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Ground squirrels (Rodentia, Sciuridae) of the late Cenozoic Meade Basin sequence: diversity and paleoecological implications

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Abstract.—The Meade Basin, SW Kansas, yields a rich vertebrate fossil record from the late Cenozoic. Here, we review fossil ground squirrels (Sciuridae) from the region as a contribution to the broader Meade Basin Rodent Project. We recognize 14 species in seven genera: two species of giant ground squirrels (*Paenemarmota* Hibbard and Schultz, 1948) from the early Pliocene, and at least 12 species in six extant genera (*Ammospermophilus* Merriam, 1892; *Otospermophilus* Brandt, 1844; *Ictidomys* Allen, 1877; *Poliocitellus* Howell, 1938; *Urocitellus* Obolenskij, 1927; *Cynomys* Rafinesque, 1817) from the Pliocene–Pleistocene sequence, including the first regional records of *Ammospermophilus*. Based on dental morphology and the ecology of modern congeners, we interpret faunal change through the sequence as primarily reflecting a shift from a Pliocene assemblage of "southwestern" taxa with granivorous/omnivorous diets (relatively low-crowned, transversely narrow cheek teeth) in warm and at least occasionally dry shrub or shrub-steppe habitats (*Ammospermophilus*, *Otospermophilus*, *Ictidomys meadensis* [Hibbard, 1941a]), to a Pleistocene temperate assemblage of grazing taxa that either exhibited relatively high-crowned, transversely wider cheek teeth (*Urocitellus*, *Cynomys*, *Ictidomys tridecemlineatus* [Mitchill, 1821]) or were otherwise dependent on grassland habitats (*Poliocitellus*). The early Pleistocene Borchers assemblage was transitional in this regard, heralding a "revolution" observed as well with other clades in the Meade Basin rodent community. This interpretation is broadly congruent with evidence of Pliocene climatic change and the staged development of regional grasslands, with the modern proportion of C_3/C_4 plants established in the Meade Basin during the early Pleistocene.

Introduction

This paper represents a contribution of the Meade Basin Rodent Project (MBRP), a long-term research program designed to examine the history of rodent diversity on the Central Great Plains. The Meade Basin, a depositional trough running through part of southwestern Kansas and the panhandle of Oklahoma, covers an area of ~50 × 150 km and includes episodic exposures from the late Miocene to Late Pleistocene (Figs. 1, 2). The primary goal of the MBRP is to create a species-level database from which a number of analyses can be generated, testing a variety of ecological and evolutionary hypotheses. For example, the database has been used to examine patterns of diversity in cotton rats and pocket gophers (Peláez-Campomanes and Martin, 2005; Martin et al., 2011) and diversity dynamics of the entire rodent community through the late Neogene and Quaternary (Martin and Peláez-Campomanes, 2014).

While the taxonomy and diversity of most rodent groups in the Meade Basin are reasonably resolved, the taxonomy of Sciuridae (squirrels and allies) has not been reviewed. Prior studies recognized the early Pliocene giant ground squirrel *Paenemarmota* and an average of two smaller ground squirrels (previously assigned to *Spermophilus* Cuvier, 1825) and one prairie dog (*Cynomys*) of unknown affinities (Martin et al., 2008; Martin and Peláez-Campomanes, 2014). Here, we review the Sciuridae within the Meade Basin, representing the culmination

of a study by the senior author of both newer material collected through the MBRP and material housed at the University of Michigan and University of Kansas collected previously by C.W. Hibbard and his students. A more comprehensive phylogenetic analysis of extinct and extant ground squirrels would be helpful, but was beyond the scope of this analysis, which is primarily concerned with taxonomy of the Meade Basin species. This review recognizes seven genera and possibly 14 species of sciurids in the Meade Basin record. The increase in number of genera reflects both recognition of additional species and application of a revised taxonomy of *Spermophilus* to existing material. Helgen et al. (2009) divided the paraphyletic *Spermophilus* into eight presumably monophyletic genera, and we recognize four of these genera from the Meade Basin fossil sequence.

Morphometric comparisons among fossil ground squirrels from the Meade Basin revealed multiple phenetic clusters of tooth size and relative tooth width. In part, these clusters helped to separate and identify species, but they also revealed a pattern of dental morphological change in *Ictidomys* during the early Pleistocene that mirrors previously reported size shifts in other Meade Basin rodents, such as the cotton rats and pocket gophers (Peláez-Campomanes and Martin, 2005; Martin, 2016). Consequently, in addition to providing basic taxonomic descriptions of the Meade Basin sciurid remains, we present some graphic comparisons suggesting that the Huckleberry
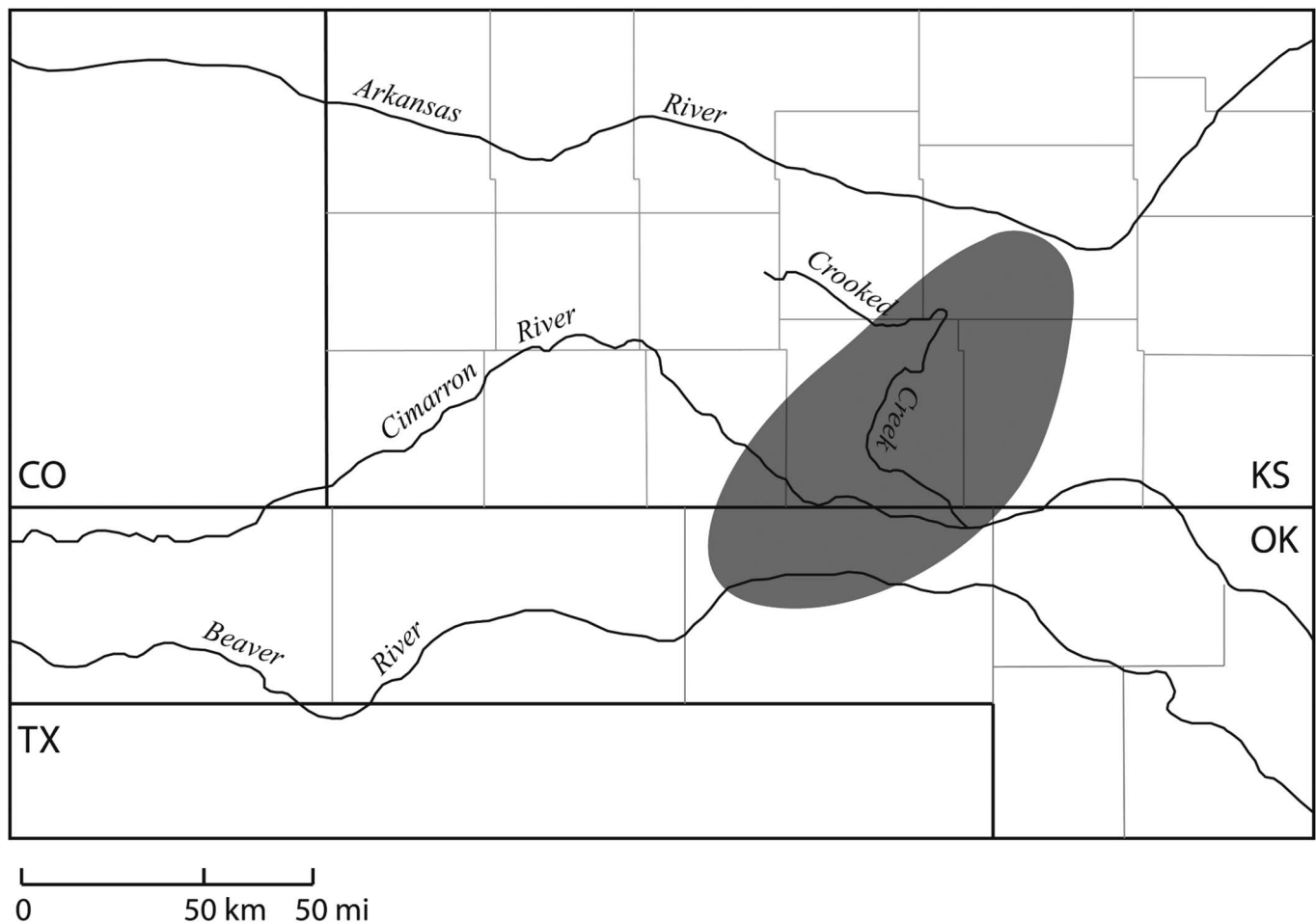
Figure 1. Location of the Meade Basin (gray ellipse).

Ridge ash-fall may have played a part in dental structural and size change within *Ictidomys*.

Materials and methods

Diagnostic dental specimens were digitally photographed in occlusal view (and usually in other views) along with a scale through a Leica MZ8 stereoscope (Leica Microsystems, Inc., Bannockburn, Illinois). Dental photographs were organized in a FileMaker Pro database (http://www.Filemaker.com), along with associated taxonomic and locality data. Specimens examined for this study are listed in the appendix (provided as Supplemental Data 1).

Digital photographs were output from the FileMaker database, calibrated to the scale, and measured digitally using GraphicConverter (https://www.lemkesoft.de/en/products/graphicconverter/) to obtain the following variables: greatest mesiodistal length of upper and lower cheek teeth; tooth width from the lingual margin of the protocone to buccal margin of the paracone on P3–M3; and tooth width across the trigonid on p4–m3, and likewise across the talonid on p4 (Fig. 3). Relative trigonid width of p4 was calculated as trigonid width/length of p4. Metric data were employed to graphically and statistically explore taxonomic and stratigraphic patterns in dental size and shape. All statistical analyses and graphing were done with SPSS (http://www-01.ibm.com/software/analytics/spss/).

