J Mammal Evol
DOI 10.1007/s10914-017-9400-2

ORIGINAL PAPER

Advantages and Limitations in the Use of Extant Xenarthrans (Mammalia) as Morphological Models for Paleobiological Reconstruction

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Abstract Extant species of Xenarthra represent a severely restricted sample of the total diversity achieved by the group. Given their shared history, the extant representatives of the three major groups of xenarthrans (Cingulata, Folivora, and Vermilingua) provide a valuable basis for paleobiological inference. However, many extinct taxa are morphologically so dissimilar from their extant relatives that they suggest very different ways of life. In these cases, extinct forms do not have modern models within the group and the application of a simplistic and strict approach can produce nonsensical reconstructions. In this contribution, we evaluate the limitations of the use of extant xenarthrans as morphological models for paleobiological reconstructions. A database of linear dimensions of the appendicular skeleton of extant and extinct xenarthrans and other mammals (marsupials, carnivorans, rodents, primates, perissodactyls, artiodactyls, and proboscideans) was constructed. Exploratory analyzes were performed on general morphometric similarity between existing and extinct xenarthrans (PCA) and the accuracy of body mass estimates of extinct xenarthrans based on their close relatives and other mammals (simple and multiple linear regressions) were tested. Extinct xenarthrans occupy similar relative positions in the morphospaces as extant mammals other than their closest relatives. Most allometric equations, particularly those based only on xenarthrans, produced remarkable underestimates. This can be explained by dimensional differences (up to four orders of magnitude) and shape differences between most of the extinct and extant xenarthrans. This does not invalidate actualism and the use of analogues, but suggests the need to apply other approaches, such as mechanics, that address form-function relationships but are not necessarily based on known biological comparators.

Keywords Xenarthra · Paleobiology · Form-function · Actualism

Introduction

In the last 15 years, molecular studies have clearly supported Xenarthra as one of the four major clades of Eutheria (e.g., Delsuc and Douzery 2008; Asher and Helgen 2010; Meredith et al. 2011; but see O'Leary et al. 2013), and provided evidence that crown placental mammalian diversification was related to ancient plate tectonic events. According to Wildman et al. (2007), when Gondwana and Laurasia separated during the Cretaceous, the Atlantogenata, the southern clades of Xenarthra (armadillos, anteaters, and sloths) and Afrotheria (hyraxes, elephants, and others) become isolated from the Boreoeutheria, the northern Laurasiatheria and Euarchontoglires, and the Late Cretaceous separation of South America and Africa resulted in the divergence of Xenarthra and Afrotheria (Fig. 1). Still, the overall morphology of xenarthrans seems radically different to that of afrotheres except in the late eruption of permanent dentition (Asher and Lehmann 2008; Asher et al. 2009).

Electronic supplementary material The online version of this article (doi:10.1007/s10914-017-9400-2) contains supplementary material, which is available to authorized users.

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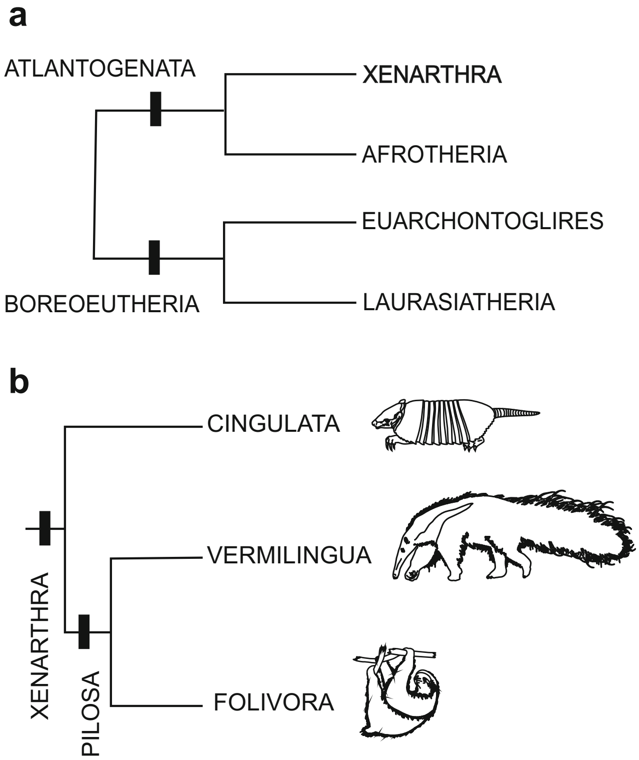

Fig. 1 Phylogenetic relationships of placental mammals. **a** Among the four major clades, following Asher and Helgen (2010). **b** Among major clades of xenarthrans

Clearly, the time elapsed since the Late Cretaceous has been sufficient to produce not only a great morphologic distance between Atlantogenata and Boreoeutheria, and between xenarthrans and afrotheres, but also within these clades. Xenarthrans have a long history in South America, with their first fossil record during the Paleocene, and an enormous disparity between extant and extinct taxonomic richness and morphological disparity, with living species representing a severely restricted sample of the total richness and diversity achieved by the group (Vizcaíno and Loughry 2008; Vizcaíno et al. 2008). There are 31 species of extant xenarthrans (Gardner 2005a, b), including armadillos (Cingulata, "Dasypodidae"), digging animals with a complete, flexible armor and diets ranging from omnivory to myrmecophagy, the strictly myrmecophagous anteaters (Vermilingua), which range from fully terrestrial to fully arboreal in habits, and the almost completely arboreal, largely folivorous, tree sloths (Folivora). Their extinct representatives, however, exhibit very peculiar features, with many taxa reaching large body sizes, particularly those of the Pleistocene, of which some achieved masses greater than a ton (Vizcaíno et al. 2012 and references therein). Cingulates are very diverse including many extinct taxa as large as or larger than extant armadillos, such as eutatine armadillos, pampatheres (Pampatheriidae), and glyptodonts (Glyptodontidae). Pilosans are also very diverse, especially the sloths (Mylodontidae, Megalonychidae, Nothrotheriidae, and Megatheriidae). Anteaters are very poorly represented, with two extant clades: Myrmecophagidae, with very few fossil representatives, and Cyclopedidae without known extinct relatives.

