



Original Investigation

Interatheriidae (Tyotheria; Notoungulata), body size and paleoecology characterization

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ABSTRACT

Size has a major influence on animal's adaptation to its environment and is central to paleobiological characterization of fossil mammals. We present new models of body mass estimation for the Interatheriidae (Notoungulata, Tyotheria). This small herbivorous mammals extends from the late Paleocene to the late Miocene and they are very well represented in the paleontological record of southern South America during a geological time lapse that witnessed extremely important events, at both climatic and biotic levels. The importance of the group as paleoecological indicators for a great part of the Cenozoic is emphasized by their long biochron and abundance in the fossil record. In this context, estimation of the body mass becomes crucial to reconstruct and infer ecological-environmental structure for a given time period. The results of the calculation of body masses from these new equations shows overall narrower range, smaller deviations, lower de-transformation correction and lower prediction error than previous equations used for body mass estimation in herbivores ungulates, establishing the maximum body mass for the Interatheriidae in 8.3 kg. These new body masses were utilized for characterization of the nutritional ecology of *Prototyotherium australe* (early Miocene), suggesting browser habits but it does not exclude grass from been part of the diet.

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Introduction

The Interatheriidae (Notoungulata, Tyotheria) are small herbivorous mammals with peculiar characteristics: apart from their small body size, roughly equivalent to that of recent Lagomorpha such as *Oryctolagus cuniculus* (maximum weight 9 kg) (Álvarez-Romero and Medellín 2005) or even smaller, one of their most remarkable traits is their complete dentition (dental formula 3/3 1/1 4/4 3/3), arranged in an almost closed series (entelodont). The cheekteeth range from brachydont (limited growth, early root differentiation) to euhypsodont (continuous growth, no root development). The biochron extends from the late Paleocene to the late Miocene (Bond et al. 1995). This group was very well represented and is frequent in the paleontological record of southern South America during a geological time lapse that witnessed extremely important events, at both climatic (e.g. climatic optima at the end of the Paleocene and early Eocene, Eocene-Oligocene transition crisis) and biotic (entrance of rodents and primates in the Oligocene, emergence of hysodonty in many mammal groups)

levels. The importance of this group is emphasized by their long biochron and the fact that some of its members have been used as paleoecological indicators for a great part of the Cenozoic. In this context, estimation of the body mass of individuals becomes crucial to reconstruct and infer ecological-environmental structure for a given time period.

Many workers have used the body mass of ungulates to make ecological inferences (e.g. Silva and Downing 1995; Pérez-Barbería and Gordon 1999; Hjeljord and Histøl 1999; Cumming and Cumming 2003; Reguero et al. 2010) which, in turn, can be the basis for notable paleoenvironmental implications (Croft 2001). Damuth and MacFadden (1990) have provided a major contribution for the estimation of body mass of ungulates, including hundreds of equations generated on the basis of living groups, which allow other researchers to estimate body masses for different groups. All these are linear equations of the type:

$$y_i = mx_i + b$$

where x_i is the independent or predictor variable (generally, a measurement taken from an anatomical structure), y_i is the dependent variable which represents body mass, and m and b are constants that describe the dependency relationship between the variables x (independent) and y (dependent).

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In this work we present a detailed account of the procedure followed for the calculation of body mass of individuals belonging to the Interatheriidae. In addition, we discuss the different algorithms used for the calculation of body mass and the implications of predicted body masses in paleobiological inferences.

Material and methods

Equations

Ideally, regression equations used for body mass prediction in fossil groups should be created on the basis of living groups, in which the proportions of the specific structures to be used as predictor variables are similar to those of the fossil groups under study; also, the grouping criteria used for the reference group, that is, the group of recent individuals from which the new prediction equations will be generated, should be applicable to the fossil species. In many cases, the best reference groups are defined by morphological or functional criteria rather than by taxonomical affinity (Damuth 1990).

