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Body mass estimation in Early Miocene native South American ungulates: a predictive equation based on 3D landmarks

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Abstract

South American native ungulates include extinct taxa that evolved within the geographical context given by the isolation of South America during most of the Cenozoic. The ungulates (orders Notoungulata, Litopterna and Astrapotheria) of the Santa Cruz Formation (late Early Miocene) are particularly interesting for paleobiological studies due to their diversity, richness and quality of preservation of the specimens. The body mass estimation of extinct species is one of the basic biological attributes for paleobiological reconstructions. The most common way to estimate body mass from fossils is using linear regression. Here, we used geometric morphometric techniques in order to estimate their body mass. We used regressions based on centroid size of 3D craniomandibular landmark configurations, including extant ungulates (their size and ecological relatives). Cases were weighted to maximize the taxonomic evenness. A broad body size range was recorded. The highest predictive power is obtained with those functions derived from the highest taxonomic and ecological diversity. The highest taxonomic richness corresponds to masses below 100 kg. Among Notoungulata, typotheres (Hegetotheriidae + Interatheriidae) vary from 1 to less than 10 kg, while the smaller toxodontid reached 100 kg and the larger 500 kg. Litoptern proterotheriid body masses vary from 10 to 50 kg, and macraucheniids surpass 100 kg. The astrapotheres (Astrapotheria) reached (or even surpassed) 1000 kg, being the only megamammal in the Santacrucian ungulate assemblage.

Introduction

South American native ungulates include several extinct taxa that evolved within the context of South American geographic isolation during most of the Cenozoic (Bond, 1999). The ungulates of the Santacrucian Age (Early Miocene), belonging to the orders Notoungulata, Litopterna and Astrapotheria, are particularly interesting for paleobiological studies due to their diversity, richness and quality of specimen preservation (Cassini *et al*., in press). Their biological diversity includes types that resemble equids, rhinos, camels and caviomorph rodents in both shape and size (see Cassini & Vizcaíno, 2011), as well as a giant form with no analogue in the current faunas.

A recent study of Santacrucian ungulates from south-east Patagonia (Cassini *et al*., in press) provides an extensive description of their diversity in a bounded geographic and stratigraphic context. Notoungulates are represented by four genera of Typotheria: *Interatherium* and *Protypotherium* (Interatheriidae), and *Hegetotherium* and *Pachyrukhos* (Hegetotheriidae). Notoungulata also comprise three genera of Toxodontia: *Nesodon* and *Adinotherium* (Toxodontidae), and *Homalodotherium* (Homalodotheriidae). The litopterns include representatives of the families Proterotheriidae (*Anisolophus*; *Diadiaphorus*; *Tetramerorhinus*; *Thoatherium*) and Macraucheniidae (*Theosodon*). Astrapotheres are represented by a single genus (*Astrapotherium*).

Toxodontids are medium- to large-sized notoungulates often compared with rhinoceroses both in appearance and ecological role. They have a long and high skull, high crowned cheek teeth, with lateral incisors developed as tusks, and a robust skeleton. Typotheres are small- to medium-sized mammals, mostly described as rodent-like in overall form, although Hegetotheriidae more closely resemble hares (Reguero, Dozo & Cerdeño, 2007) and Interatheriidae resemble a composite of a small mustelid's body with a hyrax's head (Croft & Anderson, 2008; Cassini *et al*., in press). Typotheres have wide and low skulls, ever growing high crowned cheek teeth, and gracile postcranial skeletons. Among Litopterna, macraucheniids include large animals with some convergences with camelids (long neck and a canal for the vertebral artery in cervicals, which passes through the neural arch; Scott, 1910). Proterotheriids are medium-sized animals, mostly described as similar to small primitive holartic horses due to their body size and overall cranial shape, but the presence of reduced digits and mesaxonic limbs makes convergent with modern equids. Their tooth crown morphology, on the other hand, resembles that of artiodactyls such as deer (Bond *et al.*, 2001). Astrapotheres are large to very large mammals (including strict megamammals, i.e. 1000 kg or more *sensu* Owen-Smith, 1988), described as morphologically intermediate between a tapir and an elephant, with large canine tusks and a putative proboscis (Scott, 1928; Riggs, 1935).

Size is one of the most variable features in the diversity of Santacrucian ungulates. Usually measured through body mass (*bm*), size is one of the most important aspects of the biology because it is highly correlated with various aspects of life such as diet, locomotion, energy, ecology, morphology and physiology (see Brown & West, 2000 and references therein).

Since the initial formalization of the allometric relationship by Kleiber (1932), various subsequent studies have applied the concept of allometry in physiological to ecological contexts (Calder, 1996). These studies demonstrated that many fundamental characteristics of biological organisms scale with corporal size following a power law formalized mathematically as $Y = aX^b$ (Savage *et al.*, 2004).

Body mass constitutes one of the first parameters to evaluate in the fossil taxa for the purpose of predicting biological attributes that are not preserved, and to propose paleoecological hypotheses (Andrews, Lord & Evans, 1979; Reed, 1998; Vizcaíno *et al.*, 2006). Although some attempts have been made to estimate the *bm* of the Santacrucian ungulates, the results are either restricted to few taxa or based only on a small set of measures. For example, Villafañe (2005) reported *bm*'s of proterotheriids, and Scarano, Carlini & Illius (2011) for the species of *Protypotherium*. Croft (2000) and Vizcaíno *et al.* (2010) used a more inclusive sample of taxa; their estimations were based on the first lower molar dimensions and the mean of a set of skull measurements, respectively.

