

**Preliminary study of rodents from the Gollither B Assemblage
of Meade County, Kansas, USA
indicates an intense cold period near the end of the Pleistocene**

Robert A. Martin, Pablo Peláez-Campomanes, and James G. Honey

ABSTRACT

An assemblage of rodents recovered from a thin layer of sediments along Sand Creek on the Gollither Ranch in Meade County, Kansas, indicates that cold steppe conditions likely prevailed for a brief time near the close of the Pleistocene around 12,500 radiocarbon years ago. This environment is suggested by the northern disjunct rodents *Zapus princeps*, *Microtus pennsylvanicus*, *Thomomys* cf. *talpoides* and the presumed cold steppe vole *Microtus (Pedomys) parmaleei*, n. sp., plus the absence of cotton rats. Comparison of meadow vole m1 crown morphology diversity through the late Pleistocene in Kansas shows that the modern pattern of diversity developed in a brief period of 1500 years, possibly during the Younger Dryas interval. A cement-filled prism fold, a feature commonly encountered in extinct species of *Mimomys* with rooted molars, appears in three rootless first lower molars of *Microtus pennsylvanicus*. The Gollither B assemblage helps to fill in the late Pleistocene history of rodents in the ongoing Meade Basin Rodent Project.

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INTRODUCTION

In an attempt to determine the timing and possible environmental influences for diversity changes in the terrestrial and freshwater molluscan fauna of the central Great Plains, Miller (1975) ana-

lyzed the species abundances, distributions and habitat tolerances of a series of radiocarbon-dated fossil mollusc assemblages from southwestern Kansas and northwestern Oklahoma. He examined seven assemblages ranging in time from about 30,000 – 10,500 radiocarbon years ago. (In the

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FIGURE 1. Upper part of outcrop along Sand Creek, Meade Co., Kansas, showing the zone (Level B) from which the Gollither B rodents were excavated. Vertical black line on rulers equals 10 cm.

present paper an assemblage, or local fauna (l.f.), and the site name from which the specimens were collected are used synonymously.) During the summers of 2004-5, the authors sampled three of these localities, Bird, Boyd and Classen, for rodent fossils as part of the Meade Basin Rodent Project, a long-term study designed to examine the history of rodent biodiversity in southwestern Kansas and northwestern Oklahoma (Martin et al. 2000; 2002; 2003; Peláez-Campomanes and Martin 2005;

Honey et al. 2005). The zones we sampled at the Bird and Boyd localities produced meager fossils, but we discovered a very rich layer for small mammals in the outcrop that produced Miller's Classen molluscan fauna. In order to avoid confusion with the Classen faunule of the Jones l.f. (Davis 1987) we here rename Miller's Classen l.f. the Gollither l.f. in honor of the current owners of the property. The organismal assemblage we report here is referred to as the Gollither B local fauna, taken from a thin

stratum above the layer of Miller's molluscan sample, the latter which will be known as the Gollither A l.f. (Figure 1). Stratigraphy of the Sand Creek section producing the fossils is described below. In addition to the stratigraphy, we will present a rodent species list from level B in the Gollither section and argue that some indicate an intense cold period near the end of the Pleistocene. An ancillary examination of variation in the crown pattern morphology of meadow vole molars from Gollither B shows that the modern crown morphology pattern in *M. pennsylvanicus* developed in a remarkably brief period of time during the late Pleistocene.

GEOLOGICAL SETTING

Late Pleistocene sediments in Meade County have occasionally been referred to formations named for sediments of this approximate age in Clark County (e.g., Kingsdown, Vanhem; Hibbard and Taylor 1960), but we doubt this nomenclature can be extended to Meade County and currently view such accumulations as localized basin-fill deposits (Martin et al. 2000). The Gollither quarries are located along about 20 m of a partly exposed bank on the north side of Sand Creek, Meade County, on the property of Dave and Kathy Gollither.

Measured section along Sand Creek at Gollither quarries in NW NE SW, Sec. 3, T. 33 S, R. 27 W, Meade County, Kansas. Measured by J. Honey, P. Peláez-Campomanes and R. Martin.

Top of Section	Thickness (m)
6. Very fine-grained sandy silt, pale yellowish brown (10YR 6/2; GSA rock color chart); lightly blocky and crumbly, contains rare quartz pebbles, some scattered white CaCO ₃ mottling at base of roots. Grades upward into 13 cm of modern soil	1.15
5. Light gray (N7) massive clayey silt, granular, crumbly; CaCO ₃ mottling at base of roots; scattered molluscs; sediments with dark yellowish-orange scattered mottling	0.45
4. Granular, crumbly brownish black (5 YR 2/1) clayey silt; scattered small CaCO ₃ nodules; blocky, soil-like with scattered molluscs	0.30
3B. Light olive-gray (5Y 5/2) silty clay, granular; crumbly. Scattered molluscs. Bone common. Source of Gollither B local fauna and radiocarbon date of 12,510 ± 80 years B.P.	0.57
3A. Very fine-grained pale olive (10Y 6/2) sandy clay fining upwards into unit above; massive vertical structure with scattered molluscs and root traces	0.24

2. Dark yellowish gray (5Y 7/2) to light olive-gray (5Y 5/2) fine-grained silty sands, clayey, massive; with floating quartz pebbles, and small CaCO₃ nodules in lowest 11 cm.

