

MAMMALS FROM THE BLUE ASH LOCAL FAUNA (LATE OLIGOCENE), SOUTH DAKOTA. RODENTIA, PART 3: FAMILY SCIURIDAE

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ABSTRACT

The Sciuridae (squirrels) are the most diverse family of rodents thus far described from the late Oligocene Blue Ash fauna of South Dakota. Nine species of sciurids are recognized: two previously described probable “flying” squirrels, *Hesperopetes jamesi* and *H. blacki*; five sciurines, *Protosciurus* cf. *P. mengi*, *P. rachelae*, *Nototamias* sp., *Miospermophilus* sp., a new species *Dougllassciurus sapphirus*; and two cedromurines, *Cedromus wilsoni* and a new species *Oligospermophilus emryi*. The recognition of these species increases the number of rodent species from the Blue Ash fauna to 20. As with the remainder of the described species from this fauna, the squirrels help little in establishing a precise age of the fauna, containing a combination of Orellan and earlier taxa, along with Arikareean or younger taxa.

INTRODUCTION

(Figure 1; Table 1)

In a preliminary faunal list of the Blue Ash fauna, Martin (1974) identified four species of squirrels (Sciurid indet., *Protosciurus* sp, *Protospermophilus* sp., and *Miospermophilus* sp.). In a later faunal list, Simpson (1985) identified only a single squirrel species (Sciurid indet.). More recently, Emry and Korth (2007) named two species of a probable “flying” squirrel, *Hesperopetes*. A detailed study of specimens from the Blue Ash fauna has yielded a much more diverse sciurid fauna, resulting in the recognition of nine species. Thus far, this is the greatest diversity of any of the families of rodents described from the Blue Ash fauna (Korth, 2007a, 2008).

All of the fossil material described herein consists of isolated cheek teeth. As with a fauna of this nature, association of upper and lower dentitions and premolars with molars was based on comparable size and morphology of the teeth. Dental terminology follows that of Wood and Wilson (1936). Upper teeth are designated by capital letters, lower teeth by lower-case letters. Abbreviation for Carnegie Museum of Natural History: CM.

SYSTEMATIC PALEONTOLOGY

Family Sciuridae Fischer de Waldheim, 1817
Subfamily Sciurinae Fischer de Waldheim, 1817
Tribe Sciurini Fischer de Waldheim, 1817
Dougllassciurus Emry and Korth, 2001
Dougllassciurus sapphirus n. sp.

Type Specimen—CM 76647, left m1 or m2.

Referred Specimens—CM 76660, 76662 - p4; CM 76621, 76648-76649, 76656, 76659 - m1 or m2; CM 76658, 76671 - m3; CM 76622, 76666, 76674, 76700, 76701 - M1 or M2; CM 76673 - M3.

Diagnosis—Smallest species of the genus, 30% smaller than type species *D. jeffersoni*; hypocone on upper molar not as large as in the type species; enamel in the basins of the cheek teeth smooth (variably rugose in *D. jeffersoni*).

Etymology—Latin, *sapphirus*, blue; in reference to the Blue Ash fauna.

Description—The anterior cingulum of M1 or M2 runs lingually from the buccal edge of the tooth to a point even with the buccal edge of the protocone. The cingulum is separated from the protoloph by a deep, wide valley. There is a short loph (=protocone crest) in this basin at the lingual end that runs buccally from the protocone. The protoloph runs directly lingually from the paracone to the protocone. A small protoconule is distinguishable near its center. The protocone is anteroposteriorly broadened. The metaloph runs slightly anterolingually from the metacone, then attaches to the protocone. There is a large, distinct metaconule just buccal to the union of the metaloph and the protocone. Buccal to it, along the metaloph is a smaller second metaconule. The posterior cingulum runs from the posterior margin of the protocone to the buccal margin of the tooth, posterior to the metacone. A hypocone is present at the

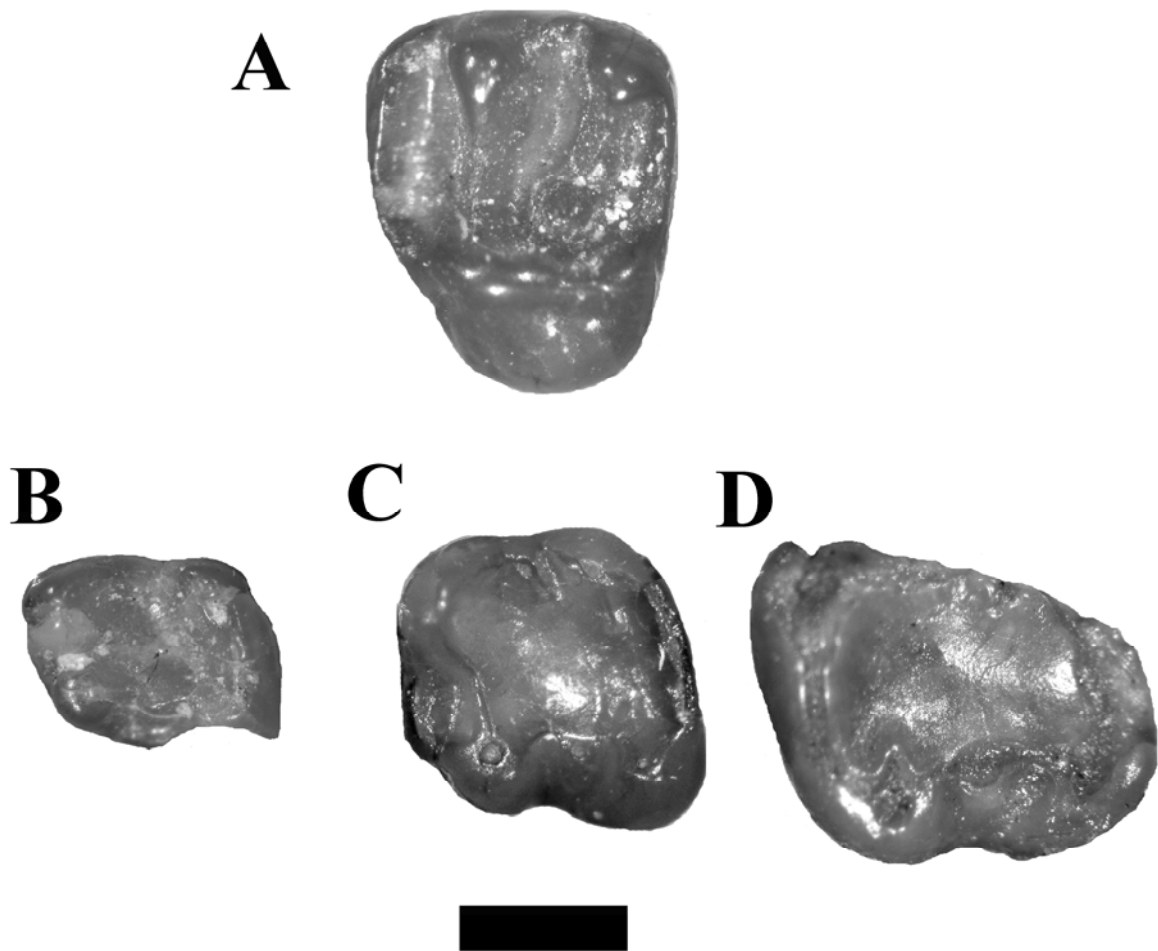


FIGURE 1. Cheek teeth of *Douglassciurus sapphirus*. A, CM 76622, right M1 or M2. B, CM 76662, left p4 (partially broken). C, CM 76647 (holotype), left m1 or m2. D, CM 76658, right m3 (reversed). Bar scale = 1 mm.

lingual base of the posterior cingulum. The cusp is larger than the conules, approximately the size of the buccal cusps (paracone, metacone). There is a minute mesostyle along the buccal margin of the tooth midway between the buccal cusps.

The M3, CM 76673, is slightly smaller than the M1 or M2. The morphology of the anterior half of M3 is very similar to that of the anterior molar. The short protocone crest on the anterior molar is not present on M3, but there is a small cuspule anterior to the lingual end of the protoloph. The posterior half of the tooth is expanded anterobuccally. There is no metacone or hypocone. There is a minute mesostyle along the buccal margin of the tooth posterior to the paracone.

