

REASSESSING THE MASS OF EXCEPTIONALLY LARGE RODENTS USING TOOTHROW LENGTH AND AREA AS PROXIES FOR BODY MASS

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A variety of estimators have been used by paleontologists for reconstructing body mass of fossil mammals. For rodents, the most commonly used proxy is m1 area, although that value is known to overestimate masses in muroid rodents and is generally problematic in rodent taxa in which the m1 is either enlarged (as in muroids) or reduced (as in extinct mylagaulids). This paper explores the potential utility of 2 alternative proxies, tooththrow length and tooththrow area; these measures are shown here to be very tightly correlated with body mass among rodents. Regression within certain clades of the Rodentia provides an even tighter fit. Applying these proxy measures to several fossil rodents provides an estimate of their masses. Comparison to published body masses of extinct rodents estimated from postcrania reveals that body masses for *Castoroides* and *Palaeocastor* estimated from femur length are consistent with those from dental proxies but that tooththrow-based estimates for *Phoberomys*, the largest known fossil rodent, are discordant with the mass estimated from limb bone diameter. This difference may be explained by both allometric scaling of limbs and locomotor differences between *Phoberomys* and the caviomorph rodents on which the limb bone diameter regression was based.

Key words: body mass, *Castoroides*, dental measurements, mass estimation, *Phoberomys*, Rodentia

Reconstructing the body mass of a fossil animal is an essential step toward understanding its paleoecological role. Many proxies have been proposed for determining body mass of fossil mammals, including molar area (Creighton 1980; Gingerich 1976, 1977; Legendre 1986; Martin 1990), dimensions of long bones (Biknevicius et al. 1993; Christiansen 2002; Egi 2001; Gingerich 1990; Reynolds 2002; Ruff 2003), and cranial measurements (Janis 1990; Reynolds 2002; Thewissen and Gingerich 1989). Area of m1 is the most commonly used because it is applicable even to specimens known only from dental remains and because it provides one of the best correlations with body mass of any skeletal or dental proxy (Gingerich et al. 1982). However, there are some cases for which none of these proxies offer a good estimate of body mass. One such case is the rodent family Mylagaulidae, species of which lose the anterior molars (the 1st and, in some cases, the 2nd) early in the clade's evolutionary history, but retain the 4th premolar and the 3rd molar. Crania are known for only

about one-half of mylagaulid species, and are often fragmentary, and limb bones of mylagaulids are very rarely associated with species-diagnostic dental and cranial material. The m1 area regression for rodents as a whole provided by Legendre (1986) also has the problem of overestimating body mass in muroid rodents (Lindsay 1988; Morgan et al. 1995), possibly because they have lost the premolar and have enlarged the upper and lower 1st molars. This study aims to solve these problems in estimation of rodent body mass by assessing the value of lower tooththrow dimensions (length and area) as proxies for body mass in rodents.

Within-species studies (Blem et al. 1993; Patton and Brylski 1987) have found tooththrow length to be a poor proxy for body mass in modern rodents, which is seemingly at odds with the strong relationship documented by paleontologists between m1 area and body mass in small mammals (Damuth and MacFadden 1990; Legendre 1986). This apparent contradiction may arise because tooththrow length varies because of differences in the dimensions of the teeth other than m1, and hence is a poor proxy for mass both intra- and interspecifically; or because within-species variations in mass are largely a result of ecophenotypic plasticity, which do not manifest as variation in size of the genetically controlled tooththrow length (Hadly 1997). These 2 alternatives are compared here using data on intra- and

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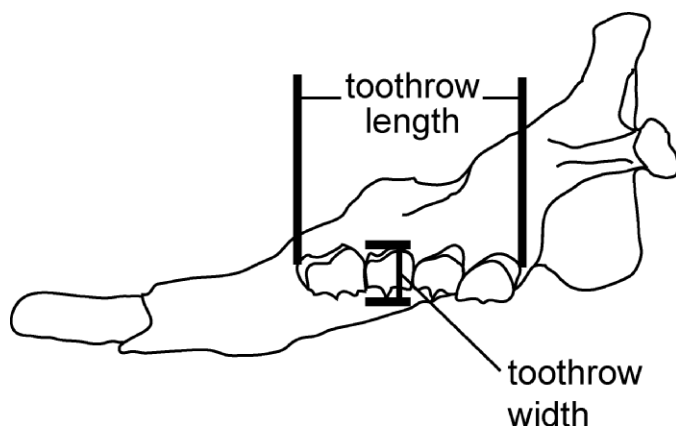


FIG. 1.—Tooththrow measurements used in this study, on a right jaw of *Aplodontia rufa* shown in occlusal view. LTRL = lower tooththrow length.

interspecific variation in dental characters and body mass in diverse species of rodents.

There are energetic reasons to expect a close relationship between the dimensions of the tooththrow and the body mass of a mammal. Particularly in a predominantly herbivorous clade such as the Rodentia, the cheek tooththrow provides the surface for processing food. Larger animals must process more (and generally larger) food items with their dentition; hence, the larger the animal, the larger the tooththrow is required to be. Gingerich and Smith (1984) suggest that this scaling may not be energetically determined because, at least in primates, dental dimensions scale geometrically rather than exponentially (as would be expected of metabolic scaling). No allometric relationships or changes have been suggested for the forces that relate dental dimensions to body mass, so their relationship should be consistent as long as the functional constraints remain similar. Functionally, the cheek tooththrow is used similarly in all rodents, so it provides an analogous measure throughout the Rodentia.

This study uses data from modern rodents to examine the utility of tooththrow dimensions as proxies for body mass in this clade. Considering the utility of both tooththrow length and area over several different taxonomic scales and including different parts of the range of modern rodent masses makes it possible to determine the best approach for estimating body mass in extinct rodents. This approach is then used to estimate mass in a fossil clade (the Mylagaulidae) for which no reliable mass estimate was previously possible, as well as to explore the reliability of estimates for several taxa that have previously had masses estimated from other proxies.

MATERIALS AND METHODS

Data on lower tooththrow length (LTRL), maximum width, and body mass were collected from 5 specimens each of 75 species of rodents housed in the collections of the University of California Museum of Vertebrate Zoology (listed in Appendix I). Taxa were chosen so as to span the evolutionary, morphological, and ecological diversity of the order Rodentia. For 5 of these species (*Aplodontia rufa*, *Thomomys bottae*,

Tamiasciurus hudsonicus, *Peromyscus maniculatus*, and *Mesomys hispidus*), measurements were collected from 10 additional specimens (for a total of 15 individuals per species) to assess the relationship between tooththrow size and body mass within a species. These additional samples were chosen to span multiple subspecies in all but *M. hispidus*, for which only a single subspecies was available. Only adult specimens with all teeth erupted were measured for this study, because the question of interest is how to estimate the body mass characteristic of a fossil species, not the mass for fossil individuals. Wherever possible, both males and females were sampled for each species; no other control was made for possible sexual dimorphism. Because there was no consistent bias in the specimens measured (e.g., only measuring females for all the smallest species), dimorphism should not be a problem for these analyses.

Lower tooththrow length is the mesiodistal distance from the posterior edge of the alveolus of m3 to the anteriormost point of p4 (Fig. 1). Maximum width is the greatest labiolingual width of the tooththrow, measured perpendicular to the long dimension of the tooththrow (Fig. 1). This dimension is equivalent to the width of m1 or m2 in all taxa included here. Rectangular lower tooththrow area (RTRA) also was estimated for all taxa examined as a possible alternative proxy for mass. Calculating actual tooththrow area is methodologically difficult, but the mammalian tooththrow more or less approximates a rectangle. In making regressions between m1 area and body mass, Legendre (1986) used rectangular area of the molar (length times width) as a predictor rather than actual area. Here, I have done the same with tooththrow area, multiplying length times the maximum width of the tooththrow. In contrast, Gingerich et al. (1982) and Gingerich and Smith (1984) summed the rectangular areas of the individual teeth to estimate total tooththrow area. This method, although effective, is a great deal more time-consuming and is unnecessary in rodents, whose teeth are generally rectangular and lack diastemata between the cheek teeth.

Specimens were measured using Mitutoyo CD-6"CS digital calipers. Average values of lower tooththrow length, maximum width, and mass were calculated for each species. All 3 average measurements were then natural log (ln)-transformed to reduce the effect of increasing variance with increasing body size. Body mass was obtained for each specimen from the data recorded on the museum specimen tag, which includes a mass recorded at the time the animal was collected. The average body mass reported by Ernest (2003) was used for 3 species (*Hydrochoerus hydrochaeris*, *Graphiurus murinus*, and *Cryptomys hottentotus*) for which museum specimens lacked data on body mass. Including these data would tend to decrease the strength of correlations if the individuals measured by Ernest (2003) are not representative of their species. However, because one point of this study was to determine whether these proxies can be used to represent the species averages for traits, including these data will add to the robustness of the conclusions drawn from this study. Furthermore, each is the only representative of its family in the study, and hence these taxa improve the general applicability of the results.

