# A new genus of eomyid rodent from the Miocene of Nevada

KENT S. SMITH, RICHARD L. CIFELLI, and NICHOLAS J. CZAPLEWSKI

Smith, K.S., Cifelli, R.L., and Czaplewski, N.J. 2006. A new genus of eomyid rodent from the Miocene of Nevada. *Acta Palaeontologica Polonica* 51 (2): 385–392.

The description of a new genus (*Apeomyoides*) of eomyid rodent from the Miocene of Nevada increases the diversity of known taxa, enhances the geographic range, and extends the biochronology for the Apeomyinae (Eomyidae). Three groups of Eomyidae are known from the fossil record of North America. Of the three groups, Neogene taxa include four genera representing the Eomyinae and two genera representing the Apeomyinae; no genera of the subfamily Yoderimyinae are known from the Neogene of the continent. This diversity represents a significant reduction of eomyid taxa compared to the Paleogene, from which 17 genera of eomyines and three genera of yoderimyines are known. In Eurasia, 11 genera of eomyids occurred during the Neogene, with a few taxa that persisted until about 2 million years before present. At present, there are no known eomyids from the last 4.5 million years of the Neogene in North America. *Apeomyoides savagei* is referable to the subfamily Apeomyinae based on several key structures of the teeth and mandible. This new eomyid is part of the Eastgate local fauna, collected from volcanic ash deposits of the Monarch Mill Formation, Churchill County, Nevada. *Apeomyoides* has an occlusal pattern that shares characteristics of apeomyines from both North America (*Megapeomys* and *Arikareeomys*) and Eurasia (*Apeomys* and *Megapeomys*). The unique occlusal pattern and large size of *Apeomyoides* demonstrates that not all eomyids from North America were small or that their lineages decreased in size through time. *Apeomyoides* also may provide evidence, which challenges the hypothesis that eomyids within a single lineage from North America became more lophodont in geologically younger genera.

Key words: Rodentia, Eomyidae, *Apeomys*, *Apeomyoides*, *Megapeomys*, Miocene, Barstovian, Nevada.

*Kent S. Smith [smithks@chs.okstate.edu], Department of Anatomy and Cell Biology, Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma 74107, and Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (corresponding author);*
*Richard L. Cifelli [rlc@ou.edu] and Nicholas J. Czaplewski [nczaplewski@ou.edu], Sam Noble Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, Oklahoma 73072.*

## Introduction

During the Paleogene (65.5–23.03 Ma) in North America, the rodent family Eomyidae consisted of two major groups, the Eomyinae and Yoderimyinae, with 17 genera and three genera, respectively (Korth 1994). The number of taxa for the former was significantly reduced to three genera (*Pseudotheridomys*, *Kansasimys*, and *Leptodontomys*) by the Neogene (23.03–1.8 Ma). No Yoderomyinae have been recorded from the Neogene of North America; presumably the group was extinct on the continent by that time. Although the number of genera from these two eomyid groups was significantly reduced or absent by the Neogene, a third group of eomyids (Apeomyinae) is known from the Hemingfordian of Nevada and includes the single genus *Megapeomys* (Morea and Korth 2002). In addition, a new genus (*Apeomyoides*) of an apeomyine eomyid from the early Barstovian in Nevada is described herein. In contrast to North America, during the Paleogene, Eurasia had two primary groups of eomyids, Eomyinae and Apeomyinae, with four genera (*Eomys*, *Rhodanomys*, *Eomyodon*, and *Pseudotheridomys*) of eomyines and a single genus (*Apeomys*) of apeomyine (Engesser 1999). Of these Paleogene taxa, three genera (*Rhodanomys*, *Eomyodon*, and *Pseudotheridomys*) from the eomyine group and one genus (*Apeomys*) from the apeomyine group persisted into the Neogene of Eurasia (Engesser 1999). Excluding the genera that persisted into the Neogene from the Paleogene, six genera (*Ritteneria*, *Ligerimys*, *Pentabuneomys*, *Keramidomys*, *Estramomys*, and *Eomyops*) of eomyines and a single apeomyine genus (*Megapeomys*) are known from the Neogene of Eurasia (Engesser 1999; Fahlbusch 1968; Fejfar et al. 1998).

In North America and Eurasia, the cheekteeth of the apeomyine group are easily distinguished from those of both the eomyine and the yoderimine groups in that the apeomyines have distinctly bilobed (bilophodont) cheekteeth that are higher-crowned, with thick enamel (Fejfar et al. 1998). The apeomyines also have a diastema and a rostrum that are greatly elongated for eomyids. These taxa are medium- to large-sized among Eomyidae, and therefore larger than most genera of eomyines that are known from the Neogene of North America and Eurasia.

The cheekteeth of Neogene eomyids from North America display basic structures of the occlusal surface (Fig. 1) which include the following: cuspate-to-lophate, brachydont-to-

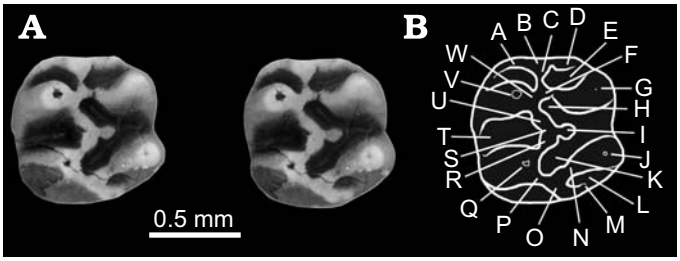


Fig. 1. *Leptodontomys* sp., Clarendonian, Whisenhunt Quarry, Beaver County, Oklahoma (see Smith 2005), OMNH 72076, left m1 or m2, occlusal view. **A**. Stereo pair. **B**. Schematic drawing of left m1 or m2. Top is mesial and left is labial; A, labial arm of anterolophid (anterior cingulid); B, anteroconid; C, adlophid; D, lingual arm of anterolophid; E, syncline I; F, lingual arm of metalophid; G, metaconid; H, syncline II (part of middle syncline); I, mesolophid; J, entoconid; K, syncline III (part of middle syncline); L, syncline IV; M, posterolophid (posterior cingulid); N, lingual arm of hypolophid; O, hypoconulid; P, labial arm of hypolophid; Q, hypoconid; R, Posterior arm of ectolophid; S, mesoconid; T, labial part of middle syncline (synclines II, III); U, anterior arm of ectolophid; V, protoconid; W, labial arm of metalophid.

