

## Comment

## The largest among the smallest: the body mass of the giant rodent *Josephoartigasia monesi*

Body mass in extant rodents covers more than four orders of magnitude, from a few grams up to 40 kg on average in the capybara (*Hydrochaeris hydrochaeris*; Silva & Downing 1995). However, rodents have been much bigger in the past. The South American fossil rodent, *Phoberomys pattersoni* (Sanchez-Villagra *et al.* 2003), found in north-western Venezuela (Mones 1980; Horovitz *et al.* 2006) had an estimated body mass of 436–741 kg (Sanchez-Villagra *et al.* 2003). Most recently, Rinderknecht & Blanco (2008, hereafter R&B 2008) described a giant fossil rodent from the Plio–Pleistocene of Uruguay. The new species *Josephoartigasia monesi* was estimated to have weighed 1211 kg on average, and perhaps as much as 2584 kg; a value well outside the range of size of any previously described rodent. However, a closer examination of R&B's (2008) methods suggests that the body mass of *J. monesi* may have been overestimated.

One approach that is commonly used to estimate body mass in extinct species is to calculate the allometric relation between a character and body mass in a number of recent species. This relation is then applied to extinct species to estimate their body mass. This procedure is in principle very straightforward, but it has a number of limitations (Smith 1980, 1996; Schmidt-Nielsen 1984; Damuth & MacFadden 1990; Egi 2001; Reynolds 2002). In particular, I have identified four main issues that place doubt on the body mass estimate of R&B (2008): the reference dataset; the choice of the character; the statistical analysis; and the presentation of the data.

The reference data used by R&B (2008) contain a rather small sample size. Ideally, the sample size should be large enough to allow as much confidence in the results as possible. Their data are a mixture of intra- and interspecific measurements taken on 13 individuals representing nine species of hystricognath rodents, all close living relatives to *Josephoartigasia*. Because the allometric model used is an evolutionary allometric model at the level of the infra-order, the dataset should only contain interspecific data (using a mean value when several individuals from the same species are measured) as opposed to a static allometric model based on intraspecific data (Klingenberg & Zimmermann 1992). Thus, the actual sample size is 9 in R&B (2008). The use of a species mean also reduces the possibility of giving too much weight to a single individual such as the small 19 kg capybara in table 1 of R&B (2008). Second, the reference dataset should cover the widest range possible. This is especially true for fossil species that fall well outside the

range of the reference group. This problem of extrapolation is regarded as one of the largest sources of error and is known to cause overestimation of body mass (Schmidt-Nielsen 1984; Damuth & MacFadden 1990; Reynolds 2002). A wider selection of taxa may offset potential bias. In the following, I use a larger dataset of 35 species of rodents that includes hystricognath species and other large rodents (see appendix A).

I recalculated the allometric models based on the data given in table 1 of R&B (2008). The body mass estimates are based on an allometric model which is expressed as a power function:  $Y = aX^b$ , where  $a$  is a constant;  $b$  is the allometric coefficient;  $Y$  is the independent variable (body mass); and  $X$  is the dependent variable (dental or skull measurements). The log transformation of the power function results in a linear relationship,  $\log Y = \log a + b \log X$ , which is then fitted to the data by a least-squares criterion (Smith 1984). All data should be log-transformed before regression. This was not carried out in R&B (2008), a fact which introduced a significant bias in some of the body mass estimates (table 1). I also calculated three additional parameters to assess the validity of the allometric models (Smith 1980, 1984, 1996): the per cent coefficient of determination (% $R$ ); the per cent standard error of the estimate (%SEE); and the average absolute value of per cent prediction errors (%PE) that determine how accurately the regression model predicts the estimate.

Despite the high correlation coefficients, which are typical of interspecific relations, the %PE and %SEE are high, no matter which measure is considered, most especially for the incisor width (IW, table 1). The estimated body mass values for *J. monesi* ranged from 272 to 1535 kg (table 1). The largest values were obtained from some length measurements of the skull, including the total length, the diastema length and the basicranial length. Large values (from 715 to 1929 kg) are also obtained from the skull length using the various models (the beaver model excluded) presented by Reynolds (2002). Despite the fact that all the upper dentition is preserved, R&B (2008) did not include molar measurements in their analysis. Estimates that I calculated based on dental measurements (upper incisor and tooth row) yielded much smaller values of 651 and 356 kg. The estimate calculated from the width of the skull (FW) yielded a comparable value of 498 kg. The value of 272 kg obtained here from the upper IW is an order of magnitude smaller than the value of 2584 kg calculated in R&B (2008), which I was not able to recalculate with their data. There is certainly some doubt associated with estimates based on IW, given the high %PE (table 1).