These peculiarities make extinct xenarthrans particularly interesting for paleobiogical studies aimed at reconstructing their appearance as living animals and describing their basic behavior, ecological role, and habitat. Vizcaíno et al. (2008) noted that many paleomammalogists apply a restrictive actualistic criterion in considering the paleobiology of extinct forms, assuming such species had habits similar to those of their extant relatives. This practice probably stems from the fact that extant mammals are very diverse and most clades include extinct forms and, reciprocally, most extinct mammals can be assigned to extant orders. In this context, the fact that there are extant representatives of the three major groups of xenarthrans (Cingulata, Folivora, and Vermilingua) provides a valuable, and tempting, basis for paleobiological inference. However, an overly straightforward approach may produce either very predictable results or nonsensical reconstructions (Vizcaíno 2014). Among cingulates, the early Miocene armadillo *Prozaedyus proximus* Ameghino, 1887, may have been very similar in behavior and played a very similar ecological role as the extant relative *Zaedyus pichiy* Desmarest, 1804, based on their notable morphological similarities (including size; Fig. 2). But among sloths, due to the unusual lateral expansion of the femur, the use of a single allometric equation based on transverse diameter -a measurement used extensively in body mass estimates of mammals- produces an overestimate of 98 tons for the elephant-sized Pleistocene ground sloth *Megatherium americanum* Cuvier, 1796 (Fariña et al. 1998; Fig. 3).

The purpose of this paper is to evaluate advantages and limitations in the use of extant xenarthrans as morphological models for paleobiological reconstructions of their extinct relatives. In doing so, some exploratory analyses on the overall morphometric similarity between extant and extinct xenarthrans were performed, and the accuracy of body mass estimations of extinct xenarthrans based on their close extant relatives and other mammals was evaluated. The results will be discussed in combination with a review of further information available in previous literature.

Materials and Methods

A database was built with ten linear dimensions of fore- and hind limbs (Table 1) of 195 specimens of mammals that include 19 marsupials, 92 xenarthrans (43 extinct and 49 extant), five aardvarks, one elephant, 31 carnivorans, nine manids, 18 primates, 14 rodents, and six ungulates (Appendix 1, Online Supplement).

Institutional Abbreviations AMNH – American Museum of Natural History, New York, USA. FMNH – Florida

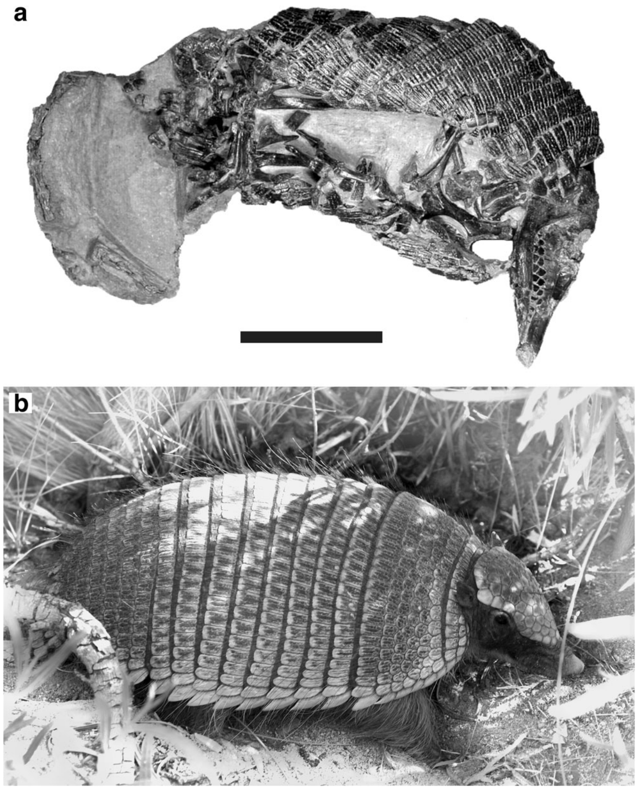

Fig. 2 **a** Complete articulated skeleton and carapace of the Miocene armadillo *Prozaedyus proximus* (MPM-PV 3506). **b** A specimen in the wild of its extant relative *Zaedyus pichiy*. Scale bar 5 cm

Museum of Natural History, Gainesville, USA. MACN – Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina. MLP - Museo de La Plata, La Plata, Argentina. MPM-PV – Museo Regional Provincial Padre M.J. Molina, Río Gallegos, Argentina. USNM – Smithsonian, National Museum of Natural History, Washington, USA. YPM-VPPU – Yale Peabody Museum-Vertebrate Paleontology Princeton University, New Haven, USA.

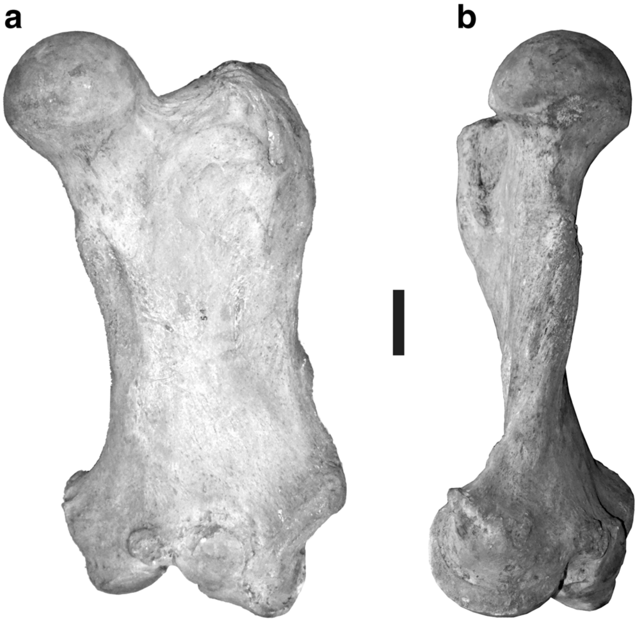

Fig. 3 Left femur of the Pleistocene giant ground sloth *Megatherium americanum* (MACN PV 54). **a** Frontal view, and (**b**) Medial view. Scale bar 10 cm

PCA

Principal Component Analysis was performed to explore the overall morphometric similarity of extant and extinct xenarthrans. Data were ten based log-transformed prior to analysis to reduce bias due to size differences among taxa. A covariance matrix was used. Different PCA were performed. Separated PCAs were also performed for forelimb and hind limb measurements. Calculations were performed in R (R Development Core Team 2008). The R command *princomp* of the R core package *stats* was used to perform calculations, and the graphics were built using the package *ggplot2* (Wickham 2009).