mesodont, and primitively with five transverse lophs (anteroloph = anterior cingulum, protoloph, mesoloph, metaloph, and posteroloph = posterior cingulum) on the upper cheekteeth and five transverse lophids (anterolophid = anterior cingulid, metalophid, mesolophid, hypolophid, and posterolophid = posterior cingulid) on the lower cheekteeth (Korth 1994; Wang and Emry 1991). Also in association with the primitive pattern of five lophs (-ids), is the presence of a transverse valley (syncline), which occurs between each pair of lophs (-ids).

Typically, Neogene North American eomyids exhibit four distinct variations of the following cheekteeth patterns of lophs (-ids) and transverse valleys (synclines), appearance of primary cusps, and crown height: (1) five lophs (-ids), four transverse valleys, entoloph and ectolophid present, primary cusps submerged, and low crowned (e.g., *Pseudotheridomys*); (2) four lophs (-ids) but not bilophed, three transverse valleys (syncline II, syncline III, and syncline IV), entoloph and ectolophid present or incomplete (anterior or posterior arm of the entoloph/ectolophid is present but not both), primary cusps submerged, and high crowned (e.g., *Arikareeomys*); (3) four lophs (-ids) and bilophed, three transverse valleys (syncline II, syncline III, and syncline IV), entoloph and ectolophid absent, primary cusps submerged, and high crowned (*Apeomys*, *Megapeomys*, and *Apeomyoides*); and (4) four to five lophs (-ids), three transverse valleys (syncline I, middle syncline = synclines II–III, and syncline IV), entoloph and ectolophid present, primary cusps distinct, and low crowned (e.g., *Leptodontomys* and *Kansasimys*). Among the apeomyines, crown height appears to vary little among the genera (*Apeomys*, *Megapeomys*, and *Apeomyoides*); however, a slight increase in crown height appears to occur from the oldest (*Apeomys*) to the youngest (*Apeomyoides*) genus.

Additional dental characteristics of eomyids are discussed in several papers (Dalquest 1983; Jacobs 1977; Kelly and Whistler 1998; Lindsay 1972, 1974; Walhert 1978; Wood 1936), which led Engesser (1979) and Korth (1994) to suggest that most eomyid genera were small, with no trend toward an increase in size. Fejfar et al. (1998) noted that Eurasian apeomyines experienced a rapid increase in size through time, ultimately leading to one of the largest taxa of eomyids (*Megapeomys*). *Megapeomys bobwilsoni* Morea and Korth, 2002, from the Hemingfordian of Nevada, is much larger than the species of *Megapoemys* from Eurasia (*M. lavocati* Fejfar, Rummel, and Tomida, 1998, *M. lindsayi* Fejfar, Rummel, and Tomida, 1998, and *M*. sp.), which are geologically older than the North American species. In addition to size, Korth (1994) noted that geologically younger genera are characterized by more lophodont cheekteeth. However, *Kansasimys,* a genus from Hemphillian deposits (geologically younger) of Kansas, Arizona, and Texas, is considered to be the largest Neogene species of any North American eomyid and is less lophodont than some geologically older taxa (Dalquest 1983; Dalquest and Patrick 1989; Jacobs 1977; Korth 1994). Compared to other genera of eomyids, *Leptodontomys* also shows less lophodonty, as well as an apparent decrease in size through time for some lineages (Engesser 1979). Other lineages increase in size and reduce lophodonty, as exemplified by eomyid specimens from Nebraska (McCann Canyon local fauna, late Arikareean) and Nevada (Massacre Lake local fauna, late Hemingfordian; and Eastgate local fauna, early Barstovian). These taxa include *Arikareeomys skinneri* Korth, 1992 from McCann Canyon, *Megapeomys bobwilsoni* from Massacre Lake, and *Apeomyoides savagei* gen. et sp. nov. from Eastgate. The Nevada genus, *Megapeomys*, indicates that at least one member of the eomyid group reached considerable size and showed a reduction in structures (absent to incomplete entoloph on M1). This taxon is also comparatively less lophodont, whereas other taxa (e.g., species of *Pseudotheridomys*) vary little in size but became more lophodont through time (Korth 1994).

*Pseudotheridomys,* known from North America and Eurasia, is the only Neogene genus of eomyids in North America with a primitive pattern of five lophs and four synclines. This basic pattern of eomyid cheekteeth appears as early as the Uintan in North America (Engesser 1979). Other eomyids that occurred during the Neogene in North America include *Arikareeomys*, *Megapeomys*, *Apeomyoides*, *Leptodontomys*, and *Kansasimys*. The last two genera have lophodont cheekteeth; however, the four primary cusps (protoconid, metaconid, hypoconid, and entoconid) are not submerged within lophs. In addition to equally sized and prominent primary cusps, *Kansasimys* also has an equally sized mesoconid and upper cheekteeth (paracone, protocone, metacone, and hypocone) with a similarly large mesocone. Therefore, the cheekteeth of *Kansasimys* are easily differentiated from those of *Arikareeomys*, *Megapeomys*, and *Apeomyoides*, which have four primary cusps submerged within the lophs and a reduction in lophs on the upper and lower molar teeth. Also, *Leptodontomys* and *Kansasimys* have a complete loph that unites the two anteriormost and posteriormost primary cusps. The arrangement of cusps and lophs for *Leptodontomys* al-

