

Original Study

Lucas C. Pasin, Daniel M. Casali, Thiago B. F. Semedo and Guilherme S. T. Garbino*

Harpy eagle kill sample provides insights into the mandibular ontogenetic patterns of two-toed sloths (*Xenarthra: Choloepus*)

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Abstract: Skeletal ontogeny of xenarthrans is poorly known, especially because of the paucity of study specimens from distinct developmental stages. Here, we investigate morphometric aspects of the mandible ontogeny in the two-toed sloths, *Choloepus* spp. We examined mandibles of infant, juveniles and subadult sloths that were present in kill assemblages of harpy eagles, *Harpia harpyja*, and complemented our study with adult museum specimens. We carried out uni- and multivariate linear morphometric analyzes to assess the growth pattern of the mandible. Harpy eagles did not prey on adult two-toed sloths, preferring younger individuals. We found an overall strong correlation between the total length of the mandible and other mandibular measurements across age classes, with some of them scaling isometrically, and others presenting allometric growth. Also, morphometric data correlated with patterns of symphyseal fusion across ontogenetic stages, rendering the latter a reliable indicator of the

animal's age category. Although it was necessary to complement our sample with museum material, individuals obtained from the harpy eagle kill assemblage proved to be a valuable complementary source of specimens to be studied.

Keywords: allometry; dentary; isometry; morphometrics; pilosa

1 Introduction

Assessing ontogenetic variation in wild medium-sized and large mammals is usually constrained by small sample sizes (Hautier et al. 2014; Rocha et al. 2014; Smith et al. 2021). Usually, there are ethical issues when collecting these species, which may occur in relatively small populations, but their sampling is also hindered by difficulties in specimen preparation and storage (Delsett 2024; Pyke and Ehrlich 2010; Rocha et al. 2014).

To avoid this sampling bias, specimens of medium-sized and large mammals may be obtained via alternative methods. For example, thousands of mammals are rescued from forested areas prior to reservoir flooding (Peres 1999). In this context of occasional sampling, hundreds of osteological materials of medium and large mammals may be collected from harpy eagle (*Harpia harpyja*) nests (Aguiar-Silva et al. 2014; Garbino et al. 2024; Miranda 2018). Depending on the fragmentation and preservation, this material can potentially cover part of this sampling gap.

Two-toed sloths, *Choloepus didactylus* and *Choloepus hoffmanni*, are arboreal folivores that are underrepresented in scientific collections (Santos et al. 2019). This sampling deficiency hinders assessing individual, geographic, and particularly ontogenetic variation in the species (Hautier et al. 2018). Although some studies have shed some light on the ontogenetic variation in mandibles of a few species of extinct sloths (e.g., Boscaini et al. 2019; Cartelle et al. 2019; Cartelle and De Iullis 2006; Cartelle et al. 2015; De Iuliis et al. 2017; De Iuliis et al. 2020; Gaudin and Scaife 2023; Pujos et al. 2023), these patterns are far from being fully understood in the group. Moreover, the mandibular ontogeny of living sloths

*Corresponding author: **Guilherme S. T. Garbino**, Departamento de Biologia Animal, Laboratório de Mastozoologia, Museu de Zoologia João Moojen, Universidade Federal de Viçosa, 36570-900 Viçosa, Minas Gerais, Brazil; and Pós-graduação em Biologia Animal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil, E-mail: guilherme.garbino@ufv.br. <https://orcid.org/0000-0003-1701-5930>

Lucas C. Pasin, Departamento de Biologia Animal, Laboratório de Mastozoologia, Museu de Zoologia João Moojen, Universidade Federal de Viçosa, 36570-900 Viçosa, Minas Gerais, Brazil

Daniel M. Casali, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, 14040-900, Av. Bandeirantes, 3900 Ribeirão Preto, São Paulo, Brazil. <https://orcid.org/0000-0002-0100-3735>

Thiago B. F. Semedo, BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal; CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus De Vairão, Universidade do Porto, 4485-661 Vairão, Portugal; and Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal. <https://orcid.org/0000-0003-4379-5993>

remains poorly explored, especially from a quantitative perspective, with other sources of intraspecific variation being more thoroughly explored (Hautier et al. 2014, 2018).

In this study, we compare mandibles of two-toed sloths from harpy eagle kill assemblages and museum specimens and provide ontogenetic information on the growth, shape modifications and symphyseal ossification patterns of the mandible in the genus.

