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Biochronology of Latest Miocene Through Pleistocene Arvicolid Rodents from the Central Great Plains of North America

Biocronología de roedores arvicólidos del Mioceno tardío al Pleistoceno de las Grandes Llanuras centrales de Norteamérica

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Abstract: The Pliocene and Pleistocene record of arvicolid rodents from the central region of North America is broadly reviewed. A new provincial rodent zonation is proposed for the central Great Plains. Hemphillian arvicolids are represented by *Promimomys* and *Protopliophenacomys.* Although primitive species of *Pliophenacomys* are known from the early Blancan of Indiana and Kansas, this genus is conspicuously absent from most of the early and middle Blancan localities of the Meade Basin of Kansas. Advanced species of *Pliophenacomys*, with positive enamel differentiation, characterize late Blancan deposits, and appear to be good index fossils for this time period, especially in combination with advanced species of *Ophiomys*. *Ogmodontomys poaphagus* is the most common arvicolid through much of the Pliocene in Kansas and Nebraska. Bog lemmings are late Blancan immigrants to the central Great Plains. The disappearance of archaic arvicolids from the Borchers local fauna of Kansas at 2.10 Ma heralds the transition from the Blancan to Irvington-ian North American Land Mammal Age (NALMA). A *Microtus* immigration event characterizes the beginning of the Pleistocene and the Irvingtonian NALMA at Nash 72, Kansas. Early Irvingtonian deposits contain *Microtus* cf. *pliocaenicus* and *Mictomys kansasensis*, whereas later ones include a more advanced suite of arvicolids such as *Microtus ochrogaster /llanensis*, *M. meadensis*, *M. paroperarius*, and *Mictomys meltoni*. Exclusively modern arvicolids are recorded in latest Irvingtonian or earliest Rancholabrean deposits above the Lava Creek B ash (0.67 Ma), such as Butler Spring.
Key words: arvicolid, rodents, Cenozoic, Pliocene, Pleistocene, voles, systematics, biochronology.

Resumen: Se revisa ampliamente el registro Plioceno y pleistoceno de roedores arvicólidos dela región central de Norteamérica. Una nueva zonación provincial es propuesta para las Grandes Llanuras centrales. Los arvicólidos Hemphillienses están representados por *Promimomys* y *Protopliophenacomys*. Aunque especies primitivas de *Pliophenacomys* son conocidas del Blanquiense temprano de Indiana y Kansas, este género esta ausente en la mayoría de las localidades del Blanquiense inferior y medio de la cuenca de Meade en Kansas. Especies avanzadas de *Pliophenacomys*, con diferenciación positiva del esmalte, caracterizan los depositos del Blanquiense superior, y parecen ser buenos fósiles indicadores para este periodo, especialmente en combinación con especies avanzadas de *Ophiomys*. *Ogmodontomys poa-phagus* es el arvicólido más comun a lo largo de gran parte del Plioceno de Kansas y Nebraska.La desaparición de los arvicólidos arcaicos de la fauna local de Borchers en Kansas a 2.10 Ma marca anuncia la transición entre las edades de mamíferos Norteamericanas (NALMA) Blanquiense e Irvingtoniense que se produse en Nash 72, Kansas. Depósitos del Irvingtoniense inferior contienen *Microtus* cf. *pliocaenicus* y *Mictomys kansasensis*, mientras que posteriormente contienen un conjunto de arvicólidos más avanzados como *Microtus ochrogaster/ llanensis*, *M. meadensis*, *M. paroperarius*, and *Mictomys meltoni*. Arvicolidos exclusivamente modernos son registrados en depósitos del Irvingtoniense tardío o Rancholabreaense temprano por encima de las cineritas Lava Creek B (0.67 Ma), como en Butler Spring.
Palabras clave:arvicólidos, roedores, Cenozoico, Plioceno, Pleistoceno, sistemática, biocronología.

