Mass estimation of Santacrucian sloths from the Early Miocene Santa Cruz Formation of Patagonia, Argentina

NÉSTOR TOLEDO, GUILLERMO HERNÁN CASSINI, SERGIO FABIÁN VIZCAÍNO, and M. SUSANA BARGO

Miocene deposits of the Santa Cruz Formation, Patagonia, comprise a diverse and excellently preserved vertebrate fauna, allowing detailed paleobiological and paleoecological studies based on three ecological parameters: body mass, diet, and substrate preference. In contrast to the small and arboreal extant sloths, *Bradypus* and *Choloepus*, Santacrucian sloths were much more diverse and larger, and comprised 11 genera previously characterized as arboreal or climbing forms. Here, we focus on body mass estimation based on measurements of postcranial elements. We present a morphometric database comprising 64 linear, base-ten logged variables applied to Santacrucian sloths and a wide sample of extant mammals, as well as the body mass of the extant taxa as reported in the literature. To detect any potential phylogenetical bias, we performed a variance decomposition test on our sample of extant mammals. Based on four orthogram statistics, logged body mass was found not to be dependent on phylogenetic tree topology. Predictive equations for the body mass of extant mammals were generated through multiple regression analysis, using weighting procedures to avoid taxonomic biases and stepwise analysis to discard redundant variables. Using this procedure, we derived separate equations for the scapula, humerus, radius, ulna, pelvis, femur, tibia plus fibula, astragalus, and calcaneum. These equations were then applied to estimate the body mass of our sample of Santacrucian sloths. We obtained an average body mass of about 70 kg for the megalonychid *Eucholoeops*. Among stem megatherioids, *Hapalops* ranged between 30 and 80 kg, *Analcimorphus* was estimated at 67 kg, and *Schismotherium* at 44 kg. Larger genera included the megatheriid *Prepotherium* (~123 kg), and the mylodontids *Analcitherium* (~88 kg) and *Nematherium* (~89 kg). The medium to large body size of Santacrucian sloths imposed constraints on their climbing abilities. Megalonychids and stem megatherioids were likely unable to access the finest branches, while megatheriids and mylodonts were more terrestrial forms.

Key words: Mammalia, Xenarthra, Folivora, Santacrucian sloths, body mass, substrate preference, paleobiology, Miocene, Argentina.

Néstor Toledo [ntoledo@fcnym.unlp.edu.ar] and Sergio Fabián Vizcaíno [vizcaino@fcnym.unlp.edu.ar], División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina and CONICET-Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina;
Guillermo Hernán Cassini [gcassini@macn.gov.ar], Departamento de Ciencias Básicas, Universidad Nacional de Luján, Ruta 5 y Av. Constitución, B6700, Luján, Buenos Aires, Argentina; CONICET-Consejo Nacional de Investigaciones Científicas y Técnicas, División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Av. Angel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina;
M. Susana Bargo [msbargo@fcnym.unlp.edu.ar], División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina and CIC-Comisión de Investigaciones Científicas, Provincia de Buenos Aires, Argentina.

Introduction

The mostly fluvial deposits of the Santa Cruz Formation (late Early Miocene, ~18–16 Ma) along the Atlantic coast of Santa Cruz Province (Patagonia, Argentina) preserve a rich and diverse vertebrate fauna, comprising xenarthrans such as sloths (Folivora), anteaters (Vermilingua), and armadillos and glyptodonts (Cingulata), as well as marsupials, astrapotheres, notoungulates, litopterns, rodents, primates, and birds (Tauber 1997a,b; Vizcaíno et al. 2012c). The remains are excellently preserved, thus offering the possibility of detailed paleobiological analyses.

Eleven genera of relatively large sloths have been iden-

Acta Palaeontol. Pol. 59 (2): 267–280, 2014

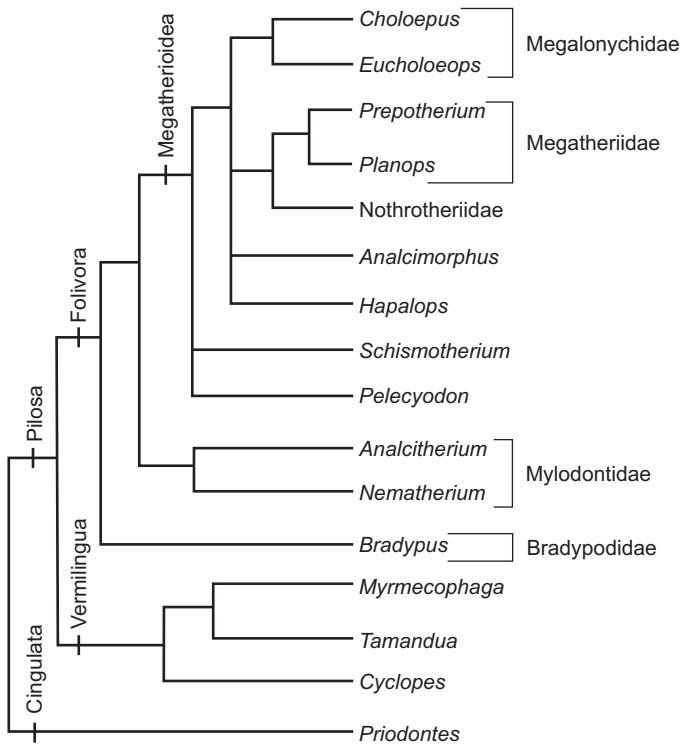http://dx.doi.org/10.4202/app.2012.0009

Fig. 1. Cladogram showing the phylogenetic relationships among the xenarthrans included in this study. Modified from Gaudin (2004).

tified from the Santa Cruz Formation. These include *Eucholoeops* and *Megalonychotherium* (forming part of the Megalonychidae); *Planops* and *Prepotherium* (Megatheriidae); *Hapalops*, *Hyperleptus*, *Analcimorphus*, *Schismotherium*, and *Pelecyodon* (stem megatherioids sensu Gaudin 2004); and *Nematherium* and *Analcitherium* (Mylodontidae). These fossil taxa contrast in their diversity and size with the extant sloths, which are represented by only two genera (*Bradypus* and *Choloepus*), both fully arboreal and weighing less than 10 kg (Nowak 1999). The Santacrucian genera are considered to represent the first major radiation of three of the five major folivoran families (Megalonychidae, Megatheriidae and Mylodontidae; see Fig. 1). By contrast, no representatives of Nothrotheriidae are known from the Santa Cruz Formation, while Bradypodidae lacks any fossil record whatsoever (see Gaudin 2004; McDonald and De Iuliis 2008).

Previous studies have analyzed the position of mammalian species within their respective communities in terms of three ecological parameters: body mass, diet, and substrate preference (including locomotion) (Andrews et al. 1979; Van Couvering 1980; Reed 1998; Kay and Madden 1997; Vizcaíno et al. 2006, 2008, 2010; Kay et al. 2012). Out of the latter, the diet and substrate preference of Santacrucian sloths have been the focus of several studies. Bargo et al. (2009) analyzed the masticatory movements and potential food sources of *Eucholoeops*, and made comparisons with other megatherioids, such as *Hapalops*, and mylodontids, such as *Nematherium*. White (1993, 1997) used several functional indices to propose that *Hapalops* and *Eucholoeops* were mainly arbo-

real or semi-arboreal, while *Prepotherium* was likely more terrestrial. Finally, a recent morphometric study focusing on the forelimbs of the Santacrucian sloths concluded that they resembled extant anteaters and pangolins, rather than extant sloths, in terms of their functional capabilities (Toledo et al. 2012). This finding potentially implies the ability to dig, and probably arboreal and semiarboreal habits for these taxa.

Body mass is among the most important variables in mammalian biology because it correlates with several significant biological parameters, such as basal metabolic rate, cardiac rhythm, sleeping times, or energetic requirements (e.g., Smith and Savage 1955; Eisenberg 1981; Hildebrand 1988; Brown and West 2000 and references therein). Previous body mass estimates for the Santacrucian sloths have mainly relied on regressions based on the bicondylar width of the femur or the diameter of the femoral head (White 1993; Croft 2000, 2001).

Obtaining reliable mass estimates of extinct mammals from allometric functions has been controversial (Millien and Bovy 2010). Mass estimates based on dental measurements were reported by Fortelius (1990) and by Millien and Bovy (2010), who concluded that, when available, other measures are preferable. Several authors have provided body mass estimates for Pleistocene ground sloths based on linear regressions (e.g., Fariña et al. 1998; Christiansen and Fariña 2003), but cautioned that taking a wider set of variables into account would likely lead to more robust estimates.

