# Paleoecological inferences about the Late Quaternary giant ground sloths from the Americas

Mário A. T. Dantas ( ✉ matdantas@yahoo.com.br )

  Universidade Federal da Bahia – Campus Anísio Teixeira, Vitória da Conquista

Sean Cody Campbell

  La Brea Tar Pits and Museum, Los Angeles, CA, USA

H. Gregory McDonald

---

---

## Abstract

The Occlusal Surface Area index together with the body mass contribute to better understanding the paleoecology and evolution of the giant sloths in the Americas. The giant sloths from southern South America probably had higher levels of fermentation/lower metabolic requirements, whereas the tropical taxa had higher metabolic requirements. The sloths that dispersed into Central and North America were most likely derived from tropical taxa based on the patterns observed in this study. Relative Muzzle Width and the Hypsodonty indices were used to infer the dietary adaptation of several late Pleistocene/early Holocene giant ground sloths from the Americas. The Nothrotheriidae and Megatheridae taxa were adapted to a browser or mixed-feeder "browser" diet, the Mylodontidae taxa to a variety of dietary types, and the Megalonychidae taxa to a mixed-feeder browser diet. However, these dietary adaptations do not necessarily reflect food niches. In general, Megalonychidae and Nothrotheriidae were climber species, Mylodontidae taxa were digger species, and Megatheriidae taxa were fully terrestrial species.

## Introduction

Late Quaternary giant sloths are among the most iconic members of the mammalian fauna of the Americas, and at present, at least 40 species are classified into four families: Megalonychidae, Nothrotheriidae, Mylodontidae, and Megatheriidae (e.g. Hoffstetter, 1952; Matthew and Paula-Couto, 1959; Cartelle, 1991; Pujos et al., 2007; De Iuliis et al., 2009; McDonald et al., 2013; De Iuliis et al., 2017; McDonald et al., 2017; Stinnesbeck et al., 2017; De Iuliis et al., 2020; McDonald et al., 2020; McAfee et al., 2021).

While many studies on the paleoecology of these taxa have been conducted; much of the paleoecology of several taxa (mainly recently described species) remains unknown. As the extant taxa are diminute in comparison and have a specialized ecology (browser diet, suspensory habit), it is difficult to compare them with extinct taxa to infer the paleoecology of the fossil species.

Past studies used to infer the paleoecology of extinct taxa had used techniques utilizing bone morphology (e.g. White, 1993; Bargo et al., 2006a; 2006b; Viscaíno *et al.*, 2006; Dantas and Santos, 2022; Santos et al., 2023), stable isotopes (e.g. Coltrain et al., 2004; Ruez, 2005; Perez-Crespo *et al.*, 2014; Fuller et al., 2014; Bocherens et al., 2017; DeSantis et al., 2019; Fuller et al., 2020; Omena et al., 2021), and tooth microwear analysis (Green, 2009; Resar et al., 2013; Oliveira et al., 2020), which have often focused on a small subset of the late Pleistocne sloths from the Pampean Region of Argentina, Brazilian Intertropical Region, and La Brea tar pits in the United States. Taxa from Central and South America have not yet been evaluated.

Thus, our goal was to use several morphologic approaches to suggest the paleoecology of 30 extinct giant sloth taxa, helping to better understand their metabolism, diet, and ecological niche and broaden our understanding of a wider diversity of extinct sloth taxa.

## Material and Methods

## Material

The skulls (in ventral view), dentaries, and ulnae of the following specimens were measured for this study: Megalonychidae, *Ahytherium aureum* (skull and dentary MCL 22834), *Australonyx aquae* (skull UHE Samuel s/n; dentary MCL 23315/04), *Meizonyx salvadorensis* (dentaries UF 27513 and INAH DP 5869), *Megistonyx oreobios* (skull MBLUZ-P-1668), *Megalocnus rodens* (skull AMNH 16876), *Parocnus browni* (skull AMNH 16877), *Parocnus serus* (skulls MHD 237, MHD 347, MHD 412, and DR PN FM 02–11; dentaries MHD 406 and MHD 408; ulnae MHD 225 and

MHD 348), *Acratocnus ye* (skull and dentary UF 170533), *Neocnus dousman* (skull UF 76363; dentary UF 76370), *Neocnus toupiti* (skull UF 156892; dentary UF 171296), *Nohochichak xibalbahkah* (skull and dentary INAH DP5832), *Xibalbaonyx oviceps* (skull, dentary and ulnae Za2014), *Xibalbaonyx exinferis* (dentary CPC-2774), *Xibalbaonyx microcaninus* (dentary INAH-MRG-10-294923), *Megalonyx jeffersonii* (skulls IMNH 23034, OMNH 4326, TMM G-333, DMNS E.P.V. 65000; dentary UCC 21429; ulnae UCC 23192); Nothrotheriidae, *Nothrotherium maquinense* (dentaries MCL 1020/2 and LEG 1461), *Nothrotheriops shastensis* (skulls LACMHC 208, LACMHC 303, LACMHC 632, LACMHC 1800-5, LACMHC 1800-7; dentaries LACMHC 1801-1, LACMHC 1801-2, LACMHC 1801-3, LACMHC 1801-5, LACMHC 1801-7, LACMHC 1801-R-4, and LACMHC 1801-L-8; ulnae LACMHC 1873-1 and LACMHC 1873-2); Mylodontidae, *Catonyx cuvieri* (skulls MAMC 18, MPAC 418; dentaries LEG 1178, MCN.P.687), *Valgipes bucklandi* (dentary LEG 1666), *Glossotherium phoenesis* (skull MCL 4303/2 and dentary MCL 4008), *Glossotherium tropicorum* (skull and dentary ROM 3146; dentaries ROM 2122 and MNHN LAR 243), *Glossotherium wegneri* (skulls MECN 356, MECN 417, MECN 505, AMNH 96216, MNHN.F.PUN220; dentaries MECN 357, AMNH 96217, AMNHH 1758; ulnae EPN V 140), *Paramylodon harlani* (skulls IMNH 15273, LACMHC 692, LACMHC 832, LACMHC 1716-2, LACMHC 1716-3, LACMHC 1716-4, LACMHC 1717-1, LACMHC 1717-2, LACMHC 1717-3, LACMHC 1717-32, LACMHC 1717-4, LACMHC 1717-6, LACMHC 1718-8, LACMHC 1717-10, LACMHC 1717-13, LACMHC 1717-14, LACMHC 1717-16, LACMHC 1717-17, LACMHC 1717-19, LACMHC 1717-20, LACMHC 1717-21, LACMHC 1717-22, LACMHC 1717-23, LACMHC 1717-24, LACMHC 1717-25, LACMHC 1717-26, LACMHC 1717-27, LACMHC 1717-28, LACMHC 1717-29, LACMHC 1717-30, LACMHC 1933, LACMHC 12369, LACMHC 14537, LACMHC 14549, LACMHC 14550, LACMHC 14551, LACMHC 14554; dentaries LACMHC 1718-1, LACMHC 1718-2, LACMHC 1718-8, LACMHC 1718-14, LACMHC 1718-15, LACMHC 1718-18, LACMHC 1718-20, LACMHC 1718-21, LACMHC 1718-25, LACMHC 1718-27, LACMHC 1718-28, LACMHC 1718-30, LACMHC 1718-31, LACMHC 1718-32, LACMHC 1718-33, UCC 21156, UCC 21158, and UCC 21170; ulnae LACMHC 1714-27), *Mylodon darwini* (ulnae CORD PZ 4570, Haro et al., 2017; FMNH P14288, McAphee, 2016); Megatheriidae, *Eremotherium laurillardi* (skulls EPN V 1508, INAH uncatalogued,; skulls and dentaries MPM702, FMNH P-26962, TMM 41075-10; dentaries MCL 1700/2, MCL 1702/2, MCL 7220−7226, MCL 7228, MCL 7229, MCL 7231−7234, MCL 7236, MCL 7237, FMNH P-26970; ulnae TMM 41075-10), *Megatherium tarijense* (skull and dentary FMNH P14216).

# Body mass estimation

In this study, we estimated the body mass of eleven extinct giant sloths from the Americas using circumference measurements from the humerus and femur, following the regression for xenarthrans presented by Dantas (2022; Tables 1 and S2). These measurements were acquired from collections or estimated through figures in publications (Hoffstetter, 1952; Mathew and Paula Couto, 1959; MacPhee et al., 2000; De Iuliis et al., 2009; McDonald and Lundelius, 2009; Stinnesbeck *et al.*, 2020; McAfee et al., 2021; Table S2).

**Table 1.** Average values of body mass (in kg), carbon isotopes through bioapatite ($\delta^{13}C_{ap}$, ‰) and collagen ($\delta^{13}C_{col}$, ‰), the proportion of $C_3$ and $C_4$ plants ($p_iC_3$, $p_iC_4$, %), relative muzzle width (RMW), occlusal superfície area (OSA, in $mm^2$), hypsodonty index (HI), index of dorsal olecranon projection (IDO), index of fossorial ability (IFA), percentage of fossorial ability (%IFA), and possible ecological habit (H; suspensory − S, climber − C, terrestrial − T, non digger − ND, digger − D, high digger − HD, and burrower - B) for the Late Quaternary giant sloths from America. **Labels.** [a] USA and Mexico; [b] Cuba, Dominican Republic, Haiti, and Honduras; [c] Venezuela, Ecuador, Peru, and Brazil; [d] Bolivia, Argentina, and Uruguay.

| taxa | BM | $\delta^{13}C_{ap}$ $(p_fC_3, p_fC_4)$ | $\delta^{13}C_{col}$ $(p_fC_3, p_fC_4)$ | RMW | OSA | HI | IDO | IFA | %IFA | H |
|---|---|---|---|---|---|---|---|---|---|---|
| **Megalonychidae** | | | | | | | | | | |
| *Mx. jeffersonii* [a] | 588[1] | -13.3 (1; 100, 0)[2] | -19.9 (85; 15)[3,4] | 0.58[1] | 1,545[1] | 1.32[1] | 0.73[1] | 0.20[1] | 35 | T, ND |
| *No. xibalbahkah* [a] | - | - | - | 0.60[1] | - | 0.90[1] | - | - | - | - |
| *X. oviceps* [a] | 189[1] | - | - | 0.63[1] | 3,699[1] | 0.65[1] | 1.15[1] | - | - | - |
| *Ms. rodens* [b] | 95[1] | - | - | 0.73[1] | 2,402[1] | - | 1.36[5] | - | - | - |
| *Pa. browni* [b] | - | - | - | 0.42[1] | - | - | - | - | - | - |
| *Pa. serus* [b] | 38[1] | - | - | 0.49[1] | 774[1] | 1.14[1] | 1.19[1] | 0.31[1] | 55 | T, D |
| *Ac. ye* [b] | 15[1] | - | - | 0.35[1] | 344[1] | 1.03[1] | 0.86[5] | - | - | - |
| *Ne. dousman* [b] | - | - | - | 0.45[1] | - | 0.88[1] | - | - | - | - |
| *Ne. toupiti* [b] | - | - | - | 0.53[1] | - | 0.75[1] | - | - | - | - |
| *Mg. oreobios* [c] | - | - | - | 0.72[1] | - | - | - | - | - | - |
| *D. nordenskioldi* [c] | 67[1] | - | - | 0.57[1] | 828[1] | 0.67[1] | 1.27[1] | 0.24[1] | 42 | T, ND |

References. [1]Our data; [2]Kohn et al. (2005); [3]Bocherens et al. (1994); [4]McDonald et al. (2019); [5]White (1993).