Two isolated p4s are referred to *D. sapphirus*. Both are at least partially broken. The metalophid consists of two cusps of equal size, metaconid and protoconid, the former being slightly larger and more anteriorly positioned. A small, crescentic trigonid basin is present between these cusps. Lingually, a low

loph runs posteriorly from the apex of the metaconid along the lingual margin of the tooth, ending in a small metastylid near the center of the lingual margin. Buccally, there is a circular mesoconid posterior to the protoconid that connects to the protoconid anteriorly, and hypoconid posteriorly by a very narrow connection. The posterior width of p4 is wider than the metalophid. The posterior cingulum runs from the hypoconid to a point just posterior to the entoconid and is separated from the latter by a narrow valley. A short loph runs from the entoconid into the talonid basin that is angled posterobuccally, joining the posterior cingulum buccal to its lingual end.

Lower m1 or m2 is just slightly wider than long, and narrower anteriorly than posteriorly. The protoconid and metaconid are more widely separated than in p4. The metaconid is larger than the protoconid. A small anteroconid is present along the anterior margin of the tooth (metalophulid I). A metalophulid II is complete from the base of the

protoconid to the base of the metaconid, enclosing a small, nearly circular trigonid basin. The mesoconid is central along the buccal side of the tooth between the protoconid and hypoconid but isolated or weakly connected to both cusps. In worn specimens the ectolophid is continuous. A low loph runs from the mesoconid toward the buccal edge of the tooth. The posterior cingulum is as in p4, ending before joining the entoconid lingually. There is a distinct hypolophid running buccally from the entoconid. It is variable in length, but always present. There is a small metastylid along the lingual margin of the tooth near its center. There is also a short loph extending into the basin from the metastylid.

TABLE 1. Dental measurements of *Dougllassciurus sapphirus* from the Blue Ash fauna. Measurements in mm. Abbreviations: L, anteroposterior length; W, transverse width; M, mean; ST, standard deviation; CV, coefficient of variation.

| CM # | | M1L | M1W | M3L | M3W | |
|-------|------|------|------|------|------|------|
| 76622 | | 1.88 | 2.23 | | | |
| 76666 | | 1.78 | 2.28 | | | |
| 76673 | | | | 1.97 | 1.90 | |
| 76674 | | 1.77 | | | | |
| 76700 | | 1.86 | 2.26 | | | |
| 76701 | | 1.90 | 2.23 | | | |
| M | | 1.84 | 2.25 | | | |
| SD | | 0.06 | 0.02 | | | |
| CV | | 3.23 | 1.09 | | | |
| CM# | p4L | p4W | m1L | m1W | m3L | m3W |
| 76621 | | | 1.85 | 1.94 | | |
| 76662 | 1.96 | | | | | |
| 76647 | | | 1.84 | 1.94 | | |
| 76648 | | | 1.85 | 2.10 | | |
| 76649 | | | 1.92 | 2.25 | | |
| 76658 | | | | | 2.44 | 2.15 |
| 76659 | | | | | 2.06 | 2.31 |
| 76660 | 2.11 | 1.96 | | | | |
| 76669 | | | 2.01 | 2.14 | | |
| 76671 | | | | | 2.48 | 2.18 |
| M | | | 1.93 | 2.09 | 2.33 | 2.21 |
| SD | | | 0.10 | 0.13 | 0.23 | 0.09 |
| CV | | | 5.34 | 6.16 | 9.96 | 3.84 |

A single specimen, CM 76658, is referred to m3. In general morphology it is similar to m1 and m2. However, the tooth is more elongated and narrower posteriorly than anteriorly, unlike the anterior molars.

The metalophid II is not complete, leaving the trigonid basin open posteriorly, and no anteroconid is present. Even though the tooth is badly abraded, there is a low hypolophid running posteriorly from the entoconid to the lingual end of the posterior cingulum. The mesoconid is relatively smaller than in m1 or m2, and the ectolophid is continuous from the protoconid to the hypoconid.

Discussion—*Dougllassciurus sapphirus* is referable to this genus based on the presence of several dental morphologies considered diagnostic for the genus but primitive for sciurids (Emry and Korth, 1996): upper molars - doubled metaconules and distinct paraconule, hypocone nearly as large as the protocone, presence of a protocone crest; lower molars - presence of a hypolophid, entoconid and mesoconid large and distinct. It differs from the type species *D. jeffersoni* mainly by its much smaller size, being at least 30% smaller (Table 1; Black, 1965:21; Emry and Korth, 1996:table 1). The hypocone on the upper molars of *D. jeffersoni* are relatively larger compared to the protocone than in *D. sapphirus*, and the irregularities of the enamel in the basins of the teeth of *D. jeffersoni* are lacking in specimens of *D. sapphirus*.

The late Whitneyan or earliest Arikareean age of *D. sapphirus* is much later than the Chadronian occurrence of *D. jeffersoni*, leaving a three to four million year gap in the record of the genus. *Dougllassciurus jeffersoni* has a protrogomorphous zygomaseteric structure of the skull, unknown in any other Sciurinae (Emry and Thorington, 1982). Unfortunately, no cranial material is known of *D. sapphirus*, so it cannot be determined whether the genus developed sciuromorphy independently from other sciurines or retained the primitive morphology until the late Oligocene.

Genus *Protosciurus* Black, 1963
Protosciurus sp. cf. *P. mengi* Black, 1963
 (Figure 2A-C; Table 2)

Referred Specimens—CM 76627, 76628 - p4; CM 76626 - m3; CM 76624, 76625, 76667 - M1 or M2.

Description and Discussion—The cheek teeth referred here to *Protosciurus* sp. cf. *P. mengi* differ little from previous descriptions of the species (Black, 1963; Korth, 1987). The upper molars have the doubled metaconules and large hypocones diagnostic for the species (Korth, 1987). The Blue Ash specimens are only slightly smaller than those previously reported (Table 2; Black, 1963:147; Korth, 1987:tables 1, 2). This is the latest occurrence of this species. Previously, *Protosciurus mengi* was only known from the Orellan (Goodwin, 2008).

