

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

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Abstract We describe a new taxon of mylodontid sloth from the late Oligocene (Deseadan South American Land Mammal “age”), Salla Beds of Bolivia. This taxon, *Paroctodontotherium calleorum*, new genus and species, is one of the oldest known sloths, but it is surprisingly derived. It is referable to the Mylodontidae and, with just a little doubt, to the Mylodontinae. It shares a number of derived characteristics with other mylodontids and even mylodontines. These include: a relatively low temporomandibular joint; a relatively short zygomatic process of the squamosal; an elongated, narrow braincase; anteriorly diverging tooththrows; broad muzzle; and greatly enlarged external nares. The relative width of the muzzle of *Paroctodontotherium* is as great as any Pleistocene mylodontid except the giant grazer, *Lestodon*. We review and critique methods of estimating diets of extinct sloths and propose a hypothesis in regard to the feeding ecology of *Paroctodontotherium*. Based upon its broad muzzle, the degree of tooth wear, and its presence in a habitat dominated by hypsodont herbivores, we propose that *Paroctodontotherium* was a bulk feeder that foraged near ground level. Grasses were likely a major component of its diet. The addition of this new taxon, along with other recently discovered taxa, illustrates that late Oligocene sloths had much greater diversity than recognized just a decade ago. This diversity is evident in species richness,

variations in body sizes, dental morphologies, and means of locomotion. We regard this relatively sudden sloth radiation as a significant component of the Eocene-Oligocene faunal turnover and was related to the development of more open habitats of post-Eocene South America.

Keywords Folivora · Sloth · Deseadan · Eocene-Oligocene turnover · Grazing · South America

Introduction

Sloth diversity is one of the great stories of the post-Eocene New World. This diversity is evident in terms of the numbers of species, the extreme variation of body sizes, diversity of locomotor and feeding adaptations, as well as the variety of habitats in which the beasts lived. The richness of species is illustrated by the approximately 90 genera recognized (Wilson and Reeder 2005; McKenna and Bell 1997), with the greatest diversity being documented for the late Miocene and the Pleistocene (McKenna and Bell 1997).

The morphological diversity of sloths is conspicuous in the extreme variation in body size. For example, the masses of extant sloths range from 2.25 to 5.5 kg in *Bradypus* spp., and 4.0–8.5 kg in *Choloepus* spp. (Nowak 1991), while that of the extinct Pleistocene giant, *Megatherium*, approached 4,000 kg (Casinos 1996; Fariña et al. 1998). Diversity of form is also seen in locomotor abilities, with some of the so-called “ground” sloths being capable of climbing (e.g., *Hapalops* and *Acratocnus*, White 1993; and *Diablolotherium nordenskioldi*, Pujos et al. 2007), others of digging (*Scelidotherium* and *Glossotherium*, Vizcaíno et al. 2001), and still others being competent swimmers (e.g., *Thalassocnus*, Muizon and McDonald 1995; Muizon et al. 2004).

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Whereas extant sloths are limited to tropical forests where they are specialized arboreal folivores, it is clear that many extinct sloths lived in various and sometime extreme habitats. For example, *Nothrotheriops* is known from arid regions of North America (Hansen 1978) and *Myiodon* from extreme southern Patagonia (Owen 1840; Smith Woodward 1900). And whereas numerous genera of megalonychids inhabited tropical isles of the West Indies (White and MacPhee 2001), the megalonychid, *Megalonyx jeffersoni*, ranged beyond the Arctic Circle (McDonald et al. 2000). Species of *Ereotherium* inhabited forested, intertropical regions of both South and North America, whereas the other well-known Pleistocene giant, *Megatherium*, lived in more open and temperate habitats (Bargo and De Iuliis 1999).

Despite the remarkable Neogene diversity of sloths, little had been known of these beasts from the Paleogene. Curiously, the oldest, but fragmentary, remains of a probable sloth come from the Eocene of the Antarctic (Vizcaíno and Scillato-Yané 1995). Questionably, *Proplatyarthrus* is known by an astragalus from the late Eocene Mustersan South American Land Mammal “age” (SALMA) of Argentina (Ameghino 1905), and the enigmatic sloth-like *Pseudoglyptodon chilensis* was recently discovered in the early Oligocene Tinguirirican SALMA (McKenna et al. 2006). Postcranial remains from the early Oligocene Juana Diaz Formation of Puerto Rico appear to be those of a sloth (MacPhee and Iturralde-Vincent 1995).

Sloths have been known from the late Oligocene Deseadan SALMA for over a century. Ameghino (1895) named two distinct genera from the Deseadan of Patagonia (*Octodontotherium* and *Orophodon*). He also questionably referred another species to *Hapalops* (?*H. antistis*). Recent work (Engelmann 1987; Carlini and Scillato-Yané 2004; Pujos and De Iuliis 2007), including the discovery reported in this work (see also Shockey and Anaya 2008), indicates a much greater taxonomic diversity of sloths in the Deseadan SALMA (late Oligocene) than previously recognized. McKenna and Bell (1997) listed only three genera of late Oligocene sloths, *Pseudoglyptodon*, *Orophodon*, and *Octodontotherium*, and suggested *Proplatyarthrus* as a possible fourth genus, but preferred the interpretation that the material (an astragalus) was referable to *Orophodon* or *Octodontotherium*. We recognize seven valid genera: *Octodontotherium*, *Orophodon*, ?*Hapalops* (sensu Ameghino, 1897 for a Deseadan species), *Chubutherium*, *Deseadognathus*, *Pseudoglyptodon*, and *Paroctodontotherium*, new genus. *Chubutherium*, the oldest known scelidotheriine mylodontid, was found in strata originally thought to be of Colhuehuapian SALMA (early Miocene) (Cattoi 1962), but has recently been ascribed to the late Oligocene Deseadan (Carlini and Scillato-Yané 2004).

The presence of sloths in the late Oligocene, Deseadan beds of Salla, Bolivia, has been known for some time (Hoffstetter 1968). However, until now, the only named taxon was *Pseudoglyptodon sallaensis*. Pujos and De Iuliis (2007) completed a descriptive survey of various fragmentary remains of sloths from Salla, mostly from the collection in the MNHN-Paris, and recognized two unnamed species of small “orophodontids,” and a small unnamed megalonychid. We (Shockey and Anaya 2008) have previously announced our discovery of this new mylodontid from the late Oligocene of Bolivia that we here formally recognize as a new taxon, *Paroctodontotherium calleorum*.

The purpose of this paper is to describe and formally name the new mylodontid from Salla. We also discuss and critique methods of determining feeding habits in extinct sloths and propose that the new Salla sloth and *Octodontotherium* were bulk feeders, likely feeding at ground level in grasslands or savannas.

Materials and Methods

Taxonomic Nomenclature For convenience sake, we frequently use the informal “sloth” to denote the last common ancestor of *Bradypus*, *Choloepus*, *Megalonyx*, *Megatherium*, and *Myiodon* and all the descendants of that common ancestor. To ease the discussion, we generally refer to *Pseudoglyptodon* as a sloth, but we note that, unless it is the sister to megalonychids, as suspected by some workers (Hoffstetter 1982; Carlini and Scillato-Yané 2002), it may not be a member of the group (McKenna et al. 2006). Also, we do not constrain “sloth” to a crown clade for the simple reason we are not sure what that would include—the phylogenetic position of *Bradypus* is too unstable to confidently define a crown clade of sloths (see “Discussion”, *Diversity above Species Level*).

