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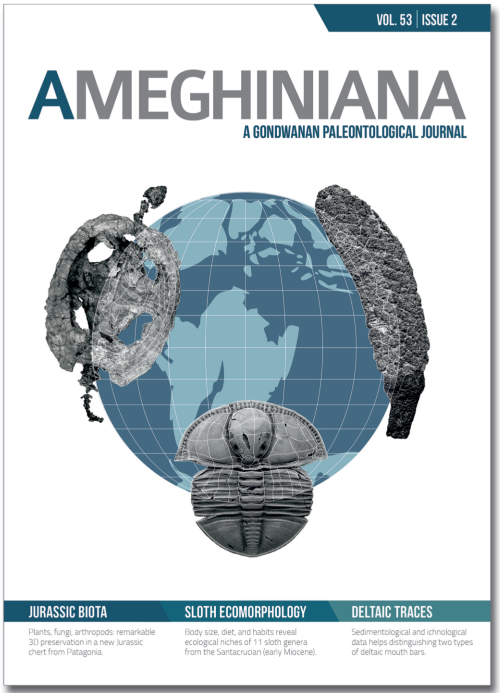

PALEOBIOLOGICAL INTEGRATION OF SANTACRUCIAN SLOTHS (EARLY MIOCENE OF PATAGONIA)

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Abstract. Paleobiological integration proceeds from descriptive morphology and paleosynecological reconstruction. This integration is achieved through modeling of function, inference of faculties, performance and resource use to hypothesize about fundamental niche. Environmental information is then incorporated to discuss biological roles and realized niche. Herein, paleobiological integration of Santacrucian (early Miocene of Patagonia) sloths is analyzed as a study case. Santacrucian sloths comprise a diversity of approximately 11 genera ranging from 40 kg to 120 kg in body mass and characterized by being morphologically different from any living relatives. In this study, the realized niche of each taxon is reconstructed via integration of three paleoecological attributes: body size, dietary habits and substrate preference. An ecomorphological approach is applied using Principal Components Analysis to explore the correlation between postcranial linear dimensions and substrate preference together with classical functional indices. Integration of these results with previous studies indicates that the mid-sized *Hapalops*, *Pelecyodon*, *Schismotherium* and *Analcimorphus* (stem Megatherioidea) and *Eucholoeops* (Megalonychidae) are members of the arboreal folivore paleoguild. In contrast, the mylodonts *Analcitherium* and *Nematherium*, marked by their greater size, may have been semiarboreal consumers of leaves, fruits and tubers due to their digging capabilities. *Prepotherium* (Megatheriidae), the largest and most terrestrial Santacrucian sloth, was also a folivore. Only the latter three genera competed for trophic resources with other coexistent mammalian herbivores. Their body size, strength and claws made Santacrucian sloths subject of predation solely for the largest Santacrucian carnivores, borhyaenoids marsupials and phorusrhacoid birds. Finally, the absence of modern analogues of these heavy-sized arboreal and semiarboreal herbivore diversity is discussed.

Key words. Form-function. Paleoecology. Xenarthra. Folivora.

Resumen. INTEGRACIÓN PALEOBIOLÓGICA DE LOS PEREZOSOS SANTACRUCENSES (MIOCENO TEMPRANO DE PATAGONIA). La integración paleobiológica procede desde la morfología hacia la reconstrucción paleosinecológica. Esta integración se produce a través de la modelización de la función, inferencia de facultades, desempeño y uso de los recursos para hipotetizar el nicho fundamental. La información ambiental es entonces incorporada para discutir el rol biológico y el nicho realizado. Se analiza la integración paleobiológica de los perezosos santacrucenses (Mioceno temprano de Patagonia). Éstos comprenden aproximadamente 11 géneros de 40 kg a 120 kg de masa corporal estimada, diferentes morfológicamente de sus parientes vivientes. El nicho realizado es reconstruido por medio de la integración de los atributos paleoecológicos: tamaño corporal, dieta y preferencia de sustrato. Se realizaron Análisis de Componentes Principales para explorar ecomorfológicamente la correlación entre medidas lineales postcraneales y preferencia de sustrato, aplicándose además índices funcionales tradicionales. La integración de estos resultados con estudios previos permite proponer que *Hapalops*, *Pelecyodon*, *Schismotherium* y *Analcimorphus* (Megatherioidea basales medianos) y *Eucholoeops* (Megalonychidae) integraban el paleogremio arborícola folívoro. Los milodóntidos *Analcitherium* y *Nematherium*, de mayor tamaño, fueron semiarborícolas con habilidades cavadoras y consumidores de hojas, frutos y tubérculos. *Prepotherium* (Megatheriidae), folívoro, fue el mayor y más terrestre. Los últimos tres géneros fueron los únicos en competir por el recurso trófico con los mamíferos herbívoros coexistentes. Su tamaño corporal, robustez y garras hicieron de los perezosos santacrucenses presas sólo de los carnívoros miocenos más grandes, como los marsupiales borhiaenoideos y aves fororracoideas. Finalmente, se discute la ausencia de análogos modernos a esta diversidad de herbívoros arborícolas y semiarborícolas.

Palabras clave. Forma-función. Paleoecología. Xenarthra. Folivora.

According to the definition coined by Abel (1911) and more recently discussed by Jackson and Erwin (2006) and Vizcaíno (2014), paleobiology encompasses reconstructing the biology and ecology of extinct organisms. As noted by Plotnick and Baumiller (2000), paleobiology relies on the assumption that functional attributes of life (whatever their organismic level may be) have ecological and evolutionary consequences and that morphology determines overall capacity to exploit resources (Wainwright, 1994). The culmination of this type of research involves the reconstruction of the entire past environment, herein referred to as "paleobiological integration". Morphology (and form) is the most

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widely available source of information provided by fossils and, hence, morphology-based approaches to paleobiology will be addressed. Through them, paleobiological integration issues constitute a complex progression from morphology to paleoecological hypotheses (both aut- and synecological).

Reconstruction of paleoecological attributes (*e.g.*, dietary habits, substrate preference and locomotion strategies) from morphology is carried out through hierarchically arranged inquiry levels, as proposed by Arnold (1983) and Reilly and Wainwright (1994: fig. 13.1) for modern ecosystems. Following Bock and von Wahlert (1965) and Plotnick and Baumiller (2000), performance can be reconstructed by inferring the function (*e.g.*, for a wing, to generate lifting) from the form (Radinsky, 1987) and then hypothesizing the faculties (to fly) based on the form-function complexes. Thus, maximum potential resource use (fundamental niche) can be inferred by estimating maximum performance based on form and function. Different methodologies can be applied at different levels of analysis of the relationship between morphology and ecology. Such methods rely, for instance, on functional morphology and biomechanics for causally reconstructing function and performance from form and ecomorphology for inferring resource use by determining the correlation between form and ecology (paleoautecology). Later in the analysis, performance becomes the foundation for speculating about the realized niche (the actual use of those resources). This process of conjecturing derives from investigating the relationships between the inferred use of resources by the studied organism and the collection paleoenvironment reconstructed on the basis of other information sources (paleosynecology).

According to the concepts discussed and applied by Vizcaíno *et al.* (2008, 2010, 2012a, b) and Vizcaíno (2014), paleobiological integration of taxa constituting fossil assemblages should be subsequent to a paleoecological characterization based on at least three main biological attributes: body size, dietary habits and substrate preference and use (including postural and locomotor patterns). Substrate preference is defined herein as the substrate where the organism carries out its activities: *i.e.*, water, ground, trees or any combination of such variables (see Miljutin, 2009 for a discussion). According to Wainwright (1994), the ecological identity of an organism is defined by the suite of environmental resources it uses. In this regard, the threefold ecological characterization explained above defines a hypothetical niche by reconstructing the organism's use of spatial and trophic resources.

The Santa Cruz Formation (early Miocene, approximately between 18–16 Ma, see Perkins *et al.*, 2012) of Patagonia (southern South America, Fig. 1) offers a unique opportunity to carry out such paleobiological integrative studies. This is due to two main factors: 1) the abundance, diversity and quality of preservation of the fossil remains and 2) the fact that sections of the outcrops representing discrete time intervals without extensive time averaging can be identified. The Santa Cruz Formation fossil assemblages include frogs, lizards, birds and a great diversity of mammals (Vizcaíno *et al.*, 2010, 2012a; Kay *et al.*, 2012b). Within these, some have traditionally been considered as characteristic of open habitats (notoungulates, litopterns, phorusrhacoid birds) while others (anteaters, primates, some marsupials) seem to suggest the presence of closed, forested areas (see, for example, Pascual and Ortiz-Jaureguizar, 1990).

Sloths are among the most noticeable vertebrates of the Santa Cruz Formation. They are striking because of their abundance and apparently high taxonomic richness (11 genera with several species, see Bargo *et al.*, 2012). Such facts contrast with their uniformity and conservative skeletal morphology marked by a limb structure more similar to extant anteaters than to extant sloths (Bargo *et al.*, 2012). As further pondered below, Santacrucian sloths have been proposed as terrestrial by Scott (1903–1904) or as semi-arboreal herbivores by White (1993; see White, 1997 for a synopsis of previous works). More recently, Bargo *et al.* (2012) characterized the preliminary paleoautecology of Santacrucian sloths considering body size, diet and substrate preference. Nonetheless, detailed paleoautecological work– particularly on substrate preference and use– is still required. Comprehensive works by Croft (2001), Vizcaíno *et al.* (2010) and Kay *et al.* (2012b) on the Santacrucian fauna included the Santacrucian sloths in paleoclimatic and paleoecological studies.

The goal of this contribution is to discuss the application and scope of paleobiological integration as defined above; that is, by using different morphology-based methodological approaches (*e.g.*, functional morphology, biomechanics and ecomorphology) to reconstruct ecological attributes of extinct organisms such as, in this case, the Santacrucian

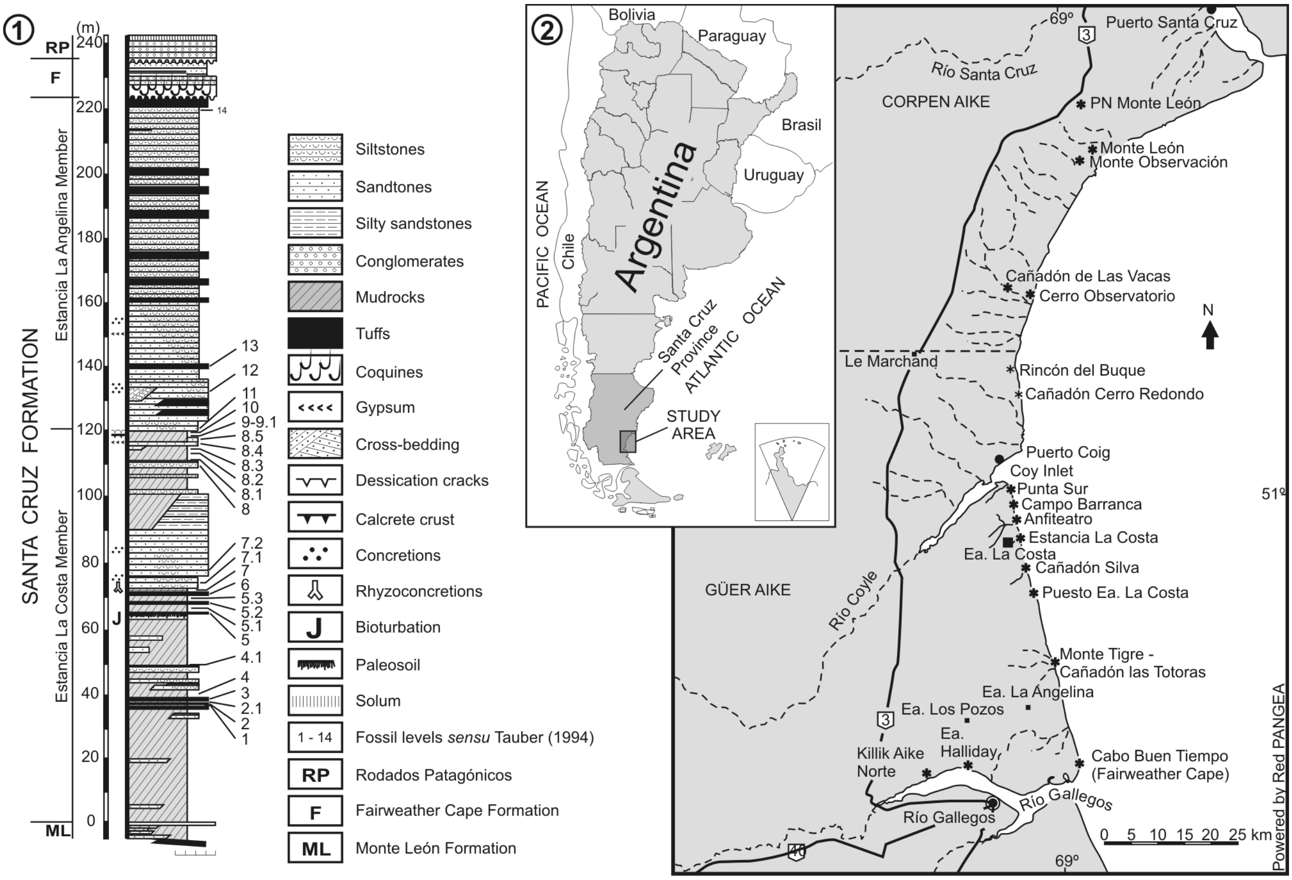


Figure 1. The Santa Cruz Formation. On the left, stratigraphic column of the Santa Cruz Formation, modified from Vizcaíno *et al.* (2010). On the right, geographic locations of main Santacrucian fossil localities, modified from Vizcaíno *et al.* (2010): *, fossil localities; ■, ranches; ●, towns and cities; **Ea**, estancia (ranch).

sloths. Results of the present analysis will be discussed in light of hypotheses on substrate preference and use proposed by previous authors (*e.g.*, White, 1993, 1997; Bargo *et al.*, 2012). Furthermore, reconstructions of body size and dietary habits provided by previous studies will be summarized in an attempt to reach paleobiological integration and to characterize Santacrucian sloths in a paleosynecological context. Through such contextual depiction, this exploration will try to reconstruct, as far as possible, the hypothetical niche of each taxon.

This work is part of a series of studies performed during the thesis project of the author on substrate preference and locomotion of Santacrucian sloths (Toledo, 2012), which in turn contributed to a long-term program on the paleoecology of the Miocene Santa Cruz Formation (Vizcaíno *et al.*, 2012a).

Geological and paleontological context of the Santa Cruz Formation

The sedimentological and biostratigraphic context for these paleobiological studies is provided by Fleagle *et al.* (1995), Tauber (1997a, b), Perkins *et al.* (2012) and Matheos and Raigemborn (2012). The Santa Cruz Formation (early Miocene, about 18 to 16 Ma BP in its coastal localities – Perkins *et al.*, 2012) is composed of pyroclastic influenced fluvial deposits comprising floodplain layered mudstones, tuffaceous psammitic riverbeds and alternating subhorizontal tuffs (Tauber, 1994; Matheos and Raigemborn, 2012; Fernicola *et al.*, 2014) (Fig. 1). Most well-known Santacrucian deposits crop out along the Atlantic coast of Patagonia between the Coyle and Gallegos Rivers. Other Santacrucian fossiliferous localities are scattered throughout Patagonia, from near Golfo San Jorge to Tierra del Fuego and from the Atlantic coast to the Andean range (see Fernicola *et al.*, 2014). These deposits were extensively explored by Carlos Ameghino and John B. Hatcher, among others, at the end of the 19th century (see Vizcaíno *et al.*, 2010, 2012b; Vizcaíno, 2011). The vertebrate remains recovered by them were mainly described by Florentino Ameghino (1887, 1889, 1891, 1894), Scott (1903–1904) and Sinclair (1906–1909). Later, Santacrucian deposits and their faunas were studied by Marshall (1975, 1976), Bown and Feagle (1993), and Tauber (1994, 1997a, b). More recently (2003 to present) the very same deposits were re-examined by the joint expeditions of Museo de La Plata, Museo Argentino de Ciencias Naturales (Argentina) and Duke University (North Carolina, USA) (see Vizcaíno *et al.*, 2012a).

The Santa Cruz Formation fossil assemblages include anurans, lizards, birds (including phorusrhacoids, see Discussion) and, among mammals, marsupials, xenarthrans (cingulates, anteaters and sloths), rodents, primates and several lineages of South American ungulates (notoungulates, litopterns and astrapotheres) (Vizcaíno *et al*, 2010, 2012a–c; Kay *et al.*, 2012b). Such diverse assemblages are a fair representation of the vertebrate communities previous to the Great American Biotic Interchange (GABI) in the southernmost part of South America (Vizcaíno *et al.*, 2010). These faunas are enormously significant because they represent a period of the South American Cenozoic when the communities consisted of a complex mixture of “ancient South American lineages” (Reig, 1981) and the first taxa originating from other continents (caviomorph rodents and primates; Simpson, 1980). The Santacrucian assemblages are among the last fossil communities before the advent of modern faunas which include taxa of North American origin and show a diversity and structure not easily comparable with extant communities considered as analogues (Vizcaíno *et al.*, 2010). Comprehensive paleoenvironmental (Pascual and Ortiz-Jaureguizar, 1990; Croft, 2001) and paleoecological (Vizcaíno *et al.*, 2010; Kay *et al.*, 2012b) studies have indicated that the Santacrucian environments exhibited a balanced mixture of humid closed areas such as forests, and relatively drier open areas (see Barreda and Palazzesi, 2007; Brea *et al.*, 2012).

The sloths of the Santa Cruz Formation

Sloths (Folivora) and anteaters (Vermilingua) comprise the Pilosa within Xenarthra which in its turn includes Cingulata (armadillos, pampatheres and glyptodonts) (see Engelmann, 1985; Delsuc and Douzery, 2008; Gaudin and McDonald, 2008). Xenarthrans are among the most prominent clades of placental mammals of the Neotropical Region (see Delsuc and Douzery, 2008; Gaudin and McDonald, 2008; Vizcaíno and Bargo, 2014). Extant sloths (*Choloepus* or two-toed-sloth, and *Bradypus* or three-toed sloth) are fully arboreal, folivorous mammals of about 5 kg that inhabit the tropical forests of Central and South America (Chiarello, 2008). The fossil record of folivorans extends from the early Oligocene to the late Pleistocene (Gaudin and McDonald, 2008; McDonald and De Iuliis, 2008; Pujos *et al.*, 2012) and presents a striking diversity and taxonomic richness comprising over 90 genera (McKenna and Bell, 1997) and that greatly exceeds that of the modern diversity. Their body mass ranges from 5 kg to several tons (Vizcaíno and Bargo, 2014). According to the most comprehensive phylogenetic analysis of the clade performed by Gaudin (2004) on craniodental traits, Folivora comprises five families: Megalonychidae (including the extant two-toed sloth), Megatheriidae, Nothrotheriidae, Mylodontidae and Bradypodidae (which includes only the extant three-toed sloth) (Fig. 2). According to these and previous (Patterson and Pascual, 1968; Webb, 1985) phylogenetic hypotheses, extant sloths are not directly related to each other. Accordingly, their unique suspensory arboreal lifestyle constitutes a wonderful example of convergent evolution (Nyakatura *et al.*, 2010). Unfortunately, fossils that are undoubtedly related to *Bradypus* are not currently known (McDonald and De Iuliis, 2008). Fossil sloths as a whole were historically considered large and lumbering ground-dwelling herbivores. It is because of such misconception that they were popularly referred to as “ground-sloths” (in opposition to the extant “tree-sloths”) therefore somewhat perpetuating the terminology coined by Owen (1842). The giant Pleistocene forms were undoubtedly quadrupedal or facultative bipedal terrestrial walkers (de Toledo, 1998; Fariña *et al.,* 1998; Bargo *et al.,* 2000; Bargo, 2003; Blanco and Czerwonogora, 2003) of which some (at least some mylodontids) were able to dig and thus probably built large burrows (Bargo *et al.*, 2000). Additionally, several studies have raised the possibility that some of the smaller forms could have been capable arboreal climbers (see White, 1993, 1997; Pujos *et al.*, 2007; Bargo *et al.*, 2012; Toledo *et al.*, 2013, 2015) or even dis-

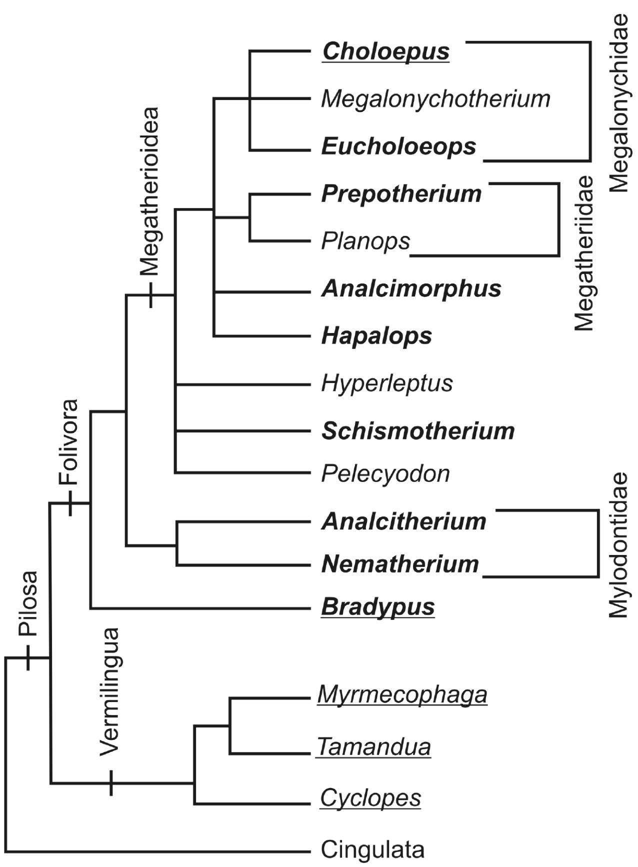


Figure 2. Cladogram showing the phylogenetic relationships among the xenarthrans included in this study. Modified from Gaudin (2004). Fossil sloths considered in this study are in bold case while extant pilosans are underlined.

played semi aquatic habits (see De Muizon *et al.*, 2004; Amson *et al.*, 2014). Such variations suggest a range of diversity in substrate preference and locomotion abilities wider than traditionally expected.

