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Rodent community change at the Pliocene–Pleistocene transition in southwestern Kansas and identification of the *Microtus* immigration event on the Central Great Plains

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ABSTRACT

A dense fossil rodent database and new paleomagnetic data from the Meade Basin of southwestern Kansas document the transition from a Pliocene community characterized by cricetids of southern aspect and archaic arvicolids with rooted molars to a Pleistocene community with cricetids of temperate aspect and arvicolids with ever-growing molars. This new information suggests a revised date for the Blancan–Irvingtonian North American Land Mammal Age boundary between 2.06 and 1.95 Ma, coincident with the extinction of the *Sigmodon minor* lineage and the immigration of *Microtus*. Carbon and oxygen isotope compositions of paleosol carbonates indicate the faunal changes occurred during the final expansion of C_4 grasses in the Great Plains to modern abundance and a strong cooling trend reflecting the end of the early Pliocene warm interval and onset of northern hemisphere glaciation. Although extinctions balance originations through the study period, pulses of enhanced extinction and origination occurring near the Pliocene–Pleistocene boundary strongly suggest environmental change as the likely forcing mechanism for rodent community compositional shifts. The Meade Basin rodent sequence provides the most complete history of any terrestrial vertebrate group in North America for this period of time.

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1. Introduction

Paleontological fieldwork in the Meade Basin of southwestern Kansas over the past 10 years has revealed a dense record of stratigraphically superposed fossiliferous localities especially rich in small mammals. Building on the framework set by the late C. W. Hibbard and his students (Hibbard, 1938, 1941, 1950, 1953, 1955, 1956, 1964; Paulson, 1961; Woodburne, 1961; Schultz, 1969; Zakrzewski, 1975), the authors have re-sampled most of Hibbard's collecting localities for vertebrate remains, discovered new quarries, remapped and redefined regional sediments, analyzed paleosol carbonates for carbon and oxygen isotopic signatures, and developed a more extensive paleomagnetic record. This interdisciplinary research program is beginning to reveal the intricacies of small mammal community change from the earliest Pliocene (and eventually the latest Miocene) through modern time. In this paper we will show that the rodent community of southwestern Kansas changed from one characterized by cricetid rodent species of southern aspect and arvicolids with rooted molars during the Pliocene to one dominated by cricetids of temperate aspect and arvicolids with rootless molars during the Pleistocene. We will further suggest that the Blancan–Irvingtonian North American Land Mammal Age boundary (NALMA) is best defined by the *Microtus* immigration event, constrained in the Meade Basin to the period between 1.95 and 2.10 Ma (million years

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Epoch	MPTS		Ma	Geol. Markers	Local Faunas	RZ	
Pleistocene	Br	C1n		Lava Crk B ash (0.64) **********		15	
			0.78		Arkalon, Cudahy (N); Couch 3,4		
	Jar	1 r n	0.99 / 1.07			14	
		C1r 2r		Cerro Tol B ash (1.23–1.47) **********	Aries B (R)		
	Ma		1.77		Nash 72 (R)	13	
	Old	C2n	1.95		Aries NE (N)	Aries A (R)		
	Reun	1 r n	2.14 / 2.15	Huck R ash (2.06) **********	Short Haul (R)	12	
					Borchers (R)		
		C2r 2r			Margaret	11	
				CCN2 ~~~~ Seger Gr. ========			
			2.58	CCN1 ~~~~	Sanders (N)	10	
Pliocene		C2an 1 n			Paloma	9	b
			3.04		Rexroad Loc. 2		a
	Kaena	r	3.11		Rexroad Loc. 2A (R) / Deer Park, Rex 3D (R)	8	
	Ga	2 n	3.22	Wolf Gr. ========	Rexroad Loc. 3A–C (N)	7	
	Mam	r	3.33		Bender 1B (N) / Hornet (R)		
		3n					
			3.58	CC2 ~~~~ CC1 ~~~~	Wiens, Vasquez, Rap3A (R)		
		C2ar			XIT1E, XIT2B (R)	6	
					Keefe C., Rap 1C (R)		
			4.18		Ripley (R), ? XIT1B-D		
	Coch	1 n r	4.29	Bishop Gr. --------	Bishop (R)		
	Nun	n	4.48		Fox Canyon (R)	5	
		2	4.62	--------			
	Gi	C3n			Fallen Angel (?R)	4	
	Sud	r n r	4.80 / 4.89 / 4.98		Argonaut / Saw Rock C. (?R)		
	Thv	4n					
			5.23				
Miocene		C3r	5.89		High Banks		
		1 n r	6.14 / 6.27				
		2 n	6.57				
		C3an					
		r					

Fig. 1. Stratigraphic, paleomagnetic, and biostratigraphic consensus chronology for mammalian local faunas from the Meade Basin of Kansas. MPTS=magnetic polarity time scale, Ma=millions of years ago, Geol.=geological, RZ=rodent zones (following Martin, 2003), Crk=Creek, Tol=Toledo, Huck R=Huckleberry Ridge, Gr.=gravel, CC, CCN=calcium carbonate marker layers, (N) and (R)=normal and reversed magnetism, Loc.=Locality, Rap=Raptor, Keefe, Saw Rock C.=Keefe and Saw Rock Canyon, ?=questionable placement or record.

ago). Enhanced rodent species turnover at this boundary and during the Pleistocene suggests that volatility characterizing the climatic record subsequent to about 2.6 Ma is the forcing mechanism for this change.

The assemblages of rodents analyzed for this study, called "local faunas," are listed chronologically in Fig. 1, with accompanying information on stratigraphic marker units, dated ashes, and paleo-

magnetic (pmag) data. Each locality from which the rodent fossils were excavated represents one quarry no more than 1.0 m in depth. If superposed quarries were discovered in the same outcrop, they were given letter designations (thus Rexroad 3A–D; Deer Park A–B, etc. "A" represents the lowest site). Chronology of local faunas below the Gauss Geomagnetic Chron is less secure because of limited

Table 1
Sites from which mean directions could be calculated

Locality	N	Dec	Inc	k	α_{95}	VGP Lat
Site 22	2	204.6°	−71.5°	520	15.6°	−64.69
Site 23	2	194.6°	−60.6°	1275	10°	−77.82
Site 25	3	155°	−17.7°	577	6.3°	−54.05
Site 26	3	93.3°	−13.3°	558	6.4°	−6.67
Site 30	3	8.9°	58.5°	240	9.8°	82.66

paleomagnetic data and dated ashes. Assignment of these older Pliocene assemblages is based on ten years of field mapping (Martin et al., 2002, 2003; Honey et al., 2005), biostratigraphic comparisons with other published faunas (Lindsay et al., 1975; Tomida, 1987; Czaplewski, 1987, 1990; Lindsay et al., 2002) and both previously published (Lindsay et al., 1975) and new pmag data presented here. Table 1 provides the rodent species examined for this study. The taxonomy of the database is in revision (Martin, 2000; Martin et al., 2000; Peláez-Campomanes and Martin, 2005), but the number of species is likely very close to a final tally. The database was corrected for pseudoextinction by collapsing known or suspected phyletic sequences into single species lineages. Sampling bias was corrected by including missing species in a local fauna if they were bracketed in time by the same species (known as "range-through" taxa in the literature; Barry et al., 1995; Martin and Fairbanks, 1999). In some circumstances (e.g., *Neotoma*, *Peromyscus*) we assumed at least one species would be present throughout the study period; for ground

squirrels, we assumed the presence of two species. Aquatic rodents (muskrats, beavers) were excluded because their presence is determined to such a great extent by available aquatic habitats. Details of field collecting and screen-washing methods have been described (Martin et al. 2002, 2003; Honey et al., 2005); 0.5 mm mesh sieves were used. The stratigraphic positions of some pmag samples and fossil localities in the Crooked Creek formation are provided in Fig. 2.