De Esteban-Trivigno et al. (2008) developed a robust set of predictive equations based on fore- and hind limb measurements from a wide sample of extant mammals, and applied them to Pleistocene xenarthrans, including ground sloths. These authors used weighting procedures to avoid taxonomic bias and indices of perceptual error to evaluate the accuracy of their estimates. Postcranial elements have been claimed as the best elements on which to base mass estimates, because they support the weight of the body (Gingerich 1990; White 1993; De Esteban-Trivigno et al. 2008 and references therein). This is especially true for fossil sloths, as their limbs supported relatively larger muscular masses than found in any living mammal, except those with fossorial adaptations (Bargo et al. 2012). Unfortunately, the equations of De Esteban-Trivigno et al. (2008) are not applicable to the Santacrucian remains, because there are few specimens retaining all of the fore- and hind limb elements, despite the generally excellent state of preservation. Here, we present a set of predictive body mass equations for fossil sloths, based on limb bone measurements, which are suitable for incomplete specimens.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; MLP, Museo de La Plata, La Plata, Argentina; MPM-PV, Museo Regional Provincial Padre M. Jesús Molina, Río Gallegos, Argentina; YPM-VPPU, Yale Peabody Museum, Vertebrate Paleontology, Princeton University Collection, New Haven, USA.
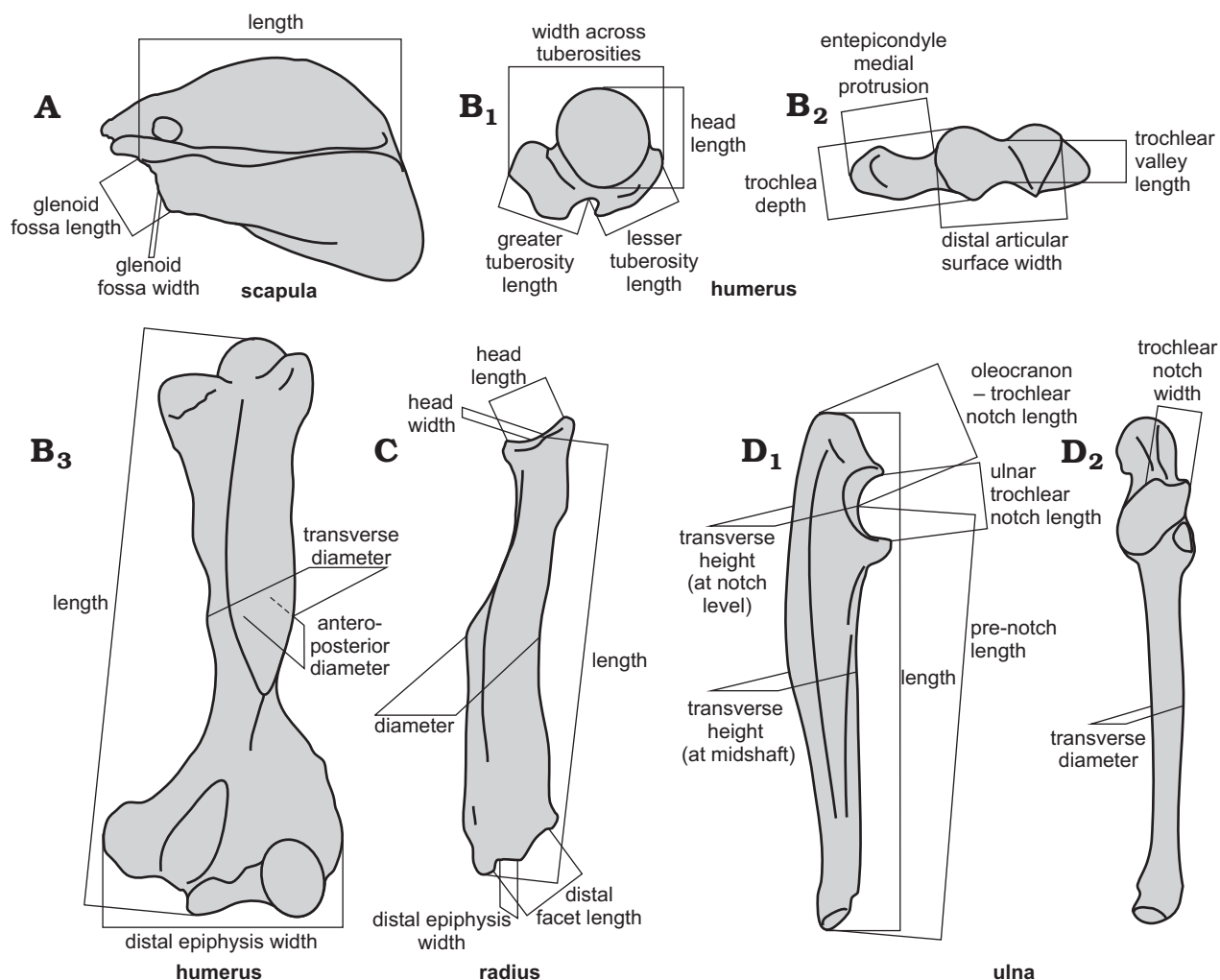
Fig. 2. Measurements used in this work, as illustrated using the left forelimb of *Hapalops*. **A**. Scapula in lateral view, anteroventral aspect to the left. **B**. Humerus in proximal view (B_1), anterior aspect down; distal view (B_2), anterior aspect up; anterior view (B_3), proximal end up. **C**. Radius in anterior view, proximal end up. **D**. Ulna in medial view (D_1), anterior aspect right; anterior view (D_2).

Other abbreviations.—QMLE, Quasi Maximum Likelihood Estimator; PE, Percentual Error of the estimate; RE, Ratio Estimator; SE, Smearing Estimator.

Material and methods

The fossil material studied here was collected by expeditions during the 19th and early 20th centuries (MLP, YPM-VPPU, AMNH, and FMNH), as well as MLP-Duke University joint expeditions (MPM-PV) over the last nine years (2003–2011). The specimens of extant mammals are housed mostly at the AMNH and the FMNH.

We constructed a morphometric database of extant mammals including xenarthrans, marsupials, pholidotans, tubulidentates, carnivorans, primates and rodents (SOM 1 and 2, Supplementary Online Material available at http://app.pan.pl/ SOM/app59-Toledo_etal_SOM.pdf), based on 64 linear variables (Appendix 1 and Figs. 2, 3) commonly used to quantify the proportions and dimensions of the appendicular skeleton

(e.g., Alexander et al. 1979; Scott 1990; Sargis 2002a, b; Elissamburu and Vizcaíno 2004; Candela and Picasso 2008; De Esteban-Trivigno et al. 2008). When available from the literature (Nowak 1999), gender-specific body mass was included. A second database of 44 Santacrucian sloths was built using the same measurements (Table 1; SOM 2).

Phylogenetic bias analysis

In order to identify a putative phylogenetic bias in the distribution of body mass within our sample of extant mammals, we performed a variance decomposition test (Ollier et al. 2006). This test decomposes the variance of a given trait with respect to the topological structure of a phylogenetic tree (in our case, the phylogeny of Asher and Helgen 2010; Fig. 4), and determines whether it is concentrated at one or more particular nodes of the latter. This method does not take into account the distance between individual nodes, but focuses only on the topology of the tree. The total absence of phy-

Table 1. Santacrucian fossil sloth specimens included in this study.

Family	Taxon	Collection number
indet.	Folivora indet.	MPM-PV 3458
		MPM-PV 3454
		MPM-PV 3462
Megalonychidae	*Eucholoeops* cf. *E. fronto*	MPM-PV 3403
	Eucholoeops ingens	FMNH 13280
		MPM-PV 3451
	Eucholoeops sp.	MPM-PV 3402
		MPM-PV 3651
	Megalonychidae indet.	AMNH 9249
		AMNH 94754
Basal megatherioids	*Analcimorphus giganteus*	YPM-VPPU 15561
	cf. *Hapalops*	MPM-PV 3404
	Hapalops angustipalatus	YPM-VPPU 15562
	Hapalops elongatus	FMNH 13133
		FMNH 13123
		YPM-VPPU 15155
	Hapalops indifferens	YPM-VPPU 15110
	Hapalops longiceps	YPM-VPPU 15523
	Hapalops platycephalus	YPM-VPPU 15564
	Hapalops rectangularis	AMNH 9222
		FMNH 13143
	Hapalops ruetimeyeri	FMNH 13128
		FMNH 13130
	Hapalops sp.	AMNH 9252
		FMNH 15103
		MLP 34-III-5-1
		MPM-PV 3412
		MPM-PV 3467
		MPM-PV 3400
		YPM-VPPU 15414
		YPM-VPPU 15597
		YPM-VPPU 15005
		YPM-VPPU 15045
		YPM-VPPU 15160
		YPM-VPPU 15183
		YPM-VPPU 15618
		YPM-VPPU 15836
		YPM-VPPU 15520
	Schismotherium fractum	FMNH 13137
Megatheriidae	Megatheriidae indet.	MPM-PV 3408
	Prepotherium potens	YPM-VPPU 15345
Mylodontidae	*Analcitherium*? sp.	FMNH 13131
	Mylodontidae indet.	MPM-PV 3406
	Nematherium angulatum	FMNH 13129

logenetic dependency was considered the null-hypothesis. Following Ollier et al. (2006), we compared the observed variance decomposition to a theoretical distribution based on 20 000 Monte-Carlo permutations using four statistics: R2Max, with high values indicating significant changes in body mass variance at a single node; Dmax, corresponding

to the Kolmogorov-Smirnov statistic, which tests whether the vector describing the studied variable matches a random sample from a uniform distribution; SkR2k, indicating the degree of asymmetry (skewness) in body mass variance; and SCE, which measures the local averaged variation in the orthogram values. All calculation were performed in R (R Development Core Team 2011) using the 'ade4' package (Dray and Dufour 2007).