Santacrucian sloths were mid-sized animals, between about 30 kg to over 100 kg (White, 1993; Toledo *et al.*, 2014) belonging to Megalonychidae (*Eucholoeops* and *Megalonychotherium*), Megatheriidae (*Planops* and *Prepotherium*), stem-megatherioids (*Hapalops*, *Hyperleptus*, *Analcimorphus*, *Schismotherium* and *Pelecyodon*) and Mylodontidae (*Nematherium* and *Analcitherium*). As noted by White (1997) and Bargo *et al.* (2012), Santacrucian sloths were the first great assemblage of excellently preserved members of the clade (Fig. 3). According to analyses of their masticatory apparatus performed by Bargo *et al.* (2009, 2012), megalonychids and megatherioids were mainly folivorous herbivores, whereas mylodontids were able to process a wider dietary spectrum including not only leaves but also fruits and tubers. Although considered to be "ground-sloths" by Scott (1903–1904), diverse studies have raised the hypothesis that most Santacrucian sloths were proficient climbers. Using functional indices, White (1993, 1997) characterized many of them as arboreal or semiarboreal. This hypothesis was later supported and expanded by Bargo *et al.* (2012) and Toledo *et al.* (2012, 2013, 2015) based on morphometric studies of limb bones, appendicular muscle reconstructions and morphofunctional analysis. Additionally, morphometric and functional similarities with extant digging mammals suggested that some Santacrucian sloths were also skilled diggers.

Institutional abbreviations. **AMNH,** American Museum of Natural History, New York, USA; **FMNH,** The Field Museum of Natural History, Chicago, USA; **MLP,** Museo de La Plata, La Plata, Argentina; **MPM-PV,** Museo Regional Provincial Padre M. Jesús Molina, Paleontología Vertebrados, Río Gallegos, Argentina; **YPM-VPPU,** Yale Peabody Museum, Vertebrate Paleontology Princeton University Collection, New Haven, USA.

MATERIALS AND METHODS

The fossil sloths analyzed comprise 51 specimens (Appendix A) and include historical specimens in the vertebrate paleontology collections of MLP, YPM-VPPU, AMNH and FMNH and new specimens deposited in MPM-PV, collected by the MLP-Duke University joint expeditions during 2003–2013. Due to unavailability of relatively complete postcranial remains, a few genera were omitted in this work (*Planops*, *Megalonychotherium*, *Hyperleptus* and *Pelecyodon*). Specimens with appendicular remains complete enough to be morphometrically meaningful for this study include the genera *Eucholoeop*s, *Prepotherium*, *Hapalop*s, *Analcimorphu*s, *Schismotherium*, *Analcitherium* and *Nematheriu*m, as well as several undetermined specimens of megalonychids, megatheriids and mylodontids. Osteological materials of the extant mammals studied are from the mammalogy collections of MLP, AMNH and FMNH.

A morphometric database of 134 extant mammals (xenarthrans, marsupials, pangolins, tubulidentates, carnivorans, primates and rodents, Appendix B) was constructed. Therein, classical linear dimensions used in postcranial morphometric studies were included (Alexander *et al.*, 1979;

Scott, 1990; Sargis, 2002a,b; Elissamburu and Vizcaíno, 2004; Candela and Picasso, 2008; De Esteban-Trivigno *et al.*, 2008). The same measurements were applied for the sample of Santacrucian sloths and correspond to those used in Toledo *et al.* (2014) (Appendix C). Measurements were taken using a common caliper and used for multivariate exploratory analyses and for constructing biomechanical and functional indices.

Normality tests *a priori* applied to both the raw (in milimeters) and log-transformed linear measurements showed non-normal distribution of the variables (see Supplementary Online Information). Therefore, multivariate statistics requiring normality (Discriminant Analysis, for instance) were not applied. Instead, Principal Component Analyses (**PCA**) were performed to explore the placing of the Santacrucian sloths in relation to the morphospace as defined by the extant mammal sample.

An exploratory analysis of linear measurements of the appendicular system of Santacrucian sloths (together with the extant mammal reference sample) was carried out in an attempt to recognize morphometric patterns in the appendicular skeleton. The starting point assumption was that comparison of the morphospace and ecospace (Reilly and Wainwright, 1994) would reveal recognizable patterns. The morphospatial exploratory comparison with the extant mammal sample was ecomorphologically interpreted for

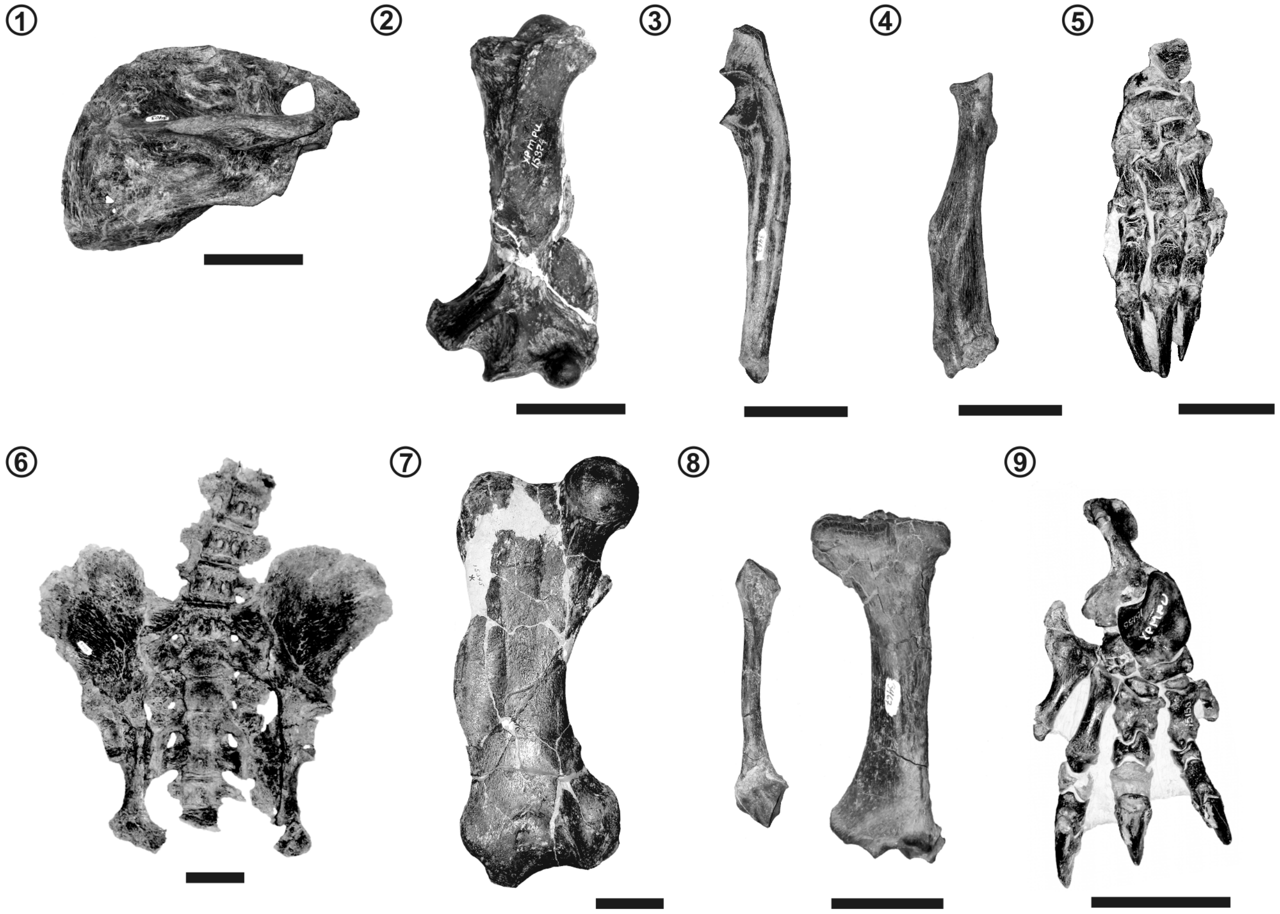


Figure 3. Santacrucian sloths appendicular skeleton. **1,** ***Eucholoeops*** **MPM-PV** 3403, right scapula, lateral view; **2,** ***Nematherium*** **YPM-VPPU** 15374, left humerus, anterior view; **3,** ***Hapalops*** **MPM-PV** 3467, left ulna, lateral view; **4,** ***Hapalops*** **MPM-PV** 3404, left radius, lateral view; **5,** ***Eucholoeops*** **MPM-PV** 3402, left manus, dorsal view; **6,** ***Eucholoeops*** **MPM-PV** 3403, pelvic girdle, ventral view; **7,** ***Prepotherium*** **YPM-VPPU** 15345, right femur, anterior view; **8,** ***Hapalops*** **MPM-PV** 3467, right tibia and fibula, anterior view; **9,** ***Hapalops*** **YPM-VPPU** 15155, right pes, dorsal view. Scale bar= 5 cm.

assessing substrate preference and/or use in Santacrucian sloths (see Appendix B). This was achieved through the conjecture of a correlation between form and ecological attributes, spatial resource use in this case, used to paleoautecologically characterize the Santacrucian sloths. These results are discussed and pondered within the context provided by the results yielded by other publications using other methodological approaches. The Principal Component Analysis was chosen to perform the exploratory analysis due to its robustness, procedural simplicity and the absence of required *a priori* grouping hypotheses. Log-transformed data were used to reduce the wide range of the records. The covariance matrix was used in order to include the largest fossil sample, in a procedure analogous to that used by Toledo *et al.* (2014) for body size estimations, and separated PCAs were performed for each of the following appendicular elements: scapula, humerus, ulna, radius, pelvis, femur, tibia, astragalus and calcaneum. Computation and graphics were performed using the open-source program R Statistical Software (R Core Team 2014) drawing on the command *princomp* of the built-in package *stats* and the graphic package *ggplot2* (Wickham, 2009).

Indices are dimensionless parameters of easy construction and calculation. They are a valuable tool in functional studies (Smith and Savage, 1955; Hildebrand, 1988; Vizcaíno *et al.*, 1999; Elissamburu and Vizcaíno, 2004) that allow simple and fast comparisons of a large number of taxa. Concerning limb function, most indices consist of a single ratio between two measures commonly modeled as a lever system examining in-lever and out-lever arms of segments of limb, consequently making their biomechanical application quite straightforward. Other indices merely describe limb proportions with functional significance. While most indices applied herein were taken from the literature, some were developed specifically for this study. Indices codification, formulae, source and functional significance are described in Table 1.

RESULTS

Principal Component Analysis

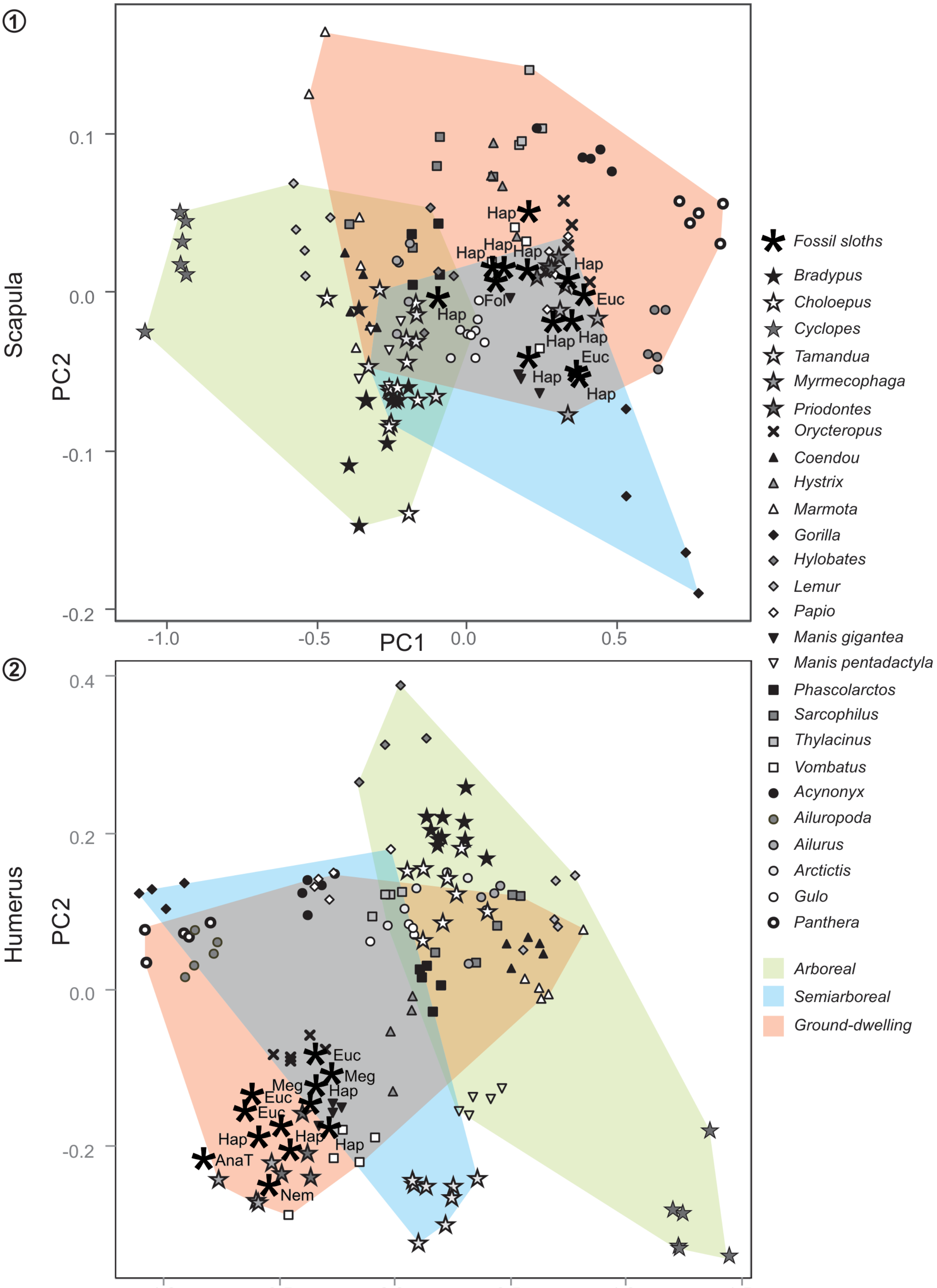
Results from the Principal Component Analyses performed in this work are depicted in Figs. 4–8 and in the Appendix D. In the PC1s, all the variables contributed in similar proportion to the eigenvector (roughly reflecting bone dimensions in the morphospace) whereas PC2s reflect changes in bone proportions related to different loadings of variables. Explanations below are therefore mainly focused on taxa scores along PC2 while PC1 can be considered to depict relative size.

Scapula (Fig. 4.1). In PCA performed with variables of the scapula (plotting PC1 *vs*. PC2), Santacrucian sloths share morphospace with the giant anteater *Myrmecophaga*, the giant armadillo *Priodontes*, the aardvark *Orycteropus*, the wombat *Vombatus*, the terrestrial pangolin *Manis gigantea* and the baboon *Papio*. All these extant mammals are proficient diggers but for the baboon, which frequently uses its forelimb for manipulating objects. They are all clearly well separated from extant sloths. In PC2, the length of the scapula increases with the positive values while the parasagittal length of the glenoid fossa increases towards the negative end of the axis. As a result, towards the positive end of PC2, elongated scapulae arise (the cheetah *Acinonyx* and the marsupial wolf *Thylacynus* for instance), indicating more cursorial locomotion. Conversely, towards the negative end of PC2, shorter scapulae with relatively longer glenoid fossae (the gorilla and some specimens of extant sloths) surface. This indicates more complex shoulder movements not restricted to parasagital movements typical of cursors. However, the separation of the taxa along PC2 is not clear enough. Accordingly, Santacrucian sloths share similar eigenvalues not only with terrestrial diggers but also with arboreal and semiarboreal taxa such as the two-toed sloth *Choloepus*, the lesser anteater *Tamandua*, the koala *Phascolarctos*, the tree-porcupine *Coendou*, the red panda *Ailurus* and the lesser pangolin *Manis pentadactyla*.

Humerus (Fig. 4.2). In PCA performed with variables of the humerus (plotting PC1 *vs*. PC2), Santacrucian sloths share a morphospace with digging forms such as the giant anteater, the giant armadillo *Priodontes*, the wombat *Vombatus* and the aardvark *Orycteropus*, therefore supporting the results obtained by Toledo *et al.* (2012). PC2 is dominated by humerus length (increasing towards positive end) and humeral diaphyseal and distal epiphyseal widths (increasing towards the negative end). Hence, towards the positive end of PC2, there are taxa with gracile humeri such as the extant sloths and the primates. In opposition, there are taxa with stouter humeri towards the negative end. Independently of their substrate preference, all of these are

Table 1 – Indices used in this work.

