A TINY DEER WITH BIG IMPLICATIONS: A NEW GENUS (*SANTUCCIMERYX*) FROM BADLANDS NATIONAL PARK HELPS BRIDGE THE GAP BETWEEN OLIGOCENE AND MIOCENE LEPTOMERYCIDAE (MAMMALIA, ARTIODACTYLA)

Mattison Shreero[1], Ed Welsh[1], Katherine Marriott[2,3], Donald R. Prothero[4,5]

[1] Badlands National Park, Interior, SD 57750

[2] Research Foundation of the City University of New York, New York, NY 10036

[3] American Museum of Natural History, New York, NY 10024

[4] Department of Geological Sciences, California State Polytechnic University, Pomona, CA 91768

[5] Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, CA 90041

ABSTRACT

In 2016, a leptomerycid skull was collected at Badlands National Park, South Dakota from the earliest Whitneyan "*Leptauchenia* beds" (early Oligocene, ~32 mya) of the Poleslide Member, Brule Formation. This specimen (BADL 64015) is the first cranium referable to *Leptomeryx elissae* and is by far the most complete specimen to date; the skull lacks only the premaxilla and has associated dentaries. Prior to the discovery of BADL 64015, only isolated dentaries from the late Orellan of northwestern Nebraska had been referred to *L. elissae*.

Previous literature reports that *L. elissae* differs from the more common *Leptomeryx evansi* in that it has smooth tooth enamel, lacks the *Palaeomeryx*-fold on the lower molars, has a rounded and evident entoconulid on m3, and is smaller in size. Based upon measurements and diagnostic characters, BADL 64015 significantly deviates from *L. evansi* beyond differences in the lower teeth.

BADL 64015 exhibits a shift towards brachycephaly, a shortening of the cranium. The weakly developed postorbital constriction and reduced length of the sagittal crest demonstrate that the cranial characters of BADL 64015 are more akin to the Hemingfordian (early Miocene) leptomerycid, *Pseudoparablastomeryx*, than to *Leptomeryx*. This affinity suggests *L. elissae* cannot be attributed to the genus *Leptomeryx*. However, in BADL 64015, characters of the premolars are more closely aligned to *Leptomeryx* than *Pseudoparablastomeryx*, with some minor differences, including the shortening of P2-3. An enigmatic Arikareean (Oligocene to early Miocene) leptomerycid, *Pronodens*, also demonstrates a shortening of the anterior dentary, but lacks associated cranial material. The *Pronodens* holotype consists of only extremely worn lower teeth, making it impossible to draw any meaningful comparisons between *Pronodens* and other leptomerycids.

Based on the combination of cranial and dental characteristics, we thus validate *L. elissae* as a distinct species and reposition it into a new genus, *Santuccimeryx*,

intermediate between *Leptomeryx* and *Pseudoparablastomeryx*. Evolutionary relationships of the Leptomerycidae will, however, remain uncertain until additional specimens can be collected that provide unambiguous characters to clarify the relationships between these taxa.

INTRODUCTION

A new specimen (BADL 64015), initially attributed to *Leptomeryx*, was discovered by a Geoscientists-in-the-Parks intern at Badlands National Park during the summer of 2016 (Figure 1). After preparation, we used dental characters to identify the specimen as *Leptomeryx elissae*, a species named by Korth and Diamond (2002) based on isolated dentaries and lower dentition (Figure 2). BADL 64015 is the first and only known specimen of *L. elissae* to contain both dentary and skull material, thereby providing the first characters beyond lower dentition and helping clarify evolutionary relationships within the genus *Leptomeryx* and the family Leptomerycidae. This work describes BADL 64015 and compares it to the only other leptomerycid genera known from skull material: *Leptomeryx* and *Pseudoparablastomeryx*.

The ruminant family Leptomerycidae is an extinct taxon endemic to North America and the longest-lived member of the Traguloidea. Leptomerycids range temporally from the late Eocene to Miocene and geographically throughout the Western Interior from Saskatchewan to Mexico, with one atypical occurrence in California (*Leptomeryx blacki*). Leptom-
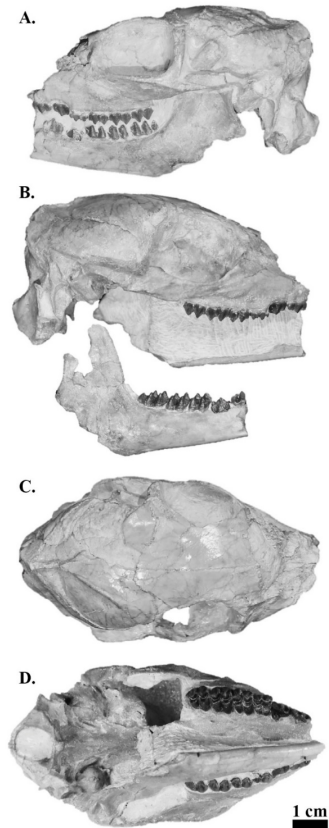

Figure 1. Skull and dentaries of BADL 64015, the first skull attributed to the species *Leptomeryx elissae* (Korth and Diamon 2002). A. left lateral view; B. right lateral view; C. dorsal view; D. ventral view.
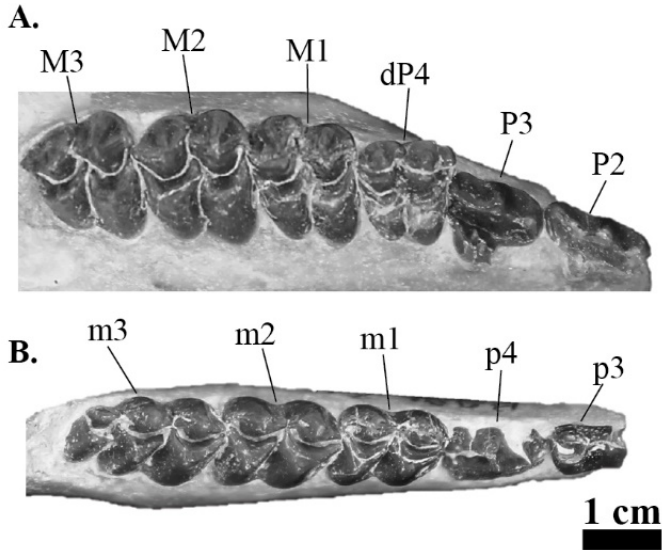
Figure 2. Dentition of BADL 64015. A. occlusal view of upper dentition; B. occlusal view of lower dentition. Lower dentition was used to initially identify BADL 64015 as *Leptomeryx elissae* (Korth and Diamond 2002).

erycidae currently contains four genera of small (~2 to 4 kg), hornless ruminants: *Hendryomeryx, Leptomeryx, Pronodens,* and *Pseudoparablastomeryx.* Of these, *Leptomeryx* is by far the most abundant genus and is also one of the most common small herbivores found in the White River Group.

Members of this genus are extremely useful in biostratigraphy. All three Eocene *Leptomeryx* species have their First Appearance Datum (FAD) in successive subdivisions, or interval zones, of the Chadronian North American Land Mammal Age (NALMA). The late early Chadronian *Leptomeryx yoderi* Interval Zone (Ch2) is followed by the *Leptomeryx mammifer* Interval Zone (Ch3) and the *Miniochoerus chadronensis* Interval Zone (Ch4) for which the last Chadronian leptomerycid, *Leptomeryx speciosus*, can be used as an index fossil (Prothero and Whittlesey 1998, Prothero and Emry 2004). The transition into the Orellan NALMA (Or1; *Hypertragulus calcaratus* Interval Zone) at the Eocene–Oligocene transition is marked by the replacement of *L. speciosus* with *Leptomeryx evansi* (Prothero and Emry 2004; see also Zanazzi et al. 2009). *L. evansi* differs from its Chadronian counterparts in that it possesses crenulated enamel and *Palaeomeryx*-folds on the lower molars (Figure 3A) (Heaton and Emry 1996, Zanazzi et al. 2009). The evolution of the *Palaeomeryx*-fold and relative proliferation of *Leptomeryx evansi* throughout the White River Group of the northern Great Plains makes it an invaluable taxon in orienting the boundary of the Eocene–Oligocene transition.

