Paludicola 9(1):13-20 November 2012

FURTHER NOTES ON THE PORT KENNEDY CAVE ARVICOLID RODENTS

Robert A. Martin

Department of Biological Sciences, Murray State University, Murray, KY 42071

ABSTRACT

Cope (1871) named five *Microtus*-like species from the Port Kennedy Cave deposit of Montgomery County, Pennsylvania, all of which he referred to the genus *Arvicola*. Using Cope's illustrations and descriptions, a review by C. W. Hibbard and examination of three Port Kennedy specimens, all of Cope's species (*Arvicola speothen, A. tetradelta. A dideltus, A. sigmodus* and *A. involutus*) are deemed *nomina dubia*. Two available specimens are clearly referable to *Pitymys cumberlandensis* van der Meulen, and another is referred to cf. *Microtus* (*Pedomys*) *llanensis* Hibbard. On the basis of these specimens and other considerations, Port Kennedy is considered to be younger than the Cumberland Cave local fauna of Maryland and approximately contemporaneous with the Trout Cave 2 local fauna of West Virginia, falling within Great Plains Rodent Zone (RZ) 14, between about 1.3 - 0.64 Ma.

The origin of *Pitymys* is obscure. Absence of a suitable North American ancestor and dental features of *P. cumberlandensis* suggest we should look for an Old World immigrant ancestor with undifferentiated enamel, a complex m3, and an m1 with five closed triangles and deep, provergent reentrants. Confluent T1-2 on lower molars and T2-3 on M3 in *P. cumberlandensis* may preclude this species as an ancestor for later North American pine voles.

INTRODUCTION

Six species of arvicolid rodents were described by Cope (1871) from the Port Kennedy Cave deposit in Montgomery County, Pennsylvania. All were referred to the genus *Arvicola*. The taxonomic history of these species was reviewed by Hibbard (1955), and he synonymized five of the *Microtus*-like species under *Microtus speothen*, "*Pedomys* or *Pitymys* " *dideltus* and "*Pedomys* or *Pitymys*" *involutus*. The sixth Hibbard identified as an extinct muskrat, *Ondatra hiatidens*, which is probably juvenile *O. annectens* (Martin et al., 2009). He also added the genus *Neofiber* to the arvicolid community. Hibbard examined material in the American Museum of Natural History (AMNH) and a few specimens from the Academy of Natural Sciences of Philadelphia (ANSP), as the Port Kennedy specimens were split between the two institutions. The holotypes were kept at the AMNH and, according to Hibbard (1955) were in the following condition when he examined them: 1) *Arvicola speothen* (AMNH 8689) – imprint of a left ramus with only m3 preserved; 2) *Arvicola tetradelta* (AMNH 8692) – according to Cope (1871) is a maxillary piece with M2-M3 but Hibbard (1955) identified the molars as m2-m3; 3) *Arvicola involuta* (AMNH 8699a) – teeth absent, presumably disintegrated. 4) *Arvicola sigmodus* (AMNH 8696) – molars missing, only piece of ramus and lower incisor remains; 5) *Arvicola didelta* (AMNH 8694) – all teeth missing, presumably disintregrated.

Hibbard (1955) valiantly attempted to make sense of the material from Cope's (1871) descriptions and comparisons made by Gidley and Gazin (1938) when they described arvicolid material from the Cumberland Cave deposit of Maryland. Van der Meulen (1978) later restudied the arvicolids from the Cumberland Cave deposit of Maryland, referring them to *Microtus paroperarius* Hibbard (1944) and the new species *Pedomys guildayi* and *Pitymys cumberlandensis*. In his paper, van der Meulen (1978) considered "*Pitymys*" *involutus* as a *nomen dubium*, but did not consider Cope's (1871) other species. From Hibbard's (1955) descriptions and illustrations of the Port Kennedy material, van der Meulen's (1978) classic work on the Cumberland Cave arvicolids and subsequent research on arvicolids from northeastern states (Pfaff, 1990) it seems likely that the Port Kennedy Cave arvicolid cadre includes a species of *Microtus* near Hibbard's (1944) *M. paroperarius* and two additional species near van der Meulen's (1978) *Pitymys cumberlandensis* and either van der Meulen's (1978) *Pedomys guildayi* or Hibbard's (1944) *Pedomys llanensis*. The first question that arises is: Are any of Cope's holotypes or topotypes sufficiently preserved to be diagnostic at the species level, perhaps supplanting one or more of Hibbard's and van der Meulen's later names? Combining information from Cope's (1871) original work, Hibbard's (1955) review and personal obervation of three specimens, I review the Port Kennedy *Microtus*-like voles and tentatively correlate the Port Kennedy Cave assemblage with other early

Pleistocene assemblages from the eastern and midwestern states.