Folivora Delsuc et al. 2001, is a satisfactory solution to the homonym problem of the two commonly used formal names for sloths: *Phyllophaga* Owen 1842, and *Tardigrada* Brisson, 1762. Both *Phyllophaga* and *Tardigrada* are homonyms for invertebrate taxa—*Phyllophaga* is a genus of beetles (e.g., “June bugs”) and *Tardigrada* is phylum of arthropod-like animals commonly known as “water bears” (see Delsuc et al. 2001; Shockey 2009 for discussion).

Dental Nomenclature To avoid implying tooth homologies with other mammals, we follow the notation of Carlini and Scillato-Yané (2004) in designating the five upper teeth of sloths as a caniniform (Cf1) plus four molariforms (Mf1–Mf4). The four lower teeth are referred to as cf1 and mf1–3. This is similar to the convention of many workers that use C for caniniform and M for molariform (e.g., McKenna et al. 2006). We find it unnecessary and confusing to use

the “orophodont” notation, where the Cf1 is designated as M1, the Mf1 as M2, etc (e.g., Hoffstetter 1956, 1982; Pujos and De Iuliis 2007), as we are content that the upper dentitions of *Octodontotherium* and the holotype of *Paroctodontotherium* are unambiguously homologous to those of other mylodontids.

Body Mass Estimates Body masses are estimated using the empirically derived allometric relationships of three linear measures with body mass from Janis (1990; see also Fariña et al. 1998). These include body mass estimates based upon total skull length (TSL), muzzle width (MZW), and upper postcanine toothrow length (PCRU). The equations (transformed to solve for mass) are as follows:

$$\text{mass} = \text{TSL}^{2.975} / 220.8;$$

where mass is in kg and TSL in cm. Likewise,

$$\text{mass} = 4.365\text{MZW}^{2.313}; \text{ and}$$

$$\text{mass} = \text{PCRU}^{3.07} / 12.599.$$

Muzzle Measures and Index We follow Bargo et al. (2006a) regarding the measures used to determine the relative width

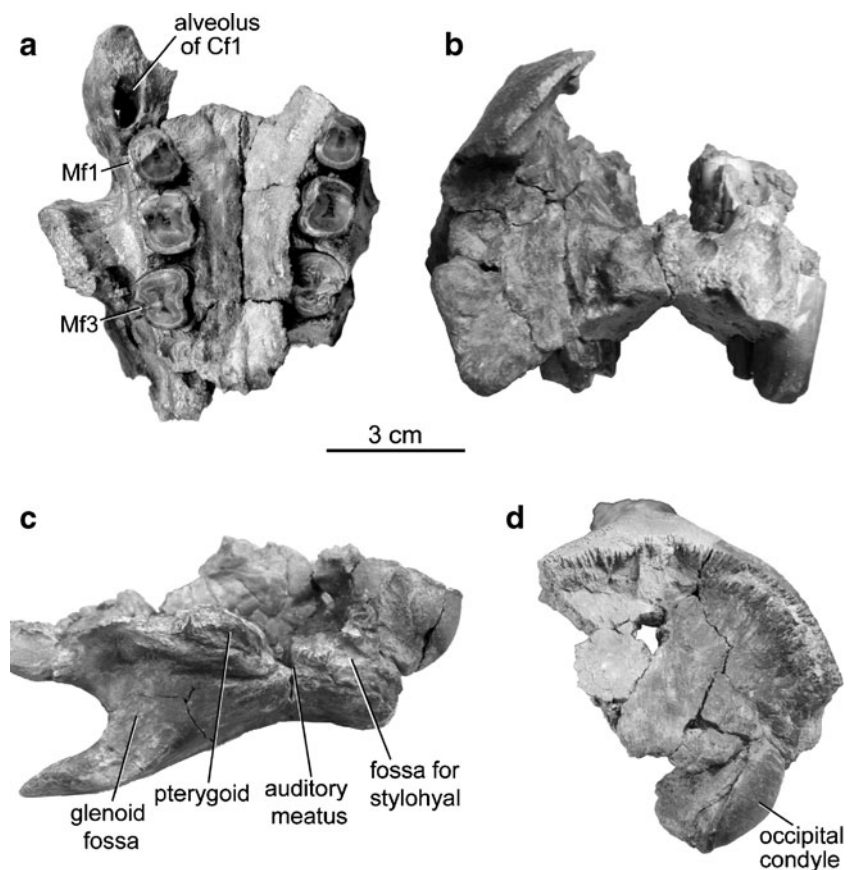
of the muzzle. However, we modify the equation so that the mathematical expression for relative muzzle width is proportional to muzzle width—larger numbers to indicate wider muzzles. (The “relative muzzle width” of Bargo et al. (2006a), following Janis and Ehrhardt (1988), is actually inversely proportional to muzzle width.) Our corrected relative muzzle width (RMW) is the maximum muzzle width (MMW) divided by the average palatal widths (PW = the mean of the anterior and posterior widths of the palate, between Mf1 and Mf4 respectively):

$$\text{RMW} = \text{MMW} / \text{PW}$$

Our principle study specimen is the holotype of *Paroctodontotherium calleorum* (UATF-V-00127). We also studied other sloth specimens of Salla at UF, YPM-PU, and MNHN-SAL collections (see abbreviations below). Comparative studies utilized fossils and casts from the AMNH, FMNH, UF, and the YPM-PU.

Institutional Abbreviations AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MNHN SAL, the Salla collection of the Laboratoire de Paléontologie, Muséum national d’Histoire naturelle, Paris, France; UATF, Universidad

Fig. 1 Holotype of *Paroctodontotherium calleorum*, new genus and species, UATF-V-000127. **a** palatal view; **b** rostral view; **c** ventral view of right basicranial region; and **d** caudal view of right occipital region.



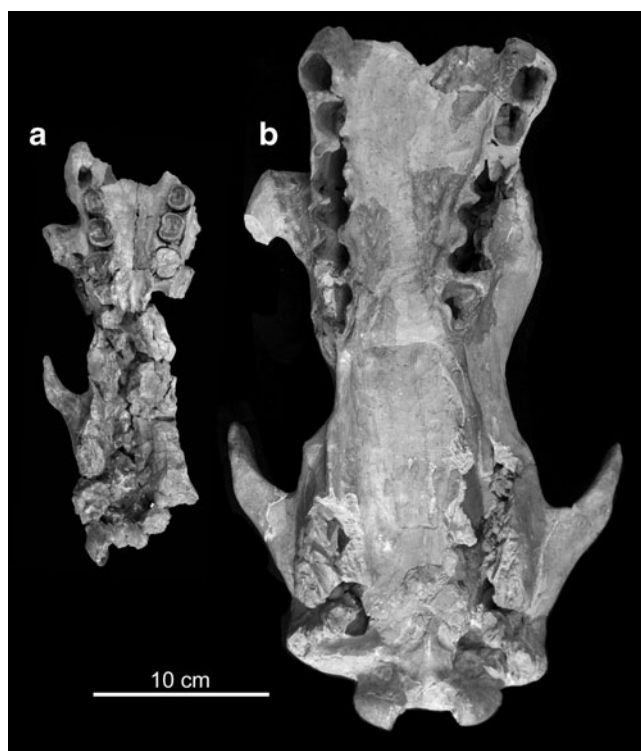


Fig. 2 Late Oligocene (Deseadan) mylodontid sloths. **a** *Paroctodontotherium calleorum*, new genus and species, UATF-V-000127; and **b** *Ocotodontotherium grande*, FMNH FMNH 13616 (see also Patterson et al. 1992: fig 2 for detail of auditory region of FMNH 13616).

