

A NEW LATE NEOGENE GROUND SQUIRREL (RODENTIA, SCIURIDAE) FROM THE PIPE CREEK SINKHOLE BIOTA, INDIANA

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ABSTRACT. The Pipe Creek Sinkhole of eastern Indiana has yielded a diverse assemblage of late Neogene plants and vertebrates, documenting a mix of local habitats including both aquatic and upland open habitat. It represents one of few late Neogene fossil assemblages from the interior of eastern North America. A new species of ground squirrel is described from this fossil assemblage based on a partial dentary with all cheek teeth and numerous isolated teeth. This moderately-sized ground squirrel exhibits generally plesiomorphic, low-crowned cheek teeth that were narrow across their trigonids. It also has a p4 that uniquely lacks a buccally-directed hypoconid. The ground squirrel is tentatively assigned to the extant genus *Ictidomys* Allen, 1877 and represents the sole Neogene ground squirrel known only from eastern North America. The presence of this new ground squirrel in the Pipe Creek Sinkhole biota suggests that the late Neogene diversification of ground squirrels, well documented in the American West and on the Great Plains, may have extended into eastern North America and confirms the presence of open habitat within the sampling area of the fossil assemblage.

Keywords: Sciuridae, *Ictidomys*, new species, Neogene, vertebrate paleontology, ground squirrel

INTRODUCTION

The Pipe Creek Sinkhole (PCS) biota has yielded a rich assemblage of fossil plants and vertebrates from eastern Indiana, with fossils recovered from unconsolidated sediments in a buried sinkhole that was exposed during limestone quarrying (Farlow et al. 2001; Farlow et al. 2010). Although many of the PCS fossils were recovered from a spoil pile of sediment removed from the sinkhole by quarriers, subsequent study of the remaining *in situ* sediment indicated that nearly all of the fossils initially came from a localized, 2-m-thick layer of dark-colored sediment interpreted to have formed in a stagnant sinkhole pond, an interpretation supported by the abundance of fossils such as frogs and pond turtles that represent aquatic communities (Farlow et al. 2001; Shunk et al. 2009; Farlow et al. 2010).

Even though aquatic forms were numerically abundant, the PCS site also preserved plants and vertebrates from upland terrestrial habitats (Farlow et al. 2001; Farlow et al. 2010). Upland regions perhaps supported open, pine-hickory

woodland with little grass and occasional fires, an interpretation suggested by pollen evidence and the presence of carbonized wood (Shunk et al. 2009; Ochoa et al. 2016). The occurrence of one or more species of extinct land tortoise (*Hesperotestudo* Williams, 1950) probably reflected a warm local climate (Farlow et al. 2001).

The PCS fossil assemblage likely represented a roughly contemporaneous (although ecologically mixed) biota, based on the apparent restriction of PCS fossils to a single layer of pond sediment and the presence of a biostratigraphically coherent mammal fauna (Farlow et al. 2001; Prothero & Sheets 2013). However, the duration of fossil accumulation is not known. Initially, the PCS assemblage was interpreted to indicate a latest Hemphillian North American Land Mammal Age based on biostratigraphically indicative taxa, such as the rhinoceros *Teleoceras* Hatcher, 1894 and dentally-plesiomorphic members of several cricetid rodent lineages (Martin et al. 2002). However, *Teleoceras* was subsequently documented in the early Blancan (Gustafson 2012), and more recent analyses of arvicolid rodents pointed to an early Blancan North American Land Mammal Age (Martin 2010; Martin et al. 2018). In either case, the PCS assemblage

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represents the late Neogene age in the global geochronology (Tedford et al. 2004). As such, the PCS assemblage is one of few Neogene (or even Cenozoic) vertebrate assemblages from the interior of eastern North America in contrast to the much richer record from the American West, Great Plains, and coastal regions of North America (Farlow et al. 2001; Shunk et al. 2009; Farlow et al. 2010). The nearest well-studied vertebrate fossil sequence with faunas of approximately equivalent age is from the Meade Basin, southwestern Kansas (Martin et al. 2002), about 1300 km to the west-southwest.

An initial tabulation of PCS fossil taxa listed nearly 40 vertebrate taxa and included eight rodents (Table 1 in Farlow et al. 2001). Rodents were represented by the beaver *Dipoides* Jäger, 1835 (Martin 2014), a pocket gopher (Geomysidae), four new species of cricetids (Cricetidae), and one or two species of small-sized ground squirrels (Sciuridae) (Martin et al. 2002). Ground squirrel identifications were based on isolated teeth, with most teeth tentatively referred to *Spermophilus howelli* (Hibbard 1941b), a species initially described from the mid-Blancan Rexroad 3 fauna (Hibbard 1941b) and subsequently identified in the earlier Fox Canyon fauna (Hibbard 1950), both from the Meade Basin sequence of Kansas. In addition to fossils assigned to *S. howelli*, a single m3 from PCS with distinctive morphology was assigned to an unknown species in *Spermophilus* Cuvier, 1825 and interpreted as probably representing a second and perhaps new species of small-sized ground squirrel (Martin et al. 2002).