2. Magnetostratigraphy and correlation with the Geomagnetic Polarity Time Scale (GPTS)

Magnetic polarity of sediments in the Meade Basin, Kansas, were presented initially by Lindsay et al. (1975), based on a limited number of samples that provided correlation of the Fox Canyon local fauna with subchron C2Ar, the Rexroad, Bender, and Sanders local faunas with subchron C2An (the Gauss polarity interval), the Borchers local fauna with subchron C2r, and the Cudahy, Mount Scott, and Butler Spring local faunas with subchron C1n. The Olduvai subchron was not identified by Lindsay et al. (1975), but the Borchers (Huckleberry Ridge) ash, dated 2.06±0.004 Ma (Obradovich and Izett, 1992; Honey et al., 1998; Lanphere et al., 2002) and strata above and below the ash were found to be reversely magnetized. Reversed polarity for this stratigraphic interval is consistent with assignment to the Matuyama subchron (C1r). Note that Lanphere et al. (2002) found the Huckleberry Ridge ash to have a transitional direction between normal and reversed, and also suggested there could be a very brief normal event during deposition of the ash which they proposed to name the Huckleberry Ridge event.
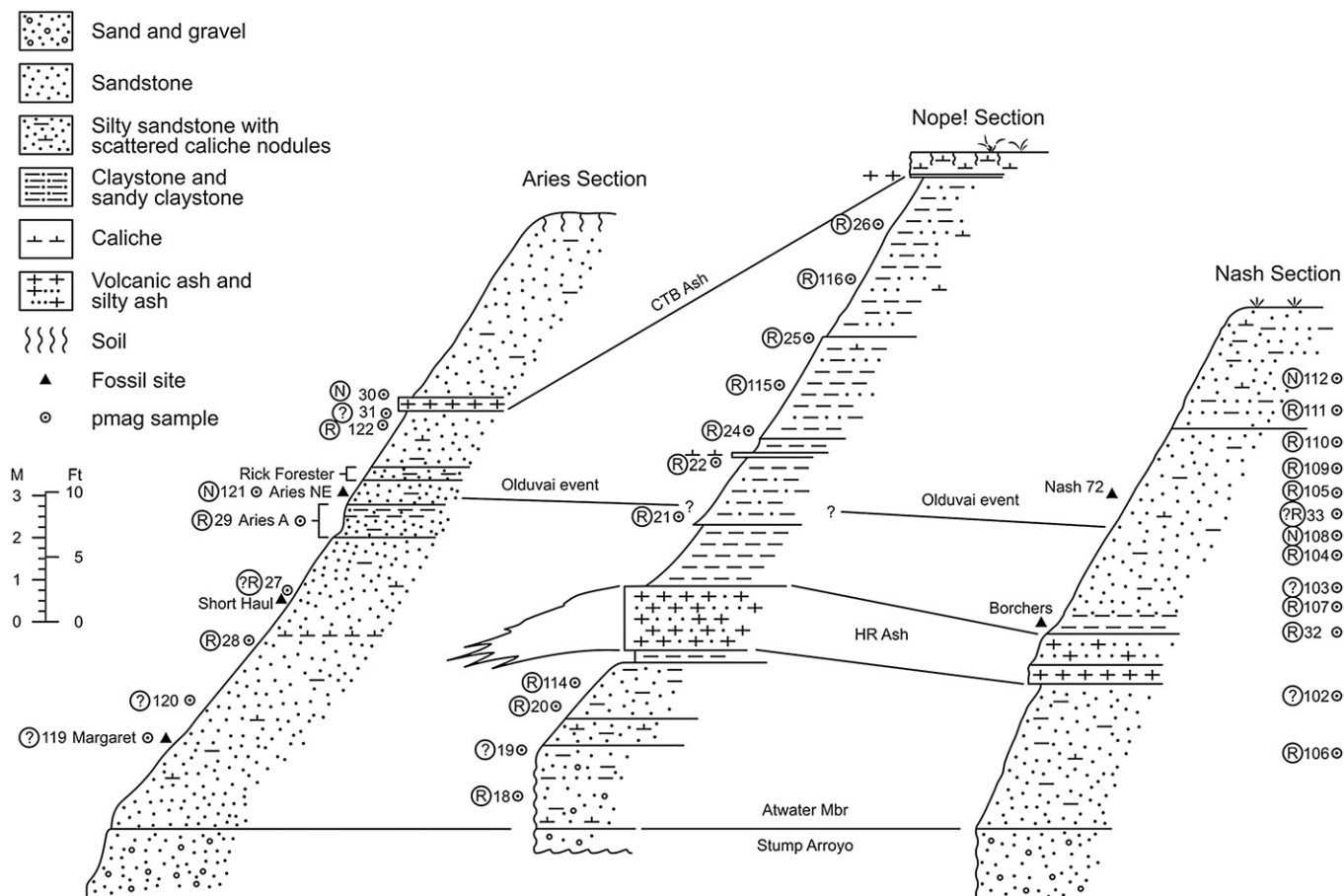

Fig. 2. Stratigraphy and paleomagnetic sampling of the Borchers Badlands area. The Aries and Nope! Sections are about 350 m apart, north of Kansas State Hwy 23. The Nash section is approximately 100 m south of the Nope! Section, on the south side of Hwy 23. Numbers represent paleomagnetic (pmag) samples. N=normal, R=reversed, ?=indecipherable signal. HR=Huckleberry Ridge, CTB=Cerro Toledo B ash, Mbr=member. Names associated with circled dots are quarries from which mammalian local faunas were recovered.

Resolution of mammal chronology with the GPTS has advanced markedly during the intervening three decades, requiring more data for better chronologic determinations. Therefore, additional paleomagnetic data were generated with hopes of placing sediments in the Meade Basin in a more refined, higher resolution temporal framework relative to the current GPTS. Although new time scales for the Paleogene and Neogene were published in 2004 (Gradstein et al., 2004), in this report we follow the GPTS of Berggren et al. (1995) for the Neogene part of the time scale.

During the 2003 summer field season B. Albright joined the Murray State University field crew, and collected 45 paleomag sites in multiple sections throughout Meade County. The following field season (2004) Albright was unable to return to Kansas, so E. Lindsay joined the Murray State team and collected paleomag samples from 42 additional sites, many of them between previously sampled localities. At each of the new pmag sites three to five oriented, fist-sized samples were collected and bedding attitudes were noted for structural corrections; dips typically measured <5°. The oriented pmag samples were reduced to 21 mm cubes, then incrementally demagnetized and measured on a 2-G Enterprises cryogenic magnetometer located in a magnetically shielded room at the Berkeley Geochronology Center (Albright's samples) or at the Geology Department at the University of Florida (Lindsay's samples measured by Opdyke). After first measuring the natural remanent magnetization (NRM) of all samples, they were then subjected to alternating field demagnetization at 4, 10, and 12 mT to erase any viscous remanent component. Stepwise thermal demagnetization followed in several steps from 130 °C to, at times, 630 °C using a modified ASC TD-48 thermal specimen demagnetizer.