Because *J. monesi* falls far outside the range of sizes known in recent rodents, I checked whether recent rodents

The accompanying reply can be viewed on page 1957 or at <http://dx.doi.org/10.1098/rspb.2008.0551>.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.0087> or via <http://journals.royalsociety.org>.

Table 1. Parameters of the equations used to estimate body mass in *J. monesi*. (FW, frontal width; IW, incisor width; ZL, zygomatic arch length; BCL, basicranial length; RL, rostral length; DL, diastema length; TL, total length (Rinderknecht & Blanco 2008); UTRW, upper tooth row length; upper T, upper incisor transverse diameter; skull, condylo-basal length of the skull; %R=100r<sup>2</sup>; %SEE=100×standard error of the estimate; %PE=average absolute value of per cent prediction error, where individual per cent prediction errors were calculated as %PE=(true mass−estimated mass)/estimated mass×100 after the data had been converted back to a linear scale; n=sample size.)

character (mm)	slope	intercept	%R	%SEE	%PE	n	body mass estimates (kg)	
							R&B (2008)	this study
FW	3.02	−4.18	91.9	24.6	35.65	9	676.24	497.84
IW	2.52	−2.16	71.8	45.9	84.53	9	2584.25	272.13
ZL	3.35	−5.13	96.5	16.2	29.25	9	468.46	493.51
BCL	3.82	−4.90	98.3	11.3	19.70	9	1519.03	1534.83
RL	3.32	−5.34	96.2	16.8	31.75	9	601.19	739.78
DL	3.53	−4.61	93.2	22.5	41.84	9	1615.64	1368.08
TL	3.56	−6.68	97.8	12.9	23.84	9	1005.48	1176.50
UTRW	2.70	−0.038	89.0	21.5	43.36	35	n.a.	356.40
upper T	2.45	2.080	83.2	26.2	54.98	34	n.a.	650.85
skull	3.49	−3.332	94.1	15.1	30.65	35	n.a.	1480.04

can actually be used as a reference sample. The analysis reveals that given the size of its upper dentition, the skull of *J. monesi* was 45% longer than expected from the sample of 35 species I used here (figure 1). The body mass estimates from skull length measurements such as the ones used in R&B (2008) may thus be greatly overestimated (out of the seven measurements in R&B (2008), five were taken along the longitudinal axis of the skull). Therefore, *J. monesi* does not fit an extant rodent model and body mass estimates for this species should be considered with caution. Whether *J. monesi* has a very elongated skull or a very short tooth row (microdonty) cannot be assessed at this point; we would need to compare the skull and teeth proportions with independent measurements, such as long bone measurements. Another possibility may be to compare *J. monesi* with extant herbivores comparable in size such as small artiodactyls.

The paper published by R&B (2008) reports a remarkable finding which widens our vision of rodent ecology and the evolution of this group of mammals. One recommendation is that future efforts should be made to take into account sources of error when estimating the body mass of extinct species. This is true not only for *J. monesi*, but also for other giant fossil rodents such as *P. pattersoni* (V. Millien & H. Bovy 2008, unpublished manuscript). In conclusion, *J. monesi* is certainly the largest rodent ever described, but, based on these calculations, its body mass may have been as low as 350 kg.

## APPENDIX A

List of species used for the reference dataset. Specimens were examined at the Museum National d'Histoire Naturelle, Paris and the Redpath Museum, McGill University, Montreal. *Atherurus macrourus*, *Castor canadensis*, *Castor fiber*, *Cavia porcellus*, *Cavia aperea*, *Chinchilla lanigera*, *Coendou prehensilis*, *Cricetomys* sp., *Cricetomys gambianus*, *Cryptomys ochraceocinereus*, *Ctenodactylus vali*, *Cuniculus paca*, *Dasyprocta* sp., *Dasyprocta leporina*, *Dinomys branickii*, *Dolichotis patagonum*, *Echymys chrysurus*, *Erethizon dorsatum*, *Galea spixii*, *H. hydrochaeris*, *Hystrix cristata*, *Lagidium peruanum*, *Makalata didelphoides*, *Marmota marmota*,