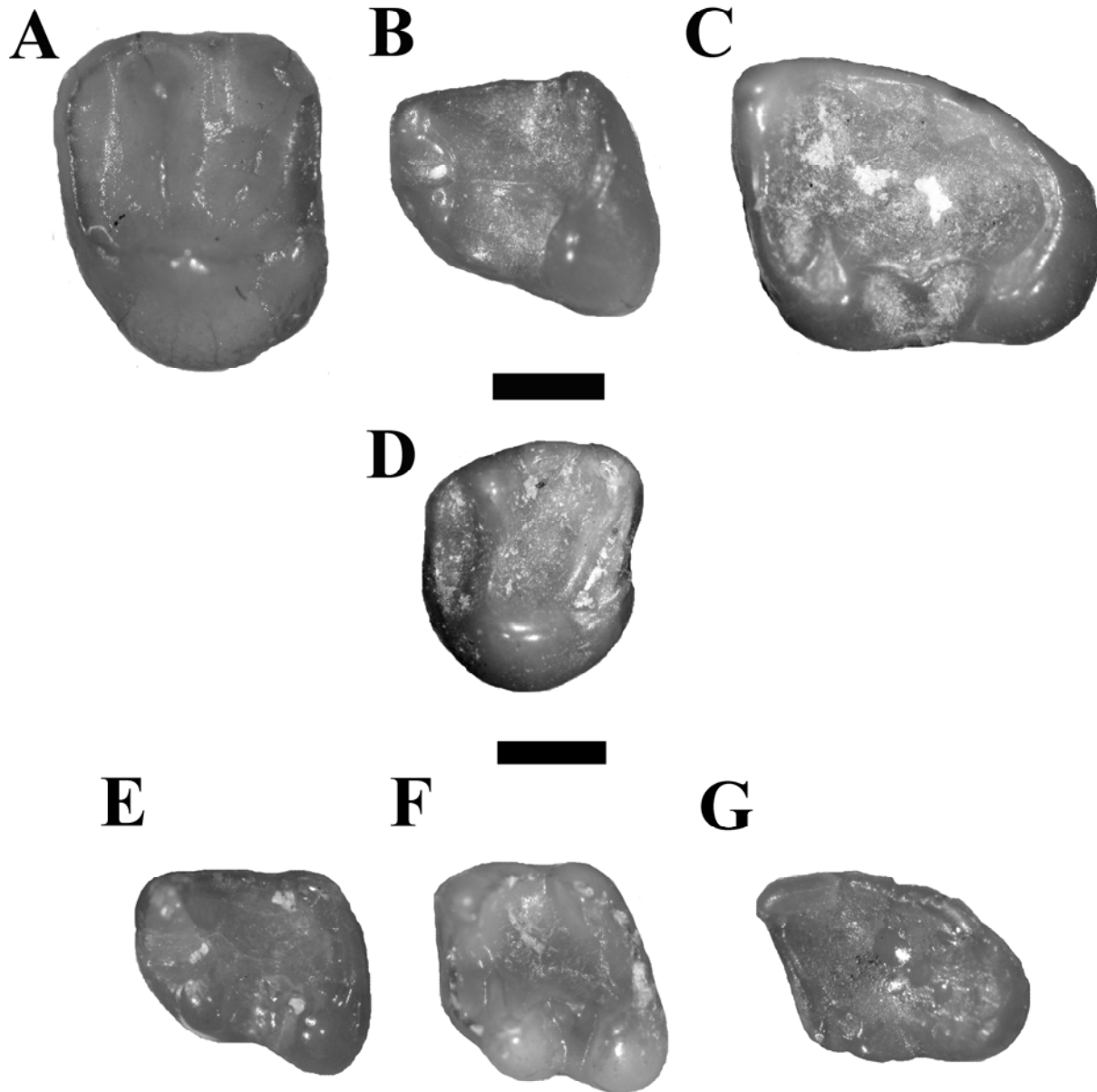


FIGURE 2. Cheek teeth of *Protosciurus* from the Blue Ash fauna. A-C, *Protosciurus* sp. cf. *P. mengi*. A, CM 76625, left M1 or M2. B, CM 76627, left p4. C, CM 76626, left m3. D-G, *Protosciurus rachelae*. D, CM 76623, left M1 or M2. E, CM 76668, right p4 (reversed). F, CM 76709, left m1 or m2. G, CM 76672, left m3. Bar scale = 1 mm.

Protosciurus rachelae Black, 1963
(Figure 2D-G; Table 3)

Referred Specimens—CM 76668 – p4; CM 76709 – m1 or m2; CM 76672 – m3; CM 76623, 76670 - M1 or M2.

Description—The upper molar is quadrate in occlusal outline. The anterior cingulum is separated by a shallow valley from the protoloph. A minute parastyle is at its buccal end. The buccal cusps, paracone and metacone, are widely spaced apart. There is a smaller, circular mesostyle along the buccal edge of the tooth near its center, slightly closer to the

paracone than metacone. The protoloph has a gentle S-curve and runs from the paracone to the anterior margin of the protocone. The metaloph runs obliquely from the metacone at the posterobuccal corner of the tooth to the posterior margin of the tooth. Both lophs are low and rounded with no indication of conules. The protocone is anteroposteriorly broadened, forming a broad U-shape along the lingual edge of the tooth. A small swelling posterior to the protocone, at the lingual end of the posterior cingulum, is the hypocone.

TABLE 2. Dental measurements of *Protosciurus* cf. *P. mengi* from the Blue Ash fauna. Measurements in mm. Abbreviations as in Table 1.

| CM # | | MIL | M1W | | |
|-------|------|------|------|------|------|
| 76624 | | 2.45 | 2.9 | | |
| 76625 | | 2.45 | 3.19 | | |
| CM# | p4L | p4W | | m3L | m3W |
| 76626 | | | | 3.30 | 2.79 |
| 76627 | 2.42 | 2.31 | | | |
| 76628 | 2.54 | 1.99 | | | |

The lower premolar is wider posteriorly than anteriorly. The metaconid is much higher than the other cusps of the tooth. The protoconid is crescentic in shape and connects to the base of the metaconid both anteriorly (metalophulid I) and posteriorly (metalophulid II), enclosing a small, oval trigonid basin. The hypoconid is the same size as the protoconid and connected to it by an ectolophid with a central mesoconid. The posterolophid runs along the posterior margin of the tooth from the hypoconid, attaching to the entoconid, which is slightly smaller than the hypoconid. There is a loph running along the lingual side of the tooth posteriorly from the metaconid, ending in a metastylid. There is a distinct, narrow valley separating the metastylid from the entoconid.

The referred lower m1 or m2, CM 76709, has very little wear, unlike the only other referred molars of *P. rachelae* (Black, 1963:pl. 6, fig. 2). The tooth is rhomboidal in occlusal outline. The four major cusps are large and nearly equal in size, the metaconid being the largest. The anterior width of the tooth is nearly as great as the posterior width; the metaconid and protoconid being widely spaced apart. The anterior cingulum is a high loph that has a small anteroconid near its buccal end. The trigonid basin is large and deep. The posterior arm of the protoconid extends lingually, ending just buccal to the base of the metaconid. A metastylid is present along the lingual border of the tooth, attached anteriorly to a loph

running posteriorly from the metaconid. The ectolophid is thin and connects the protoconid to the hypoconid, well lingual to the buccal edge of the tooth. A distinct, circular mesoconid is present at its center with a minute loph running from the mesoconid buccally. The hypoconid and entoconid are of equal size. The posterolophid is continuous between the two cusps. There is a minute loph running buccally from the entoconid.

The m3, CM 76672, is worn and very similar to that previously described for this species. There is no indication of a trigonid basin, the entoconid is reduced in size (compared to m1 or m2), and expanded posteriorly.

Discussion—The Blue Ash teeth referred to *Protosciurus rachelae* is indistinguishable from the topotypic material of this species from the John Day Formation in size and morphology (Black, 1963:pl. 6). It is distinguished from the Blue Ash specimens of *P. mengi* by its smaller size and lack of conules on the upper molars. It differs from other Arikareean species of *Protosciurus* by its smaller size (Black, 1963:147).

The occlusal morphology of the lower molars of the original material of *P. rachelae* is not known in detail because the molars are badly worn and no p4 was not known. The Blue Ash specimens are the first unworn or little worn specimens of lower dentitions. It is evident from Blue Ash material that there is a well-developed entoconid on the p4 and lower molars, producing the rhomboidal shape of the tooth evident in the original lower molars referred to *P. rachelae*.

The type and originally referred specimen of *P. rachelae* are from an unknown level in the John Day Formation (Black, 1963:145). This formation has a long temporal range, from the latest Whitneyan to the earliest Hemingfordian (Tedford et al., 2004:fig. 6.2) which clearly overlaps with the latest Whitneyan-earliest Arikareean age of the Blue Ash fauna.

TABLE 3. Dental measurements of *Protosciurus rachelae* from the Blue Ash fauna. Measurements in mm. Abbreviations as in Table 1.

| CM # | | MIL | M1W | | | |
|-------|------|------|------|------|------|------|
| 76623 | | 1.97 | 2.39 | | | |
| 76670 | | 2.02 | | | | |
| CM# | p4L | p4W | m1L | m1W | m3L | m3W |
| 76668 | 2.13 | 2.87 | | | | |
| 76672 | | | | | 2.46 | 1.86 |
| 76656 | | | 2.13 | 2.55 | | |
| 76709 | | | 2.09 | 2.19 | | |

Tribe Tamiini Weber, 1928

Genus *Nototamias* Pratt and Morgan, 1989

Nototamias sp.
(Figure 3A-C)

Referred Specimens—CM 76616, left M1 or M2; CM 76617 left p4; and CM 76618, right m1 or m2.

Measurements—M1 or M2: length = 1.25 mm, width = 1.44 mm; p4: length = 1.05 mm, width = 1.02 mm; m1 or m2: length = 1.36; width = 1.25.

Description—The upper molar, CM 76616, is rectangular in occlusal outline and wider than long. The buccal cusps are equal in size, and there is a minute mestostlye between them along the center of the anteroposteriorly elongated buccal margin of the tooth. The protoch and metaloph are continuous with the protocone and there are no conules. The protocone is slightly crescentic but not markedly elongated anteroposteriorly. There is a minute hypocone at the posterolingual corner of the tooth. The anterior and posterior cingula run the entire width of the tooth with wide, shallow basins separating them from the protoch and metaloph, respectively.

The lower premolar, CM 76617, is markedly narrower anteriorly than posteriorly. The metaconid and protoconid are of equal size and positioned very close to one another. There is no trigonid basin. The ectolophid runs from the protoconid to the hypoconid with a slight swelling at its center indicating a small mesoconid. The posterior cingulum is continuous from the hypoconid to the entoconid. The entoconid is slightly anterior to the level of the hypoconid and obliquely compressed into the posterolingual corner of the tooth.