In general, the magnetic intensity of samples are weak considering the fine-grained lithology of the beds from which the samples were collected, with many samples yielding undecipherable paleomagnetic signatures. In most of the samples that did provide usable information, demagnetization failed to result in a stable, linear vector decay toward the origin of the orthogonal vector diagrams on which the demagnetization data were plotted (Fig. 3A, B). The polarity of these samples, therefore, was inferred on the basis of the position and trend of the horizontal and vertical components as seen in equal area stereo plots of the data (Fig. 3C–E). For the few sites from which mean directions could be obtained (Fig. 4A–E), this was accomplished by averaging a sequential series of thermal demagnetization steps using principal components analysis (Kirschvink, 1980), or by selecting a single temperature step considered representative of the mean direction of that sample. Table 1 summarizes the data from which mean directions could be calculated.

One of the prime objectives of this paleomag resampling program was to locate the Olduvai subchron (C2n) in the stratigraphic interval of the Meade Basin as this had not been identified in the previous study. Fig. 2 illustrates the interval that should include subchron C2n within three separate but nearby stratigraphic sections occurring both north and south of Kansas State Highway 23 in Meade County. These sections, each spanning about 12–16 m, include the base of the Atwater Member of the Crooked Creek Formation to the level (if present) of the Cerro Toledo B (CTB) ash, dated 1.23–1.47 Ma by Izett et al. (1981) and should include the Huckleberry ridge (HR) ash as well as the Olduvai subchron (C2n), considered 1.77–1.95 Ma in duration. The Atwater Member contains a number of important fossil sites and their local faunas, including C. Hibbard's Borchers and Nash 72 faunas, plus our Margaret, Short Haul, Aries A and B, and Rick Forester faunas, as well as the Huckleberry Ridge (HR) and the Cerro Toledo B (CTB) ashes. Note that these three sections are not exactly comparable, in that the polarity sequence is dominantly reversed in all three but with two very narrow normal magnetozones recorded in two of the three sections. Also, either the CTB ash or the HR ash is missing in one of the three sections, The missing features that should be seen in these nearby and comparable stratigraphic sequences force us to conclude that either 1) significant gaps occur in individual sections throughout

the Borchers Badlands sequence, or 2) low depositional rates may have resulted in thin strata during various times in the sequence, making sampling of the Olduvai subchron problematic. Fortunately, the combination of complimentary pmag, radioisotopic and faunal information from these three well-exposed sections allows us to reconstruct a consistent and parsimonious sequence of events.

The three sections in Fig. 2 include a total of 33 pmag sites, of which 23 sites have reversed polarity, four sites have normal polarity, and six sites have indeterminate polarity. Two of the four normal polarity sites (site 30 and, presumably, site 112) occur above the Cerro Toledo B ash and are here correlated with the Cobb Mountain (1.24–1.21 Ma) or Jaramillo (1.07–0.99 Ma) normal subchrons based on the 1.23–1.47 Ma date of the CTB ash (Izett et al. 1981, Izett and Honey, 1995). It is conceivable that the sediments from which samples 111 and 112 were taken represent a much later depositional period, perhaps within the Brunhes normal chron (because the CTB ash is absent from the Nash section), but our stratigraphic interpretation correlates these sediments with those just above the CTB ash in the Aries section. Another normal polarity site (site 108) in the Nash Section occurs about 2.5 m above the top of the Huckleberry Ridge ash. This site is correlated with normal polarity site 121 in the Aries section. The polarity direction of samples from these sites is relatively close and magnetization is sufficiently strong such that these sites can be considered "Class 1" sites. Reversed polarity sites occur approximately 0.5 m above and below both of these normal sites, indicating that the normal zone is very thin in this section. Although the 180 ka (1.77–1.95 Ma) Olduvai interval is commonly about one meter thick in many other stratigraphic sections, we nevertheless interpret this normal magnetozone as representing the Olduvai subchron,. This correlation places the Olduvai subchron between the HR and CTB ashes, at about the same level in the Nash section as in the Aries section (Fig. 2).

3. Summary of rodent community turnover

For this study rodent community changes were determined by the nature and number of species immigrations and extinctions (turnover). Turnover in the Meade Basin rodents from Saw Rock Canyon (SRC) through modern time is shown in the mirror diagram of Fig. 5. The absolute number of species immigrations and extinctions is shown for 19 intervals from about 5.0 Ma (million years ago) to modern time. The width of each vertical rectangle is scaled to interval length. Expected values for species immigrations and extinctions were determined from equations published by Martin and Fairbanks (1999), as follows: $E = 6.96$ $L^{0.39}$ and $I = 7.24$ $L^{0.39}$, where E = number of extinctions, I = number of immigrations and L = interval length in millions of years. From Fig. 5 we can observe four bouts of enhanced turnover; extinctions from about 2.9–2.6 Ma, both extinctions and immigrations from about 2.1–2.0 Ma, and extinctions from about 0.67–0.30 Ma. It is noteworthy that the number of extinctions balances the number of immigrations through the study period, thus conforming to the basic tenets of MacArthur–Wilson equilibrium theory (MacArthur and Wilson, 1967). This aspect of the results and correlated survivorship patterns will be presented elsewhere.

