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SIZE AND SHAPE VARIATION IN LATE PLEISTOCENE PINE VOLE (MAMMALIA: ARVICOLIDAE: *PITYMYS PINETORUM*) FIRST LOWER MOLARS FROM THREE CAVES IN KENTUCKY AND GEORGIA

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ABSTRACT

Excavation and screen-washing of sediments in Hill Top Cave and Cutoff Cave in northwestern Kentucky and Yarbrough Cave in northwestern Georgia provided the material for an examination of temporal variation in *Pitymys pinetorum* first lower molar (m1) size and shape during the late Pleistocene.

Analysis of variance of six measurements and four ratios of pine vole m1s from Hill Top Cave (late Pleistocene), Cutoff Cave (Holocene) and a modern sample from northwestern Kentucky revealed significant differences in three measures of closure between the anteroconid and triangle (T)5 and between T4-5. However, the oldest and modern means for these variables were virtually identical, showing that, despite a few embedded significant perturbations, measurements and ratios were in overall stasis for the past 30,000 (30K) years.

Student's t-tests showed that size change of the m1s, and thus body size, decreased significantly in the past 24K years in pine voles from northwestern Georgia. The results from both cave systems are interpreted with a model invoking climate-forcing (natural selection) for body size variation and random walks for minor shape changes.

INTRODUCTION

In order to understand the tempo and mode of morphological evolution we need dense fossil records at a number of temporal and geographic scales. Because of their high population numbers and rapid evolution towards the end of the late Neogene, arvicolid rodents make ideal subjects for the study of morphological evolution. Both interspecific and intraspecific variation have been documented in North American arvicolids during time periods from a few thousand to more than a million years ago (Barnosky, 1990; Martin 1995; Marcolini and Martin, 2008). Particularly comprehensive are studies of dental evolution in late Pleistocene samples of the meadow vole, *Microtus pennsylvanicus* (Semken, 1966; Davis, 1987; Barnosky, 1990, 1993; Martin and Prince, 1990; Gordon 1998; Martin et al., 2011). These detailed investigations have been helpful, but it would also be useful to examine variation in other arvicolids, especially those that inhabit forested or near-forested ecosystems, over similar time horizons. Fossilized remains of pine voles, genus *Pitymys*, are commonly encountered in late Pleistocene deposits in eastern North America and will be the focus for this study. The genus *Pitymys* includes three extant species in the United States and Mexico: *P. pinetorum*, *P. quasiater*, and *P. oaxacensis*. Extinct species are known from the early Pleistocene of Maryland and Pennsylvania (*P. cumberlandensis*; van der Meulen, 1978; Martin, 2012) and the middle Pleistocene of Florida (*P. hibbardi*; Holman, 1959; *P. aratai*; Martin, 1974). Absence of suitable Pleistocene ancestors for *Pitymys* in North America suggests that the earliest pine voles originated in the Old World and dispersed to North America in the early Pleistocene (Martin, 2012).

In this study we first examined variation in six standard m1 measurements and four ratios from three pine vole samples from northwestern Kentucky, representing late Pleistocene, Holocene, and modern time. We found that these measures were static over the entire study period, although we also observed temporary but significant shifts in three variables. For comparison, we examined variation in a single variable, m1 length (a proxy for body size), in one late Pleistocene and one modern sample from northwestern Georgia. The sample means were significantly different. Based on an additional small sample of modern *P. pinetorum* from the mountains of Tennessee, we propose a model that combines both random walks and natural selection to explain the full set of results from both states.

STRATIGRAPHIC SETTING AND SAMPLING

In 1989 Mr. Russell Kyler of Cadiz, Kentucky discovered a specimen of an extinct tapir in Hill Top Cave that formed the basis of the only report of fossil specimens from the cave (Graham, 2003). Graham reported both extinct tapir (*Tapirus veroensis*) and peccary (*Platygonus compressus*) and also provided a map of the cave interior. In 1994 Mr. Kyler led R. Martin to Hill Top Cave, and the cave was subsequently explored by R. Martin and Murray State University graduate student C. Gordon in 1994-95 for sediments for a stratigraphically controlled excavation. This proved difficult, as the cave sediments appeared to have been disturbed significantly, apparently by amateurs in search of Indian artifacts. An excavation was begun in presumed undisturbed sediments near the site where Kyler had found the tapir specimen. On Graham's (2003) fig. 5.1, a map of the cave, the excavation site is located in the small alcove just north of his marker No. 9. The excavation was halted because the site was turned over by persons unknown during a period when we were absent from the cave. Two AMS radiocarbon dates were run on sub-surface bone, yielding dates of 32,410 ± 810 years BP (Geochron Labs, GX-21317-B-AMS, on *Dasypus bellus* dermal plate) and 28,860 ± 1720 years BP (Geochron Labs, GX-21316-AMS, on *Platygonus compressus* tooth). We consider an average of these dates, 30,635 years BP, to represent the approximate age of the fossils recovered from our excavations and the surface finds of extinct tapir and peccary reported by Graham (2003). The full rodent assemblage, recovered from screen-washing approximately 500 kg of matrix, is being studied by C. Gordon (U. Oklahoma) and will be reported elsewhere.

