

When teeth and bones disagree: body mass estimation of a giant extinct rodent

VIRGINIE MILLIEN* AND HELENE BOVY

Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec H3A 2K6, Canada

* Correspondent: virginie.millien@mcgill.ca

Body size is correlated with virtually every morphological, physiological, and life-history trait in mammal species. As a consequence, estimates of body size of fossil species are often used for paleoecological reconstructions. Characters used as proxies for body mass in extinct species include teeth, skull, and skeletal measurements. We show that the body-mass estimates of extinct species from living taxa can be misleading and depend largely on the morphological variable selected as a proxy for body mass. We also discuss statistical tools that are available to assess the accuracy of body-mass estimates in extinct species. Here, we focus on the revision of the mass estimate of the giant Miocene fossil rodent *Phoberomys pattersoni* (Venezuela), the 2nd largest rodent ever reported, with an estimated body mass between 436 and 741 kg. This is far beyond the range of average body masses in living rodents, which vary from several grams to 40 kg. We conclude that body mass of *Phoberomys* was most likely overestimated. The species *P. pattersoni* likely weighed between 220 kg and 280 kg, the mass of a horse or a large antelope. DOI: 10.1644/08-MAMM-A-347R1.1.

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Body size is probably the single most obvious and important character of an organism. Most physiological and life-history traits scale with size, including life span, metabolic rate, fasting endurance, rate of development, fecundity, interspecific relations, and numerous other morphological, physiological, behavioral, and ecological factors (Calder 1984; Peters 1983; Schmidt-Nielsen 1984).

For these reasons a long-standing tradition has persisted among vertebrate paleontologists of estimating body mass in fossil mammal species (Damuth and MacFadden 1990). Body size in fossil species is, in principle, relatively easy to characterize, and this has led to comparisons across a wide range of taxa (Alroy 1998; Damuth and MacFadden 1990). Compared to bones or other tissues, teeth are favored material for paleontologists because they are typically well preserved. For instance, body mass of many fossil mammals has been estimated from the length or the surface of the 1st lower molar (Conroy 1987; Creighton 1980; Gingerich et al. 1982; Legendre 1989; Martin 1990). Other dimensions of the upper and lower 2nd molars (Schwartz et al. 1995) and upper and lower incisors (Millien-Parra 2000; Parra and Jaeger 1998) also have been used to estimate body size in fossil rodents. Because they are related to locomotion and body support, measurements of postcranial elements such as the length of the humerus (Gingerich 1990), the diameter of long bones (Biknevicius et al. 1993), diameters of metapodials (Alberdi

et al. 1995), or the area of the astragalus (Martinez and Sudre 1995) are also strongly related to body mass in mammals and are used as a proxy for body mass in extinct species.

Rodents represent nearly one-half of all mammalian species (Wilson and Reeder 2005). Since their origin, rodents have dominated communities of mammalian herbivores in both number of species and biomass. This diversity, both taxonomic and ecological, means that rodent species are found in a wide range of environments (Landry 1970), which makes this group an excellent system for both paleontological and ecological studies.

Body mass in extant rodent species covers more than 4 orders of magnitude, from as little as 3.7 g on average in the African pygmy mouse (*Mus minutoides*) to 40 kg on average in the largest rodent, the South American capybara (*Hydrochoeris hydrochaeris*—Silva and Downing 1995). Some individuals of *H. hydrochaeris* can weigh as much as 81 kg in the wild (Ferraz et al. 2005), but the largest rodent species ever described are now extinct. Gigantism has been documented in numerous island rodents (review in Millien et al. 2006). For instance, the large extinct rodent genus *Amblyrhiza* was described from Quaternary deposits in the West Indies



(Cope 1883). Cope (1883) estimated the largest *Amblyrhiza* to be “larger than a male Virginian deer.” This was confirmed by Biknevicius et al. (1993), who proposed an estimated body mass for *A. inundata* of 50 to >200 kg. Extremely large forms of fossil rodents also are known from the Pleistocene of North America and the Pliocene of South America. Giant beavers of the Quaternary of North America represent a classic example of gigantism. Although the 2 living species, *Castor canadensis* and *C. fiber*, weigh on average between 9 and 42 kg (Silva and Downing 1995), the body mass of their extinct relative *Castoroides ohioensis* was estimated between 46 and 202 kg (Reynolds 2002).

