

Recent Advances on Variability, Morpho-Functional Adaptations, Dental Terminology, and Evolution of Sloths

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Abstract The occasion of the Xenarthra Symposium during the ICVM 9 meeting allowed us to reflect on the considerable advances in the knowledge of sloths made by the “X-community” over the past two decades, particularly in such aspects as locomotion, mastication, diet, dental terminology, intraspecific variation, sexual dimorphism, and phylogenetic relationships. These advancements have largely been made possible by the application of cladistic methodology

(including DNA analyses) and the discovery of peculiar forms such as *Diabolotherium*, *Thalassocnus*, and *Pseudoglyptodon* in traditionally neglected areas such as the Chilean Andes and the Peruvian Pacific desert coast. Modern tree sloths exhibit an upside-down posture and suspensory locomotion, but the habits of fossil sloths are considerably more diverse and include locomotory modes such as inferred bipedality, quadrupedality, arboreality or semiarboreality, climbing, and an aquatic or semi-aquatic lifestyle in saltwater. Modern tree sloths are generalist browsers, but fossil sloths had browsing, grazing, or mixed feeding dietary habits. Discovery of two important sloth faunas in Brazil (Jacobina) and southern North America (Daytona Beach and Rancho La Brea) have permitted evaluation of the ontogenetic variation in *Eremotherium laurillardii* and the existence of possible sexual dimorphism in this sloth and in *Paramylodon harlani*. A new dental terminology applicable to a majority of clades has been developed, facilitating comparisons among taxa. An analysis wherein functional traits were plotted onto a phylogeny of sloths was used to determine patterns of evolutionary change across the clade. These analyses suggest that megatherioid sloths were primitively semiarboreal or possessed climbing adaptations, a feature retained in some members of the family Megalonychidae. Pedolateral stance in the hind-foot is shown to be convergently acquired in Mylodontidae and Megatheria (Nothrotheriidae + Megatheriidae), this feature serving as a synapomorphy of the latter clade. Digging adaptations can only be securely ascribed to scelidotheriine and mylodontine sloths, and the latter are also the only group of grazing sloths, the remainder being general browsers.

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Introduction

Since the 18th century, the scope of research in vertebrate paleontology has evolved considerably. Although the discovery, systematic descriptions, and anatomical comparisons of vertebrate specimens remain at the heart of the discipline, cladistic phylogenetic reconstructions based on mitochondrial DNA as well as traditional osteological characters, biomechanical and paleobiological reconstructions using morpho-functional analysis, and an appreciation of variation (among others) have significantly altered our views and enhanced our understanding of fossil organisms.

South America was an island continent during much of the Cenozoic. This insulation, similar to that of Madagascar and Australia, helped produce several peculiar endemic mammalian groups, including Xenarthra, which Hoffstetter (1982) referred to as “un groupe singulier de la faune néotropicale.” Xenarthra comprises three distinct types: the armored xenarthrans or Cingulata (armadillos, pampatheres, and glyptodonts), and, united in Pilosa, Vermilingua (South American anteaters) and Tardigrada (or Folivora, fossil sloths and the modern tree sloths *Bradypus* and *Choloepus*).

In contrast with other mammals, tree sloths are not pronograde but exhibit an unorthodox upside-down posture and locomotory style (e.g., Nyakatura and Fischer 2010; Nyakatura 2012). These highly specialized, almost completely arboreal and folivorous mammals move very slowly but are also excellent swimmers. Paleontologists, however, have long recognized that the pronounced skeletal differences between modern and fossil sloths largely preclude the use of modern sloths as analogues for inferring the locomotor habits of their fossil kin. Workers have thus, particularly over the last few decades, devised novel research strategies to investigate the locomotion, mastication, diet, and other aspects of the life habits of fossil sloths (e.g., Vizcaíno 2009). Combined with studies that have broadened our concept of interspecific variation and the discovery of new fossil sites in South America, these recent developments have had a considerable impact on our concept of extinct tardigrades.

