

Muscular Reconstruction and Functional Morphology of the Hind Limb of Santacrucian (Early Miocene) Sloths (*Xenarthra*, *Folivora*) of Patagonia

NÉSTOR TOLEDO,^{1,2*} M. SUSANA BARGO,^{1,3} AND SERGIO F. VIZCAÍNO^{1,2}

¹División Paleontología de Vertebrados, Unidades de Investigación Anexo Museo FCNyM-UNLP, A. 60 y 122, 1900, La Plata, Buenos Aires, Argentina

²CONICET—Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

³CIC—Comisión de Investigaciones Científicas, Provincia de Buenos Aires, Argentina

ABSTRACT

This article presents a morphofunctional analysis of the hind limb of Santacrucian (Early Miocene) sloths from southernmost Patagonia (Argentina). These fossil sloths were mid sized to large animals, ranging from 40 to 120 kg, and their postcranial skeleton was markedly different in shape compared with that of extant tree sloths, which vary from 2 to 10 kg. The functional anatomy of the hind limb of Santacrucian sloths was compared with that of living xenarthrans (tree sloths, anteaters, and armadillos), which involved reconstruction of the hind limb musculature and comparative and qualitative morphofunctional analyses, and hypotheses on the biological role of the hind limb in terms of preferences in substrate, posture, and strategies of locomotion were formulated. The hind limb of Santacrucian sloths bears strong resemblances to that of living South American anteaters in stoutness of skeletal elements, form of the characteristics related to muscular and ligamentous attachments, and conservative, pentadactylous strong-clawed pes. The musculature was very well developed, allowing powerful forces, principally in entire limb adduction, crus flexion and extension, pes extension, and toe prehension. These functional features, together with those of the forelimb, are congruent with climbing behavior, and support the hypothesis that Santacrucian sloths were good but slow climbing mammals. However, their climbing strategies were limited, owing principally to their comparatively large body size, and they relied to a large extent on their powerful musculature and curved manual and pedal unguals for both moving and standing on the arboreal supports. *Anat Rec*, 298:842–864, 2015. © 2015 Wiley Periodicals, Inc.

Key words: paleoecology; Santa Cruz Formation; climbing; substrate use; substrate preferences

Grant sponsor: National Science Foundation; Grant numbers: 0851272, 0824546, PIP-CONICET 1054, PICT 2008-0143, PICT 2013-0389, PICT 2013-0386, UNLP N647 and N750.

*Correspondence to: N. Toledo; División Paleontología Vertebrados, Unidades de Investigación Anexo Museo FCNyM-UNLP, Av. 60 y 122, 1900, La Plata, Argentina.
E-mail: ntoledo@fcnym.unlp.edu.ar

Received 5 March 2014; Revised 26 June 2014; Accepted 13 November 2014.

DOI 10.1002/ar.23114

Published online 23 January 2015 in Wiley Online Library (wileyonlinelibrary.com).

This article is our second contribution to the functional morphology of the postcranial skeleton of fossil sloths of Santacrucian Age (Early Miocene) from southernmost Patagonia (Argentina). A functional analysis of the forelimb was performed by Toledo *et al.* (2013) and a similar study is presented here for the hind limb.

Sloths, together with anteaters, belong to Pilosa (Fig. 1), one of the two major groups of the Xenarthra; the other is represented by Cingulata (armadillos, pampatheres, and glyptodonts; Delsuc and Douzery, 2008; Gaudin and McDonald, 2008). Extant anteaters (Vermilingua) include three genera: the completely arboreal silky anteater *Cyclopes* (~0.5 kg), the semi-arboreal *Tamandua* (~5 kg) and the ground-dwelling giant anteater *Myrmecophaga* (~35 kg) (Nowak, 1999). The fossil record of vermilinguans is extremely scarce (McDonald and De Iuliis, 2008). The sloths (Folivora) are represented by two extant genera (ranging from ~2 to 10 kg; Nowak, 1999), mainly folivorous, and arboreal: *Choloepus* (two-toed sloth) and *Bradypus* (three-toed sloth), both denizens of tropical forests (Chiarello, 2008). Conversely, the fossil record of sloths is astonishingly abundant, principally in the South American Early Miocene and both the North and South American Pleistocene.

The sloths studied here are from the Santa Cruz Formation (Early Miocene) that crops out along the southern Atlantic coast of continental Patagonia and has been dated as approximately between 18 and 16 Ma (Perkins *et al.*, 2012). This sedimentary unit bears an assemblage of noticeably well-preserved fossil vertebrates of a wide size range from a few grams to about a ton, including marsupials, xenarthrans (armadillos, glyptodonts, anteaters in addition to the sloths), notoungulates, litopterns, astrapotheres (the largest vertebrates), rodents, primates, lizards, frogs, and birds (Vizcaíno *et al.*, 2012).

As in Toledo *et al.* (2013), sloths from the Santa Cruz Formation are referred as “Santacrucian sloths”. This expression does not have significance in terms of ecology or systematics, as is the case for other such generalized, often encountered terms (e.g., living sloths; ground sloths). Santacrucian sloths include the mylodontids *Nematherium* and *Analcitherium* and several megatherioids (Figs. 1–3), including the basal *Hapalops*, *Analcimorphus*, *Schismotherium*, *Hyperleptus* and *Pelecycodon*, *Planops* and *Prepothierium* (Megatheriidae), and *Eucholoeops* and *Megalonychotherium* (Megalonychidae). Nothrotheriids are not known from Santacrucian deposits. For this work we followed Gaudin’s (2004) phylogenetic hypothesis (Fig. 1).

As proposed by different authors, integrative paleobiological and paleoecological studies on mammals should characterize all taxa of a community through three aspects of ecological importance: body mass, diet, and substrate preference, including posture and locomotor strategies (Andrews *et al.*, 1979; Van Couvering, 1980; Kay and Madden, 1997; Reed, 1998; Vizcaíno *et al.*, 2006; Vizcaíno *et al.*, 2008; Vizcaíno *et al.*, 2010; Kay *et al.*, 2012). Toledo *et al.* (2014) proposed that the diversity of Santacrucian sloths encompassed small to medium-sized forms (mean values: 38 kg for *Hapalops*, 44 kg for *Schismotherium*, 66 kg for *Analcimorphus* and 77 kg for *Eucholoeops*) as well as large forms (~90 kg *Nematherium* and *Analcitherium* and 120 kg for *Prepothierium*). White’s (1993b) work produced similar estimates. Results of the efforts of Bargo *et al.* (2009, 2012) on the masticatory apparatus morphology of

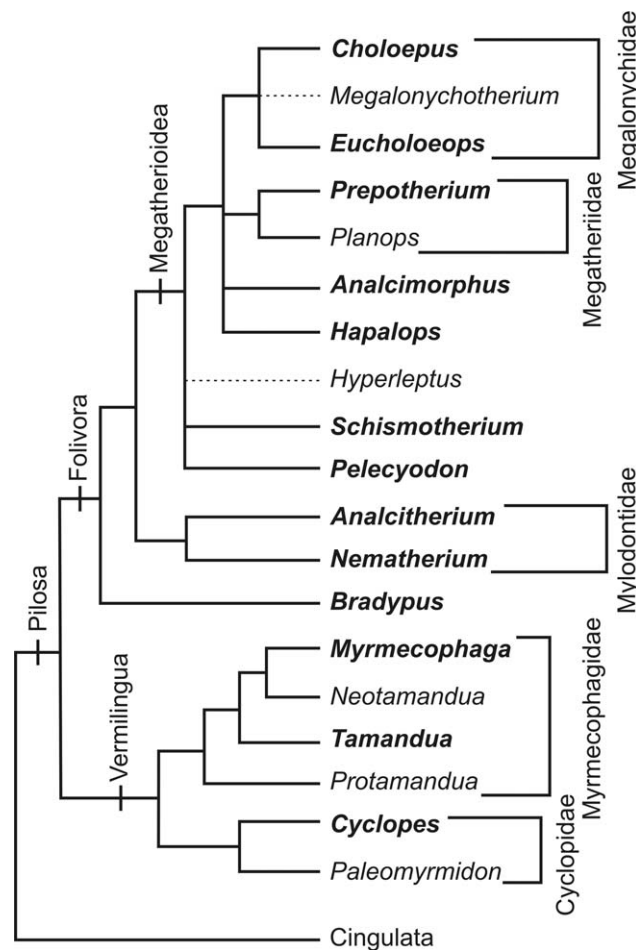


Fig. 1. Cladogram showing phylogenetic relationships among xenarthrans included in this work. Modified from Gaudin (2004). Pilosan taxa considered here are bolded.

Santacrucian sloths characterized megatherioids as mainly folivores, whereas mylodontids were considered to have probably been capable of acquiring other fibrous items (e.g., tubers, fruits).

In relation to substrate preference and locomotion, White’s (1993a,b, 1997) comprehensive morphometric studies on limb function in these sloths employed several functional indices of the extremities in discriminating among modes of locomotion. According to this author, several Santacrucian genera were apparently capable of arboreality or semiarboreality (*Hapalops*, *Eucholoeops*, *Pelecycodon*, *Schismotherium*, and *Analcimorphus*), while *Nematherium* and *Prepothierium* tended to be ground-dwellers, and none of them were suspensory, in contrast to extant tree sloths (White, 1997). A preliminary morpho-functional study of qualitative and quantitative aspects of the skeleton by Bargo *et al.* (2012) and a morphometric analysis of the forelimb by Toledo *et al.* (2012) produced similar results. Finally, Toledo *et al.* (2013) performed a detailed qualitative morphofunctional study of the forelimb, involving soft tissue reconstruction, proposing that the forelimb of these forms was well suited for climbing behavior, while also allowing digging capabilities. This contribution offers a similar analysis for the hind limb, as

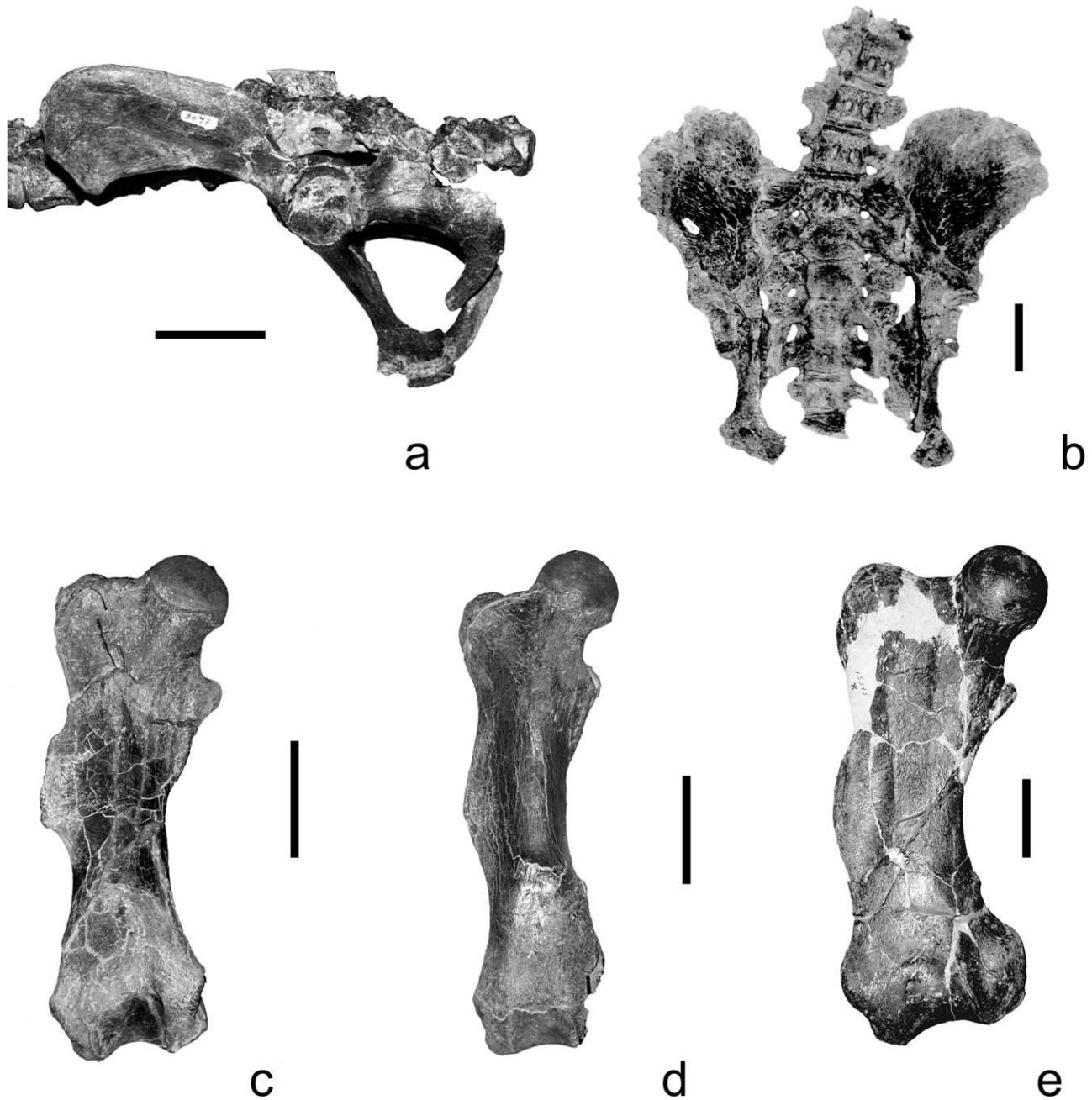


Fig. 2. Santacrucian sloth hind limb elements. a, *Hapalops* sp. MPM-PV 3467, pelvic girdle in left lateral view; b, *Eucholoeops* cf. *E. fronto*. MPM-PV 3403, pelvic girdle in ventral view; c, *Hapalops* sp. MPM-PV 3467, right femur, anterior view; d, *Eucholoeops* cf. *E. fronto*. MPM-PV 3403, right femur, anterior view; e, *Prepotherium potens* YPM-VPPU 15345, right femur, anterior view. Scale bar = 5 cm.

well as a comprehensive discussion on several paleoecological attributes of the Santacrucian sloths.

In paleontology, the biology of extinct forms cannot be observed as in extant animals, so it is usually reconstructed from the form (shape and size) of preserved body parts, such as bones and teeth. As remarked by Toledo *et al.* (2013), the investigation of causality between form and biology requires consideration of function and its relationship with form. Only after that, the

relationship between function and the biology of the organism can be considered. The inference of function from form was formalized by Radinsky (1987) as the “form-function paradigm”. To study these relationships, we adhere to the theoretical formalizations defined by Bock and Von Wahlert (1965) and Plotnick and Baumiller (2000): function is what a feature does; faculty is the form-function complex, defined as what a function (or the suite of functions) is able to perform in the life of

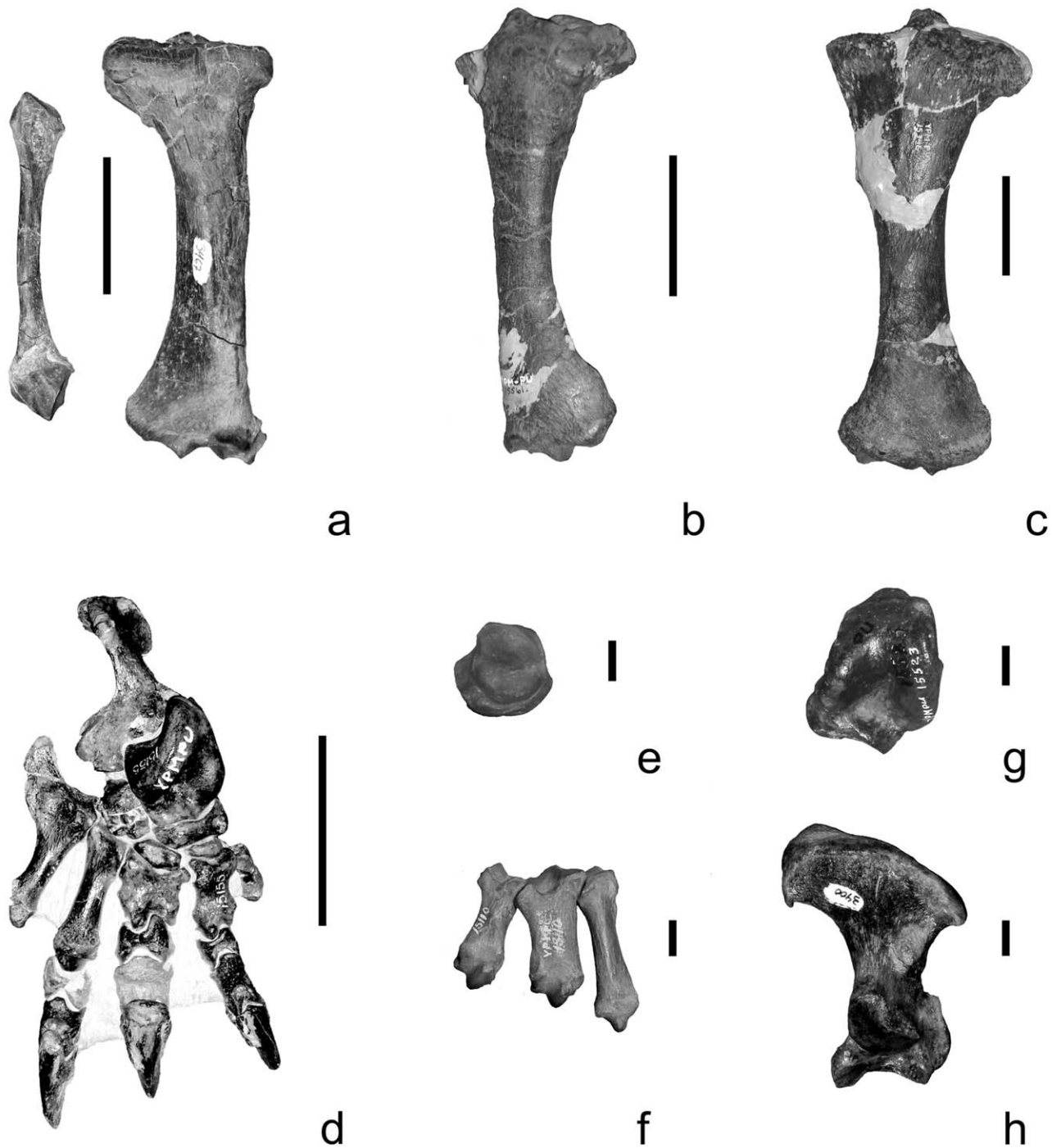


Fig. 3. Santacrucian sloth hind limb elements. a, *Hapalops* sp. MPM-PV 3467, right tibia, and fibula in anterior view; b, *Analcimorphus giganteus* YPM-VPPU 15561, left tibia, anterior view; c, *Prepothierium potens* YPM-VPPU 15345, left tibia, anterior view; d, *Hapalops elongatus* YPM-VPPU 15155, right pes, dorsal view; e,