The largest estimated body masses for fossil rodents were assigned to the South American rodents *Phoberomys pattersoni* (Sanchez-Villagra et al. 2003) and *Josephoartigasia monesi* (Rinderknecht and Blanco 2008). A genus in the family Neopiblemidae, *Phoberomys* (Bondesio and Bocquentin Villanueva 1988) encompasses 7 South American species (Horovitz et al. 2006; Negri and Ferigolo 1999), of which *P. pattersoni* is the 2nd largest. A nearly complete skeleton of *P. pattersoni* was found in the Urumaco formation in northwestern Venezuela (Horovitz et al. 2006; Mones 1980), and its body mass was estimated at >700 kg based on femur diameter (Sanchez-Villagra et al. 2003). Most recently, however, 2 studies based on tooth size revised body-mass estimates of *P. pattersoni* (Hopkins 2008) down to 200–300 kg and that of *J. monesi* (Millien 2008) to as low as 350 kg, lower than the estimate of 1,000 kg proposed by Rinderknecht and Blanco (2008). These conflicting results highlight the controversy associated with estimating body mass of fossil species that have no Recent equivalent and estimates that depend on the methods that are used. For this study we used many different measurements of the fossil giant rodent *Phoberomys* and assessed the level of confidence in the body-mass estimates derived from each one.

The most commonly used method of estimating body mass in extinct species begins by calculating the allometric relation between a given skeletal character and body mass in a number of extant species. This relation is then applied to extinct species to estimate body mass. This procedure is very straightforward but requires a number of assumptions and therefore has limitations (Damuth and MacFadden 1990; Egi 2001; Reynolds 2002; Schmidt-Nielsen 1984; Smith 1980, 1996). These limitations derive from the reference data set, the choice of the skeletal character, and the statistical analysis and presentation of the data (Reynolds 2002).

When estimating body mass in extinct taxa, researchers often assume that the relation between a skeletal character and body mass is the same for recent and extinct species (i.e., the allometric coefficient is constant). Because this is impossible to validate empirically, the choice of the reference data set used to reconstruct body mass in extinct species is critical. First, some researchers suggest that the taxa chosen to calculate the allometric relation should be close relatives of the extinct species, but others argue that a wider taxonomic sample offsets other potential bias (Schwartz et al. 1995).

Second, because one is looking for the allometric relation at the level of the order (or maybe family), the data set should be composed only of interspecific data and the intraspecific variability is of no interest for estimating body mass in extinct species. Third, allometric relations should be applied to extinct species that fall within the range of size and body proportions observed in the reference data set (Damuth and MacFadden 1990; Reynolds 2002; Schmidt-Nielsen 1984). Last, as in any statistical procedure, sample size should be large enough to allow as much confidence in the results as possible.

A 2nd set of assumptions centers on the choice of the skeletal character used to estimate body mass. Limb bones are widely accepted as a good indicator of body mass because of their role in skeletal support (Damuth and MacFadden 1990; Egi 2001). However, dental and other cranial features also provide accurate estimations of body mass (e.g., Damuth and MacFadden 1990). Because of different functional constraints on teeth and the appendicular skeleton, body-mass estimation from tooth measurements (i.e., feeding attributes) can lead to values consistently different from those estimated from long-bone measurements (i.e., locomotor attributes).

To assess the validity of the regression equation, some crucial descriptive statistics, such as the standard error of the estimate and prediction errors, are often overlooked (Smith 1980, 1996). These statistics provide an indication of the accuracy of the body-mass estimate and should always accompany it. We examine the limitations described above of the allometric method for estimating body mass in extinct species and focus on the revision of the mass estimate of the giant Miocene fossil rodent *P. pattersoni* from Venezuela.

MATERIALS AND METHODS

Data set.—Data were collected for 36 species belonging to 32 genera and 18 families of rodents (Appendix I). A sizeable majority (28 species) of the species were hystricomorph rodents, the suborder of Rodentia to which *P. pattersoni* also belongs. Because *P. pattersoni* is one of the largest rodents ever described, we also included representatives of large species of myomorph, castorimorph, and sciurimorph rodents. Taxonomy followed Wilson and Reeder (2005). Body-mass data were obtained from specimen tags and from average values published in the literature (Silva and Downing 1995). The data set covered a large range of average body masses, from 124 g in the Val's gundi (*Ctenodactylus vali*), to 40 kg in the capybara (*H. hydrochaeris*). Measurements for the extinct giant rodent *P. pattersoni* and other *Phoberomys* species were obtained from the literature (Horovitz et al. 2006; Sanchez-Villagra et al. 2003) and by us from undescribed material from Universidad Nacional Experimental Francisco de Miranda Venezuela (UNEFM).

