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The Forelimb of Early Miocene Sloths (Mammalia, Xenarthra, Folivora): Morphometrics and Functional Implications for Substrate Preferences

N. Toledo · M. S. Bargo · G. H. Cassini · S. F. Vizcaíno

Abstract Early Miocene sloths are represented by a diversity of forms ranging from 38 to 95 kg. Their forelimb bones differ in shape from those of their closest living relatives (less than 10 kg), *Bradypus* and *Choloepus*. Such differences in shape could be related to differences in substrate preference (arboreal, semiarboreal, or ground-dwelling) or substrate use (climbing, digging, etc.). In order to detect putative patterns related to substrate preference, 21 linear measurements were defined and taken on the forelimb bones. The sample was composed of 22 specimens of fossil sloths and 134 specimens of extant mammals (marsupials, xenarthrans, pangolins, rodents, primates, and carnivorans), including arboreal, semi-arboreal, and ground-dwelling taxa. Principal Components Analyses were performed on logarithms of original measurements, while functional indexes (Index of Fossorial Ability, Brachial Index, and Distal Epiphyseal Index) were calculated on raw data. The first three PCs accounted for 93.8% of the cumulative variability. PC1 roughly represented size, while positive values of PC2 represented mechanical advantage for features related to digging habits. Fossil sloths were clearly separated from living ones, sharing a common morphospace with anteaters and other good diggers. Conversely, living sloths shared a morphospace with primates. Similar results were obtained for DEI and IFA, with fossil sloths showing similar values to extant digging mammals. These results suggest that fossil sloths have a different functional pattern of forelimb use than that of extant ones, probably more similar to vermilinguas and pangolins, including putative good digging capabilities and/or semiarboreal habits. Substrate use seems to be interfering in the analysis of substrate preference based on forelimb morphology.

Keywords Miocene sloths · Morphometry · Substrate preference · Substrate use

Introduction

Interpreting limb function is one of the main approaches to elucidating the paleobiology of vertebrates (Vizcaíno et al.

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2008, 2010). A plethora of studies about locomotor behavior (one of the main limb functions) in fossil mammals has been published, employing a comparative approach with extant forms classified by locomotor category (e.g., White 1993, 1997 on fossil sloths; Elissamburu and Vizcaíno 2004 on caviomorph rodents; Argot 2004 on fossil marsupials; Croft and Anderson 2008 on the notoungulate *Protypotherium*). Many mammals can perform different locomotor behaviors depending on the substrate they use. For instance, the lesser anteater *Tamandua* walks quadrupedally on the ground, and climbs slowly on branches. Other animals walk quadrupedally both on ground and on branches, and yet others can walk and run on either substrate. Moreover, locomotor behavior can change according to the animal's activity. As Oxnard (1984) claimed in his book on primates, a fixed locomotor categorization would be impossible to propose because each animal uses a wide spectrum of locomotor modes. However, many studies use discrete unimodal categorization for each animal. It is common to use "arboreal" and "terrestrial" as locomotor categories although they are not locomotor modes, but categories of substrate preference. Developing a multimodal and exhaustive, but simple, categorization of locomotor behavior exceeds the scope of this work. Instead, in this contribution we focus on substrate preferences and their patterns of mechanical requirements.

Sloths (Folivora) and anteaters (Vermilingua) constitute Pilosa, which together with Cingulata (armadillos and glyptodonts) form the Xenarthra, one of the four major clades of placentals (see Delsuc and Douzery 2008; Gaudin and McDonald 2008) and probably the most conspicuous group of mammals from South America. Living sloths are represented by two genera, *Bradypus* (three-toed sloth) and *Choloepus* (two-toed sloth), which are small animals (less than 10 kg, Nowak 1999). They are almost completely arboreal, slow climbers, and are folivorous denizens of tropical forests (Chiarello 2008). By contrast, their fossil record is exceptionally rich and diverse, the great majority of specimens being known mostly from two time periods, the early Miocene (particularly the Santacrucian Age) and the Pleistocene of South and North America.

The most comprehensive morphology-based phylogenetic analyses of sloths are those of Gaudin (2004) and Pujos et al. (2007). Gaudin proposed *Bradypus* as the sister taxon to all other sloths, and placed *Choloepus* within Megalonychidae, a clade that includes the extinct Antillean sloths and the Santacrucian *Eucholoeops*. He corroborated the monophyly of the four clades of sloths: Megatheriidae, Nothrotheriidae, Megalonychidae, and Mylodontidae. The first three clades plus a few stem Santacrucian sloths (*Hapalops*, *Analcimorphus*, *Schismotherium*, and *Pelecyodon*) constitute the Megatherioidea. The sister group to the megatherioid radiation is the Mylodontidae (see Fig. 1). Pujos et al. (2007) support Megalonychidae and Megatherioidea but consider *Hapalops* to be a stem folivoran. Additionally, monophyly of Mylodontidae is not supported by the analysis of Pujos et al. (2007). Although the relationships among tree sloths and ground sloths are different in both analyses


Fig. 1 Cladogram showing phylogenetic relationships among xenarthrans included in this work. Modified from Gaudin (2004)
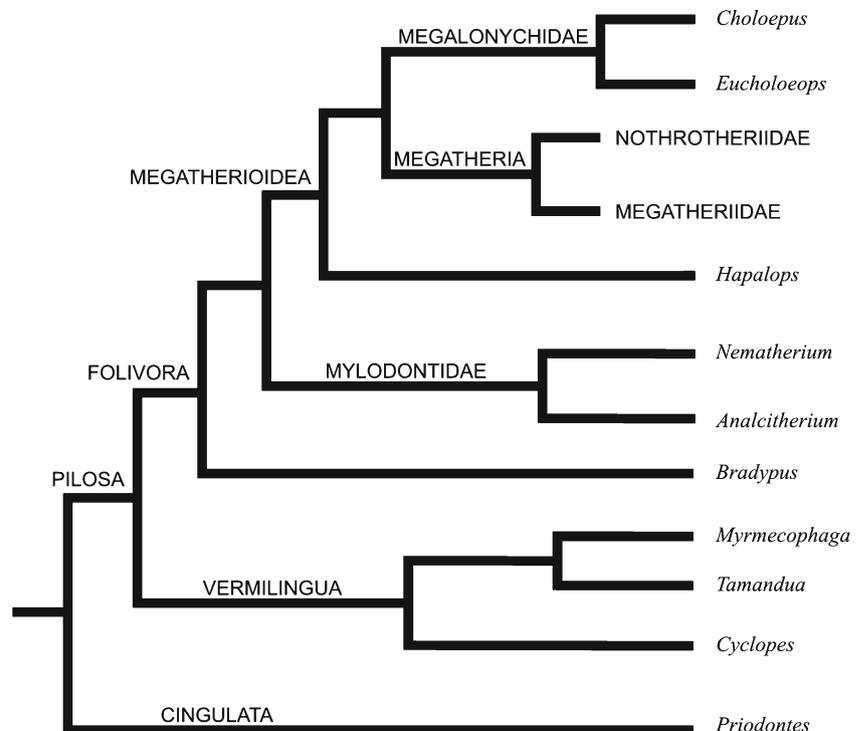
and in a previous one by White and MacPhee (2001), it is remarkable that all analyses support the diphyly of tree sloths. Thus, the hypothesis that living sloths evolved their distinctive arboreal suspensory specializations independently from different ground sloth groups is supported. For this study, we followed the phylogenetic proposal of Gaudin (2004).

