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Estimates of body mass for fossil giant ground squirrels, genus *Paenemarmota*

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Paenemarmota Hibbard and Schultz, 1948 includes 3 species of giant ground squirrels within Marmotini (Rodentia, Sciuridae) from the Late Miocene and Pliocene of central and western North America. We developed skeletal and dental models for estimating body mass across modern species of Marmotini and apply these models to *Paenemarmota*. The most reliable models for estimating body mass of modern species (on the basis of length and width of femur, lengths of p4 and P4) generally yielded lower estimates of body mass for *Paenemarmota* than less reliable models (on the basis of lengths of m1, m2, M1, and M2). Models that were most reliable across modern species yielded 2 nonoverlapping estimates for *P. barbouri* Hibbard and Schultz, 1948: 9.5–9.8 kg on the basis of femur dimensions, and 14.4–16.2 kg on the basis of lengths of premolars. On the basis of lengths of premolars, *P. mexicana* (Wilson 1949) closely resembled *P. barbouri* in estimated mass (14.4–15.7 kg), but *P. sawrockensis* (Hibbard 1964) was smaller (10.0–12.4 kg). These large ground squirrels probably differed in mass-dependent biological attributes from all modern marmotines.

Key words: body mass, Marmotini, *Paenemarmota*

Numerous physiological and ecological attributes of mammals scale with body mass (McNab 1990; Schmidt-Nielsen 1984). Paleontologists thus often seek to estimate body mass for fossil mammals by regressing mass on 1 or more skeletal or dental dimensions across modern taxa and applying the resultant model(s) to fossils (e.g., Damuth and MacFadden 1990a). In general, proximal weight-bearing limb bones are superior to distal limb elements and teeth as estimators of body mass (Damuth and MacFadden 1990b). However, teeth are more likely to be preserved as fossils and often yield realistic estimates of body mass (e.g., Gingerich et al. 1982; Millien and Bovy 2010). Resulting estimates offer insights into the physiology, ecology, and behavior of fossil mammals (e.g., Martin 1986) but must be evaluated with care, especially when estimated body masses of fossils fall well outside the range of values among modern reference species (Reynolds 2002).

Here, we provide estimates of body mass for species of the giant ground squirrel, *Paenemarmota* Hibbard and Schultz, 1948, first described from early Pliocene localities in Kansas and Nebraska (Hibbard and Schultz 1948) and known from multiple late Miocene through late Pliocene localities as far north as Idaho (Zakrzewski 1998) and as far south as Mexico (Wilson 1949). The genus includes 3 known species: *P. barbouri* Hibbard and Schultz, 1948, the type and most widely distributed species (Hibbard and Schultz 1948; Repenning

1962); *P. sawrockensis* (Hibbard 1964), first described as *Marmota* Blumenbach, 1779 but subsequently recognized as *Paenemarmota* (Voorhies 1988); and *P. mexicana* (Wilson 1949). The latter was initially described as *Marmota* (Wilson 1949) but was subsequently treated as a synonym of *P. barbouri* (Repenning 1962) or a distinct species in *Paenemarmota* (Dalquest and Mooser 1980). All 3 species are substantially larger than modern woodchucks and marmots (*Marmota*) in skeletal and dental dimensions. *P. barbouri* was reported to resemble a modern beaver in size and to be almost twice as large as the largest modern ground squirrels in dental dimensions (Repenning 1962). *P. sawrockensis* is ∼10–15% smaller in dental dimensions than is *P. barbouri* (Voorhies 1988).

Paenemarmota is phylogenetically within and shares semi-fossorial adaptations with the crown clade of the tribe Marmotini (family Sciuridae), a clade that includes ground squirrels, marmots, and prairie dogs (Goodwin 2008; Repenning 1962; Samuels and Van Valkenburgh 2008). Thus, modern marmotines represent a valid reference group for developing skeletal and dental models to estimate its body

mass. Marmotini comprises 13 modern (Helgen et al. 2009; Wilson and Reeder 2005) and 4 extinct genera (Goodwin 2008). Modern genera range widely in skeletal dimensions (Fig. 1:inset) and body mass (Hayssen 2008a), from *Tamias* Illiger, 1811 (chipmunks; species means = 0.05–0.10 kg) to *Marmota* (species means = 3.0–8.0 kg), and the fossil *Paenemarmota* was larger yet (Fig. 1:inset). Body-mass estimation in this clade is complicated by strong seasonal variation and sexual dimorphism in body mass among species that store fat for winter. Body mass may double between spring minima and fall maxima in these species (Davis 1976), and adult females typically weigh 60–90% of conspecific adult males (Schulte-Hostedde 2007; table 10.2). Despite these limitations, prior analysis demonstrated a good correlation between dental size and published body masses across the tribe (Goodwin 2009; Fig. 1). Thus, we develop clade-specific models for estimating body masses across modern marmotines, and we cautiously apply these models to estimate body mass for species of *Paenemarmota*.

MATERIALS AND METHODS

Modern and fossil specimens examined for this study are listed in Appendix I. Most fossils of *Paenemarmota* preserve 1 or more cheek teeth; thus we developed multiple dental models for estimating body mass. One fossil was a partial skeleton lacking teeth but with a preserved humerus and femur. Because *Paenemarmota* was semifossorial (Samuels and Van Valkenburgh 2008) and thus would use its forelimbs for digging as well as locomotion, we excluded the humerus but used the femur to develop 2 additional models for estimating body mass.