Measurements.—Eleven measurements were taken from the skull, teeth, and appendicular skeleton of each specimen: the condylobasal length of the skull, the length of the upper cheek toothrow, the anteroposterior diameter of the lower and upper incisors, the transverse diameter of the lower and upper

incisors, the maximum length and width of the 1st lower molar, the length of the humerus and femur, the anteroposterior diameter at 65% from the distal articular surface of the femur, and the anteroposterior diameter at 35% from the distal articular surface of the humerus. Incisor measurements were defined in Millien-Parra (2000), and long-bone measurements were as in Biknevicius et al. (1993). We used the mean value in the analyses when several specimens were available from a single species. Only adult specimens for which we could record both dental and skeletal measurements were considered. Measurements were taken with Mitutoyo digital calipers (Mitutoyo Corporation, Kanogawa, Japan) to the nearest 0.02 mm.

Statistical analyses.—All measurements were log transformed before further analyses. The log-transformed values were tested for normality by 1-sample Kolmogorov–Smirnov tests (Zar 1999). Pairwise relationships between body mass and skeletal or dental measurements were fitted to an allometric model that is expressed by a power function: $Y = aX^b$, where a is a constant, b the allometric coefficient, Y is the dependent variable (body mass, in g), and X is the independent variable (dental or long-bone measurements, in mm). The log transformation of this function results in a linear relationship, $\log Y = \log a + b \log X$, which was fitted to the data by a least-squares criterion (Smith 1984). Three additional parameters were computed: the coefficient of determination (r^2); the standard error of the estimate (SEE), which provides a comparative index of the accuracy of the different models computed (Smith 1984); and the average absolute value of individual percent prediction errors (%PE). Individual percent prediction errors were calculated as $\%pe = [(true\ mass - estimated\ mass)/estimated\ mass] \times 100$ after the data had been converted back to linear scale (Smith 1980). A stepwise multiple regression model (backward, automatic, P to enter = 0.15, P to remove = 0.15) was then applied to the data. All statistical analyses were performed using SYSTAT software (SYSTAT Software Inc. 2004).

Skeletal analysis.—Because *Phoberomys* specimens fall far outside the range of sizes known in Recent rodents, we investigated whether extant rodents can be used as a reference sample to estimate body mass in the extinct taxon. Our approach was to compare bone and teeth proportions in living species and to assess whether these proportions are conserved in the giant fossil species. Bivariate plots were used to compare bone and teeth proportions in living species with those observed in *Phoberomys*. These visual examinations of the data helped us to detect the models that, although statistically significant, may not be the most appropriate to estimate body mass in *Phoberomys*. We also assessed the relevance of the allometric models by calculating ratios between various measurements of the fossil taxon and comparing them to values obtained from reference specimens of Recent species.

RESULTS

Models calculation.—A Kolmogorov–Smirnov statistic adjusted for multiple tests showed that all variables were normally

TABLE 1.—Parameters of the equations used to estimate body mass (g) in *Phoberomys*. Skull: condylobasal length of the skull; UTRL: upper tooththrow length; Lower AP and Upper AP: lower and upper incisor anteroposterior diameters (mm); Lower T and Upper T: lower and upper incisor transverse diameters (mm); m1 length and m1 width: 1st lower molar maximum length and width (mm); n : sample size; r^2 : coefficient of determination; SEE : standard error of the estimate; %PE: average absolute percent prediction error. $n = 35$.

Character (all in mm)	Slope	Intercept	r^2	SEE	%PE
Skull	3.488	−3.332	0.94	0.157	30.65
UTRL	2.698	−0.038	0.89	0.215	43.36
Upper AP	3.237	1.315	0.82	0.274	57.17
Upper T ^a	2.445	2.080	0.83	0.262	54.98
m1 length ^b	2.902	1.434	0.89	0.218	44.62
m1 width	3.177	1.351	0.87	0.226	45.76
Lower AP	2.926	1.601	0.82	0.273	46.03
Lower T ^a	2.274	2.257	0.82	0.269	56.74
Femur length	2.825	−1.964	0.86	0.240	48.59
Femur diameter	2.635	0.903	0.84	0.257	47.45
Humerus length	2.827	−1.678	0.85	0.249	50.06
Humerus diameter	2.526	1.457	0.88	0.217	39.42

^a *Cryptomys ochraceocinereus* removed from the data set, $n = 34$.

^b *Ondatra zibethicus* removed from the data set, $n = 34$.

distributed. All regressions using log body mass as the dependent variable were significant (all $P < 0.0001$). For 3 of the allometric relations calculated, some individual data points had high leverage values (leverage > 0.3 —Fox 2008), and the models were recalculated without these individual points (Table 1). The capybara had relatively long m1 and upper tooththrow compared to other rodents, which resulted in high leverage values (0.29 in both cases). Although coefficients of determination were high for all allometric relations calculated (r^2 -values ranging between 0.82 and 0.89; Table 1), $SEEs$ also were relatively high, ranging from 0.21 to 0.27 (Table 1). Estimation of body mass from dental or skeletal measurements thus can vary within an interval of ± 21 –27% around its real value.