Predicting *bm* of extinct species using allometric functions is the most common approach (e.g. Fariña, Vizcaíno & Bargo, 1998; Millien & Bovy, 2010). Some authors postulated that some postcranial elements (e.g. humerus and femur) are more accurate estimators of *bm* because they provide body support (Damuth & MacFadden, 1990), especially for species lacking modern representatives or falling outside the size ranges of extant species. Thus, postcrania have been extensively used as *bm* proxies (e.g. Alexander *et al.*, 1979; Scott, 1990; Farlow *et al.*, 2005). However, in the mammalian fossil record, cranial remains are more frequently recovered and much easier to assign taxonomically and therefore are frequently used as *bm* estimators as well (e.g. Gingerich, Smith & Rossenberg, 1982; Myers, 2001; Mendoza, Janis & Palmqvist, 2006).

In geometric morphometric analyses, shape and size are decomposed and centroid size (*cs*) is used as a proxy for size (Goodall, 1991; Dryden & Mardia, 1998). In the absence of allometry, *cs* is not correlated with shape (Bookstein, 1986; Kendall, 1986). Hood (2000) evaluated the potential use of *cs* in the study of size sexual dimorphism in the muskrat *Ondatra zibethicus* (Rodentia: Muridae, Arvicolinae) as well as eight bat species (Chiroptera, Pteropodidae). He concluded that *cs* is a geometric measure of size that follows the same mathematical behaviour as *bm*, indicating that *cs* is an excellent variable indicative of *bm*. Meloro & O'Higgins (2011) showed that mandibular *cs* is highly correlated with mean body weight in Carnivora. Ercoli & Prevosti (2011) obtained significant log-linear regressions between *bm* and *cs* for appendicular skeleton of extant carnivorous marsupials and placental mammals, and used *cs* to estimate the *bm* of species of Santacrucian Sparassodonta metatherians.

In this contribution, we attempt to obtain equations to predict *bm* from *cs* of three-dimensional (3D) landmark configurations of cranium and mandible using a broad taxonomical and ecological diversity of extant ungulates.

Materials and methods

Data

Fifty-nine specimens of ungulates with little to no apparent deformation from the Patagonian Santa Cruz Formation (late Early Miocene) were analyzed: 19 toxodontids and 24 typotheres (Notoungulata), 11 proterotheriids and 1 macraucheniid (Litopterna), and 3 astrapotheres (Astrapotheria) (see Appendix SI – online supporting information).

The reference sample of extant ungulates consisted of 505 individuals belonging to 155 species (134 Artiodactyla, 16 Perissodactyla and 5 Hyracoidea; Appendix SII – online supporting information). All extant families and subfamilies were represented (Table 1). Only adult specimens with third molar erupted and in occlusion were included, and captive animals were avoided as much as possible.

Landmark data

3D landmark coordinates were acquired with a Microscribe G2L digitizer (Immersion Corporation, San José, CA, USA); they are defined in Tables 2 and 3 and are shown in Fig. 1a–c. Both sides and midline landmarks were included. These comprise 36 cranial (see Milne & O'Higgins, 2002) and 14 mandibular landmarks including type I (or anatomic) and II (or mathematic).

Regression functions

All statistics, mathematical operations, regression functions and prediction of mass were carried out in R.

Museum specimens rarely include body weight; therefore, analyses were performed using the mean *bm* values reported in the literature (see Appendix SII). The reference sample includes species with sexual dimorphism; when information on male and female *bm* data was available, they were differentiated. We also obtained equations using the mean *bm* by

Table 1 Number of species/genera sampled in relation to the total number of species/genera in each family/subfamily

Taxa	Species sampled	Total of species	% species	Genera sampled	Total of genera	% genera
Perissodactyla						
Equidae	8	8	100%	1	1	100%
Tapiridae	4	4	100%	1	1	100%
Rhinocerotidae	4	5	80%	3	4	75%
Artiodactyla						
Suidae	9	19	47%	5	5	100%
Tayassuidae	3	3	100%	3	3	100%
Hippopotamidae	2	2	100%	2	2	100%
Camelidae	6	6	100%	3	3	100%
Ruminantia						
Tragulidae	3	8	38%	3	3	100%
Giraffidae	2	2	100%	2	2	100%
Antilocapridae	1	1	100%	1	1	100%
Moschidae	2	7	29%	1	1	100%
Cervidae						
Capreolinae	13	22	59%	8	9	89%
Hydropotinae	0	1	0%	0	1	0%
Muntiacini	3	12	25%	2	2	100%
Cervini	10	16	63%	6	7	86%
Bovidae						
Bovinae	10	24	42%	6	9	67%
Reduncinae	8	9	89%	3	3	100%
Antilopinae	15	38	39%	10	15	67%
Caprinae	25	35	71%	11	12	92%
Aepycerotinae	1	1	100%	1	1	100%
Cephalophinae	9	18	50%	3	3	100%
Hippotraginae	6	8	75%	3	3	100%
Alcelaphinae	6	10	60%	4	4	100%
Hyracoidea						
Procaviidae	5	7	71%	3	3	100%
Total	155	266	58%	85	98	87%

species. Centroid size (*cs*) of landmark configuration (***M***) is a size function defined as the square root of the sum of squared distances from each landmark to the centroid of the configuration and is independent of position or orientation of the configuration (Claude, 2008). The *cs* of each specimen was calculated using this R command: ***cs*<–sqrt(sum(apply (M,2,var))*((dim(M)[1])–1)** (modified from Claude, 2008).

