

## LATE NEOGENE BEAVER *DIPOIDES* FROM THE PIPE CREEK SINKHOLE OF GRANT COUNTY, INDIANA

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### ABSTRACT

Two upper fourth premolars of the diminutive beaver *Dipoides* from the early Blancan Pipe Creek Sinkhole of Indiana were compared with new *Dipoides wilsoni* material from the Saw Rock Canyon 1 and Fallen Angel B assemblages of Seward County, Kansas and published accounts of other North American *Dipoides*. The Pipe Creek Sinkhole teeth are larger than those of most other late Neogene *Dipoides*. Although high-crowned and ever-growing, upper fourth premolars of the Pipe Creek Sinkhole beaver are less hypsodont than other samples with which they were compared. Despite this, both teeth are relatively advanced, with complete or nearly complete pseudostria 3 and the absence of dentine channels connecting lophs 2 and 3. The Pipe Creek *Dipoides* is probably not referable to *D. wilsoni*, but the small sample size does not currently allow allocation to other named species or the naming of a new species. A revised dental terminology is presented for the castoroidinid beavers.

### INTRODUCTION

The Pipe Creek Sinkhole in Grant County, Indiana, uncovered accidentally during limestone quarrying operations (Farlow et al., 2001; Martin et al., 2002; Farlow et al., 2010a), represents an important window into the early Pliocene biota of the central United States in an area generally devoid of localities from that time period (Farlow and Argast, 2006; Dawson et al., 2008; Shunk et al., 2009; Farlow et al., 2010b). The sinkhole was apparently extensive enough to have attracted a wide range of animals, including the presumably semi-aquatic rhinoceros *Teleoceras*. In a study of the rodents, Martin (et al., 2002) reported a humerus fragment from a beaver, allocating it to either *Castor* or *Dipoides*. Since that time, two arhizodont *Dipoides* cheek teeth were recovered from the Pipe Creek Sinkhole (hereafter referred to as "Pipe Creek"). The purpose of this study is to describe these teeth and, to the extent possible, identify them to species. A revised dental terminology for the castoroidinid beavers is presented in Figure 1 and explained in detail below.

Small beavers of the genus *Dipoides* are characteristic members of late Miocene (Hemphillian) and Pliocene (Blancan) mammalian lacustrine and palustrine assemblages through the western and central United States. Eight species have been named, including *D. stirtoni* Wilson, 1934, *D. williamsi* Stirton, 1935, *D.*

*wilsoni* Hibbard, 1949, *D. rexroadensis* Hibbard and Riggs, 1949, *D. smithi* Shotwell, 1955) *D. vallicula* Shotwell, 1970, *D. intermedius* Zakrzewski, 1969 and *D. tanneri* Korth, 1998. *D. intermedius* has since been referred to *Procastoroides* (Ruez, Jr., 2009). Shotwell (1955) observed that the holotype of *D. rexroadensis*, KU 7693, a left M1 or M2 from Keefe Canyon (Rexroad Loc. 22; Hibbard and Riggs, 1949), was so large that it likely represented another beaver taxon other than *Dipoides*. The holotype of *Dipoides rexroadensis* from Keefe Canyon is inseparable from the same molars of small adult *Procastoroides sweeti*. The specimens of *D. rexroadensis* illustrated by Woodburne (1961) from Rexroad Loc. 3 are juvenile *P. sweeti*, as can be seen by the extra flexa(ids) so characteristic of juvenile teeth in a hypsodont species. As a number of specimens of adult *P. sweeti* have also been collected at Rexroad Loc. 3, *D. rexroadensis* is here synonymized with *P. sweeti*.

The remaining small *Dipoides* form a fairly homogeneous group, although it is clear that *D. tanneri* from the late Clarendonian Pratt Quarry of Brown County, Nebraska is the most dentally primitive of the known species, as roots form late in development on the premolars (Korth, 1998). Korth (1998) noted some similarities between *D. tanneri* and *D. stirtoni* (Wilson, 1934), most notably a shorter parastriid than mesostriid on p4 (Figure 1), and for now *D. tanneri* can be considered as a general ancestral grade of dental