Linear Single and Multiple Regressions for Body Size Estimations

A number of regression equations were performed attempting to describe correlations between limb dimensions and body mass. Calculations were performed in R (R Development Core Team 2008). These allometric equations were achieved by an iterative process, beginning with the total extant sample, then repeating the regression only with xenarthrans, then only pilosans, and then only cingulates, in order to test changes in estimations related to the extant sample. In addition, progressively more simple equations were calculated, beginning with several variables for each limb, then with two variables, and finally with only one variable. Permutations tests were used to avoid biases derived from small sample size and non-normal distribution of data, especially for the xenarthran and cingulate samples. Finally, each equation was used to compute body mass estimates for the extinct xenarthrans sample. In the case of equations developed only from the extant xenarthran sample, predictions calculated for extinct xenarthrans beyond the interval of extant sample body masses lack statistical accuracy and are considered only as mathematical simulations to understand the behavior of the variables. R command *lmp* from the package *lmPerm* (Wheeler 2016) was used for calculations, and Smearing Estimator (SE) of Duan (1983) was computed to detect potential bias introduced by log-transformation. The datasets generated during the current study are available from the corresponding author on reasonable request.

Table 1 Measurements of fore- and hind limb elements

	Element	Measurement	Abbr.
1	Humerus	Humerus Length - between head and trochlea	HL
2		Antero-Posterior Diameter of Humerus - at midshaft	APDH
3	Ulna	Ulnar Length	UL
4		Olecranon - Trochlea notch length	OTL
5	Radius	Radius Length	RL
6		Radius Diameter - at midshaft	RH
7	Femur	Femoral Length - between head and medial condyle	FL
8		Antero-Posterior Diameter of Femur - at midshaft	APDF
9	Tibia	Tibial Length- from interfacet eminence to tibial malleolus	TL
10		Antero-Posterior Diameter of Tibia - at midshaft	APDT

Results

PCA

For both forelimb and hind limb dimensions taken together (Table 2, Fig. 4), the first two components concentrated more than 90% of total variance. In the first PC, all variables contributed in similar proportion, reflecting overall dimensions, while the second PC was dominated by humerus and radius lengths (negative) and olecranon length (positive). Extinct xenarthrans are concentrated around the quadrant defined by positive scores of PC2 and negative loadings of PC1, which are the largest animals with comparatively short humeri and radii and long olecrana. While clearly separated from extant sloths (grouped with primates), they occupy the same region of the morphospace as large and massive ungulates (rhinoceros, hippopotamus, and elephant), and along PC2 they share coordinates with extant diggers such as anteaters, armadillos, pangolins, aardvarks, and wombats.

The pattern is very similar for the forelimb dimensions (Table 2, Fig. 5). The first two PCs concentrated more than 90% of variance. PC1 received similar contributions from all variables while PC2 was dominated again by humerus and radius lengths (negative) and olecranon length (positive). Early Miocene sloths (not represented in the previous analysis due to missing data) share morphospace with the giant anteater, while giant Pleistocene xenarthrans are placed in a similar area as in the previous analysis. Noteworthy is the metric similarity between the giant ground sloth *Megatherium* and the elephant *Loxodonta*.

Finally, in the analysis using only hind limb dimensions (Table 2, Fig. 6), the first two PCs concentrated more than 90% of variance. The first PC reflected similar contributions of all variables, while the second was dominated by tibia length and femur length (negative) and antero-posterior diameter of tibial and femoral diaphyses (positive). The most interesting pattern is that glyptodonts are clearly separated from rest of the sample, in the very positive extreme of PC2 (relatively shorter and stouter femur and tibia). Most extinct sloths share morphospace with digging mammals, clearly separated again from extant sloths (especially from the two-toed *Choloepus*, while they are a bit closer to the three-toed *Bradypus*).

Linear Single and Multiple Regressions for Body Size Estimations

Results of regressions are summarized in Appendix 2 (Online Supplement). Most of the multiple linear equations showed good R and R-squared parameters (around 0.9–0.8), good SE values (around 1.00, indicating absent or negligible distortion induced by log-transformation), and significant p-values. Lowest reliability of equations is for ulnar length and olecranon length. Broadly, equations for xenarthrans, pilosans, and cingulates are slightly less reliable than equations based on the total sample. In some specific equations (for instance hind limb: Femur Total Length and Tibial Length), the xenarthran database rendered slightly higher R parameters than the total extant sample. In many cases pilosan equations showed slightly higher parameters than xenarthran equations (six of 11 total equations), while cingulate equations rendered the lowest parameters in all but the Ulnar Length Olecranon Length equation.

