



Taxonomic revision of maned sloths, subgenus *Bradypus* (*Scaeopus*), *Pilosa*, *Bradypodidae*, with revalidation of *Bradypus crinitus* Gray, 1850

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We present a taxonomic revision of maned sloths, subgenus *Bradypus* (*Scaeopus*), a taxon endemic to the Brazilian Atlantic Forest and currently composed of a single species, the vulnerable *Bradypus torquatus*. Our review is based on coalescent species delimitation analyses using mitochondrial and nuclear DNA, morphological analyses, and field observations. Our integrative approach demonstrates that two species of maned sloth can be recognized: the northern maned sloth (*Bradypus torquatus* Illiger, 1811) occurring in the Brazilian states of Bahia and Sergipe, and the southern maned sloth (*Bradypus crinitus* Gray, 1850), occurring in Rio de Janeiro and Espírito Santo states. The two species diverged in the Early Pliocene and are allopatrically distributed. We discuss the biogeographic pattern of the two maned sloth species, comparing it with other Atlantic Forest mammals. We also suggest that the conservation status of both maned sloths needs to be reassessed after this taxonomic rearrangement.

Key words: Atlantic Forest, *Bradypus torquatus*, integrative taxonomy, molecular, morphology, species delimitation, Xenarthra

Apresentamos uma revisão taxonômica das preguiças-de-coleira, subgênero *Bradypus* (*Scaeopus*), um táxon endêmico da Mata Atlântica do Brasil e atualmente composto por uma única espécie, a vulnerável *Bradypus torquatus*. Nossa revisão é baseada em análises de delimitação coalescente usando DNA mitocondrial e nuclear, análises morfológicas e observações de campo. Nossa abordagem integrativa demonstra que duas espécies de preguiça-de-coleira podem ser reconhecidas: a preguiça-de-coleira do nordeste (*Bradypus torquatus* Illiger, 1811), que ocorre nos estados brasileiros da Bahia e Sergipe; e a preguiça-de-coleira do sudeste (*Bradypus crinitus* Gray, 1850), que ocorre nos estados do Rio de Janeiro e no Espírito Santo. Essas espécies divergiram no início do Plioceno e atualmente apresentam distribuição alopátrica. Discutimos o padrão biogeográfico das duas espécies de preguiça-de-coleira, comparando-o com outros mamíferos da Mata Atlântica. Também sugerimos que o estado de conservação de ambas as preguiças-de-coleira seja reavaliado após este rearranjo taxonômico.

Palavras-chave: *Bradypus torquatus*, delimitação de espécies, Mata Atlântica, molecular, morfologia, taxonomia integrativa, Xenarthra

Extant sloths are relict members of a clade that was much more diverse in the past (McDonald and De Iuliis 2008). Two extant families are currently recognized, two-toed sloths of the family Megalonychidae, and three-toed sloths of the family Bradypodidae. The latter includes a single genus, *Bradypus* Linnaeus, 1758, that occurs from southern Mexico to southern Brazil (Gardner 2008; Santos et al. 2019b). Morphological data suggest that *Bradypus* is the sister group of Eufolivora, a clade containing most other sloths, both living and extinct (Gaudin 2004; Varela et al. 2019), whereas molecular evidence points to a closer affinity with extinct terrestrial megatherioid sloths (Slater et al. 2016; Delsuc et al. 2019; Presslee et al. 2019).

The genus *Bradypus* contains two subgenera of three-toed sloths, the widely distributed *Bradypus*, comprising three species—*B. variegatus* Schinz, 1825, *B. tridactylus* Linnaeus, 1758, and *B. pygmaeus* Anderson and Handley, 2001—and the Brazilian Atlantic Forest endemic *Scaeopus* Peters 1864, currently including a single species—*B. torquatus* Illiger, 1811, the maned sloth (Wetzel 1985; Gardner 2008; Hayssen 2009a). Maned sloths have a restricted range comprising the Atlantic coast of the Brazilian states of Sergipe, Bahia, Espírito Santo, and Rio de Janeiro (Hayssen 2009a; Hirsch and Chiarello 2012; Santos et al. 2019b). Due to habitat loss, maned sloths are currently classified as Vulnerable by the IUCN Red List (Chiarello and Moares-Barros 2014).

Although the distinctiveness of *Scaeopus* in relation to *Bradypus* has long been recognized, including differences in skull, skeleton, pelage, and karyotype (Gray 1850; Peters 1864; Wetzel and Avila-Pires 1980; Azevedo et al. 2012), only a few studies have attempted to investigate the diversity within the subgenus. Previous molecular-based investigations (Lara-Ruiz et al. 2008; Schetino et al. 2017) showed that *B. torquatus* can be subdivided into at least three distinct populations, associated with the Brazilian states of Bahia (BA), Espírito Santo (ES), and Rio de Janeiro (RJ), although no molecular data of specimens from the Brazilian state of Sergipe were analyzed. Based on mitochondrial (mtDNA) and nuclear (nuDNA) genes, Schetino et al. (2017) suggested a relatively deep temporal divergence between BA and ES + RJ (5.36 Ma) within the single recognized species, whereas the populations of ES and RJ would have diverged much recently (390 Ka). They also found that most of the molecular variance is distributed between populations (mtDNA 98.29%, nuDNA 83.7%) rather than within populations (mtDNA 1.71%, nuDNA 16.3%). Nevertheless, no species delimitation analyses were carried out. Moreover, discrete phenotypic variation within maned sloths has yet to be addressed, with only intrapopulation size and pelage variation being previously reported (Pinder 1993; Lara-Ruiz and Chiarello 2005).

Here, we investigate the genetic and phenotypic variation in *Bradypus* (*Scaeopus*) applying an integrative approach (Dayrat 2005). Based on molecular coalescent species delimitation analyses and on discrete and continuous phenotypic characters, we argue for the recognition of two species of maned sloths.

MATERIALS AND METHODS

Molecular data

Nucleotide sequences.—Most of the nucleotide sequences used in this study were generated by Schetino et al. (2017). Sequences for each individual were kindly made available by M.A. Schetino, and unique haplotypes are available in GenBank (Supplementary Data SD1). These sequences include two mitochondrial (COI and cyt-b) and three nuclear (ADRB2, APOB, and vWF) genes, for 24 individuals (four from BA, 18 from ES, and two from RJ). All sequences were previously aligned and nuclear loci phased, as reported in Schetino et al. (2017). Additionally, COI and cyt-b sequences for the outgroups *Bradypus* (*B.*) *variegatus*, *Bradypus* (*B.*) *tridactylus*, *Bradypus* (*B.*) *pygmaeus*, and *Choloepus didactylus* (Linnaeus, 1758) were obtained from GenBank (Supplementary Data SD1). Individual alignments are available in https://figshare.com/authors/Daniel_Casali/11756480.

Unilocus coalescent species delimitation.—We pruned the concatenated mitochondrial alignment in order to keep only unique haplotypes and added outgroups. These alignments were submitted to partitioning and substitution model selection in ModelFinder in IQ-TREE (Nguyen et al. 2014; Kalyaanamoorthy et al. 2017), using the Bayesian information criterion. Both genes (COI and cyt-b) were submitted to ModelFinder considering each codon position as a possible data partition. The best-fitting partitioning scheme and substitution models (Supplementary Data SD2) were applied in a phylogenetic analysis conducted in IQ-TREE (Chernomor et al. 2016). Supports were assessed with ultrafast bootstrap (Minh et al. 2013).

Unilocus species delimitation was investigated with the mitochondrial tree resulting from that analysis, with a multi-rate Poisson tree process (mPTP; Kapli et al. 2017), considering the minimum branch length according to the distances obtained from the nucleotide alignment. This analysis was conducted in the mPTP webservice (<https://mcmc-mptp.h-its.org/mcmc/>), using a Markov chain Monte Carlo (MCMC) approach to assess speciation supports, with two independent runs of 1 M generations each, sampling at every 100, and applying a 25% burn-in.

Multilocus coalescent species delimitation.—Using all four loci (MIT, APOB, ADRB2, and vWF), we jointly inferred the best-supported species delimitation and species tree according to a full-Bayesian multispecies coalescent analysis in BPP 4.0 (Yang and Rannala 2010; Yang 2015), applying algorithm “1” of species delimitation. We assigned sequences to three populations (i.e., putative species) according to their geographic provenance, and used (BA, (ES, RJ)) as the initial tree, following the topology obtained with mitochondrial data and previously published results (Schetino et al. 2017). We verified the stability of the results in face of alternative nucleotide substitution models and prior probabilities for population size (θ) and root divergence time (τ). For each unique combination of model and priors (Supplementary Data SD3), we considered a strict clock and estimated loci rates in all analyses, defining heredity

probabilities as 0.25 for the mitochondrial and 1.0 for nuclear loci. Two RJMCMC runs were performed, with 2 M iterations (400,000 samples \times 5 sample frequency), 10% being discarded as burn-in.

Species tree and divergence times estimation.—The best-fitting substitution model for each locus was obtained with ModelFinder in IQ-TREE, with the Bayesian information criterion (Supplementary Data SD4). Using all four loci, species and gene trees were co-estimated in *Beast2 (Heled and Drummond 2010), with a constant population size model, a strict molecular clock (with unlinked rate estimates for mitochondrial and nuclear genes), and a Yule tree prior. To accelerate convergence, initial values of parameters were informed according to estimates obtained during model selection. Since there is no fossil record associated with *Bradypus* (McDonald and De Iuliis 2008), the root was calibrated using a normal distribution, with mean = 5.36 and sigma = 1.33, approximating the estimates (mean and 95% Highest posterior density interval [HPD]) obtained by Schettino et al. (2017). Four MCMC runs were conducted, with 10 M generations each, sampling every 5,000th generation. The initial 25% generations were discarded as burn-in, and species and gene trees were summarized with major clade credibility (MCC) trees. Convergence was checked in Tracer 1.7.1 (Rambaut et al. 2018) and supports were assessed with posterior probabilities.