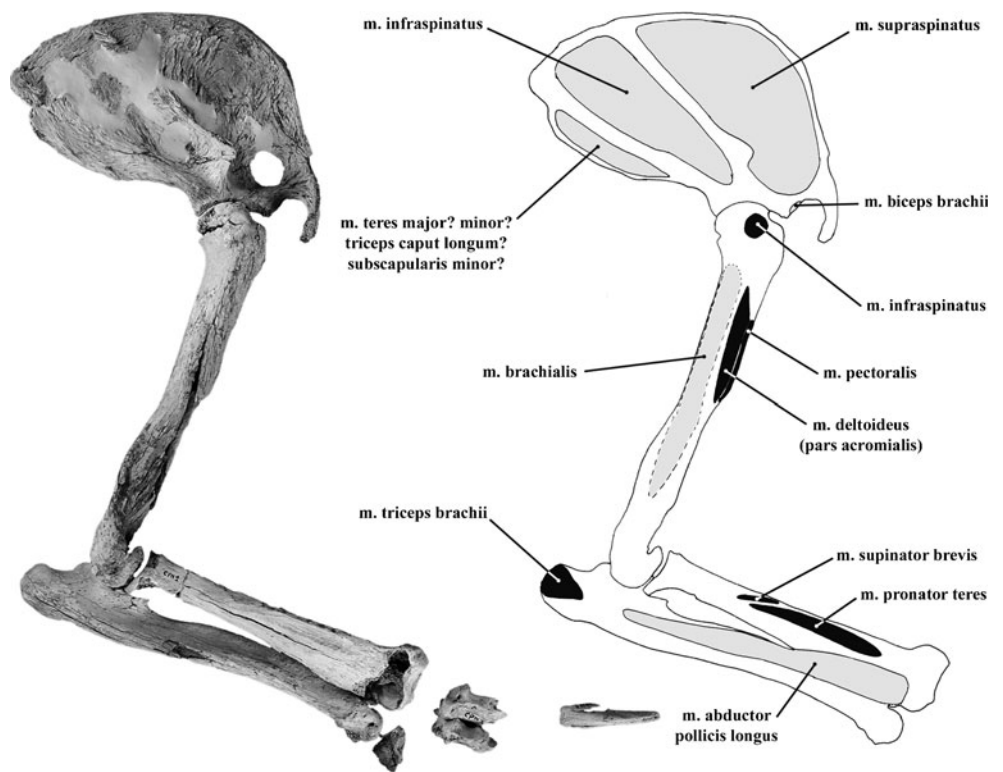
Locomotion Diversity

As with most modern taxa, early primitive xenarthrans (i.e., armadillos) were fossorial. The quadrupedal suspensory locomotion present in modern sloths has not been recorded among fossil sloths. The latter are commonly considered “ground sloths,” reflecting the striking contrast in their habits and locomotion compared to the unique (though almost certainly convergent) arboreal lifestyle of tree sloths. The latter are represented by six species (assigned to the genera *Bradypus* and *Choloepus*) exclusively restricted to forested regions of Central and South America (Reid 1997;

Gardner 2008). Ground sloths were much more diverse (at least 400 taxa distributed among 90 genera), abundant and widespread, and colonized a diversity of environments: from the Patagonian steppes during the Oligocene to the plains of Quaternary Alaska; and the Miocene deserts of the Peruvian Pacific coast to the Oligo-Pliocene Andean Altiplano. Modern tree sloths are relatively small (2.5–8.5 kg), whereas ground sloths, commonly called “giant,” ranged in mass from tens of kilograms (e.g., *Hapalops* and the Megalonychidae *Neocnus*) to hundreds of kilograms (e.g., Nothrotheriidae and Scelidotheriinae) or several tons (e.g., Lestodontinae and Megatheriinae) (see Fariña et al. 1998 and Christiansen and Fariña 2003 for detailed estimations). Given the great mass of many fossil sloths (and those initially known from the fossil record were extremely heavy) – it is difficult to imagine them as having suspended themselves from branches – most fossil forms have traditionally been considered terrestrial. Taking Megatheriinae as an example, skeletal remains of *Megatherium* and a trackway attributed to this genus (from Pehuén-Có, Casinos 1996; Blanco and Szerwonogora 2003) suggest that these sloths were likely quadrupedal and “capable of positioning themselves in an upright position on their hind limb” (McDonald 2007: 206). A common condition among ground sloths is a rotation of the feet so that they contact the ground on their lateral and plantolateral portions. This pedolateral stance occurs in most sloth lineages but not in all taxa (see below), and also occurs in Vermilingua. Orr (2005) suggests convergent knuckle-walking adaptations between African hominids and modern anteaters. A similar condition occurred in giant megatheriine and mylodontid ground sloths. Finally, Quaternary mylodontid sloths (i.e., *Scelidotherium* and *Glossotherium*) are considered as the probable builders of paleoburrows discovered in Argentina based on size and the presence of claw marks preserved on their walls and ceilings (Vizcaíno et al. 2001).

Despite the stereotypical concept of large, ground-walking sloths, recent analyses have suggested arboreality or semi-arboreality for several smaller-sized Santacrucian and Antillean fossil sloths (White 1993) and *Diabolotheium* from Pleistocene levels of the Peruvian desert coast (Pujos et al. 2007). Climbing capabilities, somewhat comparable to those of some marsupials and primates, were proposed for the Peruvian taxon based on such features as the considerable mobility of the elbow, hip, and ankle joints, the posterior convexity of the ulna, a very short olecranon, a proximodistally compressed scaphoid, and a wide range of digital flexion (Pujos et al. 2007; Fig. 1). However, recent and more abundant discoveries of this species in caves of Peru and Argentina (Pardiñas et al. 2008; Shockey et al. 2009) may suggest that *Diabolotheium* was more of a rock climber, capable of moving easily on rocky, uneven terrain, rather than a tree climber,

Fig. 1 Reconstruction of arm musculature origins (grey raster) and insertions (black raster) of late Pleistocene “climber sloth” *Diabolootherium nordenskioldi* (after Pujos et al. 2007: fig. 9)



an ability that might also explain its presence in remote caves. Additionally, the discovery of the Mio-Pliocene nothrotheriid *Thalassocnus* from the Peruvian coast (e.g., *T. natans*; Muizon and McDonald 1995) revealed an unsuspected diversity in the locomotion of fossil “ground sloths.” Nearly complete specimens of this nothrotheriid sloth have been recovered from marine deposits of the Pisco Formation in association with sharks, marine bony fishes, and marine mammals. Taphonomic arguments combined with peculiar anatomical adaptations (mainly of the femur and caudal vertebrae) permitted the authors to suggest the novel (for a sloth) possibility of an aquatic or semi-aquatic lifestyle in saltwater. If *Thalassocnus* was a terrestrial mammal, arid conditions during the Neogene on the Pacific coast may have obliged it to enter the sea to feed on seaweed or seagrass (McDonald and Muizon 2002).

The ancestral locomotory condition of Tardigrada is uncertain. The earliest form, *Pseudoglyptodon chilensis* (early Oligocene 31.5 Ma, McKenna et al. 2006), is not represented by postcranial elements. The mylodontine *Octodontotherium* (late Oligocene, 27–29 Ma, Flynn and Swisher 1995) is the most basal sloth represented by abundant skeletal elements (Gaudin 2004). It is a robust, medium- to large-sized form. Its postcranial elements (e.g., tibia and carpal-tarsal elements such as the astragalus) exhibit strong similarities to more recent mylodontine forms that are generally considered terrestrial and quadrupedal. During this period, the small-sized megalonychid *Deseadognathus* is recorded from the late Oligocene of Patagonia, but is represented only by mandibular remains, so

that the locomotory habits of early Megalonychidae are unknown.

