

A Paleogeographic Overview of Tropical Fossil Sloths: Towards an Understanding of the Origin of Extant Suspensory Sloths?

François Pujos, Gerardo De Iuliis & Cástor Cartelle

Journal of Mammalian Evolution

ISSN 1064-7554

Volume 24

Number 1

J Mammal Evol (2017) 24:19-38

DOI 10.1007/s10914-016-9330-4

Volume 24, Number 1

March 2017

24(1) 1-126 (2017)
ISSN 1064-7554

JOURNAL OF MAMMALIAN EVOLUTION



 Springer

 Springer

Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media New York. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



A Paleogeographic Overview of Tropical Fossil Sloths: Towards an Understanding of the Origin of Extant Suspensory Sloths?

François Pujos¹ · Gerardo De Iuliis^{2,3} · Cástor Cartelle⁴

Published online: 28 May 2016

© Springer Science+Business Media New York 2016

Abstract Modern sloths are among the more characteristic mammals of South and Central American faunas. Recent discovery in four Paleogene, 22 Neogene, and dozens of Pleistocene fossiliferous localities in the tropics has revealed an unexpected paleobiodiversity constituted by some 81 fossil sloth species. Probably originating in southern South America near the Eocene/Oligocene transition, sloths were represented in the tropics during the late Oligocene by *Pseudoglyptodon*, Mylodontidae, and Megalonychidae. The latter occupied the West Indies between at least the late early Miocene and late Pleistocene, and two mylodontid clades, Octodontobradyninae and Urumacotheriinae, were characteristic of Amazonian localities from the Colhuehuapian and the Laventan periods, respectively, until the end of the Miocene. Megatheriinae and Nothrotheriidae appeared during the middle Miocene, colonizing the tropics and then North America, where Mylodontidae and Megalonychidae had already been present since the early late Miocene. Nothrotheriids are more abundant and diversified during the late Miocene in the tropics than in southern South America. Remains closely related to either of the modern sloths are absent from the fossil record,

including those in the tropics. The characteristic suspensory posture of *Bradypus* and *Choloepus* appeared independently and likely after the Miocene epoch, and thus well after the hypothesized split suggested by molecular studies of the respective clades of these genera. Given their current widespread distribution in and reliance on the tropics, prospecting efforts for the direct fossil kin of suspensory sloths should concentrate on deposits in the Amazonian region, as this area has shown promise in producing fossil sloths.

Keywords Tropics · Paleogene · Neogene · Pleistocene · Sloths · Systematics

Introduction

Xenarthra is among the most enigmatic and characteristic groups of the South American mammalian fauna. Anyone may expect to be surprised and fascinated by the ability of armadillos to bury themselves in seconds despite the presence of their armor, the ease with which anteaters can rise on their hind legs to insert their long tongue deep into an anthill in search of food, and the slow sloths, hanging upside down for most of their life yet able to swim across rivers.

What is the origin of Xenarthra? Evidence for such origins should probably be sought near the end of the Cretaceous or perhaps the beginning of the Paleocene as suggested by molecular clocks (e.g., Delsuc et al. 2004, 2012; Delsuc and Douzery 2009; Emerling and Springer 2015; Gibb et al. *in press*). We might expect this ancestor to have been small to medium-sized, mobile, with its body probably covered with dermal scutes (which may be the primary way of recognizing its xenarthran affinities), to have possessed a strengthened vertebral column (with xenarthry and ischiosacral fusion), and many homodont and hysodont teeth. Indeed, many

✉ François Pujos
fpujos@mendoza-conicet.gov.ar; fpujos@yahoo.fr

¹ Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET-Mendoza, Avda. Ruiz Leal s/n, Parque Gral., San Martín 5500, Mendoza, Argentina

² Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada

³ Department of Palaeobiology, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada

⁴ PUC Minas, Avenida Dom José Gaspar, 290 Coração Eucarístico, Belo Horizonte, Minas Gerais, Brazil

Tertiary placental mammals share several convergent similarities with xenarthrans without belonging to this particular clade (see Storch 2003 for a review). As well, we would expect its teeth to have lacked or least possessed only traces of enamel. Recently, Emerling and Springer (2015) and Gaudin and Croft (2015) suggested that “proto-xenarthrans” might have been myrmecophagous diggers and climbers.

The fossil record suggests that armored Xenarthra (armadillos and glyptodonts) have been present in South America since at least the early Eocene (Itaboraian South American Land Mammal Age [SALMA], Scillato-Yané 1976). Pilosa (sloths and anteaters) appear later in the fossil record, with the earliest sloths reported from the early Oligocene Tinguirirican SALMA (McKenna et al. 2006) and the earliest anteaters at the beginning of the Miocene Colhuehuapian SALMA (McDonald et al. 2008). Modern armadillos, represented by about 20 species, and anteaters, represented by four species, are very similar to their earliest representatives, but this is not the case for the six species of suspensory sloths. An unresolved aspect of xenarthran evolution that has generated numerous debates among zoologists and paleontologists over several decades is the origin of current and fossil sloths. Although they are ultimately of South American origin, the factors and place are still uncertain.

Modern suspensory sloths are represented by the genera *Bradypus* and *Choloepus* and are distributed in Bradypodidae and Megalonychidae, respectively, with the former generally being considered as the sister clade of other sloths (e.g., Gaudin 2004; Pujos et al. 2012c; Gibb et al. in press). Suspensory sloths are relatively small compared to fossil sloths, slow-moving mammals utilizing a mainly suspensory posture in arboreal environments of the tropical rainforests of South and Central America and some Antillean islands. It is generally suspected that the very peculiar upside-down posture and suspensory locomotion were acquired independently in these genera but presumably under similar ecological conditions. The diphyletic origin of modern suspensory sloths has been commonly supported by osteological (Gaudin 2004), morphofunctional (Nyakatura 2012), and molecular (Höss et al. 1996) studies. The beginning of their independent evolutionary paths is thought to date back to the early late Oligocene (~27 mya; Delsuc et al. 2012; ~30 mya, Pant et al. 2014; Gibb et al. in press).

However, “suspensory” sloths’ fossil kin, generally referred to as “ground” sloths, displayed a much wider range of body size (from dozens of kilograms to several tons; Toledo et al. 2014), diet (mixed feeding, browsing, grazing, subterranean grubbing, and aquatic grazer; Bargo et al. 2006; Pujos et al. 2012c), and locomotory modes (bipedal, quadrupedal, aquatic or sub-aquatic, and climbing), and a much broader geographic distribution (Pujos et al. 2012c). *Pseudoglyptodon* from the early Oligocene of Chile (McKenna et al. 2006) is a peculiar basal sloth considered as

the earliest member of Pilosa. Indeed, sloths colonized much of the Americas (including the West Indies) during the Paleogene, Neogene, and Quaternary periods, extending from Patagonia to Alaska (Pujos and De Iuliis 2008). It is generally accepted that sloths first colonized North America during the late middle Miocene and more extensively at the end of the Pliocene after the formation of the Panamanian Isthmus (McDonald 2005; Fariña et al. 2013). Sloths, along with native ungulates, were the most diversified and represented herbivorous mammals of South America until about 10,000 years ago and they seem to have had little geographical or ecological limitation (Pujos et al. 2012c). However, dramatic climatic and environmental changes at the end of the Pleistocene probably combined with the arrival of humans contributed to the extinction of this group of giant xenarthrans, as well as of many other groups of megamammals (Fariña et al. 2013).

Fossil sloths are distributed in four commonly recognized clades (rather than the seven recognized by Pant et al. 2014) (Gaudin 2004; De Iuliis et al. 2011): Mylodontidae, Megalonychidae, Megatheriidae, and Nothrotheriidae (Fig. 1a). The majority of fossil sloths discovered in the Americas since the end of the 18th century have been recovered from Argentina and North America, although a few other well-known localities have yielded fossil sloths, such as Tarija (late Pleistocene, Bolivia; Boule and Thévenin 1920), late Pleistocene Cuban caves (Matthew 1931), and La Venta (late middle Miocene, Colombia; McDonald 1997). Given that modern suspensory sloths are so characteristic of tropical mammalian communities, it is paradoxical that our knowledge of fossil sloths from the tropics is relatively poorly and the data sporadic.

The aim of this contribution is to present the first extensive systematic and paleobiogeographic review of Cenozoic sloths recovered from the tropics. By gathering such disparate records into a single dataset, our aim permits a synthesis of information that would shed light on the appearance, disappearance, migration, and possible adaptations of major groups of sloths and allow some evaluation of the possible origin(s) of suspensory sloths.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; **FLMNH**, Florida Museum of Natural History, Gainesville, USA; **FMNH**, Field Museum of Natural History, Chicago, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, USA; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; **MCL**, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN**, Muséum national d’Histoire

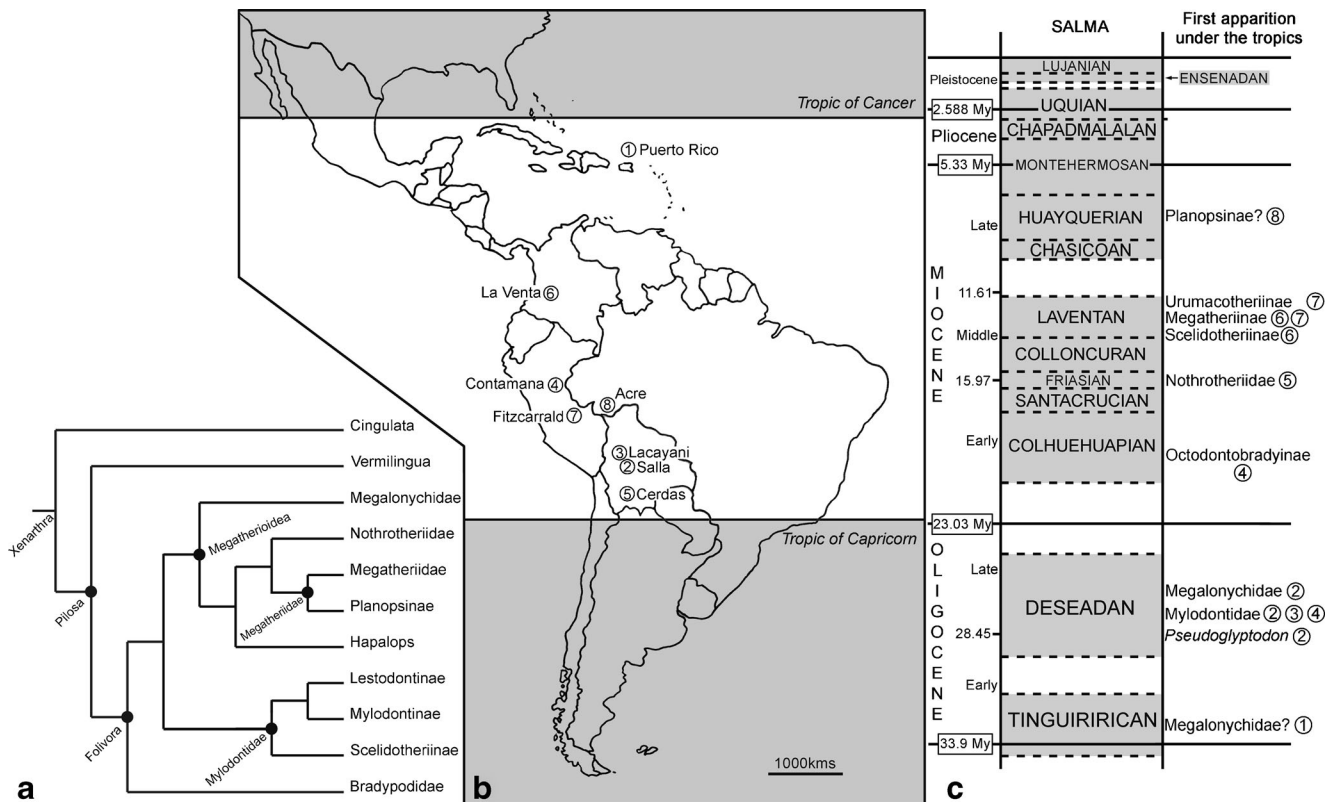


Fig. 1 a, cladogram showing the phylogenetic relationships among sloths (based on Gaudin 2004); b, study area between Tropics of Cancer and Capricorn showing the tropical localities from which the

oldest members of major clades of sloths have been recovered; c, location on the time scale of the South American Land Mammal Ages for the first appearance of major clades of sloths in the tropics

naturelle, Paris, France; **MNHN-Bol**, Museo Nacional de Historia Natural de Bolivia, La Paz, Bolivia; **MUSM**, Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima, Peru; **PUC**, Pontificia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; **UFAC**, Universidade Federal do Acre, Rio Branco, Brazil; **YPM**, Yale Peabody Museum, New Haven, USA.

