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MAMMALS FROM THE BLUE ASH LOCAL FAUNA (LATE OLIGOCENE), SOUTH DAKOTA. RODENTIA, PART 1: FAMILIES EUTYPOMYIDAE, EOMYIDAE, HELISCOMYIDAE, AND *ZETAMYS*

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ABSTRACT

More than twenty species of rodents have been listed from the Blue Ash local fauna of South Dakota in preliminary surveys, but only four species have been formally identified and described. Species of rodents from the families Eutypomyidae, Eomyidae, and Heliscomyidae are described here. There are one species of eutypomyid, *Eutypomys wilsoni* (new species); three species of eomyids, *Paradjidaumo* sp., *Leptodontomys* sp. cf. *L. douglassi*, and *Zophoapeomys indicus* (new genus and species); and two heliscomyids, *Heliscomys medius* (new species) and *Heliscomys* sp. An additional specimen of the problematical rodent *Zetamys* sp. is also cited. This increases the number of described taxa from the Blue Ash fauna to seven. There appears to be some ambiguity as to the age of the fauna, latest Whitneyan or earliest Arikareean. Unfortunately, the species described here (and previously) are unique to this fauna and cannot be used to correlate with other North American faunas to determine the exact biostratigraphic age.

INTRODUCTION

The Blue Ash fauna from Fall River County, South Dakota was first mentioned by Martin (1974) who identified it as Whitneyan in age and presented a preliminary faunal list that included over 20 species of rodents (Table 1). He suggested that the fauna was transitional between typical Orellan and Arikareean faunas of the Great Plains. The geology of the area was described by Simpson (1985), who similarly recognized approximately the same number of rodent taxa from what he called the Blue Ash Channel. Simpson (1985:fig. 2, 3) determined that the Blue Ash Channel rested on top, and cut into rocks of the Whitney Member of the Brule Formation, source of the type Whitneyan Land Mammal Age (Wood et al., 1941: Prothero and Emry, 2004). He was unable to determine whether fossils from the Blue Ash Channel were latest Whitneyan or earliest Arikareean. Bailey (2004) came to a similar conclusion when he compared a number of early Arikareean faunas and estimated that the Blue Ash fauna was near the Whitneyan-Arikareean boundary in age.

Only four species of rodents have been formally described from the Blue Ash local fauna thus far: the aplodontid *Ansomys* (Korth, in press), two new sciurids (Emry and Korth, in press), and the problematical *Zetamys* sp. (Martin, 1974). All of these species are unknown from elsewhere, so they cannot be used in any faunal correlation. Generically, *Zetamys* is known only from the early Arikareean Gering fauna (Tedford et al., 2004), *Ansomys* is known from Orellan to Barstovian of North America (Hopkins, 2004), and the genus of a new squirrels is known elsewhere only from the Chadronian (Emry and Korth, in press). The specimens described below, and those of the species previously described from the Blue Ash fauna, were collected from several anthills. Because of this, the vast majority of the specimens are isolated cheek teeth. However, the sample consists of nearly 1000 individual specimens. This paper is intended to be the first in a series of systematic descriptions of the rodents from the Blue Ash fauna.

Abbreviations.—Dental measurements: L, anteroposterior length; W, transverse width; H, crown height. Institutions: CM, Carnegie Museum of Natural History. Dental terminology follows that of Wood and Wilson (1936). Upper teeth are indicated by capital letters, lower teeth by lower-case letters.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1827

Family Eutypomyidae Miller and Gidley, 1919

Eutypomys Matthew, 1905

Eutypomys wilsoni n. sp.

(Figure 1A, B)

Type Specimen—CM 76293, left M1 or M2

Referred Specimen—CM 76292, left P4.

Diagnosis—Small species, similar to *E. parvus* in size; accessory lophules on cheek teeth as high and pronounced as major lophs (major lophs nearly indistinguishable); upper cheek teeth proportionally elongated (longer than wide) as in *E. montanensis*; M1 markedly longer than P4 (P4 longer or slightly shorter in length than M1 in other species); cheek teeth higher crowned than in other species.

Etymology—Patronym for R. W. Wilson.

Description—The upper premolar is roughly square in outline, being nearly equal in length and width (L = 2.52 mm; W = 2.55 mm). The buccal cusps (paracone and metacone) are rounded and there is a deep valley along the buccal margin of the tooth between them. A distinct parastyle (anterocone) is present at the anterobuccal corner of the tooth. This cusp is anteroposteriorly compressed, smaller than the major buccal cusps, and extends the buccal corner of the tooth farther forward than the rest of the anterior margin. There is a narrow valley on the occlusal surface between the parastyle and the paracone. The mesostyle is doubled on the margin of the tooth between the paracone and metacone, the posterior of the two being the larger. The lingual cusps are crescentic and slightly smaller than the buccal cusps. There is only a shallow emargination between the lingual cusps. The central basin of the tooth and the narrow valley between the paracone and parastyle are filled with numerous lophules. A metaloph and very short protoloph are recognizable, but are very irregular. There is no obvious mesoloph or other complete loph on the occlusal surface of the tooth, which is a complex of numerous lophules. A posterior cingulum forms the posterior margin of the tooth connecting the hypocone and metacone posteriorly. The lophules are only slightly lower than the protoloph and metaloph. There is no indication of a distinct conule on either of the major lophs of the tooth. The tooth shows the beginnings of wear only on the occlusal surface, and there is no recognizable facet on the anterior side of the tooth to accommodate a P3.