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INTRODUCTION

It is axiomatic that evolutionary studies with paleontological data require an accurate sequence of fossil sources, preferably with associated chronological information. One of the ongoing activities of paleontology is to generate such information, using a variety of methods including geologic mapping, radiometric dating, paleomagnetic analysis, and biochronology. Mammalian fossils have long been used for biochronological purposes in North American terrestrial deposits, and arvicolid rodents in particular have been utilized effectively to help sequence late Neogene and Pleistocene localities. An excellent review was presented by BELL (2000), and only the highlights will be discussed here. L. MARTIN (1979) suggested six North American arvicolid zones, with one for the Hemphillian, two for the Blancan, one for part of the Irvingtonian, another for the late Irvingtonian and early Rancholabrean, and a sixth for the remainder of the Rancholabrean. REPENNING (1987) recognized two Hemphillian arvicolid zones, five in the Blancan, two in the Irvingtonian, and two in the Rancholabrean. BELL (2000) maintained REPENNING's five Blancan zones, expanded the Irvingtonian to three zones, and reduced the Rancholabrean to a single zone. SCHULTZ *et al.* (1978), L. MARTIN (1979), L. MARTIN and SCHULTZ (1985) proposed a provincial zonation of mammalian local faunas for the central Great Plains, based on mammalian assemblages from Nebraska and Kansas. The Rexroadian and Senecan represented the Blancan; the Sappan and the Sheridinian covered the Irvingtonian and earliest Rancholabrean. L. MARTIN and SCHULTZ (1985) also suggested the possible need for the "Cudahyan" to cover such Great Plains local faunas as Cudahy, from Kansas. A developing database generated by the Meade Basin Rodent Project (MARTIN *et al.*, 2000), plus the discovery of new arvicolids from Indiana (FARLOW *et al.*, 2001; MARTIN *et al.*, 2002a), allow a more refined arvicolid biostratigraphy to be constructed for the central Great Plains region, with primary emphasis on the Pliocene and early Pleistocene Meade Basin sequence of Kansas. A new zonation terminology, somewhat similar to that used in Europe (the "MN" zones) is proposed, but here restricted in usage to the central Great Plains. The classification of North American arvicolids from MARTIN (2002) is used here, and is presented as Appendix I.

METHODS AND TERMINOLOGY

Data from the literature and unpublished information from the Meade Basin Rodent Project (MARTIN *et al.*, 2000) were used for this synthesis. Calibration points include the radiometric data from the Huckleberry Ridge, Lava Creek B, and Cerro Toledo B ash dates in the Meade Basin (IZETT and HONEY, 1995; MARTIN *et al.*, 2000), and reported position of various localities relative to other datable rock units (VOORHIES, 1977; REPENNING, 1987). Paleomagnetic data reported by LINDSAY *et al.* (1975) for Meade Basin localities was also helpful. For instance, sediments at Bender (presumably Loc. 1c), Rexroad Loc. 3, and Sanders are magnetically normal, suggesting these sites and others positioned between them were active during the Gauss chron. Additionally, field mapping by the author and colleagues J. HONEY and P. PELÁEZ-CAMPOMANES continues to provide new and revised information regarding stratigraphic position of many classic and new Meade Basin localities. Our most recent evaluation is presented as a stratigraphic hypothesis in Figure 1. In Figures 1 and 2 we also include local faunas from depositional regions outside the Meade Basin, but as no paleomagnetic or radiometric data are available from these faunal sources (e.g., Sand Draw, White Rock, Dixon, Big Springs), their exact temporal position relative to the Magnetic Polarity Time Scale (MPTS) cannot be determined at this time. I follow the recent treatment of LINDSAY *et al.* (2002) in defining the Hemphillian/ Blancan boundary.

Arvicolid dental terminology follows VAN DER MEULEN (1973), RABEDER (1981), and MARTIN (1987, 2001). A new biochronological category, the North American rodent zone (RZ), is introduced here. A RZ is defined on the basis of one or more rodent index fossils, and includes one or more representative local faunas. The term "rodent" rather than "arvicolid" is used because in the near future results from studies of other rodent families will contribute to this zonation. In this paper a mammalian local fauna is considered an aggregate of mammalian fossils taken from a single quarry or set of quarries at the same presumed stratigraphic level. The author has less confidence in the application of this approach to assemblages outside of the Meade Basin (such as Sand Draw and White Rock), but will tentatively assume they are temporally homogeneous until further study proves otherwise.