Two sets of equations from Damuth and MacFadden (1990) were selected based on generalized ungulates (Appendix A). In addition, new regression equations were also created for the same predictor variables included in the equations taken from the literature, but using small ungulate herbivores as reference group; this reference group include species with body mass of less than 13.5 kg (Appendix B). This limit was chosen so as to not exceed the maximum hypothetical average weight estimated in previous works for some members of the Interatheriidae, by more than 30–35% (Croft 2000; Elissamburu 2004; Croft and Anderson 2008), and thus maintain, with a high degree of certainty, the morphological features and body proportions characteristic of small ungulate herbivores. These new equations obtained from small herbivores will be used to test the results from the ungulate equations provided by Damuth and MacFadden (1990). In addition, they allow to calculate more statistical parameters and several correction coefficients, such as SE (smearing estimate) and RE (ratio estimator) which will be detailed below, as well as confidence intervals for equation parameters (intercept and slope), which provide clearer understanding of the fit and behavior of each independent variable included in the prediction of body mass for fossil species.

The confidence intervals for the parameters were calculated using bootstrapping as resampling method (Manly 2004), with 1000 repetitions for each model.

The value of SEE (standard error of estimate) was calculated following Van Valkenburgh (1990), in order to enable comparison with equations available in the literature. The value of PE (prediction error) was calculated also following Van Valkenburgh (1990) but by cross-validation (leave-one-out) (Kohavi 1995). This method allows to remove one observation from the data set, recalculate the equation without it, and calculate the body mass for the excluded observation using this new equation; this procedure is repeated as many times as there are observations. Thus, the same number of observations is used to calculate PE and to generate the regression equation for each variable.

The equations were generated using least squares as fitting method. All the methods for correction to the de-transformation error (see below), as well as the equations taken from the literature, were designed for this type of fit (Smith 1993; Riska 1991). There has been much debate on which method should be used when (Smith 1994; Quinn and Keough 2002; McArdle 2003; Warton et al. 2006 and references therein), but a major review on bivariate line-fitting methods has been made by Warton et al. (2006). In this work the authors emphasize the importance of least squares fitting method for prediction models (Warton et al. 2006).

Predictor variable selection

The first step was an assessment of the availability of materials corresponding to interatheriids included in paleontological collections. These comprise mostly dental remains; the degree of accuracy and predictive power of this type of remains is not equivalent to that of variables such as body length (measurement of a cylinder that encompasses most of the body mass of the individual) or femur diameter, which is directly related to the way that mass is supported; however, dental materials are highly diagnostic at species level compared to other skeletal structures, and their preservation in the fossil record is much more frequent. The available cranial materials are frequently deformed and/or fragmented, and postcranial remains may be inappropriate for their use because of their scarcity, heterogeneity, and in some cases, unreliable association and provenance. The second step consisted of measuring the length of each dental piece and of the dental series (for instance, length of the molar series) to be used as independent variables. Tooth width and other measurements that include width were avoided because they present a much higher level of variation in ungulates, according to Damuth (1990), and also Janis (1990) and Fortelius (1990). In addition, the equations using *width* as predictor variable show the highest values of PE; consequently, length is to be preferred if both measurements are available for the same dental element. Following Janis (1990) criterion, the length of each element of the lower molar series (m_1 , m_2 and m_3) was used as predictor (independent) variable, along with the length of the second upper molar (M^2) and the total length of the lower molar series ($m_1 + m_2 + m_3$). These are the measurements with lowest variation and highest correlation with body mass in herbivorous ungulates (Janis 1990).

Data collection

A total of 35 specimens were measured; these correspond to 12 species in 10 genera according to the systematic scheme of Reguero et al. (2003).

The values for each independent variable were log-10 transformed. This transformation was based on two criteria: first, it is useful to reduce statistical problems associated with extreme data values (outliers); the procedure does not determine if highly deviant points should be excluded or not, but reduces the importance of this decision; and second, it is an efficient method of changing data distribution to fulfill the statistical assumptions of normality and homoscedasticity (Smith 1980; Zar 1996).

Correction coefficients

In general, when body mass is calculated from a regression equation, the variables are measured in arithmetic units, then they are log-transformed, and the estimate values are de-transformed to the original arithmetic units for subsequent interpretation. Several authors follow this procedure, considering that it has no effect on the final values obtained; however, an error is introduced during this process (Smith 1993) (Table 1).

The problem lies in the fact that the value of the dependent variable predicted from a regression equation is the arithmetic mean of the conditional distribution of y for a given x (Smith 1993). However, the arithmetic mean calculated in the logarithmic space is the geometric mean of the data de-transformed back into the arithmetic space, because the calculation of an arithmetic mean using logarithmic units, which entails addition of logarithms, results in the multiplication of the equivalent arithmetic units (Smith 1993).