Body mass (*bm*) grows at cube rates, while *cs* does so linearly, so the two variables were log(base 10) transformed, converting the relationship of these variables from a power formula ($\boldsymbol{bm} = \mathrm{a}\boldsymbol{cs}^{\mathrm{b}}$) to a straight line: $\log(\boldsymbol{bm}) = \log(\mathrm{a}) + \mathrm{b}\log(\boldsymbol{cs})$. Variable normality was analyzed with a Shapiro–Wilk test and normal quantile-quantile plot on log-transformed variables (Shapiro & Wilk, 1965). We assessed the extent and significance of the association between *cs* and *bm* via Spearman rank non-parametric correlations. We used the original non-transformed data because it tests how monotonically they are related, even if their relationship is not linear (Zar, 1999).

The regression functions were fitted to the data by means of ordinary least squares (OLS) models on log10-transformed variables. The OLS regression model is recommended if the main aim of our regression analysis is prediction (Warton *et al.*, 2006). Additionally, quantile regression analysis was performed. It was developed by Koenker & Bassett (1978) as a new class of robust alternatives to the OLS regression. This method is suitable for estimating functional relations between variables for all portions of a probability distribution (Cade & Noon, 2003). Quantile regression estimates can be used to construct prediction and tolerance intervals without assuming any parametric error distribution. Also, the estimates retain their statistical properties under any linear or non-linear monotonic transformation (e.g. logarithmic) as a consequence of this ordering property (Koenker & Machado, 1999). This allows the back transformation of the *bm* estimates to the original scale without any loss of information (Cade & Noon, 2003).

Some groups are widely represented in the database, while others (e.g. Procaviidae) are under-represented. The number of taxonomic groups is limited by the available sample (see Table 1), but their taxonomic evenness can be maximized (for an extensive discussion, see Mendoza *et al.*, 2006). In order to avoid biases, the taxa were weighted so each taxon contributes equally in the *bm* function; that is, in a family with one genus with four species and another with only two, both genera contribute in the same way to the equation. For this purpose, a

Table 2 Cranial landmarks, names and definitions used in the present study (see also Milne & O'Higgins, 2002)

Number	Name	Definition of *landmark*
1 & 22	*Stephanion*	*Sutura coronalis* at the intersection with the *linea temporalis*
2 & 23		*Sutura frontolacrimalis* at the *margo orbitalis*
3 & 24	*Dacryon*	*Sutura zygomaticolacrimalis* at the *margo orbitalis*
4 & 25		Anterior point of the *processus zygomaticus* of the *os temporale*
5 & 26		*Sutura zygomaticotemporal* on the *margo dorsal* of the *arcus zygomaticus*
6 & 27		*Superior root of the zygoma (on the temporal bone)*
7 & 28		*Sutura zygomaticotemporal* on the margo ventrale of the *arcus zygomaticus*
8 & 29		Anteriormost origin of *musculus masseter*/Lowest point of the '*masseteric process*'
9 & 30		Distal *margo alveolare* of the last molar
10 & 31		Mesial *margo alveolare* of first functional premolar
11 & 32		*Foramen infraorbitale*
12 & 33		*Sutura maxilloinsiciva* at the *margo intralveolaris*
13 & 34		Distal *margo alveolare* of the lateralmost incisor or horny pad scar
14 & 35		*Sutura nasoinsiciva* at the margin of the nasal aperture
15 & 36		*os nasale, frontale* and *maxilla* junction
16	Lambda	*Sutura occipitoparietalis*
17	Bregma	*Sutura coronalis* in the midline
18	*Nasion*	*Sutura frontonasalis* on the sagittal plane
19	*Rhinion*	Rostral edge of the *os nasale* on the *sutura internasalis*
20	*Nasospinale*	*Sutura interincisiva* on the mid-sagittal plane of nasal aperture
21	*Prosthion*	*Sutura interincisiva* on the *margo alveolaris*

Table 3 Mandibular landmarks, names and definitions used in the present study

Number	Name	Definition of landmarks
1	*Gnathion*	Caudo-ventral margin of the mandibular symphysis on the midline
2	*Infradentale*	*Alveoli dentalis* of i1 in the midline
3		Distal margin of *alveoli dentalis* of the last lower incisor
4		Distal margin of *alveoli dentalis* of the lower canine
5		Mesial margin of the *alveoli dentale* of the first functional premolar
6		*Margo interalveolaris* between last premolar and first molar
7		Distal margin of the *alveoli dentale* of the last molar
8	*Coronion*	The most superior point on the *processus coronoideus*
9	Mandibular notch	The most inferior point on the *incisura mandibulae*
10	*Condylion medial*	Most medial margin of mandibular condyle
11	*Condylion lateral*	Most lateral margin of mandibular condyle
12		Most dorsal-caudal rugosity from *musculus masseter* insertion
13		Most anterior roughness from *musculus masseter* insertion
14		*Foramen mandibulae*

new weighing variable was obtained following two approaches: one developed by Mendoza *et al*. (2006) and the other by De Esteban-Trivigno, Mendoza & De Renzi (2008). This variable is implemented as a 'weight' argument of 'lm' R function.

When predicted *bm* values from a least squares regression are retransformed back to arithmetic units, log-adjustment could yield biased estimates (Smith, 1993). In order to correct this potential bias, the ratio estimator (RE) (Snowdon, 1991) was applied. This ratio consisted of the mean of the observed values divided by the mean of retransformed predicted values. The predicted masses for the South American ungulates were retransformed back and then multiplied by the corresponding RE.

Although the correlation coefficient is one of the commonest ways to evaluate regressions, it poorly indicates the independent variable predictive power because it is affected by the range of values of the dependent variable and, therefore, it could be high even with high residuals (Smith, 1984). Thus, function reliability was evaluated by directly using their percent prediction error as **%PE = 100 × [observed − predicted]/predicted** (Smith, 1984).