Morphological data

Specimens examined.—We examined 55 specimens of *Bradypus* (*Scaeopus*), the largest sample ever gathered for the study of the subgenus and covering most of its known distribution (Taxonomic Accounts and Supplementary Data SD5). These samples included skins, skulls, mandibles, humeri, and scapulae. Specimens are deposited in the following collections: Natural History Museum, London, United Kingdom (BMNH); Museu de Biologia Professor Mello Leitão, Instituto Nacional da Mata Atlântica, Santa Teresa; Brazil (MBML); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MN); Museu de Zoologia João Moojen, Universidade Federal de Viçosa, Viçosa, Brazil (MZUFV); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH); Coleção de mamíferos Alexandre Rodrigues Ferreira, Universidade Estadual de Santa Cruz, Ilhéus, Brazil (CMARF); Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG); and Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro, Macaé, Rio de Janeiro, Brazil (UFRJ/NUPEM). The examined specimens include the lectotype of *Bradypus crinitus* Gray, 1850 (BMNH 47.4.6.5) and the holotype of *Bradypus affinis* Gray, 1850 (BMNH 46.4.21.3). The two name-bearing types were examined through photographs.

Age determination.—Specimens were classified as adults based on the patterns of cranial suture closure and, when available, complemented by observations of epiphyseal fusion in

humeri and ossification of scapulae. We classified individuals in three age groups—(i) juveniles, in which skulls are substantially smaller and with most sutures still open; (ii) subadults, which presented some sutures closed, but clearly discernible; and, for those that postcranial skeleton was available, incompletely fused epiphyses in humeri and partially ossified scapulae; (iii) adults, in which most cranial sutures are closed or nearly so, and only faintly marked or not observable at all, and fully fused epiphyses in humeri and complete scapular borders. Only adults (age 3) were considered while evaluating discrete morphological variation, whereas for skull biometry and morphometry, subadults were also included (ages 2 and 3) to increase sample sizes (Supplementary Data SD5).

Discrete characters.—We evaluated the variation in discrete morphology in skulls ($N = 23$, [BA 10, ES 5, RJ 8]), mandibles ($N = 24$, [BA 10, ES 5, RJ 9]), and humeri ($N = 8$, [4 BA, 4 RJ]), resulting in 12 binary characters (Fig. 1). For character coding, see Supplementary Data SD6. Anatomic nomenclature for the osteological characters follows Gaudin (2004), Weksler (2006), Toledo et al. (2013), and Hautier et al. (2014).

To summarize this variation for the populations, we produced frequency plots for each character and state. To evaluate the presence of morphological patterning among groups, we conducted a hierarchical cluster analysis on the between-individual square-root Gower distance (Gower 1971). Because this method requires traits to be coded on the same individual, we only evaluated craniomandibular traits. The matrix of distances among skull traits was subjected to a series of hierarchical clustering algorithms to identify morphological clusters. Specifically, we investigated the unweighted and weighted average linkage clustering (UPGMA and WPGMA, respectively), the complete linkage method, and the squared-ward clustering method (ward D²).

We also reconstructed the ancestral states for craniomandibular characters, in order to explore the polarity of their evolution. The mitochondrial tree was used, pruning each population (BA, ES, and RJ) to a single tip. Since most characters showed polymorphisms within populations, we applied the *PolyMk* model, which explicitly accounts for polymorphic taxa, with the package Phytools (Revell 2010) in R programming environment (R Development Core Team 2021). The other three species of the genus *Bradypus* were included as outgroups, being coded after the photos in the literature (Anderson and Handley 2001; Hayssen 2008, 2009b, 2010; Hautier et al. 2014).

Geometric morphometrics.—To validate the quantitative assessment of the morphological variation in *Scaeopus*, we used 2D geometric morphometric analysis based on photos of the skull and mandible of 36 specimens. Skulls were photographed in ventral ($n = 30$) and lateral ($n = 33$) views, and hemimandibles were photographed in lateral view ($n = 34$). Photos were taken by both the authors and, due to COVID-19 restrictions, also third parties, to increase sample sizes. Landmarks and semi-landmarks were placed on regions identified on the morphological analyses as potentially important for between-taxon discrimination using the software TpsDig 1.32 (Rohlf 2015). We digitized 20 landmarks (18 bilaterally symmetric and two along the midline) and four bilaterally symmetric

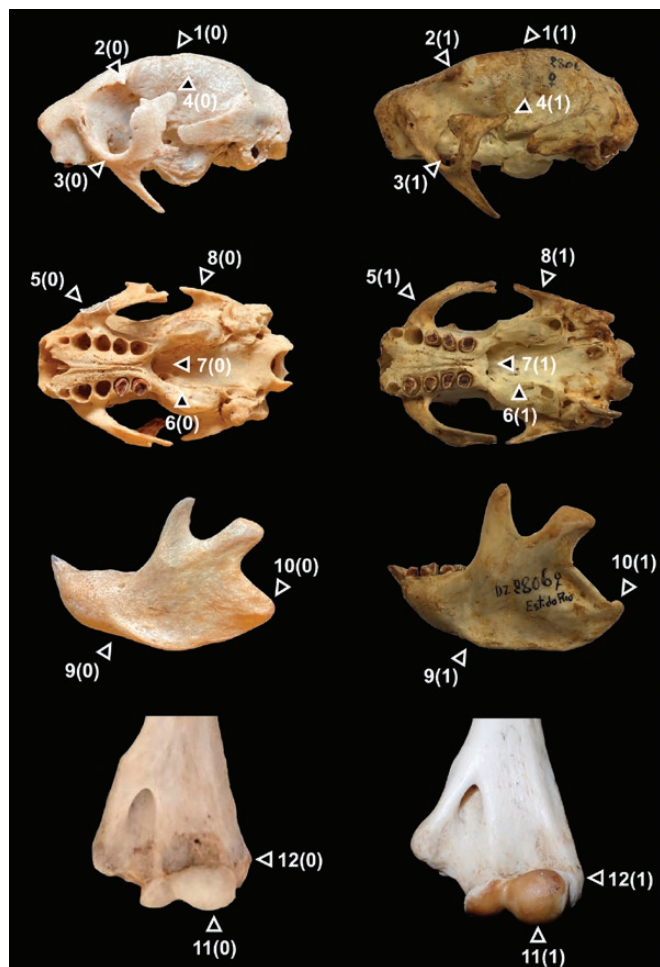


Fig. 1.—Discrete osteological characters and states observed in *Bradypus* (*Scaeopus*). 1. Dorsal contour of the cranium (lateral view): 1(0)—rounded, 1(1)—flattened; 2. Postorbital process of frontal (lateral view): 2(0)—process more laterally and ventrally projected, rendering the orbit deeper, 2(1)—process less laterally and more dorsally projected, rendering the orbit shallower; 3. Ventral margin of the orbit (lateral view): 3(0)—margin level with or above alveolar line, 3(1)—margin below alveolar line; 4. Orientation of the ascending process of jugal (lateral view): 4(0)—oblique (posterodorsal), 4(1)—horizontal (posterior); 5. Direction of the root of the jugal (ventral view): 5(0)—directed posterolaterally, rendering zygomatic arch narrower and closer to the cranium, 5(1)—directed laterally, rendering the zygomatic arch broader and displaced from the cranium; 6. Shape of medial margins of pterygoids (ventral view): 6(0)—margins gradually diverge posteriorly, 6(1)—margins proximally wider, with a constrained median region, from which margins follow subparallel or slightly divergent toward the posterior end of the pterygoids; 7. Exposition of nasopharyngeal foramina (ventral view): 7(0)—foramina exposed in mesopterygoid fossa, 7(1)—foramina mostly covered by the secondary palate; 8. Profile of lateral margin of zygomatic process of squamosal (lateral view): 8(0)—slightly curved medially, 8(1)—straight or roughly so; 9. Profile of ventral mandibular margin (lateral view): 9(0)—angle between symphyseal region and horizontal ramus more marked, 9(1)—angle less marked, with a rounder outline; 10. Shape of angular process of mandible (lateral view): 10(0)—angular process of mandible rounded posteriorly, 10(1)—angular process of mandible tapers posteriorly; 11. Shape of humeral capitulum (anterior view): 11(0)—wider than higher, roughly rectangular, 11(1)—width and

curves (22 semi-landmarks) for the ventral view, 12 landmarks and two curves (34 semi-landmarks) for the lateral view, and five landmarks and four curves (42 semi-landmarks) on the mandible (Supplementary Data SD7). For the ventral view, each landmark configuration was superimposed on its mirror image to avoid redundancy due to bilateral symmetry and to input missing data (Cardini 2016). Each configuration was subjected to a general Procrustes alignment (GPA) with a bending energy minimization sliding step for the semi-landmarks. For the mandible, because photos were taken by multiple researchers, the inclination of the structure varied in a discrete manner (either “inclined” or “parallel” in relation to the plane of the photo). A linear model was used to remove the effect of inclination, centering the sample around the “parallel” average. For all views, shape differences between the consensus landmark configuration and each specimen (i.e., Procrustes residuals) were subjected to a principal component analysis (PCA) to reduce dimensionality.