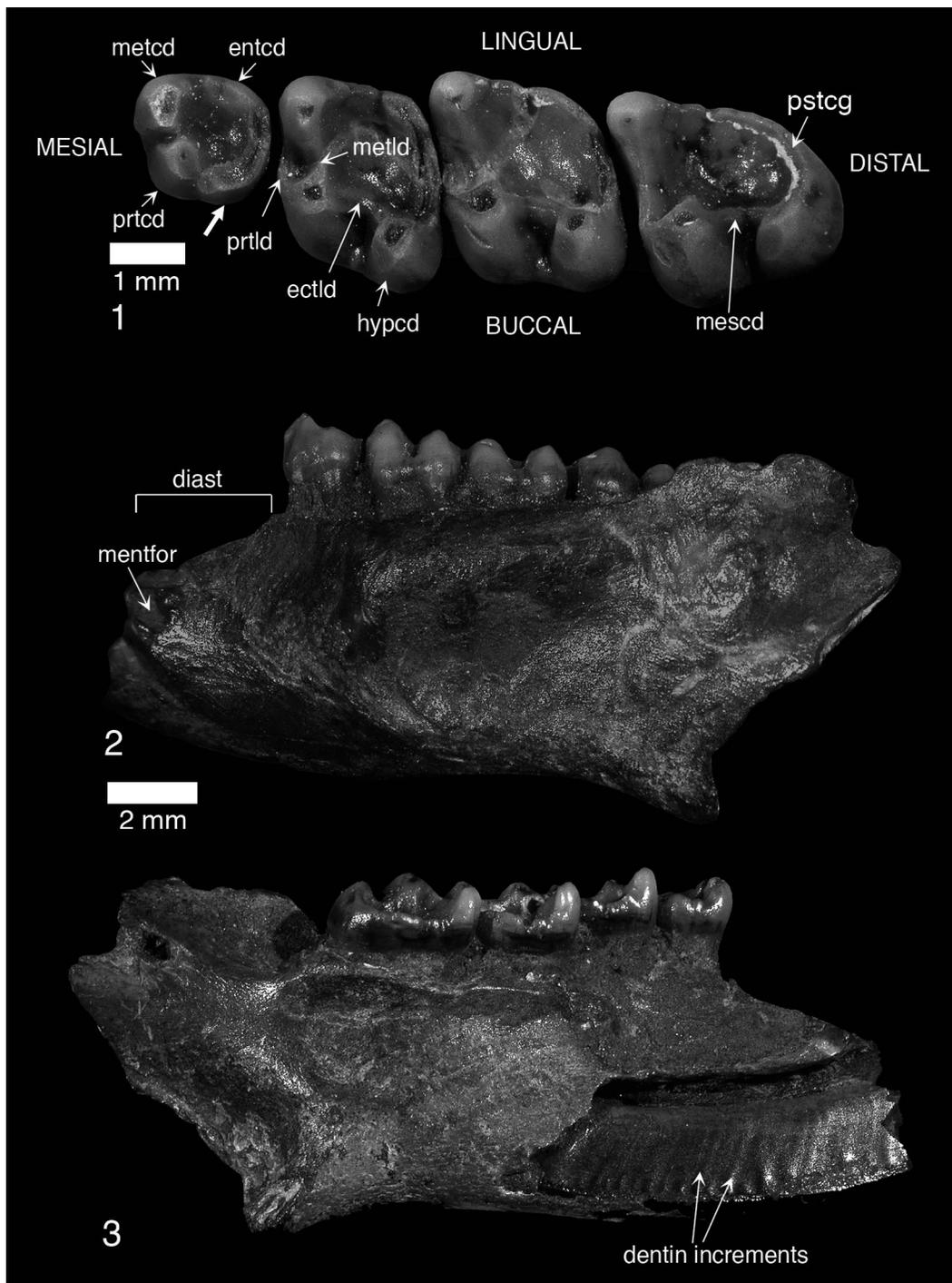
Here, we provide an updated description of PCS ground squirrel fossils based on additional and more complete material, including a dentary fragment with p4–m3. A revised generic taxonomy is also incorporated that splits the paraphyletic *Spermophilus* into multiple, presumably monophyletic genera (Helgen et al. 2009), and recent taxonomic revision of *S. howelli* (Goodwin & Martin 2017) that tentatively assigns this species to the genus *Ictidomys* Allen, 1877 and treats it as a junior synonym of *Ictidomys? meadensis* (Hibbard 1941a), described from the earliest Pleistocene Borchers local fauna. Based on this updated analysis, we tentatively attribute all PCS ground squirrel fossils to a single, morphologically variable lineage, which is described as a new species.

METHODS AND MATERIALS

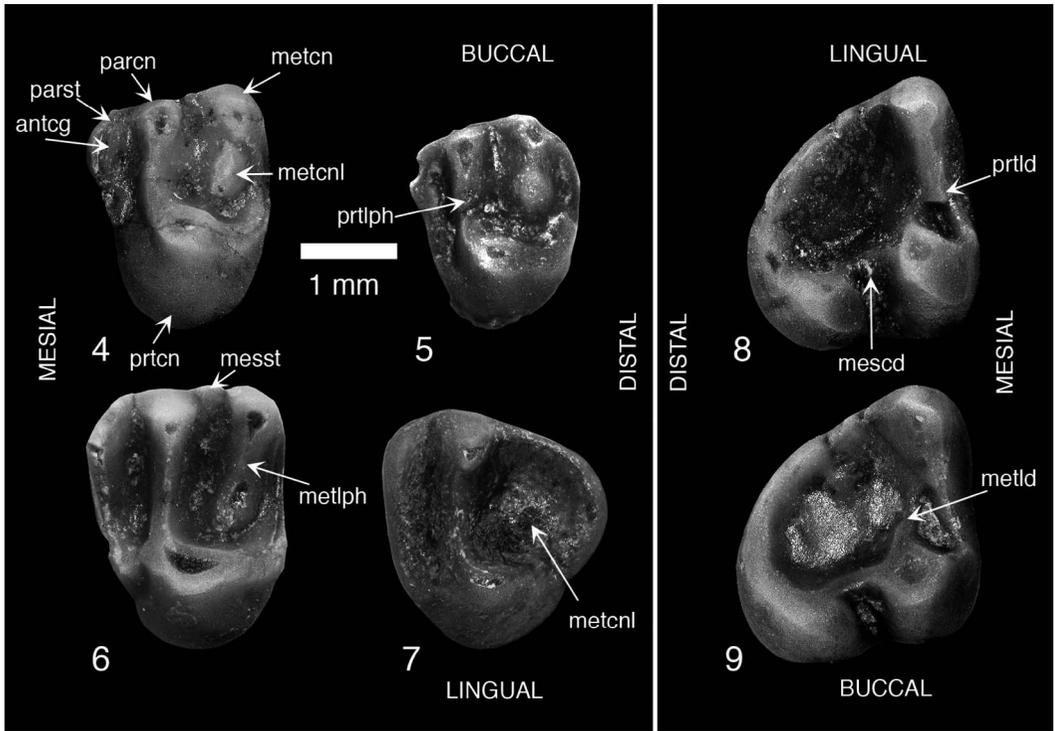
Examination and identification of fossil squirrels were done by one of us (HTG). PCS fossils were photographed digitally in multiple views along with a scale through a Leica MZ8 stereo microscope, and digital photographs were stored in a FileMaker Pro database (www.filemaker.com). Images were used for morphological description and to compare with a large series of fossil and modern squirrels, using databases of modern and fossil ground-squirrel dental images described elsewhere (Goodwin 2009; Goodwin & Martin 2017). Scaled photographs were subsequently measured digitally using GraphicConverter (<https://www.lemkesoft.de/en/products/graphicconverter/>).