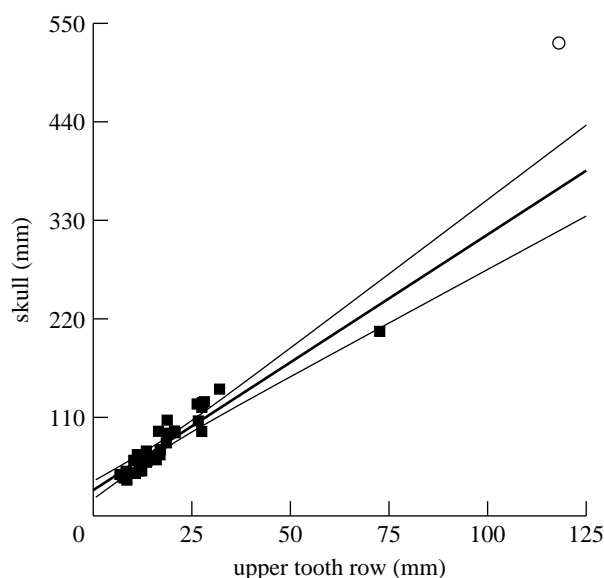


Figure 1. Bivariate plot of the skull length against the upper tooth row length. Filled squares, reference sample for 35 rodent species; open circle, *J. monesi*.

*Myocastor coypus*, *Myoprocta acouchy*, *Octodon degus*, *Ondatra zibethicus*, *Petaurista petaurista*, *Proechimys cuvieri*, *Rattus norvegicus*, *Sciurus niger*, *Spermophilus mexicanus*, *Sphiggurus insidiosus*, *Thryonomys swinderianus*, *Trichomys apereoides*.

Virginie Millien\*

Redpath Museum, McGill University,  
859 Sherbrooke Street West,  
Montreal, Quebec H3A 2K6, Canada  
\*virginie.millien@mcgill.ca

## REFERENCES

- Damuth, J. & MacFadden, B. J. 1990 *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge, UK: Cambridge University Press.
- Egi, N. 2001 Body mass estimates in extinct mammals from limb bone dimensions: the case of North American hyaenodontids. *Palaeontology* **44**, 497–528. (doi:10.1111/1475-4983.00189)

- Horovitz, I., Sanchez-Villagra, M. R., Martin, T. & Aguilera, O. 2006 The fossil record of *Phoberomys pattersoni* Mones 1980 (Mammalia, Rodentia) from Urumaco (Late Miocene, Venezuela), with an analysis of its phylogenetic relationships. *J. Syst. Palaeontol.* **4**, 293–306. (doi:10.1017/S1477201906001908)
- Klingenberg, C. P. & Zimmermann, M. 1992 Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. *Am. Nat.* **140**, 601–620. (doi:10.1086/285430)
- Mones, A. 1980 Un Neopiblemidae del Plioceno medio (Formacion Urumaco) de Venezuela (Mammalia: Rodentia: Caviomorpha). *Ameghiniana* **17**, 277–279.
- Reynolds, P. 2002 How big is a giant? The importance of method in estimating body size of extinct mammals. *J. Mammal.* **83**, 321–332. (doi:10.1644/1545-1542(2002)083<0321:HBIAGT>2.0.CO;2)
- Rinderknecht, A. & Blanco, R. E. 2008 The largest fossil rodent. *Proc. R. Soc. B* **275**, 923–928. (doi:10.1098/rspb.2007.1645)
- Sanchez-Villagra, M. R., Aguilera, O. & Horovitz, I. 2003 The anatomy of the world's largest extinct rodent. *Science* **301**, 1708–1710. (doi:10.1126/science.1089332)
- Schmidt-Nielsen, K. 1984 *Scaling. Why is animal size so important?* Cambridge, UK: Cambridge University Press.
- Silva, M. & Downing, J. A. 1995 *CRC handbook of mammalian body masses*. London, UK: CRC Press.
- Smith, R. J. 1980 Rethinking allometry. *J. Theor. Biol.* **87**, 97–111. (doi:10.1016/0022-5193(80)90222-2)
- Smith, R. J. 1984 Allometric scaling in comparative biology: problems of concept and method. *Am. J. Physiol.* **246**, R152–R160.
- Smith, R. J. 1996 Biology and body size in human evolution. *Curr. Anthropol.* **37**, 451–481. (doi:10.1086/204505)