Despite their abundance and relevance to biostratigraphy, the taxonomic organization of leptomerycids has confounded researchers for more than a century, and their evolutionary relationships remain primarily unresolved in the literature. Zittel (1893) was the first to distinguish Leptomerycinae as a distinct subfamily
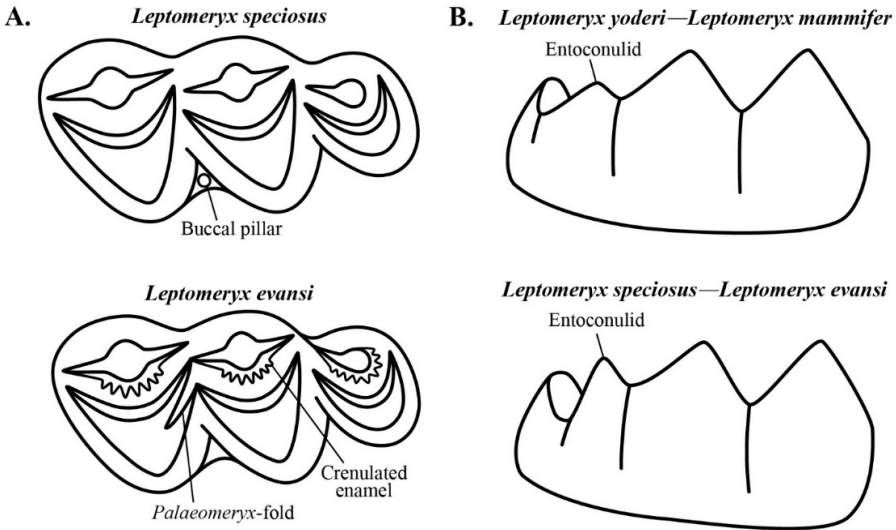
Figure 3. A. Idealized comparative diagram highlighting diagnostic molar features of *L. speciosus* (Chadronian) and *L. evansi* (Orellan). The *Palaeomeryx*-fold and crenulated enamel of *L. evansi* are used to indicate the beginning of the Orellan NALMA. **B.** Idealized comparative diagram of m3 entoconulid morphology illustrating the two recognized lineages of Leptomeryx: the *L. yoderi–L. mammifer* lineage and *L. speciosus–L. evansi* lineage. Modified from Heaton and Emry (1996) and Korth and Diamond (2002).

within the Tragulidae. Shortly thereafter, Scott (1899) first utilized Leptomerycidae as a distinct family, but provided no justification and was dismissed by subsequent authors who placed members within the Hypertragulidae (Frick 1937, Scott 1940, Simpson 1945, Macdonald 1963, 1970). Scott (1899) also included hypertragulids (*Hypertragulus* and *Hypisodus*) and protoceratids (*Protoceras*) within the family Leptomerycidae. Character differences to distinguish Leptomerycidae as a distinct family were not described until Gazin (1955), who focused on dental characters. However, Gazin's "leptomerycids" are no longer considered members of the family and are instead early members of the Protoceratidae and Camelidae (Wortman 1898, Matthew 1903, Scott 1899, Taylor and Webb 1976). Taylor and Webb (1976) provided the first cranial and postcranial characteristics, alongside dental characters, to further justify the distinction of the family Leptomerycidae, and this justification was supported by subsequent works (Webb and Taylor 1980, Webb 1998, Vislobokova 2001). Taylor and Webb (1976) also document the survival of two leptomerycid genera—*Pronodens* and *Pseudoparablastomeryx*—into the late Oligocene and Miocene, respectively. To clarify relationships within Hypertraguloidea and Traguloidea, Vislobokova (2001) elaborated on diagnostic characters through phylogenetic analyses and repositioned taxa previously and erroneously placed within Leptomerycidae (e.g., *Archaeomeryx*). Currently, taxa that can be confidently included in Leptomerycidae are *Hendryomeryx*, *Leptomeryx*, *Pronodens*, and *Pseudoparablastomeryx*. Another genus, *Pipestoneia*, was tentatively referred to Leptomerycidae (Tabrum

and Métais 2007); however, no further study had been undertaken to resolve the position of this taxon relative to other leptomerycids or tragulids. Métais and Vislobokova (2007) further expanded upon phylogenetic relationships of basal ruminants, reaffirming leptomerycids within the Traguloidea. Spaulding et al. (2009) provided a phylogenetic analysis of Artiodactyla, focusing on Cetacea, and added confusion by placing *Leptomeryx* within the Pecora as the sister group to Moschidae. However, this work did not include basal, hornless ruminants accounted for in other studies which consistently place *Leptomeryx* close to the Tragulidae (Webb and Taylor 1980, Bouvrain and Geraads 1985, Geraads et al. 1987, Janis 1987, Gentry and Hooker 1988, Vislobokova 2001, Métais and Vislobokova 2007).

Heaton and Emry (1996) provided the first thorough analyses of the genus *Leptomeryx*, employing a large sample size of Chadronian specimens from Wyoming and Montana. They statistically accounted for every character variation that could be found within the genus, provided a synopsis of reliable characterization for the four species they considered valid (*L. yoderi*, *L. mammifer*, *L. speciosus*, and *L. evansi*), and analyzed which characters could be attributed to individual variation. As with most other works on the genus, Heaton and Emry (1996) relied on characters from the lower dentition because upper dentitions are considered less diagnostic and are rarely found with associated dentaries. Heaton and Emry's (1996) diagnostic characters are based on size, morphology of the m3 entoconulid, and presence or absence of the *Palaeomeryx*-fold. Korth and Diamond (2002) continued the reliance on dental characters in their reevaluation of Orellan *Leptomeryx* species when they resurrected *L. exilis* (Cook, 1934) and named a new species, *Leptomeryx elissae*. Mathis and MacFadden (2010) used enamel thickness and complexity data to verify species separation along the Eocene–Oligocene transition, corroborating Korth and Diamond's (2002) claim that there was at least one other species of leptomerycid in addition to *L. evansi* during the Oligocene.

Heaton and Emry (1996) proposed two evolutionary lineages, simplified as the *L. yoderi*–*L. mammifer* and *L. speciosus*–*L. evansi* lineages, based on the morphology of the m3 entoconulid. The m3 entoconulid either possesses a posterior ridge (*L. yoderi*–*L. mammifer*) or the ridge is lost and the m3 entoconulid is a pillar-like cuspid (*L. speciosus*–*L. evansi*) (Figure 3B). Korth and Diamond (2002) elaborated on these lineages with their analysis of *L. elissae* and *L. exilis*. They defined *L. elissae* based on a left dentary containing p3-m3 (UNSM 119638) with a unique combination of characters–smooth tooth enamel, *L. speciosus*–*L. evansi* type of m3 entoconulid, absence of a *Palaeomeryx*-fold on the lower molars, and smaller size than *L. evansi*–and provided several referred specimens. Thus, *L. elissae* seems to have stemmed from the *L. speciosus*–*L. evansi* lineage since it shares the same m3 morphology, whereas *L. exilis* shares the m3 morphology of the *L. yoderi*–*L. mammifer* group and implies a ghost lineage somewhere in the early Orellan NALMA (Korth and Diamond 2002). Korth and Diamond (2002) also elaborated on the relationship of *L. obliquidens* (Lull 1922), a species not discussed by Heaton and Emry (1996). They position *L. obliquidens* within the *L. yoderi*–*L. mammifer*–*L. exilis* lineage on the basis of the m3 entoconulid and lack

of *Palaeomeryx*-fold but note that *L. obliquidens* has highly crenulated enamel, a trait typical of the *L. speciosus–L. evansi* lineage.

Considering the confusion surrounding the evolutionary relationships of the Leptomerycidae, this work endeavors to not only describe new material of *L. elissae*, but also compare it to all leptomerycid genera known from skull material in order to provide an impartial analysis of the position of *L. elissae* within Leptomerycidae. As mentioned, only the genera *Hendryomeryx*, *Leptomeryx*, *Pronodens*, and *Pseudoparablastomeryx* are considered valid leptomerycids (Webb 1998, Vislobokova 2001). *Hendryomeryx* contains three species: *H. defordi, H. wilsoni,* and *H. esulcatus.* The holotype of *Hidrosotherium transpecosensis* (Wilson 1974) was synonymized with *H. defordi* (Prothero and Emry 1996) and is the only reported skull of any *Hendryomeryx* species. The characters in *Hendryomeryx* are basal and differ enough from the other leptomerycids that they do not merit detailed comparison to *L. elissae* for the purposes of this study. Aside from *L. elissae*, *Leptomeryx* contains the species *L. blacki, L. yoderi, L. mammifer, L. speciosus, L. evansi, L. exilis,* and *L. obliquidens.* Of these, only *L. evansi, L. obliquidens,* and now *L. elissae* are known from skull material. However, the poor condition of the only known skull of *L. obliquidens* precludes it from reliable comparison. Two other species, *L. transmontanus* and *L. agatensis*, have been plagued with vague reclassifications and require additional review. *Pronodens* contains one species, *P. silberlingi*, which is known from an isolated dentary with very worn teeth. Though no *Pronodens* skull material has been reported, this problematic genus merits discussion due to its temporal intermediacy between *Leptomeryx* and *Pseudoparablastomeryx* and its lack of species-defining characters. All referrals of material to this genus are tentative at best. *Pseudoparablastomeryx* contains the species *P. scotti* and *P. francescita.* Of these, *P. scotti* is known from a single skull (Frick 1937, Taylor and Webb 1976). As such, *Leptomeryx* and *Pseudoparablastomeryx* are currently the only leptomerycid genera with defined cranial characters, meriting their detailed comparison to BADL 64015.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York; BADL, Badlands National Park, Interior, South Dakota; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; F:AM, Frick Collection, American Museum of Natural History, New York, New York; SDSM, South Dakota School of Mines and Technology Museum of Geology, Rapid City, South Dakota; UNSM, University of Nebraska State Museum, Lincoln, Nebraska; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut; YPM-PU, Princeton University Museum of Natural History (now in the collection of the Yale Peabody Museum of Natural History).