METHODS

Upper molars are abbreviated by upper case letters (e.g., M3), lowers by lower case letters (e.g., m3). Three arvicolid specimens from the Port Kennedy Cave deposit housed at the Philadelphia Academy of Natural Sciences (ANSP) were examined and measured for this study: ANSP 141 (figured by Hibbard, 1955; fig. 2D): part right (R) mandible with incisor and m1-m3; ANSP 142 (figured by Hibbard, 1955; fig. 2B): part left (L) mandible with m1; ANSP 18907: part L mandible with m1-m3.

Measurements were made with an AO filar micrometer coupled to an AO binocular microscope. The micrometer was calibrated with a 2.0 mm AO slide and measurements were multiplied by the appropriate correction factor (0.615 in this case). Measurements made on m1 are shown in Figure 1. Ratios calculated from the measurements are as follows: A/L = 100a/L, a measure of the relative length of the ACC; W'/W = 100w'/W, a measure of the relative width of the anterior cap; B/W = 100b/W, a measure of the degree of confluency between the anterior cap and the triangles 4 and 5; C/W = 100c/W, a measure of the degree of confluency between triangles 4 and 5 (Martin, 1991).

I follow van der Meulen (1978) in assuming that T1 is not expressed on M2-M3; consequently the triangles begin on these teeth after the anterior loop with T2 instead of T1 as illustrated by Pfaff (1990; fig. 3). Dental abbreviations in the text are as follows: BRA = buccal re-entrant angle, LRA = lingual re-entrant angle.

Figure 2 was traced from a digital photograph, reduced and darkened. Parts of some of the triangle edges were obscured by thick glue and are therefore best estimates. Nevertheless, most triangles clearly displayed undifferentiated enamel.

SYSTEMATIC PALEONTOLOGY
FAMILY ARVICOLIDAE
COPE'S SPECIES
Arvicola speothen Cope, 1871
Arvicola tetradelta Cope, 1871

Comments—Despite the presence only of m3 (m1 and m2 are missing), Hibbard (1955) retained AMNH 8689 as the holotype of *Microtus speothen* and, without explanation, suggested that *M. speothen* and *M. paroperarius* from the Cudahy and Subrite local faunas of Kansas (Hibbard, 1944) might be conspecific. However, the m3 of most *Microtus*, including the extant subgenera *Microtus, Pedomys* and the extinct *Allophaiomys,* are generally indistinguishable, and as such it would not be possible (at least currently) to distinguish *M. paroperarius* from *P. guildayi* based on this molar. Relying on Cope's (1871) description of the m1-m2 of AMNH 8689 before it was lost, Hibbard (1955, p. 90) further referred the ambiguous AMNH 8692, the holotype of Cope's *Arvicola tetradelta,* to *M. speothen*. However, even if the two molars of AMNH 8692 are eventually identified correctly, they cannot be used to identify the subgenus *Microtus*, let alone *M. speothen* or *M. paroperarius*. In the absence of additonal material that could be construed to be part of a "type series," I recommend we consider *Arvicola speothen* and *A. tetradelta* as *nomena dubia*.

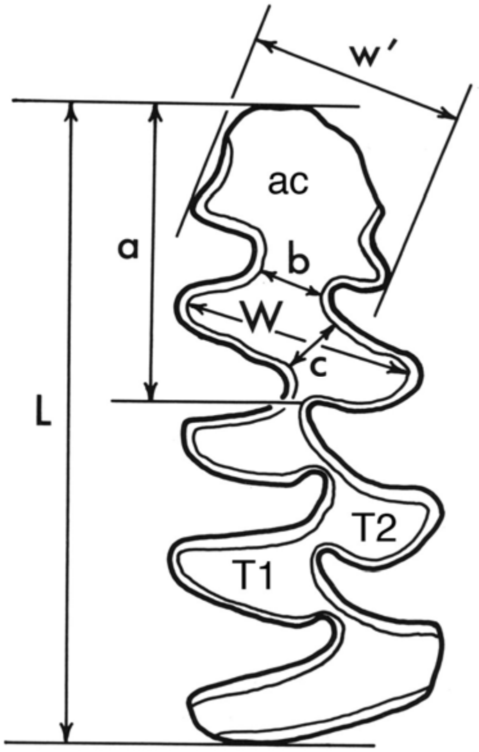

FIGURE 1. Topography of a *Microtus* left m1 (after Pfaff 1990). ac = anterior cap (sometimes also referred to as the acd, or anteroconid); L = occlusal length; a = length of ACC (anteroconid complex; all structures anterior to T3); W = greatest width ACC; w'= greatest width of anterior cap; b = width of dentine isthmus connecting T4-T5 and the anterior cap; c = width of dentine isthmus connecting T4 - T5; T1, T2 = triangles 1 and 2 (to identify other triangles, continue counting from T2; buds from the ac are considered "incipient" triangles).