Table 1
Example of transformation error (modified from Helsel 1990).

Original data	Transformed values (log-10)
1	0
10	1
100	2
1000	3
10,000	4
Mean 2222.2	Mean 2 exp(2)=100

Consequently, a Correction coefficient (CF) is calculated and applied as follows:

$$\text{Corrected value} = (\text{biased value from regression equation}) \times (\text{correction factor})$$

In this case, three correction factors were calculated: Quasimaximum likelihood estimator (QMLE), Smearing estimate (SE) and Ratio estimator (RE). These correction factors are discussed in detail by Smith (1993).

Quasi-maximum likelihood estimator

The quasi-maximum likelihood estimator (QMLE) correction coefficient is calculated as follows:

$$\text{QMLE} = \exp\left(\frac{s^2}{2}\right)$$

where s^2 is the residual mean square of the regression equation. This correction coefficient was applied to all the results obtained from equations taken from the literature, as well as to the equations generated from small herbivores. This coefficient is very sensitive to the assumption of normal distribution of the residues in logarithmic space; furthermore, it was frequently found to over-compensate the correction.

The calculation of the next correction coefficients requires the use of the original data from which the equation was obtained, which are not available in the case of the regressions from Damuth and MacFadden (1990).

Smearing estimate

It was developed by Duan (1983), and is calculated as follows:

$$\text{SE} = \frac{1}{n} \sum \exp(\log r_i)$$

where n is the number of cases, and $\log r_i$ is the residue for each point in logarithmic units. If the residues are normally distributed, the smearing estimate closely approximates the QMLE.

Ratio estimator

This estimator, proposed by Snowdon (1991), is calculated as follows:

$$\text{RE} = \frac{y}{z}$$

where y is the arithmetic mean of the observed y_i values in original scale z is the arithmetic mean of predicted y_i values detransformed back to original scale (Smith 1993).

In the equations taken from the literature, for which only %PE and %SEE of the regression are available, only the QMLE correction factor can be calculated; this factor requires a single parameter, s^2

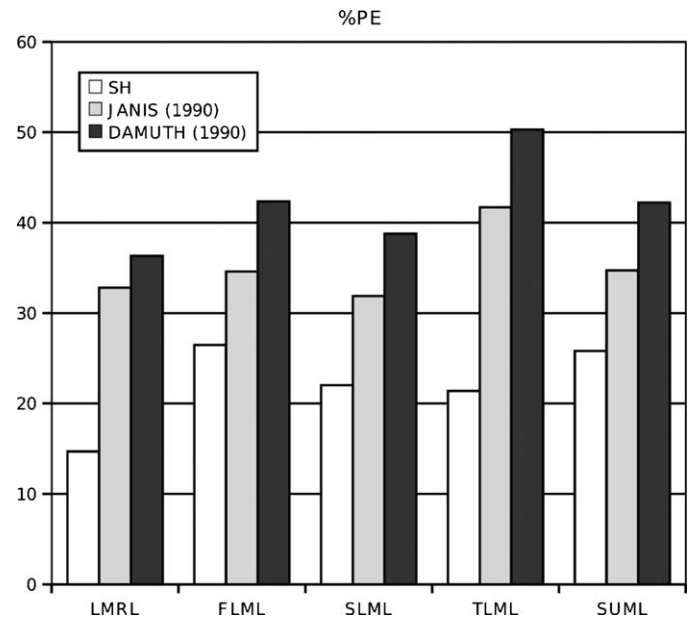


Fig. 1. Comparison of %PE values. LMRL, lower molar series length; FLML, first lower molar length; SLML, second lower molar length; TLML, third lower molar length; SUML, second upper molar length. SH, models from Small Herbivores.

residual mean square) from the regression equation, after accounting for the dependency of Y on X .