To evaluate group differences, we employed a Mahalanobis distance permutation procedure and a linear discriminant analysis (LDA) on the geographical groups. Because both methods require matrix inversion and are prone to sampling noise (Strauss 2010; Mitteroecker and Bookstein 2011), we only used the leading five principal components for each view. The Mahalanobis distance was then calculated between-group averages and confronted against a null distribution generated by 1,000 permutations of individuals among groups. Because the permutation procedure only focuses on differences in the central tendencies of groups, we also employed the LDA to characterize the overlap between groups (Machado and Hingst-Zaher 2009; Machado and Teta 2020). This was done by employing a jackknife cross-validation procedure, in which individuals are removed from the sample one at a time and reclassified according to the LD estimated for the remaining individuals. Large correct classification rates imply less overlap among groups, while higher misclassification rates imply a large overlap. Lastly, we projected the LD function back on the shape space to visualize the morphological differences associated with each group and compare these graphical representations to the differences described in the discrete morphology analysis. All statistical analyses were performed with the R programming environment. Geometric morphometric analyses were performed using the packages Morpho (Schlager 2017) and geomorph (Adams and Otárola-Castillo 2013).

Size differences.—To evaluate potential size and allometric differences between groups we compiled biometric information about weight and body length of live individuals measured in the field (Pinder 1993; Lara-Ruiz 2004). We supplemented this data set with new field observations made by the leading author, totaling 60 observations for

height subequal, roughly rounded; 12. Humeral ectepicondyle (anterior view): 12(0)—laterally protruding dorsal to capitulum, forming a triangular lateral margin, 12(1)—laterally protruding at the level capitulum, forming a straight lateral margin.

weight and 57 for body length (Supplementary Data SD8). Because *B. torquatus* has been described as having altitudinal variation in body weight (Lara-Ruiz 2004; Lara-Ruiz and Chiarello 2005), we also classified each sample as either originating from “lowlands” or “highlands,” following Lara-Ruiz and Chiarello (2005). We evaluated the difference between geographical groups and altitudinal categories by performing an allometric regression analysis of body length on body weight on the logarithmic scale, using the populational and altitudinal categories as covariates. The effects of individual factors and their interactions were evaluated using a type II nonparametric linear model (RRPP) that is well suited for small sample sizes (Collyer and Adams 2018). Additionally, we evaluated osteological differences between individuals from BA and RJ with 13 linear measurements (Table 1; Supplementary Data SD9). Between-group difference was tested using a nonparametric analysis of variance with the package RRPP, and *P*-values were adjusted for multiple comparisons with Bonferroni corrections (Bonferroni 1936).

Pelage.—We analyzed the pelage of 18 museum skins and 14 live captures to assess variation in color pattern (Taxonomic Accounts and Supplementary Data SD5). Permits to capture and handle the animals were duly provided by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Ministry of the Environment (process no. 67274-2) and approved by an ethics committee (CEUA 014/21—Universidade Estadual de Santa Cruz). Research on live animals followed ASM guidelines (Sikes et al. 2016).

Geographic distribution.—Geographical coordinates were obtained using GPS data in the field, from museum specimens labels, and published articles, including a data set of occurrence of xenarthran species in the Neotropics (Santos et al. 2019b). Approximate coordinates based on the municipality were used when more precise information was not available. Maps were

produced in QGIS 3.16.3, and the Multiscale Hydrographic Base (BHO50k).

Conceptual framework applied for taxonomic decisions.—We interpreted our data in light of the General Lineage Concept of species, in which species are broadly defined as “separately evolving metapopulation lineages” (de Queiroz 1998). In this sense, other proposed species concepts are subsumed as operational criteria or secondary species concepts (Mayden 1997; de Queiroz 2007). This framework has the advantage to recognize that the speciation process is continuous, and some properties—diagnosed using operational criteria—can be present at a given moment, whereas others may be absent (de Queiroz 1998, 2007). For example, two species may have acquired phenotypic diagnosability and ecological specializations at a given point of their separated evolutionary paths, but no reproductive isolation, or they may be reproductively isolated, but have not yet achieved reciprocal monophyly. That means that no single criterium is necessary, but a single one is sufficient to diagnose species, with each additional criterion applied providing cumulative evidence relative to the species limits (de Queiroz 2007). Here, we focus specifically in the criteria of genetic/geographic exchangeability (Templeton 1989), morphological clustering (Sokal and Crovello 1970), and reciprocal monophyly (Donoghue 1985).

RESULTS

Molecular data

Mitochondrial haplotype network and conspecificity matrix.—The mitochondrial haplotype network recovered four unique haplotypes for BA, two for ES, and one for RJ (Supplementary Data SD10A). This result indicates a substantial genetic divergence between BA and ES + RJ populations, which were separated by 86 mutational steps. ES and RJ populations, on the other hand, were only separated by 11 mutational steps, and all other haplotypes within these three populations were separated by 1–3 steps. See Supplementary Data SD11 for the association of individual sequences and haplotypes. Conspecificity matrix indicated a clearer subdivision associated with each of the three geographic regions, but also some lesser similarity among some ES specimens with those from RJ and some other ES specimens with those from BA (Supplementary Data SD10B).

Coalescent species delimitation.—The concatenated mitochondrial phylogeny recovered a BA clade as sister to a clade composed of ES + RJ (Supplementary Data SD12). Those three clades were highly supported by bootstrap values (>90). The results of mPTP indicated two putative species—BA and ES + RJ—with this speciation event being highly supported by posterior probability in both runs (PP = 0.97/0.99). The divergence between ES and RJ was not supported (PP = 0.03/0.03), and a division among the northern and southern BA populations was not supported as well (PP = 0.43/0.44). Multilocus species delimitation with BPP provided consistent support for the recognition of three species (PP = 1.0) (BA, (ES, RJ)), irrespective of the substitution model and priors applied.

Table 1.—Osteological linear measurements of *Bradypus* (*Scaepus*) taken in this study.

SL	Skull length, measured from the tip of nasal to the nuchal crest
SH	Skull height, measured from the dorsum of the skull to the ventral surface of the pterygoid
IJW	Inter-jugal width, measured at the base of the ascending process of jugal
POCW	Postorbital constriction width
PL	Palatal length, measured at the midline
CfD	Distance between upper caniniforms, measured at the labial side
Mf1D	Distance between first upper molariforms, measured at the labial side
Mf4D	Distance between last upper molariforms, measured at the labial side
OW	Occipital width, measured at the level of paroccipital process
OH	Occipital height, measured from the nuchal crest to ventralmost extension of the occipital condyle
ML	Mandibular length, measured from the tip of the spout to the angular process
MH	Mandibular height, measured from the coronoid process to the ventral surface of the horizontal ramus
HL	Humeral length

Gene trees, species tree, and divergence times.—In all gene trees co-estimated along with the species tree in *Beast2, BA and ES + RJ are reciprocally monophyletic and highly supported (PP > 0.95). For MIT and ADRB2 loci, RJ and ES are also reciprocally monophyletic and well supported, whereas for APOB and vWF, RJ clade is nested within the ES clade, rendering the latter paraphyletic according to these loci. The species tree indicates that BA, ES, and RJ are monophyletic, and the species tree (BA, (ES, RJ)) was recovered as in BPP, with maximum support for ES + RJ clade. The average estimated age for the divergence of BA and ES + RJ was 4.24 Ma [95% HPD, 1.59–6.74], and for ES and RJ, 0.25 [0.03–0.54] Ma. Gene and species tree files are available in https://figshare.com/authors/Daniel_Casali/11756480.

Morphological data

Discrete characters.—The distribution of craniomandibular discrete characters shows a clear distinction between BA and ES + RJ (Fig. 2A). The ES population has a somewhat mixed signal, with some traits clearly aligning with the RJ population (characters 1, 2, 6, 8, 9, and 10) and some with the BA population (characters 4, 5, and 7). Character 3, the ventral margin of the orbit relative to the alveolar line, was not clearly diagnostic of the geographic groups, with much variation observed within groups. The ancestral states reconstructions indicate that the characters that render ES more similar to BA are most likely the retention of a primitive morphology in the subgenus *Scaeopus* (character 4) or a retention of ancestral polymorphism (character 5 and 7, Supplementary Data SD13). Other characters rendering ES and RJ more similar were also associated with a greater probability of having a polymorphic ancestor population (characters 1, 8, and 9, Supplementary Data SD13).

Humeral characters 11 and 12 fully corroborate the distinction of BA and RJ, but no sample from ES was evaluated. Table 2 summarizes the frequency of each craniomandibular character state among specimens of each group.

The hierarchical cluster analyses of discrete traits showed the formation of two clear clusters: one containing ES + RJ individuals, without any clear geographical pattern among them, and one containing all BA samples—Fig. 2B shows the result for the UPGMA method. Other clustering algorithms (Ward D², WPGMA, and complete linkage) also showed the same pattern of differentiation between both morphotypes. We therefore only show the result of UPGMA for simplicity. See the taxonomic accounts for a detailed list of the character states used to diagnose these two morphotypes.

Geometric morphometrics.—The inspection of the scores for the two LD axes shows that there is a gradient between the northern population (BA) with lower scores, and the southern populations (RJ and ES) with higher scores on LD1 (Fig. 3). The differentiation between groups is more pronounced in ventral view than in lateral views of the skull or mandible. The deformation grids associated with LD1 depict a differentiation on all views that reflects the morphological differences described on the discrete morphological analysis (see above). Because no group was differentiated on the LD2, we do not show here the shape changes associated with that axis.

