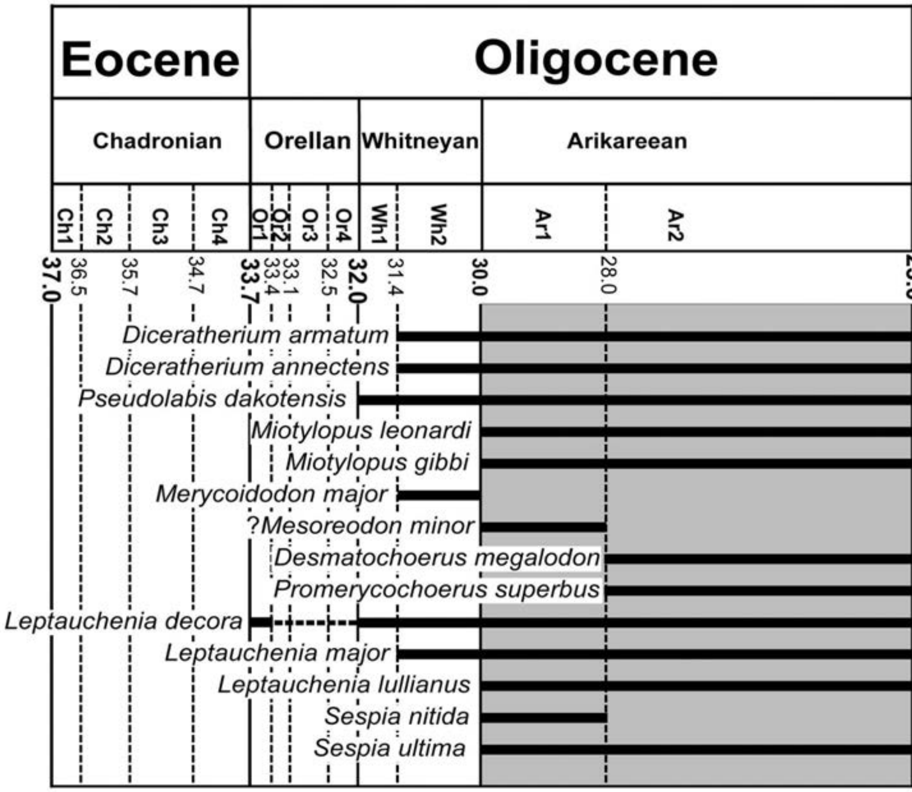

Figure 3. Little Muddy Creek local fauna, Part 2. Diagram displaying known biochronologic ranges of ungulates previously described from the Little Muddy Creek site and the ranges of each known taxa (Hoffman and Prothero 2004; Hone et al. 1998; Lander 1998; Prothero 1996; Prothero 1998; Prothero 2005; Prothero and Sanchez 2008; Schultz and Falkenbach 1954, 1968; Stevens and Stevens 2007). Gray area represents the biostratigraphic zones previously recognized in the area.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1785
Order CARNIVORA Bowdich, 1821
Suborder FELIFORMIA Kretzoi, 1945
Family NIMRAVIDAE Cope, 1880
Nimravus Cope 1879

Type species—*Nimravus brachyops* (Cope 1878)

Other Included Species—*Nimravus intermedius* (Filhol 1872)

Diagnosis—The following revised differential diagnosis is taken directly from Barrett (2015:116-117): “Sutural contact between the lacrimal and jugal; presence of lateral and medial fossae on the zygomata; broadly circular zygomata in dorsal view; presence of discrete petrobasilar and posterior lacerate foramina; postglenoid foramen present; nasals extend posterior to the maxillofrontal suture;

reduced mastoid with large plate-like paroccipital process; posterior lip of the glenoid socket projects more ventrally than anterior lip; oblique angle between the braincase and axial plane of the cranium; horizontally projecting postorbital process of frontal; posteriorly orientated posterior border of coronoid process; no genial flange, but the ventral rim of the chin is distinctly angulate; presence of fossa on ventral face of chin; spatulated incisors, with accessory denticules especially on the lower incisors, I3 slightly caniniform and distinctly larger than the other incisors; mesial-distal length of C1 less than that of P4; ratio of height of P3 to P4, 0.71 and greater; parastyle absent from P4; P4 protocone reduced, short, crest-like; M1 transversely reduced, crest-like, with low cusps and near absent to absent protocone; lower incisor arcade not or little curved, so as i1 is not visible in lateral view; p3 height is as tall or slightly taller than p4; anterior cusp on p4 mesially/distally longer than the posterior cusp; p4 as tall as or taller than the paraconid of m1; m1 metaconid absent; trigonid proportion of m1 is 77-87%; serrations absent on adult minimally worn cheek teeth; ratio of tibia to femur 87% and higher; articulation between the calcaneum and navicular present."

