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MAMMALS FROM THE BLUE ASH LOCAL FAUNA (LATE OLIGOCENE), SOUTH DAKOTA. RODENTIA, PART 4: FAMILY APLODONTIDAE

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ABSTRACT

Ten species of aplodontid rodents are present in the Blue Ash local fauna, which currently represents the most diverse family of rodents in the assemblage. One new genus, *Disallomys*, is described with *Allomys storeri* Tedrow and Korth as the type species. Four new species are described, *Disallomys robustus*, *D. intermedius*, *Prosciurus clausulus*, and *Niglarodon brachyodon*. The aplodontids from the Blue Ash fauna suggest that it is more likely Whitneyan than Arikareean in age because of the abundance and diversity of prosciurines (=basal aplodontids) that are more common from earlier horizons and fewer, generally more poorly represented species referable to the otherwise Arikareean genera, *Allomys*, *Downsimus*, and *Niglarodon*. The species of these genera from Blue Ash, *Allomys* sp., *Downsimus* sp., and *N. brachyodon*, differ from all other recognized species of these genera in being smaller with more primitive cheek tooth morphologies.

INTRODUCTION

Previously, only one species of aplodontid rodent had been described from the Blue Ash fauna of southwestern South Dakota, *Ansomys cyanotephrus* (Korth, 2007). A detailed study of the aplodontid material from an anthill collection of this fauna at the Carnegie Museum of Natural History demonstrates that the aplodontid fauna is much more extensive. Ten species of aplodontids are recognized, making this family the most diverse yet described from this fauna. Previously, the Sciruidae (known from nine species) was the most diverse rodent family in the assemblage (Emry and Korth, 2007; Korth, 2009).

The aplodontids differ markedly between the Arikareean and Orellan and earlier horizons. The Arikareean is dominated by allomyine and meniscomyine aplodontids, whereas the Orellan and earlier Oligocene faunas are dominated by more primitive prosciurines [=basal aplodontids] (Korth, 1994a; Flynn and Jacobs, 2008). The intervening Whitneyan age is poorly documented and aplodontids are represented mainly by poorly known taxa that are almost exclusively limited to this interval, such as *Dakotallomys*, *Epeiromys*, and *Oropyctis* and some relict prosciurines (Korth, 1989; Tedrow and Korth, 1997; Flynn and Jacobs, 2008). With the distinctions between the aplodontid faunas from the Orellan, Whitneyan and Arikareean, it seems that this family would be the most promising for a more definite assignment of the Blue Ash fauna to a North American Land Mammal Age.

Dental terminology used follows that of Rensberger (1975) and Korth (1994b) with modifications for meniscomyines (Rensberger, 1981). Upper teeth are designated by capital letters, lower teeth by lower-case letters. Abbreviations for institutions: CM, Carnegie Museum of Natural History; LACM, Museum of Natural History, Los Angeles County; MCZ, Museum of Comparative Zoology, Harvard University; SDSM, South Dakota School of Mines and Technology, Museum of Geology; UCMP, University of California Museum of Paleontology.

SYSTEMATIC PALEONTOLOGY

Family Aplodontidae Brandt, 1855

Subfamily Prosciurinae Wilson, 1949

Discussion—Recent authors (McKenna and Bell, 1997; Hopkins, 2008; Flynn and Jacobs, 2008) have abandoned the use of Prosciurinae as a subfamily of the Aplodontidae because it has been considered a paraphyletic group, consisting of unrelated primitive aplodontids. Flynn and Jacobs (2008:379) referred to this group as "basal aplodontids". It does appear that the Prosciurinae is a "waste basket" taxon. However, it remains a useful grouping of the more primitive aplodontids, and is used here as such.

Prosciurus Matthew, 1903

Prosciurus clausulus n. sp.

(Figure 1A-E; Table 1)

Type Specimen—CM 54074, right M1 or M2.

Referred Specimens—CM 54069, 76711, P4; CM 54088, 54090, M1 or M2; CM 76713, p4; CM 54077, CM 54086, m1 or m2; CM 54068, 76712, m3.

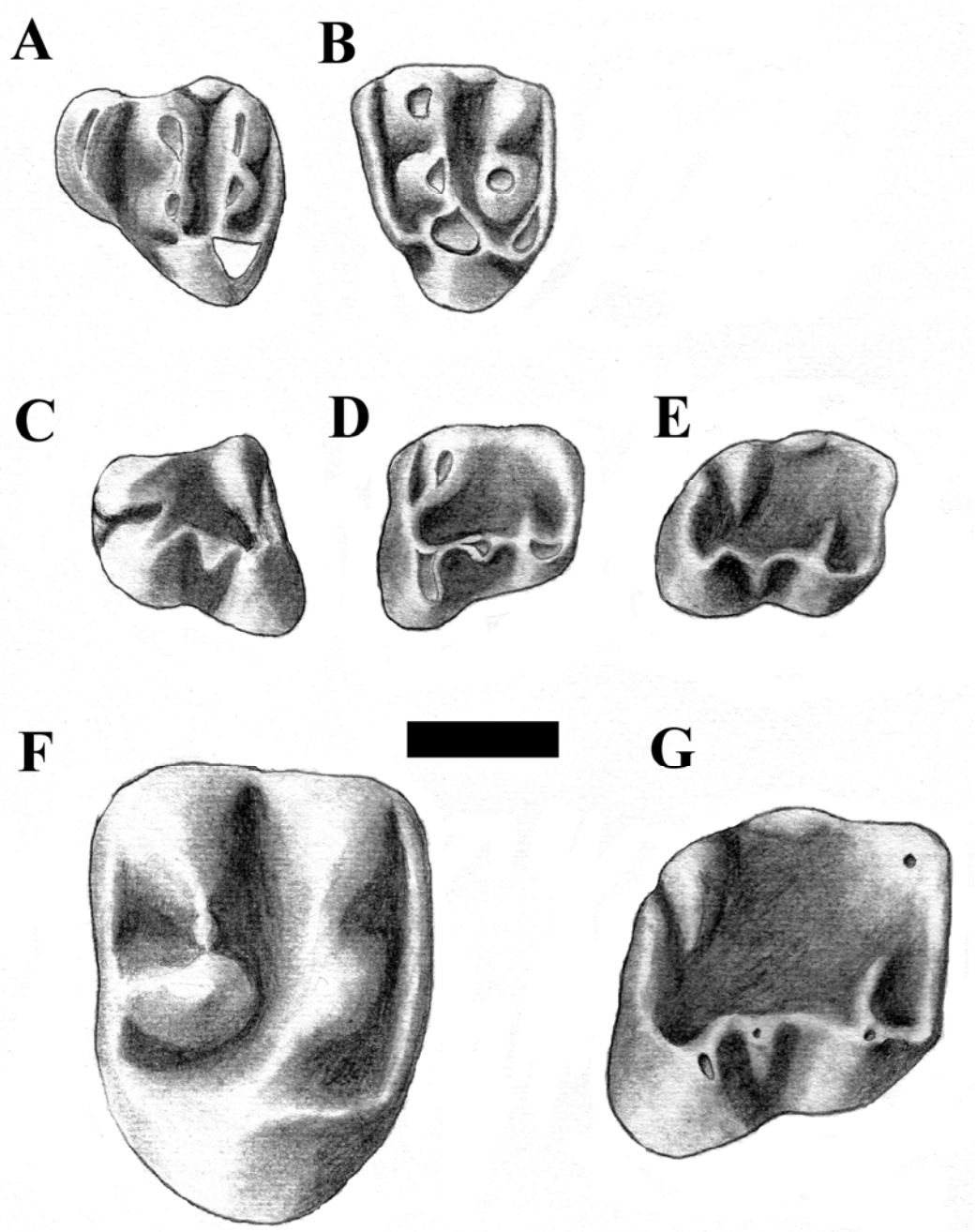

FIGURE 1. Cheek teeth of *Prosciurus* from the Blue Ash fauna. A-E, *P. clausulus*. A, CM 76711, LP4. B, CM 54074 (type), LM1. C, CM 76173, Lp4. D, CM 54077, Rm1 or m2. E, CM 76712, Rm3. F-G, *P. magnus*. F, CM 76714, RM1 or M2. G, CM 76716, Rm1 or m2. Bar scale = 1 mm.

Diagnosis—Smallest species of the genus; protocone crest on upper molars smaller than in other species (nearly absent).

Etymology—Latin, *clausula*, end or conclusion; reference to the occurrence of the species as the last of the genus.

Description—Size of the cheek teeth of *Prosciurus clausulus* is less than in any other species of the genus (Black, 1965:6; Korth, 1989:tables 1 and 2). The cheek teeth are very similar in morphology to those of other species of the genus described elsewhere (Matthew, 1903; Wood, 1937; Black, 1965; Korth, 1989, 1994b). *P. clausulus* differs from other species in the reduction of the protocone crest on the upper cheek teeth. In other species the protocone crest is a small but distinct loph running buccally from the

protocone (Wood, 1937:figs. 8, 9; Korth, 1989:fig. 1A-B). The protocone crest is a minor swelling on the anterobuccal side of the protocone on molars of *P. clausulus*. The metaconule is single on *P. clausulus*, as in most other species of the genus, unlike that of *P. vetustus*, which has a doubled metaconule.