Hapalops indifferens YPM-VPPU 15110, right navicular, proximal view; f, *Hapalops indifferens* YPM-VPPU 15110 metatarsals II to IV, dorsal view; g, *Hapalops longiceps* YPM-VPPU 15523 left astragalus, dorsal view; h, *Hapalops* sp. MPM-PV 3400 left calcaneus, dorsal view. Scale bar = 5 cm.

the organism, and biological role describes the use of the faculty (form-function complex) in the organism's environment. A single function can be involved in different faculties and perform several biological roles and vice versa. Hypothesis on the biological role has to be devel-

oped in the context of approaches based on present information. Hence, inference of biological role for a hypothesized particular function of a fossil organism must be made from the knowledge about the relation between function and biology in extant organisms.

TABLE 1. Santacrucian Sloths Studied in This Work

Family	Taxon	Collection number
Folivora	Folivora indet.	AMNH 9537
	Folivora indet.	MPM-PV 3454
	Folivora indet.	MPM-PV 3458
Megalonychidae	Megalonychidae indet.	AMNH 9227
	Megalonychidae indet.	AMNH 9237
	Megalonychidae indet.	AMNH 9249
	Megalonychidae indet.	AMNH 9279
	Megalonychidae indet.	AMNH 9305
	Megalonychidae indet.	AMNH 9518
	Megalonychidae indet.	AMNH 94749
	Megalonychidae indet.	AMNH 140824
	<i>Eucholoeops fronto</i>	AMNH 9241
	<i>Eucholoeops ingens</i>	FMNH 13125
	<i>Eucholoeops</i> cf. <i>fronto</i>	MPM-PV 3403
	<i>Eucholoeops</i> sp.	MPM-PV 3651
	<i>Eucholoeops</i> sp.	MPM-PV 3402
	Megatheriidae indet.	MPM-PV 3408
	<i>Prepootherium potens</i>	YPM-VPPU 15345
Megatheriidae	<i>Prepootherium potens</i>	YPM-VPPU 15568
	<i>Analcimorphus giganteus</i>	YPM-VPPU 15561
Basal megatherioids	<i>Analcimorphus</i> sp.	YPM-VPPU 15192
	<i>Hapalops angustipalatus</i>	YPM-VPPU 15562
	<i>Hapalops elongatus</i>	FMNH 13123
	<i>Hapalops elongatus</i>	YPM-VPPU 15011
	<i>Hapalops elongatus</i>	YPM-VPPU 15155
	<i>Hapalops elongatus</i>	YPM-VPPU 15160
	<i>Hapalops elongatus</i>	YPM-VPPU 15545
	<i>Hapalops elongatus</i>	YPM-VPPU 15597
	<i>Hapalops gracilidens</i>	YPM-VPPU 15595
	<i>Hapalops indifferens</i>	YPM-VPPU 15110
	<i>Hapalops longiceps</i>	AMNH 9289
	<i>Hapalops longiceps</i>	YPM-VPPU 15523
	<i>Hapalops longipalatus</i>	FMNH 13146
	<i>Hapalops platycephalus</i>	YPM-VPPU 15536
	<i>Hapalops platycephalus</i>	YPM-VPPU 15564
	<i>Hapalops ponderosus</i>	YPM-VPPU 15034
	<i>Hapalops ponderosus</i>	YPM-VPPU 15520
	<i>Hapalops rectangularis</i>	AMNH 9222
	<i>Hapalops rectangularis</i>	FMNH 13143
	<i>Hapalops ruetimeyeri</i>	FMNH 13128
	<i>Hapalops ruetimeyeri</i>	FMNH 13130
	<i>Hapalops</i> sp.	AMNH 9252
	<i>Hapalops</i> sp.	MPM-PV 3462
	<i>Hapalops</i> sp.	AMNH 94752
	<i>Hapalops</i> sp.	FMNH 13211
	<i>Hapalops</i> sp.	MPM-PV 3400
	<i>Hapalops</i> sp.	MPM-PV 3404
	<i>Hapalops</i> sp.	MPM-PV 3467
	<i>Hapalops</i> sp.	YPM-VPPU 15045
	<i>Hapalops</i> sp.	YPM-VPPU 15112
	<i>Hapalops</i> sp.	YPM-VPPU 15129
	<i>Hapalops</i> sp.	YPM-VPPU 15173
	<i>Hapalops</i> sp.	YPM-VPPU 15184
	<i>Hapalops</i> sp.	YPM-VPPU 15259
	<i>Hapalops</i> sp.	YPM-VPPU 15313
	<i>Hapalops</i> sp.	YPM-VPPU 15347
	<i>Hapalops</i> sp.	YPM-VPPU 15355
	<i>Hapalops</i> sp.	YPM-VPPU 15376
	<i>Hapalops</i> sp.	YPM-VPPU 15515
	<i>Hapalops</i> sp.	YPM-VPPU 15527

TABLE 1. (continued).

Family	Taxon	Collection number
Mylodontidae	<i>Hapalops</i> sp.	YPM-VPPU 15594
	<i>Hapalops</i> sp.	YPM-VPPU 15600
	<i>Hapalops</i> sp.	YPM-VPPU 15617
	<i>Hapalops</i> sp.	YPM-VPPU 15628
	<i>Hapalops</i> sp.	YPM-VPPU 15836
	<i>Hapalops</i> sp.	YPM-VPPU 15890
	<i>Hapalops</i> sp.	YPM-VPPU 15913
	<i>Peleciodon arcuatus</i>	AMNH 9240
	<i>Peleciodon arcuatus</i>	FMNH 12062
	<i>Schismotherium fractum</i>	AMNH 9244
	<i>Schismotherium fractum</i>	FMNH 13137
	<i>Schismotherium fractum</i>	YPM-VPPU 15524
	<i>Mylodontidae</i> indet.	MPM-PV 3406
	<i>Nematherium angulatum</i>	FMNH 13129
	<i>Nematherium</i> sp.	FMNH 13258
	<i>Nematherium</i> sp.	YPM-VPPU 15965

The question about substrate preference (including locomotor behavior) of the Santacrucian sloths is in turn a question about function of the appendicular skeleton. Thus, this contribution is framed within the methodological context of functional morphology.

MATERIALS AND METHODS

Institutional Acronyms

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.

The fossil sloths analyzed comprise 76 specimens (Table 1), housed in the vertebrate paleontology collections of MLP, YPM-VPPU, AMNH and FMNH and new material collected by the MLP-Duke University joint expeditions during 2003–2012, that belongs to MPM-PV. Hind limb remains for *Planops*, *Megalonychotherium*, *Hyperleptus* and *Analcitherium* are not known, so this contribution treats only *Eucholoeops*, *Prepootherium*, *Hapalops*, *Analcimorphus*, *Peleciodon*, *Schismotherium*, and *Nematherium*, as well as several undetermined specimens of megalonychids, megatheriids and mylodontids. Osteological material of extant mammals studied is housed in the mammalogy collections of MLP, AMNH, and FMNH.

Following the anatomical framework provided by descriptions of fossil and extant Folivora (Ameghino, 1891; Scott, 1903–1904; Mendel, 1981; McDonald, 2003; McDonald and De Iuliis, 2008), we qualitatively described the hind limb skeleton of Santacrucian sloths. The analysis was carried out by visual observation and comparison with homologous elements of extant sloths (*Bradypus* and *Choloepus*), anteaters (*Myrmecophaga*, *Tamandua*, and *Cyclopes*) and armadillos (*Priodontes*,

Cabassous and *Chaetophractus* - see Appendix I). Anatomical background includes references on extant mammals (Lessertisseur and Saban, 1971; Polly, 2007; De Iuliis and Pulerá, 2010) and humans (Gray, 1918, revised edition of 2000). To avoid the abundance of anatomical terms and their redundancy, we follow the nomenclature of muscles and ligaments proposed by Mendel (1981) and De Iuliis and Pulerá (2010). In some instances, especially regarding tarsal articular facet terminology, we also refer to Szalay and Schrenk (1998). Among the terms related to muscle and ligament attachment sites, we use the term “enthesis” as defined by Mariotti *et al.* (2007): simple surface irregularities, or osteo-productive/erosive formations, both produced by the bone as a response to mechanical loads related to movements and exerted by tendons and/or ligaments.

Muscular reconstruction was performed by identifying their bony entheses in extant sloths, anteaters and armadillos, and analyzing fossil sloths by searching for homologous features. Preserved specimens for dissection are scarce (anteaters) or unavailable (extant sloths), and we have thus relied largely on muscular descriptions in the literature (Macalister, 1869; Humphry, 1869–1870; Macalister, 1875; Windle and Parsons, 1899; Jouffroy, 1971; Mendel, 1981). Appendix II offers a brief explanation of the muscles studied here. As explained for the forelimb (Toledo *et al.*, 2013), the degree of confidence in the muscular reconstruction decreased proximo-distally along the hind limb. Most entheses of the distal half of the zeugopodium correspond to ligaments. The same applies to most of the entheses recognized in the pes.

The reconstruction of muscles and ligaments of the appendicular apparatus allowed us to make qualitative inferences on mechanical capabilities of Santacrucian sloths (function). These hypotheses were based on previous works, mainly those dealing with extant xenarthrans (Mendel, 1981; Nyakatura, 2010), but also from other mammals such as tupaiids (Sargis, 2002), marsupials (Szalay and Sargis, 2001; Argot, 2002), and rodents (Candela and Picasso, 2008). The interface between function and biological role is the averaged biomechanical situation proposed by Oxnard (1984), which integrates functional information of each feature and element in a mechanical profile comprising the suite of functions that the structure can perform. Thus, in the present qualitative biomechanical analysis of the hind limb, functional inferences were formulated that allowed hypotheses on the biological and ecological significance of such functions (biological role).

RESULTS

Comparative Description of the Hind Limb Elements and Muscular Reconstruction

In this section, the hind limb elements of the Santacrucian sloths are described, with emphasis on functionally significant features (i.e., articular surfaces, entheses of tendons of muscles and ligaments), and compared with homologous bony elements of extant sloths, anteaters, and armadillos. Inferences on the presence and development of specific muscles and ligaments are also provided.

Pelvic Girdle - Pelvis

Pelves of Santacrucian sloths are poorly preserved and relatively scarce in collections. Most of them include only

the acetabular region, while the iliac wings and pubic symphysis are usually incomplete. The pelvis analyzed here are those of *Hapalops* (YPM-VPPU 15523, MPM-PV 3467), *Eucholoeops* (MPM-PV 3403), *Analcimorphus* (YPM-VPPU 15561) and *Schismotherium* (FMNH 13137) (Figs. 4 and 5). Unfortunately, no pelvis have been recorded for mylodonts. In overall morphology, the pelvis of Santacrucian sloths exhibits a combination of some features seen in extant sloths and anteaters. As in other xenarthrans (see McDonald, 2003), the pelvis is robustly fused to a synsacrum developed by inclusion of a variable number of caudal vertebrae into the sacral segment, as well as extensive synostosis between not only ilia and sacral vertebrae, but also between ischia and caudal vertebrae.

The ilium has flat and wide iliac wings, bearing on its very lateral border a rough entheses for the *m. sartorius* and/or the *tensor fasciae latae* tendon (Fig. 4). The margin of the iliac crest is more rounded in *Eucholoeops*, *Analcimorphus*, and *Schismotherium*, whereas it projects laterally and forms an angular margin in *Hapalops*, as in the giant anteater *Myrmecophaga*. The iliac wings accommodated very well-developed gluteal muscle groups. A strong tubercle for attachment of the origin of the *m. rectus femoris* tendon is located anterior to the acetabulum. The ischiatic bodies are robust, laterally inclined, and about one half of the length of the iliac spine (Fig. 4). The ischiatic tuberosity is robust and the origin site of the muscle group comprising the *mm. biceps femoris*, *semitendinosus*, and *semimembranosus* (hamstring group—Figs. 4 and 5). The *m. quadratus femoris* (a lateral rotator of the femur) arises also from this region, although its entheses is difficult to distinguish from that of the hamstring group. The ventral ischiatic branches are deflected anteriorly. The pubis is straight and posteriorly inclined, resembling that of the semiarboreal anteater *Tamandua* and the armadillo *Priodontes* in being of similar length to the ischiatic ventral branches. On its ventral surface, a well-marked crest adjacent to the border of the acetabulum corresponds to the origin entheses of *m. pectineus* (Figs. 4 and 5). The pelvic basin is piriform in ventral view, more so than in extant sloths (Fig. 5). The symphysis, relatively more robust and longer than that of extant sloths and the tiny anteater *Cyclopes*, is more similar to that of *Tamandua*. The acetabulum faces ventrally in *Analcimorphus* and *Eucholoeops*, while in *Hapalops* it is more laterally disposed, as in *Tamandua*, but not as much as in extant sloths. The acetabular notch (for the *teres femoris* ligament) extends posteriorly, being relatively wider than in extant sloths, but narrower than in *Tamandua* and *Myrmecophaga*. The relatively wide acetabular notch makes the ventral border of the acetabulum appear open, resembling that of *Myrmecophaga* and *Tamandua*.