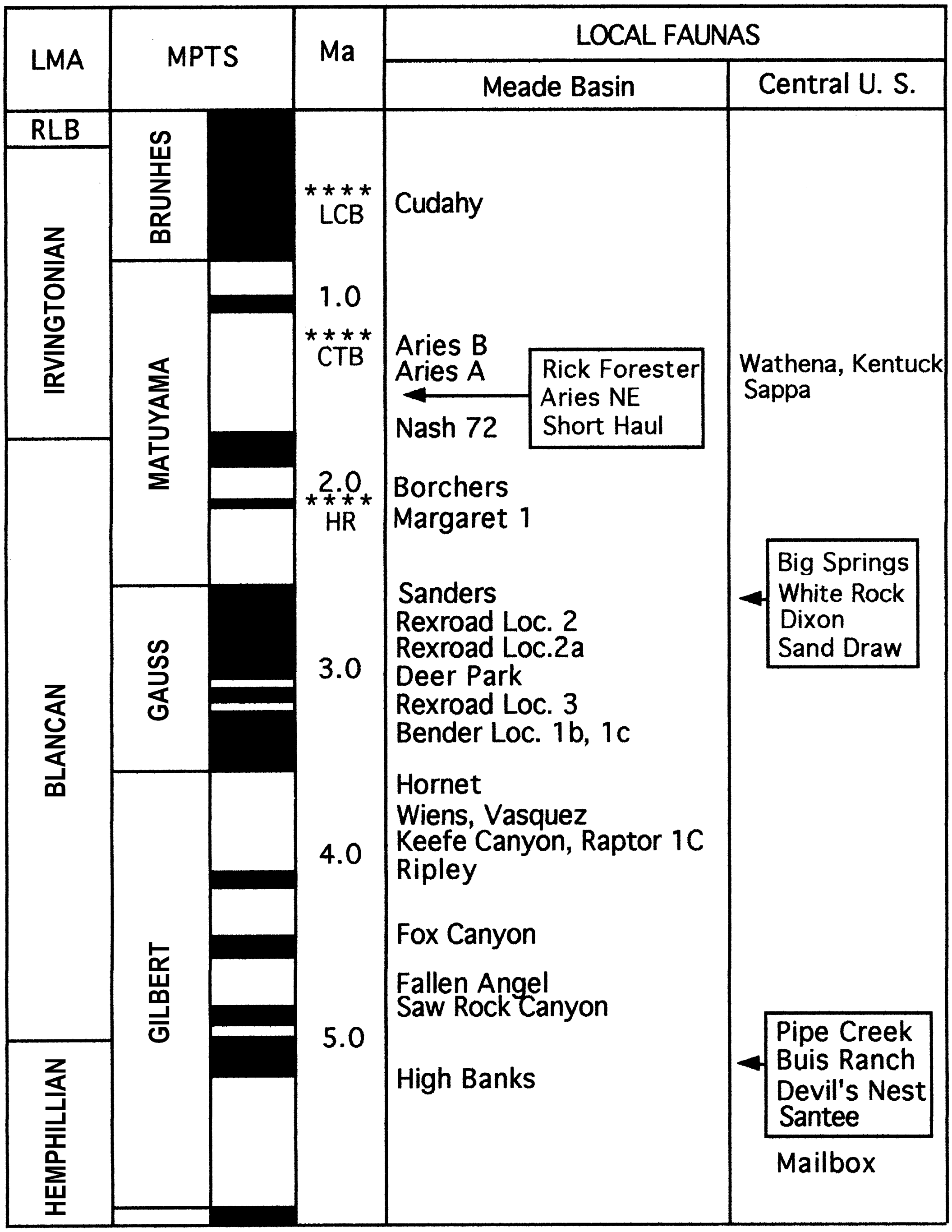

Figure 1.- Proposed stratigraphic hypothesis for local faunas of the Meade Basin from southwestern Kansas, compared to the presumed stratigraphic occurrences of other local faunas from the central United States (U.S.). Relative position of faunas within boxes from the central U. S. has not been determined. Line of stars = volcanic ash; HR = Huckleberry Ridge, CTB = Cerro Toledo B, LCB = Lava Creek B. LMA = North American land mammal age, MPTS = magnetic polarity time scale, Ma = Million years ago, RLB = Rancholabrean.

Figura 1.- Hipótesis estratigráfica propuesta para las faunas locales de la Cuenca de Meade en el Suroeste de kansas, comparada con la ocurrencia de otras faunas del centro de los Estados Unidos (U.S.). La posición relativa de las faunas del centro de los Estados Unidos que se encuentran en los marcos no ha sido determinada. Las líneas de estrellas representan cenizas volcánicas.