Predictive equations for body mass estimation

We developed separate multiple regression models for the scapula, humerus, ulna, radius, pelvis, femur, tibia-fibula, astragalus, and calcaneum, using the 64 size variables as predictors and body mass as the dependant variable. Owing to the volumetric nature of body mass, and to ensure a normal distribution, all of the data were base-ten log-transformed prior to the analysis. Following De Esteban-Trivigno et al. (2008), a weighting factor was introduced to account for the over-representation of some clades (xenarthrans and carnivorans). Redundant variables were discarded from all models using a stepwise method (backwards-forwards; Hocking 1976), based on the Akaike Information Criterion (Sakamoto et al. 1986; SOM 1). The final models were then used to estimate the body mass of Santacrucian sloths.

When body mass values inferred using least squares regression are transformed back to arithmetic units, log-adjustment can result in biased estimates (Smith 1993). We corrected for this potential bias (and thus restored dimensionality) by applying the "Ratio Estimator" (RE) of Snowdon (1991), the "Quasi Maximum Likelihood Estimator" (QMLE) of Fergusson (1986), and the "Smearing Estimator" (SE) of Duan (1983).

The equation reliability was evaluated using the Percent Prediction Error %PE = 100 x [observed-predicted]/predicted (Smith 1984). This index is more reliable than the correlation coefficient, which is affected by the range of values of the dependent variable and thus a poor indicator of the predictive power of the independent variable(s) (e.g., De Esteban-Trivigno et al. 2008; Cassini et al. 2012).

All calculations were performed using the open-access statistical package R (R Development Core Team 2011). Details of the scripts and modules used here are provided in SOM 1.

Results

Phylogenetic bias analysis.—None of the four orthogram statistics for variance independence resulted in significant values (see Table 2 and Fig. 5), thus indicating that the (log-transformed) body mass of extant mammals is not dependent on tree topology.
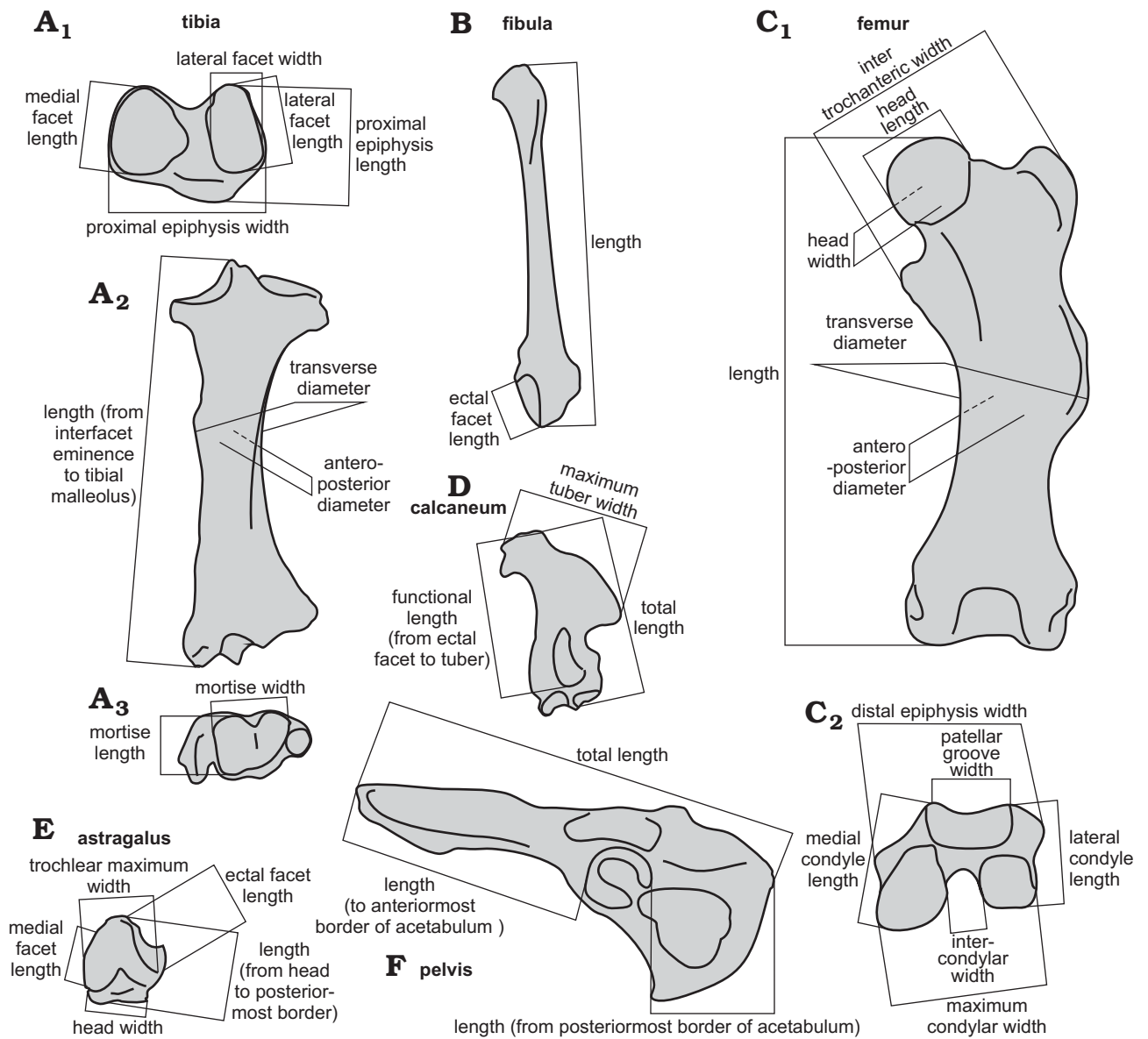
Fig. 3. Measurements used in this work, as illustrated using the left hind limb of *Hapalops*. **A**. Tibia in proximal view (A_1), anterior aspect down; anterior view (A_2), proximal end up; distal view (A_3), anterior aspect up. **B**. Fibula in anterior view, distal end down. **C**. Femur in anterior view (C_1), distal end down; distal view (C_2), anterior aspect up. **D**. Calcaneum in dorsal view, anterior aspect down. **E**. Astragalus in dorsal view, anterior aspect down. **F**. Pelvis in left lateral view.

Predictive equations for body mass.—Those equations with lower R^2 values (radius and calcaneum) showed higher %PE values, and vice versa (humerus and femur). The former also showed higher QMLE values. All the SE and QMLE values were very close to 1, which suggests little, but not necessarily no bias. We therefore conservatively used the RE coefficient to re-transform the logged body size estimates (Table 3; see also Christiansen and Harris [2005] and De Esteban-Trivigno et al. [2008]). While all equations showed high R^2 (>0.80) and highly significant P values, the humeral and femoral equations stood out as those with the lowest %PE (~9 and ~8%, respectively). Therefore, we assumed that the most reliable equations were those corresponding to the humerus and femur, while those based on the radius,

calcaneum and ulna were less accurate (Table 3). The final equations used to estimate the body mass of the Santacrucian sloths are shown in Table 4. No fibular variable was conserved in the final equations.

Table 2. Obtained values for the four statistics for variance independence, based on 20 000 Monte-Carlo permutations.

Test	Observed values	Standard deviation of observed values	Alternative hypothesis	Probability values (P)
R2Max	0.2279288	-0.25450430	greater	0.50160
SkR2k	12.2341244	-0.36863125	lesser	0.36445
Dmax	0.1521757	0.05894575	two-tailed	0.95880
SCE	0.1498420	-0.66036589	greater	0.73910

Table 3. Statistics for each of the predictive equations. R^2, coefficient of determination; adjusted-R^2, coefficient of determination adjusted by the number of explanatory terms in the model; F, value of Fisher Test for null dependency and associated degrees of freedom (df); p-F, probability of the F-test; RE, "Ratio Estimator"; QMLE, "Quasi Maximum Likelihood Estimate"; SE, "Smearing Estimate"; %PE, Percent Prediction Error of the estimate.

