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EARLY ARIKAREEAN (LATE OLIGOCENE) EOMYIDAE (MAMMALIA, RODENTIA) FROM NEBRASKA

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ABSTRACT

Five species of eomyid rodents are recognized from the earliest Arikareean (late Oligocene) Ridgeview local fauna of Nebraska. This is the greatest diversity of Arikareean eomyids of any fauna known from North America. The species recognized are *Leptodonotmys douglassi* (Burke), *Leptodontomys* sp., *Neoadjidaumo hemedapus* n. gen. et n. sp., *Pentabuneomys engesseri* n. sp., and *Zophoapeomys* sp. It is suggested that nearly all of these species were derived from earlier North American eomyids. Based on the early occurrence in the Ridgeview fauna, *Pentabuneomys* and subfamily Apeomyinae likely migrated to Europe from North America near the beginning of the Miocene. *Neoadjidaumo* is viewed as being derived from earlier North American eomyids but developed some dental morphologies convergent with those of the European Miocene genus *Ritteneria* Stehlin and Schaub.

INTRODUCTION

Eomyid rodents first appear in North America in the Uintan (middle Eocene) and persist until the end of the Hemphillian (late Miocene), reaching their greatest diversity in the Chadronian and Orellan (latest Eocene to early Oligocene [Korth, 1994]). Since the Orellan, no more than four species of eomyids are known from any time interval. Although eomyids are known from several North American Arikareean faunas (Macdonald, 1972; Korth, 1992; Albright, 1996, 1998; Storer, 2002), they are usually represented by only a few isolated cheek teeth. The most diverse Arikareean eomyid fauna previously cited was from Saskatchewan, where three different species have been recognized, but this fauna was based on only ten isolated cheek teeth (Storer, 2002).

The best represented species of eomyid previously known from the Arikareean was *Leptodontomys douglassi*, known from several jaws and maxillary fragments from a single fossil quarry in Dawes County, Nebraska (Korth and Bailey, 1992). This quarry has since been more extensively excavated and referred to as the Ridgeview local fauna (Bailey, 2004). The material described below is from the Ridgeview fauna and is the most diverse and best represented fauna of eomyids (greater number and more complete specimens) from the Arikareean of North America. Five species of eomyids are recognized from the Ridgeview fauna, based on over 60 specimens including complete upper and lower dentitions. The diversity of eomyids from the Ridgeview fauna increases the number of known eomyids from the Arikareean of North America to six genera and at least seven different species.

All of the specimens described below are from the Ridgeview local fauna that is dated as the earliest Arikareean (Ar1 of Tedford et al., 2004), which has been referred to the latest Oligocene. The stratigraphy, locality data, and age of this fauna are described in detail by Bailey (2004).

Dental nomenclature used below is modified from Wood and Wilson (1936). Abbreviation used for University of Nebraska State Museum specimens and localities is UNSM.

SYSTEMATIC PALEONTOLOGY

Family Eomyidae Winge, 1887
Subfamily Eomyinae Winge, 1887
Leptodontomys Shotwell, 1956
Leptodontomys douglassi (Burke, 1934)
(Figures 1, 2B; Table 1)

Adjidaumo douglassi Burke, 1934
Leptodontomys douglassi (Burke) Korth and Bailey, 1992

Referred Specimens—UNSM 26533, 130288 to 130295, 130398 to 130425, 130431, 130432, lower dental elements; UNSM 26511, 26523, 130284, 130426 to 130430, maxillae with upper cheek teeth.

Description—Specimens of *Leptodontomys douglassi* from UNSM locality Dw-121 (Ridgeview fauna) have been described previously (Korth and Bailey, 1992). However, the description of the upper cheek teeth was based on a specimen (UNSM 26531)

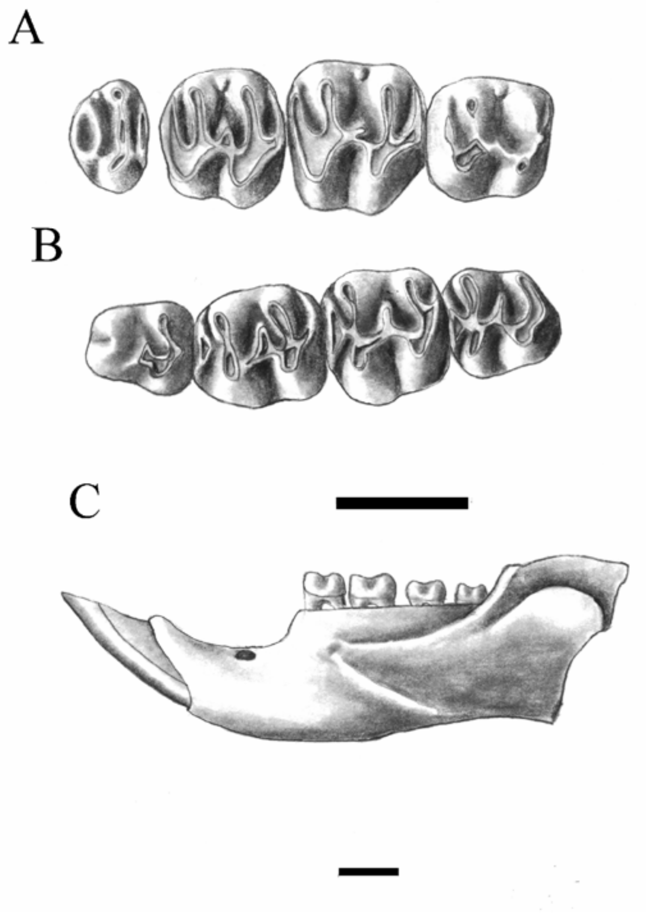

FIGURE 1. Dentition and mandible of *Leptodontomys douglassi* from the Ridgeview fauna (locality UNSM Dw-121). A, Right P^4-M^3, UNSM 130430. B, Left P_4-M_3, UNSM 26533. C, Same specimen as B, lateral view of mandible. Bar scales = 1 mm.