Table 1 (continuation).

| taxa | BM | $\delta^{13}C_{ap}$ ($p_iC_3$, $p_iC_4$) | $\delta^{13}C_{col}$ ($p_iC_3$, $p_iC_4$) | RMW | OSA | HI | IDO | IFA | %IFA | H |
|---|---|---|---|---|---|---|---|---|---|---|
| **Megalonychidae** | | | | | | | | | | |
| *A. aureum* [c] | 186[6] | -14.4 (100, 0)[7] | - | 0.54[1] | 1,370[8] | 0.94[1] | 0.75[9] | 0.11[9] | 20 | C, ND |
| *Au. aquae* [c] | 226[6] | - | - | 0.83[1] | 2,606[8] | 0.77[1] | 1.05[9] | 0.09[9] | 16 | C, ND |
| **Nothrotheridae** | | | | | | | | | | |
| *Nh. shastensis* [a] | 339[1] | 1.7 (0, 100)[10] | -19.5 (82, 18)[11,12] | 0.66[1] | 1026[1] | 1.09[1] | 1.12[1] | 0.11[1] | 19 | T, ND |
| *N. maquinense* [c] | 157[4] | -12.4 (96; 4)[13] | - | 0.74[7] | 574[7] | 0.77[1] | 0.85[9] | 0.12[9] | 21 | C, ND |
| **Mylodontidae** | | | | | | | | | | |
| *P. harlani* [a] | 798[1] | 3.3 (7, 93)[10,14,15] | -20.8 (91, 9)[12,16] | 0.49[1] | 3,314[1] | 0.62[1] | 1.03[1] | 0.45[1] | 80 | T, HD |
| *My. ibseni* [c] | 1,020[1] | - | - | 0.53[9] | - | - | - | - | - | - |
| *O. giganteum* [c] | 842[4] | - | - | 0.39[9] | 2,096[9] | - | 1.39[9] | 0.40[9] | 71 | T, HD |
| *G. phoenesis* [c] | 463[4] | - | - | 0.50[9] | 2,837[9] | 0.56[1] | 1.12[9] | 0.46[9] | 82 | T, HD |
| *G. tropicorum* [c] | 610[1] | - | - | 0.53[1] | 3,149[1] | 0.60[1] | - | - | - | - |
| *G. wegneri* [c] | 436[1] | - | - | 0.40[1] | 1,924[1] | 0.66[1] | 0.72[1] | 0.49[1] | 87 | T, HD |
| *M. darwini* [d] | 689[4] | - | - | 0.58[17] | 1,319[16] | 0.78[17] | 0.74[1] | 0.39[1] | 69 | T, D |
| *G. robustum* [d] | 627[4] | -9.8 (77, 23)[20] | -20.0 (83, 17)[20,21] | 0.43[17] | 1,076[18] | 0.71[19] | - | 0.56[17] | 100 | T, B |

**References.** [1]Our data; [6]Dantas (2022); [7]Costa et al. (in press); [8]Dantas & Santos (2022); [9]Santos et al. (2023); [10]DeSantis et al. (2019); [11]Fuller et al. (2014); [12]Fuller et al. (2020); [13]Omena et al. (2021); [14]Ruez (2005); [15]Perez-Crespo et al. (2014); [16]Coltrain et al. (2004); [17]Bargo et al. (2006a); [18]Vizcaino et al. (2006); [19]Bargo et al. (2006b); [20]Bocherens et al. (2017).

Table 1 (continuation).

| taxa | BM | $\delta^{13}C_{ap}$ ($p_iC_3$, $p_iC_4$) | $\delta^{13}C_{col}$ ($p_iC_3$, $p_iC_4$) | RMW | OSA | HI | IDO | IFA | %IFA | H |
|---|---|---|---|---|---|---|---|---|---|---|
| Mylodontidae | | | | | | | | | | |
| L. armatus [d] | 1,155[4] | - | -18.6 (75, 25)[21] | 0.28[17] | 1,111[18] | 0.62[19] | - | 0.53[17] | 94 | T, HD |
| V. bucklandi [c] | 463[4] | -10.2 (80; 20)[13] | - | 0.49[9] | 2,804[9] | 0.48[1] | 1.29[9] | 0.24[9] | 43 | T, ND |
| C. cuvieri [c] | 598[4] | -7.3 (59; 41)[13] | - | 0.39[9] | 3,103[9] | 0.62[1] | 1.31[9] | 0.40[9] | 71 | T, HD |
| C. cuvieri [d] | - | - | - | 0.40[1] | - | - | - | - | - | - |
| S. leptocephalum [d] | 616[6] | - | - | 0.49[17] | 775[18] | 0.91[19] | - | 0.54[17] | 96 | T, HD |
| Megatheriidae | | | | | | | | | | |
| E. laurillardi [a] | 1,763[1] | -7.7 (62, 38)[22] | - | 0.69[1] | 9,625[1] | 0.50[1] | 0.74[1] | 0.10[1] | 17 | T, ND |
| E. laurillardi [a] | - | - | - | 0.63[1] | - | - | - | - | - | - |
| E. laurillardi [b] | - | - | - | 0.63[1] | - | 0.81[1] | - | - | - | - |
| E. laurillardi [c] | 2,361[6] | -5.4 (46, 54)[13] | -14.2 (44, 56)[23] | 0.66[9] | 11,340[9] | 0.75[1] | 1.76[9] | 0.09[9] | 16 | T, ND |
| Me. tarijense [d] | 947[1] | - | - | 0.63[1] | 9,137[1] | 0.84[1] | - | - | - | - |
| Me. americanum [d] | 1,468[6] | -7.5 (60, 40)[20,24] | -17.9 (71, 29)[20] | 0.84[17] | 10,818[18] | 1.02[19] | - | 0.26[17] | 46 | T, ND |

References. [1]Our data; [6]Dantas (2022); [9]Dantas & Santos (2022); [13]Omena et al. (2021); [17]Bargo et al. (2006a); [20]Bocherens et al. (2017); [21]Czerwonogora et al. (2011); [22]Perez-Crespo et al. (2015); [23]Dantas et al. (2021); [24]Lopes et al. (2021).

For *Diabolotherium nordenskioldi*, *Glossotherium tropicorum*, and *Mylodonopsis ibseni* as there is only one humerus for adults individuals (Cartelle, 1991; Pujos et al., 2007; De Iuliis et al., 2017), the circumference (C) of the femur was estimated using the proportion (humerus: femur; 1:1.35 for *D. nordenskioldi*; 1:1.40 for *G. tropicorum* and *M. ibseni*) determined from the relationship between the circumference of the femur and humerus found in *Ahytherium aureum*, *Australonyx aquae*, *Glossotherium wegneri*, and *Paramylodon harlani* (Table S2).

These taxa were classified based on the stage of epiphysis–diaphysis fusion in the humerus and femur as juveniles (clear separation between the epiphysis and diaphysis), subadults (a visible scar between the epiphysis and diaphysis), or adults (epiphysis–diaphysis completely fused).

# Occlusal Surface Area

The occlusal surface area (OSA in mm$^2$) of each extinct giant sloth skull was estimated only for the species for which body mass could also be estimated (i.e. taxa for which both the humerus and femur are known; Table S2) adapted from the technique proposed by Vizcaíno et al. (2006). OSA was calculated using ImageJ software (Abràmoff et al., 2004), utilizing freehand selection to determine the exact area of each molariform. Only the skulls of adult individuals were measured (except for *Xibalbaonyx oviceps*, which is known only from a single immature skull). When the molariform was absent, measurements were made from either the tooth alveolus, or on one side when a single tooth was present and multiplied by two to estimate the total OSA of the studied individual. All OSA measurements are presented in Table S1.

OSA values were plotted against body mass (kg) of each sloth taxon (Tables 1 and S2; Dantas, 2022). The two variables (OSA and body mass) of each extinct giant sloth examined were log-transformed and compared with the OSA data presented by Vizcaíno et al. (2006) and Dantas and Santos (2022).

## Relative Muzzle Width

To infer the diet of the BIR late Quaternary giant ground sloths, we use the muzzle width technique for giant ground sloths proposed by Bargo *et al.* (2006a). For all sloths, the maximum muzzle width (MMW) was measured on the maxilla at the premaxillo-maxillary suture. The palatal width (PW) was based on the mean width between the anterior (M1) and posterior width of the last molariform (M3 in Megalonychidae and Nothrotheriidae, and M4 in Mylodontidae and Megatheriidae; Fig. 1).