The Mahalanobis permutation procedure on the geographical groups showed differentiation between the extremes of the distribution (BA and RJ) on all views of skull and mandible (Supplementary Data SD14), but comparisons between neighboring populations (BA–ES and ES–RJ) did not show a consistent differentiation. The ventral view of the skull showed a significant difference between BA and ES, and the lateral view showed a significant difference between ES

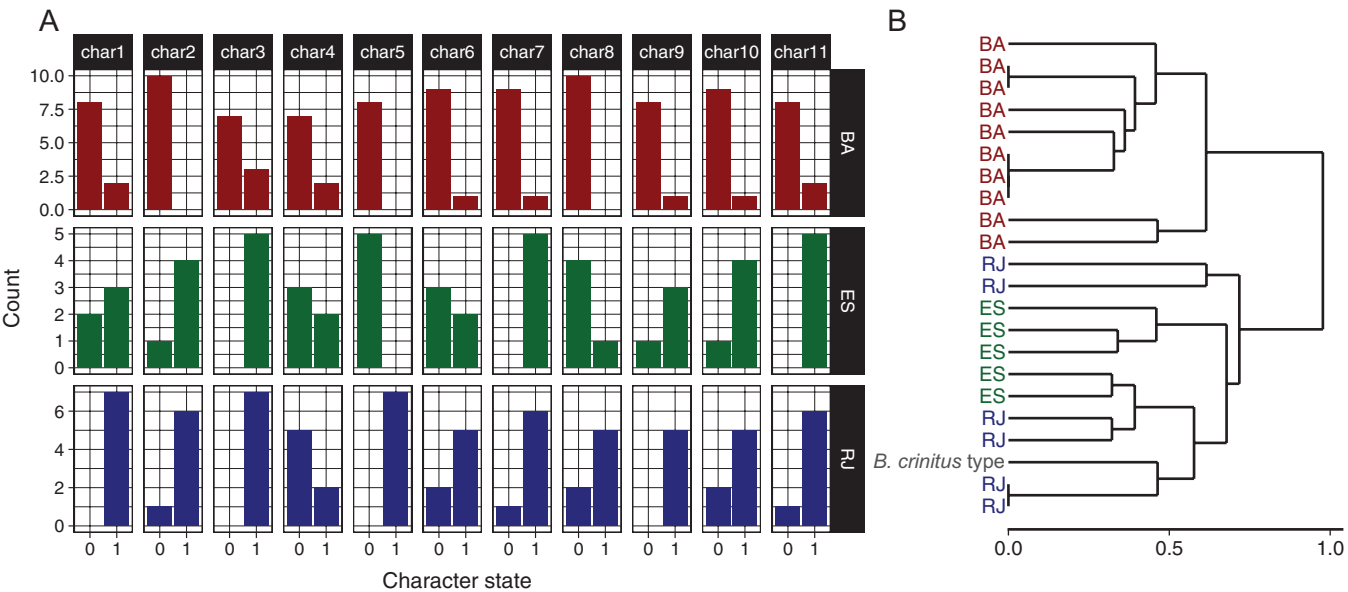


Fig. 2.—(A) Frequency of character states for the skull (char1–8) and mandible (char9–10) for the Bahia (BA), Espírito Santo (ES), and Rio de Janeiro (RJ) populations of *Bradypus* (*Scaeopus*). (B) Hierarchical cluster analysis of craniomandibular traits, highlighting the presence of two morphotypes (BA and ES + RJ).

Table 2.—Relative frequencies for craniomandibular character states among *Bradypus (Scaeopus)* specimens associated with each of the two main groups recognized here. Missing data “?” indicates unpreserved or ambiguous morphology. BA = Bahia; ES = Espírito Santo; RJ = Rio de Janeiro.

Character/state (%)	BA (N = 10)			ES + RJ (N = 13)		
	0	1	?	0	1	?
1	80	20	0	15	85	0
2	70	30	0	0	100	0
3	70	20	10	62	38	0
4	80	0	20	38	62	0
5	90	10	0	38	62	0
6	90	10	0	8	92	0
7	100	0	0	46	54	0
8	80	10	10	8	69	23
9	90	10	0	23	77	0
10	80	20	0	8	92	0

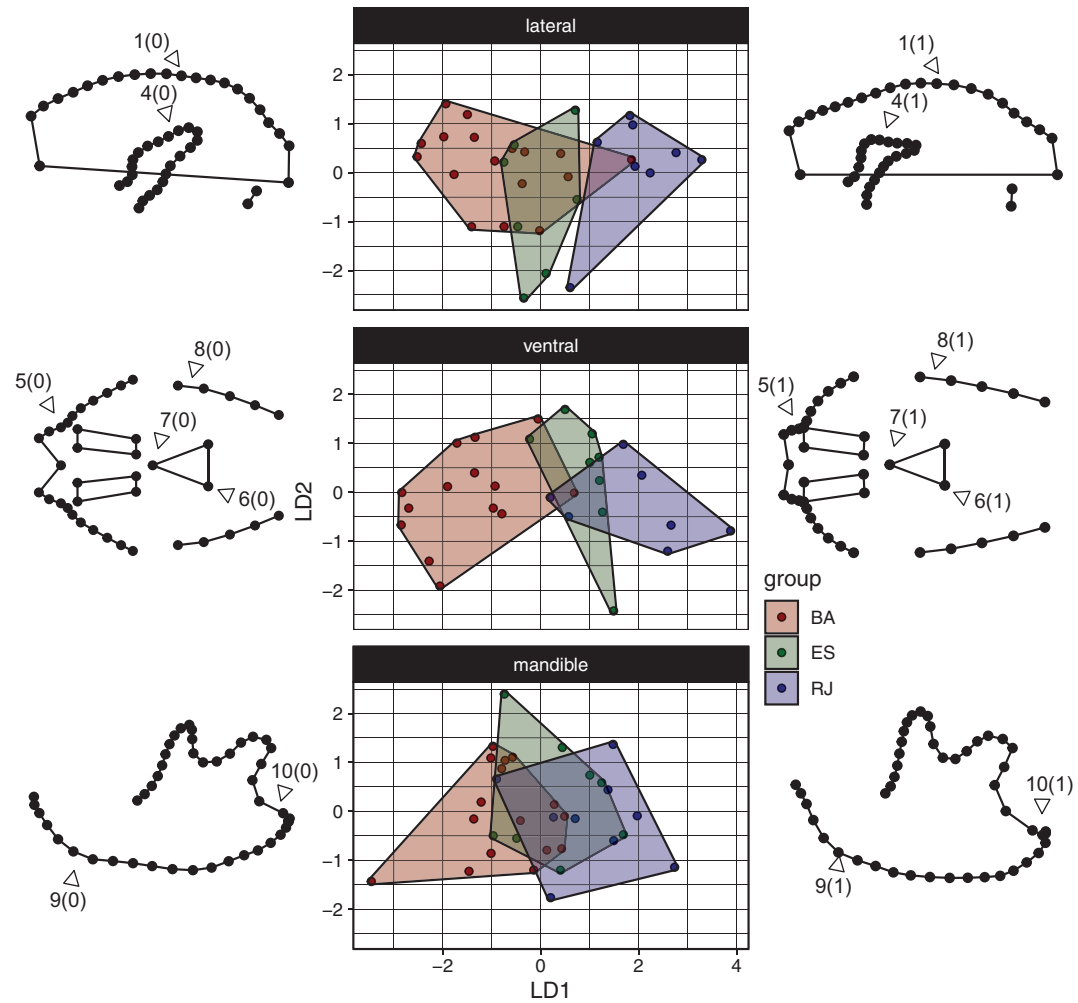


Fig. 3.—Linear discriminant analysis of the lateral (top) and ventral (central) views of the skull and lateral view of the mandible (bottom) of *Bradypus (Scaeopus)*. Central column represents the distribution of scores for each individual on the two first discriminant axes (LD1 and LD2). The left and right column highlights the shape associated with negative and positive values on LD1, respectively. Shape changes were calculated at 2 SDs from the grand mean. Arrows and numbers represent the shape changes similar to the discrete traits identified in Fig. 1.

and RJ, in addition to the differentiation between BA and RJ. These patterns are reflected on the estimation of the superimposition through the jackknife procedure. For the

ventral view, BA shows very little overlap with the southern groups, while both ES and RJ overlap with each other to a greater extent (Table 3A). For the lateral view of the skull

and mandible, there is a great overlap among all groups, with individuals from the ES being consistently classified outside of their original group (Table 3B and C). Overall, these analyses point to a detectable statistical differentiation between North and South genetic groups, and no differences between ES and RJ populations within the southern group. Analyses performed on the genetic groupings are consistent with the results depicted here, even depicting the same shape changes, but show even more differentiation (not shown). Therefore, the results obtained here for the geographical groups can be considered conservative.

Size differences.—The regression analysis shows a strong effect of both body length and altitude on body weight, but no effect of the geographic group after accounting for length and altitude (Supplementary Data SD15). We also did not find evidence of interaction between altitude and body length, which suggests that the allometric relation between body weight and length is the same between altitudes (Supplementary Data SD15). Specimens from lowland areas fall within the same allometric relation, with no clear geographical gradient (Supplementary Data SD16). This similarity is also reflected in the analysis of the osteological measurements between RJ and BA groups (Supplementary Data SD17), where we did not detect any significant difference between groups. This suggests that the shape differences observed in the geometric morphometric analysis are not likely the consequence of allometric differences. Table 4 summarizes the linear measurements for BA and ES + RJ groups.

Pelage.—No consistent geographic variation was detected. Body pelage in adults varies from buff-brown to gray. The face is always ocher-brown. Juveniles have a darker tone of buff-brown pelage. The mane varies ontogenetically being better defined in adults.

DISCUSSION

Integration of evidence

Unilocus species delimitation suggests two putative species, related to northern (BA) and southern (ES and RJ) distribution of *Bradypus* (*Scaeopus*), attributing a very low probability for further distinction of ES and RJ populations as independent entities. This method, mPTP, was shown to be more accurate and conservative than other unilocus methods, leading to delimitations more aligned to classical taxonomy (Kapli et al. 2017). This pattern is consistent with the number of mutational steps between populations in the mitochondrial haplotype network.