Discussion

Principal Components Analysis

The morphospace defined by the eigenvalue decomposition roughly describes limb proportions. The most evident pattern emerging from the relative position of taxa along the morphospaces is that extinct xenarthrans are quite different in shape from their closest extant relatives. This is especially remarkable for sloths (both for fore- and hind limbs). While extant sloths cluster with primates due to their relatively long

Table 2 PCA results for fore- and hind limb dimensions. Abbreviations as in Table 1

Total PCA (both fore and hindlimb): HL + APDH + RL + RH + OTL + FTL + APDF + TL + APDT

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Importance of components									
Standard deviation	2.783	0.913	0.361	0.296	0.270	0.180	0.142	0.108	0.098
Proportion of variance	0.866	0.093	0.015	0.010	0.008	0.004	0.002	0.001	0.001
Cumulative Proportion	0.866	0.959	0.974	0.984	0.992	0.995	0.998	0.999	1.000
Contribution of each variable									
HL	-0.332	-0.371	0.060	0.353	0.280	0.210	0.293	-0.499	0.408
APDH	-0.340	0.255	0.141	0.303	0.521	-0.595	-0.260	0.113	-0.054
RL	-0.302	-0.575	0.103	-0.060	0.247	0.283	-0.050	0.430	-0.486
RH	-0.338	0.099	0.816	-0.323	-0.295	-0.053	0.098	-0.059	0.062
OTL	-0.305	0.530	-0.189	-0.428	0.418	0.476	0.052	-0.008	0.053
FTL	-0.352	-0.138	-0.235	-0.064	-0.259	-0.033	-0.241	0.496	0.653
APDF	-0.347	0.172	-0.078	0.357	-0.391	0.306	-0.559	-0.291	-0.268
TL	-0.339	-0.248	-0.400	-0.510	-0.122	-0.438	0.011	-0.401	-0.191
APDT	-0.342	0.257	-0.209	0.318	-0.305	-0.078	0.679	0.242	-0.232

Forelimb PCA: HL + APDH + RL + RH + OTL

	PC1	PC2	PC3	PC4	PC5
Importance of components					
Standard deviation	0.630	0.262	0.104	0.070	0.036
Proportion of variance	0.822	0.142	0.022	0.010	0.003
Cumulative Proportion	0.822	0.965	0.987	0.997	1.000
Contribution of each variable					
HL	0.415	-0.394	0.251	-0.177	0.761
APDH	0.439	0.216	0.136	-0.785	-0.354
RL	0.415	-0.634	0.174	0.329	-0.536
RH	0.487	0.071	-0.860	0.107	0.080
OTL	0.475	0.625	0.386	0.482	0.049

Hindlimb PCA: FTL + APDF + TL + APDT

	PC1	PC2	PC3	PC4
Importance of components				
Standard deviation	0.566	0.125	0.051	0.031
Proportion of variance	0.944	0.046	0.008	0.003
Cumulative Proportion	0.944	0.990	0.997	1.000
Contribution of each variable				
FTL	-0.476	-0.415	-0.134	0.763
APDF	-0.540	0.332	-0.720	-0.282
TL	-0.398	-0.678	0.212	-0.580
APDT	-0.569	0.507	0.647	0.034

and gracile limbs, extinct ones cluster in the opposite quadrant with large herbivores and diggers, all of them with stout limb bones with marked crests and tuberosities. This pattern was recognized previously for Caribbean Pleistocene sloths (White 1993, 1997) and Miocene sloths from Patagonia (White 1993, 1997; Bargo et al. 2012; Toledo et al. 2012; Toledo 2016). These differences in the appendicular skeleton shape suggest that using extant sloths as models for their extinct relatives could introduce strong biases, and that comparison with other mammals (e.g., anteaters and koalas) could provide much more heuristic functional hypotheses. In the case of glyptodonts, the overall similarity of the forelimb with that of extant armadillos is greater, but the same is true for other digging mammals, such as aardvarks and anteaters. Many of the humeral features of glyptodonts seem to be related to their large body size (Milne et al. 2009). Instead, the shape of the hind limb skeleton is pretty different from that of extant cingulates (as in Milne et al. 2012) and using the