Index	*Formulae*	*Author*	*Index explanation*
Brachial Index (BI)	*BI=RL/HL*100*	*Sargis, 2002a, b*	*The Brachial Index abridges the proportion between the upper arm (brachium) and forearm (antebrachium), reflecting indirectly the relative leverage for forearm extension. High values of this index would indicate forelimb configuration optimal for fast forearm extension at the expense of power applied.*
Scapulo-Humeral Index (SHI)	*SHI=SL/HL*100*	*this work*	*The SHI index reflects the origin extension of the* m. deltoideus *relative to the out-lever arm, represented by the humerus length.*
Humeral Robusticity Index (HRI)	*HRI=TDH/HL*100*	*Elissamburu and Vizcaíno, 2004*	*This index allows visualizing the proportion between the length and width of the humerus, giving a clear idea of their comparative slenderness or robusticity and, indirectly, their potential compliance to facing mechanical loads. It also reflects the amount of available space for musculature, especially true for xenarthrans.*
Humeral Distal Epiphysis Depth (HDED)	*HDED=HDASW/HL*100*	*this work*	*This index describes the relative depth of the distal humeral facet, which reflects the stabilization of the elbow joint and its relative degree of constraint to parasagittal movements.*
Entepicondyle Index (EPI)	*EPI=HDEW/HL*100*	*this work*	*This index depicts the proportional width of the distal humeral epiphysis, describing indirectly the available space for hand and digit flexor musculature.*
Index of Fossorial Ability (IFA)	*IFA=OTL/UL-OTL*100*	*Elissamburu and Vizcaíno, 2004*	*Describes the relative mechanical advantage of the* m. triceps *for forearm extension by means of calculating the ratio between in-lever (ulnar olecranon process) and out-lever (representd by the rest of the ulna) arms.*
Ulnar Robusticity Index (URI)	*URI=TDU/UL*100*	*Elissamburu and Vizcaíno, 2004*	*In addition to describing the relative toughness of the ulnar diaphysis, this index describes the available space for hand flexor and pronator-supinator musculature.*
Radial Head Index (RHI)	*RHI=RHL/RHW*100*	*Sargis, 2002a, b*	*This index describes the roundness of the radial head and, indirectly, its capacity to rotate around the humeral capitulum and to slide on the radial notch of the ulna during pronation-supination.*
Crural Index (CI)	*CI=TL/FL*100*	*Sargis, 2002a, b*	*This index depicts, similarly to the BI, the relative length of the shin with respect to the thigh and, indirectly, the out-lever arm for lower leg extension. Typically those animals with limbs equipped for optimization of speed against force showed the highest values, but some exceptions are notable.*
Femoral Robusticity Index (FRI)	*FRI=TDF/FL*100*	*Elissamburu and Vizcaíno, 2004*	*Highest values for this index, as for the HRI, represent femora with relatively stouter diaphyses, more resistant to mechanical loads.*
Tibial Robusticity Index (TRI)	*TRI=TDT/TL*100*	*Elissamburu and Vizcaíno, 2004*	*Similarly to previously explained robusticity indices, this one provides insight about the compliance of the tibial diaphysis against mechanical loads.*
Medial Condyle Depth Index (MCDI)	*MCDI=MCL/FL*100*	*Sargis, 2002a, b*	*Similarly to the HDED, this index provides information about the stabilization of the knee joint: narrower and deeper femoral distal epiphyses are involved in more stabilized knee joints.*
Tibial Proximal Epiphyseal Index (TPEI)	*TPEI=TPEL/TPEW*100*	*Sargis, 2002a, b*	*This index represents proportionally the shape of the proximal epiphysis of the tibia, and like the MCDI, is related to knee joint stabilization. High values correspond to deeper tibial plateaus, whereas low values describe wide and shallow ones.*


①
Scapula
PC2
PC1
0.1
0.0
-0.1
-0.2
-1.0
-0.5
0.0
0.5
Hap
Fol
Euc
②
Humerus
PC2
0.4
0.2
0.0
-0.2
-1.0
-0.5
0.0
0.5
1.0
1.5
Euc
Meg
Hap
AnaT
Nem
Fossil sloths
Bradypus
Choloepus
Cyclopes
Tamandua
Myrmecophaga
Priodontes
Orycteropus
Coendou
Hystrix
Marmota
Gorilla
Hylobates
Lemur
Papio
Manis gigantea
Manis pentadactyla
Phascolarctos
Sarcophilus
Thylacinus
Vombatus
Acynonyx
Ailuropoda
Ailurus
Arctictis
Gulo
Panthera
Arboreal
Semiarboreal
Ground-dwelling

diggers (anteaters, the giant armadillo, pangolins, the wombat and the aardvark). The results for the Santacrucian sloths are not conclusive with respect to substrate preference.

Ulna (Fig. 5.1)**.** When plotting PC1 *vs*. PC2, Santacrucian sloths occupy the middle central morphospace together with the greater pangolin *Manis gigantea*, the giant panda *Ailuropoda* and the baboon *Papio*. PC2 is mainly influenced by the olecranon length (positive end) and by transverse diameter of the diaphysis and semilunar notch length. Thus, towards the positive end of PC2, there are some taxa with an elongated olecranon and short semilunar notch (the giant anteater *Myrmecophaga*, the giant armadillo *Priodontes*, the lesser pangolin *Manis pentadactyla*, the African porcupine *Hystrix*, the groundhog *Marmota*). In contrast, towards the negative end of the axis, taxa with relatively short olecranon (primates and extant sloths) appear. Although digging forms are clearly situated at the positive end of PC2, there is no clear separation of the taxa with respect to their substrate preference. Santacrucian sloths are scattered in the mid region of PC2 together with a spectrum of both arboreal and terrestrial animals.

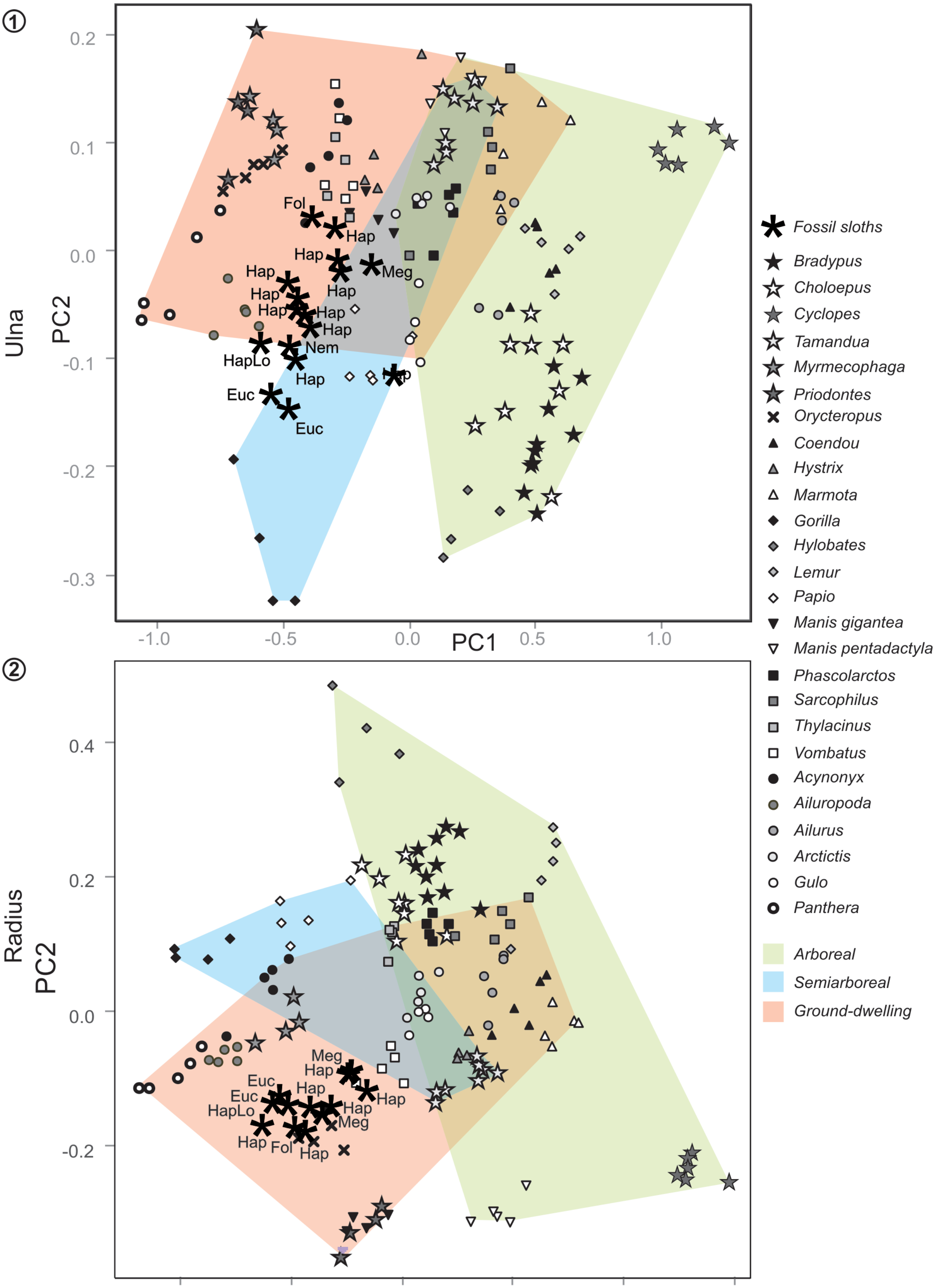
Radius (Fig. 5.2)**.** Concerning PCA of the variables of the radius, Santacrucian sloths occupy a relatively isolated position near the aardvark *Orycteropus* and the wombat *Vombatus* in the morphospace. Due to the lack of complete radii, mylodonts could not be included in this analysis. The PC2 is dominated by the radius length (increasing positively) while the rest of the variables increase negatively. Thus, towards the positive end of the axis there are taxa with elongated, gracile radii (primates, extant sloths). Conversely, towards the negative end, there are taxa with stout, short radii (anteaters, the giant armadillo, pangolins, the wombat, the tiger). Once again, with Santacrucian sloths sharing morphospace with digging mammals, a clear pattern regarding substrate preference is not apparent.

Pelvis (Fig. 6.1)**.** PC2 is dominated by the ilium length (increasing negatively) and the ischium length (increasingly positively). Therefore, on the one hand, the fact that taxa with pelves with long iliac wings and short ischiadic rami would be placed towards the positive end of PC2 (extant sloths and primates for instance) could be expected. On the other hand, taxa with a comparatively longer ischiadic ramus would be conversely placed towards the negative end of the component (*e.g.*, greater pangolin *Manis gigantea* and aardvark *Orycteropus*). However, most of the taxa are scattered along PC2, thus only indicating a very general ordination. Santacrucian sloths follow this general trend.

Femur (Fig. 6.2)**.** When plotting PC1 *vs*. PC2, most of the taxa are arranged in globular clusters with clear separation between them. PC2 is dominated by femur length and lateral condyle length increasing positively, and diaphyseal transverse width increasing negatively. Thus, located towards the positive end of the axis, taxa with elongated femora (felids and primates for instance) arise. Conversely, towards the negative end, taxa with robust and stouter femora (extant sloths, silky and lesser anteaters, pangolins and the aardvark) appear. Santacrucian sloths surface, clearly branched out from other taxa, as a separate cluster in the negative-most end of PC2. Due to the presence of a third trochanter, they present the most robust femora along with the silky anteater *Cyclopes* and the giant armadillo *Priodontes*. However, a well-defined pattern related to substrate preference is not visibly evident.

Tibia (Fig. 7.1)**.** Because of the fact that taxa were arranged in clearly separate clusters, the PCA of tibia variables shows similarities with the analyses of humeri and femora. Santacrucian sloths share the morphospace with the giant armadillo *Priodontes*, the greater pangolin *Manis gigantea* and the aardvark *Orycteropus*. The PC2 is dominated by the tibia length, which increases positively, together with the proximal epiphyseal and mid-diaphyseal widths, which increase negatively. Therefore, while in the positive extreme of PC taxa with elongated and gracile tibiae (primates, extant

Figure 4. Distribution of modern mammals and Santacrucian sloths in the morphospaces depicted in PC1 and PC2. Santacrucian sloths are depicted with text codes. Substrate preference is depicted by using convex hulls. **1,** scapula; **2,** humerus. **Fol:** Folivora indet; **Meg:** Megalonychidae indet; **Euc:** *Eucholoeops*; **Prep**?**:** cf.*Prepotherium*; **Prep:** *Prepotherium potens*; **Hap:** *Hapalops*; **HapLo:** *Hapalops longiceps*; **AnaM:** *Analcimorphus giganteus*; **Schi:** *Schismotherium fractum*; **Myl:** Mylodontidae indet; **AnaT:** *Analcitherium?* sp.; **Nem:** *Nematherium*. See Appendix D for contribution of each variable to components.


①
Ulna
PC2
0.2
0.1
0.0
-0.1
-0.2
-0.3
-1.0
-0.5
0.0
0.5
1.0
PC1
Fol
Hap
Meg
Nem
HapLo
Euc
②
Radius
PC2
0.4
0.2
0.0
-0.2
-1.0
-0.5
0.0
0.5
1.0
1.5
Meg
Hap
Euc
HapLo
Fol
Fossil sloths
Bradypus
Choloepus
Cyclopes
Tamandua
Myrmecophaga
Priodontes
Orycteropus
Coendou
Hystrix
Marmota
Gorilla
Hylobates
Lemur
Papio
Manis gigantea
Manis pentadactyla
Phascolarctos
Sarcophilus
Thylacinus
Vombatus
Acynonyx
Ailuropoda
Ailurus
Arctictis
Gulo
Panthera
Arboreal
Semiarboreal
Ground-dwelling

sloths, the cheetah and the marsupial wolf) surface, in the negative end, taxa with comparatively shorter and stouter tibiae (the silky anteater *Cyclopes*, the giant armadillo and both pangolins) materialize. No clear pattern related to substrate preference is visible; nevertheless, PC2 (as in some of the previous analyses) exhibits a weak gradient from robust, powerful limb elements to gracile, slender ones.

Astragalus (Fig. 7.2)***.*** When plotting PC1 *vs*. PC2 of the analysis performed using astragalar variables, Santacrucian sloths share the morphospace with the giant anteater *Myrmecophaga*, the giant armadillo *Priodontes* and the gorilla *Gorilla*. PC2 is dominated by trochlear width (increasing negatively) and length of the medial facet of the trochlea (increasing positively). Thus, taxa with wide talar trochleae are placed in the negative region of the axis (*e.g.*, both pangolins and, to a lesser degree, anteaters) while, in contrast, taxa with narrower talar trochleae are placed in the positive region (extant sloths, rest of the primates, the marsupial wolf *Thylacynus* and the red panda *Ailurus*, among others). Santacrucian sloths are placed slightly beyond the mid of PC2, towards the negative end. No clear pattern related to substrate preference is evident.

Calcaneum (Fig. 8)***.*** The PCA with calcaneal variables shows Santacrucian sloths occupying an isolated morphospace and forming a cluster clearly separated from the extant sample. The PC2 is dominated by the calcaneal tuber width, which increases positively, and the calcaneal total length, which increases negatively. In general, taxa with a wide calcaneal tuber (both Santacrucian and extant sloths) are placed towards the positive end of the component. Conversely, taxa with a relative narrower calcaneal tuber (giant and lesser anteaters, the cheetah *Acynonyx,* the tiger *Panthera* and the aardvark *Orycteropus*, among others) are placed towards the negative end of PC.

Functional Indices

Results obtained from functional indices (defined and explained in Tab. 1) are represented by means of boxplots arranged vertically through systematic groups along the y axis (Figs. 9–15).

Brachial Index (**BI**, Fig. 9.1)***.*** The Santacrucian sloths *Hapalops* and *Eucholoeops* show intermediate values similar to those of three-toed sloth *Bradypus*, lesser anteater *Tamandua,* Tasmanian devil *Sarcophilus*, marsupial wolf *Thylacynus*, tiger *Panthera tigris*, gorilla *Gorilla* and tree-porcupine *Coendou*. While a relatively longer forearm is observed in climber taxa such as the koala *Phascolarctos*, the tree-porcupine *Coendou* and the most arboreal primates; the same is not the case for the carnivorans, where the cursorial *Acynonix* has a longer forearm than the arboreal *Arctictis*. Similarly, among anteaters the terrestrial *Myrmecophaga* has the longest forearm when compared with the short forearm of the arboreal *Cyclopes*.

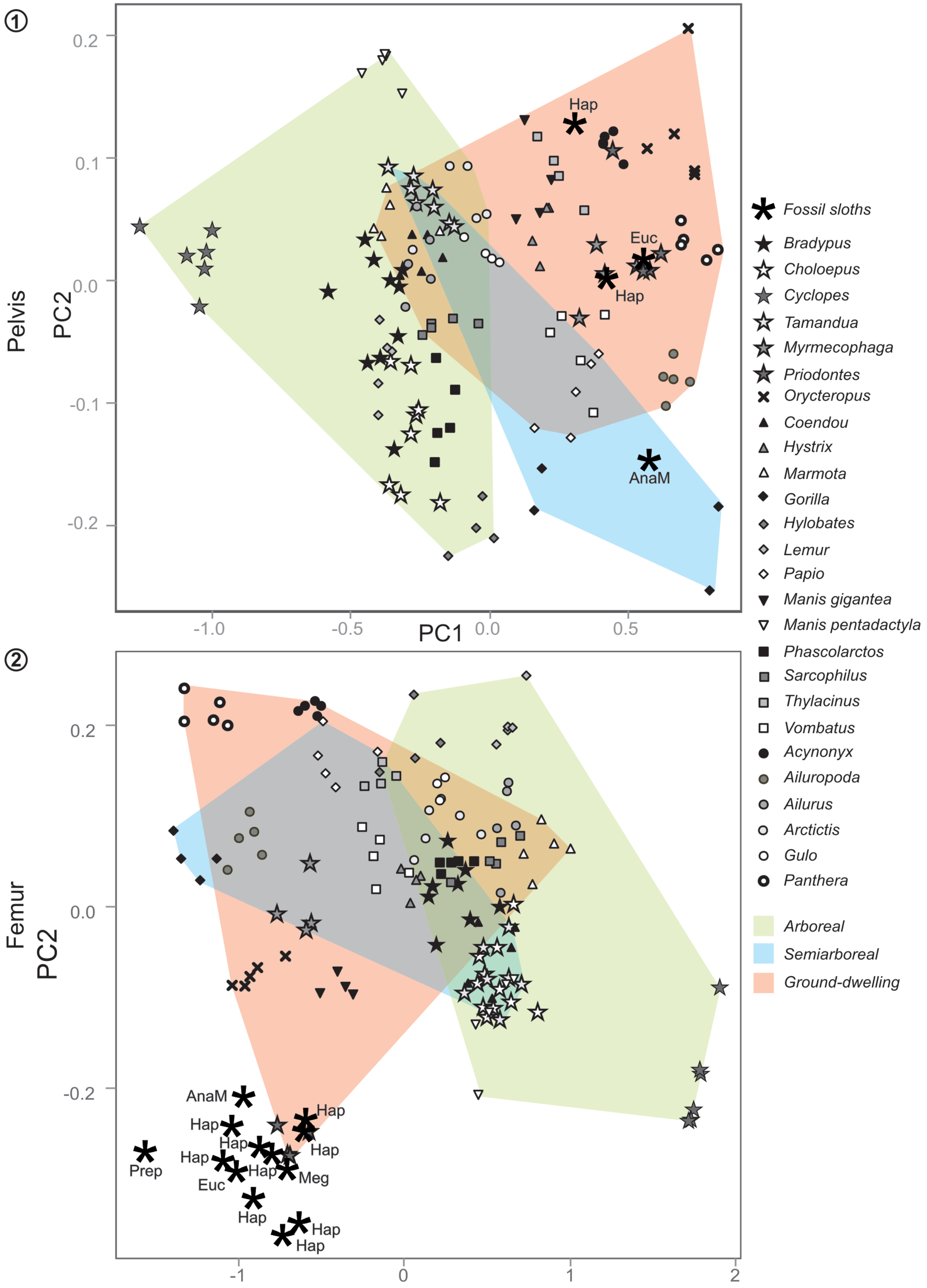
Scapulo-Humeral Index (**SHI**, Fig. 9.2)***.*** Santacrucian sloths with scapular remains (*Eucholoeops* and *Hapalops* only) show intermediate values similar to those of the lesser anteater, the terrestrial carnivores of the sample (*Acynonyx*, *Ailuropoda* and *Gulo*), the koala *Phascolarctos* and the tree-porcupine *Coendou*. Higher values are depicted by digging taxa such as the giant armadillo *Priodontes*, the aardvark *Orycteropus*, the wombat *Vombatus* and the African porcupine *Hystrix*.

Humeral Robusticity Index (**HRI**, Fig. 10.1)***.*** Santacrucian mylodontids exhibit a stouter humerus comparable to that of the anteaters and giant armadillo. *Hapalops* and *Eucholoeops* present a slightly slender humeri similar to that of the wombat *Vombatus* and both pangolins though more robust than that of the rest of the extant sample. Lowest values are displayed by extant sloths and the gibbon.

Humeral Distal Epiphysis Depth (**HDED**, Fig. 10.2)***.*** Santacrucian sloths present intermediate values similar to those exhibited by anteaters, the giant armadillo, the terrestrial marsupials, pangolins, the cheetah, the tiger, the groundhog and the tree-porcupine. The highest values are represented by the most terrestrial taxa, with the lesser anteater, the lesser pangolin and the baboon being exceptions.

Entepicondyle Index (**EPI**, Fig. 11.1)***.*** Santacrucian sloths show intermediate values equivalent to those of the giant armadillo and wombat, and lower than those of anteaters and pangolins. Digging taxa within each clade yield the highest values.

Figure 5. Distribution of modern mammals and Santacrucian sloths in the morphospaces depicted in PC1 and PC2. **1,** ulna; **2,** radius. Codes as in Fig. 4.


①
Pelvis
PC2
0.2
0.1
0.0
-0.1
-0.2
-1.0
-0.5
0.0
0.5
PC1
Hap
Euc
Hap
AnaM
②
Femur
PC2
0.2
0.0
-0.2
-1
0
1
2
AnaM
Hap
Hap
Hap
Hap
Hap
Prep
Hap
Euc
Meg
Hap
Hap
Hap
Fossil sloths
Bradypus
Choloepus
Cyclopes
Tamandua
Myrmecophaga
Priodontes
Orycteropus
Coendou
Hystrix
Marmota
Gorilla
Hylobates
Lemur
Papio
Manis gigantea
Manis pentadactyla
Phascolarctos
Sarcophilus
Thylacinus
Vombatus
Acynonyx
Ailuropoda
Ailurus
Arctictis
Gulo
Panthera
Arboreal
Semiarboreal
Ground-dwelling

Index of Fossorial Ability (**IFA**, Fig. 11.2)***.*** Santacrucian sloths display relatively high values similar to those of anteaters, pangolins, the wombat, the African porcupine and the groundhog. As noted by Vizcaíno *et al.* (1999), within each clade, digging taxa present the highest values of this index. Among the Santacrucian sloths, *Eucholoeops* show the lowest value while *Nematherium* show the highest.