M1 is larger than P4. It is markedly longer and only slightly wider (L = 2.95 mm; W = 2.73 mm). M1 is longer than wide, a proportion known only in one other species of *Eutypomys*, *E. montanensis*. The four major cusps of the tooth are relatively more reduced than in P4. The buccal cusps (paracone and metacone) are only small swellings along the buccal margin of the tooth, and the lingual cusps (protocone and hypocone) are strongly obliquely compressed, entirely incorporated in lophs, and are not distinguishable on the occlusal surface as cusps. The anterior and posterior cingula run the entire width of the tooth from the buccal to the lingual cusps, and form the anterior and posterior margins of the tooth. Across the center of the tooth are six transverse lophs that run the width of the tooth. Both the paracone and metacone have lophs running lingually from them across the occlusal surface, which may be interpreted as the protoloph and metaloph; but they are not any higher or wider than the remainder of the transverse lophs. The most posterior of the transverse lophs extends only about half the width of the tooth, joining the posterior cingulum lingual to its center. There are also several shorter anteroposterior lophs that connect the transverse lophs. These lophs are as high and thick as the transverse lophs. There is no indication of conules. The tooth is clearly higher-crowned lingually than buccally (unilateral hypsodonty). The height of the crown at the protocone is apporoximately 90% of the width of the tooth (H = 2.42 mm).

TABLE 1. Rodents previously listed from the Blue Ash fauna.

Martin, 1974	Simpson, 1985
Aplodontidae	
Prosciurus sp.	*Prosciurus* sp.
Pelycomys sp.	?*Haplomys* indet.
?*Allomys* sp.	?Prosciurine indet.
Haplomys sp.	
?*Meniscomys* sp.	
Sciuridae	
Squirrel indet	Squirrel indet
Protosciurus	
Protosphermophilus	
Miospermohilus	
Castoridae	
Agnotocastor	castorid gen. et. sp. new
	castorid gen. et. sp. indet
Eutypomyidae	
Eutypomys	
Eomyidae	
Small eomyid	*Adjidaujmo* cf. *douglassi*
Paradjidaumo	*Paradjidaumo trilophus*
Cricetidae	
Eumys brachyodus	*Eumys brachyodus*
Leidymys cf. *blac*ki	*Eumys* cf. *parvidens*
Geringia mcgregori	*Eumys* indet.
Scottimus cf. *kellamorum*	*?Leidymys* cf. *blacki*
	Leidymys sp. indet.
	Geringia cf. *mcgregori*
	Scottimus exiguus
	Scottimus longiquus
	Scottimus sp. indet.
Heliscomyidae	
Helisomys	*?Helisomys* sp. indet.
Heteromyidae	
Proheteromys	
Geomyidae	
Tenudomys	
Florentiamyidae	
Florentiamys	*?Florentiamys* sp. indet
Family uncertain	
Zetamys sp.	

Discussion—*Eutypomys wilsoni* is distinguished from all other species of the genus by its small size, being smaller than all others except the Chadronian *E. parvus* and the Duchesnean species, *E. acares* and *E. obliquidens*, described by Storer (1988). The occlusal pattern of the cheek teeth of *E. wilsoni* is similar to that of Orellan and later species of the genus, with accessory lophules as high and distinct as the major lophs. Proportions of the upper molars are similar to those of Arikareean *E. montanensis* (Wood and

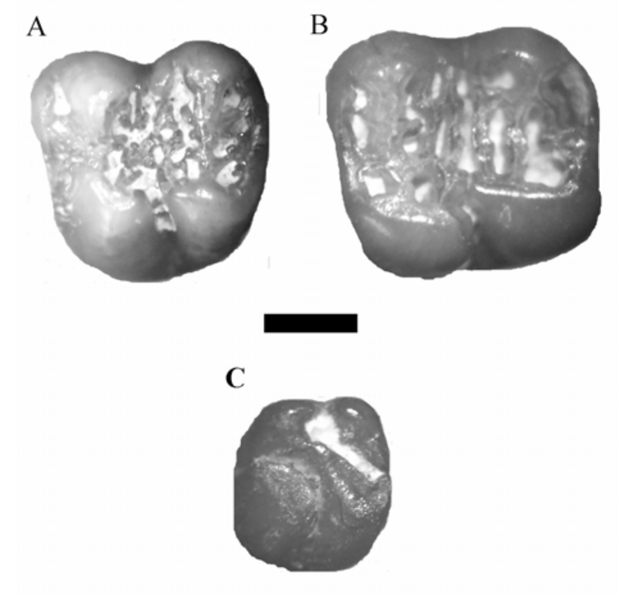

FIGURE 1. Cheek teeth of *Eutypomys wilsoni* and *Zetamys* sp. A-B, *E. wilsoni*. A, CM 76292, left P4. B, CM 76293, left M1 or M2 (holotype). C, *Zetamys* sp., CM 76301, left P4. Bar scale = 1 mm.