Yellowish-orange mottling common. Root traces and molluscs common. Source of Miller's mollusc assemblage and radiocarbon date of 16,100 ± 250 years B.P.

1.30.

Irregular contact

1. Dark yellowish-orange (10 YR 6/6) unconsolidated sand and gravel.

Not measured.

METHODS, MEASUREMENTS AND ABBREVIATIONS

Rodent specimens were recovered from the Gollither B zone using the collection and washing methods described for previous field seasons of the Meade Basin Rodent Project (e.g., Martin et al. 2002, 2003). Approximately one and one-half tons of matrix were washed to extract the rodent remains in 2004 and 2005.

Dental measurements were made with an ocular micrometer and binocular microscope, calibrated with an AO 2.0 mm slide. Measurements are greatest occlusal lengths and widths taken only on adult molars. Uppercase letters indicate upper dentition; lower case, lower dentition. Left and right are indicated by L and R, respectively. T = a triangle on an arvicolid molar. Arvicolid dental terminology follows van der Meulen (1973), Rabeder (1981) and Martin (1987). Five- and six-triangle m1 morphotypes (5T, 6T, respectively) of *Microtus pennsylvanicus* were scored as in Martin and Prince (1989; figures 1, 2); an m1 was recorded as a 6-T form if no distinct band of reparative dentin connected T6 to the anteroconid, even if the external enamel bands from buccal reentrant angle 4 (BRA4) and lingual reentrant angle 4 (LRA4) were not touching.

Specimens are catalogued in the Fort Hays Sternberg Museum (FHSM). Other abbreviations appearing in the text are as follows: CM = Carnegie Museum of Natural History; UT = McClung Museum, University of Tennessee. The material from Yarbrough Cave, Georgia, collected while the senior author was teaching at Berry College (BC), has been donated to the Florida State Museum and will eventually bear FSM numbers. Average calendar year B.P. ages were generated from ¹⁴C years B.P. using the CalPal calibration program at www.calpal-online.de/index.html.

RODENT PALEONTOLOGY

The following is a list of rodent taxa identified from Gollither B:

TABLE 1. Rodent species from select Pleistocene local faunas of the Central Great Plains. N = northern Kansas or southern Nebraska, S = southern Kansas or Oklahoma.

See Table 2 for local fauna ages.

	Cudahy (S)	Jinglebob (S)	Tesequite (S)	Taylor (S)	Jones (S)	Washita (S)	Coon Crk (N)	Duck Crk (N)	Trapshoot (N)	N Cove (N)	Gollifer B (S)	Elm Crk (S)	Robert (S)	Domebo (S)	Modern KS (S)
RODENTIA															
<i>Sciuridae</i>															
<i>Eutamias sp.</i>										x					
<i>Tamias quadrivittatus</i>			X												
<i>Tamias striatus</i>												x			
<i>Tamiasciurus hudsonicus</i>										x					
<i>Spermophilus franklinii</i>	cf		X		x							x			K
<i>Spermophilus tridecemlineatus</i>	cf			cf	x							x	x		x
<i>Spermophilus richardsoni</i>	x				x		x	x		x			x		
<i>Spermophilus spilosoma</i>															x
<i>Spermophilus sp.</i>		x		x				x			x				
<i>Cynomys ludovicianus</i>			X			x						x			x
<i>Cynomys sp.</i>					x								x		
<i>Marmota flaviventris</i>										x					
<i>Geomyidae</i>															
<i>Geomys bursarius</i>	cf							x				x		x	x
<i>Geomys sp.</i>		x		x	x								x		
<i>Thomomys talpoides</i>								x	cf		cf	x	cf		
<i>Thomomys bottae</i>			X												
<i>Thomomys sp.</i>	x			x	x		x			x					
<i>Heteromyidae</i>															
<i>Dipodomys ordii</i>			cf												x
<i>Perognathus flavescens</i>															x
<i>Perognathus flavus</i>				X											x
<i>Perognathus sp.</i>		x		x	x										
<i>Chaetodipus hispidus</i>		x												x	x
<i>Cricetidae</i>															
<i>Onychomys leucogaster</i>		x		cf	x						cf				x
<i>Reithrodontomys megalotis</i>															x

TABLE 1 (continued).

