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MAMMALS FROM THE BLUE ASH LOCAL FAUNA (LATE OLIGOCENE), SOUTH DAKOTA, MARSUPIALIA AND LAGOMORPHA

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ABSTRACT

Two marsupials (*Herpetotherium fugax* and *Herpetotherium* sp.) and three lagomorphs (*Palaeolagus subhypsodus* n. sp., *Palaeolagus* sp. cf. *P. philoi*, and *Palaeolagus* sp.) are identified from the Blue Ash local fauna of South Dakota. Of the species identified here, *H. fugax* is otherwise known from the Orellan to early Arikareean, *Herpetotherium* sp. is morphologically closest to the middle to late Arikareean *H. youngi* but is smaller in size, *Palaeolagus subhypsodus* is intermediate between the Whitneyan *P. burkei* and the Arikareean *P. hypsodus*, and the other lagomorphs are closest to Arikareean species morphologically. The age of the fauna is still not definite based on these species but it is suggested that it is slightly earlier than previously described Arikareean faunas.

INTRODUCTION

To date, only rodent species have been formally recognized from the Blue Ash local fauna (Martin, 1974; Korth, 2007, in press; Emry and Korth, in press). Earlier preliminary faunal lists presented by Martin (1974) and Simpson (1985) included all of the mammalian species present. Martin (1974:3) listed two lagomorphs, the otherwise Arikareean *Palaeolagus hypsodus* and *P. philoi*, but did not list any marsupials. Simpson (1985:table 1) cited three species of marsupials, the Orellan *Herpetotherium fugax*, and two uncertain species, *Herpetotherium* sp. and *Nanodelphys* sp. cf. *N. minutus* (=*N. hunti*: only known from Orellan). He also cited four species of lagomorphs, all species previously known from the Orellan, *Megalagus turgidus, Palaeolagus intermedius, P. haydeni,* and *P. burkei*. Of these, all but *P. haydeni* have been reported also from the Whitneyan (Wood, 1940; Dawson, 1958; Korth and Hageman, 1988). Simpson's (1985) preliminary identifications tended toward earlier species (Orellan and Whitneyan) whereas Martin (1974) assigned the specimens to Arikareean species. In part, this is likely due to the uncertain age of the fauna, being near the temporal boundary of the Whitneyan and Arikareean (Simpson, 1985; Bailey, 2004).

An extensive anthill fauna from the Blue Ash Channel in the collections of the Carnegie Museum of Natural History (CM) has yielded over 1000 specimens, almost entirely isolated teeth. Analysis of the marsupials and lagomorphs in this collection increases the number of formally described taxa from the fauna that can potentially help in the determination of the biochronologic age of the fauna.

Dental nomenclature for marsupials is from Crochet (1980); that for lagomorphs is from White (1987) for P2 and p3, and Dawson (1958) for the molariform cheek teeth. Capital letters (e.g., M1) indicate upper teeth, lower-case letters indicate lower teeth (e.g., m1).

SYSTEMATIC PALEONTOLOGY

Order Marsupialia Illiger, 1811

Family Didelphidae Gray, 1821

Herpetotherium Cope, 1873

Herpetotherium fugax Cope, 1873

(Figure 1A-D; Table 1)

Referred Specimens—CM 76305, partial maxilla with M1-M2; CM 76302, 76303, 76304 – M1s; CM 76306, 76307 – M2s; CM 76308 through 76313 – M3s; CM 76314 – M4; CM 76315, 76317, 76318, 76320, 76321, 76323 - lower molars; CM 76322 – mandibular fragment with p2.

Description—On M1, there are always three recognizable stylar cusps: B, C and D. D is the largest, being only slightly larger than B, and C is a minute cuspule, just anterior and slightly lingual to cusp D (Figure 1C). The arrangement and relative size of the stylar cusps is nearly identical to that of M1 on all of the referred M2s. In all other features of occlusal morphology, M1 and M2 do not differ from those of the genus (see Korth, 1994:379; Hayes, 2005:346).