Multiple regressions included only the following independent characters: Upper tooththrow length, Lower anteroposterior diameter of the incisor, Femur diameter, Humerus length, and Humerus diameter (model 1; Table 2). This last model, with an SEE of 0.12, is more accurate in estimating body mass than any of the pairwise models. Because not all variables were available for individuals of *Phoberomys*, a 2nd multivariate model was calculated that included the following independent variables: Upper tooththrow length, Femur diameter, Humerus length, and Humerus diameter (model 2; Table 2). A 3rd model, which did not include long-bone diameters, also was calculated (model 3, variables included: Upper tooththrow length, Femur length, and Humerus length).

Skeletal analysis.—Scatter plots of humerus diameter against its length (Fig. 1a) and femur diameter against its length (Fig. 1b) show that the giant fossil rodent *Phoberomys* has relatively large bone diameters. The linear relation between log-transformed diameter (independent variable) and log-transformed length (dependent variable) were used to calculate percent prediction errors (%pes) of estimated diameters from the length of long bones. The specimen *P. pattersoni* UNEFM-VF-

TABLE 2.—Parameters of the multivariate predicting equation (model 2) used to estimate body mass (g) in *Phoberomys*; R^2 : square multiple coefficient of determination; SEE : standard error of the estimate; PE: average absolute prediction error; $n = 35$. Model 1: $F_{5,29} = 188.66$, $P < 0.001$, $SEE = 0.119$, $R^2 = 0.97$, PE = 0.208; model 2: $F_{4,30} = 193.61$, $P < 0.001$, $SEE = 0.131$, $R^2 = 0.96$, PE = 0.206; model 3: $F_{3,31} = 129.50$, $P < 0.001$, $SEE = 0.181$, $R^2 = 0.93$, PE = 0.351. UTRL: upper tooththrow length; Lower AP: lower incisor anteroposterior diameter (mm).

Effect	Coefficient	t	P
Model 1			
Constant	-1.060	-3.118	0.004
UTRL	1.519	5.976	0.000
Lower AP	1.066	2.694	0.012
Femur diameter	1.303	5.110	0.001
Humerus length	1.065	4.026	0.001
Humerus diameter	-1.616	-2.943	0.006
Model 2			
Constant	-0.915	-2.479	0.019
UTRL	1.288	4.897	0.000
Femur diameter	1.292	4.610	0.000
Humerus length	1.059	3.639	0.001
Humerus diameter	-0.553	-1.318	0.198
Model 3			
Constant	-1.019	-3.110	0.004
UTRL	1.613	4.984	0.000
Humerus length	0.942	0.451	0.655
Femur length	0.360	1.262	0.216

020 has a humerus diameter 47% and a femur diameter 82% larger than in a ‘‘normal’’ rodent. On the contrary, *Phoberomys* spp. specimens CIAAP-1438 and UNEFM-VF-010 seem to better fit a rodent design with %pe values of -3% and -4%, respectively, for humerus diameter. Yet the %pe for the femur diameter in specimen CIAAP-1438 is 163%. Both of these specimens each represent a single individual and may belong to *Phoberomys* species other than *pattersoni*. The large size in *Phoberomys* thus seems to be accompanied by an increase in the

robustness of the long bones, and body-mass estimates from long-bone diameters are likely to be overestimated.

When compared with recent rodents, *P. pattersoni* possessed an upper tooththrow of usual length relative to the lengths of its humerus and femur (Fig. 2). The capybara has a relatively long tooththrow compared to its femur length and humerus length. The upper tooththrow length and the lengths of the humerus and femur are thus recommended for the estimation of body mass in the extinct rodent *Phoberomys* spp.

Unfortunately, the dimensions of the 1st lower molar are known for only 1 specimen of *P. pattersoni* (UNEFM-VF-025) and 1 specimen of *Phoberomys* sp. (CIAAP-1449) for which no other measurement is available. The same problem existed for the diameters of the upper and lower incisors that are known from only 3 isolated incisors. These dimensions cannot be compared to other skeletal dimensions of *Phoberomys*. As a consequence, although they may be accurate, one has to be extremely cautious in the interpretation of body-mass estimates for *Phoberomys* based on measurements on incisors and on the 1st lower molar.