All measurements were made using ImageJ software (Abràmoff et al., 2004) on photographs of *Megalonyx jeffersonii*, *Nothrotheriops shastensis*, and *Paramylodon harlani*, as well as published figures (Matthew and Paula Couto, 1959; MacPhee et al., 2000; Lindsey and Lopez, 2005; McDonald, 2006; Pujos et al., 2007; Lucas, 2008a, 2008b; De Iuliis et al., 2009; Corona et al., 2013; McDonald et al., 2013; 2017; Stinnesbeck et al., 2017; De Iullis *et al.*, 2017; De Iullis *et al.*, 2020; McAfee et al., 2021; Table S1).

The relative muzzle width (RMW) index is the ratio of MMW/PW. We suggest modifying the interpretation of Bargo *et al.* (2006a): so that animals with an RMW index between 0 to 0.30, and a wide muzzle, are interpreted as being adapted to feed primarily as a grazer; when this index is between 0.31 to 0.70, and with an intermediate muzzle, those taxa with values between 0.31 to 0.50 are considered mixed-feeders "grazers", while those with an RMW index between 0.51 to 0.70 are considered mixed-feeders "browsers". Finally, taxa with RWM values between 0.71 to 1.00 and with a narrow muzzle are considered an obligatory browser (Tables 1 and S1).

For comparison, we include the values obtained by Bargo *et al.* (2006a) and Dantas and Santos (2022) for the South American giant ground sloths: *Eremotherium laurillardi*, *Megatherium americanum*, *Glossotherium robustum*, *Glossotherium phoenesis*, *Mylodon darwini*, *Mylodonopsis ibseni*, *Lestodon armatus*, *Ocnotherium giganteum*, *Scelidotherium leptocephalum*, *Catonyx cuvieri*, *Valgipes bucklandi*, and *Nothrotherium maquinense* (Table 1). The RMW for *Ahytherium aureum* and *Australonyx aquae* was recalculated because Dantas and Santos (2022) incorrectly measured the premaxillo-maxillary suture of these taxa.

## Hypsodonty index

The degree of hypsodonty for several extinct giant sloth taxa in the Americas (Tables 1 and S2) was estimated following the criteria of Bargo et al. (2006b): depth of the mandible (DM) measured at the level of the third molariform tooth divided by the length of the molariform tooth row (LTR). All measurements were performed using ImageJ software (Abràmoff et al., 2004).

It should be noted that the lower tooth rows of megalonychids and nothrotheres include only three molariforms while in megatheres and mylodonts there are four molariforms. Calculations of the relationship between mandible depth and the lower tooth row length do not significantly alter the hypsodonty index (Fig. 2).

For comparison, we included the values obtained by Bargo et al. (2006b) for the South American extinct giant sloths: *Megatherium americanum*, *Glossotherium robustum*, *Mylodon darwini*, *Lestodon armatus*, and *Scelidotherium leptocephalum* (Table 1).

# Index of dorsal olecranon projection (IDO)

The Index of Dorsal Olecranon projection (IDO) is calculated by the division of the dorsal extent of the olecranon process by the length of the trochlear notch from the most proximal, anterior point to the junction of the trochlear and radial notches (Fig. 3A; Tables 1 and S1).

Here, we use the proposition of Santos et al. (2023), which uses the body mass (BM; transformed to logarithm values at base 10) associated with IDO. This could separate the animals into suspensory, climbing, and terrestrial modes of locomotion.

Based on data from the Primate and Xenarthra taxa, animals with suspensory or climber habits present IDO values varying between 0.52 to 1.24, and separated as suspensory based on the body mass log-transformed varying between 0.68–1.30 (BM = 5–20 kg), and climbers with body mass log-transformed varying between 1.70–2.40 (BM = 50–250 kg). Those taxa with a body mass log-transformed value higher than 2.40 (BM > 250 kg) should be considered terrestrial.

# Index of Fossorial Ability (IFA)

The Index of Fossorial Ability (IFA), developed by Vizcaíno *et al.* (1999), is calculated by dividing the length of the olecranon (OI) by the difference between the total length of the ulna (UI) and the olecranon: IFA = OI/(UI − OI) (Table S1; Fig. 3B). In this way, it is possible to calculate the movement capacity and strength of the triceps muscle, which is mainly responsible for the extensor movement of the forearm and is widely used by mammals that dig with the movement of the entire arm. Burrowing animals generally have a higher index result than non-digging animals (Hildebrand 1985).

Here, we used the adaptation of Bargo *et al.* (2000) made by Santos et al. (2023). To estimate the percentage of IFA (%IFA), the IFA of each giant sloth is divided by the value of *G. robustum* (IFA/0.56*100), which has the highest value of the late Pleistocene giant sloths from South America. Thus, values lower than 50% indicate non-digging mammals, between 51–70% diggers, values between 71–95% are highly specialized diggers, and values between 96–100% indicate burrowers.

# Analytical methods

We used Student's t-test ($p = 0.05$) and ANOVA ($p = 0.05$) to compare similarities between the RMW, OSA, and HI values of the studied taxa. Tukey's test was used to identify species that presented similar values. These analyses were performed using PAST 3.11 (Hammer et al., 2001).

# Results

# Body mass

The estimated body mass of continental Megalonychidae from the Americas was 67 kg for *Diabolotherium nordenskioldi* (Peru) and 189 kg for a juvenile individual of *Xibalbaonyx oviceps* (Mexico), which is the only known specimen of this taxon to date. The body mass of *X. oviceps* approximates the 200 kg estimate of Stinnesbeck et al. (2020) based on femur length. For *Megalonyx jeffersonii* (USA), based on the bones of several adults from three localities, we suggest a body mass of 527–668 kg (mean value 588 ± 71 kg; Tables 1 and S2), which is lower than the estimate of 1,090 kg of McDonald (2005) based on femur length.

Three members of the Megalonychidae from the Caribbean Islands were included: *Megalocnus rodens* (Cuba, BM = 95 kg), *Parocnus serus* (Dominican Republic, BM = 38 kg), and *Acratocnus ye* (Haiti, BM = 15 kg). The only late Pleistocene nothrothere in North America, *Nothrotheriops shastensis*, had a mean body mass of 339 kg (Tables 1 and S2) based on adult individuals, which is slightly lower than the 463 kg estimate of McDonald (2005) based on femur length.

For the Mylodontidae, the body mass of the South American *Mylodonopsis ibseni* (Brazil) was 1,020 kg, *Glossotherium tropicorum* (Ecuador) was 610 kg, and *Glossotherium wegneri* (Ecuador) was 439 kg. For the North American *Paramylodon harlani* was 798 kg, which is less than the estimated 1,392 kg reported by McDonald (2005). For Megatheriidae taxa, the body mass of the South American *Megatherium tarijense* (Bolivia) was 947 kg, and for an individual of *Eremotherium laurillardi* from North America, the body mass was 1,763 kg (Tables 1 and S2).

## Occlusal Surface Area

The OSA values of *Nothrotheriops shastensis* (1026 ± 350 mm$^2$), *Glossotherium wegneri* (1,924 ± 374 mm$^2$), *Paramylodon harlani* (3,314 ± 772 mm$^2$), and *Eremotherium laurillardi* (9,625 ± 4,528 mm$^2$) are different from each other, the only exception is between *Nh. shastensis* and *G. wegneri*, which are similar (ANOVA, $F = 40.01$, $p < 0.05$). Since these represent three families it seems reasonable that the values would be different, what is unexpected is that *Nh. shastensis* and *G. wegneri* had similar values.

*Glossotherium tropicorum*, *Megatherium tarijense*, and megalonychid taxa presented only one OSA value each and could not be statistically tested. The OSA value of *Acratocnus ye* (OSA = 344 mm$^2$, Table 1) was the lowest of all taxa and cannot be compared, however, the OSA values of *Parocnus serus* (OSA = 750 mm$^2$, Table 1), *Diabolotherium nordenskioldi* (OSA = 828 mm$^2$, Table 1), and *Megalonyx jeffersonii* (OSA = 1,545 mm$^2$, Table 1) are similar to those found for *Nh. shastensis* and *G. wegneri*, respectively, while the OSA values from *Megalocnus rodens* (OSA = 2,402 mm$^2$, Table 1), *G. tropicorum* (3,149 mm$^2$, Table 1), and *Xibalbaonyx oviceps* (OSA = 3,699 mm$^2$, Table 1) are similar to those for *P. harlani*. The *Me. tarijense* (OSA = 9,137 mm$^2$; Table 1) values were similar to the *E. laurillardi* RMW values (Table S1).

## Relative Muzzle Width

The RMW values (Table S1) for members of the Megalonychidae (*Megalonyx jeffersonii*, *Xibalbaonyx oviceps*, *Nohochichak xibalbahkah*, *Megalocnus rodens*, *Parocnus browni*, *Parocnus serus*, *Acratocnus ye*, *Neocnus dousman*, *Neocnus toupiti*, *Diabolotherium nordenskioldi*, and *Megistonyx oreobios*), Nothrotheriidae (*Nothrotheriops shastensis*), Mylodontidae (*Catonyx cuvieri*, *Glossotherium wegneri*, *Glossotherium tropicorum*, and *Paramylodon harlani*), and Megatheriidae (*Eremotherium laurillardi*, *Megatherium tarijense*) taxa were statistically different from each other (ANOVA, $F = 90.59$, $p < 0.05$), an exception to the RMW values found for *Nothrotheriops shastensis* (RMW = 0.66 ± 0.04), *Eremotherium laurillardi* (RMW = 0.64 ± 0.03), and *Megatherium tarijense* (RMW = 0.63) which was similar.

The mixed-feeder "grazers" included the majority of Megalonychidae from the Caribbean Islands, *Acratocnus ye* (Haiti, RMW = 0.35), *Parocnus browni* (Cuba, RMW = 0.42), *Neocnus dousman* (Haiti, RMW = 0.45), and *Parocnus serus*

(Dominican Republic, RMW = 0.49 ± 0.06). The mylodontids group included *Catonyx cuvieri* (Uruguay, RMW = 0.40 ± 0.01), *Glossotherium wegneri* (Ecuador, RMW = 0.40 ± 0.04), and *Paramylodon harlani* (USA, RMW = 0.49 ± 0.04).