GEOLOGICAL SETTING AND PALEOENVIRONMENT

Badlands National Park is characterized by the White River Group siltstones and mudstones, which were deposited in the northern Great Plains between 37 and 30 million years ago (Figure 4). The White River Group contains two formations, the late Eocene Chadron Formation and the early Oligocene Brule
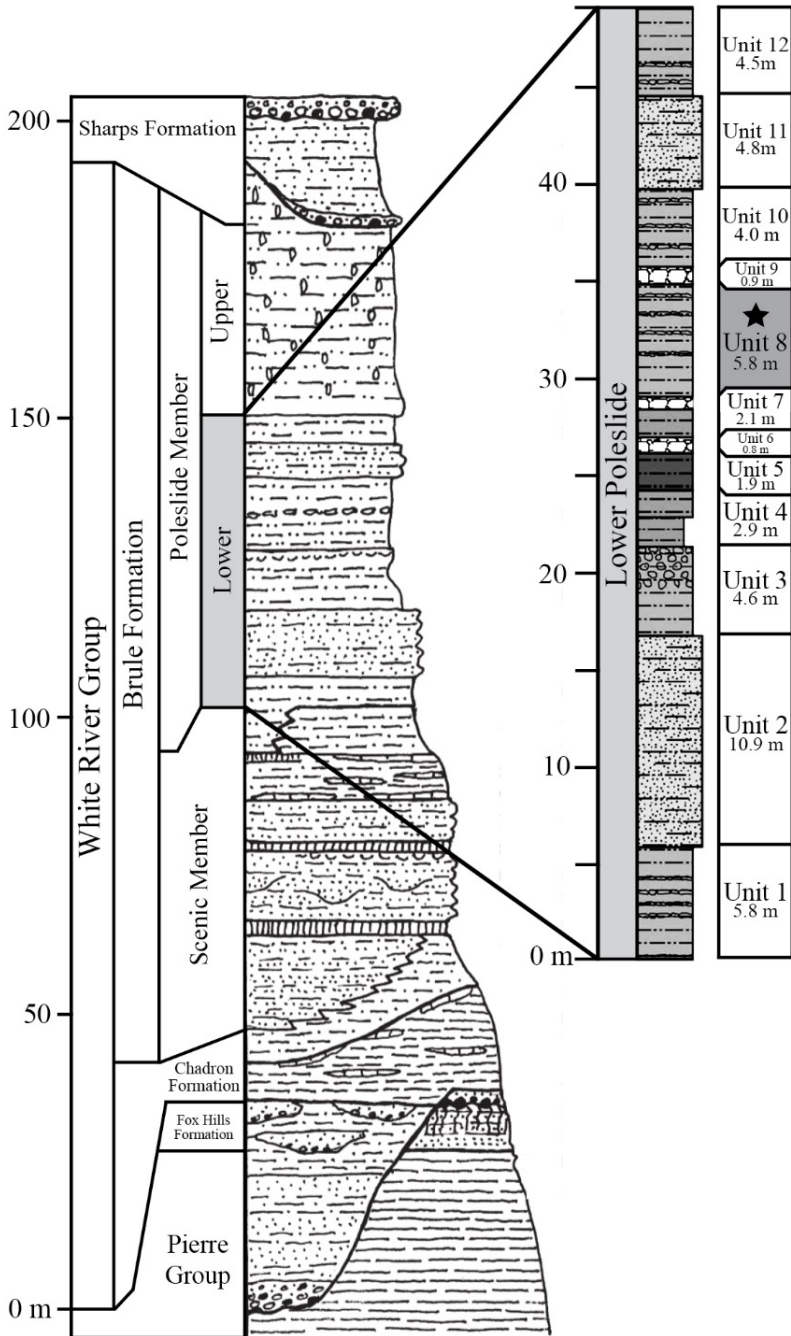
Figure 4. General stratigraphic column of Badlands National Park and inset showing detailed stratigraphy of the Lower Poleslide Member. BADL 64015 was found within Unit 8 of the Poleslide. Modified from Evanoff et al. (2010).

Formation. The Brule Formation in South Dakota is subdivided into the Scenic Member (34–32 mya) and Poleslide Member (32–30 mya). In the Cedar Pass area of the Badlands, the lower Poleslide is primarily lithologically composed of tan to light gray eolian siltstone but also contains mudstone and well-bedded river channel sandstone complexes (Benton et al. 2015). The specimen of *L. elissae* described herein (BADL 64015) was found in the Cedar Pass area within Unit 8 of the Poleslide Member, which has also been referred to as the Bjork Siltstone or the *Leptauchenia* Beds (Figure 4) (Evanoff et al. 2010). Biostratigraphically, Unit 8 correlates with the base of the *Leptauchenia major* Interval Zone as defined by Prothero and Whittlesey (1998) and Prothero and Emry (2004) because it contains the zone's characteristic fauna. Stevens et al. (2023) provides a synopsis of oreodont zonation that narrows the Orellan–Whitneyan transition in the Cedar Pass Area, which corroborates rodent data supplied by Korth (2014). Unit 8 thus records the early Oligocene, about 32 mya, and the earliest Whitneyan NALMA (Wh1).

In stark contrast to wetter, more tropical Eocene environments, around 32 mya the area that is now Badlands National Park was an open savanna with few trees. Paleosols of the lower Poleslide indicate that the environment here was a dry, distal floodplain (Benton et al. 2015). The prolific Cedar Pass fossil assemblage reveals a diverse collection of Cenozoic animals that roamed this landscape including, most commonly, oreodonts (*Leptauchenia* and *Merycoidodon*), hyracodontids (*Hyracodon*), ancient dogs (*Archaeocyon* and *Mesocyon*), false saber-toothed cats (*Nimravus*), tortoises (*Stylemys*), and small deer-like artiodactyls (*Leptomeryx* and *Hypertragulus*).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus 1758
Order ARTIODACTYLA Owen 1848
Family LEPTOMERYCIDAE Scott 1899
Genus *SANTUCCIMERYX* new genus
Santuccimeryx elissae (Korth and Diamond 2002)
Leptomeryx elissae Korth and Diamond 2002

Holotype—UNSM 119638, mandible with left p3-m3 (Korth and Diamond 2002).

Etymology—"Santucci's ruminant". Named in honor of Vincent L. Santucci, the Senior Paleontologist at the Geologic Resources Division of the National Park Service, for his contributions to NPS paleontology, support of and advocacy for the paleontology program at Badlands National Park, and work conducted in the Cedar Pass area for his master's thesis.

Referred Specimens—Specimens referred to *L. elissae* by Korth and Diamond (2002) from the Orella Member, Brule Formation, Sioux County, Nebraska: CM 73416; UNSM 119636, 119637, 119639, 119640; AMNH 53626A, 606-25868, 606-25873.

From the Poleslide Member, Brule Formation, Jackson County, South Dakota: BADL 64015, skull and dentaries with left and right P2-3, dP4, M1-3, left and right p3-4, m1-3, and articulated atlas; BADL 24824, partial skull with left P3-M3 and right P4-M2; BADL 64245, partial skull and dentaries with right dP4, M1-3, left and right dp4, m1-3.

Locality and Horizon—Holotype from UNSM locality Sx-8, Orella Member (Orella C; Or3) of the Brule Formation, Sioux County, Nebraska. Other specimens referred to by Korth and Diamond (2002) are from the upper Orella Member (Orella C and D; Or3 and Or4), Brule Formation, Sioux County, Nebraska.

New BADL material is from the Cedar Pass area, North Unit, Badlands National Park, Jackson County, South Dakota. These specimens were collected from Unit 8 of the Poleslide Member, Brule Formation, White River Group, based on Evanoff et al. (2010) (Figure 4). This unit is classically known as the base of the "*Leptauchenia* beds" (Schultz and Falkenbach 1968). Specific site information is protected under federal law. To request precise locality data, qualified researchers should inquire with Badlands National Park's on-staff paleontologist.