lows it to be easily separated from that of *Pseudotheridomys*, which has its primary cusps submerged into the lophs. According to Korth (1992), *Arikareeomys* has a small ovoid-shaped depression in the maxilla anterior to the P4, which may have housed a P3. This was the only character that Korth (1992) used in placing *Arikareeomys* in the yoderimyine group. However, a P3 is also present in the Uintan eomyid *Metanoiamys*, which is clearly not a yoderimyine (Walsh 1997). This may indicate that the presence of a P3 is a primitive character for all eomyids regardless of subfamily. Other characters of *Arikareeomys* that aid in separating it from *Leptodontomys* and *Kansasimys* include presence of an anteroconid on the p4 and a D-shaped enamel lake on the trigonid of the p4 (Korth 1994). Following Fejfar et al. (1998), *Arikareeomys* has several characteristics that prompt us to tentatively place it within the apeomyine group rather than with the yoderimyines (Korth 1992, 1994). These characters include a P4 with a false bilophodonty tooth pattern (four lophs that do not form complete loops, as in true bilophodonty, because the lingual ends of the lophs do not unite and the lophids do not unite labially; and so the synclines between each loph only close on one end) and an M2 that is bilobed. For eomyids, these characters are only known for the apeomyine group (Engesser 1999; Fejfar et al. 1998; Morea and Korth 2002).

Herein we describe a new genus and species (*Apeomyoides savagei*), based on eighteen specimens discovered at a single Miocene local fauna (Eastgate) in Churchill County, Nevada. These specimens include upper and lower cheekteeth and mandibles. A noteworthy change in occlusal attributes of the cheekteeth includes the lack of several structures that results in fewer lophs and transverse valleys (similar to other apeomyines). Except for *Megapeomys bobwilsoni*, this new taxon from Eastgate is also larger than all apeomyines from the Neogene of North America and most genera from Eurasia (Tables 1–3). The Eastgate local fauna also has genera from the eomyine group of eomyids, which include *Pseudotheridomys* and *Leptodontomys* (Smith 2002). Since Smith's (2002) work, we have made additional comparisons and examinations of the Eastgate eomyid materials, which included more extensive comparisons of appropriate eomyid material from North America and Eurasia (Wang and Emry 1991; Fejfar et al. 1998; Engesser 1999; Morea and Korth 2002). Based on the information provided herein, we believe the large-sized eomyid from the Eastgate local fauna merits new generic status (*Apeomyoides*) and belongs to the Apeomyinae group. We follow Wang and Emry (1991) for dental terminology, which is modified from Engesser (1979), Fahlbusch (1973), Kelly and Whistler (1998), Wood (1936), and Wood and Wilson (1936).

*Institutional abbreviations*.—OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA.

*Other abbreviations*.—Ma, meganna, or millions of years ago; V, vertebrate paleontology locality number for the University of California Museum of Paleontology; DP4, upper fourth deciduous premolar.

Table 1. Measurements (mean, observed range, and n; in mm) of upper cheekteeth of *Apeomyoides*, *Megapeomys*, and *Arikareeomys*. Data for *Megapeomys bobwilsoni* from [a]Morea and Korth (2002). Data for *Arikareeomys* from [b]Korth (1992).

| Tooth and character | | *Apeomyoides savagei* | [a]*Megapeomys bobwilsoni* | [b]*Arikareeomys skinneri* |
|---|---|---|---|---|
| DP4 | AP | 2.00, 1.88–2.03, 2 | – | – |
| | T | 1.79, 1.79–1.80, 2 | – | – |
| P4 | AP | – | 2.88, 2.85–2.91, 2 | 2.28, 1 |
| | T | – | 3.10, 3.00–3.20, 2 | 2.05, 1 |
| M1/2 | AP | 2.00, 1.92–2.07, 2 | 2.61, 2.49–2.69, 4 | 1.90, 1 |
| | T | 2.22, 2.12–2.33, 2 | 2.85, 2.66–3.09, 4 | 2.13, 1 |
| M3 | AP | – | 2.12, 2.07–2.17, 2 | – |
| | T | – | 2.45, 2.28–2.61, 2 | – |

Table 2. Measurements (mean, observed range, and n; in mm) of lower cheekteeth of *Apeomyoides*, *Megapeomys bobwilsoni*, and *Arikareeomys*. Data for *Megapeomys* from [a]Morea and Korth (2002). Data for *Arikareeomys* from [b]Korth (1992); * indicates incomplete data.

| Tooth and character | | *Apeomyoides savagei* | [a]*Megapeomys bobwilsoni* | [b]*Arikareeomys skinneri* |
|---|---|---|---|---|
| p4 | AP | 2.35, 2.27–2.43, 7 | – | – |
| | T | 2.17, 2.09–2.29, 7 | – | 2.22, 1 |
| m1/2 | AP | 2.00, 1.74–2.58, 11 | 2.65, 2.50–2.91, 3 | 1.92* |
| | T | 2.23, 2.08–2.33, 11 | 2.91, 2.79–3.11, 3 | – |
| m3 | AP | 1.86, 1.56–2.19, 3 | 2.39, 2.29–2.49, 2 | – |
| | T | 1.92, 1.82–2.02, 3 | 2.38, 2.32–2.43, 2 | – |

Table 3. Measurements (mean in mm) of lower cheekteeth of *Megapeomys* and *Apeomys*. The numbers listed below were derived from scatter plots from Fejfar et al. (1998). These are maximum values observed in the scatter plots taken for each tooth locus listed below.

| Tooth and character | | *Megapeomys* | | | *Apeomys* cf. *tuerkheimae* |
|---|---|---|---|---|---|
| | | *M. lavocati* | *M. lindsayi* | *M.* sp. | |
| p4 | AP | 2.00 | 2.53 | 2.10 | 1.58 |
| | T | 2.17 | 2.50 | 2.30 | 1.45 |
| m1 | AP | 1.94 | – | – | – |
| | T | 2.20 | – | – | – |
| m2 | AP | 1.93 | – | – | – |
| | T | 2.25 | – | – | – |

# Systematic paleontology

## Order Rodentia Bowdich, 1821

## Family Eomyidae Winge, 1887

## Subfamily Apeomyinae Fejfar, Rummel, and Tomida, 1998

## Genus *Apeomyoides* nov.

*Etymology*: Greek *ides*, suffix indicating similarity—similar to eomyid genus *Apeomys*.