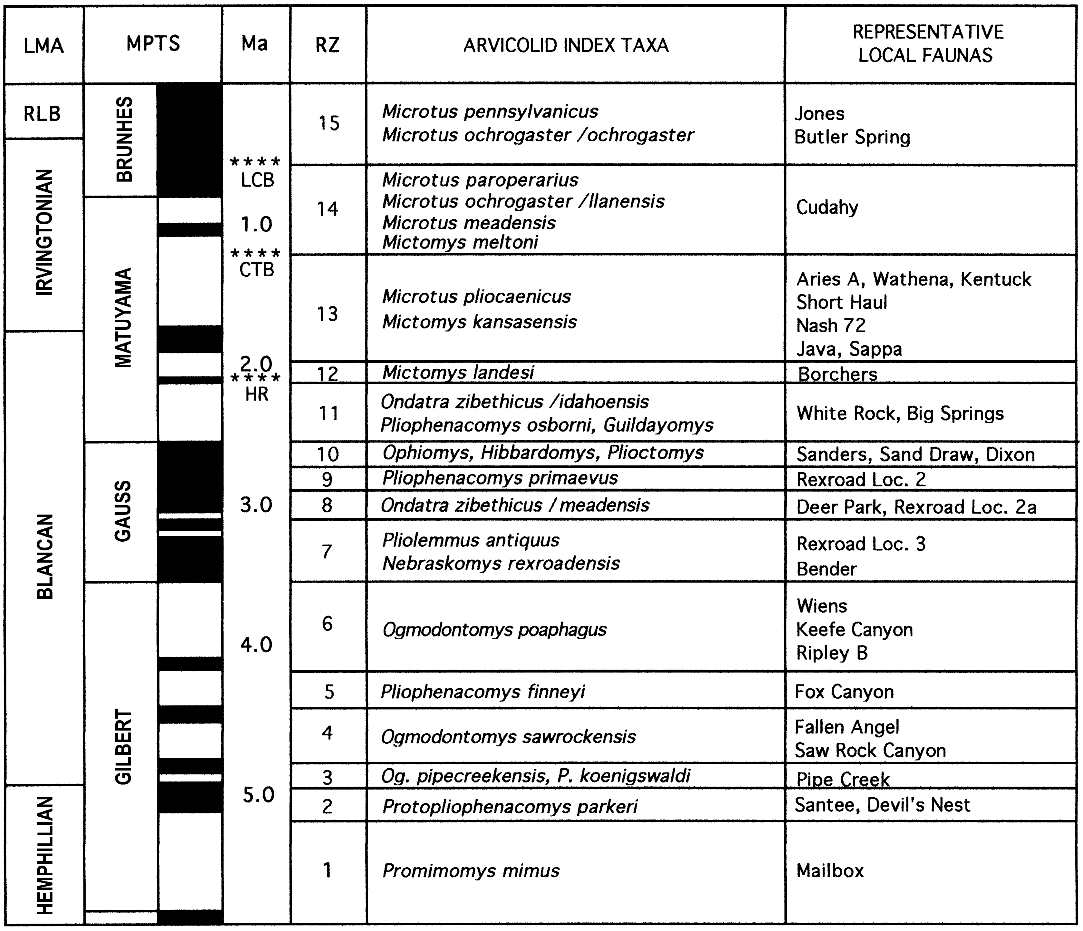

Figure 2.- Arvicolid index taxa and rerpesentative local faunas for central Great Plains rodent zones. Og. = *Ogmodontomys*, P. = *Pliophenacomys*; other abbreviations as in Fig. 1.
Figura 2.- Taxones de arvicólidos indicadores y faunas locales representativas para la zonación de roedores de las Grandes Llanuras centrales.

THE GREAT PLAINS RECORD

A minimum of fifteen rodent zones can be recognized from mammalian deposits on the Great Plains. Figure 2 presents characteristic index arvicolid species and representative local faunas for each zone. However, it is as much the combination and sometimes the lack of species that characterizes a given interval, and therefore the identifying spectrum of arvicolids for each zone is more fully elaborated in the review of each zone presented below. The complete stratigraphic ranges of the arvicolids considered here are provided in Fig. 3.

RZ 1

Index fossils- *Promimomys mimus* SHOTWELL, 1956

Characteristic local faunas- Mailbox, NE.

Comments- *Promimomys mimus* is the earliest and most primitive arvicolid on the Great Plains. The Mailbox locality is considered to be of late Miocene age and probably earlier than 5.5 Ma, but a more precise date is currently unavailable (REPENNING *et al.*, 1990; BELL, 2000).

RZ 2

Index fossils- *Protopliophenacomys parkeri* (L. MARTIN), 1975.

Rodent Zones (RZ)	1	2	3	4		5	6				7		8			9	10				11		12	13			14	15
Species	Mbx	STE	Pcr	SRC	FA	FC	Rip	KC	Wns	Hor	Ben	RR3	DPA	DPB	RR2a	RR2	Sdr	Sand	Dix	BD	WR	BS	Bor	Jav	N72	ArA	Cud	BS
Promimomys mimus	x																											
Protopliophenacomys parkeri		x																										
Pliophenacomys koenigswaldi			x																									
P. finneyi						x																						
P. primaevus																x	x	—	—	x								
P. dixonensis																			x									
P. osborni																					x	x	—	x?				
Ogmodontomys pipecreekensis			x																									
O. sawrockensis				x	x																							
O. poaphagus						x	x	x	x	x	x	x	x	x	x	x	x											
Ondatra zibethicus /meadensis													x	—	—	—	x	—	x	x								
O. z. /idahoensis																					x	—	x					
O. z. /annectens																								x				
Ophiomys meadensis																	x	x	x	x	x							
Guildayomys hibbardi																					x	x	—	x?				
Pliolemmus antiquus											x	—	x	—	—	—	x	x										
Nebraskomys rexroadensis											x	x	—	x														
N. mcgrewi																	x											
Hibbardomys marthae																					x	x	—	x?				
H. skinneri																	x											
H. fayae																			x									
H. voorhiesi																					x	x						
Mictomys vetus																												
M. landesi																							x					
M. kansasensis																								x	x	x		
M. meltoni																											x	
Plioctomys rinkeri																			x	x	x							
Microtus cf pliocaenicus																								x	x	x		
M. ochrogaster /llanensis																											x	
M. o. /ochrogaster																												x
M. meadensis																											x	
M. paroperarius																											x	
M. pennsylvanicus																												x

Figure 3.- Known stratigraphic ranges of arvicolid taxa included in this study. Mbx = Mailbox, STE = Santee, Pcr = Pipe Creek, SRC = Saw Rock Canyon, FA = Fallen Angel, FC = Fox Canyon, Rip = Ripley B, KC = Keefe Canyon, Wns = Wiens, Hor = Hornet, Ben = Bender, RR3 = Rexroad Loc. 3, DPA = Deer Park A, DPB = Deer Park B, RR2a = Rexroad Loc. 2a, RR2 = Rexroad Loc. 2, Sdr = Sand Draw, Sand = Sanders, Dix = Dixon, BD = Boyle Ditch, WR = White Rock, BSp = Big Springs (Nebraska), Bor = Borchers, Jav = Java, N72 = Nash 72, ArA = Aries A, Cud = Cudahy, BS = Butler Spring.
Figura 3.- Distribución estratigráfica conocida delos taxa de arvicólidos incluidos en este trabajo.