Distribution—Late Orellan of Sioux County, Nebraska and earliest Whitneyan of Jackson County, South Dakota.

Emended Diagnosis—**Cranium:** *Santuccimeryx* is brachycephalic, exhibiting a short cranium and relatively large orbits. In BADL 64015, the orbit length is 61.2% of the cranium length measured from the postorbital process of the frontal. In *Santuccimeryx*, the postorbital bar is formed primarily by the jugal. The postorbital constriction is shallow and poorly developed. The distance between frontal-parietal contact and sagittal crest is double the length of the sagittal crest. The sagittal crest has weak insertions for nuchal ligaments. The angle between the temporal crests is 64°, and they converge with the anterior sagittal crest dorsal to the external auditory meatus. The sagittal crest does not overhang the occipital region. The basioccipital is posteriorly expanded and trapezoidal, and the auditory bullae are sculptured, defined, and possess an anterior spur.

Dentition*: S. elissae* has smooth tooth enamel. P2 and P3 have distinct preprotocrista and lack a cusp-like protocone. The margin of the P3 postprotocrista is posterolabially expanded, and the P3 posterostyle is reduced. BADL 64015 possesses upper deciduous P4s, but lower deciduous teeth are lost, and all upper and lower molars are fully erupted, indicating an adult specimen. The dP4 is strongly molariform, nearly as robust as M1, and possesses a lingual cingulum and buccal pillar. The styles of all upper molars are reduced or nearly absent and antero-posteriorly shortened.

The lower premolars are complex. The p3 possesses a protoconid with posterior ridges to the entoconid and hypoconid, and p4 has a well-developed paraconid, metaconid, protoconid, entoconid, and hypoconid. The dp4 in referred *S. elissae* specimen BADL 64245 is molariform with three characteristic lobes, as in all artiodactyls. On the lower molars, *S. elissae* has smooth enamel, anterior cingula on the protoconids, and lacks *Palaeomeryx*-folds. The posterior ridge on m3 is lost and the entoconulid is a pillar-like cuspid (*L. speciosus–L. evansi* morphology).

Differential Diagnosis—Overall, the cranial features of BADL 64015 are closest to *Pseudoparablastomeryx*, while the dental characters are more akin to

TABLE 1 – Differential characters among all leptomerycids observed in this study. "✓" indicates character is present, "X" indicates character is absent, "?" indicates character is unknown.

	Palaeomeryx-Fold	Crenulated Enamel	m3 Entoconulid Ridge	Buccal Pillar	Elongate P2-3 Posterior Ridge	Posterior Basin in P2-3 Postprotocrista	Well-Developed Upper Molar Styles
Hendryomeryx	X	X	?	✓	✓	X	?
Leptomeryx yoderi	X	X	✓	X	?	?	?
Leptomeryx mammifer	X	X	✓	X	?	?	?
Leptomeryx exilis	X	X	✓	X	✓	X	✓
Leptomeryx obliquidens	X	X	✓	X	✓	X	✓
Leptomeryx speciosus	X	X	X	✓	?	?	X
Leptomeryx evansi	✓	✓	X	X	✓	X	✓
Santuccimeryx elissae	X	X	X	✓	X	✓	X
Pseudoparablastomeryx	X	X	X	✓	X	✓	X
"Leptomeryx" transmontanus	?	X	?	?	X	?	?
"Leptomeryx" agatensis	?	X	X	X	✓	X	✓
Pronodens silberlingi	?	X	?	X	?	?	?
Pipestonia	X	✓	X	X	✓	X	✓

	Postorbital Bar Formed Primarily By Jugal	Well-Developed Postorbital Constriction	Ratio of Sagittal Crest Length to Distance Between Frontal-Parietal Suture is ≤ 1/2	Temporal Crests Converge Above External Auditory Meatus	Angle of Temporal Crests ≥ 60°	Basioccipital is trapezoidal	Spherical Auditory Bulla
Leptomeryx evansi	X	✓	X	X	X	X	✓
Santuccimeryx elissae	✓	X	✓	✓	✓	✓	X
Pseudoparablastomeryx	X	X	✓	✓	✓	?	X

Figure 5. Artistic reconstruction of *Leptomeryx* (left) meeting *Santuccimeryx* (right). Note the overall smaller size, proportionally larger orbits, and brachycephaly of *Santuccimeryx*. Illustration by Mattison Shreero.

TABLE 2 – Cranial measurements of *Santuccimeryx elissae*, *Leptomeryx evansi*, and *Pseudoparablastomeryx scotti*. All measurements in mm unless otherwise notated.

	BADL 64015 *Santuccimeryx elissae*	SDSM 62381 *Leptomeryx evansi*	BADL 53936 *Leptomeryx* cf. *evansi*	F:AM 95490* *Pseudoparablastomeryx scotti*
Maximum Width of Cranium	33.5	33.8	28.4	35.9
Cranial Length From Postorbital Process of Frontal	36.4	44.7	45.8	38.3
Width at Postorbital Constriction	29.9	23.1	19.3	27.9
Length of Sagittal Crest	10.3	30.5	30.8	11.3
Distance Between Frontal-Parietal Suture & Sagittal Crest	22.0	7.4	9.5	18.9
Angle Between Temporal Crests	64°	44°	40°	60°
Depth at Malar	12.0	14.0	18.0	N/A
Height of Orbit	17.4	19.2	17.0	N/A
Length of Orbit	22.3	N/A	18.2	N/A

* F:AM 95490 exhibits some dorsal–ventral crushing

Leptomeryx, specifically *L. speciosus* (Table 1). Therefore, this taxon cannot be confidently placed within either genus, justifying repositioning *L. elissae* into a new, intermediate genus: *Santuccimeryx*. See figure 5 for artistic reconstruction of both *Leptomeryx* and *Santuccimeryx*.

Comparison to *Leptomeryx*: The orbit in *Santuccimeryx* is proportionately larger than observed in *Leptomeryx* (Table 2). The orbit length in BADL 53936 (*L.* cf. *evansi*) is 39.7% of the cranium length measured from the postorbital process of the frontal whereas this ratio is 61.2% in BADL 64015 (*S. elissae*). In *L. evansi* (and in all leptomerycids known from cranial material), the postorbital bar is composed of equal proportions of the frontal and jugal. In *Santuccimeryx*, the jugal comprises the majority of the postorbital bar. The postorbital constriction is shallow and poorly developed, but well-developed in *L. evansi* (Figures 6 and 7). The cranium is shortened in *Santuccimeryx* with a reduced sagittal crest length of 10.3 mm; *L. evansi* exhibits a 33.8 mm long sagittal crest in SDSM 62381, a specimen of nearly identical cranial width (Table 2 and Figure 7). The shortening of the sagittal crest increases the distance between the frontal-parietal contact and the anterior margin of the sagittal in *Santuccimeryx* (Figures 6 and 7; Table 2). The ratio of these measurements is inversely proportional in observed specimens of *L. evansi* (SDSM 62381 and BADL 53936) (Table 2). The angle between temporal crests is 64° in contrast to 40-44° in *L. evansi* (Table 2). In *Santuccimeryx*, the anterior sagittal crest begins to form dorsal to the external auditory meatus; in *L. evansi,* the anterior sagittal crest is formed anterior to the lateral expansion of the squamosal for the zygomatic (Figures 6 and 7). The basioccipital in *Santuccimeryx* is trapezoidal whereas it is subrectangular in *L. evansi*.