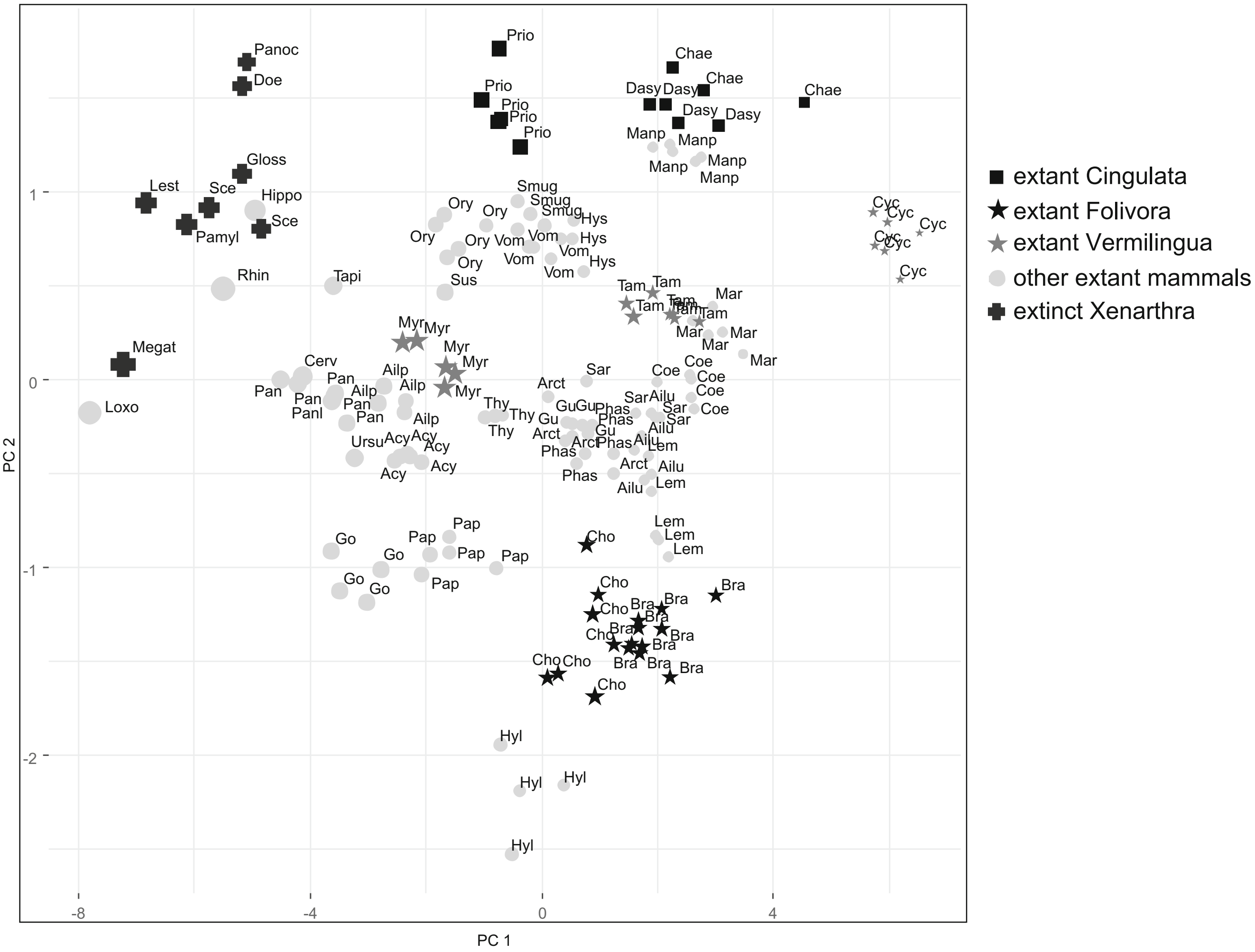

Fig. 4 Scatterplot of the first two components of PCA of both fore- and hind limb dimensions. Symbols were scaled using the geometric mean of the taxa dimensions to allow quick depiction of relative body sizes. Abbreviations: extinct xenarthrans, **Prop** *Propalaehoplophorus*, **Glyp** *Glyptodon*, **Panoc** *Panochthus*, **Doe** *Doedicurus*, **Megat** *Megatherium*, **Prep** *Prepotherium*, **Lest** *Lestodon*, **Gloss** *Glossotherium*, **Sce** *Scelidotherium*, **Pamyl** *Paramylodon*, **Anat** *Analcitherium*, **Nem** *Nematherium*, **Euc** *Eucholoeops*, **Anam** *Analcimorphus*, **Hap** *Hapalops*; extant xenarthrans, **Prio** *Priodontes*, **Chae** *Chaetophractus*, **Dasy** *Dasypus*, **Cho** *Choloepus*, **Bra** *Bradypus*, **Tam** *Tamandua*, **Myr** *Myrmecophaga*, **Cyc** *Cyclopes*; other extant mammals, **Sar** *Sarcophilus*, **Thy** *Thylacinus*, **Phas** *Phascolarctos*, **Vom** *Vombatus*, **Ory** *Orycteropus*, **Lox** *Loxodonta*, **Acy** *Acinonyx*, **Pan** *Panthera tigris*, **Panl** *Panthera leo*, **Arct** *Arctictis*, **Ailu** *Ailurus*, **Ursu** *Ursus*, **Ailp** *Ailuropoda*, **Gu** *Gulo*, **Smug** *Smutsia gigantea*, **Manp** *Manis pentadactyla*, **Pap** *Papio*, **Go** *Gorilla*, **Hyl** *Hylobates*, **Lem** *Lemur*, **Coe** *Coendou*, **Hys** *Hystrix*, **Mar** *Marmota*, **Rhin** *Rhinoceros*, **Tapi** *Tapirus*, **Hippo** *Hippopotamus*, **Camel** *Camelus*, **Cerv** *Cervus*, **Sus** *Sus*

latest as models for interpreting glyptodont hind limbs could be inconvenient too. However, no other extant mammal in our sample places near glyptodonts in the morphospace. This suggests two possible procedures to generate hypotheses with higher heuristic value: expand extant comparative sample and/or use non-biological models (i.e., biomechanics).

Xenarthran Based Equations for Body Mass Estimate

Allometric equations have been used by a plethora of researchers in estimating body size (e.g., see Damuth and McFadden 1990). Fariña et al. (1998), De Esteban-Trivigno et al. (2008), Vizcaíno et al. (2011), and Toledo et al. (2014) discussed issues involved in the development and application of allometric equations for extinct xenarthrans. Fariña et al. (1998) applied and discussed equations achieved for other clades of mammals, while De Esteban-Trivigno et al. (2008) focused on developing equations especially suited for xenarthrans.

After averaging all the results, Fariña et al. (1998) obtained mass estimations reasonably similar to those obtained with different methods such as scale and computer-generated models (see also Bargo et al. 2000; Vizcaíno et al. 2011). However, as mentioned above, Fariña et al. (1998) recognized that some estimations obtained from equations based on anatomical proportions were radically different in xenarthrans with respect to those of other mammals, and indeed may