Santacrucian sloths are represented mainly by megatherioids (the megatheriid *Planops*, the megalonychid *Eucholoeops,* and the basal *Hapalops*, *Analcimorphus*, *Schismotherium*, and *Pelecyodon*), but also mylodontids (the scelidotheres *Nematherium* and *Analcitherium*). Nothrotheres have not been recorded yet from Santacrucian beds. The Santacrucian sloths include a diversity of small to medium-sized forms, with average body mass estimates of about 38 kg for *Hapalops*, 77 kg for *Eucholoeops*, and 95 kg for one specimen of *Nematherium* (Vizcaíno et al. 2010; Bargo et al. in press). The morphology of the masticatory apparatus of Santacrucian sloths suggest that megatherioids were mainly folivorous (Bargo et al. 2009) and mylodontids may include also other fibrous food items as fruits and tubercules (Bargo et al. in press). Their limb bones (Fig. 2) strongly differ in shape from those of their living relatives (Fig. 3). White (1993, 1997) performed the most comprehensive morphometric analysis of limb function in Santacrucian sloths, as well as in Antillean fossil sloths, using multiple functional indices of the fore- and hind limb to discriminate locomotor modes. She obtained very good
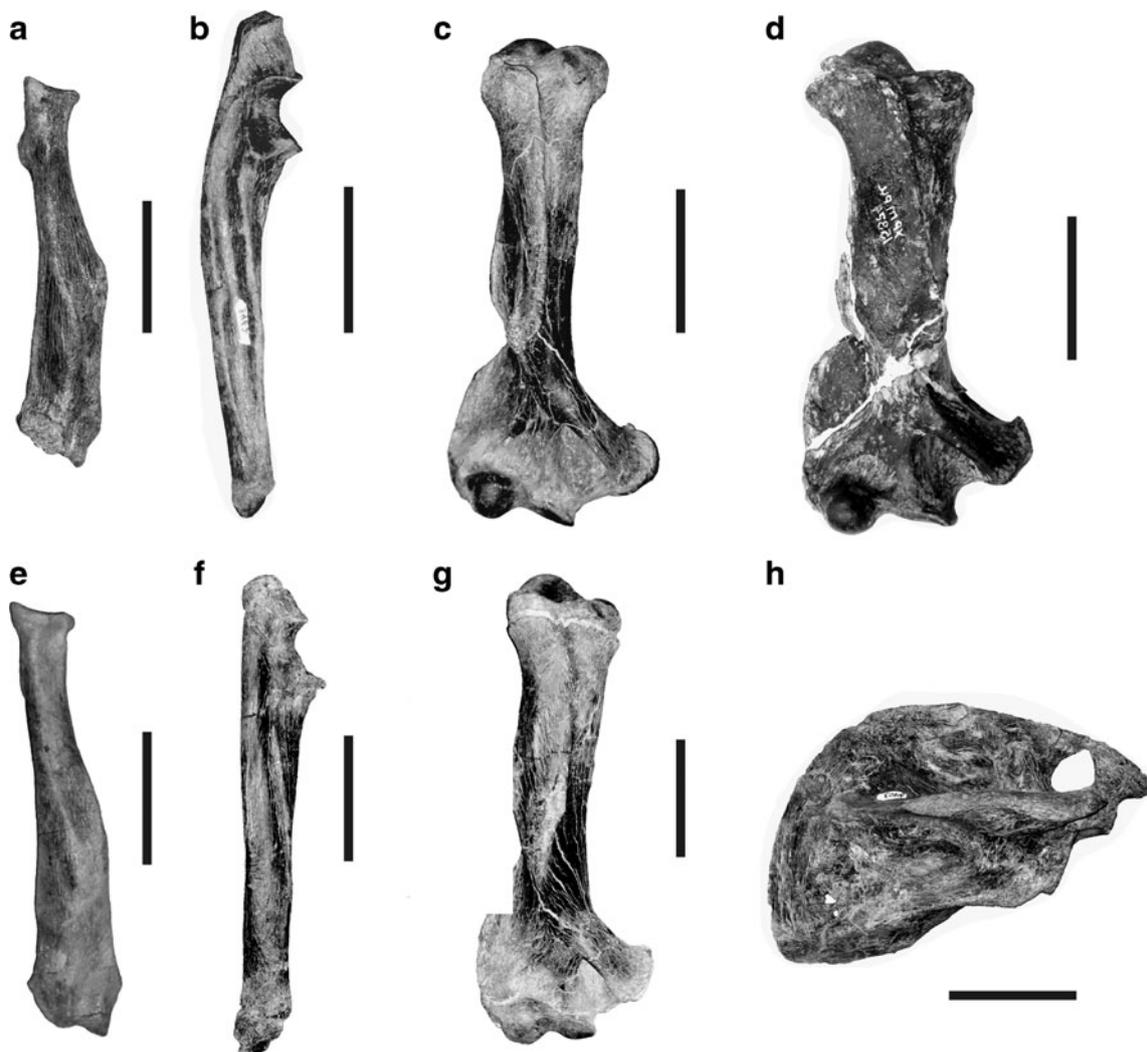
Fig. 2 Santacrucian sloth forelimb elements. **a** *Hapalops* sp., MPM-PV 3404, left radius, lateral view (reversed image); **b** *Hapalops* sp., MPM-PV 3467, left ulna, lateral view (reversed image); **c** *Hapalops* sp., MPM-PV 3467, right humerus, anterior view; **d** *Nematherium* sp., YPM-PVPU 15374, left humerus, anterior view (reversed image); **e** *Eucholoeops* sp., MPM-PV 3651, left radius, lateral view (reversed image); **f** *Eucholoeops* cf. *E. fronto.*, MPM-PV 3403, left ulna, lateral view; **g** *Eucholoeops* cf. *E. fronto.*, MPM-PV 3403, right humerus, anterior view; **h** *Eucholoeops* sp., MPM-PV 3403, rigth scapula, lateral view. Scale bars=5 cm
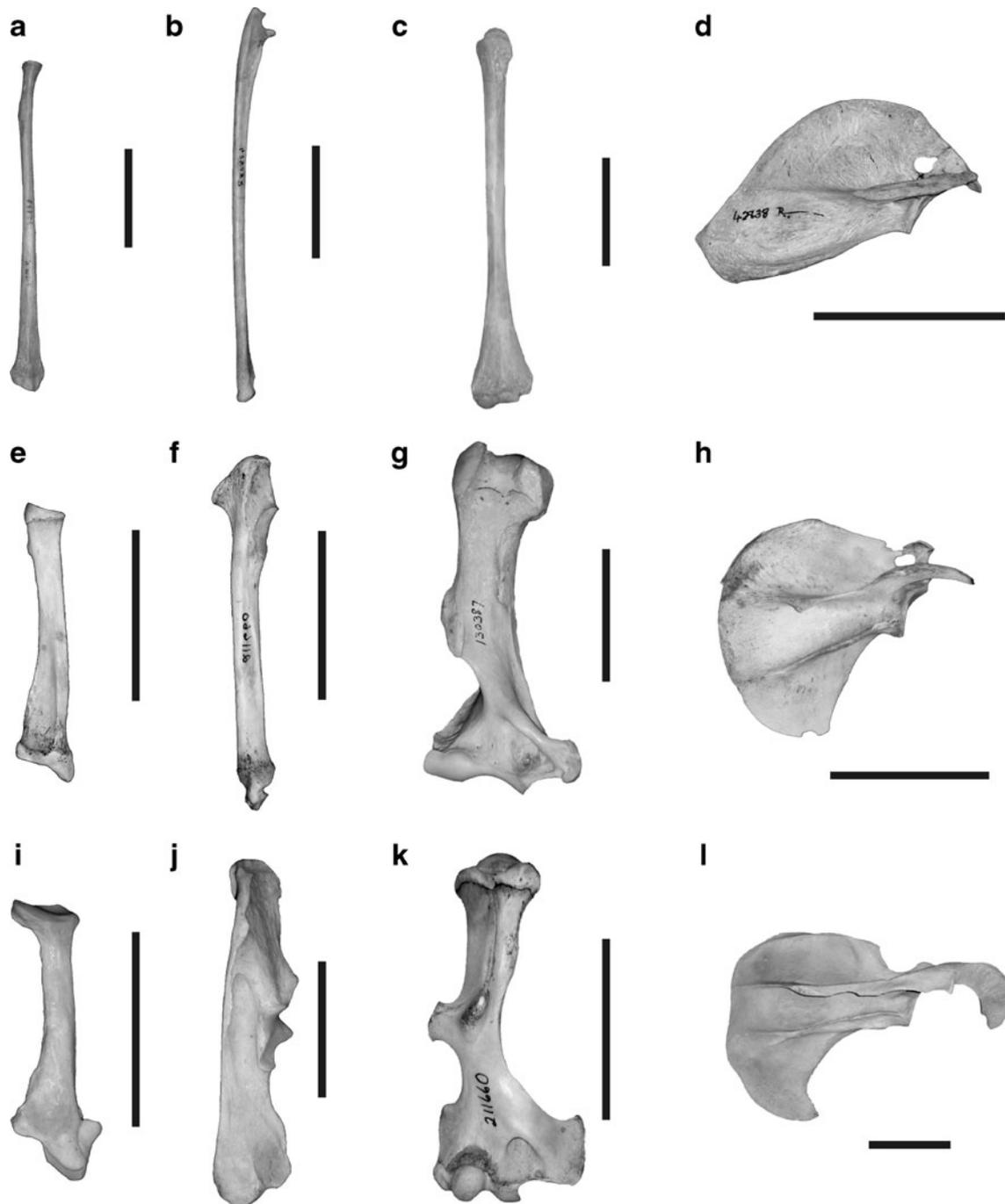
Fig. 3 Forelimb elements of living xenarthrans. **a**, **b**, **c**, and **d**, *Bradypus* sp., right radius in lateral view, left ulna in medial view (reversed image), right humerus in anterior view, and right scapula in lateral view; **e**, **f**, **g** and **h** *Tamandua* sp., right radius in lateral view, left ulna in medial view (reversed image), right humerus in anterior view, and right scapula in lateral view; **i**, **j**, **k** and **l** *Priodontes* sp., right radius in lateral view, right ulna in lateral view, right humerus in anterior view, and right scapula in lateral view. Scale bars=5 cm