Femur

The femur of Santacrucian sloths is massive and wide transversely and the proximal and distal ends are approximately in the same frontal plane (Fig. 6). It is more robust in *Prepothierium* (YPM-VPPU 15345) and *Hapalops* (MPM-PV 3467, YPM-VPPU 15520, 15110, 15594), but more slender in *Eucholoeops* (MPM-PV 3403 and AMNH 9241), *Peleciodon* (AMNH 9240) and *Analcimorphus* (YPM-VPPU 15561). The femoral head is hemispheric, as in the extant xenarthrans analyzed

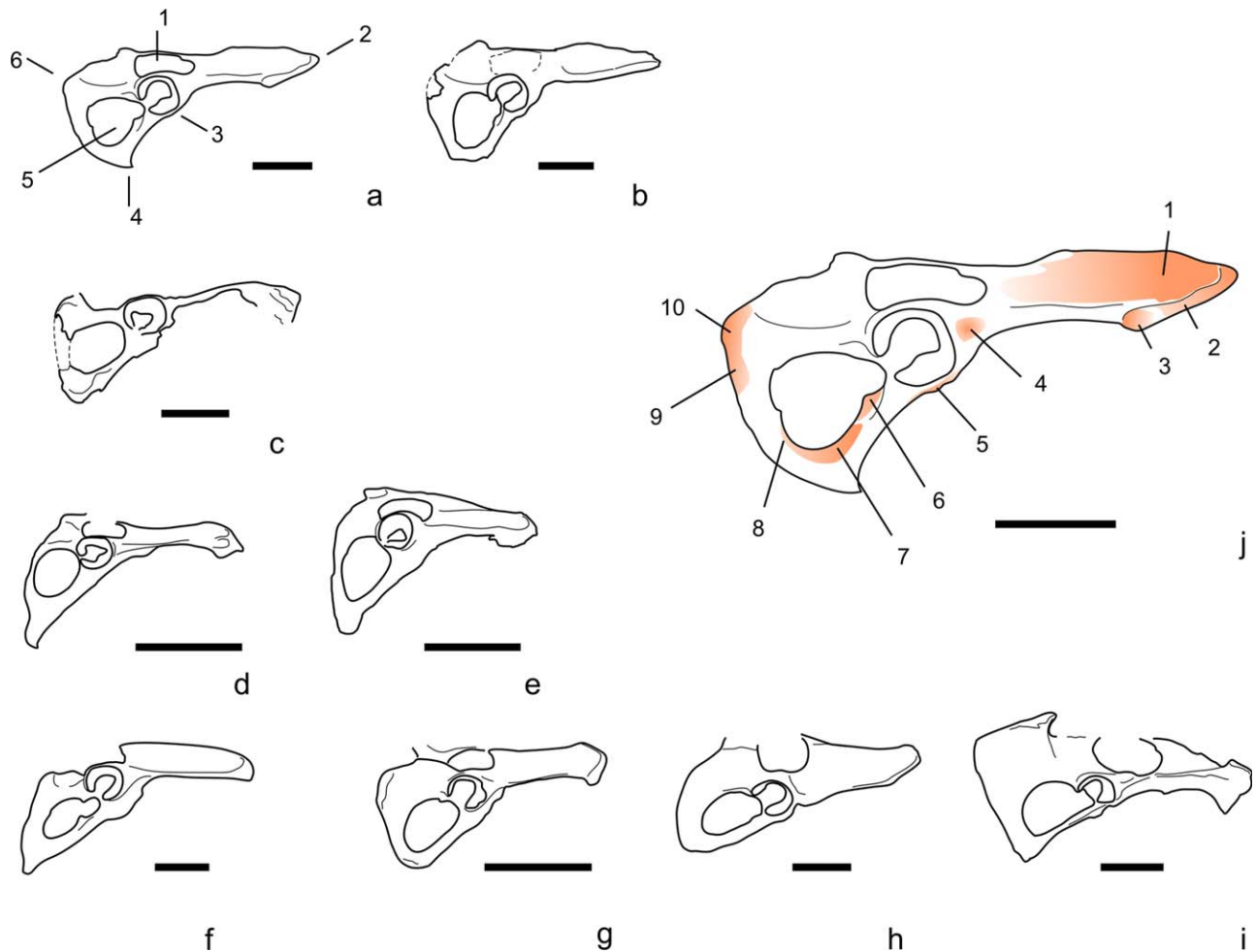


Fig. 4. Pelvic girdles in lateral view, sacral vertebrae were omitted for clarity, cranial aspect to right. a, *Hapalops* YPM-VPPU 15011, 1- Ischial-ilio-sacral fenestra; 2- iliac crest; 3- acetabulum; 4- pubic symphysis; 5- obturator fenestra; 6- ischiatic tuberosity; b, *Analcimorphus* YPM-VPPU 15561; c, *Schismotherium* FMNH 13137; d, *Bradypus* AMNH 42838; e, *Choloepus didactylus* AMNH 35483; f, *Cyclopes didactylus* FMNH 81889; g, *Tamandua mexicana* AMNH 23565; h, *Myrmecophaga tridactyla* FMNH 26563; i, *Priodontes maximus* FMNH

25271; j, entheses of pelvis, in lateral view, of *Hapalops* YPM-VPPU 15011: 1- gluteal complex, 2- tendon *tensor fasciae latae*, 3- *m. sartorius*, 4- *m. rectus femoris* (*m. quadriceps femoris*), 5- *mm. pectineus*, 6- *m. obturator*, 7- *m. gracilis*, 8- group of adductors, 9- *m. semimembranosus*, 10- *mm. biceps femoris* and *semitendinosus*. Scale bar = 5cm (except in f-, scale bar = 1 cm.). Origin entheses in orange, insertion entheses in light blue, speculative entheses in gray.

here. It is relatively large, inclined anteriorly, and the *fovea capitis* is very well developed (especially in *Analcimorphus* and *Prepothierium*), suggesting a robust *teres femoris* ligament. The neck is short and not well defined, as in the extant *Choloepus*. In *Hapalops* the articular surface extends onto the dorsal surface of the neck. The angle between the neck and the femoral diaphysis varies slightly among the genera, as noted by White (1993a). The anterior inclination of the head does not implies that proximal and distal femoral epiphysis are not aligned in the same, frontal plane. The greater trochanter is robust (especially in *Prepothierium*) and large, as in *Myrmecophaga*, but is laterally directed and does not reach as far proximally as the femoral head, as in extant sloths (Fig. 7). It bears a robust entheses for *mm. gluteus medius*, *minimus* and *piriformis* (Fig. 6). The lesser trochanter, triangular in anterior view, is well developed, projecting farther medially than in extant

sloths and anteaters, and resembling more the condition in the armadillos *Priodontes* and *Chaetophractus*. The lesser trochanter is the attachment site for *m. ilio-psoas*, a flexor and lateral rotator of the thigh. The intertrochanteric fossa is wide and deep, indicating a well-developed *m. obturator externus*. The femoral diaphysis is wide transversely, especially in the largest Santacrucian sloths such as *Prepothierium*, due to the large greater trochanter, the expanded third trochanter and the wide distal epiphysis. This widening of the diaphysis provided extensive attachment sites for the very well-developed *mm. quadriceps femoris* (complex of *vastus*, anteriorly) and *quadratus femoris* (posteriorly). The diaphysis is slightly bent showing some variation among the different genera. Its medial border shows a robust entheses for the adductor muscle group. The large and prominent third trochanter, placed approximately at midshaft or very slightly distal to midshaft

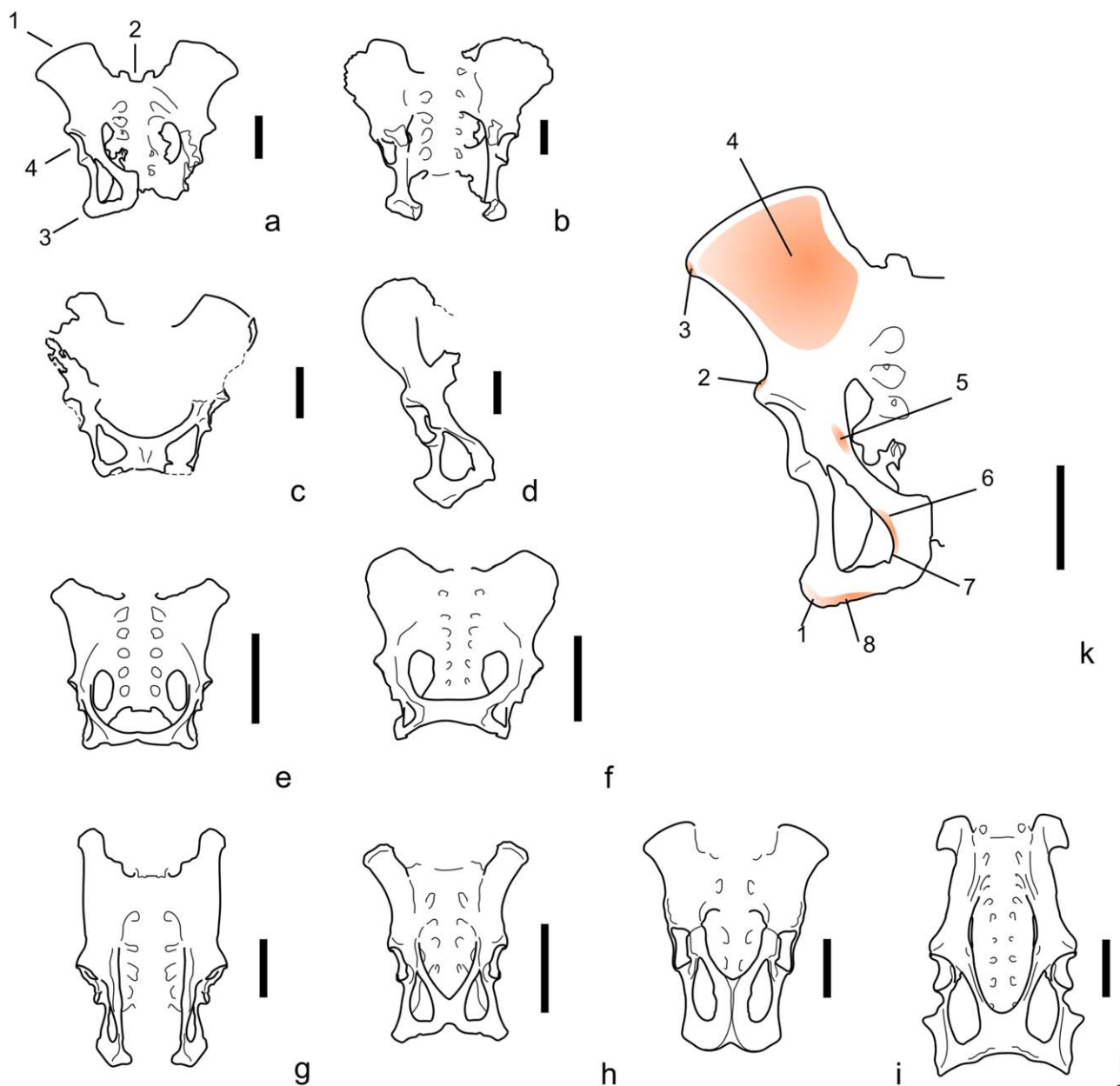


Fig. 5. Pelvic girdles in ventral view, anterior surface upwards. a, *Hapalops* YPM-VPPU 15011, 1- iliac crest, 2- sacrum; 3- ischiatic tuberosity; 4- acetabulum; b, *Eucholoeops* MPM-PV 3403; c, *Schismotherium* FMNH 13137; d, *Analcimorphus* YPM-VPPU 15561; e, *Bradypus* AMNH 42838; f, *Choloepus didactylus* AMNH 35483; g, *Cyclopes didactylus* FMNH 81889; h, *Tamandua mexicana* AMNH 23565; i, *Myrmecophaga tridactyla* FMNH 26563; j, *Priodontes maxi-*

mus FMNH 25271; k, entheses of pelvis, in ventral view, of *Hapalops* YPM-VPPU 15011: 1- *mm. biceps femoris* and *semitendinosus*, 2- *m. rectus femoris* (*m. quadriceps femoris*), 3- *m. sartorius*, 4- *m. iliopsoas*, 5- *m. pectineus*, 6- *m. gracilis*, 7- group of adductors, 8- *m. semimembranosus*. Scale bar = 5 cm. (except in g-, scale bar = 1 cm.), colours as in Fig. 4.

(*Prepootherium*), protrudes more than in extant sloths and anteaters, resembling in this aspect those of extant armadillos (*Priodontes*, *Cabassous* and *Chaetophractus*), indicating powerful *mm. gluteus maximus* and *tensor fasciae latae* (ilio-tibial tract) (Fig. 6).

The distal femoral epiphysis of the Santacrucian sloth is medio-laterally widened and antero-posteriorly depressed (Fig. 7). The lateral epicondyle bears strong attachment sites for *m. plantaris* and/or collateral liga-

ments. The articular condyles have different sizes, the medial condyle having greater anteroposterior diameter than the lateral, in contrast to the subequal condyles of extant sloths and resembling more those of *Myrmecophaga* and extant armadillos (Fig. 7). Both condyles are posteriorly inclined. A well-marked entheses for *m. gastrocnemius* is placed in the posterior aspect of the distal epiphysis, proximal to the medial condyle (Fig. 6). The intercondylar fossa is wide, providing extensive

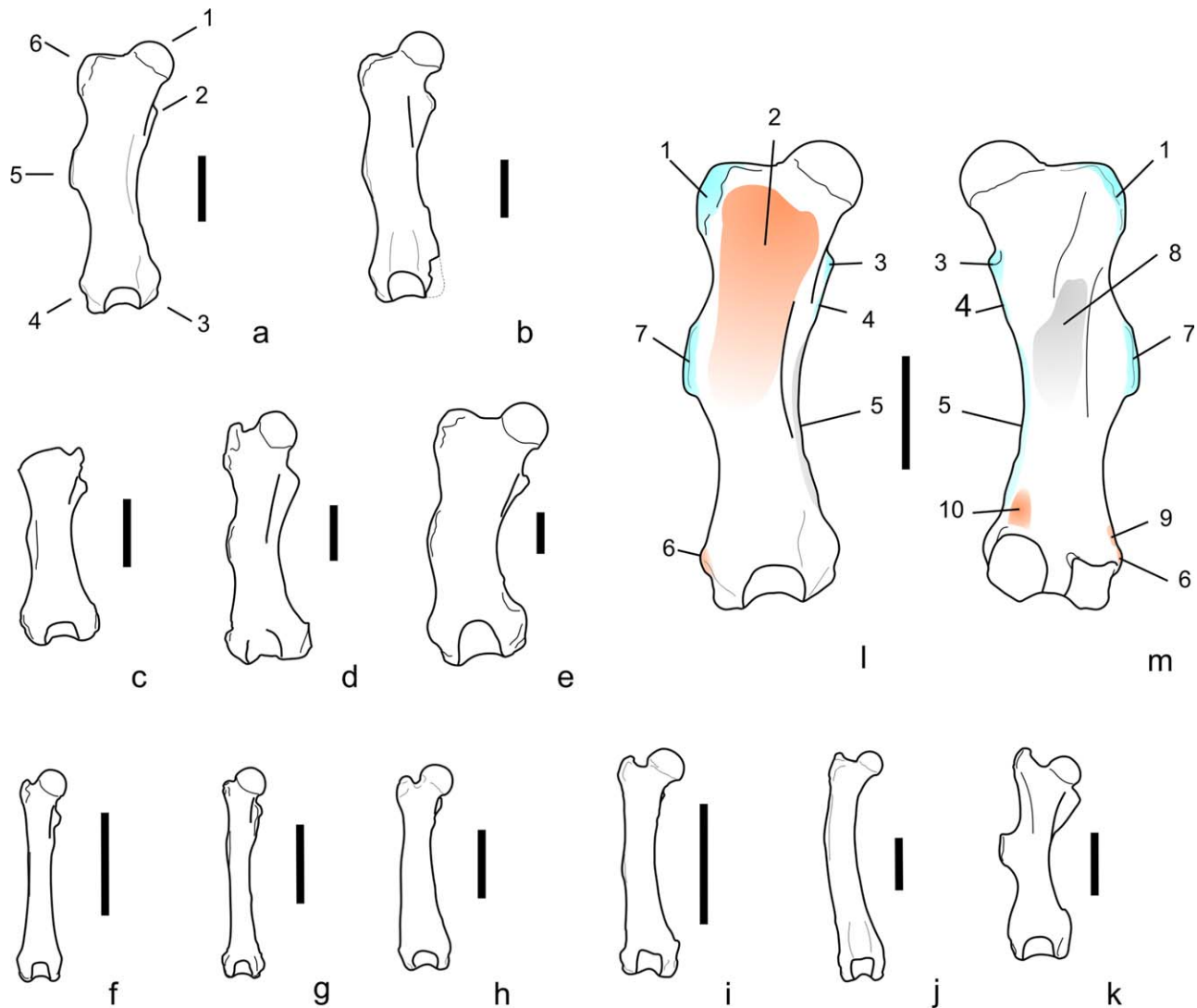


Fig. 6. Right femora in anterior view, distal epiphysis downwards. a, *Hapalops* YPM-VPPU 15011 (left femur reversed), 1- femoral head; 2- lesser trochanter; 3- medial epicondyle; 4- lateral epicondyle; 5- third trochanter; 6- greater trochanter; b, *Eucholoeops* MPM-PV 3403; c, *Pelecyodon* AMNH 9240; d, *Analcimorphus* YPM-VPPU 15561; e, *Prepothierium* YPM-VPPU 15345; f, *Bradypus* AMNH 42838; g, *Choloepus didactylus* AMNH 35483; h, *Cyclopes didactylus* FMNH 81889; i, *Tamandua mexicana* AMNH 23565; j, *Myrmecophaga tridac-*

tyla FMNH 26563; k, *Priodontes maximus* FMNH 25271; l, entheses of the right femur, anterior view (a) and posterior view (b) of *Hapalops* YPM-VPPU 15110: 1- *mm. gluteus medius, minimus, and piriformis*, 2- complex of *m. quadriceps femoris*, 3- *m. ilio-psoas*, 4- *m. pectineus*, 5- *m. adductores*, 6- *m. plantaris*, and fibular collateral ligament, 7- *m. gluteus maximus* and ilio-tibial tract, 8- *m. quadratus femoris*, 9- *m. popliteus*, 10- *m. gastrocnemius*. Scale bar = 5 cm (except in h-, scale = 1 cm.), colors as in Fig. 4.

attachment site for cruciate ligaments. The patellar groove is wide and shallow, as in extant sloths and the anteaters *Cyclopes* and *Tamandua* (Figs. 6 and 7). In *Prepothierium*, *Analcimorphus* and some specimens of *Hapalops*, the medial lip of the patellar groove is more pronounced than the lateral one, while in *Eucholoeops* and the remaining *Hapalops* specimens both lips of the groove are subequal. The patella is subtriangular in anterior view, robust, and with a well-marked distal apex.