Body-mass estimates.—Estimated body-mass values for *P. pattersoni* ranged from 221 to 460 kg and from 565 to 774 kg in UNEFM-VF-020 and UNEFM-VF-025, respectively (Table 3). Estimates for UNEFM-VF-025 were based on the dimensions of the 1st lower molar only. Average prediction errors for each of the allometric relations indicate that *P. pattersoni* may have weighed as little as 111 kg but also could have weighed over a ton. This last figure was based on a body-mass estimate from the length of the 1st lower molar. Allometric models based on the length of the upper tooththrow and the humerus and femur lengths yielded an estimated body mass of 221–281 kg. Estimated body mass for *P. pattersoni* UNEFM-VF-020 was 568 kg and 346 kg based on multivariate models 2 and 3, respectively. As opposed to model 2, model 3 did not include long-bone diameters. The other smaller species of *Phoberomys* had estimated body masses ranging from 53 to 912 kg. When considering values obtained from the upper tooththrow and from the humerus and femur

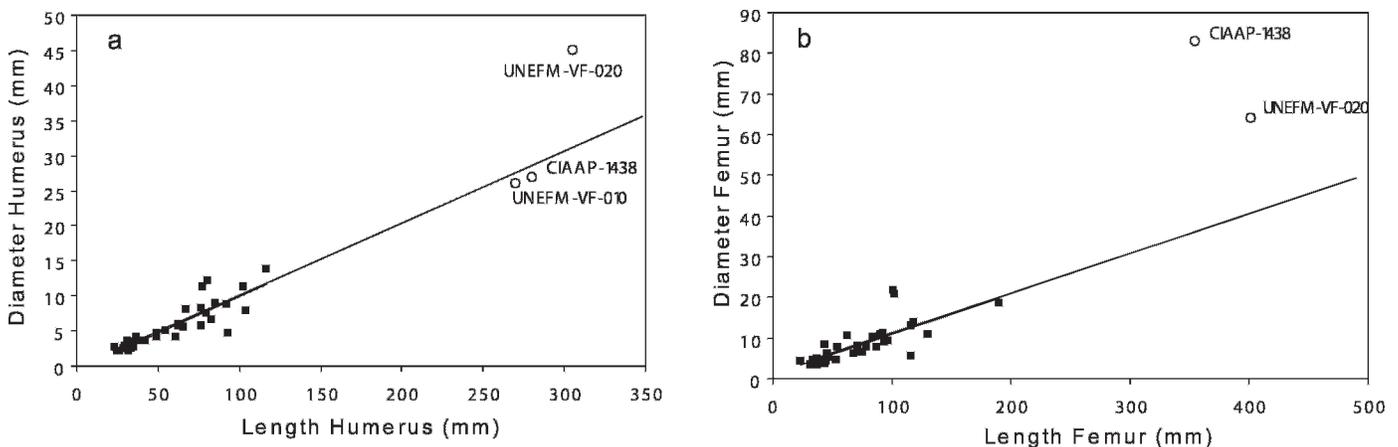


FIG. 1.—Bivariate plots of a) humerus diameter against humerus length and b) femur diameter against femur length. Regression equations used to calculate the estimated value of diameters from length were as follow: diameter = $1.049 \times \text{length} - 1.121$ (humerus, log-transformed) and diameter = $0.099 \times \text{length} - 0.977$ (femur, log-transformed). Filled square: reference sample for 35 rodent species; open circles: *Phoberomys pattersoni* and *Phoberomys* spp.