The resulting body masses were used for dietary characterization of *Protypotherium australe* (early Miocene) using a nutritional ecology model (Illius and Gordon 1992). This model predicts the daily energy needs for maintenance obtained on herbage of a potential digestibility for a particular type of ungulate (ruminant or hindgut fermenter) and body mass. In this paper, we run the model at a particular body mass and ungulate type (see below) in different herbage types (grass and browse) to assess the potentially dietary preferences for *Protypotherium australe*. In order to do this, some assumptions were taken. A hindgut digestive system was proposed for Interatheriidae (Scarano 2009) using predictive models based on craniodental characteristics of extant ungulates, an approach developed by Janis and Constable (1993). The body mass used in the model was the maximum value estimated in this work (see 'Results' section). For detailed aspects of the model see Illius and Gordon (1992).

Results

Body mass estimation

The values of PE and SEE are very useful values for algorithm selection, but the evaluation should not be based on one of them only but both should be taken into account, since in these cases, they are better indicators of the performance of predictor equations than the coefficient of determination can be (Smith 1980, 1984). Figure 1 shows a comparison of different PE values for each predictor variable, differentiating the reference groups used. It can be seen that the PE values for the equations based on Small Herbivores are markedly lower than the rest.

The value of SEE is the square root of the residual mean square of the model. It is a general indicator that measures the accuracy with which the calculated regression function predicts the dependency of Y on X (Zar 1996).

Figure 2 shows the different SEE values for each equation; the values for Small Herbivores are seen to be markedly lower. All the SEE values from Generalized Ungulates depart significantly from

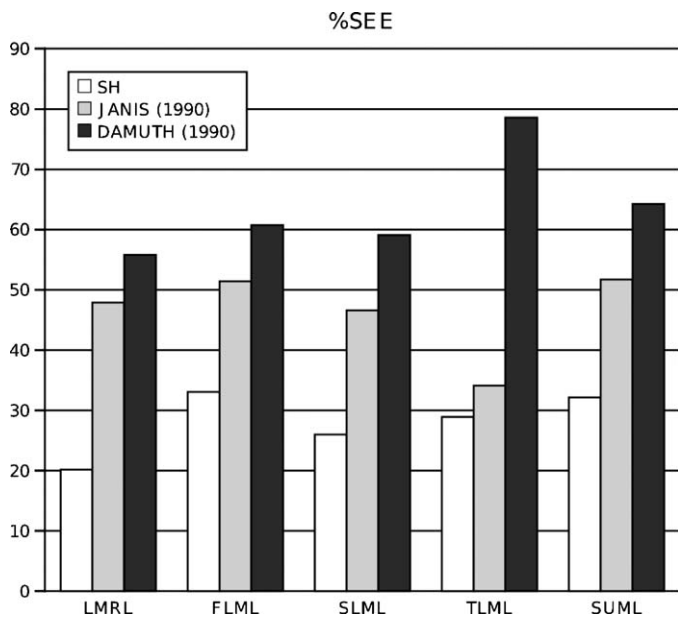


Fig. 2. Percentage of SEE for each model by group. LMRL, lower molar series length; FLML, first lower molar series; SLML, second lower molar length; TLML, third lower molar length; SUML, second upper molar length. SH, models from Small Herbivores.

those generated from Small Herbivores. It is important to consider that the value of SEE is directly linked to the calculation of the QMLE correction coefficient, and higher SEE values will increase the magnitude of this correction coefficient. The QMLE tends to overestimate the magnitude of the correction, and therefore it is recommended to also calculate the other two correction coefficients, so that more than one criterion is available to assess the degree of correction. Smith (1996) also recommends using RE as correction coefficient. Unless the predicted values are kept in logarithmic units, one of the criteria to use when selecting regression equations for body mass estimation is the degree of correction for the de-transformation of predicted values. Smith (1993) does not recommend using regression equations with corrections higher than 6%, or with a difference between correction coefficients (RE, SE and QLME) higher than 3–4%; this limit varies according to the intended use of the predicted values. Estimated body masses for fossil species that are intended to be used for inferences on their morphology, physiology, ecology, etc. should fulfill these criteria.

The equations based on Small Herbivores (Appendix C) have the lowest correction values and the predictor variable LMRL is the one with the lowest values of %PE and %SEE. Body masses of 12 species of Interatheriidae were predicted using this model (Table 2) with a maximum body weight of 7.4 kg for *Protypotherium australe* with an upper confidence interval (99%) for this prediction of 8.3 kg.

Table 2
Predicted body mass values for species of Interatheriidae using LMRL model.