Element	R^2	adjusted-R^2	F(df, df)	p-F	RE	QMLE	SE	%PE
Scapula	0.916	0.908	125.048 (2, 23)	4.39E-13	1.018	1.005	1.005	13.963
Humerus	0.970	0.963	130.357 (5, 20)	1.49E-14	0.979	1.002	0.999	9.263
Ulna	0.880	0.875	175.608 (1, 24)	1.56E-12	1.213	1.008	1.041	21.167
Radius	0.862	0.849	71.548 (2, 23)	1.34E-10	1.031	1.009	1.014	41.363
Pelvis	0.836	0.821	58.448 (2, 23)	9.62E-10	1.301	1.011	1.040	18.663
Femur	0.968	0.955	77.674 (7, 18)	3.76E-12	1.055	1.003	1.014	7.833
Tibia-fibula	0.934	0.917	56.428 (5, 20)	4.17E-11	1.126	1.005	1.023	13.598
Astragalus	0.862	0.850	72.080 (2, 23)	1.24E-10	1.034	1.009	0.996	18.419
Calcaneum	0.802	0.794	97.417 (1, 24)	6.34E-10	1.270	1.012	1.048	47.838

Table 4. Final predictive equations for each of the studied elements of the appendicular skeleton. See Appendix 1 for explanations of abbreviations.

Element	Equation
Scapula	$-2.737 + 1.767 \times SGL1 + 0.8131 \times SL$
Humerus	$-1.971 + -0.925 \times TDH + 1.993 \times APDH + 0.553 \times HDASW + 0.599 \times HTVL + 0.5127 \times HEMP$
Ulna	$-0.701 + 2.0634 \times TDU$
Radius	$-1.764 + 1.0822 \times RHL + 1.645 \times RDEW$
Pelvis	$-4.049 + 3.895 \times PL + -1.669 \times ILL$
Femur	$-1.116 + -1.437 \times TDF + 1.026 \times WTroc + -1.026 \times FL + 1.2154 \times FHL + -1.505 \times FCW + 2.388 \times MCL + 1.762 \times PGW$
Tibia and fibula	$-1.592 + 1.079 \times APDT + -0.531 \times TMW + 2.115 \times LTFW + -2.638 \times LTFL + 2.011 \times TPEW$
Astragalus	$-1.209 + -0.780 \times ATMW + 3.099 \times AHW$
Calcaneum	$-1.898 + 2.1308 \times FCL$

Estimated body mass of Santacrucian sloths.—The mean body mass and ponderated mean value (weighted by the %PE value; see Christiansen and Harris 2005) for each specimen are listed in Table 5. Mean values for each genus are shown in Table 6. Estimated body mass values ranged between 40 and 80 kg (Tables 5, 6), except for the megatheriids and mylodontids. The genus with the most reliable estimates was the stem megatherioid *Hapalops*, owing to the great number of available specimens and preserved elements, followed by the megalonychid *Eucholoeops*. Conversely, the estimates for the remaining genera were less reliable, owing to the relatively small number of specimens and/or elements on which they were based.

Eucholoeops showed an average body mass of about 60 kg, with *E. fronto* weighing about 65 kg, and *E. ingens* estimated at 53 kg (Table 5). For *Hapalops*, the mean was about 45 kg, but with high intra- and interspecific variability (Table 5). Thus, for example, the smallest and largest specimens of *H. ruetimeyeri* and *H. elongatus* differed by more than 10 kg. *Hapalops rectangularis*, on the other hand, showed less variation, ranging between 31.5 and 38 kg. Other species of

the genus were heavier, reaching weights of 49.4 kg (*H. platycephalus*) and 56 kg (*H. indifferens*). Finally, *H. longiceps* was the biggest species of the genus (83.8 kg). The remaining basal megatherioids included *Analcimorphus* (67 kg) and *Schismotherium* (44 kg).

Larger genera were represented by the megatheriid *Prepotherium* (123.2 kg), the mylodontids *Analcitherium* (88.2 kg) and *Nematherium* (89.3 kg), and some taxonomically unassigned specimens showing even larger estimates. Based on the tibial, astragalar and calcaneal equations, the mylodontid MPM-PV 3406 was about 170 kg, which was only surpassed by the megatheriid MPM-PV 3408 at around 200 kg (based on the astragalar equation).
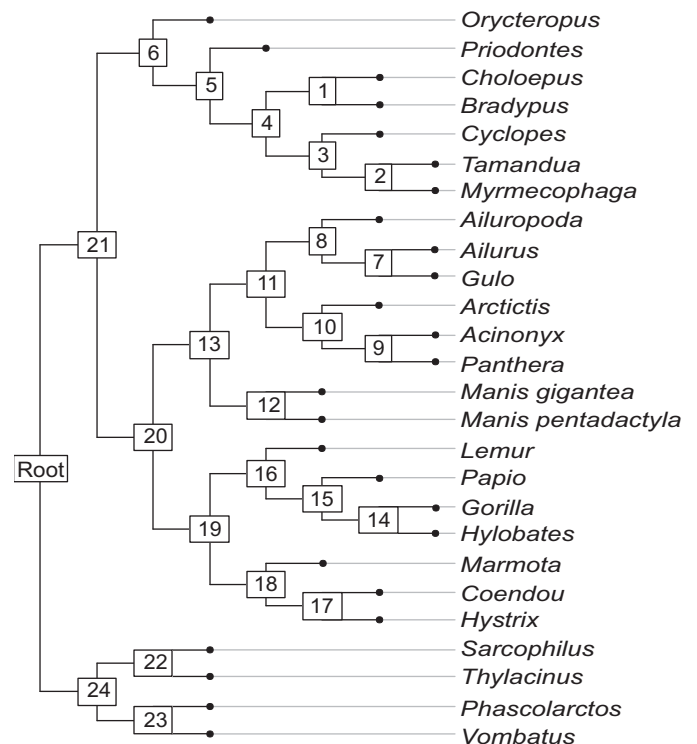

Fig. 4. Phylogenetic tree following Asher and Helgen (2010), as used in the variance decomposition test. The nodes are arbitrarily labeled with numbers.

Table 5. Mean and weighted estimates of body mass (in kg) for specimens analyzed in this work. Weighted means were calculated taking into account %PE. Abbreviations: Pond. Mean, mean ponderated by the %PE index for each equation; Pond. #, number of equations per specimen. SD, standard deviation.