Autónoma Tomás Frías, Potosí, Bolivia; UF, Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; YPM-PU, Princeton University Collection in the Peabody Museum of

Table 1 Measures (mm) of selected cranial elements of *Paroctodontotherium calleorum*, new genus and species. Parentheses indicate estimates due to damage. Estimates of symmetric dimensions (e.g., maximum muzzle width) were obtained by measuring one side and multiplying by two. Tooth lengths are their mesial-distal dimensions and widths are their transverse dimensions

Element	Length (mm)	Width (mm)
Total length of skull (basal-nasal length)	224	
Maximum braincase width	–	(75)
Maximum muzzle width (MMW)		(67)
Palatal width at Mf1 (PW _{ant})		30
Palatal width at Mf4 (PW _{post})		21
Dentitions		
Toothrow length (Cf1-Mf4)	(67.1)	
Cheek toothrow length (Mf1-Mf4)	(55.3)	
Cf1 (right alveolus)	12.1	6.9
Mf1 (right)	12.8	10.0
Mf2 (right)	13.4	11.9
Mf3 (right)	14.0	13.0
Mf4 (right alveolus)	(10)	(10)

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Other Abbreviation SALMA, South American Land Mammal “age.”

SYSTEMATIC PALEONTOLOGY

MAGNORDER XENARTHRA Cope, 1889

ORDER PILOSA Flower, 1883

SUBORDER FOLIVORA Delsuc et al., 2001

SUPERFAMILY MYLODONTOIDEA Gill, 1872

FAMILY MYLODONTIDAE Gill, 1872

cf., SUBFAMILY MYLODONTINAE Gill, 1872

PAROCTODONTOTHERIUM, new genus

Type Species *Paroctodontotherium calleorum*

Diagnosis Same as for species.

Etymology-Para (L., besides)+*Octodontotherium*, in reference to its similarity to and to imply a relationship with the Patagonian sloth of the late Oligocene, *Octodontotherium*.

Paroctodontotherium calleorum, new species

Figures 1 and 2; Table 1; Shockey and Anaya 2008:142–143, fig. 7.4

Holotype UATF-V-000127, partial cranium containing much of the cranial vault, palate with right and left Mf1-3s, an isolated tooth (Mf4?), and a small portion of the basicranium containing both condyles, and a portion of the right otic region from the uppermost horizon of Unit 3 in Calabozza Pata.

Referred Specimens UATF-V-00128, a maxillary fragment from a larger individual containing Mf1-2, broken at the occlusal level, found about a meter from the holotype; UATF-V-00130, fragments of Mf 1-3, fragment of maxilla with alveolus, and both occipital condyles, found in the Unit 3 beds at Cerro El Flaco.

We also tentatively include UATF-V-00133, postcranial fragments found near (3-4 m), but not in close association with UATF-V-00130. These fragments include distal and proximal ends of a right humerus and some caudal vertebrae.

Locality Along with Luis Lopez of UATF, we discovered the holotype at Calabozza Pata (S 17° 9.897' W 67° 37.729'). Stratigraphically, it was at the contact of the upper horizon of Unit 3 (the “Red Rodent Zone” of MacFadden et al. 1985; Kay et al. 1998) with the base of Unit 4. Remains found at Cerro El Flaco (S 17° 9.499' W

67° 37.583') were lower in the section but still in the “Red Rodent Zone.” These upper regions of Unit 3 and all of Unit 4 are composed of paleomagnetic normal sediments, interpreted to be C8n.2n in the “best-fit” correlation to radiometric ages obtained from sediments above and below the Red Rodent Zone (Kay et al. 1998). This suggests an age between 25.99 and 26.55 Ma (Berggren et al. 1995; Kay et al. 1998) or perhaps a little younger (25.49–26.15 Ma), according to the revised geomagnetic polarity time scale of Ogg and Smith (2004), if the upper part of Unit 3 and all of Unit 4 do indeed pertain to C8n.2n.

Etymology The specific name, *calleorum*, is Latinized to indicate the Calle family, in honor of Don Primitivo Calle, his sons, Jacinto and Daniel Calle, and nephew Natalio Calle of the Aymaran village of Sahalla (the correct spelling of the pueblo for which the Salla Beds are named). For over the past ten years the help of the Calle family has made our projects at Salla relatively easy and most enjoyable.

Diagnosis Moderately small mylodontid sloth, much smaller than species of *Octodontotherium* (Fig. 2) and a little smaller than *Orophodon*. Molariform upper teeth ovoid to bilobate (Fig. 1a), subtly figure-eight shaped (“octodont”) in cross section; temporomandibular joint just above the plane formed by the occlusion of the upper and lower tooththrows; zygomatic process of squamosal relatively short; occiput inclined, with condyles posterior to nuchal crest; and greatly enlarged external nares (Fig. 1b). Outline of alveolus for Mf4 suggests that this tooth could not have been widely lobate as in most mylodontids. Anterior divergence of cheek teeth with resultant broad muzzle (Fig. 1a) is similar to that of species of *Glossotheriopsis*, *Thinobadistes*, *Lestodon*, and *Glossotherium*. There is no diastema separating the caniniforms of *Paroctodontotherium* from the rest of the cheek teeth, nor are the caniniforms enlarged.

Differs from *Octodontotherium grande* and *O. crassidens* by its smaller size; its absolutely and relatively smaller caniniforms; greater quantities of cementum and internal vascular dentine (=vasodentine); Mf3 more circular (less “octodont” [“figure-eight”]) in cross section, lacking an elongated isthmus between the anterior and posterior lobes. The molariforms of *Paroctodontotherium* are worn fairly evenly, forming a shallow transverse crest, but without forming a cusp-like projection as seen in some specimens of *Octodontotherium* (Ameghino 1897: fig. 82; Hoffstetter 1956: fig. 1).

Similar in size to *Orophodon*, but differs by the relatively simple columnar shape of Mf1-2, smaller Mf4, relatively larger and bilobed nature of Mf3, greater quantity of cementum, and by the formation of transverse crests during occlusal wear, rather than the strongly oblique crests seen in *Orophodon* (Hoffstetter 1956).

Differs from *Glossotheriopsis* by its relatively broader muzzle and even greater inflation of the external nares, smaller caniniform, greater separation between the cheek teeth, and the subtle “octodont” (“figure-eight”) form of Mf2-3.

Differs from *Pseudopreotherium confusum* by its more lobate, figure-eight shaped Mf3, its anterior divergence of the tooththrow, broad muzzle, and relatively smaller size of Mf4 and Cf1, and by the lower placement of the dentary-squamosal articulation, which is above the level of the tooththrow in *P. confusum*, but at the tooththrow level in *P. calleorum*.

Not directly comparable to *Pseudoglyptodon sallaensis*, which is known only by its mandible and lower teeth, but some distinctive differences may be reasonably deduced. *Paroctodontotherium* differs by its larger size and lack of palpable ridge around the toothcore by the orthodentine (less durable, the orthodentine wears smoothly in *Paroctodontotherium*, but it forms a palpable ridge around the toothcore in *Pseudoglyptodon sallaensis*). Also the relatively large cf1 of *P. sallaensis* suggests that its Cf1 is also enlarged (as in *P. chilensis*), unlike that of *Paroctodontotherium*.

Differs from *Pseudoglyptodon chilensis* by the presence of five upper teeth (*P. chilensis* has only four), rounded to bilobed (not trilobed) molariform teeth, and much smaller Cf1.