SP	Mean	Max	Min	n
<i>Notopithecus adapinus</i>	1.25	1.47	0.97	4
<i>Antepithecus brachystephanus</i>	1.61	1.63	1.6	2
<i>Santiagorothia chiliensis</i>	4.2	4.78	3.62	2
<i>Archaeophylus patrius</i>	0.95	–	–	1
<i>Plagiathrus clivus</i>	4.12	–	–	1
<i>Proargyrohyrax curanderensis</i>	5.49	5.79	5.18	2
<i>Progaleopithecus tournoueri</i>	2.7	–	–	1
<i>Cochilius volvens</i>	2.05	2.29	1.75	4
<i>Protypotherium australe</i>	5.86	7.39	3.79	12
<i>Protypotherium attenuatum</i>	2.85	3.1	2.59	2
<i>Protypotherium praeutilum</i>	4.57	5.8	3.87	3
<i>Interatherium rodens</i>	1.25	–	–	1

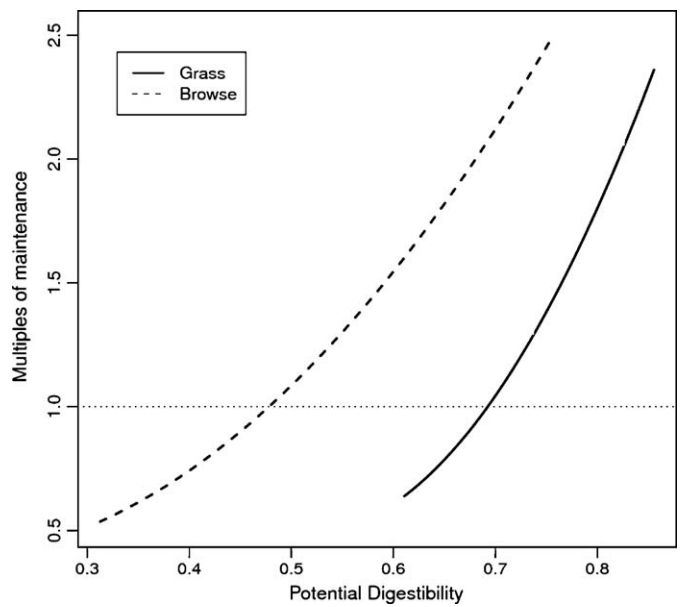


Fig. 3. Predictions of energy intake (in multiples of maintenance) for different levels of potential digestibility for browse and grass.

Therefore, the maximum body mass for Interatheriidae now was established in 8.3 kg.

Nutritional ecology prediction

Because of the scaling of nutritional requirements with body mass, the absolute mass of a mammalian herbivore has implications for the minimum quality of food necessary for survival, and hence for the feeding niche occupied (Illius and Gordon 1992; Janis et al. 1994). Figure 3 shows the predictions of the model for energy intake (in multiples of maintenance) for a hindgut fermenter ungulate of 8.3 kg, using different herbage types (grass and browse) at different potential digestibility (the sum of cell contents and digestible cell wall) levels. The model predicts that a browse diet has an advantage over grass. Browse material full-fit maintenance energy (1 × maintenance) at a lower level of digestibility.

Discussion

For the calculation of body mass in groups such as the interatherids, for which diverse types of restrictions exist (availability of remains, fragmentary elements, no living descendants, etc.), least squares simple regression is the approximation that makes best use of the available materials and allows a more precise evaluation of predictive capacity of the selected variables (Warton et al. 2006). In addition, being a widely applied methodology (Damuth and MacFadden 1990), it allows direct comparison with studies made for other mammalian groups and evaluation of the performance of the criteria used.

The results of the calculation of body masses from the equations based on small herbivores show overall narrower range (Table 3), smaller deviations, lower de-transformation correction and lower prediction error, demonstrating the importance of the reference group of choice used to generate new algorithms for the prediction of body mass, especially when trying to predict body masses from extreme groups like these. In previous works, body masses for *Protypotherium* were reported between 2.8 and 10 kg, without publication of any kind of confidence interval for predictions or any parameter of dispersion (Elissamburu 2004; Croft and Anderson 2008; Reguero et al. 2010). Such absence of data do not allow to establish parameters and set statistical limits that inform about the