We calculated mean body mass for each modern species used in our study by averaging mean values for males, females, and adults of unknown sex from a published compilation (Hayssen 2008a). In most cases, mean body masses probably represent an average of values recorded throughout the active season, but the published compilation did not specify season of measurements.

We used 58 species representing all modern genera of Marmotini to develop dental models for estimation of body mass, and we applied these models to 3 species of *Paenemarmota* (Appendix I). We obtained individual tooth lengths of P4, M1, M2, p4, m1, and m2 by measuring maximum tooth lengths from scaled digital photographs of modern and fossil specimens (Fig. 2) using GraphicConverter (www.lemkesoft.com), and then calculated species means. Tooth widths (and thus tooth areas) and lengths of P3, M3, and m3 were excluded because in Marmotini, these dimensions vary with dietary adaptation in addition to body size (Goodwin 2009). Tooth width also varies with functional groups among ungulates (Fortelius 1990).

We used 25 species representing 12 of 13 modern marmotine genera (lacking only the Chinese rock squirrels, *Sciurotamias* Miller, 1901) to develop femur-based models for estimating body mass (Appendix I). Femurs were photo-
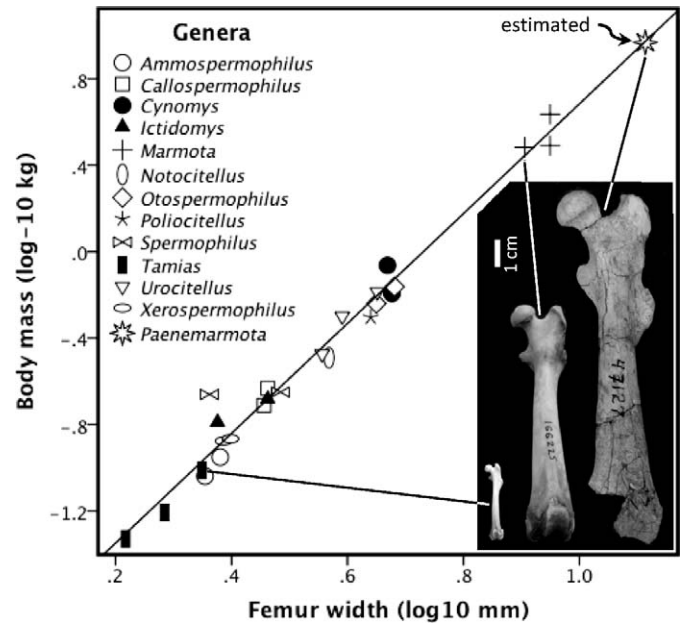

FIG. 1.—Body mass as a function of femur width (both $\log_{10}$-transformed) across modern marmotine species and applied to estimate body mass of *Paenemarmota barbouri*. Regression statistics are given in Table 1. Inset depicts left femurs (to scale) of (from left to right): eastern chipmunk, *Tamias striatus* (Linnaeus, 1758; UMMZ 124622); woodchuck, *Marmota monax* (UMMZ 166225); and *Paenemarmota barbouri* (UMMP 47127).

graphed with a scale and measured digitally using GraphicConverter. We measured maximum length (parallel to its long axis) and minimum shaft width of the femur on 1–8 specimens ($n \geq 3$ for 19 of 25 species) with fused epiphyses and calculated species means for femur length and width. The same protocol was used to measure 1 femur of *P. barbouri*.

Mean lengths of teeth and mean length and width of the femur were individually used to estimate mean body mass per species. Each scaled linearly with body mass when both axes were $\log_{10}$ transformed. A separate linear regression, each using ordinary least squares, was performed with each variable to facilitate application to fragmentary fossils. Ordinary least-squares regression assumes that the independent variable is measured without error, which is never the case with morphometric variables. However, this approach may be acceptable for predicting Y on the basis of X even when this assumption is violated (Sokal and Rohlf 1981), and it is widely used in studies that estimate body mass of fossils (e.g., references in Damuth and MacFadden 1990a).

For each regression we recorded r^2 and the standard error of the estimate (*SEE*) and saved estimated and leverage values and standardized residuals. We inspected leverage values for cases that unduly influenced regression and tested standardized residuals for normality (1-sample Komolgorov–Smirnov test; $P = 0.05$). Statistical analyses were done with SPSS 19 (http://www-01.ibm.com/software/analytics/spss/products/statistics/).

We assessed model sensitivity to sample selection and to male–female differences by performing 2 additional analyses
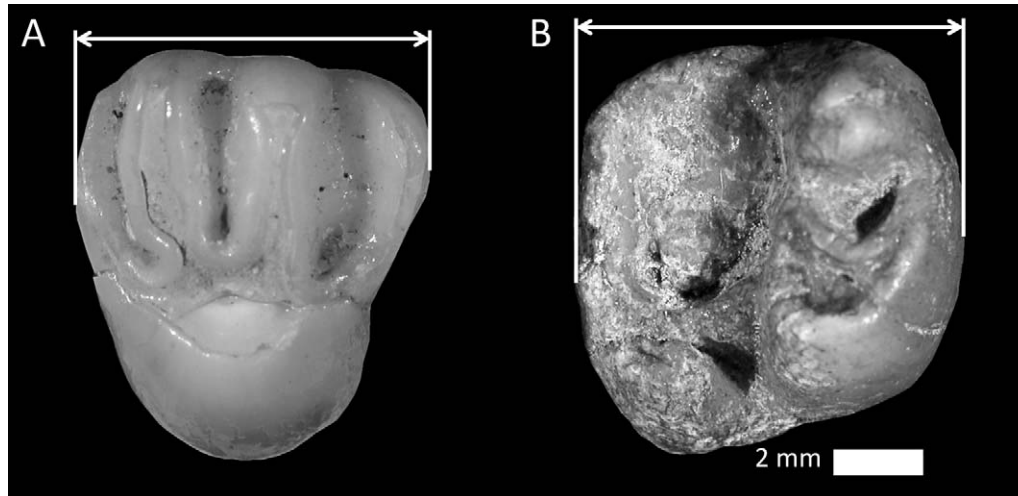
Fig. 2.—A) Right P4 (UMMP 47886) and B) left p4 (UMMP 33367) of *Paenemarmota barbouri* depicting how length was measured on each tooth.