These data document a change from a community characterized by the cricetids *Bensonomys*, *Baiomys*, *Symmetrodontomys*, *Sigmodon* (extinct *S. minor* lineage)and the archaic vole *Ogmodontomys* and, to a much lesser extent, the archaic voles *Pliophenacomys* and *Ophiomys* (with rooted molars) to ones characterized by arvicolids of the genus *Microtus* (with ever-growing molars) and advanced cricetids of the genera *Sigmodon*, *Reithrodontomys* and *Peromyscus*. The shift to *Microtus* at this time appears to be almost a globally instantaneous event, as indicated by the observation that archaic species of *Microtus* morphologically indistinguishable from one another and treated as *M. (Allophaiomys) pliocaenicus* are recorded from latest Pliocene and early Pleistocene sediments throughout the Holarctic region in both
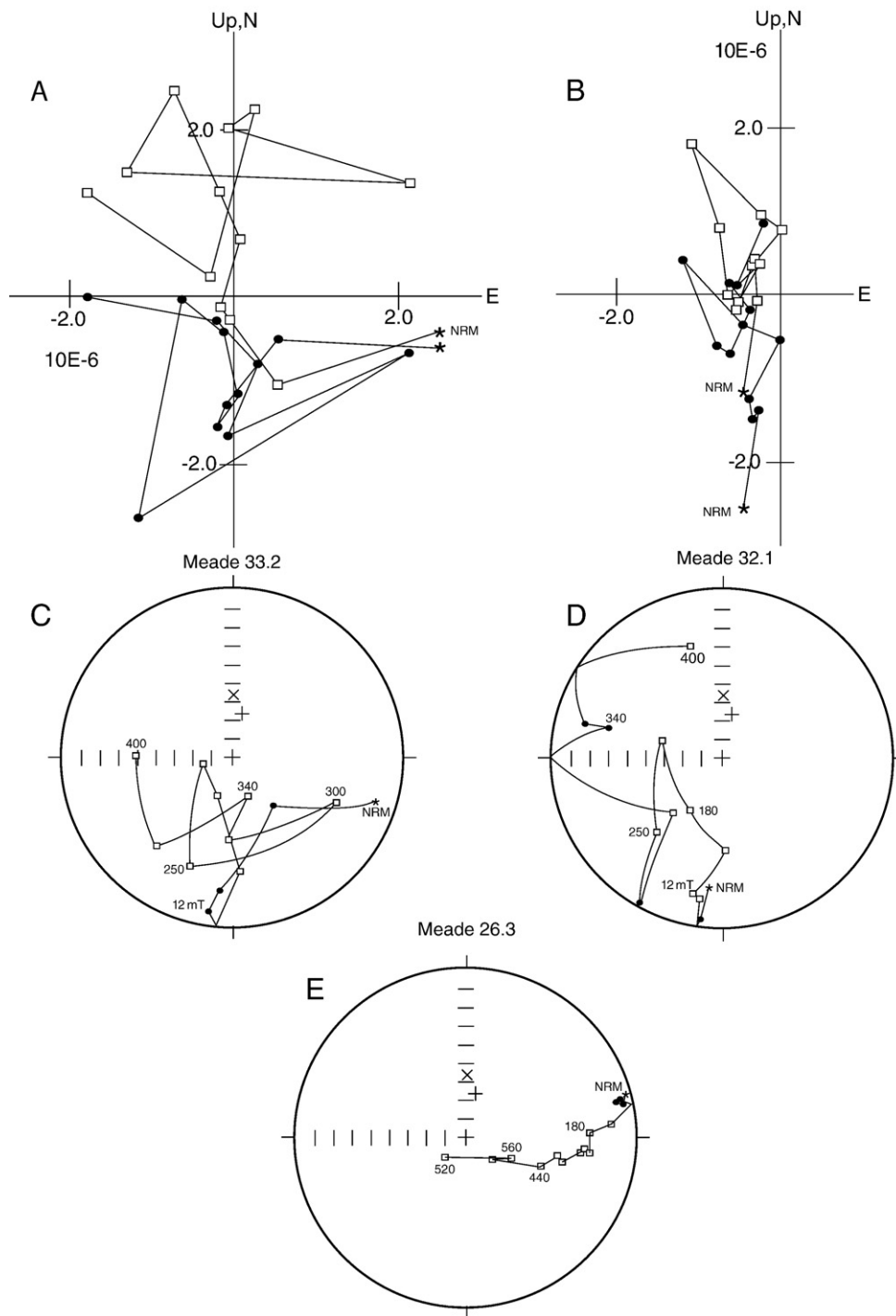
Fig. 3. A, B. Representative orthogonal vector diagrams from which mean directions of magnetization could not be determined. C, D. Equal area stereo plots of same data indicating the position and trend of the horizontal and vertical components. E. Equal area stereo plot indicating the position and trend of the horizontal and vertical components from which a determination of polarity is obtainable.

Eurasia and North America (Pevzner et al., 1998; Martin, 2003; Tesakov, 2004). *Microtus* then undergoes an explosive radiation, becoming the dominant rodent taxon in much of the world's Holarctic grasslands from that time. It seems likely that the paedomorphic appearance of rootless molars in *Microtus* was associated with precocious and amplified fecundity, leading to higher fitness over competitors in Holarctic environments.

Morphologically, the dentition of *Bensonomys* resembles that of the South American genus *Calomys*; indeed, for some years fossil *Bensonomys* from North America were referred to *Calomys* (Baskin,

1978). There is little doubt that late Miocene and early Pliocene species of *Bensonomys* were ancestral to their extant South American relatives (Baskin, 1978; Jacobs and Lindsay, 1984; Baskin, 1986; Carranza-Castañeda and Walton, 1992; Pardiñas et al., 2002). The molar pattern of *Symmetrodontomys* can be derived from that of *Bensonomys*, and it seems likely they shared similar environmental preferences, as they appear together early in Meade Basin history (both present in the Saw Rock Canyon l.f.) and became extinct during the latest Pliocene, between about 2.9 and 2.1 Ma (Table 2). Between 2.6 and 2.1 Ma we also see the demise of *Baiomys*, the pygmy mice, an
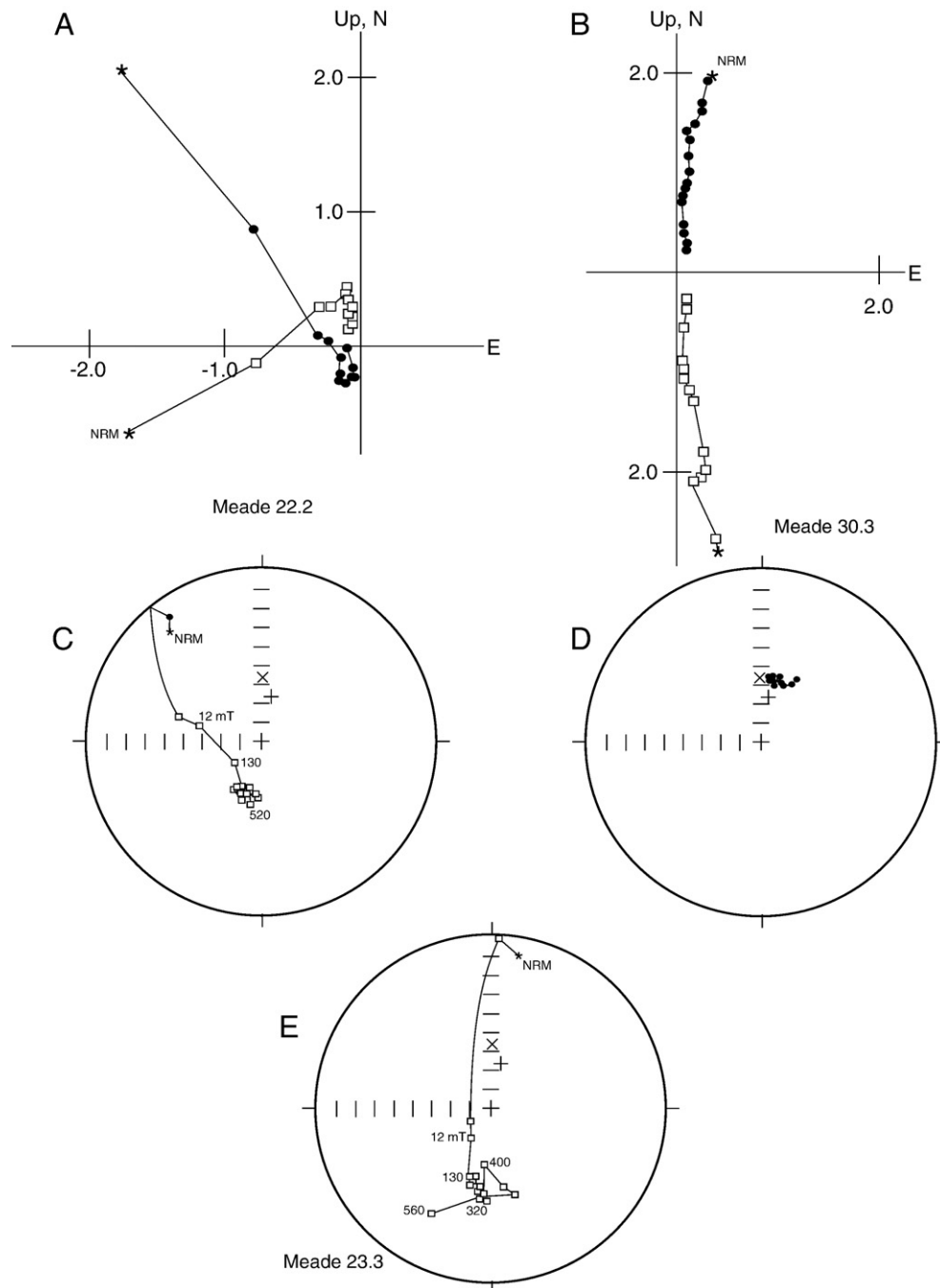
Fig. 4. A–D. Orthogonal vector diagrams and equal area stereo plots from which site mean directions could be determined through principle components analysis of a sequential series of thermal demagnetization steps. E. Equal area stereo plot from which a site mean direction could be determined by selecting a single temperature step considered representative of the mean direction.

extant genus found today in eastern Texas, extreme southern New Mexico and Arizona and throughout Mexico (Hall, 1981). Ground squirrels, gophers, heteromyids and the insectivorous cricetid *Onychomys* persisted for the entire 5.0 my, and lemmings have been continuously present from about 2.1 Ma, presumably in suitable marshy habitats. Only one species of jumping mouse *Zapus* has been recorded at any given time in the Meade Basin.