Table 3.—Classification rates for the jackknife cross-validation procedure for the ventral (A) and lateral (B) views of the skull and of the mandible (C) of *Bradypus* (*Scaeopus*). Comparisons that were significantly different on the Mahalanobis permutation approach are indicated with *.

A. Ventral	BA	ES	RJ	B. Lateral	BA	ES	RJ	C. Mandible	BA	ES	RJ
BA	85.71	14.29*	0.00*	BA	76.47	17.65	5.88*	BA	68.75	12.50	18.75*
ES	12.50*	37.50	50.00	ES	42.86	28.57	28.57*	ES	50.00	12.50	37.50
RJ	0.00*	42.86	57.14	RJ	0.00	12.50*	87.50	RJ	33.33*	22.22	44.44

The multilocus delimitation performed with BPP, on the other hand, suggests that the population of RJ could also constitute a distinct species. Nonetheless, this method has been recently criticized for overestimating the number of species for some data sets, and for not delimiting species, only population genetic structure (Sukumaran and Knowles 2017). These putative species can or cannot be indicative of taxonomic differences, and it is recommended that its results be evaluated along with other sources of evidences before taxonomic decisions are made (Leaché et al. 2019; Sukumaran et al. 2021).

Previous studies also discarded a simple isolation-by-distance scenario between all three populations, in favor of one of allopatry, with the northern–southern division being much older than the split between ES and RJ lineages (Lara-Ruiz et al. 2008; Schetino et al. 2017). As discussed by Schetino et al. (2017), BA and ES share one haplotype of the nuclear gene APOB, which is more likely a retention of ancestral polymorphisms due to incomplete lineage sorting rather than recent or historical gene flow. We concur with Schetino et al. (2017) that a scenario of migration among males of each population is not impossible, but would be unlikely given the natural gap in their distribution in northern ES (Fig. 4), where decades of survey have failed to detect maned sloths (Oliver and Santos 1991; Hirsch and Chiarello 2012; Santos et al. 2019b).

Osteological evidence also suggests two species, with humeral characters fully differentiating between two groups, despite the limited sample. Cluster analyses of cranial characters indicate that ES and RJ populations show considerable overlapping, but BA constitutes a single cluster distinguishable from ES + RJ when multiple characters are considered. Nevertheless, some ES individuals show a mosaic of character states from both northern and southern populations, somewhat aligned with nonsignificant differences between ES and BA in some morphometric geometric analyses and the patterns obtained in the conspecificity matrix analysis.

Although a quantitative inference regarding the polarity of the discrete characters of maned sloths is beyond the scope of this study, a tentative discussion about character evolution in *Bradypus* (*Scaeopus*) may be warranted, especially for the three characters that render some or all ES individuals more similar to those of BA. Character 4, the orientation of the ascending process of jugal in lateral view, also presents a posterodorsal orientation in the three species of subgenus *Bradypus* (depicted in Hayssen 2008, 2009a, 2010; Hautier et al. 2014), suggesting that BA and ES populations retained this purportedly primitive morphology, whereas RJ presents the derived horizontal orientation. Character 5, the direction of the root of the jugal in

Table 4.—Summary statistics of quantitative measurements for Bahia (BA) and Espírito Santo + Rio de Janeiro populations (ES + RJ) of *Bradypus* (*Scaepus*). Cranial measurements were not obtained for the ES population. Mean \pm SD [range] sample size.

	BA	ES + RJ
Body mass	5.33 \pm 0.59 [4.64–6.38] 15	6.25 \pm 1.52 [3.7–10.1] 45
Body length	634.6 \pm 58.12 [519–722] 15	645.52 \pm 59.56 [535–765] 42
SL	76.64 \pm 2.95 [71.1–79.9] 10	77.94 \pm 4.73 [72–84.1] 7
SH	41.28 \pm 1.19 [39.1–42.9] 10	39.26 \pm 2.45 [35.8–43] 7
IJW	47.76 \pm 2.68 [42.9–51.7] 9	49.25 \pm 2.63 [44.8–52] 6
POCW	26.79 \pm 2.06 [22.2–28.9] 10	24.97 \pm 2.36 [22–28.9] 7
PL	29.04 \pm 1.53 [27.5–32.2] 8	29.42 \pm 2.62 [25–34] 8
CfD	16.99 \pm 0.49 [16.3–17.7] 8	17.7 \pm 1.65 [15.6–19.5] 6
Mf1D	19.31 \pm 0.9 [18.1–21] 8	19.36 \pm 1.19 [17.8–21.4] 8
Mf4D	13.94 \pm 0.75 [13.1–15.6] 9	15.47 \pm 2.61 [13–19.7] 8
OW	34.7 \pm 1.85 [32.6–38] 10	38.31 \pm 3.37 [35–44.9] 7
OH	22.06 \pm 1.2 [20.1–23.7] 10	21.67 \pm 0.82 [20.5–23] 7
ML	57.61 \pm 2.08 [54.2–61.5] 12	59.08 \pm 2.89 [56–64] 9
MH	32.03 \pm 1.9 [29.7–34.7] 12	31.89 \pm 2.3 [28–35] 9
HL	175.35 \pm 11.17 [160–195.5] 8	179.22 \pm 21.89 [155.3–205.1] 4

Body mass in kg, measurements in mm.

ventral view, is more frequently directed posterolaterally in the species of the subgenus *Bradypus* (depicted in Hayssen 2008, 2009a, 2010; Hautier et al. 2014), similar to most BA and ES specimens of *Scaepus* studied here, with only two individuals from RJ presenting this morphology. The last character that would render ES specimens more similar to those of BA, character 7, is of a more ambiguous polarity, since the nasopharyngeal foramina are absent in *B. (B.) variegatus* and in *B. (B.) pygmaeus* and is present as a single pair of large foramina in *B. (B.) tridactylus* (depicted in Hayssen 2008, 2009a, 2010; Hautier et al. 2014), whereas in *Scaepus* multiple small foramina are present (Anderson and Handley 2001). Our ancestral state reconstructions suggest that the similarity of BA and ES individuals most likely indicates the retention of a primitive morphology (character 4) or the retention of ancestral polymorphism (characters 5 and 7), with this last pattern being already observed in other taxa (Corl et al. 2010).

Size and body mass differences were observed between specimens from ES and those from BA and RJ. Nevertheless, this pattern does not immediately correlate to population differences. Lara-Ruiz et al. (2008) showed that size differences in ES maned sloths are associated with altitudinal variation within the state. We further confirmed this when, removing larger highland individuals, no significant size difference is observed between the three populations.

Pelage variation could not be consistently associated with taxonomic differences, possibly related to ontogenetic, sexual, environmental, or individual variation (Pinder 1993; Lara-Ruiz and Chiarello 2005). However, the low sample size of skins in collections hampers definitive conclusions. Additionally, the variable presence of algae covering the pelage can further confound the assessment of the coloration. Future efforts in that direction are necessary to better understand pelage variation in *Bradypus* (*Scaepus*).

Taking all the evidence together, we argue that the recognition of two species is a better fit for the data available than the alternatives (one or three species). There is a considerable genetic divergence between northern and southern populations, corroborated by

evidence provided by osteological characters. Also, the temporal divergence between northern and southern populations occurred in the Early Pliocene, whereas ES and RJ diverged much more recently, in the Middle Pleistocene (Fig. 5).

Taxonomic history

The existence of maned sloths has been known by Europeans at least since the 16th century (Gray 1850; Moreira and Mendes 2016). However, scientific nomenclature of the maned sloths begins in 1811, with *Bradypus torquatus* (Illiger 1811). Illiger described *B. torquatus* based on a specimen collected by Francisco Gomes in Brazil. The specimen assumed to be the type (ZMB_MAM 1895, Fig. 6) was donated by Hoffmannsegg to the Berlin Museum (now Museum für Naturkunde) and its label reads that it comes from Cametá, a region of Amazon rainforest in the Brazilian state of Pará (Vaz 2003). This locality falls outside the known range of maned sloths, and it is plausible that some of Hoffmannsegg's specimens were mislabeled, as one of his collectors, Friedrich Sieber, did collect in Cametá (Papavero 1971). In the mammalogical literature, there is at least one example of an Atlantic Forest endemic species, the porcupine *Chaetomys subspinosus*, whose type specimen label also reads "Cametá," where Sieber collected (Avila-Pires 1967). Other mislabeling cases of early 19th century specimens in the Museum für Naturkunde collection are evidenced by Voss and Angermann (1997) and Garbino and Nogueira (2017). Based on the fact that Gomes was hired by Hoffmannsegg to collect specimens in the Brazilian states of Pernambuco, Sergipe, and Bahia, the type locality of *B. torquatus* was restricted to the vicinities of Salvador, in the state of Bahia, Brazil (Papavero 1971; Vaz 2003).