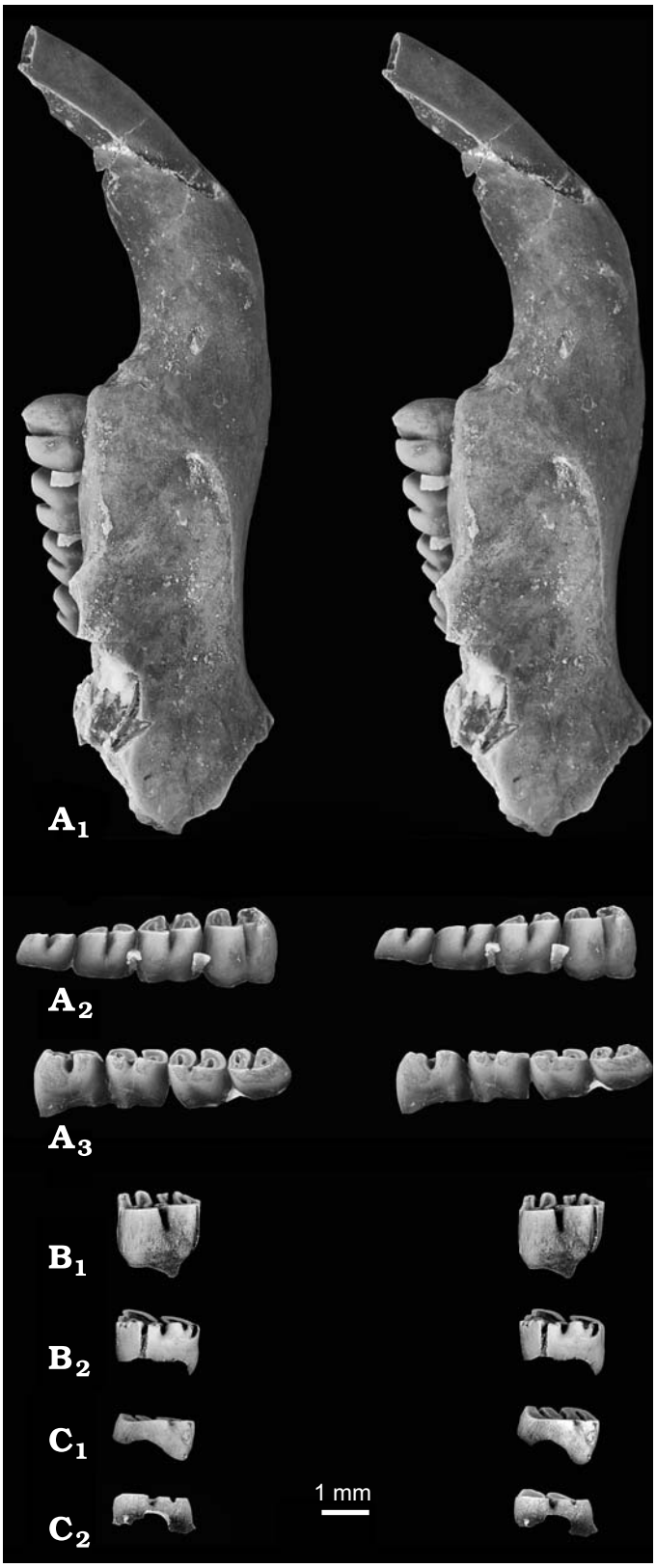


Fig. 2. Labial and lingual views (stereo pairs) of *Apeomyoides savagei* gen. et sp. nov., Eastgate local fauna, Monarch Mill Formation, early Barstovian Churchill County, Nevada. **A**. UCMP 109300; $A_1$, $A_2$, holotype, dentary with p4–m3 in labial views; $A_3$, p4–m3 in lingual view. **B**. UCMP 141774-01, left M1 or M2 in labial ($B_1$) and lingual ($B_2$) views. **C**. UCMP 141774-08, left DP4 in labial ($C_1$) and lingual ($C_2$) views.

*Type species*: *Apeomyoides savagei* gen. et sp. nov. UCMP 109300, dentary with p4–m3.

*Diagnosis and distribution*.—The same as for the type and only species, below.

## *Apeomyoides savagei* gen. et sp. nov.

Figs. 2, 3.

*Etymology*: Species named in honor of Donald E. Savage, for his contributions to the study of Tertiary mammals and for helping the senior author with the loan of important material and innumerable other courtesies.

*Holotype*: UCMP 109300, right dentary with p4–m3 (Figs. 2A, 3A).

*Hypodigm*.—Holotype, UCMP 109300, right dentary with p4–m3 (Figs. 2A, 3A); OMNH 54618, right p4; OMNH 54619, left m1 or m2; OMNH 54620, left m3; and OMNH 54621, right dentary fragment with p4–m2.

*Referred material*.—OMNH 54746, left m1 or m2; OMNH 54747, left m1 or m2; UCMP 109301, left dentary fragment with m3; UCMP 141564, left dentary fragment with p4–m2; UCMP 141774-01, left M1 or M2 (Figs. 2B, 3C); UCMP 141774-02, left M1 or M2; UCMP 141774-03, left m1 or m2; UCMP 141774-04, right p4; UCMP 141774-06, right m1 or m2; UCMP 141774-07, left p4; UCMP 141774-08, left DP4 (Figs. 2C, 3B); UCMP 141818-02, left p4; UCMP 141818-03, right m1 or m2.

*Locality and age*.—UCMP V70139, V70140, and V70147, Monarch Mill Formation, Eastgate local fauna, Churchill County, Nevada; early Barstovian.