Konizeski, 1965:table 2; Macdonald, 1970:table 31); longer than wide (wider than long in other species). In all other species, P4 is nearly equal to M1 in length; in *E. wilsoni*, P4 much shorter.

Crown-height of cheek teeth of *E. wilsoni* is greater than all other species of *Eutyopmys*. Storer (1988) measured the height of the upper molars of *E. acares* and *E. obliquidens* and stated that the crown height was nearly identical to that of the Duchesnean to early Chadronian *E. inexpectatus* from Texas (Wood, 1974). Using Storer's (1988:tables 8, 9) measurements, the height of the protocone on the upper molars relative to the width of the tooth ranged from 61 to 65%. The same ratio on the upper molar of *E. wilsoni* is approximately 90%. Comparisons to other species of *Eutypomys* are a little more difficult because crown-height measurements are rarely recorded and there is no standard method for this measurement. However, Korth (2000:table 2) compared the crown height of lower molars of *E. inexpectatus* and the Orellan *E. thompsoni* and *E. hibernodus*. According to these measurements, *Eutypomys thompsoni* had cheek teeth approximately 10% higher crowned than *E. inexpectatus* (presumably equivalent to the other Duchesnean species), and *E. hibernodus* was approximately 20% higher crowned than the Duchesnean species. If measurements of crown-height are proportional, then the cheek teeth of *E. wilsoni* are approximately 50% higher-crowned than the Duchesnean species and 30-40% higher than the Orellan species. Unfortunately, the crown-height of *E. montanensis* has not been reported. According to the published figures of *E. montanensis* (Wood and Konizeski, 1965:text-fig. 2; Macdonald, 1970:fig. 25), the crown height is about the same as *E. thompsoni*.

Storer (1988) argued that *Eutypomys acares* had greater dental similarity to *E. inexpectatus* and the Chadronian *E. parvus* than other species of the genus (also see Russell, 1972; Storer, 1978), and that they were slightly more primitive than the Orellan and later species of *Eutypomys*. He viewed *E. obliquidens* as an early, more specialized species, not directly related to any other. *E. wilsoni* is most similar to *E. montanensis* than other species of the genus because of the proportions of the upper molars. Only in *E. montanensis* are the upper molars wider than long, as in *E. wilsoni* (Macdonald, 1970:table 31). This distinctive feature appears to unite the latter two species together, distinct from all of the earlier species. *Eutypomys wilsoni* differs from *E. montanensis* in its smaller size, greater crown height of the cheek teeth, and having P4 much sorter than M1. In *E. montanensis*, P4 is nearly equal in length to M1.

Family Uncertain
Zetamys Martin, 1974
Zetamys sp.
(Figure 1C)

Referred Specimen—CM 76301, left P4.

Measurements—L = 1.55 mm; W = 1.76 mm.

Discussion—Martin (1974) previously reported three isolated teeth of *Zetamys* sp. from the Blue Ash fauna, including an isolated P4. The P4 assigned here to this species does not differ from the P4 described and figured earlier in size or morphology (Martin, 1974:fig. 2D, table 1).

Family Eomyidae Winge, 1887
Subfamily Eomyinae Winge, 1887
Paradjidaumo Burke, 1934
Paradjidaumo sp.
(Figure 2A, B)

Referred Specimens—CM 76137, left p4; CM 76294, left M1 or M2; and CM 76295, right M1 or M2.

Measurements—CM 76137, p4: L = 1.22 mm; W = 1.04 mm. CM 76294, M1 or M2: L = 1.20 mm; W = 1.33 mm. CM 76295, M1 or M2: L = 1.23; W = 1.40.

Description—The two upper molars, CM 76294 and CM 76295, do not differ from the upper molars of other species of *Paradjidaumo* described or figured elsewhere (Black, 1965; Setoguchi, 1978; Storer, 1978; Korth, 1980). The teeth are mesodont with thin lophs and long mesolophs. The anterior cingulum runs approximately half the width of the tooth from the