Temminck (1820) reported on additional specimens of maned sloths in the Rijksmuseum van Natuurlijke Historie (now Naturalis Biodiversity Center), Leiden. Based on one specimen he acquired from the British Museum of Natural History (now Natural History Museum), London, and another donated by Wied, he described the pelage and confirmed the species occurrence in eastern Brazil. However, he also reproduced the erroneous locality of Cametá,

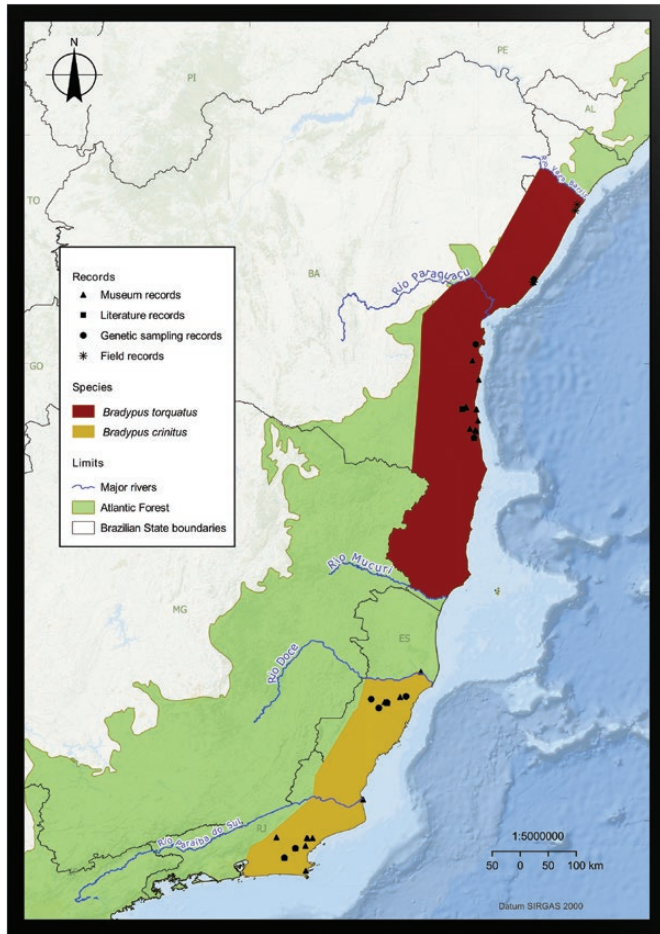


Fig. 4.—Geographical distribution of *Bradypus (Scaeopus) torquatus* and *Bradypus (Scaeopus) crinitus* in the Brazilian Atlantic Forest (minimum convex polygons depicting all known records, modified from Santos et al. 2019a). The points indicate individuals sampled for this study from museum collections (triangles), genetic samples (circles), field observations (asterisk), and a single literature photograph used to complement osteological evaluations (square).

in the Amazon (Temminck 1820). The publication of Temminck is the first to show a plate of the collared sloth, which was based on the Natural History Museum specimen.

The second oldest name for a maned sloth appeared in the 16-volume English translation of Cuvier's *Règne Animal*, published between 1824 and 1835. In the Mammals volume, Hamilton-Smith notes that Temminck gave the name *Cristatus* to the maned sloth represented by the specimen he acquired from the British Museum of Natural History (Griffith et al. 1827). From this publication it is also evident that the maned sloth brought from London by Temminck (1820) was collected by William Swainson in Brazil. In the same publication, there is a color plate resembling the plate published by Temminck (1820).

Swainson (1835), claiming authority for his maned sloth taxon, argued that *Bradypus cristatus* should be replaced by his new name, *Bradypus melanotus*. This replacement is not in accordance with the principle of priority of the International Code of Zoological Nomenclature (ICZN 1999). Therefore, *melanotus* Swainson, 1835 may be considered a

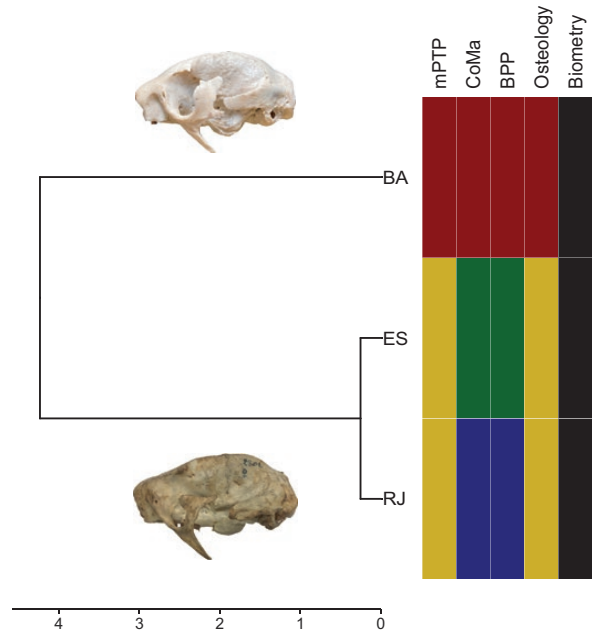


Fig. 5.—*Bradypus (Scaeopus)* time-scaled species tree (scale in My) and a summary of the evidence used to delimitate the species recognized in the present study. Osteology comprises both geometric morphometrics and discrete characters, whereas biometry encompasses body mass, body length, and cranial linear measurements.



Fig. 6.—Skin of the holotype of *Bradypus torquatus* (ZMB_MAM 1895) in dorsal view.

junior objective synonym of *cristatus* Hamilton-Smith, 1827. Although Swainson does not mention the collecting locality of the maned sloth, most of his collections in Brazil were made in Pernambuco, Sergipe, and Bahia, so we assume that the specimen came from the Brazilian state of Bahia (Swainson 1835; Papavero 1973).

The maned sloth specimen collected by Swainson and acquired by Temminck, which would be the type of both *cristatus* Hamilton-Smith, 1827 and *melanotus* Swainson, 1835,

could not be located in the Naturalis Biodiversity Center collection. There is a maned sloth specimen from “near Bahia” (RMNH.MAM.1612.a) in the collection, but it was acquired by the museum in 1927, so it could not represent Swainson’s specimen (Kamminga P., personal communication).

Gray (1850) described two new species of maned sloth based on specimens donated to the Natural History Museum in London. He described *B. crinitus* based on a specimen from Guiana and on another from Brazil donated by Becker. As the specimen from Brazil (BMNH 1847.4.6.5) is the one figured in his plate X, we designate it as the lectotype of *B. crinitus*. The lectotype of *crinitus* Gray, 1850 has the cranial characters of the southern species of maned sloth, and is the oldest available name for this taxon. However, its type locality was not given in the original description.

The other species described by Gray (1850), *B. affinis*, was based on an immature skeleton donated by J.F. von Brandt (BMNH 1846.4.21.3), with no more specific locality than “Brazil” (Gray 1850). Considering that Brandt was the curator of the St. Petersburg Museum (Russia), which at the time housed the specimens collected in Brazil by the Langsdorff expedition, the type specimen could have been collected in the state of Rio de Janeiro (Papavero 1971; Abramov and Baranova 2008). However, the data presently at hand do not allow for restriction of the type locality. Being an immature specimen, the type of *affinis* Gray, 1850 does not have definite characters that allow us to allocate this name in the northern or southern species of maned sloth.

Gray (1873), in a list of the “edentates,” “pachyderms,” and ruminants in the Natural History Museum, mentions a skull specimen of *B. crinitus* from Rio de Janeiro labeled “923 b.” The lectotype of *crinitus* Gray, 1850 is listed in the same catalog under the number “923 a” (Gray 1873), which is still readable on the specimen’s cranium (Fig. 7). We consider that this, allied to the observed morphological characters, reinforces the possibility that the lectotype of *crinitus* came from Rio de Janeiro. Therefore, we restrict the type locality of *B. crinitus* Gray, 1850, to the northern portion of Rio de Janeiro state, Brazil.

Gray (1850) was the first author to classify the maned sloth in a distinct genus from the other three-toed sloths, using *Bradypus* for the former and *Arctopithecus* for the latter. Peters (1864), recognizing that *Bradypus* was the available generic name for the three-toed sloth excluding the maned sloths, described the subgenus *Scaeopus* for the maned sloths.

Anthony (1906) subsequently described genus *Hemibradypus*, with no included species, based on a juvenile maned sloth specimen, arguing that Peters’ description of *Scaeopus* was insufficiently distinguishable from *Bradypus* (Anthony 1906). The same Anthony described the species *mareyi* in the genus *Hemibradypus* (Anthony 1907a). In the same year, Anthony designated *H. mareyi* as the type species of *Hemibradypus*, stating that the type specimen came from the physiological station of the Collège de France and that its geographical provenance was unknown (Anthony 1907b).

The validity of both genus *Hemibradypus* and species *H. mareyi* were questioned by contemporary authors (Poche 1908;

Menegaux 1909), and at present it is not possible to determine to which species of maned sloth *H. mareyi* belongs to. Conservatively, we consider *Hemibradypus mareyi* as a junior synonym of *B. torquatus*.

Taxonomic accounts

Subgenus *Scaeopus* Peters, 1864

Synonyms:

Bradypus Gray, 1850: 65; not *Bradypus* Linnaeus, 1758.

Scaeopus Peters, 1864: 678. Type species *Bradypus torquatus* Illiger, 1811, by monotypy.

Hemibradypus Anthony, 1906: 292. Type species *Hemibradypus mareyi* Anthony, 1907, by subsequent designation (Anthony 1907b).

Remarks.—*Scaeopus* Peters, 1864 has been used as a genus or a subgenus by many authors (Peters 1864; Thomas 1917; Cabrera 1958; Wetzel and Avila-Pires 1980; Hayssen 2009a). Considering the presence of several characters distinguishing it from other three-toed sloths and their deep molecular divergence, the distinction of maned sloths at the generic level would be justifiable. Nevertheless, to preserve nomenclatural stability, and to convey the information that the three-toed sloths form a monophyletic group, we propose to keep *Scaeopus* as a subgenus of *Bradypus* (Voss et al. 2014; Garbino 2015; Teta 2018).