discrimination for living anteaters. Some genera of Santacrucian sloths appeared to be arboreal or semiarboreal (*Hapalops*, *Eucholoeops*, among others), while *Nematherium* was probaly more terrestrial. White (1997) remarked that none of Santacrucian sloths seems to be suspensory like the extant ones.

The goal of this contribution is to test if the morphological differences in the forelimb between Santacrucian sloths and extant ones are related to substrate preferences, and/or substrate use. We employ a morphometric approach, including comparisons with a wide sample of extant mammals.

Materials and Methods

Acronyms: 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.

Specimens used in this study are listed in Appendix I. The fossil specimens studied include those collected by expeditions carried out during the nineteenth and early twentieth centuries (MLP, YPM-VPPU, AMNH, and FMNH) and material collected by MLP-Duke University joint expeditions (MPM-PV) over the last eight years (2003–2010). This new sloth material was collected in coastal Santacrucian outcrops (Santa Cruz Formation, late-early Miocene) of Patagonia, Argentina, and often includes complete and very well-preserved specimens that complement the samples analyzed by previous researchers (e.g., White 1997). The fossil sloth sample comprises 22 specimens representing *Hapalops* (12 specimens), *Eucholoeops* (4), *Nematherium* (2), and *Analcitherium* (1) (Appendix I). Some (3) specimens of indeterminate taxonomic allocation were included because of their completeness.

Paleobiological approaches based on morphology usually are not sensitive enough to discriminate between species of the same genus (Vizcaíno et al. 2010). Consequently, and following the taxonomic overview, genus was chosen as the working taxonomic level, except for *Manis*, regarding the great differences existing in body size and substrate preference between *M. gigantea* (the ground-dwelling African giant pangolin) and *M. pentadactyla* (the arboreal Chinese pangolin). These taxa are considered separate subgenera of *Manis*, or even different genera by Gaudin et al. (2009), who proposed the giant pangolin as belonging to the genus *Smutsia*. As most of the specimens collected recently are megalonychids and basal megatherioids, while mylodontids and megatheriids are very rare, our analysis is based largely on the better preserved and more complete specimens of *Eucholoeops* and *Hapalops*. Specimens of the Mylodontidae, *Nematherium* and *Analcitherium*, although not complete, were also included. Other Santacrucian genera were unsuitable for this analysis due to the incompleteness of their forelimbs.

A sample of 134 specimens of extant mammals, including marsupials, xenarthrans, pangolins, rodents, primates, and carnivorans, was analyzed. Data of extant mammals were collected mostly at the AMNH and the FMNH Mammalogy collection (see Appendix II).

Twenty-one linear measurements were defined and taken on bones of the forelimb and pectoral girdle (scapula,

humerus, ulna, and radius; see Fig. 4). Measurements are in most cases those traditionally used in morphometric studies (by Sargis 2002 on tupaiids; and by Elissamburu and Vizcaíno 2004, and Candela and Picasso 2008 on caviomorph rodents; see Table 1). The measurements were taken directly from bones with hand calipers or from photographs in standard orientation by suitable software (ImageJ® Wayne Rasband, NIH, public domain). Some measurements were unattainable, especially among the fossil specimens, and these were estimated from global mean values for the Principal Component Analysis (PCA).

A PCA was performed on all 21 forelimb measurements of the 15 most complete specimens of Santacrucian sloths and all included extant mammals, in order to explore shape variation. PCA was chosen for robustness, simplicity, and ease of interpretation. The correlation matrix was used. Because of the large variability in body size in the extant mammal sample, i.e., from *Cyclopes* (0.5 kg, Nowak 1999) to *Panthera* (300 kg, Nowak 1999), base-ten logarithms of the raw measurements were used to perform the analysis.

Some of the variables were combined to calculate three functional indices as another way to potentially distinguish taxa by substrate preference or use. All specimens were analyzed, including those fossil specimens not included in the PCA due to their incompleteness but that allowed indices to be calculated. These indices represent functionally significant variables such as in-lever/out-lever ratios and proportional width of elements and were calculated as the ratio of two measures multiplied by 100 (Table 2):

1. The Brachial Index (BI – Howell 1944), represents the antebrachium-brachium ratio (out-lever/in-lever ratio) for the forelimb. This index roughly represents the mechanical advantage for extension/flexion of forearm, that is correlated with substrate preference and locomotion style (for its application see Elissamburu and Vizcaíno 2004; Croft and Anderson 2008; among others)

2. The Index of Fossorial Ability (IFA) represents the ratio of olecranon process length to ulna length and is correlated with increasing the length of the lever arm (and mechanical advantage) of the triceps muscle and the dorsoepitrochlearis muscle during powerful elbow extension (Smith and Savage 1956; Vizcaíno et al. 1999; Elissamburu and Vizcaíno 2004). IFA has been used as a proxy for digging ability (Vizcaíno et al. 1999).