Family	Collection number		Taxon	Mean	Pond. mean	Pond #	SD
indet.	MPM-PV	3458	Folivora indet.	98.130	88.220	3	62.864
indet.	MPM-PV	3454	Folivora indet.	90.383	90.383	1	
indet.	MPM-PV	3462	Folivora indet.	15.823	15.823	1	
Megalonychidae	MPM-PV	3403	*Eucholoeops* cf. *E.fronto*	66.610	64.668	3	18.100
Megalonychidae	FMNH	13280	*Eucholoeops ingens*	35.728	35.728	1	
Megalonychidae	MPM-PV	3451	*Eucholoeops ingens*	53.248	53.248	1	
Megalonychidae	MPM-PV	3402	*Eucholoeops* sp.	62.168	62.168	1	
Megalonychidae	MPM-PV	3651	*Eucholoeops* sp.	73.575	72.081	6	30.464
Megalonychidae	AMNH	9249	Megalonychidae indet.	31.775	33.874	3	6.172
Megalonychidae	AMNH	94754	Megalonychidae indet.	25.854	27.242	3	8.211
Megatheriidae	MPM-PV	3408	Megatheriidae indet.	200.321	200.321	1	
Megatheriidae	YPM-VPPU	15345	*Prepotherium potens*	107.793	123.227	2	81.142
Basal Megatherioidea	YPM-VPPU	15561	*Analcimorphus giganteus*	64.395	66.908	4	10.849
Basal Megatherioidea	MPM-PV	3404	cf. *Hapalops*	57.388	65.313	2	17.674
Basal Megatherioidea	YPM-VPPU	15562	*Hapalops angustipalatus*	47.338	33.862	5	31.876
Basal Megatherioidea	YPM-VPPU	15155	*Hapalops elongatus*	27.685	27.685	1	
Basal Megatherioidea	FMNH	13133	*Hapalops elongatus*	36.557	31.283	3	17.388
Basal Megatherioidea	FMNH	13123	*Hapalops elongatus*	53.593	45.019	3	25.218
Basal Megatherioidea	YPM-VPPU	15110	*Hapalops indifferens*	72.292	56.077	3	39.865
Basal Megatherioidea	YPM-VPPU	15523	*Hapalops longiceps*	84.288	83.772	7	37.624
Basal Megatherioidea	YPM-VPPU	15564	*Hapalops platycephalus*	51.627	49.390	2	37.825
Basal Megatherioidea	FMNH	13143	*Hapalops rectangularis*	30.115	31.481	4	8.335
Basal Megatherioidea	AMNH	9222	*Hapalops rectangularis*	40.426	38.050	5	21.359
Basal Megatherioidea	FMNH	13128	*Hapalops ruetimeyeri*	23.815	20.312	2	18.413
Basal Megatherioidea	FMNH	13130	*Hapalops ruetimeyeri*	37.058	36.841	4	15.226
Basal Megatherioidea	AMNH	9252	*Hapalops* sp.	7.944	7.944	1	
Basal Megatherioidea	YPM-VPPU	15414	*Hapalops* sp.	16.160	16.160	1	
Basal Megatherioidea	YPM-VPPU	15597	*Hapalops* sp.	19.694	18.166	2	4.278
Basal Megatherioidea	FMNH	15103	*Hapalops* sp.	19.851	19.626	2	0.986
Basal Megatherioidea	YPM-VPPU	15005	*Hapalops* sp.	29.414	25.104	3	10.235
Basal Megatherioidea	YPM-VPPU	15045	*Hapalops sp.*	32.226	29.264	3	11.798
Basal Megatherioidea	YPM-VPPU	15160	*Hapalops* sp.	30.069	29.509	2	2.024
Basal Megatherioidea	MLP	34-III-5-1	*Hapalops* sp.	40.581	40.581	1	
Basal Megatherioidea	YPM-VPPU	15183	*Hapalops* sp.	43.152	43.152	1	
Basal Megatherioidea	YPM-VPPU	15618	*Hapalops* sp.	48.487	48.487	1	
Basal Megatherioidea	MPM-PV	3412	*Hapalops* sp.	48.580	48.580	1	
Basal Megatherioidea	MPM-PV	3467	*Hapalops* sp.	52.648	52.395	4	6.167
Basal Megatherioidea	MPM-PV	3400	*Hapalops* sp.	68.013	59.402	6	40.209
Basal Megatherioidea	YPM-VPPU	15836	*Hapalops* sp.	68.113	68.113	1	
Basal Megatherioidea	YPM-VPPU	15520	*Hapalops* sp.	95.175	74.513	3	48.160
Basal Megatherioidea	FMNH	13137	*Schismotherium fractum*	37.992	43.722	2	18.250
Mylodontidae	FMNH	13131	*Analcitherium*? sp.	88.226	88.226	1	
Mylodontidae	MPM-PV	3406	Mylodontidae indet.	181.167	168.262	3	38.735
Mylodontidae	FMNH	13129	*Nematherium angulatum*	89.329	89.329	1	

Discussion

Estimation of body mass.—The absence of any obvious phylogenetic bias in our analysis of extant mammals likely is a result of the wide range of sampled taxa, and corroborates the conclusions of Mendoza et al. (2006). However, this finding does not exclude the possibility that phylogenetic biases may affect patterns within particular clades, such as folivorans. Most of our predictive equations include the diaphyseal width of each bone (humerus, ulna, femur, and tibia), as well as the width and depth of the distal epiphysis, thus reflecting the overall robustness of the element.
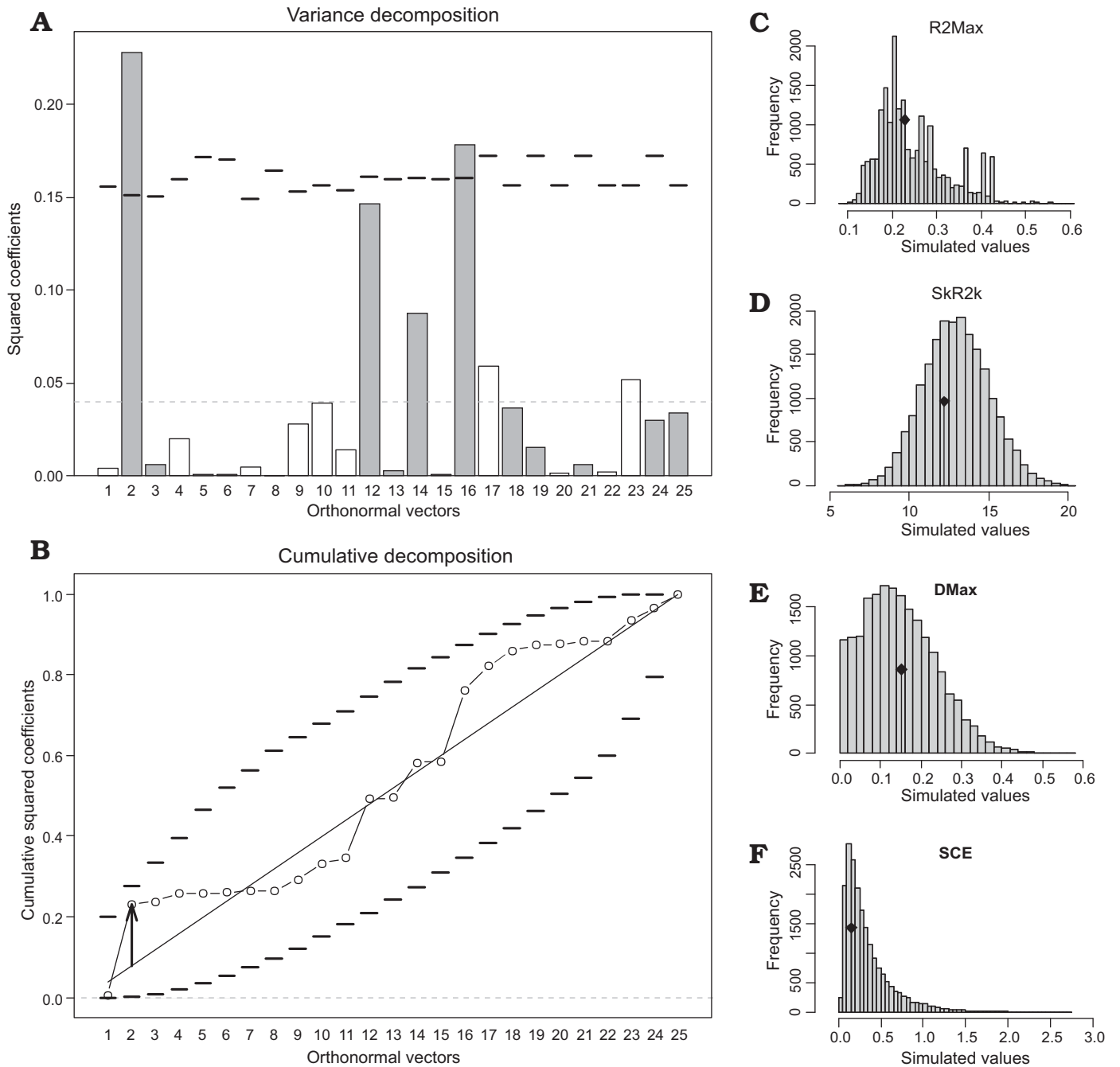
Fig. 5. **A**. Orthogram plot. The bars are proportional to the squared coefficients (white and gray bars stand for positive and negative coefficients, respectively). The dashed line is the upper confidence limit at 5%, deduced from 20000 Monte Carlo permutations (mean value indicated by the horizontal solid line). **B**. Cumulative orthogram plot. Circles represent observed values of cumulated squared coefficients, expected values under H0 are along the straight line, and dashed lines stand for the bilateral confidence interval. The cumulative decomposition remained between the confidence limits. **C–F**. Histograms of observed values for the four test statistics, all of which were non-significant after 20 000 Monte-Carlo permutations. The black dot depicts the observed parameter value.

Our equations represent an improvement on those of White (1993, 1997) and Croft (2000, 2001) in including more than one variable, more than a single postcranial element, and being derived from a more diverse sample of extant mammals. In addition, although our equations are not as robust as the ones provided by de Esteban-Trivigno et al. (2008), they have the advantage of being applicable to incomplete specimens—a very common situation in pale-

ontology. The best estimators are the humeral and femoral equations (lowest %PE values), while were radial and calcaneal equations show a greater degree of distortion. These findings are in agreement with those of Gingerich (1990) and Biknevicius (1993).

Our body mass estimates for *Eucholoeops* differ markedly from the 40 kg obtained by Croft (2000) based on regressions against the femoral bicondylar width, and are closer

Table 6. Mean and weighted estimates of body mass (in kg) for the genera included in this study. Abbreviations: Pond. Mean, weighted mean; Pond. Estimate, body mass estimate weighted by the number of equations instead of number of specimens (only for *Hapalops* and *Eucholoeops*), SD, standard deviation.