using the dental model that yielded the highest r^2 and lowest *SEE* in estimating body mass: length of p4 (Table 1). First, we regressed body mass on length of p4 using a randomly selected subsample of 29 species (marked with an asterisk in "Appendix I") from the 58 in the original sample and compared results with the total sample. Second, we analyzed male and female body masses separately. This analysis used sex-specific means for body mass, but species-specific means for length of p4 because males and females did not differ in length of p4 (Wilcoxin related-sample signed rank test, $P > 0.30$).

Regression models were tested for isometry by inspecting confidence intervals for each slope. In log-log space, isometric slopes should be no different from 3.0 for models that estimate body mass from length of a skeletal or dental element because mass increases in proportion to length cubed in original units.

When log-transformed estimated values derived from linear regression are detransformed to original units, the results are systematically biased: they estimate the geometric instead of the arithmetic mean of the dependent variable and thus

underestimate values in original units (discussed and applied to body-mass estimation by Smith 1993). Thus, a model-specific correction factor should be developed and applied to each detransformed estimate. Several methods for correcting this bias have been proposed (Smith 1993); the most commonly used method derives the correction factor from the *SEE* or residual mean square of the regression. This method assumes normal distribution of residuals and works best when residual mean square is less than 0.75 (Smith 1993). We used this method because both criteria were met by all models in the present study: residuals were always normally distributed ($P > 0.35$; one-sample Kolmogorov–Smirnov test for normality), and residual mean squares were always low (<0.025).

When estimated values are detransformed from $\log_{10}$ units, the correction factor (*CF*) is computed as: $CF = \exp([SEE \times 2.3026]^2/2)$, where exp() represents e raised to the power of the parenthetical expression, *SEE* is the standard error of the estimate from the regression model, and 2.3026 is an adjustment needed for $\log_{10}$ values because the formula is based on natural logarithms (see Smith 1993 for an extended

TABLE 1.—Regression statistics and calculated correction factor and *PPE* for models that estimate $\log_{10}$ body mass (kg) on the basis of the indicated $\log_{10}$-transformed variable. *CI* is confidence interval; *CF* is a correction factor applied to detransformed estimates of body mass, n is sample size, *PPE* is mean absolute percent prediction error per model, r^2 measures variance explained by each model, and *SEE* is standard error of the estimate. *CIr²* and *SEE* obtained from SPSS statistical output; *CF* and *PPE* calculated as described in methods.

Independent variables (all $\log_{10}$ transformed from mm)	n	Intercept	Slope	95% CI of slope	CIr^2	SEE	CF	PPE (%)
Femur length	25	−5.34	3.00	2.75–3.26	0.96	0.100	1.03	18.7
Femur width	25	−1.86	2.54	2.37–2.72	0.98	0.081	1.02	14.5
Length p4: total sample	58	−1.37	2.81	2.68–2.95	0.97	0.101	1.03	16.4
Randomly-selected subset	29	−1.36	2.79	2.61–2.96	0.98	0.082	1.02	13.9
Predicting male body mass	42	−1.36	2.82	2.64–2.99	0.96	0.108	1.03	19.5
Predicting female body mass	47	−1.37	2.72	2.57–2.86	0.97	0.097	1.03	17.6
Length m1	58	−1.55	3.27	3.03–3.52	0.93	0.153	1.06	30.0
Length m2	58	−1.67	3.33	3.08–3.57	0.93	0.148	1.06	27.3
Length P4	58	−1.42	2.87	2.70–3.04	0.95	0.121	1.04	19.8
Length M1	58	−1.60	3.22	3.00–3.44	0.94	0.140	1.05	25.9
Length M2	58	−1.63	3.23	3.02–3.45	0.94	0.135	1.05	25.3

TABLE 2.—Mean observed body mass, and mean % deviations of corrected estimates of body mass on the basis of length of p4 for each genus in Marmotini. Percent deviations calculated per species as ([corrected estimate of body mass − observed body mass]/observed body mass × 100) and averaged per genus. n = number of species per genus for which we had observed and estimated body masses. One-sample t-tests used to assess whether % deviations were significantly different from 0; none was significant. See "Materials and Methods" for how corrected estimates of body mass were calculated.