Results

Figure 2 shows the box and whisker plot diagram of both variables *bm* and *cs*. They are discriminated between families across the three orders of extant ungulates and subfamilies among Bovidae and Cervidae. The *cs* values in these taxonomic groups show a pattern similar to *bm* (Fig. 2). Both log-transformed variables show no significant deviations from normality. Spearman's rank non-parametric correlation shows that cranial and mandibular *cs* are highly correlated with mean *bm* in the extant ungulates (cranial: $n = 155$, $r_s = 0.968$, $P < 0.0001$; mandibular: $n = 147$, $r_s = 0.976$, $P < 0.0001$).

All regressions obtained were statistically significant (Table 4). The *bm* range for all regressions is from 1.46 kg (represented by the bush hyrax *Heterohyrax brucei*) to 1750 kg (represented by the javan rhino *Rhinoceros sondaicus*). All determination coefficients (R^2) are high (Table 4) and the mean prediction error (%PE) is low. The relationship between the two variables, both for cranium and mandible, was isometrical [i.e. slope values around three expected under geometric similarity between a variable that grows linearly (*cs*) and cube (*bm*); Peters, 1983]. Based on %PE, we chose the

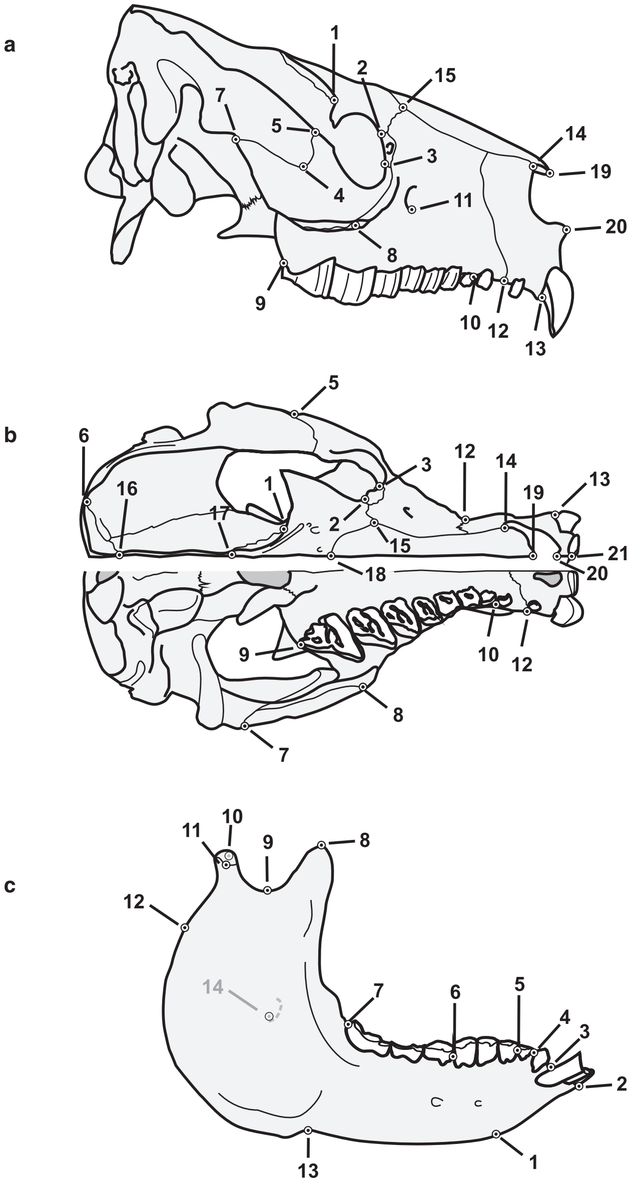

Figure 1 Landmark configuration on *Adinotherium* cranium (a, b) and mandible (c). See Tables 2 and 3 for their definition. The landmarks are shown on the right side and midline.

equations for cranium and mandible obtained using the Mendoza *et al*. (2006) weighted approach (i.e. Cr.4 and Md.4 equations).

Only for two cranial regressions outliers were found. The outlier species are listed in Table 5 and eliminated from dataset for the calculation of regressions.

The distribution of extant taxa around regression line is shown in Fig. 3. Those groups with proportionately large skulls (consequently high *cs*) relative to their *bm* lie below the regression line (among others, suids, equids, and some alcelaphine bovids). On the other hand, some taxa with proportionately short skulls (e.g. tapirs, rhinos and saiga) lie above the regression line. However, they are not outliers.

Figure 4 presents a summary of quantile regression results for Cr.4 regression. The horizontal axis represents the quantile scale and the vertical indicates the estimates. The conditional median and mean fits for both estimates (intercept and slope) are very similar as both 90% confidence intervals overlap. Also, the quantile intercepts and slopes between 0.15 and 0.7 remain enclosed to OLS estimate confidence intervals. Note that one consequence of this is that the OLS fit provides a very good estimate of the conditional mean in the sample. However, departures of the OLS model are represented by the larger than 0.7 quantile.

Estimated *bm* of each specimen of Santacrucian ungulates are listed on Appendix SI. Additionally, the minimum and maximum *bm* based on quantile regression are shown.

Mean *bm* at species level are listed in Table 6, discriminated between cranial and mandibular equations. Also, mean max *bm* are shown. The values obtained for these two elements are quite similar, except for *Astrapotherium magnum* (higher *bm* from mandible) and *Nesodon imbricatus* (lower *bm* from mandible). Except for typotheres, mandible mean max *bm* are always greater than cranial ones. For less-abundant species, the value for a single specimen is presented.