Cutoff Cave was also brought to our attention in 1994 by Mr. Kyler. Cutoff Cave is located at the base of a hill on the south side of Sinking Fork Creek, directly opposite the hill in which Hill Top Cave is found. Hill Top Cave, according to Graham (2003), is about 137 m above mean sea level. Cutoff Cave is about 15 m below the entrance to Hill Top Cave. The cave is predominantly a tube running from near the creek bank at about a 10-20^{o} incline into the limestone embankment; it likely floods completely when the creek rises after a prolonged rain. Loose brown sediments, with obvious rodent bones on the surface, had accumulated on the cave floor to a depth of perhaps 0.3 m. A single sediment sample of about 50 kg provided the *P. pinetorum* specimens from this cave. Wilson (1985) reported remains of the extinct giant beaver, *Castoroides ohioensis*, from "Cutoff Caves." A recent phone conversation with Dr. Wilson confirmed that a piece of a giant beaver upper incisor was found within a rich localized concentration of bone at the base of a stalagmite in a cave that may be our Cutoff Cave at a point where light no longer penetrates. If Wilson's Cutoff Cave and ours are the same, this area was not accessible to us; all of our material came from floor matrix within the photic zone, and we recovered no extinct vertebrates. Consequently, we consider the Cutoff Cave sample of *P. pinetorum* to be "sub-Recent," deposited within the current warm interstadial after 10,000 years ago (10 Ka).

Pine vole specimens from Georgia came from stratified excavations in the Peccary Room of Yarbrough Cave, Floyd County, made by R. Martin and student crews at Berry College between 1988 - 1991. Gordon (1998) examined dental variation in *Microtus pennsylvanicus* throughout the excavations in the Peccary Room, representing about 7,000 years of the late Pleistocene. We measured only the sample of pine vole m1s from level 14, the lowest level, associated with an AMS radiocarbon date of 23,880 ± 200 years BP (Gordon, 1998).

SPECIMENS AND MEASUREMENTS

Lower molars are represented by lower case letters, uppers by upper case letters (e.g., m3, M3), left and right by the capital letters L and R. Specimens reported here were catalogued in the University of Oklahoma, Sam Noble Museum of Natural History (OMNH), and University of Florida, Florida State Museum (UF), collections and include the following: Hill Top Cave: OMNH 76943-76944: 1L, 1R m1; 76945: 1 L m1; 76946-76954: 6 L m1s, 3 R m1s; 76955: 1 part R mandible with m1; 76956-76972: 7 L m1s, 10 R m1s; 76973: 2 L m1s, 2 R m1s; 76977-76979: 1 L m1, 2 Rm1s; 76980-76981: 1 L m1, 1 Rm1; 76982-786990: 5 Lm1s, 4 R m1s; 76991-76994: 2 L m1s, 2 R m1s. Cutoff Cave: OMNH 76995-77002: 4 L m1s, 4 R m1s; 77003-77015: 2 part L mandibles with m1-m2, 3 part R mandibles with m1-m2, 3 L m1s, 5 R m1s. Yarbrough Cave (Peccary Room, stratum 14): UF 276816-276822, 7 Rm1s; 276823-276833, 11 L m1s.

The modern sample from Kentucky (KY) includes 30 specimens from northwestern Kentucky in the mammal collection at Murray State University. The Georgia modern sample (GA) includes five uncatalogued specimens in the Berry College collections trapped in Floyd County. Three additional modern specimens of *P. pinetorum* from the University of Florida mammal collections from Mascot, Monroe, and Loudon Counties in the mountains of eastern Tennessee (TN) were measured and compared with the GA sample.

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.

Statistical comparisons were made with the Data Analysis add-in from Microsoft Excel. All Student's t-tests were unpaired, two-tailed tests assuming unequal variances. An alpha level of 0.05 was assumed in all cases.