PCS fossil teeth that were figured in the paper were lightly dusted with ammonium chloride to enhance photographic contrast, by placing the fossil in the column of smoke above a heated test-tube of ammonium chloride enclosed within a fume hood (method 1 outlined at: <https://wikis.utexas.edu/display/specify6/NPL+Photography+Ammonium+Chloride+whitening>). Dusted fossils were photographed at multiple focal planes, and the multiple images were focus-stacked in Photoshop CS 5 (<http://www.adobe.com/products/photoshop.html>) to improve depth of field for visualization.

Qualitative and morphometric comparisons were made with modern and fossil specimens assigned to genera with generally plesiomorphic cheek teeth (p4–m2 relatively narrow across the trigonid compared to tooth length, low to moderately low crown height (Goodwin 2009)). Measured dental dimensions were lengths of all cheek teeth; widths of upper cheek teeth from the buccal margin of the paracone to the lingual margin of the protocone; trigonid widths of lower teeth from the lingual margin of the metaconid to the buccal margin of the protoconid; and, for p4, talonid width from the lingual margin of the entoconid to the buccal margin of the hypoconid. These dimension were figured by Goodwin & Martin (2017, Fig. 3). To aid the reader in interpretation of dentary and dental images, we label selected features of the dentary as well as at least one example of each dental structure used in descriptions (Figs. 1–9). For lower teeth, cuspids and lophids were labeled (Figs. 1, 8–9); and for upper teeth, cusps and lophs were labeled (Figs. 4–7). We also labeled directional terms that were used when describing dentition (mesial to distal



(Plate 1) Figures 1–3.—Holotype of *Ictidomys? pipecreekensis* (INSM 71.3.144.4049) from Pipe Creek Sinkhole, Indiana; a left dentary fragment preserving a partial incisor and complete p4 through m3. 1. Occlusal (chewing surface) view of cheek teeth; heavy arrow points to distinctive lack of buccally expanded hypoconid on p4. Directional terms for teeth given in all caps (mesial, distal, lingual, buccal). 2. Lateral view of dentary, anterior to the left; 3. Medial view of dentary, anterior to the right; dorsal is toward the top in both 2–3. Scale beneath 2 applies also to 3. Labeled cusplids, lophids, and features of the dentary are: diast = diastema; ectld = ectolophid; entcd = entoconid; hypcd = hypoconid; mentfor = mental foramen; mescd = mesoconid; metcd = metaconid; metld = metalophid; prtcd = protoconid; prtld = protolophid; pstcg = posterior cingulum.



(Plate 2) Figures 4–9.—Occlusal (chewing surface) views of isolated teeth of *Ictidomys? pipecreekensis* from Pipe Creek Sinkhole, Indiana; scale applies to all teeth. 4–7. Upper cheek teeth; all displayed as left teeth (4 and 7 reversed to facilitate comparisons). 4–5. Right (reversed) and left P4 (INSM 71.3.144.83 and 71.3.144.31, respectively); the tooth in Fig. 5 has been eroded chemically. 6. Left M1 or M2 (INSM 71.3.144.4046); 7. Right (reversed) M3 (INSM 71.3.144.86). 8–9. Right m3s (INSM 71.3.144.19 and 71.3.144.4045, respectively). Directional terms in all caps; those left of vertical white line apply to upper teeth (Figs. 4–7), those right of white line apply to lower teeth (Figs. 8–9). Labeled features: antcg = anterior cingulum; mescd = mesoconid; messt = mesostyle; metcn = metacone; metcnl = metaconule; metld = metalophid; metlph = metaloph; parcn = paracone; parst = parastyle; prtcn = protocone; prtld = protolophid; prtph = protoloph.

[anterior to posterior], and lingual to buccal [toward the tongue and cheek] (Figs. 1, 4–7, 8–9).

A lower jaw with p4–m3 from Pipe Creek was compared morphometrically with modern and fossil reference specimens using both bivariate and multivariate methods. The latter employed principal components 1 and 2 derived from a principal component analysis (PCA) of \log_{10} -transformed measures of length and trigonid widths for each of p4–m3, and talonid width of p4. PCA reduces multiple, correlated variables to few, orthogonal (uncorrelated) variables and in morphometric comparisons typically differentiates size (PC 1) from aspects of shape (PC 2 and higher). Statistical and graphical analyses were done with SPSS (<https://www.ibm.com/analytics/us/en/technology/spss/>).