3. The Distal Epiphyseal Index (DEI = EI of Elissamburu and Vizcaíno 2004) represents the available space for musculature involved in hand retraction and prehension, very important functions during digging. Thus, DEI represents the ratio of humeral distal width with respect to total length of the humerus.
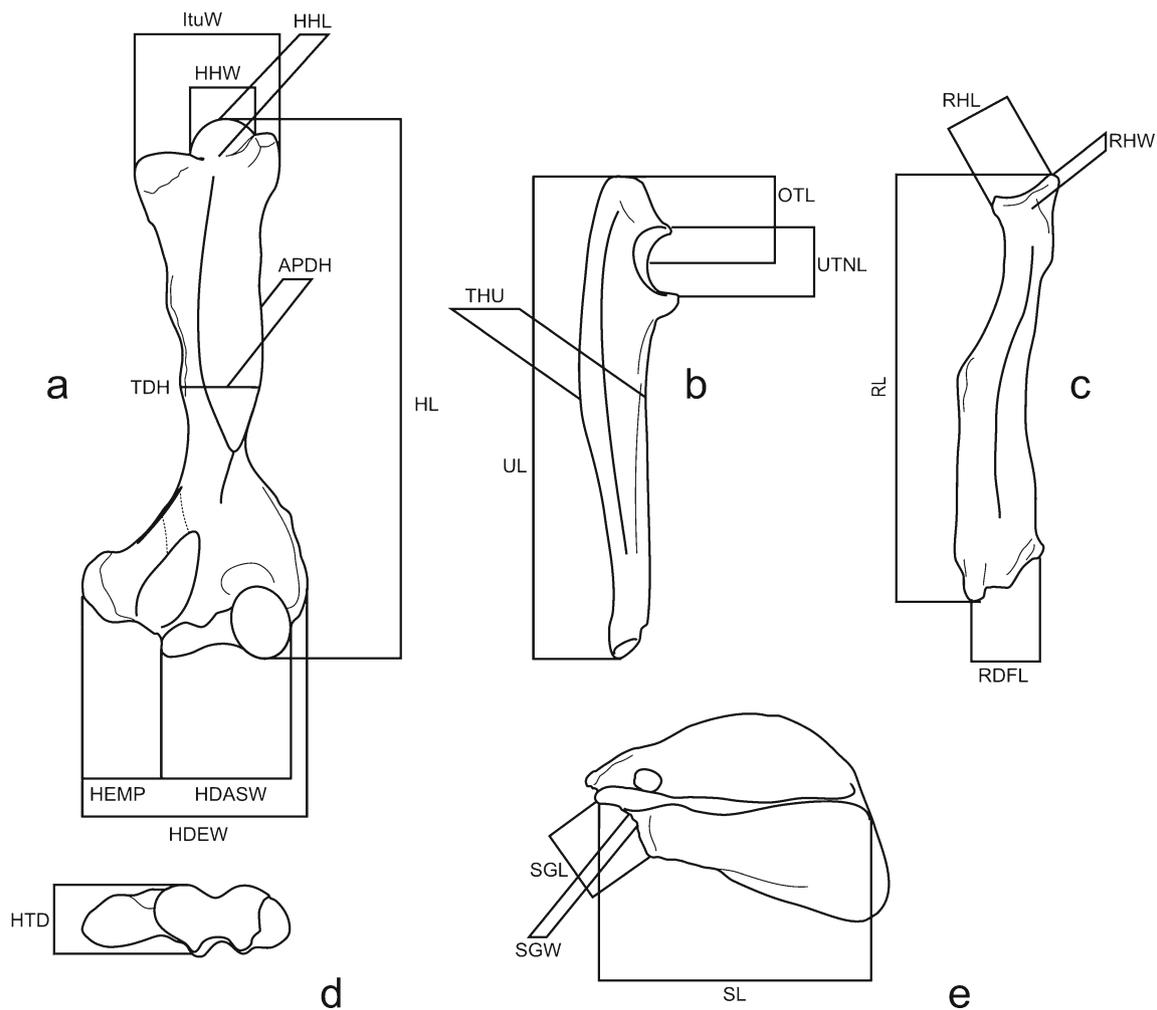
Fig. 4 Measurements used in this work. **a** left humerus, anterior view; **b** left ulna; medial view; **c** left radius, lateral view; **d** left humerus, distal view; **e** left scapula, lateral view. For explanation and references see Table 1

Functional indices were plotted in boxplots, showing the same data in two different ways: index values for extant mammals were plotted using alternately substrate preference categories (arboreal, semi-arboreal, and ground-dwelling) and substrate-use categories regarding digging activity (digger and non-digger). Santacrucian fossil sloths were treated as a separate, non-functional category. For this analysis, "arboreal" mammals were considered those spending most of their time in trees; "semi-arboreal" included those forms spending similar proportions of their time on the ground and in trees, showing some climbing capabilities; and "ground-dwelling" included only terrestrial forms that do not climb trees. Within "diggers" were included mammals that usually dig, scratch, or rip the substrate (not only the ground, but also tree bark) to obtain food items and/or shelter. The fact that both non-digger and digger categories included arboreal, semi-arboreal, and ground-dwelling mammals must be noted: digging behavior is present all along the substrate preferences continuum.

All calculations and graphics were performed in R (R Development Core Team 2011), and suited using free graphical software.

Results

The appendicular skeleton of Santacrucian sloths is very conservative compared with their living relatives (Figs. 2–3). Their overall features are more similar to the limb elements of anteaters and cingulates than to those of extant sloths, especially *Bradypus*. Except for the scapula (which resembles more closely that of extant sloths), the general robustness and diaphyseal proportions of the limb elements, the great development of tuberosities, ridges, and crests for muscular attachment, and the morphology of articular surfaces resemble those of the anteaters. The mylodontids

Table 1 Measurements used in this work, and represented in Fig. 3

	Measurement definition	Abbrev.	Source
Scapula	Length from supraglenoid apophysis to ventral border of glenoid fossa (lateral aspect)	SGL	Sargis 2002
	Maximum width of glenoid fossa in ventral view	SGW	Sargis 2002
	Length from supraglenoid apophysis to posterior border of scapula (at level of spine)	SL	This work
Humerus	Anteroposterior diaphyseal width at midshaft.	APDH	Sargis 2002; Elissamburu and Vizcaíno 2004; Candela and Picasso 2008
	Width from medialmost border of trochlea to lateralmost border of capitulum	HDASW	Sargis 2002; Candela and Picasso 2008
	Width from medialmost border of entepicondyle to lateralmost border of epicondyle	HDEW	Sargis 2002; Elissamburu and Vizcaíno 2004; Candela and Picasso 2008
	Medial protrusion of entepicondyle	HEMP	This work
	Length from anteriormost edge of head to posteriormost border	HHL	Candela and Picasso 2008
	Head width between posteriormost edges of both tuberosities	HHW	Candela and Picasso 2008
	Length from proximalmost border of head to distalmost border of the capitulum	HL	Elissamburu and Vizcaíno 2004; Candela and Picasso 2008
	Width from anteriormost border of trochlea to posteriormost border of entepicondyle	HTD	Candela and Picasso 2008
	Maximum width between both tuberosities	ItuW	This work
	Transverse diaphyseal width at midshaft	TDH	Sargis 2002; Elissamburu and Vizcaíno 2004; Candela and Picasso 2008
Ulna	Length from semilunar notch midpoint to the superior end of olecranon process	OTL	Elissamburu and Vizcaíno 2004; Candela and Picasso 2008
	Diaphyseal height at midshaft	THU	This work
	Total length	UL	Sargis 2002; Elissamburu and Vizcaíno 2004; Candela and Picasso 2008
	Proximo-distal length of semilunar notch	UTNL	Sargis 2002; Candela and Picasso 2008
Radius	Width of carpal fossa	RDFL	Sargis 2002; Candela and Picasso 2008
	Maximum diameter of capitular fossa	RHL	This work
	Minimum diameter of capitular fossa	RHW	Sargis 2002
	Total length	RL	Sargis 2002; Candela and Picasso 2008

Nematherium and *Analcitherium* have more robust humeri than the megatherioids *Eucholoeops* and *Hapalops*.

Principal Component Analysis

The first three principal components account for 93.8% of the total variability among taxa; PC1 alone explains about 83% of total variance, whereas PC2 and 3 together explain about 10% (Table 3).

The contributions of each variable on PC1 are very similar (15 of 21 variables range from −0.9 to −0.97; Table 4) whereas the smallest contribution was from RL (−0.75; Table 4). This indicates that PC1 is negatively correlated with size of forelimb elements (*Cyclopes* and *Panthera*, being the smallest and largest forms included in

Table 2 Functional indices used in this work

Index	Abbrev. and equation	Functional significance
Index of Fossorial Ability	$IFA = OTL/UL * 100$	In-lever/out-lever ratio for ulna
Brachial Index	$BI = RL/HL * 100$	Out-lever/in-lever ratio for forelimb
Distal Epiphyseal Index	$DEI = HDEW/HL * 100$	Relative width of humeral distal epiphysis

Table 4 Contribution of the variables to each Principal Component (PC)

Variable	PC1	PC2	PC3
SL	−0,937	0,005	−0,310
SGL1	−0,958	−0,019	−0,075
SGW	−0,967	−0,016	−0,152
TDH	−0,858	0,357	0,226
HL2	−0,862	−0,479	0,076
APDH	−0,949	0,167	−0,056
HHL	−0,971	−0,083	−0,015
HDASW	−0,969	0,000	0,097
HTD	−0,944	−0,024	−0,089
HEMP	−0,789	0,414	0,410
HDEW	−0,923	0,212	0,293
ItuW	−0,921	0,182	−0,008
HHW	−0,969	−0,050	−0,083
UL	−0,836	−0,518	0,044
THU	−0,918	0,254	−0,140
OTL	−0,830	0,403	−0,302
UTNL	−0,957	−0,025	−0,063
RL	−0,747	−0,633	0,109
RDFL	−0,955	−0,002	0,020
RHL	−0,963	0,003	−0,011
RHW	−0,901	−0,219	0,126

this study, are at opposite extremes of PC1; Fig. 5). In this PC, Santacrucian sloths occupy a position between *Panthera*, *Gorilla*, and the giant panda *Ailuropoda* (the largest taxa analyzed) on one side, and the giant armadillo *Priodontes* on the other, showing similar loading as the giant anteater *Myrmecophaga*, *Manis gigantea*, and the cheetah *Acinonyx* (Fig. 5, x-axis).