Data were analyzed using the statistical software JMP IN 5.1 (SAS Institute Inc., Cary, North Carolina). To get an overall picture of how well the metric of tooththrow length predicts body mass, I plotted $\ln(\text{average body mass})$ against $\ln(\text{tooththrow length})$ for each species. The relationship between tooththrow length and body mass should actually be best fit by a cubic equation, because the linear measurement of length is being compared to mass, which is a function of volume; a cubic relationship is the best fit for the untransformed values. However, taking the natural log of the tooth measurement removes much of the curvature in the relationship. Linear regressions provide the additional benefit of being easier to use to reconstruct body mass of species known only from dental remains. Cubic regressions in data with so little curvature have a tendency to track variation in the data, rather than creating a more biologically realistic model, so they were not used here. Parameter values given for all regressions correspond to the terms in the following equation:

$$\ln \text{ body mass} = a + b \ln \text{ LTRL}.$$

Confidence limits can be placed on the body mass predicted from a regression based on the following formula (Zar 1999:339) for standard error of an estimated y value ($s_{\hat{y}_i}$):

$$s_{\hat{y}_i} = \frac{s_{y \cdot x}}{\sqrt{n}} \sqrt{1 + \frac{(x_i - \bar{X})^2}{\text{var}(x)}},$$

where $s_{y \cdot x}$ is the standard error of the regression, n is the number of samples, x_i is the natural log of the tooththrow length of the fossil species (input into the regression equation to estimate body mass), \bar{X} is the mean value of the natural log of the tooththrow measurement, and $\text{var}(x)$ is the population variance in the tooththrow measurement. All terms in this equation except x_i are determined from the data used to generate the regression. The parameters of this equation are computed for each of the regressions performed in this study. The standard error of y allows calculations of upper and lower 95% confidence limits of body mass according to the following formulae:

$$\text{upper 95\% limit} = e^{\ln(\text{predicted mass}) + t_{\alpha(2), (n-2)} s_{\hat{y}_i}}$$

$$\text{lower 95\% limit} = e^{\ln(\text{predicted mass}) - t_{\alpha(2), (n-2)} s_{\hat{y}_i}}.$$

There are relatively few rodents with body masses greater than 5 kg; only 4 are included in this analysis and, although log-transformation of the data reduces their influence on the overall result, their dentitions may be shaped by different factors than those affecting smaller mammals. Alroy (1998) has pointed out that a “gap” (an area occupied by a lower density of species) appeared in the distribution of masses of North American mammals in the late Eocene. This gap occurs between approximately 10^3 and 10^4 g body mass; because the 4 rodents with masses >5 kg are within or above the gap, it may be misleading to include them in a regression intended to estimate body mass for rodents as a whole. Furthermore, the sparse distribution of points above a mass of 5 kg makes for a nonuniform difference in the distribution of the variance, a potential problem for regression analysis. To determine

whether the inclusion of these large species disproportionately influenced my regression analyses, I removed these large species (*Erethizon dorsatum*, *Castor canadensis*, *H. hydrochaeris*, and *Cuniculus paca*) from the data set and then reran the regressions. Regressions also were performed within narrower subclades to determine whether scaling of mass to tooththrow size differed notably between rodent lineages.

One source of error in the prediction of body mass from the length of the tooththrow is variation in the relative width of the teeth, which enables an animal with a shorter tooththrow to have functionally the same surface area for processing food as one with a longer, narrower tooththrow. Because this relationship is expected to be constrained by the need to process food, area may provide an even better proxy for body mass. The same regressions were performed for $\ln(\text{tooththrow area})$ as for $\ln(\text{tooththrow length})$ to determine whether adding tooththrow width to the prediction equation yielded a significant improvement in the performance of the proxy.

In order to explore the conflict between within-species studies that find tooththrow dimensions to be a poor proxy for mass in rodents and among-species studies that find the dimensions of individual molars to be good proxies for rodent body mass, regressions between tooththrow size and body mass were run for the 5 species with larger ($n = 15$) sample sizes to assess the utility of these proxies in predicting the masses of conspecifics. Comparing these results with the results of interspecific regressions makes it possible to determine whether the conflicting results of past studies arose because tooththrow length is simply not strongly related to body mass in rodents at any level of examination, or if the problem arises because body mass and tooththrow length are constrained at different taxonomic levels.

RESULTS

Intraspecific relationship between tooththrow size and body mass.—The 5 species for which larger sample sizes were obtained allow assessment of the relationship between tooththrow size and body mass within a species. The results of regressions of $\ln(\text{mass})$ against $\ln(\text{lower tooththrow length})$ and $\ln(\text{lower tooththrow area})$ are presented in Table 1. The outcomes of these analyses are generally consistent with more exhaustive within-species studies of cranial measurements and body mass (Blem et al. 1993; Patton and Brylski 1987) in revealing generally positive but nonsignificant relationships between dental measures and body mass.

Comparing within-species variation in body mass and tooththrow length reveals an important difference between interspecific and intraspecific studies of mass proxies. For each of the intraspecific analyses, the coefficient of variation (CV) is 2–9 times greater for body mass than for tooththrow length (Table 1). In all but *T. hudsonicus*, the CV also is greater for the tooththrow area than for body mass. This is even more striking given that the sample contains only individuals with a full adult dentition. For the interspecific regressions, variance is generally more similar between body mass and tooththrow length. In the regression including all taxa, the CV is 4.86 for

TABLE 1.—Parameters for within-species regressions of tooththrow dimensions and body mass. See text for equation. *df.* = degrees of freedom; *a* = regression intercept; *b* = regression slope; *SE(a)* = standard error of *a*; *SE(b)* = standard error of *b*; *CV* = coefficient of variation; LTRL = lower tooththrow length; RTRA = rectangular lower tooththrow area.

	<i>df.</i>	<i>a</i>	<i>b</i>	<i>SE(a)</i>	<i>SE(b)</i>	<i>P</i>	<i>R</i> ²	<i>CV</i>	<i>CV (mass)</i>
LTRL									
<i>Apodonta rufa</i>	14	−7.77	5.11	4.63	1.62	0.008	0.43	0.0354	0.281
<i>Mesomys hispidus</i>	14	6.36	−0.644	4.88	2.38	0.791	0.006	0.0235	0.208
<i>Peromyscus maniculatus</i>	14	1.27	1.29	2.45	1.89	0.508	0.03	0.0410	0.299
<i>Tamiasciurus hudsonicus</i>	14	4.68	0.382	1.14	0.547	0.497	0.04	0.0398	0.0784
<i>Thomomys bottae</i>	14	2.60	1.03	1.63	0.764	0.202	0.12	0.0716	0.208
RTRA									
<i>Apodonta rufa</i>	14	−2.78	2.31	4.47	1.07	0.495	0.27	0.0615	0.281
<i>Mesomys hispidus</i>	14	2.93	0.786	1.80	0.673	0.264	0.09	0.0809	0.208
<i>Peromyscus maniculatus</i>	14	2.13	0.657	1.28	1.04	0.538	0.03	0.0744	0.299
<i>Tamiasciurus hudsonicus</i>	14	4.61	0.295	0.635	0.217	0.197	0.12	0.0942	0.0784
<i>Thomomys bottae</i>	14	3.15	0.570	1.42	0.494	0.269	0.09	0.113	0.208

body mass and 1.02 for tooththrow length. Both values are much higher than for the intraspecific analyses, and the difference between them (~4 times) is less than most of the intraspecific studies.

Interspecific relationship between tooththrow length and body mass.—The linear regression between $\ln(\text{lower tooththrow length})$ and $\ln(\text{body mass})$ for all 75 species examined is highly significant ($P < 0.0001$, $R^2 = 0.94$), providing a very good predictor of body mass (Table 2; Fig. 2A). The linear regression for rodents with body masses less than 5 kg (Table 2; Fig. 2B) has somewhat lower explanatory power ($R^2 = 0.89$), likely due in part to the greater density of sampling through the range of masses included. A *t*-test comparing the slope of the regression including all taxa with that of the regression including only rodents less than 5 kg in body mass finds no significant difference between the two ($P = 0.727$). Hence, the large taxa are not solely responsible for the relationship found between tooththrow length and body mass, although some of the variance around the relationship is obscured by looking at the wider range of body masses. Even if only small rodent species (<500 g body mass) are included (Table 2; Fig. 2C), the regression is not significantly different from the original values ($P = 0.34$), although the R^2 value is reduced even further (0.81).

A great deal of the scatter in the regression for small (<500-g) species is created by the Muroidea; for nonmuroid rodents with

body masses below 500 g, tooththrow length and body mass are much more tightly correlated ($R^2 = 0.93$). Nonmuroids also are less variable among species less than 5 kg (Table 2; Figs. 2D and 2E; $R^2 = 0.94$). Clearly, mureids have a much more variable relationship between body mass and tooththrow length, although these parameters are still strongly associated ($R^2 = 0.75$ for mureids < 500 g; $R^2 = 0.83$ for mureids < 5 kg).