Nimravus brachyops (Cope 1878)

Diagnosis—The following differential diagnosis is taken directly from Barrett (2015:119) "A nimravine of moderately large size with basilar length ranging from 159 to 194 mm, mean of 177 mm, [n=9]; lambdoid crest angle ranging from 133 to 146 degrees, mean of 138 degrees, [n=10]; serration density per millimeter on upper canines ranging from 2.2 to 2.3, mean of 2.2, [n=4]; C1 compression ranging from 1.56 to 1.84, mean of 1.74, [n=11]; lacrimal process absent; presence of alveolar torus variable; anterior P3 cusp absent; presence of anterior p3 cusp variable."

Referred Specimen—F:AM 99259: Complete skull and mandible (Figures 4 and 5).

Locality and Horizon of Referred Specimen—Recorded as: "1st DRAW E OF ROBERTSON DRAW WYO." The town name "LUSK" is also written on the skull in two places, referring to the town of that name in Niobrara County, Wyoming. Robertson Draw is located approximately 17.5 miles southwest of Lusk, Wyoming, and 0.5 miles east of Robertson Draw is Little Muddy Creek, which is inferred to be the collection area. The stratigraphic position and age of the specimen is interpreted as: Undifferentiated Arikaree Group (Arikareean; Ar1 or Ar2).

Basis of Referral—Examination of F:AM 99259 reveals the presence of a suite of characters that support the referral of this specimen to *Nimravus brachyops*, including the presence of spatulate incisors, absence of a metaconid on the exposed adult m1, and the presence of a fossa on the ventrointernal face of the zygomatic arch below the postorbital process.

Comments—Peigné and de Bonis (2003) described a juvenile skull and jaws referred to the Hoplophoneini (FSP-ITD 342) from the Phosphorites du Quercy, France. Specimen F:AM 99259 appears to share a similar ontogenetic age with FSP-ITD 342, approximately 5-6 months of age (Peigné and de Bonis 2003). There are some clear contrasts between the two specimens that also distinguish F:AM 99259 from members of the Hoplophoneini, including a relatively uninflated infraorbital foramen, lack of a glenial phlange on the dentary, and the presence of a relatively large talonid on dp4. The relative size and morphology of the lower and upper canines are important characters for differentiating nimravids. In basal taxa, like *Nimravus*, the lower canines are substantially larger than the adjacent lower incisors. Taxa within the Hoplophonini and the infant specimen FSP-ITD 342 display lower canines that are roughly the same size and morphology as the adjacent lower incisors. Another trend in nimravid canine morphology is the increased serration density of the adult upper canines from relatively coarse serrations in shorter canines, as observed in *Nimravus*, to fine and condensed serrations in enlarged canines, as observed in the Hoplophoneini