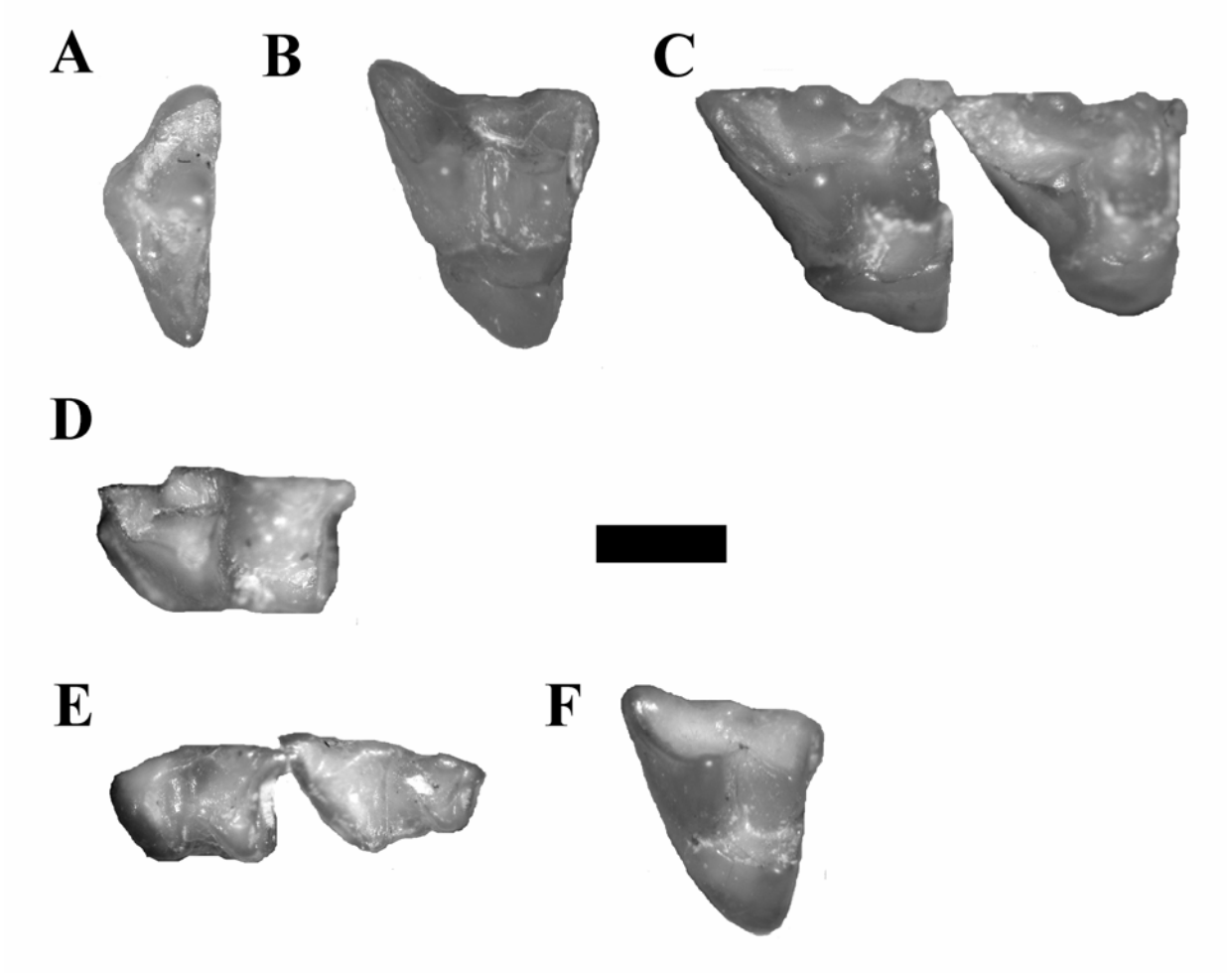

FIGURE 1. Marsupials from Blue Ash. A-D, *Herpetotherium fugax*. A, left M4 (reversed), CM 76214. B, right M3, CM 76312. C. right M1-M2, CM 76305. D, left m2, CM 76315. E-F, *Herpetotherium* sp. E, left m3(broken)-m4, CM 76319. F, right M3, CM 76311. Bar scale = 1 mm.

On M3 there is a large, central stylar cusp (cusp C) and a minute cusp B (Figure 1B). One specimen retains a minute cuspule on the anterior slope of C, similar to the condition figured by Green and Martin (1976:fig. 2a), suggesting the fusion of cusps C and D. There is only one specimen of M4, CM 76314 (Figure 1A). It is much smaller than the other molars. There is no recognizable stylar cusp. The metacone is along the posterior margin of the tooth, near the center. The lower molars do not differ in morphology from any of the species of the genus (see Korth, 1994:380; Hayes,2005:348).