Description and diagnosis.—Dorsal pelage vary from yellowish buff to light gray. The face is homogeneously colored ocher-brown, differing from subgenus *Bradypus* where there is a horizontal white stripe connecting the eyes. Posterior to the face, the crown and nape have the same color as the rest of the body, usually lighter than the ocher face. A dark brown mane is present in adult individuals. Density and color intensity of the mane may be related to ontogeny and sex (Pinder 1993; Lara-Ruiz and Chiarello 2005). Dorsum, venter, forelimbs, and hindlimbs have the same color, varying from light gray to yellowish buff. Shoulders have a slightly darker tone. Dorsal hairs may have a dark base or a pale base. There is no yellowish dorsal speculum as is present in males of subgenus *Bradypus*.

In the jugal bone, the orbital processes are more developed in the subgenus *Scaeopus* than in *Bradypus*. The pterygoid sinuses are inflated in *Scaeopus* but not in *Bradypus*. The mandibular spout of *Scaeopus* is well-developed relative to that of *Bradypus*, although not so prominently as observed in *Choloepus* Illiger, 1811. In *Scaeopus*, the horizontal ramus of the mandible is deeper and more ventrally curved than in subgenus *Bradypus*, leading to a posteriorly projected angular process in the former, whereas, in the latter, the angular is projected ventrally. A constriction between the horizontal ramus and the base of angular is well-marked in *Bradypus*, but it is weak or absent in *Scaeopus*. In *Bradypus*, the base of the angular process is dorsoventrally narrower than in *Scaeopus*, rendering the angular process slender in the former and broader in the latter. The coronoid process of the mandible is broader in *Scaeopus* and subequal or only slightly taller than the condylar process, whereas in *Bradypus*, the coronoid is slender and extends well above the condyle. An entepicondylar foramen of the humerus

is present, as in *Choloepus*, whereas in the subgenus *Bradypus* it is absent. Both species of *Bradypus* (*Scaeoepus*) have a chromosomal complement of $2n = 50$, one of the smallest numbers among Pilosa (Pinder 1993; Azevedo et al. 2012).

Bradypus torquatus Illiger, 1811

Northern Maned Sloth (English)

Preguiça-de-coleira do nordeste (Portuguese)

Synonyms:

Br[adypus]. *Torquatus* Illiger, 1811:109; type locality “Brasília.” Restricted to “arredores de Salvador, Estado da Bahia, Brasil” (vicinities of Salvador, state of Bahia, Brazil) by Vaz (2003).

[*Bradypus*] *Cristatus* Hamilton-Smith in Griffith, Hamilton-Smith & Pidgeon, 1827:278; type locality subsequently identified as Brazil (Swainson, 1835) and here restricted to the state of Bahia, Brazil based on Swainson’s itinerary.

[*Bradypus*] *melanotus* Swainson, 1835:207; type locality “interior of Brazil”; here restricted to the state of Bahia, Brazil based on Swainson’s itinerary.

Bradypus affinis Gray, 1850:68; type locality “Tropical America”; restricted to Brazil based on the locality of the holotype.

Hemibradypus Mareyi Anthony, 1907:220; no locality mentioned.

Type material.—The type (ZMB_MAM 1895), by monotypy, is a flat skin, without associated skull (Fig. 6). The label reads that it comes from Cameté, but the original catalog entry originally read “Bahia,” which was crossed-out and replaced by “Cameté.” Vaz (2003) further restricted the type locality to the vicinities of Salvador, in the Brazilian state of Bahia.

Distribution.—The northern maned sloth is distributed in the Brazilian states of Bahia and Sergipe (Fig. 4). It occurs from Itaporanga d’Ajuda in Sergipe, on the southern (right) margin of Rio Vaza-Barris, to the northern (left) margin of Rio Mucuri in Bahia (Oliver and Santos 1991; Hirsch and Chiarello 2012; Fig. 4).

Bradypus torquatus occurs in humid and seasonal forests of the Atlantic Forest, in transitional areas with the Cerrado, and in restingas (Hirsch and Chiarello 2012). The species has been recorded from sea level to ca. 1,000 m of altitude.

Description and diagnosis.—Cranial dimensions similar to *B. crinitus* (Table 4). Rounder braincase in lateral view relative to *B. crinitus*; postorbital process of frontal more laterally and ventrally projected, rendering the orbit deeper relative to that observed in *B. crinitus*; root of jugal directed posterolaterally, rendering zygomatic arch narrower and closer to the cranium; medial margins of pterygoid gradually diverge posteriorly; palatine foramina more exposed in mesopterygoid fossa; lateral margin of zygomatic process of squamosal slightly medially curved; angle between symphyseal region and horizontal ramus of mandible more marked; angular process of mandible rounded posteriorly; humeral capitulum wider than higher, roughly rectangular; and humeral ectepicondyle laterally protruding dorsal

to capitulum, forming a triangular lateral margin. The frequencies in which these character states occur in *B. torquatus* are summarized in Table 2.

Specimens examined ($N = 27$).—Brazil: Bahia, without specific locality (RMNH MAM 1612, UFMG 3111), Camamu (MN 84576), Ilhéus (MN 10981, 11204, 11206, 11395, CMARF 1347, 1841), Ilhéus (uncertain) (MN 23933), Itabuna (MZUSP 3506–3507), Itacaré (CMARF 3124, 3126), Itapoã (CMARF 1847), Praia do Forte (CMARF 3946), Una (CMARF 1823, 1828, 1831, 1834, 3123, 3128, 3150–3151, 3153, UFMG 1033). Locality unknown: BMNH 47.4.6.5 (holotype of *B. affinis*).

Bradypus crinitus Gray, 1850

Southern Maned Sloth (English)

Preguiça-de-coleira do sudeste (Portuguese)

Synonyms:

Bradypus crinitus Gray, 1850:67; type locality originally “British Guiana”; here redefined to the northern portion of the state of Rio de Janeiro, Brazil, based on the selection of specimen BMNH 1847.4.6.5 as the lectotype.

Type material.—The lectotype of *B. crinitus* (BMNH 1847.4.6.5) is an adult specimen, with preserved cranium and mandible in good condition (Fig. 7).

Distribution and habitat.—Records of the southern maned sloth are known from the Brazilian states of Espírito Santo and Rio de Janeiro (Fig. 4). The species occurs from the southern (right) margin of Rio Doce in Espírito Santo to the municipality of Arraial do Cabo, in Rio de Janeiro (Hirsch and Chiarello 2012; Ferreira et al. 2018; Fig. 4). The westernmost limit of the species is in Nova Friburgo, Rio de Janeiro.

The records of *B. crinitus* are from humid lowland and montane forests of the Atlantic Forest and it occurs also in the restinga, a coastal habitat associated with the Atlantic Forest (Hirsch and Chiarello 2012). The altitude where individuals were observed ranges from sea level to 1,290 m (Hirsch and Chiarello 2012).

Description and diagnosis.—cranial dimensions similar to *B. torquatus* (Table 4). Flatter braincase in lateral view, when compared to *B. torquatus*; postorbital process of frontal less laterally and more dorsally projected, rendering the orbit shallower relative to that observed in *B. torquatus*; root of jugal directed laterally, rendering the zygomatic arch broader and displaced from the cranium; medial margins of pterygoid proximally wider, with a constrained median region, from which margins follow subparallel or slightly divergent toward the posterior end of the pterygoids; palatine foramina mostly covered by the bony palate; lateral margin of zygomatic process of squamosal straight or roughly so; angle between symphyseal region and horizontal ramus of mandible less marked relative to *B. torquatus*, with a rounder outline; angular process of mandible tapers posteriorly; humeral capitulum with width and height subequal, roughly rounded; and humeral ectepicondyle laterally protruding at the level of capitulum, forming a straight

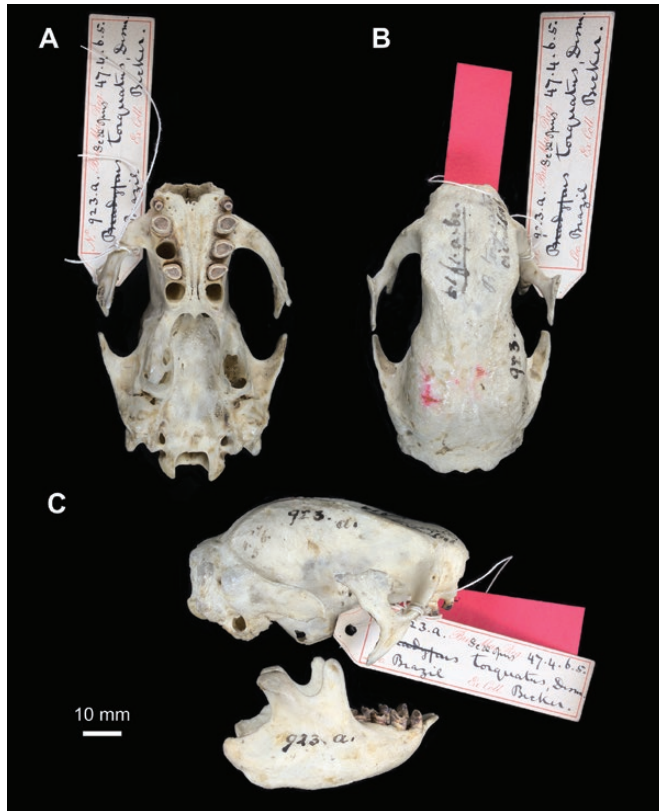


Fig. 7.—Skull and mandible of the lectotype of *Bradypus crinitus* (BMNH 1847.4.6.5) in ventral (A), dorsal (B), and lateral (C) views.

lateral margin. The frequencies in which these character states occur in *B. crinitus* are summarized in Table 2.