Mastication, Diet, and Dental Terminology

Skull and mandibular morphology, muscular attachment sites, tooth morphology, and cusp organization have recently been studied to try to obtain new information on diet and mastication of sloths and to contribute to our understanding of their paleoecology. Tardigrada do not possess incisors or true canines, and the cheek teeth are located exclusively on the maxilla and defined functionally as caniniforms or molariforms. The plesiomorphic dental formula observed in the Oligocene *Pseudoglyptodon* and *Octodontotherium* is comprised of 1/caniniform-4/3 molariforms (Pujos and De Iuliis 2007). Xenarthran teeth lack enamel [except for the Eocene armadillo *Utaetus buccatus* (Simpson 1932; Kalthoff 2011) and juveniles of the extant armadillo *Dasypus* (Martin 1916)] and each tooth is composed of dentine, a layer of outer hard orthodentine surrounding a core of softer inner vasodentine, and cementum, covering the non-occlusal periphery (Green 2009; Kalthoff 2011). The outer dentine functions like enamel (MacFadden et al. 2010) and retains compositional similarities to the dentine of non-xenarthran eutherian mammals. For these reasons, several xenarthran clades, particularly giant extinct cingulates (glyptodonts and pampatheriids), have adopted hypselodont teeth (high crowned and ever growing; also applicable to

sloths) as a feeding strategy (Vizcaíno 2009). Ground sloths, like modern tree sloths, are generally considered to have been herbivorous. Depending on the authors and the taxa analyzed, however, browsing, grazing, or mixed feeding dietary habits have been proposed.

The dental terminology applied to the highly specialized teeth of xenarthrans is ambiguous and the teeth have never been correlated to the tribosphenic dentition of most other mammals. Bargo et al. (2009) proposed a new dental terminology for molariform teeth based on the early Miocene Miocene Megalonychidae *Eucholoeops*. Pujos et al. (2011), following Bargo et al. (2009), refined the terminology, making it applicable to all tardigrade clades. A caniniform tooth, when present, exhibits a single cusp/cuspoid. The molariform teeth bear three cusps/cuspids organized on two approximately transverse loph/lophids. Following Bargo et al. (2009), Pujos et al. (2011) described the following cusps and cuspids: cusp/cuspoid C: mesial (or sometimes slightly mesiolingual); cusp/cuspoid A: distolingual or lingual cuspoid on m4 of *Hiskatherium*; and cusp/cuspoid B: distolabial. The mesiolingual or mesial loph/lophid connects cusp/cuspids A and C and extends labially from cusp/cuspoid C in the direction of the labial opening of the central valley (modified from Bargo et al. 2009); and the distal loph/lophid: connects cusp/cuspids A and B and extends slightly labially from cusp/cuspoid B in the direction of the labial opening of the central valley (see Bargo et al. 2009). Cusps/cuspids are not, or are not easily, observable in molariform teeth of *Pseudoglyptodon*, terminal scelidotheres, Mylodontidae (Bargo 2003), and all members of the megatheriine clade (Pujos et al. 2011). This terminology permits a straightforward nomenclature based on cusp/cuspoid position and facilitates comparisons among sloths.

Microwear studies are useful in reconstructing diet in extant sloths. Orthodontine microwear analysis allows recognition of functional division of modern Xenarthra (except edentulous anteaters) into four dietary categories (Green 2009). Armadillos are carnivore-omnivores or insectivores, and sloths arboreal folivores (*Bradypus*) or frugivore-folivores (*Choloepus*). High scratch values and the number and depth of scratches present on the teeth of the nothrotheriid *Nothrotheriops shastensis* suggest an herbivorous paleodiet for this Quaternary North American sloth comparable to that of extant folivores (Green 2009). This is consistent with previous analyses of its diet based on coprolites assigned to this taxon (e.g., Hansen 1978). Geochemical analysis using stable isotopes have been performed on xenarthran outer dentine (which presents a mineralogy and composition similar to regular dentine) to obtain information on their diets (Green 2009; MacFadden et al. 2010). The diets of extant tree sloths have been carefully investigated (especially *Bradypus*, *Choloepus* to a lesser extent), and both are generalist browsers (Chiarello 2008). In contrast, the dietary habits of most giant ground

sloths were, until about a decade ago, poorly known. Studies of the masticatory apparatus of sloths by Bargo (2001a, b), Bargo et al. (2006a, b), Bargo and Vizcaíno (2008), and Vizcaíno et al. (2006) investigated several aspects of ground sloth feeding paleobiology, such as masticatory musculature and muzzle reconstruction (Bargo et al. 2006a; Fig. 2); hypsodonty variation as related to dietary preferences, habitat and habits; the development of morpho-functional analyses of the masticatory apparatus to obtain information on dietary habits; and the relationship between dental occlusal surface area and diet. The main results of these and other studies (e.g., Naples 1987, 1989; Muizon et al. 2004) indicate several possibilities for ground sloths within the general herbivore regimes, such as mixed feeding, browsing, grazing, subterranean grubbing, and aquatic grazer.