Ulnar Robusticity Index (**URI**, Fig. 12.1)***.*** Among Santacrucian sloths, the highest value, similar to that of the aardvark and the greater pangolin, is obtained for *Prepotherium*. *Hapalops* and *Eucholoeops* present more slender ulnae which are equivalent to those of anteaters, the giant panda, the tiger and the African porcupine. While the giant armadillo has the stoutest ulnae, extant sloths together with the cheetah and the gibbon exhibit the most gracile. Among marsupials, primates and rodents, the arboreal forms have more slender ulnae. Yet, the same is true for the specialized cursor cheetah. Regarding the anteaters and pangolins, terrestrial forms have more slender ulnae than climbing ones.

Radial Head Index (**RHI**, Fig. 12.2)***.*** Santacrucian sloths present intermediate values similar to those of the lesser anteater, the marsupial wolf, the giant pangolin, the tree-porcupine and the placental carnivorans of the sample. The extant sloths and primates exhibit more rounded radial heads. In general, within each clade, arboreal taxa display more rounded radial heads which enhance radial rotation. The exceptions to this rule, as demonstrated for other indices, are the anteaters and the lesser pangolin.

Crural Index (**CI**, Fig. 13.1)***.*** *Hapalops*, *Analcimorphus* and *Prepotherium* display relatively low values (equivalent to those of the gorilla, the koala and the wombat) while *Analcimorphus* presents the lowest, which is similar to that of the giant panda. As transpires with the BI, anteaters show a decrease in relative tibia length from the arboreal silky anteater to the terrestrial giant anteater. A similar phenomenon can be seen in the arboreal to terrestrial pangolins.

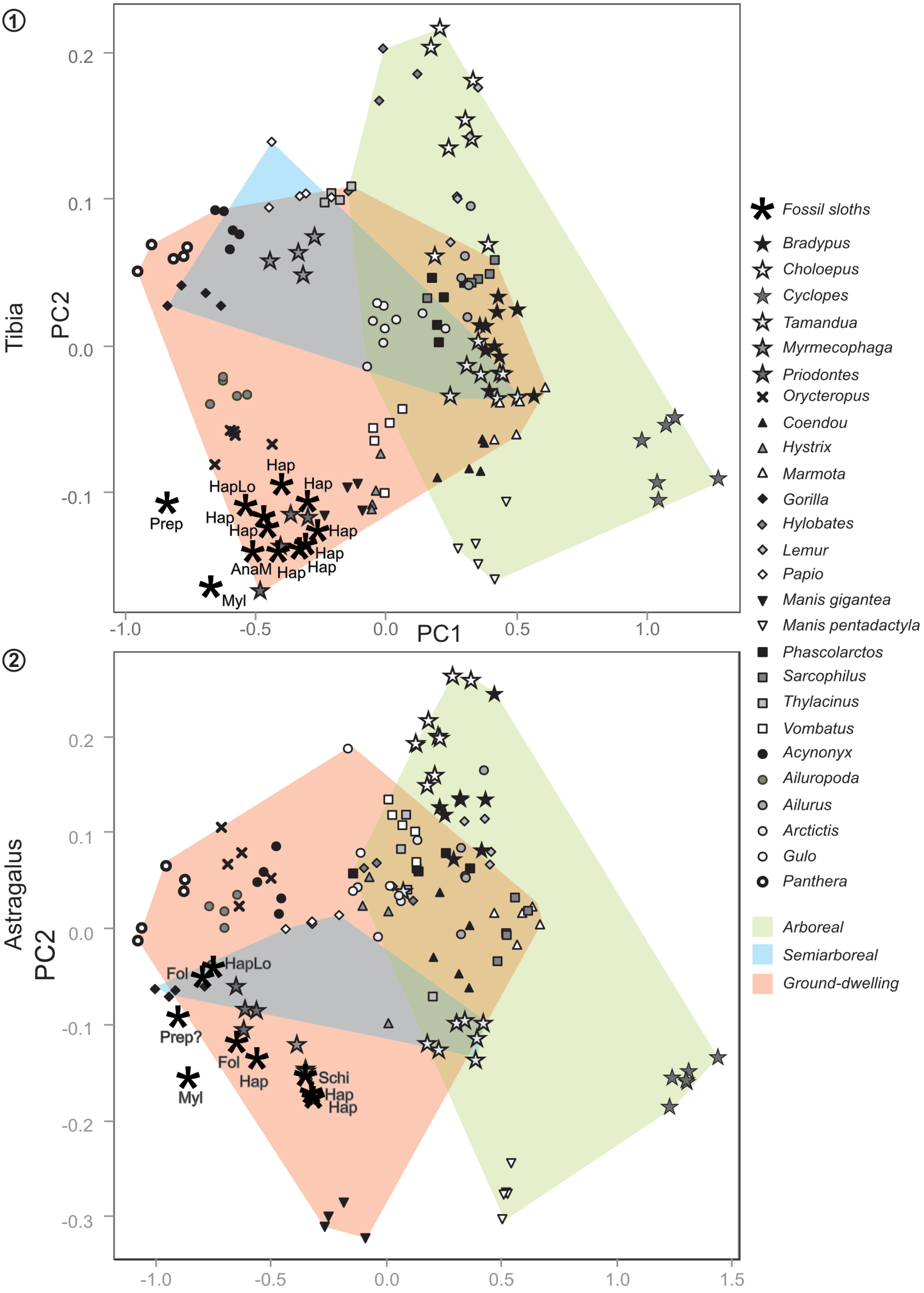
Femoral Robusticity Index (**FRI**, Fig. 13.2)***.*** Santacrucian sloths display a comparatively wide range of values for this index. However, overall they possess relatively high values when compared to those of the giant armadillo and the aardvark. *Analcimorphus* exhibit the most gracile femur among Santacrucian sloths. *Eucholoeops* and *Hapalops* present in turn, intermediate femurs while *Prepotherium* display the stoutest of all, even when compared to the rest of the sample. Note that all these taxa have a well-developed third trochanter followed by the anteaters, the pangolins, the tree-porcupine and the African porcupine. Armadillos also have a prominent third trochanter.

Medial Condyle Depth Index (**MCDI**, Fig. 14.1)***.*** Santacrucian sloths exhibit comparatively low values describing wide and shallow femoral distal epiphyses (similar to those of extant sloths, the giant armadillo and the koala) which indicate the presence of flexed stances and a lesser degree of stabilization. The highest values correspond to the more terrestrial taxa within each clade (except for the giant armadillo and the gorilla).

Tibial Robusticity Index (**TRI**, 14.2)***.*** Santacrucian sloths display the highest values of the entire sample. Among the extant mammals, it is the giant armadillo, the greater pangolin, the aardvark, the African porcupine and the giant panda that present stouter tibiae. Conversely, the two-toed sloth and the primates (except for the gorilla) have the most slender tibiae. In general, within each clade, the more slender tibiae correspond to the most arboreal taxa. Yet, these forms also present the smallest body size.

Tibial Proximal Epiphyseal Index (**TPEI**, Fig. 15)***.*** The Santacrucian sloths, especially *Prepotherium*, display comparatively low values that are similar to those of the three-toed sloth, the lesser anteater, the pangolins, the gorilla and the gibbon. *Hapalops* and *Eucholoeops* exhibit higher values that are comparable to those of the giant anteater, the Tasmanian devil, the lemur and rodents. Some cursorial forms such as the marsupial wolf and the cheetah present the highest values. In opposition, extant sloths and pangolins show evidence of the lowest ones.

Figure 6. Distribution of modern mammals and Santacrucian sloths in the morphospaces depicted in PC1 and PC2. **1,** pelvis; **2,** femur. Codes as in Figure 4.


①
Tibia
PC2
0.2
0.1
0.0
-0.1
-1.0
-0.5
0.0
0.5
1.0
PC1
Prep
HapLo
Hap
Hap
Hap
Hap
Hap
Hap
Hap
Hap
AnaM
Hap
Myl
②
Astragalus
PC2
0.2
0.1
0.0
-0.1
-0.2
-0.3
-1.0
-0.5
0.0
0.5
1.0
1.5
Fol
HapLo
Prep?
Fol
Hap
Myl
Schi
Hap
Hap
Fossil sloths
Bradypus
Choloepus
Cyclopes
Tamandua
Myrmecophaga
Priodontes
Orycteropus
Coendou
Hystrix
Marmota
Gorilla
Hylobates
Lemur
Papio
Manis gigantea
Manis pentadactyla
Phascolarctos
Sarcophilus
Thylacinus
Vombatus
Acynonyx
Ailuropoda
Ailurus
Arctictis
Gulo
Panthera
Arboreal
Semiarboreal
Ground-dwelling

DISCUSSION

Results obtained in the present contribution and in Toledo *et al.* (2012) are overall consistent with those of other morphofunctional studies of Santacrucian sloths (Bargo *et al.*, 2012; Toledo *et al.*, 2013, 2015).

Overview of PCAs

All PCAs performed show similar results highlighting the following aspects: 1) primary separation between arboreal and terrestrial taxa occurs along PC1s. This can be considered a size proxy because, as previously summarized in Toledo *et al.* (2014), body size is a primary constraint for arboreality. Remarkable exceptions to this rule are the orangutan *Pongo* and (among extant sample used herein) the gorilla; 2) a relatively clear separation of taxa with elongated slender limb elements from those with robust stouter ones is detected. In most cases, PC2 may reflect a gradient between optimization of speed and optimization of power applied by the limbs. Fast-moving animals (cursorials) and fast brachiating climbers (but also extant sloths, which are slow-climbers) occupy one end of the gradient. Conversely, walking (ambulatory *sensu* Polly, 2007) and slow-climbing forms (many of them also good diggers, such as the silky and lesser anteaters) occupy the other; and 3) besides size as a primary classifier for substrate preference, no other clear pattern separating arboreal taxa from terrestrial ones is detected based on the measurements used in this analysis.

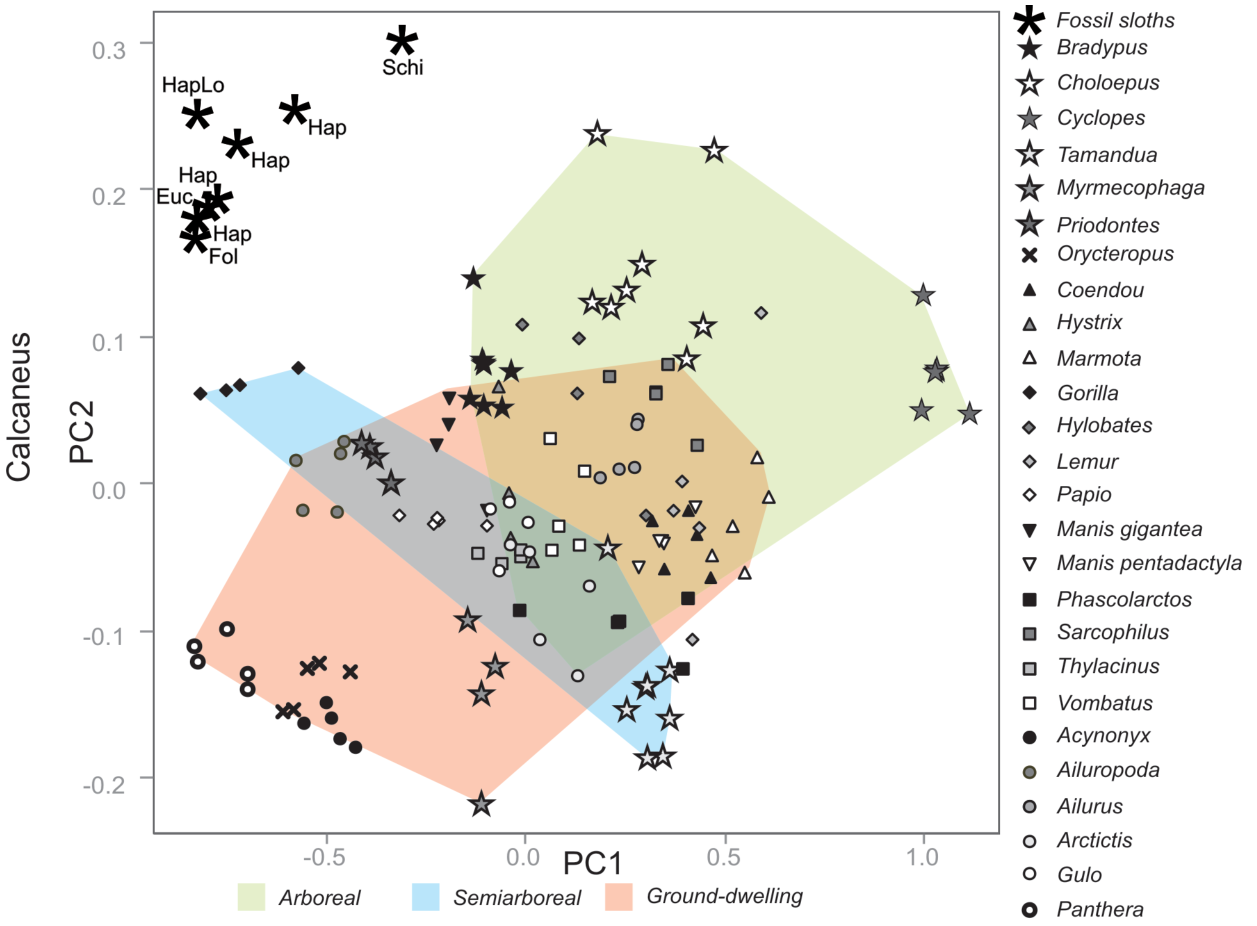


Figure 8. Distribution of modern mammals and Santacrucian sloths in the morphospaces depicted in PC1 and PC2. Calcaneus. Codes as in Figure 4.

Figure 7. Distribution of modern mammals and Santacrucian sloths in the morphospaces depicted in PC1 and PC2. **1,** tibia; **2,** astragalus. Codes as in Figure 4.

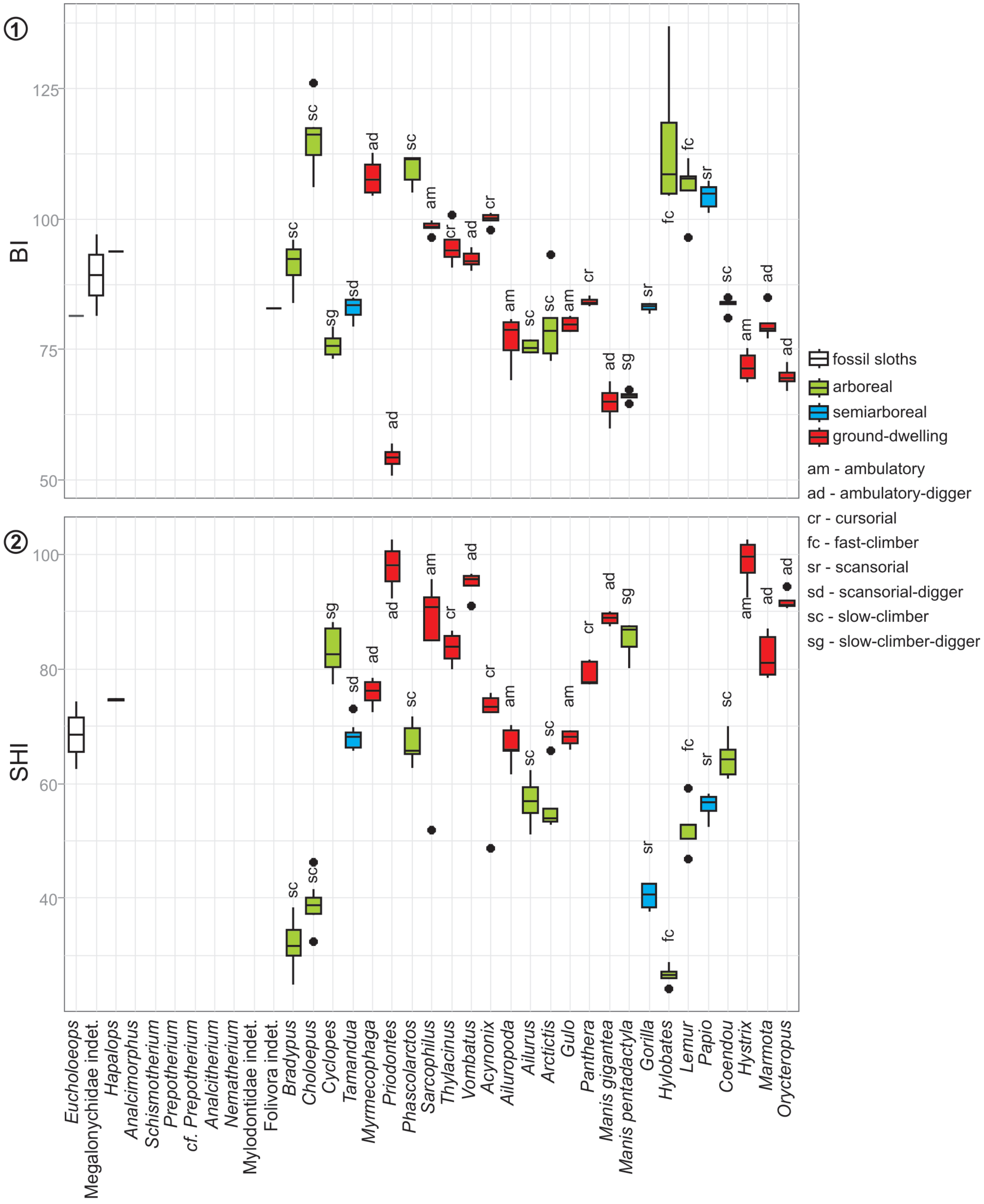


Figure 9. Boxplot of functional indices: **1,** BI; **2,** SHI. Missing values implies unavailable specimens for required measurements.

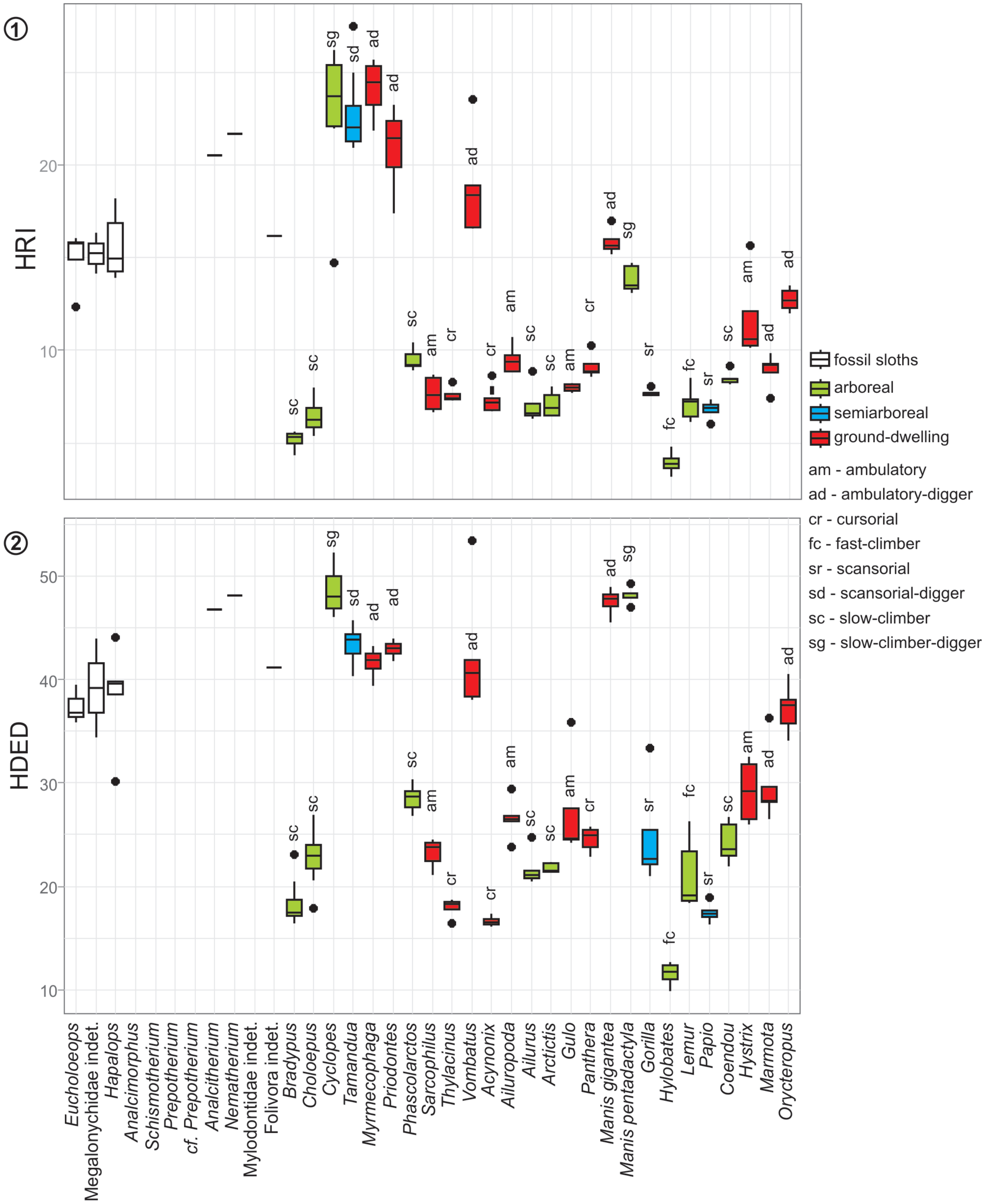


Figure 10. Boxplot of functional indices: **1,** HRI; **2,** HDED.