Tibia

The tibia of Santacrucian sloths is short compared with the femur. It is robust, and mediolaterally and

anteroposteriorly bent, as in extant sloths, *Cyclopes*, and the armadillos *Priodontes* and *Chaetophractus* (Fig. 8). Tibia and fibula were not co-ossified as in cingulates and some Pleistocene sloths (de Toledo, 1998), but were tightly articulated. The proximal epiphysis is wide and anteroposteriorly compressed, with a wide, short and barely protruding tibial tuberosity, the insertion entheses for a very robust *m. quadriceps femoris* and the *tensor fasciae latae* tendon (Fig. 8). The tibial tuberosity is especially wide and flattened in *Hapalops* (MPM-PV 3467) and *Prepothierium* (YPM-VPPU 15345). The tibial condyles resemble those of *Priodontes*: the medial condyle is concave and flattened, while the lateral one is slightly more convex (Fig. 8). The medial condyle

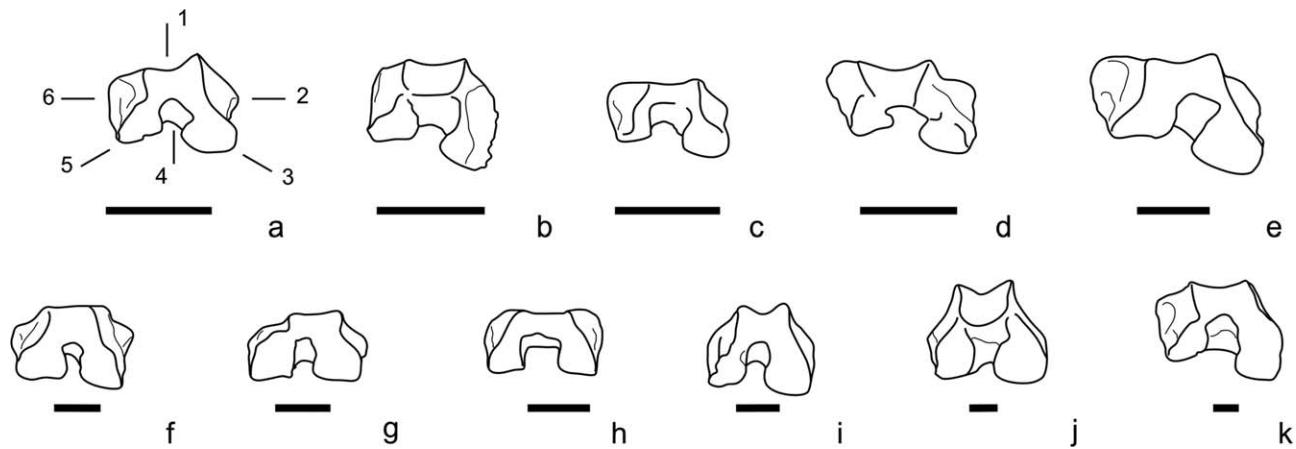


Fig. 7. Right femora in distal view, anterior aspect upwards. a, *Hapalops* YPM-VPPU 15011 (left femur reversed) 1- patellar groove; 2- medial epicondyle, 3- medial condyle, 4- intercondylar fossa, 5- lateral condyle, 6- lateral epicondyle; b, *Eucholoeops* MPM-PV 3403; c, *Pelecypodon* AMNH 9240; d, *Analcimorphus* YPM-VPPU 15561; e,

Prepootherium YPM-VPPU 15345; scale bar = 5 cm. f, *Bradypus* AMNH 42838; g, *Choloepus didactylus* AMNH 35483; h, *Cyclopes didactylus* FMNH 81889; i, *Tamandua mexicana* AMNH 23565; j, *Myrmecophaga tridactyla* FMNH 26563; k, *Priodontes maximus* FMNH 25271. Scale bar = 1 cm.

extends farther distally than the lateral condyle. The posterior surface of the condyle extends in a well-developed lip for the tendon of the *m. popliteus*, suggesting the presence of a sesamoid ossification on this tendon (*cyamella* or *cyamo-fabella*, Lessertisseur and Saban 1971; see Salas *et al.* 2005 for a discussion). On the posterior surface of the proximal third of the diaphysis, distal to the intercondylar eminence, lies a deep fossa that serves as an insertion entheses for a robust *m. popliteus* (Fig. 8). The tibial diaphysis, as mentioned above, is bent, especially in *Analcimorphus*, the Mylodontidae indet. MPM-PV 3406, *Pelecypodon* and in some specimens of *Hapalops*. In *Eucholoeops* and *Prepootherium* the diaphysis is straighter. In all cases, the shaft is more convex along its medial surface, just distal to a well-developed insertion site for a powerful *pes anserinus* muscle group (*mm. gracilis*, *semitendinosus* and *sartorius*) (Fig. 8). This tibial curvature results in a wide separation between tibia and fibula, providing abundant space for accommodation of a powerful *m. flexor digitorum*. The distal epiphysis is wide and massive. The tibial malleolus is reduced and does not bear articular facets, similar to the extant xenarthrans analyzed here. Posteriorly it extends as a robust trochlea with at least two deep grooves for a very powerful ankle joint extensor and toe flexor musculature (*mm. tibialis posterior* and *extensor digitorum longus*) (Fig. 9). The articular facet for the astragalus is longer than wide. It is somewhat triangular in *Pelecypodon*, the Santacrucian mylodonts and *Analcimorphus*, while in *Prepootherium*, *Hapalops* and *Eucholoeops* it is more squared. Its lateral border is straight, bearing a flat articular facet for the fibular distal epiphysis. The posterior border extended in a lip, as in *Priodontes*, *Myrmecophaga*, *Tamandua*, and *Bradypus*.

Fibula

The fibula of Santacrucian sloths is straight (as in *Choloepus* and *Tamandua*) and robust when compared with the tibia, resembling that of *Priodontes*. The proxi-

mal epiphysis is stout, bearing a well-marked attachment site for a robust *m. biceps femoris* (Fig. 8). The distal epiphysis is massive and large, exhibiting a very well-developed fibular malleolus similar to that of extant sloths. Both facets (proximal and distal) for articulation with the tibia are flat. The facet for articulation with the ectal facet of the astragalus is large, flat, and crescent-shaped. A fibulo-calcaneal joint is absent, a basal feature common to all xenarthrans (see McDonald, 2003).

Posterior Autopodium - Pes

The pes of Santacrucian sloths is fairly conservative in morphology and configuration, as is the manus (Toledo *et al.*, 2013). It is pentadactyl, with no loss, reduction, or fusion of elements, being thus comparable to the autopodium of generalized mammals (Polly, 2007). The astragalus is narrow when compared to those of extant anteaters, and armadillos such as *Cabassous*, *Priodontes* and *Chaetophractus*, only roughly resembling those of extant sloths (Fig. 10). The medial condyle of the *trochlea tali* is short, small and rounded, but without forming a well-defined odontoid process as in the Pleistocene megatherians and mylodontids (see McDonald, 2012). The lateral condyle of the *trochlea tali* shows a gentler curve, having a greater anteroposterior diameter. The difference between the condyles is more pronounced in *Analcimorphus* (YPM-VPPU 15561), *Nematherium* (YPM-VPPU 15965), the mylodontid indet. (MPM-PV 3406), and *Pelecypodon* (FMNH 12062). However, the overall configuration is quite different from that present in Plio-Pleistocene sloths, which exhibit a small, subspherical medial condyle and a large discoidal lateral one (see De Iuliis, 1994; McDonald and De Iuliis, 2008 and McDonald, 2012). The astragalo-fibular facet is well developed, flat, and crescent-shaped, bearing a deep postero-ventral depression, the entheses of the lateral talo-calcaneal ligament. The astragalar head is concave, mediolaterally elliptical and medially inclined, bearing a well-marked medial articular surface for the navicular medial lip (see below). The

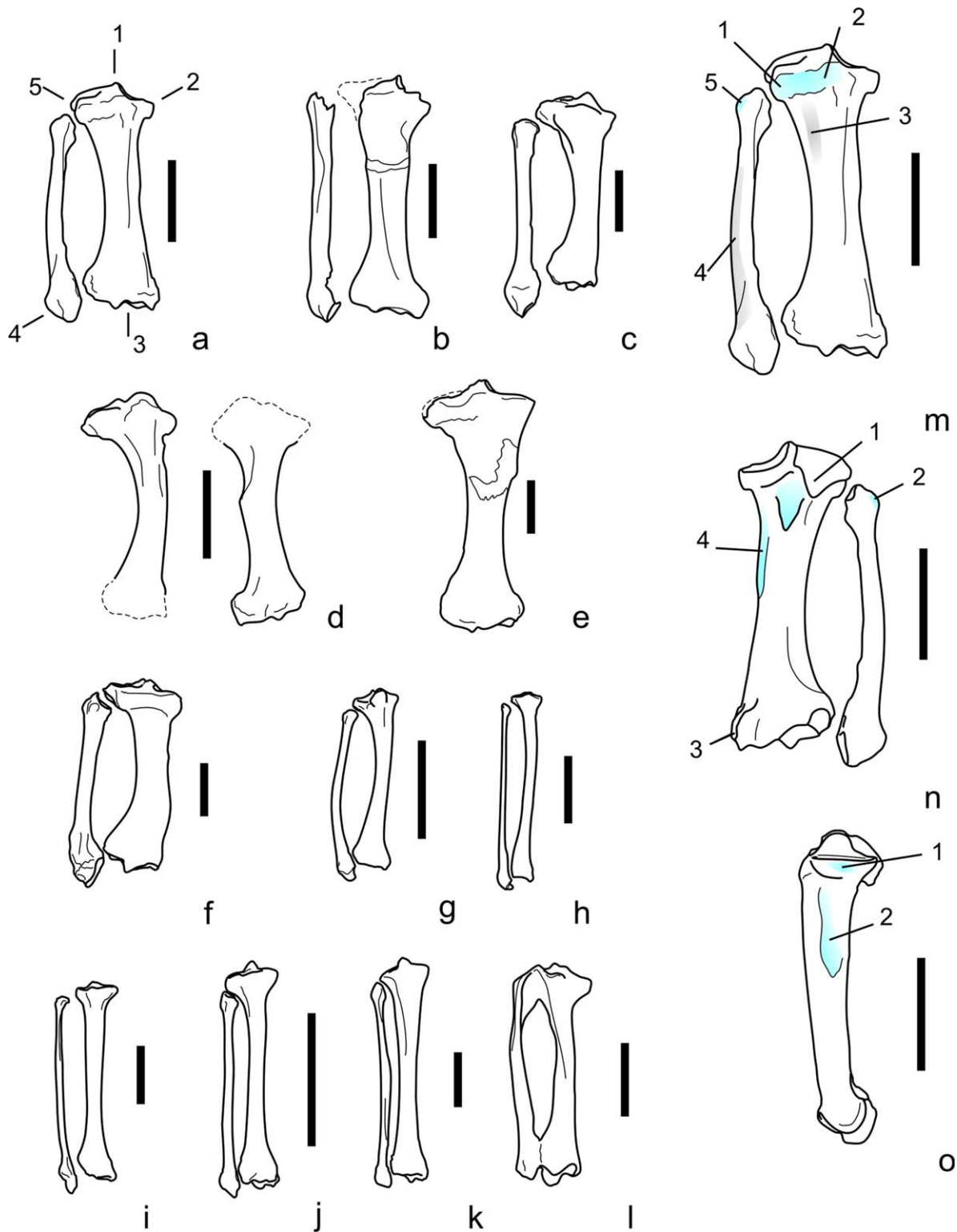


Fig. 8. Right tibiae and fibulae in anterior view. a, *Hapalops* YPM-VPPU 15045 (left fibula reversed), 1- intercondyloid tubercle; 2- medial facet; 3- astragalar facet; 4- fibular malleolus; 5- lateral facet; b, *Eucholoeops* MPM-PV 3403 (tibia) and FMNH 13125 (fibula); c, *Analcimorphus* YPM-VPPU 15561; d, *Pelecypodon* AMNH 9240; e, *Prepothierium* YPM-VPPU 15345 (left tibia reversed); f, Mylodontidae indet. MPM-PV 3406 (left tibia and fibula reversed); g, *Bradypus* AMNH 74136; h, *Choloepus didactylus* AMNH 35483; i, *Cyclopes didactylus* AMNH 171297; j, *Tamandua mexicana* AMNH 23565; k, *Myrmecophaga tridactyla* FMNH 26563; l, *Priodontes maximus* FMNH 25271; m, entheses of the right tibia and left fibula (reversed) of *Hapalops* YPM-VPPU

15045, anterior view: 1- *m. tensor fasciae latae*, 2- *m. quadriceps femoris*, 3- *m. tibialis anterior*, 4- joined fibular entheses (*mm. peroneus longus, brevis, tertius, extensor digitorum longus, tibialis anterior*), 5- *m. biceps femoris*; n, entheses of right tibia and left fibula of the same specimen of *Hapalops*, posterior view: 1- articular facet for *m. popliteus* and its sesamoid bone, 2- *m. biceps femoris*, 3- trochleae for tendons of *mm. tibialis posterior* and *flexor digitorum*, 4- tendon of *pes anserinus* group; o- entheses of right tibia and left fibula of the same specimen of *Hapalops*, medial view: 1- *m. semimembranosus*, 2- tendon of *pes anserinus* group (*mm. gracilis, semitendinosus, and sartorius*). Scale bar = 5 cm. (except in i- scale bar = 1 cm), colors as in Fig. 4.

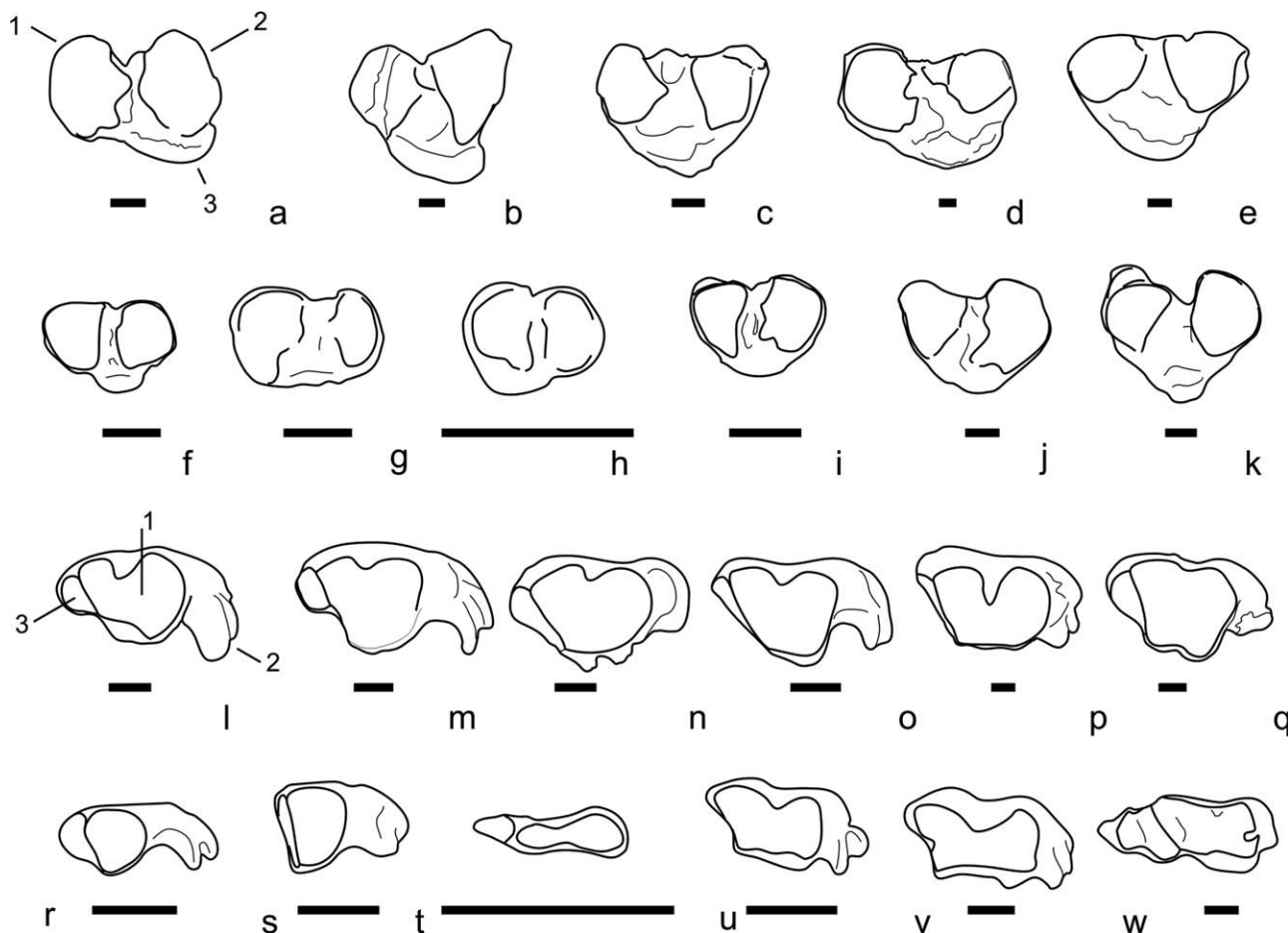


Fig. 9. Above. Right tibiae in proximal view, anterior aspect downwards. a, *Hapalops* YPM-VPPU 15045, 1- lateral facet, 2- medial facet; 3- tibial tuberosity; b, *Analaimorphus* YPM-VPPU 15561; c, *Pelecypodon* AMNH 9240; d, *Prepothierium* YPM-VPPU 15345 (left tibia reversed); e, *Myiodontidae* indet. MPM-PV 3406 (left tibia reversed); f, *Bradypus* AMNH 74136; g, *Choloepus didactylus* AMNH 35483; h, *Cyclopes didactylus* AMNH 171297; i, *Tamandua mexicana* AMNH 23565; j, *Myrmecophaga tridactyla* FMNH 26563; k, *Priodontes maximus* FMNH 25271. Below. Right tibiae in distal view, anterior aspect

upwards. l- *Hapalops* YPM-VPPU 15045, 1- astragalar facet; 2- trochlea for flexor tendons; 3- distal fibular facet; m, *Eucholoepus* MPM-PV 3403; n, *Analaimorphus* YPM-VPPU 15561; o, *Pelecypodon* AMNH 9240; p, *Prepothierium* YPM-VPPU 15345 (left tibia reversed); q, *Myiodontidae* indet. MPM-PV 3406 (left tibia reversed); r, *Bradypus* AMNH 74136; s, *Choloepus didactylus* AMNH 35483; t, *Cyclopes didactylus* AMNH 171297; u, *Tamandua mexicana* AMNH 23565; v, *Myrmecophaga tridactyla* FMNH 26563; w, *Priodontes maximus* FMNH 25271. Scale bar = 1 cm.

sustentacular facet for the calcaneus, almost vertically oriented, is located posterior to the astragalar head, similarly to *Tamandua*. The astragalar head is also almost sessile, in contrast to extant sloths. The ectal, posterior calcaneal facet (calcaneo-astragalar facet *sensu* Szalay and Schrenk, 1998) is crescent-shaped (Fig. 10).