The mixed-feeder "browsers" include the megalonychids *Neocnus toupiti* (Haiti, RMW = 0.53), *Ahytherium aureum* (Brazil, RMW = 0.54), *Diabolotherium nordenskioldi* (Peru, RMW = 0.57), *Megalonyx jeffersonii* (USA, RMW = 0.58 ± 0.09), *Nohochichak xibalbahkah* (Mexico, RMW = 0.60), and *Xibalbaonyx oviceps* (Mexico, RMW = 0.63); the mylodontid *Glossotherium tropicorum* (Ecuador, RMW = 0.53); the megatheriid *Eremotherium laurillardi* (Ecuador, RMW = 0.63; Honduras, RMW = 0.63; USA, RMW = 0.69), *Megatherium tarijense* (Bolivia, RMW = 0.63), and the nothrotheriid *Nothrotheriops shastensis* (USA, RMW = 0.66 ± 0.04).

The browser category included *Megistonyx oreobios* (Venezuela, RMW = 0.72), *Megalocnus rodens* (Cuba, RMW = 0.73), and *Australonyx aquae* (Brazil, RMW = 0.83).

# Hypsodonty index

The Hypsodonty index (HI) of the extinct giant sloths was not statistically different among the four families (ANOVA, $F$ = 28.96, $p < 0.05$), varying between 0.48 to 1.32, and could be compared between the giant sloth families due to the isometric increase in the length of the tooth row associated with the depth of the dentary ($R^2 = 0.81$; Fig. 2). The lowest HI values were observed in members of the Mylodontidae (HI = 0.62 ± 0.06), followed by the Megatheriidae taxa (HI = 0.75 ± 0.08). Megalonychidae (HI = 0.91 ± 0.22) and Nothrotheriidae taxa (HI = 1.02 ± 0.18) had the highest values.

# Index of dorsal olecranon projection (IDO)

All Megalonichidae taxa (except *Megalonyx jeffersonii*; Tables 1 and S1) were within the limit of body mass × IDO, suggesting suspensory or climber habits (*Ac. ye*, 15 kg, IDO = 0.86; *Pa. serus*, 38 kg, IDO = 1.19; *D. nordenskioldi*, 71 kg, IDO = 1.27; *Ms. Rodens*, 95 kg, IDO = 1.36; *X. oviceps*, 189 kg, IDO = 1.15). The remaining giant sloths were probably terrestrial (*Nh. shastensis*, 339 kg, IDO = 1.12; *Mx. jeffersonii*, 588 kg, IDO = 0.73; *G. wegneri*, 627 kg, IDO = 0.72; *M. darwini*, 689 kg, IDO = 0.74; *P. harlani*, 798 kg, IDO = 1.03; *E. laurillardi* from the USA, 1,763 kg, IDO = 0.74).

# Index of Fossorial Ability (IFA)

Based in the proportion of the Index of fossorial ability (%IFA) *D. nordenskioldi* (%IFA = 42), *Mx. jeffersonii* (%IFA = 35), *Nh. shastensis* (%IFA = 19), and *E. laurillardi* from USA (%IFA = 17) were non digger mammals. *Pa. serus* (%IFA = 55) and *M. darwini* (%IFA = 69) were classified as digger mammals, while *G. wegneri* (%IFA = 87) and *P. harlani* (%IFA = 80) are higher specialized diggers (Table 1).

# Discussion

# Metabolism inferences

The pioneering work of Vizcaino *et al.* (2006) was based on the analysis of five giant sloth species from the Pampean Region (Argentina and Uruguay) from only two families, four mylodontids (*Glossotherium robustum*, *Lestodon armatus*, *Mylodon darwini*, and *Scelidotherium leptocephalum*), and one megatheriid *Megatherium americanum*. Mylodontids presented lower OSA values, whereas *M. americanum* had high OSA values. Vizcaino *et al.* (2006) suggest that the lower values of the mylodontids could indicate a higher level of fermentation in the digestive system and a possible lower metabolic requirement, while *Me. americanum* could present similar metabolic requirement to Epitherian taxa of the same size.

Dantas and Santos (2022) used the same approach to study giant sloths from the Brazilian Intertropical Region, that included all four sloth families, Megalonychiidae (*Ahytherium aureum*, *Australonyx aquae*), Nothrotheriidae (*Nothrotherium maquinense*), Mylodontidae (*Glossotherium phoenesis*, *Ocnotherium giganteum*, *Catonyx cuvieri*, *Valgipes bucklandi*), and Megatheriidae (*Eremotherium laurillardi*). The mylodontid and megathere giant sloths from BIR have OSA values higher than those from the Pampean Region and all taxa, with the exception of *N. maquinense* and *O. giganteum*, which fell on the regression line of epitherians, suggesting higher levels of oral food processing and metabolic requirements.

Excluding *D. nordenskioldi* and *Mx. jeffersonii*, all the megalonychids studied (*Xibalbaonyx oviceps*, *Megalocnus rodens*, *Parocnus serus*, *Acratocnus ye*, *A. aureum*, and *Au. aquae*), mylodontids (*Paramylodon harlani*, *Glossotherium tropicorum*, and *Glossotherium wegneri*), and megatheriids (*Megatherium tarijense* and *Eremotherium laurillardi*) had high OSA values that fell above the Xenarthra regression line (Fig. 5), showing the same pattern observed for giant sloths from BIR.

If this pattern is correct, all megalonychids may have had higher metabolic requirements than other sloths, which allows a review of the interpretation proposed by McDonald et al. (2013) for *Megistonyx oreobios*. The unique exception was *D. nordenskioldi* and *Mx. jeffersonii*, which fell on the Xenarthra regression, probably because of larger body mass relative to its OSA capability, which could have a direct effect, causing a high energy cost, probably lowering its metabolism.

The OSA × body mass of *Nothrotheriops shastensis* suggests that members of the Nothotheriidae probably had low oral food processing and metabolic requirements, together with *D. nordenskioldi*, *Megalonyx jeffersonii*, *Ocnotherium giganteum*, and the mylodontid species from the Pampean Region (Fig. 4). This hypothesis for *Nh. Shastensis* is supported by the size of plant fragments in its dung which are large and not fully chewed, may be related to long transit time in the gut to absorb nutrients (Lindsey et al., 2020).

Dantas and Santos (2022) proposed that giant sloths from temperate regions would have adapted to a lower oral food processing capability, together with a higher fermentation need. However, data from the North American temperate zones allowed us to disregard this hypothesis (Table 1; Fig. 4). This could reflect the evolution of North American taxa from tropical forms (McDonald, 2006; McDonald et al., 2017; Varela et al., 2019), and feeding on new types of vegetation promotes different metabolic requirements from giant sloths from the temperate zones of South America.

In terms of time to adapt to North American vegetation, *Megalonyx jeffersonii* would have had the greatest amount of time, *Paramylodon harlani* and *Eremotherium laurillardi* arrived later in Blancan, and *Nothrotheriops shastensis* was the last to reach North America and had the least amount of time to adapt, and all of these taxa reached more temperate latitudes in North America. Because *Nohochichak xibalbahkah* and *Xibalbaonyx oviceps* were restricted to in tropical habitats in North America, they do not appear to have adapted to different vegetation types in their diet.

# Diet inferences

The Relative Muzzle Width index and hypsodonty index provide a means to suggest the different feeding adaptations of extinct giant sloths within the environment in which they lived, allowing an interpretation of their diet and habitat. These indices may allow for the interpretation of niche partitioning when multiple sloths are associated in a fauna, as well as how they may have avoided competition with other megaherbivores in the fauna.

The Hypsodonty index values (Table 1) did not differ between the extinct giant sloth families (ANOVA, $F = 28.96$, $p < 0.05$), suggesting adaptation to a similar degree of tooth wear between all taxa. As all sloths lack enamel on their teeth and the teeth are composed of similar types of dentine (Kalthof, 2011), as well as hypselodont and ever-growing, the

rate of growth to compensate for tooth wear during mastication may be essentially the same in all sloths; therefore, the height of the teeth, as indicated by depth of the mandible, may not be a critical factor.

Available RMW values for the extinct giant sloths (Bargo *et al.*, 2006; Dantas and Santos, 2022; Table S1) confirm the families Megalonychidae (13 species), Nothrotheriidae (two species), Mylodontidae (12 species), and Megatheriidae (three species) present different RMW values (Table 1). The unique exception was between Nothrotheriidae and Megatheriidae, which had similar values (ANOVA, $F = 36.12$, $p < 0.05$).

The RMW and HI values for megalonychid taxa showed an adaptation to a mixed-feeder to a browser diet (RMW = 0.35−0.85; HI = 0.65−1.32; Fig. 5). This partially agrees with the interpretation of a browser diet for members of this family (McDonald et al., 2017), for example, the diet of *Xibalbaonyx oviceps* is proposed to be composed of leaves and fruits (Stinnesbeck et al., 2021).

Unfortunately, only a limited number of other techniques can provide inferences on the diet of extinct species. However, dental microwear analyses have indicated that *Acratocnus* (*Ac. odontrigonus*) could have a mixed-feeder "browser" diet, while *Megalonyx* (*Mx. wheatleyi*) was a grazer (Resar et al., 2013). In marked contrast, carbon isotopic analysis of bioapatite and collagen ($\delta^{13}C_{ap}$ = -13.3‰; $p_iC_3$ = 100%; $\delta^{13}C_{col}$ = -19.9‰; $p_iC_3$ = 85%; Bocherens *et al.*, 2004; McDonald et al., 2019; Table 1) suggest that *Mx. jeffersonii* is a browser. The same interpretation was made for *Ahytherium aureum* ($\delta^{13}C_{ap}$ = -14.4‰; $p_iC_3$ = 100%; Costa *et al.*, in press).

Both nothrotheres, *Nothrotheriops shastensis* and *Nothrotherium maquinense*, had RMW values indicative of adaptation as browsers (RMW = 0.66−0.74; Fig. 5), the HI values suggesting an adaptation to a less abrasive diet for *N. maquinense* (HI = 0.77; Table 1), but a high abrasive diet for *Nh. shastensis* (HI = 1.09; Table 1), confirmed by direct evidence of the diet by the diversity of plants it consumed in preserved coprolites (Hansen, 1978; Thompson et al., 1980).