performance of the equation used and the dispersion of the data obtained. The use of these values for posterior analysis must be accompanied by the researcher's criterion, since inferences based on them will have an even greater uncertainty (Smith 2002). In this work, the maximum body mass for patagonian members of the Interatheriidae was established in 8.3 kg (99% upper limit of maximum estimated body mass for *Protypotherium australe*), and this value was used for prediction of intake energy in a nutritional ecology model. The results show that, with this body mass, browse has an advantage over grass, but it does not exclude grass from being part of the diet, at least seasonally. The quality of food required for the animals' survival (i.e. $1 \times$ maintenance) is indicated by the horizontal dotted line (Fig. 3) and browse with a potential digestibility of ~ 0.48 full-fit maintenance energy while grass do the same but at a higher value (~ 0.69). The quality of forages can be seen as the inverse of fibre content and its degree of lignification and small bodied ungulates are more selective feeders than large animals (Jarman 1974; Illius 1997). Furthermore, there is a strong tendency in small species to select against stem and leaf sheath in favour of leaf lamina (Illius 1997) and have botanically diverse diets where in large species this is almost absent. This is in concordance with previous works where browser habits were inferred for *Protypotherium australe* from microwear analysis (Townsend and Croft 2008) and from craniodental morphology (Scarano and Carlini 2007; Scarano et al. 2009). All these suggest that size is an important adaptation in ungulates (Illius 1997), so body mass estimation in fossil

All this evidence shows that *Protypotherium australe* most likely had browser habits, but this could change seasonally depending on food availability.

Conclusions

The body masses from the equations based on small herbivores show overall higher performance compared to previous works, demonstrating the importance of the reference group of choice used to generate new algorithms for the prediction of body mass especially, when trying to predict body masses from groups like these.

The body masses for the Interatheriidae ranges from ~ 1 kg in *Archaeophylus patrius* to 7.4 kg for *Protypotherium australe* with an upper confidence interval (99%) for this prediction of 8.3 kg, establishing the maximum expected body mass for Interatheriidae in 8.3 kg.

The use of the maximum estimated body mass in a nutritional ecology model (Illius and Gordon 1992) predicts that a browse diet has an advantage over grass since full-fit maintenance energy ($1 \times$ maintenance) at a lower level of digestibility (~ 0.48) than grass (~ 0.69).

Appendix A.

Regression equations taken from the literature (in Damuth and MacFadden 1990).

		r^2	%SEE	%PE
Janis (1990)				
LMRL (length $m_1 + m_2 + m_3$)	$\log \text{Mass} = 3.28 \times (\log \text{lmrl}) - 0.552$	0.94	47.9	32.8
FLML (m_1 length)	$\log \text{Mass} = 3.26 \times (\log m_1 \text{ length}) + 1.337$	0.93	51.4	34.6
SLML (m_2 length)	$\log \text{Mass} = 3.20 \times (\log m_2 \text{ length}) + 1.130$	0.94	46.6	31.9
TLML (m_3 length)	$\log \text{Mass} = 3.18 \times (\log m_3 \text{ length}) + 0.801$	0.90	64.1	41.7
SUML (M^2 length)	$\log \text{Mass} = 3.18 \times (\log m_2 \text{ length}) + 1.091$	0.93	51.7	34.7
(Masses in kg, lengths in cm, log = log base 10)				
Damuth (1990)				
LMRL (length $m_1 + m_2 + m_3$)	$\log \text{Mass} = 3.14 \times (\log \text{lmrl}) - 0.6$	0.93	55.8	36.3
FLML (m_1 length)	$\log \text{Mass} = 3.11 \times (\log m_1 \text{ length}) + 1.24$	0.92	60.7	42.3
SLML (m_2 length)	$\log \text{Mass} = 3.07 \times (\log m_2 \text{ length}) + 1.07$	0.92	59.0	38.7
TLML (m_3 length)	$\log \text{Mass} = 2.99 \times (\log \text{length}) + 0.80$	0.88	78.5	50.2
SUML (M^2 length)	$\log \text{Mass} = 3.03 \times (\log m_2 \text{ length}) + 1.06$	0.91	64.2	42.4
(Masses in g, lengths in mm, log = log base 10)				

LMRL: Lower molar row length; FLML: First Lower Molar Length; SLML: Second Lower Molar Length; TLML: Third Lower Molar Length; SUML: Second Upper Molar Length.

species have central importance when posterior inferences are needed.

