



Morphological disparity and evolutionary rates of cranial and postcranial characters in sloths (Mammalia, Pilosa, Folivora)

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Abstract: Sloth morphological evolution has been widely studied qualitatively, with comparative anatomy and morpho-functional approaches, or through quantitative assessments of morphological variation using morphometrics. Only recently, however, have folivoran morphological disparity and evolutionary rates begun to be evaluated using discrete character data. Nonetheless, patterns of morphological evolution in separate character partitions have not been investigated, neither the relative influence of, on the one hand, phylogeny, and on the other, dietary and locomotory adaptations of sloths. Here we evaluate those patterns using a phylomorphospace approach, quantifying morphological disparity and evolutionary rates, and investigating possible drivers of morphological evolution for cranial and postcranial characters

in Folivora. The evolution of the morphology in those partitions is associated with distinct patterns of disparity among clades and ecological groups, even though the two partitions do not differ substantially in overall evolutionary tempo. Historical processes shaped the morphological evolution of sloths more consistently than ecological ones, although changes in postcranial characters also seem to be associated with locomotory adaptations, in which morphological convergences were much more common. We also discuss important methodological trade-offs in investigations of partitioned datasets mostly composed of fossil taxa.

Key words: sloth, morphology, partition, phylomorphospace, diet, locomotion.

SLOTHS (Folivora), along with anteaters (Vermilingua), are members of the clade Pilosa and, together with its sister clade Cingulata (armadillos and their fossil kin), comprise Xenarthra (Gaudin & McDonald 2008; Gibb *et al.* 2016), one of the main placental mammal lineages (O’Leary *et al.* 2013; Upham *et al.* 2019). Folivora is a diversified group, with *c.* 100 recognized genera, most of them extinct. The extant diversity of the group is restricted to only two genera, *Bradypus* Linnaeus and *Choloepus* Illiger (McKenna & Bell 1997; Gardner 2008; McDonald & De Iuliis 2008). Overall sloth diversity is also reflected in morphology, with marked differences associated with the main clades (Gaudin 2004; Varela *et al.* 2019; Casali *et al.* 2022). According to the most recent and comprehensive morphological phylogeny, most sloths can be included in one of two major clades, Mylodontoidea and Megatherioidea, the first being composed of Scelidotheriidae and Mylodontidae and the second, of Megalonychidae and Megatheriidae (Casali *et al.* 2022).

Sloths present disparate ecological adaptations (Pujos *et al.* 2012; Gaudin & Croft 2015). Although all living and fossil sloths are considered herbivorous, dietary specializations have been inferred for several taxa, which have been classified as browsers, mixed-feeders or grazers (Naples 1982, 1987, 1989; Bargo & Vizcaíno 2008; Bargo *et al.* 2009, 2012; Naples & McAfee 2012; Saarinen & Karme 2017; Kalthoff & Green 2018). However, for some taxa (mostly among mylodontoids), data from cranio-mandibular morphology and dental wear patterns point to conflicting dietary classifications, making the distinction between grazers and mixed feeders less clear (Bargo & Vizcaíno 2008; Saarinen & Karme 2017).

Locomotory habits are also diverse throughout the evolutionary history of sloths, but can be more generally associated with either climbing or terrestrial (including graviportal) adaptations (White 1993, 1997; Pujos *et al.* 2007; Bargo *et al.* 2012; McDonald 2012; Nyakatura 2012;

Toledo *et al.* 2012, 2013, 2015). Nevertheless, other types of substrate use, such as digging (Bargo *et al.* 2000; Pujos *et al.* 2012; Toledo *et al.* 2012; Gaudin & Croft 2015) or semi-aquatic adaptations, can also be recognized (Amson *et al.* 2014, 2015a, 2015b, 2015c). Climbing habits range from facultative semi-arboreal forms (White 1993, 1997; Toledo *et al.* 2013, 2015) to fully suspensory taxa (living sloths; Nyakatura 2012), also encompassing climbing capabilities probably unrelated to an arboreal lifestyle (Pujos *et al.* 2011). Additionally, some terrestrial taxa may have been able to assume a bipedal posture (Casinos 1996; Blanco & Czerwonogora 2003; Brandoni *et al.* 2004).

Empirical morphospaces have been widely used to investigate patterns of morphological evolution, including adaptation, convergence, morphological disparity and evolutionary rates (Sidlauskas 2008; Lloyd 2016, 2018). Previous studies on sloth morphology applied a morphospace evaluation for morphometric data from dental (Green 2009; Green & Resar 2012; Resar *et al.* 2013; Saarienen & Karme 2017; Kalthoff & Green 2018) and postcranial elements (White 1997; Bargo *et al.* 2012; Toledo *et al.* 2012; Toledo 2016; Amson & Nyakatura 2018; Oliveira & Santos 2018; Vizcaíno *et al.* 2018; Grass 2019; Serio *et al.* 2020). Often, and especially for postcranial data, this was done in broader taxonomic contexts, along with other xenarthrans and placental mammals, providing some insights on how their morphology relates to phylogeny and/or adaptation. One of the limitations of this approach is that the morphology of sloths in particular, and xenarthrans in general, is unique when compared to other placental mammals, presenting a distinctive combination of primitive and derived traits (McDonald 2003).

Other studies examined the evolution of adaptive ecological characters themselves, suggesting an ancestral browsing diet and scansorial locomotory adaptations for sloths (Pujos *et al.* 2012; Gaudin & Croft 2015), whereas Varela *et al.* (2019) were the first to use discrete morphological characters to investigate patterns of disparity and morphological evolutionary rates for different folivoran clades, an approach further explored in the present study.

The vertebrate skeleton is a modular morphological complex, and it is well known that different character partitions may evolve at different rates and thereby lead to distinct phylogenetic patterns (Clarke & Middleton 2008; Mounce *et al.* 2016). Recent studies investigating morphological disparity and evolutionary rates for discrete character partitions in vertebrates have shown that, when all morphological characters are treated as a homogeneous source of evidence, unique patterns exclusive to some of these character subsets may be obscured (Stubbs *et al.* 2019; Brocklehurst & Benevento 2020; Simões *et al.* 2020; Wang *et al.* 2021; Brocklehurst *et al.* 2022; Müller 2022).

We apply here a partition-oriented approach, separately investigating cranial and postcranial morphological evolution in sloths. This allows us to provide a general characterization of the patterns of evolution in these morphological complexes for a broad sample of sloths, also investigating the degree to which they are associated with historical (phylogenetic) and ecological (adaptive) factors.

MATERIAL AND METHOD

Morphological dataset and phylogenetic tree

We obtained discrete morphological characters from a previous phylogenetic study of Folivora (Casali *et al.* 2022), a dataset comprised of 510 characters (383 binary, 127 multistate, of which 63 were ordered). The characters were separated into two data partitions. The cranial partition (326 characters, 240 binary, 86 multistate, of which 38 were ordered) was composed of characters from the skull (including ear region characters), mandible, teeth and hyoid apparatus. The postcranial partition (184 characters, 143 binary, 41 multistate, of which 25 were ordered) was composed mostly of appendicular skeleton characters, with a few characters from the axial skeleton. For a detailed account of these characters, see Casali *et al.* (2022). The complete dataset is available in the Dryad Digital Repository (Casali *et al.* 2023).

Partitions were pruned of outgroups and of sloth taxa that were associated with incalculable distances (due to the absence of at least a single character coded for a given pair of taxa). For evaluating the minimum number of taxa to be removed, we calculated the maximum observable rescaled distance (MORD) with functions *calculate_morphological_distances* and *trim_matrix* in the R package Claddis v.0.6.3 (Lloyd 2016) in the R programming environment (v.4.2.0; R Core Team 2013). This distance metric produced higher fidelity in simulations considering datasets with intermediate amounts of missing data and including ordered characters (Lloyd 2016), as is the case with our dataset. Also, we removed taxa that presented a 75% or higher proportion of missing data in at least one of the two partitions (Table S1). Preliminary explorations showed that most taxa with this high level of missing data were artificially displaced to extreme values along the axes of the morphospace, which resulted in their isolation from all other data points, even from those similar in character coding. In both cases, if a taxon was removed from one partition, it was also removed from the other, ensuring that results of partitions were fully comparable. The resulting datasets included 41 taxa, with at least one representative of all major groups recognized in the classification of Casali *et al.* (2022), which is herein considered as the preferred systematic hypothesis.

As a reference tree, we adopted the Bayesian chronogram from the best-fitting model of Casali *et al.* (2022), pruned to match the taxonomic sample of the present dataset (Fig. 1). The complete tree is available in Dryad Digital Repository (Casali *et al.* 2023).