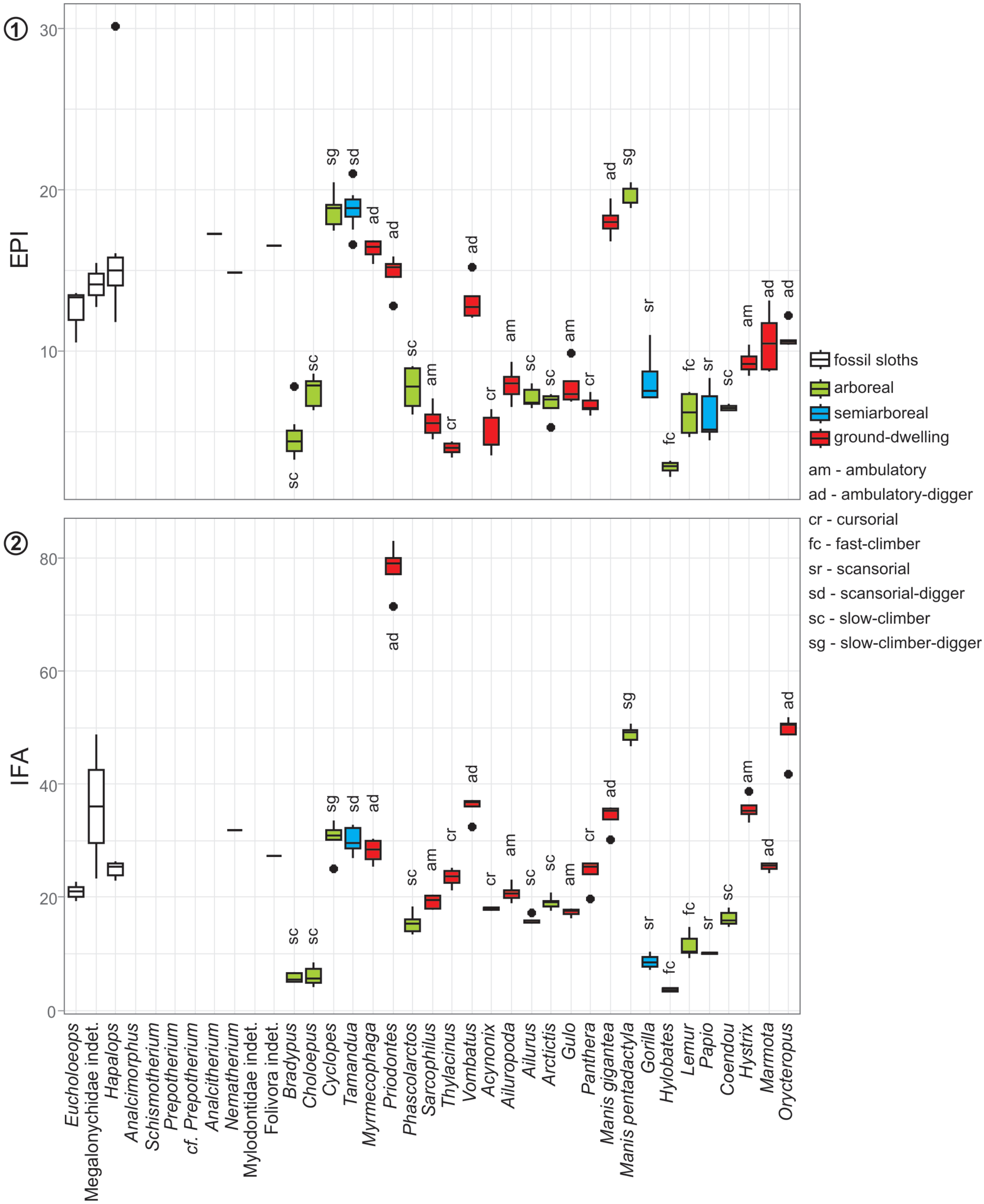


Figure 11. Boxplot of functional indices: **1,** EPI; **2,** IFA.

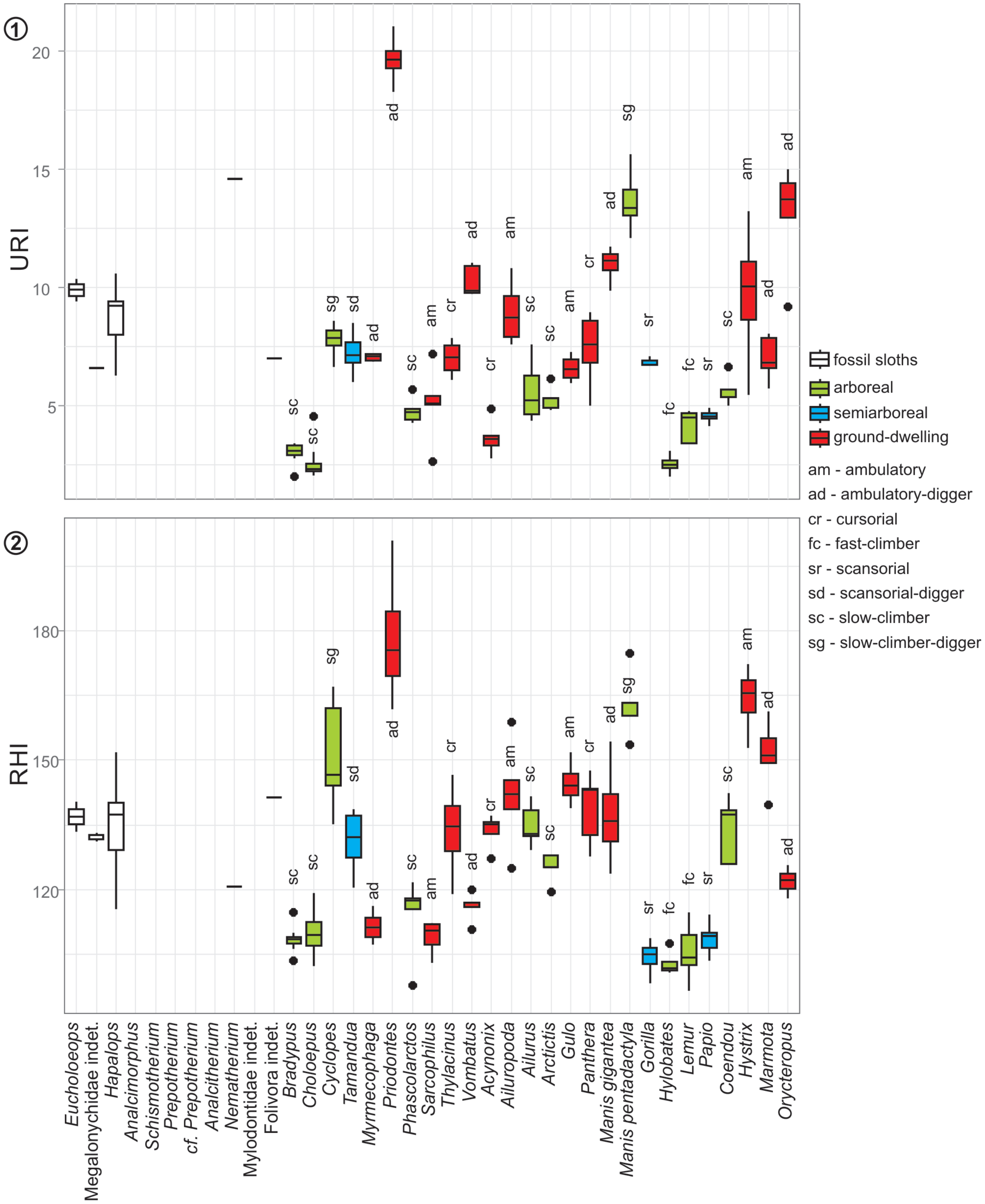


Figure 12. Boxplot of functional indices: **1,** URI; **2,** RHI.

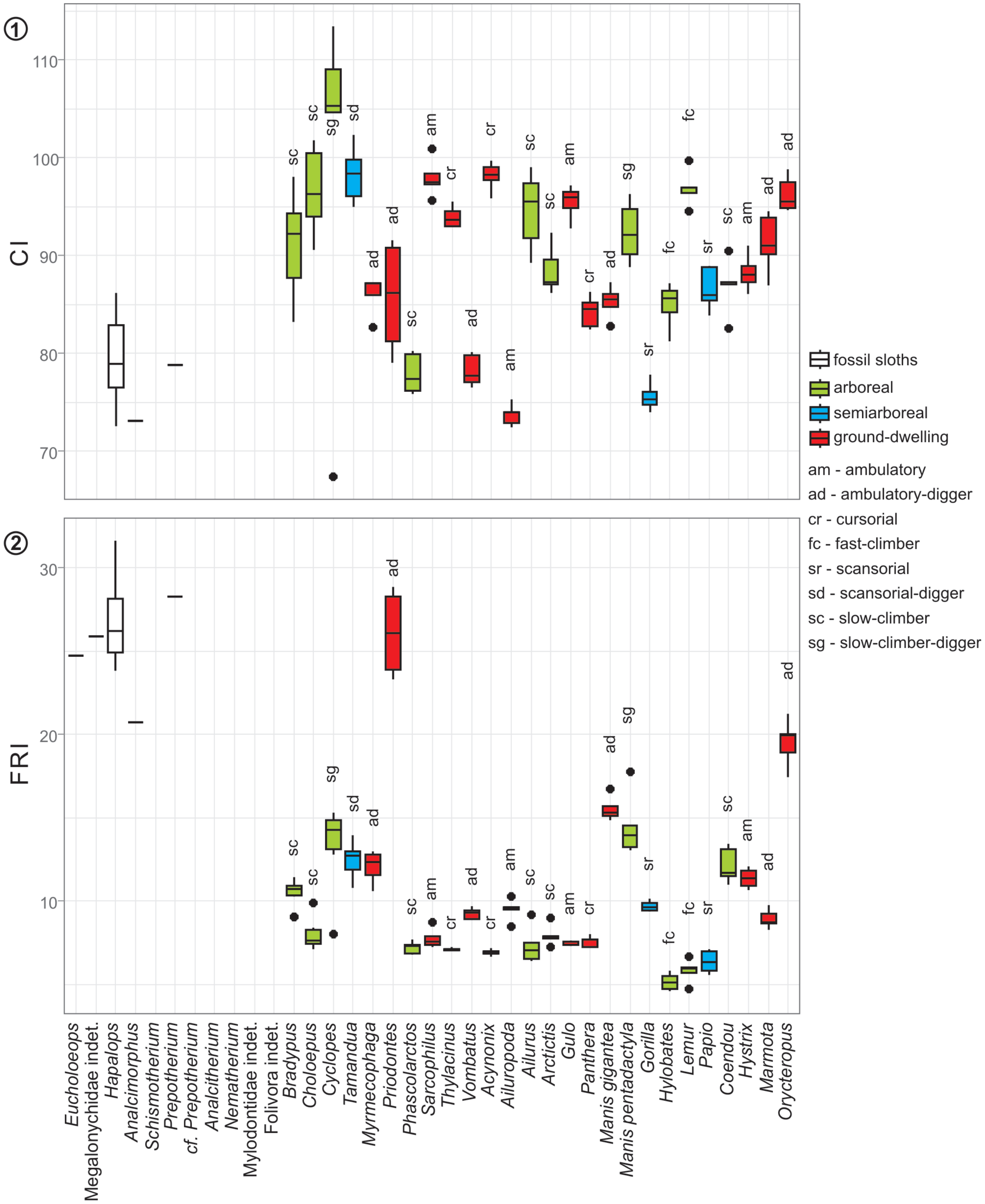


Figure 13. Boxplot of functional indices: **1,** CI; **2,** FRI.

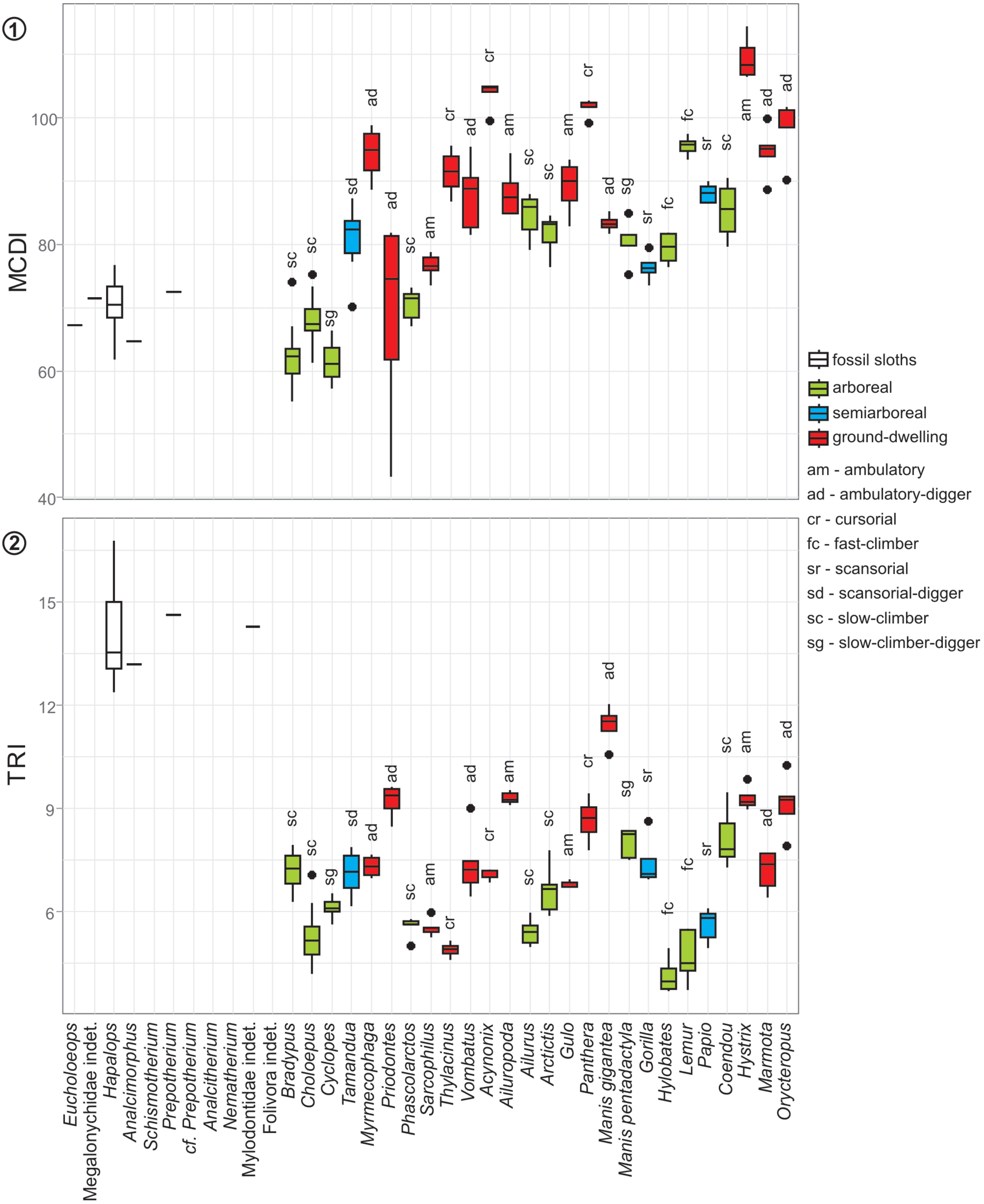


Figure 14. Boxplot of functional indices: **1,** MCDI; **2,** TRI.

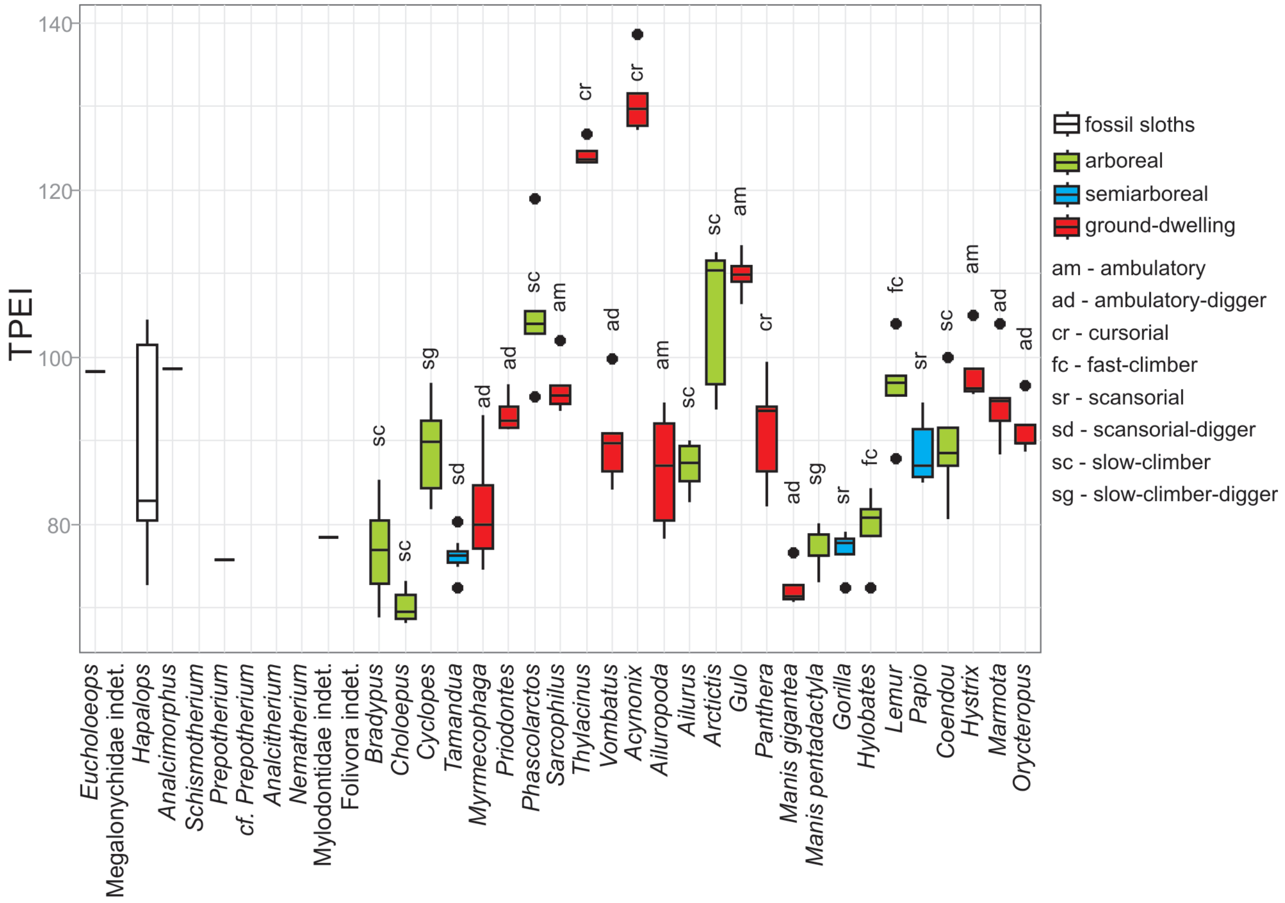


Figure 15. Boxplot of functional indices: TPEI.