2 Materials and methods

2.1 Analyzed sample and linear measurements

We have analyzed 24 complete mandibles and 11 disarticulated dentaries of two-toed sloths collected in harpy eagle nests from Mato Grosso, central Brazil. Complementarily, we have also examined nine mandibles of adult specimens from Brazilian Amazonia (Amazonas, Pará, and Rondônia states). Specimens are deposited in the Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV), and Museu de Zoologia da Universidade de São Paulo (MZUSP) collections (Appendix 1). All specimens were considered as *Choloepus* sp. in the present study, since the characters' states traditionally used for cranial identification of the two currently recognized species can be observed in both, sometimes showing intraspecific variation as well (Hautier et al. 2014). Hence, the available information does not allow us to unequivocally identify to which species an individual belongs. In addition, not all mandibles had associated skulls, and mandibles alone are not diagnostic of their specific characteristics.

Skeletal material was collected in harpy eagle nests following the protocol described in Miranda et al. (2021). Permits to collect the material were provided by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Brazilian Ministry of the Environment (SISBIO process No. 58533). We chose to examine mandibles because these were the most well-preserved part of the skeleton of the two-toed sloths in the kill assemblage.

The following eight measurements (Figure 1) were taken with a digital caliper (precision 0.01 mm):

- TML: total mandibular length; distance from the most posterior point of the mandibular condyle to the most anterior point of the spout.
- LAM: length of the anterior part of the mandible; taken from the anteriormost tip of the mandibular spout to the posteriormost tip of the symphysis.
- BCC: breadth between lower caniniform teeth; measured between the most labial surfaces of the caniniform teeth.
- LCD: length from caniniform to diastema; taken from the mesial surface of the caniniform to the mesial surface of the first molariform.
- LMS: length of molariform series; distance from the mesial surface of the first molariform to the distal surface of the last molariform.
- BAC: mandibular breadth across condyles; greatest transverse width across mandibular condyles.
- HCC: distance between condylar and coronoid processes; distance from the most dorsal point of the coronoid process to the mandibular condyle.

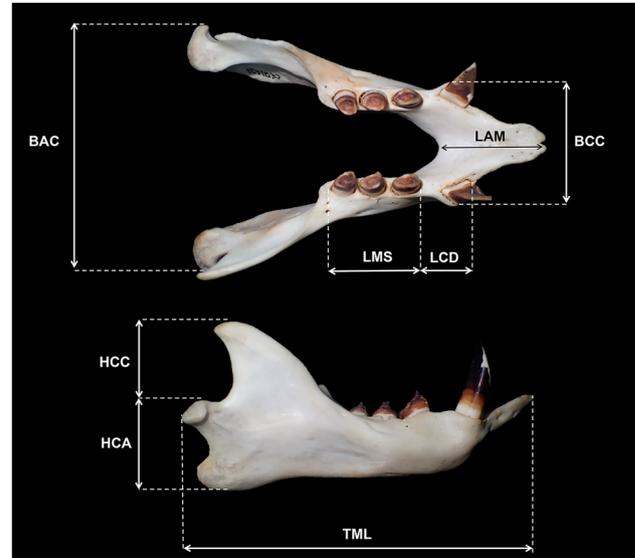


Figure 1: Mandible of an adult *Choloepus didactylus* (MZUSP 21328), showing the limits of the mandibular and dental measurements.

- HCA: distance between condylar and angular processes; distance from the most ventral point of the angular process to the dorsal surface of the mandibular condyle.

We then classified *a priori* the mandibles into four age classes, based on TML. Infants were defined as having $50.5 \text{ mm} \leq \text{TML} \leq 61.0 \text{ mm}$; Juveniles had $62.5 \text{ mm} \leq \text{TML} \leq 68.6 \text{ mm}$; Subadults were defined as having $69.0 \text{ mm} \leq \text{TML} \leq 75.0 \text{ mm}$; Adults were categorized as $81.0 \text{ mm} \leq \text{TML} \leq 92.0 \text{ mm}$ (Figure 2). We also evaluated the degree of symphyseal fusion in the specimens, classifying them in unfused, partially fused, and completely fused. Mandibular measurements were \log_{10} transformed for statistical analyzes.

2.2 Statistical analyzes

We chose TML as a proxy for overall mandibular size and regressed the other variables against it to test for linearity and quantify correlation. We inspected slopes to evaluate if mandibular measurements scale isometrically or allometrically with TML, regarding as isometric variables whose slope confidence interval (CI) included the value of 1.0. Significance was assessed with *F*-tests, with $\alpha = 0.05$, and the degree of correlation was evaluated using the adjusted coefficient of determination (R^2). We corrected for the family-wise error rate stemming from multiple comparisons using Holm's correction (Holm 1979).

