

THE EARLY PLEISTOCENE HAMILTON CAVE MUSKRATS AND A REVIEW OF MUSKRAT SIZE CHANGE THROUGH THE LATE NEOGENE

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ABSTRACT

Recently collected fossil muskrat first lower molars from early Pleistocene deposits in the Cheetah Room and *Smilodon* Pit, Hamilton Cave, Pendleton County, West Virginia, are described and referred to *Ondatra zibethicus /annectens*. Measurements from these molars are incorporated into an analysis of muskrat body size through the late Neogene. Size change is best modeled by a third order polynomial, with the most rapid increase in m1 length, and thus body mass, occurring since deposition of the Cudahy local fauna at 0.64 Ma. This pronounced size increase, leading to Wisconsinan giants, is followed by a rapid dwarfing event over about the last 12,300 ¹⁴C years B.P. to muskrats of modern body size. The cause for the dwarfing event is unknown; natural selection and PaleoIndian culling are possible mechanisms.

INTRODUCTION

As part of their description of arvicolid rodents from the Cheetah Room of Hamilton Cave, West Virginia, Repenning and Grady (1988) listed eight first lower molars (m1) of *Ondatra annectens*, an extinct species originally named by Brown (1908) from the Conard Fissure locality of Arkansas. Confirming Semken's (1966) observation that changes in lower first molar (m1) size in muskrats formed a chronocline through the Pliocene and Pleistocene with new data, Martin (1993, 1996) subsumed all fossil and modern muskrats (not including the round-tailed muskrat, *Neofiber alleni*) into the modern species *Ondatra zibethicus*, recognizing a series of informal populations, called chronomorphs, as potential biostratigraphic markers. One of these was *O. z. /annectens*. We have not seen the original muskrat specimens, which were in C. A. Repenning's possession at the time of his death and are currently not in the U. S. National Museum (USNM) collections. We report here on specimens collected in Hamilton Cave by F. Grady since the 1988 report.

Since Semken's (1966) seminal paper, a number of authors have attempted to utilize the muskrat chronocline to infer information about climate or to support various models of evolutionary tempo and mode (Nelson and Semken, 1970; Martin and Tedesco, 1976; review in Martin, 1996). L. D. Martin's (1979) analysis of size and character evolution in muskrats

first suggested that the majority of change was concentrated in the last 640,000 years of an almost four million year record, and based on m1 measurements, Martin (1993, 1996) agreed with that conclusion and also suggested that a late Pleistocene dwarfing event led to the current average size for modern muskrats. Based on fossil muskrat data from two sites in South Carolina, Bentley and Knight (1994) questioned the dwarfing event, but it was supported in an extensive statistical analysis of fossil muskrat samples from radiocarbon-dated sites in Florida by Milbacher et al. (2002). They also recognized a significant regional difference in average m1 lengths among modern muskrat samples, with the largest m1s from the northeast, the smallest from the midwest, and intermediate-sized m1s from the southeast.

As part of a series of studies we began on North American arvicolid evolution a few years ago, we decided to review the evidence for size change in North American muskrats. One of our first conclusions was that the dates for many of the fossil sites used in the databases of L. D. Martin (1979) and R. A. Martin (1996) for their regressions of m1 length against time were very imprecise, often based on a limited understanding of the evolutionary relationships of fossil animals in those aggregations and devoid of radioisotopic confirmation. Consequently, we decided to reproduce their analyses with a more limited, but more chronologically secure database. Below, we describe the new Hamilton Cave *Ondatra* material, and

then incorporate measurements from these specimens into a new quantitative evaluation of size change through the late Neogene.

MATERIALS AND METHODS

Five muskrat specimens were measured from various levels in the Cheetah Room (N=3) and *Smilodon* Pit (N=2) of Hamilton Cave, Pendleton County, West Virginia. Three were adult and two were juvenile teeth. Material was collected from the top 75 cm in both localities, and they are presumed to be contemporaneous. Morphology of the *Ondatra* specimens does not contradict that hypothesis. Length and width of the m1s were measured 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 factor (0.615 in this case). Length measurements on two juvenile m1s were made halfway down the sides of the teeth as they were lying on their side. Width measurements are notoriously imprecise for muskrat m1s because of tooth curvature and wear differences. On the juveniles, width was approximated by taking the greatest width from the outside of the lingual edge of the triangles to a point that included about 50 percent of the observed curvature on the labial side. Widths on the three adult m1s were greatest widths of the occlusal surface.