Description The skull is tubular and modestly long for its depth and width (Fig. 2a; Shockey and Anaya 2008: fig. 7.4). The anterior region remains about as high as the posterior, ending abruptly at the grossly enlarged external nares (Fig. 2a). The palatal region is likewise enlarged, diverging anteriorly from the mid-sagittal plane such that the muzzle is broad, similar to that of various geologically younger mylodontids (e.g., *Glossotheriopsis*, *Thinobadistes*, *Glossotherium*, and *Lestodon*). As in most, if not all, sloths, the maxillary region of the palate is rugose with much pitting. The medial portion of the maxillary palate (that medial to the teeth) is inclined such that the posterior end is more ventral than the anterior end. The posterior palatal region is also ventral to the edge of the facial process of the maxilla and lateral to the posterior cheek teeth.

The upper tooththrow of the animal has five teeth, of which the second through the fourth (Mf1-Mf3) are preserved (the Cf1 and Mf4 were not preserved within their alveoli). These teeth show three distinctive tissues (Fig. 1a): a central core of vasodentine, a denser orthodentine, and an outer layer of thick cementum. *Paroctodontotherium calleorum* has greater amounts of cementum than *Octodontotherium* (compare Fig. 1 with Ameghino 1897: fig. 82). The borders where the orthodentine contacts the

cementum and the vasodentine are not as distinct as in geologically younger mylodontids (e.g., *Paramylodon*, *Thinobadistes*, *Lestodon*, and *Glossotherium*). In these mylodontids and *Pseudoglyptodon*, the orthodentine is more resistant to wear, such that it forms a palpable ridge above the wear plane of the other dental tissues. In contrast to most other mylodontids, the teeth of *Paroctodontotherium* have worn smoothly, without regard to tissue type.

The alveolus of Cf1 on the right side (Fig. 1a) outlines the general form of the tooth, indicating that the Cf1 was oval in cross section and had but a slight posterior curvature. It is the smallest tooth, with the possible exception of the Mf4. It is positioned lateral to the axis of the anteriorly diverging tooththrow, such that the line formed by Cf1-Mf1 diverges at a greater angle than the axis formed by Mf2-4. There is no real diastema, just a slight gap between Cf1 and the first molariform (Mf1) that is no greater than the gaps between the other cheek teeth.

The Mf1 is oval in cross section, with but a slight pinching of the mid region of both labial and lingual sides, suggestive of the “octodont” form of the teeth that follow. The vertical axis of the first molariform is curved posteriorly. Two distinct wear facets, mesial and distal, occur on the Mf1 and are inclined such that they form a distinct transverse crest anterior to the mid section of the occlusal surface. This has not worn as sharply as that shown for *Octodontotherium grande* by Hoffstetter (1956: fig. 2) (note: Hoffstetter uses the M1-M5, “orophodont” scheme; thus, our Mf1 = his M2). Such wear suggests that the Mf1 occluded with two lower teeth, as shown in *Thinobadistes* (Webb 1989: fig. 4). Almost certainly, the anterior surface of Mf1 occluded with the posterior surface of cf1, whereas the posterior surface of Mf1 occluded with the anterior surface of mf1. There is no lateral wear facet on the Mf1, as seen in some specimens of *Octodontotherium* (FMNH P-13512).

The Mf2 is subtly octodont, i.e., figure-eight shaped. The vasodentine is butterfly-shaped, with each “wing” suggesting the form of the mesial and distal lobes of the tooth. A weak vertical groove defines the labial and lingual boundaries between the mesial and distal lobes. The occlusal surface is worn to form a gently convex surface with a palpable transverse crest. Its wear is very unlike that of the Mf2 on a comparative specimen of *Octodontotherium* (FMNH P-13512) on which the distal loph is much more heavily worn (deeply concave) than the lightly and convexly worn mesial lobe.

The mesial lobe of the Mf3 is larger than the distal lobe (best seen on the right Mf3 as the left Mf3 is damaged). Although the lobes are distinct, there is no elongated narrow isthmus separating them as in the Mf3 of *Octodontotherium* (see Hoffstetter 1956: fig. 2). Also, the long axis

of the tooth lacks the distinctive rostral curve seen in that of *Octodontotherium*. Both the Mf2 and Mf3 wear such that the occlusal surfaces of these teeth are convex in lateral view with but a single, shallow transverse crest.

The Mf4 is not preserved on either side. Enough of the alveoli are preserved to indicate that Mf4 was a much smaller tooth than the preceding one, but the condition of the alveoli are too poor to define the outline of the tooth.

The premaxilla was not recovered. Enough of the maxilla is present to indicate that the muzzle of the animal was quite broad. This is illustrated by the diverging tooththrow and the maxilla extending anterior and laterally to the Cf1.

The anterior lateral region of the maxilla is expanded and outlines all but the most dorsal margins of the external nares (the nasals were not preserved). The external nares were large (Fig. 1c), comparable in relative size to the huge external nares of *Glossotherium* and *Lestodon* (see Bargo et al. 2006a, b). Anteriorly, the nasal passage is expanded ventrally and laterally, but less so dorsally.

The zygomatic region of the squamosal is broad at the base, but the zygomatic process is not greatly elongated (compare our Fig. 1c with that of *Octodontotherium* in Fig. 2b and Patterson et al. 1992: fig. 2a). The glenoid fossa is broad and poorly defined, similar to those seen in our comparative specimens of *Paramylodon* sp. Its position is near the level of the tooththrow.

The pterygoid is laterally rugose, descends ventrally and appears semicircular in lateral view. Its base, just anterior to the external auditory meatus, is thick but is not greatly inflated. A groove on the medial side of the damaged pterygoid descending lamina runs parallel to the long axis of the skull. Its position suggests that it contained the vidian nerve.

The ectotympanic and entotympanic were not found and the promontorium of the petrosal is likewise missing. The fossa for the stylohyal is conspicuous but not greatly enlarged.

There is no distinctive sagittal crest and the damaged nuchal crest is rounded and does not overhang the occiput. As in other mylodontids, the occiput is inclined such that the occipital condyles lie posterior to the nuchal crest.

Discussion

Affinities of Paroctodontotherium The phylogenetic analysis of Gaudin (2004) defines a monophyletic Mylodontidae that includes *Octodontotherium*, a taxon Ameghino (1895) initially and tentatively referred to the Mylodontidae, but that he and others later regarded as an “orophodontid” (Ameghino 1897; Simpson 1945; Hoffstetter 1956, 1982; Carlini and Scillato-Yané 2004; Pujos and De Iuliis 2007). Our evaluation of *Paroctodontotherium* strongly suggests that it is also a mylodontid. Although the absence of a

mandible and various regions of the skull did not allow us to evaluate many characters in Gaudin's (2004) character-taxon matrix, several characters of *Paroctodontoherium* allow us to confidently refer it to the Mylodontidae. These character states of *Paroctodontoherium* are given below in terms of Gaudin's character numbers and states shown within brackets and parentheses as follows: [character number (state)]. Character numbers and states of unambiguous synapomorphies are shown in bold:

Character states observed in *Paroctodontoherium* that suggest a relationship among the Mylodontidae include: temporomandibular joint near, but just above, the plane formed by the occlusion of the upper and lower tooththrows [53(1)]; and zygomatic process of squamosal relatively short [168(1)]. Synapomorphies of basal mylodontid nodes (within Mylodontidae, but outside of the subfamilies Mylodontinae and Scelidotheriinae) shared by *Paroctodontoherium* include: skull elongated with narrow braincase [82(0)]; snout elevated, lacking anterior constriction [87(1)]; pterygoid inflated [137(1)]; and frontal sinus large and extensive [174(3)]. An ambiguous synapomorphy with the Mylodontinae shared by *Paroctodontoherium* is: left and right tooththrows diverge anteriorly [4(1)]. Synapomorphies for nodes within Mylodontinae shared by *Paroctodontoherium*

include: external nares greatly enlarged [98(1)]; and palate long and strongly widened anteriorly [122(3)].