Material and Methods

As mentioned above, the fossil record of sloths is particularly well known from the austral regions of South America, North America, and the West Indies. Based on the study of the collections of fossil sloths in several institutions mentioned above combined with a detailed revision of the available literature and personal field experience in the Peruvian Amazon, Bolivian Altiplano, southern North America, and Brazil, we have gathered into a single dataset records of the better known taxa of fossil sloths recovered from between the tropics of Cancer and Capricorn. With this information, we try to identify the more important Paleogene and Neogene localities yielding fossil sloths in a region that spans from northern Argentina to Mexico and includes the West Indies. Quaternary tropical fossiliferous localities are too numerous

for exhaustive inclusion, so we have included those that have yielded the most characteristic and abundant sloths during this recent period (Tables 1 and 2).

Systematic and Paleobiogeographic Review of Fossil Sloths in the Tropics

The monogeneric Bradypodidae (Fig. 1a) is not recorded in the fossil record. The four other clades of Folivora (Phyllophaga = Tardigrada sensu Delsuc et al. 2001), those noted above as commonly recognized (Pujos et al. 2012c), do not appear synchronously or in the same geographical area; moreover their evolution, geographical distribution, and diversity are clearly distinct. In the tropics, sloths are present at least in four Paleogene, approximately twenty Neogene, and dozens of Pleistocene localities (Tables 1 and 2).

MacPhee and Iturralde-Vinent (1995) reported the presence of a megalonychid in the early Oligocene of Yauco, Puerto Rico. The age of this fragmentary but fundamental material attributed tentatively (but reasonably) to a megalonychid sloth is highly questionable (McDonald and De Iuliis 2008; but see also Vélez-Juarbe et al. 2014). However, if its age is confirmed, it would require reconsideration of the early paleobiogeographic history of early sloths.

Table 1 Tropical Cenozoic localities yielding fossil sloths

Period	Locality and country	Age	References
Oligocene	1 Juana Díaz Fm., Yauco, Puerto Rico	Early Oligocene	MacPhee and Iturralde-Vinent 1995; White and MacPhee 2001
	2 Contamana, CTA-61 locality (Chambira Fm.), Peru	Late Oligocene	Antoine et al. 2016a
	3 Salla, Bolivia	Late Oligocene	Engelmann 1987; Pujos and De Iuliis 2007; Shockey and Anaya 2011
Miocene	4 Lacayani, Bolivia	Late Oligocene	Hoffstetter et al. 1971
	5 Contamana, CTA-63 locality, (Pebas Fm.), Peru	Early Miocene	Antoine et al. 2016a
	6 Domo de Daza, Cuba	Late early Miocene	MacPhee et al. 2003
	7 Cerdas, Bolivia	Early middle Miocene	Croft et al. 2009
	8 Fitzcarrald, Peru	Middle Miocene	Salas-Gismondi et al. 2006; Antoine et al. 2007; Pujos et al. 2013; Tejada-Lara et al. 2015
	9 Socorro Fm., Venezuela	Middle Miocene	Carlini et al. 2006b
	10 La Venta (Villavieja Fm.), Colombia	Upper middle Miocene	Hirschfeld 1985; McDonald 1997; Villarroel 1998, 2000
	11 Quebrada Honda, Bolivia	Early late Miocene	Croft 2007; Pujos et al. 2011, 2014
	12 Contamana (Pebas Fm.), Peru	Late Miocene	Antoine et al. 2016a
	13 Urumaco Fm., Venezuela	Late Miocene	Carlini et al. 2006a; Rincón et al. 2015
	14 San Pedro, Venezuela	Late Miocene	Collins 1934; Hoffstetter 1961; Marshall et al. 1983
	15 Acre (Upper Solimões Fm.), Brasil	Late Miocene	Frailey 1988; Santos et al. 1993; Cozzuol 2006; Negri et al. 2010; De Iuliis et al. 2011; Ribeiro et al. 2013
	16 Sacaco-Aguada de Lomas, Peru	Late Miocene	Pujos and Salas 2004a
	17 Achiri, Bolivia	Late Miocene	St-André 1996; Pujos et al. 2012a
	18 Maímara, Argentina	Late Miocene	Pujos et al. 2012b
19 San Gerardo de Limoncito, Costa Rica	Late Miocene	Laurito and Valerio 2012	
20 Estado Zacapeta (Juchipita Fm.), Mexico	Late Miocene	Carranza-Catañeda et al. 2008	
Pliocene	21 Pomata-Ayte, Bolivia	Early Pliocene	St-André et al. 2010; Pujos et al. in press
	22 Choquecota, Bolivia	Early Pliocene	St-André et al. 2010
	23 Yauca, Peru	Early Pliocene	Muizon et al. 2004
	24 Ayo Ayo – Vizcachani, Bolivia	Early and middle Pliocene	St-André 1994; St-André and De Iuliis 2001; St-André et al. 2010
	25 Codore Fm., Venezuela	Pliocene	Carlini et al. 2006b
Pleistocene	26 Inchasi, Bolivia	Late Pliocene	Anaya and MacFadden 1995
	27 El Bosque, Nicaragua	Early Pleistocene	Page 1978
	28 Barranca del Sisimico, El Salvador	Early-middle Pleistocene	Webb and Perrigo 1985
	29 Río Tomayate, El Salvador	Early-middle Pleistocene	Cisneros 2005
	30 Tarapoto, Peru	Late Pleistocene	Pujos and Salas 2004b
	31 “Amazona,” Brasil	Late Pleistocene	Marshall et al. 1984
	32 Río Napo, Ecuador	Late Pleistocene	Marshall et al. 1984
	33 Amazonas State, Brasil	Late Pleistocene	Fátima Rossetti et al. 2004
	34 Curaçao	Late Pleistocene	White and MacPhee 2001
	35 Puerto Rico	Late Pleistocene	White and MacPhee 2001
	36 Cuba	Late Pleistocene	White and MacPhee 2001
	37 Hispaniola	Late Pleistocene	White and MacPhee 2001
	38 El Hatillo and La Coca, Panama	Late Pleistocene	Gazin 1957
	39 Hormiguero Quarry Site, El Salvador	Late Pleistocene	Stirton and Gealey 1949
	40 Río de la Pasión, Guatemala	Late Pleistocene	Woodburne 1969
	41 Actun Lak, Belize	Late Pleistocene	De Iuliis et al. 2015
	42 La Brea – Talara, Peru	Late Pleistocene	Lemon and Churcher 1961; Pujos and Salas 2004b

Table 1 (continued)

Period	Locality and country	Age	References
43	La Huaca, Piura, Peru	Late Pleistocene	Pujos and Salas 2004b
44	Cupisnique desert, Peru	Late Pleistocene	Marshall et al. 1984; Pujos 2000; Pujos and Salas 2004b; Pujos et al. 2007
45	Uyujalla, Ocucaje, Peru	Late Pleistocene	Pujos and Salas 2004a, 2004b
46	Sacaco and Aguada de Lomas, Peru	Late Pleistocene	Pujos and Salas 2004b
47	Celendin, Peru	Late Pleistocene	Pujos 2006
48	Chingas, Peru	Late Pleistocene	Pujos and Salas 2004b
49	Cerro de Pasco, Peru	Late Pleistocene	Pujos and Salas 2004b
50	Yantac, Peru	Late Pleistocene	Pujos and Salas 2004b
51	Tres Ventavas Cave, Peru	Late Pleistocene	Engel 1970; Pujos and Salas 2004b
52	Tirapata, Peru	Late Pleistocene	Pujos and Salas 2004b; Pujos et al. 2007
53	Tarija, Bolivia	Late Pleistocene	Marshall et al. 1984
54	Ulloma, Bolivia	Late Pleistocene	De Iuliis and St-André 1997; Marshall et al. 1984; Marshall and Salinas 1991
55	Minas Gerais caves, Brasil	Late Pleistocene	Cartelle 2012
56	La Carolina, Ecuador	Late Pleistocene	Hoffstetter 1952; Marshall et al. 1984; Román-Carrión 2007
57	Punin, Ecuador	Late Pleistocene	Hoffstetter 1952; Marshall et al. 1984
58	Riacho Negro and General Bruguer, Paraguay	Late Pleistocene	Hoffstetter 1978; Marshall et al. 1984
59	Muaco, Venezuela	Late Pleistocene	Marshall et al. 1984
60	Sao Paulo, Brasil	Late Pleistocene	Dias Régo 1992
61	Bahia, Brasil	Late Pleistocene	Cartelle 1991; Cartelle et al. 2008, 2009
62	Sergipe, Brasil	Late Pleistocene	Dantas et al. 2011
63	Rondônia, Brasil	Late Pleistocene	Rodrigues do Nascimento 2008; De Iuliis et al. in press
64	Mato Grosso, Brasil	Late Pleistocene	Cartelle and Hiroka 2005
65	Serra da Capivara, Piaui, Brasil	Late Pleistocene	Guérin and Faure 2008
66	Ceará, Brasil	Late Pleistocene	Ximenes 2008; Araújo-Júnior et al. 2013
67	Rio Grande do Norte, Brasil	Late Pleistocene	Cabral de Carvalho et al. 1969
68	Mato Grosso do Sul, Brasil	Late Pleistocene	Salles et al. 2006
69	Cerro Pintado, Zulia State, Venezuela	Late Pleistocene	McDonald et al. 2013

During the late Paleogene, sloths are predominantly represented in the late Oligocene Patagonian locality of La Flecha with the mylodontoids *Octodontotherium* and *Orophodon* and the megalonychid *Deseadognathus* (Pujos et al. 2012c). Sloth remains are generally scarce and fragmentary in other Oligocene localities (McDonald and De Iuliis 2008; Pujos et al. 2012c; Gaudin and Croft 2015). In the tropics, sloths are recorded from three late Oligocene localities from Peru (Contamana, Antoine et al. 2016a) and Bolivia (Salla and Lacayani, Hoffstetter et al. 1971; Engelmann 1987; Pujos and De Iuliis 2007; Shockey and Anaya 2011). The enigmatic “glypto-sloth” *Pseudoglyptodon*, present since the early Oligocene in Chile and Patagonia (McKenna et al. 2006), is

also present later in the Bolivian locality of Salla (Engelmann 1987; Pujos and De Iuliis 2007). It is commonly considered as the first sloth and characterized by trilobed molariform teeth (as occurs also in glyptodontid armored xenarthrans; Fig. 2a–b). The presence of Megalonychidae is demonstrated in Salla by fragmentary remains (isolated teeth and mandibular remains, Pujos and De Iuliis 2007) that are sufficiently diagnostic to be assigned to this clade. Mylodontidae are represented at the end of the Paleogene by a fragment of a robust tooth from Contamana (CTA-61 locality, Antoine et al. 2016a), the distal extremity of a femur from Lacayani (Hoffstetter et al. 1971), and a partial skull (i.e., *Paroctodontotherium*, Shockey and Anaya 2011) belonging

to a small-sized taxon that presents affinities with *Octodontotherium* from La Flecha (Hoffstetter 1956).