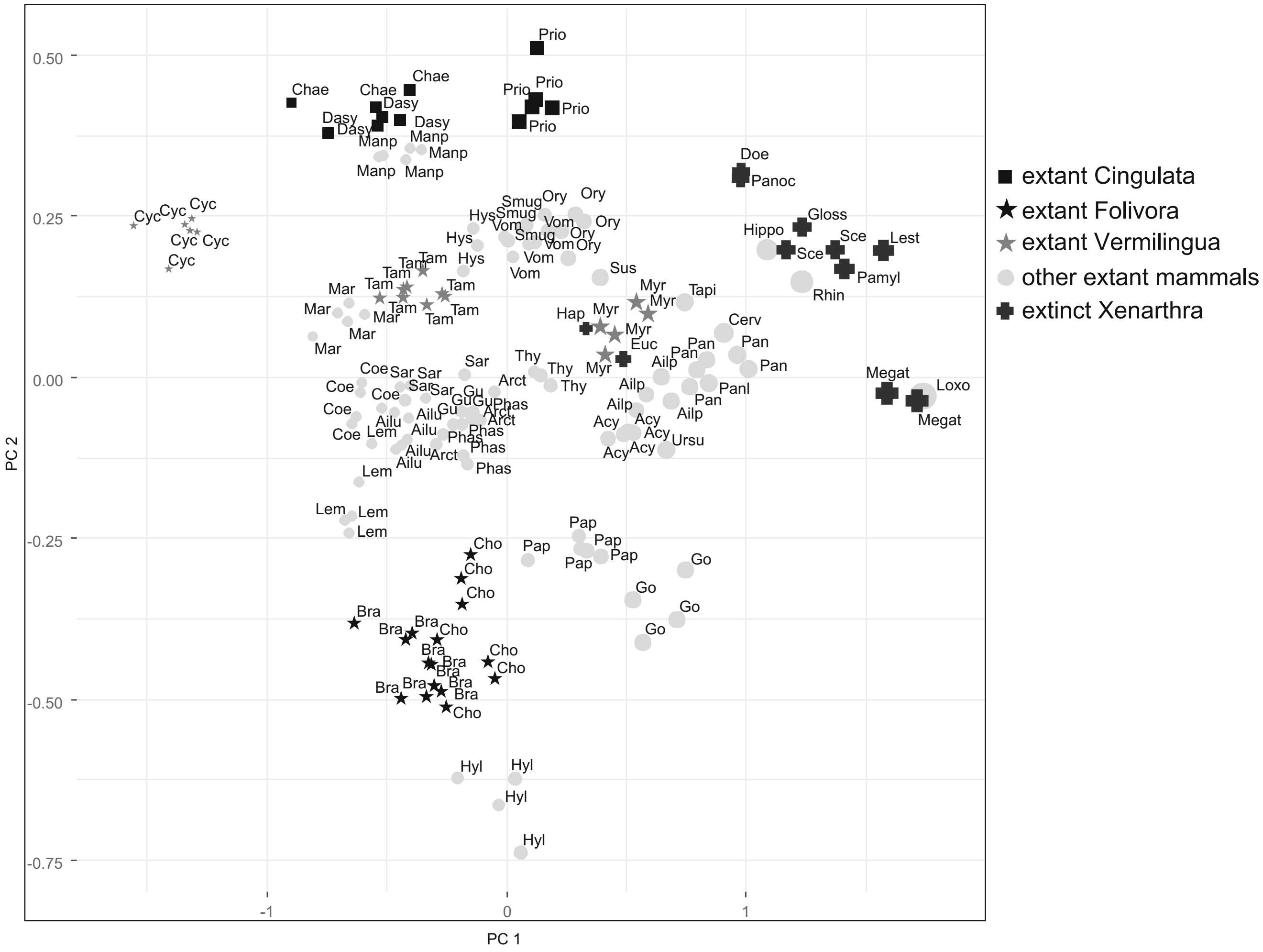

Fig. 5 Scatterplot of the first two components of PCA of forelimb dimensions. Symbols and abbreviations as in Fig. 4

produce nonsensical results that both grossly underestimate or overestimate body mass (e.g., using the tooth row length or the transverse diameter of the femur). Fariña et al. (1998) clearly established that most used ungulate cranial equations were inappropriate for xenarthrans and proposed that one solution would be to develop xenarthran-specific equations. These authors also remarked on the paucity or absence of body size data available for osteological specimens in collections, an issue that remains unresolved nearly two decades after their article was published.

A decade later, De Esteban-Trivigno et al. (2008) performed a regression protocol based on a mixed extant ungulate-xenarthran postcranial database, selecting only equations with stable percent errors when estimating body size of a test sample. Their results for the Miocene glyptodont *Propalaehoplophorus australis* Ameghino, 1887, and the Pleistocene ground sloth *Lestodon armatus* Gervais, 1855, were not particularly different from estimates using scale and computer models. They also pointed out that such equations worked well for other clades of mammals. Vizcaíno et al. (2011) again used scale and computer models based on their own life reconstructions of glyptodonts, obtaining mass estimations on average similar to those obtained by Fariña (1995) and Fariña et al. (1998). More recently, Toledo et al. (2014) developed ad hoc postcranial allometric equations for extinct sloths from a wide extant mammal database, obtaining values reasonably similar those of previous works (White 1993; Croft 2001).

In this contribution, most xenarthran, pilosan, and cingulate equations produced remarkable underestimations when compared with previously published body size estimations (close estimations were obtained only for a few cases; Table 3). Such departures can be explained not only by the dimensional differences (up to four orders of magnitude) between most extinct taxa considered in this contribution and extant xenarthrans, but also (and more importantly here) by the shape differences between them. For instance, in all groups the third trochanter on the lateral side of the femur, one of the most conspicuous features of the xenarthran femur (McDonald and De Iuliis 2008), becomes more distal as size increases (Milne et al. 2012) in a way that is consistent with a stress reducing strategy (Milne et al. 2012; Milne and