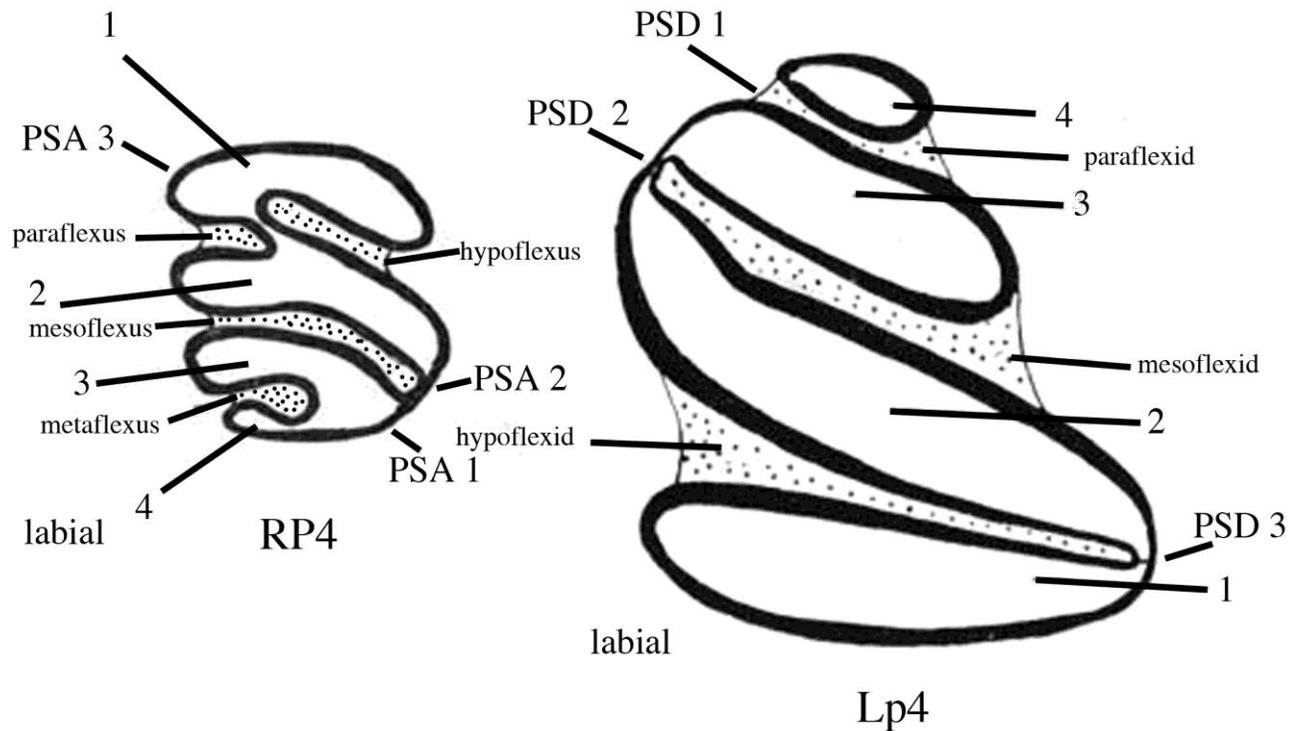


FIGURE 1. Castoroidinin dental terminology. Numbers by themselves = lophi, PSA = pseudostria, PSD = pseudostrid. When viewed from labial or lingual views, the cement-filled flexae(ids) are also known as striae(ids); e.g., the mesoflexid on p4, from lingual view, is referred to as the mesostrid.

morphology for the genus. There are few dental characters that serve to unequivocally separate the various species except the presence of roots in adult teeth, as in *D. tanneri*. Unlike most arvicolid and muroid rodents, the occlusal morphology and size of castoroidinin cheek teeth change considerably after birth. Juvenile teeth hardly resemble those of adults, and often retain occlusal features of their Miocene ancestors (Shotwell, 1955; Korth, 1998). Because ontogenetic changes in dental morphology have not been systematically described, the range of intraspecific and interspecific variation in *Dipoides* is essentially unknown. Nevertheless, it may be possible to determine some developmental tendencies from published accounts.

For example, as shown by Shotwell (1955), juvenile upper teeth of *Dipoides* and *Procastoroides* (the *Dipoides rexroadensis* of Woodburne, 1961) often display a metaflexus and paraflexus (Figure 1), both of which disappear with later wear (age). During wear and prior to its disappearance, the metaflexus may become isolated as a metafossette. Likewise in the lowers, the

paraflexid may either disappear with wear or remain through life, depending on the depth of the parastrid. Certain striae on the upper teeth, such as the parastria and metastria, reach the base of the crown in the Cretaceous *Dipoides tanneri* (Korth, 1998), but in all other *Dipoides* with arhizodont, ever-growing teeth, downward developmental extension of these striae does not keep pace with upward growth from the tooth base, resulting in disappearance of the paraflexus and metaflexus soon after tooth wear begins. On the other hand, as the cheek teeth enlarge over evolutionary time in the castoroidinins, pseudostriae(ids)(PSA, PSD; Figure 1) may appear, representing weak points on the enamel surface at the termination of ancestral flexa(ids). Thus, in *Castoroides* M3s, both PSA1 and PSA2 may be well-developed, and PSD2 and PSD3 are often present in the lower cheek teeth (Martin, 1969). Understanding castoroidinin phylogeny will depend, to a great extent, on understanding these tendencies, well appreciated by Shotwell (1955).