*Diagnosis*.—A large eomyid that is bigger than *Apeomys* and *Megapeomys lavocati* Fejfar, Rummel, and Tomida, 1998 from Eurasia, smaller than *Megapeomys lindsayi* Fejfar, Rummel, and Tomida, 1998 and *Megapeomys* sp. from Eurasia, and *Megapeomys bobwilsoni* from North America. Differs from all known Neogene eomyids in North America and Eurasia in having a very long diastema and a procumbent incisor (except *Megapeomys*). A mental foramen is anterior to p4 near the level of the ventral shelf of the masseteric scar, whereas in *Apeomys* and *Megapeomys* it occurs near the level of the dorsal shelf. Both shelves are weak, but strong in *Apeomys*. A rounded masseteric scar terminates below the anterior roots of the m1, but in *Apeomys* and *Megapeomys* it ends below the anterior root of p4. All cheekteeth are bilobed and higher crowned than *Apeomys*, *Megapeomys*, and *Arikareeomys*. An entoloph is incomplete on M1 and M2, but is complete in *M. bobwilsoni*, and reduced but more prominent in *Arikareeomys*. The transverse valley (syncline IV) between the hypolophid and posterolophid is closed labiolingually on the m1–3, whereas in *M. bobwilsoni* it is open. The posteriormost valley (syncline IV) opens into the central transverse valley (syncline III), whereas they are closed in *Arikareeomys*. An ectolophid is absent from all lower cheekteeth, but present in *Arikareeomys*. The cheekteeth are rectangular in occlusal outline, not barrel-shaped as in other apeomyines (e.g., *M. bobwilsoni*). The lophids of unworn cheekteeth are very rugose. Two roots occur on the p4 and

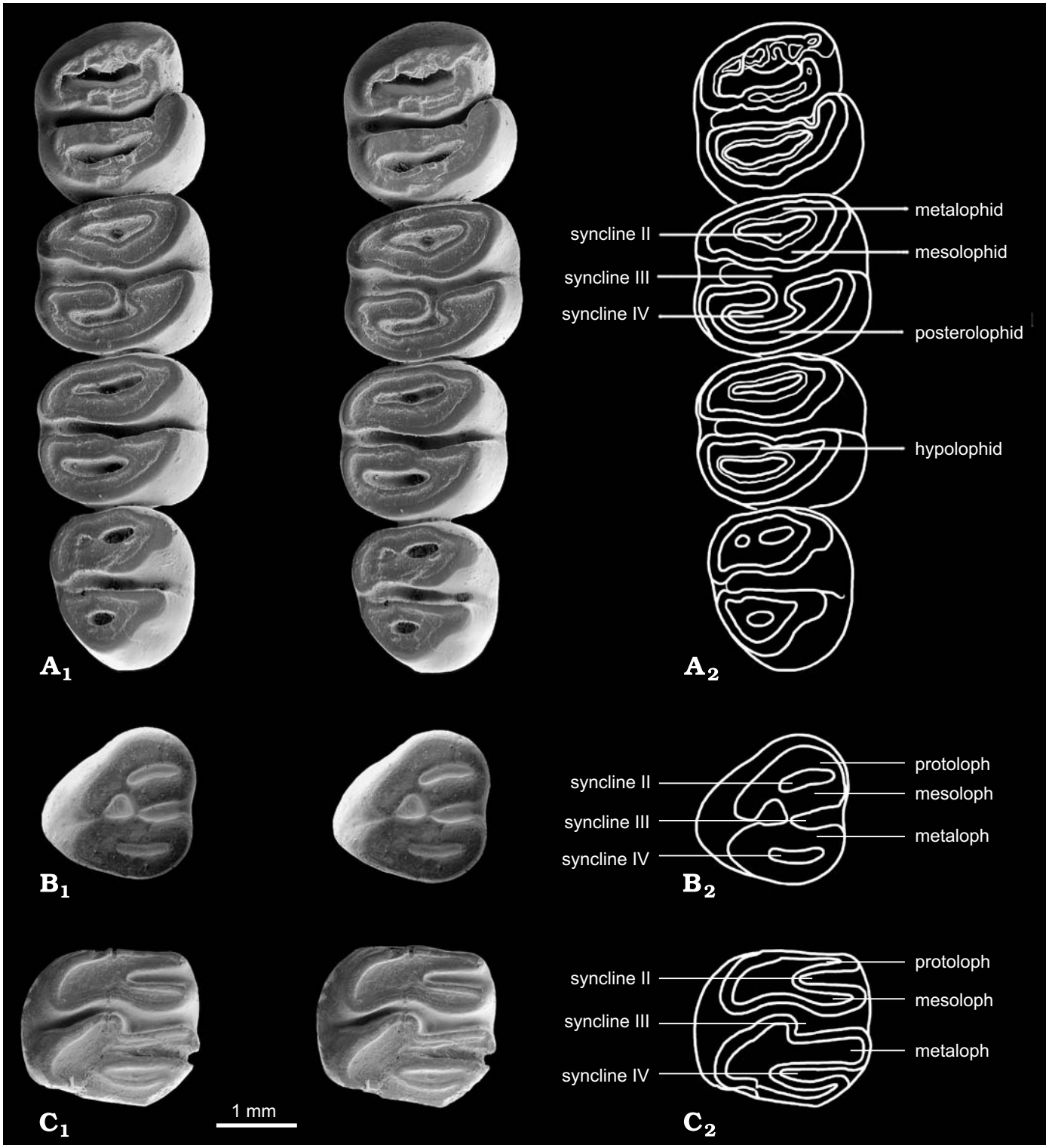


Fig. 3. Scanning micrographs of cheekteeth of *Apeomyoides savagei* gen. et sp. nov. in occlusal view, Eastgate local fauna, Monarch Mill Formation, early Barstovian, Churchill County, Nevada. **A**. The p4–m3 of the holotype, UCMP 109300, stereopair ($A_1$) and explanatory drawing of the same ($A_2$). **B**. Left DP4, UCMP 141774-08, stereopair ($B_1$) and explanatory drawing of the same ($B_2$). **C**. Left M1 or M2, UCMP 141774-01, stereopair ($C_1$) and explanatory drawing of the same ($C_2$).

three roots occur on the m1–m3; in *M. bowilsoni*, however, the p4 has three roots and the m1–m3 possess four roots. The p4 is the largest of the lower cheekteeth, whereas the p4–m2 are subequal in size for *Apeomys*.