Definition of clades and ecological groups

To study the influence of historical factors in the morphological evolution of Folivora, we applied two different phylogenetic division schemes for sloths: (1) less inclusive clades, Scelidotheriidae, Mylodontidae, Megatheriidae and Megalonychidae; and (2) more inclusive clades, Mylodontoidea and Megatherioidea (Fig. 1).

Dietary and locomotory categories were obtained from the literature (Tables S2, S3). To classify taxa that were not previously evaluated, we applied the same criteria used by studies which investigated morphologically similar and phylogenetically related taxa. We worked with

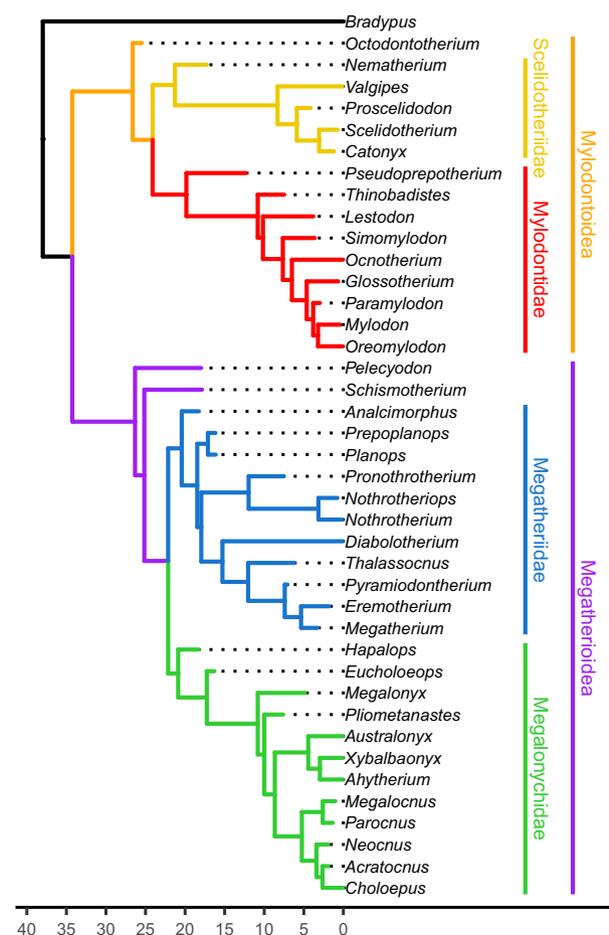


FIG. 1. Bayesian chronogram from (Casali *et al.* 2022), pruned for the taxonomic sample evaluated in the current study. Clades considered during analyses are named and coloured.

general but still biologically meaningful ecological categories, avoiding overly small groups, which could affect the precision of estimates of morphological disparity (Lloyd 2016; Gerber 2019).

For dietary categorization, we relied on previous classifications that considered evidence from anatomical features of the muzzle and mandibular spout, as well as overall tooth morphology and dental wear patterns. More rarely, data from masticatory musculature reconstructions and palaeofaecal content was available, and was also considered. Since there are considerable disagreements among classifications stemming from alternative sources of evidence for taxa associated with mixed feeding and grazing, we considered both diets in a single category (mixed/grazer), whereas all other folivorans were classified as browsers.

We assigned sloth taxa to one of two locomotory categories: scansorial and terrestrial. These assignments were also informed by literature that applied anatomical and morpho-functional inferences to assess locomotory habits in sloths. We considered both the living fully arboreal and the extinct semi-arboreal sloths as scansorial. This category was also applied to *Diabolootherium* Pujos, which presents climbing adaptations probably unrelated to arboreal substrates (Pujos *et al.* 2011). All the other taxa possessing terrestrial (= ambulatory) adaptations were grouped together in a single category, irrespective of substrate use. When different species of a genus differed in their locomotory adaptations, as is the case for *Thalassocnus* Muizon & McDonald, we assigned the genus the primitive condition, to avoid introducing categories that would include only one or a couple of taxa, which could make quantitative analyses impossible.

Morphological disparity

For each partition, we inferred character ancestral states with the function *estimate_ancestral_states* in the R package Claddis, only inferring nodes with observed states for both descendants, whereas tip states were not inferred. Ancestral states for inapplicable characters were also not estimated, and polymorphic states were considered equally probable. The threshold used to collapse ancestral states to the most probable state was kept at the default value (= 0.01), meaning that any minor preference (1% of the marginal likelihoods) for the best supported state (or states within this threshold) relative to the alternatives will be taken as evidence of this state being present at the given node. As discussed in Casali *et al.* (2022), higher threshold values may be more conservative, but it is unclear which value should be used and how they must be adjusted according to the number of states observed in each character. Then we calculated morphological distances of discrete characters with

MORD (Lloyd 2016), applying an arcsine square root transformation with the function *calculate_morphological_distances*, in Claddis. Polymorphisms were evaluated using their minimum distances, inapplicable characters were treated as missing, and character dependencies were disregarded. With the distances obtained, we conducted principal coordinate analyses (PCoA) with the function *pcoa* available in the R package *ape* (v.5.6.2; Paradis & Schliep 2019), applying a Cailliez correction for negative eigenvalues (Cailliez 1983). The first two PCoA axes were used for plotting graphs to visualize the data, but disparity analyses were conducted considering all 79 axes. Estimated ancestors were included in the phylomorphospace visualizations, but were not shown in non-phylogenetic morphospaces and were removed from disparity analyses.

Disparity for dietary category groups was investigated using the cranial partition exclusively, whereas for locomotory categories, only data from postcranial characters were considered. Before calculating the disparity index, we performed 1000 bootstrap replications for each group, rarefying the samples according to the size of the smallest group involved in each comparison, to ensure that differences in sample sizes were not affecting results. Disparity was assessed with the widely used sum of variances (SV) metric, which is relatively insensitive to outliers and a good descriptor of changes in space occupancy (Guillaume *et al.* 2020), and not much affected by moderate differences in group sizes and levels of missing data (Ciampaglio *et al.* 2001; Hopkins & Gerber 2017). To assess significance in disparity differences between groups, we applied a two-sided Wilcoxon rank-sum test (Wilcoxon 1945), with $\alpha = 0.01$. In cases of multiple comparisons, a Holm–Bonferroni *p*-value correction was used (Holm 1979). To evaluate the degree of overlap among distributions of SV values obtained from bootstrapped data for each group, we applied the Bhattacharyya coefficient (BC; Bhattacharyya 1946). Those calculations and tests were conducted in R package *dispRity* (v.1.7.0; Guillaume 2018), with functions *custom.subsets*, *boot.matrix*, *dispRity* and *test.dispRity*.

Ancestral state estimations and phylogenetic signal of ecological characters

To be able to associate ecological categories with all branches of the tree for subsequent rate analyses, we estimated the ancestral diet and locomotion for all nodes of the tree. We estimated ancestral states with the R package *corHMM* (v.2.8; Beaulieu *et al.* 2021), using marginal inferences (Joy *et al.* 2016). We fitted alternative versions of the Mk model (Pagel 1994; Lewis 2001), considering the equal rates (ER) and all rates different (ARD) models of among-state rate heterogeneity (Paradis *et al.* 2004),

and evaluated the presence of one or two rate regimes across branches (Beaulieu *et al.* 2013), resulting in four alternative models for each ecological character (ER1, ER2, ARD1 and ARD2).

Those models were compared using sample size corrected Akaike information criteria (AICc) and Akaike weights (AICw) (Burnham & Anderson 2002). Following Harmon (2018), a best-fitting model was only considered if there was a difference of at least four AICc units between it and the next best-fitting model; we also required an AICw value greater than 0.9. Otherwise, the less parametrized model was applied irrespective of its relative fit (Harmon 2018). We also investigated the phylogenetic signal of ecological characters using the D statistic (Fritz & Purvis 2010), calculated by function *phylo.d* in the R package *caper* (v.1.0.1; Orme *et al.* 2018). Values of D less than or equal to 0 relate to a strongly clumped distribution of character states in the tree, indicating a strong phylogenetic signal, with 0 being the value expected when characters evolved by a Brownian motion process. Values between 0 and 1 suggest a progressively weaker signal, with 1 indicating that characters evolved according to a stochastic process obtained by randomly permutating the data across the tips. Finally, values greater than 1 indicate an overdispersion of character states in the phylogeny, beyond random expectation. Significance was assessed relative to Brownian motion and a random pattern obtained using 10 000 permutations of the tip values.

Morphological convergence

We evaluated the statistical support for four hypotheses of morphological convergence considered here, based on patterns observed in the phylomorphospace and the morphological adaptations shared by taxa which are not closely related in our reference tree. For the cranial dataset, we evaluated the hypotheses of convergence among *Bradypus*, stem megatherioids and Megatheriidae, and of convergence among *Choloepus* and Mylodontinae taxa. For the postcranial dataset, we tested for convergence among taxa with adaptations to a pedolateral stance, including taxa showing fully pedolateral morphologies and those with incipient modifications, and the convergence among taxa showing scansorial adaptations. We considered data from the first two principal coordinates for each terminal taxon and ancestral node, since these were the same axes applied to construct the phylomorphospace, but also because the other axes accounted for a much smaller fraction of the total morphological variance (see Results).