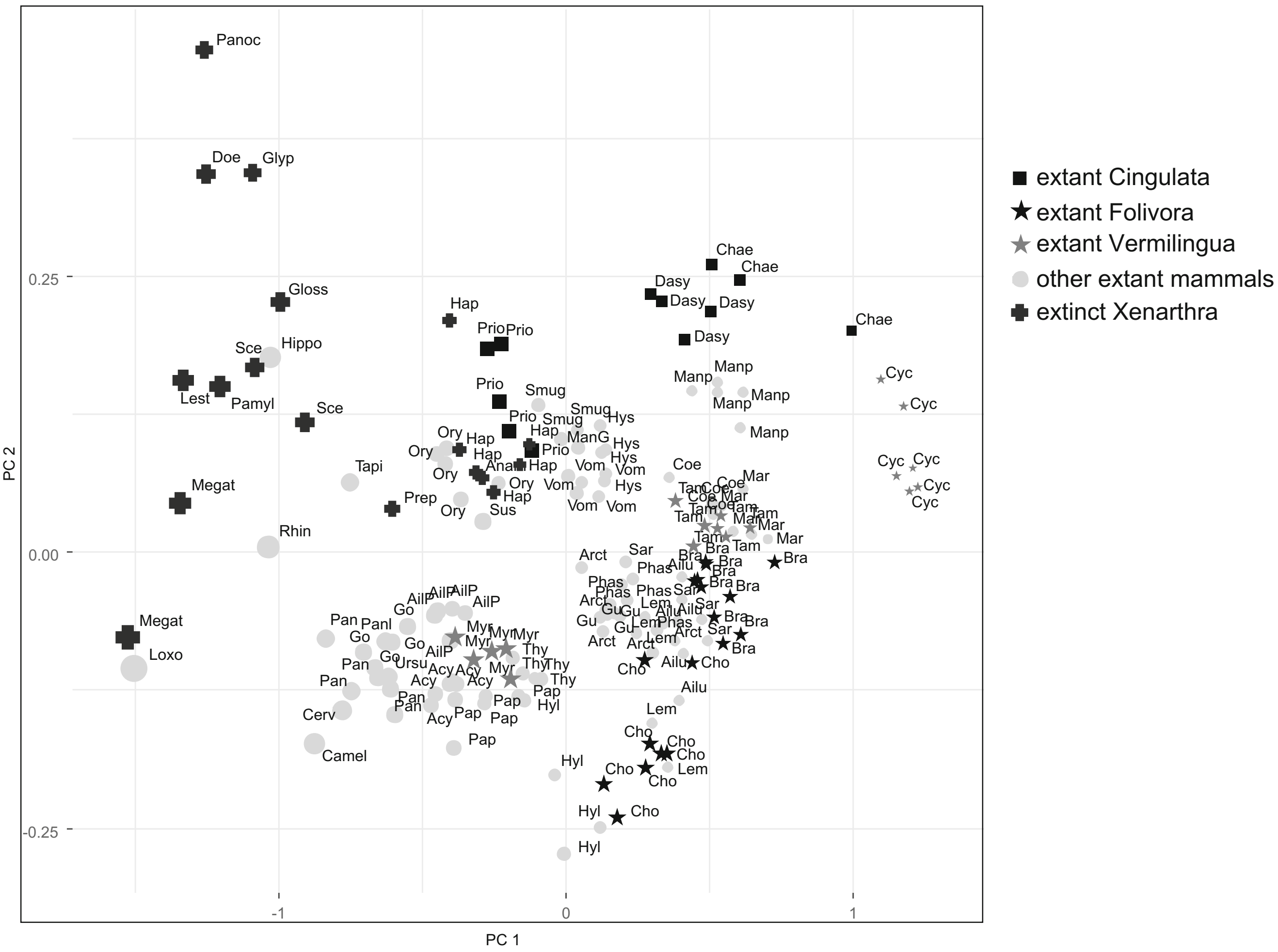

Fig. 6 Scatterplot of the first two components of PCA hindlimb of dimensions. Symbols and abbreviations as in Fig. 4

O'Higgins 2012). In the giant Pleistocene glyptodonts and ground sloths, this trochanter is situated at the level of the knee, and particularly in Megatheriidae and Mylodontidae, the complete lateral border of the femur is expanded above that level. This clearly increases the mass of the musculature associated with the hind limbs, clearly reproduced in the scale and computer-generated models, but not in the estimations based on the anteroposterior diameter of the bone. The same applies to equations based on a broad dataset of extant mammals albeit less marked, because they do include animals of sizes equivalent to the largest xenarthrans.

It is worth restating that over- and underestimations indicate shape differences between fossil and extant xenarthrans that are larger than expected based only on allometry (that is, a glyptodont cannot be modeled merely as an allometrically-scaled armadillo). This is also supported by the position of extinct xenarthrans through the morphospaces defined by postcranial dimensions. As mentioned above, extinct cingulates and sloths occupied the same morphospaces as those of other extant mammals rather than those of their closest relatives (especially obvious for sloths), making comparison more informative that merely depicting morphometric differences with extant xenarthrans (see Toledo et al. 2014; Toledo 2016).

According to results obtained herein and supporting previous proposals by Fariña et al. (1998), problems related to the modeling of biological attributes of extinct xenarthrans by comparison with a phylogenetically restricted sample of extant xenarthrans involve several issues. One, the reduced diversity of extant xenarthrans, in addition to the scarcity of detailed biological data of available specimens (which forces the use of mean values from the literature for generic or species level averages), introduces limitations when applying parametrical modeling (low *n* of extant sample). Second, due to marked differences in biological design, this kind of modeling commonly extends well beyond the range of the extant sample (many extinct taxa are dimensionally markedly different from their extant relatives, and such differences account for much of the extinct diversity of the clade). And third, bias is introduced by differences in anatomical proportions – extinct taxa are very different in shape compared to their extant relatives, which is a particularly important factor for most glyptodonts and giant ground sloths.

Table 3 Comparison of averaged body mass estimations of extinct xenarthrans obtained using allometric equations developed in this work, and other estimations from the literature

Ground sloths	Mean all mammals	Mean xenarthrans	Mean Pilosa	Mass estimations from other sources
Megatherium americanum *	2024.57	502.39	944.87	6073.00 [a]
Prepotherium potens *	236.47	72.20	104.84	134.19 [b]; 107.79 [c]
Eucholoeops sp. *	75.54	29.49	31.11	37.55 [b]; 58.66 [c]
Hapalops sp.*	50.19	21.85	25.41	39.80 [c]
Hapalops angustipalatus	110.82	44.00	92.11	47.34 [c]
Hapalops indifferens	50.05	22.67	23.85	46.50 [b]; 84.29 [c]
Hapalops longiceps	99.17	38.35	53.34	60.63 [b]; 72.29 [c]
Hapalops elongatus *	47.68	19.77	25.39	21.08 [b]; 39.28 [c]
Hapalops platycephalus *	44.05	19.49	21.58	31.20 [b]; 51.63 [c]
Hapalops ruetimeyeri *	48.50	22.29	27.53	30.43 [c]
Hapalops rectangularis	46.89	18.62	22.46	35.27 [c]
Analcimorphus giganteus	62.55	31.15	43.14	66.91 [c]
Lestodon armatus	1846.73	678.77	1141.48	3397.00 [a]; 3925.00 [d]; 3616.00 [f]
Glossotherium robustum	688.50	279.95	498.14	1713.00 [a]; 1350.00 [d]
Scelidotherium sp.*	627.39	191.24	348.84	1057.00 [a]; 840.00 [d]; 581.80 [f]
Paramylodon harlani	1203.34	514.63	881.89	1153.64 [e]
Analcitherium sp.	116.75	44.32	46.79	88.23 [c]
Nematherium *	59.23	20.33	20.03	89.33 [c]
R	0.880	0.854	0.844	
SE	1.046	1.025	1.019	
p(F)	0.000	0.005	0.008	
Glyptodonts	Mean all mammals	Mean xenarthrans	Mean Cingulata	Mass estimations from other sources
Propalaehoplophorus australis	73.92	28.88	28.35	81.10 [f]; 76.00 [g]
Glyptodon reticulatus	1028.14	355.77	327.53	862.30 [a]; 380.50 [g]
Glyptodon clavipes	435.52	102.90	83.00	1730 [g]
Panochtus intermedius	1086.30	251.91	146.04	
Panochthus tuberculatus	1840.88	584.22	1172.12	1061.00 [a]; 1185,00 [g]
Doedicurus clavicaudatus	1568.00	524.25	680.57	1468.00 [a]; 1410.00 [g]
R	0.880	0.854	0.785	
SE	1.046	1.025	1.021	
p(F)	0.000	0.005	0.011	