that appears to be referable to a different, smaller species. The description of the lower dentition and mandible are not changed from that of Korth and Bailey (1992). The only lower tooth not described earlier was M_3. The last molar is smaller than the first two. The anterior half of the tooth is very similar to the anterior molars. The anterior cingulum attaches to the metalophid near its center and extends both lingually and buccally, but not for the entire width of the tooth. The metaconid and protoconid are slightly anteroposteriorly compressed. The metalophid is continuous and forms a straight line from the metaconid to the protoconid. The ectolophid is complete from the protoconid to the hypoconid. The mesolophid is relatively long, usually longer than in the anterior molars, but never reaches the lingual margin of the tooth. The hypolophid is a posteriorly bowed loph connecting the entoconid and hypoconid. The entoconid is reduced in size, smaller than any of the other cusps. There is no indication of a posterior cingulum.

P^4 is smaller than the first two molars and quadrate. The four major cusps (paracone, metacone, hypocone, protocone) are of equal size and show a minor degree of anteroposterior compression. There is a small anterior cingulum originating in the middle of the protoloph with a minute capsule and running along the anterior slope of the paracone. The endoloph is variably complete. In specimens where it is not complete, a narrow valley separates the protocone from the anterior end of the mesoloph. A mesoloph is present but short on all specimens. The protoloph is slightly bowed anteriorly. The metaloph runs directly lingually from the metacone to the center of the hypocone. A distinct but small mesostyle is present along the buccal margin of the tooth, equally spaced between the paracone and metacone. The posterior cingulum runs the entire width of the tooth, arising from the hypocone and running to the buccal edge of the tooth.

The first two molars are nearly identical in occlusal morphology, M^2 being only slightly smaller than M^1. The anterior cingulum is much stronger than in the premolar and runs from the centerline of the tooth to the buccal margin, isolating a transverse valley between it and the protoloph and paracone. The protoloph runs directly lingually from the paracone to the protocone, joining the latter cusp just anterior to its center. The endoloph is always complete with a short mesoloph or small, triangular mesocone. The mesostyle is always present and more strongly developed than on P^4. The posterior cingulum is as in the premolar.

M^3 is greatly reduced in size, especially its (anteroposterior) length. The protoloph is similar to that of the anterior molars, but the paracone and protocone are reduced in size. The anterior cingulum parallels the protoloph, and both are oriented directly buccolingually. The posterior half of the tooth is greatly reduced. The metacone is a minute cusp at the buccal end of the metaloph and the hypocone is not recognizable. The metaloph and posterior cingulum join at their ends forming on ovate loop with a shallow central depression. The mesostyle is minute. The very short endoloph is reduced to a minute connection between the lingual end of the metaloph and the protocone.

Discussion—*Leptodontomys douglassi* is the most abundant eomyid in the Ridgeview fauna. It is easily distinguishable from the species described below by its smaller size (except *Leptodontomys* sp.) and morphology of the cheek teeth (lower crown height; complete ectolophids; longer mesolophids; longer posterior cingula; anterior cingulum not as closely appressed to the metalophid).

TABLE 1. Dental and mandibular measurements of *Leptodontomys douglassi* from the Ridgeview fauna, Nebraska. Abbreviations used: L, anteroposterior length; W, transverse width; N, number of specimens; M, mean; OR, observed range; S, standard deviation; CV, coefficient of variation. Measurements in mm.

		N	M	OR	S	CV
P^4	L	15	0.81	0.73-0.88	0.05	6.07
	W	15	0.91	0.81-0.96	0.05	5.62
M^1	L	7	0.93	0.89-0.95	0.03	2.82
	W	7	1.03	0.97-1.08	0.04	3.61
M^2	L	2	0.91	0.90-0.92		
	W	2	1.08	1.04-1.12		
M^3	L	2	0.69	0.63-0.75		
	W	2	0.93	0.86-0.99		
P^4-M^3		1	3.57			

		N	M	OR	S	CV
P_4	L	38	0.72	0.65-0.93	0.06	7.57
	W	38	0.72	0.54-0.80	0.06	7.89
M_1	L	38	0.95	0.85-1.06	0.05	5.03
	W	36	0.85	0.77-0.93	0.05	5.36
M_2	L	31	0.89	0.73-1.02	0.06	6.64
	W	31	0.88	0.80-0.99	0.05	5.86
M_3	L	8	0.84	0.78-0.91	0.04	4.70
	W	8	0.78	0.71-0.82	0.04	4.92
P_4-M_3		16	3.62	3.16-3.85	0.16	4.31
I1	L	13	0.87	0.69-1.00	0.08	9.75
	W	14	0.57	0.47-0.66	0.05	8.59

	N	M	OR	S	CV
length of diastema	13	2.83	2.47-3.15	0.21	7.51
depth of mandible at M_1	22	2.53	2.18-2.75	0.16	6.22

Leptodontomys. sp.

(Figure 2A, Table 2)

Leptodotomys douglassi (Burke) Korth and Bailey, 1992 (in part)

Referred Specimen—UNSM 26531, right maxilla with P^4-M^3.