Intraspecific Variation and Possible Sexual Dimorphism

Since the last half of the 19th century, isolated vertebrate remains, including those of ground sloths, have commonly been interpreted as new taxa, often without consistent diagnoses. During the last few decades, however, several researchers have begun analyzing the abundant and

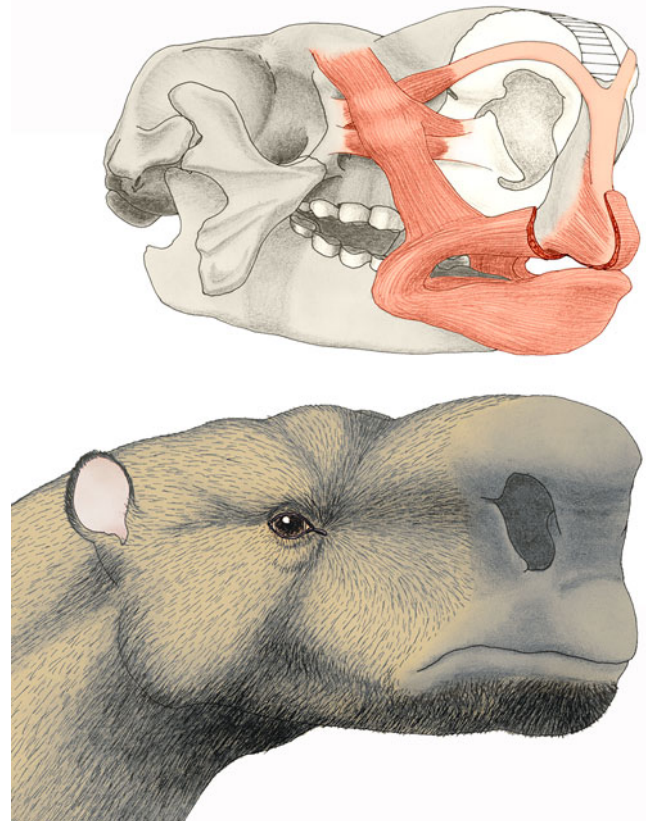


Fig. 2 Reconstruction of muscles (*top*) and external appearance (*bottom*) of skull and mandible of Quaternary giant ground sloth *Mylodon darwini* (after Bargo et al. 2006a: fig. 6)

exceptionally well-preserved Quaternary sloth assemblages discovered, some rather recently, in North and South America (e.g., Rancho La Brea and Daytona Beach in USA; Minas Gerais in Brazil) with the aim of synthesizing a broad range of information, rather than creating new taxa. Such systematic and morphometric analyses on ground sloth communities (many from the same stratigraphic level of a single locality) suggest the possible existence of intraspecific variation and sexual dimorphism in these large mammals. Knowledge of variation in living Tardigrada would be extremely useful for interpreting fossil forms. For example, a large sample of 62 modern tree sloths (including 48 specimens of the three-toed sloth *Bradypus torquatus*) studied by Lara-Ruiz and Chiarello (2005) revealed notable size variation and sexual dimorphism. In *B. torquatus*, females are generally larger than males and exhibit external differences in color and, of course, in the shape of the external genitalia. However, skeletal differences have not, to our knowledge, been assessed for modern forms.

Sexual dimorphism is suggested in the Panamerican giant megatheriid ground sloth *Eremotherium laurillardii*. Based on large collections recovered from caves near Jacobina (Bahia State, Brazil), Cartelle and Bohórquez (1982) suggested that in specimens considered males the sagittal crest is more developed and bifurcated and the dorsal border of the skull is more horizontal and less convex than in females. De Iuliis (1996) and Cartelle and De Iuliis (2006), studying North American specimens of the same taxon from the Daytona Beach Bonebed in combination with the Brazilian material, identified notable differences in the transverse diameter of the pelvis and shape of the pelvic canal as “possible evidence for sexual dimorphism” (Cartelle and De Iuliis 2006: 201). Possible sexual dimorphism was also suggested in Mylodontidae by McDonald (2006), who studied 39 skulls of *Paramylodon harlani* from Rancho La Brea (California, USA). This author separated the specimens into two distinct morphs based on differences related to skull proportions and robustness of the caniniform. Effectively, these were the characters on which Stock (1917) separated *Paramylodon harlani* from Rancho La Brea in two subspecies: *P. harlani harlani* and *P. harlani tenuiceps*. These two morphotypes could also be interpreted as male and female of a single species where the female is represented by the more slender skulls with reduced caniniform teeth. Similar differences have been also observed in another Quaternary Mylodontidae, *Glossotherium robustum* (Christiansen and Fariña 2003). Sexual dimorphism is probably present in other clades but its demonstration will require more abundant samples than are currently available. Intraspecific variation, long ignored for ground sloths, has been recently established for some ground sloths, such as the megatheriines *Megatherium* and *Eremotherium* (Fajardo and Lague 1999; De Iuliis and Pujos 2006; De Iuliis et al. 2009). However, several specimens

of the mylodontid scelidotheriine *Scelidodon chiliensis* discovered in Peru do not present much variation in size and form (F.P. pers. obs). Given the probable existence of sexual dimorphism and intraspecific variation in several ground sloth clades, judicious assessment of characters should be practiced in the erection of new taxa, particularly (as is often the case) when our samples are exceedingly small and fragmentary (see De Iuliis 2010).

Discovery of “Peculiar” Sloths and New Prospecting Areas

Advances in paleontological knowledge are clearly related to new discoveries and, more generally, field work — this is especially true for South American endemic mammals. Since the latter part of the 19th Century, the “cradle” of sloth evolution was widely considered to have been located in Argentina and Brazil. This perception was due largely to the abundance of material recovered and the existence of strong paleontological traditions in these countries, led by such pioneers as J. Reinhardt, P.W. Lund, F. and C. Ameghino, and W. B. Hatcher. As well, these countries have large areas that are reasonably accessible and that preserve fossils in relatively recoverable positions. It is no coincidence, therefore, that the majority of current South American paleontologists are Argentinean and Brazilian. Sloths colonized the West Indies early (probably during the late Oligocene) and, slightly later, North America, first during the late Miocene and then more abundantly during the late Pliocene-Pleistocene over the Isthmus of Panama (McDonald and De Iuliis 2008). It is clear, then, that sloths must also have been important biotic elements in other parts of South America, for such as in the more northerly parts of the continent. However, the geography of South America has been an important limiting factor in fossil research. For example, Patagonia, the Pampas of Buenos Aires Province, and the caves of Brazil are reasonably accessible and rich in fossils, facilitating repeated prospecting and collecting. In contrast, most areas of the Andes are extremely difficult to access (principally in Peru, Bolivia, and Chile); and the Amazon region, which represents a third of the continent, was long ignored on the assumption that it was fossil poor (forest regions are generally considered poorly fossiliferous fossils based on bedrock acidity).