## Description

**Upper premolars**.—P3 is absent and the P4 is not known at present. The DP4 possesses four major cusps (protocone,

paracone, hypocone, and metacone) and four lophs (protoloph, mesoloph, metaloph, and posteroloph) with three transverse valleys (synclines II, III, IV). The anteriormost valley forms an isolated lake (syncline II). The protoloph extends labially from the anterolabial margin of the protocone but does not reach the paracone. The protocone and paracone are not joined directly by the mesoloph; instead, the mesoloph joins the protoloph lingual to the protocone. Absent are the anteroloph, mesocone and mesostyle. Unlike the mesoloph, the metaloph is complete and joins the hypocone to the metacone. The posteroloph arises along the posteromedial margin of the hypocone and joins the metacone. The posteroloph is anteroposteriorly narrow and closed labially, forming a D-shaped enamel lake (syncline IV).

**Upper molars**.—The M1 and M2 are subquadrate, trigon and talon equal, high crowned, and similar in size to the DP4. The protoloph arises high on the anterolabial margin of the protocone and traverses the anteriormost edge of the tooth but does not join the paracone. The protoloph and mesoloph do not join at the paracone; thus, the anterior transverse valley (syncline II) is open lingually (lacks a D-shaped enamel lake). A prominent mesocone is present. The posterior arm of the entoloph (spur or endoloph; see Korth 1992; Morea and Korth 2002) is distinct and arises from the labial part of the metaloph. A mesostyle is absent. The hypocone and metacone are joined by a metaloph. A posteroloph arises along the posterolabial margin of the hypocone and does not reach the metacone; thus, the posterior valley does not form a D-shaped enamel lake and is open lingually. However, after heavy wear to the occlusal surface, a D-shaped enamel lake may appear.

**Dentary**.—The dentary has a very long diastema. A very small, anteriorly open mental foramen occurs along the dorsoventral midline of the dentary in the diastema, anterior to the p4, and near the level of the ventral shelf of the masseteric scar. The masseteric scar is rounded anteriorly, ends below the anterior margin of m1, and has weak ventral and dorsal shelves. A fossa occurs anterior to the distal end of the masseteric scar, below the p4, and may house a foramen. On the lingual surface of the dentary there are many foramina below the cheekteeth.

**Lower cheekteeth**.—The p4–m3 are high crowned, possess four cusps (metaconid, protoconid, entoconid, and hypoconid), four lophids (metalophid, mesolophid, hypolophid, and posterolophid), and three transverse valleys (synclines II, III, IV). The four lophids and their completeness (labial and lingual arms present) for the p4–m3 are as follows: metalophid complete, mesolophid variably complete (labial and lingual arms may not unite centrally), hypolophid variably complete (labial and lingual arms may not unite), and posterolophid complete. Based on specimens with a complete dentary (UCMP 109300 and OMNH 54621), it appears that the completeness of lophids (mesolophid and hypolophid) changes with wear to the occlusal surface from incomplete to complete, respectively. The metalophid and mesolophid of unworn cheekteeth are very rugose. Thus, heavily worn lower molars have complete lophids. There are three roots on all lower cheekteeth except p4, which has two large roots. The m1–m3 have two small anterior roots and a single, large, posteromedial root that occurs along the posterior part of the tooth.

The p4 is molariform and larger than the molars, is longer than wide, and has a metalophid that runs from the anteromedial margin of the protoconid and extends lingually to join the anterolingual margin of the metaconid. The protoconid and metaconid are joined centrally by a mesolophid. The ectolophid is absent. An anterolophid, mesoconid, and mesostylid are absent. A hypolophid arises along the labial margin of the entoconid and joins the posterolophid posterior to the hypoconid. A posterolophid arises along the posterolingual margin of the hypoconid and ends along the posteromedial margin of the entoconid; no hypolophulid is present. The posterolophid is anteroposteriorly narrow and closed labially forming a D-shaped enamel lake.

The m1 is slightly wider than long; on the anterolingual surface of this tooth, the metalophid arises high on the anterolabial margin of the protoconid and traverses the anterior margin of the tooth to join the anteromedial margin of the metaconid. The protoconid and metaconid are joined centrally by a mesolophid after late stages of wear. The ectolophid, mesoconid, and mesostylid are absent. The hypolophid is incomplete (it is incised mesiodistally along its midline), and therefore does not join the hypoconid and entoconid until very late stages of wear. The posterolophid arises along the posterolingual margin of the hypoconid and ends along the posteromedial margin of the entoconid. The posterolophid forms a D-shaped enamel lake. The m2 does not differ significantly in any characters or size from m1. The m3 is distinguished from the preceding molars only by its smaller size and a more rounded, narrower posterior margin that is triangular in shape.

## Discussion

A combination of defining features for *Apeomyoides savagei* gen. et sp. nov. clearly distinguishes it from other Neogene eomyids. These characters include large size; high crowned cheekteeth with thick enamel; very long diastema; p4 largest of lower cheekteeth; and arrangements of lophs, transverse valleys, and submerged cusps. In addition to size, *Apemyoides* is unlike any other genus of Neogene eomyid from North America in that it lacks an anteroloph on all cheekteeth, has four lophs and three transverse valleys, and is bilophed (except *Megapeomys*). Most North American eomyid genera possess an anteroloph, entoloph and ectolophid (both may vary from complete to incomplete), and have five lophs and four transverse valleys. The absence of an ectoloph or entolophid is also evident in *Pseudotheridomys hesperus* Wilson, 1960 from the Miocene of Colorado (Wilson 1960; Korth 1992) and *Apeomys* from the Oligocene of Europe (Fahlbusch 1968; Korth 1992; Engesser 1999). *Apeomyoides savagei* gen. et sp. nov. also lacks an ectolophid but is larger than *P. hesperus* or *Apeomys*. However, *A. savagei* gen. et sp. nov. is

smaller than *Megapeomys bobwilsoni* and slightly larger than *Arikareeomys*. This arrangment of characters clearly separates *A. savagei* from other described genera of eomyids.