Forelimb and scapular girdle indices. There is no clear pattern associated with substrate preference that can be derived from BI values of the modern mammal sample. Elissamburu and Vizcaíno (2004) described intermediate BI values (upper arm and forearm similar in length) for caviomorph rodents that move in a limb-flexed posture. In this posture, the stride length is more related to scapular rotation than to forearm extension. There is an observable pattern linking BI and substrate use: lower BI values (forearm shorter than upper arm) are exhibited by digging taxa such as the giant armadillo, the giant pangolin and the aardvark. Therefore, this corresponds to an optimization of power over speed during activities other than locomotion, plus an associated reduction of the bending forces on the forearm. Thus, there are overlapping locomotion pattern and substrate preference requirements (see also URI and TRI). The calculated values for SHI probably reflect the deltoid musculature arising from the scapular spine in *Eucholoeops* and *Hapalops* and functioning to stabilize the shoulder joint rather than facilitating humeral protraction and elevation. Additionally, the relatively highly-movable shoulder joint of *Hapalops* and *Eucholoeops* as proposed by Toledo *et al.* (2013), supports the interpretation of their hypothetical climbing abilities (see Argot, 2001). Values obtained for HRI indicate that the humeri of Santacrucian sloths, particularly of the mylodontids *Analcitherium* and *Nematherium,* were capable of remarkable compliance when faced with high mechanical loads. In contrast, *Hapalops* and *Eucholoeops* were instead exposed to lower levels of mechanical stress. The same can be stated regarding the ulna: values of URI indicate a relatively strong ulnar diaphysis. Additionally, the space available for the accommodation of hand flexor and pronator-supinator musculatures was wide, fact also noted by Bargo *et al.* (2012) and Toledo *et al.* (2013). The megathere *Prepotherium* showed the strongest ulnar diaphysis while *Hapalops* and *Eucholoeops* proved less robust. Elissamburu and Vizcaíno (2004) described an increase of URI in diggers with respect to non-digger ambulatory taxa. Such increas relates to greater development of hand and digital flexor muscles as well as greater strength of the diaphysis. Both these two mechanical aspects are linked to digging performance. However, as discussed by Argot (2001) for fossil didelphids, the very same mechanical context is also consistent with climbing behavior. High IFA values, analogous to those of digging mammals in the extant sample, support previous hypotheses of digging abilities for some Santacrucian sloths (mainly mylodonts, Bargo *et al*., 2012 and Toledo *et al*., 2013). On the other hand, non-digging extant taxa present consistently low IFA values (see Vizcaíno *et al*., 1999, 2003; Elissamburu and Vizcaíno, 2004; Croft and Anderson, 2008; Toledo *et al*., 2012). *Eucholoeops* exhibit the lowest values among Santacrucian sloths while *Nematherium* display the highest. Evidence indicating restricted forearm extension and habitually flexed stances, especially in *Nematherium* and *Hapalops* (Bargo *et al*., 2012; Toledo *et al*., 2013), is consistent with this interpretation. In contrast, *Eucholoeops* and *Prepotherium* were less capable diggers. Pronation-supination capabilities, as described by RHI values, are comparable to those of the extant anteaters and more restricted than those in extant sloths. *Eucholoeops* and *Nematherium* appear to have possessed radii capable of significant rotation while that of *Hapalops* was more restricted. Note that this pattern is compatible with inferred digging capabilities. Nevertheless, although pronation-supination capabilities of the silky and lesser anteaters are restricted (Yalden, 1966) when compared to those of other climbing mammals (for example, see Szalay and Sargis, 2001; Sargis, 2002a; Candela and Picasso, 2008), this does not in any way impede them from moving and standing in arboreal substrates (Taylor, 1978). This pattern suggests that anteaters (and perhaps all Pilosa) share morphofunctional solutions to climbing that are different from those of other mammals. Finally, as shown by high EPI values, a large available space for hand and digital flexor musculature (indirectly indicating powerful hand prehension) is consistent with both climbing (see Argot, 2001; Candela and Picasso, 2008) and digging faculties (Milne *et al*., 2009; see Bargo *et al*., 2012; Toledo *et al*., 2013). Among Santacrucian sloths, the mylodontid *Analcitherium* has the largest entepicondyle while *Hapalops* and *Nematherium* exhibit intermediate values and *Eucholoeops* possess the least protruding entepicondyle. Such values suggest a more powerful manual and digital flexion in the former cases than in *Eucholoeops*. Milne *et al.* (2009) detected a strong positive correlation between high IFA values and well-developed entepicondyles among cingulates. Likewise, similar findings were attained by Elissamburu and Vizcaíno (2004) for caviomorph rodents. On the other hand, powerful hand prehension using the thumb is important for didelphids (Argot, 2001) and for hystricognath rodents (Candela and Picasso, 2008). Nevertheless, this adaptation has not been described for sloths.

Hindlimb and pelvic girdle indices. As with PCA results, to discern a biomechanical pattern for hindlimb and pelvic girdle indices was difficult. Low CI values indicating relatively short tibiae in *Hapalops*, *Analcimorphus* and *Prepotherium* suggest that Santacrucian sloths were not well-adapted for fast lower-leg extension needed for fast movements but rather for applying power instead. In other mammalian clades (*e.g.*, rodents; Elissamburu and Vizcaíno, 2004), these values would also indicate movement in flexed stances. FRI values reveal that femoral diaphyses of Santacrucian sloths were well-adapted to resist strong mechanical demands. *Analcimorphus* was the most gracile Santacrucian sloth while *Eucholoeops* and *Hapalops* were intermediate, and *Prepotherium* the more robust. Elissamburu and Vizcaíno (2004) remarked that FRI in caviomorph rodents could not be correlated with a functional sequence from cursorial to fossorial lifestyles or with body size, but was only an indication of relative femur length. This could be the case for *Analcimorphus* whereas, in opposition, in *Prepotherium,* the robustness of its femur could merely reflect its greater body size (see Bargo *et al*., 2012; Toledo *et al*., 2015). Considering MCDI values obtained for Santacrucian sloths, their knee joint was well-adapted for transmission of high mechanical loads in habitually flexed stances and with abducted knees (de Toledo, 1998; Bargo *et al*., 2012; Toledo *et al*., 2015). MCDI is similar to the Distal Femur Shape index utilized by White (1993). In White's study, values obtained for more robust specimens of *Hapalops* were similar to those obtained for the silky anteater. In contrast, values for *Prepotherium* and smaller *Hapalops* specimens were closer to those of the lesser anteater. Transmission of mechanical loads, mainly through the medial femoral condyle, is also related to climbing faculties (Sargis, 2002b; Candela and Picasso, 2008). Nevertheless, Argot (2002) argues that this is a measure of agility more than substrate preference. TPEI is also related to knee-joint stabilization. The heaviest Santacrucian sloths, such as *Prepotherium* and the mylodontids, exhibit low values. Conversely, *Hapalops* and *Eucholoeops* display higher values, a fact suggesting slightly less-flexed stances and/or less mechanical requirements in accordance to their lighter body size (see Toledo *et al.*, 2014). As indicated by TRI, the robust tibial diaphysis of the Santacrucian sloths was well-adapted to cope with high mechanical stresses. This feature is more likely related to body mass support during posture and locomotion (as explained for armadillos by Vizcaíno and Milne, 2002) than to substrate preference. Use of hindlimbs to assist digging behaviour cannot be ruled out based on these findings. Analyses considering potential upright postures of Santacrucian sloths are still in progress.

White (1997) utilized indices to perform Principal Coordinates Analysis only including a single very complete specimen of *Hapalops* (the type specimen of *H. longiceps* from YPM-VPPU). She found that it shared morphospace with the more highly-arboreal xenarthrans. In this study, a greater number of fossil sloth specimens were compared with a larger sample of extant mammals by means of using separate PCAs on measurements of each limb element. Summarizing the results presented by White (1993, 1997), Bargo *et al.* (2012), Toledo *et al.* (2012, 2013, 2015), and the work herein introduced, the following functional inferences can be stated:

Santacrucian sloths were robust quadrupedal animals with relatively short and stout limb elements with proportions similar to those of extant anteaters, tree and greater pangolins, aardvarks and wombats (Bargo *et al.*, 2012; Toledo *et al.*, 2012; and the present contribution). Differences observed in taxa presenting more slender limbs seem to be independent of body size. When compared to extant mammals, limb proportions of Santacrucian sloths are optimized to apply power at the expense of speed or agility. In this sense, in addition to the results obtained from the indices, PC2 could be considered to reflect the "cursorial-graviportal continuum" proposed by Carrano (1999) in an analysis of limb proportions of dinosaurs and mammals. Thus, Santacrucian sloths occupy the region between "mid-grades" and graviportal forms (*sensu* Carrano, 1999). Taking into account that extant sloths present extremely slow movements associated with their particular lifestyles and physiologies (Chiarello, 2008), the utility of this gradient for inferring locomotion speed in xenarthrans needs to be further discussed. Santacrucian sloths can be characterized as forceful animals able to apply concentrated muscular force through their appendicular skeleton to meet their ecological needs.

Shoulder and hip joints were highly mobile but resilient at the same time (Toledo *et al.*, 2013, 2015). Extant sloths have in turn maximized such features (see Mendel, 1981; Nyakatura *et al.*, 2010). Conversely, both elbow and knee joints appear to be well-suited for posture and movement in flexed and abducted stances (see also White, 1997; Toledo *et al.*, 2013, 2015).

The reconstructed musculature of Santacrucian sloths (Bargo *et al.*, 2012; Toledo *et al.*, 2013, 2015) indicates that these animals were able to apply great muscular power during abduction, adduction, flexion and retraction of limb elements. Accordingly, long-clawed digits in both hands and feet were able to be forcefully flexed in a powerful grasp. This mechanical context is compatible with climbing abilities but may also facilitate digging.

Performance of the appendicular form-function complex: faculties

As detailed above, biomechanics, functional morphology and ecomorphology approaches support the hypothesis that some Santacrucian sloths analyzed herein (*Eucholeops*, *Hapalops*, *Schismotherium*, *Analcimorphus*, *Prepotherium*, *Analcitherium* and *Nematherium*) were at least semiarboreal climbing mammals, a form of locomotion seen today in the collared anteater *Tamandua*, if not fully arboreal in substrate preference. Digging abilities appear to have been well-developed too, especially in the case of the mylodontids. The functional demands for climbing and digging overlap to some degree (see Argot, 2001 for a discussion on fossil didelphids; see also Croft and Anderson, 2008) thus making it difficult to specifically assign these taxa to one or the other category without invoking contextual information. In accordance with the theoretical framework imparted in the introductory section of this contribution, the presented morpho-functional characterization together with the results provided by White (1993, 1997), Bargo *et al.* (2012) and Toledo *et al.* (2012, 2013, 2015), suggest the following hypothetical faculties:

A. Santacrucian sloths were good climbing animals.

B. Some Santacrucian sloths presented digging abilities.

C. Santacrucian sloths were quadrupedal plantigrade walkers in a flexed stance with abducted elbows and knees.

But, what hypotheses can be proposed of their maximal performance as climbing mammals? The previously discussed form-function complexes can be used to qualitatively define a hypothetical maximal appendicular performance for Santacrucian sloths.

Posture and movement over arboreal substrates imply a number of physical issues that must be sorted out through evolution of design for animals to face climbing requests. As detailed in a plethora of works and summarized by Cartmill (1985), these physical issues can be synthesized as:

1. Problem A: to maintain the body over the support by working out the rotational moment around it and, also, to avoid sliding over sloped or vertical surfaces.
2. Problem B: to transfer the body mass from one support to another by handling the gap between them and avoiding falling.
3. Problem C: to ensure that chosen supports do not break due to the animal's weight.

Extant climbing animals display a number of morphofunctional tools that allow them to figure out these issues such as, as summarized by Cartmill (1985) and Hildebrand (1988):

1. Problem A: Solving the rotational moment can be achieved by:
   a. Diminishing the moment arm (rotational radius) by means of a small body size relative to the diameter of the support and/or adopting a flexed limb posture (most climbing mammals).
   b. Suspending below the branch in a dynamically stable position (extant sloths-see also Nyakatura *et al.*, 2010, and orangutan *Pongo pygmaeus*).
   c. Applying forces opposed to rotational moment and maximizing the frictional component by means of prehensile hands and feet, prehensile tails, curved claws, opposition of limbs to the sides of the support and maximization of frictional forces via rugose or adhesive pads (most climbing mammals).
2. Problem B: Transferring the body mass to another support by eluding the gap can be achieved by:
   a. Overcoming the gap using a flying stage (leaping, gliding and fast brachiating) analogous to that of the fastest terrestrial gaits in which duty factor (the time proportional to the step cycle during which the limb is in contact with the substrate) is diminished to 0.
   b. Overcoming the gap without a flying stage by means of ensuring the grasping of the next support before leaving the previous one (slow brachiating and bridging). Duty factor is maximized.
3. Problem C: ensuring the compliance of the support can be achieved by:
   a. Diminishing the time of contact (leapers and brachiators).
   b. Distributing the body weight among several supports (extant sloths and orangutans, among others).
   c. Simply not moving or standing on unreliable supports by previously choosing them (most arboreal mammals).

All these strategies are applied to different extents by extant climbing mammals (Cartmill, 1985; Hildebrand, 1988). Each animal presents a particular spectrum of functional capabilities that can be analogized to the Averaged Biomechanical Situation (Oxnard, 1984) which describes its maximal postural and locomotor performance. In this sense, Santacrucian sloths can be characterized as follows:

1. Problem A: Unquestionably, Santacrucian sloths cannot be considered small-sized climbing mammals. Essentially based on comparisons of limb proportions to extant sloths, suspended posture has been ruled out by White (1993, 1997) and by Toledo *et al.* (2013, 2015). In this respect, Santacrucian sloths seem well-prepared for posture and movement in flexed stances. Although an analysis of caudal vertebrae of Santacrucian sloths has yet to be made, their proportional length and robustness do not match those of extant mammals with prehensile tails such as the tropical porcupine *Coendou* or the collared anteater *Tamandua*. Bargo *et al.* (2012) and Toledo *et al.* (2013, 2015) found no evidence of opposable digits in their hands and feet. Nevertheless, these animals appear to have been capable of "trunk-hugging" (opposition of the limbs to the sides of the support, see Toon and Toon, 2004) and using their curved claws (see White, 1997 for an ungual morphometric

analysis) to cling to supports.

2. Problem B: As discussed above, the appendicular skeleton of Santacrucian sloths was well-suited for power application rather than for speed. However, considering their body size, leaping, jumping and gliding need be dismissed as working hypotheses. Proportions and joint extension capability of the forelimbs do not support slow brachiating locomotor hypotheses (White, 1997) either. Therefore, slow and careful bridging was probably the preferred method for Santacrucian sloths to transfer body mass between supports.

Problem C: As discussed in Bargo *et al.* (2012) and Toledo *et al.* (2014), body size is a primary constraint for climbing abilities. Most agile and acrobatic climbing mammals are very small while terrestrial forms are larger (Eisenberg, 1978). In this sense, and as noted by White (1993), body size is a good predictor for substrate preference in extant anteaters though not in primates. Even so, it seems plausible to propose that the smallest Santacrucian sloths (*Schismotherium*, *Eucholoeops*, *Analcimorphus* and *Hapalops*) were more arboreal than the heavier ones (mylodonts *Analcitherium* and *Nematherium*, and megatheriids such as *Prepotherium*). In fact, as observed by Toledo *et al.* (2014), mylodontids lie close to the maximum operational body size of around 90 kg (*Pongo pygmaeus*) for an arboreal lifestyle as defined by Cartmill (1985). *Prepotherium*, in their turn, clearly surpassed such limit. Santacrucian sloths were surely quite restricted in terms of needing to stand and move only on the thickest of branches, or at least would have needed to distribute their weight on several supports (albeit limited by their limb joints morphology which suggests they were not capable of hyper-extension-see Bargo *et al.*, 2012).

In summary, the climbing performance of Santacrucian sloths is comparable to that of extant mammals that climb slowly and by relying on grasping branches carefully while applying great muscular power. Such is the case of the silky and lesser anteaters, lesser pangolins and koalas (Hildebrand, 1988). Regarding their locomotion on the ground, not much can be proposed: according to the results obtained in this study, Santacrucian sloths were probably fairly quadrupedal plantigrade mid- to large-sized mammals of an ambulatory (*sensu* Polly, 2007) walking nature not well-suited for fast locomotion. Analysis of any putative bipedal stance either for feeding or locomotion, such as proposed for later taxa (see Blanco and Czerwonogora, 2003), awaits further research in these sloth taxa.

Morphology-based paleoautecology of Santacrucian sloths: inferring hypothetical fundamental niche according to body size, dietary habits and substrate preference and use

As aforementioned, comprehensive paleoautecological characterization following the above-mentioned protocol (Vizcaíno *et al.*, 2008, 2012b) integrates information from three main biological attributes (deemed the most relevant for interpreting the biology of extinct mammals; Bargo, 2003): body size, dietary habit, and substrate preference and use.

Based on the body size estimates of White (1993, 1997), Bargo *et al.* (2012) and Toledo *et al.* (2014), Santacrucian sloths were mid to large sized mammals ranging from about 30 kg in the smaller genera up to 200 kg. As White (1993) and Toledo *et al.* (2014) discussed, arboreal Santacrucian sloths exhibit body size heterogeneity, comprising both small and relatively large genera (from *Pelecyodon* to *Hapalops longiceps*). *Prepotherium*, the largest of the Santacrucian sloths, is likely to be the most terrestrial form and probably not arboreal.

As explained in the literature, access to arboreal substrates allows animals to obtain food resources unavailable at ground level and/or forage on them while safe from predators (Hildebrand, 1988). According to Vizcaíno (2009), unique features in xenarthran dental morphology would have allowed Santacrucian sloths to establish a subtle partitioning of their food resources that cannot be easily estimated by analyzing modern arboreal herbivore mammalian guilds. Bargo *et al.* (2009) analyzed dental morphology and reconstructed masticatory movements of the megalonychid *Eucholoeops* and then compared them to those of other Santacrucian sloths. This genus, mainly presenting orthal masticatory movements and teeth well suited for shearing and tearing, may have been predominantly folivorous. This characterization was extended by Bargo *et al.* (2009) to other megatherioid Santacrucian sloths which share the same overall dental morphology. Such is the case of *Hapalops, Pelecyodon* and *Prepotherium*. On the other hand, the mylodontids *Nematherium* and *Analcitherium* exhibited a pattern similar to that of Pleistocene mylodontids such as

Scelidotherium (Bargo and Vizcaíno, 2008; Bargo *et al.*, 2012). Marked by essentially lateral masticatory movements and a tooth morphology more capable of crushing and grinding, this pattern suggests a more varied diet composed of not only of leaves but also of fibrous and turgid items such as fruits and tubers.

These dietary habits –in conjunction with the substrate preference and use hypotheses and locomotory inferences summarized herein– suggest that megatherioid Santacrucian sloths spent time on arboreal substrates while possibly feeding on leaves yet avoided the smaller branches that could not support their weight (see Toledo *et al.*, 2014). The Santacrucian mylodontids were bigger sloths with putatively more terrestrial habits. Their good digging abilities allowed them to obtain food from the ground (as partially suggested by their dentition) while also being facultative climbers that turned to trees for resting and sheltering. Finally, the folivorous megatheriid *Prepotherium*, the biggest Santacrucian sloth, was most likely a predominantly terrestrial herbivore and, perhaps, an occasional digger.

By integrating estimates of body size with reconstructed feeding habits and substrate preference/locomotion, the Santacrucian sloths can be characterized in three paleoautecological groups:

A- Arboreal and semiarboreal folivores ranging in body size from 30 to 80 kg (*Eucholoeops*, *Hapalops*, *Schismotherium* and *Analcimorphus*, but probably also *Pelecyodon*).

B- Semiarboreal mixed consumers of leafs, fruits and tubers presenting good digging capabilities and ranging in body size to about 80 kg (the mylodontids *Nematherium* and *Analcitherium*).

C- Terrestrial folivores capable of facultative climbing and ranging from 120 to around 200 kg (*Prepotherium*).

According to the theoretical framework discussed in the introductory section, the abovementioned groups describe the maximum inferred spatial and trophic resource use of Santacrucian sloths and consequently define their hypothetical fundamental niche.

This paleoautecological characterization thus describes Santacrucian sloths as mid to heavy-sized arboreal and semiarboreal herbivores that either inhabited forested zones or at least required the presence of tree-habit flora in their environment.

Paleosynecology of Santacrucian sloths and the Santa Cruz Formation arboreal guild: inferring biological roles and putative realized niche in a reconstructed paleoenvironment

At this stage, inferences and hypotheses exclusively based on the skeletal remains of the Santacrucian sloths are not enough to hypothesize on their ecological role in the Santacrucian assemblages. Contextual information provided by other reconstructed components of the environment is needed. In the following sections, concurrent evidence drawn from researching into the biodiversity of Santacrucian assemblages is discussed in order to develop a putative realized niche reconstruction for Santacrucian sloths.