Genus	n	Observed body mass (kg)		Deviation of corrected estimate from observed body mass (% of observed)		
		Mean	SD	Mean	SD	t-value
Ammospermophilus Merriam, 1892	4	0.12	0.03	13.7	13.4	2.05
Callospermophilus Merriam, 1897	3	0.19	0.04	22.2	12.8	3.01
Cynomys Rafinesque, 1817	5	0.79	0.18	25.8	32.0	1.80
Ictidomys Allen, 1877	2	0.19	0.03	−0.7	16.5	−0.06
Marmota Blumenbach, 1779	9	4.52	1.59	−4.1	18.8	−0.65
Notocitellus Howell, 1938	1	0.32	–	2.7	–	–
Otospermophilus Brandt, 1844	3	0.56	0.13	−2.7	15.5	−0.30
Poliocitellus Howell, 1938	1	0.50	–	−26.4	–	–
Sciurotamias Miller, 1901	1	0.26	–	14.0	–	–
Spermophilus Cuvier, 1825	6	0.30	0.09	38.4	54.2	1.73
Tamias Illiger, 1811	7	0.07	0.02	−0.1	10.4	−0.03
Urocitellus Obolenskij, 1927	12	0.33	0.19	−8.5	16.4	−1.80
Xerospermophilus Merriam, 1892	4	0.15	0.02	1.7	17.8	0.19

discussion of correction factors). We then applied the *CF* to all estimates of body mass to adjust for transformation bias.

We computed the absolute percent prediction error (*PPE*) for each model and species as: *PPE* = absolute value of ([observed body mass − corrected estimate of body mass]/corrected estimate of body mass) × 100. For each model, we then computed the mean *PPE* across species. We used corrected estimates of body mass in this calculation instead of uncorrected estimates because these were the values we report for *Paenemarmota*. The *PPE* provides a comparative, but not statistical, estimate of confidence in a given estimate of body mass (e.g., Millien and Bovy 2010).

For the dental variable that estimated body mass with highest r^2 and lowest *SEE* and *PPE* (length of p4), we explored the degree to which regression over- or underestimated observed body mass per modern genus. We computed the deviation between corrected estimates of body mass and observed body mass, as percentage of observed body mass, for each species. We then computed mean deviation per genus and tested the hypothesis that deviations per genus did not differ from 0, using one-sample t-tests.

Because we intended to apply regression models to giant fossil ground squirrels, we assessed the effectiveness of each model in estimating body masses of the largest modern marmotines, the marmots and woodchucks (*Marmota*). For each model and marmot species, we computed and graphed the deviations between corrected estimates of body mass and observed body masses, as percentage of observed body mass. Finally, we applied these models to each species of *Paenemarmota* with relevant material and calculated corrected estimates of body mass. We also calculated a comparative (but not statistical) measure of "confidence" in these estimates as corrected estimate ± (*PPE* × corrected estimate; Millien and Bovy 2010).

RESULTS

All regression models displayed a strong, linear relationship between $\log_{10}$-transformed body mass and the $\log_{10}$-transformed independent variable (illustrated for width of femur; Fig. 1). Leverage values were low to moderate for all cases in each model (always <0.10 for dental models and ≤0.22 for femur models); thus all cases were included in each model. Models accounted for ≥93% of variation in $\log_{10}$ body mass ($R^2 \geq 0.93$), exhibited relatively low *SEE* (<0.16), and displayed *PPE* ≤ 30% (Table 1). Correction factors ranged from 1.02 to 1.06, indicating that uncorrected, detransformed estimates of body mass were below "true" estimates in original units by 2–6% (Table 1). Models based on the femur, p4, and P4 had the highest r^2 and lowest *SEE* and *PPE* (Table 1). Subset and sex-specific models based on length of p4 did not differ in slope or intercept from the overall p4-based model (Table 1). Within upper and lower cheek-tooth series, 4th premolars exhibited higher r^2 and lower values of *SEE* and *PPE* than molars (Table 1).

Three models had slopes that met isometric expectations: lengths of femur, P4, and M1 (Table 1). Width of the femur and length of p4 exhibited negative allometry (slopes < isometric expectations), whereas lengths of m1, m2, and M2 all displayed positive allometry (slopes > isometric expectations). Models that exhibited negative allometry exhibited higher r^2 and lower *SEE* and *PPE* than those that exhibited positive allometry.

Per modern genus, mean deviation of corrected estimates of body mass from observed body mass, on the basis of length of p4, ranged from −26% for *Poliocitellus* Howell, 1938 to 38% for *Spermophilus* Cuvier, 1825. However, none of these deviations significantly differed from 0 (Table 2).