The lower cheek teeth vary little from other species except in their smaller size (Wood, 1937:fig. 12; Black, 1965:fig. 1a; Korth, 1989:fig. 1C).

TABLE 1. Dental measurements of *Prosciurus causulus* from Blue Ash fauna. Abbreviations: L, anteroposterior length; W, transverse width. Measurements in mm.

CM#	P4L	P4W	M1L	M1W	M3L	M3W
54069	1.58	1.67				
54074			1.40	1.75		
54088			1.46	1.88		
54090			1.51	1.88		
76711	1.47	1.57				
	p4L	p4W	m1L	m1W	m3L	m3W
54068					1.68	1.40
54077			1.44	1.45		
54086			--	1.27		
76712					1.61	1.47
76713	1.47	1.47				

Discussion—*Prosciurus clausulus* is the smallest species of the genus, having little or no overlap in size with the next larger species *P. parvus* from the Orellan (Korth, 1989:table 2). The only other aplodontid from the Blue Ash fauna of similar size is *Ansomys cyanotephrus* (Korth, 2007:table 1), which is easily distinguished from *Prosciurus* by the complex pattern of lophules on the cheek teeth, morphology of the mesostyle on the upper molars, and compression of the metaconid on the lower molars. Morphologically, the cheek teeth of *P. clausulus* are very similar to those of other species of *Prosciurus*, differing only in having a relatively smaller hypocone and a protocone crest on the upper molars.

Prosciurus clausulus is also one of the last occurring species of the genus. Previously, the only species known from later than the Orellan was *P. magnus*, which also occurs in the Blue Ash fauna and elsewhere in the late Orellan and Whitneyan (Korth, 1989).

Prosciurus magnus Korth, 1989
(Figure 1F-G)

Referred Specimens—CM 76714, right M1 or M2; CM 76716 and CM 84646, m1 or m2.

Measurements—CM 76714 (M1 or M2): L = 2.35 mm; W = 3.11 mm. CM 76716 (m1 or m2): L = 2.40 mm; W = 2.48 mm. CM 84646 (m1 or m2): L = 2.45 mm; W = 2.35 mm.

Description—The M1 or M2 is similar in overall morphology to that of other species of the genus. There is no indication of an ectoloph or mesostyle. The protoconule is greatly reduced as part of the protoloph. Both the protoloph and metaloph converge lingually on the protocone. The protocone crest is reduced to a low swelling at the base of the transverse valley between the anterior cingulum and protoloph. The metaconule is doubled. The lingual metaconule is large and fuses posteriorly with the posterior cingulum. The buccal metaconule is much smaller, a distinct swelling of the metaloph lingual to the metacone. The hypocone is a small swelling at the posterolingual corner of the tooth. The lower molars referred here do not differ from those previously described (Korth, 1989).

Discussion—The teeth referred to *Prosciurus magnus* from Blue Ash are much larger than any of the specimens of *P. clausulus*. They are also larger than the upper molars of the large Orellan species *P. albiclivus* (Korth, 1994:table 1). The Blue Ash lower molars most closely approach the size of *P. magnus* and do not differ in morphology from them. In an unpublished thesis, Simpson (1986) cited a nearly complete lower jaw of *Prosciurus* from the Blue Ash fauna, SDSM 9462, that is equal in size and similar in morphology to *P. magnus*. This specimen verifies the identification of the isolated teeth referred here.

No upper cheek teeth have been previously assigned to *P. magnus*. CM 76714 is referred to *P. magnus* based on its greater size than other species of *Prosciurus* in the fauna, and similar size to the lower molars of *P. magnus. P. albiclivus* is similar in size to *P. magnus*, but the upper molar from Blue Ash lacks the diagnostic central ridge from the mesostyle that is present on upper molars of the former. The upper molar of *P. magnus* is similar to those of *P. albiclivus* in the lack (or great reduction) of the protocone crest that is present on all other species of the genus except *P. clausulus*. CM 76714 also has a doubled metaconule that is elsewhere only known in the Chadronian *P. vetustus* (Wood, 1937:fig. 8). The larger size of CM 76714 and lack of a protocone crest

distinguish it from the Chadronian species. The previously reported Whitneyan occurrence of *P. magnus* (Korth, 1989) suggests a similar age for the Blue Ash fauna.

Camprestrallomys Korth, 1989
Campestrallomys dawsonae (Macdonald, 1963)
(Figure 2A-C; Table 2)

Referred Specimens—CM 76725, 76726, P4; CM 54092, 76730, 76731, 73733, 76735, 76736, 76738, 76739, M1 or M2; CM 76740, M3; CM 76742, 76743, m1 or m2.

Description—The only cheek teeth not previously figured or described for *Campestrallomys dawsonae* are P4 and M3 (see Macdonald, 1963; Korth, 1989). P4 of *C. dawsonae* described here differs little from that of *C. siouxensis* (Korth, 1989:fig. 4C) except in its larger size. The tooth is roughly triangular in occlusal outline. A large anterocone forms the anterobuccal corner of the tooth. The anterior cingulum runs lingually from the anterocone to the base of the protocone. A second ridge runs from the anterocone to the paracone, dividing the valley between them. The paracone and metacone are flattened buccally. The ectoloph runs from the anterocone to the posterobuccal corner of the tooth. Between the paracone and metacone, the ectoloph extends buccally and forms a V-shaped mesostyle that extends buccally to the major cusps. A small metastyle is at the posterior end of the ectoloph at the posterobuccal corner of the tooth. The protocone is broad (anteroposteriorly). Both the protoloph and metaloph converge toward the center of the buccal margin of this cusp. The metaconule and protoconule are similar in size, the latter being only slightly larger, and single. The posterior cingulum runs along the posterior margin of the tooth from the protocone to the posterolingual base of the metacone. There is no indication of a hypocone.

As with P4, M3 of *C. dawsonae* is very similar in morphology to that of *C. siouxensis*. The tooth is expanded posterobuccally. The protocone and paracone are the only recognizable cusps. The paracone is flattened buccally and the ectoloph extends posterobuccally, ending at the center of the buccal margin of the tooth. The protoloph is a straight ridge from the paracone to the protocone with no indication of a protoconule. The anterior cingulum, which runs the width of the tooth along its anterior border, forms a shallow, wide valley between it and the protoloph. Posterior to the protoloph the tooth is essentially flattened with no indication of any cusps or metaloph.

Discussion—The Blue Ash specimens referred to *Campestrallomys dawsonae* do not differ in size or morphology from those previously described (Macdonald, 1963:table 5; Macdonald, 1970:tables 10, 11). The only record of this species previously was from the Arikareean Sharps Formation of southwestern South Dakota.

Campestrallomys siouxensis Korth, 1989
(Figure 2D-F; Table 3)

Referred Specimens—CM 76723, 76724, P4; CM 76727 to 76729, 76732, 76734, M1 or M2; CM 76741, p4; CM 76744, m3 (partial).

Discussion—The complete dentition of *Campesterallomys siouxensis* has been described elsewhere (Korth, 1989). The morphology and size of the Blue Ash specimens is the same as the originally reported specimens of *C. siouxensis* (Korth, 1989:table 3; Table 5 this paper).

Specimens of *C. siouxensis* and *C. dawsonae* from Blue Ash are separated by size (Tables 3 and 4). The Mann-Whitney nonparametric statistical test was run on the dimensions of the upper molars of the sample of *C. dawsonae* and *C. siouxenis* from Blue Ash and the two samples were demonstrated to be distinct (significant to 0.01). Other than size, only a few morphologies distinguish *C. siouxensis* from *C. dawsonae*: 1) presence of an anterior cingulum on p4 of *C. dawsonae*; and 2) a minor lophule in the talonid basins of m1 and m3 of the latter (Korth, 1989). Unfortunately, no lower molars of *C. siouxensis* are present in the Blue Ash collections. However, the single p4 of *C. siouxensis*, CM 76744, does not have the diagnostic anterior cingulum of p4s of *C. dawsonae*.

Campestrallomys siouxensis was previously reported from the Whitneyan and possibly the earliest Arikareean of Nebraska (Korth, 1989).

Disallomys n. gen.

Type Species—*Disallomys storeri* (Tedrow and Korth, 1997).

Referred Species—*D. robustus* n. sp., *D. intermedius* n. sp., and *Disallomys* sp. (=cf. *Sespymys* sp., Wood, 1937).

Range—Whitneyan and possibly earliest Arikareean of northern Great Plains.

Etymology—Latin, *dis-*, prefix meaning not; and *Allomys* genus to which the type species was originally referred.