Digital photographs were also used in detailed qualitative comparisons within and across putative taxa, across sites, and with relevant modern taxa using a companion photographic database of modern ground squirrels described elsewhere (Goodwin, 2009). Genus and species assignments were informed by both quantitative and qualitative comparisons; descriptions in the text employ standard dental terminology (Fig. 3). We followed the taxonomy of Helgen et al. (2009) when assigning fossil species to genera.

The way that paleontologists recognize and describe species in the fossil record strongly affects subsequent diversity analyses. Our perspective since beginning the MBRP was to make the database as biologically realistic as possible. Consequently, we do not accept anagenesis, the phyletic origin of new species. New species are recognized only as the result of cladogenesis, or lineage-splitting. The criteria for recognizing cladogenesis in the Meade Basin were delimited by Martin and Peláez-Campomanes (2014), and no intra-basin speciation events have been recognized to this point, though the origin of the diminutive gopher *Geomys tyrioni* Martin, 2016 was likely induced by the Huckleberry Ridge ash-fall on the Central Great Plains (Martin, 2016).

During the previous generation of work in the Meade Basin, C.W. Hibbard and his students attempted to fit their fossil localities in Meade, Seward, and Clark counties into a common

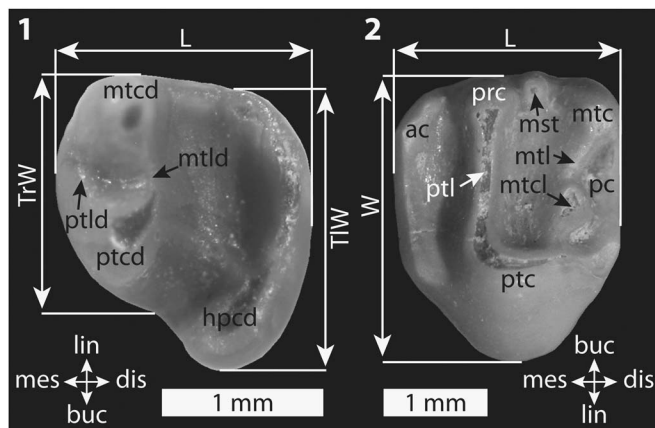| Epoch	MPTS		Ma	Geol. Markers	Assemblages	RZ
Pleistocene	Br	C1n	0.78	Lava Crk B ash (0.63) ************	Various late Pleistocene; Arlene's Ledge, Robin's Roost Arkalon, Cudahy (N); Couch 3,4	15
	Jar	1n r	0.99 / 1.07			14
		C1r 2r		Cerro Tol B ash (1.23-1.47) ************	Aries B (R)	13
	Ma		1.77	CCN3 ~~~~~~~~~~	Rick Forester Nash 72 (R)	
	Old	C2n	1.95		Aries NE (N) | Aries A (R) / Short Haul (R)	
	Reun	1n r	2.14 / 2.15	Huck R ash (2.11) ************	Borchers (R)	12
		C2r 2r			Margaret	11
			2.58	CCN2 ~~~~~~~~~~ Seger Gr. ------------		
Pliocene		C2an		CCN1 ~~~~~~~~~~	Sanders (N) Paloma	10
		1n	3.04			9 B / A
	Kaena	r	3.11	Wolf Gr. ------------	Rexroad Loc. 2; Rexroad Loc. 2A (R) Deer Park, Rex 3D (R)	8
	Ga	2n	3.22		Rexroad Loc. 3A-C (N) Bender 1B (N)	7
	Mam	r	3.33		Hornet (R)	
		3n	3.58			6
		C2ar			Wiens (R), Vasquez-Newt XIT 1E, 2B	
	Coch	n	4.18		Keefe C., Rap 1C (R)	
		1 r	4.29	CC2 / CC1 ------------	Ripley (R), XIT 1B	
	Nun	r / n	4.48	Bishop Gr.	Bishop	
		2	4.62	------------	Fox Canyon (R)	5
	Gi	C3n			Fallen Angel (?R) Argonaut	4
	Sud	r / r / n	4.80		Saw Rock C. (?R)	
		3 r	4.89 / 4.98			
	Thv	4n	5.23			
		C3r			? High Banks	
Miocene			5.89			
		1 n / r	6.14 / 6.27			
		2 n	6.57			
		C3an				
		r				

Figure 3. Measured dimensions, and orientation and dental terminology for (**1**) lower (FHSM VP-18159; left p4 of *I. tridecemlineatus* from Cudahy) and (**2**) upper teeth (UMMP 42319C; left M1 or M2 of *P. franklinii* from Cudahy). Scale bars = 1 mm Abbreviations: ac = anterior cingulum, buc = buccal, dis = distal, hpcd = hypoconid, L = length, lin = lingual, mes = mesial, mst = mesostyle, mtc = metacone, mtcd = metaconid, mtcl = metaconule, mtl = metaloph, mtld = metalophid, pc = posterior cingulum, prc = paracone, ptc = protocone, ptcd = protoconid, ptl = protoloph, ptld = protolophid, TlW = width across the talonid, TrW = width across the trigonid, W = width at paracone.

stratigraphic framework by allocating geographically isolated sites to the same "formations" based on faunal content rather than lithology. For example, the Kingsdown Formation, originally named for late Pleistocene sediments in Clark County, was extended by Hibbard and Taylor (1960) to the Big Springs Ranch in Meade County to include the Cragin Quarry vertebrate assemblage. Schultz (1969) continued this approach, applying the name Cragin Quarry to one of four superposed Late Pleistocene faunal levels that he recognized farther south in Meade County on the XI Ranch. Our current perspective is that it is very difficult to correlate the many isolated Late Pleistocene depositional environments, and we pursue a more cautious interpretation. Primarily through the careful field-mapping program directed by the late J. Honey, we have been able to determine the stratigraphic position of most of Hibbard's fossil assemblages, but we have refrained from using many of Hibbard's geologic names and marker units (e.g., the Angel gravel) or extending formational names beyond the sediments in which they were initially described (Martin et al., 2000). Late Pleistocene sediments on the Big Springs Ranch containing the Cragin Quarry assemblage cannot be securely correlated in time with sediments on the XI Ranch, with the latter apparently representing localized sinkhole and collapse features (Kapp, 1965). Because the name Cragin Quarry in both places has led to considerable confusion regarding faunal composition and could potentially create mistaken conclusions regarding faunal turnover, we here name the Kapp horizon for the Cragin Quarry level of Schultz (1969) on the XI Ranch, in honor of Ronald O. Kapp's (1965) detailed fossil pollen analyses on both the Big Springs and XI ranches.

Localities from which rodent assemblages were collected within the Meade Basin system are shown in Fig. 2. Because

rodent assemblages were collected from a limited vertical horizon (<1.0 m) at each locality noted in Figure 2, the name of the locality and the assemblage derived from it are here used synonymously. A few Neogene assemblages including sciurid remains listed in Table 1 do not appear in Figure 2, either because rodents were poorly represented or their stratigraphic positions were not precisely determined. None of the late Pleistocene assemblages (from Adams through Robert) in Table 1 is shown in Figure 2, but their temporal placement can be found in Martin and Peláez-Campomanes (2014). We follow the International Commission on Stratigraphy 2015 International Chronostratigraphic Chart and consider the base of the Pleistocene at 2.58 Ma. The early Pleistocene ranges from 2.58–0.78 Ma (million years ago), Middle Pleistocene from 0.78–0.13 Ma, and Late Pleistocene from 0.13–0.01 Ma.

Fossils referred to each of the following species are listed in the appendix (provided as Supplemental Data 1), organized alphabetically by genus and species, stratigraphically by age (early and late Pliocene; early, Middle, and Late Pleistocene), alphabetically by locality within age category, by element (skulls, maxillae, upper cheek teeth, dentaries, lower cheek teeth), then alphanumerically by museum acronym and catalog number.

Repositories and institutional abbreviations.—One of us (HTG) inspected sciurid fossils (skulls, jaws, maxillae with teeth; most isolated teeth; N > 1,000) from the Meade Basin in the vertebrate fossil collections of the University of Kansas (KUVP) and University of Michigan Museum of Paleontology (UMMP), as well as more recent collections made during the MBRP and curated by the Fort Hayes State Museum (FHSM).