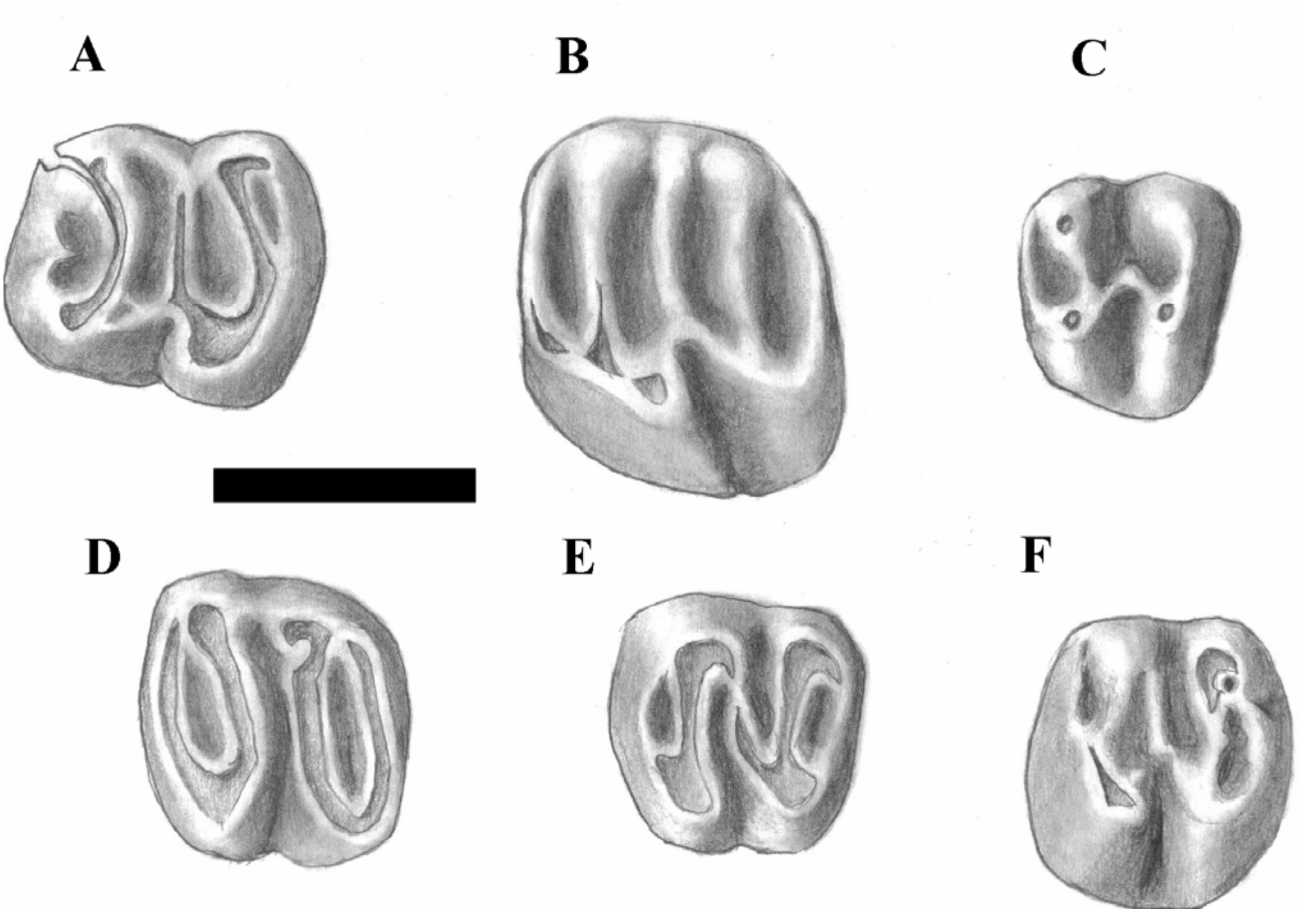

FIGURE 2. Eomyids from Blue Ash fauna. A-B, *Paradjidaumo* sp. A, CM 76137, left p4. B, CM 76294, left M1 or M2. C, *Leptodontomys* sp. cf. *L. douglassi*, CM 76296, right P4. D-F, *Zophoapeomys indicum*, D, CM 76136, right m1or m2 (holotype). E, CM 76135, left P4. F, CM 76134, left M1 or M2. Bar scale = 1 mm.

paracone at the buccal end to about the center of the anterior margin where it joins the protoloph. The posterior cingulum runs the entire width of the tooth. CM 76295 has a distinct mesostyle at the buccal end of the mesoloph, not present in CM 76294. This character is variable in species of the genus. In size, these specimens are within the size ranges of other *P. hypsodus*, *P. hansonorum*, and *P. trilophus* (Setoguchi, 1978:table 7; Storer, 1978:32; Korth, 1980:table 2), but are at the very lowest end of the size range.

The lower premolar, CM 76137, is similar in size to the upper molars and is mesodont as well. The lophs are high and thin. A small trigonid basin is formed by the metalophid fusing at both of its ends with the anterior cingulum. The mesolophid is long, reaching the lingual margin of the tooth. The posterior cingulum is short, extending only about one-third the width of the tooth from the entoconid buccally. In size, p4 is smaller than any specimen of *P. trilophus* or *P. hansonorum* (Storer, 1978:32; Korth, 1980:table 2), at the very lowest end of the size range of *P. hypsodus* (Setoguchi, 1978:table 7) and slightly larger than the p4 of *P. alberti* (Russell, 1954:103).

Discussion—The crown-height and occlusal morphology of these three isolated teeth are identical to that of other species of *Paradjidaumo*. *Padjidaumo. alberti* from the Chadronian of British Columbia is the smallest species of the genus and slightly smaller than the specimens from Blue Ash (Russell, 1954:103). *Paradjidaumo. spokanensis* and *P. validus* from the Orellan are the largest species of the genus, clearly larger than the specimens from Blue Ash (White, 1954:410; Korth, 1980:table 3). The size of the Blue Ash teeth is included in the range of size of the Orellan *P. hypsodus* and *P. trilophus*, and the Chadronian *P. hansonorum*, but they are always at the very lowest end of the size range, well below the mean (Setoguchi, 1978:table 7; Storer, 1978:32; Korth, 1980:table 2).