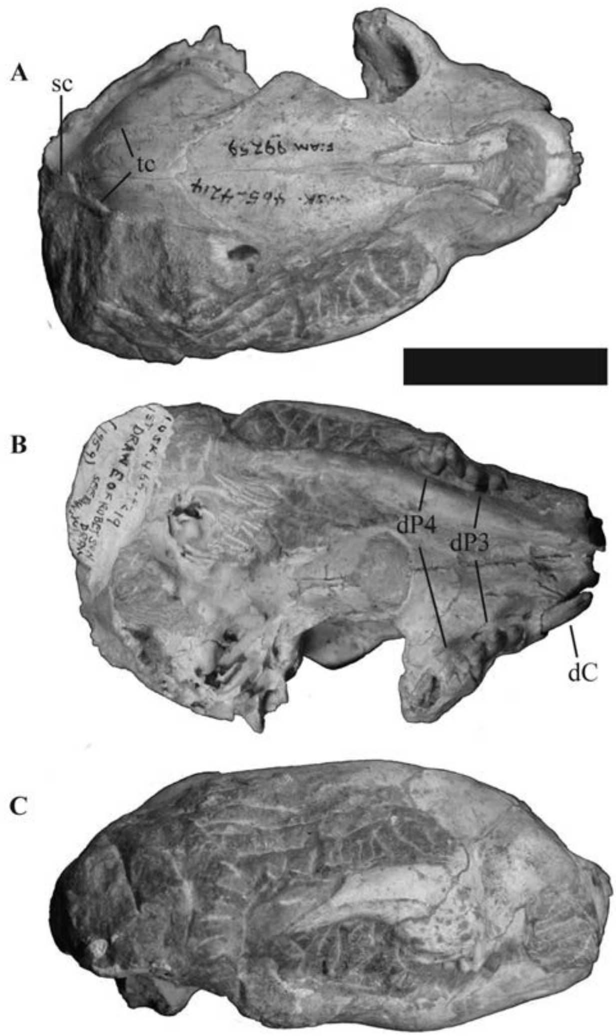

Figure 4. Skull of F:AM 99259 in A) dorsal, B) ventral, and C) right lateral views. Saggital crest (sc) and temporal crests (tc) are labeled. Scale bar = 5cm.

(Barrett 2015; Boyd and Welsh 2013). F:AM 99259 exhibits a coarse serration density within the parameters of *Nimravus* (average of 2.0 serrations per millimeter: Barrett 2015). Thus, the overall morphology of F:AM 99259 is consistent with a referral to *Nimravus brachyops*, and not to the hoplophonin taxon *Eusmilus (contra* Holliday and Steppan 2004; Holliday 2010).

Preliminary Overview of Ontogenetic Changes in Nimravus brachyops—A full description of the morphology of F:AM 99259 and a discussion of ontogenetic change within *Nimravus brachyops* will be provided elsewhere, but a few important insights can be made here. Bryant (1988) provided a detailed study of the tooth eruption sequence of *Barbourofelis* in comparison with members of the Nimravidae and Felidae. The nimravids included in that study were *Eusmilus*, *Hoplophoneus*, *Dinictis,* and a brief mention of canine replacement