The hypotheses of convergence were tested with the function *search.conv* in the R package *RRphylo* (v.2.7.0;

Castiglione *et al.* 2018, 2019). This function calculates the angle (θ) between vectors of multivariate phenotypes for each pair of species associated with the convergent state, and return a mean θ for all pairwise comparisons. Then it compares the empirical mean θ to a random distribution of θ values. If the mean empirical θ is smaller than random θ values, this is taken as evidence of convergence. Angles are calculated both disregarding and considering the temporal distances among taxa informed by the branch lengths in the chronogram. Significance was assessed comparing the mean empirical θ with 1000 samples taken from a distribution obtained after 1000 random permutations of tip values, with $\alpha = 0.05$. In order to avoid false positives due to putatively convergent taxa showing a phylogenetic proximity greater than that expected by chance, the *declust* option was applied.

Morphological evolutionary rates

Branch rates were evaluated with the function *test_rates* in Claddis, which first estimates ancestral states for all morphological characters. Subsequently, this method considers the number of changes observed on each branch, calculated over the product of the branch duration (in millions of years) and the number of characters that can be observed at both ends of this given branch, controlling for missing data (Lloyd 2016). Ancestral states were estimated by applying the same settings as those used in the disparity analyses, and for branch rate calculations, all polymorphic, uncertain and inapplicable states were considered missing.

To test the influence of historical factors on morphological evolutionary rates, we considered models with one to five rate regimes for each partition, totalling 18 alternative models: (1) a null model, with no rate differences among groups (one rate regime); (2) six individual clade models (same clades as in disparity analyses), comparing the focal clade average morphological evolutionary rate relative to a background average rate comprised of the rates of all other branches not associated with the focal clade (two rate regimes); (3) six models assuming that two of the less inclusive clades had distinct rates from the background (three rate regimes); (4) four models assuming that three of the less inclusive clades had distinct rates from the background (four rate regimes); and (5) a model considering distinct average rates for each less inclusive clade, plus a background average rate (five rate regimes). To evaluate the influence of ecological factors, we applied a model assigning branches associated with the derived ecological category an average rate different from those associated with the primitive state (two rate regimes). Finally, to evaluate the influence of convergent morphologies in morphological evolutionary rates, we

assigned four models comparing convergent with non-convergent taxa (two rate regimes), two for each partition. The fit of these models to the data was evaluated with AICc and AICw, using the same thresholds as defined above. For the cranial partition, we should note that Mylodontoidea and the diet rate regimes are identical, and for the postcranial partition, the rate regimes associated with the locomotory categories and the convergent scansorial taxa are also the same, but were included for the sake of completeness. To allow comparison among partitions, branch rates (i.e. the number of character changes per million years) were normalized by their respective partition size.

Plots were produced using R packages phytools (v.1.2.0; Revell 2012), ggplot2 (v.3.3.6; Wickham 2016), ggphylo (v.0.2; Barr 2017), ggtree (v.3.4.0; Yu *et al.* 2017), ggpubr (v.0.4.0; Kassambara 2020), ggrepel (v.0.9.1; Slowikowski 2021) and deeptime (v.0.2.3; Gearty 2021). An R script to fully reproduce all analyses employed in this study, a modified version of the function *ggphylo* and a file associating each branch of the chronogram with phylogenetic, ecological and convergence categories is available in Casali *et al.* (2023).

Abbreviations. AICc, sample size corrected Akaike information criteria; AICw, Akaike weights; ARD, all rates different; BC, Bhattacharyya coefficient; ER, equal rates; MORD, maximum observable rescaled distance; PCoA, principal coordinate analysis; SV, sum of variances.

RESULTS

Overall phylomorphospace patterns

As is usual for morphospaces/phylomorphospaces obtained from discrete morphological characters (Gerber 2019), especially when PCoA analyses are performed applying corrections for negative eigenvalues, the variance explained by each axis is quite modest. For cranial data, PCo1 explained 22.93% of the variance, and PCo2 13.24% (Fig. 2A). For postcranial data, PCo1 was responsible for 9.48% of the variance, whereas for PCo2, 4.38% was explained (Fig. 2B). PCoA eigenvalues and eigenvectors are available in Casali *et al.* (2023).

For the cranial partition, the first axis of phylomorphospace provided evidence of a clear separation between megatherioid and mylodontoid sloths (Fig. 2A). In this axis, *Bradypus* was closely associated with stem megatherioids and to a lesser extent, to Megatheriidae (Fig. 2A), and the test of cranial convergence associated with this pattern was statistically significant (Table S4). The other living genus, *Choloepus*, although clearly associated with

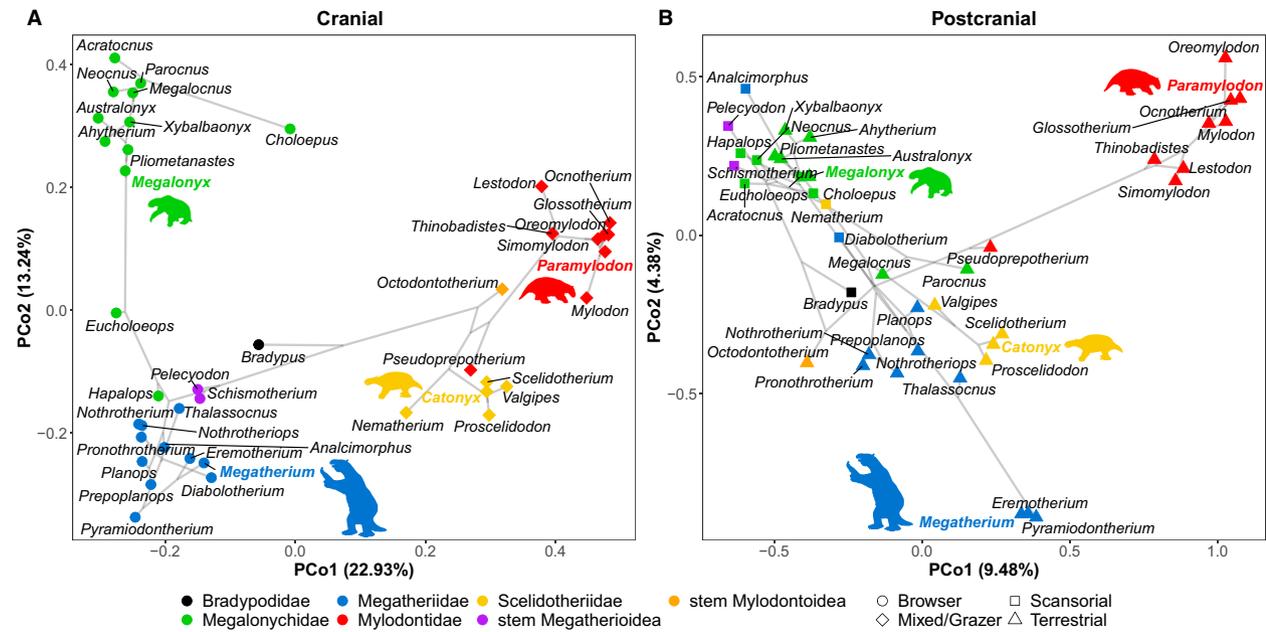


FIG. 2. Phylomorphospaces depicting the first two axes of the principal coordinate analyses. A, cranial partition. B, postcranial partition. Silhouettes indicate representatives of less inclusive clades with names indicated in bold colour ((*Catonyx* (*Scelidodon*), *Paramylodon harlani* and *Megatherium*, all from <http://phylopic.org>, artist Zimices (CC BY-NC 3.0), modified; *Megalonyx wheatleyi* created by DC after the illustration by ДибГД (CC BY-SA 4.0; https://commons.wikimedia.org/wiki/File:Megalonyx_wheatleyi12.jpg).

megalonychids in phylomorphospace, was somewhat separated from the other genera of this clade and displaced towards higher values of PCo1, a region of the phylomorphospace occupied by mylodontines (Fig. 2A). This pattern was also associated with a statistically significant result in the test of morphological convergence (Table S4). Both living genera occupy a central position in PCo1, between megatherioids and mylodontoids. PCo2 roughly separates the Megalonychidae from Megatheriidae and Mylodontidae from Scelidotheriidae, although stem members of some of those clades were associated with the clusters of other clades (Fig. 2A). Among megatherioids, the stem genera *Pelecypodon* Ameghino and *Schismotherium* Ameghino, as well as the stem megalonychids *Hapalops* Ameghino and *Euchloeops* Ameghino, were placed closer to megatheriids. For mylodontoids, the stem genus *Octodontotherium* Ameghino was associated with mylodontids, whereas *Pseudopreotherium* Hoffstetter, a stem mylodontid, was closely associated with scelidotheriids (Fig. 2A). These cases are suggestive of the retention of an ancestral morphology, according to the disposition of the branches in the phylomorphospace.