All fossil specimens utilized in this study are catalogued in the collection of the Indiana State Museum (INSM). Abbreviations used in subsequent tooth identifications include: L, R = side (left, right); P, p = upper and lower premolars (followed by specific numbered premolar); M, m = upper and lower molars (followed by specific numbered molar).

SYSTEMATIC DESCRIPTION

Family Sciuridae Fischer de Waldheim, 1817

Subfamily Xerinae Osborn, 1910

Tribe Marmotini Pocock, 1923

Ictidomys Allen, 1877

Ictidomys? pipecreekensis sp. nov., Figs. 1–9

2002 *Spermophilus* cf. *howelli* Martin et al. (2002), p. 138.

2002 *Spermophilus* sp. Martin et al. (2002), p. 139, Fig. 2A.

Holotype.—INSM 71.3.144.4049: left dentary fragment preserving a partial incisor, complete p4 through m3.

Type locality.—Pipe Creek Sinkhole, Grant Co., Indiana; collected *in situ* from pit 8, level 1 [2004 collection; see Farlow et al. (2010) for a description of *in situ* sample units].

Referred material (all from Pipe Creek Sinkhole).—2 L P4s (INSM 71.3.144.31, 71.3.144.83), R P4 (INSM 71.3.144.18), 4 L M1 or M2s (INSM 71.3.144.82, 71.3.144.84, 71.3.144.85, 71.3.144.4046), 3 R M1 or M2s (INSM 71.3.144.32, 71.3.144.88, 71.3.144.89), R M3 (INSM 71.3.144.86), 2 R m1 or m2s (INSM 71.3.144.87, 71.3.144.4047), L m3 (INSM 71.3.144.4048), 2 R m3s (INSM 71.3.144.19, 71.3.144.4045)

Diagnosis.—Moderately-sized ground squirrel, similar in size of upper and lower molars to the Mexican ground squirrel *Ictidomys mexicanus* (Erxleben, 1777). Talonid of p4 proportionally narrow compared to trigonid width of molars, particularly of m3. Metaconid of p4 offset mesially compared to protoconid and bears a small swelling at its mesiobuccal margin. The p4 differs from the p4 of all other marmotine ground squirrels in the absence of a buccally-deflected hypoconid.

Description and comparisons.—Dental dimensions of the holotype and all referred specimens are provided (Table 1). The holotype dentary lacks the portion anterior to the mental foramen as well as the coronoid, condyloid, and much of the angular processes; but it preserves a partial incisor and complete cheek-tooth series (Figs. 1–3). The mental foramen is situated well anterior to the plane of the anterior root of p4 (Fig. 2), and the dorsal margin of the diastema of the dentary drops gradually from the p4 alveolus (Figs. 2–3), in both respects resembling typical extant specimens of *Otospermophilus* Brandt, 1844. The incisor displays distinctly incremented dentin (Fig. 3) with increments averaging 0.38 mm in width, similar to average increment widths reported for extant ground squirrels of the genus *Urocitellus* Obolenskij, 1927 (Goodwin et al. 2005).

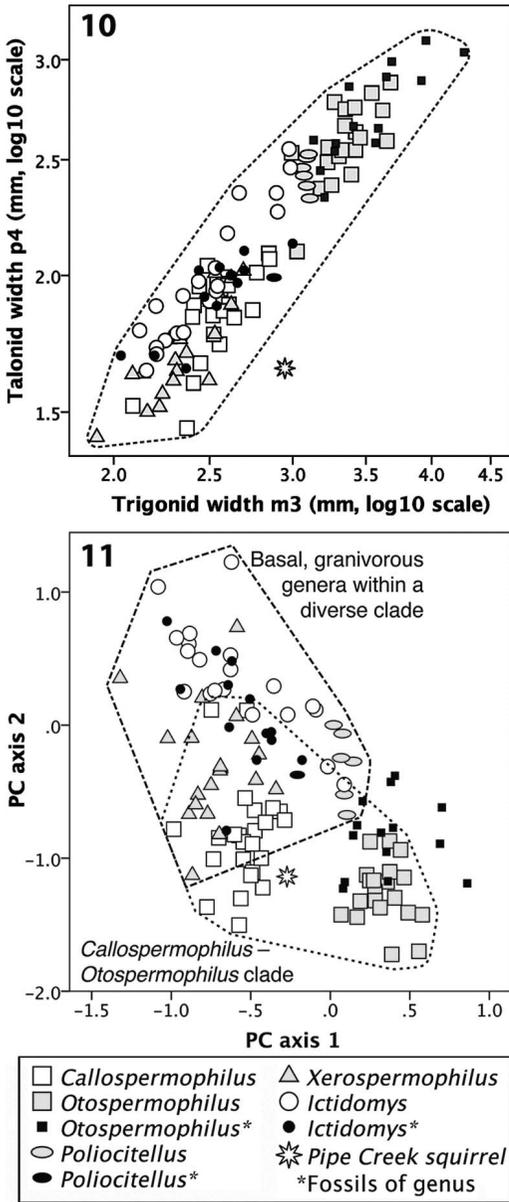
The associated p4–m3 of the holotype documents a unique p4 morphology coupled with m1–m3 morphologies typical for small to moderately-