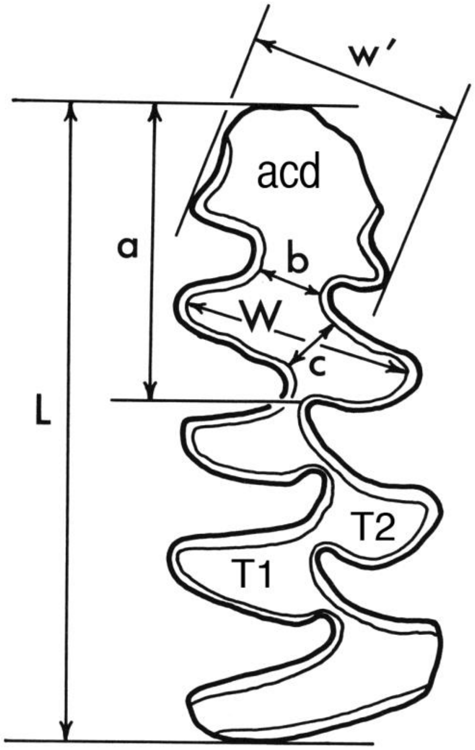

FIGURE 1. Topography of a *Pitymys or Microtus* right m1 (modified from Pfaff, 1990). acd = anteroconid; L = occlusal length; a = length of ACC (anteroconid complex; all structures anterior to T3); W = greatest width ACC; w'= greatest width of acd; b = width of dentine isthmus connecting T4-T5 and the acd; 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).

RESULTS

Measurements and ratios from the Hill Top Cave (HTC), Cutoff Cave (CC), Yarbrough Cave (YC), and Kentucky (KY), Georgia (GA), and Tennessee (TN) modern pine vole m1s can be found in Appendix I. One-factor ANOVAs were run on all measurements and ratios of the Hill Top Cave, Cutoff Cave, and Kentucky modern specimens. The only significant ANOVAs were for b, c and C/W, measures of closure, either between T5 and the anteroconid or between T4-5. However, as can be seen from Appendix I, the mean values for these measures were virtually identical for the HTC and KY samples, indicating an overall pattern of stasis for all measurements and ratios over the past 30,000 years.

A Student's t-test of mean m1 length between the YC and GA specimens was significant (t = 4.022, p = 0.0024). This reduction in m1 length corresponds to a decrease in average body mass, as shown by the tight correlation between m1 length (*L*) and body mass (*W*) in extant arvicolid rodents (Martin, 1996). Applying Martin's (1996) equation ($W = 0.71L^{3.59}$) to the GA and YC means generates an average body mass of 22.9 g for the GA sample and 30.5 g for the YC sample, resulting in a 25% decrease in the past 24K years. These body mass estimates are within the range of body mass data reported for living pine voles (Smolen, 1981).

A Student's t-test between the GA and TN mean m1 length samples also was significant (t = -4.4177, p = 0.0045). The small sample of pine vole m1s from the mountains of eastern Tennessee is significantly larger than the sample from the Piedmont of northwestern Georgia.

DISCUSSION

As noted above, there was no statistically significant difference between the HTC and KY samples for any variables or ratios, indicating stasis in morphology and size over the past 30K years, despite significant departure from average in three measures of closure for the CC sample, likely representing a period <10Ka. Differences in closure between the acd and T5 of a qualitative nature have been reported for a number of *Pitymys* and *Microtus* (*Pedomys*) species, and can be used as an informal, macroscopic means to differentiate between subspecies of *P. pinetorum* (Arata, 1965; Martin, 1987, 1991), but have not been statistically examined in comparative studies of fossil or modern pine vole populations. Shifts in closure of various molar regions in both m1 and M3, however, are well documented in fossil sequences of the meadow vole, *Microtus pennsylvanicus*, over a number of temporal scales, from stratified sequences in single deposits over a few thousand years to superposed sequences spanning hundreds of thousands of years (Semken, 1966; Davis, 1987; Barnosky, 1993; Gordon, 1998; Martin et al., 2011). In particular, on the Central Great Plains there is a shift from predominantly 5T (5 triangle) to 6T m1s during the late Pleistocene in a brief 1500 year period. Davis (1987) preferred an adaptive explanation for this change, suggesting that the 6T morphs were from larger m1s and could process grasses more effectively than 5T m1s. However, Martin and Prince (1990) found no correlation between tooth size and closure of T5-6 in *M. pennsylvanicus*, and we consider it just as likely that the latter trend represents a biased random walk. This is one explanation for the departure of closure from average values in the Kentucky CC sample, though we also recognize that sampling bias is possible.