Diagnosis—Cheek teeth brachydont; minute lophules in basins of teeth weak or absent; P4 equal to or smaller than M1 in size; anterocone of P4 transversely expanded; mesostyle squared and anteroposteriorly compressed on upper cheek teeth; ectoloph only slightly crescentic on upper cheek teeth; transverse loph runs lingually from mesostyle toward

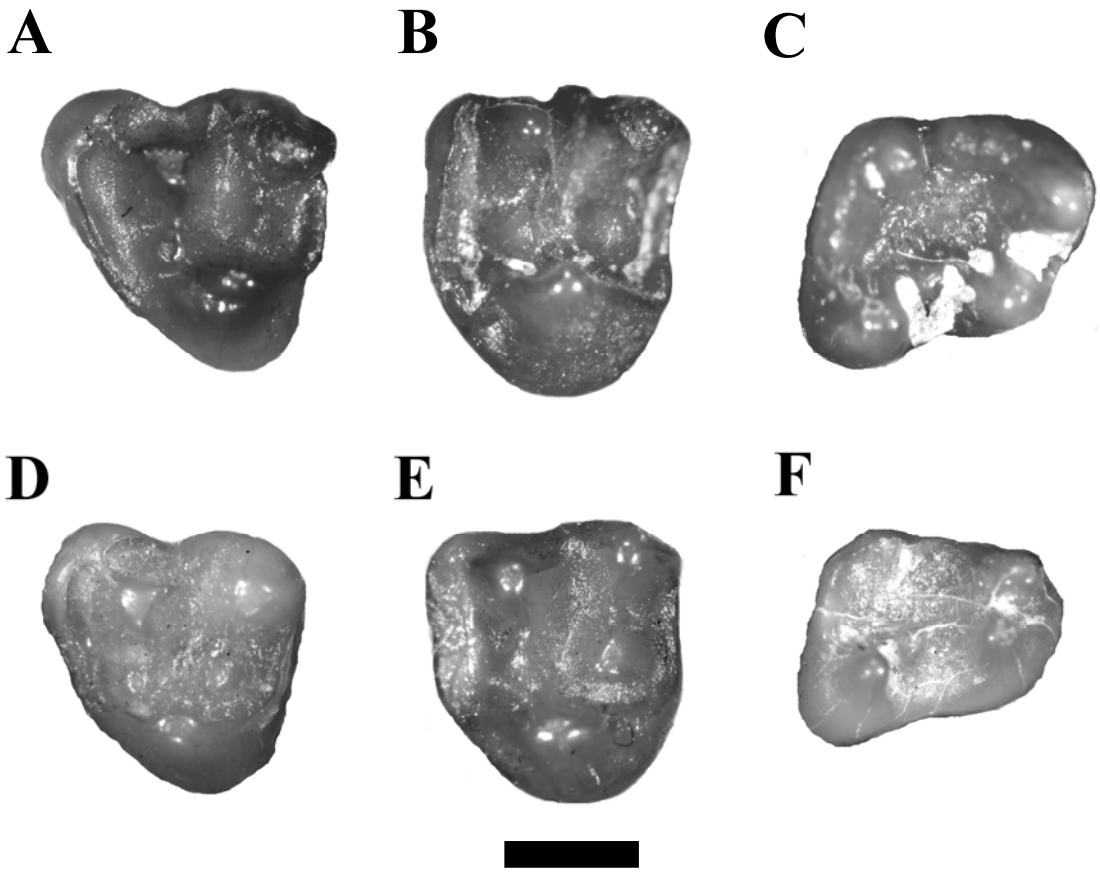

FIGURE 2. Cheek teeth of *Campestrallomys* and *?Downsimus* from the Blue Ash fauna. A-C, *C. dawsonae*. A, CM 76725, LP4. B, CM 76731, LM1 or M2. C, CM 76742, Rm1. D-F, *C. siouxensis*. D, CM 76723, LP4. E, CM 76734, RM1 or M2 (reversed). F, CM 76741, Rp4. Bar scale = 1 mm.

center of the tooth on upper molars; metacone and paracone with slight convexity buccally on P4-M2; metaconule large and isolated from protocone and protoconule on M1-M2; protoconule nearly as large as metaconule on P4, smaller than metaconule on upper molars; second metaconule buccal to main metaconule minute or absent on upper cheek teeth; protocone crest strongly developed in upper cheek teeth; small hypocone or angular cingulum at posterolingual corner of the tooth; p4 wider than long; partial hypolophid joins posterolophid near its center on lower molars; metalophulid II complete or nearly complete on m1-m2, enclosing trigonid basin; metaconid not compressed anteroposteriorly on lower molars; posterobuccal fossettid between mesoconid and hypoconid forms in late stages of wear on m1-m2; metastylid may be multiple on lower cheek teeth.

Comparisons—*Disallomys* has brachydont cheek teeth unlike all aplodontines and meniscomyines. *Disallomys* differs from allomyines by lacking the following: 1) strongly cresentic ectoloph on the upper molars, 2) network of fine lophules filling the basins of the teeth, and 3) doubled metaconule on the upper molars (buccal metaconule nearly as large as lingual metaconule in allomyines). *Disallomys* also differs from aplodontines, meniscomyines and allomyines in having a last premolar equal to or smaller than the fist molar. *Disallomys* differs from other prosciurines in the unique shape of the mesostyle in the upper cheek teeth and lack of compression of metaconid on lower molars (as in *Prosciurus*).

Disallomys shares a similar shape of the mesostyle of the upper cheek teeth with that of *Ansomys*, but the mesostyle differs in being deeper (transversely), having two distinct swellings, and not being as anteroposteriorly elongated as in *Ansomys*. The accessory lophule that runs lingually from the mesostyle toward the center of the upper cheek teeth also is not present in *Ansomys*. Other features of the upper cheek teeth of *Disallomys* that are distinct form those of *Ansomys* are: 1) a large isolated metaconule (in *Ansomys* the metaconule is connected by a short

loph to the protocone or protoloph near the protoconule); 2) the paracone and metacone in *Ansomys* are flattened buccally, whereas in *Disallomys* the ectoloph is gently concave with buccal bulges at the paracone and metacone; 3) the metaconule is variably doubled in *Disallomys* (buccal metaconule minute), whereas in *Ansomys* the metaconule is single (except in the most primitive species *A. cyanotephrus*); and 4) the protocone crest is strongly developed on the upper molars of *Disallomys* but absent or very weakly developed in *Ansomys*.

The lower cheek teeth of *Disallomys* differ from those of *Ansomys* in having: 1) having an uncompressed metaconid; 2) a partial hypolophid joining the posterolophid; 3) a ridge running from the hypoconid anteriorly that joins with the buccal end of the mesoconid, forming a posterobuccal fossettid after wear, as in allomyines. The multiple metastylids of *D. robustus* and *Disallomys* sp. are also unknown in *Ansomys*.

TABLE 2. Dental measurements of *Campestrallomys dawsonae* from Blue Ash fauna. Additional abbreviations: M, mean; STD, standard deviation; CV, coefficient of variation. Other abbreviations as in Table 1. Measurements in mm.

CM#	P4L	P4W	M1L	M1W	M3L	M3W
76725	2.62	2.62				
76726	--	2.45				
76730			2.62	3.20		
76731			2.38	2.90		
76733			2.47	2.98		
76735			2.32	2.92		
54092			2.34	2.88		
76738			2.50	3.15		
76739			2.58	2.99		
76740					2.85	2.95
M	2.62	2.54	2.46	3.00	2.85	2.95
STD		0.12	0.12	0.12		
CV		4.74	4.76	4.16		
	m1L	m1W	m2L	m2W		
76742	2.65	2.36				
76743			2.71	2.60		

TABLE 3. Dental measurements of *Campestrallomys siouxensis* from Blue Ash fauna. Abbreviations as in Tables 1 and 2. Measurements in mm.

CM#	P4L	P4W	M1L	M1W
76723	2.34	2.47		
76724	2.46	2.42		
76727			2.14	2.45
76728			2.17	2.6
76729			--	2.59
76732			2.28	2.57
76734			2.29	2.57
M	2.40	2.45	2.22	2.56
STD	0.08	0.04	0.08	0.06
CV	3.54	1.45	3.43	2.37
	p4L	p4W	m3L	m3W
76741	2.37	1.91		
76744			--	2.28

Discussion—Tedrow and Korth (1997) first described *Allomys storeri* from the Whitneyan of South Dakota. They placed the species in *Allomys*, but noted that it lacked some of the derived diagnostic characters of the genus, as defined by Rensberger (1983). The differences were explained as being due to its more primitive morphology, supported by its earlier occurrence than all other species of *Allomys*. Recently, Hopkins (2008) viewed *A. storeri* as a sister taxon to all of the species of *Ansomys*. She did not refer it to a different genus, but placed it as the most primitive member of the Ansomyinae (Hopkins, 2008:figs. 2, 3, 5, 8), clearly distinct from *Allomys* and other Allomyinae. However, the morphology of the mesostyle on the upper cheek teeth appears to be the only shared character between *Ansomys* and *Disallomys*, and differs as noted above. In *Ansomys*, the mesostyle is much more anteroposteriorly elongated and shallow (not extending into the center of the tooth), whereas in *Disallomys* it is shorter anteroposteriorly, extends much farther lingually, and has an associated transverse loph running lingually from the mesostyle. The remainder of the features of the cheek teeth of *Disallomys* that separate it from *Ansomys* (listed above) make it unlikely that the former

is very closely related to *Ansomys* or the Ansomyinae, and suggests that the similar morphology of the mesostyle on the upper cheek teeth is due to convergence.

