



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).

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