sized, plesiomorphic ground squirrels. On the p4, a continuous ridge arcs from the entoconid to buccodistal base of the protoconid, and the ridge lacks a buccally-deflected hypoconid (Fig. 1). This morphology is unique among > 700 p4s that were examined for this feature, representing modern or fossil species within 13 extant and at least 4 extinct genera of ground-dwelling squirrels. The metaconid of p4 is offset mesially compared to the protoconid, bears a distinct swelling on its mesial face near the contact with the protoconid, and borders a small trigonid pit that is incompletely closed mesially (Fig. 1). The p4 is low-crowned (protoconid crown height of 1.6 mm; ratio of protoconid height to total length of p4=0.90) and narrower across the trigonid than it is long (TrW/L = 0.92), in both respects reflecting plesiomorphic dental morphology for ground squirrels (Goodwin 2009). Widths across the trigonid and talonid of p4 are equal, unlike most specimens of dentally plesiomorphic lineages, which display greater talonid versus trigonid widths on p4. The relatively narrow talonid of p4 is striking when compared to trigonid widths of associated molars from the same dentary, especially of m3, falling well outside observed variation in a bivariate plot of talonid width of p4 versus trigonid width of m3 across modern and fossil reference specimens (Fig. 10).

It is unlikely that the distinctive p4 is a deciduous p4 (dp4); the dp4 typically bears widely diverging roots, a feature not observed in the fossil. Furthermore, dp4 always displays a buccally directed hypoconid in the specimens we have examined (34 extant specimens representing 10 genera and 28 species; 49 fossil specimens representing at least 6 genera and 8 species). Finally, there is no evidence of a permanent p4 coming into place, as would be expected given the otherwise fully erupted cheek teeth.

The m1 and m2 of the holotype display a well-developed protoconid and metaconid that, together with a complete protolophid and metalophid, bound an elevated trigonid pit. The bounding metalophid is better developed on m1 than on m2 of the holotype, or on one isolated m1 or m2 (INSM 71.3.144.87). The entoconid of m1 and m2 is bounded mesially by a distinct notch and subsumed within the posterior cingulum buccodistally; and both teeth display a prominent, buccally-deflected hypoconid that connects to the protoconid via a prominent ectolophid (Fig. 1).

The m3 of the holotype is likewise typical for moderately-sized, dentally plesiomorphic ground



(Plate 3) Figures 10–11.—Odontometric relationships between the holotype of *Ictidomys? pipecrekensis* and specimens of extant and fossil reference taxa that exhibit similarly plesiomorphic dental morphology. Each plotted point was based on dental measurements of a single dentary. 10. Holotype of the Pipe Creek squirrel exhibits a distinctively narrow talonid on p4 compared to trigonid width of m3, falling outside variation exhibited across specimens representing extant and fossil reference taxa that exhibit similarly plesiomorphic dental morphology. 11. Morphometric position of the Pipe Creek squirrel compared to reference specimens of two marmotine

squirrels in most respects: it bears a prominent protoconid and metaconid connected by a continuous protolophid, an incomplete metalophid that does not close the trigonid pit distally, a distally expanded posterior cingulum that arcs from a poorly-defined entoconid to a prominent, mesiobuccally deflected hypoconid, and a distinct ectolophid connecting the hypoconid with protoconid (Fig. 1). The m3 of the holotype bears a small swelling on the ectolophid, adjacent to the protoconid, that may represent a rudimentary mesoconid (Fig. 1), a feature likewise exhibited by one isolated m3 (INSM 71.3.144.19; Fig. 8). Two of three isolated m3s differ from the holotype in exhibiting a complete metalophid that encloses a distinct trigonid pit (INSM 71.3.144.19 and 71.3.144.4045; Figs. 8–9). One of these m3s uniquely displays abrupt, distal expansion of the protolophid at the lingual margin of the trigonid pit (INSM 71.3.144.19; Fig. 8). Of all other m3s examined (modern and fossil), only one specimen of *Otospermophilus rexroadensis* (Hibbard 1941b) from the Blancan Rexroad 3 locality of the Meade Basin, Kansas (UMMP 117829) approached this morphology.

All upper cheek teeth were isolated when recovered, thus no associations among upper teeth can be made. The P4 is subtriangular in shape, bears a metacone that extends further buccally than does the paracone or parastyle, and exhibits a swollen metaconule (Figs. 4–5). On two of three P4s (INSM 71.3.144.18 and 71.3.144.83), the anterior cingulum is restricted to the buccal ½ of the mesial face of the tooth (Fig. 4). A third, somewhat corroded P4 (INSM 71.3.144.31) differs from the other two P4s in greater lingual extension of the anterior cingulum, a pronounced constriction in the protoloph, and lesser relative width compared with length (Fig. 5).

All M1s or M2s are similar morphometrically, display a mesostyle that differs in size across

clades: *Callospermophilus*–*Otospermophilus*, and *Poliocitellus*–*Xerospermophilus*–*Ictidomys*. Axes represent tooth shape (PC 2) and tooth size variables (PC 1) extracted by principal component analysis of log₁₀-transformed measurements of tooth length and width. Envelopes of variation in Fig. 11 correspond to variation across modern reference specimens for each clade; some fossils assigned to *Otospermophilus* fall outside variation exhibited among extant species of the genus.

specimens, and exhibit constriction or interruption of the metaloph between the moderately developed metaconule and the protocone (Fig. 6). A single M3 (INSM 71.3.144.86) is subtriangular in shape and bears the remnant of a low metaconule evident as a circular patch of dentin exposed by wear on the expanded posterior cingulum. This M3 does not display a metaloph (Fig. 7).