Systematic paleontology

Family Sciuridae Fischer de Waldheim, 1817
Tribe Marmotini Pocock, 1923
Genus *Ammospermophilus* Merriam, 1892
Ammospermophilus sp.
Figure 4.1

Remarks.—*Ammospermophilus* today incorporates four or five extant species of antelope squirrels (Hall, 1981; Alvarez-Castaneda, 2007) of the southwestern deserts, with the closest approach to the Meade Basin being populations of Texas antelope squirrels (*Ammospermophilus interpres* [Merriam, 1890]), ~600 km to the WSW in central New Mexico (Hall, 1981). Early Pliocene fossils from XIT 1B and Wiens B are assigned to *Ammospermophilus* based on small size (all teeth; Table 2) and, for m1 or m2, narrow transverse width and well-developed metalophid (Fig. 4.1) that resemble some individuals of extant *Ammospermophilus* (Fig. 4.2), but differ sharply from Pliocene *Ictidomys meadensis* in tooth size and proportions (Fig. 4.3). *Ammospermophilus* has not previously been recognized in the

Species	HB	SRC	FC	RipB	XIT1B	RapIC	WnsB–D	Vas/Nwt	Hor	R3A–C	WFP*	Wb*	R2A	R2	DP	HD,Pal	Mar	Bor	SH	ArA	ArNE	RF	Na72	Cud	Sun	RR	AD	BS	MS*	Kapp	CQ	Jin	Jon	Tay*	GolB,C	Rob	Mod
Ammospermophilus sp.											cf		cf	cf																							
Otospermophilus rexroadensis		x	x	x	x		x		x	x	x	x	x	x	x	x																					
Otospermophilus sp.		x	x																																		
Ictidomys meadensis	x		x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x																	
Ictidomys tridecemlineatus																					x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Xerospermophilus spilosoma																																					x
Poliocitellus franklini																							x	x									x				
Urocitellus cragini																							cf	x													
Urocitellus richardsonii																							x	x								x	x				
Urocitellus "morph A"																				cf	cf																
Cynomys hibbardi																									x	x											
Cynomys ludovicianus																											x										
Cynomys niobrarius																									x	x											
Cynomys? n. sp. (small)																														x			x				
Cynomys sp.																													x								
Paenemarmota sawrockensis		x				x																															
Paenemarmota barbouri					x																																

Meade Basin, and its presence implies at least a brief episode of increased early Pliocene aridity.

Three specimens from the late Pliocene (Rexroad 2, 2A, Wendell Fox Pasture) may represent additional records of *Ammospermophilus*. The dp4 from Rexroad 2 differs from fossil and extant *Ictidomys*, but resembles *Ammospermophilus* in very small size, transversely narrow trigonid, and closely adjacent protoconid and metaconid. P4s from Rexroad 2A and Wendell Fox Pasture are much smaller than in coeval *I. meadensis* (Table 2; Fig. 5.2) and have a reduced anterior cingulum, in both features resembling *Ammospermophilus*, but exhibit a more developed connection between the metaloph and protocone than is typical for the genus. We tentatively assign both specimens to *Ammospermophilus*.

Genus *Otospermophilus* Brandt, 1844
Otospermophilus rexroadensis (Hibbard, 1941c)
Figure 4.7

1941c *Citellus rexroadensis* Hibbard, p. 348, fig. 7.
1961   *Citellus (Otospermophilus) rexroadensis* Hazard, p. 477, figs. 1, 2.
1980   *Spermophilus rexroadensis* Kurtén and Anderson, p. 213.

Holotype.—KUVP 4608, left dentary with I, p4–m3 from Rexroad Loc. 3, Meade Co., KS (Hibbard, 1941c, fig. 7).

Remarks.—Assignment to *Otospermophilus* is supported by multiple characters, including moderately large size (Fig. 5.1, 5.2), low relative trigonid width of p4 (Figs. 5.3, 6.1), low tooth crown height, and incomplete metaloph on M1 and M2 (constricted at contact with the base of the protocone). *Otospermophilus rexroadensis* (Hibbard, 1941c) from the type locality (Rexroad Loc. 3; Hibbard, 1941c) and other late Pliocene localities display significantly larger teeth (and presumably body mass) than fossils from Fox Canyon and other early Pliocene localities (Table 2; length of p4: $t = 2.93$, $df = 20$, $p < 0.01$; length of P4: $t = 6.26$, $df = 20$, $p < 0.001$), a difference previously noted by Hazard (1961) that we attribute to phyletic evolution.

Otospermophilus spp.

Remarks.—Both Saw Rock Canyon and Fox Canyon include *O. rexroadensis* and probably a second, larger species of *Otospermophilus* (UMMP 117762, P4, from Saw Rock Canyon in Fig. 5.2) that we cannot presently identify to species. *Otospermophilus* was not observed in early Pleistocene or the Middle Pleistocene Cudahy assemblages, but a single p4 from the Adams local fauna (UMMP 34735; Fig. 5.1) is clearly assignable to the genus. We are unable to confidently assign this tooth to species, but it plausibly represents a temporary northeastern range expansion of the extant rock squirrel, *Otospermophilus variegatus* (Erxleben, 1777), a species that ranges today from northern Utah to southern Mexico and from far southeastern California to the panhandle of Oklahoma, ~60 km SW of Meade County (Helgen et al., 2009).

Genus *Ictidomys* Allen, 1877
Ictidomys meadensis (Hibbard, 1941a)
Figures 4.3–4.5, 7.1

1941a   *Citellus meadensis* Hibbard, p. 203, Plate 1, figs. 2, 7.
1941c   *Citellus howelli* Hibbard, p. 347, fig. 6.
1980   *Spermophilus howelli* Kurtén and Anderson, p. 212.
1980   *Spermophilus meadensis* Kurtén and Anderson, p. 214.

Holotype.—KUVP 6169, right dentary with p4–m2 from Borchers, Meade Co., KS (Hibbard, 1941a, pl. 1, fig. 2). Paratype KUVP 6119, left maxillary fragment with P4–M2 (Hibbard, 1941a, pl. 1, fig. 7).
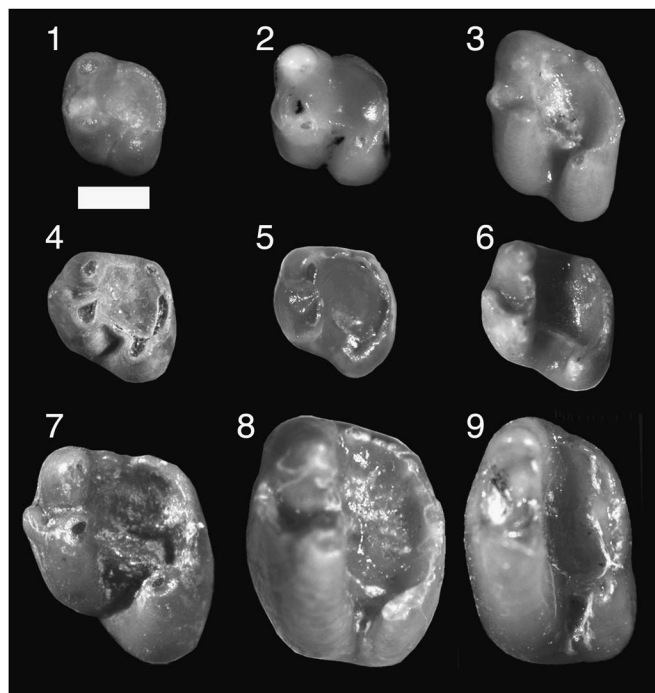

Figure 4. Lower cheek teeth (p4, m1 or m2) of Meade Basin ground squirrels. Scale bar = 1 mm. To facilitate comparisons, all are displayed as left specimens (reversed right teeth are indicated). (**1–3**) Lower m1 or m2 of (**1**) *Ammospermophilus* sp. from Wiens B (FHSM VP-18438; R reversed), (**2**) extant *A. interpres* from Dona Ana Co., NM (KUVP 131708; m1), and (**3**) *Ictidomys meadensis* from Rexroad 3 (UMMP 35057). (**4–9**) Lower p4s of (**4**) *I. meadensis* from Rexroad 3C (FHSM VP-18365; R reversed), (**5**) *I. meadensis* from Borchers (KUVP 156258), (**6**) *Poliocitellus franklinii* from Cudahy (UMMP 36796; R reversed), (**7**) *Otospermophilus rexroadensis* from Rexroad 3B (FHSM VP-18348), (**8**) *Urocitellus*? *cragini* from Borchers (UMMP 50136), and (**9**) *Cynomys*? sp. from Sunbrite (KUVP 6704; R reversed).

Remarks.—Hibbard described two small-sized ground squirrels from the Meade Basin sequence in the same year: *Citellus meadensis* Hibbard, 1941a from the early Pleistocene Borchers locality and *Citellus howelli* Hibbard, 1941c from the late Pliocene Rexroad Locality 3 (Hibbard, 1941a, 1941c). We assign both to the genus *Ictidomys* (*Citellus* is no longer regarded as a valid name).

Hibbard distinguished *Ictidomys meadensis* from the Pliocene *Ictidomys howelli* by its lesser molar tooth width, better developed trigonid pit, and more pronounced metalophid that reaches to the base of the metaconid on lower molars (Hibbard, 1941b). However, we observed that the trigonid pit was variably developed in both species, and average width of m1 or m2 did not differ significantly between late Pliocene *I. howelli* (2.3 mm, sd = 0.14, N = 21) and *I. meadensis* (2.4 mm, sd = 0.14, N = 24; t = −1.61, p = 0.998).

The Borchers and Margaret specimens of small ground squirrels (early Pleistocene) differ significantly from the combined Pliocene *Ictidomys* sample in frequencies of two attributes. First, ~60% of measured M3s from Borchers (10 of 17) display a ridge coursing buccodistally from the protocone (dashed line in Fig. 7.1) that does not merge with the margin of the posterior cingulum, with the contact between this ridge and the posterior cingulum typically marked by a distinct notch or groove (arrow in Fig. 7.1). This feature was not observed on Pliocene M3s (0 of 22; $\chi^2 = 17.40$, df = 1, p < 0.001). Second, only 30% of Borchers and Margaret M1s or M2s (7/23) display a mesostyle, compared to 60% of Pliocene M1s and M2s (14/23; $\chi^2 = 4.29$, df = 1, p < 0.05). We did not observe other consistent morphological differences that separated the Pliocene and early Pleistocene Borchers samples.