Arvicola involuta Cope, 1871

Comments—Molars of the holotype of *Arvicola involuta* (AMNH 8694) have disintegrated and the illustration of an m1 provided by Cope (1871, fig. 16) is not definitive of any *Microtus*-like subgenus or species, and it does not resemble the m1 of extant *Pitymys pinetorum*, despite Cope's suggestion to the contrary (Cope, 1871, p. 90). I recommend we consider *Arvicola involuta* as a *nomen dubium*.

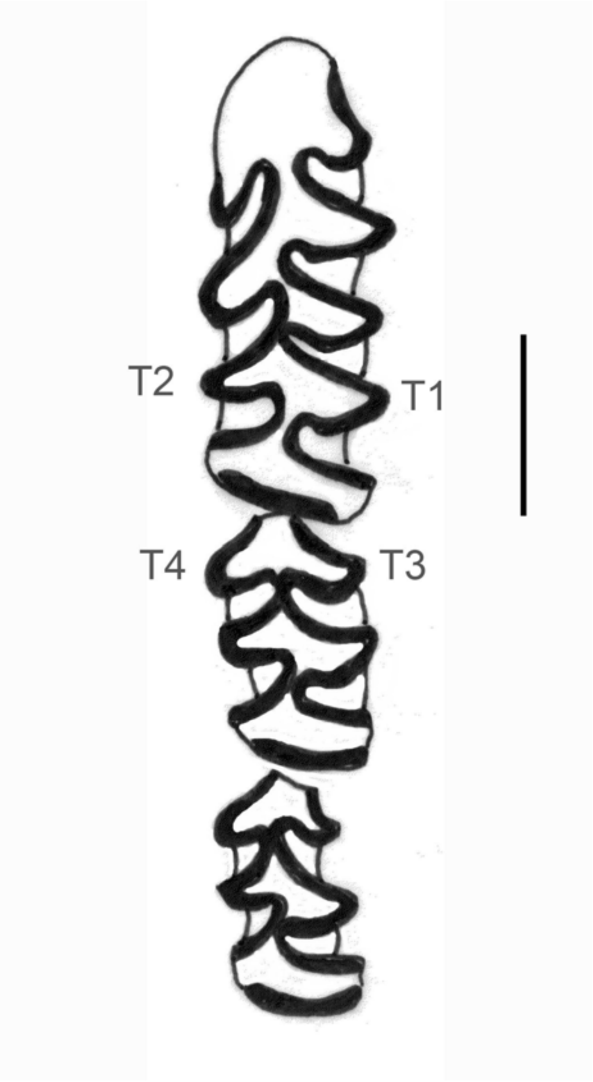

FIGURE 2. Occlusal morphology of Lm1-3 of *Pitymys cumberlandensis* (ANSP 18907) from Port Kennedy Cave. Scale bar = 1.0 mm.

Arvicola didelta Cope, 1871

Microtus dideltus (Cope, 1896)
Pedomys or *Pitymys dideltus* (Hibbard, 1955)

Comments—Illustrations of three m1s and an M3 in an M1-M3 series of *Arvicola didelta* (Cope, 1871; fig. 15) are similar to the same teeth of *Pedomys guildayi* van der Meulen (1978) based on occlusal morphology. The shallow and C-shaped BRA3 on m1, clearly distinguishable in Cope's illustration in his fig. 15, suggest *didelta* is a member of the taxon *Pedomys* (Martin, 1991; Pfaff, 1990). However, both the series of isolated m1s and the holotype of *A. didelta* are missing. The topotype m1-m3 illustrated by Hibbard (1955) is not advanced enough in dental anatomy to be distinguishable from Great Plains Pleistocene *Microtus* referred to *M.* (*Allophaiomys*) *pliocaenicus* (Martin, 1989). Although the molars of AMNH 8688 display positive enamel differentiation (unlike *Pitymys cumberlandensis*, in which the enamel is undifferentiated) both *M. pliocaenicus* and *M.* (*Pedomys*) *guildayi* from Cumberland Cave display positive enamel differentiation (van der Meulen, 1978; Martin, 1989, 1995). Because the remaining material of *Arvicola didelta* is not sufficient to define a distinct *Microtus* species, I recommend that *A. didelta* be considered a *nomen dubium*.

Arvicola sigmodus Cope, 1871

Comments—The molars from the holotype mandible of *A. sigmodus*, AMNH 8606, are missing, and none of the uncatalogued individual molars illustrated by Cope (1871, fig. 17) are currently recognized in the AMNH collections (R. Oleary, personal commmunication). Cope's (1871) diagnosis of *A. sigmodus* is contradictory, indicating some similarity to species we currently recognize as *Microtus* (*Pedomys*) *ochrogaster* and *Pitymys pinetorum*, which is not surprising because he illustrated a combination of species under *A. sigmodus* in his fig. 17, one of which, fig. 17a, may not even be a *Microtus* or *Pitymys*. Fig. 17b of *A. sigmodus* is roughly similar to the m1 of a *Pitymys* species, but as it is missing we cannot be sure. I recommend we consider *A. sigmodus* as a *nomen dubium*.