4. Climatic forcing as a likely mechanism for rodent turnover from 2.6–0.3 Ma

The change in continental climate associated with the onset of global cooling subsequent to 2.7 Ma is probably best reflected in the

transition of some rodent species from the Borchersl.f. at 2.06 Ma to a series of stratigraphically higher assemblages in the Crooked Creek formation of the Borchers Badlands in Meade County. These assemblages were excavated from single superposed quarries in sediments that also preserve two dated volcanic ashes and paleomagnetic signals (Fig. 2). The Borchersl.f. represents the youngest expression of the more equable later Pliocene assemblages compared to those slightly higher in the Borchers Badlands sequence. The Borchers locality is one of the most prolific in North America. Thousands of rodent teeth have been collected from this site. By far, the most common species represented is the diminutive *Sigmodon minor*, a species recovered from most earlier Pliocene local faunas. As Peláez-Campomanes and Martin (2005) showed, *S. minor* from
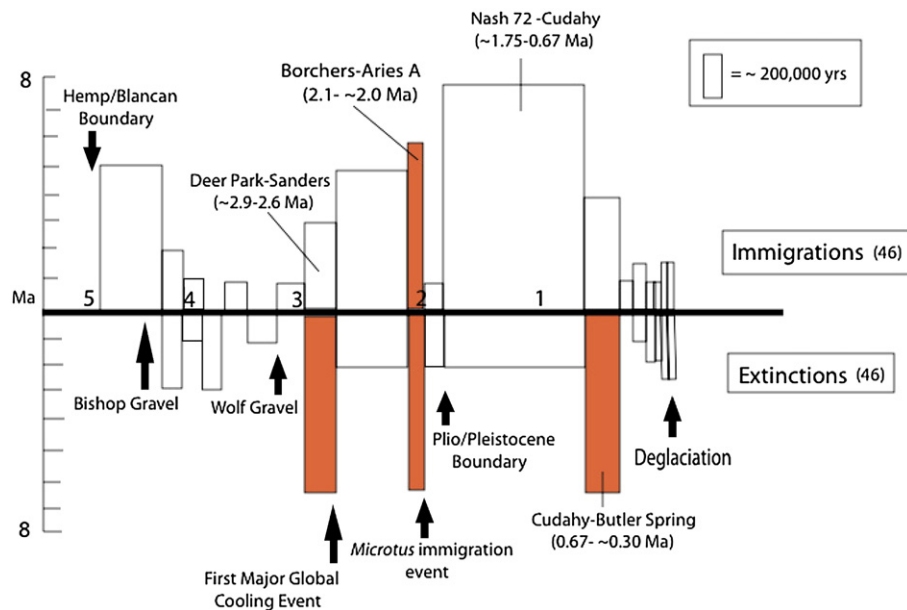
Fig. 5. Mirror diagram of rodent turnover during the late Pliocene and Pleistocene in the Meade Basin. Hemp = Hemphillian, Ma = millions of years ago. The left scale indicates number of species. Each rectangle represents the number of immigrations (above the line) or extinctions (below the line) scaled for interval length. Rectangles in the latest Pleistocene (Wisconsinan) not as accurately drawn to scale. Gray rectangles indicate bouts of immigration or extinction that exceeded expected values.

Borchers expressed a dwarfing event just prior to its extinction. The Pliocene gopher *Geomys quinni* became giant at this time, and then also disappeared (Flynn et al., 2008). The last appearance of the giant tortoise *Hesperotestudo* (=*Geochelone*) in the Meade Basin, other than a brief appearance in a presumed warm period during the late Pleistocene (Cragin Quarry, loc. 1; Schultz, 1969), is from Borchers. Less than 2.0 m above the Borchers l.f., and probably less than 0.10 Ma later, a new climatic regime is recorded.

The Short Haul l.f. records the first appearances in the Meade Basin of the vole *Microtus* cf *pliocaenicus*, the lemming *Mictomys kansasensis*, and the advanced, large cotton rat *Sigmodon curtisi*. These species are also present in the superposed Aries A l.f. Both assemblages were excavated from sediments beneath the Olduvai subchron. (Fig. 2; and see below). The *Microtus* cf *pliocaenicus* record at about 2.0 Ma is the oldest documented record of an archaic *Microtus* with positively differentiated enamel in the world. The most dentally primitive *Microtus*, *M. deucalion*, with negatively differentiated enamel (as in its ancestral genus *Mimomys*), has been identified from the Kryzhanovka 4 and Tizdar localities in the Taman Peninsula of Russia (Pevzner et al., 1998; Tesakov, 2004) from sediments lying just beneath the Olduvai event, basically synchronous with *M. pliocaenicus* from the Meade Basin. Nash 72, also with *M. pliocaenicus* but without *Sigmodon curtisi*, marks the first appearance datum for prairie dogs, genus *Cynomys*, in the Meade Basin.

Sediments above the Cerro Toledo B ash (~1.35 Ma; this ash was identified chemically, and the date represents an average between two ash-falls at 1.23 and 1.47 Ma; Izett et al., 1981) are sparse in the Borchers Badlands, and we have no fossil assemblages from them. Sections in the Borchers Badlands area are frequently truncated above the CTB ash. The next youngest rodent assemblage is the Cudahy l.f., from central Meade County, approximately 20 km northeast of the Borchers Badlands sections. Directly underlying the Lava Creek B ash, dated at 0.64 Ma (Lanphere et al., 2002), the Cudahy l.f. exemplifies the transformation from the Pliocene assemblages with southern affinities to a completely temperate fauna, dominated as it is by five arvicolid species (Table 2). Although there is considerable spread to the data, Montuire et al. (1997) have shown a significant correlation in modern rodent assemblages between the number of arvicolid species and mean annual temperature. With five species, the mean annual temperature ranges between slightly less than 0° to about 13° C, with an average of about 7° C. The current average temperature for

southwestern Kansas is in the neighborhood of 12° C, and three arvicolid species are found there today. For three species, the Montuire et al. (1997) estimate falls almost exactly at 12° C. The Cudahy l.f. existed on the Great Plains at approximately the time of the glacial interval expressed by Marine Isotope Stage 16. We can conclude from these data that Cudahy time was considerably colder than today, and it is no surprise that cotton rats are absent from the Cudahy assemblage whereas they are common throughout the Meade Basin during the remaining Pleistocene (Peláez-Campomanes and Martin, 2005).