The presumed ages, average m1 length and number of specimens is provided for 12 fossil assemblages in Table 1. There are no North American mammalian fossil localities securely dated between the Cudahy site at 0.64 Ma and those at the upper limit for ¹⁴C dating, in part because of a lack of dates using thermoluminescence or other methods that are available for this time period in terrestrial continental sediments. Nevertheless, the 0.25 and 0.35 Ma estimates for the Doby Springs and Hay Springs localities seem eminently plausible based upon their fossil mammalian microfaunas. Both localities include *Microtus pennsylvanicus*, and there is presently no confirmed record of this species earlier than the late Pleistocene (Rancholabrean). We are concerned that the Hay Springs material could be from a mixture of different Rancholabrean levels, but the m1 measurements do not indicate contamination from two or more distinctly different temporal levels. The Doby Springs, Oklahoma mammalian contingent fits well into the refined Meade Basin, Kansas sequence somewhere between Cudahy and Jinglebob, and its age was estimated to be about 0.30 Ma by Martin and Fairbanks (1999). The difference of 0.10 My between the localities is based on subjective evaluation of the published faunas and stratigraphic interpretations, but in fact there is no conclusive evidence for this

assumption and the relative positions of these assemblages could easily be reversed.

Age of the Cheetah Room local fauna from Hamilton Cave was reviewed by Martin (2003a), who concluded that it was deposited between 1.3-1.6 Ma. We currently view the Java l.f. (Martin, 1989) to be a combination of reworked late Blancan and early Pleistocene material, the majority of fossils coming from the early Pleistocene. Thus, *Pliolemmus*, *Pliophenacomys* and *Hibbardomys* probably were not contemporaneous with the remainder of the fauna. The presence of copious *Microtus pliocaenicus* and a few other rodent species strongly suggests the Java l.f. was deposited in an early phase of the Pleistocene, probably between about 2.0-1.5 Ma (Martin et al., 2008). The Dixon local fauna (l.f.) was recovered from a site in Kansas to the east of the Meade Basin, but its contingent of rodents, especially *Ophiomys meadensis*, *Ondatra zibethicus /meadensis*, *Pliolemmus antiquus*, and *Pliotomys rinkerii*, places it securely in Great Plains Rodent Zone (RZ) 10 (Martin, 2003b), between about 2.5-3.0 Ma, probably closer to the younger limit.

TABLE 1. Mean length of the m1 (L) and body mass (W) in Quaternary North American muskrats, *Ondatra zibethicus*. Modern and Aucilla River data from Milbacher et al. (2002). Ardis data from Bentley and Glass (1994). N = number of specimens; Spr = Springs, Ham. = Hamilton, SH = Sloth Hole, PL = Page Ladson, LS = Latvissimpson.

| Site | Age (Ma) | Mean L (mm) | Mean W (g) | N |
|--------------|----------|-------------|------------|----|
| Modern | 0 | 7.63 | 1046 | 85 |
| Aucilla (SH) | 0.012 | 8.08 | 1285 | 61 |
| Aucilla (PL) | 0.012 | 7.74 | 1101 | 4 |
| Ardis | 0.019 | 7.39 | 933 | 18 |
| Aucilla (LS) | 0.032 | 8.19 | 1349 | 50 |
| Doby Spr | 0.25 | 6.5 | 588 | 11 |
| Hay Spr | 0.35 | 6.72 | 663 | 7 |
| Cudahy | 0.64 | 5.7 | 367 | 5 |
| Leisey | 1.3 | 5.6 | 345 | 1 |
| Ham. Cave | 1.45 | 5.76 | 381 | 5 |
| Java | 1.8 | 5.7 | 367 | 8 |
| Inglis 1A | 2 | 4.5 | 222 | 12 |
| Borchers | 2.1 | 5 | 229 | 1 |
| Dixon | 2.6 | 4.8 | 198 | 7 |
| Hagerman | 3.75 | 4.15 | 117 | 9 |

Inglis 1A (with *Ondatra zibethicus /idahoensis*) is likely older than Java (with *O. z. /annectens*), occurring in Florida after the *Sigmodon minor* extinction event, and therefore probably slightly postdating the Borchers

l.f. Thus, we view the Florida DeSoto Limepit l.f. (with *Sigmodon minor*) as late Blancan and the Inglis 1A l.f. (with *Sigmodon curtisi*, *Ondatra zibethicus* /*idahoensis* but lacking *Microtus*) as latest Blancan or possibly earliest Irvingtonian, if *Microtus* was in North America at the time but restricted to more northern environments (Morgan and White, 1995; Martin, 2005). In any case, Inglis 1A very likely was deposited only slightly later than Borchers, at about 2.0 Ma. The Leisey Shell Pit l.f. of Florida was estimated at between 1.0-1.6 Ma (Morgan and White, 1995), and the midpoint of 1.3 Ma was used for this sample

We recorded the dataset in Table 1 on a Microsoft Excel spreadsheet and used the Excel graphing module to determine the best curve fit for the data on a bivariate plot. Equations and correlation coefficients were generated from that module, and the mathematical model with the highest correlation coefficient was considered to represent the best approximation of evolutionary response of m1 length over time.