The deviations between corrected estimates of body mass and observed body masses of *Marmota* varied substantially across species and models (Fig. 3). For the Siberian marmot,
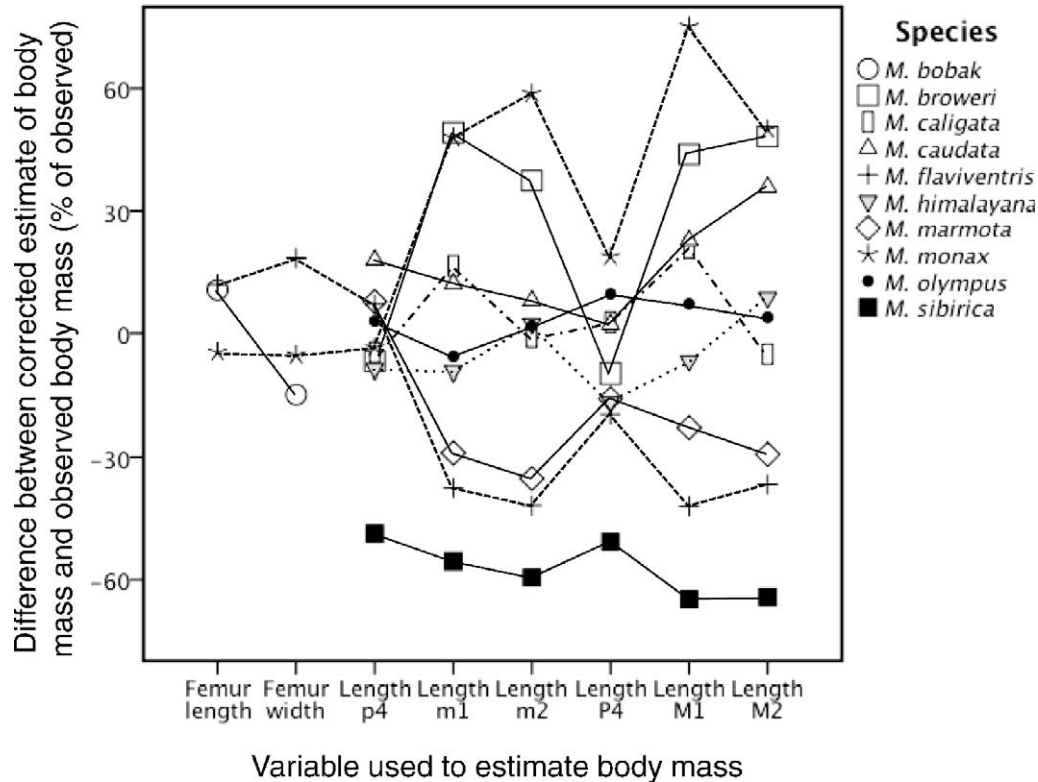
Fig. 3.—Variation in reliability of models that estimate body mass when applied to modern species of *Marmota*. Reliability measured as deviation between corrected estimates of body mass (corrected by appropriate correction factor in Table 1) and observed body mass, as percentage of observed body mass.

M. sibirica (Radde, 1862), corrected estimates of body mass were >45% below observed body mass (8.0 kg) across all models, but for all other species at least 1 model yielded corrected estimates within ± 10% of observed body mass. Four species exhibited high variation in corrected estimates of body mass across models (ratio of maximum to minimum corrected estimates ≥1.65). The best models for estimating body mass of these species were consistently those that used (in order) length of p4, length of the femur (when available), width of the femur (when available), and length of P4 with estimates based on lengths of molars either divergently large (Alaskan marmot, *M. broweri* Hall and Gilmore, 1934 and woodchuck, *M. monax* [Linnaeus, 1758]) or small (yellow-bellied marmot, *M. flaviventris* [Audubon and Bachman, 1841] and alpine marmot, *M. marmota* [Linnaeus, 1758]; Fig. 3). Overall, the most reliable dental model for estimating body mass among marmots used length of p4. This model yielded corrected estimates of body mass within ± 10% of observed body masses for 7 of 9 and ± 20% of observed body masses for 8 of 9 modern marmots (Fig. 3).

Corrected estimates of body mass for *Paenemarmota* likewise varied across species and models (Table 3). *P. barbouri* and *P. mexicana* exhibited similar estimated body masses per model (within 14 % of each other) and were always estimated to be larger than *P. sawrockensis* (by ≥29% in lower and ≥14 % in upper dental models; Table 3). Estimated body masses varied markedly across models for *P. barbouri* and *P.*

mexicana (ratio of maximum to minimum corrected estimates: 2.33 [1.47 excluding the femur-based models] and 1.53, respectively) but somewhat less so for *P. sawrockensis* (ratio of maximum to minimum corrected estimates: 1.28). The four models that exhibited highest r^2 and lowest *SEE* among modern species (Table 1), and that yielded the most reliable estimates of body mass for modern marmots (length and width of femur and length of p4 and P4; Fig. 3), typically yielded lower estimates of body mass than other models (with the exception of P4 for *P. sawrockensis*; Table 3).

Femur-based estimates for *P. barbouri* (9.5–9.8 kg) were 32–41% less than the most reliable dental estimates (on the basis of lengths of P4 and p4: 14.4–16.2 kg; Table 3). When sex-specific p4-based models (Table 1) were applied to *Paenemarmota*, males were estimated to be ~25% larger than females in all species (Table 3).

DISCUSSION

The most reliable models for estimating body mass among modern marmotines in general (Table 1) and species of *Marmota* in particular (Fig. 3) were those based on length and width of the femur and lengths of p4 and P4. Application of these models to *P. barbouri* (the only species of *Paenemarmota* with relevant material for all 4 variables) produced 2 divergent estimates: 9.5–9.8 kg based on femur dimensions, and 14.4–16.2 kg based on lengths of premolars (Table 3). *P.*

TABLE 3.—Sample size, corrected estimates of body mass, and "confidence interval" of corrected estimates (minimum–maximum) for 3 species of *Paenemarmota* on the basis of separate regression models. n = number of specimens; min–max = minimum–maximum estimates of body mass per model calculated as min = estimated mass – ($PPE \times$ estimated mass), max = estimated mass + ($PPE \times$ estimated mass). PPE = percent prediction error (see "Materials and Methods"). Estimated masses are corrected by model-specific correction factors from Table 1 to minimize detransformation bias (see "Materials and Methods").