Discussion—Korth and Bailey (1992) described UNSM 26531 in detail believing that it belonged to *Leptodontomys douglassi*. However, now that more complete maxillary dentitions are available for the latter, it is clearly distinguishable as a separate species. The only known specimen of *Leptodontomys* sp. is nearly 20% smaller than specimens of *L. douglassi*, and similar in size to the Barstovian species *L. quartzi* and *L. russelli* (Shotwell, 1967; Storer, 1975). The premolar differs from that of *L. douglassi* in lacking a mesostyle. The anterior cingulum on UNSM 265631 is reduced to a minute cuspule on the anterior slope of the paracone. M^1 and M^2 are nearly square, having nearly the same width as length (Table 2), whereas in other *Leptodontomys* the first two upper molars are distinctly wider than long (Table 1; Shotwell, 1967:table2; Lindsay, 1972:table 8). On the upper molars of *Leptodontomys* sp., the metaloph is slightly bowed anteriorly (metacone attaches to endoloph lingually, anterior to the hypocone). In *L. douglassi* the metaloph is straight and the loph from the metacone joins the hypocone at its center or slightly anterior to it. The cups of the upper molars in *L. douglassi* appear slightly anteroposteriorly compressed (especially the lingual cusps) and those on the molars of *Leptodontomys* sp. are not compressed at all.

It is likely that *Leptodontomys* sp. represents a new species. However, it is not appropriate to name a new species at this time based on a single specimen. If additional specimens, including lower dentitions, can be referred to the same species as UNSM 26531, then it should be formally named.

Genus *Pentabuneomys* Engesser, 1990

Type Species—*Pentabuneomys rhodanicus* (Hugueney and Mein, 1968).

Referred Species—*P. engesseri* n. sp.

Range—Early Miocene (early Orleanian, MN 3-4a) of Switzerland and late Oligocene (early Arikareean) of Nebraska.

Pentabuneomys engesseri n. sp.

(Figure 3; Table 3)

Type and Only Specimen—UNSM 130278, partial right mandible with incisor, P_4-M_1, and roots for M_2-M_3.

Diagnosis—Differs from the type species in being smaller; having lophs more poorly developed on cheek teeth; having lower cheek teeth with the mesoconid larger and more isolated; and a shorter posterior cingulum.

Etymology—Patronym for Burkhart Engesser, in reference to his extensive work on European eomyids.

Description—The mandible is slender. None of the mandible is preserved anterior to P_4, so there is no evidence of the mental foramen or diastema. The masseteric scar is similar to that of some species of *Eomys* (Engesser, 1990:abb. 28, 29). The masseteric scar is marked by dorsal and ventral ridges that are concave upward and meet below the posterior margin of P_4, fusing into a low, long protuberance. The morphology of the ascending ramus is unknown due to the posterior portion of the mandible being broken away. The base of the incisor is evident on the lateral side of the mandible, posterior to the alveolus for M_3.

The lower incisor is oval in cross-section and narrower (buccolingually) than it is high. The anterior enamel surface is gently convex with no ornamentation.

The cheek teeth are brachydont and bunodont, showing very little evidence of loph development. The premolar is two-rooted, and the molars are three-rooted (two anterior, one posterior). The premolar is much

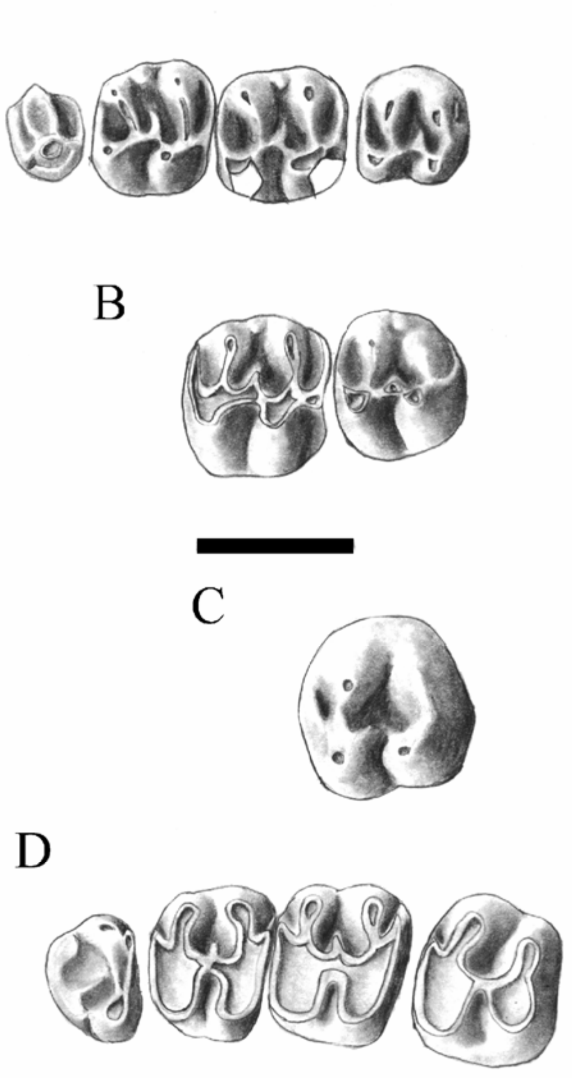

FIGURE 2. Upper cheek teeth of eomyids. A, *Leptodontomys* sp., UNSM 26531 (holotype), right P^4-M^3. B. *L. douglassi*, UNSM 130426, right P^4-M^1. C, *Neoadjidaumo hemedapus*, UNSM 130285, right P^4. Bar scale = 1 mm.

smaller and narrower anteriorly than M_1 (Table 4). The protoconid and metaconid are equal in size and separated from one another by a narrow, deep valley. The protoconid is slightly anterior to the metaconid. In the center of the tooth is a large, circular mesoconid. It is not connected to the metalophid cusps, and only a very low, short connection is present between the mesoconid and the hypoconid. The hypoconid and entoconid are connected by a thin loph (hypolophid) that forms a posteriorly pointing V. At the center of the hypolophid is a short posterior cingulum that is separated from the hypolophid by a small, deep valley. The posterior cingulum is oriented nearly at a 90° angle from the hypolophid, bends lingually, and ends before reaching the level of the apex of the entoconid.