Among the assemblage of Santacrucian ungulates, *Astrapotherium* reaches higher *bm* (*c*. 700 kg). Among Notoungulata, *Nesodon* is the largest within Toxodontia (*c*. 400 kg), while both *Adinotherium* species are below 100 kg. All Typotheria are smaller than 10 kg; among them, *Protypotherium australe* and *Hegetotherium mirabile* are the largest (4.6 and 3.6 kg, respectively), and *Interatherium* spp. and *Pachyrukhos moyani* are the smallest (just below of 2 kg). Among Litopterna, all the Proterotheriidae fall in the 10–60 kg range. Only the Macraucheniidae *Theosodon* reaches more than 110 kg, being the largest Santacrucian litoptern.

Discussion

All regression equations have similar parameters (Table 4), indicating minor differences between the weighted and unweighted methods. In agreement with Mendoza *et al*. (2006) and De Esteban-Trivigno *et al*. (2008), this suggests that high taxonomical diversity leads to good predictive power functions. The equations obtained here have very low %PE values (6%) when compared with simple regressions that use skull or dental measurements of different mammalian lineages (16–97 %PE extracted from the literature; De Esteban-Trivigno *et al*., 2008: table 3). Our results match the smallest %PE of multiple regressions previously reported (4.5–7.5%; Mendoza *et al*., 2006: table 2). Although working with fragmentary fossils using equations based on a single variable (e.g. Janis, 1990) is convenient for simplicity, with almost complete specimens, our model predictions are more accurate due to smaller prediction errors and absence of allometry.

The distribution of taxa around the regression line indicates that if the taxon whose *bm* we attempt to estimate has a large

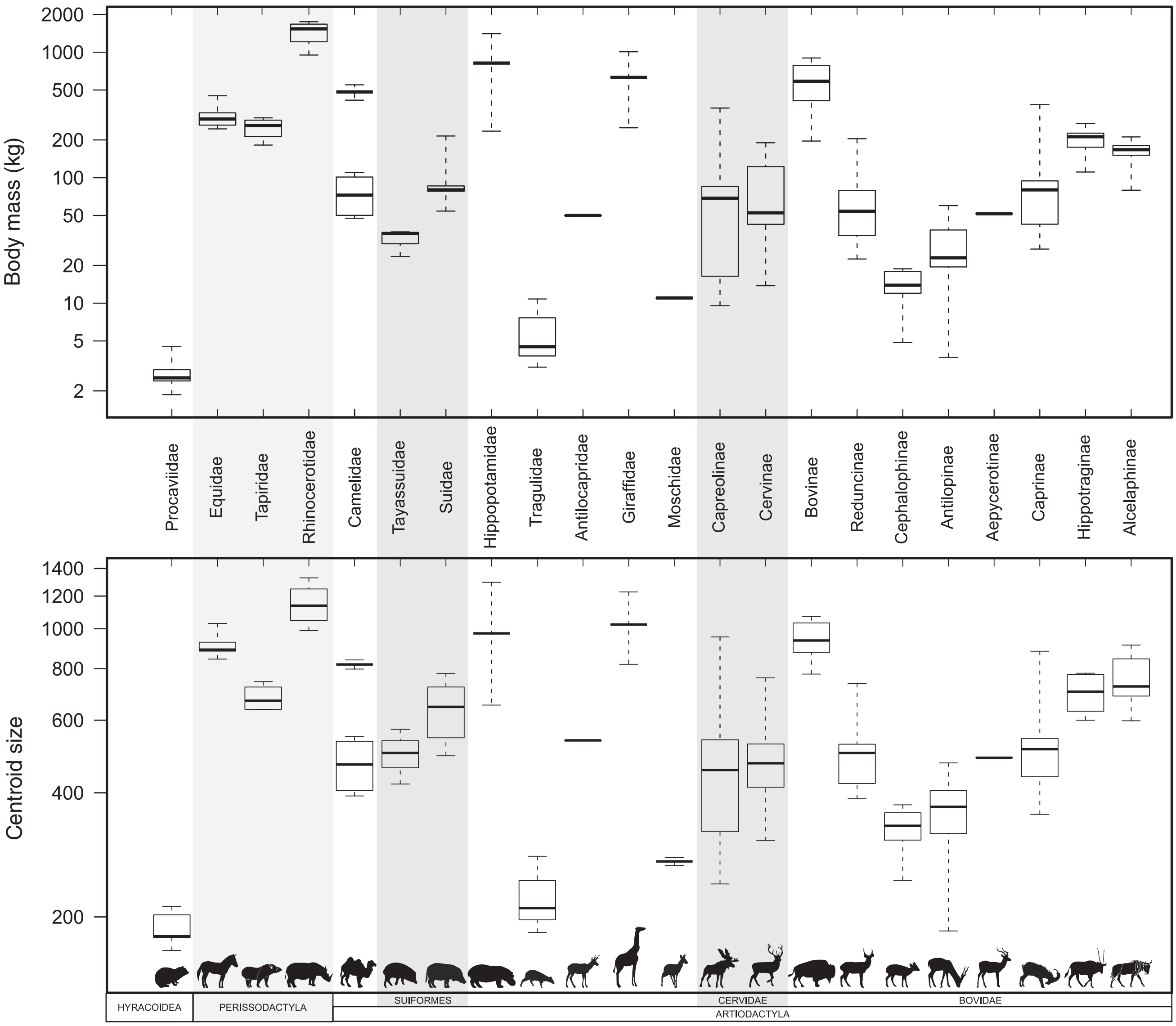

Figure 2 Box plot diagram (median, first and third quartile, and range) of body mass (top) and centroid size (bottom) within families and subfamilies categories of extant mammal sample.

skull relative to the body, the *bm* obtained could be overestimated. On the contrary, if they have a typical skull size, the OLS regression provides a reliable estimate.