Table 2. Measurements of p4 and P4 (in mm) in composite stratigraphic samples used for statistical analysis. L = length, W = width. Cell values represent mean (standard deviation) *n*. See Table 1 for assemblage abbreviations.

| Taxon	Age (Assemblages)	L p4	Trigonid W p4	L P4	W P4
Paenemarmota sawrockensis	early Pliocene (SRC)	6.62 (—) 1	6.11 (—) 1		
Paenemarmota barbouri	early Pliocene (FC)	8.24 (0.67) 3	8.30 (0.62) 2	7.76 (0.49) 3	8.50 (0.88) 3
Ammospermophilus sp.	early Pliocene (WnsB)			1.38 (—) 1	1.80 (—) 1
Ammospermophilus? sp.	late Pliocene (R2A)			1.45 (—) 1	1.87 (—) 1
Otospermophilus rexroadensis	early Pliocene (FC, SRC, Vas, WnsD, XIT1B)	2.34 (0.12) 8	2.09 (0.08) 8	2.28 (0.08) 8	2.96 (0.15) 7
	late Pliocene (HD, R2A, R3, R3A, R3B, WFP)	2.51 (0.14) 14	2.32 (0.13) 12	2.56 (0.11) 14	3.19 (0.16) 11
Otospermophilus sp.	early Pliocene (SRC)			2.9 (—) 1	3.43 (—) 1
	Middle Pleistocene (AD)	2.70 (—) 1	2.40 (—) 1		
Ictidomys meadensis	early Pliocene (FC)	1.88 (0.10) 13	1.72 (0.12) 13	1.82 (0.09) 14	2.36 (0.09) 14
	Late Pliocene (HD, R2A, R3, R3C)	1.79 (0.06) 5	1.58 (0.05) 5	1.79 (0.03) 5	2.25 (0.08) 5
	earliest Pleistocene (Bor)	1.78 (0.11) 24	1.65 (0.10) 24	1.76 (0.06) 19	2.30 (0.08) 18
Ictidomys tridecemlineatus	early Pleistocene (N72, RF, SH)	1.51 (0.06) 8	1.49 (0.07) 7	1.50 (0.09) 13	1.96 (0.10) 12
	Middle Pleistocene (CQ, Cud, Jin, MS, Sun)	1.69 (0.12) 6	1.69 (0.10) 6	1.56 (0.13) 8	2.10 (0.23) 8
	Late Pleistocene (GolB, GolC, Jon, Rob, Tay)	1.42 (0.09) 6	1.46 (0.09) 5	1.43 (0.07) 3	1.88 (0.12) 3
Poliocitellus franklinii	Middle Pleistocene (Cud)	1.95 (—) 1	1.90 (—) 1	2.06 (0.04) 3	2.51 (0.01) 3
	Late Pleistocene (Jon)	2.25 (—) 1	1.97 (—) 1		
Urocitellus cragini	earliest Pleistocene (Bor)	2.80 (0.19) 8	3.44 (0.24) 8	2.83 (0.14) 7	3.82 (0.11) 6
Urocitellus cf. *richardsonii*	Middle Pleistocene (Ad, BS, Cud)	1.87 (0.03) 3	2.27 (0.30) 2	1.99 (0.09) 3	2.53 (0.14) 3
	Late Pleistocene (GolB, Jon)	2.07 (0.10) 8	2.51 (0.10) 8	2.15 (0.06) 3	2.87 (0.21) 3
Cynomys hibbardi	early Pleistocene (N72)	2.85 (—) 1			
Cynomys ludovicianus	Middle Pleistocene (BS)	3.44 (—) 1			
Cynomys niobrarius	Middle Pleistocene (Kapp)	3.15 (0.01) 2	4.60 (0.10) 2		
Cynomys sp.	Middle Pleistocene (RR)	3.43 (0.05) 2	4.45 (0.01) 2		
Cynomys? new sp.	Middle Pleistocene (Sun)	2.39 (—) 1	3.53 (—) 1		
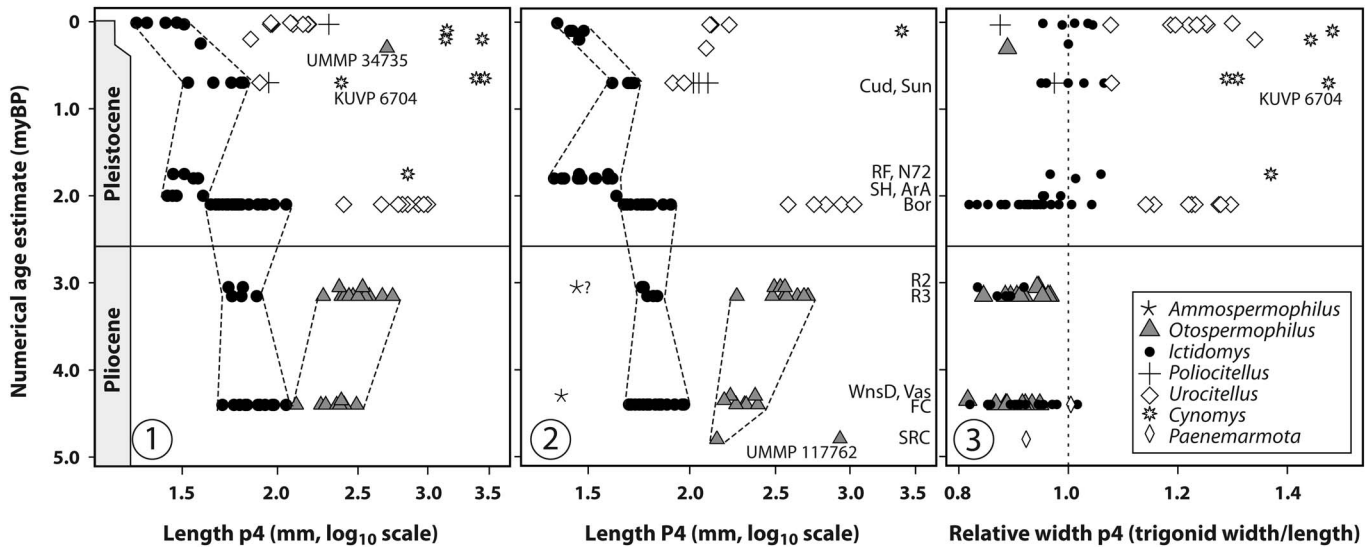
Figure 5. Stratigraphic variation in (**1**) lengths of p4 and (**2**) P4 of fossils from the Meade Basin, excluding *Paenemarmota* (log₁₀-scale for tooth lengths). Envelopes of size variation in *Ictidomys* and *Otospermophilus* given by dotted lines. (**3**) Stratigraphic variation in relative width of p4 (trigonid width/length). Dashed vertical line represents equivalence of trigonid width and tooth length. Dark horizontal line in all panels represents the Pliocene-Pleistocene boundary. Representative localities indicated in (**2**); locality abbreviations defined in Table 1.
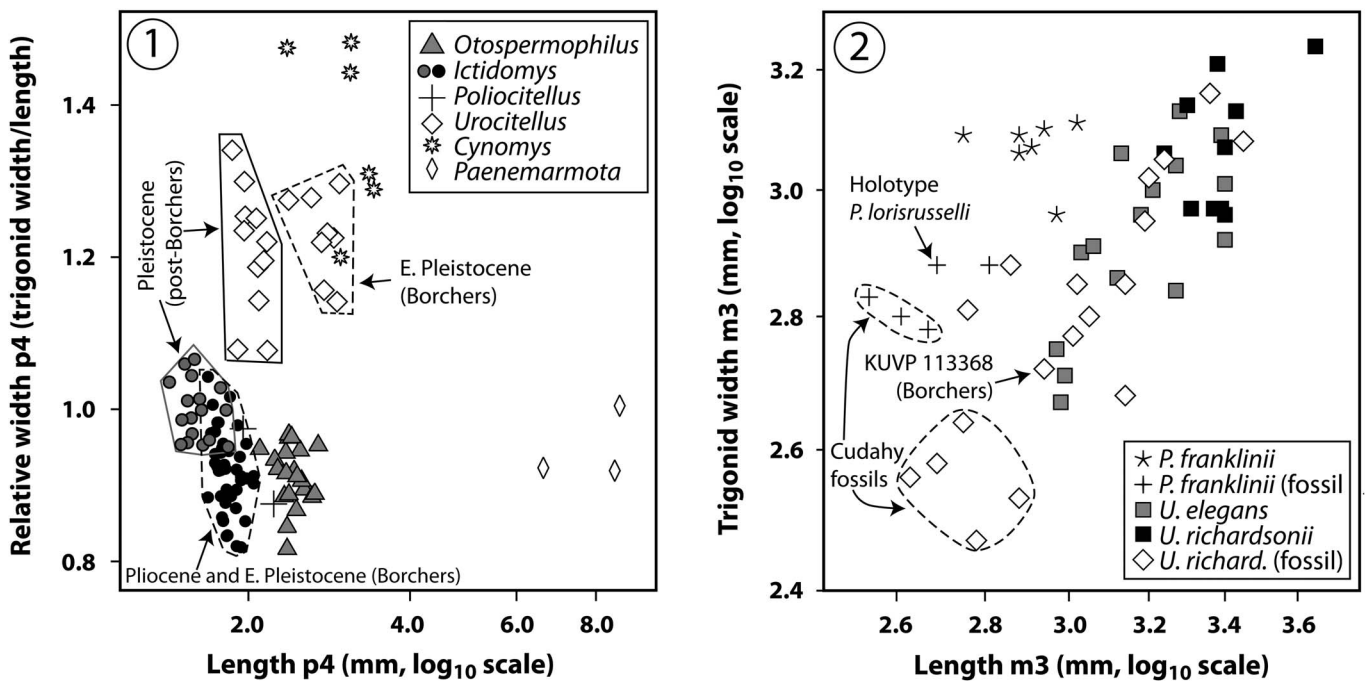
Figure 6. (**1**) Scatter plot of relative trigonid width of p4 (trigonid width/tooth length) versus p4 length (log₁₀ scale) for all Meade Basin fossils of p4 that can be identified to genus. Genera marked with different symbols; stratigraphic samples distinguished for *Ictidomys* and *Urocitellus*. (**2**) Scatter plot of trigonid width versus tooth length (log₁₀ scale for both) of the m3 for fossils of *Poliocitellus franklinii*, and *Urocitellus* cf. *U. richardsonii*, and for comparative extant species (*P. franklinii*, *U. elegans*, and *U. richardsonii*). One fossil outside the Meade Basin (holotype of *P. lorisrusselli*; UMMP 61136) is plotted and labelled. Fossils from Borchers and Cudahy are indicated.