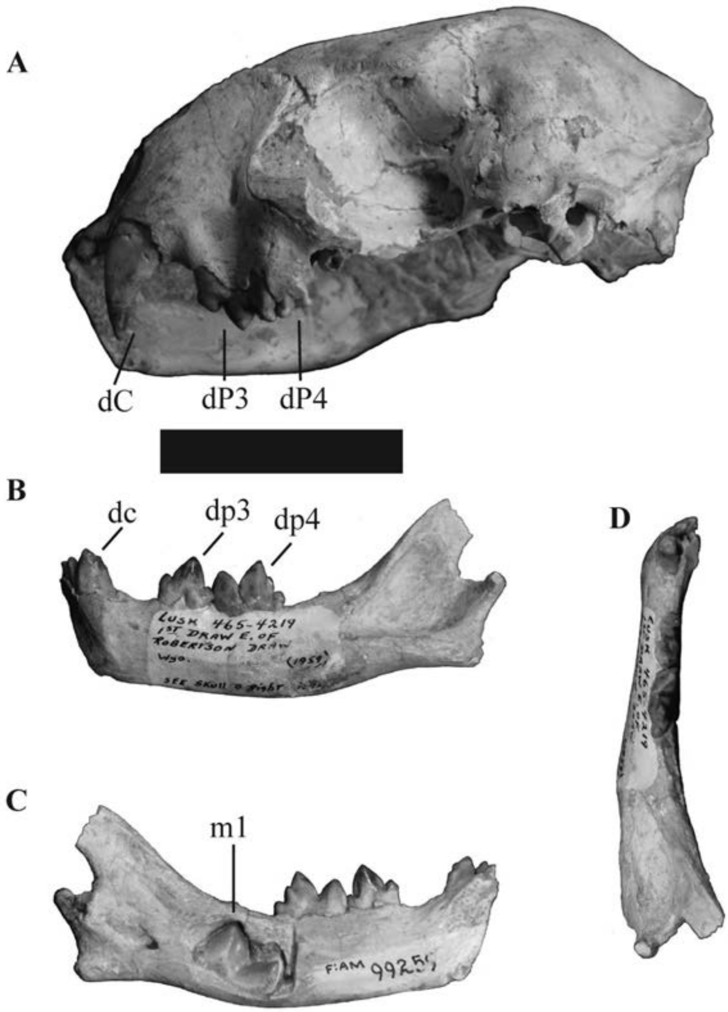

Figure 5. Skull of F:AM 99259 in A) left lateral view, with left dentary in B) labial, C), lingual, and D) occlusal view. Scale bar = 5cm.

in *Nimravus* (Bryant 1988). Bryant (1998) was able to demonstrate that the adult canines were the last teeth to be replaced in *Barbourofelis* and nimravids, as opposed to early canine replacement prior to the P^3 and P_4 in felids. This trend is also demonstrated by a specimen of *Eusmilus villebramarensis* (Peigné and Brunet 2001). Owing to the trend towards brachycephaly in more derived nimravids, compounded by the loss of anterior premolars in many derived taxa (e.g., *Hoplophoneus*), the timing of canine replacement in nimravids that retain the full premolar dentition was previously unclear. Most specimens of *Nimravus* possess a complete upper premolar count, but the presence of a P1 is variable within the taxon. This can also vary between the left and right sides as observed in SDSM348. F:AM 99259 and a handful of specimens from the collections at SDSM provide a thorough view into the dental ontogeny of that taxon, in order from youngest to oldest: F:AM 99259, SDSM 15012, BADL 52047 (= SDSM 12530), and SDSM 348. In those specimens, the upper premolars erupt/are replaced in sequential order from posterior to anterior, P^4 to P^1. P^1 first erupts posterolingual to the canine, as observed in BADL 52047. During elongation of the muzzle, the P^1 migrates posterolaterally, eventually being positioned posterior to the C as observed in SDSM 348. The adult upper canine is indeed the last tooth to erupt, following the full eruption of the upper premolars.

Also of note, the cranium of F:AM 99259 possesses laterally expanded or lyrate temporal crests that converge and join near the posterior end of the skull. During ontogeny, the temporal crests reduce anteromedially as the sagittal crest forms, relocating the temporal crest junction to the fronto-parietal suture, as observed in other adult nimravids.

CONCLUSIONS

Specimen F:AM 99259 represents the earliest ontogenetic stage of development yet reported for the nimravid taxon *Nimravus* based on the clear morphologic contrast of the canines and the dentary when compared to contemporaneous hoplophonins, confirming the interpretation provided by Peigné and de Bonis (2003). Matrix appended to the specimen best matches with Arikaree Group sandstones and sharply contrasts with White River Group sandstones. The faunal constituents in the Robertson Draw and Little Muddy Creek area are almost entirely representative of the Arikareean NALMA, which remains consistent with previous interpretations of the stratigraphy by Schultz and Falkenbach (1968).

The present study was focused on identifying the provenance and taxonomic affinities of F:AM 99259. Further research is underway on this and other specimens to describe in detail the series of ontogenetic changes that occur from infancy to adulthood in *Nimravus brachyops*, since no other juvenile or infant specimens are thoroughly described. Once that information is compiled, comparisons to known ontogenetic series for other nimravid taxa can be made and broad trends in the ontogenetic development of nimravids can be understood. These comparisons will also reveal any impact heterochrony had on the evolution of nimravids, particularly in the transition from the basally-placed scimitar-toothed forms to the derived dirk-toothed taxa.

LITERATURE CITED

Barrett, P. 2015. Valid Species and Sub-Family Relationships of the North American Nimravidae (Mammalia: Carnivora). MS Thesis (unpublished). South Dakota School of Mines and Technology, Rapid City, South Dakota.

Boyd, C.A., and E. Welsh. 2013. Investigating the Taxonomic Utility of Serration Density on the Canines of North American Nimravid Feliforms (Poster): In Geological Society of America Annual Meeting, Denver, CO.