We compared mandibular measurements among the four age classes with a Kruskal-Wallis test, assessing significance ($\alpha = 0.05$) and effect-size. Additionally, we performed sequential pairwise comparisons for age classes (i.e. infant x juvenile, juvenile x subadult, and subadult x adult) using a Wilcoxon rank-sum test ($\alpha = 0.05$, with Holm's correction), also calculating the effect sizes.

Lastly, we conducted a multivariate exploration using all eight variables with a principal component analyzes (PCA), and tested for age group differences using a non-parametric multivariate analyzes of variance (NP-MANOVA, Anderson 2001) taking the square root of the dissimilarities, and also considering subsequent pairwise tests between



Figure 2: Four age classes the *Choloepus* mandibles were grouped into. From left to right: infant, juvenile, subadult, adult. Specimens photographed, from left to right: MZUFV B0401, CE01109, CE0101, MZUSP 3651.

age groups. For these comparisons, 9999 permutations were applied to evaluate significance ($\alpha = 0.05$, with Holm's correction).

All analyzes and plots were done in R (R Core Team 2023), with packages *rstatix* (Kassambara 2023a), *vegan* (Oksanen et al. 2022), *pairwiseAdonis* (Martinez Arbizu 2017), *ggplot2* (Wickham 2016), *ggpubr* (Kassambara 2023b) and *ggfortify* (Tang et al. 2016). Tables were exported using package *openxls* (Schauberg and Walker 2023).

3 Results

Although TML in measured adult *Choloepus* specimens can reach up to 91.9 mm, none of the mandibles in the harpy eagle kill assemblage had a TML greater than 74.5 mm. Patterns of symphyseal fusion were correlated with the predefined length-based age classes. Every infant had unfused symphyses and they were completely fused in every adult and subadult specimens. Out of 18 juveniles, three had unfused symphysis, nine were partially fused, and in six individuals the mandibular symphysis was completely fused. Fusion begins in dorsal surface of the symphyseal region, and some specimens had a completely fused symphysis dorsally but with the suture still visible ventrally. It is also evident, based on specimens with varying degrees of fusion, that, anteroposteriorly, the process of suture closure begins from the middle portion, with the anterior and posterior sutures closing later (Figure 2).

Linear regressions indicate that there are significant and strong ($R^2 \geq 0.8$) correlations between most of the other variables and overall mandibular size (Figure 3, Supplementary Table S1). The only variables associated with slightly weaker correlations were LCD ($R^2 = 0.68$) and HCA ($R^2 = 0.77$), even though they still showed significant correlation with TML (Supplementary Table S1). Besides that, only three measurements (BAC, LAM and LCD) showed a slope CI including the estimated value of 1.0, indicating isometry, with BCC, HCA and HCC growing slower and LMS faster than TML.

In univariate comparisons, at least two age classes were found to be significantly different, and this difference was associated with a large effect size for all variables (Supplementary Table S2). Sequential pairwise comparisons indicate that sequential age group pairs are, in almost all cases, significantly different, with measurements for age groups showing little or no overlapping (Table 1, Supplementary Figure S1). Non-significant differences were obtained only when comparing subadults and adults, for LAM and LCD. For most pairwise comparisons, large effect sizes were obtained, excepting for HCA, juvenile x subadult (moderate); HCC, infant x juvenile (moderate); LAM, subadult x adult (moderate), and LCD, subadult x adult (small) (Supplementary Table S3).

In PCA, all four groups are clearly separated in PC1, which accounts for most of the variance (~88%), but less so on PC2 (~5%), both summing up to more than 90% of the total variance in the dataset (Figure 4, Supplementary Table S4). For PC1, the sign of all factor loadings is the same, indicating its correspondence to size (Table 2). Also, the magnitude of loadings show that variables contribute very similarly to the variance of the first axis (Table 2). General and pairwise multivariate tests were significant, further supporting the differences observed among age groups (Supplementary Table S5).