CM 76618 is a lower molar and is rhomboidal in occlusal outline. The metaconid and protoconid are widely separated, unlike p4, but there appears to be little if any trigonid basin. The remainder of the cusps are as in the premolar, with a much reduced and obliquely compressed entoconid.

Discussion—The specimens referred to *Nototamias* sp. are the smallest sciurids in the Blue Ash fauna. They are just slightly smaller than specimens identified as “*Tamias* sp.” by Black (1963:134) from the early Arikareean Sharps Formation of South Dakota, but are very similar in occlusal morphology. The Blue Ash specimens differ from specimens of *N. quadratus* from the Arikareean of Nebraska in being smaller, having a less well developed entoconid, and lacking the enclosed trigonid basin on the lower cheek teeth (Korth, 1992:fig. 12 C-E; table 6). The Blue Ash specimens differ from the later Hemingfordian and Barstovian species of *Nototamias* in having less lophate cheek teeth (Hall,

1930; Black, 1963; Pratt and Morgan, 1989). As with other species of the genus, the Blue Ash specimens of *Nototamias* have two-rooted lower molars rather than the four-rooted molars of *Tamias* and *Eutamias* (Pratt and Morgan, 1989).

Tribe Marmotini Pocock, 1923

Genus *Miospermophilus* Black, 1963

Miospermophilus sp.
(Figure 3D-F)

Referred Specimens—CM 76704 – right p4; CM 76703 – left m1 or m2; CM 76620 - left M1 or M2.

Measurements—p4: length = 1.70 mm, width = 1.55 mm; m1 or m2: length = 1.53 mm, width = 1.50; M1 or M2: length = 1.60 mm; width = 2.09 mm.

Description—Similar in size to *Miospermophilus bryanti* (Wilson, 1960:59; Black, 1963:191), smaller than other species. Anterior cingulum separated from protoch by deep valley. Protoch oriented directly lingually. Protocone rises well above the level of the protoch. There is a faint outline of a protoconule. The metaloph is directed slightly anterolingually from the metacone which, is at the posterobuccal corner of the tooth. The metaloph consists of a low but wide swelling for the metaconule, and is only weakly connected to the protocone. The protocone is the highest cusp on the tooth and is anteroposteriorly lengthened. At the posterolingual corner of the tooth is a small hypocone that is separated from the posterior end of the protocone by a small but distinct notch. The posterior cingulum runs buccally from the hypocone to the base of the metacone.

The lower cheek teeth referred here to *Miospermophilus* are done so based on appropriate size and the reduction of the entoconid, a character of the genus (Black, 1963). The lower premolar is wider posteriorly than anteriorly but more elongated than that of *M. bryanti* (Wilson, 1960:fig. 67a; Black, 1963:pl. 16, fig. 1a). The metaconid is the largest of the cusps and is positioned more anterior than the protoconid. These cusps are closely appressed, and there is only a minute trigonid basin. Along the anterior margin of the trigonid basin is a distinct but small anteroconid. The majority of the tooth is a shallow basin. The ectolophid is thin, and runs posterobuccally from the protoconid to the hypoconid. There is no indication of a mesoconid on the ectolophid. The hypoconid and entoconid are similar in size and connected by a continuous posterolophid. The entoconid is more anterior than the hypoconid. A short, posterior loph runs from the metaconid to a point just anterior to the entoconid, and is separated from the latter by a small valley.

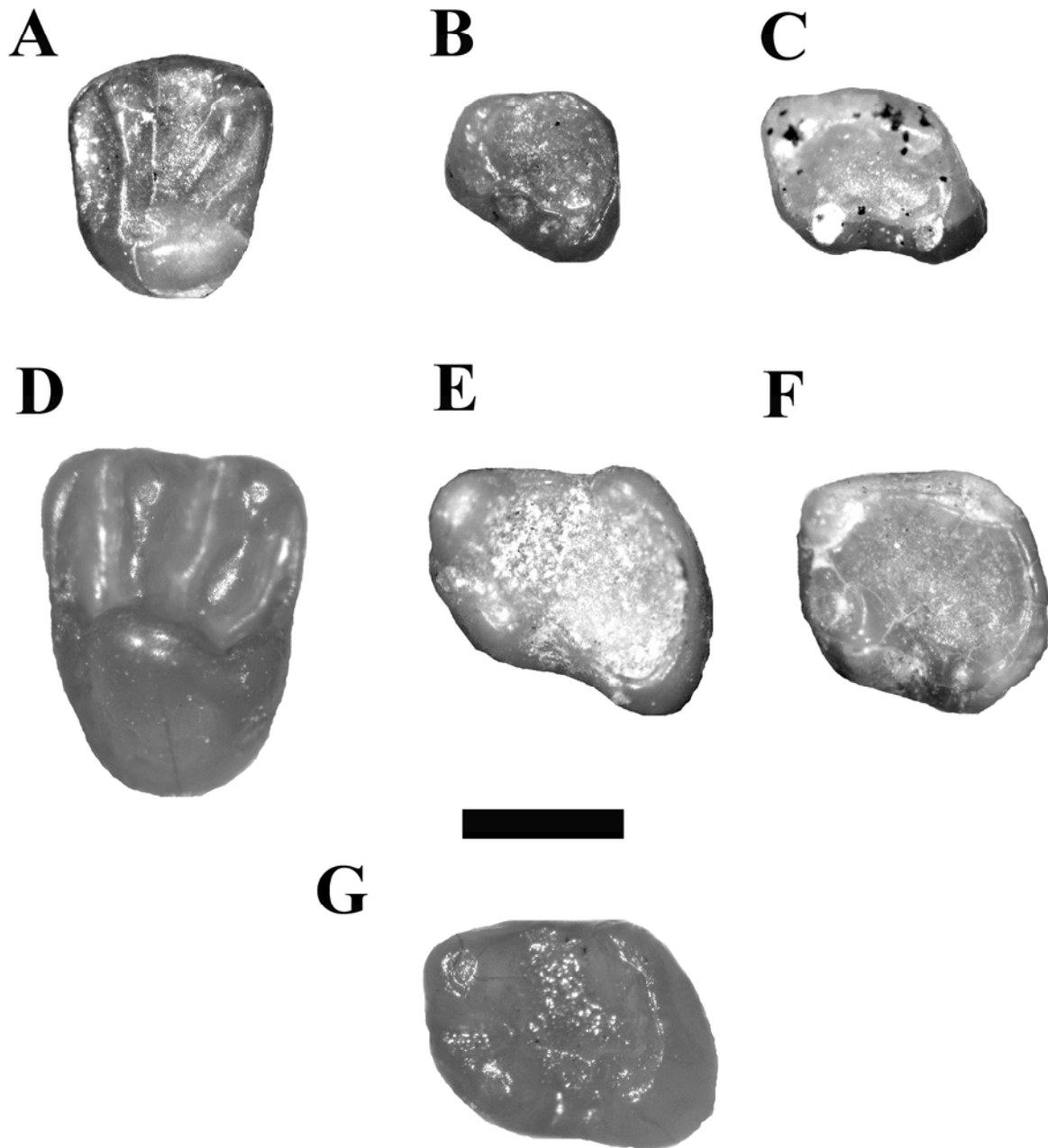


FIGURE 3. Cheek teeth of sciurids from Blue Ash fauna. A-C, *Nototamias* sp. A, CM 76616, left M1 or M2. B, CM 76617, left p4. C, CM 76618, right m1 or m2 (reversed). D-F, *Miospermophilus* sp. D, CM 76620, left M1 or M2. E, 76704, right p4 (reversed). F, CM 76703, left m1 or m2. G, *Hesperopetes jamesi*, CM 76619, left p4. Bar scale = 1mm.

The lower molar, CM 76703, is abraded, the tips of the buccal cusps and some of the lingual margin has been broken away. Similar to the premolar, the tooth consist mainly of a shallow basin. The trigonid basin is

larger than in the p4, but is not closed posteriorly, the posterior arm of the protoconid ending lingually well short of the base of the metaconid. The ectolophid is weakly developed and oriented as in p4, but there is a

small wear facet at its center marking the presence of a mesoconid. As in p4, the entoconid is more anterior than the hypoconid, rounding-off the posterolingual corner of the tooth.