The modern rodent fauna of southwestern Kansas is mostly in place by the early Rancholabrean, after about 0.30 Ma, but a variety of transient species provide clues to late Pleistocene climatic regimes that may have varied significantly from current conditions. For instance, the meadow vole is almost a constant member of the late Pleistocene rodent community of southwestern Kansas, but is not found there today. Cooler conditions in the late Pleistocene are also indicated by other species, such as the northern pocket gopher *Thomomys* and the western jumping mouse, *Zapus princeps*, both of which are recorded from the Golliher B l.f., recently AMS radiocarbon dated to 12,510 + 80 years B.P. (Geochron Laboratories, sample No. GX-31988-AMS). *Thomomys* seems to be a good indicator of cool weather, as it was also a transient during the depositional interval of the Cudahy l.f. After the local extinctions of *Microtus pennsylvanicus* and *Thomomys*, both present in the Robert l.f. (11,110 + 350 years B.P.; Schultz, 1969) near the start of North American deglaciation, the hispid cotton rat entered the Meade Basin, documenting the beginning of the warm interstadial that defines modern time.

Taken collectively, the turnover in rodent species throughout the late Pliocene and Pleistocene suggests a climatic shift that eliminated a coterie of warm-adapted cricetid species of southern aspect along with archaic arvicolids with rooted cheek teeth, and replaced them having more temperate-adapted species and, at least in the case of *Microtus*, with ever-growing molars and likely with higher reproductive potential.

5. Stable oxygen isotopes from paleosol carbonates support a climatic change at the end of the Pliocene

We collected and analyzed 58 pedogenic carbonates from three measured sections: two in the Borchers Badlands area that includes

Table 2
Rodent species recovered from selected local faunas from the Meade Basin of southwestern Kansas

Rodentia	SR	F C	RipB	Rap1C	WnsB	Hor	R3	DP	Ss	Bor	SH	ArA	Na72	Cud	B S	CQ	Jin	GolB	Jon	Rob	Mod
Sciuridae																					
Spermophilus rexroadensis		x					x														
Spermophilus howelli		x					x														
Spermophilus meadensis										x	x										
Spermophilus tridecemlineatus												cf	x	cf	cf	x		o	x	x	x
Spermophilus cragini										x											
Spermophilus franklini										cf	o	o	cf	cf					x		K
Spermophilus richardsoni										cf				x	x			o	x	x	
Spermophilus spilosoma																					x
Spermophilus sp.	x		x	o	x	x	x	x									x				
Spermophilus sp.	o		o	o	o	o	o	o							o	o					
Cynomys ludovicianus /sappaensis													cf								
Cynomys l. /spenceri															x						
Cynomys l. /ludovicianus																	cf	o	x	x	x
Cynomys niobrarius																x					
Cynomys sp.														cf							
Paenemarmota barbouri /sawrockensis	x																				
Paenemarmota b. /barbouri		x	o	x																	
Geomyidae																					
Geomys adamsi		x																			
Geomys minor		x	x		x	x	x	x													
Geomys quinni				cf	cf		x	x		x											
Geomys bursarius														cf	cf	x	cf	cf	x	cf	x
Geomys sp.	x			x					x	x	x	x	x								
Thomomys sp.														x				x	x	x	
Heteromyidae																					
Prodipodomys centralis /griggsorum	x																				
Prodipodomys c. /centralis		cf					x		x												
Prodipodomys c. /tiheni										x		o	cf								
Prodipodomys sp.			x	x	x	o	x					o									
Dipodomys hibbardi										x											
Dipodomys ordii														o	cf	cf	cf	o	o	o	x
Perognathus mclaughlini /mclaughlini	x																				
Perognathus m. /rexroadensis		x																			
Perognathus pearlettensis		x								cf	cf		cf	cf							
Perognathus gidleyi						x	cf							cf							
Perognathus flavescens																					x
Perognathus flavus																		cf			x
Perognathus sp.	x		x	x	x	x					x			o	x	o	x		x	o	
Chaetodipus hispidus														x	x	x					x
Cricetidae																					
Symmetrodontomys stirtoni	x																				
Symmetrodontomys simplicidens		x	x	cf	cf	x	x	x													
Bensonomys eliasi		x	x	x																	
Bensonomys meadensis							x	x	x												
Bensonomys sp.	x				x	x															
Baiomys rexroadi	x	x	cf	x	x	x	cf	x													
Onychomys leucogaster /gidleyi	x	x					x														
Onychomys l. /pedroensis											x	cf									
Onychomys l. /leucogaster											cf			cf	cf	cf	cf		x	o	x
Onychomys hollisteri								cf		x											
Onychomys sp.			x	o	x	x			o				x	o							
Reithrodontomys wetmorei		x	x	x																	
Reithrodontomys moorei										x	x	x	x	x							
Reithrodontomys megalotis															cf	cf					x
Reithrodontomys montanus																	cf				x
Reithrodontomys sp.								x	o			x	x					x	o	x	
Peromyscus baumgartneri		x			x																
Peromyscus kansasensis					x																
Peromyscus cragini														x							
Peromyscus maniculatus /progressus															x	x					
Peromyscus m. /cochrani																	x				
Peromyscus m. /maniculatus																				x	x
Peromyscus leucopus																				x	x
Peromyscus sp.	x	x	o	x	x		x	o	x	o	o	o					x	x	x		
Oryzomys palustris																		x			
Neotoma sawrockensis	x																				
Neotoma quadriplicata		x	x	o	x	x	x	x													
Neotoma taylori										x											
Neotoma micropus																x					x
Neotoma sp.									o			o	o	o	o	o	x	o	o	o	o
Sigmodon holocuspis			x																		

Table 2 (continued)

Rodentia	SR	F C	RipB	Rap1C	WnsB	Hor	R3	DP	Ss	Bor	SH	ArA	Na72	Cud	B S	CQ	Jin	GolB	Jon	Rob	Mod
Cricetidae																					
Sigmodon minor			cf			x	x	x	x	x											
Sigmodon curtisi											x	x									
Sigmodon hispidus																					x
Arvicolidae																					
Ogmodontomys sawrockensis	x																				
Ogmodontomys poaphagus		x	x	x	x	x	x	x													
Pliophenacomys finneyi		x																			
Ophiomys meadensis									x												
Pliolemmus antiquus								x	x												
Nebraskomys rexroadensis							x	x													
Mictomys landesi											x										
Mictomys kansasensis												x	o	x							
Mictomys meltoni														x							
Mictomys sp.																					
Synaptomys australis																	x				
Synaptomys cooperi																				x	x
Microtus pliocaenicus												x	x	x							
Microtus paroperarius														x							
Microtus meadensis														x							
Microtus ochrogaster /llanensis														x							
Microtus o. /ochrogaster															x	cf	x		x	x	x
Microtus o. /parmaleei																		x			
Microtus pennsylvanicus															x	x	x	x	x	x	
Zapodidae																					
Zapus rinkeri		x																			
Zapus sandersi			o	o	o	cf	x	cf	x	o	o	o	o	cf							
Zapus hudsonius															o	o	x		o	x	K
Zapus princeps																		x			
Species totals	14	18	16	16	14	15	17	18	14	17	13	14	15	18	14	14	17	14	15	16	17
Mean = 15.5																					