4 Discussion

The absence of larger two-toed sloth specimens in the kill sample indicate prey selectivity by harpy eagles. Adult two-toed sloths are notoriously aggressive and are able to fend off predators, which may explain why they are largely absent from our sample (Bastidas-Domínguez et al. 2023). Moreover, it has been observed (E.B.P. Miranda pers. comm.) that harpy eagles frequently perch on nearby branches to snatch juvenile sloths from their mothers. Absence of adult

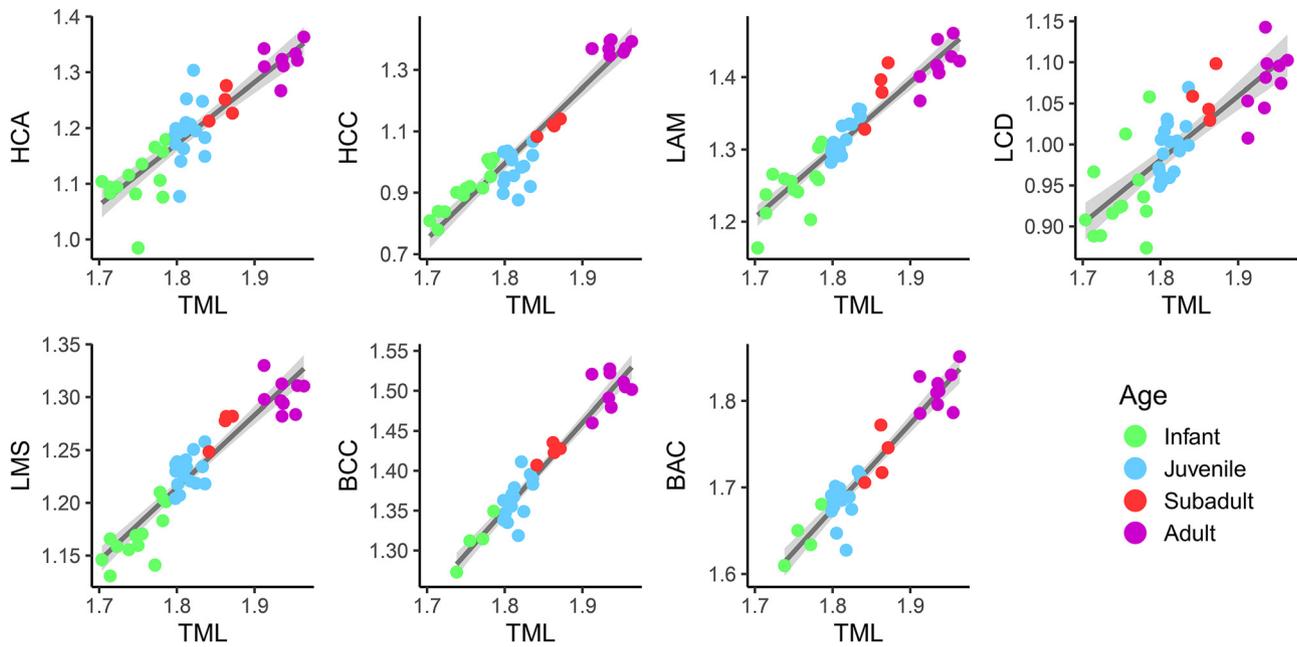


Figure 3: Linear regression of mandibular measurements of *Choloepus* sp. on total mandibular length (TML). Age groups indicated by colors. See main text for measurement abbreviations.

Table 1: Summary statistics for mandible measurements (in mm) of each age group of *Choloepus* (mean \pm standard deviation [range] sample size).