Regression model (independent variable)	*P. barbouri*			*P. mexicana*			*P. sawrockensis*		
	n	Estimated mass (kg)	Min–max estimate (kg)	n	Estimated mass (kg)	Min–max estimate (kg)	n	Estimated mass (kg)	Min–max estimate (kg)
Femur length	1	9.8	8.0–11.6	–					
Femur width	1	9.5	8.1–10.9	–					
Length p4: total sample	3	16.2	13.6–18.9	1	15.7	13.1–18.3	2	10.0	8.4–11.6
Randomly-selected subset	3	15.8	13.6–18.0	1	15.3	13.1–17.4	2	9.7	8.4–11.1
Predicting male body mass	3	17.0	13.7–20.3	1	16.4	13.2–19.6	2	10.4	8.4–12.5
Predicting female body mass	3	13.4	11.1–15.8	1	13.0	10.7–15.3	2	8.4	6.9–9.9
Length m1	4	17.3	12.1–22.5	1	17.3	12.1–22.5	2	12.3	8.6–16.0
Length m2	4	19.4	14.1–24.7	1	22.1	16.1–28.1	2	12.8	9.3–16.3
Length P4	3	14.4	11.5–17.2	1	14.4	11.5–17.2	1	12.4	9.9–14.8
Length M1	2	17.3	12.8–21.8	1	15.2	11.3–19.1	1	12.1	8.9–15.2
Length M2	3	21.2	15.8–26.5	2	20.3	15.2–25.5	–	–	–

mexicana was estimated to be similar in body mass to *P. barbouri* (14.4–15.7 kg based on premolars), and *P. sawrockensis* to be somewhat smaller (10–12.4 kg based on premolars). Less-reliable models for estimating body mass of modern marmotines used lengths of M1, M2, m1, and m2 (Table 1). When applied to *Paenemarmota*, these models typically yielded higher estimated body masses than did more reliable models (Table 3).

Alternate models for estimating body mass commonly yield divergent estimates when applied to fossil species, especially when fossils fall well outside the size range of modern reference taxa. For example, estimates of body mass for a giant fossil rodent from South America, *Phoberomys pattersoni* (Mones 1980), range from 221 to 745 kg depending on the variables and reference taxa used (Hopkins 2008; Millien and Bovy 2010; Sánchez-Villagra et al. 2003). In general, estimates of body mass obtained from weight-bearing proximal limb bones such as the femur are considered superior to those obtained from teeth (Damuth and MacFadden 1990b), although models based on teeth often yield reasonable estimates (e.g., Gingerich et al. 1982; Millien and Bovy 2010).

We do not know why estimates of body mass derived from the length and width of the femur were substantially lower than those derived from lengths of P4 and p4 for *P. barbouri* (Table 3). We were able to measure only 1 femur of *P. barbouri* (Appendix I), but it came from a full adult with fused epiphyses and was collected from the same locality as dental remains of typical size for *P. barbouri*. Also, we used fewer modern marmotine species when building the femur-based models (25 versus 58 for dental models), but this probably does not explain the divergent estimates; differences persist when femur-based estimates are compared with those derived from length of p4 but using a random subset of 29 species (Table 3).

Despite uncertainties about precise body masses, species of *Paenemarmota* were very large squirrels, ~3–5 times larger than is typical for *M. monax* (3.0 kg). Furthermore, if *Paenemarmota* exhibited significant seasonal variation in body

mass as do all modern large marmotines, it likely attained substantially larger late-season body masses than we estimated. Our estimates are based on regressing mean body masses obtained from a published compilation (Hayssen 2008a; see "Materials and Methods") against skeletal or dental dimensions, and these body masses appear to represent an average of values recorded throughout the annual cycle. The Siberian marmot may be an exception; its body mass (8 kg) was substantially larger than predicted on the basis of any model (Fig. 3), perhaps because this value was obtained from late-season adults. Many species attain substantially higher body masses before hibernation than reported in this compilation. For example, Edelman (2003) reported mean prehibernation body masses for adult female (7.1 kg) and male (9.3 kg) Olympic marmots (*M. olympus* [Merriam, 1898]) that were 65–116% larger than the mean value (4.3 kg) used in our study.

Modern ground squirrels commonly exhibit strong sexual dimorphism in body mass (Schulte-Hostedde 2007). Thus, gender-specific estimates of body mass for species of *Paenemarmota*, with males estimated to be ~25% larger than females (Table 3), are biologically plausible. Across modern species within Marmotini, neonatal and litter masses at birth scale positively with mass, whereas overall reproductive effort as a percentage of body mass scales negatively with mass (Hayssen 2008b, 2008c). Therefore, because of their larger estimated size, species of *Paenemarmota* likely exhibited even larger neonatal and litter masses but lower weight-specific overall reproductive effort than any modern species within the tribe. Other paleobiological inferences may be drawn from broad relationships between body mass and physiology, behavior, and/or ecology across modern mammals (e.g., Eisenberg 1990; McNab 1990). Compared with modern marmotines, species of *Paenemarmota* likely exhibited higher absolute and lower mass-specific metabolic rates, required more food and water, could move more rapidly, and had a larger home range. Finally, the large size of *Paenemarmota* likely affected its susceptibility to predation, perhaps offering

size-based protection against some common predators of ground squirrels (e.g., mustelids), but making it more difficult to escape larger predators by rapidly entering burrows (Samuels and Van Valkenburgh 2008).