Carbon isotopic values for *N. maquinense* ($\delta^{13}C_{ap}$ = -12.4 ± 0.06; $p_iC_3$ = 96%; Omena et al., 2021; Table 1) and *Nh. shastensis* ($\delta^{13}C_{col}$ = -19.5 ± 0.02‰; $p_iC_3$ = 82%; Fuller et al., 2014; Table 1) confirm a browser diet for both. In *Nh. shastensis*, microwear analysis (Green *et al.*, 2009), coprolite analysis based on macrobotanical composition (Hansen, 1978), and molecular data (Hofreiter et al., 2000) reinforce this interpretation. However, the available carbon isotopic values in bioapatite indicate an opposite diet rich in $C_4$ plants ($\delta^{13}C$ = 1.7 ± 0.04‰; $p_iC_4$ = 100%; DeSantis et al., 2019; Table 1).

The Mylodontidae species presented the widest RMW in comparison with the other families (RMW = 0.28−0.58; Table 1; Fig. 5), indicative of a mixed-feeder diet, in agreement with the results presented by Naples (1989). The only exception was *L. armatus*, which was adapted to the grazer diet (RMW = 0.28; Table 1). The HI values reinforce this interpretation, suggesting an adaptation to less abrasive food items (HI = 0.48−0.91; Bargo et al. 2006b; Table 1).

Currently the only taxa in the family, for which carbon isotopic data acquired from collagen and bioapatite is available are *Glossotherium robustum*, *Catonyx cuvieri* (from Brazil), *Valgipes bucklandi* (Brazil), *Paramylodon harlani* (United States), and *Lestodon armatus* (Uruguay).The data for these taxa indicate a mixed-feeder "browser" diet for *G. robustum* and *C. cuvieri*, and a browser diet ($p_iC_3$ > 80%) for *P. harlani*, *V. bucklandi*, and *L. armatus* (Table 1). As occurred in *Mx. jeffersonii*, the carbon isotopic data acquired through bioapatite for *Paramylodon harlani* indicates a diet that is opposite to that indicated by the collagen analysis data (Ruez, 2005; Perez-Crespo *et al.*, 2014; DeSantis et al., 2019; Table 1).

Finally, the HI index suggests that all megatherines were adapted to abrasive food items (HI = 0.50–1.02; Table 1), the RMW index suggesting that *Eremotherium laurillardi* and *Megatherium tarijense* were adapted to a mixed-feeder "browser" diet (RMW = 0.63–0.69; Fig. 5), whereas *Megatherium americanum* was a strict browser (RMW = 0.84; Fig. 5). The limited carbon isotopic (bioapatite) data from the *E. laurillardi* in Mexico ($\delta^{13}C$ = -7.7‰; piC3 = 62%; Perez-Crespo *et al.*, 2015; Table 1) seems to confirm this dietary pattern, however, the data from Brazil (bioapatite and collagen) suggest a mixed-feeder "grazer" diet ($p_iC_4$ = 54–56%; Dantas et al., 2020; Omena et al., 2021; Table 1), These differences may reflect greater dietary flexibility in *E. laurillardi*, which may explain its wide latitudinal distribution and a range greater than any other sloth.

Microwear analyses of *E. laurillardi* in Brazil also confirmed a mixed-feeder diet (Oliveira et al., 2020). The carbon isotopic values of bioapatite and collagen suggest that *Me. americanum* had a mixed-feeder "browser" diet ($p_iC_3$ = 60–71%; Bocherens et al., 2017; Lopes et al., 2021; Table 1).

Dantas (2022) discussed how body mass strongly influenced the variation in carbon isotopic values in giant sloths from the Brazilian Intertropical Region (n = 4; $R^2$ = 0.90), which represented changes in habitat use and consequently their diet. However, body mass did not seem to affect the RMW index in giant sloths (n = 23; $R^2$ = 0.30; Fig. 6A).

When all available $\delta^{13}C_{collagen}$ data for giant sloths from the Americas were interpreted together, a moderate correlation between $\delta^{13}C_{collagen}$ and body mass was observed (n = 7; $R^2$ = 0.48; Fig. 6B), similar to that observed by Dantas (2022). However, $\delta^{13}C_{bioapatite}$ showed no correlation with body mass (n = 10; $R^2$ = 0.04; Fig. 6C), with results opposite to those reported by Dantas (2022). This occurs because of the discordant carbon isotopic data acquired through bioapatite found for *Mx. jeffersonii* ($\delta^{13}C$ = 1.7 ± 0.04‰; Table 1) and *P. harlani* ($\delta^{13}C$ = 3.3 ± 4.2‰; Table 1), which differ strongly from the carbon isotopic data found in collagen. Without these values, the correlation coefficient increased to 0.62.

# Niche differentiation

The niche differentiation of the Late Quaternary giant sloths has been studied and currently we have a view that mostly Megalonychidae and Nothrotheriidae could be mainly climbers, the Mylodontidae mainly diggers, while the Megatheriidae were fully terrestrial animals (Bargo *et al.*, 2000; Vizcaino *et al.*, 2006; Santos et al., 2023).

Our results suggest that within the Megalonychidae, *Acratocnus ye* could be a suspensory species, while *Parocnus serus*, *Mesocnus rodens*, *Xibalbaonyx oviceps*, and *Diabolotherium nordenskioldi* were climber species (Fig. 7), with *Pa. serus* probably also being a digger species (Table 1). The results for *D. nordenskioldi* were in accordance with the interpretation made by Pujos et al. (2007). Unfortunatelly *Megistonyx oreobios* and *Nohochichak xibalbahkah* do not have preserved ulnae, which prevents us from proposing their ecological niche based on this bone.

As in the case of *Mx. jeffersonii* the larger body mass of *Nothrotheriops shastensis* probably prevented it from being considered to be a climber species (as *N. maquinense*, Fig. 7; Santos et al., 2023), it also was not a digger species (Table 1). It is possible that immature juvenile individuals of *Megalonyx* could climb until they reached a critical size, but the paucity of juvenile skeletons at different growth stages, prevents a resolution of this question at this time.

Within the Mylodontidae *Mylodon darwini* was probably a digger species, while *Paramylodon harlani* and *Glossotherium wegneri* were specialized diggers, as the species *O. giganteum*, *G. phoenesis*, *L. armatus*, and *C. cuvieri*. The Megatheriidae *E. laurillardi* from USA, does not differ from the South American relatives, being a fully terrestrial species, as expected (Fig. 7; Table 1).

# Final remarks

The giant sloths which lived in southern South America, probably had a higher level of fermentation/lower metabolic requirement, which was reflected in the late Pleistocene taxa found in the Pampean Region. As these taxa migrated to tropical regions, they probably evolved higher metabolic requirements, and these tropical taxa migrated to Central and North America, explaining the pattern observed in this study.

We have a paradox here, the more southern giant sloths in South America would have been at higher latitudes and in the more temperate zones, as for example the Pampas in Buenos Aires Province is (34 to 38 degrees south), which is roughly the same latitude as the southern third of the United States. So sloths in these two regions are living in climatically comparable regions which is what Webb argued for in his savanna taxa interchange papers. We point out that tropical adapted sloths in southern Mexico and Central America did not move into temperate habitats.

The relative muzzle width and hypsodonty indices suggest dietary adaptation of several late Pleistocene/early Holocene giant sloths in the Americas. Nothrotheriidae and Megatheridae taxa were adapted to a browser or mixed-feeder "browser" diet, Mylodontidae taxa to a variety of diet types, and Megalonychidae taxa to a mixed-feeder to a browser diet. The Occlusal Surface Area index together with the body mass allows a better understanding of the paleoecology and evolution of the giant sloths in the Americas.

These dietary adaptations did not necessarily reflect their food niche; the RMW diets for some Mylodontidae taxa were different from what RMW and HI suggested. Similarities between RMW, HI, and isotope/microwear analysis were observed for Megalonychidae, Nothrotheriidae, and Megateridae taxa.

Finally, two indices based on ulna measurements allowed us to differentiate the ecological niche of giant sloths. A probable pattern is that Megalonychidae and Nothrotheriidae could include mainly climber species, while Mylodontidae taxa are mainly diggers, and Megatheriidae, due to their higher body mass, a fully terrestrial species.

# Declarations

## Acknowledgments

## Declaration of competing interest

The authors do not have any conflict of interest to report.

## Author contributions

All authors contributed equally to the manuscript.

## Data availability

All used data is available in the manuscript.

# References

1. Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics Int 11(7):36-42.

2. Bargo MS, Toledo N, Vizcaíno SF (2006ª) Muzzle of South American Pleistocene ground sloths (Xenarthra, Tardigrada). J Morphol 267:248-263.

3. Bargo SM, Iuliis GD, Vizcaíno, SF (2006b) Hypsodonty in Pleistocene ground sloths. Acta Palaeontol 51(1):53-61.

4. Bocherens H, Fizet M, Mariotti A, Gangloff RA, Burns JA (1994) Contribution of isotopic biogeochemistry ($^{13}$C, $^{15}$N, $^{18}$O) to the paleoecology of mammoths (Mammuthus primigenius). Hist Biol 7(3):187-202.

5. Bocherens H, Cotte M, Bonini RA, Straccia P, Scian D, Soibelzon L, Prevosti FJ (2017) Isotopic insight on paleodiet of extinct Pleistocene megafaunal Xenarthrans from Argentina. Gondwana Res. 48:7-14. https://doi.org/10.1016/j.gr.2017.04.003.

6. Cartelle C (1991) Um novo Mylodontinae (Edentata, Xenarthra) do Pleistoceno final da regiao intertropical brasileira. An Acad Bras 63(2):161-170.

7. Coltrain JB, Harris JM, Cerling TE, Ehleringer JR, Dearing MD, Ward J, Allen J (2004) Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of late Pleistocene, coastal southern California. Palaeogeogr Palaeoclimatol Palaeoecol 205(3-4):199-219.