| Measurement | Age classes | | | |
|-------------|-----------------------------------|-----------------------------------|----------------------------------|----------------------------------|
| | Infant | Juvenile | Subadult | Adult |
| BAC | 44.08 \pm 3.04 [40.7–47.92] 4 | 48.54 \pm 2.65 [42.39–52.29] 15 | 54.46 \pm 3.79 [50.78–59.2] 4 | 65.12 \pm 3.28 [61.05–71.01] 9 |
| BCC | 20.57 \pm 1.47 [18.76–22.35] 4 | 23.08 \pm 1.33 [20.83–25.78] 16 | 26.51 \pm 0.73 [25.53–27.25] 4 | 31.81 \pm 1.59 [28.84–33.69] 9 |
| HCA | 12.84 \pm 1.41 [9.66–15.12] 13 | 15.66 \pm 1.74 [11.95–20.11] 18 | 17.48 \pm 1.13 [16.32–18.88] 4 | 21 \pm 1.25 [18.49–23.08] 9 |
| HCC | 8.16 \pm 1.4 [6.01–10.29] 13 | 9.65 \pm 1.23 [7.52–11.68] 15 | 13.08 \pm 0.72 [12.11–13.83] 4 | 23.68 \pm 0.98 [22.16–25.02] 9 |
| LAM | 17.74 \pm 1.57 [14.58–20.44] 13 | 20.6 \pm 1.15 [19.15–22.72] 18 | 24.11 \pm 2.11 [21.29–26.3] 4 | 26.28 \pm 1.67 [23.31–28.9] 9 |
| LCD | 8.69 \pm 1.11 [7.48–11.43] 13 | 9.88 \pm 0.75 [8.89–11.73] 18 | 11.43 \pm 0.8 [10.7–12.54] 4 | 12 \pm 1.07 [10.18–13.89] 9 |
| LMS | 14.78 \pm 0.84 [13.52–16.22] 13 | 16.98 \pm 0.54 [16–18.11] 18 | 18.74 \pm 0.69 [17.72–19.15] 4 | 20.06 \pm 0.71 [19.15–21.38] 9 |
| TML | 56.3 \pm 3.76 [50.53–61.07] 13 | 64.9 \pm 1.99 [62.81–68.57] 18 | 72.42 \pm 2.12 [69.41–74.39] 4 | 86.67 \pm 3.52 [81.7–91.93] 9 |

See main text for measurement abbreviations.

specimens has also been noted in a previous study on harpy eagle kill assemblages (Garbino et al. 2024).

Our results indicate a consistent linear relationship between some mandibular measurements and the total mandibular length. Nonetheless, only about half of the variables considered here scale isometrically with overall mandibular size, suggesting that some degree of allometry is present during mandibular growth. Moreover, this study has focused exclusively on linear morphometrics, and it is possible that some patterns that could only be captured by geometric morphometrics could be present, deviating from our observations here. For instance, it has been shown, with geometric morphometrics, that at the phylogenetic level, allometry explains a substantial part of the variation

observed between living sloths (Hautier et al. 2014), so it is not surprising that some degree of ontogenetic allometry is also present in mandibular shape within genera or species.

Our results are in overall consistent with those reported in the literature, in which some mandibular measurements are compatible with isometric and others with allometric patterns of growth. For instance, as reported for both extant and some extinct sloths, ontogenetic variation can be observed in mandibles, such as in the dental morphology, the curvature of the ventral and lateral edges of horizontal ramus, the shape and orientation of mandibular processes, the degree of fusion of the symphysis, formation of the mandibular canal and the number of mental foramina (Boscaini et al. 2019; Cartelle and De Iuliis 2006, 2014; De

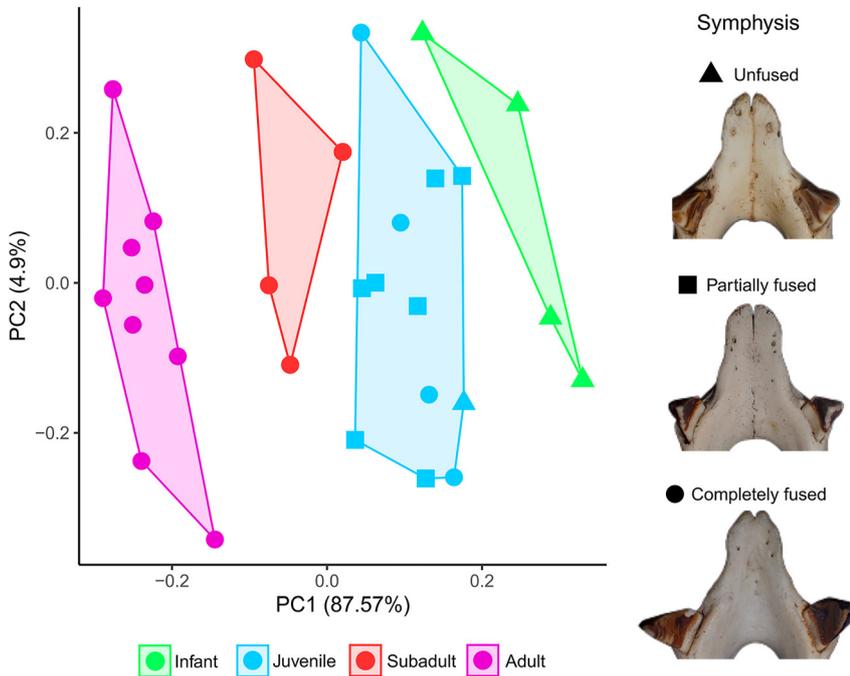


Figure 4: The first two principal components of a multivariate analysis of eight mandibular measurements of *Choloepus* sp., with their associated variance at axis titles. Age groups are indicated by colors and the degree of symphyseal fusion by shapes.