With respect to PC2, major negative contributions correspond to total length of limb elements (humerus HL~−0.48, ulna UL~−0.52, and radius RL~0.63; Table 4), with some minor positive contributions, such as olecranon length and medial protrusion of the entepicondyle (OTL and HEMP~ 0.4; Table 4). In that sense, positive values for PC2 indicate relatively short and massive forelimb elements, traits that improve force (leverage) rather than speed in flexion or extension of the proximal and medium segments of the forelimb [i.e., long OTL, increased humerus midshaft diameter (TDH), and a wide entepicondyle]. Species with high negative scores have slender, gracile bones with less development of such features (e.g., the gibbon and extant sloths; see Fig. 5).

Positive contributions of variables on PC3 are HEMP (~ 0.4; Table 4), width of entepicondyle (HDEW~0.3; Table 4), and TDH (~ 0.2; Table 4), and negative values are scapula and olecranon lengths (SL and OTL~−0.3). Positive values of PC3 represent a medially protruding humeral entepicondyle and increased humeral midshaft diameter, but also relatively short scapula and olecranon process, while negative values represent a narrower distal humeral epiphysis and less well-developed entepicondyle with more elongated scapula and olecranon. However, PC3 accounts for only 3%

Table 3 Eigenvalues, proportion, and cumulative variance explained by Principal Component (PC) (see Fig. 1)

PC	Eigenvalue	% Total Variance	Cumulative eigenvalue	Cumulative%
1	17,50	83,34	17,50	83,34
2	1,59	7,57	19,09	90,91
3	0,61	2,90	19,70	93,80

of the variance and does not make a clear separation between functional groups (Table 3; Fig. 6: y-axis).

To summarize, in bivariate plots of PC1 and PC2 (91% of variance; Table 3; Fig. 5), Santacrucian sloths share a common morphospace with anteaters, the giant armadillo *Priodontes*, the African porcupine, pangolins, the aardvark, and the wombat, being clearly separated from their extant sloth relatives.

Functional Indexes (Fig. 7)

High values of BI represent comparatively long antebrachia, as seen in many non-digger and arboreal forms, while low BI values are seen in forms with shorter antebrachia, such as many digging mammals. Santacrucian sloths show similar forelimb proportions to digging mammals, and show little distinction based on substrate preference.

As seen in Fig. 7, Santacrucian sloths show mean values of IFA intermediate between extant digging mammals and non-diggers. Using substrate preference categorization, the similarity due to this index is greater with ground-dwelling and to a lesser degree with semi-arboreal forms.

Santacrucian sloths show very similar values of DEI to those of diggers, not allowing a clear discrimination between substrate preference categories.
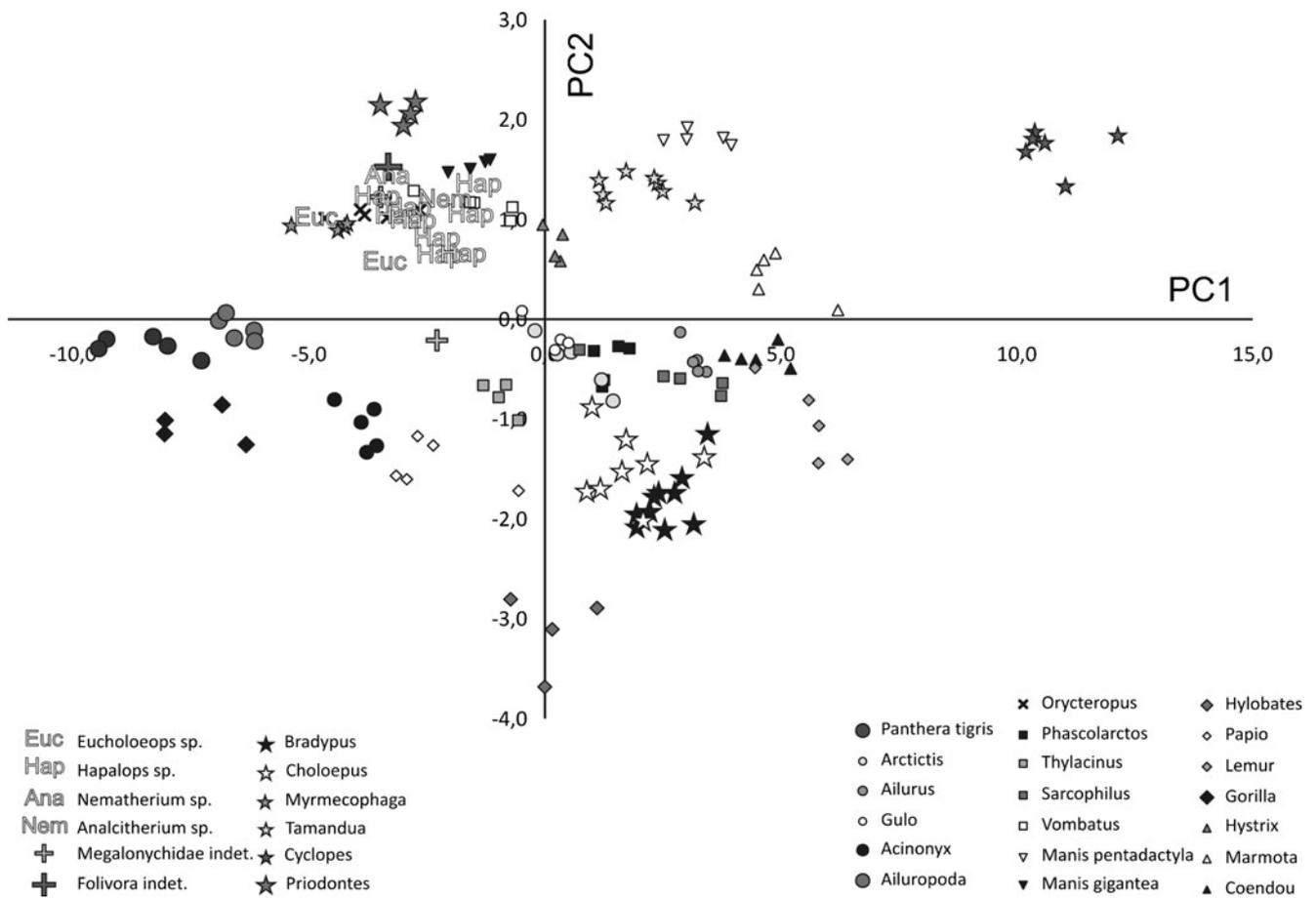
Fig. 5 Distribution of the 26 taxa of living mammals and 15 specimens of Santacrucian sloths in the morphospace depicted by PC1 and PC2. See Table 4 for the contributions of individual variables to each factor

Discussion

PCA shows that while extant sloths are sharing a common forelimb morphospace with primates (both groups being arboreal, non-digging mammals with slender and gracile forelimbs), Santacrucian sloths are clearly separated from their living relatives and share a morphospace with anteaters and other efficient-digging forms, such as pangolins, aardvarks, and wombats. The latter includes ground-dwelling as well as semi-arboreal and arboreal forms. Thus, the results of the PCA seem to reflect to a great extent the way the animals use the substrate, obscuring inferences about substrate preferences.

This morphometric similarity between Santacrucian sloths and extant digging mammals is characterized by the combination of length of forelimb elements (RL, UL, and HL) with olecranon process length (OTL) and entepicondylar width (HEMP). The amount of epicondylar space available for hand retractor and prehensor musculature is captured by DEI, where the separation between non-diggers and diggers becomes more pronounced. DEI values of Santacrucian sloths resemble more those of diggers than those of non-diggers, suggesting powerful hand prehension and retraction

capabilities. A long olecranon is linked to mechanical advantage of the triceps muscle. This feature is in fact reflected by IFA (combination of most positive and negative variables in PC2: OTL and UL, respectively). Thus, as depicted by the PC1 vs PC2 plot (Fig. 5) and the DEI and IFA boxplots (Fig. 7), diggers and Santacrucian sloths show relatively short and massive forelimb elements, as well as wider epicondyles and slightly longer olecranon processes than non-diggers, especially the mylodontid *Nematherium*.