The calcaneus is fairly atypical. The *tuber calcanei* is large, robust, and mediolaterally expanded, forming a medioventrally projecting wing that is particularly prominent in *Hapalops* (e.g., YPM-VPPU 15523 and FMNH 13123) and *Analaimorphus* (YPM-VPPU 15561) (Fig. 10). This expansion of the tuber provides an extensive attachment site for powerful *mm. gastrocnemius*, *soleus*, and *plantaris* (Figs. 10 and 11). The ectal, posterior facet (calcaneo-astragalar facet of Szalay and Schrenk, 1998) that articulates with the astragalus is convex and anteroposteriorly disposed. The body of the calcaneus anterior to this facet is comparatively short, bearing a well-developed groove that accommodated the

interosseous ligament for the astragalus. The cuboidal facet is slightly medially directed, while the sustentacular facet is placed almost perpendicular to the anteroposterior axis of the calcaneus (Fig. 10). At the level of the sustentacular facet but on the lateral side of calcaneus, there is a well-developed trochlear process showing a deeply concave surface for passage of the tendons of toe flexor and plantarflexor muscles (Figs. 10 and 11).

The navicular is rounded in anterior view. The proximal facet, for the astragalar head, is convex and its medial border forms a thick margin or lip, the entheses for the calcaneo-navicular ligament. The postero-medial surface of this lip bears a very marked articular surface for a corresponding articular surface on the medial aspect of astragalar head. The cuboid and cuneiforms are squared in shape and slightly anteroposteriorly compressed. Metatarsals I, II, and in particular III are shorter and stouter than IV and V (Fig. 11). Metatarsal V has an expanded wing-like postero-lateral border that

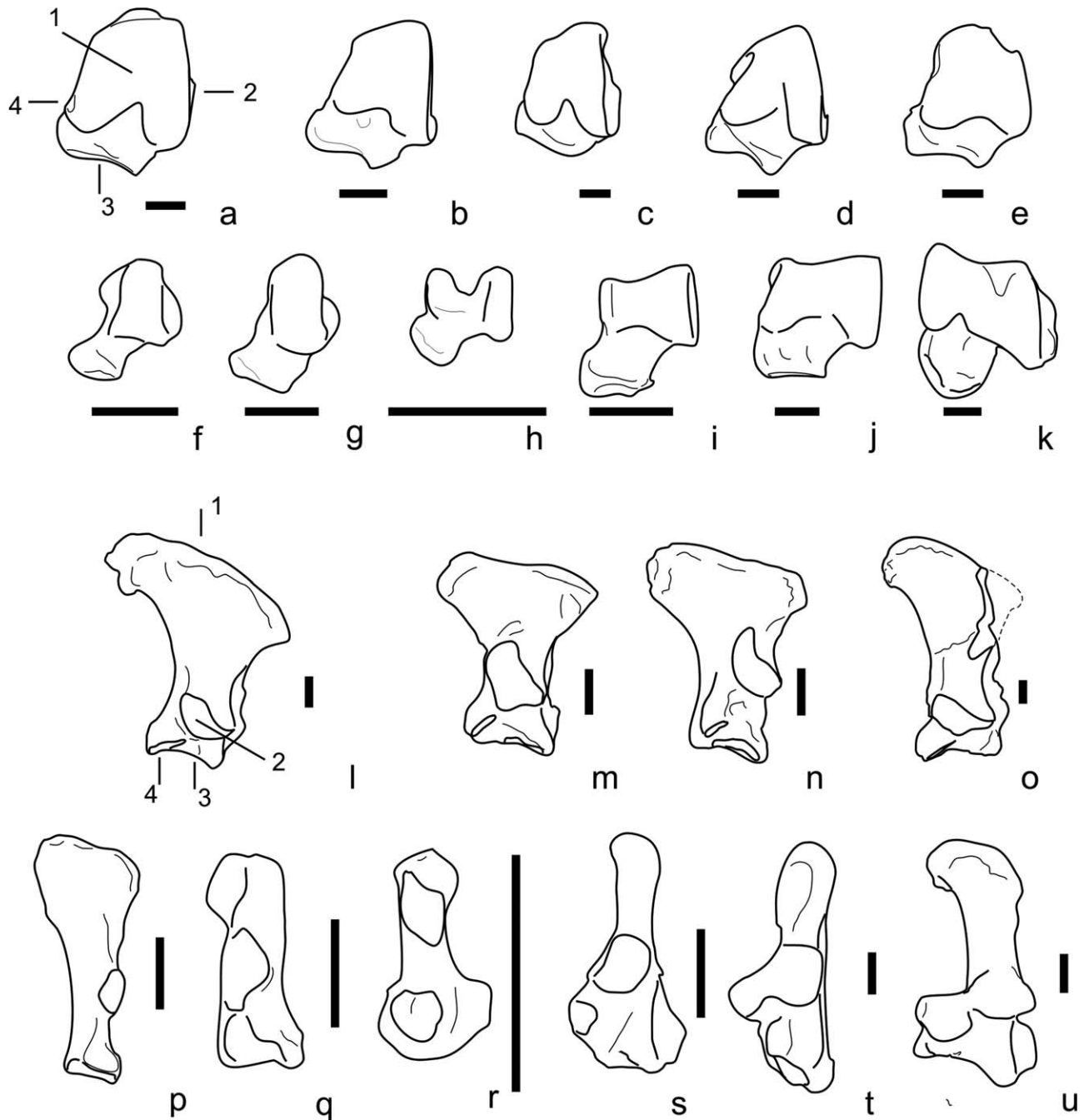


Fig. 10. Above. Left astragali in dorsal view, anterior aspect downwards: a, *Hapalops* YPM-VPPU 15523, 1- astragalar trochlear surface; 2- fibular facet; 3- head, 4- medial condyle; b, *Schismotherium* FMNH 13137; c, *Analcimorphus* YPM-VPPU 15561; d, *Peleciodon* FMNH 12062; e, *Nematherium* YPM-VPPU 15965; f, *Bradypus* AMNH 42838; g, *Choloepus didactylus* AMNH 139772; h, *Cyclopes didactylus* FMNH 81889; i, *Tamandua mexicana* AMNH 23565; j, *Myrmecophaga tridactyla* MLP 8-X-01-9; k, *Prionodites maximus* FMNH 25271. Below. Left

calcaneus in dorsal view, anterior aspect downwards: l-*Hapalops* YPM-VPPU 15523, 1- *tuber calcanei*, 2- ectal facet; 3- cuboidal facet; 4- sustentacular facet; m, *Schismotherium* FMNH 13137 (right calcaneus reversed); n, *Peleciodon* FMNH 12062; o, *Myiodontidae* indet. MPM-PV 3406; p, *Bradypus* AMNH 42454; q, *Choloepus didactylus* AMNH 139772; r, *Cyclopes didactylus* FMNH 81889; s, *Tamandua mexicana* AMNH 23565; t, *Myrmecophaga tridactyla* MLP 8-X-01-9; u, *Prionodites maximus* FMNH 25271. Scale bar = 1 cm.

provides attachment sites for ligaments, and extensor (*mm. peroneus longus* and *brevis*) and toe flexor (*m. flexor digiti quinti*) muscles (Fig. 11). All the phalanges are short and massive, especially the proximal phalanx

of digits I, II, and III. In all cases the proximal phalanx articulated tightly with the metatarsal. All ungual phalanges are well developed and less curved than those of the manus (see Toledo *et al.*, 2013), and bear very

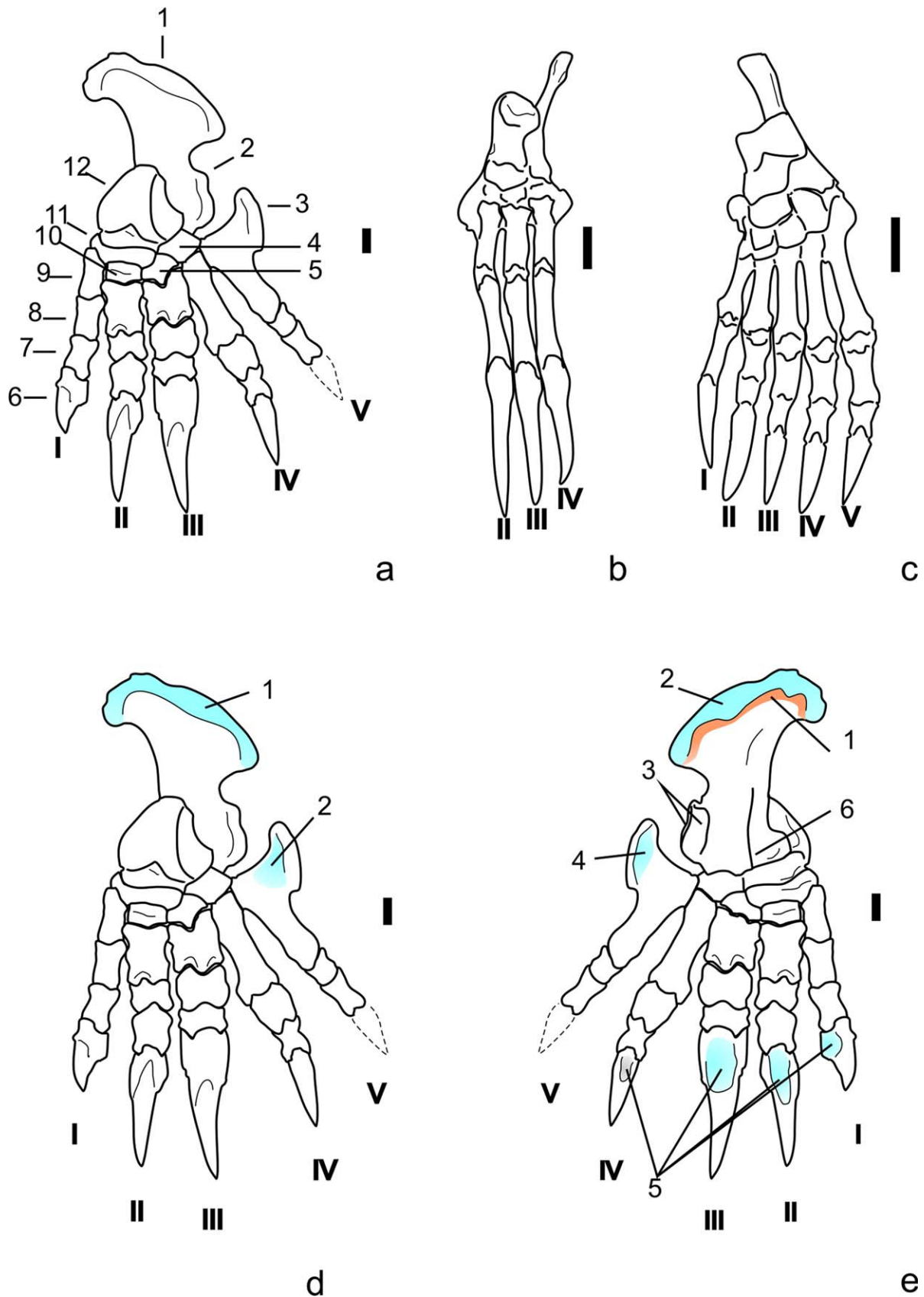


Fig. 11. Left pes in dorsal view. a, generalized pes constructed from several specimens of *Hapalops* (mainly YPM-VPPU 15523): 1- calcaneus, 2- trochlea for flexor tendons, 3- expanded winged postero-lateral border of metatarsal V, 4- cuboid, 5- lateral cuneiform, 6- ungual phalanx, 7- proximal phalanx, 8- metatarsal, 9- medial cuneiform, 10- central cuneiform, 11- navicular, 12- astragalus; b, *Bradypus* AMNH 97315; c, *Tamandua* AMNH 23437; d, entheses of the same generalized pes, in

dorso-lateral view: 1- joined entheses of *m. soleus*, *m. gastrocnemius* and *m. plantaris*, 2- *m. peroneus longus* and *brevis*; e, entheses of the same generalized right pes, in ventro-medial view: 1- *m. quadratus plantae*, 2- joined entheses of *m. soleus*, *m. gastrocnemius* and *m. plantaris*, 3- trochleae for tendons of *m. peroneus longus* and *brevis*, 4- *m. flexor digiti quinti*, 5- *m. flexor digitorum longus*, 6- groove for tendon of *m. flexor digitorum longus*. Scale bar = 1 cm., colors as in Fig. 4.

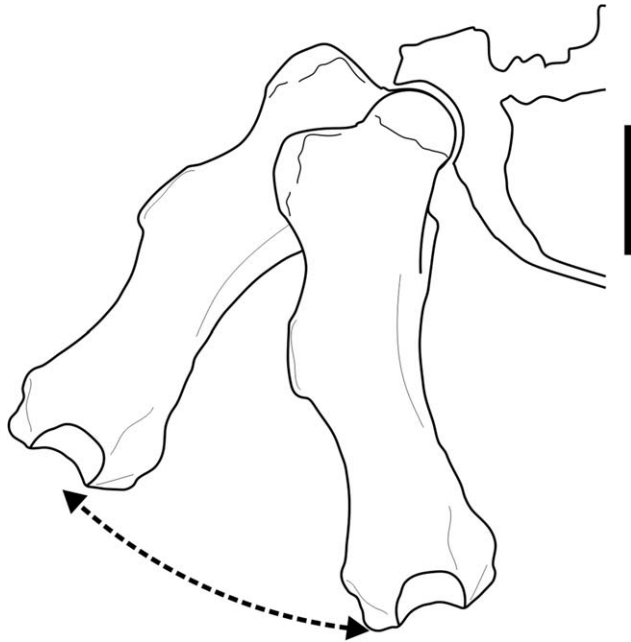


Fig. 12. Range of femoral abduction in *Hapalops* (YPM-VPPU 15011), in anterior view. Pelvis is depicted with the iliac blade removed for greater clarity. Scale bar = 5 cm.

prominent subungual tubercles for attachment of a powerful flexor musculature (mainly *mm. flexor digitorum communis* and *flexor digitorum profundus*) (Fig. 11).

Qualitative Functional Morphology

Pelvic girdle. The great development of the gluteal musculature indicates powerful thigh abduction and stabilization of the hip-joint, especially when the contralateral limb was in recovery phase. The development of this muscle group also suggests powerful extension of the limb. The long and laterally deflected dorsal ischiatic branches provide large leverage for muscles of the hamstring group and *m. quadratus femoris*, suggesting that Santacrucian sloths were capable of powerful thigh adduction. These muscles also acted as potent extensors of the limb, especially when knee was flexed.

The ventrally oriented acetabulum of *Analcimorphus* and *Eucholoeops* indicates lesser capabilities of extensive thigh abduction than in *Hapalops*, where the acetabulum is laterally oriented (Fig. 12). The great development of the ligament *teres femoris* (as indicated by the acetabular notch) suggests that the hip joint faced great mechanical stress, especially in abduction and lateral rotation of the femur.