MICROTUS-LIKE SPECIES FROM PORT KENNEDY CAVE

Microtus (*Pedomys*) cf. *llanensis*

Referred Material—ANSP 142, left mandibular fragment with juvenile m1 (illustrated by Hibbard, 1955).

Comments--As documented by Martin (1987) and confirmed statistically by Pfaff (1990), the subgenus *Pedomys* can be recognized by a relatively shallow and C-shaped BRA3 (the anterior enamel border of T4 is relatively horizontal [rather than provergent] compared to this border in *Pitymys*). This feature is observable in ANSP 142 (Hibbard, 1955, fig. 2B and personal obervation). The relatively thin enamel and acute enamel borders identify ANSP 142 as a juvenile, and thus measurements and ratios of those measurements (after van der Meulen, 1978) are needed to at least tentatively determine the identity of this specimen. Measurements and ratios from ANSP 142 are presented in Table 1. In measurements and ratios ANSP 142 is indistinguishable from both *M. llanensis* and *M. guildayi*. Nevertheless, the relatively advanced form of the anteroconid on ANSP 142 as a juvenile suggests that it would have more approximated average *M. llanensis* in its adult configuration than average *M. guildayi*, and is tentatively referred to *M. llanensis*.

In a review of fossil *Pedomys*, Martin (1995) synonymized *Pedomys guildayi* (van der Meulen, 1978) under *M. pliocaenicus* and *M. llanensis* (Hibbard, 1944) under *M. ochrogaster* to reflect the likelihood, first expressed by van der Meulen (1978), that the extant *M. ochrogaster* evolved by phyletic evolution from early Pleistocene Great Plains populations referred to *Microtus pliocaenicus* (Martin, 1989). Whereas *M. ochrogaster* certainly evolved from a species similar to *M. pliocaenicus* of the Java local fauna from South Dakota, the recognition of two new extinct *Pedomys* species, *M. australis* from Florida and Texas (Martin, 1995), and *M. parmaleei* from Kansas and the Appalachian chain in the eastern United States (Martin, 1991; Martin et al., 2012) demonstrates that a single species phyletic model is no longer tenable. Because some specimens of *M. guildayi* demonstrate the shallow, C-shaped BRA3 of *Pedomys*, it now appears more prudent to resurrect both *M. guildayi* and *M. llanensis*, and then to try to determine their relationships to other extinct and extant species of the prairie vole clade with a more complete phylogenetic analysis. *Pedomys* is here retained within *Microtus* until an analysis demonstrates that early Pleistocene North American *Microtus* cf. *pliocaenicus* molars can be separated unequivocally from Eurasian *Microtus pliocaenicus* molars. If they cannot, then it seems reasonable to assume that many extant *Microtus* in both the Old and New World with positive enamel differentiation are descended from the evolutionary queen species *M. pliocaenicus* (Martin, 1995). This was essentially the conclusion reached earlier by van der Meulen (1978, 114).

Pitymys cumberlandensis van der Meulen, 1978

Pedomys or *Pitymys involutus*? (Hibbard), 1955 (fig. 2D)

Referrred Material—ANSP 141, part right mandible with m1-m3; ANSP 18907, partial left mandible with m1-m3.

Comments—*Pitymys cumberlandensis* (van der Meulen, 1978) is a medium-sized *Pitymys* characterized by the following: 1) relatively thick, undifferentiated enamel, 2) relatively simple anteroconid on m1 in which BRA4 and LRA5 are shallow and rarely contain cementum, complex m3 with well-developed T4, and 3) deep penetration of BRA3 and LRA3, almost closing T4 from T5. North American *Pitymys* can be identified by a prevalence of m1s with deep and provergent BRA2, BRA3 and LRA3 and LRA4. Deep penetration of BRA3 into the acd often isolates T6 as a sausage or finger shape with the apex pointing posteriorly (Figure 2). ANSP 141 (illustrated by Hibbard, 1955) and ANSP 18907 (Figure 2) display the salient features of *P. cumberlandensis*, although T4 is somewhat reduced on m3 in ANSP 141. Van der Muelen (1978) did not provide description of variation in the m3 of *P. cumberlandensis*, and for now the differences between ANSP 141 and 18907 are considered to represent population variation.

The B/W measurement for ANSP 18907 (Table 1), representing the relative width of the dentine isthmus connecting T5 with the anteroconid and therefore the tendency for T5 to be closed from the acd, is outside the small end of the range for B/W in *P. cumberlandensis* from Trout Cave 2, implying a very narrow connection. This condition is certainly derived in North American voles as compared with early *Microtus* (*Allophaiomys*) from the Java local fauna (Martin et al. 1998), but it appears to have evolved independently a number of times in unrelated voles, including other *Pitymys* (e.g., *P. aratai*, *M. guatemalensis*; Martin, 1987,1995). Currently, this condition in ANSP 18907 is considered to represent an extreme in *P. cumberlandensis* population variation, but without taxonomic significance.