Pujos et al. (2007) performed an extensive morphofunctional description of the Pleistocene climbing megalonychid *Diabolotherium*. In that study, the authors considered both *Diabolotherium* and *Hapalops* to have a relatively short olecranon process when compared with Pleistocene mylodontids, which show a particularly well-developed olecranon and were good diggers as proposed by Bargo et al. (2000). In the latter study, the authors analyzed limb proportions and resistance to bending forces in the Pleistocene mylodontids *Scelidotherium*, *Glossotherium*, and *Lestodon* to infer their locomotor abilities. Their conclusion was that the forelimbs of these ground sloths were well suited for activities such as digging where force is favored over velocity. Indeed, these forms were proposed as
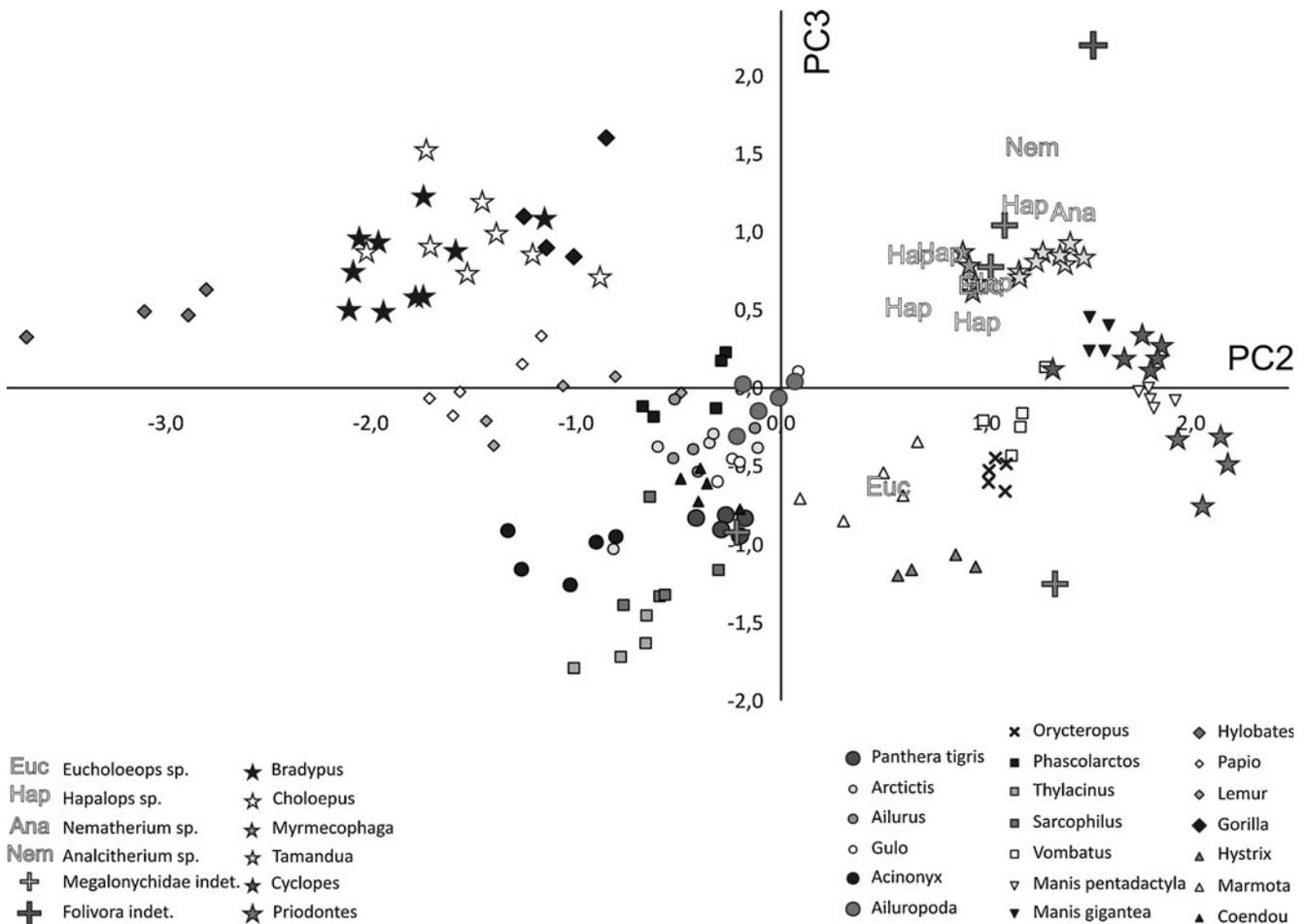
Fig. 6 Distribution of the 26 taxa of living mammals and 17 specimens of Santacrucian sloths in the morphospace depicted by PC2 and PC3. See Table 4 for the contributions of individual variables to each factor

cave-builders (see Vizcaíno et al. 2001). It is noteworthy that the mylodontid *Nematherium* exhibits the most robust and massive humerus among Santacrucian sloths (Fig. 2), suggesting that mylodontids would have a very long phylogenetic history of digging habits.

The shared possession of a relatively extended olecranon process in both non-suspensory climbers and diggers was recognized previously by White (1993). Non-digging forms show low values of this variable, as noted by Elissamburu and Vizcaíno (2004) and Croft and Anderson (2008), while the arboreal suspensory forms are those with shortest olecranon processes (e.g., living sloths, gibbon; Fig. 5). Although the measurements used in this work do not explain sufficiently the variability in ulnar shape between *Eucholoeops* and *Hapalops,* a detailed qualitative morphofunctional analysis recently performed (Toledo submitted) provides more insight into these issues.

It is interesting to think that the mechanical requirements for most characteristic locomotor behaviors of suspensory climbers (brachiation, where tensile forces are applied to bones; Oxnard 1984) could be considered opposite to the

mechanical requirements for digging (where primarily compressive forces are applied).

Santacrucian sloths had a functional pattern of forelimb use that differed from the extant ones, and were probably more similar to living anteaters and pangolins, which were able to dig, or at least to rip the substrate to obtain their food. A few of these living mammals are semiarboreal or arboreal, like the lesser anteaters, *Tamandua* and *Cyclopes*, and the Chinese pangolin, *Manis pentadactyla*. It is interesting to note that no separation between substrate preference groups within digging mammals is apparent from the PCA. The very slender and gracile forms, such as the extant sloths and the gibbon *Hylobates* at one extreme of the PC2 axis, are strictly arboreal and do not dig. At the other extreme are diggers. Between these extreme morphologies there are several generalized ground-dwelling, semi-arboreal, and arboreal mammals without derived morphologies suited for digging. The Santacrucian sloths also show positive values of HEMP, a variable that can be related to powerful hand prehension: that is, a medially protruding humeral entepicondyle. This trait implies increased area available for well-developed carpal and digital flexor