The first molar is larger than the premolar and more nearly rectangular in shape. The lingual cusps (metaconid and entoconid) are anteroposteriorly compressed and the buccal cusps (protoconid and hypoconid) are circular in outline. The anterior cingulum does not extend for the entire width of the tooth, but runs from the lingual side of the tooth buccally to a point even with the apex of the protoconid, well short of the buccal margin of the tooth. The cingulum is closely appressed to the metalophid and widest at its center. The rounded cusps of the metalophid are subequal in size. These cusps are connected by a short, low ridge. The mesoconid, as in P_4, is large and round, nearly the size of the major cusps of the tooth. It is not connected to the metalophid, but is close to the hypoconid and forms a minute connection with it. The hypolophid, connecting the entoconid and hypoconid, is slightly posteriorly bowed. Similar to P_4, the posterior cingulum arises from the center of the hypolophid, extends directly posteriorly, then turns lingually (at approximately a 90° angle) and ends well before the level of the apex of the entoconid. A small, deep valley separates the posterior cingulum from the hypolophid.

TABLE 2. Dental measurements of *Leptodontomys* sp., UNSM 26531. Measurements in mm. Abbreviations as in Table 1.

P^4L	0.64
P^4W	0.72
M^1L	0.82
M^1W	0.85
M^2L	0.80
M^2W	0.80
M^3L	0.52
M^3W	0.70
P^4-M^3	2.94

Discussion—*Pentabuneomys engesseri* is referable to this genus based on Engesser's (1990) diagnosis of the genus: 1) brachydont and bunodont cheek teeth; 2) large, circular mesoconid on the lower cheek teeth; and 3) deep valley between the hypolophid and posterior cingulum. *P. engesseri* differs from the type species, *P. rhodanicus* from Europe, in being smaller, having a lesser degree of loph development on the cheek teeth, and shorter posterior cingula on the lower cheek teeth. In all known characters, *P. engesseri* is more primitive than *P. rhodanicus*.

All of the previously described material of the type species of *Pentabuneomys* has been isolated cheek teeth (Hugueney and Mein, 1968; Engesser, 1990). The type specimen of *P. engesseri* is the first described mandible and incisor of the genus. The masseteric scar on the mandible most closely approaches that of *Leptodontomys douglassi*, also from the early Arikareean (Fig. 1C; Korth and Bailey, 1992:fig. 1g), and species of *Eomys* from Europe (Engesser, 1990:abb. 28, 29).

Engesser (1990, 1999) noted that *Pentabuneomys* was clearly not derived from any European eomyid from the late Oligocene or earlier Miocene because of its lack of lophodonty, and suggested that it was an immigrant species. Recognition of an earlier, more primitive species of *Pentabuneomys* from North America substantiates this idea and indicates the source of the immigrant taxon.

The origin of *Pentabuneomys engesseri* is uncertain. Similar to the record in Europe, there is no obvious ancestor in the North American record. Even with the diversity of Chadronian eomyids, none appears to retain the bunodonty of the cheek teeth of *Pentabuneomys*. It is possible that *Pentobuneomys* originated from an early *Leptodontomys*-like ancestor with the simplification (reduction of lophodonty) of the cusps of the cheek teeth.

The only North American eomyids with similar bunodonty of the cheek teeth are the large Hemphillian eomyids referred to *Kansasimys* (Wood, 1936; Wahlert, 1978; Korth, 1994). Except for its size, *Kansasimys* has the same degree of bunodonty of the cusps and large central mesoconid of the lower cheek teeth of *Pentabuneomys*. Fahlbusch (1979) was unable to relate *Kansasimys* to any other North American or Eurasian eomyid. Wahlert (1978) described the skull of *Kansasimys* and considered it distinct from all other eomyines as well.

TABLE 3. Measurements of the holotype of *Pentabuneomys engesseri,* UNSM 130278. Abbreviations as in Table 1.

P_4L	0.74
P_4W	0.62
M_1L	0.90
M_1W	0.77
I_1L	0.80
I_1W	0.58
P_4-M_3	3.34
Depth of mandible below M_1	1.94

Genus *Neoadjidaumo* n. gen.

Type Species—*Neoadjidaumo hemedapus* n. sp.

Referred Species—Only known species of the genus.

Range—Early Arikareean (late Oligocene) of Nebraska.

Diagnosis—Cheek teeth mesodont; anterior cingulum on lower molars indistinct (fused to metalophid); posterior cingulum on P_4-M_1 more greatly reduced than in *Metadjidaumo*, completely lacking on M_2, reduced to small wrinkle in wear fossettid of hypolophid of M_1; mesolophid on P_4 lacking, and on lower molars is very short and positioned posterior to the midline of the tooth; connection of mesoconid to protoconid very weak or absent (ectolophid only weakly developed); small enclosed trigonid basin on P_4; P^4 larger than M^1, lacking anterior cingulum; massteric scar on mandible U- or V-shaped anteriorly.