Discussion—The upper molar of *Miospermophilus* sp. can be distinguished from the upper tooth identified as *Nototamias* sp. based on its larger size, proportionally wider shape (upper molars of *Nototamias* sp. more nearly equidimensional), and better development of conules and hypocone. The p4 is more elongated with a larger entoconid than in other species of *Miospermophilus*. Similarly, the molar has a minute mesoconid and is slightly more squared in the posterolingual corner than the later species of *Miospermophilus*.

The morphology of the Blue Ash *Miospermophilus* specimens closely matches that of later species. However there are a few characteristics of the Blue Ash teeth that distinguish it from other described species. On upper molars of other species of *Miospermophilus*, the conules and hypocone are extremely small or completely absent and the teeth are more lophate. The greater prominence of these cusps on the Blue Ash specimen suggests that it is more primitive than other species. The less reduced entoconid and mesoconid on the lower cheek teeth is also a more primitive morphology than in later species.

The occurrence of *Miospermophilus* in the Blue Ash fauna is the earliest recorded of the genus. Macdonald (1972) referred several isolated teeth from the Arikarean Monroe Creek Formation of South Dakota to “Sciurid, small species.” Later, Martin (1976) described specimens of “cf. *Miospermophilus*” from the early Hemingfordian of South Dakota (also see Martin and Green, 1984), and suggested that the Monroe Creek specimens represented the same species. The specimens figured by Macdonald (1972:fig. 9) appear to represent more than a single species. Some of the specimens may be referable to *Nototamias*. However, if Martin (1976) is correct and at least some of these specimens are *Miospermophilus*, they are more lophate with less well developed conules, hypocone, and entoconids than the Blue Ash specimens (Martin, 1976:fig. 3f; Martin and Green, 1984:fig. 17).

Other than the Monroe Creek specimens, the earliest occurrence of *Miospermophilus* is from the Arikarean of California (Whistler and Lander, 2003). However, this record only appears on a faunal list and no specimens have been described or figured. All other previously described species of *Miospermophilus* are Hemingfordian to Clarendonian in age (Goodwin, 2008). It is not surprising that the earliest occurrence of the genus would have the most primitive dental morphology.

Subfamily uncertain

Genus *Hesperopetes* Emry and Korth, 2007

Discussion—In the original description of *Hesperopetes*, Emry and Korth (2007) did not present a direct comparison between their new genus and the propable “flying” squirrel *Sciurion* from the Hemingfordian of Saskatchewan (Skwara, 1989). However there are several morphological differences between these two genera. First, in overall size, the type and only species of *Sciurion*, *S. campestre*, is smaller than the smallest species of *Hesperopetes*, *H. blacki* (Skwara, 1989:table 1; Emry and Korth, 2007:table 1). The crenulations of the enamel in the basins on the cheek teeth of *Sciurion* are more delicate and distinct than in *Hesperopetes*, the former more closely resembling that of the European *Blackia*, as noted by Skwara (1986).

In the upper cheek teeth of *Sciurion*, the protoloph and metaloph are nearly parallel, whereas in *Hesperopetes* these lophs converge on the protocone. This is true of the P4 as well as the molars. Related to the latter morphology, the protocone on *Sciurion* upper cheek teeth forms a much wider U-shape (lengthened anteroposteriorly) than in *Hesperopetes*. The occlusal shape of P4 in *Hesperopetes* is triangular, whereas in *Sciurion* it is more nearly rectangular (=subquadrate). On both P4 and upper molars of *Sciurion* an ectoloph connects the paracone to the mesostyle, and variably connects posteriorly to the metacone. None of the upper cheek teeth of *Hesperopetes* have a loph connecting the mesostyle to either of the major buccal cusps.

In the lower dentition, the trigonid basin of the molars is blocked posteriorly by the metalophule II in *Hesperopetes* specimens, but is always open posteriorly on specimens of *Sciurion*. The anteroconid on the lower molars of *Hesperopetes* is absent or very small, whereas in *Sciurion* it is a small but distinct cusp, much larger than in the former. The entoconid on the lower molars of *Sciurion*, especially m3, is much more reduced than in any of the species of *Hesperopetes*.

Based on the differences cited above, it appears that *Sciurion* is morphologically closer to *Blackia* from the Miocene of Europe (Skwara, 1986), and *Hesperopetes* is morphologically more similar to *Oligopetes* from the Oligocene of Europe.

Hesperopetes jamesi Emry and Korth, 2007
(Figure 3H)

Additional Referred Specimens—CM 76619 - right p4; CM 76705 – right M1 or M2.

Measurements—p4: length = 1.77 mm, width = 1.48 mm; M1 or M2: length = 1.85 mm, width = 2.34 mm.

Description—CM 76619 is nearly rectangular in occlusal outline, and longer than wide. The anterior width of the tooth is nearly equal to that of the posterior width. The metaconid is the largest cusp of the tooth and slightly anterior to the level of the protoconid. The trigonid basin is closed posteriorly by a small metalophulid II. There is no anteroconid on the anterior cingulum. The protoconid is crescentic in shape. The ectolophid consists of a triangular mesoconid. The hypoconid and entoconid are subequal in size, and the posterior cingulum is continuous between these cusps with no indication of a hypoconulid. The metastylid is distinct, but smaller than the other lingual cusps. The talonid basin has very delicate crenulations.

Discussion—The p4 is referred to *Hesperopetes jamesi* because of its equivalent size to the other specimens of the latter from this fauna (Emry and Korth, 2007:table 1) and because of the delicate crenulations in the basin of the tooth. The only previously described p4 of *Hesperopetes* is that of the Chadronian *H. thoringtoni* (Emry and Korth, 2007). The Blue Ash p4 is very similar to that of *H. thoringtoni*, differing mainly in the proportions of the tooth. The p4 of *H. thoringtoni* is nearly equidimensional, whereas the p4 of *H. jamesi* is distinctly longer than wide. The anterior width of the p4 of *H. thoringtoni* is distinctly less than the posterior width of the tooth, whereas in the p4 of *H. jamesi* the anterior and posterior widths are nearly the same, giving the tooth a rectangular shape.

The morphology of the additional referred upper molar does not differ in size or morphology from the original material (Emry and Korth, 2007).

Hesperopetes blacki Emry and Korth, 2007

Discussion—No additional specimens of this species have been recovered since its original description (Emry and Korth, 2007), so no additional comments can be made here.

Subfamily Cedromurinae Korth and Emry, 1991

Genus *Cedromus* Wilson, 1949

Cedromus wilsoni Korth and Emry, 1991
(Figure 4; Table 4)

Referred Specimens—CM 76708 – dp4; CM 76710 = p4; CM 76650, 76652, 76654, 76655 – m1 or m2; CM 76653, 76657, 76661 – m3; CM 76630, 76706 – dP4; CM 76633, 76634, 76637, 76646, 76707 – P4; CM 76629, 76631, 76635, 76651 – M1 or M2; CM 76632, 76636 – M3.

Description—The only teeth not previously described for this species present in the Blue Ash fauna is dP4 and dp4. A single specimen, CM 76630, is referred to dP4 based on appropriate size and similar morphology to the permanent P4. The tooth is triangular in shape, and more expanded in the anterobuccal and posterolingual corner than P4. The parastyle is greatly enlarged and anteroposteriorly compressed, nearly as large as the paracone. The paracone is large and oval (transversely elongated). The protoloph is short, extending from the paracone to the protocone. The protocone is smaller than in the permanent cheek teeth and positioned more buccally. A short partial ectoloph connects the paracone to the mesostyle as in the molars. The metaloph curves anteriorly from the metacone to weakly connect to the protocone. The hypocone is small but its apex is lingual to that of the protocone. The posterior cingulum is continuous from the hypocone to the metacone.

The single dp4 is referred to this species based on its comparable size to the rest of the sample of *C. wilsoni*. It is smaller than p4 and narrower anteriorly than p4. The metaconid and protoconid are positioned close to one another, the metaconid being slightly more anterior. The trigonid basin is shallow and open anteriorly but closed posteriorly by a short metalophulid II. The ectolophid is a high, thin ridge running posteriorly from the protoconid to the hypoconid. There is a small but distinct mesoconid at the center of the ectolophid. The posterolophid is also a thin, high loph that runs along the posterior margin of the tooth from the hypoconid to the entoconid. The entoconid is smaller than the remainder of the major cusps. A lower, thin ridge connects the metaconid to the entoconid along the lingual edge of the tooth.