Femur

The relatively large femoral head of Santacrucian sloths suggests that the hip joint was highly mobile. The great development of the *fovea capitis* supports the presence of a robust ligament *teres femoris*, especially in *Analcimorphus* and *Prepothierium*. The position of the greater trochanter distal to the femoral head suggests that, as in extant sloths, *Tamandua* and *Cyclopes*, the

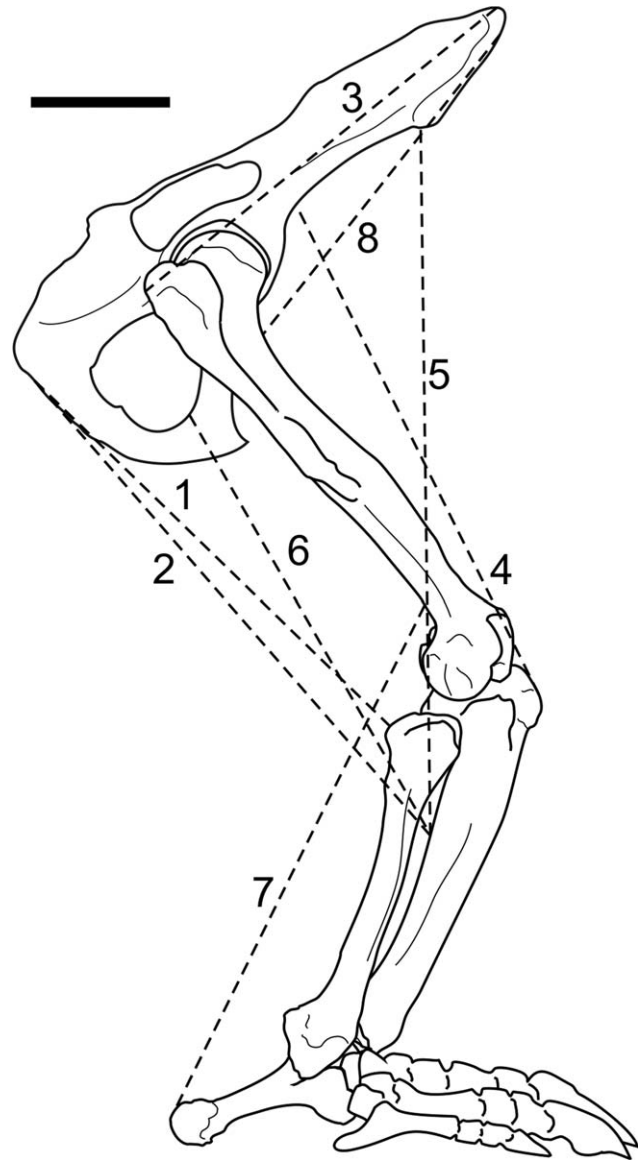


Fig. 13. Inferred extensor and flexor musculature of the hind limb, depicted in *Hapalops* (YPM-VPPU 15011 pelvis, MPM-PV 3467 femur, tibia, and fibula, and YPM-VPPU 15155 pes). Elements were rescaled to preserve proportions. The dotted lines correspond to action lines of muscles, as follows: 1- *m. biceps femoris*, 2- *m. semitendinosus*, 3- *mm. gluteus medius and minimus*, 4- *m. rectus femoris*, 5- *m. sartorius*, 6- *m. gracilis*, 7- *m. gastrocnemius*, 8- *m. ilio-psoas*. Scale bar = 5 cm.

hip joint was capable of a wide range of abduction, more so than in *Myrmecophaga* and armadillos such as *Priodontes*. Additionally, a more distal greater trochanter decreases the leverage for the gluteal muscle group as a thigh extensor (Fig. 13), but improves its leverage as an abductor, especially if the trochanter is expanded laterally, as occurs in the Santacrucian sloths analyzed here. The conspicuous and medially directed lesser trochanter increases the lever arm for the *m. ilio-psoas*, allowing powerful lateral rotation of the thigh (lateral excursion) in addition to the flexion exerted by this muscle. Furthermore, the wide and deep intertrochanteric

fossa, indicating a powerful *m. obturator externus*, also points to good capabilities for abduction and lateral rotation of the femur.

The well-developed *m. quadriceps femoris* and its extensive origin entheses on the femoral diaphysis (mainly *m. vastus*) indicate that extension of the zeugopodium was powerful. The anatomy of the tibia provides more detailed information about this muscle (see below). On the other hand, the well-developed thigh adductor muscle group suggests powerful limb adduction. The robust third trochanter, providing great leverage for the powerful *m. gluteus maximus* (Fig. 13), indicates potent extension and abduction of the thigh, as well as stabilization of the hip joint when the contralateral limb was in recovery phase. In *Prepothierium*, where the third trochanter is slightly more distally placed, the lever arm of this muscle was greater. Regarding the *m. tensor fascia latae*, a robust third trochanter also indicates increased hip stabilization during extension and maybe reduced bending stresses (Milne *et al.*, 2012). Another function of the *fascia latae* was surely containing and surrounding the bulky thigh muscles of these sloths. Functional implications of the expanded diaphysis other than muscle attachment requires further study, as proposed by Milne *et al.* (2012).

The asymmetry of the femoral condyles can be related to several functional issues. First, load transmission between tibia and femur would mainly be through the larger medial condyle. Second, knee flexion may have imparted lateral rotation of the tibia, as the femoral medial condyle has a greater diameter than the lateral condyle. On the other hand, the placement of the condyles, inclined on the posterior aspect of the femur, suggests that flexed stances of the knee were usual. The wide space for cruciate ligaments also indicates that the knee joint was able to withstand high mechanical demands involving anteroposterior and rotational movements.

The wide and relatively shallow patellar groove accommodated a very robust tendon of the well-developed *m. quadriceps femoris*, main extensor of the crus during the propulsive phase of the pace. The morphology of the patellar groove implies slow movements in flexed stances. The larger medial margin of the groove in *Prepothierium*, *Analcimorphus* and in some specimens of *Hapalops* would have prevented medial displacement of the tendon of *m. quadriceps* during lateral excursion of the femur when the knee was flexed. On the other hand, in *Eucholoeops* and the remaining *Hapalops* specimens the requirements for tendon stabilization could have been reduced. Additionally, the long and acuminate patella also indicates that complete extension of the knee was not usual.

Tibia

The relative proximodistal displacement between the medial and lateral proximal tibial condyles, and the asymmetry of the femoral condyles, indicate knee stabilization. Another functional feature inferred is that flexion of the knee joint involved a sliding movement of the femoral lateral condyle on the corresponding tibial facet, compared with the more rotational movement of the medial condyle. The robust but flattened tibial tuberosity supports the presence of a powerful *m. quadriceps*

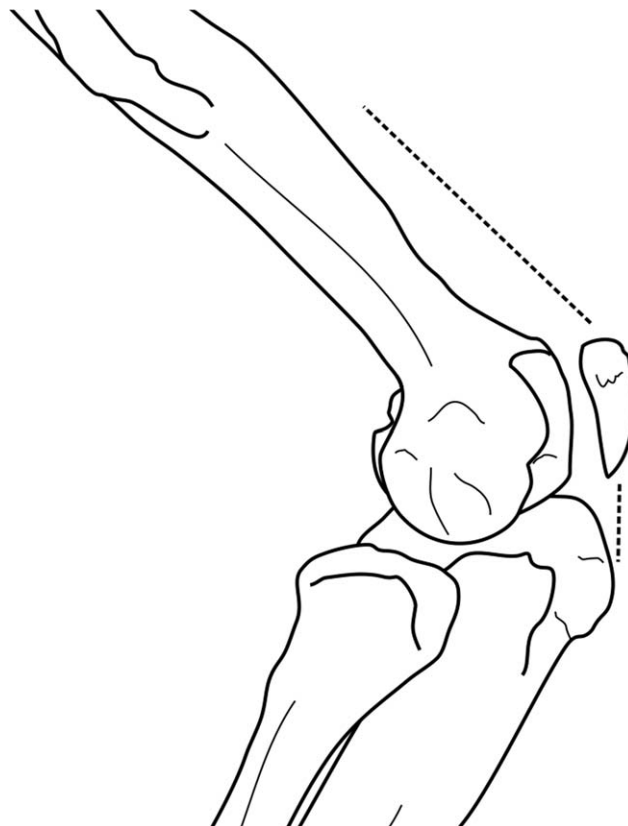


Fig. 14. Inferred action lines of the complex *m. quadriceps femoris* (dotted lines) in *Hapalops* (same specimens as in Fig. 22, plus FMNH 13130 patella).

femoris, but, on the other hand, indicates a very short lever arm for this muscle (Fig. 14). Thus, a functional hypothesis for *m. quadriceps femoris* would be that it was capable of powerful but slow extension of the zeugopodium. Additionally, its wide insertion tendon may have collaborated with other knee ligaments in stabilizing the knee joint.

The curvature of the tibial diaphysis displaced the line of load transmission more medially. The fact that this curvature was adjacent to the insertion entheses of *mm. semitendinosus*, *gracilis*, and *sartorius* would suggest that the influence of the action of these muscles could modify the morphology of the diaphysis during development. Another consequence is the abundant available space for a very powerful *m. flexor digitorum*, indicating forceful flexion of toes and indirectly extension of the entire pes.

The well-developed posteromedial trochlea for ankle extensor (plantarflexor) muscles indicates a very potent plantarflexion of the pes and flexion of the toes. The morphology of the tibial facet for the astragalus, longer than wide, indicates parasagittally restricted movements of the ankle joint. Coincidentally, the flattened nature of the distal facet for the fibula indicates that swinging movements of the fibula (equivalent to pronation-supination of the radius) were restricted or prevented. The inclination of the axis of the ankle joint would position the pes parallel to the substrate when the knee was abducted during lateral excursion of the thigh.

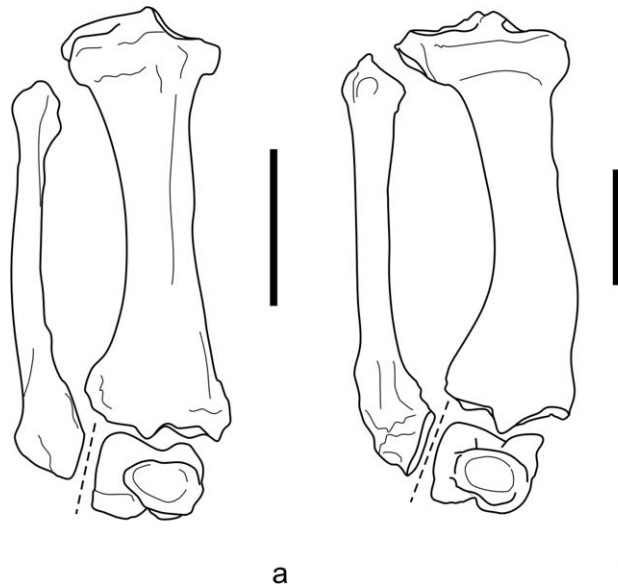


Fig. 15. Astragalar mobility. a, *Hapalops* YPM-VPPU 15045 (right tibia and fibula) and YPM-VPPU 15523 (left astragalus reversed), both specimens were rescaled; b, *Mylodontidae* indet. MPM-PV 3406 right tibia, fibula, and astragalus. Note the flat nature of fibular-astragalar joint, represented by dotted lines. Scale bar = 5 cm.

Fibula

The robustness of the fibular diaphysis indicates important mechanical requirements applied to the crus (Fig. 8). The morphology of the distal epiphysis, with its flattened facet for the ectal facet of the astragalus, suggests that eversion–inversion movements at the ankle were severely restricted.

Pes

The tight fit between the fibular facet and the ectal facet of the astragalus indicates that the ankle joint was restricted to parasagittal rotation, precluding eversion–inversion movements at this level (Fig. 15), similar to described by McDonald (2012) for Plio-Pleistocene megalonychids. Restricted mediolateral rotation of the pes by pivoting on the medial astragalar condyle is also suggested by the low angle between both trochlear surfaces, following the criteria provided by McDonald (2012) for later fossil sloths. The morphology of the astragalar head and the navicular suggest that the navicular was able to perform rotatory movements on the astragalar head, but functional implications of this feature require further analysis. The short neck of the astragalar head and the short length of the part of the calcaneum anterior to the astragalocalcaneal articulation suggest a plantigrade pes. The vertically placed sustentacular facet precluded anteroposterior sliding movements of the astragalus with respect to the calcaneus, only permitting slight mediolateral movements (Fig. 16). The great length of the *tuber calcanei*, when compared with the part of the calcaneum anterior to the astragalocalcaneal articulation, optimized force against velocity during pes extension, providing a very long lever arm for powerful action of *mm. gastrocnemius* and *plantaris*. The

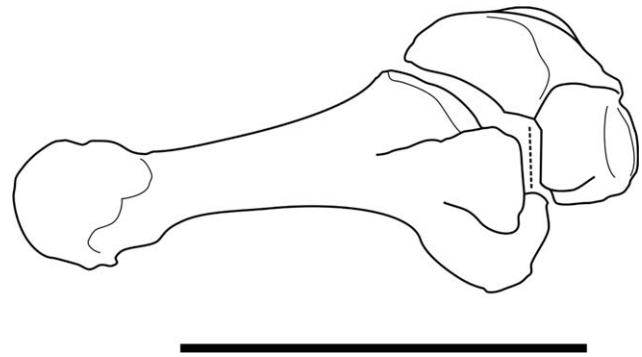


Fig. 16. Articular relationship between astragalus and calcaneus in MPM-PV 3406. The dotted line represents the plane of articulation between the sustentacular facet of the calcaneus and the corresponding facet in the posterior aspect of the astragalar head. Scale bar = 5 cm.

expanded *tuber calcanei* provided an extensive contact surface, also indicating a plantigrade pes. The metatarsal arch was wide, giving ample space to accommodate the powerful tendons of flexor muscles. The morphology of joints between metatarsals and proximal phalanges suggests great stability for facing high mechanical demands. The ungual phalanges were also very tough, indicating they were capable for strenuous activities involving powerful claws. The great development of digital flexor musculature indicates that Santacrucian sloths were able to undergo forceful phalangeal flexion, especially of the ungual phalanges.

DISCUSSION

Biological Role of Functional Features of the Hind Limb

As defined in Toledo *et al.* (2013), the biological role is the use or uses to which a given function is put to by an organism. We provide and consider here hypotheses on the biological role of the functions of the hind limb of Santacrucian sloths proposed in the previous section, largely through comparison with knowledge of extant mammals.

Acetabulo-Femoral Joint

The functional features of the hip joint described are consistent with climbing activities, which require high mobility of the hip and great mechanical efforts applied on the joint, mainly in abduction. The lateral orientation of the acetabulum, mainly in *Hapalops* and *Schismotherium*, permitted well abducted stances as in extant sloths, while *Eucholoeops* and *Analcimorphus* would have had narrower ranges of mobility. The more distal position of the greater trochanter of Santacrucian sloths also allowed an extensive range of abduction of the hip joint, as discussed by Pujos *et al.* (2007) for the fossil sloth *Diabolotheirus* from the Pleistocene of Peru. In the extant xenarthrans analyzed here, the greater trochanter is more distally located in arboreal forms (the silky and lesser anteaters, *Cyclopes* and *Tamandua*, and sloths) than in ground-dwelling forms (the giant anteater *Myrmecophaga*, and the armadillos *Priodontes*, *Cabassous* and *Chaetophractus*), as Candela and Picasso (2008) described for hystricognath rodents. Sargis (2002)

related high mobility of the hip joint in tupaiids with climbing abilities, as similarly described by Szalay and Sargis (2001) for some marsupials.

Femoral Abduction and Extension

With regard to the gluteal musculature, the laterally expanded iliac wings of Santacrucian sloths would have emphasized the function of this musculature as a fast extensor of the hind limb, diminishing its effectiveness as a femoral abductor. However, leverage for femoral abduction is increased by the laterally expanded greater trochanter. The lever arm for the muscles of the hamstring group, important as slow extensors of the limb when flexed, is proportionately similar to the lever arm for the gluteal group, a fast extensor of thigh. Argot (2002) described the gluteal group as more developed than the hamstring group in fast cursorial didelphids. The opposite pattern is verified in some arboreal carnivorans, in which the hamstring group is predominant (Jenkins and Camazine, 1977). Thus, it is noteworthy that Santacrucian sloths exhibit morphologies that increased the leverage of both muscle groups, without predominance of the faster or the stronger muscle groups. In this sense, the laterally expanded third trochanter of Santacrucian sloths increased leverage for femoral abduction by the *m. gluteus maximus*. As discussed below, this functional feature may be explained in the mechanical context of climbing, but the similar third trochanter morphology in extant armadillos (e.g., *Chaetophractus* and *Priodontes*) and other ground-dwelling mammals (see Sargis, 2002 and Candela and Picasso, 2008) begs a more careful consideration of its correlation with substrate preference.

Lateral Rotation of Femur

The great leverage for extensive lateral rotation of the femur provided by the medially protruding lesser trochanter is consistent with climbing abilities, as noted by several authors with respect to other mammals (Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002; Candela and Picasso, 2008) and related to extensive lateral rotation during the recovery phase in climbing. In ground-dwelling forms, the need for such lateral excursion would not be necessary. In extant anteaters, protrusion of the lesser trochanter increases from the most ground-dwelling to most arboreal forms, that is, from *Myrmecophaga* to *Tamandua* to *Cyclopes*. However, the lesser trochanter also protrudes medially in extant armadillos, which are all ground-dwelling.