Table 2: Principal components' factor loadings of eight mandibular measurements of *Choloepus* sp.

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|-----|----------|----------|----------|----------|----------|----------|----------|----------|
| BAC | -0.36419 | -0.03257 | -0.37585 | -0.00685 | 0.21989 | 0.78839 | 0.12241 | 0.20027 |
| BCC | -0.37306 | -0.05151 | -0.04782 | 0.07696 | 0.19834 | 0.01218 | -0.59374 | -0.67672 |
| HCA | -0.33771 | -0.40931 | 0.39166 | 0.70764 | -0.04241 | -0.03279 | 0.01090 | 0.24754 |
| HCC | -0.35614 | -0.02746 | -0.63993 | 0.00627 | -0.09856 | -0.50959 | -0.20713 | 0.38803 |
| LAM | -0.35690 | 0.09563 | 0.39899 | -0.44229 | -0.55334 | 0.16929 | -0.33608 | 0.24672 |
| LCD | -0.31297 | 0.86221 | 0.17765 | 0.23890 | 0.18636 | -0.10852 | 0.14633 | 0.04581 |
| LMS | -0.35341 | -0.25972 | 0.29043 | -0.48950 | 0.58561 | -0.26349 | 0.25401 | 0.08244 |
| TML | -0.37024 | -0.08940 | -0.13581 | -0.03065 | -0.46577 | -0.08763 | 0.62497 | -0.46940 |

See main text for measurement abbreviations.

Iuliis et al. 2020; Hautier et al. 2016). On the other hand, it has been suggested that, at least for some taxa, the overall mandibular shape remains largely unaffected as the mandible increases in size during ontogeny (Boscaini et al. 2019; Pujos et al. 2023), suggestive of the presence of a dietary uniformity during the development of sloths.

Sloths' dietary habits can vary across species, ranging from selective browser to bulk-feeding grazer habits (Bargo et al. 2006; Pujos et al. 2012), and possibly including opportunistic omnivory as well (Tejada et al. 2021). The presence of isometric and allometric patterns does not appear to be associated with taxa presenting any of these dietary adaptations, although more studies are necessary to investigate this in greater detail.

Our study shows that osteological material from raptor kill samples can provide valuable clues on the morphology and ontogeny of poorly sampled species. However, a caveat

of this study is that harpy eagles select younger individuals of two-toed sloths, biasing the sample towards these ontogenetic stages. To mitigate this, our examination of museum specimens obtained through traditional collecting methods provided an adequate sample of individuals of later ontogenetic stages.

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Research ethics: Licenses and permits to collect the osteological material and install the camera traps in the nests were provided by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Brazilian Ministry of the Environment (SISBIO process No. 58533). The study was also approved by the Ethics Committee on Animal Use (CEUA) of the Universidade Federal de Viçosa (UFV) – process no. 1106/2021. No live animal was handled and/or injured.

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Data availability: The raw data can be obtained on request from the corresponding author.

Appendix 1

Specimens of *Choloepus* from Brazil used in this study are deposited in the Museu de Zoologia João Moojen (MZUFV), and Museu de Zoologia da Universidade de São Paulo (MZUSP) collections. Localities are arranged by the Brazilian federal state (in bold) and municipality or specific locality. Decimal geographic coordinates (latitude and longitude, respectively) are between parentheses, when available. Disarticulated dentaries were counted as separate specimens.

C. didactylus – Adult specimens in MZUSP ($N = 5$): **Amazonas**, Rio Juruá: 781; **Maranhão**, Miritiba: 2899; **Pará**,

Cachoeira do Espelo, Altamira: 21328; Cametá: 19925; Óbidos: 3651.

C. hoffmanni – Adult specimens in MZUSP ($N = 4$): **Amazonas**, Eirunepé: 19926; Igarapé Grande, Rio Juruá: 5446, Santa Cruz, Rio Eiru: 5461; **Rondônia**: 32340.