Disallomys robustus n. sp.
(Figure 3A-F; Table 4)

Type Specimen—CM 54062, right M1 or M2.

Referred Specimens—CM 54061 (partial), 54066, 83714, 83722 (partial), 83723, 83724, P4; CM 54076, 83715, 83717 (partial), 83721, M1 or M2; CM 54079, 54085, M3; CM 83718, p4; CM 83720, m1; CM 83719, m2; CM 76715, (partial) m1 or m2; CM 84647, 84651, 84652, m3.

Diagnosis—Largest species of the genus; mesostyle on upper cheek teeth doubled; no hypocone on upper molars (present in *D. storeri*); lophs higher and more distinct on cheek teeth than in other species; metastylid multiple on lower molars.

Etymology—Latin, *robustus*, larger or stronger.

Description— P4 is triangular in occlusal outline. The major cusps (paracone, metacone, protocone) are large. The anterocone is large and limited to the anterobuccal corner of the tooth. It is flattened posteriorly, giving it a D-shaped occlusal outline. At the posterobuccal corner of the anterocone is a parastyle of variable size that connects via a short, thin loph to the anterobuccal side of the paracone. A short accessory lophule is present along the posterior side of the anterocone on two specimens (CM 54066, CM 83724), and runs lingually from the posterobuccal corner. CM 83714 has two accessory lophules on the posterior side of the anterocone, one as in the other specimens and a second running buccally from the anterolingual part of the anterocone. The paracone and metacone are equal in size, flattened slightly, and sloped on the buccal side of the cusps. The paracone and metacone are connected along the buccal border of the tooth by an inverted U-shaped mesostyle that appears as two small swellings on either side of the midline. The protoconule and metaconule are only slightly smaller than the buccal cusps. The protoloph is a low, thin loph that is continuous from the paracone to the protocone, connecting the protoconule on its posterior side, and joining the protocone at the center of its buccal side. A minute loph runs anteriorly from the protoconule to join the anterocone on one of the specimens, CM 83723. It appears that this connection is homologous to the more lingual lophule on the posterior side of the anterocone present in CM 83714. The metaloph is not continuous with the protocone, ending as a short anteriorly directed spur from the metaconule. On one specimen, CM 83724, the metaloph is not continuous with the metaconule, although there is a low ridge running lingually from the metacone. There is a minute secondary metaconule between the metacone and metaconule along the metaloph on CM 54066. A long, narrow central transverse basin is present between the metaloph and protoloph. A short, low, straight loph runs lingually in the central valley from the split mesostyle, ending even with the buccal cusps. The protocone is large and semicircular in outline. There is a minute swelling on the anterobuccal side of the cusp that appears to be a much reduced protocone crest. The posterior cingulum runs along the posterior margin of the tooth from the metacone to the poserolingual corner of the tooth, then bends anteriorly at a right angle, joining the posterior side of the protocone. On CM 83724, the metaconule joins the posterior cingulum. The anterior cingulum is short, extending from the anterobuccal corner of the protocone to the lingual end of the anterocone.

M1 and M2 cannot be distinguished from one another and their is very similar to that of P4. The molars are approximately the same width as the referred P4, but are shorter (anteroposteriorly) due to the lack of development of the large anterocone on the premolar. M1 or M2 are nearly rectangular in occlusal outline, being much wider than long. The anterocone is absent and the anterior cingulum runs the width of the tooth from the anterobuccal corner to the protocone. The buccal cusps are similar to those of P4, but the paracone is more crescentic. The structure of the doubled mesostyle and associated loph running lingually from it is the same as in P4. The only difference in the protoloph of the molars is that the protconule is relatively smaller than in P4 (smaller than the metaconule) and triangular in shape. The protocone crest is longer and more distinct on the molars than on P4. The metaloph is also similar to that of P4. The metaconule is oval in outline (transversely compressed) and connects with the posterior cingulum on three of the four specimens that preserve this cusp. On four of the five specimens, a minute secondary metaconule (variable in size) is present between the metacone and metaconule. The posterior cingulum and posterolingual corner of the tooth resemble those of P4.

M3 is smaller than M1 or M2. The protoloph is nearly identical to that of the anterior molars. The protocone crest is present, but appears as a short stub arising from the protocone. The posterior half of the tooth is much different in the two specimens of M3. On CM 54079, the anterior half of the ectoloph is as in the anterior molars with the associated short lingual loph. The central basin of the tooth is divided by a short loph between the metaloph and protoloph, isolating a smaller basin just buccal to the protocone. There is no recognizable metacone. The metaloph runs from the buccal edge of the tooth, posterior to the mesostyle, and connects to the metaconule. The metaconule is an anteroposteriorly directed loph that

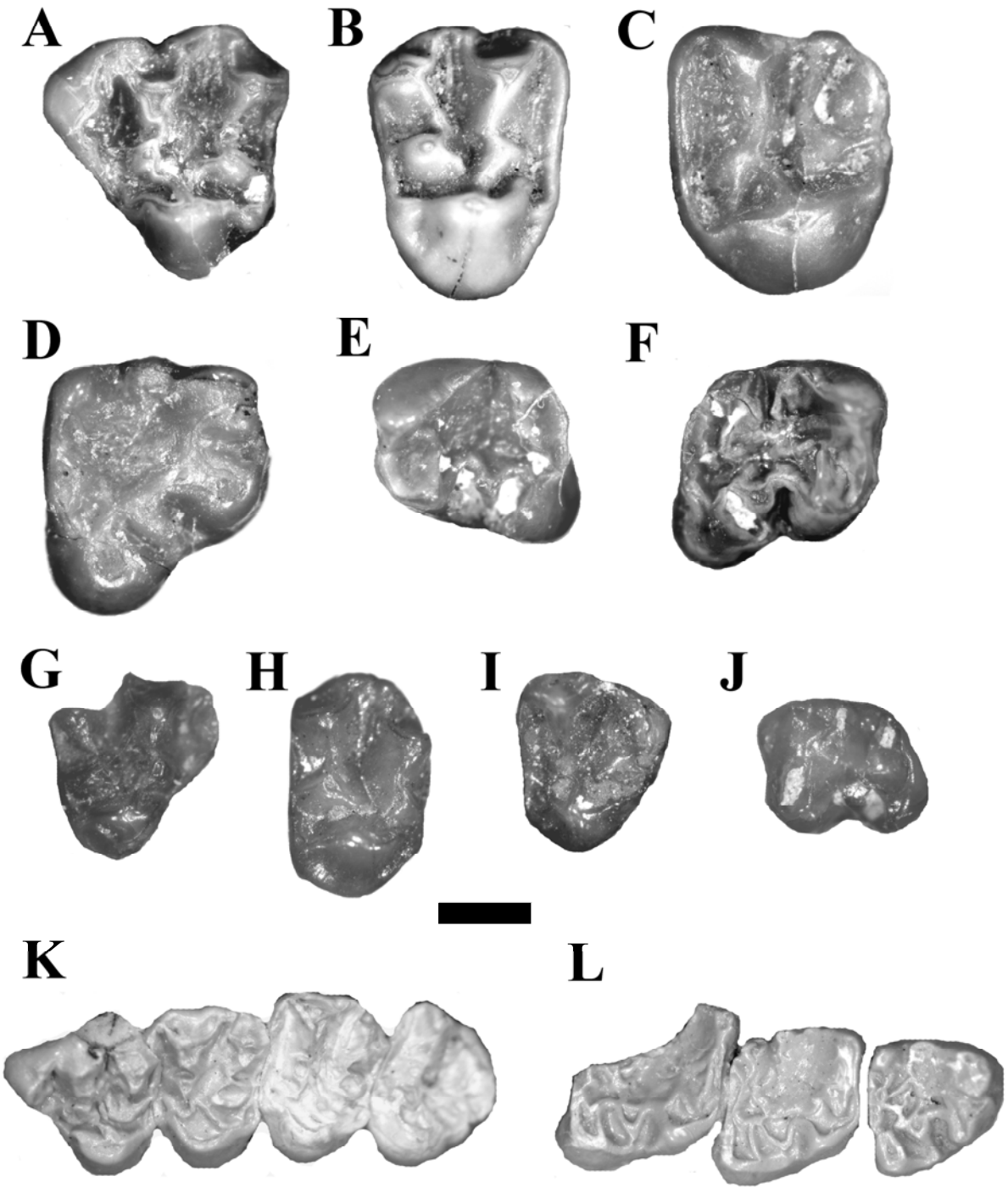

FIGURE 3. Cheek teeth of *Disallomys*. A-F, *D. robustus*. A, CM 54066, LP4. B, CM 54062 (type), RM1 or M2. C, CM 54085, LM3. D, CM 83718, Rp4. E, CM 83720, Lm1. F, CM 83719, Rm2. G-J, *D. intermedius*. G, CM 54073, RP4 (partial). H, CM 83713 (type), RM2. I, CM 83716, LM3. J, CM 76717, Lm3. K-L, *D. storeri*. K, Cast of UCMP 82832 (type) LP4-M3. L, Cast of SDSM 15612, Rp4-m2 (partial). Bar scale = 1 mm.