Characteristic local faunas- Santee, NE; Devil's Nest, NE.

Comments- Originally described as "*Proplio-phenacomys*"*parkeri* (L. Martin, 1975), *Protopliophenacomys* was reconstituted and redefined by L. Martin (1994). It is intermediate in dental complexity between *Promimomys mimus* and the genus *Pliophenacomys* (Martin *et al.*, 2002a). The Santee and Devil's Nest local faunas are considered to be at the same stratigraphic level and may underlie a tuff dated at 5.0 Ma (Voorhies, 1977).

RZ 3

Index fossils- *Ogmodontomys pipecreekensis* Martin *et al.*, 2002; *Pliophenacomys koenigswaldi* Martin *et al.*, 2002.

Characteristic local faunas- Pipe Creek Sinkhole, IN

Comments- The rhinoceros *Teleoceras* was recovered with the Pipe Creek arvicolids, and on this basis the locality and biota were referred to the late Hemphillian (Martin *et al.*, 2002a). However, Lindsay *et al.* (2002) provided a cogent argument for using the first appearance of either *Ophiomys* or *Ogmodontomys* (= their *Mimomys*) as an indication of early Blancan time, and I will follow that boundary definition here, thus referring Pipe Creek to the early Blancan NALMA. *Ophiomys* and *Ogmodontomys* are likely early immigrants, whereas the Pliophenacomyinae (see Appendix) appears to be a North American endemic subfamily, derived from *Promimomys*.

Ogmodontomys pipecreekensis is a primitive species, but probably was not ancestral to *O. sawrockensis. Pliophenacomys koenigswaldi* is morphologically intermediate between *Protopliophenacomys parkeri* and later species of *Pliophenacomys*.

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RZ 4

Index fossils- *Ogmodontomys sawrockensis* HIBBARD, 1957.

Characteristic local faunas- Saw Rock Canyon, KS; Saw Rock Canyon 1, KS; Fallen Angel, KS; Argonaut, KS.

Comments- Neither the rhinoceros *Teleoceras* nor the primitive geomyid *Pliogeomys* can be confirmed in collections from HIBBARD's original Saw Rock Canyon sites (despite publication to the contrary; HIBBARD, 1953; PROTHERO & MANNING, 1987), and neither have been recovered from new localities at the presumed same stratigraphic level in and around Saw Rock Canyon. Consequently, these sites are now considered as earliest Blancan, rather than as late Hemphillian, but slightly later in time than the Pipe Creek Sinkhole.

RZ 5

Index fossils- *Pliophenacomys finneyi* HIBBARD & ZAKRZEWSKI, 1972.

Characteristic local faunas- Fox Canyon, KS.

Comments- Thousands of teeth and jaws of *Pliophenacomys finneyi*, which has undifferentiated molar enamel, have been recovered only from the original Fox Canyon locality (HIBBARD, 1950). No additional rodent localities have been found at this stratigraphic level, although Bishop, a large mammal locality, was likely contemporaneous (MARTIN *et al.*, 2000). ZAKRZEWSKI (1967) presented a quantitative analysis of *Ogmodontomys* from the Meade Basin, and suggested that *O. poaphagus* m1s from Fox Canyon were more primitive than samples of m1s of *O. poaphagus* from other Meade Basin localities.

RZ 6

Index fossils- *Ogmodontomys poaphagus* HIBBARD, 1941.

Characteristic local faunas- Ripley B, KS; Keefe Canyon, KS; Raptor 1C, KS; Wiens, KS.

Comments- Blancan local faunas from the Meade Basin younger than Fox Canyon and older than Bender have only one arvicolid, *Ogmodontomys poaphagus*. This is not an artefact of sampling, as Ripley B, for example, has produced thousands of rodent molars. Neither is the reasoning circular; the sequence of these faunas has been determined by careful field mapping.

RZ 7

Index fossils- *Pliolemmus antiquus* HIBBARD, 1938; *Nebraskomys rexoadensis* HIBBARD, 1970; in combination with *Ogmodontomys poaphagus*.

Characteristic local faunas- Bender (Localities 1b and 1c combined), KS; Rexroad Loc. 3, KS.

Comments- The immigration of *Nebraskomys* and *Pliolemmus* into the Meade Basin is considered a significant event identifying RZ 7.