SR=Sawrock Canyon, FC=Fox Canyon, RipB=Ripley B, Rap1C=Raptor 1C, WnsB=Wiens B, Hor=Hornet, RR3=Rexroad Loc. 3, DP=Deer Park A, Ss=Sanders, Bor=Borchers, ArA=Aries A, Na72=Nash 72, Cud=Cudahy, BS=Butler Spring, CQ=Cragin Quarry, Jin=Jinglebob, Jon=Jones, GolB=Golliher B, Rob=Robert, Mod=Modern, o=range-through taxon (see text).

the Nash 72 and Borchers fossil localities and one through the Aries Quarry section that includes the Short Haul and Aries local faunas. The dominant carbonate morphology in these sections is distributed nodules that are ca. 5 cm in diameter, but disseminated carbonate and thin caliche beds (typically less than 25 cm thick) also occur. In each section, we collected a stratigraphic series of samples, usually collecting several nodules or caliche samples per sampling level. Samples were collected *in situ* either from trenches or from caliche beds following removal of the weathered surface. None of the sections had distinct preserved A horizons or obvious zonation despite the abundance of carbonate nodules and occasional caliches. We interpreted these intervals as cumulative soils and sampled opportunistically or at intervals of 50, 75, or 100 cm depending on abundance of carbonate. Caliche beds were sampled from the lowermost indurated surface or from the entire thickness.

Samples for carbonate analysis were roasted *in vacuo* at 400° C for at least 1 h to eliminate water and organic matter. Samples were analyzed at both the Stable Isotope Laboratory at the University of California, Santa Cruz (UCSC) and the Stable Isotope Laboratory at the University of Minnesota (UM). At UCSC, samples were reacted with 100% H_3PO_4 at 90° C in a MicromassIsocarb automatic carbonate extraction system. The isotope composition of the resulting CO_2 was measured using either a Micromass Prism or Optima isotope-ratio mass spectrometer in the Stable Isotope Lab at the UCSC and sample values were normalized to the mean isotope composition of six to eight samples of granular Carrera marble analyzed as a laboratory standard with each set of paleosol samples. Normalizations for the UCSC data were confirmed by analysis of NBS-19 in parallel with the paleosol carbonates at UCSC. At UM, carbonate samples were reacted with 100% H_3PO_4 at 71° C in Finnigan "Kiel" automatic extraction line coupled to the ion source of a Finnigan MAT 252 isotope ratio mass spectrometer; and sample values were compared with NBS-18 and

NBS-19 and two laboratory standards. Analytical precision of results from both labs is better than 0.1‰ for both $\delta^{13}C$ and $\delta^{18}O$ values.

To examine isotopic variation within individual field samples, we analyzed two discrete nodules from each of 31 samples. Five samples were analyzed at both UCSC and UM to compare treatment and analysis of samples. Variation within nodules was generally low for both $\delta^{13}C$ and $\delta^{18}O$. Mean difference within nodules was <0.2‰ for both, the maximum range within a sample was 0.72‰ for $\delta^{13}C$ and 0.56‰ for $\delta^{18}O$ and the mean difference within nodules was <0.2‰ for both $\delta^{13}C$ and $\delta^{18}O$ values. For $\delta^{13}C$ values, this variation within samples is small relative to the range expected due to variation in the $C_3:C_4$ ratio. We present results of these analyses as sample means. For the remaining samples we made single determinations of the isotopic composition. In total, we report 38 carbon and oxygen isotope values resulting from 64 individual analyses.

We use a simple linear mixing model between end-members with mean C_3 and C_4 carbon isotope compositions to estimate the percentage of C_4 biomass implied by paleosol carbonate $\delta^{13}C$ values. For simplicity, we assume a pre-industrial atmospheric CO_2 carbon isotope composition of −6.5‰ (Friedli et al., 1986). Using a time series of $\delta^{13}C$ values from planktonic foraminifera to estimate secular change in the $\delta^{13}C$ value of atmospheric CO_2 (Passey et al., 2002) would have a negligible impact on our interpretations (Fox and Koch, 2004). The assumed $\delta^{13}C$ value for atmospheric CO_2 implies mean $\delta^{13}C$ values for C_3 and C_4 plant biomass of −25.5 and −11.5‰, respectively. We assume a fractionation factor between soil CO_2 and soil carbonate of +15.5‰, which is roughly the midpoint of observed modern values (Cerling and Quade, 1993). Water stress under arid growing conditions would shift organic matter compositions to less negative $\delta^{13}C$ values and would lead to an overestimate of C_4 biomass (Farquhar et al., 1989). However, the offsets between $\delta^{13}C$ values of co-occurring Great Plains paleosol carbonate and organic matter do not suggest high aridity (Fox

and Koch, 2003). Under closed canopy cover, mixing of atmospheric CO_2 with plant and soil respired CO_2 previously fractionated by photosynthetic processes reduces the $\delta^{13}C$ value of plant biomass (vanderMerwe and Medina, 1991) and could lower soil carbonate $\delta^{13}C$ values, leading to an underestimate of C_4 biomass.

Both $\delta^{13}C$ and $\delta^{18}O$ values of paleosol carbonates from measured sections in the Borchers Badlands and the section containing the Short Haul and Aries l.f.s have strong trends that reflect environmental changes during the late Pliocene and early Pleistocene that are associated with faunal turnover during that interval (Fig. 6). The $\delta^{13}C$ value of carbonate that precipitates at depth in a soil in equilibrium with soil-derived CO_2 reflects the proportion of isotopically distinct C_3 and C_4 plants that were growing in the soil. C_3 plants are trees, shrubs, and cool growing season grasses with pre-industrial mean $\delta^{13}C$ value of ca. −25.5±3‰; C_4 plants are primarily warm growing season grasses with pre-industrial mean $\delta^{13}C$ value of ca. −11.5±2‰ (Cerling and Quade, 1993). Paleosol carbonate $\delta^{13}C$ values increase steadily through time from about −4‰ below the Huckleberry Ridge Ash in the Borchers Badlands to −2 to 0‰ above the Cerro Toledo B ash above the Aries A fauna. The trend in $\delta^{13}C$ reflects the final step in the multi-stage development of the modern C_4-dominated grassland of the southern Great Plains (Fox and Koch, 2003). The $\delta^{13}C$ values at the base of the Borchers sections are higher than those for all older Blancan localities in the Meade Basin, which do not exhibit a secular trend (mean $\delta^{13}C = -4.9 \pm 0.95$‰, $n = 135$; Fox, unpublished). The values at the top of the Aries section are similar to Holocene soil carbonate $\delta^{13}C$ values from northern Kansas (0 to 2‰; Kelly et al., 1991). Assuming simple mass balance with mean plant $\delta^{13}C$ values and temperature dependent fractionation of +15.5‰ (Cerling and Quade, 1993), the proportion of C_4 biomass increased from ca. 45% below the HRA to 58–78% at the top of the composite section.