TABLE 4. Dental measurements of *Disallomys robustus* from Blue Ash fauna. Abbreviations as in Tables 1 and 2 Measurements in mm.

CM#	P4L	P4W	M1L	M1W	M3L	M3W		
54066	3.07	3.26						
83714	3.3	3.73						
83723	3.27	3.54						
83724	3.02	3.24						
83715			2.73	--				
54062			2.52	3.62				
54076			2.82	3.79				
83721			2.44	--				
83717			2.74	--				
54079					2.72	2.96		
54085					2.82	3.28		
M	3.17	3.44	2.65	3.71	2.77	3.12		
STD	0.14	0.24	0.16	0.12	0.07	0.23		
CV	4.44	6.84	6.10	3.24	2.55	7.25		
	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
83718	2.90	3.36						
83719					2.69	2.85		
83720			2.60	2.55				
84647							2.63	2.86
84651							3.10	--
86452							3.49	--

connects the posterior margin of the tooth to the metaloph, just buccal to the protocone. A few accessory lophules run toward the center of the tooth from the buccal and posterior margins of the posterior half of the tooth. CM 54085 has an isolated, round metacone at the posterobuccal corner of the tooth. The metaloph runs from an enlarged mesostyle to a large, round metaconule. The metaconule is not connected to the protocone as in the anterior molars, and is connected by a short posterior loph to the posterior margin of the tooth. The posterior cingulum on both specimens is continuous from the protocone to the mesostyle, wrapping around the posterobuccal corner of the tooth.

The p4 referred to *D. robustus* has a greater posterior width than anteroposterior length. The anterior width (metalophid) is much less than the posterior width of the tooth. The four major cusps (metaconid, protoconid, hypoconid, entoconid) are large and of equal size. The protoconid and metaconid are very close together, but border a small trigonid basin. There is a small anterostylid on the anterobuccal slope of the metaconid. There is a low loph running lingually from the front of the protoconid (metalophulid I) that encloses the trigonid basin

anteriorly. Posteriorly, the trigonid basin is enclosed by a short, curved metalophulid II, that connects the posterior sides of the protoconid and metaconid. On the lingual side of the tooth, just posterior to the metaconid is a large metastylid. There is a narrow, deep valley that separates the metastylid from the entoconid. On the anterior slope of the entoconid is a minute accessory metastylid. The ectolophid is obliquely oriented, uniting the lingual sides of the protoconid and hypoconid. It is recessed from the buccal margin of the tooth and has a large mesoconid with a loph extending buccally to the base of the tooth, dividing the lingual valley between the protoconid and hypoconid. The posterior cingulum runs the entire width of the tooth from the hypoconid to the entoconid. At its center is a large hypoconulid that is only slightly smaller than the entoconid. Some minor lophules run anteriorly from the posterior cingulum and lingually from the ectolophid into the talonid basin. These are not very high and will likely be worn away after moderate wear.

Although the two lower molars referred to *D. robustus* are isolated, they can be differentiated as m1 and m2 by their proportions, m2 being wider anteriorly than m1. The m1s are narrower anteriorly than posteriorly. The metaconid is slightly anterior to the protoconid. A small trigonid basin is enclosed anteriorly by a short metalophulid II that connects the anterolingual corner of the metaconid to the anterolingual corner of the protoconid. A thin but high metalophulid II extends lingually from the protoconid, curves anteriorly at its lingual end, but does not reach the metaconid, leaving the trigonid basin slightly open posteriorly. The metastylid crest runs posteriorly from the metaconid along the lingual edge of the tooth, ending in a small metastylid. There is a slight flexure in the metastylid crest, just anterior to the metastylid. A minute secondary metastylid is present at this flexure, just anterior to the terminal metastylid. The ectolophid is set well toward the center of the tooth and connects the hypoconid and protoconid on their lingual sides. A large, anteroposteriorly compressed mesoconid is at the center of the ectolophid. There is a sharp ridge extending buccally from the mesoconid to the base of the crown at the buccal edge of the tooth. The anterior slope of the hypoconid is a sharp ridge that extends anterobuccally. It is likely that a small basin will form between the mesoconid and hypoconid in later stages of wear. The entoconid is anteroposteriorly compressed. A short hypolophid extends buccally from it into the center of the tooth, then bends posteriorly, joining the posterior cingulum lingual to its center and forming a small basin. The posterior cingulum is a high ridge that runs lingual from the hypoconid along the posterior margin of the tooth, fusing with the entoconid lingually. Lingual to the center of the posterior cingulum is a broad, flattened hypoconulid. The talonid basin contains some short lophules that will likely disappear with wear.

The m2, CM 83719, is very similar to m1 but is wider anteriorly. The trigonid basin is wider and completely closed posteriorly by the metalophulid II. The metastylid crest is similar to that of m1, but the flexure is not as pronounced, and the accessory metastylid is larger than on m1. The mesoconid is circular in outline rather than compressed as in m1, but the buccal loph extends to the base of the tooth and joins the anterior loph from the hypoconid. The hypolophid is also similar to that of m1, but does not completely fuse with the posterior cingulum, being separated by a narrow, shallow valley. The irregularities of the enamel in the talonid basin of m2 are slightly more pronounced than in m1.

The m3 is wider than long and much wider anteriorly than posteriorly. The metaconid is the highest cusp and is connected along a straight metalophulid I to the protoconid. The protoconid is positioned more posteriorly than the protoconid. The metalophulid II is very short, extending from the protoconid less than half the way across the tooth to the base of the metaconid. The ectolophid is oriented directly posterior to the hypoconid. The mesoconid is very large and central. The hypoconid is smaller than the mesoconid and at the posterobuccal corner of the tooth. The entoconid is variable in size, from barely distinguishable on CM 84647, to a large cusp on the other two specimens. The posterior cingulum is a loph that runs along the posterior margin of the tooth to the posterolingual corner from the hypoconid. There are some minor irregularities of the enamel along the posterior cingulum and into the talonid basin. The metastylid is posterior to the metaconid along the lingual side of the tooth and varies in size from minute to nearly equal to the entoconid on CM 84652.

Discussion—*Disallomys robustus* is distinct from the type species, *D. storeri* in being nearly 60% larger and having a twinned mesostyle and no hypocone on the upper molars.

Wood (1937) described a single mandible with p4-m3, MCZ 5056, from the Whitneyan of Nebraska as "cf. *Sespemys* sp". Later, Korth (1989) listed the specimen as "Aplodontidae, genus and species uncertain," and described the specimen in detail. He noted that it was clearly not referable to *Sespemys* and was more likely a primitive aplodontid, as suggested earlier by Stehlin and Schaub (1951). Korth (1989) suggested that this specimen was closest in morphology to species of *Campestrallomys* because of the multiple metastylids on the lower molars, but differed from the latter in its much larger size and the shape and proportions of p4. MCZ 5056 has heavily

worn cheek teeth (Wood, 1937:fig. 31; Korth, 1989:fig. 6) so much of the occlusal morphology cannot be discerned. However, the proportions of p4 (wider than long) and the relative robustness of the cheek teeth with multiple metastylids are very similar to the morphology of *Disallomys robustus*. It appears that MCZ 5056 is referable to *Disallomys* but is too large to be referred to *D. robustus* (Wood, 1937:209). This specimen is here referred to *Disallomys* sp.

Disallomys intermedius n. sp.
(Figure 3G-I)

Type Specimen—CM 83713, right M2.

Referred Specimens—CM 54073, P4; CM 83716, M3; CM 76717, left m3.

Diagnosis—Intermediate in size (approximately 30% smaller than *S. robustus*, 25% larger than *D. storeri*); mesostyle doubled and hypocone lacking on upper molars as in *D. robustus*; accessory lophules on cheek teeth greatly reduced or absent (present in other species); lophs and cusps less robust than in *D. robustus*.

Etymology—Latin, *intermedius*, in between.

Measurements—CM 54073 (P4): length = 2.16 mm; width = 2.62 mm. CM 83713 (M2): length = 1.81 mm; width = 2.82 mm. CM 83716 (M3): length = 1.94 mm; width = 2.25 mm. CM 76717 (m3): length = 1.83 mm; width = 1.54 mm.

Description—The P4 referred here, CM 54073, is lacking most of the anterocone and metacone, along with the mesostyle. Other than its smaller size, the P4 is very similar to that of *D. robustus*. Due to breakage, it is not possible to determine whether there is a large parastyle as in the latter. The ectoloph running posteriorly from the paracone is the same as in P4 of *D. robustus*, but the rest of the parastylar area and buccal half of the metacone is broken off. It is apparent that there are no accessory lophules posterior to the anterocone in the valley separating it from the protoloph. There is no indication of a second, smaller metaconule on the metaloph. The metaconule is transversely compressed and joins the posterior cingulum. All other observable features are as in P4 of *D. robustus*.

CM 83713 is identified as M2 rather than M1 because of its much shorter length relative to width. The buccal cusps of CM 83713 are crescentic in shape and the paracone is more lingually placed than the metacone. The ectoloph between the buccal cusps in *Haplomys liolophus* forms an inverted U-shape at the mesostyle, which is doubled. The loph running posteriorly from the protocone in CM 83713 extends directly posteriorly to the posterolingual corner of the tooth, then bends directly buccally, forming a right angle at the corner of the tooth and making the lingual margin look squared. There is a minute transverse loph in the centeral basin of the tooth as in the upper molars of *D. robustus*, but it does not extend buccally to meet the ectoloph as in the latter.