During the last decade, a *corpus* of studies focusing on the Miocene flora of Patagonia has become available (Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2007; Brea *et al.*, 2012). The paleopalynologic and paleobotanical studies of Miocene sequences of Patagonia carried out by Barreda and Palazzesi (2007) and Palazzesi and Barreda (2007) described the increase of xerophytic and megathermal taxa (for instance, bushes and palms) during the early Miocene, therefore illustrating a progressive importance of the herbaceous and arbustive elements. Brea *et al.* (2012) described the flora of the Santa Cruz Formation as consisting of both herbaceous and tree elements which formed a heterogeneous environment constituted by intermingled temperate semiarid and temperate-warm humid forests. These findings suggest a semiarid environment in temperate to warm-temperate conditions marked by the presence of dense and localized more-humid forested areas. The vegetation cover probably shifted along the fluvial plain, with open areas separating mixed woods and dense forests (Brea *et al.*, 2012). Similar florae (with respect to composition and physiognomy) are present nowadays in central Chile, southeastern Australia and New Zealand (Brea *et al.*, 2012).

Extended paleoecological analyses performed by Kay *et al.* (2012b) based on a comparison between the Santa Cruz Formation's non-volant mammalian fauna and selected modern mammalian faunas from other localities from Argentina and South America, indicated that the Santa Cruz Formation landscape was composed of a "mosaic of open temperate humid and semi-arid forests" (Kay *et al.*, 2012b, p. 313). Such conditions were more specifically characterized by the presence of forest coverage similar in composition to those existing today in the Andes area and its piedmont, which in their coexist with grasslands and both permanent and temporary water bodies. Kay *et al.* (2012b) remarked that the proportion of vertebrate paleoguilds and their niche composition was equivalent to modern subtropical environments with a vegetational mosaic of open and closed habitats. The Santacrucian landscape was more humid and warmer than Patagonia today, with average annual rainfall of more than 1000 mm and average annual temperatures of about 14 C° as well as noticeable daylight seasonality (Kay *et al.*, 2012b).

In this sense, paleobotanical and paleoclimatical data support the presence of plant communities that would have allowed considering the Santacrucian sloths as putative arboreal and semiarboreal herbivores.

Hypothesizing the ecological roles of Santacrucian sloths

The mammal assemblage of the Santa Cruz Formation is dominated by taxa below 500 kg in body size and only one genus almost reaching a ton (*Astrapotherium*) (see Cassini, 2011, 2013; Cassini *et al.*, 2012). Apart from sloths, the herbivore assemblage (Fig. 16) comprises glyptodonts, notoungulates, litopterns, rodents and primates (Vizcaíno *et al.*, 2012b). Sloths are among the heaviest herbivores recorded in the Santa Cruz formation and are only surpassed by the largest ungulates.

Plotnick and Baumiller (2000) defined a guild as a group

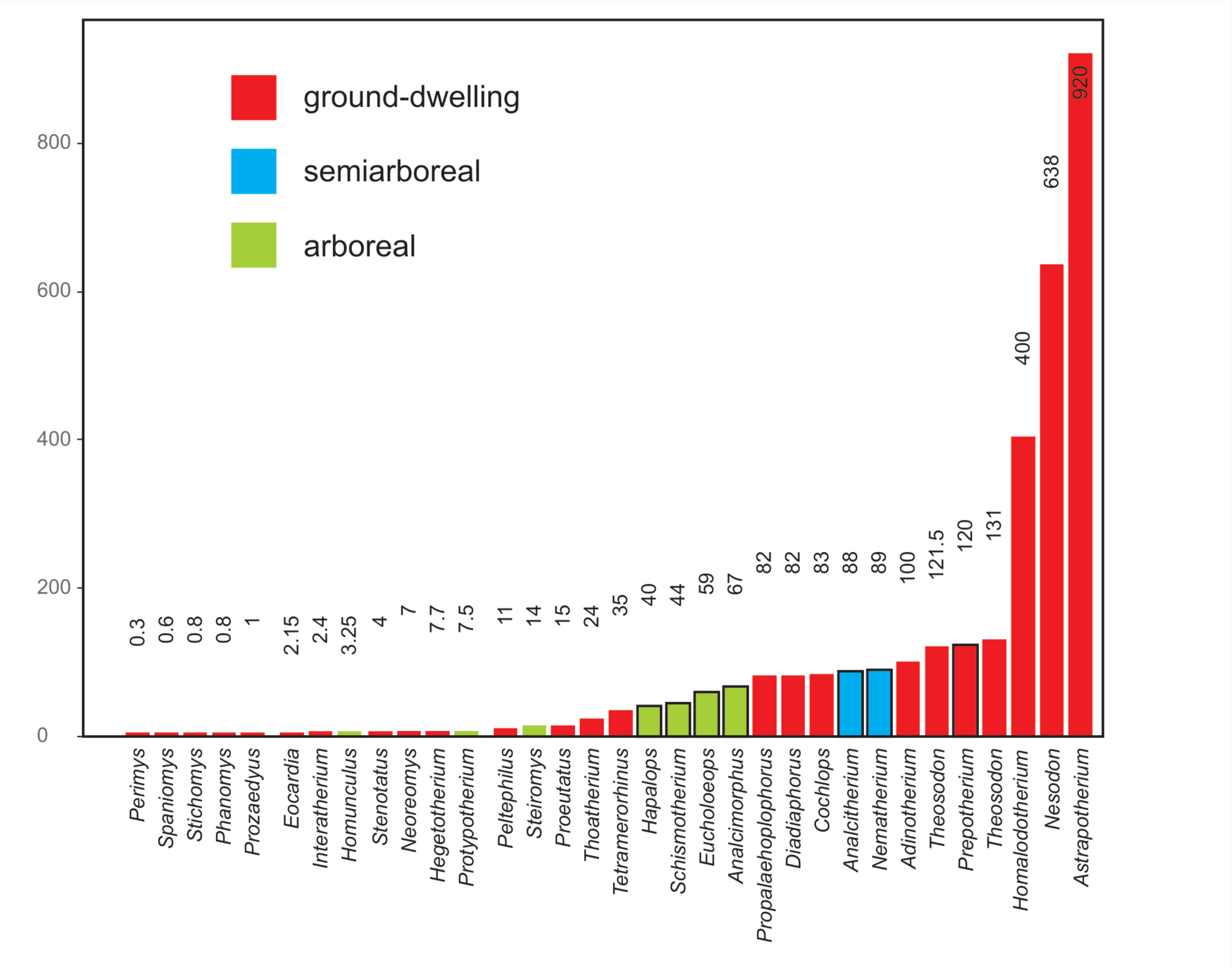


Figure 16. Body size distribution of Santacrucian herbivorous genera (in kg). Santacrucian sloths's bars with black outline. Based on data from Bargo *et al.* (2012), Candela *et al.* (2012), Cassini *et al.* (2012), Kay *et al.* (2012a, b), Prevosti *et al.* (2012), Vizcaíno *et al.* (2010, 2012b), and Toledo *et al.* (2014).

of species that exploit environmental resources in a similar way. Santacrucian sloths from group A shared their spatial and trophic resources solely with the porcupine *Steiromys*, the only other semiarboreal herbivore surpassing 10 kg (Candela and Picasso, 2008; Candela *et al.*, 2012). The inferred diet of *Steiromys* is composed of coniferous aciculae, seeds and bark (Candela *et al.*, 2012) while the plants consumed by the sloths would have consisted mainly of leaves. Based on its smaller body size, this porcupine was potentially able to forage on relatively thin branches in which sloths were not able to move or stand. Thus, what is proposed herein is that porcupines and group A of Santacrucian sloths did not markedly compete for either trophic or spatial resources. Santacrucian sloths could have shared or competed with other taxa for spatial and trophic resources. Yet, they were clearly the heaviest arboreal mammals and completely dominated the herbivore arboreal guild over 10 kg in body size (Fig. 17). Only the marsupial *Prothylacinus* (about 37 kg, Prevosti *et al.*, 2012) is close in body size to the smallest representatives of the genus *Hapalops*. Nevertheless, hitherto untested functional attributes of members of the arboreal guild, such as different daytime activity patterns (diurnal habits for the primate *Homunculus* were proposed by Kay *et al.*, 2012a), could have been involved in potential niche partitioning. The two-toed sloth and, to a certain degree, the three-toed sloth, are nocturnal or crepuscular (Chiarello, 2008). Consequently, potential crepuscular habits of Santacrucian sloths can be considered valid hypotheses to be tested in futures studies.

The taxonomic diversity of group A is interesting for at least three genera (*Eucholoeops*, *Hapalops* and *Analcimorphus*) may have probably coexisted (see Vizcaíno *et al.*, 2010; Kay *et al.*, 2012b). Such fact raises questions about possible competition for trophic resources among sloths. Some of the previously described slight functional differences between these genera could suggest variations in locomotor

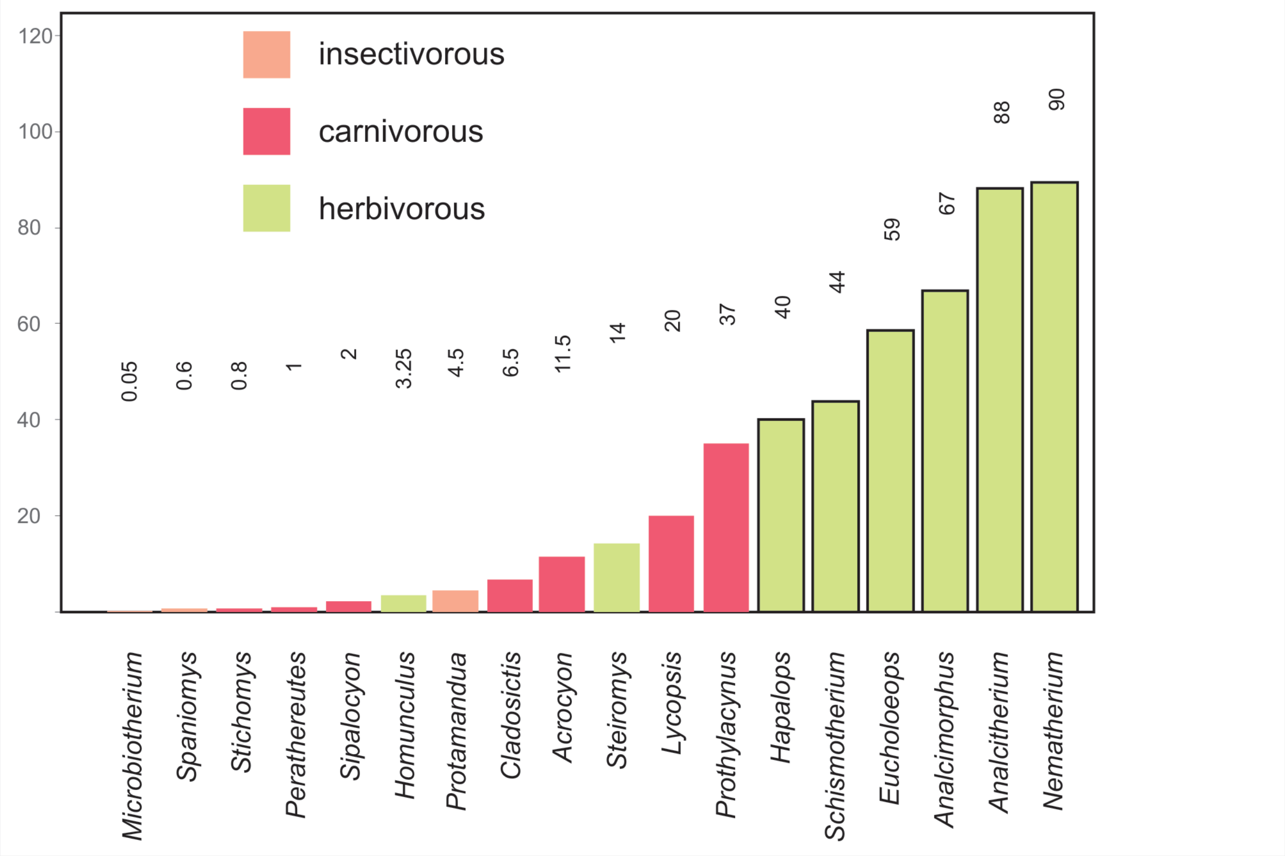


Figure 17. Body size distribution of the Santacrucian arboreal and semiarboreal mammalian genera (kg). Santacrucian sloths's bars with black outline. Based on data from Bargo *et al.* (2012), Candela *et al.* (2012), Prevosti *et al.* (2012), Kay *et al.* (2012a, b), and Toledo *et al.* (2014).

performance and, hence, access to diverse levels of the arboreal substrate. Heavier members of the genus *Hapalops* were, in comparison to relatively more gracile taxa capable of greater limb extension such as species of *Eucholoeops* and *Analcimorphus*, robust sloths with flexed limb posture possibly restricting them to thicker branches.

The genera comprising paleoautecological groups B and C shared the trophic resources within closed vegetation habitats with a greater diversity of terrestrial mammalian herbivores. Such diversity encompasses a range of body sizes, including small cingulates such as *Peltephilus* (11 kg) and *Proeutatus* (15 kg) as well as glyptodonts of about 80 to 100 kg (Vizcaíno *et al.*, 2006, 2011a, b, 2012c) and litopterns of more than 130 kg (*Theosodon*; Cassini, 2011). It cannot be discarded that these Santacrucian sloths ventured into open areas.

Regarding group B, the fact that Santacrucian mylodonts competed to a certain degree with larger litopterns inhabiting closed areas, such as *Diadiaphorus* and *Theosodon* (Cassini, 2011, 2013), or with the glyptodonts *Propalaehoplophorus* and *Cochlops* (Fig. 18) is quite probable. All of the aforementioned species are considered selective herbivores in mixed-closed environments (Vizcaíno *et al.*, 2011b, 2012c). Nonetheless, the digging abilities of the Santacrucian sloths (especially mylodontids) allowed them to gain access to food resources probably not exploited by non-digging similar-sized herbivores such as the glyptodonts.

Group C taxa, such as the heavy terrestrial sloth *Prepotherium*, possibly used their forelimbs to reach leaves on the lowest tree branches thus avoiding competition with glyptodonts though potentially sharing food resources with the aforementioned litopterns. *Prepotherium* is more frequently recorded from sediment deposits corresponding to more arid environments (see Matheos and Raigemborn, 2012). Such location supports the hypothesis that *Prepotherium* may have been well-suited for living in open habitats, where they may have competed for dietary resources with other heavy-sized herbivores such as the notoungulates *Adinotherium* (100 kg) and *Nesodon* (630 kg) (Cassini, 2011, 2013).

When considering Santacrucian sloths as potential food resources for other Santacrucian vertebrates, the fact that

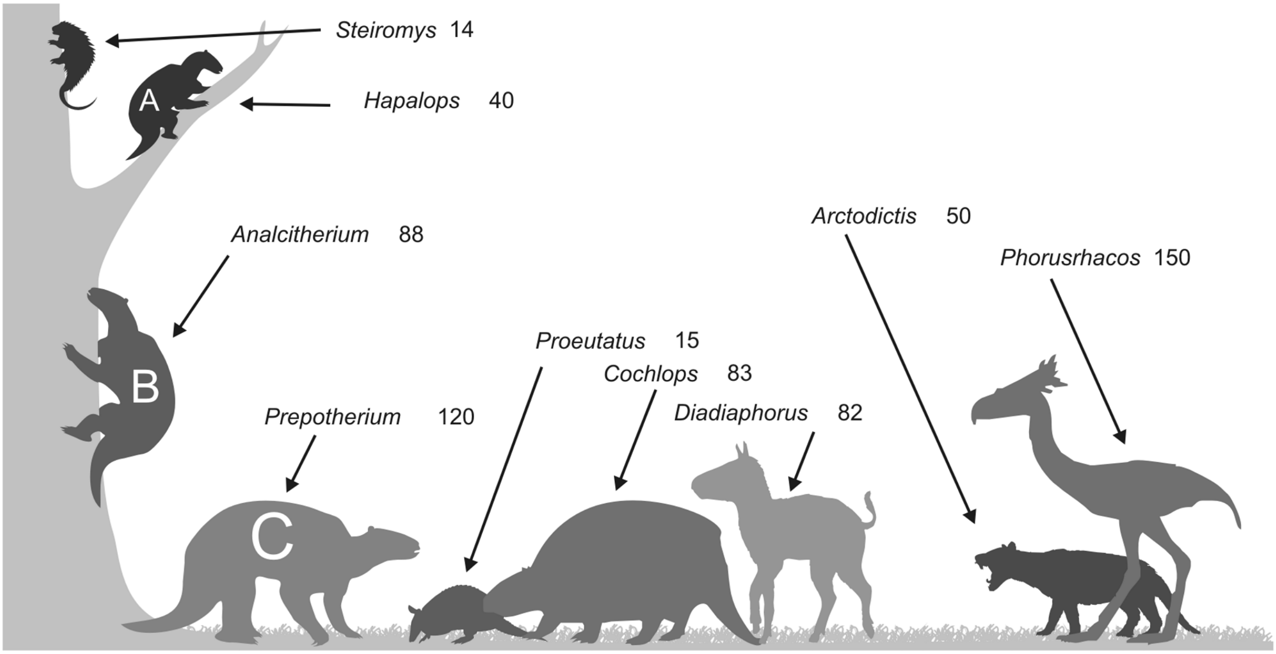


Figure 18. Schematic illustration of the proposed paleosynecological relationships of Santacrucian sloths (paleoautecological groups A, B and C) with other coeval taxa, including potential predators. Body sizes depicted in kg.

the largest sparassodonts could have been their predators seems reasonably probable. Among these carnivorous marsupials, *Prothylacynus* were semiarboreal animals weighing about 32 kg. In contrast, the heavier *Borhyaena* and *Arctodictis* (Fig. 18) were terrestrial animals weighing about 36 kg and 50 kg respectively (Prevosti *et al.*, 2012). Consequently, they may only have been predators of the sloths in groups B and C. However, taking into account the robustness, muscular power and well-developed ungual phalanxes of Santacrucian sloths, it is not improbable that they were hard-to-kill animals (at least the adults). Putative defensive behaviors similar to those of living anteaters (Taylor, 1978; Nowak, 1999) may have further increased the level of difficulty for a predator to easily take down an adult Santacrucian sloth. Note that, in addition to digging for food and climbing, a hypothetical defensive biological role for the forelimbs is suggested here. In this sense, it seems probable that the carnivorous marsupials preyed only occasionally on adult Santacrucian sloths and focused more on juvenile or weakened individuals, both on the ground or in trees.

Vizcaíno *et al.* (2010) adhered to an approach based on the analysis of body size, diet and basal metabolic rate to develop a reconstruction of the structure of the Santacrucian mammal assemblage. Several ecologically relevant parameters such as population density, biomass, metabolic rate, and both primary and secondary productivity, were therein calculated. Resulting data revealed that secondary productivity surpassed the estimated resource requirements of the carnivorous mammalian guild. Similar results led Croft (2001) to propose that depauperate carnivore paleoguilds were characteristic of South American Cenozoic communities prior to the Great American Biotic Interchange. However, as discussed by Prevosti and Vizcaíno (2006) in their analysis of the Pleistocene carnivorous paleoguild and by Kay *et al.* (2012b) for the Santacrucian community, several factors could be affecting carnivore density at local levels; more specifically, the presence of competitors (*e.g.*, carnivorous birds such as Phorusrhacidae), among others.

It is plausible that other potential predators of Santacrucian sloths were phorusrhacoid birds (terror-birds, Fig. 18). This extinct group included several genera of active, fast, terrestrial and carnivorous birds. One of the largest genera, *Phorusrhacos*, is estimated to have weighed about 150 kg and reached 2.5 m high when upright (Degrange *et al.*, 2012). This animal could have hunted and consumed Santacrucian sloths using its tall stature and speed to avoid defensive behaviors.

At this point, it should be noted that, nowadays, there is no community of mammals including an arboreal herbivore guild with such a diversity of large-bodied forms. Although in Africa and Oceania there are arboreal and semiarboreal large-bodied primates (*Gorilla* adult males over 150 kg, *Pan* between 30 and 60 kg and *Pongo* around 90 kg, Nowak, 1999), in general, they are not sympatric. In other forested regions of the world, there are ursids (*Tremarctos ornatus* or spectacled bear around 120 kg, Nowak, 1999) presenting well-developed climbing abilities yet, again, without diversity comparable to that of Santacrucian sloths.