Bryant, H.N. 1988. Delayed Eruption of the Deciduous Upper Canine in the Sabertoothed Carnivore Barbourofelislovei (Carnivora, Nimravidae). Journal of Vertebrate Paleontology 8:295-306

Bryant, H.N. 1996. Nimravidae. Pages 453-475 in Prothero D.R., R. Prothero and R.J. Emry, editors. The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, Cambridge, UK.

Clark, J., J.R. Beerbower, and K.K. Kietzke. 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota. Field Museum of Natural History, Fieldiana Geology Memoirs 5:1-158.

Cope, E.D. 1878. On some of the characters of the Miocene fauna of Oregon. Proceedings of the American Philosophical Society, 18:63-78.

Cope, E.D. 1879. On the genera of Felidae and Canidae. Proceedings of the Academy of Natural Sciences, Philadelphia 31:168–194.

Cope, E.D. 1880. On the extinct cats of America. American Naturalist 14:833-858.

Filhol, H. 1872. Note relative à la découverte dans les gisements de phosphate de chaux du Lot d'un mammifère fossile nouveau. Bulletin de la Société des Sciences Physiques et Naturelles, Toulouse 1:205-208.

Flynn, L.J., and L.L. Jacobs. 2008. Castoroidea. Pages. 391-405 in C.M. Janis, G.F. Gunnell, and M.D. Uhen, editors. Evolution of Tertiary Mammals of North America. Volume 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge, UK.

Flynn, L.J., E.H. Lindsay, and R.A. Martin. 2008. Geomopha. Pages 428-455 in C.M. Janis, G. F. Gunnell, and M.D. Uhen, editors. Evolution of Tertiary Mammals of North America Volume 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge, UK.

Harksen, J.C. and J.R. Macdonald. 1969. Type sections for the Chadron and Brule Formations of the White River Oligocene in the Big Badlands of South Dakota. South Dakota Geological Survey Report of Investigations 99:1-23.

Hoffman, J.M., and D.R. Prothero. 2004. Revision of the Late Oligocene Dwarfed Leptaucheniine Oreodont Sespia (Mammalia: Artiodactyla). New Mexico Museum of Natural History and Science Bulletin 26: 155-164.

Holiday, J.A. 2010. Evolution in Carnivora: identifying a morphological bias. Pages 189-224 in A. Goswami and A. Friscia, editors. Carnivoran evolution: new views on phylogeny, form and function. Cambridge University Press, Cambridge, UK.

Holiday, J.A. and S.J. Steppan. 2004. Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. Paleobiology 30:108-128.

Hone, J.G., J.A. Harrison, D.R. Prothero, and M.S. Stevens. 1998. Camelidae. Pages 439-462 in C.M. Janis, K.M. Scott, and L.L. Jacobs, editors. Evolution of Tertiary Mammals of North America Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, UK.

Janis, C.M., G.F. Gunnell, and M.D. Uhen. 2008. Introduction. Pages 1-6 in C.M. Janis, G.F. Gunnell, and M.D. Uhen, editors. Evolution of Tertiary Mammals of North America Volume 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge, UK.

Korth, W.W. 1992. Small mammals from the Harrison Formation (late Arikareean, early Miocene), Cherry County, Nebraska. Annals of Carnegie Museum 61:69–131.

Kretzoi, M. 1929. Materialien zur phylogenetischen Klassifikation der Aeluroideen. 10th International Congress of Zoology 1293-1355.

LaGarry, H.E. 1998. Lithostratigraphic revision and re-description of the Brule Formation (White River Group) of northwestern Nebraska. Geological Society of America Special Paper 325: 63-91.

Lander, B. 1998. Oreodontoidea. Pages 574-580 in C.M. Janis, K.M. Scott, and L.L. Jacobs, editors. Evolution of Tertiary Mammals of North America. Cambridge University Press, Cambridge, UK.

Martin, LD. 1998. Nimravidae. Pages 228-242 in C.M. Janis, K.M. Scott, and L.L. Jacobs, editors. Evolution of Tertiary Mammals of North America Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, UK.

Osborn, H.F. 1929. Titanotheres of ancient Wyoming, Dakota, and Nebraska. U.S. Geological Survey Monography 55:1-953.

Peigné, S., and M. Brunet. 2001. Une nouvelle espéce du genre Eusmilus (Carnivora: Nimravidae) de l'Oligocéne (MP 22) d'Europe. [A new species of the genus Eusmilus (Carnivora: Nimravidae) from the European Oligocene]. Geobios 34:657-672.