The M3 referred here is smaller than the referred M2. The paracone is only weakly crescentic and the ectoloph ends at the center of the buccal margin of the tooth in a small mesostyle. The protoloph is continuous from the paracone to the protocone with a small protoconule between them. A small loph running posteriorly from the protoconule connects to a buccally running loph from the protocone, forming a small accessory basin between the protocone and protoconule. There is no protocone crest, but the anterior connection of the protocone and protoconule may represent the fusion of the protocone crest to the protoconule. The anterior cingulum runs the entire width of the tooth, forming a long, shallow basin between the cingulum and the protoloph. The metaloph originates at the buccal edge of the tooth at a small cuspule (?accessory mesostyle) and extends lingually to a round metaconule. The metaconule is not connected to the protocone, but a short spur extends anteriorly from it toward the protocone, and a second spur extends posteriorly, joining the posterior cingulum. The metacone is a low, round swelling at the posterobuccal corner of the tooth. The morphology of CM 83716 is nearly identical to that of M3 of *D. robustus*, CM 54085.

The m3 is longer than wide. The metaconid is anteroposteriorly compressed into a flat ridge. The protoconid is positioned posterior to the metaconid, and a small trigonid basin is enclosed posteriorly by a broad metalophule II, which extends to the lingual border of the tooth. There is a minute metastylid on the posterior slope of the metaconid, and a much larger second metastylid posterior to the first along the lingual edge of the tooth. A short, broad spur extends posteriorly from metalophulid II into the center of the tooth. The hypolophid is complete from the entoconid to the mesoconid. The ectolophid is complete from the protoconid to the hypoconid, but situated well buccal of the edge of the tooth. A ridge descends the mesoconid buccally, dividing in half the valley between the protoconid and hypoconid. The anterior slope of the hypoconid forms a ridge that will in later stages of wear likely enclose a small basin between it and the mesoconid. The posterior border of the tooth is convex posteriorly, and the posterior cingulum runs from the hypoconid to the entoconid, enclosing a small basin between the posterior cingulum and the hypolophid.

Discussion—Other than its smaller size, the morphology of the cheek teeth of *Disallomys intermedius* is nearly identical to that of the larger *D. robustus*. The most striking difference in the cheek

teeth of these species is the heavier and higher lophs on the teeth of *D. robustus* compared to those of *D. intermedius*. *Disallomys intermedius* differs from *D. storeri* (Figure 3J-K) in the same morphologies as does *D. robustus* (described above) and loss of accessory lophules on the cheek teeth, as well as being nearly 25% larger in dental dimensions.

Downsimus Macdonald, 1970
Downsimus sp.
(Figure 4A)

Referred Specimens—CM 54078, left M1 or M2; and CM 54084, right M1 or M2.

Measurements—CM 54078: length = 1.65 mm; width = 2.37 mm. CM 54084: length = 1.71 mm; width = 2.25 mm.

Description—The upper molar is much wider than long. The buccal cusps (paracone, metacone) are crescentic in shape and the ectoloph forms a W-shape, connecting these two cusps. The ectoloph between the cusps is an inverted U-shape and extends more buccally than any other part of the tooth. The parastyle and metastyle are very small, and serve as the posterior and anterior ends of the ectoloph. The protoloph is low and runs from the base of the paracone to the protocone. The protoconule is an anteroposteriorly compressed minor swelling along the protoloph, just lingual to the paracone. A very short protocone crest extends anterobuccally from the protocone. The anterior cingulum extends the entire width of the tooth, isolating a deep valley between it and the protoloph. The metaloph is also a low loph but is continuous from the metacone to the protocone. The metaconule is as large as the metacone and round in outline. It is connected to the metaloph anteriorly. There is no connection of the metaconule to the posterior cingulum. The ridge running posteriorly from the apex of the protocone extends to the posterolingual corner of the tooth, then turns buccally and extends the remainder of the width of the tooth. A small but distinct hypocone is present at the bend in the posterior cingulum at the posterolingual corner of the tooth.

Discussion—The only species originally referred to this genus was *Downsimus chadwicki* from the early Arikareean Sharps Formation of South Dakota (Macdonald, 1970). Rensberger (1975) suggested that the contemporaneous *Allomys sharpi* was a junior synonym. These species were both known only from lower dentitions. Storer (2002) referred upper molars to *D. chadwicki* from the Arikareean of Saskatchewan. The Blue Ash specimens are very similar in morphology to the upper molars described by Storer (2002) but have a smaller protoconule and a metaconule that is connected to the protocone (isolated from protocone in *D. chadwicki*). The Saskatchewan specimens are also larger than those from Blue Ash (Storer, 2002:table 5).

Macdonald (1963) originally referred a maxilla with M1-M3 to ?*Prosciurus dawsonae*, SDSM 5598, from the Sharps Formation. Korth (1989) argued that this specimen was not referable to *Campestrallomys dawsonae* and probably represented a different, unnamed aplodontid. The morphology of the upper molars in this specimen is very similar to that of *Downsimus* from Blue Ash and those described from Saskatchewan (Storer, 2002). According to Macdonald's (1970:table 11) measurements of this specimen, it is slightly larger than would be expected for the upper molars of either *D. chadwicki* or the possibly synonymous *Allomys sharpi* (Macdonald, 1970:tables12, 13), also from the Sharps Formation. SDSM 5598 is also distinctly larger than the Blue Ash specimens, but likely represents a distinct species of *Downsimus*.

Subfamily Ansomyinae Qiu, 1987
Ansomys Qiu, 1987
Ansomys cyanotephrus Korth, 2007

Additional Referred Specimens— CM 76721, left P4; CM 76718, M1 or M2; CM 76719, left m1; CM 76720, right p4.

Measurements—CM 76721 (P4): length = 1.92 mm. CM 76718 (M1 or M2): length = 1.85 mm; width = 2.14 mm. CM 76720 (p4): length = 1.48 mm; width = 1.54 mm. CM 76719 (m1): length = 1.44 mm; width = 1.36 mm.

Discussion—Korth (2007) fully described the cheek teeth of *Ansomys cyanotephrus* from the Blue Ash fauna. The only difference between the newly referred material and the previous description of the species is that there is a minute second metaconule buccal to the larger metaconule on the upper molar CM 76718. In the original diagnosis of the genus, the metaconule was identified as single on the upper molars (Hopkins, 2004). Korth (2007) demonstrated that *A. cyanotephrus* was the most primitive species of the genus. The presence of an accessory, minute metaconule on upper molars of *A. cyanotephrus* demonstrates that this is a variable character (in *A. cyanotephrus*) and suggests that its presence was primitive for this genus, but lost in all later, more derived species.

Subfamily Allomyinae Marsh, 1877
Allomys Marsh, 1877
Allomys sp.
(Figure 4B)

Referred Specimens—CM 54083, left M1 or M2; CM 76722, right M1 or M2.

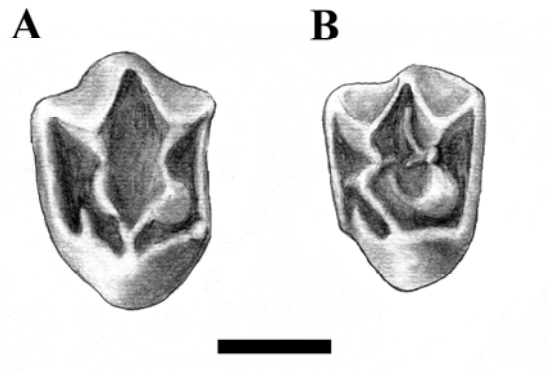

FIGURE 4. Cheek teeth of *Downsimus* sp. and *Allomys* sp. from the Blue Ash fauna. A, *Downsimus* sp., CM 54078, LM1 or M2. B, *Allomys* sp., CM 54083, LM1 or M2. Bar scale = 1mm.

Measurements—CM 54083; length = 1.46 mm; width = 1.89 mm. CM 76722: length = 1.42 mm; width = 1.91 mm.

Description—The upper molar is wider than long. The buccal cusps are slightly crescentic and sloped buccally and the ectoloph forms a W-shape as in other species of *Allomys*. The protoloph zig-zags from the paracone to the protocone. The protoconule is small, single and triangular in shape. A short protocone crest extends into the tranverse valley formed between the protoloph and anterior cingulum. The central basin of the tooth has several low, minute lophules emanating from the protoloph, metaloph and ectoloph. The metaconule is slightly smaller than the metacone and is transversely compressed, but does not connect either to the protocone or posterior cingulum. A second accessory metaconule is present on the metaloph between the metacone and metaconule. The second metaconule is very small but distinct. A minute hypocone is present posterior to the apex of the protocone, along the posterior border of the tooth. The posterior cingulum extends the entire width of the tooth, enclosing a third transverse basin between it and the metaloph.