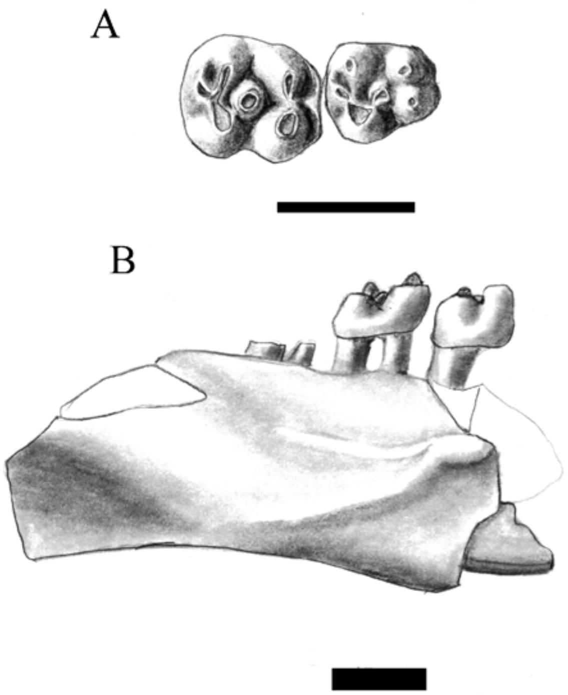

FIGURE 3. Dentition and mandible of *Pentabuneomys engesseri*, UNSM 130278. A, occlusal view, P_4-M_1. B, lateral view of mandible. Bar scales = 1 mm.

Etymology—Greek, *neos*, new; *Adjidaumo*, related North American eomyid.

Discussion—*Neoadjidaumo* differs from the *Leptodontomys* from Dw-121 in being slightly larger, having weaker anteroposterior connections of the lophs (endoloph on uppers, ectolophid on lowers), and having the anterior and posterior cingula fusing with the primary lophs (no distinct cingula) on all cheek teeth. The massteric scar on the mandible of *Neoadjidaumo* is typical of earlier North American eomyids such as *Adijdaumo* and *Paradjidaumo*, with the dorsal and ventral ridges converging anteriorly and ending in a U-shape below P4. The scar on specimens of *Leptodontomys* is similar to that of European species of *Eomys* where both dorsal and ventral ridges are dorsally concave and do not form the U at its anterior extent (see above description of *L. douglassi*).

Metadjidaumo has a similar reduction of the posterior cingulum on the lower molars as in *Neoadjidaumo* (Setoguchi, 1978), but is distinguished from the latter by having more distinct anterior cingula, a stronger connection of the protoconid to the mesoconid, and having lophs that are high and thin rather than broad.

The early Miocene European genus *Ritteneria* has similar occlusal morphology of the cheek teeth with reduction of the endoloph-ectolophid and dominance of two broad, transverse lophs and reduction of the cingula as in *Neoadjidaumo*. However, Engesser (1990) demonstrated that *Ritteneria* was directly derived from the late Oligocene *Rhodanomys*, which in turn, was derived from earlier Oligocene *Eomys*. Based on Engesser's (1990) derivation, the mesoloph on the upper molars in *Rhodanomys* is very long (reaching the buccal margin of the tooth) and ultimately fuses with the protoloph. In *Neoadjidaumo* the mesoloph on the upper molars is very short. Even the most derived species of *Ritteneria* maintain a distinct, detached anterior cingulum on the lower molars (Engesser, 1999:fig. 30.4), whereas the anterior cingulum on the lower molars of *Neoadjidaumo* fuses with the metalophid, forming a broad loph. The masseteric scar on the mandible of *Neoadjidaumo* is similar to that of Orellan eomyids from North America rather than that of European eomyids from which *Rhodanomys* and *Ritteneria* were derived. Therefore, it appears that the similarities in the occlusal morphology of the cheek teeth between *Neoadjidaumo* and *Ritteneria* were attained convergently.

Neoadjidaumo hemedapus n. sp.
Figures 2C, 4; Table 4

Type Specimen—UNSM 26597, right mandible with incisor and p4-m2.

Referred Specimens—UNSM 26552, 130280 to 130282, mandibles with lower cheek teeth; UNSM 130285, 130286, 130287, partial maxillae with P^4, and UNSM 130510, maxilla with P^4-M^3.

Diagnosis—Only species of the genus.

Etymology—Greek, *hemedapos*; native or indigenous.

Description—The cheek teeth are submesodont, higher crowned than *Adjidaumo*, near that of *Paradjidaumo*. The lower premolar is smaller than M_1 and narrower anteriorly than posteriorly. The metalophid consists of two subequal cusps, protoconid and metaconid, that are separated by a narrow valley. There is a minute transverse loph that connects the protoconid and metaconid blocking the trigonid basin anteriorly. Posteriorly, the cups are tapered medially, and fuse posteriorly forming a V-shape, enclosing the trigonid posteriorly. These cusps fuse after only moderate wear into a broad transverse loph. The hypolophid is separated from the metalophid by a deep transverse valley. The hypolophid cusps are marginal and wear into a transverse loph. The posterior cingulum is minute but present posterior to the entoconid. Running anteriorly from the hypoconid is a low ectolophid. It tapers anteriorly and either ends before reaching the protoconid, or is connected by a very thin, low loph that is continuous with the protoconid. There is no distinct mesoconid or mesolophid.