Van der Meulen (1978) was impressed by the tendency in some extant *P. pinetorum* to retain undifferentiated enamel, but this must be rare, as most of the specimens of extant *P. pinetorum* I have studied display positive differentiation, although enamel on the anterior triangle borders in *Pitymys* is distinctly thicker than in *Microtus* at the same relative molar size (Martin, 1991: table 2). The m3 is also simpler (T4 reduced) in extant *P. pinetorum* then it is in *P. cumberlandensis*. The shift to positive enamel differentiation and change in form of m3 are dental changes that characterize the evolution of later *Pitymys* species as they branched from *P. cumberlandensis* or a related species. In his diagnosis of *P. cumberlandensis* van der Meulen (1978) also included the form of M3, which he labeled as unreduced, in combination with the m3. Judging by his illustrations, I assume van der Meulen was referring primarily to the relatively deep and postvergent LRA3, but this feature is highly variable in extant *P. pinetorum,* as shown by Arata (1965: fig. 4). M3s of extant *P. pinetorum* from the northeastern and midwestern United States display an equal complexity to those of *P. cumberlandensis*. Only *P. pinetorum parvulus* from Florida displays reduced

TABLE 1. Comparative measurements (in mm) of *Pitymys cumberlandensis* (ANSP 141, 142) and *Microtus* (*Pedomys*) sp. (ANSP 18907) from Port Kennedy Cave with other Pleistocene samples. Cumberland Cave data from van der Meulen (1978), Trout Cave 2 data from Pfaff (1990). Numbers for samples other than Port Kennedy Cave include the mean and observed range.

	L	a	w’	W	b	C	A/L	W’/W	B/W	C/W
Pitymys cumberlandensis										
Port Kennedy Cave										
ANSP 141	2.28	1.13	0.78	0.84	0.12	0.06	48.56	92.86	14.30	7.14
ANSP 18907	2.56	1.00	0.81	0.95	0.05	0.12	39.06	85.26	5.26	12.63
Cumberland Cave	2.54						48.2	92.6	16.2	15.1
	(2.28-2.87)						(44-53)	(84-102)	(6-27)	(6-32)
Trout Cave 2	2.62						47.5	91.5	14.1	15.4
	(2.36-2.92)						(42.2-53.1)	(79-101.2)	(7.3-24.1)	(8.5-26.0)
M. (*Pedomys*) *llanensis*										
Trout Cave 2	3.18						47.2	84.8	19.8	21.0
	(2.51-3.59)						(39.5-52.1)	(73.7-98.5)	(9.9-30.6)	(13.3-29.0)
M. (*Pedomys*) *guildayi*										
Cumberland Cave	2.58						45.7	80.4	26.0	20.4
	(2.27-3.07)						(42-50)	(70-91)	(13-36)	(9-31)
M. (*Pedomys*) sp.										
Port Kennedy Cave										
ANSP 142	2.57	1.18	0.87	1.11	0.12	0.23	45.91	78.38	14.29	27.38

complexity of the M3, with shallow and generally horizontal reentrants. What separates *P. cumberlandensis* M3s from those of *P. pinetorum* and other known North American *Pitymys* is that the apices of T2-3 are directly opposite and the dentine fields of these triangles are entirely confuent (Pfaff, 1990: fig. 8). Confluence of T2-3 in M3 was reported only in modern *P. pinetorum parvulus* from Florida (Arata, 1965), which as we discussed above has the simplest M3 in *P. pinetorum*. As illustrated by Arata (1965, fig. 4D) M3s of *P. pinetorum* from the late Pleistocene Reddick 1A deposit of northcentral Florida demonstrate a tendency towards confluent and opposite T2-3, but were not as extreme in their morphology as the M3s of *P. cumberlandensis* or those from living Florida pine voles. These observations lead to the following tentative conclusions: 1) the confluent T2-3 on a complex M3 as in *P. cumberlandensis* is likely a derived, rather than primitive condition; 2) the confluent M3 of extant *P. pinetorum* evolved relatively recently, during the late Pleistocene, and is convergent, rather than homologous, with the condition in *P. cumberlandensis.*

Another unusual dental feature of *P. cumberlandensis* is the tendency in all lower molars for the dentine fields of T1-2 to be confluent (Figure 2). The well-developed dentine field of T4 on M3, another distinguishing feature of *P. cumberlandensis*, is also directly opposite, rather than alternating with, the dentine field on T3. Taken collectively, the open and confluent dentine fields in both upper and lower molars probably preclude the known populations of *P. cumberlandensis* from direct ancestry to *P. pinetorum* and other modern and extinct pine voles in which these fields are mostly closed. Thus, *P. cumberlandensis* likely represents a sister species of the species ancestral to later pine voles. The ancestral North American pine vole likely displayed some of the features of *P. cumberlandensis*, such as thick, undifferentiated enamel, unreduced m3 and a tendency in m1 for T4-5 to be closed, but it would also display closed or nearly closed T2-3 on M3 and closed or nearly closed T1-2 on m1 and m2. It is conceivable that this “missing link” is simply another population of *P. cumberlandensis* in which these features are expressed. In some support for this idea is the observation in the Trout Cave 2 population of *P. cumberlandensis* that the dominant m1 morphology is one in which T1-2 are closed rather than open (Pfaff, 1990: fig. 8).