This suggests an overall smaller size of the Blue Ash species. However, it cannot be referred to any currently recognized species of *Paradjidaumo*, nor is it possible to name a new species based on such a small sample.

Both Martin (1974) and Simpson (1985) listed *Paradjidaumo* in their respective preliminary faunal lists of the Blue Ash fauna (Table 1). This represents the latest occurrence of the genus. Previously, *Paradjidaumo* was only known definitely from the Chadronian and Orellan (Korth, 1980, 1994)

Leptodontomys Shotwell, 1956
Leptodontomys sp. cf. *L. douglassi* (Burke, 1934)
(Figure 2C)

Referred Specimen—CM 76296, maxillary fragment with right P4.

Measurements—L = 0.82 mm; W = 0.85 mm.

Discussion—The single maxillary fragment with P4, CM 76296, is nearly identical in size and morphology to the P4 of *Leptodonotmys douglassi* previously described and figured (Korth and Bailey, 1992: fig. 2a, table 1). The type of *L. douglassi* was originally reported from the Whitneyan (Burke, 1934; Wood, 1937). Korth and Bailey (1992) suggested that it may have been Arikareean based on the occurrence of this species from the early Arikareean of Nebraska. The uncertainty of the age of the Blue Ash fauna, latest Whitneyan or earliest Arikareean, makes this occurrence of the species compatible with either of these proposed ages.

Subfamily Apeomyinae Fejfar, et al., 1998
Zophoapeomys n. gen.

Type and Only Species—*Zophoapeomys indicum* n. sp.

Range—Late Oligocene (latest Whitneyan or earliest Arikareean) of South Dakota.

Diagnosis—Small eomyid, similar in size to *Apeomys*, much smaller than other apeomyines; cheek teeth lower crowned than in *Apeomys*; lophate cheek teeth; lophs on lower molars form two oval loops as in *Apeomys*; occlusal surface of lower molars slightly concave; lower molars two-rooted (three-rooted in *Apeomys*); no "spur" on lower molars lingual to the metaconid (present on *Apeomys*).

Etymology—Greek, *zophos*, west; and *Apeomys* a related genus.

Discussion—This genus clearly belongs to an apeomyine because of the diagnostic double-loop occlusal morphology of the lower molars and concave occlusal surface of the cheek teeth (Fejfar, et al., 1998). It is distinct from other genera of apeomyines based on several features: 1) there are only two roots on the lower molars (three in others); 2) there is no "spur" connected to the metaconid on the lower molar; and 3) the cheek teeth are slightly lower crowned.

Zophoapeomys indicum n. sp.
(Figure 2D-F)

Type Specimen—CM 76136, right M_1 or M_2.

Referred Specimens—CM 76134, left M^1 or M^2; CM 76135, maxillary fragment with left P^4.

Diagnosis—Same as for genus.

Etymology—Latin, *indicum,* deep blue or indigo; intended to refer to the fauna, Blue Ash, from which the specimens were recovered.

Measurements—CM 76136, m1 or m2: L = 0.92 mm; W = 1.02 mm. CM 76135, P4: L = 0.95 mm; W = 1.07 mm. CM 76314, M1 or M2: L = 0.99 mm; W = 1.13 mm.

Description—The lower molar is very low crowned, lophate, and two-rooted. The occlusal surface is gently concave upwards. The tooth is only slightly wider than long. There are four distinct lophs that cross the entire occlusal surface transversely. The anterior cingulum and metalophid are parallel to one another and enclose a transversely wide, anteroposteriorly narrow valley. The metaconid is a distinguishable cusp at the anterolingual corner of the tooth. The anterior cingulum ends just anterior to this cusp, so the "loop" typical of other apeomyines is not complete. Just buccal to the facet for the metaconid, the metalophid has a small irregularity that appears in the shape of a question mark. The remainder of the metalophid is a straight ridge that meets the anterior cingulum buccally at the protoconid. Both buccal cusps, protoconid and hypoconid, are barely recognizable as such, and are V-shaped junctions of the lophs that fuse on the buccal side of the tooth. There is no short lophid or "spur" running buccally from the metaconid into the anterior valley that is present on *Apeomys* (Fahlbusch,1968:abb. 7). The entoconid is represented by a round facet at the posterolingual corner of the tooth. The hypolophid runs directly buccally and joins the posterior cingulum at the hypoconid. The posterior cingulum runs the entire width of the posterior margin of the tooth and ends just posterior to the entoconid. These latter two lophids form an oval that is transversely long and anteroposteriorly narrow, nearly identical to that of the anterior lophids. There is a narrow valley separating the metalophid from the hypolophid that extends the entire width of the tooth, but is blocked lingually by the posterior side of the metaconid and anterior side of the entoconid. It appears that after only a little more wear, the anterior cingulum will join the metaconid, the posterior cingulum will join with the entoconid, and the two lingual cusps will fuse along the center of the lingual border of the tooth.