The relationship between tooththrow length and body mass is generally tighter within a more narrowly defined taxonomic group, as is apparent from the results of the within-clade regressions presented in Table 3. For all but the Murinae and the Sigmodontinae, the R^2 values are as good as or better than the overall analysis. Although none of these regressions is significantly different from the others based on *t*-tests comparing the slopes (all $P > 0.05$), the parameter values are more specific to the clade of interest, and hence provide a better estimate of body mass. Arvicolines, for example, generally lie below the line for rodents as a whole, having very long tooththrows relative to their body mass. Murines, on the other hand, generally lie above the line, having a tooththrow that is short relative to their mass.

The results of regressions of $\ln(\text{tooththrow area})$ against $\ln(\text{body mass})$ are presented in Fig. 3. The parameters from these analyses are presented in Table 4. The decision to use maximum width and whole tooththrow length (rather than the rectangular areas of individual teeth) to estimate tooththrow area seems to be supported, because the R^2 value (0.96) is comparable to that reported by Gingerich and Smith (1984) for the more labor-intensive method. For the more taxonomically inclusive analyses of tooththrow area, R^2 is a bit higher than for the corresponding analyses of tooththrow length, although relatively little difference between dental measures is apparent in the regressions within narrower clades. In fact, in 2 of these clades, the Arvicolinae and the Sciuridae, mass is more tightly correlated with tooththrow length than with rectangular area. This is not simply a function of the inaccuracy of a rectangular description of the tooththrow in these clades, because the morphology of the tooththrow in both these groups is relatively rectangular. Rather, this result appears to reflect the weaker relationship between tooththrow width and body mass in these 2 clades.

TABLE 2.—Parameters for interspecific regressions of lower tooththrow length against body mass. See text for equation. LTRL = lower tooththrow length; *df.* = degrees of freedom; *a* = regression intercept; *b* = regression slope; *SE(a)* = standard error of *a*; *SE(b)* = standard error of *b*.

LTRL	<i>df.</i>	<i>a</i>	<i>b</i>	<i>SE(a)</i>	<i>SE(b)</i>	<i>P</i>	<i>R</i> ²
All species	74	−0.6909	2.7813	0.1753	0.0844	<0.0001	0.94
All < 5 kg	70	−0.5992	2.7283	0.2254	0.1156	<0.0001	0.89
All < 500 g	60	−0.3024	2.5426	0.2901	0.1599	<0.0001	0.81
Muroidea < 500 g	40	−0.6196	2.7020	0.4410	0.2518	<0.0001	0.75
Non-Muroidea < 500 g	19	0.2931	2.2734	0.2874	0.1485	<0.0001	0.93
Muroidea < 5 kg	43	−0.6449	2.7160	0.3545	0.1944	<0.0001	0.83
Non-Muroidea < 5 kg	26	−0.2175	2.5909	0.2787	0.1303	<0.0001	0.94

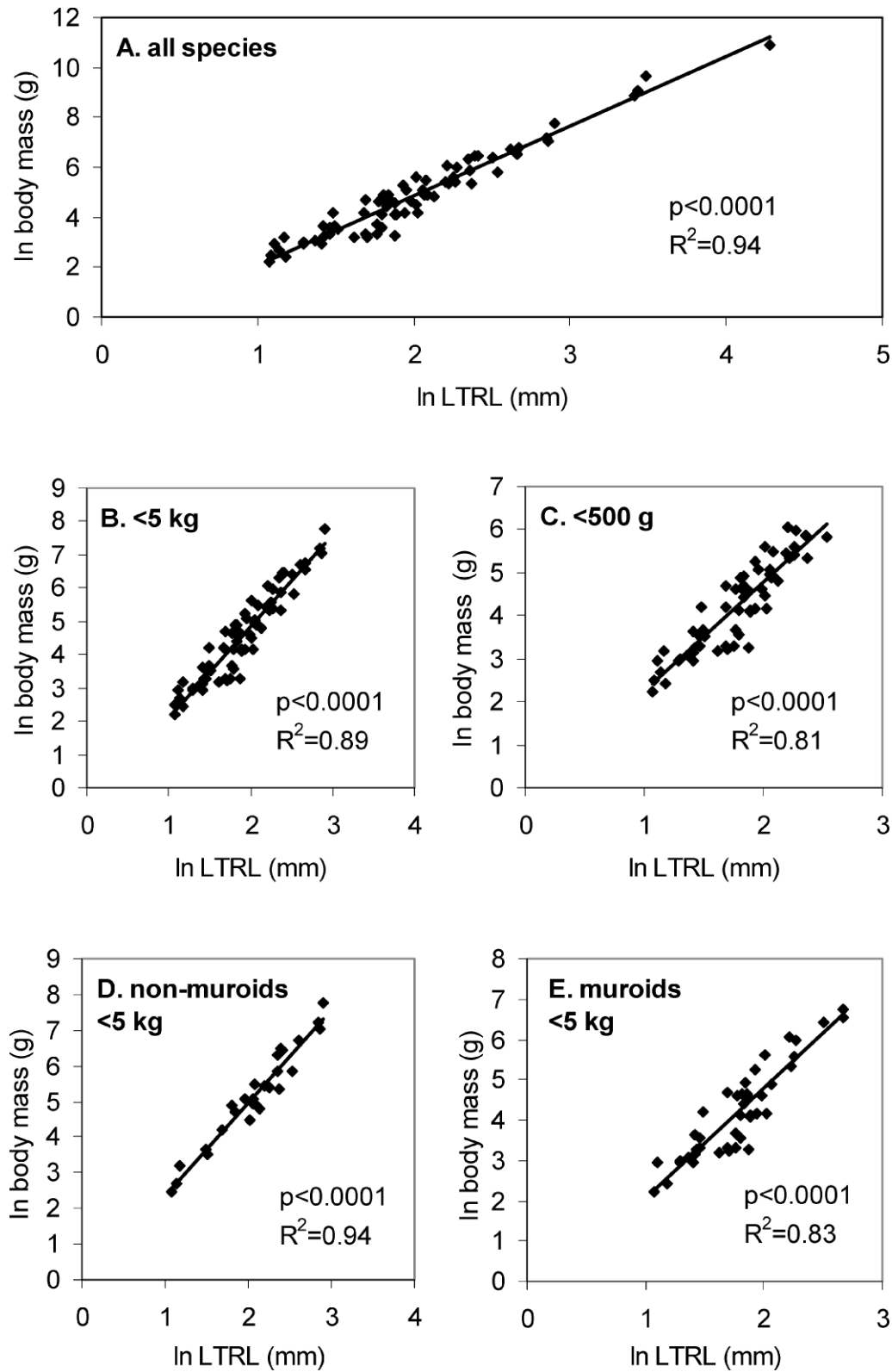


FIG. 2.—Regressions of lower tooththrow length against body mass in A) all rodent species, B) rodents < 5 kg body mass, C) rodents < 500 g body mass, D) nonmuroid rodents < 5 kg body mass, and E) muroid rodents < 5 kg body mass. See Table 2 and text for regression parameters and statistics.

TABLE 3.—Parameters for analysis of lower tooththrow length against body mass of selected subordinal clades. See text for equation. LTRL = lower tooththrow length; *d.f.* = degrees of freedom; *a* = regression intercept; *b* = regression slope; *SE(a)* = standard error of *a*; *SE(b)* = standard error of *b*.

LTRL	<i>d.f.</i>	<i>a</i>	<i>b</i>	<i>SE(a)</i>	<i>SE(b)</i>	<i>P</i>	<i>R</i> ²
Arvicolinae	10	−2.3641	3.3073	0.5361	0.2816	<0.0001	0.94
Geomyoidea	6	0.0523	2.3238	0.4226	0.2538	0.0003	0.94
Hystricomorpha	9	−0.9125	2.8134	0.3624	0.1269	<0.0001	0.98
Murinae	10	−0.2474	2.6926	0.6446	0.3560	<0.0001	0.86
Neotominae	7	−0.7237	2.7540	0.1218	0.0726	<0.0001	0.996
Sciuridae	9	−0.9466	3.0060	0.5186	0.2286	<0.0001	0.96
Sigmodontinae	9	−1.0419	3.1078	0.8156	0.4776	0.0002	0.84

Reconstruction of body masses of extinct mylagaulids.—The regressions generated here between tooththrow area and body mass for extant rodents provides a method for reconstructing the average body masses of extinct rodent species. One clade for which preexisting regressions using M1 area were not applicable is the Mylagaulidae, which has lost the 1st molar. Using the regression for nonmuroid rodents under 5 kg, the mass of *Alphagaulus vetus*, a mid-Miocene mylagaulid, is reconstructed to be roughly 1,100 g, similar to the larger subspecies of its modern relative, *A. rufa* (1,261 g for 5 specimens of *A. rufa californica* in this analysis). The horned mylagaulid *Ceratogaulus hatcheri*, one of the largest mylagaulids according to skull size, is reconstructed to be approximately 1,900 g, the mass of a small marmot. Known species of mylagaulids are estimated to range from 230 g (*Trilaccogaulus montanus*) to 1,900 g (*Ceratogaulus hatcheri*), or from roughly the mass of a woodrat to that of a marmot.