Discussion—*Allomys* sp. from the Blue Ash fauna is the smallest of all previously described species of the genus as well as species of *Parallomys* (see appropriate tables in Rensberger, 1983). *Allomys* sp. also differs from other species of *Allomys* by having lower lophules, and a minute buccal metaconule (much larger and transversely compressed in other species). It differs from *Parallomys* by having the basins of the teeth filled with irregular lophules and having a smaller, circular buccal metaconule on the upper molars (Rensberger, 1983; Korth, 1992). *Allomys* sp. differs from species of *Alwoodia* by being markedly smaller, having much less robust cusps and lophs and possessing the minute lophules in the basin of the teeth (absent in *Alwoodia*). *Allomys* sp. differs from *Ansomys* in lacking the specialized mesostyle on the upper molars (Hopkins, 2004; Korth, 2007). *Allomys* sp. differs from *Disallomys storeri* in being smaller and in the morphology of the mesostyle and the buccal cusps of the upper molars (Tedrow and Korth, 1997).

Hopkins (2008) redefined *Allomys* and excluded previously included species, *A. cavatus* and *A. stirtoni*, referring them to *"Parallomys"*, and including the species previously included in *Alwoodia* (*A. magnus* and *A. harkseni*) as species of *Allomys*. However, according to her definition of the genus (Hopkins, 2008:table3), the first diagnostic character of *Allomys* is the presence of complex accessory lophules in the basins of the teeth. Specimens of *A. cavatus* possess these lophules (Rensberger, 1983:pl. 7), and specimens referred to *Alwoodia* lack these lophules (Rensberger, 1983:fig. 17). It is also evident from the cladograms presented by Hopkins (2008:figs. 4, 5, 6) that *A. magnus* and *A. harkseni* form their own clade, separate from the remainder of species of *Allomys*. The Blue Ash specimen has the doubled metaconule and presence of minor lophules that are diagnostic for *Allomys*.

All previously described species of *Allomys* are Arikareean in age. The smaller size, weak development of the small lophules on the teeth, and smaller buccal metaconule of *Allomys* sp. are viewed as primitive conditions for *Allomys*. The stage of development of these features suggests an earlier temporal occurrence of the Blue Ash specimen. *Allomys* sp. from Blue Ash is clearly distinct from all other species of the genus, but is not formally named here because of its poor representation.

Meniscomyinae Rensberger, 1981
Niglarodon Black, 1961
Niglarodon brachyodon n. sp.
(Figure 5, 6; Table 5)

Type Specimen—CM 54070, right M2.

Referred Specimens—CM 54063, CM 83726 to 83729, 83731, 83732, 84649, M1; CM 83725, 83730, M2; and CM 54065, 54067, 54091, M3; CM 83733, 83734, 84650, m1 or m2.

Diagnosis—Small species; cheek teeth lower-crowned than in all other species of *Niglarodon*; no posterior enamel chevron on M1; mesostyle rib on buccal surface of upper molars less well developed than in other species of *Niglarodon*; protoconule on M2 and M3 oriented obliquely (anteroposteriorly in

other species); protocone crest present on little worn M1 (absent in all other species of *Niglarodon*); mesoconid on lower molars divides labial inflection into two (single in other species) and poterolabial fossettid does not form until very late stages of wear (formed in early wear in other species).

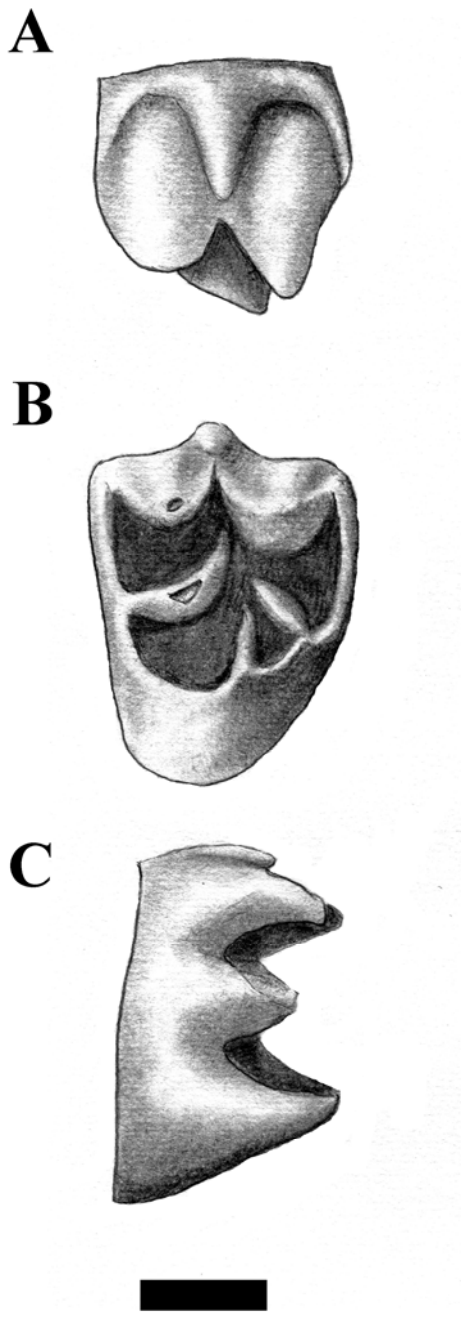

FIGURE 5. Holotype of *Niglarodon barchyodon* CM 54070, RM2. A, Buccal view (occlusal surface to bottom of page). B, Occlusal view. C, Posterior view (occlusal surface to right). Bar scale = 1mm.

Etymology—Greek, *brachys*, short; and *odon*, tooth.

Description—The upper molars from Blue Ash are submesodont to mesodont in crown-height, higher crowned than prosciurines, but slightly lower crowned than in other species of *Niglarodon*. M1 is much wider than long. The buccal cusps (paracone, metacone) are transversely flattened and a prominent mesostyle extends well buccal to the cusps. There is also a small parastyle at the anterobuccal corner of the tooth. In other species of *Niglarodon*, the mesostyle and parastyle form distinct columns that run dorsally from the occlusal surface of the tooth (Rensberger, 1981:fig. 16a). These styles on M1 from Blue Ash are much smaller, slightly conical, and do not reach the occlusal surface of the little-worn M1s. The protocone is flattened buccally, but slightly rounded lingually. The protoloph is zig-zag shaped between the paracone and protoconule. The protoconule is transversely compressed and does not reach the anterior cingulum. There is a protocone crest of variable size just anterior to the protocone, extending buccally into the anterior basin between the protoloph and anterior cingulum. Three lophs extend outward from the apex of the protocone; one anteriorly, joining the lingual end of the anterior cingulum, one posteriorly, joining the lingual end of the posterior cingulum, and one directly buccally, ending near the center of the tooth and joining the posterior end of the metaconule. On some specimens, the central buccally directed loph from the protocone extends buccally slightly beyond its connection with the protoconule. Similarly, a short anteriorly directed loph extends into the central transverse basin from the metaconule. The cingula are much lower than the cusps. The flat side of the D-shaped metaconule, is on the posterobuccal side. Posteriorly, the metaconule attaches to the posterior cingulum. The anterior arm of the metaconule extends anterobuccally, joining the ectoloph lingual to the mesostyle (diagnostic of the genus). The central transverse basin is J-shaped, bending posteriorly at its lingual end. There is no indication of a hypocone.

M2 is similar in most characters to M1. The protoconule attaches to the paracone by a low protoloph that runs from the posterior side of the protoconule to the posterolingual side of the paracone. The metaconule is obliquely oriented (anterobuccal-posterolingual). The anterior arm extends to a point on the posterior side of the paracone. Posteriorly, the metaconule meets the posterior cingulum. The protoconule is obliquely compressed (posterobuccally-anterolingually), joins the anterior cingulum and forms a triangular basin between it and the ridges of the protocone.

There are three M3s referred to *N. brachyodon*. It is nearly as long as wide (Table 5). The paracone is

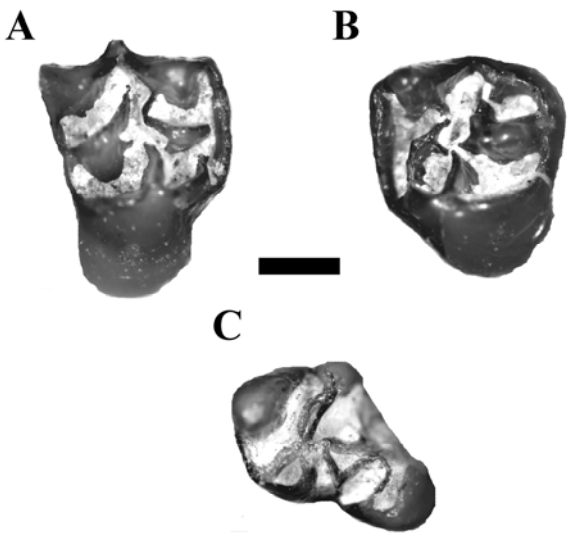

FIGURE 6. Cheek teeth of *Niglarodon brachyodon* from the Blue Ash fauna. A, CM 54063, RM1. B, CM 54067, LM3. C, CM 83733, Lm1 or m2 (partial). Bar scale = 1 mm.

only slightly flattened, much less than in M1 and M2. The protoconule is small and oriented anterolingually-posterobuccally. Anteriorly it joins the anteriorly directed loph from the protocone rather than the anterior cingulum. Posteriorly, the protoconule joins the posterobuccal side of the paracone. The central loph from the protocone ends at the center of the tooth, but does not connect with the metaconule or protoconule. The metaconule is as large as in M1 and M2, and transversely or obliquely compressed, joining the posterior cingulum. The metacone is reduced to a low ridge along the posterobuccal corner of the tooth. The posterior cingulum is very low, leaving the posterobuccal and posterolingual basins (=fossettes) open posteriorly.