AGE OF THE PORT KENNEDY CAVE ASSEMBLAGE

Daeschler (1996) published a complete list of vertebrates from the Port Kennedy assemblage and concluded that the site was late Irvingtonian in age, possibly comparable to Hamilton Cave in West Virginia (Repenning and Grady, 1988) and older than Cumberland Cave (Gidley and Gazin, 1938) in Maryland and Trout Cave 2 (Pfaff, 1990) in West Virginia. Based on the rodents, Daeshler’s (1996) general estimate of age for these early Pleistocene sites

TABLE 2. *Microtus* and *Pitymys* species from select midwestern and eastern early and middle Pleistocene assemblages. Subg, indet. = Subgenus indeterminate.

Approx. age (Ma)	(2.0)	(1.6-1.3)	(0.64)	(0.35)
Species	Aries A	Cumberland Cave, Hamilton Cave	Port Kennedy Cave, Trout Cave 2, Cudahy	Coleman 2A
Microtus (*Allophaiomys*)				
M. pliocaenicus	X			
Microtus (*Pedomys*)				
M. guildayi		X		
M. llanensis			X	
Microtus (subg. indet.)				
M. paroperarius		X	X	
M. meadensis			X	
Pitymys				
P. cumberlandensis		X	X	
P. aratai				X

from the northeastern United States seems reasonable, but a different temporal order is likely.

The combination of *Ondatra annectens* (= *O. hiatidens*), *Pitymys cumberlandensis* and *Microtus* (*Pedomys*) cf. *llanensis* suggests that the Port Kennedy assemblage is referable to Martin's (2003) Rodent Zone (RZ) 14, originally developed for the Great Plains region. RZ 13 includes a series of local faunas with the archaic arvicolid *Microtus pliocaenicus*, and RZ 14 includes *M.* (*Pedomys*) *llanensis* (=*M. ochrogaster* /*llanensis* of Martin et al. [2008]) as well as *M. paroperarius*, also found at Trout Cave 2 (Pfaff, 1990) and Cumberland Cave (van der Meulen, 1978). Midwestern and western assemblages of RZ 14 also usually include *Microtus meadensis* (sometimes referred to *Terricola*), but the absence of this species in the eastern United States is likely due to ecological rather than temporal factors.Thus, Trout Cave 2 and Port Kennedy Cave may be approximately coeval eastern equivalents of the Cudahy and Sunbrite local faunas of Kansas (Martin et al., 2003b). The Cudahy local fauna lies directly beneath the Lava Creek B ash at 0.64 Ma, but we do not know either the earliest or latest records of the arvicolids rcorded from this site. Only *Microtus pliocaenicus* has been recorded beneath the Cerro Toledo B ash (about 1.35 Ma) in the Meade Basin of Kansas (Martin et al., 2008) and the extant *M. ochrogaster* is found in Great Plains assemblages of the late Pleistocene. RZ 14, therefore, conceivably could extend from about 1.35-0.30 Ma. For now, it would not be unreasonable to provide an approximate correlation of the Trout Cave 2 and Port Kennedy Cave assemblages with Cudahy, at about 0.64 Ma.

Microtus (*Pedomys*) *guildayi* from Cumberland Cave displays a simpler dentition than that of *M. llanensis* from Trout Cave 2 and Cudahy (van der Meulen, 1978; Pfaff, 1990) and may be directly ancestral to at least the eastern populations of *M. llanensis*. Consequently, Cumberland Cave is likely older than Trout Cave 2 and Port Kennedy Cave (assuming the *M.* cf. *llanensis* identification of ANSP 142 is correct).