<i>Reithrodontomys montanus</i>	cf			x				cf		x
<i>Reithrodontomys sp.</i>							x		x	
<i>Peromyscus leucopus</i>							x		x	x
<i>Peromyscus maniculatus</i>		X					x		x	x
<i>Peromyscus sp.</i>	x		x	x			x			
<i>Oryzomys palustris</i>	x									
<i>Neotoma micropus</i>								cf		x
<i>Neotoma floridana</i>						x				
<i>Neotoma sp.</i>	x									x
<i>Sigmodon hispidus</i>										x
<i>Arvicolidae</i>										
<i>Ondatra zibethicus /annectens</i>	x									
<i>Ondatra zibethicus /zibethicus</i>									x	x x
<i>Phenacomys intermedius</i>						x	x	x	x	
<i>Clethrionomys gapperi</i>						x	x	x	x	
<i>Mictomys meltoni</i>	x									
<i>Mictomys sp.</i>				x						
<i>Synaptomys australis</i>	x									
<i>Synaptomys cooperi</i>								cf		x x x
<i>Synaptomys borealis</i>						x	x		x	
<i>Microtus paroperarius</i>	x									
<i>Microtus meadensis</i>	x									
<i>Microtus llanensis</i>	x									
<i>Microtus pennsylvanicus</i>		x	X	x	x		x	x	x	x x x
<i>Microtus xanthognathus</i>							x			x
<i>Microtus montanus</i>							x		x	x
<i>Microtus ochrogaster</i>		x	X		x	x		x	x	
<i>Microtus parmaleei</i>									x	cf
<i>Microtus sp.</i>										x
<i>Dipodidae</i>										
<i>Zapus princeps</i>							x		x	x cf

Family Sciuridae

Spermophilus sp. – ground squirrel

Family Geomyidae

Thomomys cf *talpoides* – northern pocket gopher

Family Arvicolidae

Microtus pennsylvanicus – meadow vole*Microtus (Pedomys) parmaleei*, n. sp. – Parmalee's steppe vole

Family Cricetidae

Onychomys cf *leucogaster* – southern grasshop-

TABLE 2. Sites from the text and Table 1, and their presumed or determined ages.

	¹⁴ C B.P.	Cal. Yrs B.P.
Cudahy, KS		670,000 yrs. B.P.
Jinglebob, KS		?70,000
Tesequite Canyon, OK	31,360 ± 570	35,466 ±640
Taylor, KS		?30,000
Jones (<i>Ambystoma faunule</i>), KS	26,700 ± 1500	31,328±1418
	29,000 ± 1300	33,367±1070
Washita, KS	18,295 ± 270	21,947 ±396
	16,350 ± 730	19,702 ±823
Coon Creek, KS	17,930 ± 360	21,526 ±598
Duck Creek, KS	17,700 ± 350	21,224 ±568
Trapshoot, KS	?17,000	
Golliher C, KS	16,100 ± 250	19,312 ±367
North Cove, NE	14,770 ± 100	18,107 ±309
Golliher B, KS	12,510 ± 80	14,826 ±312
Elm Creek, OK	11,410 ± 110	13,314 ±164
Robert, KS	11,000 ± 390	12,838 ±458
Domebo, KS	11,220 ± 220	13,133 ±231
	11,200 ± 600	13,074 ±767
Boyd, KS	10,790 ± 280	12,619 ±371

per mouse

Peromyscus sp. – white-footed or deer mouse*Reithrodontomys cf montanus* – Plains harvest mouse

Family Dipodidae

Zapus princeps

The Golliher B rodent assemblage is compared with a few radiocarbon-dated rodent assemblages from southern Nebraska, Kansas and Oklahoma in Table 1. Dates for these localities are provided in Table 2. The rodents of an earlier, cold-adapted fauna (Cudahy; Paulson, 1961), those of the Jinglebob l.f. (Hibbard 1955) and the modern rodent fauna of Meade County are also listed. The Jinglebob l.f. of Meade County, Kansas, lacks a radiometric date, and its fauna is not sufficient to establish a precise age, though it was most recently allocated to the “Wisconsinan” by Miller (1975). The combined presence of *Microtus pennsylvanicus*, *M. ochrogaster* and the extinct *Synaptomys australis* certainly suggest a late Pleistocene (Rancholabrean) age, and likely younger than assemblages such as Butler Spring and Mt. Scott (Schultz 1969). The extralimital record of *Oryzomys palustris* also suggests that Jinglebob was deposited during a relatively warm period, and it provides a useful contrast both for the earlier Cudahy l.f. with its host of extinct arvicolid and the radiocarbon-dated sites in Table 1 with their boreal affinities. Those species of climatic importance from Golliher B are considered individually below.

Family Geomyidae

Thomomys cf talpoides – northern pocket gopher**Material examined.** FHSM 17027, Lp4, LM3; FHSM 17028, Lp4, L upper molar.

Discussion. *Thomomys* species are easily diagnosed by upper incisors without grooves and p4 with V-shaped reentrant folds lacking cement. The lower molars also tend to be asymmetrical, or “tear-dropped” shaped, and have enamel on both leading and trailing edges. *Thomomys* first appears in the Cudahy l.f. at 0.64 Ma (Paulson 1961), associated with other species indicating a cold temperate climate, and it is present in all later Pleistocene faunas subsequent to Jinglebob (Hibbard 1950). The Jinglebob l.f. was first considered by Hibbard (1950) to be of “Sangamon” age, but it was later placed by Miller (1975) in a later, colder period of the late Pleistocene. Without radiometric dates the age of this site cannot be secure, and despite Miller’s (1975) analysis, the presence of the rice rat *Oryzomys palustris* and southern bog lemming, *Synaptomys australis*, suggest that if the fauna accumulated during the latest Pleistocene, it was probably during a warm interstadial period.