Since the 1980s several unexpected forms have helped change our views on the origin, locomotion, diet, migrations, and adaptations of sloths. In Peru, two peculiar sloths have been recently described: *Thalassocnus* (Muizon and McDonald 1995) and *Diabolotherium* (Pujos et al. 2007), two small- to medium-sized taxa that have considerably expanded our knowledge of locomotion in fossil sloths. *Thalassocnus* was recovered from Mio-Pliocene marine

deposits of the Pisco Formation. This coastal Peruvian area, a northern extension of the Atacama Desert, is a paleontological outcrop notable for its marine vertebrate and invertebrate faunas. Some few isolated remains of continental mammals found (F.P. pers. obs.) probably represent individuals swept away by coastal marine currents, whereas the sloth *Thalassocnus* is the only nonmarine vertebrate abundantly recovered in this area. One surprising aspect of *Thalassocnus* is its extraordinary adaptation to a marine habitat. As the Peruvian coast was a desert during the Neogene, Muizon et al. (2004) suggested that this nothrotheriid had aquatic or semi-aquatic habits, living on the coast, and entering the water to feed on seaweed or seagrass (McDonald and Muizon 2002). The excellent preservation of vertebrate fossils from the Pisco Formation yielded five *Thalassocnus* species, the first well-preserved and nearly continuously represented xenarthran lineage for which it is possible to trace the evolution of feeding and aquatic adaptations (Muizon et al. 2004). *Thalassocnus* remains have recently been described from the late Miocene of northern Chile (Bahía Inglesa Formation), expanding its range outside the Pisco Formation (Canto et al. 2008).

The first remains of *Diabolotherium* were discovered at the beginning of the 20th century from the Peruvian Andes close to Lake Titicaca, but this genus was only recently formally presented to the scientific community by Pujos et al. (2007), thanks to the discovery by Hoffstetter in 1975 of a partial skeleton near the northern Peruvian coastal city of Trujillo. Initially interpreted as a possible climbing tree sloth (Pujos et al. 2007), recent discoveries of more complete skeletons from caves in the Peruvian Andes (Shockey et al. 2009) may shift our perspective with respect to the significance of the anatomical features first noted by Pujos et al. (2007), so that *Diabolotherium* might more appropriately be considered as adapted to clamber over rocky terrain. Such ability would have facilitated extensive migration between Peru, Chile (F.P. pers. obs), and Argentine Patagonia (Pardiñas et al. 2008).

The origin of sloths is unclear. Remains of the early mylodontoid sloth *Octodontotherium* are abundant in Deseadan levels of Argentina, but the early and late Oligocene *Pseudoglyptodon* is considered the earliest member of Tardigrada (Engelmann 1987; McKenna et al. 2006; Pujos et al. 2007), and it may alter our view of ancestral conditions in sloths (Fig. 3). This taxon, of uncertain phylogenetic affinities and only represented by badly preserved cranio-mandibular remains, may not possess the commonly accepted plesiomorphic sloth dental formula (i.e., 1/1 caniniform – 4/3 molariform) (Engelmann 1987). *Pseudoglyptodon chilensis* apparently lacks an upper tooth; its dental formula is 1/1 caniniform – 3/3 molariform according to McKenna et al. (2006). As the two most anterior upper teeth of *Octodontotherium* are caniniform, and as the rostral region



Fig. 3 Hypothetical life reconstruction of oldest Tinguirirican sloth *Pseudoglyptodon chilensis*

of *Pseudoglyptodon* (SGO PV 2995) is missing, it may be that a more anterior tooth (presumably a first anterior caniniform) is not preserved in this skull. In any event, the phylogenetic relationships of *Pseudoglyptodon* to primitive members of other sloth families have not been resolved.

Tree sloths have not migrated far north of the Panamanian isthmus because of their peculiar locomotory style and lack of suitable habitat, but members of the major tardigrade clades (Megalonychidae, Mylodontidae, Megatheriidae, and Nothrotheriidae) penetrated far and wide into the North American continent, beginning in the late Miocene with the early mylodontid *Thinobadistes* (Webb 1989) and megalonychid *Pliometanastes* (Hirschfeld and Webb 1968). Among the best known representatives of the tardigrade clades in North America, we may note *Paramylodon* (Mylodontidae), *Megalonyx* (Megalonychidae), *Eremotherium* (Megatheriidae), and *Nothrotheriops* (Nothrotheriidae). The Megatheriinae *Eremotherium eomigrans*, about equal in size to its more widespread relative *E. laurillardii* (also present in North America), was described from Florida by De Iuliis and Cartelle (1999). It is characterized by a plesiomorphic pentadactyl manus and two distinct carpal arrangements, a striking example of the considerable plasticity of ground sloths. The taxon is important not only because it illustrates the plesiomorphic megatheriine condition of the manus, but also because it is the first member of Megatheriinae to have migrated to North America during the Great American Biotic Interchange (De Iuliis and Cartelle 1999).