There are no molars in the collection that are completely unworn. On the least worn M_1, the anterior cingulum is entirely included in the metalophid. The only evidence of an anterior cingulum is a slight wrinkle in the wear fossett anterior to the metaconid. The metalophid wears to a broad, gently anteriorly convex loph. The hypolophid similarly wears to a broad loph that bows posteriorly. The posterior cingulum on M_1 is minute, smaller than on P_4. There is no evidence of it on specimens with only moderate wear. The central transverse valley is wide and deep. The ectolophid runs anterolingually from the hypoconid to a small mesolophid, just posterior to the center of the tooth. The position of the mesolophid is closer to the hypolophid than metalophid. With wear, a small circular fossettid develops between it and the hypolophid. From the center of the tooth the ectolophid continues anterobuccally to meet the protoconid. However, the anterior half of the ectolophid is very low and thin. In some worn specimens there is no evidence of this connection between the metalophid and hypolophid.

All specimens of M_2 or M_3 are heavily worn into two broad transverse lophs with either no, or very small connection (ectolophid). The last molar is smaller than either of the first two.

On P^4, the protoloph consists of the two major cusps, paracone and protocone that are equal in size and wear to a broad transverse loph. There is no indication of an anterior cingulum. In some specimens the protocone and paracone are the same distance from one another as the cusps of the metaloph, in others they are slightly closer together. The metacone and hypocone are equal in size and form the metaloph. The endoloph is complete only on P^4 of UNSM 130510 where it is a short, thin anteroposterior loph. Where incomplete, the endoloph is poorly developed and appears as a small spur extending anterobuccally from the hypocone, making the central transverse valley complete for the entire width of the tooth.

The first and second upper molars on UNSM 130510 are nearly identical to one another and moderately worn. Both molars are slightly smaller

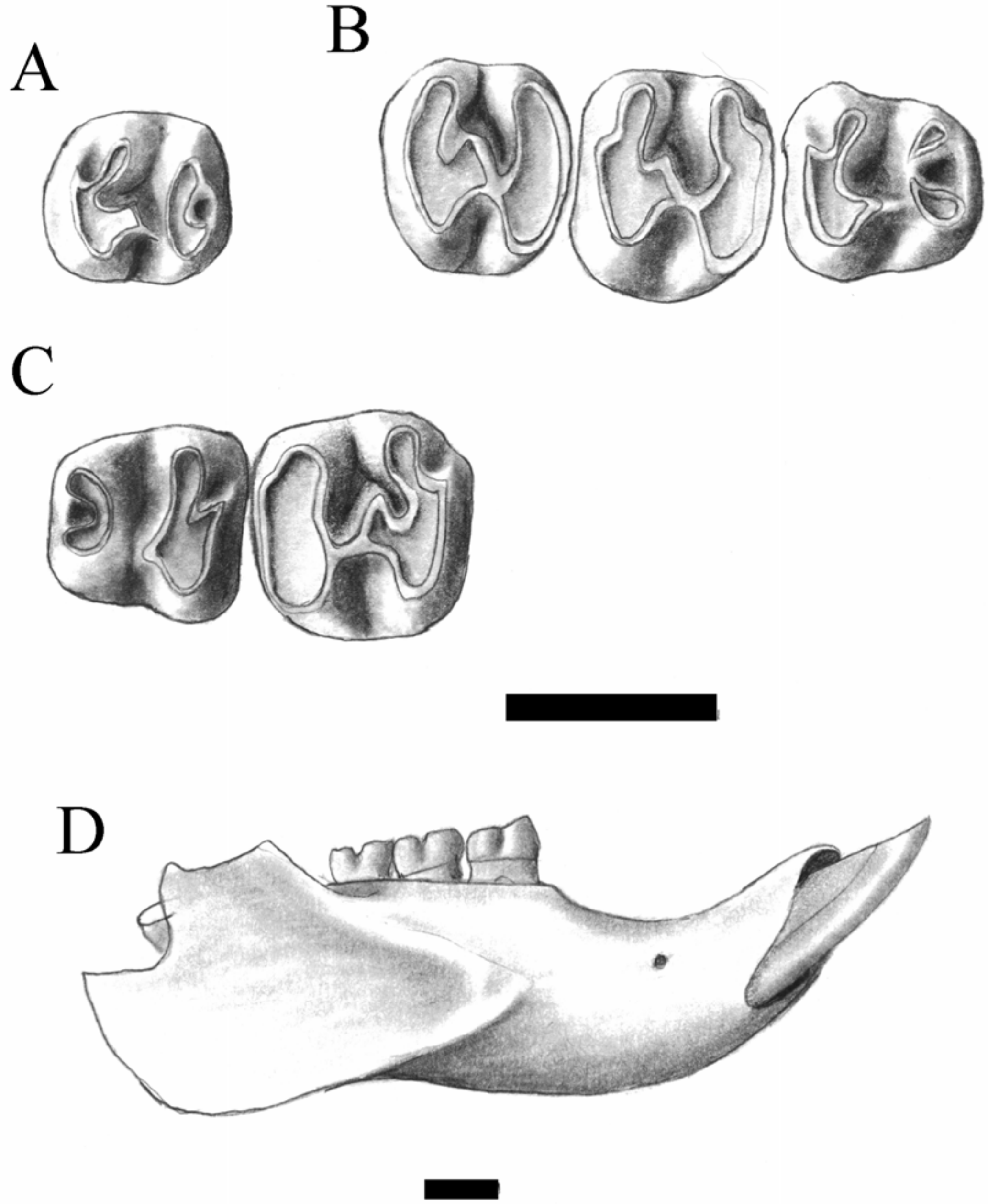

FIGURE 4. Dentition and mandible of *Neoadjidaumo hemedapus*. A, Right P_4, UNSM 130281. B, Right P_4-M_2 (holotype), UNSM 26597. C, Left P_4-M_1, UNSM 130282. D, Right lateral view of mandible, UNSM 26597. Bar scales = 1 mm.

than P^4. The occlusal pattern is quadrate with four subequal sized cusps. The only remnants of the cingula are short spurs anterior to the paracone and posterior to the metacone, respectively. The endoloph is complete but is very short and thin. A minute mesoloph extends buccally.