Comparison with other estimators of body mass.—The regressions developed above can be used to provide a check on existing estimates of body mass for extinct rodents. Comparing body mass estimates from different proxies requires some measure of the error in an estimation of body mass. This error is estimated using the confidence limits generated with the parameters in Table 5.

Body masses for several fossil rodent species have been reconstructed using regressions based on dimensions of the femur. Reynolds (2002) reconstructed masses for *Palaeocastor* and *Castoroides*, 2 extinct castorids, based on femur length. The values obtained here agree very well with those computed from femur length. Using the regression for all rodents, a mass of approximately 67 kg (95% confidence interval [95% CI] = 62–73 kg) is estimated for *Castoroides leiseyorum* (LTRL = 69.6 mm—Parmalee and Graham 2002). Reynolds' (2002) estimation of 60–100 kg for the mass of *Castoroides* is consistent with this result. Similarly, the regression for nonmuroid rodents less than 5 kg provides an estimate for *Palaeocastor nebrascensis* (LTRL = 15.8 mm—Stirton 1935) of roughly 1 kg (between 0.96 and 1.10 kg), which is in accord with Reynolds' (2002) result of 0.8–1.2 kg. Reynolds' (2002) regressions have slightly lower *R*² values (0.81–0.91) than those presented here, suggesting that the dental dimensions used here may provide a slightly better predictor of mass than femur length or skull length.

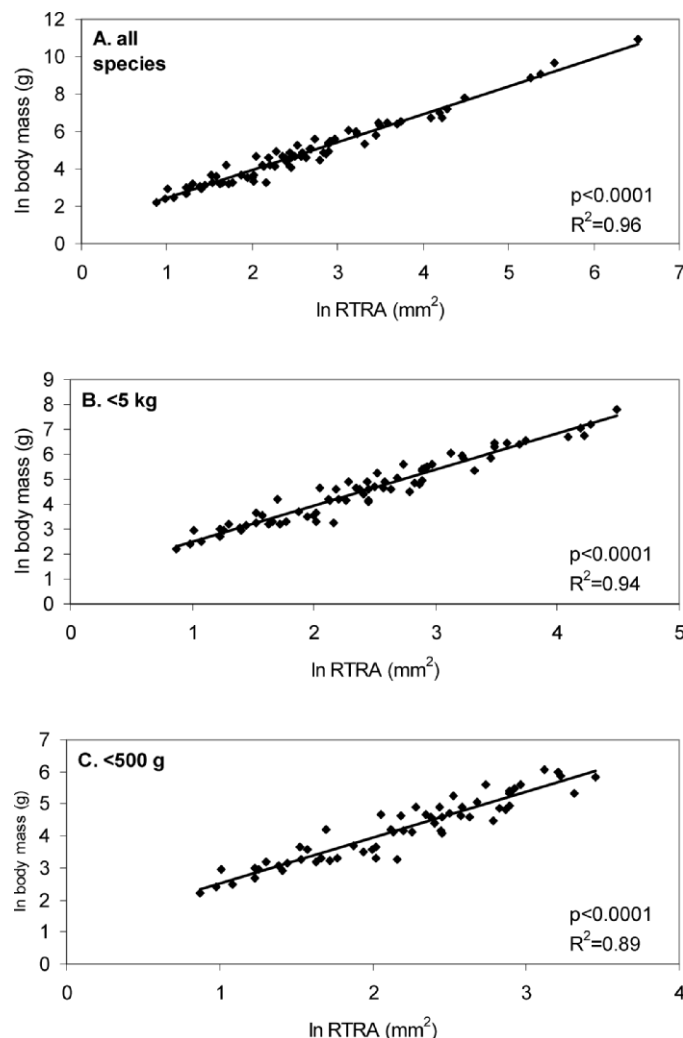


FIG. 3.—Regressions of rectangular lower tooththrow area against body mass in A) all rodent species, B) rodents < 5 kg body mass, and C) rodents < 500 g body mass. See Table 4 and text for regression parameters and statistics.

A more difficult problem is estimating the masses of rodents well outside the range of masses represented by extant rodents. *Phoberomys pattersoni* is an extinct caviomorph suggested to be roughly the size of a buffalo (Alexander 2003). Sánchez-Villagra et al. (2003) computed a mass of approximately 741 kg based on femur diameter and roughly 436 kg based on humerus diameter; based on the inference that hind limbs were more important in locomotion, they determined that the body mass from the femur was more reliable. Using the regression for tooththrow length of hystricomorphs, I find a dramatically different estimate, approximately 234 kg (95% CI = 164–334 kg based on a tooththrow length of 112 mm, as measured from the published image of the lower jaw [Sánchez-Villagra et al. 2003]). Even the maximum estimate based on tooththrow length is less than one-half the estimate made from femoral diameter. A mismatch this large is not unexpected when extrapolating so far outside the range of sizes of extant taxa, and suggests that one or both estimates are far off the correct value.

TABLE 4.—Parameters for interspecific regressions of rectangular lower tooththrow area against body mass. See text for equation. RTRA = rectangular lower tooththrow area; *df.* = degrees of freedom; *a* = regression intercept; *b* = regression slope; *SE(a)* = standard error of *a*; *SE(b)* = standard error of *b*.

RTRA	<i>df.</i>	<i>a</i>	<i>b</i>	<i>SE(a)</i>	<i>SE(b)</i>	<i>P</i>	<i>R</i> ²
All species	74	0.9386	1.4968	0.0962	0.0339	<0.0001	0.96
All < 5 kg	70	1.0484	1.4473	0.1167	0.0451	<0.0001	0.94
All < 500 g	60	1.0502	1.4442	0.1531	0.0668	<0.0001	0.89
Muroidea < 500 g	40	0.9320	1.5199	0.2055	0.0965	<0.0001	0.86
Non-Muroidea < 500 g	19	1.0853	1.4002	0.2425	0.0935	<0.0001	0.93
Muroidea < 5 kg	43	1.0516	1.4565	0.1689	0.0737	<0.0001	0.90
Non-Muroidea < 5 kg	26	0.9407	1.4715	0.1823	0.0606	<0.0001	0.96
Arvicolinae	10	0.3871	1.6150	0.3592	0.1615	<0.0001	0.92
Geomyoidea	6	1.0057	1.3446	0.2964	0.1350	0.0002	0.95
Hystricomorpha	9	0.7376	1.5427	0.2643	0.0632	<0.0001	0.99
Murinae	10	1.3517	1.4047	0.4448	0.1886	<0.0001	0.86
Neotominae	7	0.9187	1.5495	0.0692	0.0349	<0.0001	0.997
Sciuridae	9	0.8756	1.5179	0.3864	0.1167	<0.0001	0.95
Sigmodontinae	9	1.0332	1.5590	0.4657	0.2218	0.0001	0.86

DISCUSSION

Utility of dental proxies for estimating body mass.—This study reveals that, although tooththrow dimensions are relatively poor predictors of intraspecific differences in body mass in rodents, they are accurate in predicting interspecific differences in body mass. Because this is generally the scale of interest for fossil organisms, tooththrow length and area are effective as proxies for the body masses of fossil rodent species. The analyses presented here indicate that although a relatively accurate proxy for body mass can be obtained from a regression based on data from diverse rodent species, even greater accuracy can be obtained using taxa from within narrowly defined subclades. Muroids in particular are characterized by a large variance in the relationship between tooththrow size and body mass, which is perhaps unsurprising given the morphological and ecological diversity encompassed by this clade. Using these predictive equations to estimate body masses of fossil organisms in many cases yields results concordant with previous studies, although the estimated body mass for the largest known rodent, *P. pattersoni*, differs greatly from estimates obtained from other proxies, a problem that requires further consideration.

Within species, tooththrow measurements are poor predictors of individual body mass, because the complete adult dentition is generally erupted early in life, whereas body mass continues to change as an animal reaches full adult mass. Further, the adult body mass of an individual varies widely as a result of factors such as ontogeny, nutrition, and reproductive state. Tooththrow length, on the other hand, varies much less within a species and almost not at all once an animal is an adult, other than as a result of wear. Because this analysis is limited to adults, it is not surprising that tooththrow length explains almost none of the variation in body mass, except in *A. rufa*. In this case, most of the significant effect seems to be generated by the

TABLE 5.—Parameters used to determine confidence limits on estimates of body mass. See text for equation and additional explanation. LTRL = lower tooththrow length; RTRA = rectangular lower tooththrow area.