For the postcranial partition, three major clusters could be recognized. There was a main group encompassing most sloths sampled here, with representatives from all less inclusive clades. The first axis separated this major group from Mylodontinae, which grouped far away due to highly positive values for PCo1, whereas PCo2 separated both clusters from Megatheriini (Fig. 2B). In the

first group, there was some spatial structure associated with less inclusive clades, despite some noticeable exceptions, like the association of the stem megatheriid *Analcimorphus* Ameghino, stem megatheriine *Diabolootherium*, and the stem scelidotheriid *Nematherium* Ameghino with megalonychids (Fig. 2B). The stem megatherioids *Schismotherium* and *Pelecypodon* were also situated close to megalonychids (Fig. 2B). The hypothesis suggesting that taxa with scansorial adaptations converged in their postcranial morphology was supported, being statistically significant (Table S4). The proximity to scelidotheriines of less derived megatheriids, of the megalonychids *Parocnus* Miller and *Megalocnus* Leidy, and of the stem mylodontid *Pseudopreotherium*, is suggestive of morphological convergence, with their branches approximating the central region of the phylomorphospace (Fig. 2B). Testing if these and other taxa associated with pedolaterality would have converged in their postcranial morphology yielded a statistically significant result (Table S4). The living genus *Bradypus* was placed between scansorial megalonychids and the terrestrial nothrotheriines, preotheriines and *Octodontotherium* in the postcranial phylomorphospace.

Morphological disparity

Bootstrapped and rarefied disparity estimates were very similar to those obtained for the original data, with little impact on the estimated sum of variances (Table 1). We

TABLE 1. Morphological disparity of clades and ecological groups in each partition.

Partition	Group	Sample size	SV (Obs.)	Median (BS)	CI (BS)
Cranial	Megatheriidae	11	0.33	0.30	0.24–0.32
Cranial	Megatheriidae	5	–	0.31	0.20–0.35
Cranial	Megalonychidae	12	0.31	0.29	0.24–0.32
Cranial	Megalonychidae	5	–	0.29	0.19–0.35
Cranial	Myodontidae	9	0.23	0.21	0.15–0.25
Cranial	Myodontidae	5	–	0.21	0.12–0.27
Cranial	Scelidotheriidae	5	0.18	0.16	0.06–0.19
Cranial	Megatherioidea	25	0.37	0.36	0.33–0.38
Cranial	Megatherioidea	15	–	0.36	0.32–0.39
Cranial	Myodontoidae	15	0.28	0.27	0.23–0.29
Cranial	Browser	26	0.38	0.36	0.33–0.39
Cranial	Browser	15	–	0.36	0.32–0.40
Cranial	Mixed/Grazer	15	0.28	0.27	0.23–0.29
Postcranial	Megatheriidae	11	3.31	3.03	2.67–3.22
Postcranial	Megatheriidae	5	–	3.03	2.21–3.45
Postcranial	Megalonychidae	12	2.99	2.76	2.45–2.93
Postcranial	Megalonychidae	5	–	2.78	2.07–3.14
Postcranial	Myodontidae	9	2.87	2.58	2.07–2.82
Postcranial	Myodontidae	5	–	2.57	1.83–3.01
Postcranial	Scelidotheriidae	5	2.94	2.45	1.29–2.94
Postcranial	Megatherioidea	25	3.23	3.11	2.94–3.22
Postcranial	Megatherioidea	15	–	3.11	2.88–3.25
Postcranial	Myodontoidae	15	3.25	3.05	2.77–3.22
Postcranial	Scansorial	11	2.96	2.71	2.35–2.91
Postcranial	Terrestrial	30	3.39	3.28	3.18–3.35
Postcranial	Terrestrial	11	–	3.29	3.04–3.44

Observed sum of variances (SV (Obs.)) do not apply to rarefied samples. Median and confidence interval (CI) values for bootstrapped and rarefied data (BS).

considered the bootstrapped and rarefied data in the following results.

Among the less inclusive clades, there was a clear separation along the first two axes of morphospace when cranial data was considered (Fig. 3A). The median disparity was greater for Megatheriidae, followed by Megalonychidae, Myodontidae, and Scelidotheriidae (Fig. 3A; Table 1). All pairwise comparison among their disparity distributions were found to be statistically significant (Table 2). Despite that, the first two axes of morphospace indicated a broader range of values for Megalonychidae relative to that of Megatheriidae (Fig. 3A), although there was considerable overlap in the disparity of those two clades (Fig. 3A; Tables 1, 2). There was also moderate overlap in the disparity of Scelidotheriidae and Myodontidae (Fig. 3A; Tables 1, 2). On the other hand, the degree of overlap for disparity among less inclusive clades pertaining to different, more inclusive clades, was much smaller (Fig. 3A; Tables 1, 2).

Morphospace occupancy of Megatherioidea was greater than that of Myodontoidae when we consider the cranial partition, and those clades occupy clearly distinct morphospace regions (Fig. 3B; Table 1). Their disparity

difference was statistically significant and there was a clear lack of overlap between the two distributions (Fig. 3B; Table 2).

For dietary categories, the results were almost identical to those observed for more inclusive clades in the cranial partition, given the high similarity among those groupings. Browsers, including *Bradypus* and all megatherioids, occupy a distinct region of the morphospace and showed greater disparity relative to mixed feeders/grazers (Fig. 3C; Table 1). Estimated disparity values did not overlap and dietary groups were significantly different from one another (Fig. 3C; Tables 1, 2).

For the postcranial partition, the morphospace yielded a much greater superposition among less inclusive clades, with only Myodontidae being well-separated from the others (Fig. 3D). The values for median disparity follow the same order as those observed for cranial data, and group differences were also statistically significant (Fig. 3D; Tables 1, 2). In contrast to the pattern observed for cranial data, the degree of overlap among estimates of postcranial disparity in Megalonychidae relative to that in Megatheriidae was only moderate, whereas that of Scelidotheriidae and Myodontidae was much greater (Fig. 3D;