Schultz (1969) tentatively identified the northern pocket gopher, *Thomomys talpoides*, from the late Pleistocene Robert l.f., and based on zoogeographic considerations and other disjunct species in the various Meade Basin assemblages indicating cooler conditions, this is the most likely species

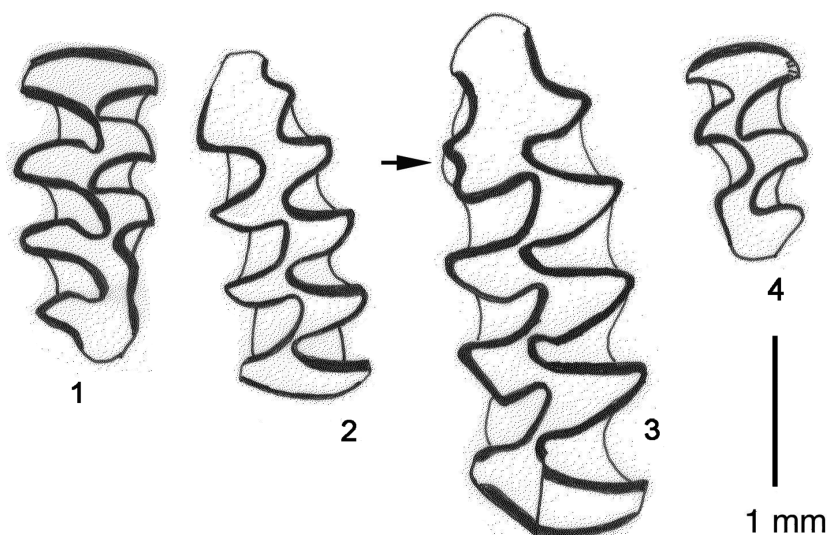


FIGURE 2. First lower and upper third molars of *Microtus pennsylvanicus* (2.1, FHSM 17019 Lm1; 2.2, FHSM 17031 LM3) and *Microtus (Pedomys) parmaleei* (2.3, FHSM 17023 holotype Lm1; 2.4, FHSM 17026 paratype RM3). Note cement-filled prism fold (arrow) in 2.3; this valley is filled with cement to the base of the tooth.

to have been present in Kansas during the late Pleistocene. The northern pocket gopher today has outlier populations in eastern Nebraska and eastern Colorado. Nevertheless, at some point it would be helpful if dental or mandibular characters could be identified to distinguish between *T. talpoides* and its southern relative *T. umbrinus*.

Family Arvicolidae

Microtus pennsylvanicus – meadow vole
(Figures 2.1 and 2.2)

Material examined. FHSM 17019, Lm1; FHSM 17020, Rm1; FHSM 17021, 18R, 14L m1s; FHSM 17022, 25R, 12L m1s; FHSM 17030, part Rm1; FHSM 17031, 12 L, 7 R M3s; FHSM 17597, 7L, 3R M2s; FHSM 17599, R mandible with m1-m2.

Discussion. Like *Thomomys*, the meadow vole is a ubiquitous presence in Meade Basin assemblages of late Pleistocene age. *M. pennsylvanicus* can be identified given adequate sample sizes of m1, M2 and M3. An M2 with incipient or closed triangle 4 (T4) is particularly diagnostic (Zakrzewski 1985; Davis 1987; Semken and Wallace 2002), although this feature does appear occasionally in other species (Bell and Repenning 1999). Ten of

TABLE 3. Measurements (in mm) of *Microtus pennsylvanicus* first lower molars from Gollieher B. N = number of specimens, s = standard deviation, O.R. = observed range.

	N	Mean	s	O.R.
Length m1	47	2.97	0.19	2.55-3.51
Width m1	48	1.14	0.07	0.96-1.36

the 14 M2s from Gollieher B examined in the size range of *M. pennsylvanicus* possessed this extra triangle. In a large sample of *Microtus* M2s from the upper *Ambystoma* faunule of the Jones l.f. of Meade County, Kansas ($26,700 \pm 1500$ and $29,000 \pm 1300$ years B.P.), Davis (1987) also noted some specimens without T4, and he speculated on the presence of another *Microtus* other than *M. pennsylvanicus* and *M. ochrogaster*, both of which he had identified from the *Ambystoma* faunule. Stewart (1987) reported *Microtus montanus* from a few late Pleistocene sites in northern Kansas and Nebraska. Conceivably, another *Microtus* species could be present in the Gollieher B l.f. in addition to *M. pennsylvanicus*, but it is also possible that there is either 1) an evolutionary tendency towards greater expression of T4 through time in the meadow vole or 2) geographic polymorphism within extant populations that has not been quantified, or both. Davis (1987), building on preliminary data presented by Semken (1966), documented clinal variation in the number of triangles on m1 in extant North American *M. pennsylvanicus*, with the most complex m1s found on specimens from the Central Great Plains. This complexity evolved through the late Pleistocene. Perhaps polymorphism and evolutionary change can also be documented for the M2. Measurements of a sample of *M. pennsylvanicus* m1s from Gollieher B are presented in Table 3.