Another problem of some concern is the difficulty in identifying specific isolated teeth. Upper first and

second and lower first and second molars are currently impossible to separate. Wilson (1934) placed a question mark next to his identification of CIT 1687 of *D. stirtoni* as an M3. Adult P4s and M3s are somewhat similar in overall morphology, but Wilson was correct in his identification, as can be seen by the triangular shape of CIT 1687 (a primitive geometry) and the curled loph 3 retaining its dentine connection with loph 2. This particular morphology is also expressed in *D. tanneri* (Korth, 1998).

## METHODS AND SPECIMENS

Upper molars are abbreviated by upper case letters (e.g., M3), lowers by lower case letters (e.g., m3). Greatest measurements of occlusal surfaces on adult teeth were made with an AO filar micrometer coupled to an AO binocular microscope. The micrometer was calibrated with a 2.0 mm AO slide and measurements were multiplied by the appropriate correction factor. Crown height was measured with a TESA digital calipers; one side of the calipers was held flat against the occlusal surface and the other manipulated until it was in contact with the longest projection of the crown base. Relative hypsodonty was calculated as follows:  $H = C/L$ , where  $C$  = crown height and  $L$  = occlusal length. Occlusal measurements of three p4s reported by Hibbard (1949, 1953) were so low that they were probably taken on juvenile teeth. Consequently, I calculated lengths of two adult p4s illustrated by Hibbard (1953:fig. 5I, J) from measurements of the tooththrow given in the text. These calculations generated estimated p4 lengths much more consistent with upper measurements and with p4s of *D. wilsoni* from FAB (Table 1). Pipe Creek specimens are housed at the Indiana State Museum (INSM) and those from Kansas at the Sternberg Museum at Fort Hays State University (FHSM).

Dental terminology for castoroidin beavers (Figure 1) follows Shotwell (1955) and Woodburne (1961), with a few minor modifications. Loph(ids) are numbered consecutively from anterior - posterior on the uppers and posterior - anterior on the lowers. Loph(ids) are *complete* when they are continuous and cementum breaks through on both the labial (buccal) and lingual tooth borders, and they are *inflated* when their enamel borders are not roughly parallel at midpoint. Following Woodburne (1961), three pseudostrids (PSD) are recognized, PSD1 for the most anterior, buccal (labial) pseudostrid when the paraflexid breaks through on the buccal side, isolating Loph 4, PSD2 for the second buccal strid when the mesoflexid breaks through on the buccal side, and PSD3 for the third posterior, lingual pseudostrid, created when the hypoflexid breaks through the enamel on the lingual tooth border. Pseudostria 1 (PSA1), pseudostria 2 (PSA2) and pseudostria 3 (PSA3) are also introduced for the stria that develop when the

metaflexus, mesoflexus and hypoflexus, respectively, break through on the lingual side of the upper cheek teeth. The parastria (the cement-filled paraflexus seen from labial view), is not the same stria seen on the buccal (lingual) side of the tooth (e.g., P4, Figure 1) when the hypoflexus is complete (breaks through buccal enamel border). It does not represent a fusion of the paraflexus and hypoflexus. Instead, a new stria forms, named here PSA3. PSA2 replaces Shotwell's (1955) medistria.