# Concluding remarks

*Apeomyoides* is a large eomyid that differs from all other known genera of Neogene eomyids from North America and Eurasia in having all cheekteeth bilobed and high crowned (except *Apeomys*), and a mandible with a long diastima (except *Apeomys* and *Megapeomys*). These characters of the cheekteeth and jaw are diagnostic for the Apeomyinae group of eomyids (Fejfar et al. 1998). A noteworthy change in occlusal attributes of the cheekteeth for *Apeomyoides* includes the lack of several structures that results in fewer lophs, which is similar to both *Megapeomys* and *Arikareeomys* of North America and *Apeomys* and *Megapeomys* of Eurasia. *Apeomyoides savagei* gen. et sp. nov. is larger than *Arikareeomys* of Nebraska but smaller than *Megapeomys* of the nearby Massacre Lake fauna (Tables 1–3). *Megapeomys bobwilsoni* from the Massacre Lake fauna of Nevada (late Hemingfordian) is geologically older than *A. savagei* from Eastgate (early Barstovian) but geologically younger than *Arikareeomys skinneri* from Nebraska (Arikareean).

A direct comparison of *Apeomyoides savagei* from the Eastgate local fauna with *Megapeomys bobwilsoni* from the Massacre Lake local fauna clearly indicates that these genera are closely related but do not belong within the same genus. As detailed above, the morphology of the lower dentition and mandible of *A. savagei* does not closely resemble that of any previously described eomyid from the Neogene of North America or Eurasia (except *Apeomys* or *Megapeomys*). These genera share two significant (and unique) features of Apeomyinae: (1) high-crowned cheekteeth, which are higher than any other North American or Eurasian eomyids; and (2) a very elongated diastema; both characters are present in *Apeomyoides savagei*. Based on the occurrence of these diagnostic characters, we suggest placing both *Arikareeomys* and *Apeomyoides* in the family Apeomyinae, which includes *Megapeomys* and *Apeomys* (Engesser 1999; Fejfar et al. 1998). Other key characteristics of apeomyines from North America and Eurasia are the presence of one or two of four distinct occlusal patterns of the cheekteeth. These patterns include a variation of the number and occurrence of lophs and transverse valleys, and the appearance of the primary cusps.

Collectively, these characters seem to be unique for each group of eomyids. For example, the yoderimyine group is identified as having one of the four occlusal patterns, while the eomyines from North America and Eurasia possess two of the four occlusal patterns. A fourth occlusal pattern is evident in the apeomyine genera (except *Arikareeomys*) from North America and Eurasia. As far as eomyids are concerned, the apeomyines tend to range in size from medium to large, with the largest being *Megapeomys bobwilsoni* from North America, followed by *M. lindsayi* of Eurasia. *Apeomyoides savagei* gen. et sp. nov. from North America is larger than all other known species of *Megapeomys* (*M. lavocati* and *M*. sp.) from Eurasia and is slightly larger than *Arikareeomys* from North America. The smallest apeomyine is *Apeomys tuerkheimae* Fahlbusch, 1968 from Eurasia.

*Apeomyoides savagei* gen. et sp. nov. shares occlusal pattern characteristics with *Megapeomys* (late Hemingfordian) and *Arikareeomys* (late Arikareean) from North America and *Apeomys* (Arikareean–Hemingfordian equivalent) and *Megapeomys* (Arikareean–Hemingfordian equivalent) from Eurasia. The distinctive occlusal pattern and large size of *Apeomyoides savagei* gen. et sp. nov. suggests that not all eomyids from North America were small and that some groups reduced the number of structures on the cheekteeth. *Apeomyoides savagei* gen. et sp. nov. may provide evidence which challenges the hypothesis that a single lineage of North American eomyids became more lophodont later in the Tertiary. According to Engesser (1999), the bunodont pattern for cheekteeth is considered the primitive condition for eomyids, remaining nearly unchanged for more than 40 Ma; hence the lophodont apeomyines appear more derived. In addition, at various spatial and temporal modes within the Northern Hemisphere, bunodont eomyids appear to have given rise to lophodont forms repeatedly, and these forms seemed to disappear as quickly as they evolved (Engesser 1999). The last occurrence of *Apeomys* and *Megapeomys* in Eurasia was about 17.4 Ma (Engesser 1999), whereas the first occurrence of *Megapeomys* in North America, *M. bobwilsoni*, was about 16.2 Ma (Woodburne and Swisher 1995; Swisher 1992; Tedford et al. 2004). The first appearance of *Apeomyoides* in North America is early Barstovian. *Apeomyoides savagei* gen. et sp. nov. increases the diversity of taxa, fills a gap in the geographic range between Nevada and Nebraska, and extends the biochronology for apeomyine Eomyidae from the Hemingfordian to the Barstovian. Prior to this study, the apeomyines were known from the Arikareean–Hemingfordian of Eurasia and North America. The absolute date for the first appearance of *Apeomyoides savagei* gen. et sp. nov. at Eastgate, Nevada and the biogeographic and systematic (phylogenetic) relationships within the family are beyond the scope of the present study, but will be pursued in a future paper.

# Acknowledgments

Special thanks are extended to the following individuals of the University of California Museum of Paleontology, Berkeley for the loan of specimens pertinent to this study: Donald E. Savage, Jere H. Lipps, J. Howard Hutchinson, and Patricia A. Holroyd. The following provided funding or support to KSS during this project: University of Oklahoma Department of Zoology; University of Oklahoma Graduate Student Senate; Oklahoma State Regents for Higher Education Doctoral Study Grant; Southern Regional Education Board Doctoral Scholars Program Dissertation Year Fellowship; the American Indian Graduate Center, Albuquerque, New Mexico; the Lt. William Johnson Scott Memorial Scholarship; and Oklahoma State University Center for Health Sciences, Department of Anatomy and Cell Biology. For providing per-

mits to collect on BLM properties, we extend our gratitude to Prill Mecham of the United States Department of the Interior, Bureau of Land Management at the Carson City District Office, Carson City, Nevada. For taking scanning electron micrographs of the type specimen, we thank Brian Davis and Christina Stewart (both from OMNH). Additional photographs were provided with the aid of Roger J. Burkhalter. KSS is especially grateful to Patty B. Smith for her continued encouragement to complete this project and reviewing an earlier version of this manuscript. We thank two anonymous reviewers for their critique of an earlier version of this manuscript, which greatly improved the final version.