Davis (1987) documented a shift in meadow vole m1 morphotype diversity on the Central Great

TABLE 4. Chronological sequence of 5- and 6-triangle m1 morphotypes (5T, 6T) in *Microtus pennsylvanicus* from Kansas. Data for samples other than Gollhofer B from Davis (1987). N= number of specimens, % = percent.

Sample	N	%5T	%6T
Modern (KS, NE, COL. NM)	116	30.1	65.5
Robert (11,000± 390)	58	36.3	62.0
Gollhofer B (12,510± 80)	60	67.0	33.0
Jones (<i>Ambystoma faunule</i>) (26,700± 1300, 29,000± 1300)	112	71.0	23.0
Mt. Scott	259	74.0	25.0
Sandahl	22	100	0

Plains, from 100% 5T forms in the late Pleistocene Sandahl l.f. through 30.1% 5T forms in extant populations. Dates are not available for the Sandahl and Mt. Scott l.f.s, but they are probably older than the Jones l.f. and definitely younger than the Cudahy l.f. (Paulson 1961) at 0.64 Ma. Part of Davis's (1987, table 8) summary is reproduced chronologically in Table 4, with comparable data for a sample from Gollhofer B (some of Davis's totals do not add to 100% because he also counted 7T forms separately and additionally has an undefined category labeled "other"). These data show that the switch from 0.67/0.33 (5T/6T) to 0.33/0.67 (5T/6T) populations occurred in Kansas in a remarkably brief 1500 year period between 12,500-11,000 radiocarbon years ago. The modern proportional representation is seen in the Robert l.f. at 11,000± 390 radiocarbon years B.P., just at the beginning of the Younger Dryas (YD) event. It is tempting to speculate that the dramatic YD climatic environment played a part in selecting for the final m1 configuration in *M. pennsylvanicus* on the Central Great Plains, but if so the YD event did not similarly influence meadow vole populations elsewhere within the species' geographic range.

Davis's (1987) Figure 12 shows that closure of T6 on m1 in extant *M. pennsylvanicus* is most common on the Central Great Plains; populations to the north, east and west more commonly display five closed triangles on m1. Martin and Prince (1989) showed that the proportion of 5T m1s in *M. pennsylvanicus* from Bell Cave in northern Alabama averaged 79% between about 26,500-11,800 radiocarbon years B.P., and Gordon (1999) reported an average of 93% 5T forms in 13 levels from Yarbrough Cave, Georgia, ranging from about 23,880-16,500 radiocarbon years B.P. Although the meadow vole resides today farther north in the southern Appalachians than either Bell Cave or Yarbrough Cave, from Davis's (1987) and Gordon's (1999) data, we could expect the modern eastern proportion to range between 70-100% 5T forms. Thus, it appears that eastern meadow vole populations retained the ancestral proportion of 5T mor-

photypes through the later Pleistocene into modern time, as Semken (1966) had earlier hypothesized. Davis (1987) speculated that the higher complexity of Great Plains meadow vole m1s was correlated both with greater tooth length and foraging on a higher proportion of harsh grasses. Martin and Prince (1989) and Gordon (1999) found no correlation between m1 length and closure of T6 in the Bell Cave and Yarbrough Cave samples of *M. pennsylvanicus*, and as there has been no quantitative assessment of diet and dental size or complexity in meadow voles, we cannot be certain of the factors contributing either to variation in the modern populations or the rapid shift from 5T to 6T morphotypes on the Great Plains during the latest Pleistocene.

The earliest appearance of *M. pennsylvanicus* in the Meade Basin is in the late Pleistocene (Rancholabrean) Adams l.f. in Meade County (Schultz 1969), and it is present in the region until it becomes locally extinct during the Holocene. In the Central Great Plains and nearby regions, the meadow vole is found today only in extreme northern Kansas and at higher elevations in Colorado and northern New Mexico, about 300 km from Meade County. Its local extirpation in southwestern Kansas appears to be roughly synchronous with the Holocene immigration of the hispid cotton rat, *Sigmodon hispidus*, both events roughly correlated with the beginning of the current interstadial warm period.

Among many first lower molars of *M. pennsylvanicus* recovered from Gollhofer B, there were three demonstrating an unusual morphology. In these specimens, a prism fold filled with cement is present (Figure 2). This feature is characteristic of *Mimomys* species with rooted molars. Rather than representing an ancient population preserving archaic characters, we suspect these specimens represent individuals in which part of the ancestral epigenetic system became functional once again. Zakrzewski (1985) also reported a prism fold in an m1 of extant *M. longicaudus*.