Femur Adduction

The greatly developed femoral adductor muscle group allowed a powerful adduction of the hind limb of Santacrucian sloths, which is consistent with the mechanical requirements for climbing arboreal supports (Fig. 17). Following Argot (2002) and Candela and Picasso (2008), adduction of the thigh would help to force both feet onto each side of the support during climbing, similar to *m. pectoralis* in the forelimb (see Toledo *et al.*, 2013).

Knee Joint

The morphology and functional features of the knee joint have been related to locomotor habits by numerous

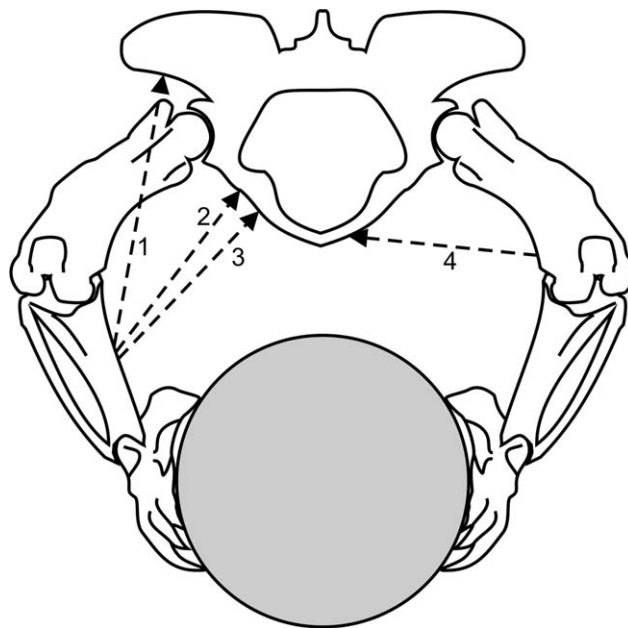


Fig. 17. Function of the adductor musculature during climbing of a support. Dotted lines represent action lines of muscles as follows: 1- *m. sartorius*, 2- *m. gracilis*, 3- *m. semitendinosus*, 4- adductor complex.

authors (Smith and Savage, 1956; White, 1993a,b; Argot, 2002; Sargis, 2002; Candela and Picasso, 2008). Regarding Santacrucian sloths, the functional properties of the knee involved usual flexed stances with great stabilization of the articulation, powerful but not fast extension of zeugopodium (as evidenced by the shallow patellar groove), prevalence of the medial femoral condyle in load transmission, and lateral rotation of the tibia during flexion. Some of these features support climbing habits. First, stabilization of the knee during flexion points to strenuous activities performed by the animal in flexed stances, as in climbing supports. Nevertheless, while it is true that many climbing mammals usually move in flexed postures, their knees are loose and mobile. Powerful action of *m. quadriceps femoris* in such flexed stances has been described for arboreal marsupials by Argot (2002), and contrasts with actions optimizing extension in cursorial forms with deep patellar grooves. However, Szalay and Sargis (2001) and Argot (2002) hypothesized that optimization of the leverage for *m. quadriceps* can be related to increased agility instead of substrate preference. In any case, it is clear that many of the functional features of the knee may be related to dealing with mechanical loads and stresses produced by body mass, as discussed by Milne *et al.* (2012).

The predominance of the medial femoral condyle in supporting mechanical loads is somewhat difficult to interpret biologically. In ground-dwelling extant xenarthrans analyzed here, the medial femoral condyle is the largest, while in arboreal xenarthrans (sloths, *Tamandua* and *Cyclopes*) the condyles are subequal. This pattern is similar to that described by Argot (2002) for arboreal marsupials and Candela and Picasso (2008) for tree porcupines. Similarly difficult to interpret is the

inferred lateral rotation of the tibia during flexion of the knee: perhaps it helped accommodate the feet to the sides of the support, but this hypothesis needs further research.

Flexion and Adduction of the Crus

The great development of leg flexor musculature (*mm. sartorius*, *semitendinosus*, *semimembranosus*, *gracilis*, and *biceps femoris*) indicates that Santacrucian sloths were capable of powerful flexion of the crus and of the entire hind limb. This functional property does not have unequivocal ecological significance itself. However, leg flexor muscles such as *mm. semitendinosus*, *sartorius* and *biceps femoris* surely collaborated to enable adduction during climbing in flexed stances with the knee abducted, as evidence noted above indicates (Fig. 17).

Ankle Joint

The ankle joint of Santacrucian sloths, as explained above, was restricted to parasagittal movements. The rotation axis of the ankle joint is inclined slightly outwardly due to tibial curvature, although the asymmetry of the astragalar trochlea partially counteracted this effect. Little or no eversion-inversion was possible at this level, in contrast to that in extant sloths (Mendel, 1981). High cruro-astragalar mobility has been related to locomotion on arboreal substrates in several groups of mammals (Mendel, 1981; Hildebrand, 1988; Meldrum *et al.*, 1997; Szalay and Sargis, 2001; Argot, 2002; Polly, 2007; Candela and Picasso, 2008). In this context, the restricted ankle mobility of Santacrucian sloths may be more consistent with locomotion on ground. However, the intriguing features of astragali of extant and fossil xenarthrans (Mendel, 1981; de Toledo, 1998; McDonald and De Iuliis, 2008) strongly suggest that further analysis is needed.

Pes

Similar to the manus (Toledo *et al.*, 2013), the pes of Santacrucian sloths had a conservative configuration, mainly when compared with extant sloths, in exhibiting no loss, fusion or reduction of elements. It presents some of the notable features that Hirschfeld (1985) recognized in relation to the acquisition of a pedolateral posture: increased size and robustness of outer digits, dorsomedial rotation of the metatarsal arch and caudal elongation of the calcaneus (see “invertigrade” in de Toledo, 1998), but without exhibiting the degree of pedolateralization as seen in later forms of Megatheria and Mylodontidae (see McDonald, 2012). The pes of Santacrucian sloths was plantigrade, with a prominent metatarsal arch, and well suited for powerful extension. As in other plantigrade mammals (Carrano, 1997), the metatarsals are not longer than the *tuber calcanei*, which represents almost a third of the total length of the pes, a configuration that optimizes force against velocity. The medioplantar prominence of the *tuber calcanei* could surely support a very developed plantar connective pad, similar to that of *Cyclopes* (Meldrum *et al.*, 1997). Other functional features allow less obvious ecological interpretations. The greatly restrictive joint between the sustentacular facet of the calcaneus and the

astragalus resembles the condition described for ground-dwelling Hystricognathi by Candela and Picasso (2008). The implications of rotation of the navicular on the astragalar head remains unclear: perhaps this capability helped to accommodate the inner toes to the substrate when climbing. The toes were capable of powerful flexion, a functional feature that is compatible with climbing faculties.

In summary, the hind limb features of Santacrucian sloths involved a mixing of possible functions, some of them are consistent with locomotion on arboreal substrates, some with locomotion on the ground (knee and ankle stabilization), and others are of ambiguous or equivocal inferential value. However, the most conspicuous functional properties are those compatible with climbing faculties, involving a highly movable hip joint, wide range of abduction of the thigh, powerful adduction and flexion of the leg, a knee joint well suited for flexed, abducted stances, and powerful toe prehension. On the other hand, the knee and ankle joints appeared to be highly stabilized, lacking the mobility described for extant arboreal mammals. This functional scenario leads us to hypothesize that Santacrucian sloths were climbing forms, but somewhat restricted in their agility.

Slight differences in the set of inferred functions of the hind limb among the different genera of Santacrucian sloths were noted, possibly related to locomotor and postural variation. For instance, the hip joint functional properties of *Hapalops* and *Schimostherium* allowed them to adopt a more abducted femoral posture, providing a more agile climbing behavior than *Euchloeops*, *Analcimorphus* and *Prepothierium*. This pattern is in accordance with some results provided by White (1993a, b). The comparatively robust and massive femur of *Prepothierium* could be related with support of its larger body mass. Considering the functional properties of the knee joint, most *Hapalops* specimens and all *Euchloeops* appeared to be slightly more agile than *Prepothierium* and *Analcimorphus*.

Paleobiological Inferences

The results of our analysis provide supplementary support for inferring climbing habits for Santacrucian sloths, as proposed by White (1993a,b,1997), Bargo *et al.* (2012) and Toledo *et al.* (2013). The morphology of the hind limbs suggests that these fossil sloths were capable climbers, but constrained in their agility, mainly by functional features of the ankle joint. Restriction to inversion-eversion movements of the pes differentiates the climbing strategies of Santacrucian sloths from those of the best-known extant climbing mammals (such as primates), suggesting that these sloths could represent a very different pattern of climbing. Here we draw attention to the frequently imprecise usage of the terms “climber” and “arboreal” as synonyms. We consider “climber” to be an animal that climbs or moves on vertical or very sloped substrates (usually branches or logs), as defined by Cartmill (1985), while “arboreal” implies that the animal lives in trees (Hildebrand, 1988) or spends most of its time on trees, especially during foraging (Eisenberg, 1978) and sheltering (Van Valkenburgh, 1987). In accordance with this, arboreal animals are climbing forms (usually very good ones), but not all climbing animals are arboreal. Therefore, the

morphofunctional evidence provided in this work does not allow us to infer how much time Santacrucian sloths spent in trees and or to categorize them as arboreal or semiarboreal animals.

As noted in the Introduction, paleoecological reconstructions must consider body size. White (1993), Croft (2000, 2001) and Bargo *et al.* (2009, 2012) provided body mass estimates of some genera of Santacrucian sloths. Toledo *et al.* (2014) analyzed a larger sample of specimens, including all genera studied here, which these authors considered as medium-sized sloths ranging from around 40 kg to 120 kg. As remarked in Toledo *et al.* (2013) the majority of extant climbing mammals are small (Cartmill, 1985; Hildebrand, 1988), with the exception of the orangutan (*Pongo pygmaeus*, ~90 kg; Nowak, 1991). Nevertheless, there are very good climbers with larger body sizes among extant mammals, such as some felids and ursids, although they are ground-dwelling animals that are not usually classified as “arboreal”. The evidence analyzed here allows the proposition that most Santacrucian sloths had good climbing capabilities, placing them among the heaviest climbing mammals together with the extinct Madagascar giant lemurs (*Megaladapis*, at about 70 kg., and *Archaeoindris*, 197 kg.; Jungers *et al.*, 2002) and Australian fossil vombatiforms (*Nimbadoron*, 70 kg.; Black *et al.*, 2012). Santacrucian sloths also show a limb configuration that would permit them to outmatch the body size constraint by relying on powerful musculature for climbing, but possibly not all of them were arboreal in their substrate preference.

As summarized in our contribution on the forelimb (Toledo *et al.*, 2013), access to an arboreal substrate has a number of advantages, including food resources not available on the ground, resting shelters, avoidance of predation, and more efficacious movement when the terrain is rough or has been flooded (Hildebrand, 1988). On the other hand, it has its disadvantages, mainly related to two mechanical issues: avoiding a fall to the ground and moving through a three-dimensional, substrate showing discontinuity. To face these difficulties, extant climbing mammals exhibit a diversity of postural and locomotor strategies, of which most are well developed in climbing forms (Cartmill, 1985; Hildebrand, 1988). Thus, many acrobatic primates and marsupials leap or glide between supports, while others such as extant sloths and orangutans move more slowly using reaching and bridging strategies *sensu* Hildebrand (1988). Beyond these differences, most climbing forms utilize opposable fingers, prehensile tails, curved claws, and flexed stances, they oppose hands and feet on either side of a branch, or they use different combinations of these functional features to cling to the support (Cartmill, 1985; Hildebrand, 1988). These issues should be considered when evaluating the potential climbing habits of Santacrucian sloths.

The locomotor strategies of Santacrucian sloths were limited in arboreal substrates in comparison to those of extant sloths and other extant climbing mammals, such as primates. This assertion is based on the following observations. First, given the limb proportions and that their morphology improved the mechanical advantage of several muscles optimizing force against speed and agility, leaping may be ruled out as a working hypothesis. Their estimated body sizes (see Toledo *et al.*, 2014)

support this assessment. Second, although capable of powerful prehension, the morphology of the manus and pes offers no evidence of opposable fingers. Third, the comparatively short and robust fore- and hind limbs of the Santacrucian sloths, well suited for the usual effort required of flexed stances, precluded them from relying on their long limbs to apply reaching and bridging strategies (Hildebrand, 1988), as extant sloths do. Due to the same reasons, distributing the body weight over two or more branches, as do extant sloths (Mendel, 1979) and the orangutan (Hildebrand, 1988), was an improbable strategy in Santacrucian sloths, except perhaps for *Eucholoeops* (Toledo *et al.*, 2013). Hence, they were constrained to move on thicker supports. However, Santacrucian sloths were especially well prepared to perform other locomotor and postural strategies exhibited by extant climbing mammals. First, they were all able to apply both manus and pedes on either side of a support with great muscular power. Second, they were capable of forcefully flexing their long-clawed manual and pedal ungual phalanges. Third, they were very well suited to moving in flexed stances and applying great muscular force in these postures. Thus, the Santacrucian sloths would have climbed in a manner resembling the climbing style of *Tamandua* and other mammals that climb slowly, such as the trunk-hugging koala *Phascolarctos cinereus* (White, 1993a, 1997; Smith and Ganzhorn, 1996; Nowak, 1999; Toon and Toon, 2004).

Some variation in posture and locomotion may be proposed among the genera analyzed. Concerning arboreal substrates, *Eucholoeops*, a comparatively graceful form of about 50 kg, exhibited an extended fore- and hind limb posture combined with movable knee and shoulder joints, allowing it a relatively agile climbing style. *Analcimorphus*, with a similar body size, also exhibited extended postures of the hind limb, although its knee was more stabilized and hence not as mobile, so this genus was perhaps a less agile climber. Evidence from the forelimb is lacking for this genus. The similarly sized *Hapalops* appeared to have been a less agile climber with a more abducted and flexed posture, but able to apply stronger muscular forces; thus, it surely relied extensively in forcefully apposing its manus and pedes to the sides of thick branches. The wide variation in body size within *Hapalops* must surely have been reflected in slight differences in climbing abilities, suggesting that further analysis focused specifically on this intrageneric variation is required. Although the functional evidence for *Schismotherium*, a gracile form of about 45 kg, is scarce, this genus showed similar properties for abducted postures of the hind limb, suggesting it was probably a more agile climber compared with *Hapalops* and *Analcimorphus*. Due to similarly scarce functional information, *Peleciodon* is equally difficult to classify, but the morphological evidence available suggests it was a climbing form. Among the larger Santacrucian sloths, *Prepothierium*, the heaviest at some 120 kg, exhibited extended posture of the forelimb and a more stabilized knee joint, suggesting that it was primarily a ground-dwelling form, but based on functional capabilities a limited climbing faculty cannot be ruled out. Due to the scarcity of hind limb material, functional inferences provided here for *Analcitherium* and *Nematherium* (~90 kg) are limited. However, as proposed previously by the authors based on the forelimb

anatomy (Toledo *et al.*, 2013) they were capable digging forms with probably limited climbing faculties. As previously mentioned, climbing animals are limited to moving or resting on supports that can accommodate their body mass, so that the diameter of the support constrains heavier animals, which must avoid the finer terminal branches. Therefore, the Santacrucian mylodonts and *Prepothierium* were probably capable of limited climbing behavior on trunks and/or on the thick branches at the base of the crown of trees, relying for such activity mostly on their powerful musculature.

In order to provide a comprehensive paleobiological characterization of Santacrucian sloths following the protocol defined in the Introduction, their dietary habits must be also considered. Bargo *et al.* (2009) performed a detailed morphofunctional analysis of the masticatory apparatus of *Eucholoeops*, focusing on tooth morphology and reconstructing masticatory mechanics and movements, and compared it with those of other Santacrucian sloths. *Eucholoeops*, with a tooth morphology well suited for shearing and cutting and employed in predominantly orthal (vertical) masticatory movements, was folivorous. This characterization can be extended to other forms with similar tooth morphology, such as *Hapalops*, *Peleciodon*, and *Prepothierium*. On the other hand, the mylodonts *Nematherium* and *Analcitherium* exhibit a pattern similar to that of Pleistocene mylodonts, such as *Scelidotherium* (Bargo and Vizcaino, 2008; Bargo *et al.*, 2012), with a tooth morphology well suited for grinding or crushing and used in mainly lateral masticatory movements. These forms probably had a more diverse diet including fibrous and turgid items such as fruits and tubers, suggesting that they probably spent time on ground, probably digging for dietary items.