These paleobiological inferences, although plausible, remain speculative and may be complicated by paleoenvironmental and paleobiological factors. For example, modern marmots exhibit the lowest mass-specific energetic investment in reproduction in the family Sciuridae (Hayssen 2008b). This may be related to their reproductive strategy as hibernators that typically occupy highly seasonal environments, and thus bear a single litter per year. The spread of C-4 grasslands during the late Miocene and Pliocene may have been associated with increased seasonality in precipitation although the signal is ambiguous in North America (Osborne 2008). However, we have no direct evidence that *Paenemarmota* was a hibernator, and we did not observe a hibernation mark on the exposed surfaces of the few incisors that we inspected (based on methodology presented in Goodwin et al. 2005).

Both body-size morphs of *Paenemarmota* had evolved by the latest Miocene, when the genus first appears, with the larger *P. mexicana* in northern Mexico and smaller *P. sawrockensis* in the central Great Plains (Goodwin 2008). *P. sawrockensis* persisted into the early Pliocene (but not later) on the central Great Plains, but, in the stratigraphic sequence of Meade County, Kansas, it was replaced by the larger *P. barbouri* during this interval (Goodwin 2008). Given the sparse fossil record of *Paenemarmota*, we cannot determine whether this represented real ecological replacement, or was an artifact of sampling. In either case, the large-sized *P. barbouri* attained a broad geographic range in the early Pliocene (northward to Idaho, southward to Arizona, eastward to Kansas and Nebraska) and persisted into the late Pliocene in New Mexico and Texas (Goodwin 2008).

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APPENDIX I
Specimens examined

Specimens examined for this study came from the following institutions: Natural History Museum, Andrews University, Berrien Springs, Michigan (AU); Mammal Collection and Vertebrate Paleontology Collection, University of Kansas Museum of Natural History, Lawrence (KU and KUVP, respectively); Vertebrate Paleontology Collection, Los Angeles County Museum of Natural History, Los Angeles, California (LACM); Mammal Collection, Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, California (LLU); Mammal Collection, National Museum of Natural History, Washington, D.C. (NMNH); University of Michigan Museum of Paleontology, Ann Arbor (UMMP); Mammal Collection, University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Vertebrate Paleontology Collection, University of Nebraska

State Museum, Lincoln (UNSM); and Field Museum of Natural History (FMNH). Species retained in a random sample of one-half of the taxa (see "Materials and Methods") are marked with an asterisk (*).

Modern Material

Dental Data—*Ammospermophilus harrisii** (KU 95267, 160101, 160104, 160109; UMMZ 108131, 77502). *A. interpres* (KU 58966, 82425, 82426, 131708; NMNH 119909). *A. leucurus* (KU 11430, 18636, 94378; UMMZ 65970, 66427, 108235). *A. nelsoni* (KU 34538, 34539, 149464–149466). *Callospermophilus lateralis* (AU 355, 356; LLU[REG] 172, 2787; UMMZ 56217, 56221, 56239, 58745, 62045, 66426, 78004, 108104, 108207). *C. madrensis* (KU 73621, 73624, 81088, 81090; NMNH 95353, 95358). *C. saturatus* (UMMZ 54618, 58110–58111, 88514, 95780). *Cynomys gunnisoni** (KU 123843, 126852; UMMZ 56956, 65919, 108028). *C. leucurus** (KU 20932, 91095, 123850, 126735, 126916, 145455). *C. ludovicianus* (KU 9426, 12001, 81884, 116380, 123277, 127066, 127925, 149477). *C. mexicanus** (KU 5740, 33097, 34576, 34929, 100423–100424). *C. parvidens** (KU 127966, 149491, 149493; UMMZ 108038, 108040). *Ictidomys mexicanus** (KU 17906, 30985, 30986, 38327, 55466; NMNH 31159, 48359, 50096; UMMZ 58055, 79346). *I. tridecemlineatus* (KU 77945; UMMZ 32797, 33689, 42872, 53846, 76201, 83634, 87358, 105212, 108334). *Marmota broweri** (KU 50417, 50418; NMNH 290273, 290274). *M. caligata* (NMNH 72226, 131437, 146358; UMMZ 54707, 58166). *M. caudata* (NMNH 35497, 62112, 173380). *M. flaviventris** (KU 7155, 45897, 112536, 123637, 142877; UMMZ 57070, 59712, 59713, 65541, 77936). *M. himalayana** (NMNH 62121, 84105, 259438). *M. marmota* (NMNH 115220, 153386). *M. monax* (KU 8570, 28632, 134367, 149581; NMNH 203286, 291554; UMMZ 53830, 125072, 170527). *M. olympus** (KU 120010–120012; NMNH 241947, 242102). *M. sibirica* (NMNH 259440, 268752). *Notocitellus annulatus** (KU 39752, 103734, 109121, 109125, 111663). *Otospermophilus atricapillus* (NMNH 79086–79087, 139744, 139746, 139748). *O. beecheyi* (AU 363; LLU[REG] 253; UMMZ 58153, 59694, 59708, 108102, 108103, 108109). *O. variegatus** (UMMZ 64000, 75251, 79331, 89994, 91884, 108350, 108353, 108354). *Poliocitellus franklinii** (UMMZ 34917, 55610, 68296, 76249, 83626, 83627). *Sciurotamias davidianus* (FMNH 25453, 25455, 32981, 45963, 45964). *Spermophilus citellus** (NMNH 248103, 327293). *S. dauricus** (NMNH 155197, 199621, 240734). *S. erethrogenys** (NMNH 251638, 254948). *S. fulvus* (NMNH 354520). *S. suslicus* (NMNH 13331). *S. xanthoprymnus* (NMNH 327276, 327277, 327290). *Tamias amoenus* (KU 32955, 41494, 46153, 142443, 149878). *T. merriami** (KU 233, 131913, 142475, 142477, 142478). *T. minimus* (KU 42671, 68195, 133310, 142526, 149965). *T. quadrivittatus* (KU 5884, 132291, 132306, 140973, 150009). *T. sibiricus** (KU 60404, 60407, 121370, 139046, 139047). *T. striatus** (KU 10095, 68598, 94635, 130420, 154163). *T. townsendii* (KU 173, 50380, 142459, 156988, 163093). *Urocitellus armatus* (KU 130567; NMNH 67213, 67214, 87783, 203737; UMMZ 65687, 65702, 65707, 108064, 108067). *U. beldingi** (AU 243, 246, 249; NMNH 108992, 108999, 203497, 205787, 272027; UMMZ 54662, 87785, 108089). *U. brunneus* (KU 45926, 45929, 45935, 45936, 45938; NMNH 201726, 201729, 201730, 202410, 265911). *U. canus** (KU 131477–131479; NMNH 78307, 78668, 78671, 78680, 80282; UMMZ 54663, 54667). *U. columbianus** (NMNH 41367, 72817, 233218; UMMZ 53873, 54673, 57977, 58151, 58152, 59545, 108121). *U. elegans** (NMNH 94292, 161510, 247284, 247767, 247768, 250459; UMMZ 56939, 56942, 65681, 65685, 80313, 87353, 87795, 87796, 162548). *U. mollis** (KU 131556, 131558, 131573, 139142, 139146; NMNH 30470, 30507, 30793, 30908, 41568, 54528, 66378, 133073, 169580, 171281, 179642, 179643, 181157, 181160, 201600, 201601, 208130; UMMZ 78833, 78834, 87790, 87791, 108315). *U. parryii** (UMMZ 94106, 94107, 94118, 94119, 158162, 146834, 158164). *U. richardsonii* (NMNH 68750, 69231, 398240, 398241; UMMZ 53282, 83643, 92691, 103265, 105204, 162551). *U. townsendii* (KU 131584, 131585, 131607, 131608; NMNH 89319, 89321, 235738, 235744). *U. undulatus* (NMNH 175286, 175293, 259717). *U. washingtoni** (NMNH 40075, 78189, 78393, 78593, 89759; UMMZ 54635, 54637, 54639, 54641, 54734). *Xerospermophilus mohavensis* (NMNH 22732, 40847, 40851, 192752, 192753). *X. perotensis** (KU 30003–30004, 30006; NMNH 54263–54264). *X. spilosoma** (KU 3454, 103744; UMMZ 66358, 66875, 66877, 92750, 108290). *S. tereticaudus** (UMMZ 53961, 53962, 56092, 61718, 98668).