Graphic plots of tooth size and relative trigonid width of p4 across early Pliocene, late Pliocene, and early Pleistocene Borchers samples of *Ictidomys* suggest overall stasis in these attributes through this interval (Fig. 5; key faunas in each stratigraphic sample are indicated in Fig. 5.2). Statistical comparisons across stratigraphic samples (one-way ANOVAs) confirm stasis in length of P4 ($F = 1.61$, $df = 2, 39$, $p > 0.05$) and relative width of p4 ($F = 2.06$, $df = 2, 35$, $p > 0.05$), but reject stasis in length of p4 ($F = 4.28$, $df = 2, 39$, $p < 0.05$),

with significant difference being a size reduction between early Pliocene and Borchers samples (Tukey's HSD, $p < 0.05$). There are no differences in these variables between the late Pliocene sample (which includes the type locality of *S. howelli*, Rexroad Loc. 3) and Borchers (the type locality of *S. meadensis*). We conclude that it is most parsimonious to infer a single, long-lived, small-sized ground squirrel species in the Meade Basin during the Pliocene and early Pleistocene (as represented at Borchers). Thus, we interpret changes in
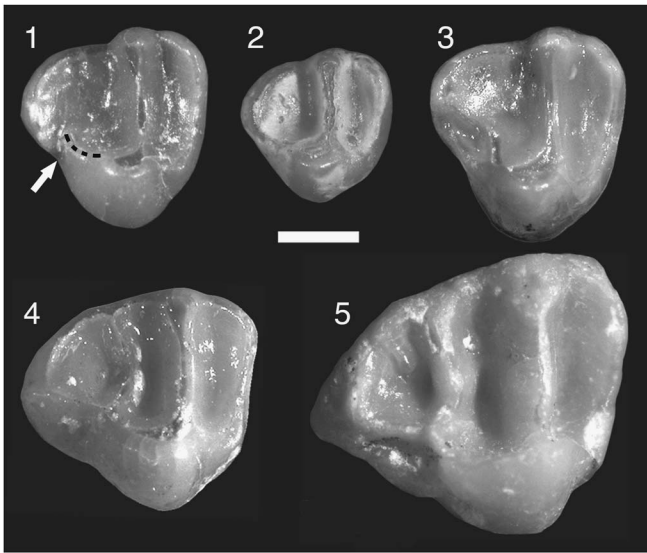
Figure 7. Upper M3 fossils, all displayed as right (indicated if reversed). Scale bar = 1 mm. (**1**) *I. meadensis* from Borchers (FHSM VP-18122; L reversed). Abrupt deflection of posterior cingulum (arrow) distal to short ridge coursing buccodistally from protocone (dotted line) noted in text. (**2**) *I. tridecemlineatus* from Short Haul (FHSM VP-18902; L reversed). (**3**) *P. franklinii* from Sunbrite (UMMP 39596). (**4**) *Urocitellus* cf. *U. richardsonii* from Adams (UMMP 34705; L reversed). (**5**) *Cynomys hibbardi* from Rick Forrester (FHSM VP-14104).

character frequency and subtle quantitative change in length of p4 as phyletic change within this lineage.

We assign the Meade Basin squirrel material described in this section to the genus *Ictidomys*, but this assignment is complicated by conservative and similar dental morphology of *Ictidomys* and *Xerospermophilus* (Merriam, 1892), both of which occur in the Meade Basin today (the thirteen-lined ground squirrel, *Ictidomys tridecemlineatus*, and spotted ground squirrel, *Xerospermophilus spilosoma* [Bennett, 1833]; Helgen et al., 2009). Cheek teeth of *Xerospermophilus* tend to be relatively narrow (Goodwin, 2009), and the hypoconid of p4 tends to be more rounded and less elongate buccally than in *I. tridecemlineatus*, but there is overlap in both features. In addition, the M1s–M2s of extant *Xerospermophilus* usually lack a mesostyle (present in one of 50 teeth observed in extant species of *Xerospermophilus*), a feature more commonly observed in extant species of *Ictidomys* (15 of 46 teeth observed). Unfortunately, fossils assigned to *I. meadensis* typically display narrow cheek teeth and a more rounded hypoconid on p4 (Fig. 4.4, 4.5) as in *Xerospermophilus*, but also may exhibit a mesostyle on M1–M2 (7 of 23), as in *Ictidomys*. Better material may clarify assignment of the fossils, but for now we assign the material to *Ictidomys*.

Ictidomys tridecemlineatus (Mitchill, 1821)
Figures 3.1, 7.2

1821 *Sciurus tridecem-lineatus* Mitchill, p. 248 [For listing of synonyms in the literature of modern *Ictidomys tridecemlineatus*, see Streubel and Fitzgerald, 1978b, p. 1].

Holotype.—Not designated. Type locality fixed as "Central Minnesota" by Allen (1895, p. 338).

Remarks.—During the early Pleistocene, an abrupt and significant reduction in tooth size between Borchers *I. meadensis* and slightly younger fossils of *Ictidomys* from the Borchers Badlands (length of p4: $t = -6.90$, $df = 30$, $p < 0.001$; length of P4: $t = -9.89$, $df = 30$, $p < 0.001$; Fig. 5.1, 5.2) was accompanied by increase in relative trigonid width of p4 ($t = 2.88$, $df = 28$, $p < 0.01$; Fig. 5.3) and decrease in frequency of the mesostyle on M1–M2 (from 30% [7 of 23] to 8% [2 of 26]). These simultaneous changes in tooth size, relative width, and mesostyle frequency indicate the appearance of a new species in the Meade Basin, which we identify as *Ictidomys tridecemlineatus* based on size and dental proportions, although extant *I. tridecemlineatus* more frequently exhibits a mesostyle on M1–M2 (~33%). Early Pleistocene *I. tridecemlineatus* usually displays a relatively elongate M3, and never displays the discontinuity between the ridge extending posterodistally from the protocone and the posterior cingulum described previously for *I. meadensis* from Borchers (compare Fig. 7.2 with Fig. 7.1).

We interpret the combination of abrupt change in size, shape, and qualitative characters as indicating immigration rather than in situ phyletic evolution. The abrupt size reduction in local *Ictidomys* immediately post-Borchers mirrors the appearance of the dwarf pocket gopher *Geomys tyrioni* at Short Haul (Martin, 2016), and may reflect dramatic restructuring of regional communities after the massive Huckleberry Ridge ash-fall (Martin and Peláez-Campomanes, 2014).

Pleistocene *I. tridecemlineatus* from the Meade Basin varies temporally in size (Fig. 5.1, 5.2), significantly so for length of p4 ($F = 13.72$, $df = 2, 17$, $p < 0.001$), but not length of P4 ($F = 2.02$, $df = 2, 21$). There was no significant stratigraphic variation in relative p4 trigonid width (Fig. 5.3; $F = 0.31$, $df = 2, 14$). In length of p4, both early and Late Pleistocene were significantly smaller than Middle Pleistocene fossils from Cudahy and Sunbrite (Tukey HSD, $p < 0.001$).

Genus *Poliocitellus* Howell, 1938
Poliocitellus franklinii (Sabine, 1822)
Figures 3.2, 4.6, 7.3

1822 *Arctomys franklinii* Sabine, p. 587 [For listing of synonyms in the literature of modern *Poliocitellus franklinii*, see Ostroff and Finck, 2003, p. 1].

1976 *Spermophilus lorisrusselli*, Hibbard, p. 282, fig. 2.

Holotype.—Not specified; type locality restricted to Carlton House, Saskatchewan, Canada by Preble (1908, p. 165).

Remarks.—*Poliocitellus franklinii* (Sabine, 1822) is an extant occupant of tall-grass prairies of the northern and central Great Plains that does not occur in the Meade Basin today, with closest populations ~200 km to the NNE (Ostroff and Finck, 2003). It is the sole extant member of its genus. Hibbard (1976) described *Poliocitellus lorisrusselli* (Hibbard, 1976) from the Cudahy-equivalent Wilson Valley local assemblage of NE Kansas, which he characterized as smaller than but otherwise similar in dental morphology to extant *P. franklinii*.