8. Corona A, Perea D, McDonald HG (2013) *Catonyx cuvieri* (Xenarthra, Mylodontidae, Scelidotheriinae) from the late Pleistocene of Uruguay, with comments regarding the systematics of the subfamily. J Vert Paleontol 33(5):1214-1225.

9. Costa JP, Araújo-Junior HI, Barbosa FHS, Dantas MAT (in press) Record of a juvenile of *Ahytherium aureum* in the Late Pleistocene of Brazilian Intertropical Region: radiocarbon dating, isotopic paleoecology, and evidence of predation by a Felidae. J Quat Sci.

10. Czerwonogora A, Fariña RA, Tonni EP (2011) Diet and isotopes of Late Pleistocene ground sloths: first results for *Lestodon* and *Glossotherium* (Xenarthra, Tardigrada). *Neues* Jahrb Geol Palaontol Abh 262(3):257-266.

11. Dantas MAT (2022) Estimating the body mass of the late Pleistocene megafauna from the South America Intertropical Region and a new regression to estimate the body mass of extinct xenarthrans. J South Am Earth Sci 119:103900. https://doi.org/10.1016/j.jsames.2022.103900

12. Dantas MA, Santos AM (2022) Inferring the paleoecology of the Late Pleistocene giant ground sloths from the Brazilian Intertropical Region. J South Am Earth Sci 117:103899. https://doi.org/10.1016/j.jsames.2022.103899

13. Dantas MAT, Cherkinsky A, Lessa CMB, Santos LV, Cozzuol MA, Omena ÉC, Silva JLL Da, Sial AN, Bocherens H (2020) Isotopic paleoecology ($\delta^{13}$C, $\delta^{18}$O) of Late Quaternary megafauna from Brazilian Intertropical Region. Rev Bras Paleontol 23(2):113-152. https://doi.org/10.4072/rbp.2020.2.05

14. Dantas MAT, Omena ÉC, Silva JLL, Sial A (2021) Could *Eremotherium laurillardi* (Lund, 1842) (Megatheriidae, Xenarthra) be an omnivore species? Anu Inst Geocienc 44:36492. https://doi.org/ 10.11137/1982-3908_2021_44_36492

15. De Iuliis G, Pujos F, Cartelle C (2009) A new ground sloth (Mammalia: Xenarthra) from the Quaternary of Brazil. C R Paleovol 8:705-715.

16. De Iuliis G, Cartelle C, McDonald HG, Pujos F (2017) The mylodontine ground sloth Glossotherium tropicorum from the late Pleistocene of Ecuador and Peru. Pap Palaeontol 3(4):613-636.

17. De Iuliis G, Boscaini A, Pujos FRF, McAfee RK, Cartelle C, Tsuji LJ, Rook L (2020) On the status of the giant mylodontine sloth Glossotherium wegneri (Spillmann, 1931) (Xenarthra, Folivora) from the late Pleistocene of Ecuador. C R Palevol 19(12):215-232. https://doi.org/10.5852/cr-palevol2020v19a12

18. DeSantis LR, Crites JM, Feranec RS, Fox-Dobbs K, Farrell AB, Harris JM, Takeuchi GT, Cerling TE (2019) Causes and consequences of Pleistocene megafaunal extinctions as revealed from Rancho La Brea mammals. Curr 29(15):2488-2495.

19. Fuller BT, Fahrni SM, Harris JM, Farrell AB, Coltrain JB, Gerhart LM, Ward JK, Taylor RE, Southon JR (2014) Ultrafiltration for asphalt removal from bone collagen for radiocarbon dating and isotopic analysis of Pleistocene fauna at the tar pits of Rancho La Brea, Los Angeles, California. Quat Geochronol 22:85-98.

20. Fuller BT, Southon JR, Fahrni SM, Farrell AB, Takeuchi GT, Nehlich O, Guiry EJ, Richards MP, Lindey EL, Harris JM (2020) Pleistocene paleoecology and feeding behavior of terrestrial vertebrates recorded in a pre-LGM asphaltic deposit at Rancho La Brea, California. Palaeogeogr Palaeoclimatol Palaeoecol 537:109383.

21. Green JL (2009) Dental microwear in the orthodentine of the Xenarthra (Mammalia) and its use in reconstructing the palaeodiet of extinct taxa: the case study of Nothrotheriops shastensis (Xenarthra, Tardigrada, Nothrotheriidae). Zool J Linn Soc 156(1):201-222.

22. Hammer Ø, Harper DA, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol electron 4(1):9pp.

23. Hansen RM (1978) Shasta ground sloth food habits, Rampart Cave, Arizona. Paleobiology 4(3)302-319.

24. Haro JA, Tauber AA, Krapovickas JM (2017) Thoracic member (pectoral girdle and forelimb) bones of *Mylodon darwinii* Owen (Xenarthra, Mylodontidae) from the Late Pleistocene of Central Argentina and their phylogenetic implications. PalZ 91:439-457.

25. Hildebrand M (1985) Digging in quadrupeds. In: Hildebrand M, Bramble DM, Liem KF, Wake DB (ed). Functional Vertebrate Morphology. Cambridge, MA, Harvard University Press, pp 89–109.

26. Hoffstetter R (1952) Les mammifères Pléistocènes de la République de l'Equateur. Mém Soc géol Fr Paléontol 66:1–391.

27. Hofreiter M, Poinar HN, Spaulding WG, Bauer K, Martin PS, Possnert G, Pääbo S (2000) A molecular analysis of ground sloth diet through the last glaciation. Mol 9(12):1975-1984.

28. Kalthoff D (2011) Microstructure of dental hard tissues in fossil and recent xenarthrans (Mammalia: Folivora and Cingulata). J Morphol 272:641–661.

29. Kohn MJ, McKay MP, Knight JL (2005) Dining in the Pleistocene—who's on the menu? Geology 33(8):649-652.

30. Lindsey EL, Lopez EX (2015) Tanque Loma, a new late-Pleistocene megafaunal tar seep locality from southwest Ecuador. J South Am Earth Sci 57:61-82.

31. Lindsey EL, Reyes EXL, Matzke GE, Rice KA, McDonald HG (2020) A monodominant late-Pleistocene megafauna locality from Santa Elena, Ecuador: Insight on the biology and behavior of giant ground sloths. Palaeogeogr Palaeoclimatol Palaeoecol 544:109599.

32. Lopes RP, Dillenburg SR, Pereira JC, Sial AN (2021) The paleoecology of Pleistocene giant Megatheriid sloths: stable isotopes (Delta C-13, Delta O-18) of co-occurring *Megatherium* and *Eremotherium* from Southern Brazil. Rev Bras Paleontol 24(3):245-264.

33. Lucas S (2008a) Pleistocene mammals from Yeroconte, Honduras. Neogene Mammals: Bulletin 44:44-403.

34. Lucas S (2008b) Late cenozoicvertebrate fossilassemblages from Jalisco, Mexico. Neogene Mammals: Bulletin 44:44-51.

35. MacPhee RD, White JL, Woods CA (2000) New megalonychid sloths (Phyllophaga, Xenarthra) from the Quaternary of Hispaniola. Am Mus Novit 2000(3303):1-32.

36. Matthew WD, Paula-Couto CD (1959) The Cuban edentates. Bull Am Mus Nat Hist 117.

37. McAfee RK (2016) Description of new postcranial elements of *Mylodon darwinii* Owen 1839 (Mammalia: Pilosa: Mylodontinae), and functional morphology of the forelimb. Ameghiniana 53(4):418-443.

38. McAfee R, Beery S, Rimoli R, Almonte J, Lehman P, Cooke S (2021) New species of the ground sloth Parocnus from the late Pleistocene-early Holocene of Hispaniola. Vertebrate Anatomy Morphology Palaeontology 9(1):52-

82.

39. McDonald HG (2005) Paleoecology of Extinct Xenarthrans and the Great American Biotic Interchange. Bull Fla Mus Nat Hist Biol sci 45(4):313-333.

40. McDonald HG (2006) Sexual dimorphism in the skull of Harlan's ground sloth. Contributions in Science 510:1-9.

41. McDonald HG (2021) Yukon to the Yucatan: Habitat partitioning in North American Late Pleistocene Ground Sloths (Xenarthra, Pilosa). Journal of Palaeosciences 70:237–251.

42. Mcdonald HG, Lundelius Jr EL (2009) The giant ground sloth *Eremotherium laurillardi* (Xenarthra, Megatheriidae) in Texas. Papers on geology, vertebrate paleontology, and biostratigraphy in honor of Michael O. Woodburne. Bulletin, Museum of Northern Arizona 65:407-421.

43. 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.

44. McDonald HG, Chatters JC, Gaudin TJ (2017) A new genus of megalonychid ground sloth (Mammalia, Xenarthra) from the late Pleistocene of Quintana Roo, Mexico. . J Vertebr Paleontol 37(3):e1307206.

45. McDonald HG, Feranec RS, Miller N (2019) First record of the extinct ground sloth, Megalonyx jeffersonii, (Xenarthra, Megalonychidae) from New York and contributions to its paleoecology. Quat Int 530:42-46.

46. McDonald HG, Arroyo-Cabrales J, Alarcón-Durán I, Espinosa-Martínez DV (2020) First record of *Meizonyx salvadorensis* (Mammalia: Xenarthra: Pilosa) from the late Pleistocene of Mexico and its evolutionary implications. J Syst Palaeontol 18(22):1829-1851.

47. Naples VL (1989) The Feeding Mechanism of the Pleistocene Ground Sloth, Glossotherium. Contributions in Science 415:1-23.

48. Oliveira JF, Asevedo L, Cherkinsky A, Dantas MAT (2020) Radiocarbon dating and integrative paleoecology ( [13]C, stereomicrowear) of *Eremotherium laurillardi* (Lund, 1842) from midwest region of the Brazilian intertropical region. J South Am Earth Sci 102:102653.

49. Omena ÉC, Silva JLLD, Sial AN, Cherkinsky A, Dantas MAT (2021) Late Pleistocene meso-megaherbivores from Brazilian Intertropical Region: isotopic diet ($\delta^{13}$C), niche differentiation, guilds and paleoenvironmental reconstruction ($\delta^{13}$C, $\delta^{18}$O). Hist Biol 33(10):2299-2304.