Despite its antiquity (only *Octodontoherium* is an older mylodontid), *Paroctodontoherium* does not appear to be very "primitive." As noted in the previous paragraph, it shares derived character states with advanced mylodontines. The relatively derived state of *Paroctodontoherium* and its differences from *Octodontoherium* hint at a likely pre-Deseadan radiation of mylodontids and probably even diversification of mylodontine sloths.

Deseadan Sloth Diversity This addition to the knowledge of the alpha diversity of sloths, along with that of other relatively recent works (Engelmann 1987; Carlini and Scillato-Yané 2004; Pujos and de Iuliis 2007; Shockey and Anaya 2008), illustrates that species richness in the late Oligocene was much greater than was known a generation ago (e.g., Simpson 1945), or even as recent as the work of McKenna and Bell (1997), which listed only three Deseadan genera. This diversity is also evident in terms of family level representation, great variation in body size (Fig 2; Carlini and Scillato-Yané 2004), variation in habitat use (Carlini and Scillato-Yané 2004), and variation in ankle form (Fig. 3; Hoffstetter 1956) and function (below).

Species Richness Carlini and Scillato-Yané (2004) recognized six species of Deseadan sloths representing three families, Megalonychidae, Megatheriidae, and Orophodontidae. Only two were congeners (*Octodontoherium grande* and *O. crassidens*), but this could actually represent variation within a single species (Pujos and De Iuliis 2007). We modify the list of Carlini and Scillato-Yané (2004) to include *Pseudoglyptodon* and the new taxon, *Paroctodontoherium*. Furthermore, we follow Gaudin (2004) and regard *Octodontoherium* as a mylodontid rather than an "orophodontid" (see above). Additionally, based upon the notched cuboid facet of the astragalus, we regard *Chubutherium* as a scelidotheriine mylodontid (see also Cattoi 1962), not an "orophodontid" (Pujos and De Iuliis 2007). Pujos and De Iuliis (2007) recognized two "orophodontids" and a megalonychid based upon fragmentary remains of Salla. They speculated that one of the "orophodontids" might be referable to the specimen that we herein designate as the holotype of *Paroctodontoherium*. We regard this as a possibility, but hesitate to refer any of their Paris specimens to *Paroctodontoherium* as they are rather fragmentary and they have thinner layers of cementum than those of the teeth of the holotype. However, to be conservative in our estimate of Deseadan sloth species richness, we count just one of their "orophodontids." Likewise, to be conservative, we do not count the megalonychid of Salla noted by Pujos and De Iuliis in our estimate of minimum species richness in the unlikely event

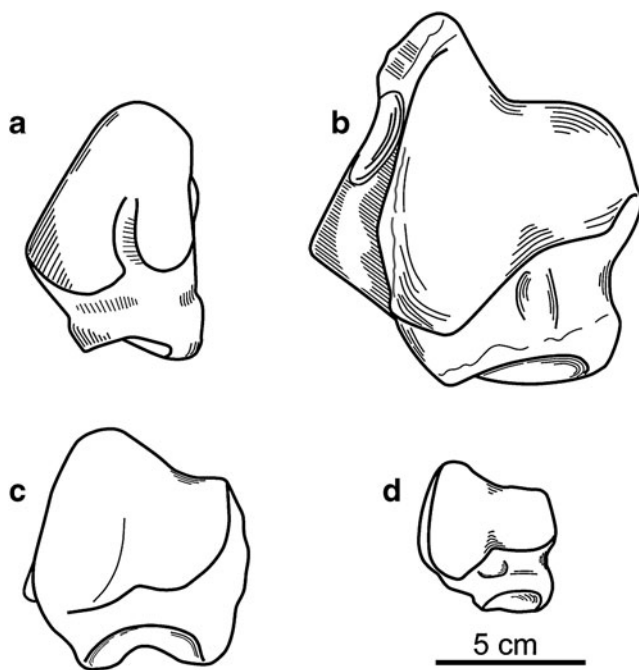


Fig. 3 Diversity of Deseadan folivoran astragali. **a** The "Haplopos-megalonychid" form is manifest in cf. *Deseadognathus*, which was originally described and figured as *Orophodon* (Hoffstetter 1956). The "odontoid" trochlear forms are manifest by **b**, *Octodontoherium* (from Hoffstetter 1956, 1982); **c** *Chubutherium* (Cattoi 1962); and **d** indeterminate folivoran astragalus from Salla (discussed by Hoffstetter 1982).

Table 2 Minimum species richness of Deseadan sloths

Species	Family	Locality	Reference
<i>Pseudoglyptodon sallaensis</i>	<i>incertae sedis</i>	Salla, Bolivia	Engelmann 1987
<i>Orophodon hapaloides</i>	“orophodontid”	“La Flecha”, Patagonia, Argentina	Ameghino 1895
unnamed “orophodontid”	“orophodontid” (possibly a mylodontid)	Salla, Bolivia	Pujos et al. 2007
<i>Octodontotherium grande</i>	Mylodontidae, cf. Mylodontinae	“La Flecha”, Patagonia, Argentina	Ameghino 1895
<i>Paroctodontotherium calleorum</i>	Mylodontidae, cf. Mylodontinae	Salla, Bolivia	new genus and species
<i>Chubutherium ferelloi</i>	Mylodontidae, Scelidotheriinae	Patagonia, Argentina	Cattoi 1962
? <i>Hapalops antistis</i>	<i>incertae sedis</i>	Patagonia	Ameghino 1895
<i>Deseadognathus riggsi</i>	Megalonychidae	“La Flecha”, Patagonia, Argentina	Carlini and Scillato-Yané 2002

it is conspecific with *Deseadognathus riggsi*. The most conservative estimate includes just one species of *Octodontotherium*. Still, with this most conservative count, there were at least eight species of sloths in the Deseadan (Table 2).

Diversity Above the Species Level Folivoran diversity includes at least three major clades, the Mylodontoidea, Megatherioidea, and a branch that includes species of *Pseudoglyptodon*. *Pseudoglyptodon* is distinct from all other known sloths because of its tri-lobed, glyptodont-like dentitions. It is sometimes regarded as being related to the Megalonychidae (Hoffstetter 1982; Carlini and Scillato-Yané 2004), but it likely falls outside the two major clades of sloths (McKenna et al. 2006). The Mylodontoidea are represented by *Octodontotherium*, *Paroctodontotherium*, *Chubutherium*, and probably *Orophodon*. The Megatherioidea are represented by *Deseadognathus* and the generically uncertain ?*Hapalops*. This diversity indicates that these two major clades of sloths had their divergence prior to the late Oligocene.

This divergence indicates an inconsistency between molecular clock studies of sloths (Delsuc et al. 2004) and the most respected sloth phylogeny (Gaudin 2004), in which *Bradypus* is the sister to both the Mylodontoidea and Megatherioidea. The molecular timescale for the separation of the extant *Bradypus* (three-toed sloth) and *Choloepus* (two-toed sloth) is 21 ± 3 MYA. This age of separation of their respective clades supports the diphyletic origins of “tree sloths,” but post dates the Mylodontoidea / Megatherioidea divergence, which must have occurred before the late Oligocene when both groups had already diversified. Thus, either the molecular clock is off by at least 5-to-10 million years or the phylogenetic hypothesis is wrong. If the molecular model is roughly correct, then the *Bradypus-Choloepus* split occurred after the Mylodontoidea / Megatherioidea split, implying that both of the extant genera had to be either megatherioids or mylodontoids (not one in each) or both had to be in a separate clade. There is a consensus for

Choloepus being a megatherioid (more specifically a megalonychid) and the evidence for this hypothesis is rather compelling (Gaudin 2004; Carlini and Scillato-Yané 2004; Pujos et al. 2007). There is, however, no consensus as to the phylogenetic position of *Bradypus*. *Bradypus* has been regarded as being allied with megatheres (Patterson and Pascual 1968), nothrotheres (Greenwood et al. 2001), megalonychids (White and MacPhee 2001; Carlini and Scillato-Yané 2004), as well as being outside the Eutardi-grada (the monophyletic clade that includes Mylodontoidea and Megatherioidea; Gaudin 2004).