The fitted values of the superior quantile regression return the maximum mean *bm* for a given *cs*. There is a low probability that an ungulate reaches a *bm* higher than that estimated by superior quantile regression. Therefore, we conclude that the superior quantile regression establishes a 'theoretical' maximum *bm* for a given centroid size.

Body mass estimation of extinct species

Applying a regression equation based on the first molar length (Damuth, 1990), Croft (2000) obtained the first *bm* estimations for Santacrucian ungulates. Croft's values for every taxon are lower than every mean value obtained here. On the contrary, *bm* estimations, which are based on a mean of several equations taken from Janis (1990), obtained by Vizcaíno *et al.* (2010) are higher (Table 6). Differences between cranial and mandibular *bm* estimates of *Astrapotherium* would reflect lower cranial *cs* due to retraction of rostral elements and a higher mandible *cs* due to a long diastema.

Most recent *bm* estimations for notoungulates (Reguero, Candela & Cassini, 2010; Elissamburu, 2011; Scarano *et al.*, 2011) provide *bm* estimates larger than those obtained here (Table 6), although our *bm* of *Pachyrukhos moyani* (1.56 kg) is very similar to the value of 1.77 kg obtained by Elissamburu (2011).

Table 4 Statistical summary of regressions obtained using the log10(centroid size) as independent variable and log10(body mass) in kg as dependent variable

Regressions	*n*	R^2	Intercept	Std. error	$t_{(n-2)}$	Slope	Std. error	$t_{(n-2)}$	RE	%PE
Sex mean										
Cr.1	238 (145 sp)	0.953	−6.506	0.120	−54.116	3.083	0.044	69.775	1.084	6.554
Md.1	230 (140 sp)	0.955	−5.665	0.109	−52.174	2.980	0.043	69.391	1.086	6.442
Species mean										
Cr.2	155	0.950	−6.539	0.155	−42.128	3.093	0.057	54.153	1.108	6.392
Md.2	147	0.956	−5.720	0.135	−42.449	3.000	0.053	56.129	1.093	6.287
A. Weighted species mean										
Cr.3	155	0.950	−6.786	0.160	−42.383	3.186	0.059	53.746	1.044	6.552
Md.3	147	0.953	−5.926	0.143	−41.525	3.085	0.057	54.134	1.033	6.748
B. Weighted species mean										
Cr.4	150	0.976	−6.701	0.113	−59.416	3.165	0.041	76.989	1.000	6.0996
Qsup			−6.926	0.178	−38.888	3.321	0.070	47.143		
Qinf			−5.902	0.385	−15.316	2.763	0.129	21.339		
Md.4	147	0.965	−5.921	0.124	−47.854	3.088	0.049	63.435	1.001	6.0604
Qsup			−6.316	0.136	−46.277	3.345	0.074	45.057		
Qinf			−5.477	0.201	−27.278	2.826	0.082	34.463		

A, weighted as in De Esteban-Trivigno *et al.* (2008); B, weighted as in Mendoza *et al.* (2006); *n*, number of observations (if not indicated correspond also to species number); Qsup, superior quantile regression (0.99); Qinf, inferior quantile regression (0.01); %PE, percent prediction error; RE, correction factor; $t_{(n-2)}$, Student's *t*-test value for both parameters. All were significant at the 0.05 level ($P < 0.00001$).

Table 5 Excluded data from indicated regression equation

Regression	Species	*r*-Student	*P*-value	*P*-Bonf
Cr.1	*Phacochoerus africanus* (M)	3.802	0.00018	0.044
Cr.4	*Catagonus wagneri*	5.161	<0.0001	<0.001
Cr.4	*Antilocapra americana*	4.646	0.00001	0.001
Cr.4	*Tayassu pecari*	4.469	0.00002	0.002
Cr.4	*Pecari tajacu*	5.435	<0.0001	<0.001
Cr.4	*Phacochoerus africanus*	4.742	<0.0001	0.001

P-value, unadjusted; *P*-Bonf, Bonferroni adjusted *P*-value. Critical value of *r*-Student equals 2.

The *bm* values obtained by the superior quantile regression should be interpreted as the maximum mean *bm* reached by an ungulate of a given *cs*. For some taxa, they are very close to the values reported in the aforementioned works. Among proterotheriids, quantile max *bm* values for *Anisolophus* and *Diadiaphorus* were very similar to those of Vizcaíno *et al.* (2010), but far lower than those of Villafañe (2005). Similarly, among notoungulates, for the toxodonts, *Adinotherium* and *Nesodon*, cranial max *bm* were similar to those obtained by Vizcaíno *et al.* (2010) and Elissamburu (2011). While in typotheres, with the exception of *Pachyrukhos moyani*, all max *bm* values were lower than previously reported.

In summary, the OLS *bm* estimates lie between those based on dental and craniomandibular measurements, suggesting that estimations based on *cs* functions could be interpreted as a 'consensus' between them. This is supported by the fact that craniomandibular measurement estimates are in the range of our 'theoretical' maximum *bm*'s obtained from quantile regression.

Paleoecology

Although the Santacrucian Age span for over several million years (~22–14 Ma, Blisniuk *et al.*, 2005), all the genera and all the size range considered in this study have been recorded in a single locality (Puesto La Costa; Tauber, 1997; Vizcaíno *et al.*, 2010; Cassini *et al.*, in press), in fossiliferous levels that may represent just different facies of the same environment.