In previous literature, differentiating species of *Leptomeryx* relies entirely on lower dentition (Heaton and Emry 1996, Korth and Diamond 2002). BADL 64015, BADL 24824, and BADL 64245 provide the first upper dentition associated with the species *S. elissae* (Figure 2). P3 is shortened in *S. elissae*, with the protocone in a medial position (Figure 8). In *L. evansi*, the posterior portion of
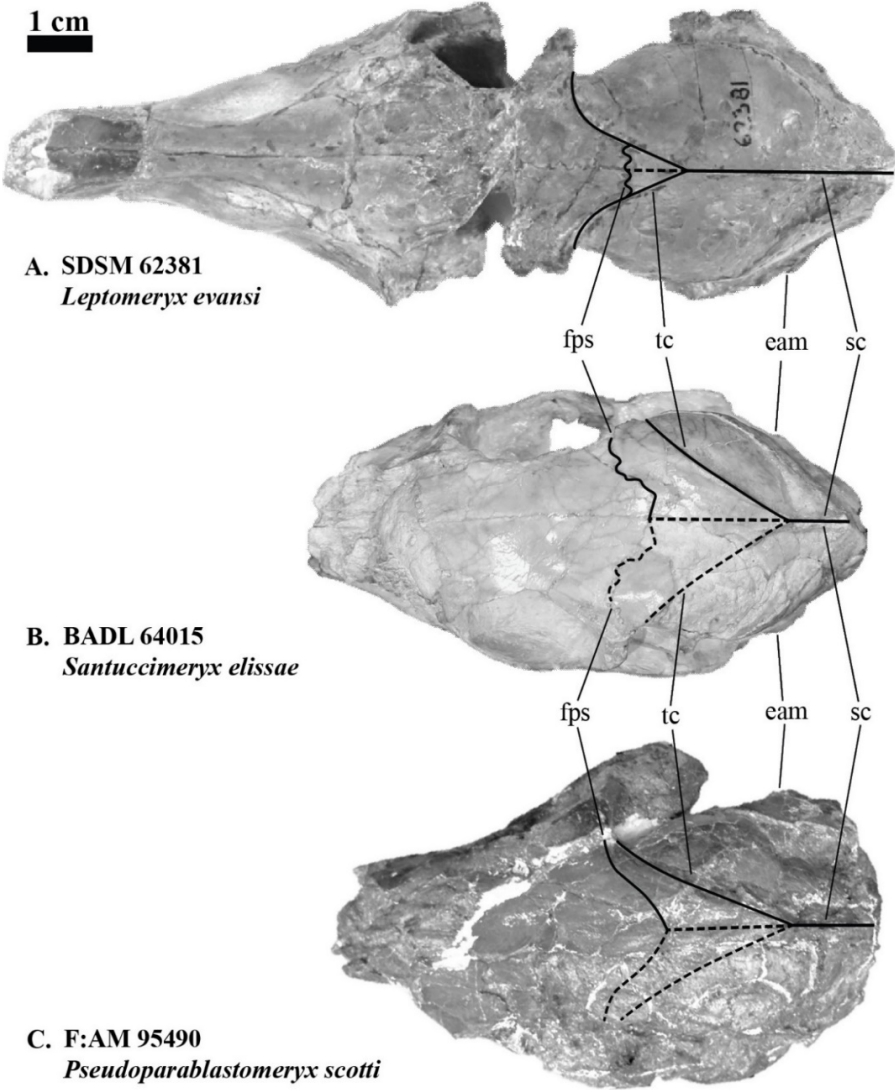
Figure 6. Comparative dorsal views of the crania of *Leptomeryx*, *Santuccimeryx*, and *Pseudo-parablastomeryx*. Lines mark the positions and orientation of the frontal-parietal suture (fps), temporal crests (tc), external auditory meatus (eam), and sagittal crest (sc). *Santuccimeryx elissae* has a cranial anatomy more akin to *Pseudoparablastomeryx* than *Leptomeryx*. In BADL 64015 and F:AM 95490, note the shortened crania, shortened sagittal crests, increased distance between the frontal-parietal sutures and sagittal crests, and increased angle between temporal crests.
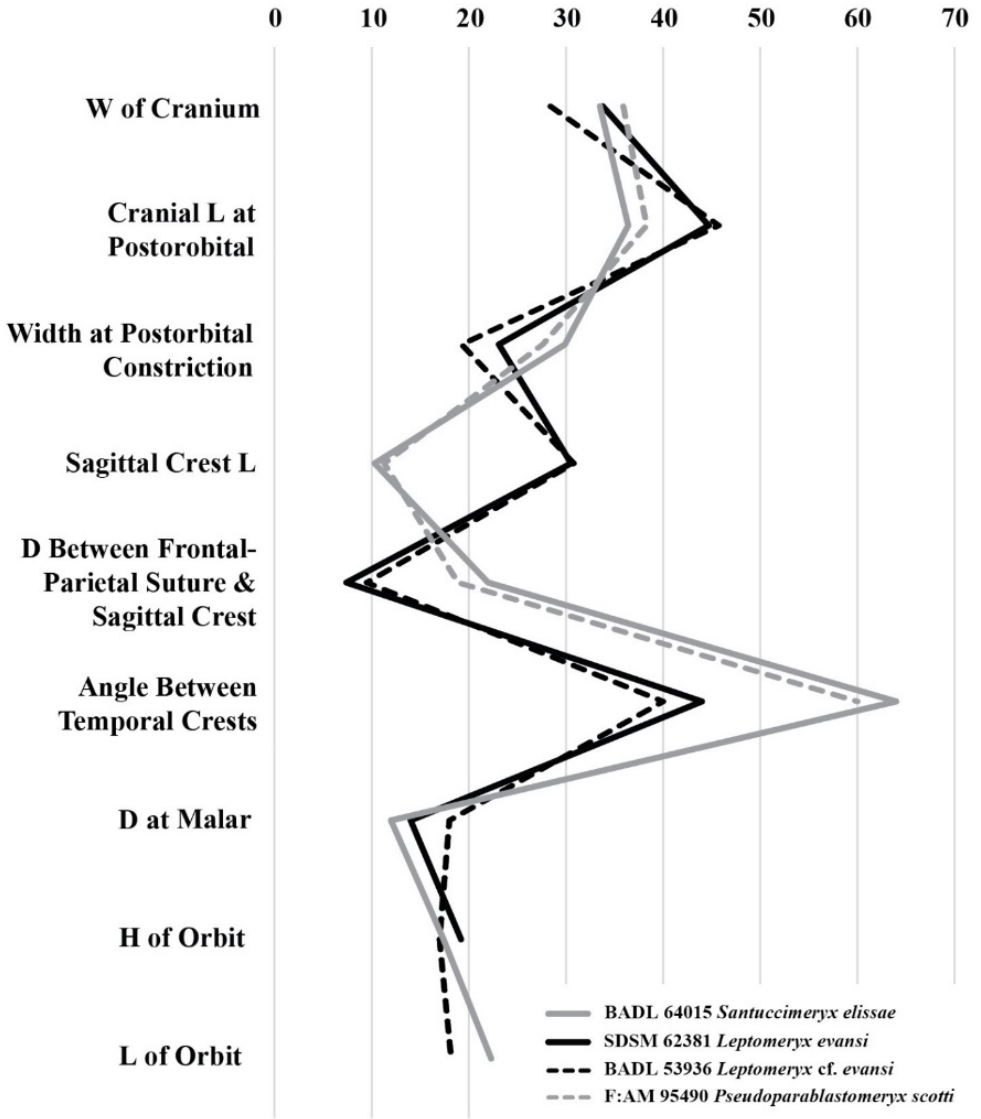
Figure 7. Simpson-ratio diagram visualizing the variation of cranial measurements for specimens of *Santuccimeryx*, *Leptomeryx*, and *Pseudoparablastomeryx*. Angle between temporal crests measured in degrees; all other measurements in mm. Note the significant deviation of cranial length at postorbital, sagittal crest length, and angle between temporal crests in BADL 64015 and F:AM 95490.
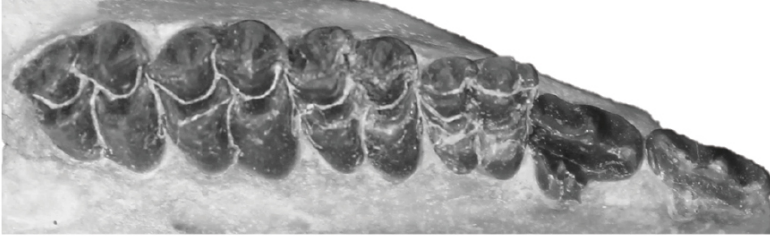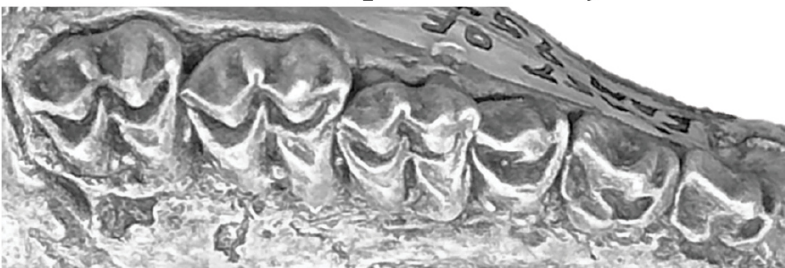
A. SDSM 62381 *Leptomeryx evansi*

1 cm

B. BADL 64015 *Santuccimeryx elissae*

C. BADL 24824 *Santuccimeryx elissae*

D. F:AM 95490 *Pseudoparablastomeryx scotti*

Figure 8. Comparative occlusal views of upper dentition for *Leptomeryx*, *Santuccimeryx*, and *Pseudoparablastomeryx* (cast of F:AM 95490). SDSM 62381, BADL 64015, and F:AM 95490 are right maxilla. BADL 24824 is a left maxilla (image has been flipped horizontally for ease of comparison). Note the submolariform P2-3 in F:AM 95490 in contrast to *Santuccimeryx* and *Leptomeryx* and the significantly increased molar styles of SDSM 62381 when compared to *Santuccimeryx* and *Pseudoparablastomeryx*.