# References

Bowdich, T.E. 1821. *An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers*. 146 pp. J. Smith Press, Paris.

Dalquest, W.W. 1983. Mammals of the Coffee Ranch local fauna, Hemphillian of Texas. *University of Texas, Pearce-Sellards Series* 38: 1–41.

Dalquest, W.W. and Patrick, D.B. 1989. Small mammals from the early and medial Hemphillian of Texas, with descriptions of a new bat and gopher. *Journal of Vertebrate Paleontology* 9: 78–88.

Engesser, B. 1979. Relationships of some insectivores and rodents from the Miocene of North America and Europe. *Bulletin of the Carnegie Museum of Natural History* 14:1–68.

Engesser, B. 1999. Family Eomyidae. *In*: G.E. Rossner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*, 319–336. Dr. Friedrich Pfeil, München.

Falhbusch, V. 1968. Neue Eomyidae (Rodentia, Mammalia) aus einer aquitanen Spaltenfullung von Weissenburg in Bayern. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 8: 219–245.

Falbusch, V. 1973. Die stammesgeschichtlichen Beziehungen zwischen den Eomyiden (Mammalia, Rodentia) Nordamerikas und Europas. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 13: 141–175.

Fejfar, O.M., Rummel, M., and Tomida, Y. 1998. New eomyid genus and species from the early Miocene (MN Zones 3–4) of Europe and Japan related to *Apeomys* (Eomyidae, Rodentia, Mammalia). *In*: Y. Tomida, L.J. Flynn, and L.L. Jacobs (eds.), Advances in Vertebrate Paleontology and Geochronology, *National Science Museum Monographs* 14: 123–143. Tokyo.

Jacobs, L.L. 1977. Rodents of the Hemphillian age Redington Local Fauna, San Pedro Valley, Arizona. *Journal of Paleontology* 51: 505–519.

Kelly, T. and Whistler, D.P. 1998. A new eomyid rodent from the Sespe Formation of southern California. *Journal of Vertebrate Paleontology* 18: 440–443.

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

Korth, W.W. 1994. *The Tertiary Record of Rodents in North America*. 319 pp. Plenum Press, New York.

Lindsay, E.H. 1972. Small mammal fossils from the Barstow Formation, California. *University of California Publications in Geological Sciences* 93: 1–104.

Lindsay, E.H. 1974. The Hemingfordian mammal fauna of the Vedder locality, Branch Canyon Formation, Santa Barbara County, California. Part II: Rodentia (Eomyidae and Heteromyidae). *PaleoBios* 16: 1–20.

Morea, M.F. and Korth, W.W. 2002. A new eomyid rodent (Mammalia) from the Hemingfordian (early Miocene) of Nevada and its relationship to Eurasian Apeomyinae (Eomyidae). *Paludicola* 4: 10–14.

Shotwell, J.A. 1956. Hemphillian mammalian assemblage from northeastern Oregon. *Bulletin of the Geological Society of America* 67: 717–738.

Smith, K.S. 2002. *Mammalian Paleontology of the Monarch Mill Formation at Eastgate, Churchill County, Nevada*. 710 pp. Unpublished Ph.D. dissertation, University of Oklahoma, Norman.

Smith, K.S. 2005. First record of *Leptodontomys* (Rodentia: Eomyidae) in the late Miocene (Clarendonian) of the Southern Great Plains. *Proceedings of the Oklahoma Academy of Science* 85: 47–53.

Swisher, C.C. 1992. *$^{40}Ar/^{39}Ar$ Dating and Its Application to the Calibration of the North American Land Mammal Ages*. 239 pp. Unpublished Ph.D. dissertation, University of California, Berkeley.

Tedford, R.H., Albright L.B. III, Barnosky A.D., Ferrusquia-Villafranca I, Hunt R.M. Jr., Storer J.E., Swisher C.C. III, Voorhies M.R., Webb S.D., and Whistler D.P. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). *In*: M.O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America*, 169–231. Columbia University Press, New York.

Wahlert, J.H. 1978. Cranial foramina and relationships of the Eomyoidea (Rodentia, Geomorpha). Skull and upper teeth of *Kansasimys*. *American Museum Novitates* 2645: 1–16.

Walsh, S.L. 1997. New species of *Metanoiamys*, *Pauromys*, and *Simimys* (Rodentia: Myomorpha) from the Uintan (middle Eocene) of San Diego County, California, and comments on the relationships of selected Paleogene Myomorpha. *Proceedings of the San Diego Society of Natural History* 32: 1–20.

Wang, B. and Emry, R.J. 1991. Eomyidae (Rodentia: Mammalia) from the Oligocene of Nei Mongol, China. *Journal of Vertebrate Paleontology* 11: 370–377.

Wilson, R.W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. *University of Kansas Paleontological Contributions* 7: 1–92.

Winge, H. 1887. Jordfundne og nulevende gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien: med udsigt over gnaveines indbyrdes Slaegtskab. *E Museo Lundii* 1 (3): 1–178. Copenhagen.

Wood, A.E. 1936. A new rodent from the Pliocene of Kansas. *Journal of Paleontology* 10: 392–394.

Wood, A.E. and Wilson, R.W. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. *Journal of Paleontology* 10: 388–391.

Woodburne, M.O. and Swisher, C.C. III 1995. Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. *In*: W.A. Berggren, D.V. Kent, M.-P. Aubry, and J. Hardenbol (eds.), Geochronology, Time Scales and Global Stratigraphic Correlation. *Society for Sedimentary Geology Special Publication* 54: 335–364.