The discovery of these new forms has changed our views on sloth origins, evolution, and adaptations, but equally, as if not more notable, is that these advances are based on material recovered from relatively recently prospected fossiliferous regions of South America. Indeed, many of these taxa were discovered beyond the traditional fossil-bearing regions of Argentina and Brazil. The emergence of a

sustained paleontological tradition, particularly in Peru, Uruguay, Chile, and Venezuela, and improvements of laws protecting these countries' paleontological heritage have permitted, over the last two decades, the discovery, preparation, and conservation in their own institutions of mammals distinct from those known from classically collected localities in Argentine Patagonia. The divergent sloth fauna from these new areas encompass some of the taxa discussed above as well as other significant new forms, including *Diabolotherium* from Quaternary Andean caves and the coastal desert (Pujos et al. 2007; Shockey et al. 2009) and *Thalassocnus* from the Mio-Pliocene of the Pisco Formation. (Muizon and McDonald 1995; McDonald and Muizon 2002) in Peru; the late Miocene Mylodontinae *Kiyumylodon* and *Lestobradys* (Rinderknecht et al. 2007, 2010) from Uruguay; late Miocene and Pliocene Mylodontidae and Megatheriidae from the Urumaco and Codore formations (Carlini et al. 2006a, b) of Venezuela; and the early Oligocene *Pseudoglyptodon* (McKenna et al. 2006) from Chile. But we may expect further advances in our knowledge from research on the traditionally neglected region of Amazonia. Preliminary results of recent explorations in late Miocene outcrops of Amazonian beds of Brazil (Frailey 1986; Cozzuol 2007) and Peru (Antoine et al. 2007), include the recent description of the Miocene nothrotheriid *Mionthropus cartellei* by De Iuliis et al. (2011). These discoveries serve to raise our hopes for filling in the picture of South American sloth history and connecting the faunas from northern and southern South America.

Phylogeny Versus Locomotion/Feeding

As should be amply clear from the preceding discussion, much progress has been made toward understanding the diet and locomotory habits within the large radiation of extinct and extant sloths. Inferences regarding modes of feeding, locomotion, and locomotory posture can be traced back to the earliest literature on sloths. Basing their functional interpretations on skeletal structures in individual taxa and extending their insights by implication to extinct sloths in general, Cuvier (1823) suggested the giant *Megatherium* was a digger that fed on roots and tubers, whereas Owen (1842) inferred that *Glossotherium* was a bipedal browser, and Stock (1925) suggested that *Paramylodon* was a grazer of grasses and low-lying shrubs. Authors like Winge (1941), Hoffstetter (1958), and Patterson and Pascual (1968) inferred that Miocene sloths such as *Hapalops* might have been semiarboreal, based on anatomical features including the reduction of xenarthrous vertebral articulations, modifications of the astragalus for pedal torsion, and increased capacity for supination of the forelimb, as indicated by the shape of the radial head. More

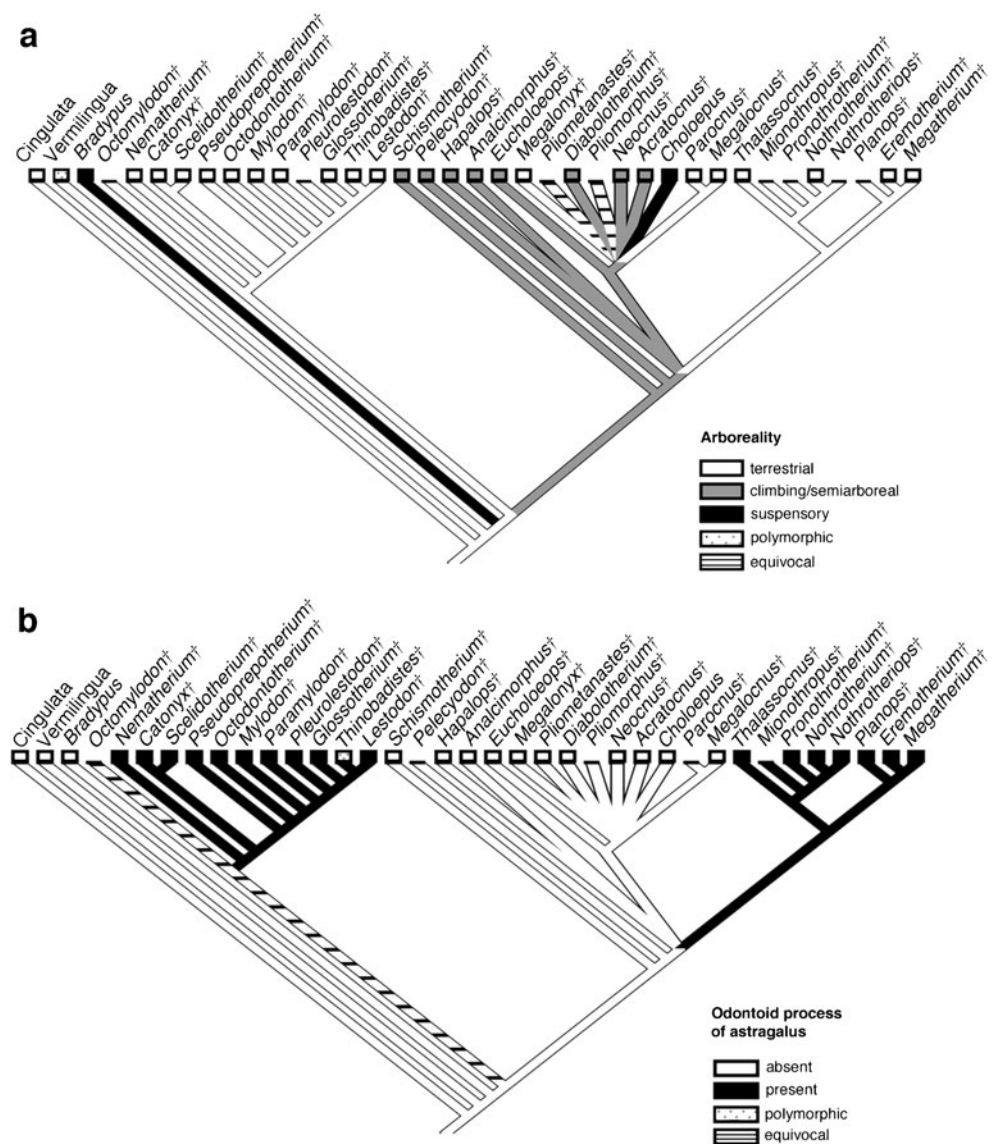
recent and sophisticated examples of such functional analyses of individual taxa can be found throughout the literature, and indeed, have been summarized in the earlier portions of this paper (e.g., Pujos et al. 2007; Green 2009). These have been supplemented by several more general functional studies of feeding and locomotion in sloths that have attempted to incorporate a wider variety of sloth taxa. These include the morphometric studies of White (1993, 1997) and the feeding studies of Bargo, Vizcaíno, and colleagues (Bargo et al. 2006a, b; Bargo and Vizcaíno 2008). While these studies are welcome and more like them are sorely needed, we felt that one element lacking in such studies was an explicit attempt to interpret these results in a phylogenetic context, so that general conclusions about sloth evolutionary patterns could be placed on a more sure phylogenetic footing.