Morphological Diversity Deseadan sloths show considerable variation in their body size, dentitions, and ankle morphology. This is remarkable, because the Deseadan (late Oligocene) is the first SALMA in which there is more than a single species known (only one sloth, *Pseudoglyptodon* is currently known from the early Oligocene (McKenna et al. 2006)).

Variation in body size is conspicuous in the two known mylodontids of the Deseadan, *Paroctodontotherium* and *Octodontotherium* (see Fig. 2). Due to the incompleteness of the material at hand, we could only obtain three estimates of masses for *Paroctodontotherium*. These estimates, obtained from the empirically derived allometric equations of Janis (1990; see “Materials and Methods” section) vary widely. That based upon the total skull length (TSL) is 47 kg, whereas those derived from the muzzle width and upper postcanine tooththrow length are 354 and 15 kg, respectively. This variability likely illustrates the morphological disparity between sloths and the non-xenarthran taxa from which the general relationships were derived (see Fariña et al. 1998 for discussion). In this particular case, we suspect that the mass obtained from the muzzle width is a gross overestimate—we have noted throughout that *Paroctodontotherium* has an unusually wide muzzle. The mass estimate obtained from the postcanine tooththrow is a likely gross underestimate—sloths are distinguished by their severely reduced tooth number.

The plesiomorphic dental formula of sloths is five uppers and four lowers, much reduced from the taxa used to derive the allometric equation by Janis (1990). The best estimate available for the mass of *Paroctodontotherium* is that from the TSL. Still, in their study of mass estimates of Xenarthra, Fariña et al. (1998) found TSL to give underestimates of probable masses. However, it is the best estimate we have and it will serve at least to compare *Paroctodontotherium* with the significantly larger Deseadan mylodontid, *Octodontotherium*.

The TSL of the reconstructed cranium of *Octodontotherium grande* (FMNH 13616, Fig. 2b) is about 40.3 cm, which yields an estimated mass of about 270 kg. This suggests that *Octodontotherium* was over 5.6 (=265 kg/47 kg) times more massive than *Paroctodontotherium*. We suspect that this large difference is actually an underestimate. From the ratio of TSL values (*Octodontotherium* / *Paroctodontotherium*=40.4 cm/22.4 cm \approx 1.8) perfect isometry would predict that *Octodontotherium* is about 5.8 (=1.8³) times more massive. However, inspection of Fig. 2 suggests that they are not isometric, but that *Octodontotherium* was a much more robust animal. This allometric relationship suggests that *Octodontotherium* was probably more than 5.8 times more massive. But even the conservative estimates of the mass differences indicate a remarkable variation in body size between these two early mylodontid sloths.

Folivorans of the Deseadan also show considerable variation in tooth forms. This includes the peg-like, rounded cheek teeth of *Orophodon*, the tri-lobed, glyptodont-like cheek teeth of *Pseudoglyptodon*, transversely bilophodont cheek teeth of *Deseadognathus*, and the figure-eight lobes of those of *Octodontotherium* and, to a lesser extent, those of *Paroctodontotherium*. Caniniforms range from being robust (e.g., *Pseudoglyptodon*, *Deseadognathus*, and *Octodontotherium*) to small (*Paroctodontotherium*) and being separated from the cheek teeth by a diastema (*Pseudoglyptodon* and *Deseadognathus*) or lacking a diastema (*Paroctodontotherium* and *Octodontotherium*). Many of the major dental forms seen in sloths appear by the late Oligocene.

The two major ankle morphologies of sloths also occur in the Deseadan (Hoffstetter 1956, 1982; Fig. 3). These are manifest in two general forms of the astragalus: the “*Hapalops*-megalonychid form” (Fig. 3a) and the “odontoid” trochlear form (Fig. 3b–d). The “*Hapalops*-megalonychid form” has a shallow, roughly heart-shaped (apex posterior) tibial articular surface, and it occurs in *Hapalops* (Scott 1903-4: fig. 27) and megalonychids (e.g., McDonald et al. 2000). The “odontoid” trochlear form has very asymmetric trochlear crests with the lateral being tall and sharp, whereas the medial is short, columnar, and oriented perpendicularly to the lateral trochlea, generally being described as “odontoid” (e.g., the “odontoid tibial process”

of De Iuliis 1994). This latter form is associated with the pedolateral rotation of the foot such that the foot is inverted with its lateral side contacting the ground (Owen 1842). This unusual stance occurs in mylodontid, nothrotheriid, and megatheriid sloths (Owen 1842; Stock 1925; De Iuliis 1994; White 1997; Argot 2008). Those with the *Hapalops*-megalonychid form are more conventionally plantigrade (White 1997).

Hoffstetter (1956) described and figured astragali of both forms from the Deseadan of Patagonia (La Flecha). He referred the large “odontoid” form to *Octodontotherium* and the smaller astragalus to *Orophodon*. Based upon its large size, the *Octodontotherium* referral is unambiguous. However, since that time a megalonychid, *Deseadognathus*, has been recognized from the fauna (Carlini and Scillato-Yane 2004), so it is possible that the astragalus Hoffstetter referred to as *Orophodon* pertains to *Deseadognathus*. Regardless of the taxon to which the astragalus pertains, it illustrates that at least one of the Deseadan folivorans had a foot structure similar to that of *Hapalops* (see White 1997) and was plantigrade, i.e., it did not walk on the lateral side of its foot. However, based upon the “odontoid” form of its astragalus, *Octodontotherium* probably did display the curious pedolateral means of locomotion.

Two other astragali from the Deseadan display the odontoid medial tibial process of the astragalus (Fig. 3c–d). Cattoi (1962) described and figured an astragalus referred to *Chubutherium* (Fig. 3c) and Hoffstetter (1982) discussed an astragalus from the Salla collection of MNHN-SAL, Paris (Fig. 3d). Both have a reduced, columnar medial tibial process; however, the cuboid articulation of *Chubutherium* is concave, like that of Pleistocene scelidotheres and a few other sloths (De Iuliis 1994).

Grazing in Mylodontid Folivorans: the Evidence

Three independent lines of evidence suggest that consuming grasses was an important means of feeding in mylodontid sloths. These include the high content of grass in feces of *Mylodon darwini* (Smith Woodward 1900; Moore 1978), inference from habitat (Stock 1925; McDonald and Pelikan 2006), and the broad muzzle of many mylodontids (McDonald 1997; Bargo et al. 2006a). Relative crown height (hypsodonty) has also been used (McDonald 1995; Bargo et al. 2006a), but we question the utility of this method for herbivores with continuously growing (hypsodont) dentitions (see below). The ever-growing (hypsodont) nature of mylodontid teeth clearly offers some protection against tooth wear caused by abrasives in and on grass, but all xenarthrans have hypselodont teeth, regardless of diet, habitat, or habits.