Comments.— *Number of ground squirrel species in the PCS sample:* Martin et al. (2002) interpreted the sciurid fossils from PCS as probably representing two species: *Spermophilus* cf. *S. howelli* (most PCS specimens; now *Ictidomys* cf. *Ictidomys?* *meadensis*), and a second, probably undescribed species represented by a single m3 that exhibits a complete trigonid pit bounded mesially by a narrow protolophid that expands abruptly at the lingual terminus of the trigonid pit (Fig. 8), a morphology that is rare in late Neogene fossils as well as modern squirrels. Subsequent discovery of the dentary with associated p4–m3 confirmed the uniqueness of at least one PCS squirrel, but the distinctive features of this dentary are those of the p4; the m3 of the holotype dentary is morphologically typical of dentally plesiomorphic ground squirrels. Thus, the PCS sample includes both distinctive p4 and m3 morphologies, but the two are not associated when preserved on the same dentary. Unfortunately, we cannot assess variability in p4 morphology given a single specimen. However, the sample of m3s indicate two specimens with complete metalophid bounding a distinct trigonid pit (Figs. 8–9), with one m3 displaying an abruptly expanded protolophid lingual to the trigonid pit (Fig. 8), and two additional specimens lacking a complete metalophid (one isolated tooth [INSM 71.3.144.4048] and the holotype; Fig. 1). We also note variation in the sample of P4 specimens (Figs. 4–5), although we caution against over-interpreting these differences given that one distinctive specimen appears to be chemically eroded (Fig. 5).

Although we recognize the possibility that Pipe Creek preserves two or more undescribed species of ground squirrel, each with a different mosaic of plesiomorphic and derived dental morphology, we consider an alternative hypothesis to be more parsimonious with present evidence: that PCS recorded a single morphologically variable ground squirrel population,

with variation perhaps increased by limited time averaging during fossil accumulation. This conservative hypothesis is supported by the similar size across teeth in each tooth class within the PCS sample (Table 1). For example, coefficients of variation for length and trigonid width of m3 (4.3% and 5.5%, respectively; Table 1) fell within the range of coefficients of variation across three extant species of *Ictidomys* (length of m3: 2.6–8.7%; trigonid width of m3: 4.5–6.2%). In addition, the hypothesis of a single species of PCS squirrel is congruent with the observation of considerable morphological variability across specimens in some modern species. For example, specimens of *Otospermophilus variegatus* (Erxleben, 1777) from Texas vary markedly in the degree of development of the metalophid and closure of the trigonid pit on m3.

Generic assignment of PCS ground squirrel: Generic assignment of the PCS ground squirrel is challenging given the conservative dental morphology characteristic of multiple ground squirrel clades that occur or once occurred within or adjacent to the Great Plains. We can exclude *Tamias* Illiger, 1811 based on its small size and complete loph on P4–M2, with the loph lacking developed conules; *Ammospermophilus* Merriam, 1892 based on its small size and typically indistinct entoconid on p4–m2; *Urocitellus* and *Cynomys* Rafinesque, 1817 which both exhibit derived teeth characterized by substantially greater crown height and relative trigonid width; and both *Marmota* Blumenbach, 1779 and the extinct *Paenemarmota* Hibbard & Schultz, 1948, which are much larger in size and exhibit rugose talonid basins on lower cheek teeth (Goodwin 2008, 2009). *Paenemarmota* also exhibits prominently striated incisors, a feature not evident on the PCS squirrel (Goodwin 2008).

However, five extant genera deserve consideration, with each including moderately-sized ground squirrels with plesiomorphic dentition (Goodwin 2009). Two genera represent a clade of western North American squirrels (Fig. 1 in McLean et al. 2018), the primarily montane *Callospermophilus* (Merriam, 1897) (mantled ground squirrels), and the wide-ranging *Otospermophilus* Brandt, 1844 (rock squirrels), with the latter inhabiting shrub- and shrub-steppe habitats of the American West, often in rocky habitats. The other three genera are dentally plesiomorphic members of a diverse

Table 2.—Loadings of original tooth measurements on principal components 1 and 2 (PC 1 and PC 2, respectively) derived from a principal component analysis; and variance explained by these two components. † = Individual measurements (mm) were \log_{10} -transformed prior to principal component analysis.

Variable†	PC 1	PC 2
Length p4	0.985	-0.104
Width trigonid p4	0.956	0.282
Width talonid p4	0.991	0.062
Length m1	0.966	-0.249
Width trigonid m1	0.991	0.088
Length m2	0.975	-0.213
Width trigonid m2	0.995	0.023
Length m3	0.981	0.103
Width trigonid m3	0.995	0.009
Variance explained (%)	96.4	2.4

clade, with all genera represented today on the Great Plains (Fig. 1 in McLean et al. 2018): *Poliocitellus* Howell, 1938 (Franklin's ground squirrel, endemic to tall-grass prairies of the eastern Great Plains), *Xerospermophilus* Merriam, 1892 (pygmy ground squirrels of the western Great Plains and Southwest that occupy a variety of open habitats, including deserts), and *Ictidomys* (lined ground squirrels that occur widely in open habitats, from southern Canada to Mexico, and from Wyoming to Michigan) (Thorington et al. 2012).

Morphometrically, the holotype of *I. pipe-creekensis* fell between smaller-bodied *Callospermophilus* and larger-bodied *Otospermophilus* on principal component 1 (PC 1; Fig. 11). PC 1 represents tooth size [loadings of all original variables on PC 1 were high (> 0.95) and positive] and accounted for 96.4% of variance across specimens (Table 2). In contrast, the holotype resembled members of *Ictidomys* and *Xerospermophilus* in tooth size (PC 1), but exhibited a more negative score on principal component 2 (PC 2; Fig. 11). PC2 represents a complex shape variable. Loadings of original variables on PC2 show that high, positive values reflect relatively great trigonid widths of p4 and m1 and elongate m3, whereas negative values on PC2 represent narrower trigonid widths and thus relatively longer p4–m2 (Table 2).