Microtus (Pedomys) parmaleei, new species

(Figures 2.3 and 2.4)

Holotype. FHSM 17023, Lm1.

Paratypes. FHSM 17024, part Lm1; FHSM 17025, part Lm1; FHSM 17026, 2 Rm2, 1L and 1R M2; 2R and 1L M3.

Referred specimens. The fossil material listed as *Microtus ochrogaster* in Martin (1991) from the following localities in the eastern United States: Yarbrough Cave, Georgia (BC 291 -- 4 Lm1, 1 R mandible; BC 292 -- 2 L mandibles, 6L and 2 R m1s; BC 293 -- 1 R mandible). Cheek Bend Cave, Tennessee (UT 135-79 -- 9 m1s; UT 113-79 -- 5 m1). Clark's Cave, Virginia (CM 24524 -- 1 L and 1 R mandible, 6 L and 3 R m1s). Natural Chimneys, Virginia (CM 7505 -- 3 R and 5 L mandibles; 18 R and 13 L m1s). The *Microtus ochrogaster* material listed by Schultz (1969) from the Robert I.f. (UM-K1-57) of Meade County, Kansas: UMMP 46016, 41469 (two right mandibles), UMMP 41470 (isolated molars).

Locality and horizon. Level B of the Gollither sequence along Sand Creek, Meade County, Kansas, $12,510 \pm 80$ ¹⁴C years B.P. (latest Pleistocene).

Diagnosis. A small *Pedomys* characterized by a combination of m1s with primitive and advanced m1 morphotypes; BRA4 and LRA5 are often absent to poorly developed and devoid of cementum. Separable from modern *M. ochrogaster* by smaller size and greater proportion of primitive m1 morphotypes. Differs from *M. ochrogaster llanensis* on basis of considerably smaller size.

Discussion. Among the numerous remains of arvicolid rodents from Gollither B, the vast majority of which were identified as *Microtus pennsylvanicus*, the meadow vole, were 10 molars from a diminutive member of the subgenus *Pedomys*. This small vole presents an enigma, as two of three m1s demonstrate a relatively primitive morphology compared to that of the modern *Microtus (Pedomys) ochrogaster* from Meade Kansas as well as some prairie vole specimens recovered from older Wisconsinan sediments in Meade County (e.g., Butler Spring, Schultz 1969). In size and morphology the small *Pedomys* from Gollither B approximates exactly a series of *Pedomys* samples from Wisconsinan localities in the eastern United States that Martin (1991) identified informally as Parmalee's steppe vole, described in the literature as a chronomorph of *M. ochrogaster*, *M. o. lparmaleei* (Martin et al. 2008). The size of the single complete m1, FHSM 17023 (Figure 2), is 2.31 mm long by 0.88

mm wide. In morphology, two of the three m1s (FHSM 17023, 17024) display three closed triangles, T4-5 confluent and a simple anteroconid (acd) in which buccal reentrant 4 (BRA4) is undeveloped and lingual reentrant 5 (LRA5) is shallow and lacks cement. Both reentrants are developed in FHSM 17025; BRA4 is filled with cement but LRA5 is not. This sort of variation is common in the *M. o. lparmaleei* from such localities as Yarbrough Cave, Georgia, Clark's Cave, Virginia, Natural Chimneys, Virginia, and Cheek Bend Cave, Tennessee (Martin 1991). The specimens reported by Schultz (1969) from the Robert I.f. as *M. ochrogaster* are small and are also referred to Parmalee's steppe vole.

Van der Meulen (1978) proposed that the extant prairie vole, *Microtus ochrogaster*, evolved from the early Pleistocene *M. guildayi*, through an intermediate species *M. llanensis* that Hibbard had named from the Cudahy I.f. (Hibbard 1944). To reflect a more biological nomenclature of phyletic series, Martin (1995) synonymized *M. guildayi* with *M. pliocaenicus* and *M. llanensis* with *M. ochrogaster*, reducing the taxa to the informal chronomorphs arranged in the following lineage: *M. p. l guildayi* -- *M. o. llanensis* -- *M. o. lochrogaster*. He also presented a preliminary phylogenetic analysis for *Pedomys*. While correct in essence (inasmuch as a binomial system can ever represent a complex evolutionary population dynamic), the evolution of modern prairie vole populations was probably not that simple.