Taxon	Family	Mean	SD	Pond. Mean	SD	Pond. Estimate
Eucholoeops	Megalonychidae	59.52	14.597	58.661	15.858	65.853
Prepotherium	Megatheriidae	107.793	NA	123.227	NA	NA
Hapalops	Basal Megatherioidea	43.266	21.216	39.799	18.578	45.042
Analcimorphus	Megatheriidae	64.395	NA	66.908	NA	NA
Schismotherium	Megatheriidae	37.992	NA	43.722	NA	NA
Analcitherium	Mylodontidae	88.226	NA	88.226	NA	NA
Nematherium	Mylodontidae	89.329	NA	89.329	NA	NA

to the results of Bargo et al. (2009), who based them on the length of the humerus using allometric equations provided by Scott (1990). The apparent variability in the body size of *Hapalops* is also consistent with the results of Bargo et al. (2009), which ranged between approximately 30 and 80 kg, but differs strikingly from the estimates of other authors. Our estimate of around 84 kg for *H. longiceps* is very similar to the 73.8–81.4 kg calculated by White (1993) based on the femoral head diameter, but lower than the 156 kg obtained by Croft (2001). The same holds true for *H. indifferens*, with our estimate of 56 kg being much higher than the 20.1 kg estimated by Croft (2000), but similar to the 58.3 kg estimated by White (1993).

At 44 kg, *Schismotherium* is one of lightest megatherioids. However, owing to its relatively poor state of preservation, we were unable to estimate the body mass of *Pelecyodon* (AMNH 9240), which seems to be a juvenile individual. By contrast, the mylodontids (*Analcitherium* and *Nematherium*, around 90 kg) and the megatheriids (*Prepotherium*, about 120 kg) are among the heaviest Santacrucian sloths. This estimate is lower than the 174–229 kg proposed for *Prepotherium* by White (1993). Cassini et al. (2012) classified Santacrucian ungulates into three base-ten logarithmic body size ranges: small-sized forms (1–10 kg), medium-sized-forms (10–100 kg), and large-sized forms (100–1000 kg). According to this scale, most of the Santacrucian sloths are therefore medium-sized, with the exception of the large-sized megatheriids and the mylodontids.

Body size and substrate preference.—Previous authors characterized the Santacrucian sloths as arboreal or semi-arboreal (White 1993, 1997). Access to arboreal substrates offers several advantages, such as food resources not available at ground level, shelter, and more efficient locomotion when the ground is rough or flooded (Hildebrand 1988). However, locomotion on arboreal substrates involves its own difficulties, which are related to two main issues: movement on a three-dimensional and discontinuous substrate, and the risk of falling during locomotion and resting. Most extant arboreal mammals are either small or medium-sized (Table 7; Eisenberg 1981). Indeed, there are no capable climbers as large as Santacrucian sloths in our sample of extant mammals, except for *Gorilla* (150 kg) and some specimens of *Acynonix* and *Panthera tigris* (50 and 200 kg, respectively).

A relatively large body size may decrease the risk of predation and allow the animal to budget its energetic resources long-term (Hildebrand 1988). The latter advantage is especially important for xenarthrans, owing to their low basal metabolic rate (McNab 1985, 2000; Vizcaíno et al. 2006; Bargo and Vizcaíno 2008; Vizcaíno 2009). On the other hand, large body size also imposes strong constraints on, for example, reproduction, substrate preference and locomotor strategies (Hildebrand 1988).

Among extant xenarthrans, anteaters, the sister group to sloths, seem to be better analogues than extant sloths in terms of understanding the relationship between the size and substrate preference of the Miocene taxa. Body size among extant xenarthrans is correlated with substrate preference: the minute *Cyclopes* (less than 0.5 kg) is strictly arboreal, *Tamandua* (around 5 kg) is a semi-arboreal form, and the giant anteater *Myrmecophaga* (about 30 kg) is terrestrial and only climbs occasionally (Taylor 1978; White 1993; Rodrigues et al. 2008). It therefore seems that body size imposes a strong constraint on arboreal capabilities (Taylor 1985), implying that some of the larger Miocene sloths, such as *Prepotherium* and the mylodonts (exceeding 80 kg), were almost certainly too heavy to be fully arboreal.

An important factor involved in arboreality is the resistance to a fall. Heavier animals reach higher kinetic energies during a fall than smaller ones for equal conditions of distance, time and gravity acceleration (Hill 1950), making them more vulnerable to injury. Thus, most of the more agile and acrobatic arboreal animals are small (Cartmill 1985). The only fully arboreal primate as heavy as the Santacrucian sloths is the orangutan (*Pongo pygmaeus*, ~90 kg; Nowak 1999), whose locomotor style consists of suspending its body from branches using most or all of its long limbs at the same time, thus distributing its weight over several supports. The animal is considered to be very close to the maximum operational body size for feeding in an arboreal substrate (Cartmill 1985). Among carnivorans, many ursids are heavier than the orangutan and are excellent climbers (e.g., the spectacled bear *Tremarctos ornatus*, and the American black bear *Ursus americanus*, both around 120 kg, Nowak 1999). However, these bears are among the smallest members of the family, and they are not as specialized as primates in their climbing abilities.

Table 7. Body mass and substrate preference of the extant mammals included in this analysis.

Taxon	Order	Family	Mean (kg)	Substrate preference
Choloepus	Folivora	Megalonychidae	6.25	arboreal
Bradypus	Folivora	Bradypodidae	4.23	arboreal
Tamandua	Vermilingua	Myrmecophagidae	4.50	semiarboreal
Myrmecophaga	Vermilingua	Myrmecophagidae	28.50	terrestrial
Cyclopes	Vermilingua	Cyclopidae	0.28	arboreal
Priodontes	Cingulata	Dasypodidae	25.50	terrestrial
Ailurus	Carnivora	Ailuridae	4.50	arboreal
Acynonyx	Carnivora	Felidae	46.50	terrestrial
Panthera tigris	Carnivora	Felidae	190.77	terrestrial
Gulo	Carnivora	Mustelidae	19.50	terrestrial
Ailuropoda	Carnivora	Ursidae	117.50	terrestrial
Arctictis	Carnivora	Viverridae	11.50	arboreal
Sarcophilus	Dasyuromorphia	Dasyuridae	7.12	terrestrial
Thylacinus	Dasyuromorphia	Thylacinidae	22.50	terrestrial
Phascolarctos	Diprotodontia	Phascolarctidae	10.22	arboreal
Vombatus	Diprotodontia	Vombatidae	25.00	terrestrial
Manis gigantea	Pholidota	Manidae	33.00	terrestrial
Manis pentadactyla	Pholidota	Manidae	17.75	arboreal
Papio	Primates	Cercopithecidae	25.60	terrestrial
Gorilla	Primates	Hominidae	155.00	semiarboreal
Hylobates	Primates	Hylobatidae	10.50	arboreal
Lemur	Primates	Lemuridae	3.00	arboreal
Coendou	Rodentia	Erethizontidae	2.95	arboreal
Hystrix	Rodentia	Histrycidae	20.00	terrestrial
Marmota	Rodentia	Sciuridae	5.25	terrestrial
Orycteropus	Tubulidentata	Orycteropodidae	60.00	terrestrial

Constraints on arboreal locomotion imposed by large body size are also related to the maximum resistance of the support. A large animal is restricted to move only on those supports that can resist its weight. Thus, *Tamandua* is unable to move along the finest, terminal branches on which *Cyclopes* moves (Taylor 1985). The same likely holds true for most of the Santacrucian sloths, especially *Prepotherium* and the mylodontids, which were characterized by White (1997) as "more terrestrial". Circumventing the problem of fine branches, many primates and extant sloths move by distributing their weight among two or more slender supports. However, the forelimbs of Santacrucian sloths are short and robust compared to those of the extant species, which are more similar to primates such as *Hylobates*. Instead, the forelimbs of the Miocene taxa resemble those of digging mammals such as anteaters, pangolins and aardvarks (Toledo et al. 2012; Bargo et al. 2012), although lacking the extreme ulnar morphology seen in armadillos (White 1993; Vizcaíno et al. 1999, 2001, 2006, 2008, 2011, 2012b; Vizcaíno and Milne 2002).