The PCS squirrel most closely resembled *Callospermophilus* in the morphometric plot

(Fig. 11). However, *Callospermophilus* has not previously been reported from the Great Plains as a fossil, and members of *Callospermophilus* differ morphologically from the PCS squirrel in that the metaloph of P4 through M2 are usually complete and the metalophid of m3 does not enclose a distinct trigonid pit. Thus, we conclude that the PCS squirrel does not represent *Callospermophilus*.

The PCS squirrel resembled *Otospermophilus* in its relatively narrow trigonid widths of p4–m1 (negative values on PC 2; Fig. 11), typically small anterior cingulum of P4 restricted to about the buccal one-half of the mesial face of the tooth (Fig. 4), swollen metaconule and interrupted metaloph between the metaconule and protocone of P4 through M2 (Figs. 4–6), common presence of a mesostyle on M1 and M2 (Fig. 6; 5 of 6 PCS specimens, 28 of 43 M1s and M2s of extant *Otospermophilus* examined for the feature), presence of a small metaconule on M3 (Fig. 7, 11 of 23 M3s for extant *Otospermophilus*), variation in development of the metalophid on m1 through m3 with some specimens showing a complete metalophid and enclosed trigonid pit on m3 (Figs. 8–9), and the gradual descent of the dorsal surface of the diastema anterior to p4 (Figs. 2–3). Furthermore, *Otospermophilus* has been identified in the late Neogene of the Great Plains (Goodwin & Martin 2017). However, all extant and known Pliocene fossils of *Otospermophilus* are substantially larger in size (Fig. 11).

The PCS squirrel differed from *Poliocitellus franklinii* (Sabine, 1822), a species endemic to the Great Plains and the only species in its genus, in its smaller size (Fig. 11), the presence of a complete metalophid on m1 and m2 of the holotype (Fig. 1) and two referred m3s (Figs. 8–9), a minute mesoconid on the ectolophid of m3 on the holotype (Fig. 1) and one referred specimen (Fig. 8), a gradual drop off of the dorsal margin of the diastema (Figs. 2–3) versus an abrupt drop off in *Poliocitellus*, the interruption of the metaloph between the metaconule and protocone of P4 and M1 or M2 (Figs. 4–6), and the presence of a subtly developed metaconule on M3 (Fig. 7). The PCS squirrel thus cannot be assigned to *Poliocitellus*.

It is difficult to reliably distinguish ground squirrels of the genus *Xerospermophilus* from those of *Ictidomys* on dental evidence, because both retain relatively plesiomorphic tooth

morphology (Goodwin 2009; Goodwin & Martin 2017). Compared with extant species of *Xerospermophilus*, extant *Ictidomys* typically exhibit proportionally wider p4-m1 and elongate m3 (but with morphological overlap; Fig. 11) and commonly exhibit a mesostyle on M1 and M2 (30%) that is infrequent on teeth of extant *Xerospermophilus* (2%; Goodwin & Martin 2017). The PCS squirrel more closely resembled *Xerospermophilus* in proportionally narrower trigonids of p4-m1 (low score on PC2; Fig. 11), but commonly exhibited a mesostyle on M1-M2 (5 of 6; Fig. 6), more closely resembling *Ictidomys* in this feature. Pliocene fossils from the Meade Basin, Kansas, tentatively assigned to *Ictidomys* (*Ictidomys?* *meadensis*) exhibited a similar mosaic dental morphology (Goodwin & Martin 2017).

Given these observations, we recognize four hypotheses for generic assignment, that the PCS squirrel represents: 1) an extinct clade not previously described, 2) the only known diminutive species within *Otospermophilus*, 3) a divergent species in *Xerospermophilus*, or 4) a dentally plesiomorphic species of *Ictidomys*, a genus widespread across the Great Plains today (assuming that relatively narrow trigonid width of p4-m1 is plesiomorphic within ground squirrels as has been argued (Black 1963; Goodwin 2009)). We tentatively support the fourth hypothesis in alignment with a recent study of ground squirrels from the Meade Basin of Kansas (Goodwin & Martin 2017) but recognize that further evidence may require revision of our interpretation.

Species assignment of the PCS ground squirrel: Initial assignment of most PCS ground squirrel teeth to the Blancan species *I.?* *meadensis* (formerly *S. howelli*) by Martin et al. (2002) reflected broadly similar dental morphology and morphometrics. However, no specimen of *I.?* *meadensis* that we have examined displayed the unique p4 morphology of *I.?* *pipecreekensis*. In addition, the variation evident in the morphology of m3 of the PCS squirrel was not incorporated in the sample of *I.?* *meadensis* that we have inspected. Two Hemphillian species from the West coast resembled *I.?* *pipecreekensis* in size. However, the p4 in both *Otospermophilus gidleyi* Merriam, Stock & Moody, 1925 (from Oregon) and *Otospermophilus argonautus* Stirton & Goeriz, 1942 (from California) differed from *I.?* *pipecreekensis* in the presence of more robust

lophids and cuspids, including a prominent, buccally deflected hypoconid. Given these distinctive differences with other Hemphillian and Blancan species, we conclude that the PCS squirrel represents a new species.

DISCUSSION

Late Neogene diversification of ground squirrels in North America.—During the Hemphillian and early Blancan North America Land Mammal Ages of the late Neogene, North American marmotines diversified markedly. First appearances have been reported for 21 species of ground squirrels during the Hemphillian and 10 additional species during the early Blancan (Goodwin 2008; this report). These first appearances represented two extinct genera (*Paenemarmota* and *Parapaenemarmota* Martin, 1998) and probably six extant genera: *Tamias*, *Ammospermophilus*, *Otospermophilus*, *Urocitellus*, *Ictidomys*, and *Marmota*.