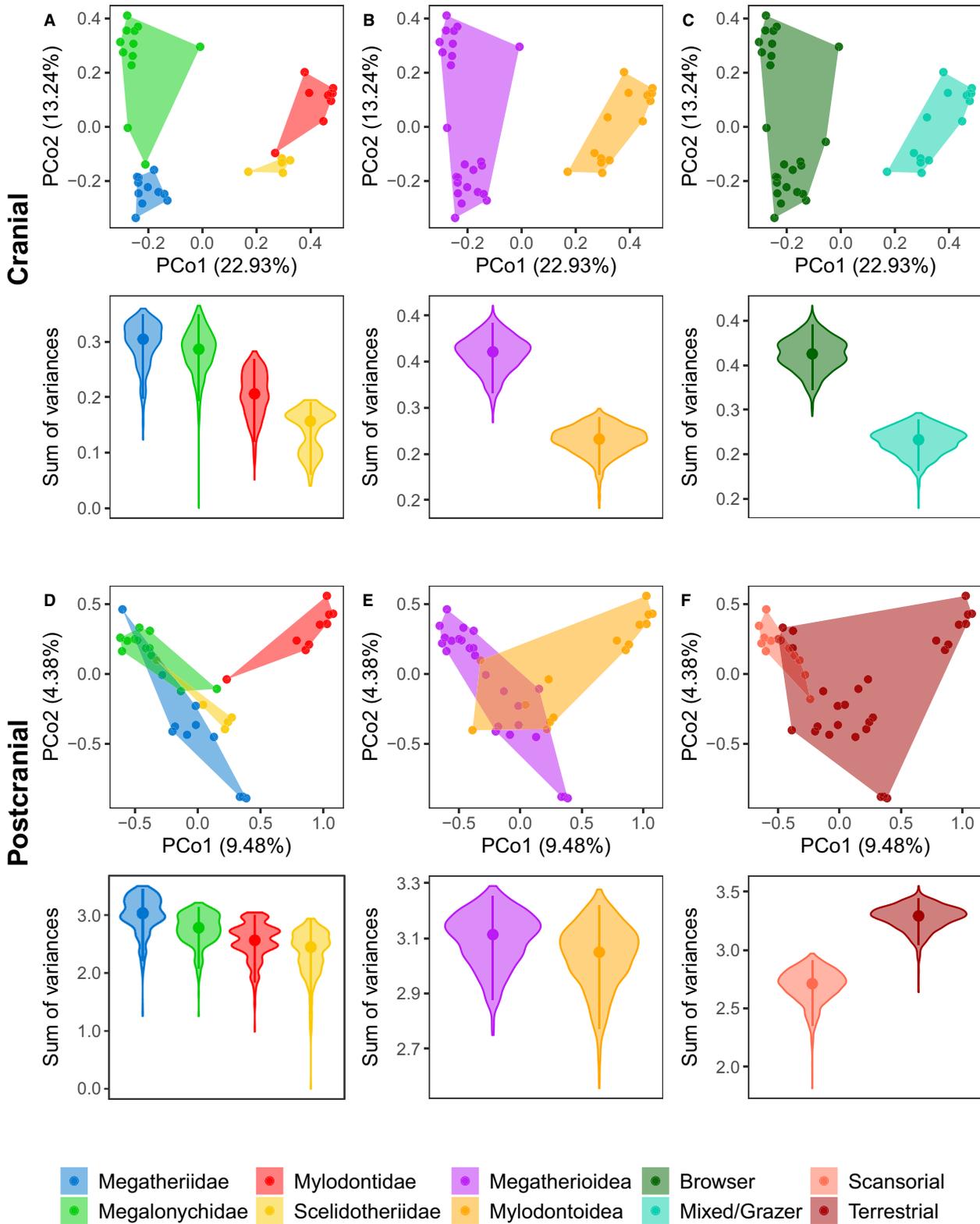


FIG. 3. Morphospace occupancy (first two PCoA axes) and morphological disparity (sum of variances) for sloths. A–C, cranial partition: A, less inclusive clades (Scelidotheriidae, Mylodontidae, Megatheriidae and Megalonychidae); B, more inclusive clades (Mylodontoidea and Megatherioidea); C, dietary categories, browser and mixed/grazer). D–F, postcranial partition: D, less inclusive clades; E, more inclusive clades; F, locomotory categories, scansorial and terrestrial.

TABLE 2. Overlap of morphological disparity for pairs of clades and ecological groups in each partition.

Partition	Groups	<i>p</i> -value	BC
Cranial	Megatheriidae Megalonychidae	<0.001	0.91
Cranial	Megatheriidae Mylodontidae	<0.001	0.15
Cranial	Megatheriidae Scelidotheriidae	<0.001	0.01
Cranial	Megalonychidae Mylodontidae	<0.001	0.16
Cranial	Megalonychidae Scelidotheriidae	<0.001	0.00
Cranial	Mylodontidae Scelidotheriidae	<0.001	0.52
Cranial	Megatherioidea Mylodontoidea	<0.001	0.00
Cranial	Browser Mixed/Grazer	<0.001	0.00
Postcranial	Megatheriidae Megalonychidae	<0.001	0.52
Postcranial	Megatheriidae Mylodontidae	<0.001	0.30
Postcranial	Megatheriidae Scelidotheriidae	<0.001	0.30
Postcranial	Megalonychidae Mylodontidae	<0.001	0.80
Postcranial	Megalonychidae Scelidotheriidae	<0.001	0.57
Postcranial	Mylodontidae Scelidotheriidae	<0.001	0.82
Postcranial	Megatherioidea Mylodontoidea	<0.001	0.90
Postcranial	Scansorial Terrestrial	<0.001	0.00

p-value for the Wilcoxon rank-sum test. BC, Bhattacharyya coefficient.

Tables 1, 2). Unlike cranial disparity, postcranial estimates of the sum of variance for Megalonychidae showed a moderate overlap with those obtained for Scelidotheriidae, and a greater similarity with the disparity observed for Mylodontidae (Fig. 3D; Tables 1, 2). On the other hand, the distribution of sum of variances for Megatheriidae presented only a small overlap with those of Scelidotheriidae and Mylodontidae, as also observed for the cranial partition (Fig. 3D; Tables 1, 2).

More inclusive clades showed a partial overlap in postcranial morphospace, with both groups having similar degrees of morphological disparity (Fig. 3E; Table 1). The difference between the disparities of these clades was statistically significant, despite their extensive overlap (Fig. 3E; Table 2).

Locomotory categories presented only a small overlap in morphospace, with terrestrial locomotory habits associated with a much greater disparity than that observed for scansorial sloths (Fig. 3F; Table 1). The disparity of the locomotory categories were significantly different and showed no overlap in disparity values (Fig. 3F; Tables 1, 2).

Ancestral states and phylogenetic signal

For both ecological traits, no model fulfilled the criteria defined *a priori* to consider it better fitted than the closest alternatives. Hence, model ER1 was applied because it was the less parametrized model tested here (Table S5).

The ancestral diet of Folivora was inferred as browsing, which was then maintained in Eufolivora and in all

Megatherioidea (Fig. 4A). The ancestor of Mylodontoidea and all nodes within this clade were estimated as mixed feeder/grazers (Fig. 4A). The D statistic ($D = -1.10$) indicates a very clumped distribution for this trait, which suggests a strong phylogenetic signal more extreme than, but still consistent with, the expectations of Brownian motion ($p = 0.99$), and significantly different from a random pattern ($p < 0.01$).

Scansorial habits were, most probably, the ancestral sloth locomotory adaptation. This was also inferred as the ancestral locomotory mode for the ancestors of Eufolivora, Megatherioidea, Megatheriidae and Megalonychidae (Fig. 4B). Three independent origins of terrestrial adaptations were observed, in Mylodontoidea, Megatheriidae minus *Analcimorphus*, and Megalonychinae (Fig. 4B). Reversions to scansorial habits evolved independently in *Nematherium*, *Diabolotherium*, and in the ancestor of the clade uniting *Choloepus*, *Acratocnus* Anthony and *Neocnus* Arredondo (Fig. 4B). The D statistic for this character ($D = 0.10$) suggested a relatively weak phylogenetic signal, not being significantly different from a pattern resulting from a Brownian motion ($p = 0.43$), but significantly different from a pattern obtained from random permutations of the data ($p < 0.01$).

Morphological evolutionary rates

Overall cranial and postcranial evolutionary rates were extremely similar, despite showing slightly different distributions (Fig. 5; Tables 3, 4). The average cranial rates of Mylodontoidea, Scelidotheriidae and Mylodontidae were lower than their respective background evolutionary rates, whereas those of Megatherioidea, Megatheriidae and Megalonychidae were higher than the background (Fig. 5; Table 3). Comparing the less inclusive clades among themselves, Megalonychidae presented a higher average morphological evolutionary rate, followed by Megatheriidae, Mylodontidae and Scelidotheriidae, and among more inclusive clades, Megatherioidea showed a higher evolutionary rate than Mylodontoidea (Fig. 5; Table 3). Among dietary categories, mixed feeders/grazers showed a lower morphological evolutionary rate than browsers (Fig. 5; Table 3), consistent with disparity results. The set of taxa associated with the convergence hypothesis uniting *Bradypus*, stem megatherioids and Megatheriidae showed lower rates relative to all other taxa, whereas for the other hypothesis, the convergent group composed of *Choloepus* and Mylodontinae were associated with a higher evolutionary rate relative to that of the remainder of sloths.

For postcranial data, clade evolutionary rates showed the same relationship to background rates as those recovered for cranial evolutionary rates, with the exception of Scelidotheriidae, which presented a slightly higher average