Choloepus sp. – Infant, juvenile, and subadult specimens in MZUFV ($N = 37$): **Mato Grosso**, Apiacás 1 (–9.383853; –57.64427): ED0116, ED0117, ED0118, ED0119, ED0201; Berneck 1 (–9.78344; –58.302317): B0111, B0401, B0750; Berneck 2 (–9.687318; –58.280317): B20101; Cotriguaçu 2 (–9.85620; –58.38038): AW0111, AW0212, AW0213; Cotriguaçu 3 (–9.990286; –58.362616): EL0219/0220, EL0528, EL0725; Cotriguaçu 4 (–9.993833; –58.280667): CE01101, CE01109, CE0196/01324, CE0197, CE0201, CE0202, CE0203, CE0204, CE0323; FSN 1 (–9.850086; –58.306281): FS0202, FS0216, FS0223, FS0224, FS0225, FS0306, FS0414; NB1 (–10.20675; –58.307479): JB0301, JB0302, JB0303; NB2 (–10.043259; –57.911096): VA0203.

References

- Aguiar-Silva, F.H., Sanaiotti, T.M., and Luz, B.B. (2014). Food habits of the Harpy Eagle, a top predator from the Amazonian rainforest canopy. *J. Raptor Res.* 48: 24–35.
- Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* 26: 32–46.
- Bargo, M.S., Toledo, N., and Vizcaino, S.F. (2006). Muzzle of South American pleistocene ground sloths (*Xenarthra*, Tardigrada). *J. Morphol.* 267: 248–263.
- Bastidas-Domínguez, M.C., Link, A., Di Fiore, A., and Mosquera, D. (2023). Sloths strike back: predation attempt by an ocelot (*Leopardus pardalis*) on a Linnaeus's two-toed sloth (*Choloepus didactylus*) at a mineral lick in Western Amazonia, Ecuador. *Food Webs* 36: e00291.
- Boscaini, A., Gaudin, T.J., Mamani Quispe, B., Münch, P., Antoine, P.O., and Pujos, F. (2019). New well-preserved craniodental remains of *Simomyiodon uccasamamensis* (*Xenarthra*: Mylodontidae) from the Pliocene of the Bolivian Altiplano: phylogenetic, chronostratigraphic and palaeobiogeographical implications. *Zool. J. Linn. Soc. Lond.* 185: 459–486.
- Cartelle, C. and De Iuliis, G. (2006). *Eremotherium laurillardii* (Lund)(*Xenarthra*, Megatheriidae), the Panamerican giant ground sloth: taxonomic aspects of the ontogeny of skull and dentition. *J. Syst. Palaeontol.* 4: 199–209.
- Cartelle, C., De Iuliis, G., Boscaini, A., and Pujos, F. (2019). Anatomy, possible sexual dimorphism, and phylogenetic affinities of a new mylodontine sloth from the late Pleistocene of intertropical Brazil. *J. Syst. Palaeontol.* 17: 1957–1988.
- Cartelle, C., De Iuliis, G., and Pujos, F. (2015). *Eremotherium laurillardii* (Lund, 1842) (*Xenarthra*, Megatheriinae) is the only valid megatheriine sloth species in the Pleistocene of intertropical Brazil: a response to Faure et al., 2014. *C. R. Palevol* 14: 15–23.
- De Iuliis, G., Boscaini, A., Pujos, F., McAfee, R.K., Cartelle, C., Tsuji, L.J., and 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: 215–232.