Specimens examined ($N = 26$).—Brazil: Espírito Santo, without specific locality (MN 23920, MZUSP 2422), Ibirapu (MN 23921), Linhares, Praia de Regência (MBML 379), Santa Teresa (MBML 281, 1836, 2798, 3475, 3841, MN 5899, UFMG 1036); Rio de Janeiro, without specific locality (BMNH 46.4.21.3 [lectotype of *B. crinitus*], MZUFV 4933, NPM TXD 367–368), Cabo Frio (CMARF 3948), Casimiro de Abreu (NPM 247, 288, 1224), Macaé (NPM 1185, 1505, 1816), Nova Friburgo (MZUSP 2806), São João da Barra (MZUSP 10074), Silva Jardim, BR-101 road (NPM 1223), Silva Jardim, Reserva Biológica Poço das Antas (MZUFV 412).

Evolution of maned sloths in the Atlantic Forest and conservation perspectives

The Atlantic Forest has long been recognized as a highly threatened ecosystem with a high level of endemism (Myers et al. 2000; Ribeiro et al. 2009). Among the 262 species of Atlantic Forest mammals, 101, or 38.5%, are endemics (Figueiredo et al. 2021). Likewise, some species are restricted to certain parts of the Atlantic Forest, and these recognized centers of endemism match the distribution of the two maned sloth species recognized here.

There are several cases among mammals and other vertebrates where phylogeographic breaks within species and separation between sister species occur at the Rio Doce (Costa and Leite 2013; de la Sancha et al. 2014). The Rio Doce, for example, separates

haplogroups of the common three-toed sloth *Bradypus* (*B.*) *variatus* (Moraes-Barros et al. 2006) and the Atlantic Forest climbing mouse *Rhipidomys mastacalis* (Costa 2003). At the species level, the Rio Doce separates the capuchin monkeys *Cebus nigritus* and *C. robustus*, with the former occurring to the south and the latter to the north of the river (Rylands et al. 1996). Nevertheless, it is unknown to what extent the river itself acts as a physical barrier, with other physical causes, like geology or climate, being proposed as the main factors responsible for the observed phylogeographic breaks (Leite et al. 2016).

Carnaval and Moritz (2008) predicted that the region between Rio Doce and Rio São Francisco, covering most of the range of *B. torquatus*, would have been a climatically stable area. However, the region south of Rio Doce, encompassing the range of *B. crinitus*, would be less stable. In fact, just a small climatically stable refuge was identified, in the border between Rio de Janeiro and Espírito Santo states, where *B. crinitus* occurs (Carnaval and Moritz 2008). Isolation in the refugia to the north and south of Rio Doce might have contributed to the separation of the two maned sloth species.

This separation was probably further aggravated by anthropogenic habitat fragmentation and deforestation in the Atlantic Forest (Chiarello 1999; Schettino et al. 2017). These processes potentially restricted the gene flow among the populations, and, combined with local effects of genetic drift, may have led to the structured pattern observed today (Lara-Ruiz et al. 2008). Additionally, a matrilineal philopatry associated with feeding preferences may have also played a role in the current restricted distribution of maned sloths (Chiarello 1998a; Lara-Ruiz et al. 2008).

The two maned three-toed sloths (*B. torquatus* and *B. crinitus*) occur in a severely fragmented region and dependent on a relatively small number of tree families for food, shelter, movement, and thermoregulation (Chiarello 1998b; Giné et al. 2015; Santos et al. 2019a). With the new taxonomic arrangement proposed here, the geographic distribution of each species becomes relatively smaller, with each one of the two species suffering under different anthropic pressures.

Bradypus crinitus occurs in a heavily fragmented region, and its apparently disjunct populations in Rio de Janeiro and Espírito Santo states may aggravate its conservation status. The Rio de Janeiro populations occur in some fairly large protected areas, such as Parque Estadual do Desengano (22,400 ha) and Reserva Biológica Poço das Antas (5,050 ha) (Pinder 1993; Modesto et al. 2008). In Espírito Santo the species occurs in medium-sized protected areas, such as Reserva Biológica Augusto Ruschi (3,570 ha) (Hirsch and Chiarello 2012), with several occurrences in montane (>600 m) areas. Although specific studies are necessary to properly evaluate this, it is likely that this species will be categorized as threatened, demanding independent management and conservation plans.

Bradypus torquatus, as redefined here, occurs in relatively large protected areas in Bahia, such as Estação Ecológica Wenceslau Guimarães (2,418 ha), Reserva Biológica Una (18,724 ha), and Parque Nacional Serra das Lontras (11,336 ha). This species uses shaded cocoa plantations, locally

known as cabrucas (Cassano et al. 2011; Giné et al. 2015). Actions needed to protect the species from local extinction include the active management of protected areas, forest fragments, cabrucas, and pastures in an integrated manner at the landscape level (Cassano et al. 2011). Due to the redefined distribution of *B. torquatus*, the species will also likely be categorized as threatened, although this will demand a proper evaluation, beyond the scope of the present study.

Future studies aiming to clarify the distribution of both maned sloth taxa, allied to the creation of protected areas and increased habitat connectivity will be necessary actions for the conservation of maned sloths.

Further directions

Further studies would benefit from investigating a broader sample of loci and evaluating patterns of genomic incongruences and how it relates with patterns of gene flow and the distribution of ancestral polymorphisms. Verifying the potential of interbreeding between the species would also be desirable, as introgression may even lead to the artificial splitting in species with allopatric distributions (Gutiérrez and Garbino 2018). Future efforts should also seek to improve sample sizes for morphological data to further address these concerns, although the inherent low number of individuals in collections might impose considerable challenges to this goal. More field studies may also be important to further characterize ecological differences between the species.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Nucleotide sequences of *Bradypus (Scaeopus)* used in this study and their respective GenBank accession number.

Supplementary Data SD2.—The best-fitting partitioning scheme and substitution models obtained with IQ-TREE for the mitochondrial data set, applied in the phylogenetic inference.

Supplementary Data SD3.—Alternative models and inverse-gamma priors for parameters of population sizes (θ) and species divergence times (τ) applied in BPP analyses.

Supplementary Data SD4.—The best-fitting substitution model for each locus, obtained with ModelFinder in IQ-TREE, with Bayesian information criteria, and applied in coalescent species tree inference and species delimitation in *Beast2.

Supplementary Data SD5.—List of specimens of *Bradypus (Scaeopus)* evaluated in this study.

Supplementary Data SD6.—Discrete osteological character coding for *Bradypus (Scaeopus)*.

Supplementary Data SD7.—Landmarks (dots) and semi-landmarks (dashed lines) used in morphometric geometric analysis of *Bradypus (Scaeopus)*. Definition of the landmarks—Skull, lateral view (upper panel)—1. Anterior- and dorsalmost point of the nasal. 2. Anterior- and ventralmost point of the maxilla. 3. Dorsal base of the ascending process of jugal. 4. Ventral base of the ascending process of jugal. 5. Dorsalmost point of the external auditory canal. 6. Ventralmost point of the external auditory canal. 7. Posterior- and dorsalmost point of the occipital region. 8. Ventral- and posteriormost point of the occipital midline, at the dorsal margin of foramen magnum. Skull, dorsal view (middle panel)—9. Lateral margin of rostrum at the level of the anterior margin of the first molariform. 10. Anteriormost point at the base of the ascending process of jugal. 11. Anteriormost point of the zygomatic process of the squamosal. 12. Posterior- and lateralmost point of the paroccipital process. 13. Anteriormost point at the suture between maxillae. 14. Lingualmost point at the first molariform. 15. Labialmost point at the first molariform. 16. Lingualmost point at the last molariform. 17. Labialmost point at the last molariform. 18. Posteriormost point at the suture between palatines. Mandible, lateral view (lower panel)—19. Tip of mandibular spout. 20. Union between the ascending ramus and the mandibular body near the toothrow. 21. Tip of the coronoid process. 22. Tip of the condylar process. 23. Tip of the angular process.

Supplementary Data SD8.—Measurements of body mass and body length of *Bradypus (Scaeopus)*.

Supplementary Data SD9.—Osteological linear measurements of *Bradypus (Scaeopus)*.

Supplementary Data SD10.—(A) A median-joining haplotype network obtained with mitochondrial data of *Bradypus (Scaeopus)*, with mutational steps indicated at the branches. (B) Conspecificity matrix (CoMa) obtained with all four loci sampled in the study.

Supplementary Data SD11.—Association of unique mitochondrial haplotypes and individual nucleotide sequences of *Bradypus (Scaeopus)*.

Supplementary Data SD12.—Maximum likelihood phylogenetic tree from concatenated mitochondrial genes (COI and cyt-b) considering the unique haplotypes of *Bradypus* (*Scaepus*). Node values indicate ultrafast bootstrap values. Geographic provenance for the ingroup (Brazilian states): Bahia (BA), Espírito Santo (ES), and Rio de Janeiro (RJ).

Supplementary Data SD13.—Ancestral states reconstructions of the craniomandibular characters of *Bradypus* (*Scaepus*).

Supplementary Data SD14.—*P*-values for the Mahalanobis permutation approach applied to groups of *Bradypus* (*Scaepus*).

Supplementary Data SD15.—Statistics of nonparametric linear models investigating size difference between geographical groups of *Bradypus* (*Scaepus*).

Supplementary Data SD16.—Relationship between total body length and body weight measured on live specimens of *Bradypus* (*Scaepus*). Lines represent linear trends between the log-transformed variables. Highland individuals indicated with a circle and these of lowlands with triangles.

Supplementary Data SD17.—Boxplots depicting the distributions of linear measurements for Bahia (BA) and Rio de Janeiro (RJ) populations of *Bradypus* (*Scaepus*). For a detailed account of the measurements, see Table 1.

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