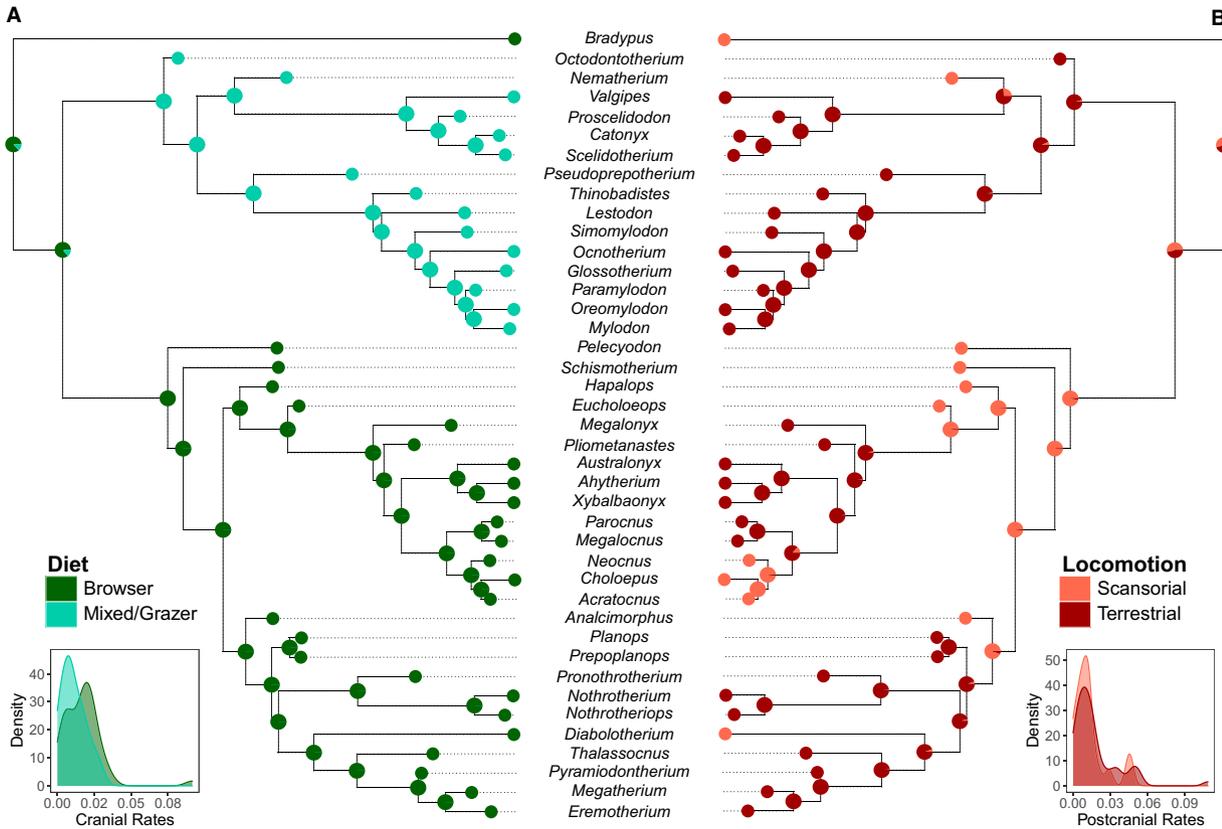


FIG. 4. Ancestral state estimations of ecological habits in Folivora. A, diet. B, locomotion. In each case, the respective distributions of morphological evolutionary rates are depicted below: cranial partition for dietary habits and postcranial partition for locomotion.

rate than the average rate of all other branches, and Mylodontoidea, which presented an average evolutionary rate similar to the background rate (Fig. 5; Table 4). Megatheriidae and Megalonychidae exhibited very similar postcranial evolutionary rates, and both showed higher rates than those observed for Mylodontidae and Scelidotheriidae (Fig. 5; Table 4). Also, Megatherioidea yielded a higher average postcranial evolutionary rate than Mylodontoidea (Fig. 5; Table 4). Sloths with terrestrial locomotory habits were associated with faster postcranial evolution than those with scansorial adaptations (Fig. 5; Table 4), aligned with the greater disparity exhibited by terrestrial sloths. The same pattern can be observed comparing taxa associated with pedolateral adaptations to all other sloths (Fig. 5; Table 4).

The best-fitting rate model for the cranial partition was associated with four rate categories, contrasting the evolutionary morphological rates of Megatheriidae, Megalonychidae and Mylodontidae with that of the remaining branches, followed by the FULL model, contrasting all four less inclusive clades with the background rate, together summing more than 0.9 of AICw (Table 3). For the postcranial partition, the best-fitting model was the FULL model (Table 4). Only in the case of the postcranial

partition, differences in AICc greater than 4 units and AICw greater than 0.9 indicated that the best-fitting model was clearly preferred relative to alternative rate models. Nevertheless, for both partitions, models associated with historical factors were preferred relative to those associated with ecological adaptations and convergent morphologies, and also relative to the NULL model with a single global rate across all branches (Tables 3, 4).

DISCUSSION

Discrete character matrices offer several advantages when comparing the morphology of fragmentary and incomplete taxa (Oyston *et al.* 2015, 2016; Schaeffer *et al.* 2020). Although Folivora as a whole possesses an outstanding fossil record, including several complete taxa, especially over the last 20 myr (Scott 1903; Stock 1925; Cartelle & Fonseca 1983; Cartelle *et al.* 2009; De Iuliis *et al.* 2016; Boscaini *et al.* 2021), it is nevertheless a clade mostly comprised of extinct taxa, many of which are missing some anatomical information. Discrete character matrices allow minimization of the loss of information in incomplete taxa, while retaining strong historical signals, since

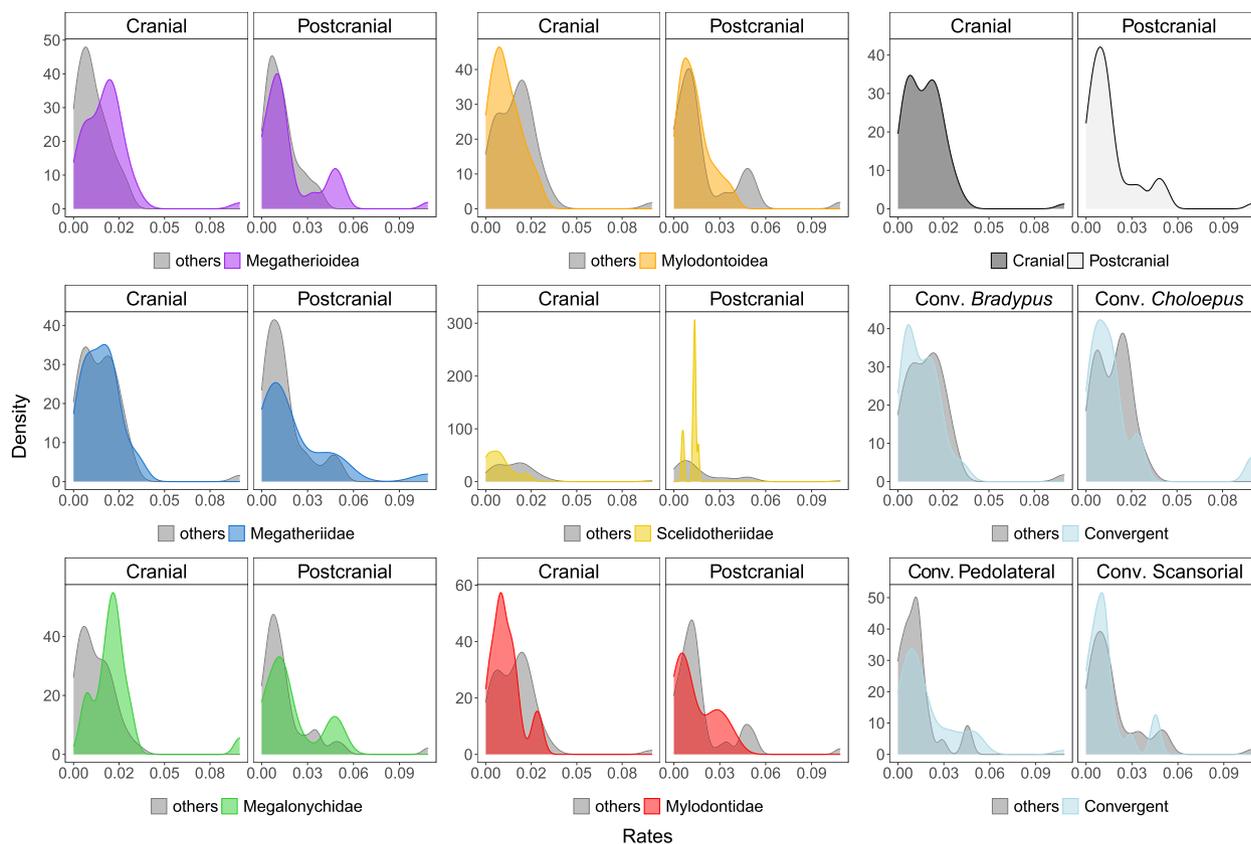


FIG. 5. Morphological evolutionary rates for cranial and postcranial partitions. Clade rates are compared to the background rate (others), and rates of morphological evolution for taxa associated with convergent morphologies are compared with these of non-convergent taxa. *Conv. Bradypus* illustrates convergence among *Bradypus*, stem megatherioids and Megatheriidae; *Conv. Choloepus*, convergence among *Choloepus* and Mylodontinae; ‘Conv. Pedolateral’ and ‘Conv. Scansorial’ compare taxa associated with these respective adaptive morphologies to those without them.

they are usually constructed with the goal of inferring phylogeny (Anderson & Friedman 2012). On the other hand, morphometric data is more closely associated with functional morphology and adaptive evolution (Anderson & Friedman 2012; Schaeffer *et al.* 2020). Nevertheless, previous studies performed on different taxonomic groups yielded congruent disparity patterns from cladistic and morphometric data (Anderson & Friedman 2012; Hetherington *et al.* 2015; Romano *et al.* 2017; Schaeffer *et al.* 2020; but see Mongiardino Koch *et al.* 2017). For rate analyses, on the other hand, discrete characters are particularly useful, since methods of ancestral state estimations are usually employed to infer branch evolutionary rates. Those methods are much better developed for discrete, rather than continuous characters (Soul & Wright 2021), and ancestral states estimates are often improved when fossil taxa are included in the taxonomic sample (Puttick 2016).