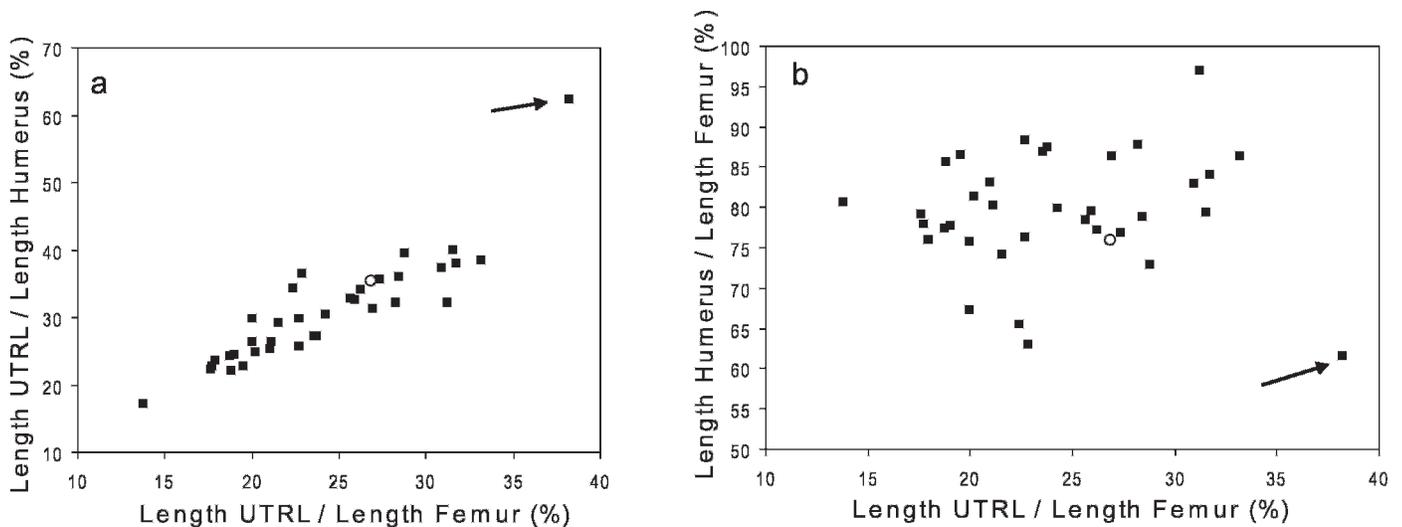


FIG. 2.—Bivariate plots of a) the ratio of upper tooththrow length (UTRL) to humerus length against the ratio of UTRL to femur length, and b) the ratio of humerus length to femur length against the ratio of UTRL to femur length. Filled square: reference sample for 35 rodent species; open circle: *Phoberomys pattersoni* UNEFM-VF-020. The arrow points to the symbol for *Hydrochoeris hydrochaeris*.

lengths only, estimated body mass for *Phoberomys* spp. ranged from 96 to 183 kg (Table 3).

DISCUSSION

Despite a relatively large sample size of reference data, the regression statistics were not sufficient to assign complete confidence to any single morphological character. The most notable results from the calculation of the allometric models were the consistently high correlation coefficients. This is typical of interspecific correlations and also of large sample size (Schwartz et al. 1995); however, the correlation coefficient is not the most convincing index value (Smith 1980). To assess the validity of the regression %PE is a much more useful tool because it determines how accurately the regression model predicts the estimate (Schwartz et al. 1995; Smith 1980). The %PE in this study is high for all equations (%PE > 30 for all characters considered). However, this does indicate that the values found for any of these equations are rough estimates because %PE and *SEE* also can be misleading (Roth 1990). Logged values when untransformed are biased (Smith 1993; Sprugel 1983). Because estimates are used in the calculation of both %PE and *SEE*, this bias is inevitably reflected in these 2 statistics. Furthermore, equations that underestimate body size lead to higher %PE values because of the smaller estimate in the denominator (Roth 1990). Other factors that could explain the high %PE values are high measurement errors or the heterogeneity of the sample (Van Valkenburgh 1990).

The choice of variables obviously has a large impact on body-mass estimates, and this is confirmed by the large variation in the present study. Estimates based on skull bones or teeth are often dismissed (Egi 2001; Smith 1996), arguably due to the lack of stress imposed on the cranium by body mass. Instead, limb-bone measurements are commonly accepted (Damuth and MacFadden 1990; Egi 2001), and it has been assumed that the size of the femur, which bears much of an

animal's body weight, should be a reliable proxy for its body mass (Sanchez-Villagra et al. 2003). However, although cross-sectional areas of long limb bones are recognized as good indicators of body mass, in certain groups (e.g., *Hyaenodontidae*) femoral cross-section equations result in overestimated body mass (Egi 2001). We showed that the range of body-mass estimates for *Phoberomys*, and in particular for *P. pattersoni*, is large and depends considerably on the character used.

Sanchez-Villagra et al. (2003) reported that the ratio of femur diameter to humerus diameter of *P. pattersoni* was 1.42, a value beyond the range of extant caviomorph rodents that were used as a reference sample in their study. Furthermore, although structural variation in limb bones of rodents is rather limited, limbs of the capybara exhibit features, such as a thick humerus and long olecranon, that most likely are related to its semiaquatic lifestyle and large body mass (Elissamburu and Vizcaino 2004). Our skeletal analysis revealed that *Phoberomys* shows some morphological peculiarities, with unusually robust long bones (i.e., large bone diameters) when compared to extant rodent species. We thus conclude that body-mass estimates of *Phoberomys* derived from diameters of long bones will tend to be overestimates. This corroborates the results presented by Sanchez-Villagra et al. (2003) in which the largest body-mass estimates were obtained from the femur and humerus diameters.