Discussion—The majority of the marsupial specimens from Blue Ash can be referred to *Herpetotherium fugax* based on the relative size of the stylar cusps on the upper molars, and overall size. In size, the Blue Ash sample overlaps that of the Orellan to early Arikareean *H. fugax* and the Arikareean *H. youngi* (Green and Martin, 1976:table 1; Korth, 1992:table 2; Korth, 1994:table 4; Hayes, 2005:fig. 5), but the mean is greater than that of *H. youngi,* and more nearly approaches that of *H. fugax* (Korth, 1994:fig. 2; Hayes, 2005:fig. 5). A recognizable stylar cusp B on M2 is also present on specimens of *H. fugax* and not *H. youngi*.

In the reviews of marsupials from the Tertiary of North America *H. fugax* (= *Peratherium fugax*) has been the most common species recognized from the Orellan, and *H. youngi* (=*Peratherium spindleri*) has been the only Arikareean species (Scott and Jepsen, 1936; Green and Martin, 1976; Korth, 1994). Hayes (2005) also recognized *H. fugax* from the early Arikareean of Nebraska and Florida. However, no species of marsupial has ever been recognized from the Whitneyan. Hayes (2005) included a sample of *Herpetotherium* from the Cedar Ridge fauna of

Wyoming (Setoguchi, 1978) as occurring in the Whitneyan, however, it has been demonstrated that this fauna is clearly Orellan in age (Korth, 1989). The presence of *H. fugax* in the Blue Ash fauna suggests that the fauna is early Arikareean at the latest. Faunas that have *H. youngi* are middle to later Arikareean (Hayes, 2005).

TABLE 1. Dental measurements of *Herptotherium fugax* from Blue Ash. Abbreviations: L, anteroposterior length; W, greatest transverse width; N, number of specimens; M, mean; OR, range; SD, standard deviation; CV, coefficient of variation. Measurements in mm.

		N	M	OR	SD	CV
M1	L	4	1.74	1.65-1.82	0.07	4.24
	W	4	1.63	1.58-1.69	0.05	3.35
M2	L	3	1.93	1.80-2.14	0.19	9.65
	W	3	1.94	1.87-2.01	0.07	3.61
M3	L	5	1.70	1.62-1.78	0.06	3.58
	W	5	2.26	2.11-2.41	0.13	5.92
M4	L	1	0.84			
	W	1	2.04			
m1	L	1	1.75			
	W	1	1.03			
m2	L	4	1.93	1.85-2.01	0.07	3.61
	W	3	1.08	1.05-1.11	0.03	2.78
m3	L	3	1.92	1.09-1.97	0.04	2.10
	W	3	1.12	1.07-1.16	0.05	4.04

Herpetotherium sp.
(Figure 1E, F)

Referred Specimens—CM 76319, partial mandible with m3 (partially broken)-m4; CM 76311, isolated M3.

Measurements—CM 76319: m3, W = 0.86 mm; m4, L = 1.49 mm; W = 0.85 mm. CM 76311: M3, L = 1.47 mm; W = 1.71 mm.

Description— These specimens are smaller in size than *Herpetotherium fugax*, and *H. youngi* (Macdonald, 1970:table 3; Green and Martin, 1976:table 1; Korth, 1992:table 2; Hayes, 2005:table 1). M3 is short anteroposteriorly, and widened transversely with a deep ectoflexus, typical of didelphid M3s. There are no recognizable conules. The only recognizable stylar cusp on M3 is a large stylar cusp C.

The trignoid on the m3 of CM 76319 is worn away. The talonid has the distinct didelphid hypoconulid that projects posteriorly, posterior to the entoconid. The remainder of the morphology of the talonid is typical of that of *Herpetotherium*. The talonid of m4 is similar in morphology to that of m3, but much smaller relative to the trigonid. This does not differ from the morphology in other species of *Herpetotherium* (see Korth, 1994).

Discussion—These specimens have the distinctive characters of didelphids (lingual, posterior projecting hypoconulid on lower molars; dilambdodonty on the upper molars with metacone higher than paracone). They are morphologically as advanced as in *H. youngi* in the morphology of the stylar cusps of the upper molars (enlarged central stylar cusp, all others unrecognizable; see Korth, 1994; Hayes, 2005) but are too small to be referred to that species.