CM 76135 has a small portion of the maxilla preserved anterior to P4. It is evident from the anterodorsal slope of the maxilla fragment that the skull was sciuromorphous. There is no indication of an alveolus for P3 or dP3. The tooth is low crowned and slightly wider than long. The anterior cingulum of P4 originates at the anterobuccal corner of the tooth and extends about half the width of the tooth lingually where it joins the protoloph near its center. The protoloph extends the entire width of the tooth from the paracone to the protocone. There is no indication of a conule on the protoloph. The protocone and paracone are anteroposteriorly compressed. The buccal end of the paracone bends back in a buccal direction forming a hook. The hypocone is anteroposteriorly compressed as is the protocone. The anterior arm of the hypocone extends anterobuccally and forms a short mesoloph that ends buccally just lingual to the end of the “hook” of the paracone. The mesoloph or anterior arm of the hypocone does not connect with the protocone or protoloph. The metaloph extends lingually from the metacone, joining the anterior arm of the hypocone at the center of the tooth, lingual to the mesoloph. The posterior cingulum forms the posterior border of the tooth and runs from the metacone to the hypocone. The union of the posterior cingulum with the buccal side of the metacone forms a hook shape, similar to that of the paracone.

The M1 or M2, CM 76134, is larger than P4 but the overall occlusal morphology is very similar. The anterior cingulum is shorter on M1 and does not expand the tooth anterobuccally as it does in P4. The only major difference between the occlusal pattern of M1 or M2 and P4 is that the anterior arm of the hypocone is continuous across the entire width of the tooth, joining the paracone along its posterior side. There is also a short spur (lophule) that runs form the apex of the protocone posterobuccally into the valley anterior to the mesoloph. This lophule does not reach the mesoloph. The junction of the metacone and posterior cingulum forms a hook, as it does on P4.

Discussion—*Zophoapeomys indicum* is the smallest species of apeomyine eomyid described. The dimensions of the cheek teeth are within the size range of *Apeomys tuerkheime* from the late Oligocene to early Miocene of Germany (MP 30) but are at the lowest end of the size range (Fahlbusch, 1968:abb. 9). It differs from *A. tuerkheime* in lacking the spur that runs buccally from the metaconid on the lower molars and appears to be slightly lower-crowned. The mesoloph of P4 of *Z. indicum* also has a longer mesoloph that nearly connects to the paracone not present in *Apeomys* (Fahlbusch, 1968:abb. 8a, b; Engesser, 1999:fig. 30.8). The lower molars of *Apeomys* are three-rooted, those of *Z. indicum* are two-rooted.

Smith et al. (2006) referred *Arikareeomys skinneri* from the Arikareean of Nebraska (Korth, 1992) to the Apeomyinae. *Zophoapeomys* cheek teeth can be distinguished from *A. skinneri* by being smaller (Korth, 1992:table 11) and lower-crowned. The P4 of *Arikareeomys* is also larger than the first molar, whereas in *Zophoapeomys* the premolar is smaller. The anterior arm of the hypocone on the upper molar of *Z. indicum* is continuous across the tooth to the paracone and in *Arikareeomys* the loph stops at a mesocone (Korth, 1992:fig. 14A).

Both *Megapeomys* and *Apeomyoides* are markedly larger than *Zophoapeomys* and the cheek teeth are much higher crowned (Fejfar et al., 1998; Morea and Korth, 2004; Smith et al., 2006).

Smith et al. (2006) recognized four genera of Apeomyinae; *Apeomys* and *Megapeomys* from late Oligocene and early Miocene Eurasia, and *Arikareeomys*, *Apeomyoides*, and *Megapeomys* from the early Miocene of North America. Previously, it was considered that the earliest occurrence of the subfamily was nearly simultaneous in the latest Oliogocene of North America and Europe, Arikareean and MP 30, respectively (Korth, 1992; Engesser, 1999). The occurrence of *Zophoapeomys* in the Blue Ash fauna (latest Whitneyan or earliest Arikareean) predates any other occurrence of the subfamily. *Zophoapeomys* also has a number of morphologies that appear to be primitive to all the later species: 1) smaller size; 2) P4 smaller than M1 (also present in *Apeomys*); 3) lower molars two-rooted; and 4) cheek teeth lower-crowned. These primitive morphological characters along with earlier occurrence suggest an ancestral position of *Zophoapeomys* to all of the later apeomyines.

The geographic occurrence of apeomyines suggests several different immigration events between Eurasia and North America from the late Oligocene to the early Miocene. Engesser (1999) could find no ancestor for *Apeomys* in Europe, and suggested that it was an immigrant taxon. The earlier occurrence of *Zophoapeomys* may be indicative of a North American origin of the subfamily that emigrated to Europe, and was later reintroduced to North America in the Hemingfordian.

Family Heliscomyidae Korth, Wahlert and Emry, 1991

Heliscomys Cope, 1873

Heliscomys medius n. sp.

(Figure 3A, Table 2)

Type Specimen—CM 76298, maxilla with left P4-M2.