The early Pleistocene Hamilton Cave arvicolids from West Virginia need restudy. Repenning and Grady (1988) listed 30 m1s of *Microtus* (*Allophaiomys*) *pliocaenicus* from the Cheetah Room of Hamilton Cave, but none of the specimens were illustrated. If this identification is confirmed, then the Cheetah Room material would be assignable to RZ 13. However, Repenning and Grady (1988) also mentioned that some of the m1s display a *Microtus* (*Pedomys*) *guildayi* morphology. In their assessment of fossil bog lemmings and muskrats from Hamilton Cave, Martin et al. (2003a, 2009) concluded that the Cheetah Room and *Smilodon* Room rodent collections from Hamilton Cave were deposited between 1.0-1.6 Ma, more likely toward the older end of the estimate (1.3-1.45 Ma). Repenning and Grady (1988) also identified *Microtus deceitensis* (as *Lasiopodomys deceitensis*), (cf.) *M. paroperarius*, and *Pitymys hibbardi* from the Cheetah Room. There is a superficial resemblance between some of the specimens illustrated by Repenning and Grady (1988) to those of *M. deceitensis* and *M. morlani* from the Yukon (Storer, 2003, 2004), but none of the Hamilton Cave m1s express the short, wide and deep lingual triangles that characterize the Alaskan species. Instead, the Hamilton Cave specimens display relatively longer and narrower triangles with more acute apices, more like *M. paroperarius* (Hibbard, 1944). Additionally, *M. deceitensis* molars display undifferentiated enamel, and if the illustrations are accurate, the specimens illustrated by Repenning and Grady (1988, fig. 4) display positive differentiation on many edges, another similarity to *M. paroperarius*. In any case, allocation to the genus *Lasiopodomys* for the Hamilton Cave specimens is certainly unwarranted at this time. Without further study of the Hamilton Cave material all we can state with certainty about the relatively advanced *Microtus* from the Cheetah Room is that it represents a species of *Microtus* with an m1 in which T4 is relatively reduced and T6 is absent or minimally expressed, both of which are features of *M. paroperarius* and the extant *M. oeconomus* group.

Pitymys hibbardi from the Williston 3A local fauna of Florida is a junior synonym of *P. pinetorum* (Martin, 1995), and differs in numerous ways from the *Pitymys* specimens from Hamilton Cave, three of which were illustrated by Repenning and Grady as *P. hibbardi* (1988, fig. 5). Illustrations B (USNM 264313) and C (USNM 264314) from their fig. 4 are very similar to specimens of *P. cumberlandensis* van der Meulen (1978), but illustration D (USNM 25431) has such a simple anteroconid complex that it is unclear if this specimen is a *Pitymys* or *Microtus* (*Allophaiomys*); Repenning and Grady (1988) mention this possibility in the legend to their fig. 5. *Pitymys cumberlandensis* thus appears to be a likely member of the Hamilton Cave assemblages, but the sample needs to be compared with those from Cumberland Cave and Trout Cave 2. Based on published information, it seems likely that a relatively primitive *Microtus* near *M. guildayi* is present at Hamilton Cave, which suggests an age for Hamilton Cave at least as old as Cumberland Cave, and likely older than Port Kennedy Cave and Trout Cave 2.

The Coleman 2A l.f. of Florida, also allocated to RZ 14 by Martin (2003), probably was deposited at the younger end of RZ 14, as the Coleman 2A *Pitymys aratai* (Martin, 1974) displays positive enamel differentiation and a reduced m3 (Martin, 1995), both advanced characters relative to *P. cumberlandensis*. The records above are summarized in Table 2.

In conclusion, due to the absence of holotypes and most paratypes, all of Cope's (1871) *Microtus*-like species from Port Kennedy Cave are declared *nomina dubia*. Two remaining specimens from Port Kennedy Cave can be assigned with certainty to *Pitymys cumberlandensis* van der Meulen (1978) and one tentatively to *M.* (*Pedomys*) *llanensis* (Hibbard, 1944). Based on these specimens, Port Kennedy Cave is allocated to the early Pleistocene in RZ 14, and is therefore younger than other eastern early Pleistocene assemblages such as Hamilton Cave and Cumberland Cave. Port Kennedy Cave is considered to be roughly coeval with Trout Cave 2 and, in the midwest, with Cudahy from the Meade Basin of Kansas at about 0.64 Ma.

ACKNOWLEDGEMENTS

Three Port Kennedy Cave arvicolid specimens from Port Kennedy Cave were provided for study by Ted Daeschler at the Philadelphia Academy of Sciences. Comparative fossil material used in this study from the Meade Basin of Kansas was collected through National Science Foundation grant EAR-0207582. The detailed review of this paper by R. Zakrzewski is much appreciated.

LITERATURE CITED

Arata, A. A. 1965. Taxonomic status of the pine vole in Florida. Journal of Mammalogy 46:87-94.

Cope, E. D. 1871. Preliminary report on the Vertebrata discovered in the Port Kennedy Bone Cave. Proceedings American Philosophical Society 12:73-102.

Daeschler, E. B. 1996. Selective mortality of mastodons (*Mammut americanum*) from the Port Kennedy Cave (Peistocene: Irvingtonian), Montgomery County, Pennsylvania. Pp. 83-96 in K. M. Stewart and K. L. Seymour (eds.), Palaeoecology and Palaeoenvironments of Late Cenozoic Mammmals: Tributes to the Career of C. S. (Rufus) Churcher. University of Toronto Press, Canada.

Gidley, J. W. and C. L. Gazin. 1938. The Pleistocene vertebrate fauna of Cumberland Cave, Maryland. Bulletin U. S. National Museum 1:1-99.