Order Lagomorpha Brandt, 1855
Family Leporidae Fischer de Waldheim, 1817
Palaeolagus Leidy, 1856
Palaeolagus subhypsodus n. sp.
(Figure 2A-C, 3; Table 2)

Type Specimen—CM 76329, right p3.

Referred Specimens—All isolated cheek teeth; CM 76385-CM 76396, lower deciduous premolars; CM 76326-CM 76329 and CM 76330-CM 76352, p3s; CM 76353-CM 76379, lower molariform cheek teeth; CM 76380-CM 76384, m3s; CM 76397-CM 76401, upper deciduous premolars; CM 76402-CM 76404, P2s; CM 76405-CM 76415, P3s; CM 76416-CM 76447, upper molariform cheek teeth.

Diagnosis—Similar in size to *P. hypsodus*, larger than *P. burkei*, smaller than *P. intermedius*; trigonid and internal reentrant on p3 obliquely oriented as in *P. hypsodus*; anterior external reentrant on p3 variably present (64% of specimens), if present is extremely shallow (less than in *P. hypsodus*).

Etymology—Latin, *sub-*, prefix meaning under or less than; and *hypsodus*, reference to a closely related *Palaeolagus* species.

Description—The specimens referred to *Palaeolagus subhypsodus* are very close in size to those of *P. hypsodus* (Dawson, 1958:table 3). All of the cheek teeth are hypsodont with no indications of roots. P3 has two anterior reentrants on the unworn and little-worn specimens, CM 76404 and CM 76403. However, the external reentrant does not extend more than approximately one-third of the height of the crown, and is only a small notch on the most worn specimen, CM 76402 (Figure 2A). The main reentrant is crescentic and extends about three-fourths the length of the tooth on the occlusal surface, and almost to the base of the crown on the anterior side of the tooth. On the intermediately worn specimen, CM 76404, there is a very shallow notch along the lingual side of the tooth, possibly homologous to the hypostria. There is no indication of this below the occlusal surface, suggesting that it will be lost after only minimal additional wear.

P3 is very similar to that of *P. hypsodus* (Figure 2B). The posterior lobe is much wider transversely than the anterior lobe. The hypostria is straight-sided and extends about half the width of the tooth on the

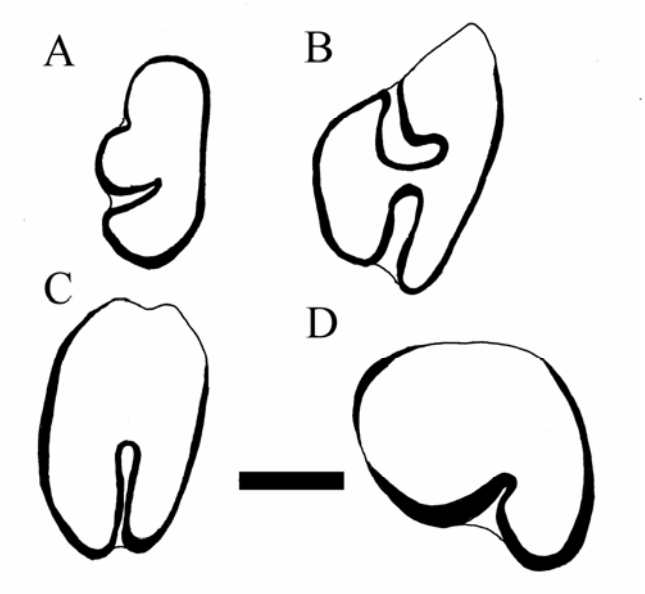

FIGURE 2. Cheek teeth of lagomorphs from Blue Ash. A-C, *Palaeolagus subhypsodus*. A, left P2, CM 76402. B, left P3, CM 76414. C, left upper molariform tooth, CM 76416. D, *Palaeolagus* sp. cf., *P. philoi*, left p3, CM 76448. Anteiror to left. Bar scale = 1 mm.

occlusal surface, and extends to the base of the crown. The external reentrant forms a J-shape, curving posteriorly at its lingual end. It appears that this reentrant remains open externally to the base of the crown. There are no specimens in the collection where it has been reduced to a crescent or eliminated. Both the hypostria and external reentrant are cement-filled.