RZ 8

Index fossils- *Ondatra zibethicus /meadensis*, in combination with *Nebraskomys rexroadensis, Ogmodontomys poaphagus*, and *Pliolemmus antiquus*.

Characteristic local faunas- Deer Park A and B, KS; Rexroad Loc. 2a, KS.

Comments- The amount of time separating RZ 7 from RZ 8 local faunas cannot be determined at present. The mammalian assemblages from these two periods are obviously very similar, and all are located relatively high in the Rexroad Formation (WOODBURNE, 1961; MARTIN *et al.*, 2000, 2002b). As an aquatic mammal, it is also possible that the muskrat was present and not recorded in earlier faunas of the Meade Basin. However, as noted above, there have been thousands of rodent fossils recovered from Ripley B and hundreds from other early Blancan sites, and no muskrat material has been found. For now, I view the Deer Park A record as the initial dispersal event of muskrats into the Meade Basin.

RZ 9

Index fossils- *Pliophenacomys primaevus* HIBBARD, 1938 with *Ogmodontomys poaphagus* and in the absence of *Ophiomys meadensis* and *Hibbardomys*.

Characteristic local faunas- Rexroad Loc. 2.

Comments- Rexroad Loc. 2 was apparently an artesian spring that developed high in the Rexroad Formation, above Deer Park A and B, possibly in deposits that contain the Rexroad Loc. 2a local fauna (MARTIN *et al.*, 2002b). Although in the same pasture and separated by no more than 300 m, Rexroad 2 and 2a clearly represent two distinct time intervals, as *Pliophenacomys* has not been recovered from Rexroad 2a (MARTIN *et al.*, 2002b). Unfortunately, Rexroad 2, a flour sand tube, was mined to a depth of over 3 m by Hibbard's field parties, and its former position is no longer observable on the high plains surface. The Rexroad Loc. 2 record of *Pliophenacomys* *primaevus*, a species with positive molar enamel differentiation (Zakrzewski, 1984), is considered the lowest stratigraphic datum (LSD) and first appearance for *P. primaevus* on the Great Plains.

RZ 10

Index fossils- *Ophiomys meadensis* HIBBARD, 1956; *Pliophenacomys dixonensis* ZAKRZEWSKI, 1984; *Hibbardomys skinneri* ZAKRZEWSKI, 1984; *H. fayae* ZAKRZEWSKI, 1984; *Nebraskomys mcgrewi* HIBBARD, 1957, in combination with *Plioctomys rinkeri* (HIBBARD), 1956.

Characteristic local faunas- Sand Draw, NE; Sanders, KS; Dixon, KS; Boyle Ditch, WY.

Comments- This time period is characterized by the dispersal of *Ophiomys* and *Plioctomys* onto the Great Plains, presumably from the western United States. Although not yet recovered from the Meade Basin, various species of *Hibbardomys* appear in Nebraska and farther east in Kansas (Dixon; HIBBARD, 1956) during this time. The Boyle Ditch local fauna is located high in the Rocky Mountains of Wyoming (BARNOSKY, 1985), but its arvicolid component shows that there was genetic continuity with Great Plains arvicolid communities, and for that reason it was included in the analysis.

RZ 11

Index fossils- *Pliophenacomys osborni* ZAKRZEWSKI, 1984; *Guildayomys hibbardi* ZAKRZEWSKI, 1984; *Hibbardomys marthae* ZAKRZEWSKI, 1984; *Hibbardomys voorhiesi* ZAKRZEWSKI, 1984; *Ondatra zibethicus /idahoensis,* in combination with *Plioctomys rinkeri.*

Characteristic local faunas- White Rock, KS; Big Springs, NE.

Comments- *Pliophenacomys osborni* exhibits the most advanced dentition of all *Pliophenacomys* species, and seems to have been convergent to some extent with *Microtus.* The molars are very high crowned, and unusually for *Pliophenacomys*, the reentrant angles are often distinctly provergent. This tendency is taken to the extreme in *Guildayomys*, which has lost the molar roots.

Because RZ 11 localities are 1) isolated from one another and from those in the Meade Basin, and 2) considerably farther north than the Meade Basin, it is conceivable, perhaps even likely, that some of the differences in arvicolid communities from those in the Meade Basin was due to differences in climate and thus environment. The temporal placement of these local faunas is therefore only tentative at this time.

RZ 12

Index fossils- *Mictomys landesi* (HIBBARD), 1954 in combination with *Ondatra zibethicus /idahoensis* and in the absence of other archaic arvicolids.

Characteristic local faunas- Borchers, KS.

Comments- At least in the Meade Basin of southwestern Kansas, Borchers (HIBBARD, 1941) is the latest Blancan local fauna, and bridges the gap between earlier Blancan local faunas with a number of archaic arvicolids and the earliest Pleistocene assemblages in which we find the first *Microtus*. The Borchers local fauna, from which thousands of rodent remains have been recovered, lies directly on the Huckleberry Ridge ash, dated at 2.10 Ma (IZETT & HONEY, 1995).