Discussion—The dentition of *Cedromus wilsoni* has been fully described elsewhere (Korth and Emry, 1991). The size of the Blue Ash material is smaller than that of *C. wardi*, but within the range of *C. wilsoni* (Table 3; Korth and Emry, 1991:tables 1, 2). The only difference between the Blue Ash material and the topotypic upper molars of *C. wilsoni* is the presence of a short protocone crest one three of the specimens. This is clearly a variable character. Similarly, the lower cheek teeth are not different from those previously described for *C. wilsoni* except that the partial hypolophid on the lower molars is more variable in length in the sample from Blue Ash than in the topotypic material.

Korth and Emry (1991) referred a single mandible from the Whitneyan to *Cedromus* sp., differs from the other species by being slightly larger and having four-rooted lower molars rather than two-rooted molars. All of the lower molars from Blue Ash are two-rooted.

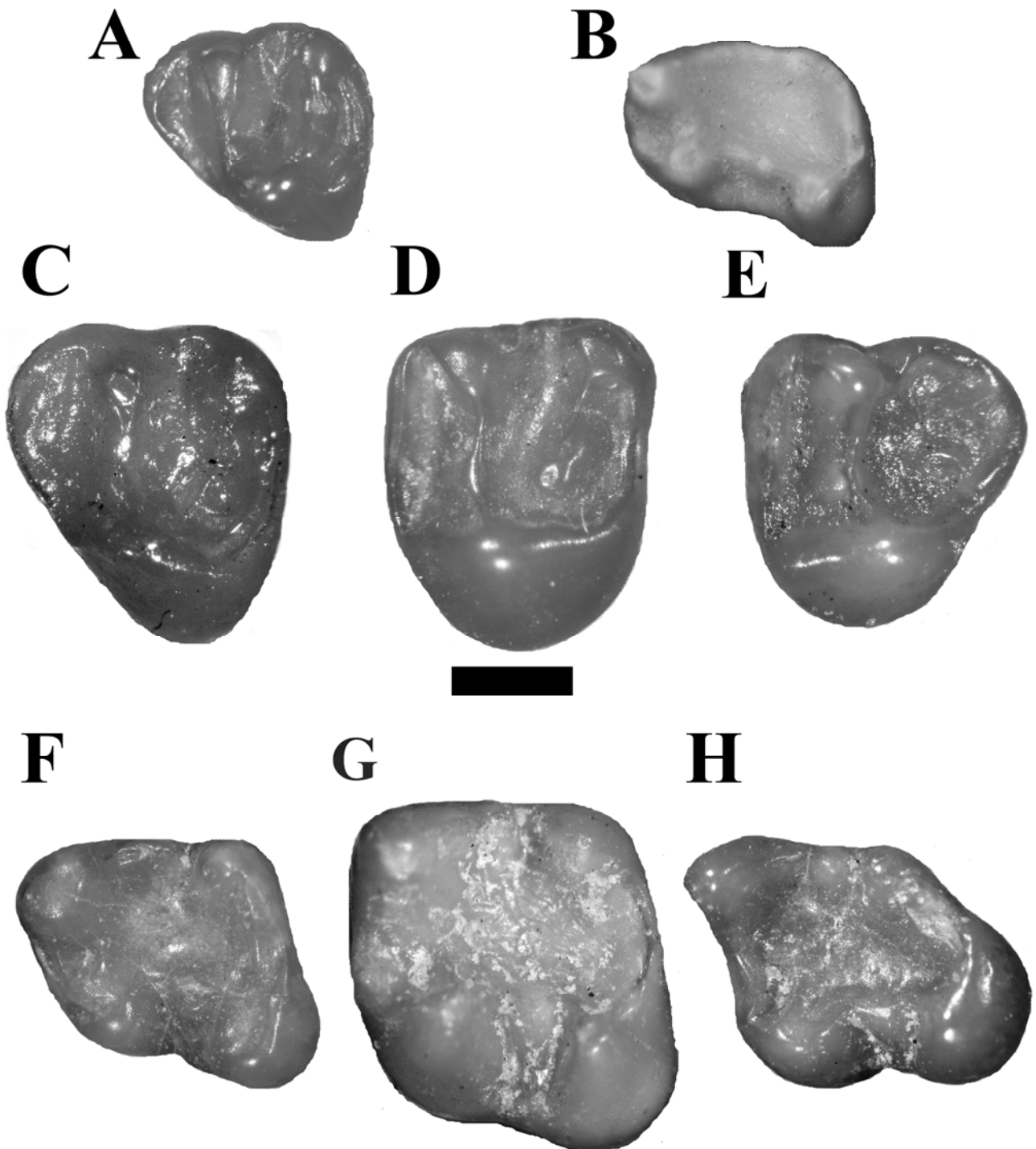


FIGURE 4. Cheek teeth of *Cedromus wilsoni* from the Blue Ash fauna. A, CM 76630, left dp4. B, CM right dp4 (reversed). C, CM 76633, left P4. D, CM 76631, left M1 or M2. E, CM 76632, left M3. F, CM 76710, right p4 (reversed). G, CM 76655, right m1 or m2 (reversed). H, CM 76653, left m3. Bar scale = 1 mm.

Genus *Oligospermophilus* Korth, 1987
Oligospermophilus emryi n. sp.
 (Figure 5; Table 5)

Type Specimen—CM 76608, left M1 or M2.

Referred Specimens—CM 76614 – p4; CM 76663 – m1 or m2; CM 76615 – m3; CM 76609 – P4; CM 76610-76612, 76664, 76702 – M1 or M2; CM 76613, 76665 – M3.

Diagnosis—Smallest species of the genus; metaconule doubled on upper molars; partial hypolophid on lower molars reduced.

Etymology—Patronym for R. J. Emry in reference to his contributions to the knowledge and understanding of Oligocene mammals of North America.

Description—P4 is smaller than the upper molars. It is oval in occlusal outline, being much wider than long. The slightly crescentic protocone is at the anterolingual corner of the tooth. A short anterior cingulum runs from the protocone to the anterobuccal corner of the tooth. The protoloph is continuous from the paracone to the protocone, parallel to and close to the anterior cingulum. There are no conules on the loph. Both loph (protoloph, metaloph) curve slightly anteriorly at their lingual ends, just before joining the protocone. The central transverse valley separating the protoloph and metaloph is blocked buccally by a small mesostyle. The posterior cingulum originates at the posterior edge of the protocone and wraps around the posterolingual corner of the tooth, then runs buccally, ending at the posterior side of the metacone. The cingulum isolates a small, circular basin between the protocone and the posterolingual corner of the tooth.

M1 or M2 is much longer than P4, and nearly equidimensional. A minute parastyle is at the anterobuccal corner of the tooth, marking the buccal end of the anterior cingulum that runs nearly the entire width of the tooth, ending lingually at the anterior border of the protocone. The protoloph runs directly lingually from the paracone to the protocone with no indication of a protoconule. The valley separating the protoloph and anterior cingulum is wide and shallow. A short loph runs from the paracone posteriorly, joining a mesostyle. This partial ectoloph extends lingual to the buccal margin of the tooth rather than along the margin. The metaloph curves anteriorly from the metacone toward the protocone. The connection of the metaloph to the protocone is weak or completely absent. Along the metaloph are two distinct metaconules, the lingual one being slightly larger than the other. A distinct hypocone is at the posterolingual corner of the tooth. The posterior cingulum runs buccally from the hypocone to the posterobuccal corner of the metacone.