50. Pérez-Crespo VA, Arroyo-Cabrales J, Alva-Valdivia LM, Morales-Puente P, Cienfuegos-Alvarado E, Otero FJ, Ochoa-Castillo P (2014) La paleodieta de cinco especies de mamíferos herbívoros rancholabreanos de Valsequillo (Puebla, México). Revista Chilena de Antropología (30):76-82.

51. Pérez-Crespo VA, Carbot-Chanona G, Morales-Puente P, Cienfuegos-Alvarado E, Otero FJ (2015) Paleoambiente de la Depresión Central de Chiapas, con base en isótopos estables de carbono y oxígeno. Rev Mex de Cienc Geol 32(2):273-282.

52. Pujos F, De Iuliis G, Argot C, Werdelin L (2007) A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implication for sloth history. Zool J Linn Soc 149(2):179-235.

53. Resar NA, Green JL, McAfee RK (2013) Reconstructing paleodiet in ground sloths (Mammalia, Xenarthra) using dental microwear analysis. Kirtlandia 58:61-72.

54. Ruez DR (2005) Diet of Pleistocene *Paramylodon harlani* (Xenarthra: Mylodontidae): review of methods and preliminary use of carbon isotopes. Texas Journal of Science 57(4):329-344.

55. Santos AMA, McDonald HG, Dantas MAT (2023) Inferences about the ecological habits of the extinct giant sloths from Brazilian Intertropical Region. J Quat Sci 2023:1-7. https://doi.org/ 10.1002/jqs.3534

56. Stinnesbeck SR, Frey E, Aviles Olguin J, González AG, Velazquez Morlet A, Stinnesbeck W (2021) Life and death of the ground sloth Xibalbaonyx oviceps from the Yucatán Peninsula, Mexico. Hist Biol 33(11):2610-2626.

57. Stinnesbeck SR, Frey E, Olguín JA, Stinnesbeck W, Zell P, Mallison H, González AG, Núñez EA, Morlet AV, Mata AT, Sanvicente MB, Hering F, Rojas Sandoval, C. 2017. Xibalbaonyx oviceps, a new megalonychid ground sloth (Folivora, Xenarthra) from the Late Pleistocene of the Yucatán Peninsula, Mexico, and its paleobiogeographic significance. PalZ 91:245-271.

58. Thompson RS, Van Devender TR, Martin PS, Foppe T, Long A (1980) Shasta ground Sloth (*Nothrotheriops shastense* Hoffstetter) at Shelter Cave, New Mexico: environment, diet and extinction. Quat Res 14:360–376.

59. Varela L, Tambusso PS, McDonald HG, Fariña RA (2019) Phylogeny, macroevolutionary trends and historical biogeography of sloths: insights from a Bayesian morphological clock analysis. Syst Biol 68(2):204-218.

60. Vizcaíno SF, Bargo MS, Cassini GH (2006) Dental occlusal surface area in relation to body mass, food habits and other biological features in fossil xenarthrans. Ameghiniana 43(1):11-26.

# Figures



## Figure 1

*Eremotherium laurillardi* skull (MCL 33068) in ventral view showing the measurements to estimate the Relative Muzzle Width (RMW). Maximum Muzzle Width (MMW); Palatal Width (PW), being an average between the first molariforms (PW$_{FM}$) and the last molariforms (PW$_{LM}$).
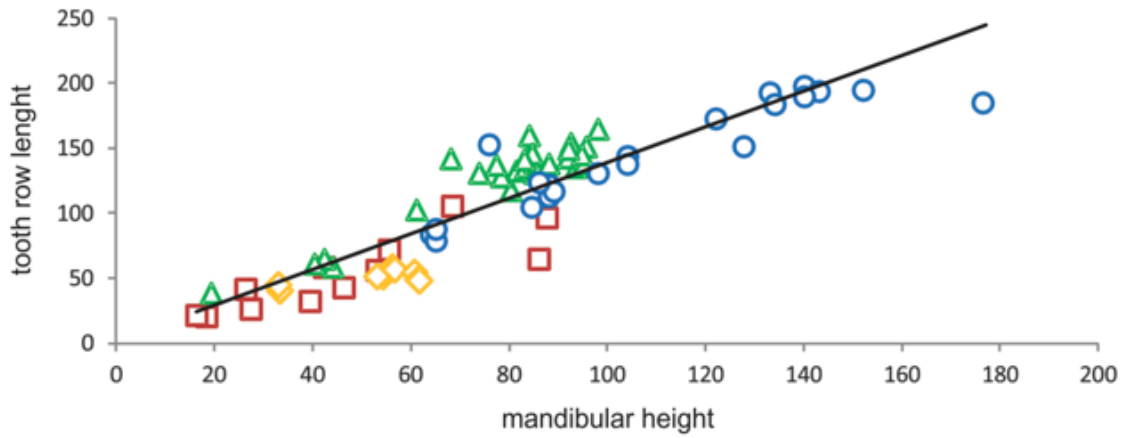
**Figure 2**

Correlation between madibular height and tooth row lenght in late Pleistocene/early Holocene giant sloths. **Labels.** Red squares = Megalonychidae; Orange diamonds = Nothrotheriidae; Green triangles = Mylodontidae; Blue circles = Megatheriidae.
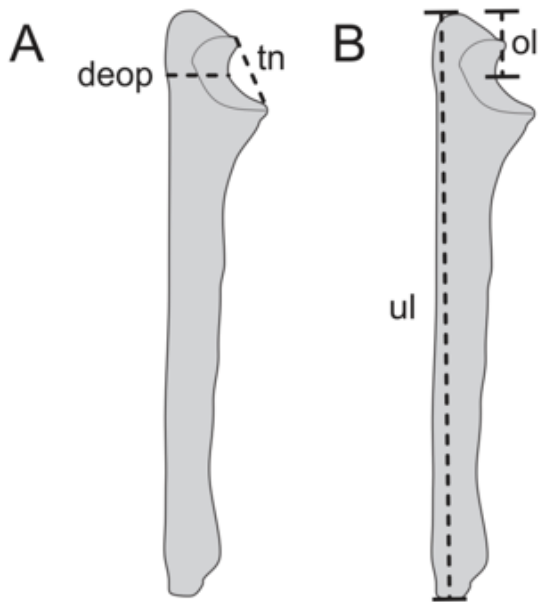


**Figure 3**

Scheme of the extinct giant sloth *Nothrotherium maquinense* bones. Ulna, (A) dorsal extent of the olecranon process (deop) and length of the trochlear notch (tn); (B) Length of the olecranon (ol) and total length of the ulna (ul).
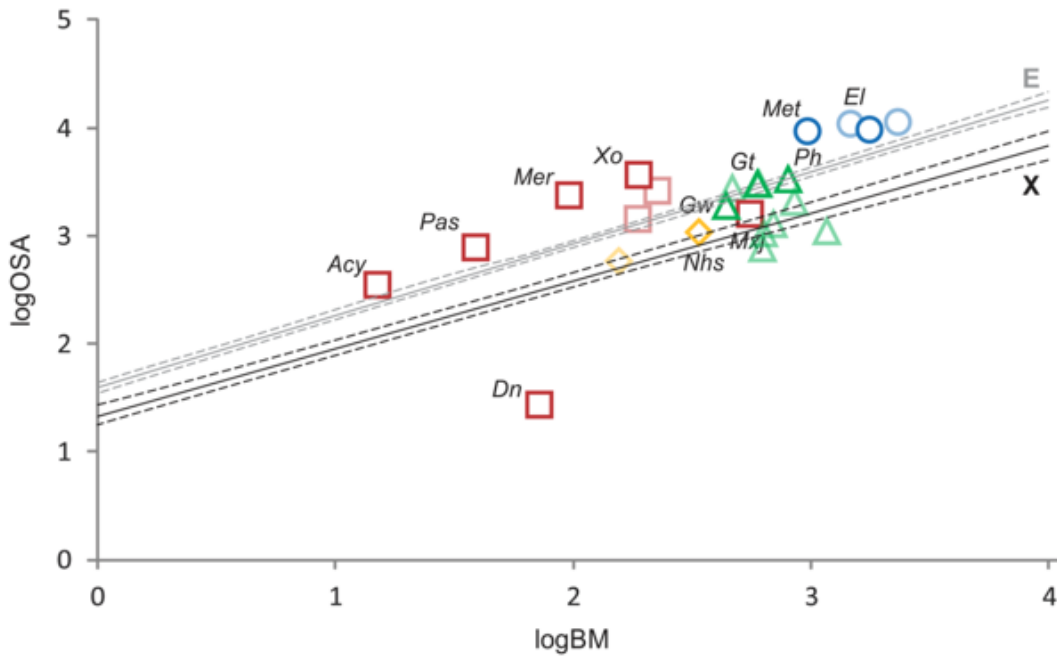
**Figure 4**