P3 is more elongate and the protocone is in a more anterior position (Figure 8). The P3 postprotocrista is directed posterolabially, creating a small basin, whereas in *L. evansi* it conforms along the margins of the tooth in a sinuous pattern, behaving more like a cingulum (Figure 8). The upper molars of *S. elissae* have greatly reduced or absent styles and are more antero-posteriorly shortened in comparison to *Leptomeryx* (Figure 8). See Table 3 for comparative measurements of upper dentition.

Unlike *L. evansi,* the lower molars in *S. elissae* lack enamel crenulation and *Palaeomeryx*-folds but retain the *L. speciosus–L. evansi* morphology of the m3 entoconulid, as described by Korth and Diamond (2002) (Figure 2). Morphologically, the lower dentition of *S. elissae* is indistinguishable from *L. speciosus* (Table 1). *S. elissae* does follow an overall decreasing size trend, from *L. speciosus* to *L. evansi* to *S. elissae*. See Table 4 for comparative measurements of lower dentition. Lambe (1908) provides the only description of upper molars attributed to *L. speciosus*, which possess styles more akin to *L. evansi* than *S. elissae*. No specimen resembling either *L. speciosus* or *S. elissae* has been confidently identified from any early Orellan site, so if there is a direct relationship between *L. speciosus* and *S. elissae*, a record gap in the early Orellan makes it difficult to demonstrate such a transition.

Comparison to Pseudoparablastomeryx—Cranial features of *Santuccimeryx* most closely resemble the Arikareean leptomerycid *Pseudoparablastomeryx* (Tables 1 and 2). As in *Santuccimeryx, Pseudoparablastomeryx* demonstrates proportionally larger orbits. In *Pseudoparablastomeryx* (and in all leptomerycids known from cranial material), the postorbital bar is composed equally of the frontal and jugal. In *Santuccimeryx*, the jugal comprises the majority of the postorbital bar. Both genera demonstrate shallow and poorly developed postorbital constrictions,

TABLE 3 – Upper dentition measurements of *Santuccimeryx elissae*, *Leptomeryx evansi*, and *Pseudoparablastomeryx scotti*. All measurements in mm.

	BADL 64015 *Santuccimeryx elissae*	BADL 24824 *Santuccimeryx elissae*	SDSM 62381 *Leptomeryx evansi*	BADL 29030 *Leptomeryx* cf. *evansi*	YPM-PU 12962* *Leptomeryx evansi*	F:AM 95490 *Pseudoparablastomeryx scotti*
P2 – P4	N/A	N/A	20.0	17.6	17.5	14.9
P2 Length	6.2	N/A	N/A	N/A	6.0	5.1
P2 Width	3.7	N/A	N/A	N/A	4.0	4.0
P3 Length	5.3	5.9	6.9	6.3	9.0	5.1
P3 Width	4.8	4.8	5.8	4.9	5.0	5.3
P4 Length	N/A	4.2	5.8	4.8	5.0	4.5
P4 Width	N/A	5.8	6.4	5.9	5.7	5.9
M1 – M3	17.9	16.8	21.7	19.2	18.5	21.4
M1 Length	5.9	5.7	7.2	6.7	8.0	7.1
M1 Width	6.5	7.1	7.6	7.1	6.0	7.3
M2 Length	6.5	6.1	7.7	6.8	6.5	8.1
M2 Width	7.2	8.0	8.5	8.1	7.0	8.8
M3 Length	6.2	5.6	7.4	7.1	7.0	7.8
M3 Width	6.2	7.1	7.9	7.6	6.5	8.9

*measurements for YPM-PU from Scott (1940).

TABLE 4 – Lower dentition measurements of *Santuccimeryx elissae*, *Leptomeryx evansi*, and *Pseudoparablastomeryx scotti*. All measurements in mm.

	BADL 64015 *Santuccimeryx elissae*	Korth & Diamond (2002)* *"Leptomeryx" elissae*	SDSM 62381 *Leptomeryx evansi*	YPM-PU 12962** *Leptomeryx evansi*	Taylor & Webb (1976)*** *Pseudoparablastomeryx scotti*
p4 Length	6.0	N/A	6.3	6.0	6.1
p4 Width	3.1	N/A	3.6	3.0	3.1
m1 – m3	20.7	19.8	24.9	23.0	N/A
m1 Length	6.0	5.6	6.9	7.0	6.4
m1 Width	4.5	4.3	4.8	5.0	4.0
m2 Length	6.4	6.4	7.5	7.0	7.0
m2 Width	5.0	4.6	4.4	5.0	4.5
m3 Length	8.0	8.6	11.2	9.0	9.6
m3 Width	4.8	4.4	5.2	5.0	4.6

* measurements for *"Leptomeryx" elissae* are mean values from Korth and Diamond (2002).
** measurements for YPM-PU from Scott (1940).
*** measurements for *Pseudoparablastomeryx scotti* are mean values from Taylor and Webb (1976).

shortened crania, and shortened sagittal crests (Figures 6 and 7). The only skull of *Pseudoparablastomeryx* (F:AM 95490) has a 11.3 mm sagittal crest (Taylor and Webb 1976), comparable to the 10.3 mm sagittal crest of *Santuccimeryx* (BADL 64015) (Table 2). When comparing both genera to *Leptomeryx*, the distance between the frontal-parietal contact and anterior margin of the sagittal is increased as well as the angle between the temporal crests (64° in *Santuccimeryx*, 60° in *Pseudoparablastomeryx*) (Figures 6 and 7; Table 2). Reliable comparison of the basicrania is not possible because of the suboptimal preservation of the only known skull of *P. scotti* (F:AM 95490).

The upper premolars in *P. scotti* develop strong anterolingual cingula, giving them a submolariform appearance with strong anterior and posterior fossettes (Figure 8). The anterolingual cingulum and corresponding fossette are lacking in the P3 for *S. elissae*. The P3 postprotocrista in *S. elissae* is directed posterolaterally, creating a small basin, similar to what is observed in *Pseudoparablastomeryx* but not as strongly pronounced (Figure 8). The upper molars of *Santuccimeryx* have reduced or absent styles and are more antero-posteriorly shortened in comparison to *P. scotti* (Figure 8). See Table 3 for comparative measurements of upper dentition.

The lower dentition of *P. scotti* resembles that of *S. elissae* in that it has smooth enamel, a well-developed buccal pillar, and lacks the *Palaeomeryx*-fold. These characters were consistent with the holotype (F:AM 95490) and all observed, referable specimens of *P. scotti*. The m3 entoconulid in *P. scotti* is, however, greatly reduced when compared to *S. elissae* or *L. evansi*. The dp4 in *S. elissae* appears to be morphologically similar to the condition in *P. scotti*, particularly with cingulum and buccal pillars separating the anteroconid, protoconid, and hypoconid, as also noted by Taylor and Webb (1976). See Table 4 for comparative measurements of lower dentition.