- De Iuliis, G., Cartelle, C., McDonald, H.G., and Pujos, F. (2017). The mylodontine ground sloth *Glossotherium tropicorum* from the late Pleistocene of Ecuador and Peru. *Pap. Palaeontol.* 3: 613–636.
- Delsett, L.L. (2024). Collecting whales: processes and biases in Nordic museum collections. *PeerJ* 12: e16794.
- Garbino, G.S.T., Semedo, T.B.F., and Miranda, E.B.P. (2024). Taphonomy of harpy eagle predation on primates and other mammals. *Am. J. Primatol.* 86: e23567.
- Gaudin, T.J. and Scaife, T. (2023). Cranial osteology of a juvenile specimen of *Acratocnus ye* (Mammalia, Xenarthra, Folivora) and its ontogenetic and phylogenetic implications. *Anat. Rec.* 306: 607–637.
- Hautier, L., Billet, G., Eastwood, B., and Lane, J. (2014). Patterns of morphological variation of extant sloth skulls and their implication for future conservation efforts. *Anat. Rec.* 297: 979–1008.
- Hautier, L., Gomes Rodrigues, H., Billet, G., and Asher, R.J. (2016). The hidden teeth of sloths: evolutionary vestiges and the development of a simplified dentition. *Sci. Rep.* 6: 27763.
- Hautier, L., Oliver, J.D., and Pierce, S.E. (2018). An overview of xenarthran developmental studies with a focus on the development of the xenarthrous vertebrae. *J. Mamm. Evol.* 25: 507–523.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* 6: 65–70.
- Kassambara, A. (2023a). *rstatix: Pipe-friendly framework for basic statistical tests*, R package version 0.7.2, <https://cran.r-project.org/web/packages/rstatix/index.html>.
- Kassambara, A. (2023b). *ggpubr: 'ggplot2' based publication ready plots*, R package version 0.6.0, <https://cran.r-project.org/web/packages/ggpubr/index.html>.
- Martinez Arbizu, P. (2017). *pairwiseAdonis: pairwise multilevel comparison using Adonis*, R package version 0.4.1, <https://github.com/pmartinezarbizu/pairwiseAdonis>.
- Miranda, E.B.P. (2018). Prey composition of harpy eagles (*Harpia harpyja*) in raleighvallen, Suriname. *Trop. Conserv. Sci.* 11: 194008291880078.
- Miranda, E.B.P., Peres, C.A., Carvalho-Rocha, V., Miguel, B.V., Lormand, N., Huizinga, N., Munn, C.A., Semedo, T.B.F., Ferreira, T.V., Pinho, J.B., et al. (2021). Tropical deforestation induces thresholds of reproductive viability and habitat suitability in Earth's largest eagles. *Sci. Rep.* 11: 13048.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., and Weedon, J. (2022). *Vegan: community ecology package*, R package version 2.6-4, <https://cran.r-project.org/web/packages/vegan/index.html>.
- Peres, C. (1999) The structure of nonvolant mammal communities in different Amazonian forest types. In: Eisenberg, J.F., and Redford, K.H. (Eds.). *Mammals of the neotropics. Volume 3. The central neotropics: Ecuador, Peru, Bolivia Brazil*. The University of Chicago Press, Chicago, pp. 564–581.
- Pujos, F., De Iuliis, G., Vilaboim Santos, L., and Cartelle, C. (2023). Description of a fetal skeleton of the extinct sloth *Nothrotherium maquinense* (Xenarthra, Folivora): ontogenetic and palaeoecological interpretations. *J. Mamm. Evol.* 30: 577–595.
- Pujos, F., Gaudin, T.J., De Iuliis, G., and Cartelle, C. (2012). Recent advances on variability, morpho-functional adaptations, dental terminology, and evolution of sloths. *J. Mamm. Evol.* 19: 159–169.
- Pyke, G.H. and Ehrlich, P.R. (2010). Biological collections and ecological/environmental research: a review, some observations and a look to the future. *Biol. Rev.* 85: 247–266.
- R Core Team (2023). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria, <https://www.R-project.org/>.
- Rocha, L.A., Aleixo, A., Allen, G., Almeda, F., Baldwin, C.C., Barclay, M.V., Bates, J.M., Bauer, A.M., Benzoni, F., Berns, C.M., et al. (2014). Specimen collection: an essential tool. *Science* 344: 814–815.
- Santos, P.M., Bocchiglieri, A., Chiarello, A.G., Paglia, A.P., Moreira, A., de Souza, A.C., Abba, A.M., Paviolo, A., Gatica, A., Medeiro, A.Z., et al. (2019). Neotropical xenarthrans: a data set of occurrence of xenarthran species in the Neotropics. *Ecology* 100: e02663.
- Schauberger, P. and Walker, A. (2023). *Openxlsx: read, write and edit xlsx files*, R package version 4.2.5.2, <https://cran.r-project.org/web/packages/openxlsx/openxlsx.pdf>.
- Smith, K.J., Mead, J.G., and Peterson, M.J. (2021). Specimens of opportunity provide vital information for research and conservation regarding elusive whale species. *Environ. Conserv.* 48: 84–92.
- Tang, Y., Horikoshi, M., and Li, W. (2016). ggfortify: unified interface to visualize statistical result of popular R packages. *R Journal* 8: 478–489.
- Tejada, J.V., Flynn, J.J., MacPhee, R., O'Connell, T.C., Cerling, T.E., Bermudez, L., Capuñay, C., Wallsgrove, N., and Popp, B.N. (2021). Isotope data from amino acids indicate Darwin's ground sloth was not an herbivore. *Sci. Rep.* 11: 18944.
- Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York, <https://cran.r-project.org/web/packages/ggplot2/index.html>.

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