New *Dipoides wilsoni* material (Figure 2) collected from the Meade Basin of southwestern Kansas was used in conjunction with previously published descriptions and measurements of this species (Hibbard, 1949, 1953) for detailed comparison with the Pipe Creek specimens. The new specimens are as follows: Saw Rock Canyon 1 (SRC1): FHSM 18071, LP4; FHSM 18072, LM1 or M2. Fallen Angel B (FAB): FHSM 18019, LM1 or M2; FHSM 18020, Rm3; FHSM 18021, Rp4; FHSM 18022, RP4; FHSM 18024, part R mandible with p4-m2. FHSM 18020 fits perfectly into the alveolus for m3 in FHSM 18024 (Figure 3) and was probably dislodged during excavation. SRC1 lies at the same stratigraphic level at the base of Saw Rock Canyon, Seward County, as Hibbard's (1949) original Saw Rock Canyon quarry (SRC), from which *D. wilsoni* was described. FAB is located in a small, unnamed canyon about 0.25 km south of Saw Rock Canyon. FAB lies directly beneath the Bishop gravel, an informal unit capping the rim of both the unnamed canyon and Saw Rock Canyon. Consequently, FAB is younger than SRC1 and SRC. Based on their rodent assemblages and the absence of *Teleoceras*, SRC, SRC1 and FAB are considered as early Blancan, probably slightly younger than Pipe Creek (Martin et al., 2008).

## AGE OF THE PIPE CREEK SINKHOLE

Lindsay et al. (2002) established the Hemphillian-Blancan North American Land Mammal (NALMA) boundary at 4.9-5.0 Ma based on a combination of radioisotopic, paleomagnetic and faunal data derived from the Panaca Formation in Nevada. A critical faunal element of the earliest Blancan horizon was the presence of the archaic arvicolid rodent *Ophiomys panacaensis* (originally referred to *Mimomys*), and the authors concluded that this record represented an approximate first appearance of the genus in North America. In the Panaca area, the rhinoceros *Teleoceras* was recovered only from earlier late Hemphillian sediments. Both *Teleoceras* and archaic arvicolid rodents have been reported from Pipe Creek (Farlow et al., 2001; Martin et al., 2002). The arvicolids include species only known from Pipe Creek, *Ogmodontomys pipecreekensis* and *Pliophenacomys koenigswaldi*. *Ogmodontomys*, restricted to early and middle Pliocene sediments of the Central Great Plains (Martin, 2008), is closely related to

TABLE 1. Measurements of the lower dentition in North American *Dipoides*. Mean, number of specimens and observed range presented for each sample. FAB = Fallen Angel B. Capital letters indicate measurement source: A = Korth (1998), B = Wilson (1934), C = Stirton (1935), D = Hibbard (1953), E = Martin (2008), F = Shotwell (1970), G = this study. # = calculated from illustration; \* = m1 or m2. L = length, W = width.

	<i>D. tanneri</i> A	<i>D. stirtoni</i> B	<i>D. williamsi</i> C	<i>D. wilsoni</i> D	<i>D. smithi</i> E	<i>D. vallicula</i> F	FAB G
Lp4	7.03 (9) (6.48-7.86)	6.4 (19)	5.3 (1)	#6.2 (2) (5.8-6.7)	5.99 (15) (4.65-7.20)	5.1 (4) (4.9-5.3)	6.72 (2) (6.42-7.01)
Wp4	3.92 (8) (3.49-4.55)	4.3 (19)	3.4 (1)	--	4.83 (15) (4.25-5.70)	3.5 (4) (3.3-3.8)	4.91(2) (4.75-5.07)
Lm1	4.34 (3) (4.14-4.59)				5.25 (11) (4.35-5.75)	*3.5 (7) (3.3-3.9)	5.02 (1)
Wm1	4.92 (3) (4.80-5.09)				4.77 (11) (4.30-5.30)	*3.8 (7) (3.2-4.2)	5.00 (1)
Lm2	3.82 (3) (3.40-4.25)				5.32 (11) (4.55-5.30)	—	5.49 (1)
Wm2	4.68 (3) (4.39-5.01)				4.79 (11) (4.20-5.30)	—	4.53 (1)
Lm3	--				4.93 (4) (4.20-5.50)	2.9 (1)	4.39 (1)
Wm3	--				4.25 (4) (3.70-4.60)	3.2 (1)	3.89 (1)

*Ophiomys* and either evolved from an early species of *Ophiomys* like *O. panacaensis* or represents a separate early Pliocene immigration from Asia across Beringia. *Pliophenacomys koenigswaldi* is the earliest *Pliophenacomys* and therefore also the earliest member of the North American endemic arvicolid subfamily, the Pliophenacomyinae. *Pliophenacomys* likely originated from *Protopliophenacomys* of the late Hemphillian Santee local fauna (l.f.) from Nebraska (Martin et al., 2002). The Santee l.f. appears to lie below a tuff that has been dated at 5.0 Ma (Voorhies, 1990). Based on the combined presence of *Teleoceras* and the arvicolids, the Pipe Creek biota is considered to have been deposited during the early Blancan, probably close to the Hemphillian-Blancan boundary.