Regression of OSA against body mass of the giant sloths of the Late Quaternary of the Americas. **Labels.** Red squares = Megalonychidae (*Dn - Diabolotherium nordenskioldi, Acy - Acratocnus ye, Pas - Parocnus serus, Msr - Megalocnus rodens, Xo – Xibalbaonyx oviceps, Mxj – Megalonyx jeffersonii*); Orange diamonds = Nothrotheridae (*Nhs - Nothrotheriops shastensis*); Green triangles = Mylodontidae (*Ph – Paramylodon harlani, Gt – Glossotherium tropicorum, Gw – Glossotherium wegneri*); Blue circles = Megatheriidae (*El – Eremotherium laurillardi, Met – Megatherium tarijense*). E – Epitheria and X – Xenarthra regression lines presented by Vizcaino *et al.* (2006). Shade figures are from giant sloths from Brazilian Intertropical Region presented by Dantas & Santos (2022). Dashed lines above and below the regression lines = 95 % confidence interval.
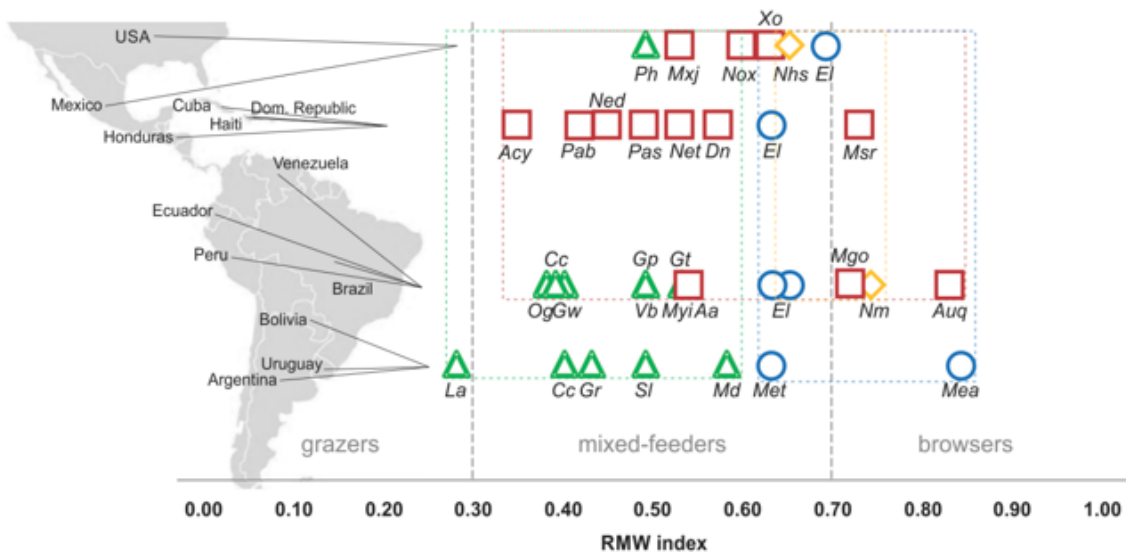


**Figure 5**

The relative muzzle width (RMW) index for the Late Quaternary giant sloths from the Americas. **Labels.** Red squares = Megalonychidae; Orange diamonds = Nothrotheridae; Green triangles = Mylodontidae; Blue circles = Megatheriidae; Mexico and USA, *Mxj* − *Megalonyx jeffersonii*, *Nox* - *Nohochichak xibalbahkah*, *Xo* - *Xibalbaonyx oviceps*, *Ph* − *Paramylodon harlani*, *Nhs* − *Nothrotherium shastensis*, *El* − *Eremotherium laurillardi*; Honduras, Cuba, Haiti, and Dominican Republic, *Acy* - *Acratocnus ye*, *Msr* - *Megalocnus rodens*, *Net* - *Neocnus toupiti*, *Ned* - *Neocnus dousman*, *Pas* - *Parocnus serus*, *Pab* - *Parocnus browni*, *El* − *Eremotherium laurillardi*; Venezuela, Ecuador, Peru and Brazil, *Dn* - *Diabolotherium nordenskioldi* ,*Mgo* - *Megistonyx oreobios*, *Aa*− *Ahytherium aureum*, *Og* − *Ocnotherium giganteum*, *Cc* − *Catonyx cuvieri*, *Gw* − *Glossotherium wegneri*, *Auq* − *Australonyx aquae*, *Vb* − *Valgipes bucklandi*, *Gp* − *Glossotherium phoenesis*, *Myi* − *Mylodonopsis ibseni*, *Gt* − *Glossotherium tropicorum*, *El* − *Eremotherium laurillardi*, and *Nm* − *Nothrotherium maquinense*; Bolivia, Argentina and Uruguay, *La* − *Lestodon armatus*, *Gr* − *Glossotherium robustum*, *Cc* − *Catonyx cuvieri*, *Sl* − *Scelidotherium leptocephalum*, *Md* − *Mylodon darwini*, *Met* − *Megatherium tarijense*; *Mea* − *Megatherium americanum*.
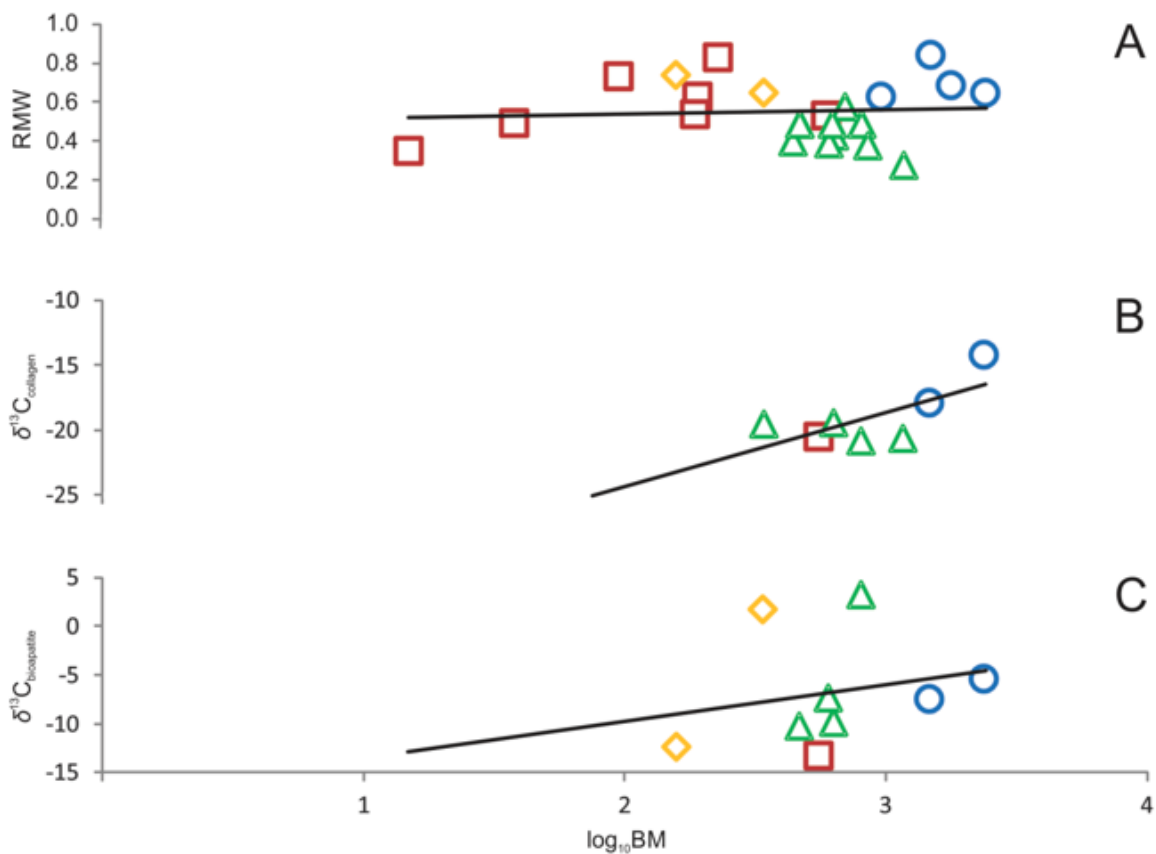


**Figure 6**

Correlation between body mass of the Late Quaternary giant sloths from Americas versus: (A) RMW ($R^2$ = 0.00); (B) carbon isotopic ($\delta^{13}C$) values acquired through collagen ($R^2$ = 0.48); (C) and through bioapatite ($R^2$ = 0.04). **Labels.** Red squares = Megalonychidae; Orange diamonds = Nothrotheridae; Green triangles = Mylodontidae; Blue circles = Megatheriidae.
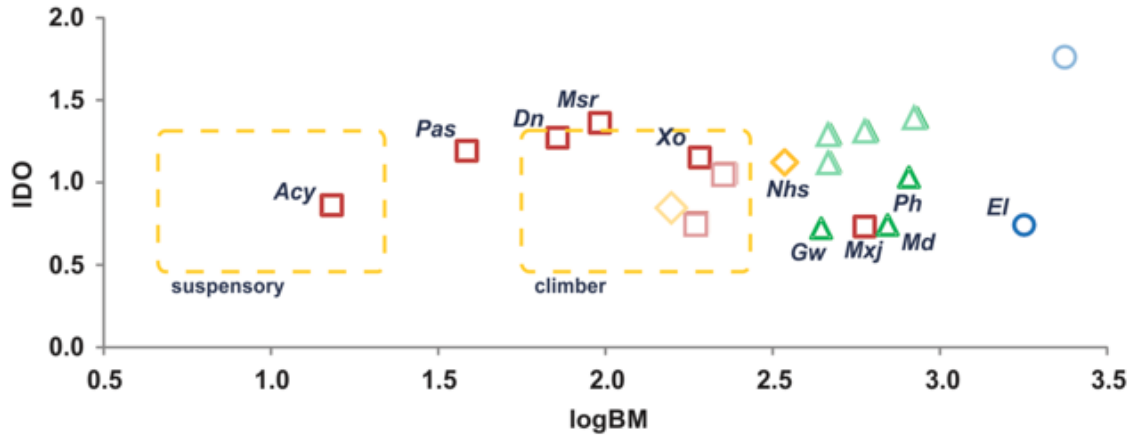
Figure 7

Bi-plot graph between log of body mass and log of Index of dorsal olecranon projection (IDO). **Labels.** Orange retangules represents animals with suspensory (S) and climber habits (C) based in extant primates and xenarthrans. Red squares = Megalonychidae (*Acy* - *Acratocnus ye*, *Msr* - *Megalocnus rodens*, *Pas* – *Parocnus serum*, *Dn* – *Diabolotherium nordenskioldi*, *Xo* - *Xibalbaonyx oviceps*, and *Mxj* – *Megalonyx jeffersonii*); Orange diamonds = Nothrotheridae (*Nhs* - *Nothrotheriops shastensis*); Green triangles = Mylodontidae (*Gw* – *Glossotherium wegneri*, *Md* – *Mylodon darwini*, *Ph* – *Paramylodon harlani*); Blue circles = Megatheriidae (*El* – *Eremotherium laurillardi*). Shade figures are from giant sloths from Brazilian Intertropical Region by Santos *et al.* (2023).

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Americagiantslothssupplementarytables.xlsx