RZ 13

Index fossils- *Ondatra zibethicus /annectens, Mictomys kansasensis* (HIBBARD), 1952; *Microtus* cf *pliocaenicus* (KORMOS), 1933.

Characteristic local faunas- Java, SD; Nash 72, KS; Short Haul, KS; Rick Forester, KS; Aries A, KS; Kentuck, KS; Wathena, KS; Sappa, NE.

Comments- The beginning of the Pleistocene and the beginning of the Irvingtonian NALMA are considered to be roughly synchronous in the Meade Basin record at about 1.8 Ma, represented by the Nash 72 local fauna, taken from a single quarry 2.5 m above the Borchers quarry (MARTIN *et al.*, 2002c). A number of local faunas from this interval have been found in Kansas and Nebraska. Other than those in superposition in the Meade Basin (MARTIN *et al.*, 2002c; Fig. 4), it is difficult to sequence them relative to one another. In the Meade Basin, RZ 13 faunas are restricted to the period of time between the Huckleberry Ridge (2.10 Ma) and Cerro Toledo B (1.23-1.47 Ma) ashes.

RZ 14

Index fossils- *Microtus paroperarius* HIBBARD, 1944; *M. meadensis* HIBBARD, 1944; *M. ochrogaster /llanensis, Mictomys meltoni* (PAULSON), 1961.

Characteristic local faunas- Cudahy, KS; Sunbrite, KS

Comments- The majority of specimens used to construct the Cudahy local fauna list were taken from the type Cudahy ash mine; a few were recovered from the nearby Sunbrite mine (PAULSON, 1961). The material was taken from a thin lens directly below the Lava Creek B ash, dated at 0.67 Ma. This aggregation of advanced arvicolids, all with rootless molars, has also been recorded from the Seymour Formation of Texas (HIBBARD and DALQUEST, 1966).

RZ 15

Index fossils- *Microtus ochrogaster/ochrogaster, M. pennsylvanicus*.

Characteristic local faunas- Butler Spring, KS; Jones, KS and numerous other Rancholabrean (late Pleistocene) assemblages from the Great Plains (e.g., see DAVIS, 1987).

Comments- Local faunas with a representation exclusively of modern arvicolids appear subsequest to 0.67 Ma on the Great Plains, but we do not currently have finer resolution for this event. With the exception of a brief appearance of *Synaptomys australis* in the Meade Basin (HIBBARD, 1955; MARTIN *et al.*, 2000), there are no extinct arvicolids recorded from the central Great Plains during the late Pleistocene.

DISCUSSION

The burgeoning rodent record in the Meade Basin will eventually lead to a very refined history of rodent communities through the Pliocene and Pleistocene in southwestern Kansas. New taxonomic assessments and stratigraphic data create a dynamic system within which even recent publications become partly obsolete. For instance, it was only during 2001 that we gained information leading to reassessment of the age and stratigraphic position of Saw Rock Canyon (now Blancan instead of Hemphillian) and some classic localities around Meade State Park (e.g., Rexroad Loc. 2, 2a, 3 and the Bender quarries). Particularly the latter information, completely unexpected, leads us to question whether there are any outcrops of Ballard Formation in Meade County other than those at the type locality on the Big Springs Ranch (not to be confused with the Big Springs local fauna from Nebraska). This area is currently inaccessible to scientists, and therefore resolution of the problem may not be quickly forthcoming.

It is critical that the geological (mapping), radiometric, and paleomagnetic work provide the primary calibrations and therefore faunal sequence, rather than invoking the circular reasoning of assuming faunal placement based solely on ad hoc assumptions of evolutionary changes in dental or skeletal morphology from recovered fossils. That is, the rodent zones should not have been created to sequence the local faunas, although once a stable sequence has been established in a region, the evolutionary data can, of course, help to determine the relative age of geographically isolated local faunas from the same general area. The chronology presented here for the Meade Basin sequence is reasonably secure, but this cannot be said for local faunas outside the basin, as noted above. Of course, the first stratigraphic record of a taxon does not necessarily represent a true first occurrence in a region, but in the case of rodent fossils, for which often hundreds or thousands of specimens may be represented, there is a greater likelihood that this is true than with other mammalian groups. Given these limitations and caveats, the Meade Basin rodent record, in concert with that of representative local faunas from other depositional regimes, provides us with a chronological framework within which some tentative distributional and evolutionary patterns can be determined, as follows:

1. Ancestral arvicolids of the genus *Promimomys* occur on the Great Plains, probably more than 5.5 Ma.
2. *Protopliophenacomys*, with dental morphology intermediate between *Promimomys* and later arvicolids, especially *Pliophenacomys*, was present in Nebraska more than 5.0 Ma.
3. Pipe Creek, an early Blancan vertebrate assemblage from Indiana, includes a possible ancestor for later members of the Pliophenacomyinae.
4. Arvicolids are rare during much of Blancan time, being represented from RZ 4-RZ 6, a period of at least 1.5 million years, by only one, or briefly two, species. The diversity of arvicolids increases dramatically during the middle and later Blancan, beginning with the Bender local fauna.
5. Muskrats enter the Meade Basin during the late Blancan, perhaps around 3.0 Ma.
6. During the late Blancan, as represented especially by RZ 10-11, arvicolid diversity is maximal on the Great Plains, dominated by species of *Pliophenacomys, Guildayomys*, *Hibbardomys*, and *Ophiomys.* However, a number of these taxa were recovered from sites to the east and north of the Meade Basin, and it is not clear if this represents either a meaningful ecological pattern or the absence of localities of similar age from southwestern Kansas.

7. By RZ 12, about 2.1 Ma, archaic arvicolids have mostly disappeared from the Meade Basin and, perhaps, from the Great Plains, unless there is still a significant climatic/ecological difference between southwestern Kansas and regions on the plains to the north. White Rock (ESHELMAN, 1975; now placed in RZ 11), for example, conceivably represents the northern equivalent of Borchers, with many more arvicolids, including *Plioctomys* rather than *Mictomys*. Perhaps a northern geographic position also explains the presence of a few arvicolids more typical of RZ 11 in the RZ 13 Java local fauna from north-central South Dakota (MARTIN, 1989). Alternatively, they could be Blancan intrusives, and that is why a question mark is associated with these records in Fig. 3.

8. Bog lemmings of the genus *Plioctomys* enter the Great Plains during the late Blancan RZ 10, slightly prior to the entrance of *Mictomys* during RZ 12.

9. Archaic arvicolids, with rooted molars, disappear from the Great Plains during late RZ 12 or early RZ 13. *Microtus* enters the Great Plains in early RZ 13. *Microtus* cf *pliocaenicus*, a species with only three triangles on m1, characterizes the central Great Plains, from Kansas through South Dakota, during RZ 13, from about 2.1-1.35 Ma (average of 1.23 and 1.47 Ma Cerro Toledo B ashfalls).

10. Sometime between about 1.35-0.67 Ma, the Great Plains arvicolid fauna changes, and *M.* cf. *pliocaenicus* gives way to *M. paroperarius, M. ochrogaster* (primitive dental morphotype), and *M. meadensis* during RZ 14.

11. Arvicolids of exclusively modern aspect are seen in the Butler Spring local fauna of Kansas and many other local faunas during RZ 15.

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APPENDIX I
Classification of North American Arvicolid Genera (from MARTIN, 2002)

Family Arvicolidae GRAY, 1821
Subfamily Promimomyinae, new
- *Promimomys* KRETZOI, 1955; synonym *Prosomys* SHOTWELL, 1956

Subfamily Arvicolinae BONAPARTE, 1837
Tribe Arvicolini KRETZOI, 1955
- *Mimomys* FORSYTH MAJOR, 1902
- *Microtus* SHRANK, 1798
- *Lemmiscus* THOMAS, 1912

Tribe Clethrionomyini, HOOPER & HART, 1972
- *Clethrionomys* TILESIUS, 1850

Tribe Phenacomyini, new
- *Phenacomys* MERRIAM, 1889
- *Hibbardomys* ZAKRZEWSKI, 1984

Subfamily Ondatrinae REPENNING, 1982
Tribe Ondatrini Repenning, FEJFAR & HEINRICH, 1990
- *Ondatra* LINK, 1795; synonym *Pliopotamys* HIBBARD, 1938

Tribe Ogmodontomyini, new
- *Ogmodontomys* HIBBARD, 1941
- *Cosomys* WILSON, 1932
- *Ophiomys* HIBBARD & ZAKRZEWSKI, 1967

Subfamily Nebraskomyinae, new
- *Nebraskomys* HIBBARD, 1957
- *Atopomys* PATTON, 1965

Subfamily Pliophenacomyinae REPENNING, FEJFAR & HEINRICH, 1990; new rank
- *Protopliophenacomys* L. MARTIN, 1995
- *Pliophenacomys* HIBBARD, 1938
- *Pliolemmus* HIBBARD, 1938
- *Guildayomys* ZAKRZEWSKI, 1984

Subfamily Lemminae GRAY, 1825
- *Lemmus* LINK, 1795
- *Plioctomys* SUCHOV, 1976
- *Mictomys* TRUE, 1894
- *Synaptomys* BAIRD, 1857

Subfamily Discrostonychinae KRETZOI, 1955
- *Predicrostonyx* GUTHRIE & MATTHEWS, 1971
- *Dicrostonyx* GLOGER, 1841

North American arvicolid genera of uncertain taxonomic affinity: *Loupomys* VON KOENIGSWALD & L. MARTIN, 1984; *Neofiber* TRUE, 1884; *Proneofiber* HIBBARD & DALQUEST, 1973.