#### STSTEMATIC PALEONTOLOGY

Order Rodentia Bowditch, 1821  
 Family Castoridae Hemprich, 1820  
 Subfamily Castoroidinae Allen, 1877  
 Tribe Castoroidini Allen, 1877  
*Dipoides* Jager, 1835  
*Dipoides* sp.

**Referred Specimens**—INSM 71.3.144.3016, LP4; INSM 71.3.144.3017, RP4

**Locality and Horizon**—Pipe Creek Sinkhole, Grant Co., Indiana. Early Blancan. Both specimens were

collected in situ, from Zone A of the southwest quadrant (Farlow et al., 2010a).

**Description of Teeth**—INSM 71.3.144.3016, RP4 (Figure 2A). The tooth is rootless, from an adult individual. Loph 1 has parallel sides and the enamel is undifferentiated (equal thickness on both anterior and posterior edges). A hypoflexus extends across the tooth and despite a hair-thin layer of enamel connecting loph 1 and loph 2 along the labial edge at the top of the tooth, a full PSA 3 runs from the occlusal surface to the base of the crown. The anterior and posterior enamel bands of loph 2 are undifferentiated and curve posteriorly. A thin enamel band runs along the lingual surface connecting loph 2 and 3, but the internal and external enamel bands are in contact and dentine is absent between them. A thick internal enamel band, representing the lingual termination of the mesoflexus, runs perpendicular to the posterior band of loph 2 and the anterior enamel band of loph 3. Part of the thin enamel band on the posterior border of loph 3 is sheared off near the occlusal surface, but its absence reduces the tooth length by only about 0.10 mm. Loph 3 is bulb-shaped, with the narrow end on the lingual side. Although the enamel is very thin opposite the mesoflexus, PSA 2 is absent.

INSM 71.3.144.3017, RP4 (Figure 2B). The tooth is rootless, from an adult individual. The long and horizontal loph 1 with parallel enamel borders identifies this tooth also as a P4, despite some morphological

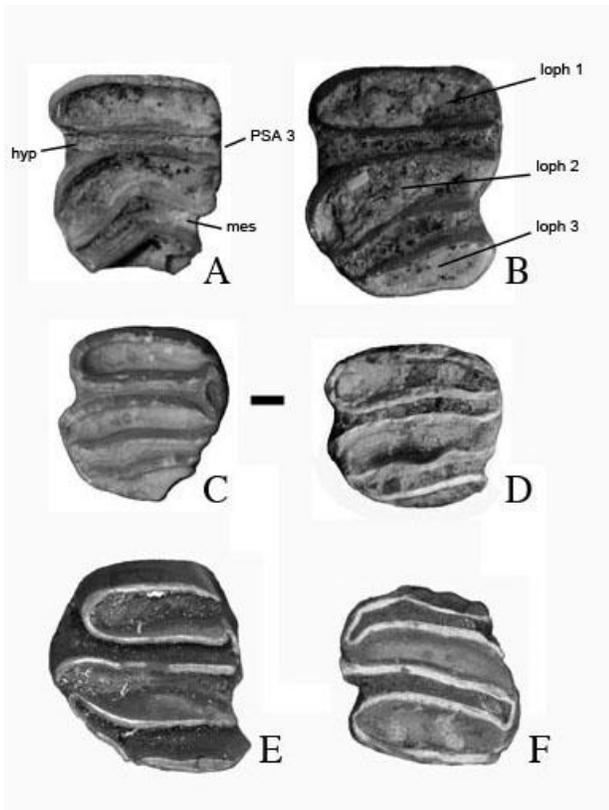


FIGURE 2. Upper cheek teeth of *Dipoides* from the central United States. *Dipoides* sp.: A, INSM 71.3.144.3016, RP4, Pipe Creek Sinkhole; B, INSM 71.3.144.3017, LP4 (reversed) Pipe Creek Sinkhole. *Dipoides wilsoni*: C, FHSM 18021, RP4, Fallen Angel B; D, FHSM 18019, LM1 or M2, Fallen Angel B; E, FHSM 18071, LP4, Saw Rock Canyon1; F, FHSM 18072 RM1 or M2, Saw Rock Canyon 1. Scale bar = 1.0 mm. See Fig. 1 for dental abbreviations.