In summary, taking into account body size (Toledo *et al.*, 2014), dietary habits and functional features of the forelimb (Toledo *et al.*, 2013) and hind limb provided here, Santacrucian sloths may be characterized ecologically as medium to large-sized quadrupedal, plantigrade herbivorous mammals capable of digging behavior and possessing good climbing abilities, though limited in their locomotor strategies on arboreal supports. These fossil mammals were probably slow climbers, relying on flexed stances, curved claws and a powerful musculature to move on the thicker branches of trees. Evidence about arboreal vegetation analyzed by Brea *et al.* (2012) indicate the presence of dense temperate tree areas in the Santacrucian paleoenvironment, as discussed by Kay *et al.* (2012), that could be used by the fossil sloths as supports for climbing activities.

The smaller genera (*Eucholoeops*, *Analcimorphus*, *Peleciodon*, *Schismotherium*, and *Hapalops*) probably demonstrated a usual climbing behavior. In contrast, the mylodonts *Analcitherium* and *Nematherium* probably moved mostly on the ground, foraging by digging, while *Prepothierium* was mainly a ground-dwelling leaf-eater.

CONCLUDING REMARKS

- The hind limb of Santacrucian sloths is very different from that of extant sloths. The robustness of elements, degree of development of features associated with muscular attachments and ligaments, and the penta-

dactyl pes are characteristics in which the hind limb is strongly similar to that of the extant anteaters *Tamandua* and *Myrmecophaga*.

- The reconstructed hind limb muscles of Santacrucian sloths show strong similarities with that of extant anteaters and, to a lesser degree, extant sloths.
- The musculature was very well developed, allowing these sloths to apply powerful muscular forces, particularly in hind limb adduction, crural flexion and extension, plantar flexion, and phalangeal prehension.
- The hip joint was capable of high mobility and extensive abduction, while the knee and ankle joints were more restricted in their mobility. The knee joint was well suited for frequent flexed stances. The ankle joint was fairly stable and inversion-eversion movements were severely restricted.
- Most of the functional properties of both the fore and hind limb are consistent with climbing faculties, allowing the proposal that Santacrucian sloths were effective climbing mammals. Their climbing strategies were constrained, so they relied largely on muscular strength, flexed stances and curved manual, and pedal unguals to move slowly along thicker branches.

APPENDIX

Extant xenarthrans considered here.

Family	Taxon	Coll. #
Bradypodidae	<i>Bradypus</i> sp.	AMNH 42454; 42838; 74136; 74137; 97315; 133437; 135474; 209940; 211663; 261304
Megalonychidae	<i>Choloepus</i> sp.	AMNH 16873; 35483; 70440; 90269; 139772; 139773; 209941; 265952
Myrmecophagidae	<i>Myrmecophaga tridactyla</i>	AMNH 1020; 100068; 100139; FMNH 15966
	<i>Tamandua</i> sp.	AMNH 23432; 23436; 23437; 23565; 23567; 96258; 211659; 211660
Cyclopedidae	<i>Cyclopes didactylus</i>	AMNH 4780; 167845; 171297; 204662; 213188; FMNH 61853
Dasypodidae	<i>Priodontes</i> sp.	AMNH 130387; 208104; FMNH 25271; 72913
	<i>Cabassous chacoensis</i>	MLP 1183
	<i>Chaetophractus villosus</i>	MLP 821; 785
	<i>Dasypus novemcinctus</i>	MLP 1.I.03.76; 1.I.03.72.

ACKNOWLEDGEMENTS

The authors want to thank M. Reguero (MLP), W. Joyce and D. Brinkman (YPM), J. Flynn, N. B. Simmons, and C. Norris (AMNH), and W. F. Simpson and K. D. Angielczyk (FMNH) for kindly providing access to the collections under their care; Dirección de Patrimonio

Cultural of Santa Cruz Province and Museo Regional Provincial P. M. J. Molina of Río Gallegos (Santa Cruz, Argentina), for support during field work. We also wish to thank J.L. White, G. De Iuliis and two anonymous reviewers for their valuable comments that greatly improved this work.

LITERATURE CITED

- Ameghino F. 1891. Observaciones críticas sobre los mamíferos eocenos de la Patagonia austral. *Revista Argentina de Historia Natural* 1: 328–382.
- Andrews P, Lord JM, Evans EMN. 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol J Linn Soc* 11:177–205.
- Argot C. 2002. Functional-adaptive anatomy of the hindlimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *J Morp* 253:76–108.
- Bargo MS, Toledo N, Vizcaíno SF. 2012. Paleobiology of the Santacrucian sloths and anteaters (Xenarthra, Pilosa). In: Vizcaíno SF, Kay RF, Bargo MS, editors. *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge: Cambridge University Press. p 216–242.
- Bargo MS and Vizcaíno SF. 2008. Paleobiology of Pleistocene ground sloths (Xenarthra, Tardigrada): biomechanics, morphogeometry and ecomorphology applied to the masticatory apparatus. *Ameghiniana* 45:175–196.
- Bargo MS, Vizcaíno SF, Kay RF. 2009. Predominance of orthal masticatory movements in the early Miocene *Eucholoeops* (Mammalia, Xenarthra, Tardigrada, Megalonychidae) and other megatherioid sloths. *J Vertebr Paleontol* 29:870–880.
- Black K, Camens AB, Archer M, Hand SJ. 2012. Herds overhead: *Nimbadon lavarackorum* (Diprotodontidae), heavyweight marsupial herbivores in the Miocene forests of Australia. *PLoS ONE* 7(11):e48213. doi:10.1371/journal.pone.0048213.
- Bock WJ, Von Wahlert G. 1965. Adaptation and the form-function complex. *Evolution* 19:269–299.
- Brea M, Zucol AF, Iglesias A. 2012. Fossil plant studies from late Early Miocene of the Santa Cruz Formation: paleoecology and paleoclimatology at the passive margin of Patagonia, Argentina. In: Vizcaíno SF, Kay RF, Bargo MS, editors. *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge: Cambridge University Press. p 104–128.
- Candela AM, Picasso MJB. 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): indicators of locomotor behavior in Miocene porcupines. *J Morphol* 269:552–593.
- Carrano MT. 1997. Morphological indicators of foot posture in mammals: a statistical and biomechanical analysis. *Zool J Linn Soc-Lond* 121:77–104.
- Cartmill M. 1985. Climbing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. *Functional Vertebrate Morphology*. Chicago: University of Chicago Press. p 73–88.
- Chiarello AG. 2008. Sloth ecology: an overview of field studies. In: Vizcaíno SF, Loughry WJ, editors. *The biology of the Xenarthra*. University Press of Florida, Gainesville. p 269–280.
- Croft DA. 2000. Archaeohyracidae (Mammalia: Notoungulata) from the Tinguiririca Fauna, central Chile, and the evolution and paleoecology of South American mammalian herbivores. PhD Dissertation, University of Chicago, USA.
- Croft DA. 2001. Cenozoic environmental change in South America as indicated by mammalian body size distributions (cenograms). *Divers Distrib* 7:271–287.
- De Iuliis G. 1994. Relationships of the Megatheriinae, Nothrotheriinae, and Planopsinae: some skeletal characteristics and their importance for phylogeny. *J Vertebr Paleontol* 14:577–591.
- De Iuliis G, Pulera D. 2010. The dissection of vertebrates: a laboratory manual. 2nd ed. Amsterdam: Academic Press. 332 p.
- de Toledo PM. 1998. Locomotor patterns within Pleistocene sloths. Unpublished Ph.D Dissertation. Boulder: University of Colorado.
- Delsuc F, Douzery EJP. 2008. Recent advances and future prospects in xenarthran molecular phylogenetics. In: Vizcaíno SF, Loughry WJ, editors. *The Biology of the Xenarthra*. University Press of Florida, Gainesville. p 11–23.
- Eisenberg JF. 1978. The evolution of arboreal herbivores in the Class Mammalia. In: Montgomery GG, editor. *The ecology of arboreal folivores: a symposium held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, 29–31 May, 1975*. Smithsonian Institution Press, Washington. 594 pp.
- Gaudin TJ. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the *craniodental evidence*. *Zool J Linn Soc-Lond* 140:255–305.
- Gaudin TJ, McDonald HG. 2008. Morphology-based investigations of the phylogenetic relationships among extant and fossil xenarthrans. In: Vizcaíno SF, Loughry WJ, editors. *The Biology of the Xenarthra*. Gainesville: University Press of Florida. p 24–36.
- Gray H. 1918. *Anatomy of the Human Body*. Philadelphia: Lea & Febiger; Bartleby 2000, 1396 p.
- Hildebrand M. 1988. *Analysis of vertebrate structure*. 3rd ed. New York: Wiley and Sons. 701 p.
- Hirschfeld SE. 1985. Ground sloths from the Friasian La Venta fauna, with additions to the Pre-Friasian Coyaima fauna of Colombia, South America. *University of California Publications in Geological Sciences* 128:1–91.
- Humphry GM. 1869–1870. The myology of the limbs of the unau, the ai, the two-toed ant-eater and the pangolin. *J Anat Physiol* 4: 17–78.
- Jenkins FAJ, Camazine SM. 1977. Hip structure and locomotion in ambulatory and cursorial carnivores. *J Zool London* 181:351–370.
- Jouffroy FK. 1971. Musculature des membres. In: Grassé PP, editor. *Traité de Zoologie, Tome XVI, 3ème Fasc, Masson, Paris*, p 1–476.
- Jungers WL, Godfrey LR, Simons EL, Wunderlich RE, Richmond BG, Chatrath PS. 2002. Ecomorphology and behaviour of giant extinct lemurs from madagascar. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP, editors. *Reconstructing behavior in the primate fossil record*. New York: Kluwer Academic/Plenum Publishers. p 371–411.
- Kay RF, Madden RH. 1997. Paleogeography and paleoecology. In: Kay RF, editor. *Vertebrate Paleontology in the Neotropics*. Washington DC: Smithsonian Institution Press. p 520–550.
- Kay RF, Vizcaíno SF, Bargo MS. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. In: Vizcaíno SF, Kay RF, Bargo MS, editors. *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge: Cambridge University Press. p 331–365.
- Lessertisseur J, Saban R. 1971. Squelette appendiculaire. In: Grassé PP, editor. *Traité de Zoologie, Tome XVI, 3rd Fasc*. p 709–1078.
- Macalister A. 1869. On the myology of *Bradypus tridactylus*; with remarks on the general anatomy of the Edentata. *Ann Mag Nat Hist* 4:51–67.
- Macalister A. 1875. Report on the anatomy of insectivorous edentates. *Trans Roy Irish Acad* 15:491–510.
- Mariotti V, Facchini F, Belcastro MG. 2007. The Study of Entheses: Proposal of a Standardised Scoring Method for Twenty-Three Entheses of the Postcranial Skeleton. *Collegium Antropol* 31:291–313.
- McDonald HG. 2003. Xenarthran skeletal anatomy: primitive or derived? (Mammalia, Xenarthra). *Seckenberg Biol* 83:5–17.
- McDonald HG. 2012. Evolution of the pedolateral foot in ground sloths: patterns of change in the astragalus. *J Mammal Evol* 19: 209–215.
- McDonald HG, De Iuliis G. 2008. Fossil history of sloths. In: Vizcaíno SF, Loughry WJ, editors. *The Biology of the Xenarthra*. Florida: University Press of Florida. p 24–36.
- Mendel FC. 1979. The wrist joint of two-toed sloths: its relevance to brachiating adaptations in the Hominoidea. *J Morphol* 162:413–424.
- Mendel FC. 1981. The foot of two-toed sloths: its anatomy and potential uses relative to size of support. *J Morphol* 170:357–372.

- Meldrum DJ, Dagosto M, White J. 1997. Hindlimb suspension and hind foot reversal in *Varecia variegata* and other arboreal mammals. *Am J Phys Anthropol* 103:85–102.
- Milne N, Toledo N, Vizcaíno SF. 2012. Allometric and group differences in the xenarthran femur. *J Mamm Evol* 19:199–208.
- Nowak RM. 1999. Walker's Mammals of the World. 6th ed. Baltimore: Johns Hopkins University Press. 1936 p.
- Nyakatura JA, Petrovitch A, Fischer MS. 2010. Limb kinematics of the two-toed sloth (*Choloepus didactylus*, Xenarthra) and its implications for the evolution of the sloth locomotor apparatus. *Zoology* 113:221–234.
- Oxnard C. 1984. The Order of Man. Hong Kong: Hong Kong University Press. 366 p.
- Perkins ME, Fleagle JG, Heizler MT, Nash B, Bown TM, Tauber AA, Dozo MT. 2012. Tephrochronology of the Miocene Santa Cruz and Pinturas Formations, Argentina. In: Vizcaíno SF, Kay RF, Bargo MS, editors. Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation. Cambridge: Cambridge University Press. p 23–40.
- Plotnick RE, Baumiller TK. 2000. Invention by evolution: functional analysis in paleobiology. In: Erwin DH, Wing SL, editors. Deep time. Paleobiology's perspective. *Suppl Paleobiol* 26:305–321.
- Polly PD. 2007. Limbs in mammalian evolution. In: Hall BK, editor. Fins into limbs: evolution, development, and transformation. Chicago: University of Chicago Press. p 245–268.
- Pujos F, De Iuliis G, Argot C, Werdelin L. 2007. A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implication for sloth history. *Zool J Linn Soc* 149:179–235.
- Radinsky LB. 1987. The evolution of vertebrate design. Chicago: University of Chicago Press. 188 p.
- Reed KE. 1998. Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. *Paleobiology* 24:384–408.
- Salas R, Pujos F, de Muizon C. 2005. Ossified meniscus and cyamofabella in some fossil sloths: a morpho-functional interpretation. *Geobios* 38:389–394.
- Sargis EJ. 2002. Functional morphology of the forelimbs of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *J Morphol* 253:10–42.
- Scott WB. 1903–1904. Mammalia of the Santa Cruz beds. I. Edentata. In: Scott WB, editor. Reports of the Princeton University Expeditions to Patagonia 1896–1899. Princeton: Princeton University Press. p 1–364.
- Smith AP, Ganzhorn JU. 1996. Convergence in community structure and dietary adaptation in Australian possums and gliders and Malagasy lemurs. *Aust J Ecol* 21:31–46.
- Smith MJ, Savage RJG. 1955. Some locomotory adaptations in mammals. *Zool J Linn Soc-Lond* 42:603–622.
- Szalay FS, Sargis EJ. 2001. Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria. *Geodiversitas* 23:139–302.
- Szalay FS, Schrenk F. 1998. The Middle Eocene *Eurotamandua* and a Darwinian phylogenetic analysis of “edentates”. *Kaupia* 7:97–186.
- Toledo N, Cassini GH, Vizcaíno SF, Bargo MS. 2014. Mass estimation in fossil sloths (Xenarthra, Folivora) from the Early Miocene Santa Cruz Formation of Patagonia, Argentina. *Acta Palaeontol Pol* 59:267–280.
- Toledo N, Bargo MS, Vizcaíno SF. 2013. Muscular reconstruction and functional morphology of the forelimb of Santacrucian (early Miocene) sloths (Xenarthra, Folivora) of Patagonia. *Anat Rec* 296:305–325.
- Toon S, Toon A. 2004. Koalas (Phascolarctidae). In: Grzimek Animals Life Encyclopedia. Detroit: Thomson Gale Group.
- Van Couvering JAH. 1980. Community evolution in Africa during the Cenozoic. In: Berensmeyer AK, Hill A, editors. Fossils in the making. Chicago: University of Chicago Press. p 272–298.
- Van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. *J Vertebr Paleontol* 7:162–182.
- Vizcaíno SF, Bargo MS, Fariña RA. 2008. Form, function, and paleobiology in xenarthrans. In: Vizcaíno SF, Loughry WJ, editors. The biology of the Xenarthra. Gainesville: University Press of Florida. p 86–99.
- Vizcaíno SF, Bargo MS, Kay RF, Fariña RA, Di Giacomo M, Perry MG, Prevosti FJ, Toledo N, Cassini GH, Fernicola JC. 2010. A baseline paleoecological study for the Santa Cruz Formation (late-Early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeogr Palaeoclimatol* 292:507–519.
- Vizcaíno SF, Bargo MS, Kay RF, Milne N. 2006. The armadillos (Mammalia, Xenarthra) of the Santa Cruz Formation (Early-Middle Miocene). An approach to their paleobiology. *Palaeogeogr Palaeoclimatol* 237:255–269.
- Vizcaíno SF, Fernicola JC, Bargo MS. 2012. Paleobiology of Santacrucian glyptodonts and armadillos (Xenarthra, Cingulata). In: Vizcaíno SF, Kay RF, Bargo MS, editors. Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation. Cambridge: Cambridge University Press. 194–215.
- White JL. 1993a. Functional and phylogenetical implications of the postcranial skeleton of fossil sloths for the evolution of arboreality in tree sloths. PhD dissertation. State University of New York at Stony Brook. p 835.
- White JL. 1993b. Indicators of locomotor habits in Xenarthrans: evidence for locomotor heterogeneity among fossil sloths. *J Vertebr Paleontol* 13:230–242.
- White JL. 1997. Locomotor adaptations in Miocene Xenarthrans. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ, editors. Vertebrate paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia. Washington DC: Smithsonian Institution Press. p 246–264.
- Windle BCA, Parsons FG. 1899. On the myology of Edentata. *P Zool Soc Lond* 1:314–339.