Toward that end, we have plotted several functional traits onto a phylogenetic tree for sloths in an attempt to understand their distribution throughout the clade (Figs. 4 and 5). The tree is based largely on Gaudin (2004), with several modifications. Three extinct taxa, *Thalassocnus* and *Diabolotherium*, have been added to the tree. Relationships among nothrotheriid sloths are based on those of De Iuliis et al. (2011). Relationships among megalonychids represent a consensus of White and MacPhee (2001), Gaudin (2004), and Pujos et al. (2007), which, because of a lack of consistency among these three studies, results in the collapse of most branches in this family tree into a large multichotomy.

The first tree (Fig. 4a) shows the distribution of arboreal/climbing adaptations in sloths. Sloths and their outgroups (Vermilingua and Cingulata) were assigned to one of three categories, terrestrial, climbing/semiarboreal, or suspensory, based primarily on the findings of White (1993, 1997 – a fourth category, semi-aquatic/aquatic, was used for *Thalassocnus*, following Muizon and McDonald 1995). This tree affirms that the suspensory locomotion of extant tree sloths is convergently acquired and unique to these two genera among sloths. It also optimizes the basal nodes of the sloth radiation as being terrestrial, and all mylodontids, nothrotheriids, and megatheriids as being terrestrial. However, the large clade Megatherioidea, including the other three sloth families, Megalonychidae, Nothrotheriidae, and Megatheriidae, is shown to be primitively semiarboreal, a feature retained at the base and on many of the branches of the megalonychid tree.

The second tree (Fig. 4a) illustrates the distribution of an odontoid process of the astragalus (see McDonald 2012). The odontoid process is a modified medial trochlea of the astragalus that is associated with a pedolateral stance in the pes (McDonald 2012). As the tree demonstrates, this too does not appear to be a feature that was present in sloths primitively, but rather is a convergently acquired characteristic of the family Mylodontidae and the Megatheria, i.e., the clade

Fig. 4 Phylogeny of Tardigrada and its nearest successive outgroups (Vermilingua and Cingulata), based largely on Gaudin (2004), showing distribution of arboreal/climbing adaptations and the odontoid process of the astragalus among extant and extinct sloths. **a** distribution of arboreal/climbing adaptations, assignments to locomotory categories (terrestrial, climbing/semiarboreal, suspensory) based primarily on White (1993, 1997); **b** distribution of odontoid process of astragalus, associated with pedolateral stance of pes. The trees were constructed using MacClade v. 4.08 OS X, and include representative genera from all five sloth families: Megatheriidae (far right clade, *Planops*-*Megatherium*), Nothrotheriidae (second clade from right, *Thalassocnus*-*Nothrotheriops*, relationships based on De Iuliis et al. 2011), Megalonychidae (third clade from right, *Eucholoeps*-*Megalocnus*, relationships based on consensus of White and MacPhee 2001; Gaudin 2004; Pujos et al. 2007), Mylodontidae (fourth clade from right, *Octomyodon*-*Lestodon*), and Bradypodidae (*Bradypus*). The genera *Schismotherium*, *Pelecycodon*, *Hapalops*, and *Analcimorphus* represent basal members of the clade Megatherioidea