Multiple fossils from the Meade Basin can be assigned to *Poliocitellus*. These fossils differ from *I. tridecemlineatus* in larger size (Fig. 5.1, 5.2) and the presence of a pronounced

protolophid on p4 (Fig. 4.6, compare with Fig. 3.1). They differ from coeval *Urocitellus* cf. *U. richardsonii* (Sabine, 1822) in much less relative trigonid width on p4 (Fig. 5.3), and relatively less-elongate M3 (Fig. 7.3) and m3 (Fig. 8.1) that lack the defined metaloph and talonid basin trench, respectively, of *Urocitellus* (Figs. 7.4, 8.2).

Middle Pleistocene m3s from Cudahy plot with the holotype of *P. lorisrusselli* and are smaller than extant *P. franklinii* (Fig. 6.2), but some later p4s were larger (Fig. 5.1). In addition, Eshelman and Hibbard (1981) tentatively identified *P. franklinii* in the early Pleistocene Nash 72 assemblage, explicitly noting that the teeth were larger than in *P. lorisrusselli*. We provisionally accept their interpretation based on published measurements, but do so with question because we were not able to inspect the specimens.

We conclude that the Meade Basin supported a single, size-variable lineage of *Poliocitellus* from the Middle (and perhaps early) to Late Pleistocene, with *P. lorisrusselli* representing an episode of reduced size. We assign all specimens to *P. franklinii*, which has priority.

<div align="center">

Genus *Urocitellus* Obolenskij, 1927
Urocitellus? *cragini* (Hibbard, 1941a)
Figure 4.8

</div>

1941a   *Citellus cragini* Hibbard, p. 204, pl. 1, fig. 13.
1980   *Spermophilus cragini* Kurtén and Anderson, p. 214.
1994   *Spermophilus*? *cragini* Goodwin and Hayes, p. 283, fig. 3.

Holotype.—KUVP 6168, right maxilla with M1–M3 from Borchers, Meade Co., KS (Hibbard, 1941a, pl. 1, fig. 13).

Remarks.—*Urocitellus*? *cragini* (Hibbard, 1941a) represents a large ground squirrel initially described solely on the holotype (Hibbard, 1941a) and subsequently described more fully and formally assigned to the derived subgenus *Spermophilus* (genus *Urocitellus* after Helgen et al., 2009) based on a larger sample (Goodwin and Hayes, 1994). It has only been reported from the type locality. The questioned assignment to *Urocitellus*? follows Goodwin and Hayes (1994), because *U.*? *cragini* could represent a small, dentally underived prairie dog (see below). It represents the first occurrence of a ground squirrel with proportionally wide p4 in the Meade Basin record (Fig. 5.3), a morphology shared by *Urocitellus* and *Cynomys* (Goodwin, 2009).

Urocitellus? *cragini* differs from all extant species of *Urocitellus* in the presence of a complete protolophid on most p4s (Fig. 4.8), a feature characteristic of *Cynomys*; but it differs from all *Cynomys* in the absence of a well-developed lophulid on the talonid of m1–m2, presence of an incomplete metalophid on m3, more circular P3, and less-elongate M3 and m3, all features of *Urocitellus* (Goodwin and Hayes, 1994). *Urocitellus*? *cragini* was a large squirrel (Table 2, Fig. 4.8) that was much larger than middle Pleistocene and later species assigned to the genus (Table 2, Figs. 5.1, 5.2, 6.1). Its dentition resembles that of the extant Arctic ground squirrel, *Urocitellus parryii* (Richardson, 1825) in p4 and P4 length, but exhibits much wider teeth (Goodwin and Hayes, 1994, fig. 1).

<div align="center">

Urocitellus cf. *U. richardsonii* (Sabine, 1822)
Figures 7.4, 8.2

</div>

1822   *Arctomys richardsonii* Sabine, p. 589 [For listing of synonyms in the literature of modern *Urocitellus richardsonii*, see Michener and Koeppl, 1985, p. 1].
1967   *Citellus kimballensis* Kent, p. 18, figs. 1–3.

Holotype.—Holotype not designated. Type locality Carlton House, Saskatchewan, Canada.

Remarks.—Fossils assigned to *Urocitellus* cf. *U. richardsonii* are smaller than fossils of *U.*? *cragini* and exhibit much greater trigonid width of p4 than in *Otospermophilus*, *Ictidomys*, and *Poliocitellus* (Fig. 6.1). The M3 usually displays a prominent metaloph (Fig 7.4), and m3 characteristically exhibits a distinct talonid basin trench adjacent to the ectolophid (Fig 8.2), in both cases resembling *Cynomys* (Figs. 7.5, 8.3.1). Morphometrically, many fossil m3s fall within the envelope of variation defined by the extant sister species *U. richardsonii* and *Urocitellus elegans* (Kennicott, 1863), although Cudahy teeth are distinctly smaller than teeth from earlier and later assemblages (Fig. 6.2).

There is considerable dental morphological overlap between extant *U. richardsonii* and *U. elegans* (Goodwin, 2002). *Urocitellus elegans* inhabits open habitats in the central Rocky Mountains and northern Basin and Range (Zegers, 1984), and was present at high elevations in central Colorado (Porcupine Cave) during the Middle Pleistocene (Goodwin, 2002). In contrast, *U. richardsonii* is an occupant of the northern Great Plains with closest extant populations ~775 km to the NNE in SE South Dakota (Michener and Koeppl, 1985). We tentatively refer the Meade Basin fossil *Urocitellus* to *Urocitellus* cf. *U. richardsonii* on geographic grounds because a number of other northern Great Plains rodent species dispersed southward into the Meade Basin,
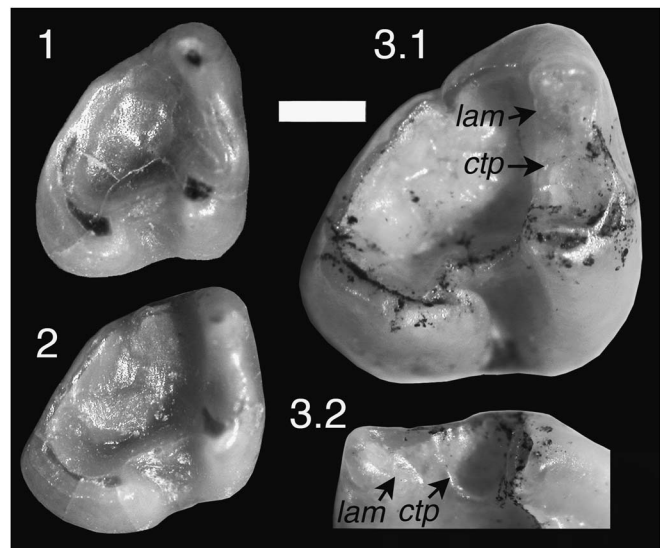

Figure 8. Lower right m3 fossils of (**1**) *P. franklinii* (UMMP 117771) and (**2**) *Urocitellus* cf. *U. richardsonii* (UMMP 117732), both from Cudahy, and (**3.1, 3.2**) of *C. hibbardi* from Nash (FHSM VP-18209). (**3.2**) represents an oblique, occlusodistal view of the trigonid. Attributes noted in text are labelled; *lam* = lingual arm of metapholophid; *ctp* = closure of trigonid pit. Scale bar = 1 mm.

rather than directly eastward from the Rocky Mountains, at various points during the Pleistocene.

Urocitellus sp.

Remarks.—Goodwin and Hayes (1994) tentatively recognized an additional species of *Urocitellus* from Borchers, which they labeled "morph A." Assignment to *Urocitellus* is supported by the large P3 relative to P4 (Goodwin and Hayes, 1994, figs. 4A, 4B). Fossils assigned to "morph A" are smaller than *U.?* cragini and larger than *Urocitellus* cf. *U. richardsonii*, and they differ from both of these species in the presence of a swollen metaconule on M3 that is constricted at its contact with the protocone (Goodwin and Hayes, 1994, fig. 4C). In addition to fossils from Borchers, a somewhat corroded M3 from Margaret (FHSM VP-18908) probably represents "morph A," bearing remnants of a swollen metaconule and resembling "morph A" in size.

Genus *Cynomys* Rafinesque, 1817
Cynomys hibbardi Eshelman, 1975
Figures 7.5, 8.3.1, 8.3.2

1975   *Cynomys hibbardi* Eshelman, p. 27, figs. 4A, 4B.
1995b   *Cynomys sappaensis* Goodwin, p. 16, figs. 2E, 3B, 4B, 4E, 4F.

Holotype.—UMMP 61648, left lower jaw with m1–m3 from locality UM-K9-72 "in the silty clay lithosome, approximately 2.2 m below the contact with the sand lithosome, Belleville Formation, SE¼, SE¼, SW¼, Sec. 34, T.1S, R.5W, Republic County, Kansas" (Eshelman, 1975, p. 27).