As pointed out by Vizcaíno *et al.* (2010, 2012a), the Santacrucian mammal assemblage includes a diversity of mammals presenting low basal metabolic rates (xenarthrans, marsupials and, very possibly, notoungulates and astrapotheres). Such fact hinders any straightforward or actualistic comparison to most of the extant mammal communities. The only extant communitiy of mammals comprising a majority of taxa with low basal metabolic rates is the Australian marsupial community, which hence becomes the only one that can be proposed as a potential analogue community (see Vizcaíno *et al.*, 2010). Australian arboreal marsupials include a great diversity of taxa ranging from minute animals such as the frugivorous and nectarivorous possums, up to taxa weighing about 10 kg such as the tree kangaroo *Dendrolagus* (frugivorous and folivorous; Smith and Ganzhorn, 1996) and the koala *Phascolarctos cinereus* (folivorous; Smith and Garzhorn, 1996). The koala, a robust animal, exhibits striking similarities with Santacrucian sloths concerning not only limb proportions but also other general features of the postcranial skeleton. Furthermore, the koala's style of arboreal locomotion, *i.e.*, the use of claws, apposition of the hands and feet on each side of the support, slow and careful movements, and "trunk-hugging" (Smith and Garzhorn, 1996; Nowak, 1999; Toon and Toon, 2004), can be considered fairly akin to that reconstructed for the smaller Santacrucian sloths (see Toledo *et al.*, 2012, 2015).

As Vizcaíno (2014) discussed, in the absence of clear actual modern analogues, restrictive actualistic approaches cannot be applied directly (for instance, as proposed by

Andrews *et al.* (1979) prediction of community structure directly drawn from modern communities). Consequently, the heuristic value of the comparison of extinct organisms to other reconstructed extinct beings (whatever their reconstructed organismical level could be) cannot be overlooked (see Vizcaíno *et al.*, 2004, 2008). In this sense, in the past there were communities including arboreal guilds with large-bodied herbivorous mammals. These include the large arboreal Miocene diprotodontids of Australia (Black *et al.*, 2012b). The genus *Nimbadon* (50–70 kg; Black *et al.*, 2012b) was an arboreal-scansorial herbivore that inhabited the middle Miocene (Woodhead *et al.*, 2014) rainforests of northern Australia. Other inhabitants of such community included a diversity of smaller arboreal marsupials such as the ringtail and brushtail possums, a fossil koala (Black *et al.*, 2014a) and other taxa considered indicators of closed forest habitats like bandicoots (Travouillon *et al.*, 2014), primitive galloping kangaroos (Black *et al.*, 2014b), hipposiderid bats and fox-sized thylacinids (see also Archer *et al.*, 1999, 2006; Black *et al.*, 2012a). Miocene Australian carnivorous marsupial diversity has been proposed to be equal or greater than that of Santacrucian taxa (Wroe and Muirhead, 1999). Predators of arboreal diprotodontids could include thylacoleonids (*Wakaleo*, with a size in between a dog and a leopard, and *Priscileo*, of the size of a cat; Gillespie, 1999; Gillespie *et al.*, 2014) and thylacinids (*Maximucinus*, of about 18 kg; Wroe, 2001). As discussed by White (1993) and Toledo *et al.* (2014), the Pleistocene giant-lemurs of Madagascar also constitute an assemblage of heavy-sized climbing herbivorous mammals including arboreal and semiarboreal forms (see Jungers *et al.*, 2002) equivalent to Santacrucian sloths in body size. Among the potential predators of these heavy-sized lemurs, were crocodiles (such as *Voay robustus,* a crocodile weighing about 170 kg, see Burness *et al.*, 2001), and later immigrants such as felids, canids and humans.

The scarcity of available data does not allow a closer comparison between these fossil faunas. While it is beyond the scope of the present work to perform a detailed and comparative paleoecological study comparing the Santacrucian assemblage with its counterparts in the Miocene of Australia and Pleistocene of Madagascar, it is clear that arboreal heavy-sized herbivore paleoguilds, although missing today, were present in past communities. Future collaborative efforts to compare the Santacrucian sloth fauna with these other faunas should be enlightening in terms of understanding this now extinct guild.

The results obtained herein, together with those provided by other works, have demonstrated the reliability of the methodological approaches used to develop quite solid hypotheses about performance and faculties and, hence, to interpret the putative fundamental niche of an organism, defined as its potential maximal spatial and trophic resource use. As Wainwright (1994) and Plotnick and Baumiller (2000) claimed, functional morphology and biomechanics are capable of producing robust and testable inferences about function, performance and resource use for fossil and living organisms. Although their inferences on spatial resource use (substrate preference) were not as detailed and heuristic as hypotheses developed through functional approaches, applied ecomorphological methods have resulted in coherent findings. In this sense, Santacrucian sloths frequently represented a unique morphospace, therefore hindering straightforward inference of ecological traits based on the extant sample. Quoting Reilly and Wainwright (1994, p. 345), there are times in which "morphology predicts ecology better than ecology predicts morphology". Besides that, it is clear that the more diverse the methodologies applied are, the more robust and integrative the resulting hypotheses will be. Finally, integration of knowledge of coeval flora and fauna has also proven useful for developing reconstructions of a taxon's realized niche according to prior clearly-delimited definitions.

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Appendix A – Santacrucian sloths studied in this work.

Taxon	***Code***	***Family***	***Museum***	***coll. #***
Folivora indet.	*Fol*	*Folivora indet.*	*MPM-PV*	*3458*
Folivora indet.	*Fol*	*Folivora indet.*	*MPM-PV*	*3454*
Folivora indet.	*Fol*	*Folivora indet.*	*MPM-PV*	*3462*
Eucholoeops ingens	*Euc*	*Megalonychidae*	*FMNH*	*13280*
Eucholoeops *sp.*	*Euc*	*Megalonychidae*	*MPM-PV*	*3401*
Eucholoeops *sp.*	*Euc*	*Megalonychidae*	*MPM-PV*	*3402*
Eucholoeops *sp.*	*Euc*	*Megalonychidae*	*MPM-PV*	*3403*
Eucholoeops *sp.*	*Euc*	*Megalonychidae*	*MPM-PV*	*3451*
Eucholoeops *sp.*	*Euc*	*Megalonychidae*	*MPM-PV*	*3651*
Megalonychidae indet.	*Meg*	*Megalonychidae*	*AMNH*	*9249*
Megalonychidae indet.	*Meg*	*Megalonychidae*	*AMNH*	*94754*
cf. **Prepotherium**	*Prep?*	*Megatheriidae*	*MPM-PV*	*3408*
Prepotherium potens	*Prep*	*Megatheriidae*	*YPM*	*15345*
Mylodontidae indet.	*Myl*	*Mylodontidae*	*MPM-PV*	*3406*
cf. **Hapalops**	*Hap*	*stem Megatherioidea*	*MPM-PV*	*3404*
Analcimorphus giganteus	*AnaM*	*stem Megatherioidea*	*YPM*	*15561*
Schismotherium fractum	*Schi*	*stem Megatherioidea*	*FMNH*	*13137*
Hapalops rectangularis	*Hap*	*stem Megatherioidea*	*FMNH*	*13143*
Hapalops angustipalatus	*Hap*	*stem Megatherioidea*	*YPM*	*15562*
Hapalops elongatus	*Hap*	*stem Megatherioidea*	*FMNH*	*13123*
Hapalops elongatus	*Hap*	*stem Megatherioidea*	*FMNH*	*13133*
Hapalops elongatus	*Hap*	*stem Megatherioidea*	*YPM*	*15155*
Hapalops indifferens	*Hap*	*stem Megatherioidea*	*YPM*	*15110*
Hapalops longiceps	*HapLo*	*stem Megatherioidea*	*YPM*	*15523*
Hapalops platycephalus	*Hap*	*stem Megatherioidea*	*YPM*	*15536*
Hapalops platycephalus	*Hap*	*stem Megatherioidea*	*YPM*	*15564*
Hapalops rectangularis	*Hap*	*stem Megatherioidea*	*AMNH*	*9222*
Hapalops ruetimeyeri	*Hap*	*stem Megatherioidea*	*FMNH*	*13128*
Hapalops ruetimeyeri	*Hap*	*stem Megatherioidea*	*FMNH*	*13130*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*MPM-PV*	*3400*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*MPM-PV*	*3412*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*MPM-PV*	*3467*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*AMNH*	*9252*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15005*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15045*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*FMNH*	*15103*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15160*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15183*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15264*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15414*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15520*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15535*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15597*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15618*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15677*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*YPM*	*15836*
Hapalops *sp.*	*Hap*	*stem Megatherioidea*	*MLP*	*34-III-5-1*
Analcitherium*? sp.*	*AnaT*	*Mylodontidae*	*FMNH*	*13131*
Nematherium angulatum	*Nem*	*Mylodontidae*	*FMNH*	*13129*
Nematherium *sp.*	*Nem*	*Mylodontidae*	*YPM*	*15374*
Nematherium *sp.*	*Nem*	*Mylodontidae*	*YPM*	*15893*

Appendix B – Modern taxa considered in this study.

	Taxon	*Code*	*Catalogue number*	*Substrate preference*	*Substrate use-locomotor mode*
XENARTHRA					
Bradypodidae	**Bradypus** *sp.*	*Bra*	*AMNH 42454; 42838; 74136; 74137; 97315; 133437; 135474; 209940; 211663; 261304*	*arboreal*	*slow-climber*
Megalonychidae	**Choloepus** *sp.*	*Cho*	*AMNH 16873; 35483; 70440; 90269; 139772; 139773; 209941; 265952*	*arboreal*	*slow-climber*
Myrmecophagidae	**Myrmecophaga** *sp.*	*Myr*	*AMNH 1020; 100068; 100139; FMNH 15966*	*ground-dwelling*	*ambulatory-digger*
Myrmecophagidae	**Tamandua** *sp.*	*Tam*	*AMNH 23432; 23436; 23437; 23565; 23567; 96258; 211659; 21660*	*semi-arboreal*	*scansorial-digger*
Cyclopidae	**Cyclopes** *sp.*	*Cyc*	*AMNH 4780; 167845; 171297; 204662; 213188; FMNH 61853*	*arboreal*	*slow-climber-digger*
Dasypodidae	**Priodontes** *sp.*	*Prio*	*AMNH 130387; 208104; FMNH 25271; 72913*	*ground-dwelling*	*ambulatory-digger*
CARNIVORA					
Ailuridae	**Ailurus** *sp.*	*AilU*	*AMNH 35433; 119474; 146682; 146778; 185346*	*arboreal*	*slow-climber*
Felidae	**Panthera** *sp.*	*Pan*	*AMNH 85396; 113743; 113744; 113748; 135846*	*ground-dwelling*	*cursorial*
Felidae	**Acynonyx** *sp.*	*Acy*	*AMNH 36426; 119654; 119655; 119656; 119657*	*ground-dwelling*	*cursorial*
Mustelidae	**Gulo** *sp.*	*Gu*	*AMNH 35054; 35081; 149692; 165766*	*ground-dwelling*	*ambulatory*
Ursidae	**Ailuropoda** *sp.*	*AilP*	*AMNH 87242; 89028; 110453; 110454; 147746*	*ground-dwelling*	*ambulatory*
Viverridae	**Arctictis** *sp.*	*Arct*	*AMNH 181; 22906; 35469; 80163; 119600*	*arboreal*	*slow-climber*
MARSUPIALIA					
Dasyuridae	**Sarcophilus** *sp.*	*Sar*	*AMNH 65670; 65672; 65673; 70406; 150211*	*ground-dwelling*	*ambulatory*
Thylacinidae	**Thylacinus** *sp.*	*Thy*	*AMNH 35244; 35504; 35866; 42259*	*ground-dwelling*	*cursorial*
Phascolarctidae	**Phascolarctos** *sp.*	*Phas*	*AMNH 65607; 65608; 65609; 65610; 107805*	*arboreal*	*slow-climber*
Vombatidae	**Vombatus** *sp.*	*Vom*	*AMNH 42997; 65619; 65622; 70209; 146850*	*ground-dwelling*	*ambulatory-digger*
PHOLIDOTA					
Manidae	**Manis gigantea**	*ManG*	*AMNH 53847; 53851; 53857; 53858*	*ground-dwelling*	*ambulatory-digger*
Manidae	**Manis pentadactyla**	*ManP*	*AMNH 60004; 60006; 60007; 172147; 184959*	*arboreal*	*slow-climber-digger*
PRIMATES					
Cercopithecidae	**Papio** *sp.*	*Pap*	*AMNH 80771; 80774; 120388; 216247; 216251*	*semi-arboreal*	*scansorial*
Hominidae	**Gorilla** *sp.*	*Go*	*AMNH 54089; 54090; 54091; 54092*	*semi-arboreal*	*scansorial*
Hylobatidae	**Hylobates** *sp.*	*Hyl*	*AMNH 90268; 102463; 106581; 106584*	*arboreal*	*fast-climber*
Lemuridae	**Lemur** *sp.*	*Lem*	*AMNH 22912; 35396; 150039; 170739; 170740*	*arboreal*	*fast-climber*
RODENTIA					
Erethizontidae	**Coendou** *sp.*	*Coe*	*AMNH 80045; 100097; 100119; 134073; 212611*	*arboreal*	*slow-climber*
Hystricidae	**Hystrix** *sp.*	*Hys*	*AMNH 51735; 87220; 87222; 119506*	*ground-dwelling*	*ambulatory*
Sciuridae	**Marmota** *sp.*	*Mar*	*AMNH 70338; 97386; 179934; 180314; 235648*	*ground-dwelling*	*ambulatory-digger*
TUBULIDENTATA					
Orycteropodidae	**Orycteropus** *sp.*	*Oryc*	*AMNH 51370; 51374; 51905; 51909; 65540*	*ground-dwelling*	*ambulatory-digger*

Appendix C – Measurements utilized in this study.

	Element	***Measurement***	***Abbreviation***
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*	*Transverse Diameter of Humerus - at midshaft*	*TDH*
5		*Humerus Length - between head and trochlea*	*HL*
6		*Antero-Posterior Diameter of Humerus - at midshaft*	*APDH*
7		*Humerus Head Length*	*HHL*
8		*Humerus Distal Articular Surface Width*	*HDASW*
9		*Humeral Distal Epiphysis Width*	*HDEW*
10	*Ulna*	*Ulnar Length*	*UL*
11		*Transverse Height of Ulna - at midshaft*	*THU*
12		*Olecranon - Trochlea notch length*	*OTL*
13		*Ulnar Trochlear Notch Length*	*UTNL*
14		*Transverse Diameter of Ulna - at midshaft*	*TDU*
15	*Radius*	*Radius Length*	*RL*
16		*Radius Diameter - at midshaft*	*RD*
17		*Radial Distal Facet Length*	*RDFL*
18		*Radial Head Length*	*RHL*
19		*Radial Head Width*	*RHW*
20		*Radial Distal Epiphysis Width*	*RDEW*
21	*Pelvis*	*Pelvis total Length*	*PL*
22		*Ilium Length- to acetabulum anterior-most border*	*ILL*
23		*Ischium Length - from acetabulum to posterior-most border*	*ISL*
24	*Femur*	*Transverse Diameter of Femur - at midshaft*	*TDF*
25		*Femoral Head Width*	*FHW*
26		*Inter trochanteric Width*	*IttW*
27		*Femoral Length - between head and medial condyle*	*FL*
28		*Antero-Posterior Diameter of Femur - at midshaft*	*APDF*
29		*Femoral Head Length*	*FHL*
30		*Femoral Distal Epiphysis Width*	*FDEW*
31		*Lateral Condyle Length*	*LCL*
32		*Medial Condyle Length*	*MCL*
33		*Patellar Groove Width*	*PGW*
34	*Tibia*	*Tibial Length- from interfacet eminence to tibial malleolus*	*TL*
35		*Transverse Diameter of Tibia - at midshaft*	*TDT*
36		*Tibial Proximal Epiphysis Length*	*TPEL*
37		*Antero-Posterior Diameter of Tibia - at midshaft*	*APDT*
38		*Tibial Proximal Epiphysis Width*	*TPEW*
39	*Astragalus*	*Astragalar Trochlear Maximum Width*	*ATMW*
40		*Astragalar Length- from head to posterior-most border*	*AL*
41		*Astragalar Ectal Facet Length*	*AEFL*
42		*Astragalar Medial Facet Length*	*AMFL*
43		*Astragalar Head Width*	*AHW*
44	*Calcaneum*	*Calcaneum total Length*	*CL*
45		*Functional Calcaneum Length- from ectal facet to tuber*	*FCL*
46		*Calcaneum maximum Tuber Width*	*CTW*

Appendix D – Contribution of each variable to PCs and variance proportion of each axis.

Scapula	***PC1***	***PC2***
log(SL)	*0.5815648*	*0.705503209*
log(SGL)	*0.5722274*	*-0.708658468*
log(SGW)	*0.5782199*	*-0.008270289*
Proportion of Variance	*0.9656027*	*0.0343973*
Cumulative Proportion	*0.9656027*	*1.0*
Humerus	***PC1***	***PC2***
log(TDH)	*-0.4270646*	*-0.60422560*
log(HL)	*-0.3880154*	*0.72289055*
log(APDH)	*-0.4321446*	*-0.10259644*
log(HHL)	*-0.3807809*	*0.18912212*
log(HDASW)	*-0.4265277*	*0.09990082*
log(HDEW)	*-0.3916515*	*-0.23678533*
Proportion of Variance	*0.8710027*	*0.08552527*
Cumulative Proportion	*0.8710027*	*0.95652801*
Ulna	***PC1***	***PC2***
log(THU)	*-0.5131158*	*-0.03204818*
log(OTL)	*-0.5430240*	*0.77780859*
log(UTNL)	*-0.3946055*	*-0.47930297*
log(TDU)	*-0.5349052*	*-0.40528431*
Proportion of Variance	*0.9148825*	*0.05187334*
Cumulative Proportion	*0.9148825*	*0.96675581*
Radius	***PC1***	***PC2***
log(RL)	*-0.4272130*	*0.86394390*
log(RD)	*-0.4337040*	*-0.30512476*
log(RDFL)	*-0.4168392*	*-0.21991343*
log(RHL)	*-0.3864950*	*-0.21173759*
log(RHW)	*-0.4064789*	*0.07409757*
log(RDEW)	*-0.3755416*	*-0.24862551*
Proportion of Variance	*0.8676865*	*0.08929278*
Cumulative Proportion	*0.8676865*	*0.95697929*
Pelvis	***PC1***	***PC2***
log(PL)	*0.5471821*	*-0.2315210*
log(ILL)	*0.5160926*	*-0.6632471*
log(ISL)	*0.6589691*	*0.7116890*
Proportion of Variance	*0.9564389*	*0.0435611*
Cumulative Proportion	*0.9564389*	*1.0*
Femur	***PC1***	***PC2***
log(TDF)	*-0.3535630*	*-0.67509969*
log(FHW)	*-0.2933961*	*-0.12816594*
log(IttW)	*-0.3332622*	*-0.08917511*
log(FL)	*-0.2739573*	*0.55883311*
log(APDF)	*-0.3090455*	*0.12528955*

Appendix D – Continuation.

log(FHL)	*-0.2860498*	*-0.01797047*
log(FDEW)	*-0.3199298*	*-0.10549061*
log(LCL)	*-0.3228115*	*0.36217080*
log(MCL)	*-0.3483587*	*0.19643062*
log(PGW)	*-0.3123234*	*-0.10327584*
Proportion of Variance	*0.9270479*	*0.03689337*
Cumulative Proportion	*0.9270479*	*0.96394122*
Tibia	***PC1***	***PC2***
log(TL)	*-0.4074091*	*0.9110595*
log(TPEL)	*-0.5351434*	*-0.1868118*
log(APDT)	*-0.5431847*	*-0.2877981*
log(TPEW)	*-0.5025830*	*-0.2285698*
Proportion of Variance	*0.9434876*	*0.03536247*
Cumulative Proportion	*0.9434876*	*0.97885005*
Astragalus	***PC1***	***PC2***
log(ATMW)	*-0.4349626*	*-0.66478448*
log(AL)	*-0.4359956*	*0.22690799*
log(AEFL)	*-0.4403537*	*-0.02370332*
log(AMFL)	*-0.4681367*	*0.66763253*
log(AHW)	*-0.4556885*	*-0.24551847*
Proportion of Variance	*0.9209805*	*0.04973715*
Cumulative Proportion	*0.9209805*	*0.97071761*
Calcaneum	***PC1***	***PC2***
log(CL)	*-0.5384013*	*-0.5331399*
log(FCL)	*-0.5629003*	*-0.3487772*
log(CTW)	*-0.6271103*	*0.7707894*
Proportion of Variance	*0.9429516*	*0.0570484*
Cumulative Proportion	*0.9429516*	*1.0*

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