We could not establish the accuracy of the estimates based on the 1st lower molar because of incompleteness of the fossil remains of *Phoberomys*. Instead, we recommend the use of the length of the upper tooththrow, length of the femur, length of the humerus, or a combination of all 3 to estimate body mass of *Phoberomys*. Using these 3 characters, *P. pattersoni* would have weighed between 220 and 340 kg. This estimate is 55–70% lower than the original figure of 740 kg proposed for *P. pattersoni* (Sanchez-Villagra et al. 2003). However, these values are still 5–8 times greater than the average body mass of the largest living rodent, the capybara, and greater than the

TABLE 3.—Body-mass estimates for *Phoberomys pattersoni* and *Phoberomys* spp. and associated prediction errors (%PEs). UTRL: upper toothrow length; Lower AP and Upper AP: lower and upper incisor anteroposterior diameters, respectively (mm); Lower T and Upper T: lower and upper incisor transverse diameters, respectively (mm); m1 length and m1 width: 1st lower molar maximum length and width, respectively (mm). Model 2: multivariate model including UTRL, Femur length, and Humerus length as independent variables. An asterisk (*) indicates that part of M3 is broken. UNEFM = Universidad Nacional Experimental Francisco de Miranda, Venezuela. CIAAP = Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro, Venezuela.

Character	Measurement (mm)	Body mass (kg)	%PE	Mass - PE (kg)	Mass + PE (kg)
<i>Phoberomys pattersoni</i>					
UNEFM-VF-020					
UTRL*	108.1	281	± 43.4	159	403
Femur length	402	247	± 48.6	127	367
Femur diameter	64	460	± 47.5	241	68
Humerus length	305	221	± 50.1	111	332
Humerus diameter	45	430	± 39.4	260	599
UNEFM-VF-025					
m1 length	34.3	774	± 44.6	429	1,119
m1 width	24.3	565	± 45.8	306	823
<i>Phoberomys</i> spp.					
CIAAP 1438					
Femur length	355	174	± 48.6	89	258
Femur diameter	83	912	± 47.5	479	1,344
Humerus length	280	174	± 50.1	87	261
Humerus diameter	26.8	116	± 39.4	70	162
CIAAP 441					
Femur length	287.5	96	± 48.6	49	142
Humerus length	284.8	183	± 47.5	96	269
UNEFM-VF-010					
Humerus length	270	157	± 50.1	78	235
Humerus diameter	26	107	± 39.4	65	150
CIAAP 1449					
m1 length	18.2	123	± 44.6	68	178
m1 width	19	259	± 45.8	141	378
UNEFM ‘‘c’’					
Lower AP	13.2	76	± 46.0	41	111
Lower T	12.7	58	± 56.7	25	92
UNEFM ‘‘f’’					
Lower AP	14.3	96	± 46.0	52	140
Lower T	12.8	60	± 56.7	26	93
UNEFM ‘‘e’’					
Upper AP	14.45	117	± 57.2	50	184
Upper T	12.1	53	± 55.0	24	83

mass of other fossil giants described in the past (e.g., the giant beaver [*C. ohioensis*] or the giant hutia [*A. inundata*]), except for the recently described *J. monesi*.

Although *P. pattersoni* is certainly one of the largest rodents ever described, because of the lack of phylogenetically similar taxa with comparable bone and tooth proportions, body-mass estimates for *P. pattersoni* should be regarded as conditional. Estimation of body mass of extinct taxa that fall outside the range of size of the reference sample has been regarded as one of the largest causes for overestimated values (Damuth and MacFadden 1990; Reynolds 2002; Schmidt-Nielsen 1984).

Factors that led *Phoberomys* and other extinct taxa to reach such gigantic sizes are unknown. Island species provide the best recorded and some of the most spectacular examples of evolution in body size, including gigantism in small mammals. However, none of the known island rodent species have reached a size comparable to those of *Phoberomys* or the even larger *Josephaartigasia*. Several hypotheses have been formulated to explain gigantism among island rodents (review in Millien and Jaeger 2001). Most of them rely on changes in interspecific interactions between species on islands, such as a reduction or loss of predation or competition, or both. Another set of hypotheses suggests the adaptation of isolated species to drastic changes in their physical environment. The sediments in the Urumaco formation indicate a coastal wetland with some lagoons separated by sandy barriers, suggesting that *P. pattersoni* was semiaquatic, similar to *H. hydrochaeris* (Horovitz et al. 2006). Other fossil rodents of unusually large size have been found in the same formation, including the genus *Telicomys*, which may have been 70% the size of *P. pattersoni* (Horovitz et al. 2006). The gigantism of *Phoberomys* may represent an adaptation to locomotion and foraging in a coastal wetland environment, a hypothesis corroborated by the morphology of its massive and heavy limbs.

It is debatable why none of the giant rodents such as *Phoberomys* or *Josephaartigasia* in South America, *Castoroides* in North America, or *Amblyrhiza* in the Caribbean persisted. The capybara is the only survivor of a once much diversified group of rodents of unusually large size. Today, the ecological niches of giant fossil rodents are filled by ungulates. The success of this group over large rodents may be related to a highly adapted digestive system that allows ungulates to rely on an entirely herbaceous diet despite their large size.