Body mass estimates were made with Martin's (1996) arvicoline equation relating mean m1 length (L) in mm to body mass (W) in g:

$$W = 0.71L^{3.59} \quad (1)$$

SYSTEMATIC PALEONTOLOGY

Family Arvicolidae Gray, 1821

Subfamily Ondatrinae Repenning, 1982

Tribe Ondatrini Kretzoi, 1955

Ondatra zibethicus (Linnaeus), 1766

=*Fiber annectens* Brown, 1908

=*Ondatra kansasensis* Hibbard, 1944

=*Ondatra annectens* Stephens, 1960

=*Ondatra zibethicus* /*annectens* Martin, 1993

Material Examined—Cheetah Room: USNM 534015 well-worn adult left (L) m1, 534016 juvenile Lm1, 534018 juvenile right (R) m1. Smilodon Pit: 534017 part R mandible with adult m1 displaying light wear, 534019 adult Lm1 with moderate wear.

Description—The material from both the Cheetah Room and *Smilodon* Pit conform to Martin's (1996) description of the chronomorph *O. z. /annectens*. In size, the average m1 length lies between 4.9-6.0 mm, the dentine tracts are moderately developed, and the molars display seven triangles and a small anterior cap as juveniles. Triangles 6 and 7 widen and broadly connect to the anterior cap with moderate wear, leaving five closed triangles posteriorly. In overall configuration they can be duplicated exactly by the sample from the Java l.f. of South Dakota (Martin, 1989 and fig. 2 in Martin, 1996). The m1s range from 5.27-6.05 in length (mean = 5.76 mm). In width, they range from 2.2-2.55 mm (mean = 2.28 mm).

RESULTS AND DISCUSSION

As concluded previously (Martin, 1996), evolution in m1 length is best modeled by a third order polynomial ($r = 0.96$). The equation for this curve (Figure 1), with each value rounded to two decimal places, is

$$y = -0.20x^3 + 1.35x^2 - 3.23x + 7.74 \quad (2)$$

where y is m1 length in mm and x is time in millions of years. An examination of the data in Table 1 and Figure 1 reveals that, as first suggested by L. D. Martin (1979), the most rapid change in m1 length, and thus body size, occurs subsequent to the middle Pleistocene, after the Cudahy l.f. at 0.64 Ma. From that point there is a rapid increase to the late Pleistocene giants seen throughout the southeast, followed by dwarfing to modern time, occurring subsequent to 12,300 ^{14}C years B. P. (Milbacher et al., 2002). The Ardis, South Carolina muskrats, with mean m1 length = 7.39 mm, are unusually small for a southeastern fauna dated at 19,000 years B.P. (Bentley and Knight, 1994). Milbacher et al. (2002:table 1) did not record a single sample this small in 13 Wisconsin sites from northern Florida ranging from about 32,000-12,000 years B. P. Martin (1996) reported large muskrat m1s (8.3 and 8.7 mm) from 15,000 and 20,000 year B. P. levels, respectively, in Bell Cave, Alabama, so the gigantism was not restricted to Florida.

When m1 length is converted to body mass in kg, the pulse towards large size is even more dramatic, with body mass basically doubling over the last 30,000 years. The late Pleistocene gigantism and subsequent dwarfing occurs in too brief a time period to be shown in Figure 1, but graphs depicting this change have been published by Martin (1996:fig. 4) and Milbacher et al. (2002:fig. 3). The cause of this size change remains unknown; it could be the result of the Younger Dryas cold interval or human (PaleoIndian) culling. Comparison of archeological and natural accumulations of ancient muskrat assemblages should provide a test for the human selection hypothesis.

Milbacher et al. (2002) also tested the use of m1 length/width ratios as a paleotemperature/climate indicator, as had been proposed by Nelson and Semken (1970). This ratio showed no latitudinal trend in modern muskrat samples, and the ratios for late Pleistocene samples were equivocal. We suspect this is because length/width ratios mostly reflect developmental tendencies of the m1 as it increases in size, as noted by Martin and Tedesco (1976). Larger m1s typically have larger length/width ratios than small m1s because, after a certain size is reached, m1 width increases at a slower rate than length. Consequently,