differences from INSM 71.3.144.3016. 3017 is reversed in Figure 2 to allow better comparison with 3016. The hypoflexus terminates broadly on the labial tooth border, and a thin enamel layer is variably developed over a distinct PSA 3 that runs the full height of the tooth crown. That is, it appears both the internal and external enamel borders of the hypoflexus termination have been dramatically thinned, allowing the cementum to show through down the tooth side; PSA 3 in the making. Enamel borders of loph 2 are undifferentiated. The posterior enamel border of loph 2 is convex anteriorly, but does not display the same distinct anterior inflection as in 3016. Loph 3 curves posteriorly on the lingual side, producing a basic S-shape to the tooth. Enamel is thin at the lingual termination of the mesoflexus, but PSA 2 is not developed. Loph 3 is bulbous, expanded towards the labial border. The posterior enamel border of loph 3 is thinner than the anterior border.

**Comments and comparisons**—The two P4s from Pipe Creek have substantially longer occlusal surfaces

than those of comparable teeth of *D. wilsoni* from the Meade Basin of Kansas (Table 2). Tooth length is generally correlated with body size (mass) in rodents (Martin, 1990), and we can tentatively conclude that the Pipe Creek beaver was near the largest size among the various late Neogene *Dipoides* species.

The P4s of the Pipe Creek *Dipoides* are proportionally longer than those of *D. wilsoni*, as can be seen in Table 2 and by comparison to P4s from SRC1 and FAB in Figure 2. Loph 1 is distinctly shorter than loph 2 in *D. wilsoni* (Figure 2C, E), whereas loph 1 is approximately the same width as loph 2 in the Pipe Creek P4s. The mesoflexus in the Pipe Creek P4s is longer and more curved posteriorly than in *D. wilsoni*. The hypoflexus of FAB 18022 is incomplete, but associated P4s of *D. wilsoni* in a single palate from Saw Rock Canyon (Hibbard, 1949, 1953) have a complete hypoflexus. The P4 morphology of the Pipe Creek specimens is sufficiently different from that of *D. wilsoni* that it is unlikely the Pipe Creek P4s are from the latter species; they more closely resemble the P4s of *D. smithi* and *D. stirtoni* (those without the paraflexus and metaflexus) illustrated by Shotwell (1955).

Shotwell (1955) constructed his own hypsodonty index using p4s and P4s, but I preferred to utilize a more standard approach, as noted above, that simply divides crown height by occlusal surface length. If we make this calculation for mean P4 data from Shotwell's (1955) Table 2,  $H = 3.57$  for *D. stirtoni* and 3.30 for *D. smithi*. A single P4 of *D. wilsoni* from FAB (FHSM 18022) has  $H = 3.37$ .  $H = 2.41$  and 2.46 for the two Pipe Creek P4s.

## DISCUSSION

Until a revision of the North American late Neogene *Dipoides* has been completed there is not much more that can be concluded about the small Pipe Creek beaver. As noted in the Introduction, we do not yet have an adequate understanding of dental development in *Dipoides* to be able to partition ontogenetic and evolutionary features. In particular, the ability of *Dipoides* teeth to increase tremendously in size during development makes it essential that investigators compare teeth at the same ontogenetic stage, or only fully adult teeth. In addition to size, it is also clear that more underived patterns are expressed in juvenile teeth than in adult teeth. Loph (ids) that may connect early in development often separate later as pseudostriae (ids) appear. It is natural to consider the S-shape pattern of adult *Dipoides* molars as the derived condition relative to the ancestral adult pattern in some *D. tanneri* and *D. stirtoni* teeth, in which additional striae(ids) are retained longer during development. However, as noted by Stirton (1935), there is a number of late Neogene Old World *Dipoides* species, such as *D. sigmodus* Gervais, 1849 and *D. major* Schlosser, 1903 with dental patterns

TABLE 2. Measurements of the upper dentition in North American *Dipoides*. \* = M1 or M2. FAB = Fallen Angel B, SRC1 = Saw Rock Canyon 1. Capital letters indicate measurement source: A = Korth (1998), B = Wilson (1934), C = Hibbard (1949, 1953), D = Martin (2008), E = Shotwell (1970), F = this study. L = length, W = width.