Fecal Contents Most compelling of the above investigative methods is the presence of grass in feces of *Mylodon*. Skin, bone, and feces of *Mylodon darwini* were collected over a hundred years ago from a cavern near Consuelo Cove, Ultima Esperanza in the Tierra del Fuego region of Chile (Smith Woodward 1900). Smith Woodward (1900), quoting a report of the botanist Spencer Moore, noted the presence of “haulms, leaf-sheaths, fragments of leaves, &c of these plants [grass].” These findings were confirmed and expanded upon much later by another Moore (D.M. Moore 1978). More specifically, the plant content of the dung was composed entirely of the families Cyperaceae (sedges) and Gramineae (grasses) (Moore 1978).

Inference from Habitat Less compelling, but none-the-less of interest, is the observation by Stock (1925) that mylodontid sloths were more likely to be found in regions that had been judged to have been grasslands. He noted the presence of mylodontids from the Pampas and Patagonia, open-habitat regions that lack significant forest. He also noted the presence of mylodontids of the treeless Altiplano regions of Bolivia and Peru. Likewise, McDonald and Pelikan (2006) noted that the presence of the open country taxa, *Bison* and *Mammuthus columbii*, in North American localities predicted the presence of *Paramylodon*.

Muzzle Morphology Relative muzzle width is another means that has been used to propose hypotheses regarding diet in extinct folivores. This is based upon observations among extant ungulates—Highly selective browsers have relatively narrow muzzles that allow them to forage upon nutrient rich buds and fruits without getting a mouthful of coarser, low protein, low calorie twigs and older, low-nutrient, leafy material, whereas grazers have relatively broad muzzles to aid in the intake of large quantities of low quality grasses (Gwynne and Bell 1968; Janis and Ehrhardt 1988; Solounias et al. 1993). McDonald (1997) applied this principle to the broad-muzzled *Glossotheriopsis pascuali* from the middle Miocene La Venta. He concluded that *Glossotheriopsis* was a grazer and, based upon the knowledge then available, was among the earliest grazing sloths.

Bargo et al. (2006a) examined the muzzle region of several Pleistocene mylodontid and megatheriid folivores. They provided detailed reconstructions of the facial muscles of the oral regions of these extinct sloths and provided measures related to their “relative muzzle widths” (see comments in “Materials and Methods” section). Due to their wide oral regions, they proposed that the large Pleistocene mylodontids, *Lestodon* and *Glossotherium*, were “bulk feeders” (likely grazers) that fairly indiscriminately took in large quantities of leafy material. *Mylodon*, with its narrower muzzle, was judged to have been a more selective feeder.

Hypsodonty High-crowned (hypsodont) teeth have long been regarded as an adaptation in ungulates to abrasive food materials, especially grasses, which wear down teeth (Kowalevsky 1873; Osborn 1910; Janis and Fortelius 1988). The adaptive nature of hypsodonty is explained by the following observations and deductions: abrasive phytoliths within leaves, and/or environmental grit resting upon low lying plants, wears down dental tissues during mastication (Janis and Fortelius 1988; Mendoza and Palmqvist 2008). This abrasion results in a decrease in the height of teeth in animals in which their dentitions have stopped developing (e.g., adult herbivores). With increased wear, the tooth may be reduced to a point where it is no longer functional. The ability to feed diminishes; thus, survival becomes less likely, and fitness is reduced. Selection for individuals with higher-crowned teeth in a population exposed to abrasives would occur because taller teeth would have longer functional lives; thus an herbivore having hypsodont teeth exposed to abrasives will have greater fitness than an identical herbivore with an identical abrasive diet that has low crowned (brachydont) teeth. Tooth longevity is the driving principle in regard to increased fitness in herbivores whose teeth are exposed to abrasives. Tooth height is a means in which tooth longevity may be obtained (see Janis and Fortelius 1988 for other means in which dental durability is increased).

There are, however, fundamental differences between teeth that are hypselodont (“ever-growing;” never form closed roots) and those having determinate growth (roots close; growth stops). For example, whereas abrasives will cause a decrease in the height of the crowns of determinate growth teeth, they might not decrease the height of the teeth in hypselodont taxa. Hypselodont teeth have the ability to continue developing, so tissue that has worn away at the crown may be replaced by new growth at the base. Thus, crown height may be maintained, despite the abrasion. On the other hand, and significantly, adult taxa with determinate growth teeth cannot replace the tissues lost.

Tooth longevity is proportional to crown height in taxa having determinate growth dentitions (i.e., if two identical taxa have identical and constant exposures to abrasives, but the teeth of Taxon A have heights twice those of Taxon B, then the teeth of Taxon A will last twice as long as those of B). However, the relationship between tooth longevity and relative crown height in taxa with ever-growing teeth is unclear. In principle, and by definition, ever-growing teeth are everlasting, regardless of how tall (or short) they are. Reality, of course, is almost certainly more complex, but if growth rate was to equal the rate of abrasion, then crown height would remain constant. In such case, there would be no relationship between relative crown height and tooth longevity. With no clear relationship between crown height and longevity in hypselodont taxa, like sloths, we cannot

assume that species with relatively higher crowned teeth are better adapted to abrasives than are those having relatively lower crown heights. To our knowledge, no such relationship has been demonstrated.

The trends seen in ungulates having determinate growth teeth have not been shown in sloths. Whereas there is a strong tendency among ungulates for browsers to have relatively low crowned teeth and open-country, ground-level feeders (e.g., grazers) to have higher crown teeth (Janis 1988; Janis and Fortelius 1988; Solounias et al. 1993), no such tendency was found in Pleistocene sloths sampled by Bargo et al. (2006b). Based upon its muzzle morphology (Bargo et al. 2006b), limb proportions and expected bending forces of limb elements (Bargo et al. 2000), the Pleistocene mylodontid, *Glossotherium* is regarded as having been a bulk feeder at ground level (e.g., grazer) and a competent digger (Bargo et al. 2000; Vizcaíno et al. 2008). This suggests that *Glossotherium* was at risk from two potential sources of tooth abrasives: phytoliths, which are in high concentrations in grasses, and environmental grit that would cover vegetation lying at or below ground level (Janis and Fortelius 1988; Mendoza and Palmqvist 2008). Despite this possible double-dose of dental abrasives, the hypsodonty indices of *Glossotherium* were, on average, only 60% those of the putative browser, *Megatherium americanum* (Bargo et al. 2006b). Plant content in the feces of *Megatherium* supports the long-held hypothesis that this giant was a browser (Carretero et al. 2004), though not necessarily a high-level browser as usually depicted in popular images (McDonald and De Iuliis 2008). One would expect a grazing digger to have greater exposure to abrasives than a browser. Yet, the putative bulk feeding and digging Pleistocene mylodontids

had lower hypsodonty indices than the browsing megatheres (Bargo et al. 2006b).

Since all other evidence discussed in the preceding sections (*Fecal Content, Inference from Habitat, Muzzle Morphology*) suggests that mylodontids tended to be bulk feeders in open habitats and due to the questionable relationship of relative crown height and abrasives in hypselodont dentitions, we do not regard the low hypsodonty indices (relative to megatheres and scelidotheres) of mylodontine mylodontids (i.e., *Glossotherium, Lestodon*) as falsifying the grazing hypothesis for these animals. For the present purposes, we are content to regard the continuous growth of the teeth of these mylodontids as being sufficient to compensate for dental tissue lost due to wear.