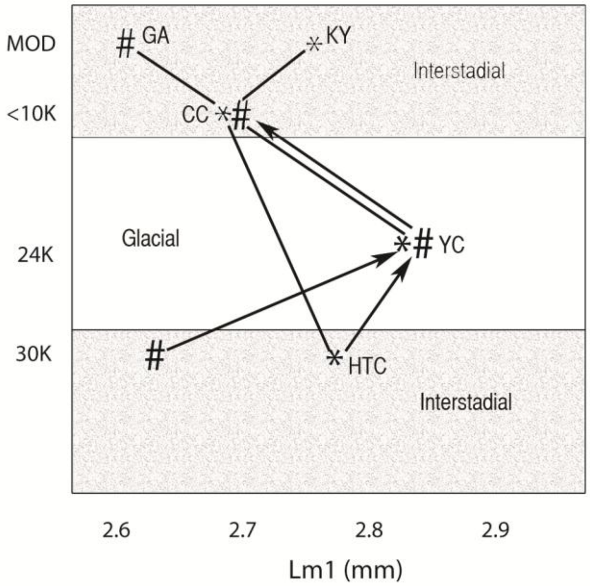

FIGURE 2. Plot of mean m1 length (abcissa) over time (ordinate). # = Georgia samples, * = Kentucky samples. GA = Georgia modern, KY = Kentucky modern, YC = Yarbrough Cave, CC = Cutoff Cave, HTC = Hill Top Cave. Symbols without locality abbreviations are hypothetical populations. Solid lines connect recorded means. Arrows represent proposed pathway of population size change, with pine voles becoming significantly larger during glacial time, returning to smaller size during the Holocene.

Variation in m1 length, and thus body size, in the Kentucky and Georgia samples appears contradictory; the pine voles from Georgia decreased significantly in size from about 24 Ka to modern time, whereas those from Kentucky show no change in size from about 30 Ka to the present. These patterns may become comprehensible if considered within the context of late Pleistocene environmental shifts. Between about 30-23Ka the vegetation of Georgia, and thus probably much of the southeastern U.S., was temperate, dominated by oak and hickory. This interstadial period was followed by a boreal coniferous forest consisting of jack pine and some spruce from about 23-11 Ka (Watts, 1973; Whitehead, 1973; Delcourt and Delcourt, 1984). Extralimital northern mammals, such as the arctic shrew, meadow vole, heather vole, fisher, caribou, and elk are common in southeastern Pleistocene assemblages during this period (Martin, 1968; Guilday et al., 1977, 1978; Grady, 1982; Martin and Sneed, 1989). An extreme cold period, the Younger Dryas event between 12,800-11,600 years BP, characterizes the transition from full glacial conditions to the current warm interstadial. The Holocene boundary is currently set at 10Ka. In the rich Quaternary record of the Meade Basin in Kansas, the Holocene sees the return of cotton rats to southwestern Kansas and the withdrawal of northern immigrants (Martin et al., 2008); in the eastern United States, the northern disjuncts noted above also disappear. Based on this information, we propose a climate-forcing model for the observed changes in pine vole body size. We suggest that the large pine voles in the Piedmont of northwestern Georgia 24 Ka (YC) represent a population that increased in average body mass as an adaptation to decreasing annual temperatures and associated habitat shifts. Whether the animals were responding directly to thermoregulatory challenges, dietary shifts, or predator associations is impossible to know at present. Furthermore, we cannot tell at this point if the shift in body size was accomplished through natural selection in a geographically restricted population or by hybridization with a northern population dispersing southward, perhaps from the mountains of northern Georgia and southern Tennessee. As shown above, the m1s of a small sample of extant *P. pinetorum* from the mountains of eastern Tennessee are significantly larger than those of extant pine voles from northwestern Georgia.

The Kentucky pine vole material includes samples from only warm periods; the mid-Wisconsinan warm interval (HTC) and two samples from the current interstadial (CC, KY). Given our current hypothesis of climate-induced size change, we propose that (ghost) samples of pine vole m1s from northwestern Kentucky during the period 24 -11 Ka would have also demonstrated the shift to larger size seen in the YC material. Likewise, (ghost) samples of pine voles from >30Ka in northern Georgia would have been smaller than those from YC at 24Ka (Fig. 2). Finally, the small size of the modern Georgia sample as compared with that from Kentucky can be explained as a result of a return to the Georgia Piedmont area of more typically smaller, southern populations as the climate warmed and plant associations shifted from sub-boreal to current southern mesic hardwood-pine associations in Georgia (Delcourt and Delcourt, 1984). This model is indirectly supported by Arata’s (1965) documentation of a south-north cline of increase in total lengths, hind foot lengths, length of M3, and length of M1-M3 combined in modern pine vole museum specimens from central Florida through Georgia, Alabama, and North Carolina.