	<i>D. tanneri</i> A	<i>D. stirtoni</i> B	<i>D. wilsoni</i> C	<i>D. smithi</i> D	<i>D. vallicula</i> E	FAB F	SRC1 F	Pipe Creek F
LP4	4.47 (11) (3.92-5.01)	4.7 (5)	4.9 (2) (4.8-5.0)	5.30(10) (4.25-6.5)	3.45 (2) (3.2-3.7)		4.82 (1)	5.76 (2) (5.50-6.02)
WP4	5.22 (8) (3.49-4.55)	5.5 (5)	5.5 (2) (4.5-6.3)	4.96 (10) (3.75-5.40)	4.1 (2) (3.7-4.5)		4.77 (1)	4.73 (2) (4.23-5.23)
LM1	3.86 (2) (3.81-3.90)		4.85 (1)	*4.62 (13) (3.80-5.30)	*3.1 (4) (2.9-3.3)	*4.61 (1)	*4.60 (1)	
WM1	4.87 (2) (4.58-5.15)		4.40 (1)	4.71 (13) (4.00-5.50)	*3.55 (4) (3.1-4.2)	*4.30 (1)	*4.08 (1)	
LM2	3.84 (2) (3.80-3.87)		5.0 (1)					
WM2	5.10 (2) (4.99-5.20)		4.15 (1)					
LM3	4.37 (2) (4.25-4.49)		4.90 (1)	4.64 (6) (4.30-5.10)				
WM3	4.11 (2) (3.93-4.29)		3.90 (1)	3.82 (6) (3.70-4.00)				

similar to North American *Dipoides*, raising the possibility that, instead of a seemingly sensible endemic radiation, North American *Dipoides* could be, as are the arvicolid rodents, the result of a number of separate dispersals across Beringia from the Old World. Nevertheless, the two Pipe Creek P4s are relatively advanced in occlusal pattern, as dentine channels do not connect lophs 2 and 3 as we see commonly in *D. stirtoni*, *D. vallicula* and *D. smithi*. Enamel borders of the lophs on the Pipe Creek specimens demonstrate undifferentiated enamel, whereas the enamel is differentiated into thick anterior and thin posterior bands in *D. smithi* (Martin, 2008). However, this derived occlusal form appears to be coupled with relatively low crown height on P4 in the Pipe Creek beaver. Additional quantitative studies of hypsodonty will be necessary to determine if this combination of features defines a new species or can be duplicated among existing museum samples of known *Dipoides* species. One of the primary characters of *Dipoides williamsi* from White Cone, Arizona provided by Stirton (1936, p. 279) was “extreme hypsodont cheek-teeth,” but H = 2.86 (16.0/5.6 mm) for the single p4 measured, which differs little from H = 2.49 (16.2/5.3 mm) for a p4 of *D. wilsoni* reported by Hibbard (1953). Mean H for the two FAB p4s is 2.14. All these p4 hypsodonty values are low when compared with H in the P4s of *D. stirtoni* and *D. smithi*. Is there a systematic difference in hypsodonty between the upper and lower cheekteeth, as seems to be the case with preliminary data for *D. wilsoni*, or are the current values

part of a wider spectrum that will be evidenced with larger sample sizes?

Anterior enamel edges of m1-m2 on the holotype of *D. williamsi* are heavily worn, giving the impression (noted by Stirton, 1936) that the anterior borders of m1-m2 are narrower than the posterior borders. This difference was used by Martin (2008) to help identify some small *Dipoides* from late Hemphillian sites in Oregon, but it may be more a function of wear than a definitive character. Other than this feature, there is little to separate *D. williamsi* from at least *D. wilsoni*.

Martin (2008) also argued that size serves to distinguish two groups of Hemphillian and Blancan *Dipoides*, with *D. stirtoni* (large) and *D. vallicula* (small) retaining more ancestral features (such as parastriae and enamel atolls) into adulthood and later species such as *D. smithi* (large) and both *D. wilsoni* and *D. williamsi* (small) that have simplified the molars into the S-pattern. He suggested (2008, p. 163) “Perhaps *D. smithi* evolved from *D. stirtoni* and *D. wilsoni* and *D. williamsi* were derived from *D. vallicula*.” Size certainly can be important, but it can also be ephemeral, related to environmental conditions. The larger size of the Pipe Creek specimens may, for example, be the result of a Bergmann’s response to the northern environment in Indiana during Pipe Creek time. As Martin (2008) further notes, most *D. vallicula* p4s retain a parastriid; however, so does the FAB *D. wilsoni*. We need a careful phylogenetic analysis to ferret out relationships to a finer degree.