MORPHOLOGICAL TRENDS

Relationships between Eocene and Oligocene leptomerycids continue to rely almost entirely on dental characters, specifically on the morphology of m3, which suggests two distinct lineages: the *L. yoderi–L. mammifer–L. exilis–L. obliquidens* lineage (Korth and Diamond 2002) and the *L. speciosus–L. evansi* lineage (Heaton and Emry 1996, Korth and Diamond 2002) (Figure 9). The *L. speciosus–L. evansi* lineage would also include the progression to *S. elissae*, as suggested by Korth and Diamond (2002) (Figure 9). We primarily agree with these assertions, given the characters provided by the material currently available. However, we believe that BADL 64015 does not bring further clarity to the *L. speciosus–L. evansi* relationship. If *S. elissae* stemmed from *L. evansi*, it would imply a new lineage that emerged in the early Oligocene and provides a link to later Oligocene and Miocene leptomerycids (Figure 9). However, because the dental characters in *S. elissae* are more akin to the condition in *L. speciosus* (Table 1), it is likely that *L. speciosus* gave rise to the two lineages of *L. evansi* and *S. elissae* at to around the Eocene–Oligocene transition (Figure 9). We recognize that once skulls of Eocene leptomerycids are discovered, additional cranial features may further complicate leptomerycid relationships. If a skull of *L. speciosus* were discovered and the cranial characters reflected a closer relationship to *S. elissae* in addition to the dental
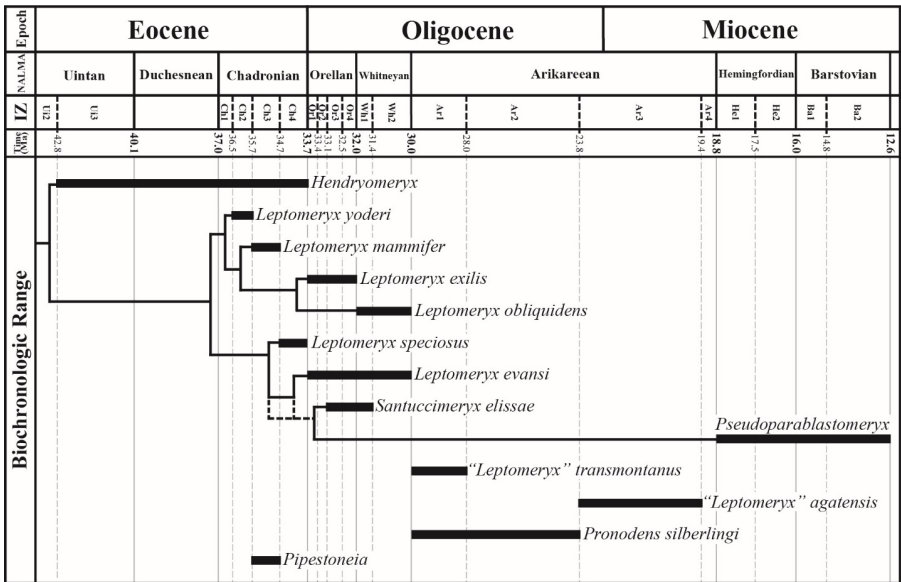

Figure 9. Biochronologic ranges of North American Leptomerycidae with hypothetical phylogenetic relationships inferred by previous authors (Heaton and Emry 1996, Korth and Diamond 2002). Hatched lines illustrate alternative branching points for the inferred *Santuccimeryx—Pseudoparablastomeryx* group. Other taxa of uncertain affinity are not positioned on branches.

characters, it could imply that the cranial anatomy of *L. evansi* is uniquely derived and not necessarily representative of other taxa currently referred to *Leptomeryx*.

Arikareean Leptomerycids: Leptomerycids identified from the Arikareean have been problematic in previous studies and are in need of careful review. Three taxa have been named from Arikareean faunae: *Leptomeryx transmontanus*, *Leptomeryx agatensis*, and *Pronodens silberlingi* (Figure 9 and Table 1). Douglass (1903) named *L. transmontanus* from a partial cranium with upper dentition from the Lower Cabbage Patch Beds of Montana (Ar1). The species was recognized by Frick (1937), but Webb (1998) suggested synonymizing *L. transmontanus* with *Hendryomeryx esulcatus*. Korth and Diamond (2002) suggest that *L. transmontanus* is synonymous with *Pronodens*, based on Rasmussen's (1977) reclassification in an unpublished dissertation. They argue that *Pronodens* likely stemmed from *L. evansi* based on a more prominent *Palaeomeryx*-fold but provide no specimens for reference. The type of *P. silberlingi* figured by Koerner (1940) and Taylor and Webb (1976) exhibits extremely worn molars that do not show features mentioned by Korth and Diamond (2002). There are no unambiguous characters to delineate *L. transmontanus* (Table 1). Therefore, on the basis of measurements alone, this species could just as easily be referred to *L. obliquidens* as to *Pronodens*.

L. agatensis is based on a partial maxilla from the *Syndyoceras* Quarry in Nebraska (Ar3) and has been synonymized with *L. obliquidens* due to morphologic similarities (Cook 1934, Taylor and Webb 1976, Webb 1998). However, Korth and Diamond (2002) again infer an equally close affinity to *Pronodens*. We maintain that, given the state of the *L. obliquidens* and *Pronodens* material, no confident synonymization is currently possible. In contrast to previous authors, Macdonald (1963, 1970) did not assign species-level designations to *Leptomeryx* specimens from the Wounded Knee Fauna (Ar1), the only other published Arikareean leptomerycid material, on account of a lack of unambiguous characters.

Aside from the procumbent incisors, no other characters link *Pronodens* to the Leptomerycidae (Table 1). The molars belonging to the holotype (YPM 13952) are extremely worn, rendering it impossible to ascertain any of the reliable characters utilized to distinguish the species of other leptomerycids. Since the molars and premolars do not provide defining characteristics, *Pronodens* is justified by the loss of p1, a shortened diastema between the canine and p2, and a more posterior position of the mental foramen—all characters found in the anterior portion of the dentary. This portion is the most likely feature of the dentary to be missing in leptomerycid specimens from the White River Group, again making it impossible to refer specimens to *Pronodens* or to synonymize *Pronodens* with other genera (Koerner 1940). Taylor and Webb (1976) attempted to refer one specimen (AMNH 13824, *Leptomeryx obliquidens*) to *Pronodens*, but this is tentative at best. *Pseudoparablastomeryx scotti* is the only other leptomerycid known to share the loss of p1, but it maintains a longer diastema between the canine and p2 despite being more brachycephalic. The dentaries of BADL 64015 are broken at the anterior side of p3, and all other referred *S. elissae* specimens are partial dentaries with cheek teeth. It is thus not possible to discern the presence of p1 or the diastema between the canines and remaining premolars without additional specimens containing these features.

Pronodens is also considered to be slightly larger than *Leptomeryx* (Webb 1998) based on molar measurements, but there is, of course, a limited sample size for this genus. Considering the shortening of the diastema and the premolars, *Pronodens* is likely brachycephalic compared to *Leptomeryx*. It is clear, however, that besides the type specimen, all specimens referred to as *Pronodens* are questionable and have no direct correlation to the type. It will be difficult to track leptomerycid diversity and evolutionary relationships from post-Whitneyan faunae until Arikareean taxa are clarified through additional material.

Convergence with the Tragulidae: *Santuccimeryx* exhibits a suite of characters that appear intermediate between *Leptomeryx* and *Pseudoparablastomeryx* (Table 1), while also demonstrating a morphologic trend of cranial features that appear to be convergent with the Eurasian and African Tragulidae. The postorbital bar is the most prominent example—in the North American leptomerycids, it is composed of equal positions of the frontal and jugal, but in *S. elissae*, the jugal comprises the majority. This trait has never before been documented in North American leptomerycids but has been used as a character used to delineate the Tragulidae from the rest of Traguloidea (Vislobokova 2001, Métais and Vislobokova 2007). The shallow and poorly-developed postorbital constriction in *S. elissae* (and in *Pseudoparablastomeryx*) is also observed in the extant tragulids, *Hyemoschus* and *Tragulus*. The basioccipital in *Santuccimeryx* is trapezoidal, again similar to the tragulid *Hyemoschus* and differing greatly from the subrectangular basioccipital in *Leptomeryx*. All of these characters—the jugal comprising most of the postorbital bar, the shortened sagittal crest, and the posteriorly expanded or trapezoidal basioccipital—have been used as synapomorphies to distinguish Tragulidae from other Traguloidea (Vislobokova 2001, Métais and Vislobokova 2007). Given that these cranial features are similar to what is documented in the evolution of the Tragulidae by previous authors (Vislobokova 2001, Métais and Vislobokova 2007), the character convergence of *Santuccimeryx* warrants future exploration.

CONCLUSIONS

The small, hornless, deer-like leptomerycids proliferated across the North American Great Plains from the late Eocene into the Miocene, leaving behind an abundant fossil record that has proven biostratigraphically valuable. Despite their significance and abundance, leptomerycid evolutionary relationships resist clarification due to both the scarcity of cranial material and the high degree of individual variation expressed in leptomerycid dentition. No non-dental cranial material has yet been reported from *Hendryomeryx*, *L. blacki*, *L. yoderi*, *L. mammifer*, *L. speciosus*, *L. exilis*, *Pronodens,* or *Pseudoparablastomeryx francescita*. Any studies into leptomerycid phylogeny up to this point have only had skulls from *L. evansi*, *L. obliquidens*, and *P. scotti* to reference and have thus been forced to rely on dental characters and temporal succession. The evolutionary relationships of the leptomerycids should thus be reevaluated if and when supplementary cranial material becomes available.