In summary, we propose that morphology and size of *P. pinetorum* m1s have been in stasis in Georgia and Kentucky for the past 30Ka. Embedded within that pattern are statistically significant departures that in the case of triangle closure likely represent random walks, but in the case of size change probably represent natural selection associated with environmental flux.

In order to test this set of hypotheses, further investigations must include: 1) larger and more diverse samples of modern pine voles from Georgia, Kentucky, and the southern U.S. and 2) late Pleistocene samples of modern pine voles throughout the southeastern U.S.

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APPENDIX I

Summary of measurements for pine vole samples. For description of measurements and ratios see Figure 1 and text. N, number of specimens; $\bar{x}$, mean; s, standard deviation; O.R., observed range.

L	N	$\bar{x} \pm s$	O.R.
Modern KY (KY)	30	2.75 ± 0.18	2.35 - 3.04
Modern GA (GA)	5	2.63 ± 0.09	2.53 - 2.74
Modern TN (TN)	3	2.84 ± 0.04	2.82 - 2.89
Cutoff Cave (CC)	16	2.69 ± 0.17	2.38 - 2.99
Hill Top Cave (HTC)	52	2.77 ± 0.14	2.51 - 3.04
Yarbrough Cave (YC)	18	2.85 ± 0.15	2.63 - 3.08

a	N	$\bar{x} \pm s$	O.R.
Modern KY	30	1.37 ± 0.13	1.04 - 1.56
Cutoff Cave	16	1.37 ± 0.13	1.10 - 1.67
Hill Top Cave	52	1.42 ± 0.13	0.79 - 1.67
Yarbrough Cave	17	1.35 ± 0.08	1.23 - 1.50

w'	N	$\bar{x} \pm s$	O.R.
Modern KY	30	0.88 ± 0.11	0.59 - 1.05
Cutoff Cave	16	0.82 ± 0.08	0.64 - 0.90
Hill Top Cave	52	0.86 ± 0.08	0.67 - 1.08
Yarbrough Cave	17	0.92 ± 0.08	0.78 - 1.07

W	N	$\bar{x} \pm s$	O.R.
Modern KY	30	0.85 ± 0.08	0.70 - 0.98
Cutoff Cave	16	0.80 ± 0.10	0.54 - 0.92
Hill Top Cave	51	0.80 ± 0.08	0.65 - 0.95
Yarbrough Cave	18	0.87 ± 0.09	0.65 - 0.99

b	N	$\bar{x} \pm s$	O.R.
Modern KY	30	0.12 ± 0.07	0.06 - 0.36
Cutoff Cave	15	0.07 ± 0.04	0.00 - 0.12
Hill Top Cave	50	0.12 ± 0.07	0.00 - 0.38
Yarbrough Cave	18	0.18 ± 0.04	0.09 - 0.24

c	N	$\bar{x} \pm s$	O.R.
Modern KY	30	0.25 ± 0.04	0.12 - 0.33
Cutoff Cave	16	0.29 ± 0.05	0.21 - 0.37
Hill Top Cave	52	0.24 ± 0.07	0.13 - 0.39
Yarbrough Cave	18	0.18 ± 0.04	0.12 - 0.23

a/L	N	x̄ ± *s*	O.R.
Modern KY	30	0.50 ± 0.03	0.42 - 0.53
Cutoff Cave	16	0.57 ± 0.26	0.43 - 1.53
Hill Top Cave	52	0.51 ± 0.04	0.31 - 0.60
Yarbrough Cave	18	0.45 ± 0.11	0.45 - 0.50

w'/W	N	x̄ ± *s*	O.R.
Modern KY	30	1.03 ± 0.11	0.75 - 1.23
Cutoff Cave	16	1.03 ± 0.09	0.85 - 1.20
Hill Top Cave	51	1.09 ± 0.12	0.86 - 1.52
Yarbrough Cave	18	1.04 ± 0.11	0.84 - 1.26

b/W	N	x̄ ± *s*	O.R.
Modern KY	30	0.15 ± 0.08	0.06 - 0.46
Cutoff Cave	15	0.1 ± 0.06	0.00 - 0.21
Hill Top Cave	49	0.15 ± 0.09	0.00 - 0.57
Yarbrough Cave	18	0.20 ± 0.05	0.11 - 0.30

c/W	N	x̄ ± *s*	O.R.
Modern KY	30	0.29 ± 0.05	.160 - .364
Cutoff Cave	16	0.36 ± 0.10	.257 - .682
Hill Top Cave	51	0.30 ± 0.09	.156 - .508
Yarbrough Cave	18	0.21 ± 0.03	0.13 - 0.25