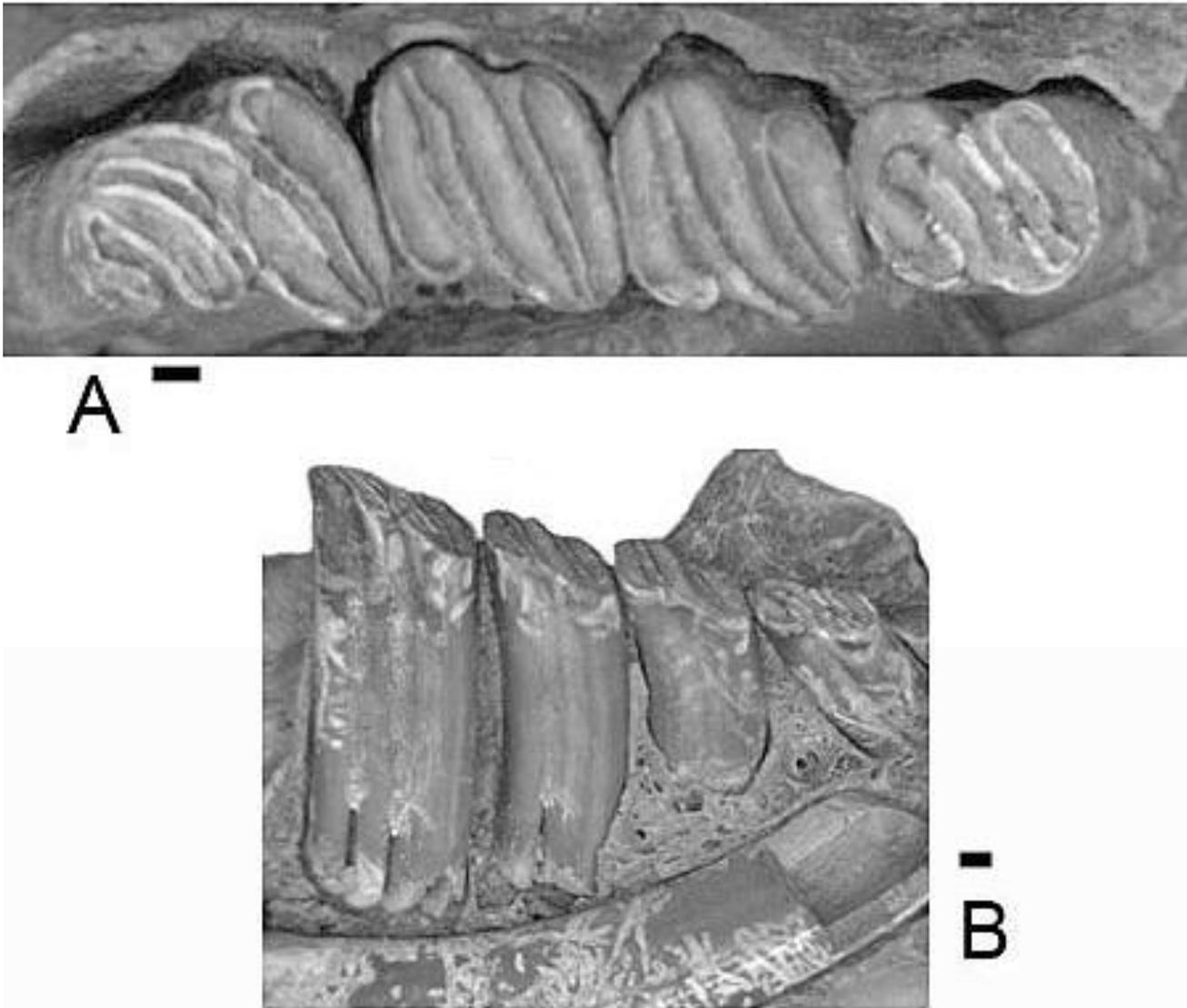


FIGURE 3. Lower dentition of *Dipoides wilsoni* from Fallen Angel B, Seward County, Kansas. The partial mandible, incisor, and p4-m2 are catalogued as FHSM 18024; the m3 is catalogued separately as FHSM 18020. Notice difference in crown height of the lower molars, further indicating that comparisons of hypsodonty must be made with the same teeth. Scale bars = 1.0 mm.

In conclusion, the Pipe Creek *Dipoides* P4s represent some of the largest individual *Dipoides* among those known from the late Neogene. The teeth are relatively advanced in that lophs 2 and 3 are not connected by dentine channels. The P4 has a long occlusal surface relative to its crown height, resulting in a hypsodonty index lower than P4s of *D. stirtoni*, *D. smithi* and *D. wilsoni*. These features are not enough to either allocate the two teeth to a known species or to name a new species, and they are identified here as *Dipoides* sp.

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