P4 is molariform and cannot be definitely separated from M1 and M2 based on morphology. On all the upper molariform cheek teeth, the hypostria is straight-sided and cement-filled, extending to the base of the crown (Figure 2C). It crosses approximately half the width of the tooth on the occlusal surface. The enamel crescent disappears in very early stages of wear because none of the specimens having any wear has preserved it. There is no enamel on the external side of the teeth, but a distinct groove extends the entire height of the tooth on the external side. No specimens in the collection have been identified as M3.

The lower third premolar (p3) is smaller than p4-m2 (Figure 3). It is widest posteriorly and rounded anteriorly. There is a persistent internal reentrant (=posterior internal reentrant of White, 1987) that is straight-sided and oriented obliquely across the occlusal surface in a lateral-posterior direction. It crosses about one-third to one-half the width of the tooth and is always cement-filled. The orientation of the internal reentrant gives the trigonid the appearance of also being oriented obliquely, similar to p3 of *P. hypsodus* (Dawson, 1958). On the external side of the tooth there is always a posterior external reentrant that is triangular in occlusal outline, extending approximately one-fourth the width of the tooth. It is also persistent to the base of the crown and cement-filled. An anterior external reentrant is variably present. When present, it forms a very small notch on the occlusal surface of the tooth, but is persistent to the base of the crown and is filled with cement. Only 64% of the specimens of p3 have an anterior external reentrant. On some specimens, the anterior external reentrant is lacking completely, whereas in others, the area of the reentrant is flattened (rounded in others), and the flattened area persists to the base of the crown (see Figure 3).

As with the upper molariform cheek teeth, p4 cannot be separated from m1 or m2. These teeth are typical of leporids, consisting to two transverse lophs; trigonid and talonid. The trigonid is always wider than the talonid. On most other early leporids, the two lophs unite lingually at very late stages of wear. There are no specimens in the collection that show this connection.

The m3 is very small relative to the other molars. The talonid is reduced to a small column with a circular occlusal outline. The talonid and trigonid fuse centrally on some of the specimens.

Discussion—*Palaeolagus subhypsodus* most closely resembles the Arikareean *P. hypsodus* in size (Dawson, 1958:table 3), and morphology of p3 (oblique trigonid and internal reentrant). It differs from *P. hypsodus* in the variable presence of an anterior external reentrant on p3. On specimens of *P. subhypsodus* that have the reentrant, it is very shallow, not as deep as in *P. hypsodus* (Dawson, 1958:fig. 10b). Both *P. intermedius* and *P. burkei* have been reported from the Whitneyan (Wood, 1940; Dawson, 1958; Korth and Hageman, 1988). *P. intermedius* can easily be distinguished from *P. subhypsodus* by larger size and presence of only a single (posterior) external reentrant on p3. *P. burkei* is smaller than *P. subhypsodus* and there is only a single external reentrant on p3 that is oriented transversely across the occlusal surface (not oblique).

Palaeolagus subhypsodus appears to be morphologically intermediate between the Orellan and Whitneyan *P. burkei* and the Arikareean *P. hypsodus*.

Palaeolagus sp. cf. *P. philoi* Dawson, 1958
(Figure 2D)

Referred Specimens—CM 76448, left p3 and CM 76449, lower molariform tooth.

Measurements— CM 76448, p3, L = 2.25 mm; W = 2.02 mm. CM 76449, lower molar, L = 2.67 mm; W = 2.24 mm.