In the present study, cranial data exhibited disparity patterns and morphological evolutionary rates clearly associated with the phylogenetic structure represented by

the less inclusive sloth clades. The first two axes of the phylomorphospace were highly informative for distinguishing these groups (Fig. 2A). The few exceptions to this clear phylogenetic pattern involved stem members of Megalonychidae and Mylodontidae, which are taxa known for retaining many primitive cranial characters in their respective clades (Gaudin 2004; Boscaini *et al.* 2019; Casali *et al.* 2022).

According to morphological phylogenies, *Choloepus* is closely related to the Antillean megalonychid taxa, whereas Bradypodidae is the sister taxon of all other sloths (Gaudin 2004; Varela *et al.* 2019; Casali *et al.* 2022). Nevertheless, it is worth noting that the proximity of *Bradypus* to megatherioids, and to a lesser extent, the displacement of *Choloepus* toward the region occupied by mylodontoids in morphospace, echoes their phylogenetic associations as recovered in recent molecular investigations including extant and extinct sloths (Slater *et al.* 2016; Delsuc *et al.* 2019; Presslee *et al.* 2019). If these molecular studies are taken at face value, this may indicate that morphology may also carry some phylogenetic signal for

TABLE 3. Model fit for each hypothesis of rate categories in the cranial partition.

Partition	Model	Rates	Focal	Backgr.	AICc	AICw
Cranial	NULL	1	0.012	0.012	862.14	0.00
Cranial	Megalonychidae (ML)	2	0.023	0.010	728.39	0.00
Cranial	Megatheriidae (MG)	2	0.013	0.012	863.99	0.00
Cranial	Scelidotheriidae (SC)	2	0.007	0.013	837.62	0.00
Cranial	Myodontidae (MY)	2	0.011	0.013	861.47	0.00
Cranial	Megatherioidea	2	0.016	0.009	786.25	0.00
Cranial	Myodontoidea	2	0.010	0.013	851.23	0.00
Cranial	ML_MG	3	0.023, 0.013	0.009	713.24	0.01
Cranial	ML_SC	3	0.023, 0.007	0.010	722.18	0.00
Cranial	ML_MY	3	0.023, 0.011	0.010	728.36	0.00
Cranial	MG_SC	3	0.013, 0.007	0.013	839.57	0.00
Cranial	MG_MY	3	0.013, 0.011	0.013	863.62	0.00
Cranial	SC_MY	3	0.007, 0.011	0.014	833.18	0.00
Cranial	ML_MG_SC	4	0.023, 0.013, 0.007	0.009	712.01	0.02
Cranial	ML_MG_MY	4	0.023, 0.013, 0.011	0.008	705.26	0.68
Cranial	ML_SC_MY	4	0.023, 0.007, 0.011	0.010	723.72	0.00
Cranial	MG_SC_MY	4	0.013, 0.007, 0.011	0.014	833.82	0.00
Cranial	FULL	5	0.023, 0.013, 0.007, 0.011	0.008	707.00	0.28
Cranial	DIET	2	0.010	0.013	851.23	0.00
Cranial	CONV. <i>Bradypus</i>	2	0.010	0.015	825.78	0.00
Cranial	CONV. <i>Choloepus</i>	2	0.016	0.012	849.27	0.00

Focal rates (Focal) refer to groups in the column 'model' and the background rates (Backgr.) for the remaining branches. Rates measured as the number of character changes per million years, standardized by the partition size.

TABLE 4. Model fit for each hypothesis of rate categories in the postcranial partition.

Partition	Model	Rates	Focal	Backgr.	AICc	AICw
Postcranial	NULL	1	0.012	0.012	542.63	0.00
Postcranial	Megalonychidae (ML)	2	0.017	0.011	533.07	0.00
Postcranial	Megatheriidae (MG)	2	0.017	0.011	532.41	0.00
Postcranial	Scelidotheriidae (SC)	2	0.013	0.012	544.70	0.00
Postcranial	Myodontidae (MY)	2	0.012	0.013	544.33	0.00
Postcranial	Megatherioidea	2	0.014	0.010	533.86	0.00
Postcranial	Myodontoidea	2	0.012	0.012	544.71	0.00
Postcranial	ML_MG	3	0.017, 0.017	0.010	513.26	0.00
Postcranial	ML_SC	3	0.017, 0.013	0.011	534.48	0.00
Postcranial	ML_MY	3	0.017, 0.012	0.011	535.16	0.00
Postcranial	MG_SC	3	0.017, 0.013	0.011	533.60	0.00
Postcranial	MG_MY	3	0.017, 0.012	0.011	534.39	0.00
Postcranial	SC_MY	3	0.013, 0.012	0.013	546.49	0.00
Postcranial	ML_MG_SC	4	0.017, 0.017, 0.013	0.009	509.88	0.00
Postcranial	ML_MG_MY	4	0.017, 0.017, 0.012	0.008	509.92	0.00
Postcranial	ML_SC_MY	4	0.017, 0.013, 0.012	0.011	536.43	0.00
Postcranial	MG_SC_MY	4	0.017, 0.013, 0.012	0.011	535.28	0.00
Postcranial	FULL	5	0.017, 0.017, 0.013, 0.012	0.006	497.43	0.99
Postcranial	LOCOMOTION	2	0.015	0.008	516.25	0.00
Postcranial	CONV. Pedolateral	2	0.015	0.008	510.75	0.00
Postcranial	CONV. Scansorial	2	0.008	0.015	516.25	0.00

Focal rates (Focal) refer to groups in the column 'model' and the background rates (Backgr.) for the remaining branches. Rates measured as the number of character changes per million years, standardized by the partition size.

placing *Bradypus* among megatherioids and *Choloepus* among mylodontoids. That said, morphospaces depict phenetic and not phylogenetic distances; hence, those patterns are also fully compatible with scenarios of evolutionary convergence (Oyston *et al.* 2016), as our results suggest. The similar position assumed by *Bradypus* and *Choloepus* on PCo1, in between mylodontoid and megatherioid sloths, is suggestive of cranial convergence between these two extant taxa, which may originate in part from allometric effects related to their relatively small body size (Hanken & Wake 1993), but also from the absence of intermediate morphologies in the sample, reflecting their long phylogenetic history, undocumented in the fossil record (McDonald & De Iuliis 2008). Unfortunately, this purportedly convergent pattern could not be investigated with the quantitative test employed here, since this would require at least three taxa associated with a hypothesis of convergence.

It was not possible to disentangle the influences of the phylogenetic relationships of more inclusive clades (Megatherioidea and Mylodontoidea) from those of dietary categories, which carry a strong phylogenetic signal (Fig. 4A). However, the poor fit of the model segregating evolutionary rates by dietary categories, which is equivalent to the model separating Mylodontoidea from all other sloths, highlights that a historical signal in morphology at the level of less inclusive clades may have been more important for cranial evolution than diet.

Some cranial characters are undoubtedly influenced by dietary adaptations in sloths, such as those from the teeth, hyoid apparatus, mandible, snout, and several other structures of the skull associated with entheses for the masticatory musculature (Naples 1987; Bargo & Vizcaíno 2008; Bargo *et al.* 2009; Pérez *et al.* 2010; McAfee 2011; Naples & McAfee 2014; Casali & Perini 2017; Saarinen & Karme 2017). Dental microwear patterns, for example, suggest that mylodontoids, which are considered grazers or mixed-feeders, present a distinct wear pattern when compared to browsing sloths, although differences within this last group are also evident, including those between *Bradypus* and *Choloepus*, suggesting some degree of dietary specialization among browsers (Green 2009; Green & Resar 2012; Resar *et al.* 2013; Saarinen & Karme 2017; Kalthoff & Green 2018).

Alternatively, other characters of the skull, like those from the ear region, have been associated with both phylogenetic and functional signals (Patterson *et al.* 1989, 1992; Gaudin 1995, 2011; Boscaini *et al.* 2018). Studies focusing on more restricted sets of characters may be necessary to properly investigate in greater detail the causal influences of cranial disparity in sloths.

Postcranial data showed less phylogenetic structure in morphospace, greater overlap in clade disparity patterns, and a marked difference in disparity among locomotory

categories (Fig. 2B). These patterns are consistent with previous results that showed that postcranial skeletal anatomy has been mostly associated with functional locomotory adaptations in sloths (Bargo *et al.* 2000; Toledo *et al.* 2013, 2015; Amson *et al.* 2014), but also with a mixture of historical and functional or ecological signals as observed in xenarthrans (Amson & Nyakatura 2018; Oliveira & Santos 2018; Serio *et al.* 2020; Toledo *et al.* 2021), which can be hard to fully disentangle, as also observed here.