Paleoecology of Paroetodontotherium Application of the broad muzzle—bulk feeder principle suggests that *Paroetodontotherium* was a bulk feeder, likely feeding upon large quantities of grasses. *Paroetodontotherium* has a relatively broad muzzle, having a maximum muzzle width to mean palate width of 2.62:1 (Table 1). This relative muzzle width (RMW) is within the range of those of the broad-muzzled folivorans sampled from the Pleistocene, *Glossotherium* (range 1.99–2.96; mean=2.37; Table 3). Only the Pleistocene grazing mylodontid, *Lestodon*, had mean RMW values greater than that of *Paroetodontotherium* (mean RMW of *Lestodon*=3.57). Both *Glossotherium* and *Lestodon* were judged to have been “bulk feeders” by Bargo et al. (2006a). *Myodon darwini*, having a narrower muzzle (mean RMW=1.89), was judged to have been a more selective feeder. However, even with its relatively narrow muzzle, *Myodon* was known to have had significant amounts of grass in its diet, as evidenced by the quantities of grass remains in its fecal samples (Moore 1978).

Independent means of testing this grazing hypothesis in *Paroetodontotherium* are equivocal but not totally wanting. We note the extremely smooth wear of the molariform teeth of *Paroetodontotherium*. This may be a result of little variability in the hardness of the dental tissues, a hypothesis that remains untested to date (Daniela Kalthoff, of the Swedish Museum of Natural History, attempted to examine the histology of the dental tissues of *Paroetodontotherium*, but the sample we provided her was too poorly preserved to yield any credible results). But the smooth wear also indicates that something abrasive “polished” the occlusal surfaces of the teeth. Also, the habitat of Salla suggests that grasses were available for exploitation by *Paroetodontotherium*. The most commonly encountered ungulates at Salla are hypsodont (Croft and Weinstein 2008; Billet et al. 2009). At least two of the notoungulates from Salla had broad muzzles, the notohippid *Pascualihippus* and the

Table 3 Relative muzzle widths (RMW) of selected extinct ground sloths. RMW defined so that RMW is proportional to maximum muzzle widths (RMW=MMW/mean PW); see Table 2). Values of the Pleistocene ground sloths (*) are from Bargo et al. (2006a), but with their “RMW” modified to be proportional to maximum muzzle width (MMW) (see “Materials and Methods”)

	<i>n</i>	mean MMW	mean PW	mean RMW	RMW range
* <i>Lestodon armatus</i>	4	239	67.0	3.57	3.28–3.95
* <i>Glossotherium robustum</i>	7	164	70.6	2.37	1.99–2.96
* <i>Scelidotherium leptcephalum</i>	9	66.7	32.8	2.04	1.72–2.39
* <i>Myodon darwini</i>	4	123	69.0	1.89	1.31–2.82
* <i>Megatherium americanum</i>	5	69.6	57.6	1.20	1.03–1.48
		MMW	PW	RMW	
<i>Paroetodontotherium calleorum</i>	1	67	25.5	2.63	–

toxodontid *Proadinotherium saltoni* (Shockey 1997; Shockey and Anaya 2008). Thus, it appears that some grasses were available in the habitat at Salla and that the hypselodont dentitions and broad muzzle of *Paroctodontotherium* gave it the tools with which it could ingest grass.

Environmental Context of the Oligocene Folivoran Radiation

The scarcity-to-absence of sloths in the Eocene of South America followed by their significant diversity in the late Oligocene suggests that a late Eocene through early Oligocene radiation of sloths occurred. This also was a time of significant faunal change in other land mammals of South America, especially notoungulates (Simpson 1950, 1980; Patterson and Pascual 1968; Pascual and Ortiz Jaureguizar 1990; Flynn et al. 2003). This late Eocene-early Oligocene faunal change is characterized by extinctions (resulting in faunal disequilibrium, sensu MacArthur and Wilson 1967), followed by radiations and the immigration of two significant taxa into South America—rodents and primates.

Simpson (1950) had defined the major faunal changes of South America in terms of “immigrations.” These were composed of three “strata:” Stratum I was recognized by the presence of only “Ancient Immigrants,” i.e., xenarthrans, marsupials, and the “condylarth-like complex” of endemic South American ungulates; Stratum II was recognized by the arrival of “Old Island Hoppers,” rodents and primates); and Stratum III was recognized by the arrival of “Late Immigrants,” e.g., various carnivorans, cervids, camelids, tayassuids, equids, tapirids, gomphotheriid proboscidiens, as well as rabbits and various rodents from North America, in what is now known as the Great America Biotic Interchange (Stehli and Webb 1985).

Later, Simpson (1980) and others (Pascual and Patterson 1968; Pascual and Ortiz Jaureguizar 1990; Flynn et al. 2003) recognized that, in addition to the immigration of caviomorphs and platyrrhines, a “modernization” of the native ungulates characterized the change between Stratum 1 and Stratum 2. Recent work in the newly recognized Tinguirirican SALMA (Flynn et al. 2003) demonstrates that this “modernization” involving hypsodonty in notoungulates as well as the arrival of rodents occurred before the Deseadan SALMA, very near the Eocene-Oligocene boundary. These events are roughly coincident with geological, climatic, and environmental changes that occurred along the Eocene-Oligocene boundary. These events include the development of deep waters between South America and Antarctica, cooling temperatures, development of the Antarctic polar ice cap, and likely drying conditions (Kennett 1977; Zachos et al. 2001; Lawver and Gahagan 2003; Flynn et al. 2003). Recent faunal studies

using new methods (i.e., cenograms [Croft 2001] and ecological diversity analysis [Croft et al. 2008]) generally confirm the precocious development of open habitats in parts of South America, with the earliest appearance of significant grasslands in the world occurring there during the Tinguirirican SALMA (early Oligocene).

The broad muzzle of the late Oligocene mylodontids, *Octodontotherium* and *Paroctodontotherium*, and their appearance in habitats dominated by hypsodont notoungulates suggests that these sloths were capable of exploiting resources in open habitats. Indeed, it is in such habitats that the sloths first become well known. Thus we propose the hypothesis that the spread of grassland was an inducement for the initial mylodontid radiation.

Summary and Conclusions

Folivoran diversity is a major feature of South American, post-Eocene faunas. These beasts ranged in size from a little over two kg up to nearly 4,000 kg. They ranged from the Pampas, to the forest, to the seas, and beyond, with some megalonychids colonizing Caribbean isles and others migrating beyond the Arctic Circle. Their origins remains a mystery; however, recent findings, including those in this work, show that they had achieved some of their significant diversity by the late Oligocene. Results of this study include the following:

New Taxon We describe a new folivoran, *Paroctodontotherium calleorum*, from the Deseadan SALMA, late Oligocene, of Bolivia (Figs. 1, and 3; Table 1). It is referable to the Mylodontidae and we also regard it as a probable member of the Mylodontinae. Its muzzle is conspicuously broad.

Grazing Hypothesis Based upon its broad muzzle, smooth dental occlusal wear, and its presence in a habitat dominated by hypsodont notoungulates, we propose grazing or other form of bulk feeding in open habitats as a hypothesis for the feeding ecology of *Paroctodontotherium*.

Deseadan Folivoran Diversity The new mylodontid, *Paroctodontotherium calleorum*, along with other relatively recent discoveries, indicates considerable sloth diversity by the late Oligocene. This diversity is seen in terms of species richness (minimum of eight spp.), phylogenetic diversity in the two major Folivoran clades (Mylodontoidea and Megatherioidea), variation in body sizes (from just under 50 kg to over 250 kg), dental morphology, and locomotion (both plantigrade and pedolateral forms).

Given that *Paroctodontotherium* and *Octodontotherium* have morphology associated with bulk feeding (i.e., broad muzzle) and that they appear in faunas dominated by hypsodont ungulates, it appears that these mylodontids

were a part of the radiation of mammals that adapted to the emerging savannas and grasslands during the Oligocene epoch of South America.

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