Sloths are poorly represented during the early Miocene in the tropics. In Patagonia, sloths are also scarce during the Colhuehuapian SALMA (McDonald and De Iuliis 2008) and the first significant diversification of sloths takes place during the late early Miocene Santacrucian SALMA, particularly from Santa Cruz Province (see list of taxa proposed by Toledo et al. 2014). Sloths are represented in two early Miocene tropical localities by an upper tooth of an octodontobradys (cf. *Octodontobradys*) from Peru (Contamana, CTA-63 locality, Colhuehuapian-Santacrucian SALMAS, Antoine et al. 2016a) and isolated remains of the megalonychid *Imagocnus zaza* from Cuba (Domo de Daza, MacPhee et al. 2003). These remains correspond to the first appearance of Octodontobradysinae mylodontid (Fig. 2c–d) in South America (Antoine et al. 2016a) and, without doubt regarding age, of sloths in the West Indies (MacPhee et al. 2003; Fig. 1b–c).

As illustrated in Tables 1 and 2, sloths were much more abundantly represented during the middle Miocene, and the first important diversification of sloths occurred during the early late Miocene. Sloths are present in four tropical middle Miocene localities in Bolivia (Cerdas, Friasian SALMA, Croft et al. 2009), Peru (Fitzcarrald, Laventan SALMA Salas-Gismondi et al. 2006; Antoine et al. 2007, 2016b; Pujos et al. 2013; Tejada-lara et al. 2015), Venezuela (Sócorro Formation, Carlini et al. 2006b), and Colombia (La Venta, Laventan SALMA; Hirschfeld 1985; McDonald 1997; Villarroel 1998, 2000). The age of the Venezuelan Socorro Formation is not known precisely. The Cerdas fauna is somewhat older than the Fitzcarrald and La Venta assemblages (see Croft et al. 2009 and Tejada-Lara et al. 2015). For the first time Megatheriinae are recorded in the tropics during the Laventan SALMA at La Venta (McDonald 1997) and Fitzcarrald local fauna in Peruvian Amazonia (*Megathericulus* sp.; Pujos et al. 2013; Fig. 2e–f). Tropical megatheriine ground sloths appear slightly later than the oldest known member of the clade, *Megathericulus patagonicus*, from the Friasian SALMA of southern Patagonia (De Iuliis et al. 2008). *Xyophorus* (Fig. 2g–h) from the early middle Miocene of Cerdas (Croft et al. 2009) is the oldest member of Nothrotheriidae in the tropics. During the middle Miocene interval, the tropics are notable for the appearance of small-sized Megatherioidea, such as the nothrotheriid *Huilabradys* and the abundance of Mylodontidae, such as *Brievabradys*, both from Colombia (Villarroel 2000), and *Eionaletherium* from Venezuela (Rincón et al. 2015). Mylodontid subfamilies Mylodontinae, Urumacotheriinae (Fig. 2i–l), and Scelidotheriinae are recognized for the first time in the Neotropics during the middle Miocene in La Venta and Fitzcarrald (McDonald, 1997; Tejada-Lara et al. 2015). *Neonematherium* from the late middle Miocene of La Venta is the oldest tropical scelidothere (McDonald 1997).

The late Miocene interval is the first golden age of sloths as reflected for example in the late Miocene fauna of “conglomerado osífero” from Entre Ríos Province (Argentina) with a great diversity of Megatheriinae, Megalonychidae, and Mylodontidae (Brandoni 2011). In the tropics, sloths are recorded in eight localities from northern Argentina to Venezuela including Bolivia, Brazil, and Peru (see Tables 1 and 2 for further details). Megalonychidae are extremely scarce during this period, represented only by *Protomegalonyx* and *Pliomorphus* in the Brazilian Amazon (Ribeiro et al. 2013). This is also true for Megatheriidae, represented by isolated remains of megatheriines in Venezuela (*Urumaquia*; Carlini et al. 2006a) and Bolivia (undetermined species from Achiri; Pujos et al. 2012a). Planopsine megatheriids appear, probably for first time in the tropics, in the Amazon of Acre (cf. *Planops* from Brazil; Ribeiro et al. 2013). Mylodontidae are abundant in Colombia, Venezuela, and Brazil (e.g., *Mirandabradys* Carlini et al. 2006b and *Pseudopreotherium* Collins 1934; Marshall et al. 1983; Hirschfeld 1985). This clade is particularly well established in the Amazon with members of the endemic clades Octodontobradysinae (*Octodontobradys*; Santos et al. 1993; Antoine et al. 2016a; Fig. 2c–d) and Urumacotheriinae (*Urumacotherium*; Negri and Ferigolo 2004; Antoine et al. 2016a; Fig. 2i–l). Although Nothrotheriidae are not common during the late Miocene in austral regions of South America, they are highly diversified in the tropics in several localities of Bolivia (*Xyophorus* sp. from Achiri; Pujos et al. 2012a; *Xyophorus villarroeli* from Quebrada Honda, Fig. 2g–h), Peruvian Amazon (Acre), with a nearly complete skeleton of the basal nothrotheriine *Mionothropus cartellei* (De Iuliis et al. 2011), and the appearance and evolution of the thalassocnine lineage (five species of *Thalassocnus*) in the Peruvian coast (Muizon et al. 2003, 2004; Pujos and Salas 2004a; Amson et al. 2015a, 2015b, 2015c). It is also during this period that sloths appear for the first time in North America (Hemphillian North American Land Mammal Age [NALMA]) with the megalonychid *Pliometanastes* and the mylodontid *Thinobadistes* (McDonald 2005). *Pliometanastes* is also present in Central America in Costa Rica (Laurito and Valerio 2012) and Mexico (Carranza-Catañeda et al. 2008). Sloths have not been recorded from the late Miocene of the West Indies.

Few Pliocene localities have yielded sloths and few genera are recorded from the tropics (half as many genera as during the late Miocene, Tables 1 and 2). These localities date from the early and middle Pliocene of Bolivia (Ayo-Ayo, Choquecota, Pomata-Ayte, and Vizcachani; St-André et al. 2010; Pujos et al. in press) and Peru (Yauca; Muizon et al. 2004), the “Pliocene” of Venezuela (Codore Formation; Carlini et al. 2006b), and the late Pliocene of Bolivia (Inchasi; Anaya and MacFadden 1995). Mylodontidae continue to be the most diverse group in the tropics (e.g.,

Glossotheridium, *Pleurolestodon*, and *Mirandabradys*) and for the first time some taxa are found in multiple localities, such as *Simomyiodon* from the Bolivian localities of Pomata Ayte and Ayo-Ayo (St-André et al. 2010). The first derived scelidotheriine is also reported in northern Argentina (i.e. *Proscelidodon*, Pujos et al. 2012b). No Amazonian localities have yielded sloth remains during the Pliocene (Antoine et al. 2016b). Two Nothrotheriidae are signaled, a peculiar form from the Bolivian Altiplano (Pujos et al. in press) and the last species of the *Thalassocnus* lineage from the Peruvian coast (Muizon et al. 2004). Several derived Megatheriinae are also present in Venezuela (*Proeremotherium elejbe*, Carlini et al. 2006b) and in several Bolivian localities (*Megatherium* (*Megatherium*) *altiplanicum*, St-André and De Iuliis 2001) and foreshadow the giant Quaternary forms.

During the Pleistocene period, sloths were the dominant terrestrial herbivores in South America and they colonized all environments of the continent. The Pleistocene mammalian localities are too numerous for exhaustive inclusion and we list the forty most representative sloth faunas and the most common sloth taxa (Tables 1 and 2).

Fourteen species of late Pleistocene small- to medium-sized Megalonychidae distributed among six genera (*Acratocnus*, *Imagocnus*, *Megalocnus*, *Neocnus* (Fig. 2m–n), *Paulocnus*, and *Parocnus*) occupied the West Indies (Curaçao, Puerto Rico, Cuba, and Hispaniola). None of these small-sized taxa has as yet been found outside the West Indies, suggesting they are confined to the West Indian islands. Giant megalonychids phylogenetically close to *Megalonyx* are present in the tropics in Venezuela (*Megistonyx*; McDonald et al. 2013) and Brazil (*Australonyx* and *Ahytherium*; Cartelle et al. 2009). Large Megalonychidae are almost absent from southern South America but identified for first time in Central America with *Meizonyx* and *Megalonyx* in the early middle Pleistocene of El Salvador (Webb and Perrigo 1985; Cisneros 2005) and *Megalonyx* in the late Pleistocene of Guatemala (Lucas et al. 2007).

During the Pleistocene, giant Megatheriinae are extremely common in Central and South America and southern areas of North America. *Eremotherium laurillardii*, the tropical giant megatheriine, is present since the early Pleistocene in nearly half of the tropical Pleistocene localities, particularly in Brazil, Ecuador, Peru, and Venezuela but also in Central America in Panama, Nicaragua, and El Salvador (see Tables 1 and 2 for further details). *Megatherium* occupies mostly the southern half of South America, with *Megatherium* (*Megatherium*) *americanum* ranging approximately from Patagonia to southern Bolivia (Tarija; Marshall et al. 1984). Several small species of “Andean” Megatheriinae grouped in the subgenus *Megatherium* (*Pseudomegatherium*) are present in Bolivia, Peru, and Ecuador. The Brazilian form *Nothrotherium maquinense* is the only nothrotheriid identified during the Pleistocene

in South American tropics. *Nothrotheriops*, the North American Pliocene-Pleistocene nothrotheriid, has been recently recorded in Belize (De Iuliis et al. 2015), which is the southernmost presence of the genus. The sudden and surprising presence of possible *Nothrotheriops* in Argentina (Brandoni and McDonald 2015) remains to be confirmed by more abundant material. *Diabolotherium*, a peculiar small-sized megatherioid, is recorded from the late Pleistocene of the Pacific Peruvian coast and several Peruvian and Chilean caves (Pujos et al. 2007).

With respect to Mylodontidae, Lestodontinae are only represented by *Lestodon* in two tropical localities in Tarija (Bolivia) and Brazil (Sao Paulo; Dias Rêgo 1992), the northernmost presence of the genus. It is, however, common in austral areas of the continent. Scelidotheriinae are abundant and diversified with three species belonging to *Catonyx* (which includes *Scelidodon*) and one species to *Valgipes*. Two species of *Catonyx* are endemic to Brazil (*C. cuvieri* cohabiting with *Valgipes*) and Bolivia (*C. tarijensis*) while *C. chiliensis* is more widespread, ranging from Ecuador to Chile including Peru and Bolivia (Cartelle et al. 2009). Four mylodontine genera are present in the tropics. *Glossotherium* is the most abundant mylodontid with four species in fifteen localities of Brazil, Peru, Bolivia, Ecuador, and Paraguay, whereas *Mylodon* is restricted to southern areas of South America (i.e., Argentina and Chile). The northernmost presence of *Mylodon* is in Ecuador (Marshall et al. 1984). Finally, among Mylodontinae, *Mylodonopsis* and *Ocnotherium* are rare endemic genera of Brazil (e.g., Cartelle 1991, 2012). The endemic Amazonian mylodontid Octodontobryinae and Urumacotheriinae are not recognized during the Pliocene or Pleistocene epochs.