	<i>n</i>	<i>S_{Y·X}</i>	\bar{X}	<i>var(X)</i>	<i>t</i> _{0.05(2), (n-2)}
LTRL					
All species	75	0.048830	1.99	87.51	1.993
All < 5 kg	71	0.051444	1.9	12.26	1.995
All < 500 g	61	0.056704	1.78	4.649	2.002
Muroidea < 500 g	41	0.077474	1.72	3.768	2.023
Non-Muroidea < 500 g	19	0.271428	1.89	6.611	2.110
Muroidea < 5 kg	44	0.071756	1.79	7.577	2.018
Non-Muroidea < 5 kg	27	0.064448	2.08	31.07	2.060
Arvicolinae	11	0.075652	1.88	6.114	2.262
Geomyoidea	7	0.10277	1.62	4.143	2.571
Hystricomorpha	10	0.09645	2.78	356.5	2.306
Murinae	11	0.114772	1.78	3.474	2.262
Neotominae	8	0.032312	1.62	6.835	2.447
Sciuridae	10	0.075307	2.24	13.16	2.306
Sigmodontinae	10	0.123885	1.69	1.801	2.306
RTRA					
All species	75	0.03987	2.61	7,476	1.993
All < 5 kg	71	0.037995	2.44	309.8	1.995
All < 500 g	61	0.043146	2.2	45.41	2.002
Muroidea < 500 g	41	0.057977	2.04	29.65	2.023
Non-Muroidea < 500 g	19	0.271429	2.51	2,802	2.110
Muroidea < 5 kg	44	0.055035	2.17	145.5	2.018
Non-Muroidea < 5 kg	27	0.052622	2.88	2,314	2.060
Arvicolinae	11	0.008736	2.15	100.8	2.262
Geomyoidea	7	0.093815	2.09	32.38	2.571
Hystricomorpha	10	0.0682	3.99	38,080	2.306
Murinae	11	0.114772	2.28	42.21	2.262
Neotominae	8	0.027983	1.81	45.28	2.447
Sciuridae	10	0.084196	3.24	554.9	2.306
Sigmodontinae	10	0.115884	2.03	15.94	2.306

inclusion of multiple subspecies that differ substantially in size. It is apparent that the limited ability of tooththrow length to predict intraspecific variation in body mass does not impact its utility as an interspecific proxy. Although it has been demonstrated that the 1st molar is less variable in size than other cheek teeth (Gingerich and Winkler 1979), the strong interspecific relationship between tooththrow length and body mass indicates that variation in dental characters is not the source of the differing predictive abilities of inter- and intraspecific body mass regressions. Rather, it appears that variation in body mass within a species is substantial, whereas variation in tooththrow length is less extreme. Thus, the differing results of intra- and interspecific studies of rodent tooth dimensions and body size appear to reflect the differing taxonomic scales at which these measurements vary. Specifically, although body mass varies on an individual level, relative tooththrow size varies primarily on a larger taxonomic scale.

At and above the species level, the relationship between tooththrow size (length and area) and body mass provides several good proxies for the average masses of rodent species. Because dental remains are by far the most common identifiable elements preserved for rodents, these proxies are important for inferring the mass of extinct species. Unlike the other

common proxy, m1 area, toothrow length and area can be used in taxa with differing dental formulae. Although there is variation between clades with regard to the closeness of the fit between toothrow size and body mass, it is quite a good predictor of mass for all rodents. For the smallest rodents, the percentage by which body masses estimated from toothrow size may err compared to actual body masses is relatively large. Nevertheless, this estimator provides a very good relative measure of body mass, particularly if the estimate is made using species within the same subordinal clade. This result is in line with the findings of Gingerich (1976, 1977) and Creighton (1980), who used the area of an individual molar as a proxy for body mass. The greater variance in the relationship between toothrow length and body mass in muroid rodents suggests that some caution should be exercised when applying this proxy to this clade, as has been found for other dental proxies for body size in muroids (Lindsay 1988; Morgan et al. 1995). Muroids, unlike almost all other rodents, have lost their premolars and possess only the 1st through 3rd molars in both the upper and lower toothrows. This modification, along with diverse changes in the morphology of these teeth, may explain why the relationship between toothrow length and body mass is more variable within this clade compared to other clades within Rodentia or among rodents as a whole.

In the taxonomically inclusive analyses, toothrow area is slightly more related to body mass than is toothrow length; within clades, however, the relationship is sometimes stronger between toothrow length and body mass. Because of the extremely tight relationship between toothrow length and width, the residuals of this relationship (which are essentially what is being added by using area, rather than length) are poorly correlated with body mass so that, within a clade, area proves to be a less effective predictor of body mass. Because tooth shapes and counts vary between the subclades included in the broader analyses, the relationship between length and width in the larger analyses is not as strong as within each individual clade, so adding width (as one does by using area) adds meaningful information and makes toothrow area a better proxy. Overall, however, either predictor provides a robust proxy for body mass.

Estimating body masses for fossil rodents.—Applying the proxy of toothrow length to a number of fossil rodents provides mass estimates for species in clades for which preexisting proxies were not applicable (the Mylagaulidae) and provides alternate estimates for species whose body mass had been reconstructed from postcranial dimensions. In most cases, the toothrow and postcranial estimators predict similar body masses in rodents. An exception occurs in the very large-bodied *P. pattersoni*, for which limb bone diameters suggest a drastically larger mass than that revealed by the dental proxy used here. Several factors may contribute to this discrepancy. First, the regression presented here may underestimate body masses of large animals. However, other body mass estimators based on dental dimensions yield results similar to the estimate of 234 kg reported here. For example, Gingerich et al. (1982) present a regression for upper cheek tooth dimensions for primates that yields an estimate of 274 kg for *Phoberomys*,

whereas Legendre's (1986) regression for m1 area of rodents yields an estimate of 219 kg, and his regression for all mammals yields an estimate of 170 kg. Legendre's regression for herbivores from all mammalian lineages yields an estimate of 323 kg. Clearly, regardless of the sample of mammals on which the regression is based, teeth indicate a body mass within the confidence interval (164–334 kg) of the estimate from toothrow length presented here.

Second, the regression for dimensions of limb bones used by Sánchez-Villagra et al. (2003) may overestimate body masses of larger mammals such as *Phoberomys*. Christiansen (2002) found that smaller mammals (<50 kg) had significantly greater positive allometry between limb dimensions and body mass than did larger mammals, an observation he explained as being due to the structural constraints of bending forces on the limb bones of large mammals. Because the regressions of the diameters of femurs and humeri on body mass on which Sánchez-Villagra et al. (2003) base their estimates were derived entirely from animals less than 50 kg in body mass (Biknevicius et al. 1993), they would be expected to substantially overestimate the body mass of an animal as large as *P. pattersoni*. Gingerich (1990) offers a regression based on the diameter of the shaft of a limb bone including animals ranging in size from shrews to elephants; his regressions suggest a mass of 1,036 kg based on the femur and of 318 kg based on the humerus, which is an even larger range of body masses than was obtained by Sánchez-Villagra et al. (2003).

Third, the persistent discrepancy between masses for *Phoberomys* estimated from dental dimensions and diameters of limb bones suggests that for 1 or more of these regressions, this taxon violates the fundamental requirement of a body mass proxy that “the fossil taxon for which a value is predicted *must* be a member of the population from which the taxa used to generate the prediction equation are a sample” (Smith 2002: 276). It seems likely that *Phoberomys* is not a member of the population of taxa used to generate these predictive equations, because the resulting estimates of mass are not concordant for the different measures (e.g., for the femur and humerus regressions), even though in many cases the taxa used to generate these regressions are the same. Sánchez-Villagra et al. (2003) conclude from this lack of agreement that *Phoberomys* probably used a different limb posture from the organisms used to generate the regression. I agree with this conclusion, but I do not agree with their subsequent statement that the larger of the estimates for body mass should be correct. Rather, neither estimate should be correct because a different locomotor habit should constrain the limbs differently and, depending on how force is applied to the limbs, could cause substantial over- or underestimation of body mass. Instead of trying to use a regression based on an admittedly nonrepresentative set of taxa, a different locomotor habit requires that the morphological consequences of associated patterns of limb use be considered before limb measurements are used to estimate mass. Better knowledge of locomotion in the fossil taxon can be used to choose a more representative sample of species from which to generate a regression to predict mass in this fossil organism. Alternatively, knowing that the locomotor habit could

confound the use of limb bone measures for estimating mass, a proxy should be chosen that is not constrained by locomotor habit.

Fourth, it is possible that dental measures underestimate the mass of *Phoberomys* because these animals consumed a diet that was drastically different from the diets of the taxa for which regressions were developed. The energetic scaling expected to constrain tooth dimensions has been found to be essentially constant across mammals (McNab 1990; West et al. 1997), and tooth dimensions are found to scale relatively consistently across wide ranges of body masses (Creighton 1980; Gingerich 1976, 1977). Without independent evidence for the dietary preferences of *Phoberomys*, it cannot be determined whether dental measures from modern mammals violate the sampling assumptions of body mass regressions. However, the dental morphology of *Phoberomys* is similar to that of other large caviomorphs, suggesting similar diets that would not violate this assumption.