The three specimens of lower molars are all partially broken. The following description combines the all three of these specimens. The lower molar is narrower anteriorly than posteriorly, the protoconid and metaconid placed closely together and connected anteriorly by a low metalophulid I. The metaconid is round in occlusal outline and the protoconid is D-shaped. The metastylid crest extends from the protoconid posterolingually, ending in a rounded metastylid. The lingual inflection is continuous from the lingual side of the tooth to the protoconid. The mesoconid is triangular in occlusal outline and connected lingually via the ectolophid to both the protoconid and hypoconid. The mesoconid is equally distinct from both of the major buccal cusps, not more posteriorly placed as in other species, producing a double labial inflection instead of a single inflection as in other species. In other species, the mesoconid fuses buccal in early wear with the hypoconid, forming a small, circular posterolabial fossettid that is eliminated in later stages of wear. However, on the Blue Ash specimens, the buccal ends of the mesoconid and hypoconid do not fuse until nearly the base of the crown. At the center of the posterior edge of the tooth is a triangular hypoconulid that extends anteriorly. The entoconid is the highest cusp of the talonid, and the hypolophid extends anterobuccally into the center of the tooth. It ends anteriorly before joining the mesoconid or ectolophid.

Discussion—*Niglarodon brachyodon* is clearly referable to this genus based on the diagnosis presented by Rensberger (1981). It is distinct from species of *Mensicomys* because of the orientation of the metaconule on upper molars (uniting with the mesostyle or parastyle), small and shallow anterolingual fossette on M1 and M2, and by the posterolingual and posterobuccal fossettes remaining open posteriorly on M3 until very heavily worn (Rensberger, 1981, 1983). *N. brachyodon* differs from all other species of *Niglarodon* in having lower crowned cheek teeth, more weakly developed mesostyle, oblique orientation of the protoconule on M1 and M3, and presence of a small protocone crest on M2. The morphology of the labial inflection and formation of the posterolabial fossettid on the lower molars are different in *N. brachyodon* than in any other reported species of *Niglarodon*. The size of the upper molars of *N. brachyodon* (Table 5) is within the range of other species of the genus, but always on the lower end (Rensberger, 1981:figs. 11, 12), making *N. brachyodon* one of the smaller species of the genus. All of these morphologies are primitive for the genus. The only species referred to the Meniscomyinae that is more primitive is the Asian *Promeniscomys* (Wang, 1987), which has cheek teeth as low-crowned as prosciurines and lacks the degree of transverse compression of the cusps present in other meniscomyines.

Niglarodon brachyodon has molars that are submesodont to mesodont in height but they are lower-crowned than in any other species of the genus. Rensberger (1981, 1983) measured crown-height of the upper molars of mensicomyines by measuring the enamel chevron on the posterior wall of M1 (CH1/). This chevron was formed because the base of the enamel descends towards the buccal side of the tooth, reaching its lowest point above the metacone, then rises sharply to the buccal edge of the tooth producing a sinuous line (Rensberger, 1983:fig. 4). The base of the enamel on the M1s of *N. brachyodon* forms a straight line with no inflections. The smallest chevron measurement on other species of *Niglarodon* was 0.4

TABLE 5. Dental measurements of *Niglarodon brachyodon*. Abbreviations as in Table 1. Measurements in mm.

CM #	M1L	M1W	M2L	M2W	M3L	M3W
83731			1.74	2.53		
54070			1.70	2.44		
83730			1.86	2.54		
83725			1.86	2.89		
54063	1.92	2.80				
83726	1.81	2.62				
83727	1.98	2.87				
83728	1.77	2.55				
83729	1.81	--				
83732	1.87	2.89				
54065					1.85	2.10
54067					1.94	2.34
54091					1.84	2.19
M	1.86	2.75	1.81	2.62	1.88	2.21
STD	0.08	0.15	0.09	0.24	0.06	0.12
CV	5.11	9.01	4.25	5.56	2.93	5.49

	m1L	m1W
83733	2.02	1.68
83734	2.24	1.73

mm (Rensberger, 1983:fig. 10). The small protocone crest present on M2 of *N. brachyodon* is not known for any other meniscomyine except *Promeniscomys* from the middle Oligocene of China (Wang, 1987), but is common in the brachydont prosciurines and allomyines, again suggesting that its presence is primitive. Rensberger (1981:fig. 4) measured the crown-height of m1 in species of *Niglarodon* by measuring the height of the enamel on the lingual side of the tooth from the base of the anterolingual inflection (HAI1). This measurement on the Blue Ash specimens is 0.4 - 0.5 mm, whereas the smallest measurement in the remaining species of *Niglarodon* was 0.80.

Niglarodon brachyodon is also the eastern-most species of Meniscomyinae. Early promylagaulines are very common in the Great Plains (McGrew, 1941; Rensberger, 1980; Korth, 1992), but meniscomyines are nearly unknown in the area. Macdonald (1963, 1970) reported two species of *Meniscomys*, *M. milleri* and *M. hippodus*, and a specimen of *Niglarodon koerneri* from the Sharps Formation of South Dakota. However, Rensberger (1980) referred *M. milleri* to a new genus of mylagaulid *Crucimys*, and determined that the specimen referred to *M. hippodus* had extremely worn teeth and was not identifiable even to genus (Rensberger, 1983). The specimen referred by Macdonald (1970) to *Niglarodon koerneri*, LACM 9269, differs from all other species by its smaller p4 and lower-crowned cheek teeth. The occlusal morphology of LACM 9269 is nearly identical to that of the early Arikareean *N. koerneri* (Black, 1961; Rensberger, 1981). It has a smaller p4 than any other species and is lower crowned. The HAI1 measurement in LACM 9269 is 0.6 mm, lower than other *Niglarodon* but higher than the Blue Ash specimens. The formation of the posterolabial fossettid occurs higher on the crown of the lower molars of LACM 9269 than on the Blue Ash lower molars as well. It is possible that the Blue Ash specimens and LACM 9269 represent the same primitive species of *Niglarodon*, but this cannot be determined at this time. All other species of *Meniscomys* and *Niglarodon* are limited to the Arikareean of Oregon and the Rocky Mountain region (Idaho, Montana, Wyoming), respectively (Rensberger, 1981, 1983; Barnosky, 1986).

CONCLUSIONS

Previous attempts to determine the provincial age of the Blue Ash fauna based on the micromammals have been inconclusive because of the occurrence of Arikareean species as well as species from the Whitneyan or earlier horizons (see Korth, 2009 and references therein). Also, the definition of the boundary between the Whitneyan and Arikareean involves very few micromammals (Prothero and Emry, 2004; Tedford et al., 2004). The single taxon used to define the beginning of the Arikareean by Tedford et al. (2004) is the zapodid rodent *Plesiosminthus*, which is lacking in the Blue Ash fauna. However, the Ridgeview fauna from Nebraska has been demonstrated to be earliest Arikareean in age, but also lacks this taxon (Bailey, 2004). For these reasons, it has been difficult to assign the fauna from Blue Ash to either the Arikareean or Whitneyan land mammal age.

The aplodontid rodents appear ideal for such a determination because of their vastly different faunas during this time interval. The Orellan to Whitneyan is dominated by morphologically more primitive or generalized species (=prosciurines), whereas the Arikareean is dominated by the radiation of the more

derived allomyines and meniscomyines (Korth, 1994:fig. 9.3; Flynn and Jacobs, 2008:fig. 22.3).

The aplodontid fauna from Blue Ash is dominated in number of specimens and number of taxa by prosciurines, with fewer taxa and fewer specimens of typically Arikareean taxa except *Niglarodon*. Of the aplodontids present in the fauna, the genus *Prosciurus* has a range from Chadronian to Whitneyan; *Prosciurus magnus* is known from the Orellan or earliest Whitneyan (Korth, 1989); *Campestrallomys siouxensis* is known elsewhere from the Whitneyan or earliest Arikareean (Korth, 1989); and all of the species of *Disallomys* are restricted to the Whitneyan of Nebraska and South Dakota. The typically Arikareean aplodontid genera present in the Blue Ash fauna, *Allomys*, *Downsimus*, and *Niglarodon*, are generally poorly reperesented (the former two being known from a total of four specimens). The species recognized from the Blue Ash fauna representing these genera (*Allomys* sp., *Downsimus* sp., *Niglarodon brachyodon*) are morphologically more primitive and smaller than the known the respective Arikareean species. The species of aplodontids from the anthill collection of the Blue Ash fauna suggest more strongly than any other group previously described that it is Whitneyan in age rather than Arikareean.

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