The addition of BADL 64015 to the known record of leptomerycid cranial material provides insights into evolutionary relationships that would not have been possible with only dental material, thereby proving that dental characters alone are problematic in delineating leptomerycid taxa and evolutionary relationships. Based solely on dental characters, BADL 64015 should undoubtedly be placed within *Leptomeryx*, as Korth and Diamond (2002) proposed, but observed cranial characters diverge vastly from *Leptomeryx* and instead suggest placement within *Pseudoparablastomeryx* and convergence with the Tragulidae. When we consider the intermediate nature of the anatomical traits exhibited by BADL 64015 in conjunction with its temporal intermediacy to *Leptomeryx* and *Pseudoparablastomeryx*, BADL 64015 not only validates Korth and Diamond's (2002) distinction of *Leptomeryx elissae* as a species but also elevates the taxon to a new genus: *Santuccimeryx*.

LITERATURE CITED

Benton, R. C., D. O. Terry Jr., E. Evanoff, and G. McDonald. 2015. The White River Badlands: Geology and Paleontology. pp. 1-222. Indiana University Press, Bloomington, Indiana.

Bouvrain, G. and D. Geraads 1985. Un squelette complet de Bachitherium (Artiodactyla, Mammalia), de l'oligocène de Céreste (Alpes de Haute Provence). Remarques sur la systématique des ruminants primitifs. Comptes Rendus de L'Académie des Sciences, Paris, Sér. 2, 300(2):75–78.

Cook, H. J. 1934. New artiodactyls from the Oligocene and Lower Miocene of Nebraska. American Midland Naturalist 15:148-165.

Douglass, E. 1903. New vertebrates from the Montana Tertiary. Annals of the Carnegie Museum 2:145-199.

Evanoff, E. E., D. O. Terry Jr., R. C. Benton, and H. Minkler. 2010. Field guide to the geology of the White River Group in the North Unit of Badlands National Park. Pages 96-127 in Terry, M.P., E.F. Duke, and J.A. Tielke, editors. Geologic field trips in the Black Hills region, South Dakota: South Dakota School of Mines and Technology Bulletin 21.

Frick, C. 1937. Horned ruminants of North America. Bulletin of the American Museum of Natural History 69:1–669.

Gazin, C. L. 1955. A review of the upper Eocene Artiodactyla of North America. Smithsonian Miscellaneous Collections 128:1–96.

Gentry, A. W. and J. J. Hooker 1988. The Phylogeny of the Artiodactyla, in The Phylogeny and Classification of the Tetrapods, vol. 2: Mammals. Oxford: Clarendon, pp. 235–272.

Geraads, D., G. Bouvrain, and J. Sudre. 1987. Relations phylétiques de Bachitherium Filhol, ruminant de l'Oligocène d'Europe occidentale. Palaeovertebrata 17(2):43–73.

Heaton, T. H. and R. J. Emry. 1996. Leptomerycidae. pp. 581-608 in D. R. Prothero and R. J. Emry (eds.) The Terrestrial Eocene-Oligocene Transition North America. Cambridge University Press, New York, New York.

Janis, C. 1987. Grades and Clades in Hornless Ruminant Evolution: The Reality of the Gelocidae and the Taxonomic Position of Lophiomeryx and Bachitherium. Journal of Vertebrate Paleontology 7(2):200–216.

Koerner, H. E. 1940. The geology and vertebrate paleontology of the Fort Logan and Deep River Formations of Montana Part I. New Vertebrates. American Journal of Science 238(12):837-862.

Korth, W. W. 2014. Rodents (Mammalia) from the Whitneyan (middle Oligocene) Cedar Pass Fauna of South Dakota. Annals of the Carnegie Museum 82(4):373-398.

Korth, W. W. and M. E. Diamond. 2002. Review of Leptomeryx (Artiodactyla, Leptomerycidae) from the Orellan (Oligocene) of Nebraska. Annals of Carnegie Museum 71:107–129.

Lambe, L. M. 1908. The Vertebrata of the Cypress Hills, Saskatchewan. Contributions to Canadian Palaeontology, Geological Survey of Canada 3(4): 1-64.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio Decima 1:1-824.

Lull, R. S. 1922. Primitive Pecora in the Yale Museum. American Journal of Science 5:111-119.

Macdonald, J. R. 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. American Museum of Natural History Bulletin 125:139–238.

Macdonald, J. R. 1970. Review of the Wounded Knee faunas of southwestern South Dakota. Bulletin of the Los Angeles County Museum of Natural History and Science 8:1-82.

Mathis, J. E. and B. J. MacFadden. 2010. Quantifying *Leptomeryx* (Mammalia, Artiodactyla) Enamel Surface Area Across the Eocene-Oligocene Transition in Nebraska. Palaios 25: 682-687.

Matthew, W. D. 1903. The fauna of the Titanotherium beds at Pipestone Springs, Montana. Bulletin of the American Museum of Natural History 19:197–226.

Métais, G. and I. A. Vislobokova. 2007. Basal Ruminants. pp. 177-188 in D. R. Prothero and S. E. Foss (eds.). The Evolution of Artiodactyls. Johns Hopkins University Press, Baltimore, Maryland.

Owen, R. 1848. Description of teeth and portions of jaws of two extinct Anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the NW coast of the Isle of Wight: with an attempt to develope Cuvier's idea of the Classification of Pachyderms by the number of their toes. Quarterly Journal of the Geological Society of London 4:103-141

Prothero, D. R. and R. J. Emry. 2004. The Chadronian, Orellan and Whitneyan North American Land Mammal Ages. Pages 156-168 in M.O. Woodburne (ed.). Late Cretaceous and Cenozoic Mammals of North America: Geochronology and Biostratigraphy. University of California Press, Oakland, California.

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 325:39-61.

Prothero, D. R. and R. J. Emry. 1996. Camelidae. pp. 609-651 in D. R. Prothero and R. J. Emry (eds.) The Terrestrial Eocene-Oligocene Transition North America. Cambridge University Press, New York, New York.

Rasmussen, D. L. 1977. Geology and mammalian paleontology of the Oligocene-Miocene Cabbage Patch Formation, central-western Montana. Unpublished Ph.D. Dissertation, University of Kansas, Lawrence, Kansas.

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

Scott, W. B. 1899. The selenodont artiodactyls of the Uinta Eocene. Transactions of the Wagner Free Institute of Science, Philadelphia 6:1-121.

Scott, W. B. 1940. Artiodactyla. Transactions of the American Philosophical Society 28:363–746.

Simpson, G. G. 1945. The Principles of Classification and a Classification of Mammals. Bulletin of the American Museum of Natural History 85:1-350.

Spaulding, M., M. A. O'Leary, and J. Gatesy. 2009. Relationships of Cetacea (Artiodactyla) Among Mammals: Increased Taxon Sampling Alters Interpretations of Key Fossils and Character Evolution. PLoS ONE 4(9): e7062. https://doi.org/10.1371/journal.pone.0007062

Stevens, M. S., D. R. Prothero, C. Cleaveland, E. Welsh, K. Marriott, T. Htun, D. Balassa, S. M. Olson, K. I. Watmore, and D. Wheeler. 2023. Systematics of the Late Oligocene and Miocene Oreodonts (Merycoidodontidae: Artiodactyla). New Mexico Museum of Natural History and Science Bulletin 93:1-226.

Tabrum, A. R. and G. Métais. 2007. *Pipestoneia douglassi*, a new genus and species of selenodont artiodactyl from the Pipestone Springs area, Jefferson County, Montana. Bulletin of the Carnegie Museum of Natural History 39:83-96.

Taylor, B. E. and S. D. Webb. 1976. Miocene Leptomerycidae (Artiodactyla, Ruminantia) and their relationships. American Museum Novitates, 2596:1-22.

Vislobokova, I. A. 2001. Evolution and classification of Tragulina (Ruminantia, Artiodactyla). Paleontological Journal, 35:69–145.

Webb, S. D. 1998. Hornless ruminants. pp. 463–476 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.) Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, U.K

Webb, S. D. and B. E. Taylor. 1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. Bulletin of the American Museum of Natural History 167:117–158.

Wilson, J. A. 1974. Early Tertiary Vertebrate Faunas, Vieja Group and Buck Hill Group, Trans-Pecos Texas: Protoceratidae, Camelidae, Hypertragulidae. Bulletin of the Texas Memorial Museum-34.

Wortman, J. L. 1898. The extinct Camelidae of North America and some associated forms. Bulletin of the American Museum of Natural History 10(7):93-142.

Zanazzi, A., M. J. Kohn, and D. O. Terry. 2009. Biostratigraphy and Paleoclimatology of the Eocene-Oligocene boundary section at Toadstool Park, northwestern Nebraska, USA. The Geological Society of America Special Paper 452:197-214.

Zittel, K. A. 1893. Handbuch der Paläeontologie. Abteilung I. Paläeozoologie. Band IV, Vertebrata (Mammalia). R. Oldenbourg, Munich, Germany, 799 pp.