Discussion

Paleogeographic Overview of Fossil Sloths in the Tropics

Although likely to appear as early as in the earliest Eocene as inferred by consensual phylogenetic relationships among Xenarthra, the earliest undisputable sloths first occur in the earliest Oligocene of southern South America, as represented by the “glypto-sloth” *Pseudoglyptodon* from central Chile and Chubut Province of southern Argentina (Mustersan? and Tinguirirican SALMAs, McKenna et al. 2006; Fig. 2a–b). The possible presence of sloths in middle Eocene levels of Antarctica (Vizcaíno and Scillato-Yané 1995), which would correspond to the oldest member of the clade, has been questioned (MacPhee and Reguero 2010). MacPhee and Iturralde-Vinent (1995) attributed a proximal femoral epiphysis from the early Oligocene of Puerto Rico to Megalonychidae (Tables 1 and 2). If this taxonomic assignment is correct (clearly more material is necessary for firm determination), the early Oligocene age for the Juana Díaz

Formation was frequently discussed (McDonald and De Iuliis 2008). Moreover, an early Oligocene age for Puerto Rican deposits has been recently confirmed (Vélez-Juarbe et al. 2014). Indeed these deposits yielded rodent incisors of undisputable caviomorph affinities, which support the existence of an early dispersal event from the Neotropics (where caviomorphs were well settled by late middle Eocene times; Antoine et al. 2012) toward the Caribbean region around the Eocene-Oligocene transition. Accordingly, this West Indian sloth would be nearly contemporaneous with the earliest *Pseudoglyptodon*, which would require a reconsideration of the early phylogenetic and paleobiogeographic history of sloths in South America and the West Indies.

By the end of the Oligocene, *Pseudoglyptodon*, mylodontids, and megalonychids were present in the southern half of the continent including the southern tropics (e.g., *Octodontotherium* and *Deseadognathus* in Argentina, *Paroctodontotherium* in Bolivia; Fig. 1b–c, Tables 1 and 2). The recent report by Antoine et al. (2016a) on the presence of isolated remains of a Mylodontidae in the Deseadan SALMA of the Peruvian Amazon greatly expands the known distribution of early sloths. Although the paleogeographical origins of Mylodontidae and Megalonychidae remain unclear, the definite presence of *Pseudoglyptodon* during the Tinguirirican SALMA in the southern part of South America would suggest Patagonia as the evolutionary cradle of sloths. The probable presence, however, of a megalonychid sloth from the Juana Diaz Formation of Puerto Rico (MacPhee and Iturralde-Vinent 1995; Vélez-Juarbe et al. 2014) gives rise to a second scenario, with the megalonychid sloths native to the West Indies and the mylodontids to central South America or Patagonia. Moreover, the presence in *Pseudoglyptodon* of a strong caniniform and multilobed molariform teeth, which never occurs in megalonychid sloths, would tend to place it closer to Mylodontidae. Only the discovery of new material in better state of preservation will contribute to increasing certainty regarding the phylogenetic affinities of *Pseudoglyptodon*. An information gap on sloths between the late Oligocene (Deseadan SALMA) and the early Miocene (Colhuehuapian SALMA) in the tropics as well as in Patagonia (Tables 1 and 2) hinders our knowledge of the evolution and diversification of Mylodontidae and Megalonychidae during this period.

In comparison with native ungulates, sloths comprised a tiny component of the tropical mammalian fauna during the late early Miocene. This period records the first certain presence of megalonychid sloths in the West Indies (i.e., *Imagocnus* from Cuba; MacPhee et al. 2003) and the first appearance in the tropics of Octodontobradyninae (Antoine et al. 2016a; Fig. 1b–c, Tables 1 and 2). The latter was an endemic Amazonian group of tropical mylodontids known only from craniodental and mandibular remains and characterized in particular by the absence of a caniniform tooth, the presence

of four lower elongated molariforms with a single transverse lophid located on the posterior third of m1–m3 and centrally on m4, a horizontal mandibular ramus with a straight ventral margin, and a thin and elongated spout (Fig. 2c–d). Megatheriidae and Nothrotheriidae are not recorded yet in Central and North America.

Sloths are not known from the middle Miocene to the early Pleistocene of the West Indies, which is probably due to the lack of the appropriate fossiliferous levels. However, sloths began colonizing the tropics of South America during the middle Miocene, with Megatheriinae and Nothrotheriidae present in several localities in the tropics (Fig. 1b–c, Tables 1 and 2). Nothrotheriid sloths appeared first during the early middle Miocene in the tropics with *Xyophorus* in the Bolivian locality of Cerdas (Fig. 2g–h, Tables 1 and 2). The *Xyophorus* specimen from Cerdas is the first recorded nothrotheriid in the tropics and suggests that this clade may have appeared first in Patagonia before spreading rapidly to the rest of the continent in the southern tropics of central South America and in Patagonia (e.g., *Pronothrotherium* from the Huayquerian SALMA of Argentina) and then North America (i.e., *Nothrotheriops* from the Irvingtonian and the RanchoLabrean NALMA of USA). Megatheriine sloths seem originally from Patagonia with *Megathericulus* spreading later into northern areas of South America and the tropics, as recorded from the Fitzcarrald fauna (Figs. 1b–c, and 2e–f, and Tables 1 and 2; Pujos et al. 2013). All groups of Mylodontidae are present during the middle Miocene in the tropics (Tables 1 and 2). Scelidotheriinae, originating probably in the Santacrucian SALMA of Patagonia, were present in the middle Miocene of Colombia (La Venta) with *Neonematherium*; simultaneously Octodontobradyninae (*Octodontobradys*, Fig. 2c–d) are joined by Urumacotheriinae (*Urumacotherium*, Figs. 1b–c, and 2e–h) in Fitzcarrald (Tejada-Lara et al. 2015). Octodontobradyninae and Urumacotheriinae are present in Acre (Brazilian Amazonia), Urumaco (Venezuela), and Contamana and Fitzcarrald (Peru). Urumacotheriinae and Octodontobradyninae are two highly specialized clades of endemically tropical Mylodontidae, and have so far been recovered only from the Amazon and surrounding areas (Tables 1 and 2, see Negri et al. 2010).

Mylodontidae and Nothrotheriidae are well represented in the tropics. Although mylodonts were generally widespread in South America, *Octodontotherium* and *Urumacotherium* were restricted to the tropics. Nothrotheriids were not particularly common in the southern part of the continent (e.g., *Pronothrotherium*), but were more abundant and diversified in the tropics, as represented by *Mionothropus* from the Peruvian Amazon, *Xyophorus* and *Lakukullus* from the Bolivian Altiplano, and *Thalassocnus* from the Pacific coast. Mylodonts extended into North America by approximately 9 my (*Thinobadistes*), and so did the megalonychid *Pliometanastes* (McDonald 2005). Recent reports (Cozzuol

2006; Ribeiro et al. 2013) suggested the presence of *Planops*, a megatheriid planopsine, in the Huayquerian of the Brazilian Amazon (Acre). This is based on isolated remains and the generic determination requires confirmation, as previous records of planopsines (e.g., *Planops* and *Prepoplanops*) are otherwise securely known only from the Santacrucian SALMA of Argentine Patagonia (Negri et al. 2010).

Only six tropical Pliocene localities have yielded sloth remains; so they are far fewer in number and diversity than the notoungulates, litopterns, and other endemic herbivores of South America. Since the end of the Oligocene, sloths are far fewer in numbers and less diversified than ungulates. Little information is available to evaluate in detail the evolution of the paleobiodiversity of sloths in the tropics during this period. The Pliocene is notable for the extinction of *Thalassocnus* and the appearance of derived giant megatheriines, *Megatherium* (*M.*) *altiplanicum* in Bolivia and *Proeremotherium elejbe* in Venezuela (St-André and De Iuliis 2001; Carlini et al. 2006a). Conversely, in southern areas of the continent, the diversity of Mylodontidae and Megatheriidae increased considerably. Megalonychidae and Nothrotheriidae, however, are not abundantly represented. During the Pliocene (late Hemphillian and early Blancan NALMA), North American Megalonychidae continued their paleobiogeographic expansion with *Pliometanastes* and *Megalonyx*.

In the Pleistocene, despite the rise of the Panamanian Isthmus and GABI (Great American Biotic Interchange), sloths became increasingly diverse and abundant. Indeed, sloths and cingulates reached their zenith and were dominant elements in South American faunas during this period, and made lasting incursions into Central and North America as well. The alteration of glacial and interglacial episodes and the arrival of humans later in the Pleistocene modified the biodiversity of South (and North) American faunas, particularly of large mammals (Barnosky et al. 2004). The end of the Pleistocene witnessed the extinction of nearly all of these mammals (see Fariña et al. 2013) and all but the smallest of sloths disappeared. Abundant remains of these mammals have been recovered from the tropics (see Tables 1 and 2).

In Central America, the presence in Guatemala of *Megalonyx* suggests an early migration from the north (where the genus had been well established since the Pliocene) towards South America. The megalonychids *Megistonyx*, *Australonyx*, and *Ahytherium*, phylogenetically close to *Megalonyx* (see McDonald et al. 2013), occupied the northern area of the South American tropics (i.e., Venezuela and Brazil). Megalonychidae are once again recorded, in abundance, from the West Indies. *Meizonyx* (El Salvador), *Nothrotheriops* (Belize), and *Eremotherium* (Panama, Nicaragua, and El Salvador) have also been recovered along

the Panamanian Isthmus and testify to the use of this corridor by several groups of sloths (McDonald et al. 2005).

Eremotherium is abundantly represented in North America during the Pliocene mainly by *E. eomigrans* (De Iuliis and Cartelle 1999) and in the Pleistocene by *E. laurillardii* (McDonald 2005), and it is possible that the latter colonized northern South America (see De Iuliis and Cartelle 1999). *Megatherium* mainly occupied the southern half of South America, with the giant *M. (Megatherium) americanum* largely in the Pampas and lowlands and the medium-sized species of the subgenus *M. (Pseudomegatherium)* (e.g., *M. (P.) tarijense* and *M. (P.) medinae*) largely in the Pacific corridor and the Andean plateau (see Pujos 2008). *Eremotherium laurillardii* seems to have largely excluded other megatheriines from its range, whereas range overlap apparently occurred among species of *Megatherium*, such as *M. (P.) tarijense* and *M. (M.) americanum* in Tarija (Tables 1 and 2). The nothrotheriid sister taxa *Nothrotherium* and *Nothrotheriops* (Nothrotheriini; De Iuliis et al. 2011) are abundantly present on either side of the equator in dozens of localities, *Nothrotheriops* to the north (McDonald and Jefferson 2008) and *Nothrotherium* to the south (Cartelle and Fonseca 1983).

Among Mylodontidae, *Lestodon* was the only Pleistocene lestodontine present in the tropics in southern Bolivia (Tarija) and Brazil (Bahia). *Lestodon armatus*, as well as the mylodontine *Mylodon darwini*, the scelidotheriine *Scelidotherium*, and the megatheriine *Megatherium (M.) americanum* are temperately adapted forms, whereas the scelidotheriines *Catonyx* sp. (including *Scelidodon*) and *Valgipes bucklandi* were abundantly present in the tropics principally in Brazil and Peru (Cartelle et al. 2009; Tables 1 and 2). The mylodontine *Glossotherium* is known from a widespread geographical area, including both the more temperate and tropical regions of South America. Although three scelidotheriine genera, (i.e., *Scelidotherium*, *Catonyx*, and *Valgipes*) inhabited South America during the Pleistocene, none participated in the GABI. As noted, *Glossotherium* species were abundant throughout South America and possibly also in North America with “*Glossotherium*” *chapadmalense* (McDonald 2005), the phylogenetic position of which within Mylodontinae remains to be resolved. The endemic tropical ground sloths Octodontobradyninae and Urumacotheriinae disappeared at the end of the Miocene (Tables 1 and 2). Two new endemic Brazilian mylodontid genera (*Mylodonopsis* and *Ocnotherium*) appeared during the late Pleistocene but they are considerably different from and not phylogenetically close to Octodontobradyninae and Urumacotheriinae.