Comparisons between estimates of body mass derived from different subsets of mammals provide some insight into the source of the disagreement between estimates of body mass for *Phoberomys*. Dental estimates are most concordant when they are derived from rodents or primates, both of which are predominantly small-bodied clades, with a few species or subclades evolving larger body masses (see Ernest [2003] for body masses of rodent and primate species). Rodents and primates also are predominantly omnivores, with diets consisting primarily of plant matter and insects. Recent phylogenetic studies suggest that primates and rodents may be relatively closely related orders of mammals (Springer et al. 2004), being members of the clade Euarchontaglres. In contrast, estimates using less closely related taxa (e.g., Legendre's [1986] analyses of "all mammals" or "all herbivores") yield wider-ranging estimates for body mass. There is no reason to prefer a regression from all mammals but, depending on whether phylogenetic effects or biomechanical constraints due to diet are more important in shaping this relationship, one of these estimates may prove to be more accurate. Certainly this study shows that, within rodents, phylogenetic effects can be important, as does Gingerich and Smith's (1984) study for primates. Hence, for *Phoberomys*, the best estimate of body mass from dental proxies is derived from regressions on cheek tooth dimensions using rodents or primates, which yield estimates ranging from 200 to 300 kg for this taxon.

Estimates of body mass from limb bone proxies are a bit more difficult to interpret. The range of these estimated values of body mass is huge, but data from humeri suggest a body mass slightly larger than that estimated from dental proxies (300–450 kg), whereas data from femora yield estimates (700–>1,000 kg) that suggest a "rodent as big as a buffalo" (Alexander 2003). This difference suggests that the femur is structured to bear more mass than the humerus and that this difference in weight distribution is more dramatic when all mammals (including a number of large extant mammals) rather than just modern rodents, are considered. Christiansen's (2002) finding of more positive limb allometry at greater than 50 kg is not sufficient to explain this finding, because the mass

estimates should decrease when a regression including animals larger than 50 kg is used; this is true for estimates using the humerus, but not for estimates based on femoral diameter. The greater disagreement between humeral and femoral estimates for larger mammals suggests that the parameter causing these estimates to diverge is more significant when an all-mammals estimate, rather than a caviomorph-specific estimate, is used to estimate body mass. If one considers that a hind-limb-dominated locomotor stance is more common among rodents than among mammals as a whole, the possibility that limb-based estimates of mass are confounded by unusual locomotion in *Phoberomys* becomes more plausible. Given that both sample populations yield discrepant humeral and femoral estimates of body mass, it is possible that each of these estimates is flawed. As a result, a better understanding of the posture of *Phoberomys* and of how limb bones would be stressed by this stance would be necessary to select an appropriate proxy. Thus, although limb bone proxies have been suggested to be preferable to dental ones because of the simple relationship between body mass and the amount of weight borne by the limbs, *Phoberomys* may provide a case where dental proxies are more trustworthy. The dental proxies developed here avoid the question of stance and locomotion while also accommodating the modified dentitions of some rodent taxa.

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APPENDIX I

Tooththrow measurements of specimens used in this study. For each species, published masses (pub mass) from Ernest (2003) are listed, followed by a list of specimens with the Museum of Vertebrate Zoology specimen number, mass in grams, lower tooththrow length in millimeters, and maximum tooththrow width in millimeters for each specimen.

Aplodontidae

Aplodontia rufa: pub mass = 687 g; 172402, 1,465, 17.53, 4.13; 22624, 1,375, 18.23, 3.83; 22626, 1,350, 17.87, 3.84; 22627, 1,048.2, 17.51, 3.61; 116278, 1,069, 17.62, 3.35; 96062, 832, 17.12, 4.01; 114341, 926, 16.40, 3.99; 96058, 760.7, 17.24, 3.82; 96063, 820.9, 16.30, 3.68; 115540, 741, 16.81, 3.76; 116294, 817, 17.72, 3.78; 114342, 685, 17.36, 3.82; 94639, 1,477, 18.30, 4.00; 94666, 744.3, 16.52, 3.85; 22618, 1,270, 17.31, 3.73.

Bathyergidae

Cryptomys hottentotus: pub mass = 132.5 g; 117785, —, 6.09, 1.88; 117787, —, 6.24, 1.74; 117788, —, 6.15, 1.70; 117803, —, 5.77, 2.01; 117804, —, 6.16, 2.10.

Castoridae

Castor canadensis: pub mass = 19,606.67 g; 33595, 14,000, 31.38, 7.44; 33608, 13,000, 33.52, 8.11; 33607, 22,700, 35.36, 8.69; 95370, 15,200, 30.23, 7.39; 33598, 15,400, 33.13, 7.44.

Dipodidae

Zapus princeps: pub mass = 28.75 g; 22582, 20, 3.99, 1.06; 22583, 19.5, 3.91, 1.00; 22584, 24.5, 4.04, 1.09; 22585, 19.5, 3.65, 0.95; 22586, 23, 3.99, 1.02.

Geomyoidea

Dipodomys merriami: pub mass = 40 g; 111638, 38.9, 4.26, 1.64; 111639, 43.6, 4.82, 1.77; 111640, 41.4, 4.34, 1.68; 111650, 32.9, 4.66, 1.67; 111651, 38, 4.26, 1.70. *Geomys arenarius*: pub mass = 210 g; 50449, 190.2, 7.39, 2.22; 50450, 132.3, 6.43, 1.95; 50451, 133, 6.69, 2.07; 50452, 175, 7.43, 2.05; 50453, 160, 7.40, 2.07. *Liomys pictus*: pub mass = 50 g; 100186, 30.3, 4.50, 1.49; 100187, 24.2, 4.51, 1.47; 100188, 37.3, 4.53, 1.53; 100190, 29.4, 4.45, 1.63; 100191, 46.5, 4.72, 1.56. *Microdipodops megacephalus*: pub mass = 13.45 g; 70859, 16.1, 3.18, 1.11; 70860, 14.8, 2.97, 1.04; 70861, 13.3, 3.05, 1.11; 70862, 14.8, 3.26, 1.06; 70863, 14, 3.14, 1.15. *Perognathus inornatus*: pub mass = 8.65 g; 47385, 16, 2.86, 1.00; 47390, 10.9, 2.85, 0.99; 47391, 12.2, 3.06, 0.96; 47392, 10, 2.93, 0.97; 47393, 10.6, 3.03, 1.08. *Thomomys bottae*: pub mass = 103.5 g; 70012, 107.5, 8.08, 2.14; 70013, 106.5, 8.41, 2.07; 70014, 137.7, 7.62, 1.99; 70015, 139.7, 7.77, 2.09; 70016, 134.2, 7.98, 1.90; 163090, 147, 8.80, 2.06; 163093, 171, 9.29, 2.29; 163151, 116, 9.19, 2.26; 163152, 155, 8.74, 2.10; 163153, 120, 9.19, 2.12; 150675, 94, 8.15, 2.19; 150744, 96, 7.59, 1.99; 150719, 97, 7.92, 2.02; 147037, 82, 8.37, 2.04; 147038, 126, 9.13, 2.18. *Thomomys monticola*: pub mass = 80 g; 33776, 77.3, 6.93, 1.89; 33777, 97.6, 8.37, 2.31; 33778, 103.8, 7.43, 2.15; 33779, 88, 7.44, 2.08; 33780, 75.1, 7.21, 2.41.