Hibbard, C. W. 1944. Stratigraphy and veretebrate paleontology of Pleistocene deposits of southwestern Kansas. Bulletin Geological Society of America 55:718-744.

Hibbard, C. W. 1955. Notes on the microtine rodents from the Port Kennedy Cave deposit. Proceedings of the Academy of Natural Sciences of Philadelphia 107:87-97.

Martin, R. A. 1974. Fossil mammals of the Coleman IIA fauna, Sumter County. Pp 35-99 in S. D. Webb (ed.), Pleistocene Mammals of Florida. University of Florida Press, Gainesville.

Martin, R. A. 1987. Notes on the classification and evolution of some North American *Microtus*. Journal of Vertebrate Paleontology 7:270-283.

Martin, R. A. 1989. Arvicolid rodents of the early Pleistocene Java local fauna from north-central South Dakota. Journal of Vertebrate Paleontology 9:438-450.

Martin, R. A. 1991. Evolutionary relationships and biogeography of late Pleistocene prairie voles from the eastern United States. Pp. 251-260 in J. R. Pordue, W. E. Klippel and B. W. Styles (eds.), Beamers, Bobwhites and Blue-Points: Tributes to the Career of Paul W.

Parmalee. Illinois State Museum Scientific Papers 23, Springfield.

Martin, R. A. 1995. A new middle Pleistocene species of *Microtus* (*Pedomys*) from the southern United States, with comments on the taxonomy and early evolution of *Pedomys* and *Pitymys* in North America. Journal of Vertebrate Paleontology 15:171-186.

Martin, R. A. 2003. Biochronology of latest Miocene through Pleistocene arvicolid rodents from the Central Great Plains of North America. Pp. 373-383 in N. López-Martinez, P. Peláez-Campomanes and M. Hernández Fernández (eds.), Surrounding Fossil Mammals: Dating, Evolution and Paleoenvironment. Colloquios de Paleontología, Volumen Extraoraordinario 1 en Honor de Dr. Remmert Daams. Madrid.

Martin, R. A., A. C. Bonk, and P. Peláez-Campomanes. 1998. Variation in enamel differentiation of *Microtus* molars from the Java local fauna, Walworth County, South Dakota. Paludicola 2:74-77.

Martin, R. A., L. Duobinis-Gray, and C. P. Crockett. 2003a. A new species of early Pleistocene *Synaptomys* (Mammalia, Rodentia) from Florida and its relevance to southern bog lemming origins. Journal of Vertebrate Paleontology 23:917-936.

Martin, R. A., R. T. Hurt, J. G. Honey, and P. Peláez-Campomanes. 2003b. Late Pliocene and Pleistocene rodents from the northern Borchers Badlands (Meade County, Kansas). With comments on the Blancan-Irvingtonian boundary in the Meade Basin. Journal of Paleontology 77:985-1001.

Martin, R. A., P. Peláez-Campomanes, J. G. Honey, D. L. Fox, R. J. Zakrzewski, L. B. Albright, E. H. Lindsay, N. D. Opdyke and H. T. Goodwin. 2008. Rodent community change at the Pliocene-Pleistocene transition in southwestern Kansas and identification of the *Microtus* immigration event on the Central Great Plains. Palaeogeography, Palaeoclimatology, Palaeoecology 267:196-207.

Martin, R. A., F. Marcolini, and F. Grady. 2009. The early Pleistocene Hamilton Cave muskrats and a review of muskrat size change through the late Neogene. Paludicola 7:61-66.

Martin, R. A., P. Peláez-Campomanes, and J. G. Honey 2012. Preliminary study of rodents from the Golliher B assemblage of Meade County, Kansas, USA indicates an intense cold period near the end of the Pleistocene. Palaeontologia Electronica, article 14.3.35A:1-13.

Meulen, A. J. van der. 1978. *Microtus* and *Pitymys* (Arvicolidae) from Cumberland Cave, Maryland, with a comparison of some New and Old World species. Annals of Carnegie Museum 47:101-145.

Pfaff, K. S. 1990. Irvingtonian *Microtus* and *Pitymys* (Mammalia, Rodentia, Cricetiade) from Trout Cave No. 2, West Virginia. Annals of Carnegie Museum 59:105-134.

Repenning, C. A. and F. Grady. 1988. The microtine rodents of the Cheetah Room fauna, Hamilton Cave, West Virginia, and the spontaneous origin of *Synaptomys*. U. S. Geological Survey Bulletin 1853:1-32.

Storer, J. E. 2003. The eastern Beringian vole *Microtus deceitensis* (Rodentia, Muridae, Arvicolinae) in late Pliocene and early Pleistocene faunas of Alaska and Yukon. Quaternary Research 60:84-93.

Storer, J. E. 2004. A middle Pleistocene (late Irvingtonian) mammalian fauna from Thistle Creek, Klondike Goldfields region of Yukon Territory, Canada. Paludicola 4:137-150.