Paleosol carbonate $\delta^{18}O$ values vary directly with soil water $\delta^{18}O$ and inversely with temperature (Friedman and O'Neil, 1977), but the effect of water composition dominates. Soil water composition is controlled by infiltration of meteoric water, seasonal variation in infiltration, and evaporative enrichment in ^{18}O. Holocene soil carbonate $\delta^{18}O$ values have a strong, positive correlation with local meteoric water $\delta^{18}O$ values, which in turn have a strong, positive correlation with local air temperature both seasonally and annually (Rozanski et al., 1993). Thus, changes in carbonate $\delta^{18}O$ values reflect changes in meteoric water $\delta^{18}O$ value, temperature, the seasonal distribution of infiltrating waters, and aridity. Paleosol $\delta^{18}O$ values in the Borchers-Aries section decrease steadily upsection by ca. 4‰, with the exception of three stratigraphically successive values in one

Borchers sections with unusually high $\delta^{18}O$ values. These values derive from otherwise typical samples and represent either a brief, extreme change in local soil hydrology (e.g., increased evaporative enrichment) or localized diagenesis that did not alter the corresponding $\delta^{13}C$ values or other levels in the section. The high values below the Huckleberry Ridge Ash are close to the $\delta^{18}O$ values of stratigraphically proximate samples in older Blancan sections in the Meade Basin (ca. 23‰; Fox, unpublished). We interpret the decrease in $\delta^{18}O$ from stratigraphic levels below to above the Huckleberry Ridge Ash as cooling associated with the termination of the early Pliocene warm period and onset of major Northern Hemisphere glaciation (NHG) at ca. 2.7 Ma (Haug et al., 2005). Assuming equilibrium fractionation and the modern meteoric water–temperature relationship (Rozanski et al., 1993), the trend in $\delta^{18}O$ values above Huckleberry Ridge Ash requires ca. 18 °C mean annual cooling in the Meade Basin following the onset of NHG, which seems extreme. As onset of NHG was controlled by cooler summers and increased winter moisture transport to high latitude (Haug et al., 2005), we interpret the isotopic trend stratigraphically above the Huckleberry Ridge Ash as a reflection of mean annual cooling driven particularly by summer cooling and an increase in the proportion of winter precipitation, which would lead to lower meteoric water $\delta^{18}O$ values and lower carbonate $\delta^{18}O$ values.

6. Reconsideration of the Blancan/Irvingtonian Boundary

Our analyses show that the sediments just above Short Haul and those in the Aries A quarry have reversed paleomagnetic signals. Normal polarity records at the levels of Aries NE and just above the Nash 72 quarry are interpreted as representing the Olduvai subchron. Since we know that the Borchers l.f. was taken from sediments developed in and just on top of the Huckleberry Ridge ash at 2.06 Ma (Fig. 2), then the age of Aries A and Short Haul must be bounded above by the base of the Olduvai event, and therefore constrained to a period between 1.95 and 2.06 Ma. Thus, assuming we have correctly identified the Olduvai event, we can conclude that the *Microtus* immigration event into the Meade Basin occurred about 2.0 Ma, slightly earlier than it had previously been estimated (Martin et al., 2003). Short Haul and Aries A also mark the earliest appearances of the lemming *Mictomys kansasensis* and the advanced, large cotton rat *Sigmodon curtisi* in the Meade Basin. We interpret these shifts to represent the continuation of continental climatic change marking the beginning of the Pleistocene, and we also recommend using the *Microtus* immigration event to identify the Blancan/Irvingtonian (B/I) North American Land Mammal Age boundary. As Cassiliano (1999; 183) aptly noted: "Selecting a taxon to define the Irvingtonian boundary is half the solution. That taxon must be located in a stratigraphic section so that its placement in the geologic record and relative to other NALMAs can be securely determined. Thus, a physical locality must also be designated." After reviewing possible candidates for a boundary stratotype, including the Meade Basin sequence, Cassiliano (1999) regretfully concluded that none provided the sufficiently detailed stratigraphic record of an appropriate taxon necessary to define the boundary, but he did suggest it should be near the Pliocene–Pleistocene boundary, and that it likely occurred between 1.95 and 2.15 Ma. Bell et al. (2004) recently reviewed the definition of the B/I boundary and, after considering the possibility of an arvicolid rodent definition, chose instead to use the immigration of *Mammuthus* and a date of about 1.35 Ma. However, the authors noted (2004, p. 269) "…we failed to reach unanimous consensus on the definition of the Irvingtonian." Further, no detailed stratigraphic section exists within which the immigration of *Mammuthus* can be clearly constrained. We appreciate the rationale for their choice of *Mammuthus*, but given the uncertainties associated with dating *Mammuthus* throughout its range, the lack of a satisfactory boundary stratotype associated with it, and the lack of an associated continental climatic regime change at 1.35 Ma, we recommend the use of *Microtus*
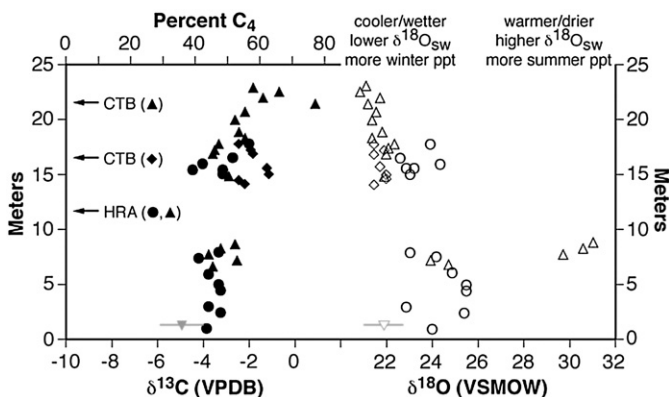

Fig. 6. $\delta^{13}C$ and $\delta^{18}O$ values of paleosol carbonates from the Borchers Badlands (black circle and triangle, open circle and triangle) and Aries quarries sections (black diamond, open diamond). Arrow and symbols indicate meter levels of Huckleberry Ridge (HRA) and Cerro Toledo B (CTB) ashes in each section; vertical offset in CTB results from paleorelief and variation in local sedimentation rates. Grey symbols and bars indicate mean and standard deviation of older Blancan samples in the Meade Basin. Percent C_4 based on simple mass balance assuming pre-industrial mean values.

in the Meade Basin and a date of about 2.0 Ma to identify the boundary. This event is one of the earliest records of *Microtus* in the world, is bounded by fossil assemblages that represent significantly different climatic regimes, and is constrained by stratigraphic, radio-isotopic and paleomagnetic data.

As presently defined, the Pliocene/Pleistocene (Pli/Ple) boundary is set at 1.8 Ma, based upon the section at Vrica, Italy (Passini and Colalongo, 1997). Thus the B/I boundary based on *Microtus* is currently within the Pliocene. However, it has been known for many years that the first evidence for global cooling appears unequivocally around 2.6 Ma (Shackleton et al., 1984), and cogent arguments have been presented that the Pli/Ple boundary should be shifted to this time (Morrison and Kukla, 1998). We strongly recommend this change, as it would better represent not only a major global climatic shift, but also the many organismal changes (both in community composition and morphology) seen in fossiliferous sediments throughout the world at this time.

7. Conclusions

The combination of detailed stratigraphic, paleontological, radio-isotopic, and paleomagnetic information for the Meade Basin of southwestern Kansas allows documentation of the most complete history of a small mammal community anywhere in the world for the past 5.0 million years. Analysis of species flux shows that species numbers remain constant while species are replaced throughout the study period, thus extending MacArthur and Wilson island biogeographic theory to continental basins. Pliocene assemblages are characterized by keystone species of cricetids of southern aspect and archaic arvicolids, which give way at the beginning of the Pleistocene to a more temperate-adapted assemblage featuring *Microtus* and a cadre of advanced cricetids and other arvicolids with ever-growing molars. The *Microtus* immigration event, constrained to a period between 1.95 and 2.06 Ma, is suggested as a replacement for the first appearance of *Mammuthus* to define the Blancan/Irvingtonian NALMA boundary.

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