Femoral data—All specimens are from UMMZ. *Ammospermophilus harrisii* (56121, 61738, 63757–63760), *A. leucurus* (80986–80988, 80990, 175462), *Callospermophilus lateralis* (54606, 56213, 56214, 56221, 62045, 62046, 162549), *C. saturatus* (54613–54615, 95781), *Cynomys gunnisoni* (56210, 56957), *C. ludovicianus* (56212, 67352, 156439), *Ictidomys mexicanus* (79344, 79345, 79347), *I. tridecemlineatus* (53728, 67095, 162783, 162785, 162789, 162809, 164036, 164051), *Marmota bobak* (122842), *M. flaviventris* (57071), *M. monax* (165973, 166225, 168141, 173712), *Notocitellus annulatus* (80978, 80979, 94630), *Otospermophilus beecheyi* (54629, 173770, 176161, 176199, 176202, 176219), *O. variegates* (79328, 79338, 90120), *Poliocitellus franklinii* (65265, 65818, 68298), *Spermophilus dauricus* (123542, 123543), *S. musicus* (123548, 123549), *S. suslicus* (123555, 123556), *Tamias minimus* (56256, 60274, 68002, 162559, 167070, 167071), *T. quadrivittatus* (56248, 56963, 56967, 56975), *T. striatus* (61928, 75981, 102531, 124622, 176372, 176807), *Urocitellus columbianus* (158284, 158300, 158414, 158432, 158459, 162472), *U. parryii* (101103, 112402, 112405, 168374–168376), *U. richardsonii* (158285, 158287, 158289, 158297, 158313, 153316), *Xerospermophilus spilosoma* (79341, 92746–92748, 92750, 92751), *X. tereticaudus* (63860).

Fossil Material

P. barbouri: KUVP 6994 (L dentary with p4–m3 [cast]), UMMP 33367 (R dentary with p4–m3 [p4 not measurable]), UMMP 42637 (R P4), UMMP 47126 (L maxilla with P4–M3, R dentary with p4–m3), UMMP 47127 (partial postcranial skeleton), UMMP 47886 (R maxilla with P4–M3, R dentary with m1–m3), UMMP 54298 (R maxilla with P3–P4, M2 [P4 not measurable]); *P. mexicana*–LACM 3546 (L maxilla with M2–M3, R maxilla with P4–M1, L dentary with P4–M3 [cast]); *P. sawrockensis*–UMMP 45775 (associated R p4–m3), UNSM 47191 (L dentary with p4–m3), UNSM 94979 (R maxilla with P4–M1).