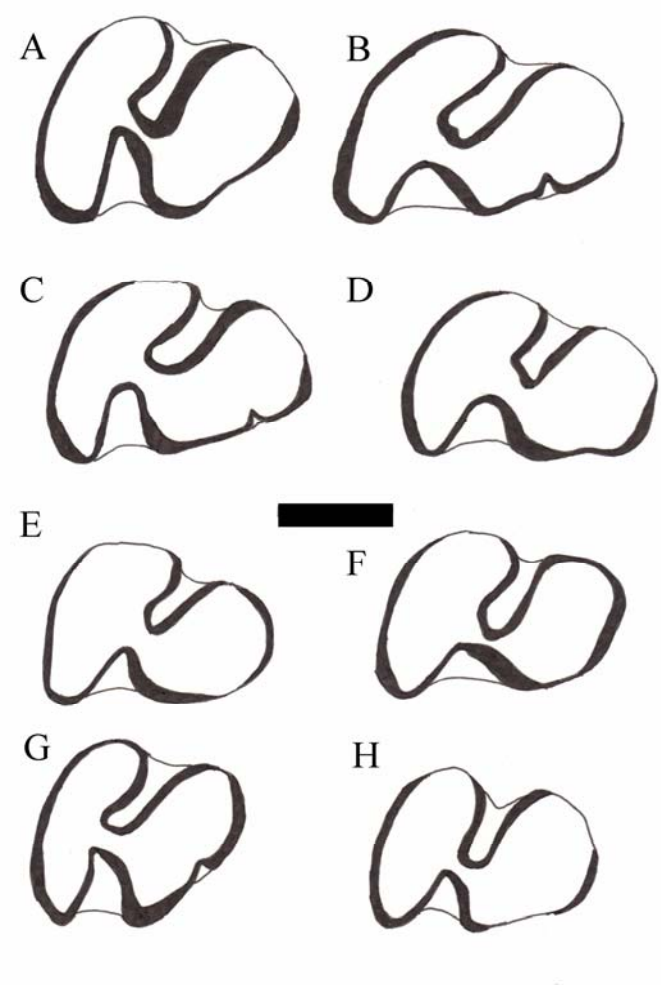

FIGURE 3. Right lower third premolars of *Palaeolagus subhypsodus* (occlusal view). A, CM 76328. B, CM 76327. C, CM 76329 (holotype). D, CM 76331. E, CM 76346. F, CM 76345. G, CM 76334. H. CM 76336. Anteiror to right. Bar scale = 1 mm.

TABLE 2. Dental measurements of *Palaeolagus subhypsodus*. Abbreviations as in Table 1. Measurements in mm.

		N	M	OR	SD	CV
p3	L	22	2.04	1.73-2.27	0.15	7.50
	W	22	1.80	1.49-2.14	0.17	9.19
p4, m1, m2						
	L	20	1.89	1.71-2.20	0.12	6.40
	W	20	2.00	1.78-2.36	0.14	7.15
m3	L	5	1.54	1.29-1.82	0.24	15.82
	W	5	1.49	1.22 1.75	0.20	13.78
P2	L	3	1.24	1.14-1.35	0.11	8.57
	W	3	2.16	2.14-2.17	0.02	0.71
P3	L	11	1.74	1.55-1.88	0.10	5.48
	W	8	2.59	2.43-2.66	0.07	2.77
P4, M1, M2						
	L	20	1.55	1.26-1.77	0.15	9.69
	W	20	2.52	2.15-2.87	0.22	8.69

Description—The p3 is longer than wide, with a single external reentrant on the occlusal surface that extends nearly half the width of the tooth and is persistent to the base of the crown. The reentrant valley is filled with cement. The molariform tooth is partially broken, but is typical of leporids with a trigonid wider than talonid. Both teeth are hypsodont.

Discussion—The specimens referred here to *Palaeolagus* sp. cf. *P. philoi* are similar in morphology to both the Arikareean *P. philoi* and the Orellan to Whitneyan *P. intermedius* (Wood, 1940;Dawson, 1958). Dawson (1958) noted that the only difference between *P. philoi* and *P. intermedius* was the crown height of the upper molars and proportions of the palate. Since there is no palate or upper molars present in the Blue Ash fauna, this material is tentatively assigned to *P. philoi* based on its slightly smaller size than *P. intermedius* (Wood, 1940:330; Dawson, 1958:table 4).

Palaeolagus sp.
(Figure 4)

Referred Specimen—CM 76450, left P2.

Measurements— L = 1.72 mm, W = 3.19 mm.

Description—The specimen is larger than any other P2 in the Blue Ash collection or any reported Whitneyan or Arikareean species of *Palaeolagus*. The tooth is unilaterally hypsodont and rootless. The enamel extends about 60% of the height of the crown on the anterior surface. At the posteroexternal corner of the tooth, the enamel is already worn away at the occlusal surface.

The tooth is roughly oval in occlusal outline. There is moderate wear on the occlusal surface, and two anterior reentrant valleys are present. The more buccal reentrant is smallest, extending less than half the anteroposterior length of the occlusal surface from the anterior margin of the tooth. The valley extends about 1.7 mm down the anterior enamel surface, less than one-quarter the height of the crown. The more lingual anterior reentrant is longer and crescent shaped, extending nearly to the posterior side of the tooth. However, the lingual reentrant does not remain open any deeper on the anterior surface of the enamel than the more buccal reentrant. This also suggests that at least the anterior opening of the valley will close at the same time as that of the more buccal reentrant.