In summary, Santacrucian sloths likely were arboreal and semiarboreal forms restricted in their climbing capabilities by their relatively large body size. While megalonychids (*Eucholoeops*) and stem megatherioids (*Hapalops*, *Analcimorphus*, *Schismotherium* and *Pelecyodon*) were probably arboreal climbers, albeit restricted to the thickest branches, megatheriids (*Prepotherium*) and mylodontids (*Analcithe-*

rium and *Nematherium*) were more terrestrial forms that climbed only occasionally, for example to avoid predation. Further morphofunctional studies are being performed to gain further insights into these issues. Our conclusions are supported by the diet of the Santacrucian mylodontids, which likely consisted of tubers and fruits (Bargo et al. 2012). In contrast to extant sloths, which generally weigh less than 10 kg, Santacrucian sloths ranged from more than 10 kg to around 120 kg. The heavier Santacrucian genera belonged to two families, Megatheriidae and Mylodontidae, which also included a range of other large genera, some with gigantic body sizes, during the Plio-Pleistocene (Vizcaíno et al. 2012a). In this lights, we interpret the small body size of *Choloepus* as a derived condition reached independently from *Bradypus*. Based on the fossil evidence, the last common ancestor of the extant *Choloepus* and *Bradypus* was likely of large body size.

Concluding remarks

- The variation in body mass shown by the extant mammals analyzed in this study does not appear to be biased by phylogeny.
- The predictive equations developed here based on several elements of the appendicular skeleton show relatively low

predictive error values, especially for the scapular, humeral, femoral, and tibia-fibular equations.

- Most Santacrucian sloths ranged between 40 and 80 kg (megalonychids and stem megatherioids), while others (megatheriids and mylodontids) ranged between 80 and 150 kg.
- Medium and large body sizes imposed constraints on climbing capabilities of Santacrucian sloths, thus likely preventing megalonychids and stem megatherioids from accessing the finest branches, while restricting megatheriids and mylodonts largely to the ground.

Acknowledgements

References

Alexander R.M., Jayes S.A.G., Maloiy, M.O., and Wathuta, M.E. 1979. Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *Journal of Zoology* 189: 305–314.

Andrews, P., Lord, J.M., and Evans, E.M.N. 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society* 11: 177–205.

Asher, R.J. and Helgen, K.M. 2010. Nomenclature and placental mammal phylogeny. *BMC Evolutionary Biology* 10: 102.

Bargo, M.S. and Vizcaíno, S.F. 2008. Paleobiology of Pleistocene ground sloths (Xenarthra, Tardigrada): biomechanics, morphogeometry and ecomorphology applied to the masticatory apparatus. *Ameghiniana* 45: 175–196.

Bargo, M.S., Toledo, N., and Vizcaíno, S.F. 2012. Paleobiology of the Santacrucian sloths and anteaters (Xenarthra, Pilosa). *In*: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (eds.), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*, 216–242. Cambridge University Press, Cambridge.

Bargo, M.S., Vizcaíno, S.F., and Kay, R.F. 2009. Predominance of orthal masticatory movements in the early Miocene *Eucholaeops* (Mammalia, Xenarthra, Tardigrada, Megalonychidae) and other megatherioid sloths. *Journal of Vertebrate Paleontology* 29: 870–880.

Biknevicius, A.R., McFarlane, A.D., and MacPhee, R.D.E. 1993. Body size in *Amblyrhiza inundata* (Rodentia: Caviomorpha), an extinct megafaunal rodent from the Anguilla Bank, West Indies: Estimates and implications. *American Museum Novitates* 3079: 1–25.

Brown, J.H. and West, G.B. 2000. *Scaling in Biology*. 352 pp. Oxford University Press, New York.

Candela, A.M. and Picasso, M.B.J. 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): indicators of locomotor behavior in Miocene porcupines. *Journal of Morphology* 269: 552–593.

Cartmill, M. 1985. Climbing. *In*: M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake (eds.), *Functional Vertebrate Morphology*, 73–88. University of Chicago Press, Chicago.

Cassini, G.H., Vizcaíno, S.F., and Bargo, M.S. 2012. Body mass estimation in Early Miocene native South American ungulates: a predictive equation based on 3D landmarks. *Journal of Zoology* 287: 53–64.

Christiansen, P. and Fariña, R.A. 2003. Mass estimation of two fossil ground sloths (Xenarthra; Mylodontidae). *Senckerbergiana Biologica* 83: 95–101.

Christiansen, P. and Harris, J.M. 2005. Body size of *Smilodon* (Mammalia: Felidae). *Journal of Morphology* 266: 369–384.

Croft, D.A. 2000. *Archaeohyracidae (Mammalia: Notoungulata) from the Tinguiririca Fauna, central Chile, and the evolution and paleoecology of South American mammalian herbivores*. 311 pp. Unpublished Ph.D. Dissertation, University of Chicago, Chicago.

Croft, D.A. 2001. Cenozoic environmental change in South America as indicated by mammalian body size distributions (cenograms). *Diversity and Distributions* 7: 271–287.

De Esteban-Trivigno, S., Mendoza, M., and De Renzi, M. 2008. Body mass estimation in Xenarthra: A predictive equation suitable for all quadrupedal terrestrial placentals? *Journal of Morphology* 269: 1276–1293.

Dray, S. and Dufour, A.B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22 (4): 1–20.

Duan, N. 1983. Smearing Estimate: A Nonparametric Retransformation Method. *Journal of the American Statistical Association* 78: 605–610.

Eisenberg, J.F. 1981. *The Mammalian Radiations*. 610 pp. University of Chicago Press, Chicago.

Elissamburu, A. and Vizcaíno, S.F. 2004. Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). *Journal of Zoology* 262: 145–159.

Fariña, R.A., Vizcaíno, S.F., and Bargo, M.S. 1998. Body size estimations in Lujanian (Late Pleistocene–Early Holocene of South America) mammal megafauna. *Mastozoología Neotropical* 5 (2): 87–108.

Ferguson, R.L. 1986. River loads underestimated by rating curves. *Water Resources Research* 22 (1): 74–76.

Fortelius, M. 1990. The mammalian dentition: a "tangle" view. *Netherland Journal of Zoology* 40: 312–328.

Gaudin, T.J. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society* 140: 255–305.

Gingerich, P.D. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. *Contributions from the Museum of Paleontology, University of Michigan* 38: 79–92.

Hildebrand, M. 1988. *Analysis of Vertebrate Structure*. 3rd ed, 701 pp. Wiley and Sons, New York.

Hill, A.V. 1950. The dimensions of animals and their muscular dynamics. *Science Progress* 38: 209–230.

Hocking, R.R. 1976. The Analysis and Selection of Variables in Linear Regression. *Biometrics* 32: 1–49.

Kay, R.F. and Madden, R.H. 1997 Paleogeography and paleoecology. *In*: R.F. Kay (ed.), *Vertebrate Paleontology in the Neotropics*, 520–550. Smithsonian Institution Press, Washington, DC.

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. *In*: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (eds.), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*, 331–365. Cambridge University Press, Cambridge.

McDonald, H.G. and De Iuliis, G. 2008. Fossil history of sloths. *In*: S.F. Vizcaíno and W.J. Loughry (eds.), *The Biology of the Xenarthra*, 24–36. University Press of Florida, Gainesville.

McNab, R.B. 1985. Energetics, population biology, and distribution of xenarthrans, living and extinct. *In*: G.G. Montgomery (ed.), *The Evo-*

lution and Ecology of Armadillos, Sloths and Vermilinguas, 219–232. Smithsonian Institution Press, Washington DC.

McNab, R.B. 2000. Short-term energy conservation in endotherms in relation to body mass, habits, and environment. *Journal of Thermal Biology* 27: 459–466.

Mendoza, M., Janis, C.M., and Palmqvist, P. 2006. Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *Journal of Zoology* 270: 90–101.

Millien, V. and Bovy, H. 2010. When teeth and bones disagree: body mass estimation of a giant extinct rodent. *Journal of Mammalogy* 91: 11–18.

Nowak, R.M. 1999. *Walker's Mammals of the World. Sixth Edition*. 1936 pp. Johns Hopkins University Press, Baltimore.

Ollier, S., Couteron, P., and Chessell, D. 2006. Orthonormal transform to decompose the variance of a life-history trait across a phylogenetic tree. *Biometrics* 62: 471–477.

R Development Core Team 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Reed, K.E. 1998. Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. *Paleobiology* 24: 384–408.

Rodrigues, F.H.G., Medri, I.M., de Miranda, G.H.B., Camilo-Alves, C., and Mourao, G. 2008. Anteater behavior and ecology. *In*: S.F. Vizcaíno and W.J. Loughry (eds.), *The Biology of the Xenarthra*, 257–268. University Press of Florida, Gainesville.

Sakamoto, Y., Ishiguro, M., and Kitagawa, G. 1986. *Akaike Information Criterion Statistics*. 290 pp. D. Reidel Publishing Company, Dordrecht.

Sargis, E.J. 2002a. Functional morphology of the forelimbs of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *Journal of Morphology* 253: 10–42.

Sargis, E.J. 2002b. Functional morphology of the hindlimbs of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *Journal of Morphology* 254: 149–185.

Scott, K. 1990. Postcranial dimensions of ungulates as predictors of body mass. *In*: J. Damuth and B.J. MacFadden (eds.), *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, 301–335. Cambridge University Press, Cambridge.