TABLE 4. Dental measurements of *Cedromus wilsoni* from the Blue Ash fauna. Measurements in mm. Abbreviations as in Table 1.

| CM # | dP4L | dP4W | P4L | P4W | M1L | M1W | M3L | M3W |
|-------|------|------|------|------|------|------|------|------|
| 76629 | | | | | 1.90 | 2.38 | | |
| 76630 | 2.02 | 2.06 | | | | | | |
| 76631 | | | | | 2.37 | 2.96 | | |
| 76632 | | | | | | | 2.48 | 2.60 |
| 76633 | | | 2.48 | 2.80 | | | | |
| 76634 | | | 2.47 | 2.92 | | | | |
| 76635 | | | | | 2.04 | 2.61 | | |
| 76636 | | | | | | | 2.84 | 2.76 |
| 76637 | | | | | 2.09 | 2.70 | | |
| 76638 | | | | | 2.18 | 2.75 | | |
| 76639 | | | | | 2.29 | 2.96 | | |
| 76640 | | | | | 2.09 | 2.54 | | |
| 76641 | | | | | | 2.76 | | |
| 76642 | | | | | 1.89 | 2.47 | | |
| 76643 | | | | | 2.30 | 2.48 | | |
| 76644 | | | | | 2.04 | 2.49 | | |
| 76645 | | | | | 2.56 | 3.11 | | |
| 76646 | | | | | 2.45 | 2.94 | | |
| 76663 | | | | | 2.13 | 2.61 | | |
| 76706 | 2.23 | 2.43 | | | | | | |
| 76707 | | | 2.44 | 2.79 | | | | |
| M | 2.13 | 2.25 | 2.46 | 2.84 | 2.18 | 2.70 | 2.66 | 2.68 |
| SD | | | 0.02 | 0.07 | 0.20 | 0.22 | | |
| CV | | | 0.85 | 2.55 | 9.37 | 8.33 | | |
| CM# | dp4L | dp4W | p4L | p4W | m1L | m1W | m3L | m3W |
| 76650 | | | | | 2.63 | 2.86 | | |
| 76652 | | | | | 2.28 | 2.63 | | |
| 76653 | | | | | | | 3.01 | 2.57 |
| 76654 | | | | | 2.69 | 2.86 | | |
| 76657 | | | | | | | 3.18 | 2.81 |
| 76661 | | | | | | | 3.06 | 2.70 |
| 76655 | | | | | 2.84 | 3.09 | | |
| 76708 | 2.21 | 1.68 | | | | | | |
| 76710 | | | 2.62 | 2.37 | | | | |
| M | | | | | 2.61 | 2.86 | 3.08 | 2.69 |
| SD | | | | | 0.24 | 0.19 | 0.09 | 0.12 |
| CV | | | | | 9.08 | 6.57 | 2.83 | 4.46 |

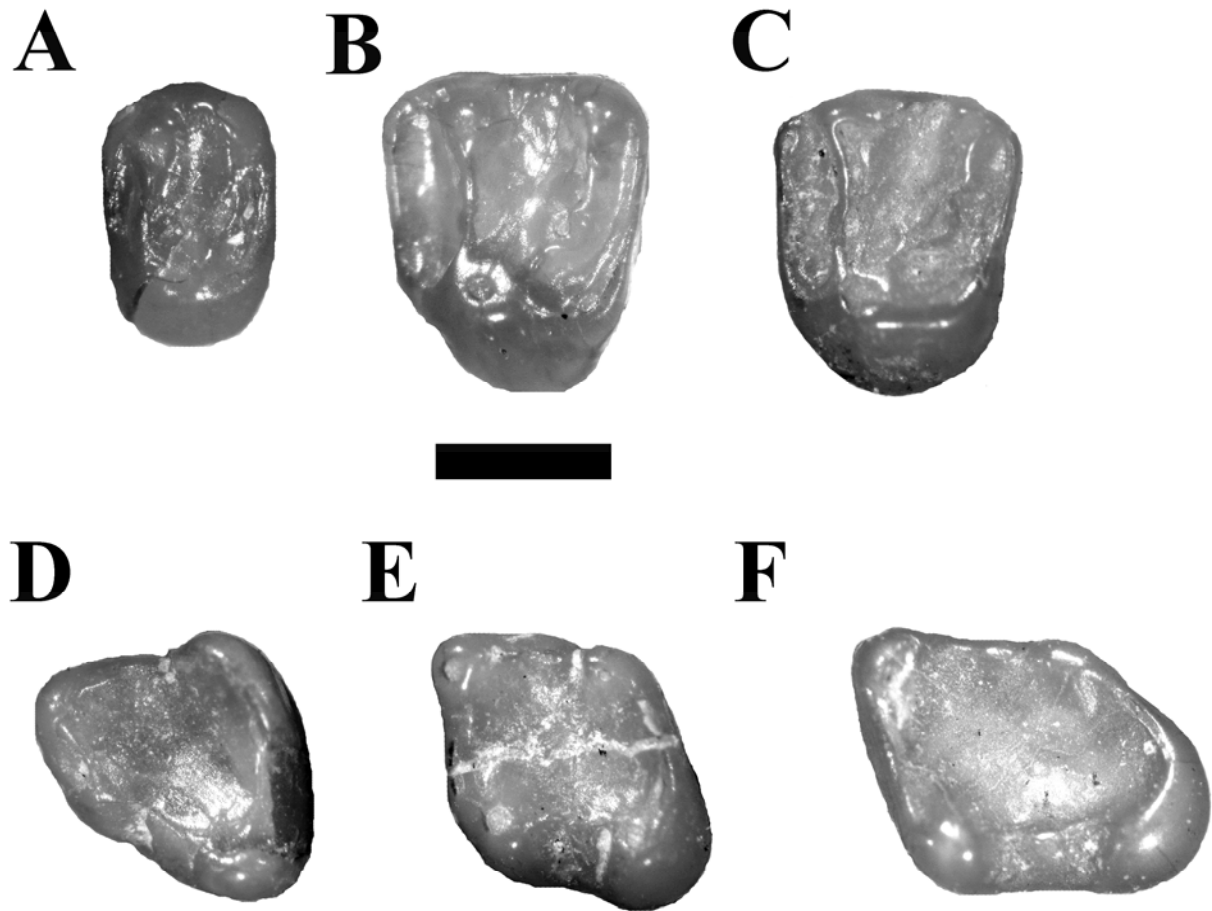


FIGURE 5. Cheek teeth of *Oligospermophilus emryi* from the Blue Ash fauna. A, CM 76609, left P4. B, CM 76608 (holotype), left M1 or M2. C, CM 76612, right M1 or M2. D, CM 76614, left p4. E, CM 7663, left m1 or m2. F, CM 76615, left m3. Bar scale = 1 mm.

Only two cusps are recognizable on M3, the paracone and protocone. Both cusps are similar to those of M1 or M2. The anterior cingulum is more closely appressed to the protoloph than in the anterior molars. The posterobuccal portion of the tooth is expanded posteriorly, but no hypocone or metacone are identifiable. The majority of the tooth is a broad, shallow basin. There is no mesostyle or partial ectolophid unlike M1 or M2.

The lower premolar is markedly narrower anteriorly than posteriorly. The protoconid and metaconid are very closely positioned. A minute, circular trigonid basin is present between the cusps. There is a minute, isolated metastylid along the lingual margin of the tooth. The entoconid and hypoconid are large and distinct. The posterior cingulum is continuous from the entoconid to the hypoconid. There is no indication of a hypolophid. The protoconid and hypoconid are connected by a low, broad ectolophid.

A small wear facet at the center of the ectolophid indicates the presence of a small mesoconid.

A single specimen, CM 76663, is referred to m1 or m2, and it is wider than long and rhomboidal in occlusal outline. The anterior cingulum (metalophid I) is continuous from the protoconid to the metaconid. There is no anteroconid. The posterior arm of the protoconid is very short, forming a very small trigonid basin that opens posteriorly. The ectolophid consists predominantly of a round mesoconid weakly connected to the hypoconid and protoconid. The posterolophid is continuous between the hypoconid and entoconid. A faintly recognizable minute loph runs buccally from the entoconid. A large mesostylid is present on the lingual edge of the tooth between the metaconid and the entoconid. It is about half the size of the other lingual cusps but as large as the mesoconid.

The only m3 referable to this species is CM 76615. The tooth is nearly rectangular in occlusal

outline, and is much longer than wide. The anterior margin of the tooth is the metalophulid I, and it connects the protoconid to the metaconid. There is no evidence of a trigonid basin or metalophulid II. A complete ectolophid is present between the protoconid and hypoconid, but it is thin and low with a slight swelling at its center indicating the mesoconid. The entoconid is well developed, and only slightly smaller than the other major cusps. The posterior cingulum is expanded posteriorly. A small metastylid is present posterior to the metaconid on the lingual margin of the tooth. The majority of the tooth is a broad, shallow basin.