The coexistence of many herbivores in a living assemblage implies partitioning of vegetation as a food source (Hirst, 1975). Size is one attribute of the niche differentiation in herbivorous mammals (Jarman, 1974; Owen-Smith, 1988): particularly among African bovids, the small-sized forms are more selective than the larger ones (Jarman, 1974). Also, food quality is inversely proportional to the fiber content (Illius, 1997), and while larger ungulates fed mainly on grasses, smaller ones do it on dicots (Gordon & Illius, 1996).

The Santacrucian ungulates can be separated into three size groups of base-10 logarithmic scale ranges, each log unit corresponding to one order of magnitude. The small-sized ungulates (1–10 kg) are exclusively typotheres; the medium-sized ungulates (10–100 kg) are the litoptern proterotheriids and the toxodontid *Adinotherium* spp.; and the large-sized ungulates (100–1000 kg) are the macraucheniid *Theosodon garretorum*, the toxodontid *Nesodon imbricatus* and the astrapothere *Astrapotherium magnum*.

According to the previous statements, we should expect typotheres to be highly selective dicot feeders, proterotheriids dicot selective feeders, *Adinotherium* spp. and macraucheniids mixed feeders, and *Nesodon* and astrapotheres grass bulk feeders. This scheme fits only partially with recent ecomorphologic and biomechanic feeding characterizations (see Cassini *et al.*, 2011; Cassini & Vizcaíno, 2011). Typotheres and

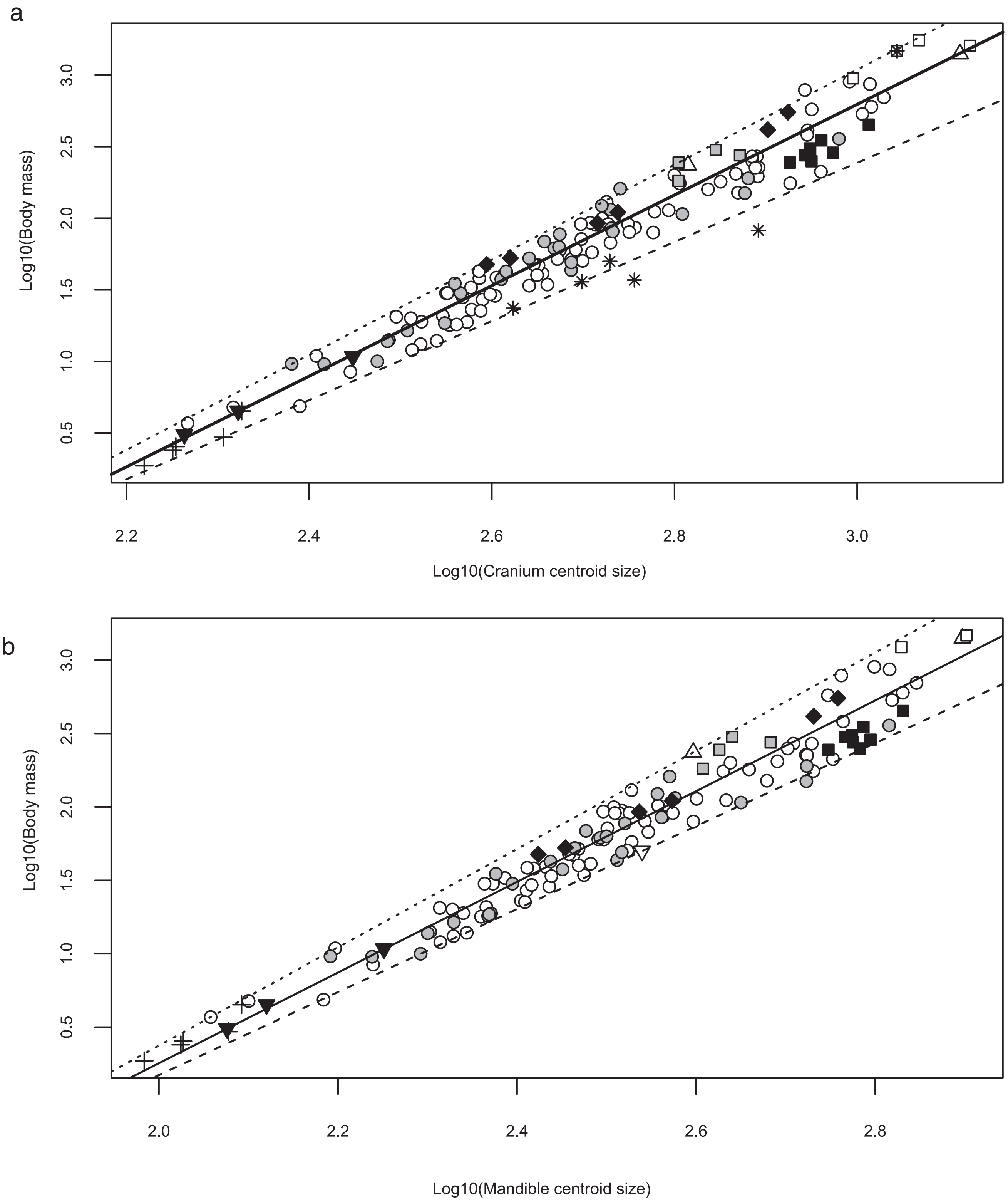

Figure 3 Dispersion diagram of cranial regression Cr.4 (a) and mandibular regression Md.4 (b). Solid line: ordinary least squares regression; dashed line: superior quantile regression; broken line: inferior quantile regression; asterisks: outliers removed from equation. Taxa symbols: cross – Hyracoidea; squares – Perissodactyla (black – Equidae; gray – Tapiridae; white – Rhinocerotidae); white triangle – Hippopotamidae; black triangle – Suiformes; black inverted triangle – Tragulidae; white inverted triangle – Antilocapridae; black rhombus – Camelidae; circle – Bovidae; gray discs – Cervidae.