Hystricomorpha

Ctenomys maulinus: no pub mass available; 154132, 254, 9.91, 2.34; 154133, 230, 12.04, 2.72; 154134, 190, 11.19, 2.67; 183310, 210, 10.84, 2.81; 183305, 158, 9.44, 2.38. *Cuniculus paca*: pub mass = 9,000 g; 116710, 8,200, 29.67, 6.95; 98880, 9,100, 30.53, 6.58; 157850, —, 30.33, 6.65; 155204, —, 32.81, 7.63; 157848, —, 30.93, 7.46. *Erethizon dorsatum*: pub mass = 9,000 g; 40874, 4,500, 29.13, 5.75; 46597, 7,264, 28.83, 6.22; 107329, 6,300, 31.28, 6.66; 58496, 6,800, 31.53, 6.44; 105680, 10,000, 31.52, 6.52. *Galea musteloides*: pub mass = 337.85 g; 114762, 360, 12.21, 2.40; 139603, 360, 12.79, 2.49; 139604, 370, 12.69, 2.70; 116708, 340, 13.49, 2.64; 166069, 275, 11.98, 2.31. *Hydrochoerus hydrochaeris*: pub mass = 55,000 g; 116818, —, 62.99, 8.44; 157846, —, 78.14, 9.77; 120922, —, 80.13, 10.29; 116819, —, 62.47, 7.85; 4836, —, 77.77, 10.29. *Lagidium peruanum*: pub mass = 1,270 g; 114772, 1,600, 17.93, 4.20; 114769, 1,100, 16.50, 3.92; 108919, 1,360, 16.98, 4.36; 108921, 1,450, 17.02, 4.30; 108922, 1,220, 17.58, 4.11. *Mesomys hispidus*: no pub mass available; 190648, 222, 8.01, 2.13; 190649, 151, 8.07, 1.76; 190650, 142, 7.75, 1.75; 190651, 193, 7.36, 1.79; 190647, 128, 7.89, 1.92; 190640, 134, 8.10, 2.02; 190644, 200, 7.88, 1.92; 190645, 196, 7.80, 2.03; 190636, 142, 7.76, 1.93; 190638, 148, 7.76, 1.91; 190643, 130, 7.68, 1.76; 190631, 110, 7.72, 1.73; 190632, 172, 7.66, 1.74; 190635, 167, 7.70, 1.81; 155158, 127, 7.82, 1.90. *Octodon degus*: pub mass = 235 g; 118664, 223, 9.19, 1.84; 150072, 272, 10.18, 1.93; 150073, 252, 10.24, 1.98; 150076, 223, 9.92, 1.95; 150077, 136, 8.40, 1.69. *Proechimys breviceauda*: no pub mass available; 190670, 345, 9.24, 2.44; 190671, 217, 8.55, 1.93; 190672, 177, 9.02, 1.80; 190673, 184, 9.52, 2.08; 190674, 226, 8.73, 1.96. *Thrichomys apereoides*: pub mass = 373.5 g; 197572, 315, 10.90, 2.43; 197616, 345, 10.45, 2.28; 145324, 294, 10.78, 2.42; 145325, 396, 10.28, 2.38; 145326, 392, 10.62, 2.33.

Muroidea

Arvicolinae.—*Arborimus pomo*: pub mass = 36 g; 99621, 24.5, 5.85, 1.31; 99622, 24.2, 5.97, 1.33; 99623, 22.3, 5.56, 1.14; 99624, 26.3, 5.48, 1.20; 120595, 38.3, 6.20, 1.49. *Myodes* (formerly *Clethrionomys*) *gapperi*: pub mass = 20.57 g; 30723, 18.6, 4.94, 0.92; 30724, 20.6, 5.06, 1.09; 30725, 20, 5.13, 1.03; 30726, 38.6, 5.22, 1.04; 30727, 22.5, 4.93, 0.95. *Myodes* (formerly *Clethrionomys*)

rutilus: pub mass = 25 g; 188639, 20.8, 5.23, 1.05; 188639, 31, 5.48, 1.13; 188639, 43.3, 5.75, 1.14; 188639, 19, 5.25, 1.10; 188639, 20.9, 5.31, 1.02. *Dicrostonyx groenlandicus*: pub mass = 55.05 g; 134428, 50.7, 7.38, 1.41; 134429, 37.3, 6.68, 1.22; 119854, 70.1, 6.51, 1.27; 119855, 86.5, 6.66, 1.25; 119856, 81, 7.48, 1.37. *Lemmys* (formerly *Lagurus*) *curtatus*: no pub mass available; 121207, 20.7, 5.48, 1.01; 121208, 20.4, 5.39, 1.01; 121238, 29.5, 5.46, 1.00; 121239, 30.1, 5.58, 0.98; 121240, 24, 5.59, 1.09. *Lemmus lemmus*: pub mass = 51.67 g; 123571, 101, 7.65, 1.62; 123572, 76, 7.59, 1.60; 173590, 66, 8.40, 1.50; 173591, 39, 7.17, 1.42; 173592, 39, 7.04, 1.49. *Microtus agrestis*: pub mass = 46 g; 179819, 60.5, 6.11, 1.15; 179820, 24.7, 5.66, 1.11; 179821, 27.8, 5.73, 1.07; 179822, 37.5, 5.68, 1.13; 179823, 49.5, 6.01, 1.14. *Microtus californicus*: pub mass = 53.5 g; 206895, 65, 6.60, 1.40; 206896, 63, 6.63, 1.25; 206897, 62, 6.46, 1.15; 136660, 53.8, 6.93, 1.38; 136661, 69.5, 6.28, 1.25. *Myopus schisticolor*: pub mass = 25 g; 173677, 32, 6.57, 1.44; 173678, 24, 6.76, 1.43; 173679, 24, 6.28, 1.26; 173680, 29, 6.50, 1.24; 173681, 22, 6.54, 1.25. *Ondatra zibethicus*: pub mass = 1,135.8 g; 61870, 726, 15.01, 2.93; 61871, 601, 13.68, 2.91; 61872, 648.7, 14.29, 3.00; 61873, 723.5, 14.43, 2.81; 61874, 777.3, 14.48, 2.94. *Phenacomys intermedius*: pub mass = 33 g; 107103, 33.6, 5.99, 1.29; 107104, 37.3, 6.48, 1.17; 107105, 43.4, 6.12, 1.28; 107106, 34, 6.03, 1.13; 107108, 28.1, 5.57, 1.23.

Gerbillinae.—*Gerbillus robustus* (formerly *Tatera robusta*): pub mass = 93 g; 149443, 127, 7.09, 2.02; 186205, 98, 6.21, 2.09; 186206, 80, 6.04, 1.98; 186207, 108, 6.50, 2.08; 186208, 104, 6.13, 2.10.

Murinae.—*Aethomys hindei*: pub mass = 107 g; 186239, 98, 6.13, 1.75; 186240, 86, 6.48, 2.00; 186241, 133, 6.26, 1.83; 186242, 104, 6.33, 1.84; 186244, 71, 6.26, 1.79. *Apodemus semotus*: no pub mass available; 174856, 27.5, 4.27, 1.13; 174860, 19, 4.09, 1.29; 174864, 28.5, 4.35, 1.18; 174868, 30, 4.36, 1.29; 174869, 30, 4.51, 1.19. *Arvicanthis abyssinicus*: no pub mass available; 186250, 94, 6.28, 1.73; 186251, 74, 6.13, 1.71; 186252, 98, 6.26, 1.79; 186253, 82, 6.37, 1.80; 186254, 63, 6.15, 1.83. *Berylmys bowersi*: no pub mass available; 186482, 427, 8.72, 2.32; 186483, 508, 9.48, 2.69; 186484, 420, 8.86, 2.47; 186485, 365, 9.22, 2.47; 186486, 412, 9.27, 2.51. *Leopoldamys edwardsi*: no pub mass available; 186496, 368, 9.44, 2.55; 186497, 435, 9.77, 2.55; 186498, 361, 10.18, 2.65; 186499, 353, 9.35, 2.44; 186501, 443, 9.69, 2.63. *Mastomys natalensis*: pub mass = 44.97 g; 149451, 56, 4.56, 1.31; 149450, 96, 4.13, 1.21; 149452, 44, 4.46, 1.27; 149455, 60, 4.31, 1.15; 149454, 76, 4.62, 1.24. *Maxomys surifer*: no pub mass available; 155534, 115, 5.75, 1.61; 155535, 128, 6.36, 1.51; 155536, 102, 5.64, 1.49; 155538, 80, 5.76, 1.50; 155539, 85, 5.84, 1.48. *Melomys cervinipes*: pub mass = 94 g; 134084, 39.1, 6.81, 1.70; 134069, 54.9, 6.50, 1.74; 126567, 96, 6.50, 1.77; 134085, 44.5, 6.40, 1.71; 134088, 65.5, 6.80, 1.88. *Mus musculus*: pub mass = 20.5 g; 135339, 22, 3.31, 0.92; 154624, 14, 2.94, 0.90; 166075, 18.5, 2.80, 0.84; 166070, 26, 3.18, 1.06; 166072, 14, 2.88, 0.84. *Rattus fuscipes*: no pub mass available; 125120, 183.5, 6.94, 1.83; 125121, 270.5, 7.27, 1.82; 125122, 122.5, 6.75, 1.82; 125123, 149.2, 6.81, 1.74; 125124, 231.5, 6.76, 1.83. *Rattus rattus*: pub mass = 246.5 g; 148410, 94, 6.30, 1.74; 148411, 94, 5.98, 1.67; 148414, 92, 5.84, 1.59; 148415, 117, 5.92, 1.67; 148416, 128, 6.73, 1.84.