Considering the Origin of Suspensory Sloths?

It is evident from our review that no fossil remains of suspensory sloths have been recovered from the tropical region, the

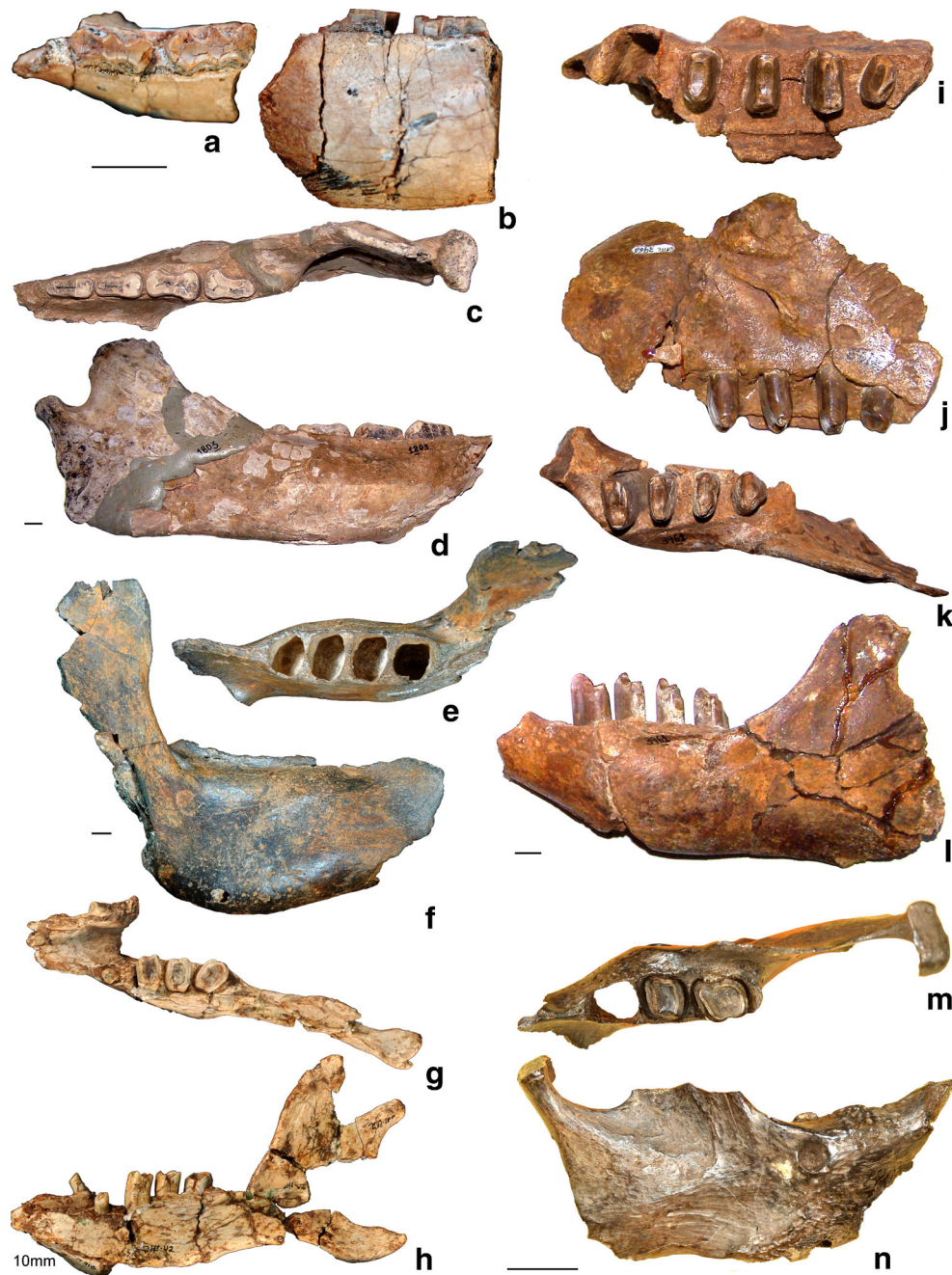


Fig. 2 **a-b**, left mandible of *Pseudoglyptodon sallaensis* (MNHN-Bol-V-009623) from the Deseadan SALMA of Salla (Bolivia) in occlusal and lateral views, respectively; **c-d**, right mandible of *Octodontobradys puruensis* (holotype, UFAC 1803) from the late Miocene of Upper Solimões Formation (Acre, Brazil) in occlusal and lateral views, respectively; **e-f**, right mandible of *Megathericus* sp. (MUSM 1564) from the Laventan SALMA of Fitzcarrald (Peru) in occlusal and lateral views, respectively; **g-h**, left mandible of *Xyophorus villarroeli* (UF 242000)

from the Laventan SALMA of Quebrada Honda (Bolivia) in occlusal and lateral views respectively; **i-l**, left maxilla (**i-j**, Holotype, UFAC 3902) and left mandible (**k-l**, holotype, UFAC 3961) of *Urumacotherium campbelli* from the late Miocene of Upper Solimões Formation (Acre, Brazil) in occlusal (**i** and **k**) and lateral (**j** and **l**) views; **m-n**, right mandible of *Neocnus gliriformis* (AMNH 16882) from the Pleistocene of Casimba (Cuba) in occlusal and lateral views, respectively

rest of continental America, or the West Indies. Over the past several decades, new Paleogene (e.g., Santa Rosa and Contamana in Peru) and Neogene (e.g., Urumaco in Venezuela, Acre in Brazil, Fitzcarrald and Madre de Dios in

Peru) localities have yielded rich and diverse vertebrate faunas from tropical rainforest habitats or “open habitats under a monsoonal-like tropical climate” (Antoine et al. 2013: 91). It is precisely in these kinds of environments

that we might expect to find forms related to modern suspensory sloths.

The very peculiar mode of life of the modern suspensory sloths *Bradypus* and *Choloepus* reflects their remarkable and independently evolved postcranial specializations. Among these features, we may note the extreme elongation of long bones, simplification of articular facets, fusion among carpal and tarsal elements, reduction in number of digits (three for *Bradypus* and two for *Choloepus*), and hook-shaped ungual phalanges (Nyakatura 2012). Both genera have an almost exclusively folivorous diet (Chiarello 1998) with a preference for the leaves of the genus *Cecropia*. It is also in this type of tree that sloths spend much of their time and assume a suspensory posture. Sloths can also consume algae-gardens present on their pelage to augment their strict diet and the existence of the mutualism characteristic of sloths (Pauli et al. 2014) further strengthens the links between tropical environment and the sloths. It would appear that modern sloths are a product of the particularities of the rainforests of Central and South America and entirely dependent on the conditions of this ecosystem. Sloths descend from trees only to defecate and predators such *Panthera* often strike during this vulnerable activity. Extant sloths are capable of only an awkward “crawl” on the ground and they are excellent swimmers in fresh and sea water (Anderson and Handley 2001). Lastly, sloths reproduce during the dry season and give birth in a suspensory posture. These characteristics clearly demonstrate that extant suspensory sloths are highly specialized mammals closely linked to the neotropical environment with functional constraint to an arboreal habitat. Although they currently range from Central America (Honduras) to southern Brazil and are relatively common, there is no evidence in the fossil record of sloths with this peculiar kind of locomotion and lifestyle.

The nonsuspensory locomotion (i.e., climbing or semi-arborality; Pujos et al. 2012c; Gaudin and Croft 2015) of fossil sloths is plesiomorphic among Pilosa. During their spread throughout South America, North America, and the West Indies, sloths diversified and adapted to various environments, ranging from the Quaternary Pampean steppes (e.g., *Megatherium*), the Mio-Pliocene Andean Altiplano (e.g., *Simomyiodon*), Quaternary Andean caves (e.g., *Diabolotherium*), the Mio-Pliocene deserts of the Pacific coast (e.g., *Thalassocnus*), and the Mio-Pliocene Amazonian rainforest (e.g., *Octodontobradys*) (Pujos et al. 2012c). They have also evolved several locomotory modes, such as possible bipedalism (e.g., *Megatherium*), quadrupedalism (e.g., *Scelidotherium*), arboreality or semiarboreality (e.g., *Hapalops*), and an aquatic or semi-aquatic lifestyle (e.g., *Thalassocnus*) (Pujos et al. 2012c; Gaudin and Croft 2015; Amson et al. 2015a, 2015b, 2015c).

We have followed above the main events in the appearance, evolution, migration, and disappearance of the

major clades of fossil sloths in the tropics, in which, at one time or another, all groups of sloths were present and within the expected area of the origin of suspensory sloths, particularly the Amazonian or proto-Amazonian rainforest. The abundance of fossiliferous localities that yield sloth remains during the Oligocene to Pleistocene (see Table 1), including the Amazonian localities of Peru, Brazil, and Venezuela, provide an excellent view of sloths in the tropics. As mentioned above, there is consensus on the diphyletic origin of modern suspensory sloths (e.g. Gaudin 2004) with an implied separation during the early late Oligocene (Delsuc et al. 2012; Gibb et al. in press), certainly before the appearance of almost all tropical fossil sloths. And yet there is total absence of fossil evidence of morphological precursors of extant suspensory sloths that currently inhabit the tropical rain forest of nearly half of South and Central America.

The most recent and comprehensive phylogenetic analysis of extant and extinct Pilosa recognized *Bradypus* as sister taxon of other sloths and *Choloepus* as sister taxon to the West Indies Quaternary genus *Neocnus* (Gaudin 2004; Fig. 2m–n). We should note that the postcranial skeleton of extant suspensory sloths is so modified that it is extremely difficult to compare it with the homologous elements of fossil sloths to obtain phylogenetic information. Indeed, the skull, teeth, and mandible of *Choloepus* exhibit synapomorphies of the megalonychid clade and are very close to those of the West Indian megalonychids (i.e., *Neocnus*, *Acratocnus*, *Megalocnus*, and *Parocnus*); however, non-postcranial elements reflecting an upside-down posture were discovered in fossiliferous Cuban localities (see White and MacPhee 2001 for an overview). With regard to *Bradypus*, its craniodental characters, including those of the ear region, separate this taxon from all other sloths, with some authors (Gaudin 2004) recognizing a separate family, Bradypodidae, which could represent a pedomorphic lineage (Patterson et al. 1992; Gaudin 1995).

The recent and abundant information of fossil sloths from the tropics, including the West Indies, and the lack of fossil sloths that share the same mode of locomotion as modern suspensory sloths suggest that the suspensory posture was not yet present in sloths at least during the Miocene and that it appeared twice and much later than the hypothetical separation suggested between *Bradypus* and *Choloepus*. The discovery of tropical Pliocene and Pleistocene localities, admittedly still very few in number, in the Amazonian region, is encouraging, and we suggest that it is important to continue prospecting for fossiliferous localities from the end of the Neogene and the Pleistocene in the Amazon in search of the close fossil kin of extant suspensory sloths.