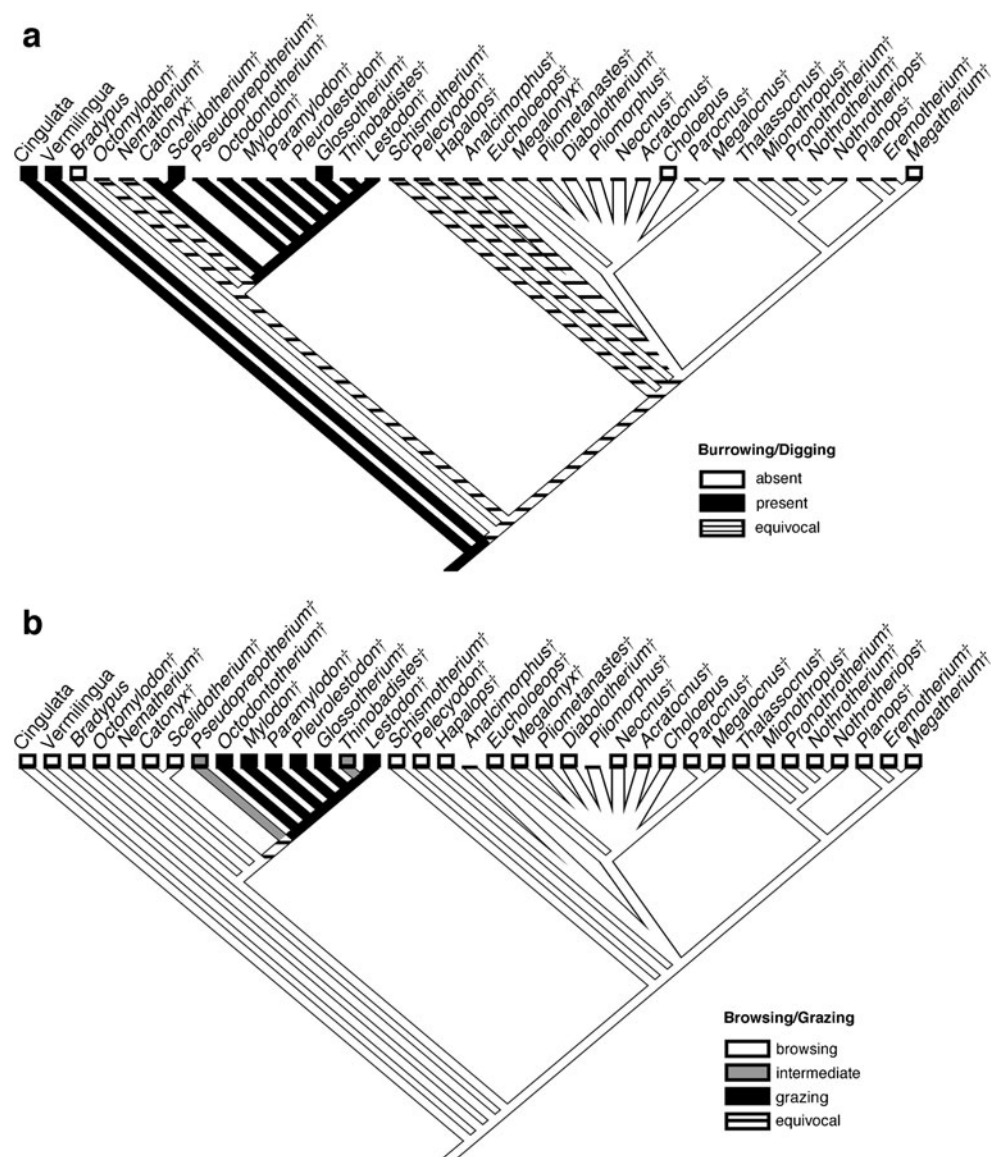
that unites the families Nothrotheriidae and Megatheriidae. It would therefore represent a mylodontid synapomorphy, as well as an additional synapomorphy supporting the monophyly of the Megatheria clade.

The third tree focuses on digging adaptations in sloths (Fig. 5a). As noted above, several Pleistocene mylodontids are thought to be burrowers (Vizcaíno et al. 2001), whereas Fariña and Blanco (1996) demonstrated that *Megatherium* lacked the forelimb strength for digging, contrary to Cuvier's (1823) suggestions. According to our phylogenetic pattern, it is possible that burrowing or digging capabilities characterized sloths primitively, although the optimization is equivocal on this point. Only scelidotheriine and mylodontine sloths are securely identified as diggers in this analysis.

The final tree (Fig. 5b) examines the distribution of feeding behaviors among sloths, using the width of the

mandibular spout as a proxy for feeding mode. Following the suggestion of Bargo et al. (2006a) that, as in modern artiodactyls, the width of the muzzle in sloths was likely correlated with foraging mode, we have identified those sloths with a mandibular symphyseal width (measured at midpoint) greater than 20% of the maximum mandibular length (data from Gaudin 2004) as likely grazers, and those with symphyseal width less than 15% of mandibular length as browsers, with a number of taxa coded as having an intermediate condition, perhaps representing incipient grazers or mixed feeders. The tree shows that the vast majority of sloths were likely to have been browsers of some sort, but that grazing is characteristic of mylodontine sloths, with the most basal mylodontine, the middle Miocene taxon *Pseudopreotherium*, perhaps representing an incipient grazer at the base of this lineage.

Fig. 5 Phylogeny of Tardigrada and its nearest successive outgroups (Vermilingua and Cingulata), based largely on Gaudin (2004), showing distribution of burrowing/digging adaptations among extant and extinct sloths. **a** distribution of burrowing/digging adaptations, based on Fariña and Blanco (1996), Vizcaino et al. (2001), and others; **b** distribution of feeding modes, assignments to browsing or grazing categories based on width of mandibular symphysis relative to mandibular length (data from Gaudin 2004), with those taxa with symphysis width <15% mandibular length considered browsers, and those taxa with symphysis width >20% mandibular length considered grazers. See Fig. 4 for detailed description of trees



Conclusion

The considerable growth in the ranks of xenarthran specialists over the past three decades, the development and application of phylogenetic and morpho-functional techniques, the discovery of large, single locality samples of ground sloth remains and new taxa such as *Pseudoglyptodon* and *Thalassocnus*, a better understanding of variation, sexual dimorphism, and ontogeny, and the establishment of dental terminology have contributed greatly in changing our views on and understanding of Tardigrada. The discovery of new remains and descriptive anatomy may still be at the core of the discipline, but the changes noted above have shifted our efforts towards a more complete and comprehensive systematic and paleobiological appreciation of ground sloths. The future looks promising, given our realization that not only is more intensive field work needed in relatively

untapped areas such as Amazonia, the Andean Altiplano, and northern regions of South America, but that renewed efforts in Patagonia, traditionally considered as the center of sloth evolution, are also required to elevate our knowledge of the earliest sloth radiation.

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