No Hemphillian or early Blancan records have yet been reported for other extant genera relevant to our study, notably *Callospermophilus*, *Xerospermophilus*, or *Poliocitellus*. It is unclear if the lack of fossils of these clades in the Hemphillian and early Blancan of North America represented their absence at that time or the difficulty of assigning fragmentary fossil material given the conservative dental morphology of many ground squirrels. However, molecular divergence-time estimates suggest that all three missing clades arose during (> 5.0 Ma) or before (> 9 Ma) the Hemphillian Land Mammal Age. These estimates were derived from Bayesian likelihood analysis of cytochrome *b* sequences (Harrison et al. 2003). We note, however, that molecular divergence-time estimates are commonly older than expected based on direct paleontological estimates (for example, Fig. 4 in Kumar & Hedges 1998; Paláez-Campomanes & Martin 2005).

Based on diversity patterns of both fossil (Goodwin 2008) and modern marmotine species (Helgen et al. 2009), speciation within the clade Marmotini in North America was concentrated in the American West and Great Plains. However, the presence of the distinctive *I.?* *pipecreekensis* in Indiana may indicate speciation in the East as well, although we cannot rule out immigration from the Great Plains. We hope that further discoveries will fill in the sparse record of fossil vertebrates from the East, both geographically and stratigraphically, facilitating more refined

understanding of regional evolutionary and biogeographic history of mammals.

Paleoenvironmental and paleoecological implications.—The three extant species of *Ictidomys*, as well as other extant marmotine ground squirrels of the Great Plains [the dentally plesiomorphic *Poliocitellus franklinii* and *Xerospermophilus spilosoma* (Bennett, 1833), and the dentally derived *Cynomys ludovicianus* (Ord, 1815) and *Urocitellus richardsonii* (Sabine, 1822)], occupy open habitat, characteristically grasslands or grassy shrub-dominated habitat (see species accounts in Thorington et al. 2012). Thus, it seems likely that *I.?* *pipecreekensis* likewise occupied an open, grassy habitat. Some extant ground squirrels differ in their specific habitat preferences. For example, *Poliocitellus franklinii* occupies tall-grass prairies whereas *Ictidomys tridecemlineatus* inhabits short-grass habitats (Thorington et al. 2012). We are not able to determine specific habitat requirements (e.g., short- or tall-grass) for *I.?* *pipecreekensis*.

Paleoenvironmental inferences from the presence of *I.?* *pipecreekensis* are broadly congruent with prior reconstructions of upland habitats around PCS: as a savannah-like habitat kept open by periodic fires and the feeding ecology of large herbivores (Farlow et al. 2001; Shunk et al. 2009; Farlow et al. 2010; Ochoa et al. 2016). Pollen evidence supports an open pine-hickory woodland, and both pollen and macrofossil evidence document a variety of herbaceous plants, in addition to the wetland and marsh plants associated with the sinkhole pond (Shunk et al. 2009; Ochoa et al. 2016). Curiously, the pollen record from PCS shows no evidence of grasses, although this pollen record is low-diversity and probably local, and captures only about one-third of plants known as macrofossils from PCS (Ochoa et al. 2016), including three leaf impressions of indeterminate grasses (Table 1 in Farlow et al. 2001).

Extant marmotine ground squirrels in *Ictidomys*, *Poliocitellus*, *Xerospermophilus*, *Otospermophilus*, and *Callospermophilus* have been classified as primarily granivorous (McLean et al. 2018), a classification congruent with their relatively low-crowned, narrow cheek teeth (Goodwin 2009; McLean et al. 2018). In contrast, high-crowned, widened cheek teeth are characteristic of ground squirrels in *Urocitellus* and *Cynomys*, classified as primarily herbivorous (McLean et al. 2018). Species in these genera

likely incorporate a greater amount of abrasive grasses into their diets (Goodwin 2009). Based on its plesiomorphic dental morphology, *I.?* *pipecreekensis* was very likely granivorous because it lacked the derived features characteristic of grazers.

Most marmotine ground squirrels in *Ictidomys*, *Poliocitellus*, *Xerospermophilus*, *Otospermophilus*, and *Callospermophilus* are obligate or facultative hibernators (Thorington et al. 2012). Individuals typically spend several months in burrows from late summer or fall to late winter or spring, with profoundly reduced metabolism punctuated by periodic arousals (Davis 1976; Michener 1984). Hibernation is reflected in a hibernation mark, a set of surface features of enamel and dentin of ever-growing lower incisors documented in multiple species of ground squirrels (Rinaldi 1999; Goodwin et al. 2005; Goodwin & Ryckman 2006; Klevezal & Anufriev 2014). This hibernation mark is preserved on an incisor for several weeks to months after hibernation, before it is lost due to wear of the ever-growing teeth, and thus allows retrospective identification of hibernation from modern and fossil museum specimens that died soon after hibernation (e.g., Goodwin et al. 2005). We did not observe a hibernation mark on the well-preserved incisor fragment of *I.?* *pipecreekensis*; thus, we have no positive evidence that this fossil species was a hibernator.

In summary, we report a new, distinctive species of ground squirrel from the late Neogene (latest Hemphillian or early Blancan) Pipe Creek Sinkhole biota, which we tentatively assign to the genus *Ictidomys*. Our findings suggest that the diversification of late Neogene ground squirrels may have extended further to the east than previously recognized, and confirms the presence of open, upland habitat in the vicinity of the Pipe Creek Sinkhole already documented from other evidence. The new ground squirrel exhibited low-crowned cheek teeth that were narrow across their trigonids; it probably was primarily granivorous in diet.

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