The prairie vole today exhibits a reverse Bergmann's response, with the smallest populations residing in southern Canada and the northern United States in primarily boreal habitat. The diminutive northern populations are recognized as the subspecies *M. o. minor*. As noted above, samples of small prairie voles are commonly encountered in late Wisconsinan Appalachian fossil assemblages noted for their boreal rodent indicators, including *Microtus xanthognathus*, *Phenacomys intermedius* and *Synaptomys borealis* (Guilday 1962; Guilday et al. 1977; Martin 1991). Occasionally, samples of larger individuals are recorded from Appalachian faunas at the same time (Martin 1991). First lower molars of the small individuals include specimens that are basically indistinguishable from those of *M. llanensis*, which are themselves only slightly advanced over *M. p. l guildayi*. Nevertheless, also among both the small Wisconsinan *Pedomys* and *M. llanensis* are some specimens indistinguishable from modern *M. ochrogaster* (Martin 1991, 1995). To make matters

more interesting, as Martin (1991) demonstrated, the small extant northern *M. o. minor* have the most complex m1s among living *M. ochrogaster*. So how do we interpret these Wisconsinan populations of small size and relatively primitive morphology? There are at least three possibilities: 1) the small animals represent a distinct, dwarf, sibling species (*M. parmaleei*) of *M. ochrogaster* with cold steppe and boreal affinities that became extinct throughout its range prior to the Holocene, 2) the small animals represent dwarf *M. o. Illanensis* that gave rise to *M. o. minor*, and as climate changed at the end of the Pleistocene they retreated to northern refugia and finalized the push for complex dentitions, or 3) the extant *Microtus ochrogaster minor* is actually a distinct species, *M. minor*, descended from dwarf *M. o. Illanensis* (= *M. o. Iparmaleei*). In scenarios 1 and 3, it is conceivable that van der Meulen's *M. p. Iguildayi* was ancestral to the diminutive species (*M. parmaleei* or *M. minor*), and that *M. ochrogaster* evolved from larger-sized Great Plains *M. pliocaenicus* through *M. o. Illanensis*. First lower molars of *M. p. Iguildayi* are decidedly smaller than those of *M. Illanensis*, thus at least giving some credence to this idea. Currently, it is difficult to test these hypotheses. A modern genetic analysis comparing *M. o. minor* and other *M. ochrogaster* subspecies would be helpful. Our current evaluation is that the samples of small *Pedomys* m1s with a high percentage of archaic morphotypes that appear in late Wisconsinan assemblages, known by independent criteria to have existed during much colder climatic periods relative to modern time, represent a distinct species *M. (Pedomys) parmaleei*. In the Meade Basin it replaced earlier, large-sized *Pedomys* referable to *M. ochrogaster*, and was later replaced by larger-sized *M. ochrogaster* in the modern rodent community of the same region. The same interpretation can be applied to late Pleistocene Appalachian assemblages. Consequently, *M. parmaleei* can be added to a small list of rodent species that generally indicate colder environments. In the east, this coterie would likely be representative of boreal or sub-boreal conditions, whereas on the Central Great Plains the environment probably ranged from boreal forest in the north to cold steppe in the south (southern Kansas and northern Oklahoma and Texas).

Family Dipodidae

Zapus princeps – western jumping mouse

Material examined. VP 17029, 1L and 1R m1.

Discussion. Jumping mice have been present in the Meade Basin since the earliest Pliocene (Fox Canyon; Hibbard 1950; Klingener 1963). Because their populations are not high in extant rodent communities, they are rarely common in fossil deposits, and their absence from any given Meade Basin assemblage is more likely an artifact of sampling rather than a climatic signal. Klingener (1963), Martin (1989, 1994) and Ruez and Bell (2004) reviewed the record of North American Pliocene and Pleistocene zapodids and presented characters used to distinguish the modern and extinct species. Characters of the first lower molar serve to distinguish the *Zapus princeps* (= *Z. trinotatus*) and *Z. hudsonius* groups. In the former, the anteroconid is a simple cone composed of a dentine island surrounded by an external enamel border. In the latter group, including the extinct *Z. rinkerii*, *Z. sandersi* (= *Z. burti*) and *Z. syksae*, as well as in extant *Z. hudsonius*, there is either a deep antero-medial fold (most species) or a central, isolated enamel atoll (*Z. syksae*). The two m1s present clearly demonstrate the *Z. princeps* morphology, and the Gollifer B *Zapus* is referred to that species. *Zapus princeps* has also been identified from three late Pleistocene sites in northern Kansas and southern Nebraska (Stewart 1987). Schultz (1969) reported *Zapus hudsonius* from the latest Pleistocene Robert l.f., but the only specimen recovered was a mandible with m2, and as the Robert l.f. has other mammalian species indicating a cooler climate (Schultz 1969; pp. 71-72), it may be that this specimen represents *Z. princeps*.

Z. princeps has a modern distribution very similar to that of *Thomomys talpoides*, *Microtus pennsylvanicus* and *Microtus ochrogaster minor*; it is confined to boreal habitats at northern latitudes or at higher elevations in the Rocky Mountain chain to the south, in central Colorado and northern New Mexico.