Neotominae.—*Neotoma cinerea*: pub mass = 335.5 g; 26340, 250, 9.11, 1.79; 26341, 175.3, 9.39, 1.92; 26342, 180, 9.08, 1.98; 26343, 181.2, 9.29, 1.93; 26346, 248.8, 9.39, 2.10. *Neotoma fuscipes*: pub mass = 233.58 g; 196368, 324, 9.20, 2.05; 196369, 239, 9.53, 2.18; 196370, 250, 9.62, 2.00; 196371, 221, 9.68, 2.04; 196372, 312, 9.61, 1.93. *Neotoma lepida*: pub mass = 125.33 g; 61850, 117.4, 8.08, 1.62; 61851, 120.7, 7.92, 1.66; 61852, 165.5, 7.94, 1.67; 61853, 127.7, 8.01, 1.74; 61854, 132.2, 7.45, 1.71. *Peromyscus boylii*: pub mass =

28.7 g; 88207, 27.5, 4.18, 1.09; 88208, 24.1, 4.08, 1.14; 88209, 23.3, 4.30, 1.09; 88210, 29.1, 3.89, 1.09; 88211, 25.4, 4.44, 1.12. *Peromyscus maniculatus*: pub mass = 20.5 g; 56315, 25.9, 3.95, 0.98; 56316, 31.6, 3.64, 0.95; 56317, 29, 3.60, 0.92; 33407, 19.2, 3.73, 0.97; 50762, 24.2, 3.57, 0.86; 50763, 25, 3.81, 1.00; 56313, 16.9, 3.77, 0.91; 33155, 13.3, 3.62, 0.97; 33405, 14.1, 3.92, 0.97; 33406, 16, 3.72, 0.93; 36327, 17.6, 3.45, 0.97; 36328, 15.7, 3.56, 0.88; 36329, 14.5, 3.48, 0.91; 36330, 16.7, 3.60, 0.94; 36331, 15.3, 3.53, 0.89. *Peromyscus truei*: pub mass = 27 g; 124549, 27.8, 4.22, 1.02; 124550, 22.1, 4.13, 0.99; 124551, 24.1, 4.05, 1.05; 124553, 19.8, 4.19, 1.05; 124554, 21.4, 3.96, 1.05. *Reithrodontomys fulvescens*: pub mass = 12.5 g; 75902, 14.7, 3.31, 0.83; 75906, 11.6, 3.29, 0.82; 75904, 9.5, 3.06, 0.77; 75905, 9, 3.29, 0.85; 85777, 11.5, 3.28, 0.84. *Reithrodontomys megalotis*: pub mass = 11.03 g; 148135, 8, 2.94, 0.84; 148136, 10, 2.92, 0.78; 148137, 7, 2.99, 0.80; 148134, 11, 2.83, 0.86; 148521, 10, 2.92, 0.82. *Uromys caudimaculatus*: pub mass = 625 g; 175371, 585, 12.37, 3.30; 175372, 708, 12.68, 3.34; 134112, 670, 12.06, 3.12; 126570, 527, 11.95, 3.15; 140440, 543, 12.44, 3.42.

Sigmodontinae.—*Akodon subfuscus*: no pub mass available; 174236, 19, 4.09, 0.98; 174237, 19, 4.07, 1.08; 174238, 17, 3.90, 0.97; 136252, 18, 4.14, 0.93; 115653, 21, 4.18, 1.05. *Graomys griseoflavus*: pub mass = 66 g; 145246, 50, 5.79, 1.48; 145247, 57, 5.26, 1.49; 145248, 54, 5.41, 1.55; 145249, 59, 4.99, 1.32; 145250, 52, 5.35, 1.52. *Nectomys apicalis*: no pub mass available; 153538, 209, 7.69, 2.06; 153539, 266, 7.57, 1.99; 153549, 392, 7.69, 2.13; 153550, 237, 7.35, 2.00; 153555, 273, 7.19, 2.13. *Nesoryzomys indefessus*: no pub mass available; 133122, 129, 5.34, 1.44; 133123, 110, 5.49, 1.43; 133125, 83, 5.50, 1.47; 133126, 110, 5.25, 1.40; 133127, 104, 5.51, 1.44. *Oecomys bicolor*: no pub mass available; 197497, 33, 4.22, 1.11; 197498, 41, 4.17, 1.16; 197499, 29, 4.41, 1.10; 197500, 40, 4.43, 1.13; 197501, 35, 4.25, 1.11. *Oligoryzomys andinus*: no pub mass available; 135649, 19, 3.78, 0.98; 135651, 17, 3.62, 0.96; 135652, 14, 3.46, 0.93; 135653, 18, 3.70, 0.94; 135653, 27, 3.64, 1.01. *Oryzomys keaysi*: no pub mass available; 171445, 64, 5.75, 1.56; 171446, 59, 6.00, 1.62; 171447, 62, 6.29, 1.66; 171448, 65, 6.21, 1.57; 171450, 64, 5.98, 1.52. *Sigmodon hispidus*: pub mass = 185 g; 92292, 137, 6.51, 1.59; 92294, 85.7, 6.28, 1.61; 92296, 112, 7.01, 1.71; 92297, 66.6, 6.17, 1.60; 92299, 86.5, 6.74, 1.74. *Thomasomys aureus*: no pub mass available; 171498, 81, 7.58, 2.07; 171499, 107, 7.29, 1.92; 114635, 78, 7.30, 1.84; 116071, 101, 6.98, 1.82; 116647, 132, 7.25, 1.90. *Zygodontomys brevicauda*: no pub

mass available; 114241, 45, 4.17, 1.15; 114244, 38.5, 4.05, 1.12; 113381, 27.8, 4.18, 1.15; 113383, 37.4, 4.14, 1.08; 113951, 42, 4.06, 1.08.

Rhizomyinae.—*Rhizomys pruinosus*: pub mass = 2,450 g; 186548, 930, 13.40, 4.33; 186543, 1,068, 15.54, 4.81; 186552, 585, 13.69, 4.73; 186544, 998, 15.06, 4.65; 186547, 721, 14.37, 5.04.

Gliridae

Graphiurus murinus: pub mass = 24 g; 117760, —, 3.20, 1.20; 124257, —, 3.14, 0.94; 117757, —, 3.27, 1.19; 117758, —, 3.24, 1.20; 117759, —, 3.25, 1.18.

Sciuridae

Ammospermophilus leucurus: pub mass = 97.5 g; 86149, 105, 6.47, 1.87; 86150, 104.1, 6.45, 2.01; 86151, 103.7, 5.99, 1.75; 86152, 126.5, 6.13, 2.02; 86153, 110, 6.49, 2.02. *Cynomys mexicanus*: pub mass = 828.1 g; 91176, 766, 14.15, 4.35; 91179, 768, 13.76, 4.28; 91180, 726, 13.26, 4.45; 91181, 866, 13.76, 4.60; 91182, 1017, 13.49, 4.16. *Glaucomys sabrinus*: pub mass = 132.17 g; 37480, 141.5, 8.28, 2.05; 37481, 151, 8.00, 2.10; 21861, 128.3, 8.14, 2.04; 22889, 128, 8.10, 2.14; 22897, 103.5, 7.91, 2.13. *Marmota flaviventris*: pub mass = 2,930 g; 149691, 3,050, 18.57, 4.98; 98957, 2,426.7, 18.52, 5.24; 98956, 1,933.2, 18.67, 4.65; 25183, 3,000, 18.11, 4.68; 105363, 1,495, 17.33, 4.75. *Sciurus aberti*: pub mass = 702.5 g; 74855, 619.5, 10.88, 2.93; 74856, 639, 10.95, 3.05; 74857, 674, 10.94, 2.95; 74858, 714.5, 11.01, 2.99; 121758, 569.2, 10.98, 2.93. *Sciurus aureogaster*: pub mass = 595 g; 106062, 475, 10.27, 2.94; 109386, 601.5, 10.46, 3.05; 106067, 548, 11.20, 3.26; 106074, 570, 9.75, 3.01; 106073, 590, 10.59, 3.35. *Spermophilus beecheyi*: pub mass = 609.33 g; 27872, 644.8, 10.97, 3.03; 27873, 774, 11.01, 3.42; 27929, 641.1, 11.36, 3.49; 27930, 584.6, 11.05, 3.13; 28024, 517.2, 11.45, 3.09. *Spermophilus lateralis*: pub mass = 157.6 g; 109266, 186.3, 7.77, 2.38; 109267, 133.4, 7.74, 2.25; 109268, 162.6, 7.72, 2.36; 109269, 75.5, 7.86, 2.14; 109270, 143.7, 7.81, 2.46. *Tamias speciosus*: pub mass = 60 g; 152332, 59, 5.41, 1.47; 152337, 84, 5.31, 1.59; 165877, 70, 5.33, 1.60; 34782, 59, 5.30, 1.57; 34780, 60.6, 5.49, 1.53. *Tamiasciurus hudsonicus*: pub mass = 194.5 g; 134488, 230, 7.87, 2.24; 134491, 214.3, 7.70, 2.21; 93370, 220, 7.92, 2.19; 93371, 263.9, 8.29, 2.39; 93372, 236.1, 8.10, 2.38; 116492, 260, 7.94, 2.41; 46989, 259, 7.93, 2.47; 46991, 267, 7.94, 2.49; 49983, 243, 8.60, 2.59; 33243, 238.5, 8.50, 2.41; 53600, 238.9, 8.04, 2.25; 53601, 255.5, 7.44, 2.06; 53602, 226.45, 7.69, 2.15; 53603, 204.28, 7.87, 2.31; 53604, 242.08, 8.41, 2.35.