Conclusion

The recent information available for fossil sloths from tropical regions during the Paleogene, Neogene, and Quaternary periods allows us to better understand this endemic South American clade. It is becoming clear that sloths were as abundant in the tropics as in the rest of South America since the end of the Paleogene. Some eighty species of fossil sloths were present in the Cenozoic: at least four Oligocene, 14 Miocene, six Pliocene, and dozens (and perhaps more than a hundred) localities in the region between the Tropics of Cancer and Capricorn. With regard to the phylogenetic and paleogeographic history of these sloths, several important events may be highlighted. Although the oldest sloths were found in the southern part of South America near the Eocene-Oligocene transition, mylodontids, megalonychids, and the “glypto-sloth” *Pseudoglyptodon* inhabited the tropics beginning in the late Oligocene. Megalonychidae are present in the West Indies in the late early Miocene and the late Pleistocene (no fossils are known from the middle Miocene to the early Pleistocene) but their relationships with other allied genera from Central, North, and South America are not yet fully resolved. During the early Miocene (Colhuehuapian SALMA) and the late middle Miocene (Laventan SALMA), two endemic groups of mylodontid sloths, Octodontobradyninae and Urumacotheriinae, appear in the tropics. The members of these clades are common in Amazonian localities, where they diversified until their probable extinction at the end of the Miocene. Megatheriinae and Nothrotheriidae appear in the tropics during the middle Miocene before members of these clades reached North America with the formation of the Panamanian Isthmus. Since the late middle Miocene, all the groups of sloths are present in the tropics except Planopsinae, given that a single record in Brazilian Amazon during the Huayquerian SALMA requires confirmation. Interestingly, nothrotheriid sloths seem to be more abundant and diversified in the tropics than in the southern part of South America during the late Miocene. It is also during this period that mylodontid and megalonychid fossil sloths began their expansion into North America, where they diversified and extended their range as far north as Alaska until their extinction at the end of the Pleistocene. The Pleistocene period might be regarded as the “golden age” of fossil sloths as they diversified into numerous large, including gigantic, forms among Megatheriidae, Mylodontidae, Megalonychidae, and Nothrotheriidae, and were, at least in South America, the dominant terrestrial herbivores, also profiting from the Panamanian Isthmus to realize new migrations probably in both directions as attested by their presence in Central America. However, highly specialized forms like Scelidotheriinae did not migrate to North America.

Despite recent advances in our understanding of fossil sloths from tropical regions, the origin of suspensory sloths remains a mystery. *Bradypus* and *Choloepus* are closely linked to the neotropical rain forests in relation to their peculiar mode of life, but their postcranial specializations appeared independently. Phylogenetic analysis based on craniodental characters suggests that *Choloepus* is a megalonychid and *Bradypus* is sister taxon to other sloths. Frustratingly, the recent available information on fossil sloths in the tropics has not shed new light on the diphyletic origins of current sloths and no fossil remains help explain the evolution of skeletal features of the suspensory posture of the extant sloths.

However, the complete absence of suspensory sloths in the tropics in dozens of Paleogene, Neogene, and Pleistocene localities discovered mainly during the last few decades suggests that the suspensory posture did not exist at least during the Oligocene and Miocene periods, contrary to what is inferred by molecular data, and appeared much later than the hypothetical separation between three- and two-toed sloths. The recent discovery of fossil mammals in numerous tropical localities should encourage us to continue to prospect and search for new remains in these areas, especially Amazonian areas of Acre and Contamana, to uncover remains of direct fossil kin of suspensory sloths.

Acknowledgments The authors thank J.J. Flynn and J. Galkin (AMNH, New York, USA), B. MacFadden, J. Bloch, and R.C. Hulbert, Jr. (FLMNH, Gainesville, USA), K.D. Angielczyk and W. Simpson (FMNH, Chicago, USA), A. Kramarz and S. Maris Alvarez (MACN, Buenos Aires, Argentina), M.A. Reguero and M.S. Bargo (MLP, La Plata, Argentina); C. de Muizon, C. Argot, and C. Sagne (MNHN, Paris, France), B. Mamani Quispe (MNHN-Bol, La Paz, Bolivia), and R. Salas-Gismondi (MUSM, Lima, Peru) for allowing us to examine specimens in their care. The authors are grateful to N. Toledo (Museo de La Plata, La Plata, Argentina) and P.-O. Antoine (ISEM, Montpellier, France) for providing and allowing us to reproduce images of *Bradypus*, *Choloepus*, *Urumacotherium*, and *Octodontobradys*. We also thank the referees, L. Hautier and two anonymous reviewers for their thorough reviews. Finally F.P. is grateful to the editors of *Journal of Mammalian Evolution*, J.R. Wible and T.J. Gaudin, for allowing the publication of the proceedings of the symposium *Cenozoic Evolution of Tropical-Equatorial Mammals* held in conjunction with the *4th International Palaeontological Congress – The history of life: a view from the Southern Hemisphere* (September 28 – October 3, 2014, Mendoza, Argentina). This project has been partially supported by the ISE-M (Paleontology Department) and by the Ecos-Foncyt A14U01 Program.

References

- Amson E, Argot C, McDonald HG, Muizon C de (2015a) Osteology and functional morphology of the forelimb of the marine sloth *Thalassocnus* (Mammalia, Tardigrada). *J Mammal Evol* 21(3):169–242
- Amson E, Argot C, McDonald HG, Muizon C de (2015b) Osteology and functional morphology of the hind limb of the marine sloth *Thalassocnus* (Mammalia, Tardigrada). *J Mammal Evol* 22(3):355–419

- Amson E, Argot C, McDonald HG, Muizon C de (2015c) Osteology and functional anatomy of the axial postcranium of the marine sloth *Thalassocnus* (Mammalia, Tardigrada) with paleobiological implications. *J Mammal Evol* 22(4):473–518
- Anaya F, MacFadden BJ (1995) Pliocene mammals from Inchasi, Bolivia: the endemic fauna just before the Great American Interchange. *Bull Florida Mus Nat Hist* 39(3):87–140
- Anderson RP, Handley CO Jr (2001) A new species of three-toed sloth (Mammalia: Xenarthra) from Panamá, with a review of the genus *Bradypus*. *Proc Biol Soc Wash* 114(1):1–33
- Antoine P-O, Abello MA, Adnet S, Altamirano Sierra AJ, Baby P, Billet G, Boivin M, Calderon Y, Candela A, Chabin J, Corfu F, Croft DA, Ganerød M, Jaramillo C, Klaus S, Marivaux L, Navarrete RE, Orliac MJ, Parra F, Pérez ME, Pujos F, Rage J-C, Ravel A, Robinet C, Roddaz M, Tejada-Lara JV, Vélez-Juarbe J, Wesselingh FP, Salas-Gismondi R (2016a) A 60 million year-long Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Res* 31(1):30–59
- Antoine P-O, Marivaux L, Croft DA, Billet G, Ganerød M, Jaramillo C, Martin T, Orliac MJ, Tejada J, Altamirano AJ, Duranthon F, Fanjat G, Rousse S, Salas-Gismondi R (2012) Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. *Proc Roy Soc B* 279:1319–1326
- Antoine P-O, Roddaz M, Bricchau S, Tejada-Lara J, Salas Gismondi R, Altamirano A, Louterbach M, Lambs L, Otto T, Brusset S (2013) Middle Miocene vertebrates from the Amazonian Madre de Dios Subandean Zone, Perú. *J S Am Earth Sci* 42:91–102
- Antoine P-O, Salas-Gismondi R, Baby P, Benammi M, Brusset S, De Franceschi D, Espurt N, Goillot C, Pujos F, Tejada J, Urbina M (2007) The middle Miocene (Laventan) Fitzcarrald Fauna, Amazonian Peru. In: Díaz-Martínez E, Rábano I (eds) Proceedings of the 4th EMPSLA, Cuad Mus Geominero (8):355–360
- Antoine P-O, Salas-Gismondi R, Pujos F, Ganerød M, Marivaux L (2016b) Western Amazonia as a hotspot of mammalian biodiversity throughout the Cenozoic. *J Mammal Evol* (in press)
- Araújo-Júnior HI, Porpino KO, Ximenes CL, Bergqvist LP (2013) Unveiling the taphonomy of elusive natural tank deposits: a study case in the Pleistocene of northeastern Brazil. *Palaeoclimatol Palaeogeogr Palaeoecol* 378:52–74
- Bargo M, Toledo N, Vizcaíno SF (2006) Muzzle of South American Pleistocene ground sloths (Xenarthra, Tardigrada). *J Morphol* 267: 248–263
- Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB (2004) Assessing the causes of the late Pleistocene extinctions on the continents. *Science* 306:70–75
- Boule M, Thévenin A (1920) Mammifères fossiles de Tarija. Imprimerie Nationale, Paris, 255 pp
- Brandoni D (2011) The Megalonychidae (Xenarthra, Tardigrada) from the late Miocene of Entre Ríos Province, Argentina, with remarks on their systematics and biogeography. *Geobios* 44:33–44
- Brandoni D, McDonald HG (2015) An enigmatic Nothrotheriinae (Xenarthra, Tardigrada) from the Pleistocene of Argentina. *Ameghiniana* 52: 294–302
- Cabral de Carvalho JN, Campos e Silva A, Oliveira LDD, Fernandes M, Carvalho SG (1969) A paleontologia no Rio Grande do Norte. *Arq Inst Antropo* 1:1–40
- Carlini A A, Brandoni D, Sánchez R (2006a) First megatheriines (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco (late Miocene) and Codore (Pliocene) formations, Estado Falcón, Venezuela. *J Syst Palaeontol* 4(3):269–278
- Carlini AA, Scillato-Yané GJ, Sánchez R (2006b) New Mylodontoidea (Xenarthra: Phyllophaga) from the middle Miocene-Pliocene of Venezuela. *J Syst Palaeontol* 4(3):255–267
- Carranza-Catañeda O, Wang X, Aranda JJ, Tzeng J, Troncoso H, Cervantes J (2008) Mastofauna del Terciario Tardío de la Formación Juchipila, Estado de Zacatecas y su correlación bioestratigráfica con las faunas del centro de México. *Geos* 28(2):191
- Cartelle C (1991) Um novo Mylodontinae (Edentata, Xenarthra) do Pleistoceno final da região intertropical brasileira. *An Acad Bras Ciênc* 63(2):161–170
- Cartelle C (2012) Das grutas à luz: os mamíferos Pleistocênicos de Minas Gerais. Bicho do Mato Editora, Belo Horizonte, 236 pp
- Cartelle C, De Iuliis G, Lopes Ferreira R (2009) Systematic revision of tropical Brazilian scelidotheriine sloths (Xenarthra, Mylodontoidea). *J Vertebr Paleontol* 29(2):555–566
- Cartelle C, De Iuliis G, Pujos F (2008) A new species of Megalonychidae (Mammalia, Xenarthra) from the Quaternary of Poo Azul (Bahia, Brazil). *CR Palevol* 7:335–346
- Cartelle C, Fonseca JS (1983) Contribuição ao melhor conhecimento da pequena preguiça terrícola *Nothrotherium maquinense* (Lund), Lydekker, 1889. *Lundiana* (2):127–181
- Cartelle C, Hiroka S (2005) Primeiro registro pleistocênico de *Pteronura brasiliensis* (Gmelin, 1788) (Carnívoro Mustelidae). *Arq Mus Nac Rio de Janeiro* 63(3):595–598
- Chiarello AG (1998) Diet of the Atlantic forest maned sloth *Bradypus torquatus* (Xenarthra: Bradypodidae). *J Zool* 246:11–19
- Cisneros JC (2005) New Pleistocene vertebrate fauna from El Salvador. *Rev Bras Paleontol* 8(3):239–255
- Collins RL (1934) Venezuelan Tertiary mammals. *Johns Hopkins Univ Stud Geol* 11:235–244
- Cozzuol MA (2006) The Acre vertebrate fauna: age, diversity, and geography. *J S Am Earth Sci* 21:185–203
- Croft DA (2007) The middle Miocene (Laventan) Quebrada Honda Fauna, southern Bolivia and a description of its notoungulates. *Palaeontology* 50(1):277–303
- Croft DA, Anaya F, Auerbach D, Garzzone C, MacFadden BF (2009) New data on Miocene neotropical provinciality from Cerdas, Bolivia. *J Mammal Evol* 16(3):175–198
- Dantas MAT, Porpino KO, Bauermann KO, Prata APN, Cozzuol MA, Kinoshita E, Barbosa JHO, Baffa O (2011) Megafauna do Pleistoceno superior de Sergipe, Brasil: registros taxonômicos e cronológicos. *Rev Bras Paleontol* 14(3):311–320
- De Iuliis G, Brandoni D, Scillato-Yané GJ (2008) New remains of *Megathericulus patagonicus* Ameghino, 1904 (Xenarthra, Megatheriidae): information on primitive features of megatheriines. *J Vertebr Paleontol* 28(1):181–196
- De Iuliis G, Cartelle C (1999) A new giant megatheriine ground sloth (Mammalia: Xenarthra: Megatheriidae) from the late Blancan to early Irvingtonian of Florida. *Zool J Linn Soc* 127:495–515
- De Iuliis G, Cartelle C, Pujos F (in press) New remains of Pleistocene megalonychid ground sloths (Xenarthra: Pilosa) from the intertropical Brazilian region. *J Paleontol*
- De Iuliis G, Gaudin TJ, Vicens M (2011) A new genus and species of nothrotheriid sloth (Xenarthra, Tardigrada, Nothrotheriidae) from the late Miocene (Huayquerian) of Peru. *Palaeontology* 54(1):171–205
- De Iuliis G, McDonald HG, Stanchly N, Spenard J, Powis TG (2015) *Nothrotheriops shastensis* (Sinclair) from Actun Lak: first record of Nothrotheriidae (Mammalia, Xenarthra, Pilosa) from Belize. *Ameghiniana* 52(1):153–171
- De Iuliis G, St-André P-A (1997) *Eremotherium sefvei* nov. sp. (Mammalia, Xenarthra, Megatheriidae) from the Pleistocene of Ulloma, Bolivia. *Geobios* 30(3):453–461
- Delsuc F, Catzeflis FM, Stanhope MJ, Douzery EJP (2001) The evolution of armadillos, anteaters and sloths depicted by nuclear and mitochondrial phylogenies: implications for the status of the enigmatic fossil *Eurotamandua*. *Proc Roy Soc B-Biol Sci* 268:1605–1615
- Delsuc F, Douzery EJP (2009) Armadillos, anteaters, and sloths (Xenarthra). In: Hedges SB, Kumar S (eds) *The Timetree of Life*. Oxford University Press, Oxford, pp 475–478