Table 3

Body mass prediction for *Protypotherium australe* using different models and reference groups.

	LMRL	FLML	SLML	TLML	SUML
Reference group: Generalized Ungulates (from Damuth 1990)					
Mean	6.43	12.16	6.89	5.5	6.77
Max	8.65	21.36	10.83	8.56	13.09
Min	3.59	6.56	3.81	1.58	3.95
SD	1.74	3.48	1.71	2.22	2.28
Range	5.06	14.8	7.01	6.98	9.14
Reference group: Generalized Ungulates (from Janis 1990)					
Mean	5.83	11.12	6.3	5.32	6.32
Max	7.95	20.03	10.07	8.48	12.61
Min	3.17	5.81	3.39	1.41	3.58
SD	1.65	3.34	1.62	2.26	2.25
Range	4.78	14.22	6.67	7.07	9.03
Reference group: Small Herbivores (this paper)					
Mean	5.86	8.29	5.48	5.85	5.38
Max	7.39	13.24	8.08	7.86	9.53
Min	3.79	5.02	3.32	2.76	3.41
SD	1.24	1.94	1.16	1.59	1.53
Range	3.6	8.23	4.75	5.1	6.12

Appendix B.

SP	BM	LMRL	FLML	SLML	TLML	SUML
<i>Heterohyrax brucei</i>	2	1.67	0.56	0.58	0.59	0.61
<i>Procavia capensis</i>	3.8	2.09	0.64	0.73	0.75	0.81
<i>Neotragus pygmaeus</i>	4	2.43	0.54	0.72	1.01	0.82
<i>Madoqua guentheri</i>	4	2.4	0.73	0.77	0.9	0.78
<i>Dendrohyrax dorsalis</i>	4	1.86	0.62	0.64	0.61	0.67
<i>Madoqua kirki</i>	5	2.24	0.71	0.85	0.77	0.84
<i>Neotragus moschatus</i>	5	2.31	0.72	0.75	0.87	0.75
<i>Tragulus napu</i>	6	2.43	0.62	0.75	0.98	0.72
<i>Cephalophus monticolor</i>	6	2.37	0.62	0.7	0.88	0.8
<i>Pudu mephistopheles</i>	9	3.26	0.92	1.02	1.3	1.08
<i>Dorcatragus megalotis</i>	9	2.82	0.82	0.87	1.08	0.89
<i>Raphicerus melanotis</i>	10.6	2.73	0.73	0.89	1.1	0.84
<i>Hyemoschus aquaticus</i>	10.8	3.35	0.93	1.02	1.29	0.97
<i>Sylvicapra grimmia</i>	11	3.18	0.9	0.93	1.24	1.03
<i>Pudu pudu</i>	11	3.4	0.91	1.1	1.29	1.19
<i>Raphicerus campestris</i>	11.8	3.11	0.84	0.95	1.28	0.98
<i>Hydropotes inermis</i>	12.6	3.35	0.95	1.04	1.3	1.06
<i>Oreotragus oreotragus</i>	12.8	3.4	0.98	1.03	1.3	1.01
<i>Ourebia ourebi</i>	13	3.4	0.85	1.18	1.55	1.19
<i>Muntiacus reevesi</i>	13.5	3.48	0.94	1.07	1.37	1.1
<i>Moschus moschiferus</i>	13.5	3.21	0.84	0.97	1.06	1.01

Body mass expressed in kg; lengths in cm.

BM: Body mass; LMRL: Lower molar row length; FLML: First Lower Molar Length;

SLML: Second Lower Molar Length; TLML: Third Lower Molar Length; SUML: Second Upper Molar Length.

Appendix C.

	LMRL	FLML	SLML	TLML	SUML
Regression					
r^2	0.9	0.73	0.82	0.79	0.74
Intercept	-0.16	1.16	1	0.84	0.99
Slope	2.38	2.55	2.61	1.85	2.59
%SEE	20.1	33	25.9	28.8	32.1
%PE	14.6	26.4	22	21.3	25.8
Correction coefficients					
QLME	1.02	1.04	1.03	1.03	1.04
SE	1.02	1.04	1.02	1.03	1.04
RE	1.01	1.02	1.01	1.02	1.01

Models based on Small Herbivores and their parameters.

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