Discussion—The isolated P2 is larger than that of the recognized species of *Palaeolagus* from Blue Ash. It is up to 25% greater in width than that of the largest species of *Palaeolagus, P. intermedius* (Wood, 1940:330). Dawson (1958) and Macdonald (1970) identified large-sized leporid specimens from the early Arikareean Sharps fauna of South Dakota as "*Megalagus* cf. *primitivus*." Dawson (1958) noted that

the specimens referred to "*M.* cf. *primitivus"* differed from other *Megalagus,* and suggested that they were more advanced and were possibly referable to *Palaeolagus*. The specimen from Blue Ash is similar in size to the lower cheek teeth from the Sharps (Dawson, 1958:table 2) but lacks the buccal roots typical of *Megalagus*. A lack of roots would fit Dawson's suggestion of a species of *Palaeolagus*. It is possible that CM 76450 from Blue Ash is a P2 of the species referred to previously as "*Megalagus* cf. *primitivus"* but since the previously recognized specimens of the latter are only lower dentitions, direct comparison is not possible. Until more material of the species can be recovered it will be included in *Palaeolagus*.

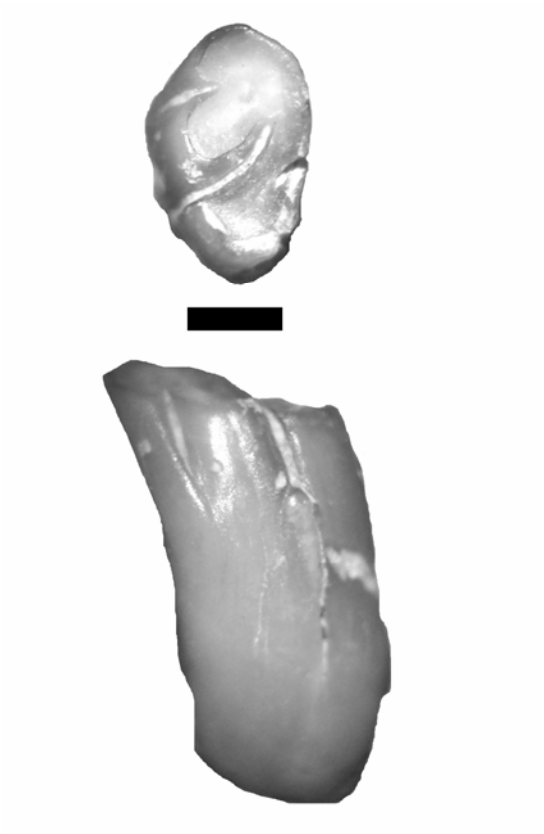

FIGURE 4. *Palaeolagus* sp., left P3, CM 76450. Occlusal view (top) and anterior view (below). Bar scale = 1 mm.

CONCLUSIONS

The five mammalian species described here increase the formally identified species from Blue Ash to fifteen (see Korth, 2007). The rodents previously described are almost entirely unique to the fauna and cannot be used to correlate to other North American faunas. The marsupial *Herpetotherium fugax* ranges from the Orellan to the early Arikareean (Hayes, 2005). The indeterminate species of *Herpetotherium* from Blue Ash is morphologically closest to the later Arikareean *H. youngi*, but is smaller. *Palaeolagus subhypsodus* is morphologically intermediate between the Whitneyan *P. burkei* and Arikareean *P. hypsodus*. The other lagomorphs identified are closest to Arikareean species, but the assignments are not definite. On the whole, the marsupials and lagomorphs appear to be a little better for age determination for the fauna because they are not unique to the fauna as the previously described rodents have been.

The combination of Orellan species and Arikareean species along with species morphologically intermediate between Whitneyan and Arikareean species (*P. subhypsodus*, *Herpetotherium* sp.) more strongly suggests that the fauna is older than previously reported Arikareean faunas. However, none of the species used to define the Whitneyan are present (see Prothero and Emry, 2004), so it cannot be determined whether the Whitneyan-Arikareean boundary is before or after the age of the Blue Ash fauna.

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