M^3 is the smallest cheek tooth and roughly triangular in outline. There is a complete anterior cingulum and protoloph that are approximately parallel and run the entire width of the tooth. They are closely appressed and converge at the protocone. The metacone and hypocone are reduced to wide wear facets along the posterior margin of the tooth which is rounded posteriorly. A thin loph arises from the hypocone and exends into the central basin of the tooth, ending posterior to the protoloph.

Discussion—Korth (1981) named a species of *Metadjidaumo* from the Orellan of Colorado, *M. cedrus*. The latter was distinguished from the type species *M. hendryi* from Wyoming by its larger size, having P_4 larger than M_1, and having the posterior cingulum on M_1 fuse lingually with the entoconid. Later, Korth (1994) questionably listed this species in *Orelladjidaumo* (a genus known only from a single species from Nebraska) without explanation. However, the presence of a small, enclosed trigonid basin on P_4, more reduced mesolophid on the lower cheek teeth, more reduced posterior cingulum on M_1, and a mesolophid posterior to the center of the tooth on M_2, suggests that *M. cedrus* is ancestral to *Neoadjidaumo* and distinct from *Metadjidaumo*. The anterior cingulum on the lower molars of "*M.*" *cedrus* is distinctly separated from the metalophid, and the ectolophid is complete. Both of these characters are different from the morphology of *Neoadjidaumo*, and are primitive for eomyids. Therefore, it is suggested here that *"M." cedrus* is an earlier, more primitive species from which *N. hemedapus* may have been derived.

TABLE 4. Dental and mandibular measurements of *Neoadjidaumo hemedapus* from the Ridgeview fauna. Measurements in mm. Abbreviations as in Table 1.

		N	M	OR	S	CV
P^4	L	4	1.05	1.00-1.10	0.04	4.08
	W	4	1.09	1.01-1.18	0.09	8.31
M^1	L	1	0.93			
	W	1	1.16			
M^2	L	1	0.87			
	W	1	1.08			
M^3	L	1	0.64			
	W	1	0.91			
P^4-M^3		1	3.68			

		N	M	OR	S	CV
P_4	L	4	0.96	0.93-0.97	0.02	1.81
	W	4	0.92	0.88-0.98	0.05	5.32
M_1	L	3	1.01	0.98-1.07	0.05	4.87
	W	3	1.05	1.04-1.07	0.02	1.45
M_2	L	1	0.99			
	W	1	1.01			
P_4-M_3		2	4.01	3.98-4.04	0.04	1.06
I1	L	2	1.01	0.98-1.03		
	W	2	0.76	0.71-0.81		

	N	M	OR
length of diastema	2	3.63	3.60-3.65
depth of mandible below M1	2	3.21	3.01-3.40

Subfamily Apeomyinae Fejfar, Rummel, and Tomida., 1998
Genus *Zophoapeomys* Korth, 2007
Zophoapeomys sp.
(Fig. 5)

Type Specimen—UNSM 26749, right mandible fragment with M_2.

Description—The only tooth with the occlusal pattern preserved is the M_2 of UNSM 26749 (mandibular fragment). The tooth is lophate, with the cusps barely distinguishable. There are two oval loops formed on the occlusal surface that are transversely elongated and separated by a deep central, transverse valley. At its lingual end, the transverse valley is pinched off between short lophs running along the lingual border of the tooth from the metaconid and entoconid. The anterior loop appears to have been formed by the anterior cingulum and metalophid, fused at opposite ends to the metaconid and protoconid. Similarly, the posterior loop consists of the posterior cingulum and the hypolophid fused to the hypoconid and entoconid. The thinnest part of the posterior loop is on the hypolophid just buccal to the hypoconid.

Measruements of M_2—Length = 1.16 mm; width = 1.19 mm.

FIGURE 5. Lower molar (M_2) of *Zophoapeomys* sp., UNSM 26749. Bar scale = 1 mm.

Discussion—The specimen referred here to Zophoa*peomys* is most similar to *Zophoapeomys indicus* from the late Oligocene (latest Whitneyan or earliest Arikareean) of South Dakota (Korth, 2007). There are a number of differences between the Ridgeview molar and European *Apeomys* (see Fahlbusch, 1968; Fejfar et al., 1998). The North American molar is two-rooted (three rooted in *Apeomys*); and is lower crowned than those of *Apeomys*. The cusps on the lower molar of *Zophoapeomys* sp. are slightly more distinct than in *Apeomys* from Europe and it lacks the "spur" that is present on the anterior loop of the Eurasian apeomyines. All of these features distinguish *Zophoapeomys* from *Apeomys*.

The single specimen from the Ridgeview fauna differs from that of *Zophoapeomys indicus* in being considerably larger in dental dimensions (13-16 %). It is possible that the Ridgeview specimen belongs to *Z. indicus*, but its considerably larger size suggests that it represents a different species.