Fig. 7 Boxplot of functional indices. **a** Brachial Index; **b** Fossorial Ability Index; **c** Distal Epiphyseal Index. Box midline represents means, and box roof and floor are first and third quartile, respectively. Whiskers represent cases lying within 1.5 times the interquartile range. Dots out of the whiskers must be considered outliers. *Fol* Folivora indet.; *Meg* Megalonychidae indet.; *Euc* Eucholoeops sp.; *Hap* Hapalops sp.; *Nem* Nematherium sp.; and *Anat* Analcitherium sp. See Table 2 for further explanations
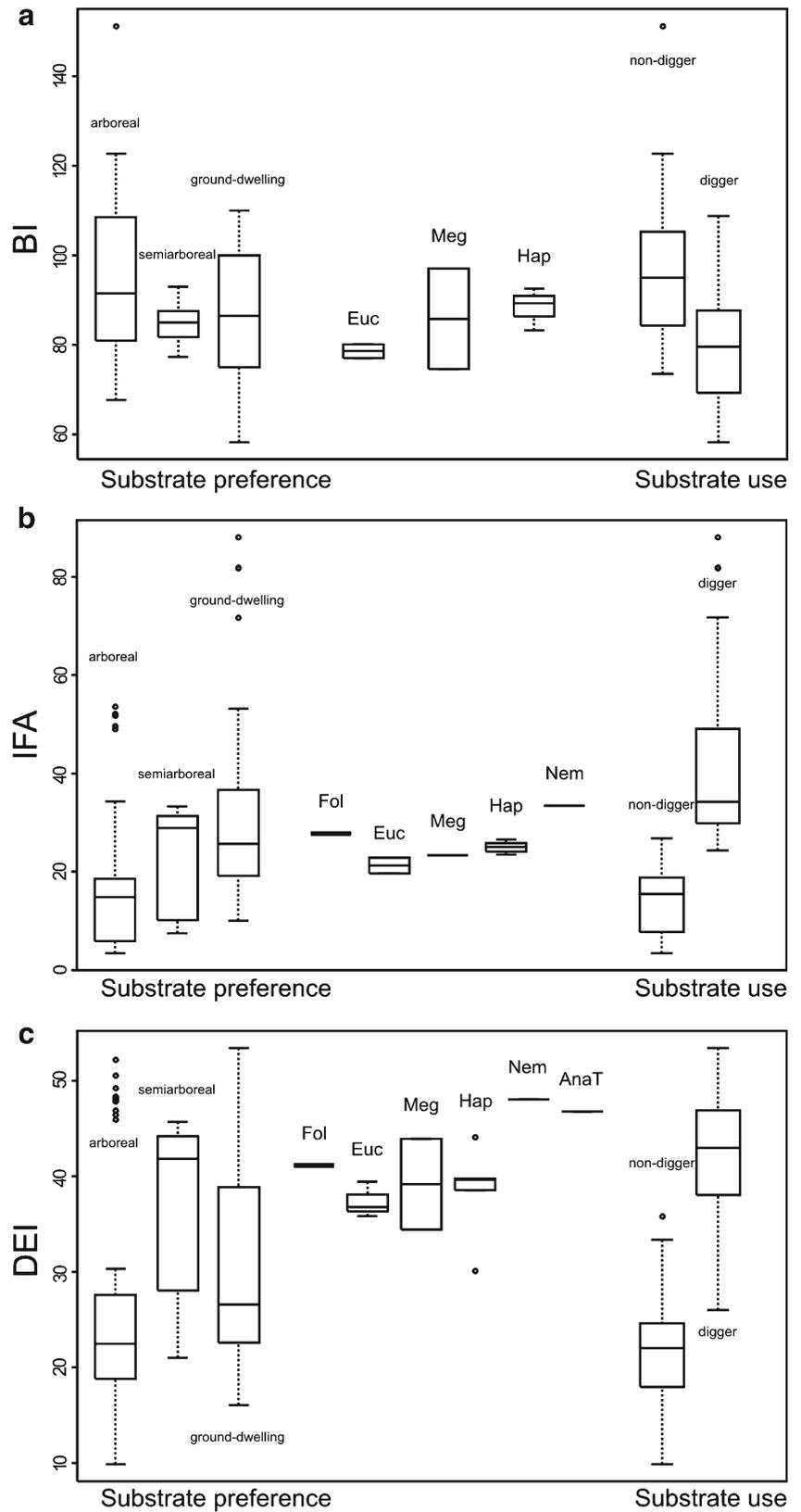
musculature, involved in climbing supports (Argot 2001; Sargis 2002) but also digging activities. This pattern is consistent with the DEI results (an index that is equivalent to the EI index of Elissamburu and Vizcaíno 2004), reflecting increasing hand flexor musculature from non-digging to digging forms. Milne et al. (2009) found a strong positive correlation between

increasing IFA values and well-developed entepicondyles in cingulates, as Elissamburu and Vizcaíno (2004) found for caviomorph rodents. A similar pattern was also described for caviomorph rodents by Candela and Picasso (2008). Thus, it can be argued that both the mechanical requirements for climbing supports and for digging activities involve powerful carpal and digital retraction and/or flexion.

To summarize, several morphological features associated with mechanical requirements for digging and climbing behaviors are similar, as noted previously by White (1997): powerful humeral adduction and retraction capabilities, as suggested by the great development of the deltopectoral ridge; powerful (more than fast) forearm extension, indicated by the relatively large olecranon process; and powerful carpal and digital flexion capacity. In their analysis of the notoungulate *Protypotherium*, Croft and Anderson (2008) found that both "semifossorial" and arboreal mammals share similar eigenvalues for many functional indices, including IFA, BI, and EI. Discriminant analysis performed by these authors using above-mentioned indices misclassified forms as "arboreal" instead of "semifossorial" and vice-versa. Interestingly, aquatic mammals seem to have similar values for IFA (Smith and Savage 1956; Elissamburu and Vizcaíno 2004), so it can be proposed that some mechanical requirements of swimming also overlap to some degree with those of digging and/or climbing.

Concluding Remarks

1   Santacrucian (early Miocene) sloths *Hapalops*, *Eucholoeops*, *Nematherium*, and *Analcitherium* occupy a morphospace closer to that of anteaters, pangolins, and other digging forms, than to highly arboreal forms such as primates and extant sloths. This conclusion differs somewhat from those of White (1993, 1997), probably because this author used both fore- and hind limb variables to state substrate preference. It is probable that the hind limb provided morpho-functional patterns more clearly related to substrate preference.

2   This similarity between Santacrucian sloths and the digging mammals of the sample is characterized by a combination of different traits, including relative length of fore limb elements, as well as protrusion of humeral entepicondyle, olecranon length, and humeral distal epiphyseal width.

3   These results suggest that the fore limbs of Santacrucian sloths had a different functional pattern from those of extant ones, probably more similar to that of anteaters and pangolins. They probably had good digging capabilities and/or semiarboreal substrate preferences.

4   Substrate use also seems to be reflected in the results, and this may be interfering with the analysis of the

substrate preferences based on fore limb morphology. It is expected that the hind limb is less involved in selective pressures related to digging capabilities.

Appendix I

Table 5 Santacrucian sloths studied in this work. Specimens included in the Principal Component Analysis are depicted in bold

	Taxon	Catalogue number
Folivora	**gen. et sp. indet.**	**MPM-PV 3458**
Megalonychidae	*Eucholoeops ingens*	FMNH 13280
Megalonychidae	*Eucholoeops ingens*	MPM-PV 3401
Megalonychidae	***Eucholoeops* cf. *E. fronto***	MPM-PV 3403
Megalonychidae	***Eucholoeops* sp.**	MPM-PV 3651
Megalonychidae	**gen. et sp. indet.**	AMNH 9249
Megalonychidae	**gen. et sp. indet.**	AMNH 94754
stem Megatherioidea	***Hapalops angustipalatus***	YPM VPPU 15562
stem Megatherioidea	***Hapalops elongatus***	FMNH 13133
stem Megatherioidea	***Hapalops longiceps***	YPM VPPU 15523
stem Megatherioidea	*Hapalops platycephalus*	YPM VPPU 15564
stem Megatherioidea	***Hapalops rectangularis***	FMNH 13143
stem Megatherioidea	***Hapalops ruetimeyeri***	FMNH 13130
stem Megatherioidea	***Hapalops* sp.**	MPM-PV 3404
stem Megatherioidea	***Hapalops* sp.**	MPM-PV 3400
stem Megatherioidea	***Hapalops* sp.**	MPM-PV 3467
stem Megatherioidea	***Hapalops* sp.**	YPM VPPU 15160
stem Megatherioidea	*Hapalops* sp.	YPM VPPU 15520
stem Megatherioidea	*Hapalops* sp.	MLP 34-III-5-1
Mylodontidae	***Analcitherium?* sp.**	FMNH 13131
Mylodontidae	*Nematherium* sp.	YPM-VPPU 15374
Mylodontidae	***Nematherium angulatum***	YPM-VPPU 15374

Appendix II

Table 6 List of specimens of extant mammals used in this work. For this study genus level was chosen as analysis unit, except for giant and Chinese pangolins, for whose we used the species