SE Smearing Estimator, *p(F)* p-value

*Average

[a] Fariña et al. (1998)

[b] White (1993)

[c] Toledo et al. (2014)

[d] Bargo et al. (2000)

[e] McDonald (2005)

[f] De Esteban-Trivigno et al. (2008)

[g] Vizcaíno et al. (2011)

In summary, previous approaches for generating allometric equations for use on extinct xenarthrans benefitted from calculations employing broad databases of extant mammals. However, the gross misestimations produced in some cases (noted above) should caution us against uncritical reliance on mathematical models (not only allometric equations, but also functional indices and ratios, and other mathematical approaches assessing relationships between dimensions and proportions with biological and ecological attributes) developed for other clades. A more desirable approach would be to combine such broad databases with ad hoc mathematical models.

Extant Xenarthrans as Morphological Models for Paleobiological Reconstruction

The previous sections indicated how distant, from a morphometric point of view, extinct xenarthrans can be from their extant relatives, and how mathematical inferences can be improved when including a wider sample for comparison.

According to Rudwick (1964), inferences of function from form in fossils commonly proceed through comparison with living organisms. However, if homology is the only criterion for comparison, the quality of the inference can be very poor when the form of the fossil is strongly different from that of its extant relatives (Rudwick gave as an example, functional inferences made on a pterosaur wing based on comparison with extant crocodile's forelimbs). More recently, Currie (2013) highlighted the philosophical value of analogy as an important empirical stream of evidence for both inspiring and corroborating adaptive hypotheses, particularly when they are incorporated into integrated explanations that use multiple evidence streams. Following the same line of thinking, Vizcaíno (2014) alleged that, although the morphology of an organism may be restricted or moderated by its evolutionary history, and thus not solely a product of a particular habitat, when structures and functions are unique to (or autapomorphic of) an extinct taxon, patterns extracted from a phylogenetic framework do not necessarily lead to paleobiologically useful information. This is precisely the case for many extinct xenarthrans that are morphologically so different from their living relatives as to readily suggest they had very (in some cases radically) different modes of life: Rudwick's rule applies when trying to make functional and paleobiological inferences about giant sloths from observations on extant tree sloths, or about glyptodonts from extant armadillos. For such cases, the extinct forms have no modern analogues and the application of an overly straightforward actualistic approach may produce nonsensical reconstructions (Vizcaíno et al. 2008; Vizcaíno 2014; Amson and Nyakatura 2017). This, however, does not invalidate actualism and the use of analogues. Rather, it requires their extension into the application of other approaches, such as mechanical, that address form-function relationships, but are not necessarily based on already-known biological comparators (Vizcaíno and De Iuliis 2003). Biomechanical models appeal to the inferred mechanical properties of the organism in question, requiring significant idealizations. According to Currie (2015), these idealizations abstract from historical information, simply considering what something of those materials could do.

As Rudwick (1964) claimed, when analogy is the criterion guiding comparison, background structural laws characterizing the similarity must be reasoned and demonstrated thoroughly: for instance, occurrence of similar structures in extant, non-related taxa could enable comparisons that would be ultimately based on (our understanding of) the shared physical-chemical operational principles underlying function. In this sense, biomechanics and functional morphology, and other form-function approaches, may be used to advantage when comparison operates without being constrained by the phylogenetic framework.

Concluding Remarks

Given the constraints imposed by shared history, the extant representatives of the three major groups of xenarthrans provide a valuable basis for paleobiological inference. For instance, the generalized low metabolism recorded in the three extant major lineages implies the same condition for the extinct taxa, and may thus have influenced virtually all other life traits, such as burrowing habits (Vizcaíno et al. 2001) and feeding (Vizcaíno 2009; Vizcaíno et al. 2006, 2011, 2012).

However, the clear and major morphological differences between extant taxa and many of their extinct relatives render the former as poor models for reliable paleobiological reconstructions. Comparisons with other mammals and the use of mechanical approaches that address form-function relationships, but are not necessarily based on already-known biological comparators, appear as some of the more promising avenues of research in overcoming such situations.

Acknowledgements This contribution was presented during the ICVM 11 meeting in Bethesda (Washington DC) in July 2016, as part of the symposium *Morphology and Evolution of the Xenarthra* organized by M. Susana Bargo and John A. Nyakatura. Attendance to the congress was partially granted by UNLP Viajes y Estadías 2016 to SFV and NT, and CIC 1827/15 (Comisión de Investigaciones Científicas de la provincia de Buenos Aires) to MSB. This is a contribution to the projects UNLP 11/N750 (Universidad Nacional de La Plata) and PICT 2013-0386 and 0389 (Agencia Nacional de Promoción Científica y Tecnológica). We thank the two anonymous reviewers for their comments, which not only improved this manuscript but inspired future work.

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