Smith, R.J. 1984. Allometric scaling in comparative biology: problems of concept and method. *American Journal of Physiology: Regulatory Integrative and Comparative Physiology* 246: R152–R160.

Smith, R.J. 1993. Logarithmic transformation bias in allometry. *American Journal of Physical Anthropology* 90: 215–228.

Smith, M.J. and Savage, R.J.G. 1955. Some locomotory adaptations in mammals. *Journal of the Linnean Society (Zoology)* 42: 603–622.

Snowdon, P. 1991. A ratio estimator for bias correction in logarithmic regressions. *Canadian Journal of Forest Research* 21: 720–724.

Tauber, A.A. 1997a. Bioestratigrafía de la formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. *Ameghiniana* 34: 413–426.

Tauber, AA. 1997b. Paleoecología de la Formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. *Ameghiniana* 34: 517–529.

Taylor, B.K. 1978. The anatomy of the forelimb in the anteater (*Tamandua*) and its functional implications. *Journal of Morphology* 157: 347–368.

Taylor, B.K. 1985. Functional anatomy of the forelimb in vermilinguas (anteaters). *In*: G.G. Montgomery (ed.), *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*, 151–171. Smithsonian Institution Press, Washington.

Toledo, N., Bargo, M.S., Cassini, G.H., and Vizcaíno, S.F. 2012. The forelimb of Early Miocene sloths (Mammalia, Xenarthra, Folivora): Morphometrics and functional implications for substrate preferences. *Journal of Mammalian Evolution* 19: 185–198.

Van Couvering, J.A.H. 1980. Community evolution in Africa during the Cenozoic, en fossils in the making. *In*: A.K. Berensmeyer and A. Hill (eds.), *Fossils in the Making*, 272–298. University of Chicago Press, Chicago.

Vizcaíno, S.F. 2009. The teeth of the "toothless": novelties and key innovations in the evolution of xenarthrans (Mammalia, Xenarthra). *Paleobiology* 35: 343–366.

Vizcaíno, S.F. and Milne, N. 2002. Structure and function in armadillo limbs (Mammalia, Xenarthra: Dasypodidae). *Journal of Zoology, London* 257: 117–127.

Vizcaíno, S.F., Bargo, M.S., and Fariña, R.A. 2008. Form, function, and paleobiology in xenarthrans. *In*: S.F. Vizcaíno and W.J. Loughry (eds.), *The Biology of the Xenarthra*, 86–99. University Press of Florida, Gainesville.

Vizcaíno, S.F., Bargo, M.S., Kay, R.F., and Milne, N. 2006. The armadillos (Mammalia, Xenarthra) of the Santa Cruz Formation (early–middle Miocene). An approach to their paleobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 237: 255–269.

Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fariña, R.A., Di Giacomo, M., Perry, M.G., Prevosti, F.J., Toledo, N., Cassini, G.H., and Fernicola, J.C. 2010. A baseline paleoecological study for the Santa Cruz Formation (late–early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292: 507–519.

Vizcaíno, S.F., Blanco, R.E., Bender, J.B., and Milne, N. 2011. Proportions and function of the limbs of glyptodonts (Mammalia, Xenarthra). *Lethaia* 44: 93–101.

Vizcaíno, S.F., Cassini, G.H., Toledo, N., and Bargo, M.S. 2012a. On the evolution of large size in mammalian herbivores of Cenozoic faunas of South America. *In*: B.D. Patterson and L.P. Costa (eds.), *Bones, Clones, and Biomes: the History and Geography of Recent Neotropical Mammals*, 76–101. University of Chicago Press, Chicago.

Vizcaíno, S.F., Fariña, R.A., and Mazzetta, G. 1999. Ulnar dimensions and fossoriality in armadillos and other South American mammals. *Acta Theriologica* 44: 309–320.

Vizcaíno, S.F., Fernicola, J.C., and Bargo, M.S. 2012b. Paleobiology of Santacrucian glyptodonts and armadillos (Xenarthra, Cingulata). *In*: S.F. Vizcaíno, R.F. Kay and M.S. Bargo (eds.), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*, 194–215. Cambridge University Press, Cambridge.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012c. *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. 370 pp. Cambridge University Press, Cambridge.

Vizcaíno, S.F., Zárate, M., Bargo, M.S., and Dondas, A. 2001. Pleistocene large burrows in the Mar del Plata area (Buenos Aires Province, Argentina) and their probable builders. *In*: S.F. Vizcaíno, R.A. Fariña, and C. Janis (eds.), Biomechanics and Paleobiology of Vertebrates. *Acta Paleontologica Polonica* 46: 157–169.

White, J.L. 1993. Indicators of locomotor habits in Xenarthrans: evidence for locomotor heterogeneity among fossil sloths. *Journal of Vertebrate Paleontology* 13: 230–242.

White, J.L. 1997. Locomotor adaptations in Miocene Xenarthrans. *In*: R.F. Kay, R. Madden, R.L. Cifelli, and J.J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia*, 246–264. Smithsonian Institution Press, Washington D.C.

Appendix 1

Measurements used in this analysis

	Element	Measurement	#
1	Scapula	Scapular Length – supraglenoid tubercle to dorso-posterior border of scapula at end of spine	SL
2		Scapular Glenoid Fossa Length – supraglenoid apophysis to ventral border of glenoid fossa	SGL
3		Scapular Glenoid Fossa Width – maximum transverse width of glenoid fossa	SGW
4	Humerus	Humeral Trochlear Valley Length	HTVL
5		Transverse Diameter of Humerus – at midshaft	TDH
6		Humerus Length – between head and trochlea	HL
7		Antero-Posterior Diameter of Humerus – at midshaft	APDH
8		Humerus Head Length	HHL
9		Humerus Distal Articular Surface Width	HDASW
10		Humeral Trochlea Depth	HTD
11		Humeral Entepicondyle Medial Protrusion	HEMP
12		Humeral Distal Epiphysis Width	HDEW
13		Humeral Greater Tuberosity Length	HGT
14		Humeral Lesser Tuberosity Length	HLT
15		Width Across Tubersities	WTub
16	Ulna	Ulnar Length	UL
17		Transverse Height of Ulna – at midshaft	THU
18		Transverse Height of Ulna – at notch level	THUn
19		Olecranon-Trochlear Notch Length	OTL
20		Ulnar pre-Notch Length	UNL
21		Ulnar Trochlear Notch Length	UTNL
22		Transverse Diameter of Ulna – at midshaft	TDU
23		Ulnar Trochlear Notch Width – at posterior border	UTNW
24	Radius	Radius Length	RL
25		Radius Diameter – at midshaft	RD
26		Radial Distal Facet Length	RDFL
27		Radial Head Length	RHL
28		Radial Head Width	RHW
29		Radial Distal Epiphysis Width	RDEW
30	Pelvis	Pelvis Total Length	PL
31		Ilium Length – to anteriormost border of acetabulum	ILL
32		Ischium Length – from posteriormost border of acetabulum	ISL
33	Femur	Transverse Diameter of Femur – at midshaft	TDF
34		Femoral Head Width	FHW
35		Width Across Trochanters	WTroc
36		Femoral Length – between head and medial condyle	FL
37		Antero-Posterior Diameter of Femur – at midshaft	APDF
38		Femoral Head Length	FHL
39		Femoral Maximum Condylar Width	FCW
40		Femoral Maximum Distal Epiphysis Width	FMDEW
41		Inter-Condylar Femoral Width	ICFW
42		Lateral Condyle Length	LCL
43		Medial Condyle Length	MCL
44		Patellar Groove Width	PGW

45	Tibia	Tibial Length – from interfacet eminence to tibial malleolus	TL
46		Transverse Diameter of Tibia – at midshaft	TDT
47		Tibial Proximal Epiphysis Length	TPEL
48		Antero-Posterior Diameter of Tibia – at midshaft	APDT
49		Tibial Mortise Length	TML
50		Tibial Mortise Width	TMW
51		Lateral Tibial Facet Width	LTFW
52		Medial Tibial Facet Length	MTFL
53		Lateral Tibial Facet Length	LTFL
54		Tibial Proximal Epiphysis Width	TPEW
55	Fibula	Fibular Total Length	FiTL
56		Ectal Fibular Facet Length	EFFL
57	Astragalus	Astragalar Trochlear Maximum Width	ATMW
58		Astragalar Length – from head to posterior-most border	AL
59		Astragalar Ectal Facet Length	AEFL
60		Astragalar Medial Facet Length	AMFL
61		Astragalar Head Width	AHW
62	Calcaneum	Calcaneum Total Length	CTL
63		Functional Calcaneum Length – from ectal facet to tuber	FCL
64		Calcaneum Maximum Tuber Width	CMTW