Remarks.—Eshelman and Hibbard (1981) tentatively referred two lower molars from Nash 72 to *Cynomys meadensis* Hibbard, 1956, a species described from the Deer Park locality (Hibbard, 1956), but recognized by Goodwin (1995b) as intrusive *Cynomys ludovicianus* (Ord, 1815). The Nash 72 prairie dog fossils were subsequently assigned to *Cynomys hibbardi* Eshelman, 1975 (Goodwin, 1995b), a species described from the late Pliocene White Rock local fauna of northern Kansas (Eshelman, 1975). A few sciurid teeth from Rick Forester represent the same taxon; a P3 with corroded enamel and fragmentary p4 from Short Haul may likewise represent a small *Cynomys*.

Three isolated M3s provide the first documentation of M3 morphology for *C. hibbardi* (Fig. 7.5). A prominent metaloph is present, and the tooth is strongly elongate posteriorly. One specimen (FHSM VP-14104) displays a short distally directed lophule connecting the lingual end of the metaloph with the posterior cingulum (Fig. 7.5).

Goodwin (1995b) also described *Cynomys sappaensis* Goodwin, 1995 from the early Pleistocene Sappa assemblage of Nebraska, which he distinguished from *C. hibbardi* by greater hypsodonty (described qualitatively, but not measured) and greater development of metalophids on lower molars. Both hypsodonty and metalophid development are temporally gradational in *Cynomys*, with greatest development in Late Pleistocene and Recent species (Goodwin, 1995b). However, we now consider *C. sappaensis* as a younger segment of the *C. hibbardi* lineage. These two species are similar in size

(Goodwin, 1995b, table 4), display a deeply notched metalophid on m1 and m2, and exhibit a similar m3 trigonid morphology. The trigonid pit is closed by a mesially directed lophid about one-half of the way between the protoconid and metaconid (Fig. 8.3.1), and the pit is separated from the lingual arm of the metalophid (Fig. 8.3.2). The latter feature is well developed on m3 fossils from Nash 72 and Rick Forester, but is absent from later prairie dog m3s.

Cynomys hibbardi resembles *U. cragini* in size (Fig. 5.1), but differs from it in multiple features, including configuration of the trigonid on m3 and development of the metaloph on M3, described above.

Cynomys ludovicianus (Ord, 1815)

1815   *Arctomys ludoviciana* Ord, p. 292 [For listing of synonyms in the literature of modern *C. ludovicianus*, see Hall 1981, p. 411, 412].
1956   *Cynomys meadensis* Hibbard, p. 172.
1995b   *Cynomys spenceri* Goodwin, p. 18, fig. 9.

Holotype.—Holotype not designated. Type locality not specified.

Remarks.—Two fossils from Butler Springs are assigned to *C. ludovicianus* (an extant black-tailed prairie dog [subgenus *Cynomys*]), based on conformation of the p4 (relatively narrow trigonid width) and m3 (mesially deflected hypoconid, absence of a bridge interrupting the talonid trench; Goodwin, 1995b). *Cynomys ludovicianus* is present in the Meade Basin today.

The Butler Springs black-tailed prairie dog was previously identified as *Cynomys spenceri* Goodwin, 1995b, a species erected for the early segment (late Middle and early Late Pleistocene) of the *C. ludovicianus* lineage, diagnosed only by smaller average size (Goodwin, 1995b). Here, we consider *C. spenceri* part of the *C. ludovicianus* lineage.

Cynomys niobrarius Hay, 1921

1921   *Cynomys niobrarius* Hay, p. 615, pl. 122, fig. 7.
1960   *Cynomys spispiza* Green, p. 545, figs. 1, 5.
1989   *Cynomys churcherii* Burns and McGillivray, p. 2637.

Holotype.—AMNH 2715, partial skull. Type locality given only as "Niobrara River, near Grayson, Nebraska" and formation as "Sheridan beds of the Pleistocene" (Hay, 1921, p. 615).

Remarks.—*Cynomys niobrarius* Hay, 1921 is a white-tailed prairie dog (subgenus *Leucocrossuromys* Hollister, 1916) that occupied the northern and central Great Plains during the late Middle and Late Pleistocene, co-occurring with *C. ludovicianus* at multiple sites on the central Plains (Goodwin, 1995a). It is known from the Kapp horizon of the XI Ranch sequence in the Meade Basin (Table 1). *Cynomys niobrarius* can be distinguished from *C. ludovicianus* by greater relative trigonid width of p4, and m3 with less mesially deflected hypoconid and a well-developed bridge connecting the talonid platform and ectolophid and interrupting the talonid trench (Goodwin, 1995b).

Cynomys sp.

Remarks.—Two well-preserved fossils (lower jaws with most teeth) from Robin's Roost, Beaver Co., OK (approximately time-equivalent with Cudahy) document the presence of a large prairie dog in the Meade Basin south of the Cimarron River. The m3s are similar to those of *C. niobrarius* based on presence of a bridge between the ectolophid and talonid on m3, but the p4s also display a relatively narrower trigonid than expected for white-tailed prairie dogs. The specimens are currently under study and are referred here to *Cynomys* sp.

A single large, somewhat worn M1 or M2 from the Cudahy time-equivalent Sunbrite assemblage (KUVP 6703) clearly represents a large *Cynomys*, but lacks diagnostic features to allow species assignment. An upper molar was likewise attributed to *Cynomys* from the Robert local fauna (Schultz, 1969). We were unable to examine this specimen, but generic identification is probably correct given that *Cynomys* molars are much larger than those of any other ground squirrel known from the Late Pleistocene of the Meade Basin, and thus unlikely to be misidentified. We identify both specimens as *Cynomys* sp.

Cynomys? new sp.
Figure 4.9

Remarks.—A single p4 from Sunbrite (KUVP 6704) documents a second prairie dog or prairie dog-like *Urocitellus* (Fig. 4.9) from that assemblage. This p4 displays great relative width (identified in Fig. 5.3) and a well-developed protolophid that lacks a distinct notch at its attachment with the protoconid (Fig. 4.9), in both respects resembling *Cynomys* more than *Urocitellus*. However, it is much smaller than all other known *Cynomys* (Table 2), plotting between *Urocitellus* cf. *U. richardsonii* and *U.*? *cragini* in length of p4 (identified in Fig. 5.1). KUVP 6704 represents an undescribed species, but more complete material will be needed to support a description. Generic assignment was queried because it could represent either a small *Cynomys* or highly derived *Urocitellus*.

Genus *Paenemarmota* Hibbard and Schultz, 1948
Paenemarmota barbouri Hibbard and Schultz, 1948

1948   *Paenemarmota barbouri* Hibbard and Schultz, p. 19, pls. 1–3.

Holotype.—KUVP 6994, left lower jaw with I, p4-m3. KUVP Locality 22, Rexroad Formation, sec. 34, T.34S., R.30W (Hibbard and Schultz, 1948).

Remarks.—*Paenemarmota* includes giant ground squirrels from the late Miocene and Pliocene (Fig. 6.1; Goodwin, 2008). *Paenemarmota barbouri* Hibbard and Schultz, 1948 had an estimated body mass of ~16 kg, extrapolated from length of p4 (Goodwin and Bullock, 2012), and was present at Fox Canyon within the Meade Basin sequence (Table 1).

Paenemarmota sawrockensis (Hibbard, 1964)

1964   *Marmota sawrockensis* Hibbard, p. 118, fig. 1.
1988   *Paenemarmota sawrockensis* Voorhies, p. 168, figs. 3, 4.

Remarks.—*Paenemarmota sawrockensis* (Hibbard, 1964) differed from *P. barbouri* in smaller size (Table 2, estimated body mass ~10 kg; Goodwin and Bullock, 2012), less molariform p4, and more elevated point of attachment of the metalophid on the metaconid (Voorhies, 1988). It was present at Sawrock Canyon within the Meade Basin.

Recognition of *P. sawrockensis* and *P. barbouri* as different lineages rather than temporal variants of a single lineage is supported by the relationship between *P. barbouri* and *Paenemarmota mexicana* (Wilson, 1949). The latter species was present in late Miocene and early Pliocene localities of northern Mexico (summarized in Goodwin, 2008), and shared with *P. barbouri* a molariform p4 and minimally developed metalophid on lower molars. These species were either closely related or conspecific (Repenning, 1962). If this relationship is correct, the *P. barbouri*–*P. mexicana* lineage must be distinct from *P. sawrockensis* because populations of the former lineage were present in the fossil record both prior and subsequent to deposition of the Saw Rock Canyon assemblage with *P. sawrockensis*.

Discussion

Temporal patterns and environmental reconstruction.—The Meade Basin sciurid record is more diverse than previously understood, with at least seven genera and 14 species present in the composite early Pliocene to Late Pleistocene sequence (Table 1). The record is discontinuous (Fig. 2), with fossil assemblages clustering at a few discrete time intervals (Fig. 5), but broad faunal patterns can be inferred.

Extinct giant ground squirrels (*Paenemarmota*) were restricted to the early Pliocene in the Meade Basin, although *P. barbouri* remained on the southern High Plains into the late Pliocene (Dalquest, 1975). In contrast, *I. meadensis* and *O. rexroadensis* persisted through the Pliocene, with the former ranging into the earliest Pleistocene at Borchers (Fig. 5). A second, larger species of *Otospermophilus* was likely also present in the early Pliocene (Fig. 5). Antelope ground squirrel fossils (*Ammospermophilus*) were relatively uncommon, present at two early Pliocene localities, and possibly present in the late Pliocene (Fig. 5.2, Table 1).