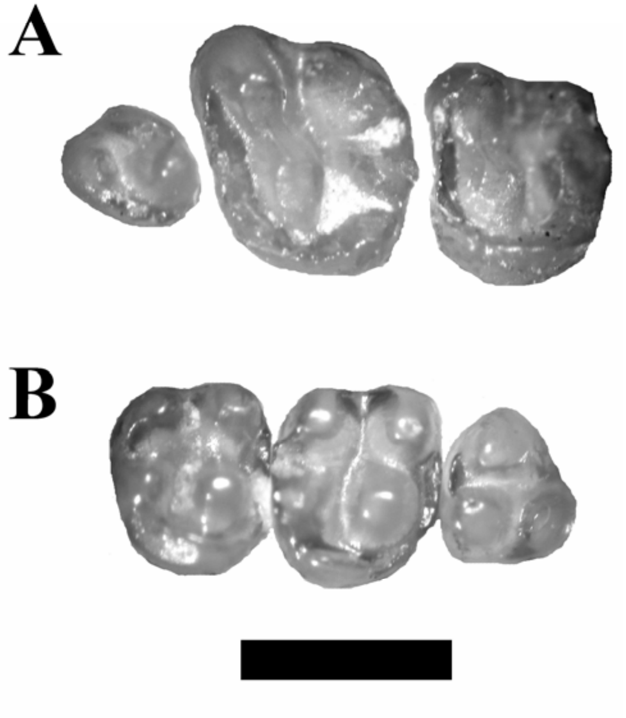

FIGURE 3. *Heliscomys* from Blue Ash fauna. A, *Heliscomys medius*, CM 76298, left P4-M2 (holotype). B, *Heliscomys* sp., CM 76297, right P4-M2. Bar scale = 1 mm.

Referred Specimens—CM 76299, maxilla with left P4-M2, and CM 76300, maxillary fragment with left M1.

Diagnosis—Intermediate sized species; P4 greatly reduced (P4 width 50-64% that of M1); protostyle and entostyle present on M1, but lingual cingulum not interrupted by valley; protostyle compressed.

Etymology—Latin, *medius*, middle.

Description—The overall size of the upper cheek teeth of *H. medius* is intermediate for species of *Heliscomys*, larger than *H. vetus* (Galbreath, 1953:table 11) and *H. senex* (Korth, 1995:table 1), and smaller than *H. mcgrewi* (Korth, 1989:table 1). P4 is greatly reduced in size compared to M1, being only 50 to 64% as wide as M1, similar to the proportions in *H. senex* and *H. mcgrewi*, relatively smaller than in all other species of the genus (Korth, 1995:table 2). P4 consists of a large cusp (hypocone) at the center of the posterior margin of the tooth, and several minute cuspules along the lingual, anterior and buccal sides. On the holotype, there is a recognizable metacone, protocone and hypostyle, but on the referred specimen CM 76299 there is no evidence of a buccal cusp (metacone).

Four major cusps are distinguishable on M1; paracone and metacone of the protoloph, and metacone and hypocone of the metaloph. The paracone and protocone are more widely separated from one another than the cusps of the metaloph, making it longer and expanding the anterobuccal corner of the tooth. The anterior and lingual cingula form a continuous ridge around the tooth beginning at the anterolingual corner of the paracone and running to the posterolingual corner of the hypocone. The central valley separating the lophs is not directly transverse, but slightly posterobuccally oriented. This valley ends at the lingual cingulum. There are two identifiable styles along the lingual cingulum. The entostyle is circular in outline and is positioned along the cingulum at the lingual end of the central valley. The protostyle is smaller than the entostyle and flattened, appearing as a small rise in the cingulum. There is a very short posterior cingulum along the posterior margin of the tooth between the hypocone and metacone.

M2 is slightly smaller than M1. The protoloph and metaloph are parallel and of equal length. The central valley of the tooth is directly transversely oriented. The anterior cingulum originates as in M1 and wraps around the lingual side of the tooth, ending at the hypocone. There is no indication of any styles or cuspules along the lingual cingulum. The posterior cingulum is as in M1.

TABLE 2. Dental measurements of *Heliscomys* from Blue Ash. Abbreviations: L = anteroposterior length; W = transverse width. Measurements in mm.

	P4		M1		M2	
	L	W	L	W	L	W
H. medius						
CM76298	0.51	0.61	1.00	1.22	0.84	1.11
CM 76299	0.71	0.75	1.11	1.25	0.98	1.09
CM 76300			0.98	1.27		
Heliscomys sp.						
CM 76297	0.69	0.75	0.77	0.94	0.66	0.90

Discussion—Korth (1995) divided the species of *Heliscomys* into two subgenera based on the relative size of the premolar compared to M1. *Heliscomys medius* has a greatly reduced premolar as in *H.* (*Heliscomys*), and clearly belongs to that subgenus. The amount of reduction of P4 is the same as in *H. senex* and *H. mcgrewi*, the species showing the greatest amount of reduction (Korth, 1995:table 2). The morphology of P4 in *H. medius* is nearly identical to that of *H. senex* and *H. mcgrewi* as well, consisting of a large hypocone and having the remainder of the cusps reduced to small, marginal cuspules. One difference between *H. medius* and the latter species is its size. It is clearly larger than *H. senex* and smaller than *H. mcgrewi* (Korth, 1989:table 1; Korth, 1995:table 1). The only difference in morphology between *H. medius* and these species is the presence of a protostyle on the lingual cingulum of M1. In *H. senex*, *H. mcgrewi* and *H. vetus* there is a distinct, circular entostyle along the lingual cingulum (variable in *H. vetus*; Korth, 1989) as in *H. medius*. However, none of these species has a protostyle. There is a protostyle on M1 of species of *Heliscomys* referred to *H.* (*Syphyriomys*) (Korth et al., 1991; Korth, 1989, 1995). However it differs from the condition in *H. medius* in that it is circular in occlusal outline, similar in size and shape to the entostyle, and there is a distinct valley separating the entostyle and protostyle. In *H. medius*, the protostyle is flattened and appears as a slight rise in the cingulum, and there is no distinct valley that separates it from the entostyle.