Zophoapeomys sp. is more primitive than Old World *Apeomys.* The Ridgeview fauna is dated at approximately 29 mya (Bailey, 2004), which predates the earliest European occurrence of around 24 mya (MP30). Engesser (1999) suggested that *Apeomys* was an immigrant to Europe in the latest Oligocene because there were no likely species from Europe from which it could be derived. Likewise, there are no North American eomyids that would be likely ancestors for Zophoa*peomys* from the earlier Oligocene. It is likely that the European *Apeomys* was directly derived from the North American species, but the origin of the North American species is uncertain.

CONCLUSIONS

The early Arikareean Ridgeview fauna contains more eomyid specimens and more species than any other Arikareean fauna in North America. *Leptodontomys* is considered to be derived from middle to late Oligocene species of *Adjidaumo*. *Neoadjidaumo* also is considered to have been derived from earlier Oligocene eomyids from North America such as "*Metajidaumo*" *cedrus* from the Orellan (early Oligocene) of Colorado. *Pentabuneomys* is problematical. The dentition is much more bunodont than in any earlier species of eomyid from either North America or Eurasia. The only other record of the genus is from later in the Miocene of western Europe. It is most likely that *Penabuneomys* evolved in North America in the late Oligocene and migrated into Europe in the Miocene.

There are no known eomyids from the Oligocene of either North America or Europe (Engesser, 1999) that are likely ancestors of apeomyines. The appearance of the primitive *Zophoapeomys* in North America predates the earliest occurrence of apeomyines in Europe by nearly four million years. This occurrence, and the more primitive cheek tooth morphology of the North American specimens, suggests that it too, like *Pentabuneomys*, migrated to Europe around the end of the Oligocene.

Although the Ridgeview eomyid fauna is the most diverse from the Arikareean of North America, there are at least two genera of eomyids known from elsewhere that are not represented. *Arikareeomys* was described from northcentral Nebraska (Korth, 1992), based on only a few specimens. The only other reference was by Tedford et al. (2004) who referred some isolated cheek teeth of undetermined eomyids from Florida to this genus. It is not surprising that this genus is lacking from the Ridgeview fauna because of its rarity elsewhere. However, a genus that is conspicuously lacking is *Pseudotheridomys*. This genus is present in a number of Arikareean localities, including some from Nebraska (Korth, 1992) and nearby South Dakota (Macdonald, 1972). This genus first appears in Eurasia and migrates to North America near the beginning of the Arikareean (Fahlbusch, 1979; Engesser, 1999).

The absence of *Pseudotheridomys* from the Ridgeview fauna appears to be due to age. Tedford et al. (2004) placed the appearance of *Pseudotheridomys* as the indicator of Ar2 (called late-early Arikareean by Bailey [2004]) around 28 mya, whereas the beginning of the Arikareean (Ar1) is cited as starting at 30 mya. Bailey (2004) noted that the Ridgeview fauna was early-early Arikareean (Ar1 of Tedford et al., [2004]) and between 28 and 30 mya. There appear to be two closely spaced immigration events near the beginning of the Arikareean. The first event included the dipodoid rodent *Plesiosminthus* (Tedford, et al., 2004), and the second included *Pseudotheridomys*, as well as seven other genera.

EOMYID MIGRATION EVENTS

Fahlbusch (1973, 1979) noted two definite migration events within the Eomyidae between Europe and North America. The first was the introduction of eomyids into Europe from North America at the beginning of the Oligocene, the second was the immigration of *Pseudotheridomys* to North America near the end of the Oligocene. Morea and Korth (2002) identified a species of *Megapeomys* from the early Miocene (Hemingfordian) of Nevada, and argued for yet another immigration event of eomyids from Eurasia to North America at that time. The occurrence of *Pentabuneomys* and the apeomyine *Zophoapeomys* in the Ridgeview fauna predates the occurrence of *Pentabuneomys* and apeomyines in Europe, and suggests an additional one or two migration events occurred from North America to Europe.

Engesser (1999), in his review of Miocene eomyids from Europe, suggested that there were as many as seven different immigration events into Europe in order to explain the occurrence of eomyids there. The first event is clearly the introduction of eomyids from North America noted by Fahlbusch (1973, 1979). The next immigration event is that of *Pseudotheridomys* which was most likely came from Asia where this genus occurred slightly earlier (Wang and Emry, 1991; Dawson, 2003). The next two immigrations into Europe are those of *Apeomys* (MP

30, 24 mya) and *Pentabuneomys* (MN3, 20 mya). The occurrence of a primitive apeomyine and *Pentabuneomys* in the early Arikareean of North America (29 mya) suggests that both of these genera migrated to Europe from North America at the end of the Oligocene and beginning of the Miocene, respectively. The appearance of *Pseudotheridiomys* in North America occurred shortly after the occurrence of *Zophoapeomys* and *Pentabuneomys* (Tedford et al., 2004), and the first appearance of *Megapeomys* in the early Miocene (nearly contemporaneous with the first occurrence of *Pentabuneomys* in Europe) demonstrates that the late Oligocene and early Miocene were times of frequent migration events between Europe and North America.

The origins of the Apeomyinae and *Pentabuneomys* are still uncertain. There are no known species of eomyids from either Europe or North America that are likely ancestors of either group. In the case of the apeomyines, the earliest record is from North America, followed by their migration to Europe at the end of the Oligocene (Engesser, 1999), and then their reintroduction to North America (as well as Asia) in the early Miocene (Fejfar et al., 1999; Morea and Korth, 2002). The record of *Pentabuneomys* is much less complex. It occurs earliest in North America in the late Oligocene (early Arikareean), and then migrates to Europe in the early Miocene (MN 3). However, there is a considerable time gap between the occurrence of *Pentabuneomys* in North America and Europe (nearly 10 million years).

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