- Delsuc F, Superina M, Tilak M-K, Douzery EJP, Hassanin A (2012) Molecular phylogenetics unveils the ancient evolutionary origins of the enigmatic fairy armadillos. *Mol Phylogenet Evol* 62:673–680
- Delsuc F, Vizcaíno SF, Douzery EJP (2004) Influence of Tertiary paleoenvironmental changes on the diversification of South American mammals: a relaxed molecular clock study within xenarthrans. *BMC Evol Biol* 4(11):1–13
- Dias Rêgo H (1992) Os Fósseis de *Lestodon Gervais*, 1855 (Edentata, Mylodontidae) da coleção de paleovertebrados do Museu Nacional/UFRJ. Estudo morfológico e comparativo. Unpublished Masters Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 141 pp
- Emerling CA, Springer MS (2015) Genomic evidence for rod monochromacy in sloths and armadillos suggests early subterranean history for Xenarthra. *Proc Roy Soc B-Biol Sci* 282:20142192
- Engel F (1970) La grotte du *Megatherium* et les écologies du Haut-Pliocène Péruvien. *Semiotica* (1):413–436
- Engelmann GF (1987) A new Deseadan sloth (Mammalia: Xenarthra) from Salla, Bolivia, and its implications for the primitive condition of the dentition in Edentates. *J Vertebr Paleontol* 7(2):217–223
- Fariña RA, Vizcaíno SF, De Iuliis G (2013) Megafauna: Giant Beasts of Pleistocene South America. Indiana University Press, Bloomington, 436 pp
- Fátima Rossetti D, Mann de Toledo P, Moraes-Santos, HM, de Araújo Santos AE (2004) Reconstructing habitats in central Amazonia using megafauna, sedimentology, radiocarbon, and isotope analyses. *Quaternary Res* 61:289–300
- Frailey CD (1988) The Miocene vertebrates of Quebrada Honda, Bolivia. II : Edentata. *Occas Pap Mus Nat Hist* (123):1–13
- Gaudin TJ (1995) The ear region of edentates and the phylogeny of the Tardigrada (Mammalia, Xenarthra). *J Vertebr Paleontol* 15(3):672–705
- Gaudin TJ (2004) Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zool J Linn Soc* 140:255–305
- Gaudin TJ, Croft DA (2015) Paleogene Xenarthra and the evolution of South American mammals. *J Mammal* 96(4):622–663
- Gazin CL (1957) Exploration for the remains of giant ground sloths in Panama. *Smithsonian Report for 1956*:341–354
- Gibb GC, Condamine FL, Kuch M, Enk J, Moraes-Barros N, Superina M, Poinar HN, Delsuc F (in press) Shotgun mitogenomics provides a reference phylogenetic framework and timescale for living xenarthrans. *Mol Biol Evol*. doi:10.1093/molbev/msv250
- Guérin C, Faure M (2008) La biodiversité mammalienne au Pléistocène supérieur – Holocène ancien dans la région du Parc National Serra da Capivara (SE du Piauí, Brésil). *FUMDHAMentos* 7:80–93
- Hirschfeld SE (1985) Ground sloths from the Friasian La Venta Fauna, with additions to the Pre-Friasian Coyaima Fauna of Colombia, South America. *Univ Calif Publ Geol Sci* 128:1–91
- Hoffstetter R (1952) Les mammifères pléistocènes de la République de l'Équateur. *Mém Soc Géol Fr* (66):1–391
- Hoffstetter R (1956) Contribution à l'étude des Orophodontoidea, Gravigrades cuirassés de la Patagonie. *Ann Paleontol* 42:27–64
- Hoffstetter R (1961) Description d'un squelette de *Planops* (Gravigrade du Miocène de Patagonie). *Mammalia* 25(1):57–96
- Hoffstetter R (1978) Une faune de mammifères pléistocènes au Paraguay. *Compt Rend Sommaire Soc Geol Fr* (1):32–33
- Hoffstetter R, Martínez C, Mattauer M, Tomasi P (1971) Lacayani, un nouveau gisement bolivien de Mammifères déséadiens (Oligocène inférieur). *C R Acad Sci* 273:2215–2218
- Höss M, Dilling A, Currant A, Pääbo S (1996) Molecular phylogeny of the extinct ground sloth *Myiodon darwini*. *Proc Natl Acad Sci USA* 93:181–185
- Laurito CA, Valerio CA (2012) Primer registro fósil de *Pliometastes* sp. (Mammalia, Xenarthra, Megalonychidae) para el Mioceno superior de Costa Rica, América Central. Una nueva pista para la comprensión del pre-GABI. *Rev Geol Am Cent* 47: 95–108
- Lemon RRH, Churcher CS (1961) Pleistocene geology and paleontology of the Talara region, northwest Peru. *Am J Sci* 259:410–429
- Lucas SG, Alvarado GE, García R, Espinoza E, Cisneros JC, Martens U (2007) Vertebrate paleontology. In: Bundschuh J, Alvarado GE (eds) Central America: Geology, Resources and Hazards. Taylor and Francis Group, Oxford, pp 443–451
- MacPhee RDE, Iturralde-Vinent MA (1995) Origin of the Greater Antillean land mammal fauna, 1: new Tertiary fossils from Cuba and Puerto Rico. *Am Mus Novitates* 3141:1–31
- MacPhee RDE, Iturralde-Vinent MA, Gaffney ES (2003) Domo de Zaza, an early Miocene vertebrate locality in south-central Cuba, with notes on the tectonic evolution of Puerto Rico and the Mona passage. *Am Mus Novitates* 3394:1–42
- MacPhee RDE, Reguero MA (2010) Reinterpretation of a middle Eocene record of Tardigrada (Pilosa, Xenarthra, Mammalia) from La Meseta Formation, Seymour Island, West Antarctica. *Am Mus Novitates* 3689:1–21
- Marshall LG, Berta A, Hoffstetter R, Pascual R, Bombin M, Mones A (1984) Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. *Paleovertebrata Mém Ext*:1–76
- Marshall LG, Hoffstetter R, Pascual R (1983) Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. *Paleovertebrata Mém Ext*:1–93
- Marshall LG, Salinas ZP (1991) The Lorenzo Sundt collection of Pleistocene mammals from Ulloma, Bolivia in the Museo Nacional de Historia Natural, Santiago, Chile. In: Suarez Soruco R (ed) Fósiles y facies de Bolivia - I - Vertebrados. *Rev Téc YPF* 12: 685–692
- Matthew WD (1931) Genera and new species of ground sloths from the Pleistocene of Cuba. *Am Mus Novitates* 511:1–5
- McDonald HG (1997) Xenarthrans: Pilosans. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington D.C., pp 233–245
- McDonald HG (2005) Paleocology of extinct xenarthrans and the great biotic interchange. *Bull Florida Mus Nat Hist* 45(4):319–340
- McDonald HG, De Iuliis G (2008) Fossil history of sloths. In: Vizcaíno SF, Loughry WJ (eds) The Biology of the Xenarthra. University of Florida Press, Gainesville, pp 39–55
- McDonald HG, Jefferson GT (2008) Distribution of Pleistocene *Nothrotheriops* (Xenarthra, Nothrotheriidae) in North America. *Sci Series* 41:313–331
- McDonald HG, Rincón AD, Gaudin TJ (2013) A new genus of megalonychid sloth (Mammalia, Xenarthra) from the late Pleistocene (Lujanian) of Sierra De Perija, Zulia State, Venezuela. *J Vertebr Paleontol* 33(5):1226–1238
- McDonald HG, Vizcaíno SF, Bargo MS (2008) Skeletal anatomy of the fossil history of the Vermilingua. In: Vizcaíno SF, Loughry WJ (eds) The Biology of the Xenarthra. University of Florida Press, Gainesville, pp 64–78
- McKenna MC, Wyss AR, Flynn JJ (2006) Paleogene pseudoglyptodont xenarthrans from central Chile and central Patagonia. *Am Mus Novitates* 3536:1–18
- Muizon C de, McDonald HG, Salas R, Urbina M (2003) A new early species of the aquatic sloth *Thalassocnus* (Mammalia, Xenarthra) from the late Miocene of Peru. *J Vertebr Paleontol* 23(4):886–894
- Muizon C de, McDonald HG, Salas R, Urbina M (2004) The youngest species of the aquatic sloth *Thalassocnus* and a reassessment of the relationships of the nothrother sloths (Mammalia: Xenarthra). *J Vertebr Paleontol* 24(2):387–397
- Negri FR, Bocquentin-Villanueva J, Ferigolo J, Antoine P-O (2010) A review of Tertiary mammal faunas and birds from western Amazonia. In: Hoorn C, Wesselingh F (eds) Amazonia: Landscape