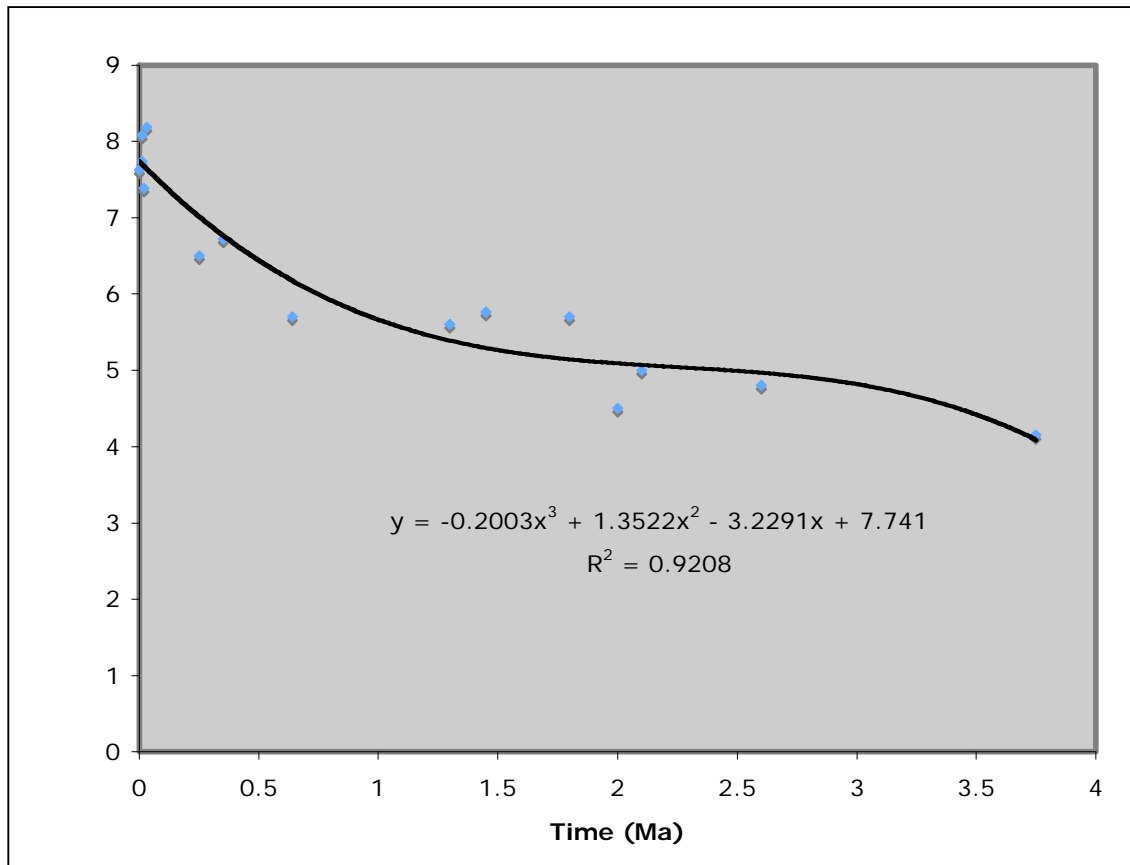


FIGURE 1. Change in length of m1 in *Ondatra zibethicus* over the past 4 million years. Mm= millimeters, Ma = millions of years ago.

either length or width taken separately (reflecting changes in body size) would likely be better indicators of climatic signals than the ratio of these two variables. However, as shown by Milbacher et al. (2002), the response in m1 length and width in modern muskrats indicates that factors other than latitude (= average temperature) controls muskrat body size. Milbacher et al. (2002) noted that Boyce (1978) found that both total annual precipitation and the variation in monthly precipitation were correlated with muskrat body size which, as they aptly note, is likely also correlated with food availability (habitat quality).

In conclusion, the muskrat fossil record remains as one of the best documented phyletic sequences in North America, testifying that significant change in dental morphology and body size can occur in an evolving lineage. However, we now suspect that phyletic sequences such as this may be relatively rare for continental mammals, being the “exceptions that prove the rule” of punctuated equilibrium. Recent studies of rodents with dense fossil records from the Meade Basin of Kansas (Peláez-Campomanes and

Martin, 2005; Marcolini and Martin, 2008) do not show these kinds of significant changes in single lineages. Rather, significant morphological change appears to be associated with speciation events. As suggested by Martin (1992), the phyletic evolutionary response of *Ondatra* may be part of a more general pattern found in aquatic mammals. Aquatic “runways” may foster genetic continuity and significantly reduce the probability of population fragmentation in aquatic mammals. Perhaps this also explains why there has been only a single beaver (*Castor*) and giant beaver (*Castoroides = Procastoroides*) alive at any point in the late Neogene. Although beyond the scope of this study, this proposition should also be testable.

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