Despite our conclusion that the mass of *P. pattersoni* was overestimated, this species, with a mass we estimated to be 220–340 kg, remains one of the largest rodents ever described. Our investigation suggests that efforts should be made to account for sources of error when estimating body mass of extinct species.

RESUMEN

El tamaño del cuerpo se correlaciona con prácticamente todos los aspectos morfológicos, fisiológicos y de historia natural de los mamíferos. Es por esto que en reconstrucciones paleoecológicas, se usan estimaciones del tamaño del cuerpo en especies fósiles. Caracteres usados como indicadores de masa del cuerpo en especies extinguidas incluyen medidas de dientes, cráneos y esqueletos. Demostramos que las estimaciones de masa del cuerpo en especies extinguidas a partir de taxa vivientes pueden ser erradas y dependen mucho de variables morfológicas que fueron seleccionadas como indicadores de masa del cuerpo. Discutimos también herramientas estadísticas disponibles para medir la precisión de las estimaciones de masa del cuerpo en especies extinguidas. Nos focalizamos en la revisión de estimadores de masa del cuerpo del roedor fósil gigante del Mioceno *Phoberomys pattersoni* (Venezuela), el segundo en tamaño reportado, con una masa estimada entre 436 y 741 kg. Este rango está más allá del

rango promedio para masas del cuerpo de roedores vivientes, rango que varía desde pocos gramos a 40 kg. Concluimos que la masa del cuerpo de *Phoberomys* fue exagerada. La especie *P. pattersoni* probablemente haya pesado entre 220 y 280 kg, que es la masa de un caballo o un antílope grande.

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APPENDIX I

List of species used for the reference data set. Specimens were examined at the Museum National d'Histoire Naturelle (MNHN), Paris, and at the Redpath Museum (RM), McGill University, Montreal. Specimen numbers for each species are given in parentheses.

Atherurus macrourus (MNHN2001-470), *Castor canadensis* (MNHN 1996-2168, MNHN 1958-203, MNHN 1996-520), *C. fiber* (MNHN1994-2961, MNHN1998-1957, MNHN1998-1941, MNHN1994-2960), *Cavia aperea* (MNHN1986-470, MNHN1986-469), *C. porcellus* (MNHN1962-2092), *Chinchilla lanigera* (MNHN1974-332, MNHN1974-333, MNHN1974-331) *Coendou prehensilis* (MNHN1997-643, MNHN1995-3239), *Cricetomys* sp. (MNHN1993-212), *C. gambianus* (MNHN1995-1565), *Cryptomys ochraceocinereus* (MNHN1956-717), *Ctenodactylus vali* (MNHN1951-254, MNHN1951-256, MNHN1951-255), *Cuniculus paca* (MNHN2005-1026), *Dasyprocta* sp. (RM2460), *D. leporina* (MNHN1998-677, MNHN1998-2253, MNHN1917-64, MNHN2006-503), *Dinomys branickii* (MNHN1990-658), *Dolichotis patagonum* (MNHN1974-87, MNHN1961-1035, MNHN1974-86), *Echimys chrysurus* (MNHN1999-1082), *Erethizon dorsata* (RM2474), *Galea spixii* (MNHN1972-857, MNHN1975-465, MNHN1975-455), *Hydrochoeris hydrochaeris* (MNHN1988-197, MNHN1962-2221, MNHN2001-1972, RM6025), *Hystrix cristata* (MNHN1990-662, MNHN1991-615), *Lagidium peruanum* (MNHN1971-361), *Makalata didelphoides* (MNHN1983-360, MNHN1972-853), *Marmota marmota* (MNHN1958-729, MNHN1996-2438), *Myocastor coypus* (MNHN1959-146, MNHN1990-651, MNHN1958-204, MNHN1952-876, RM1161), *Myoprocta acouchy* (MNHN1962-1329), *Octodon degus* (MNHN1958-747), *Ondatra zibethicus* (MNHN1983-865, MNHN1983-863, RM2475, RM2725), *Petaurista petaurista* (MNHN1982-843), *Proechimys cuvieri* (MNHN1998-689, MNHN1998-696, MNHN1995-3218, MNHN1981-409), *Rattus norvegicus* (VM0), *Sciurus niger* (MNHN2001-106), *Spermophilus mexicanus* (RM1178, RM1139), *Sphiggurus insidiosus* (MNHN1997-641), *Thrichomys apereoides* (MNHN1972-853), *Thryonomys swinderianus* (MNHN1964-204, MNHN2003-70).