- and Evolution - A Look into the Past. Blackwell Publishing, Oxford, pp 245–258
- Nyakatura JA (2012) The convergent evolution of suspensory posture and locomotion in tree sloths. *J Mammal Evol* 19: 225–234
- Page WD (1978) The geology of El Bosque Archaeological Site, Nicaragua. In: Bryan AL (ed) Early Man in America from a Circum-Pacific Perspective. Occas Pap Dept Anthropol Univ Alberta (1):231–260
- Pant SRA, Goswami A, Finarelli JA (2014) Complex body size trends in the evolution of sloths (Xenarthra: Pilosa). *BMC Evol Biol* 14:1–8
- Patterson B, Tumbull WD, Seagall W, Gaudin TJ (1992) The ear region in xenarthrans (=Edentata: Mammalia). Part II. Pilosa (sloths, anteaters), palaeodonts, and a miscellany. *Fieldiana Geol* 1438:1–78
- Pauli JN, Mendoza JE, Steffan SA, Carey CC, Weimer PJ, Peery MZ (2014) A syndrome of mutualism reinforces the lifestyle of a sloth. *Proc Roy Soc B-Biol Sci* 281:20133006
- Pujos F (2000) *Scelidodon chiliensis* (Xenarthra, Mammalia) du Pléistocène terminal de “Pampa de los Fósiles” (Nord – Pérou). *Quaternaire* 11(3-4):197–206
- Pujos F (2006) *Megatherium celendinense* sp. nov. from the Pleistocene of Peruvian Andes and the megatheriine phylogenetic relationship. *Palaeontology* 49(2):285–306
- Pujos F (2008) Paleogeographic repartition and anatomical adaptations in Peruvian Megatheriine ground sloths (Edentata: †Megatherioidea). In: Vizcaino SF, Loughry J (eds) The Biology of the Xenarthra. University of Florida Press, Gainesville, pp 56–63
- Pujos F, Antoine P-O, Mamani Quispe B, Abello A, Andrade Flores R (2012a) The Miocene vertebrate faunas of Achiri, Bolivia. *J Vertebr Paleontol* 32(suppl to no 3):159
- Pujos F, Candela A, Galli CI, Coira BL, Reguero MA, De los Reyes M, Abello MA (2012b) The scelidotheriine *Proscelidodon* (Xenarthra: Mylodontidae) from the late Miocene of Maimará (northwestern Argentina). *Ameghiniana* 49(4):668–674
- Pujos F, De Iuliis G (2007) Late Oligocene Megatherioidea fauna (Mammalia: Xenarthra) from Salla-Luribay (Bolivia): new data on basal sloth radiation and Cingulata-Phyllophaga split. *J Vertebr Paleontol* 27(1):132–144
- Pujos F, De Iuliis G, Argot C, Werdelin L (2007) A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implications for sloth history. *Zool J Linn Soc* 149(2):179–235
- Pujos F, De Iuliis G, Mamani Quispe B (2011) *Hiskatherium saintandrei* gen. et sp. nov.: an unusual sloth from the Santacrucian of Quebrada Honda (Bolivia) and an overview of middle Miocene, small megatherioids. *J Vertebr Paleontol* 31(5):1131–1149
- Pujos F, De Iuliis G, Mamani Quispe B, Adnet S, Andrade Flores R, Billet G, Fernández Monescillo M, Marivaux L, Münch P, Prámparo MB, Antoine P-O (in press) A new nothrotheriid xenarthran from the late early Pliocene of Pomata-Ayte (Bolivia): new insights into the caniniform-molariform transition in sloths. *Zool J Linn Soc*
- Pujos F, De Iuliis G, Mamani Quispe B, Andrade Flores R (2014) *Lakukullus anatisrostratus*, gen. et sp. nov., a new massive nothrotheriid sloth (Xenarthra, Pilosa) from the middle Miocene of Bolivia. *J Vertebr Paleontol* 34(5):1243–1248
- Pujos F, Gaudin TJ, De Iuliis G, Cartelle C (2012c) Recent advances on variability, morpho-functional adaptations, dental terminology, and evolution of sloths. In: Gaudin TJ, Pujos F (eds) Proceedings of the Symposium Form and Function of the Xenarthra, ICVM9. *J Mammal Evol* 19(3):159–170
- Pujos F, Salas R (2004a) A new species of the genus *Megatherium* (Mammalia: Xenarthra: Megatheriidae) from the Pleistocene of Sacaco and Tres Ventanas, Peru. *Palaeontology* 47(3):579–604
- Pujos F, Salas R (2004b) A systematic reassessment and paleogeographic review of fossil Xenarthra from Peru. *Bull Inst Fr Et And* 33(2):331–377
- Pujos F, Salas-Gismondi R, Baby G, Baby P, Goillot C, Tejada J, Antoine P-O (2013) Implication of the presence of *Megathericulus* (Xenarthra: Tardigrada: Megatheriidae) in the Laventan of Peruvian Amazonia. *J Syst Palaeontol* 11(8):973–991
- Ribeiro AM, Madden RH, Negri FR, Kerber L, Schmaltz Hsiou A, Rodrigues KA (2013) Mamíferos fósiles y biocronología en el suroeste de la Amazonia, Brasil. In: Brandoni D, Noriega JI (eds) El Neógeno de la Mesopotamia Argentina. APA, Pub Esp 4:207–221
- Rincón AD, McDonald HG, Solórzano A, Núñez Flores M, Ruiz-Ramoni D (2015) A new enigmatic late Miocene mylodontoid sloth from northern South America. *Roy Soc Open Sci* 2: 140256
- Rodrigues do Nascimento A (2008) Os Xenarthra Pilosa (Megatheriidae), Notoungulata (Toxodontidae) e Proboscidea (Gomphotheriidae) da Formação Madeira do Pleistoceno superior do Estado de Rondônia, Brasil. Monografia de Mestrado, UFRGS, Porto Alegre, 113 pp
- Román-Carrion JL (2007) Nuevos datos sobre la distribución geográfica de los “perezosos gigantes” del Pleistoceno del Ecuador. *Politécnica* 27:111–124
- Salas-Gismondi R, Baby P, Antoine P-O, Pujos F, Benammi M, Espurt N, Brusset S, Urbina M, De Franceschi D (2006) Late middle Miocene vertebrates from the Peruvian Amazonian Basin (Inuya and Mapuya Rivers, Ucayali): Fitzcarrals expedition 2005. XIII Cong Peruano Geol, Res Ext:643–646
- Salles LO, Cartelle C, Guedes PG, Boggiani PC, Janoo A, Russo CAM (2006) Quaternary mammals from Serra da Bodoquena, Mato Grosso do Sul, Brazil. *Bol Mus Nac Rio J Zool* 52:1–12
- Santos JCR, Rancy A, Ferigolo J (1993) Octodontobryinae, una nova subfamília de Orophodontidae (Edentata, Tardigrada) do Mioceno Superior - Plioceno do Estado do Amazonas, Brasil. *Ameghiniana* 30(3):255–264
- Scillato-Yané GJ (1976) Sobre un Dasypodidae (Mammalia, Xenarthra) de edad Riochiquense (Paleoceno superior) de Itaboraí, Brasil. *An Acad Bras Ciênc* 48(3):527–530
- Shockey BJ, Anaya F (2011) Grazing in a new late Oligocene mylodontid sloth and a mylodontid radiation as a component of the Eocene-Oligocene faunal turnover and the early spread of grasslands/savannas in South America. *J Mammal Evol* 18:101–115
- St-André P-A (1994) Contribution à l'étude des grands mammifères du Néogène de l'altiplano bolivien. Unpublished PhD Thesis, MNHN, Paris, 564 pp
- St-André P-A (1996) Deux nouveaux Édentés (Mammalia, Xenarthra) *Trachycalyptoides achirensis* nov. gen. et nov. sp. (Glyptodontidae, Sclerocalyptinae) et *Xyophorus villarroeli* nov. sp. (Megatheriidae, Nothrotheriinae) du Huayquerien (Miocène supérieur) de l'Altiplano bolivien. *Bull Mus Natl Hist Nat* 4(1):79–106
- St-André P-A, De Iuliis G (2001) The smallest and most ancient representative of the genus *Megatherium* Cuvier, 1796 (Xenarthra, Tardigrada, Megatheriidae), from the Pliocene of the Bolivian Altiplano. *Geodiversitas* 23(4):625–645
- St-André PA, Pujos F, De Iuliis G, Cartelle C, Gaudin TJ, McDonald HG, Mamani Quispe B (2010) Présentation préliminaire de deux nouveaux paresseux terrestres (Mammalia, Xenarthra, Mylodontidae) du Néogène de l'Altiplano bolivien. *Geodiversitas* 32(2):255–306
- Stirton RA, Gealey WK (1949) Reconnaissance geology and vertebrate paleontology of El Salvador, Central America. *Geol Soc Am Bull* 60:1731–1754
- Storch G (2003) Fossil old world “edentates.” In: Fariña RA, Vizcaino SF, Storch G (eds) Morphological Studies in Fossil and Extant Xenarthra. *Senckenb Biol* 83(1):51–60
- Tejada-Lara J, Salas-Gismondi R, Pujos F, Baby P, Benammi M, Brusset S, De Franceschi D, Espurt N, Urbina M, Antoine P-O (2015) Life in protoamazonia: middle Miocene mammals from the Fitzcarrald arch (Peruvian Amazonia). *Palaeontology* 58(2):341–378

- 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(2):267–280
- Vélez-Juarbe J, Martin T, MacPhee RDE, Ortega-Ariza D (2014) The earliest Caribbean rodents: Oligocene caviomorphs from Puerto Rico. *J Vertebr Paleontol* 34:157–163
- Villarroel CA (1998) Los *Nothrotheriinae* (*Megatheriidae*, *Gravigrada*) del Mioceno de La Venta (Colombia). Descripción de *Huilabradys magdaleniensis*, nuevos genero y especie. *Rev Acad Colomb Ci Exact* 22(85):497–506
- Villarroel CA (2000) Un Nuevo *Mylodontinae* (*Xenarthra*, *Tardigrada*) en la Fauna de La Venta, Mioceno de Colombia: el estado actual de la familia *Orophodontoidae*. *Rev Acad Colomb Ci Exact* 24(90):117–127
- Vizcaíno SF, Scillato-Yané GJ (1995) An Eocene tardigrade (*Mammalia*, *Xenarthra*) from Seymour Island, West Antarctica. *Antarctic Sci* 7: 407–408
- Webb SD, Perrigo S (1985) New megalonychid sloths from El Salvador. In: Montgomery GG (ed) *The Evolution and Ecology of Armadillos, Sloths and Vermilinguas*. Smithsonian Institution Press, Washington, D.C., pp 113–120
- White JL, MacPhee RDE (2001) The sloths of the West Indies: a systematic and phylogenetic review. In: Woods CA, Sergile FE (eds) *Biogeography of the West Indies: Patterns and Perspectives*. CRC Press, Boca Raton, pp 201–236
- Woodburne MO (1969) A late Pleistocene occurrence of the collared peccary, *Dicotyles tajacu*, in Guatemala. *J Mammal* 50: 121–125
- Ximenes CL (2008) Tanques fosilíferos de Itapipoca, CE: bebedouros e cemitérios de megafauna pré-histórica. In: Winge M, Schobbenhaus C, Souza CRG, Fernandes ACS, Berbert-Born M, Queiroz ET, Campos DA (eds) *Sítios Geológicos e Paleontológicos do Brasil*. SIGEP, Brasília, pp. 465–478