The early Pleistocene Borchers assemblage displays a diverse sciurid assemblage with transitional character. *Ictidomys meadensis* persisted from the Pliocene. The larger-bodied *Otospermophilus* was notably absent, but a similar-sized, dentally derived species probably representing the Holarctic genus *Urocitellus* (*U.*? *cragini*) was abundant. Two additional species of *Urocitellus* were likely present, including the lineage leading to the extant *U. richardsonii* (Table 1). Prairie dogs (*Cynomys*) were absent.

The transition between Borchers and slightly younger early Pleistocene faunas in the Meade Basin (e.g., Short Haul, Aries, Rick Forester, and Nash 72) was abrupt, both taxonomically (Table 1) and temporally (Fig. 5). None of the ground squirrels present at Borchers was recorded at higher localities in the same outcrops, although *Urocitellus* cf. *U. richardsonii* returned later in the Pleistocene. *Ictidomys tridecemlineatus* first appeared in the Meade Basin along with an extinct prairie dog, *C. hibbardi*. *Cynomys hibbardi* was present by the late Pliocene in northern

Kansas (Goodwin, 1995b), but apparently did not expand its range southward until the early Pleistocene, essentially coincident with the *Microtus* Schrank, 1798 immigration event in the Meade Basin (Martin et al., 2008).

The composite Middle Pleistocene record from Cudahy and Sunbrite yields a diverse sciurid assemblage distinct from that of the early Pleistocene. *Ictidomys tridecemlineatus* persisted, but was larger in size than early Pleistocene populations, and both *Urocitellus* cf. *U. richardsonii* and Franklin's ground squirrel, *P. franklinii*, were present (Table 1; Fig. 5) well south of their current ranges. Prairie dogs were absent from the rich Cudahy fauna, but two prairie dog species were present at the coeval Sunbrite locality: a large form probably representing an extant lineage, but known only from a single heavily worn upper molar, and a diminutive form representing a new species (Fig. 4.9). The roughly time-equivalent Robin's Roost assemblage from northwestern Oklahoma likewise yielded a large prairie dog. Absence of prairie dogs from Cudahy is puzzling; Cudahy is <25 km from Sunbrite and fossils collected from both localities were excavated from the same limited 20 cm horizon beneath the primary ash-fall of the Lava Creek B Tuff (0.627 ± 0.015 Ma; Mark et al., 2017). Both assemblages share the same species of *Microtus* and other rodents (Martin and Peláez-Campomanes, 2014), suggesting similar paleoecology. We speculate that the absence of prairie dogs from Cudahy may be an artifact of localized taphonomic sampling, which by chance did not encompass a prairie dog town.

Late in the Pleistocene, *I. tridecemlineatus* persisted, but returned to the same smaller size as during the early Pleistocene, *Urocitellus* cf. *U. richardsonii* remained abundant, and *P. franklinii* was present at least intermittently (Table 1). Both black-tailed (*C. ludovicianus*) and white-tailed (*C. niobrarius*) prairie dogs were present, but were not found in the same assemblages (Table 1). A single fossil from the Adams locality demonstrated at least a temporary Late Pleistocene presence of *Otospermophilus* in the Meade Basin, perhaps representing the extant rock squirrel (*O. variegatus*) that today occurs <100 km to the SW.

Two of five Late Pleistocene ground squirrels (*Urocitellus* cf. *U. richardsonii* and *P. franklinii*) disappeared from the Meade Basin near the end of the Pleistocene, but persisted farther north on the Great Plains, and a third (*C. niobrarius*) became globally extinct at this time. The modern Meade Basin ground squirrel community was assembled from the remaining two Pleistocene species (*I. tridecemlineatus* and *C. ludovicianus*), along with the spotted ground squirrel (*Xerospermophilus spilosoma*), with the latter reaching the eastern margin of its modern range in southwestern KS (Streubel and Fitzgerald, 1978a). While the dentition of *X. spilosoma* cannot reliably be distinguished from that of *I. tridecemlineatus*, the consistency of size and characters in Pliocene and Pleistocene *Ictidomys* from the Meade Basin and the current predominantly western and southwestern distribution of *X. spilosoma* suggest that the spotted ground squirrel, like the hispid cotton rat (*Sigmodon hispidus* Say and Ord, 1825) and fox squirrel (*Sciurus niger* Linnaeus, 1758), may be a Holocene immigrant to the basin.

Overall, the record of ground squirrels is congruent with two early Pliocene to Pleistocene trends in paleoenvironments inferred from stable isotopic and faunal evidence in the Meade Basin. First, carbon isotopic investigation of paleosol soil carbonates demonstrates a step-wise increase in regional abundance of C_4 vegetation (mostly grasses) leading to emplacement of essentially modern-type grassland ecosystems in at least some habitats during the early Pleistocene (Fox et al., 2012b). Pliocene squirrels of the Meade Basin were likely granivorous to omnivorous (they lacked dental specializations of small grazers, such as high-crowned, transversely wide cheek teeth; Goodwin, 2009), and, based on modern analogs, at least *Otospermophilus* and *Ammospermophilus* probably occupied shrub to shrub-steppe environments (Oaks et al., 1987; Best et al., 1990a, 1990b; Belk and Smith, 1991). In contrast, species with high-crowned, transversely wider cheek teeth known to occupy grassland ecosystems abruptly appeared in the early Pleistocene (Fig. 5.3), at or just above Borchers, and were dominant in later Pleistocene assemblages (*Ictidomys tridecemlineatus*, *Urocitellus*, and *Cynomys*). A similar pattern is evident in arvicolid rodents—*Microtus*, with ever-growing cheek teeth, first appears in the Borchers Badlands at Short Haul, dated to ca. 2.0 Ma (Martin et al., 2008).

Second, oxygen isotopic analysis of paleosol carbonates suggests an association between the stepwise increase in C_4 abundance and a combination of cooling temperatures, increased winter precipitation, and/or increased soil moisture, with particularly significant change across the Pliocene–Pleistocene transition (Fox et al., 2012a)—a change reflected in the replacement of a more southern-adapted rodent community with one more adapted to temperate conditions (Martin et al., 2008). Based on the distribution and ecology of modern representatives, the same pattern holds for sciurids; Pliocene species with modern congeners either permit (*I. meadensis*) or support (*O. rexroadensis* and *Ammospermophilus* sp.) warmer and/or more-arid paleoenvironments, whereas Pleistocene faunas incorporate species of cooler, more-temperate aspect (*Urocitellus* spp., *Cynomys* spp., *I. tridecemlineatus*, and *P. franklinii*).

The presence of *Ammospermophilus* at two early Pliocene localities slightly younger than Fox Canyon (XIT 1B, Wiens B) may indicate an episode of significant aridity in the early Pliocene. All extant species of *Ammospermophilus* occupy desert habitats (Best et al., 1990a, 1990b; Belk and Smith, 1991), thus it seems probable that fossil *Ammospermophilus* were likewise arid-adapted. This interpretation is consistent with the absence of cotton rats from the Meade Basin during the early Pliocene (Peláez-Campomanes and Martin, 2005), although cotton rats were present at the later Pliocene Rexroad Locs. 2 and 2A, from which *Ammospermophilus* was also tentatively identified. Today, *Sigmodon arizonae* Mearns, 1890 can be found in limited mesic habitat along small streams coursing through Arizona deserts, so the association of *Ammospermophilus* with *Sigmodon minor* Gidley, 1922 during the middle Pliocene could still be consistent with an arid period.

Ictidomys and the Huckleberry Ridge Tuff.—There is growing evidence that eruptions from the Yellowstone Caldera, resulting in huge accumulations of volcanic ash hundreds of km from the source, contributed to disruption of community structure and influenced cladogenesis in the Meade Basin rodents (Martin and

Peláez-Campomanes, 2014; Martin, 2016). The rapid dwarfing in *Ictidomys* from Borchers to slightly higher assemblages, such as Short Haul, Aries A, and Nash 72, may provide another example. As noted above, because there is a dental shape as well as size change, we interpret the post-Borchers early Pleistocene *Ictidomys* samples to represent immigration of the extant *I. tridecemlineatus*, perhaps originating from populations of *I. meadensis* outside of the Meade Basin as a result of natural selection during the post-ashfall environment. This hypothesis is congruent with similar dwarfing in pocket gopher populations of *Geomys tyrioni*, likely originating from the Borchers *Geomys floralindae* Martin et al., 2011. *Geomys tyrioni* was also recovered from the Short Haul, Aries A, and Nash 72 assemblages, and was replaced by modern-sized *Geomys bursarius* (Shaw, 1800) at Rick Forester. It is conceivable that *I. tridecemlineatus* originated in the Meade Basin, but given the widespread distribution of the Huckleberry Ridge Tuff and the likely wide geographic distribution of *I. meadensis*, the probability that we have recorded the *I. tridecemlineatus* speciation event is very unlikely and, in any case, impossible to distinguish from immigration. The important point is that widespread, devastating ash-falls may have contributed significantly to today's North American rodent diversity.

In conclusion, taxonomic revision of the Meade Basin sciurids results in the recognition of seven genera and at least 14 species, with changing Pliocene–Pleistocene associations consistent with environmental reconstructions made previously on the basis of other rodent clades and geochemical environmental proxies. The rapid size shift in *Ictidomys* and appearance of the modern *I. tridecemlineatus* provides further circumstantial evidence for the influence of volcanic eruptions and subsequent ash-falls on rodent community structure and cladogenesis.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.7h398

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