Korth (1995) noted that species of *Heliscomys* (*Syphyriomys*) continued into the Barstovian, but those of *H.* (*Heliscomys*) had their last occurrence in the Orellan. *H. medius* is the latest occurrence of *H.* (*Heliscomys*) recorded, extending its range into the late Oligocene (latest Whitneyan or earliest Arirkareean).

Heliscomys sp.
(Figure 3B, Table 2)

Referred Specimen—CM 76297, maxilla with right P4-M2.

Description—The cheek teeth of CM 76297 are smaller than those of the common Orellan species (Wood, 1939:table I; Galbreath, 1953:table 11; Setoguchi, 1978:table 10). P4 is smaller than M1 but not appreciably so, having a width approximately 80% that of M1. It is triangular in occlusal outline with three cusps of nearly equal size. Buccally there is a metacone, anteriorly a protocone, and at the posterolingual corner of the tooth is a hypocone. The metacone is only slightly smaller than the other two cusps. There is no indication of an entostyle or hypostyle along the lingual side of the tooth. A short posterior cingulum runs along the posterior margin of the tooth buccally from the apex of the hypocone and ends before it reaches the metacone.

M1 and M2 are nearly identical. M2 is only slightly smaller than M1. On both molars the paracone, protocone, metacone and hypocone are nearly equal in size and arranged in two transverse rows (protoloph and metaloph) that are of equal length. There is a valley separating the lophs that runs transversely across the tooth. The anterior cingulum runs from a point between the paracone and protocone and reduces in height at the anterolingual corner of the tooth until it ends at a small notch in the cingulum lingual to the protocone. The lingual cingulum starts just posterior to the end of the anterior cingulum and runs along the lingual margin of the tooth, fusing with the hypocone at the posterolingual corner of the tooth. The posterior cingulum is a low ridge that runs from the apex of the metacone and joins the apex of the hypocone.

Discussion—CM 76297 is unique among species of *Heliscomys* in the morphology of P4. In all other species of the genus, whether the upper premolar is reduced or not, the typical geomyoid pattern of a single-cusped protoloph (protocone) and a three-cusped metaloph (metacone, hypocone, entostyle) is maintained. In species of *Heliscomys* (*Heliscomys*) the premolar is greatly reduced, but it still maintains this pattern even though all but the hypocone are reduced to small cuspules (Korth, 1995). The premolar of CM 76297 has cusps unreduced in size, but the entostyle is completely lacking, forming a three-cusped rather than a four-cusped pattern. The size of the premolar is not greatly reduced in size as in *H.* (*Heliscomys*) even though one of the major cusps is lacking. In all species of *H.* (*Syphyriomys*) the premolar is approximately the same size as CM 76297 but the entostyle is always present (Korth et al., 1991; Korth, 1995). The molars are distinct as well. M1 is not markedly larger than M2 as in *H. medius* and other species of *H.* (*Heliscomys*), but there are no distinct styles diagnostic of species of *H.* (*Syphyriomys*).

The Arikareean *Heliscomys woodi* is only known from a mandible with p4-m1, but is similar in age to the Blue Ash specimen (McGrew, 1941). It may be possible that CM 76297 represents the upper cheek teeth of *H. woodi*. However, there are a few differences between them, even though *H. woodi* is only known from lower dentition and CM 76297 is a maxilla. The amount of reduction in the p4 of *H. woodi* is greater than in any other species of the genus, whereas the P4 of CM 76297 is not reduced in size compared to other species of *Heliscomys*. The second difference is in size. CM 76297 (Table 2) is smaller than all other reported species except the Chadronian *H. ostranderi* (Korth et al., 1991:table 1) and *H. woodi* has a larger m1 than any reported species (McGrew, 1941:57).

It appears that CM 76297 cannot be referred to a currently known species of *Heliscomys* or even to either of the recognized subgenera, based on the size and morphology of P4 and the upper molars. Clearly, additional material of the species represented by CM 76297 is necessary before a specific or generic identification can be made.

CONCLUSIONS

The number of species formally described from the Blue Ash local fauna is now ten, including those described previously. Unfortunately, none of the species described is diagnostic for either the Whitneyan or Arikareean Land Mammal Age (see Prothero and Emry, 2004; Tedford et al., 2004). Previously published faunal lists from the Blue Ash fauna are clearly preliminary (Martin, 1974; Simpson, 1985) and cannot be used for definite comparisons with other published faunas. Until the remainder of the fauna can be described, the exact age of the fauna cannot be determined.

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