	Taxon	Catalogue number	Substrate preference
Xenarthra			
Bradypodidae	*Bradypus* sp.	AMNH 42454; 42838; 74136; 74137; 97315; 133437; 135474; 209940; 211663; 261304	arboreal
Megalonychidae	*Choloepus* sp.	AMNH 16873; 35483; 70440; 90269; 139772; 139773; 209941; 265952	arboreal
Myrmecophagidae	*Myrmecophaga tridactyla*	AMNH 1020; 100068; 100139; FMNH 15966	ground-dwelling
Myrmecophagidae	*Tamandua* sp.	AMNH 23432; 23436; 23437; 23565; 23567; 96258; 211659; 211660	semi-arboreal
Cyclopidae	*Cyclopes didactylus*	AMNH 4780; 167845; 171297; 204662; 213188; FMNH 61853	arboreal
Dasypodidae	*Priodontes* sp.	AMNH 130387; 208104; FMNH 25271; 72913	ground-dwelling
Carnivora			
Ailuridae	*Ailurus fulgens*	AMNH 35433; 119474; 146682; 146778; 185346	arboreal
Felidae	*Panthera tigris*	AMNH 85396; 113743; 113744; 113748; 135846	ground-dwelling
Felidae	*Acinonyx jubatus*	AMNH 36426; 119654; 119655; 119656; 119657	ground-dwelling
Mustelidae	*Gulo gulo*	AMNH 35054; 35081; 149692; 165766	ground-dwelling
Ursidae	*Ailuropoda melanoleuca*	AMNH 87242; 89028; 110453; 110454; 147746	ground-dwelling
Viverridae	*Arctictis binturong*	AMNH 181; 22906; 35469; 80163; 119600	semi-arboreal
Marsupialia			
Dasyuridae	*Sarcophilus laniarius*	AMNH 65670; 65672; 65673; 70406; 150211	ground-dwelling
Thylacinidae	*Thylacinus cynocephalus*	AMNH 35244; 35504; 35866; 42259	ground-dwelling
Phascolarctidae	*Phascolarctos cinereus*	AMNH 65607; 65608; 65609; 65610; 107805	arboreal
Vombatidae	*Vombatus ursinus*	AMNH 42997; 65619; 65622; 70209; 146850	ground-dwelling
Pholidota			
Manidae	*Manis gigantea*	AMNH 53847; 53851; 53857; 53858	ground-dwelling
Manidae	*Manis pentadactyla*	AMNH 60004; 60006; 60007; 172147; 184959	semi-arboreal
Primates			
Cercopithecidae	*Papio ursinus*	AMNH 80771; 80774; 120388; 216247; 216251	semi-arboreal
Hominidae	*Gorilla gorilla*	AMNH 54089; 54090; 54091; 54092	semi-arboreal
Hylobatidae	*Hylobates syndactylus*	AMNH 90268; 102463; 106581; 106584	arboreal
Lemuridae	*Lemur catta*	AMNH 22912; 35396; 150039; 170739; 170740	arboreal
Rodentia			
Erethizontidae	*Coendou prehensilis*	AMNH 80045; 100097; 100119; 134073; 212611	arboreal
Hystricidae	*Hystrix cristata*	AMNH 51735; 87220; 87222; 119506	ground-dwelling
Sciuridae	*Marmota monax.*	AMNH 70338; 97386; 179934; 180314; 235648	ground-dwelling
Tubulidentata			
Orycteropodidae	*Orycteropus afer*	AMNH 51370; 51374; 51905; 51909; 65540	ground-dwelling

References

Argot C (2001) Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 247: 51–79

Argot C (2004) Evolution of South American mammalian predators (Borhyaenoidea): anatomical and palaeobiological implications. Zool J Linn Soc 140: 487–521

Bargo MS, Toledo N, Vizcaíno SF (in press) Paleobiology of the Santacrucian sloths and anteaters (Xenarthra, Pilosa). In: Vizcaíno SF, Kay RF, Bargo MS (eds.) Early Miocene Paleobiology in Patagonia: High-latitude Paleocommunities of the Santa Cruz Formation. Cambridge University Press, Cambridge

Bargo MS, Vizcaíno SF, Archuby FM, Blanco RE (2000) Limb bone proportions, strength and digging in some Lujanian (late Pleistocene-early Holocene) mylodontid ground sloths (Mammalia, Xenarthra). J Vertebr Paleontol 20: 601–610

Bargo MS, Vizcaíno SF, Kay RF (2009) Predominance of orthal masticatory movements in the early Miocene *Eucholaeops* (Mammalia, Xenarthra, Tardigrada, Megalonychidae) and other megatherioid sloths. J Vertebr Paleontol 29: 870–880.

Candela AM, Picasso MBJ (2008) Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): indicators of locomotor behavior in Miocene porcupines. J Morphol 269: 552–593

Chiarello AG (2008) Sloth ecology: an overview of field studies. In: Vizcaíno SF, Loughry WJ (eds) The Biology of the Xenarthra. University Press of Florida, Gainesville, pp 269–280

Croft DA, Anderson LC (2008) Locomotion in the extinct notoungulate *Protypotherium*. Paleontol Electron 11: 1–20

Delsuc F, Douzery EJP (2008) Recent advances and future prospects in xenarthran molecular phylogenetics. In: Vizcaíno SF, Loughry WJ (eds) The Biology of the Xenarthra. University Press of Florida, Gainesville, pp 11–23

Elissamburu A, Vizcaíno SF (2004) Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). J Zool Lond 262: 145–159

Gaudin TJ (2004) Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. Zool J Linn Soc 140: 255–305

Gaudin TJ, McDonald HG (2008) Morphology-based investigations of the phylogenetic relationships among extant and fossil xenarthrans. In: Vizcaíno SF, Loughry WJ (eds) The Biology of the Xenarthra. University Press of Florida, Gainesville, pp 24–36

Gaudin TJ, Emry RJ, Wible JR (2009). The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: a morphology based analysis. J Mammal Evol 16 (4): 235–305

Howell BA (1944) Speed in Animals. Their Specialization for Running and Leaping. University of Chicago Press, Chicago.

Milne N, Vizcaíno SF, Fernicola JC (2009) A 3D geometric morphometric análisis of digging ability in the extant and fossil cingulate humerus. J Zool Lond 278: 48–56

Nowak RM (1999) Walker's Mammals of the World, Sixth Ed. Johns Hopkins University Press, Baltimore

Oxnard C (1984) The Order of Man. Hong Kong University Press, Hong Kong

Pujos F, De Iuliis G, Argot C, Werdelin L (2007) A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implication for sloth history. Zool J Linn Soc 149: 179–235

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Sargis EJ (2002) Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. J Morphol 253: 10–42

Smith MJ, Savage RJG (1956) Some locomotory adaptations in mammals. Zool J Linn Soc 42: 603–622

Vizcaíno SF, Bargo MS, Fariña RA (2008) Form, function and paleobiology in xenarthrans. In: Vizcaíno SF, Loughry WJ (eds) The Biology of the Xenarthra. University Press of Florida, Gainesville, pp 86–99

Vizcaíno SF, Bargo MS, Kay RF, Fariña RA, Di Giacomo M, Perry MG, Prevosti FJ, Toledo N, Cassini GH, Fernicola JC (2010) A baseline paleoecological study for the Santa Cruz Formation (late-early Miocene) at the Atlantic coast of Patagonia, Argentina. Palaeogeog Palaeoclimat Palaeoecol 292: 507–519

Vizcaíno SF, Fariña RA, Mazzetta G (1999) Ulnar dimensions and fossoriality in armadillos and other South American mammals. Acta Theriol 44: 309–320

Vizcaíno SF, Zárate M, Bargo MS, Dondas A (2001) Pleistocene large burrows in the Mar del Plata area (Buenos Aires Province, Argentina) and their probable builders. In: Vizcaíno SF, Fariña RA, Janis C (eds) Biomechanics and Paleobiology of Vertebrates. Acta Paleontol Pol Special Issue 46: 157–169

White JL (1993) Indicators of locomotor habits in xenarthrans: evidence for locomotor heterogeneity among fossil sloths. J Vertebr Paleontol 13: 230–242

White JL (1997) Locomotor adaptations in Miocene xenarthrans. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, DC pp 246–264

White JL, MacPhee RD (2001) The sloths of the West Indies: a systematic and phylogenetic review. In: Woods CA (ed) Biogeography of the West Indies: Patterns and Perspectives. CRC Press, New York, pp 201–235