Peigné, S., and L. de Bonis. 2003. Juvenile cranial anatomy of Nimravidae (Mammalia, Carnivora): biological and phylogenetic implications. Zoological Journal of the Linnean Society 138:477-493.

Prothero, D.R. 1996. Camelidae. Pages 609-651 in D.R. Prothero and R.J. Emry, editors. The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, Cambridge, UK.

Prothero, D.R. 1998. Rhinocerotidae. Pages 595-605 in C.M. Janis, K.M. Scott, and L.L. Jacobs, editors. Evolution of Tertiary Mammals of North America Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, UK.

Prothero, D.R. 2005. The Evolution of North American Rhinoceroses. Cambridge University Press, 1-218.

Prothero, D.R., and F. Sanchez. 2008. Systematics of the Leptaucheniine Oreodonts (Mammalia: Artiodactyla) from the Oligocene and earliest Miocene

of North America. New Mexico Museum of Natural History and Science Bulletin 44:335-356.
Prothero, D.R., and K.E. Whittlesey. 1998. Magnetic stratigraphy and biostratigraphy of the Orellan and Whitneyan land mammal "ages" in the White River Group. Geological Society of America Special Paper 325:39–59.
Schultz, C.B., and C.H. Falkenbach. 1954. Desmatochoerinae, a New Subfamily of Oreodonts. Bulletin of the American Museum of Natural History 105:143-256.
Schultz, C.B., and C.H. Falkenbach. 1968. The Phylogeny of the Oreodonts. Part 1: Merycoidodontinae, Eporeodontinae, and Leptaucheniinae, Three subfamilies of oreodonts, with an appendix to the revision of the Merycoidodontidae, and Part 2. Summary and conclusions concerning the Merycoidodontidae. Bulletin of the American Museum of Natural History 139:1-498
Schultz, C.B., and T.M. Stout. 1955. Classification of Oligocene Sediments in Nebraska: A Guide for the Stratigraphic Collecting of Fossil Mammals. Bulletin of The University of Nebraska State Museum 4:16-52.
Stevens, M.S., and J.B. Stevens. 1996. Reevaluation of the taxonomy and phylogeny of some oreodonts (Artiodactyla, Merycoidodontidae): Merycoidodontinae and Miniochoerinae. Pages 498-573 in D.R. Prothero and R.J. Emry, editors. The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, Cambridge, UK.
Stevens, M.S., and J.B. Stevens. 2007. Family Merycoidodontidae. Pages 157-168 in D.R. Prothero and S.E. Foss editors. The Evolution of Artiodactyls. The Johns Hopkins University Press, Baltimore, MD.
Swinehart, J.B., V.L. Souders, H.M. Degraw, and R.F. Diffendal, Jr. 1985. Cenozoic paleogeography of western Nebraska. Pages 209-229 in R.M. Flores and S. Kaplan, editors. Cenozoic paleogeography of the west-central United States, Special Publication, Rocky Mountain Section: Tulsa, Society of Economic Paleontologists and Mineralogists.
Terry, D.O. 1998. Lithostratigraphic revision and correlation of the lower part of the White River Group: South Dakota to Nebraska. Geological Society of America Special Papers, 325:15-37.
Wahlert, J.H. 1983. Relationships of the Florentiamyidae (Rodentia, Geomyoidea) Based on Cranial and Dental Morphology. American Museum Novitates 2769:1-23
Wang, X. 1994. Phylogenetic systematics of the Hesperocyoninae (Carnivora: Canidae). Bulletin of the American Museum of Natural History 221:1-207
Wang, X., R.H. Tedford, and B.E. Taylor. 1999. Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). Bulletin of the American Museum of Natural History 243:1-392.
Woodburne, M.O. 2004. Principles and Procedures. Pages 1-20 in M.O. Woodburne, editor. Late Cretaceous and Cenozoic Mammals of North America Biostratigraphy and Geochronology. Columbia University Press, New York, NY.
Xu X. 1996. Castoridae. Pages 417-432 in D.R. Prothero, R. Prothero and R.J. Emry, editors. The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, Cambridge, UK.