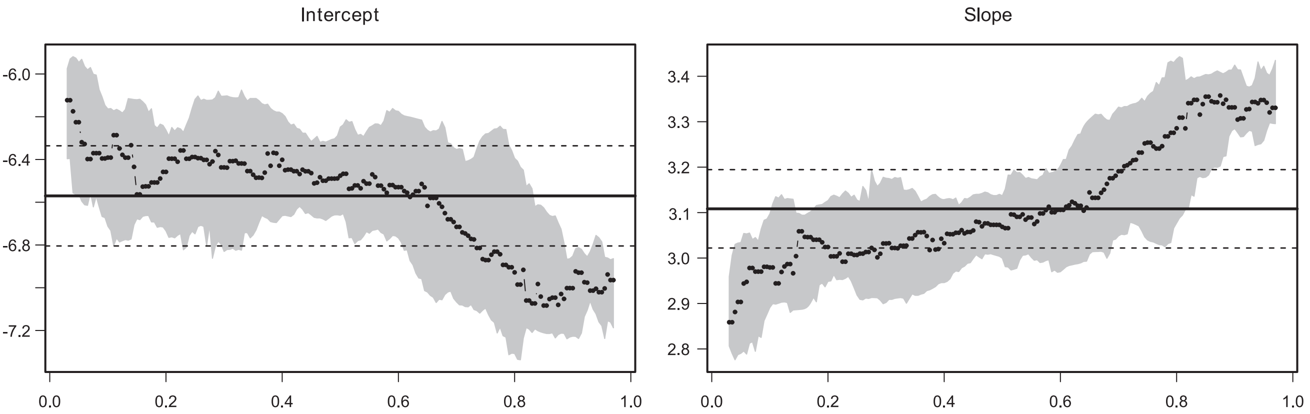

Figure 4 Ordinary least squares and quantile regression estimates for **Cr.4** model. Solid line: ordinary least squares (OLS) estimate; dotted lines: 90% confidence intervals of OLS estimates. Shaded gray area: 90% pointwise confidence band for the quantile regression estimates.

Table 6 Mean body mass (kg) of Santacrucian ungulates obtained by the regressions equations and those previously reported in the literature

	Cranium			Mandible			Croft	Other	Vizcaíno
Species	Mean ± SD	Max	*n*	Media ± SD	Max	*n*	(2000)	sources	*et al.* (2010)
Astrapotherium magnum	704.08 ± 260.18	1241.98	2	656.13 ± 213.75	1416.22	3	503.8		1021.63
Theosodon garrettorum				113.09 ± 0.00	210.14	1	46.04[a]		
Anisolophus australis				13.13 ± 0.00	20.40	1	8.84[b]	62.63(a)	18.14
Diadiaphorus majusculus	47.49 ± 1.19	73.23	4	56.08 ± 1.54	98.31	2	26.48	190.11(a)	70.25
Tetramerorhinus cingulatum	27.08 ± 0.59	40.61	2					82.76(a)	
Tetramerorhinus mixtum	19.33 ± 0.00	28.52	1					65.58(a)	
Thoatherium minusculum	19.79 ± 0.00	29.23	1	15.16 ± 0.00	23.83	1	6.25	45.00(a)	21.0
Hegetotherium mirabile	4.67 ± 0.70	6.42	3				2.190	9.69[b](b)	14.23
Pachyrukhos moyani	1.56 ± 0.00	2.04	1					1.77[b](b)	
Interatherium robustum	1.81 ± 0.43	2.37	5	1.62 ± 0.36	2.12	6	0.399	3.33[b](b)	3.5
Interatherium excavatum	1.40 ± 0.00	1.82	1						
Interatherium extensum	1.33 ± 0.00	1.72	1						
Protypotherium australe	3.63 ± 0.36	4.93	5	3.82 ± 0.00	5.35	1	2.817	6.74[b](b)/ 5.86(c)	7.8
Protypotherium attenuatum	1.93 ± 0.00	2.54	1	1.84 ± 0.00	2.43	1	0.906	2.85(c)	4.4
Protypotherium praerutilum	2.38 ± 0.10	3.16	3				0.976	4.57(c)	
Adinotherium ovinum	58.40 ± 11.67	91.07	9				33.75	119.45[b](b)	121.0[b]
Adinotherium robustum	82.06 ± 6.46	130.00	2				24.32		
Nesodon imbricatus	320.25 ± 38.34	542.59	3	429.67 ± 88.13	893.72	7	293.66	587.9[b](b)	554.0[b]

[a] Body mass obtained for *Theosodon lydekkeri*.

[b] When body mass was reported only for the genus.

Other sources: (a) Villafañe (2005); (b) Elissamburu (2011); (c) Scarano *et al.* (2011).

SD, standard deviation.

Astrapotherium depart from this pattern, the former being highly grazers and the latter a selective feeder. As described earlier, both have morphologies much different from extant ungulates toxodontids and litopterns. Typotheres, in particular, are usually described as rodent-like. Perhaps like rodents (Langer, 2002) and unlike ungulates (Pérez-Barbería & Gordon, 2001) in typotheres, fiber content was not correlated with *bm*. This issue remains as a working hypothesis for future works.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix SI Species of Santacrucian ungulates analyzed and their body mass estimates.

Appendix SII Extant ungulates reference sample.

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