Discussion—*Oligospermophilus emryi* is distinct from the Chadronian-Orellan type species *O. douglassi* in being considerably smaller (Table 4; Korth, 1987: tables 1, 2), lacking the parastylar expansion on P4 of *O. douglassi*, having a doubled metaconule on the upper molars, and having the trigonid basin open posteriorly and the hypolophid reduced on the lower molars.

Korth (1987) reported a specimen from the Whitneyan of Wyoming (CM 21244) that was referred to *Oligospermophilus* sp. This latter specimen cannot be referred to *O. emryi* because it is distinguished from *O. douglassi* by its slightly larger size rather than smaller, as in *O. emryi*.

TABLE 5. Dental measurements of *Oligospermophilus emryi* from the Blue Ash fauna. Measurements in mm. Abbreviations as in Table 1.

| CM # | P4L | P4W | M1L | M1W | M3L | M3W |
|-------|------|------|------|------|------|------|
| 76608 | | | 1.50 | 1.74 | | |
| 76609 | 1.00 | 1.59 | | | | |
| 76610 | | | 1.20 | 1.81 | | |
| 76611 | | | 1.33 | 1.86 | | |
| 76612 | | | 1.40 | 1.65 | | |
| 76613 | | | | | 1.41 | 1.49 |
| 76664 | | | 1.20 | 1.57 | | |
| 76702 | | | 1.40 | 1.81 | | |
| M | | | 1.34 | 1.74 | | |
| SD | | | 0.12 | 0.11 | | |
| CV | | | 8.97 | 6.36 | | |
| CM# | p4L | p4W | m1L | m1W | m3L | m3W |
| 76614 | 1.57 | 1.56 | | | | |
| 76615 | | | | | 2.01 | 1.71 |
| 76663 | | | 1.37 | 1.58 | | |
| 76665 | | | | | 2.10 | 1.71 |

CONCLUSIONS

Recent attempts to determine the age of the Blue Ash fauna which includes taxa from as early as Chadronian and as late as Arikareean horizons (Korth, 2007a, 2007b, 2008) have resulted in tentative results. Even at the generic level, the sciurids from the Blue Ash fauna include a combination of both earlier and later occurring taxa. *Douglassciurus* was previously known only from the Chadronian (Emry and Korth, 1996, 2001) as was *Hesperopetes* (Emry and Korth, 2007). *Oligospermophilus* has been reported from the Chadronian through Whitneyan (Korth, 1987) and *Cedromus* is from the Orellan and Whitneyan (Korth and Emry, 1991). *Protosciurus* is from the Orellan through Arikareean (Black, 1963), and both *Nototamias* and *Miospermophilus* were previously known to first occur in the Arikareean (Goodwin, 2008). At the species level, *Cedromus wilsoni* is from the late Orellan or early Whitneyan (Korth and Emry, 1991), *P. mengi* is restricted to the Orellan (Black, 1963; Korth, 1987), and *P. rachelae* is believed to be Arikareean (Black, 1963).

The specimens referred to *Miospermophilus* sp. from Blue Ash are more primitive than other species of the genus from the Arikareean or Hemingfordian. Simpson (1985) suggested that there might be a mixing of Whitneyan and Arikareean horizons in the Blue Ash fauna. However, the preservation and degree of abrasion of the specimens are similar for all represented species, thus indicating that reworking was unlikely and that they all came from the same horizon.

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LITERATURE CITED

- Black, C. C. 1963. A review of the North American Tertiary Sciuridae. *Bulletin of the Museum of Comparative Zoology, Harvard University* 130:1-248.
- Black, C. C. 1965. Fossil mammals from Montana. Pt. 2. Rodents from the early Oligocene Pipestone Springs local fauna. *Annals of Carnegie Museum* 38:1-48.
- Emry, R. J. and W. W. Korth. 1996. The Chadronian squirrel "*Sciurus*" *jeffersoni* Douglass, 1901: a new generic name, new material, and its

- bearing on the early evolution of Sciuridae (Rodentia). *Journal of Vertebrate Paleontology* 16:770-775.
- Emry, R. J. and W. W. Korth. 2001. *Douglassciurus*, new name for *Douglassia* Emry and Korth, 1996, not *Douglassia* Bartsch, 1934. *Journal of Vertebrate Paleontology*, 21:400.
- Emry, R. J. and W. W. Korth. 2007. A new genus of squirrel (Rodentia, Sciuridae) from the mid-Cenozoic of North America. *Journal of Vertebrate Paleontology* 27:693-698.
- Emry, R. J. and R. W. Thorington, Jr. 1982. Descriptive and comparative osteology of the oldest fossil squirrel, *Protosciurus* (Rodentia: Sciuridae). *Smithsonian Contributions to Paleobiology* 47:1-35.
- Goodwin, H. T. 2008. Sciuridae. Pp. 355-376, in C. M. Janis, G. F. Gunnell, and M. D. Uhen (eds.), *Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals*. Cambridge Press, New York.
- Hall, E. R. 1930. Rodents and lagomorphs from the Barstow beds of southern California. *University of California, Bulletin of the Department of Geological Sciences* 19:313-318.
- Korth, W. W. 1987. Sciurid rodents (Mammalia) from the Chadronian and Orellan (Oligocene) of Nebraska. *Journal of Paleontology* 61:1247-1255.
- Korth, W. W. 1992. Small mammals from the Harrison Formation (late Arikareean, early Miocene), Cherry County, Nebraska. *Annals of Carnegie Museum* 61:69-131.
- Korth, W. W. 2007a. Mammals from the Blue Ash local fauna (late Oligocene), South Dakota. Rodentia, Part 1: Families Eutypomyidae, Eomyidae, Heliscomyidae, and *Zetamys*. *Paludicola* 6:31-40.
- Korth, W. W. 2007b. Mammals from the Blue Ash local fauna (late Oligocene), South Dakota. Marsupialia and Lagomorpha. *Paludicola* 6:111-117.
- Korth, W. W. 2008. Mammals from the Blue Ash local fauna (late Oligocene), South Dakota. Rodentia, Part 2: Families Florentiamyidae and Geomyidae. *Paludicola* 7:14-25.
- Korth, W. W. and R. J. Emry. 1991. The skull of *Cedromus* and a review of the Cedromurinae (Rodentia, Sciuridae). *Journal of Paleontology* 65:986-994.
- Macdonald, L. J. 1972. Monroe Creek (early Miocene) microfossils from the Wounded Knee area, South Dakota. *South Dakota Geological Survey Report of Investigations* 105:1-43.
- Martin, J. E. 1976. Small mammals from the Miocene Batesland Formation of South Dakota. *Contributions to Geology, University of Wyoming* 14:69-98.
- Martin, J. E. and M. Green. 1984. Insectivora, Sciuridae, and Cricetidae from the early Miocene Rosebud Formation in South Dakota. *Carnegie Museum of Natural History Special Publication* 9:28-40.
- Martin, L. D. 1974. New rodents from the Lower Miocene Gering Formation of western Nebraska. *University of Kansas Museum of Natural History, Occasional Papers* 32:1-12.
- Pratt, A. E. and G. S. Morgan. 1989. New Sciuridae (Mammalia: Rodentia) from the early Miocene Thomas Farm local fauna, Florida. *Journal of Vertebrate Paleontology* 9:89-100.
- Simpson, W. F. 1985. Geology and paleontology of the Oligocene Harris Ranch Badlands, southwestern South Dakota. *Dakoterra* 2:303-333.
- Skwara, T. 1986. A new "flying squirrel" (Rodentia: Sciuridae) from the early Miocene of southwestern Saskatchewan. *Journal of Vertebrate Paleontology* 6:290-294.
- Tedford, R. H., L. B. Albright, III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt, Jr., J. E. Storer, C. C. Swisher, III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). Pp. 169-231, in M. O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America, Biostratigraphy and Geochronology*. Columbia University Press, New York.
- Whistler, D. P. and E. B. Lander. 2003. New late Uintan to early Hemingfordian land mammal assemblages from the undifferentiated Sespe and Vaqueros formations, Orange, County, and from the Sespe and Equivalent marine formations in Los Angeles, Santa Barbara, and Ventura counties, southern California. *Bulletin of the American Museum of Natural History* 13:231-268.
- Wilson, R.W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. *University of Kansas, Paleontological Contributions* 7:1-92.
- Wood, A. E. and R. W. Wilson. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. *Journal of Paleontology* 10:388-391.