DISCUSSION

A survey of the literature pertaining to the late Pleistocene small mammals of Kansas and adjoining states, including the excellent reviews of Stewart (1987), Wells and Stewart (1987a, b) and Davis (1987), provides an interesting view of climatic change at the end of the Pleistocene in this region. Table 1 reinforces the conclusion from many other studies that late Pleistocene climate was considerably different from that of today, bringing extralimital modern rodent species, mostly of boreal affinities, into the central Great Plains. These records include ground squirrels, gophers, arvicol-

ids and dipodids. The faunas represented in Table 1 range in age from about 31,000 to around 11,000 radiocarbon years B.P. The invasion of a group of species including the red-backed vole (*Clethrionomys gapperi*), yellow-cheeked vole (*Microtus xanthognathus*), boreal lemming (*Synaptomys borealis*) heather vole (*Phenacomys intermedius*), northern pocket gopher (*Thomomys talpoides*), motane vole (*Microtus montanus*) and the western jumping mouse (*Zapus princeps*) onto the Great Plains seems to have mostly occurred after the deposition of the Jones l.f. of Meade County, Kansas, dated at 27-29,000 years B.P. and also, at least in central Oklahoma, subsequent to the deposition of the Washita l.f. with radiocarbon dates ranging from 16-18,000 years B.P. (Kirkland et al. 2000). However, some of these boreal indicators were present in the Coon Creek l.f. of northern Kansas 18,000 years ago (Stewart 1987), and may simply not have reached central Oklahoma at this time. Twelve thousand five hundred years ago, the association of rodents at Gollieher B in southwestern Kansas indicates that cold steppe conditions were likely present at this latitude. Assuming that *M. parmaleei* had environmental requirements similar to that of the modern diminutive subspecies *M. o. minor*, the “area of sympatry,” or area where most of the rodents of the Gollieher B l.f. all overlap today, is in southeastern North Dakota. The western harvest mouse, *Reithrodontomys montanus*, is restricted to the northern Great Plains, but does extend into southern North Dakota.

Patterns indicated from the mammals are generally substantiated by molluscan and pollen studies on the Great Plains covering the same time periods and, in the case of the Gollieher B l.f., from the same outcrop. Miller (1975) compared the molluscs from a sequence of radiocarbon-dated sites in southwestern Kansas and northwestern Oklahoma, including our level A of the Gollieher sequence. A radiocarbon date of $16,100 \pm 250$ years B.P., about 4,000 years older than level B, was obtained for this unit. The molluscs from Level A were dominated by cold-adapted species with southern distributions controlled by high summer temperatures (42%, as compared with 7% in that category today). According to Miller (1975), there was a gradual decrease in these species and an increase in species of southern affinities through the late Pleistocene, with a particularly emphatic shift in the last 10,000 years. Both the Jones and Robert l.f.s also maintain a high percentage of northern mollusc species, testifying to the pres-

ence of cool summer temperatures through the latest Pleistocene.

Pollen profiles are unfortunately not available for the Gollieher sequence, but published reviews of late Pleistocene palynology for the Great Plains and Missouri Ozarks (King 1973; Fredlund and Jaumann 1987) clearly demonstrate the presence of boreal conditions during “Woodfordian” time (~22,000-10,000 years B.P.). White spruce has been recovered from a peat dated at $19,340 \pm 200/210$ years B.P. near Wichita, Kansas. Spruce and arboreal pollen dominate in the North Cove site in southern Nebraska (Table 1). Wells and Stewart (1987a) reported Rocky Mountain limber pine (*Pinus flexilis*) and spruce from sites in Graham (Coon Creek; see Table 1) and Logan Counties (unnamed; no small mammals-- $10,245 \pm 335$ years B.P.), northwestern Kansas. Wells and Stewart (1987a, b) also confirmed changes in the land snail fauna first observed by Miller (1975). As they note (p. 131):

“Perhaps the outstanding event of the North American molluscan history in the late Quaternary was the virtual disappearance of this [northern, “pleniglacial”] land-snail fauna from upland habitats of the Great Plains.”

Further, on the same page, they observe:

“Aside from the deciduous-forest species, all of the landsnails that suffered extinction on the Plains survived in the Rocky Mountains...”

In their review of the history of cotton rats, genus *Sigmodon*, in the Meade Basin, Peláez-Campomanes and Martin (2005) noted that cotton rats were absent from the known Wisconsinan-age assemblages. As mentioned above, the extant hispid cotton rat, *S. hispidus*, was apparently a Holocene immigrant into the Basin, characterizing the current interstadial warm period. The small mammal fauna at Gollieher B 12,510 Years B.P. (= 14,826 calendar years ago) is consistent with these reports and provides further documentation of the considerable changes in climate and habitat that have occurred in southwestern Kansas since the deglaciation phase of the latest Pleistocene.

In summary, rodent, mollusc and botanical assemblages from the Meade Basin of southwestern Kansas and adjoining regions document a period of extreme climatic conditions and associated habitat modification on the Central Great Plains near the close of the Pleistocene. Further collecting from among a series of latest Pleisto-

cene sections in Meade County may help reveal the intricacies of environmental and climatic change at the Pleistocene-Holocene boundary, thus providing important background data for comparison with global climatic changes during modern time.

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Comment from R. Martin—stimulating correspondence with the late Charles Repenning was occasionally the catalyst for some of my best work, and despite our differences of opinion on many issues, I will miss his astute observations and amazingly detailed and helpful reviews of my papers.

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