Morphometric data separates suspensory extant sloths from terrestrial and semi-arboreal sloths, the latter usually being recovered close to taxa with inferred digging capabilities (Bargo *et al.* 2012; Toledo *et al.* 2012; Toledo 2016; Oliveira & Santos 2018; Vizcaíno *et al.* 2018; Serio *et al.* 2020). This pattern was observed especially when anterior appendicular elements were investigated, and is in contrast to our results, which, like morphometric evaluations of scapular morphology, suggest a lesser degree of differentiation between suspensory and semi-arboreal taxa (Toledo 2016; Grass 2019). Some studies of humeral morphology that included a larger taxonomic fossil sample also recovered some historical signal, with terrestrial mylodontoids and megatheriids occupying slightly distinct morphospace regions, whereas stem megatherioids, megalonychids, stem megatheriids and nothrotherines clustered together, along with other semi-arboreal taxa (Oliveira & Santos 2018; Serio *et al.* 2020), which is also similar to the pattern observed here.

The adaptive influence is quite distinct from that of the phylogeny, as indicated by the lower phylogenetic signal of locomotory adaptations (Fig. 4B). The fit of the model considering rate differences among ecological categories (the sixth best-fitting model), and the model considering rate differences among taxa with and without pedolateral morphological adaptations (the fourth best-fitting model), provided some indirect evidence that locomotory adaptations may have also played an important role in postcranial evolutionary tempo, in addition to historical contingencies. Although long-term evolutionary change is continuously shaped by extrinsic ecological factors, historical factors result in developmental constraints, which limit or bias morphological evolution within clades (Oyston *et al.* 2015; Jablonski 2020).

The phylomorphospace also indicated multiple instances of convergent evolution among sloths, further supported by quantitative tests of morphological convergence. Some of those convergences may be related to locomotory adaptations, like the association of *Nematherium*, *Analcimorphus* and *Diabolotherium* with scansorial megalonychids, and that of *Parocnus* and *Megalocnus* to terrestrial taxa occupying a position in the centre of the phylomorphospace. The closer association of *Octodontotherium*, scelidotheriines and *Pseudopreotherium* to

terrestrial megatherioids may reflect a mixture of the retention of primitive characters along with derived convergent morphologies related to pedolateral stance, especially for Scelidotheriinae (McDonald 2012). Another noticeable pattern indicated in the postcranial morphospace is that of *Bradypus* towards the morphospace region occupied by terrestrial megatheriids. This clearly derives from its stem position as sister to all other sloths associated with a morphology adapted to climbing, which was recovered as primitive for sloths here, and for *Pilosa* as a whole in Gaudin and Croft (2015).

The members of Megalonychidae associated with terrestrial adaptations, such as *Megalonyx* Harlan, and the genera included in Ahytheriini, did not show much dissimilarity relative to their scansorial kin, and it is unlikely that adult individuals of these taxa possessed a semi-arboreal lifestyle (De Iuliis *et al.* 2009; Grass 2019). One possible explanation for this pattern would be that those taxa adapted to terrestrial habits with little postcranial modification, co-opting the semi-arboreal skeleton of stem megalonychids to perform exclusive ambulatory functions.

The isolated position of Mylodontinae on PCo1 may be related to several postcranial characters which distinguish its skeleton from that of Scelidotheriidae and primitive Mylodontidae, especially in the forelimb (Boscaini *et al.* 2019, 2021; Casali *et al.* 2022). However, associating this pattern with ecological adaptations is not straightforward since Scelidotheriidae and primitive Mylodontidae were also terrestrial and probably possessed digging and burrowing capabilities (Coombs 1983; Pujos *et al.* 2012). Megatheriini was also recovered well-separated from other megatheriids due to strongly negative values for PCo2, a distribution probably related to the presence of facultative bipedality (Coombs 1983; Casinos 1996), the lack of a morphological signal for digging (Fariña & Blanco 1996; Bargo *et al.* 2000), and their large body size (Raj Pant *et al.* 2014; Toledo *et al.* 2017).

Body size imposes important physical constraints on scansorial adaptations, which are restricted to smaller sloth species, whereas terrestrial taxa can achieve much larger body sizes, as observed in Megatheriini, most mylodontoids and, to a lesser extent, in *Megalonyx* (Toledo *et al.* 2017). The reduced disparity and morphological evolutionary rates in scansorial sloths may be the product of strong stabilizing selection for climbing adaptations, despite variations associated with particular alternative climbing habits in sloths (White 1993, 1997; Pujos *et al.* 2007, 2011; Bargo *et al.* 2012; Nyakatura 2012; Toledo *et al.* 2012, 2013). In contrast, much more disparate morphologies and faster evolutionary rates were observed among terrestrial taxa, and it is possible that specific substrate uses, like digging in Mylodontinae

(Bargo *et al.* 2000; Pujos *et al.* 2012) should also be considered in order to fully understand sloth postcranial evolution. The inclusion of those fine-grained categories is challenging, though. For example, we still have a very incomplete understanding of digging adaptations in sloths, which were probably not restricted to terrestrial taxa (Toledo *et al.* 2012; Gaudin & Croft 2015). Also, those substrate uses may interact with the locomotory categories as applied here, generating even more restricted groups, which may lead to reduced sample sizes, which then would make disparity analyses much less precise (Lloyd 2016; Gerber 2019).

Morphological disparity and evolutionary rates in Folivora were, in general, greater for megatherioids than for mylodontoids (Figs 3, 5), and this was compatible with the overall rate, but not disparity patterns observed by Varela *et al.* (2019). Nevertheless, this comparison should be viewed with caution, because there are important differences in the scope and methodology between our studies. We investigated disparity and morphological evolutionary rates for separate partitions, investigating how their evolutionary patterns differ, whereas Varela *et al.* (2019) analysed how disparity and rates changed through time for the entire skeleton. Working with a complete dataset may lead to the least loss of information caused by incompatible distances among taxa or distortions caused by taxa with higher levels of missing data (Lloyd 2016; Gerber 2019; Schaeffer *et al.* 2020). On the other hand, separate partitions may elucidate patterns that are unique for subsets of characters, which may be obscured by evaluating complete datasets (Stubbs *et al.* 2019; Brocklehurst & Benevento 2020; Simões *et al.* 2020; Wang *et al.* 2021; Brocklehurst *et al.* 2022; Müller 2022), but with the cost of losing information due to unequal completeness for some taxa in a given partition. This latter aspect can be further aggravated with the multiple time-bins required in disparity and rates through time analyses.

Another trade-off was also observed here, between using a sufficiently detailed ecological categorization on the one hand, and, on the other, ensuring adequate sample sizes for each of the groups being investigated. The proposed practice of including estimated ancestors in disparity analyses (Brusatte *et al.* 2011; Butler *et al.* 2012; Varela *et al.* 2019) could help to minimize this problem to some extent, but also introduces an undesirable phylogenetic smoothing to morphological distances (Lloyd 2016, 2018). As new taxa and additional fossil material becomes available, it will be more practical to evaluate multiple partitions with minimal taxonomic exclusion, whereas rare ecological adaptations may be more feasible to apply in species-level datasets, potentially improving sample sizes for those smaller groups.

CONCLUSION

The evolution of cranial and postcranial morphology in sloths is associated with distinct patterns of disparity among clades and ecological groups, even though the two partitions do not differ substantially in overall evolutionary tempo. Historical processes shaped the evolution of sloths more consistently than ecological ones, although changes in postcranial characters seem also to be associated to locomotory adaptations, at least more than cranial characters are affected by variations in diet. Nevertheless, this may be in part due to the greater overall variation in locomotory mode and more uniformity in dietary adaptations, which, in turn, may stem from our limited ability to infer fine distinctions in the diet of extinct taxa. Exploration of cranial subdivisions may prove to be more informative in understanding the possible drivers of the evolution of this morphological complex. Nonetheless, the usage of fine-grained partitions and ecological categories is associated with methodological trade-offs that should be taken into account when these evolutionary patterns are investigated quantitatively.

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Author contributions. DMC collected and analysed the data, and led the writing of the manuscript. All authors made substantial contributions to conception and design of the study, interpretation of data, drafting the manuscript or revising it critically for important intellectual content. All authors gave final approval of the version to be published and agreed to be accountable for all aspects of the work.

DATA ARCHIVING STATEMENT

Eigenvectors and eigenvalues obtained in PCoA analyses and code for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gmsbcc2rw>

Editor. Mary Silcox

SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12639>):

Appendix S1. Contains Tables S1–S5.

Table S1. Proportion of missing data (per partition) for taxa originally included in the dataset and their status in the current study (included or excluded).

Table S2. Assigned dietary categories.

Table S3. Assigned locomotory categories.

Table S4. Results of quantitative tests of morphological convergence.

Table S5. Fit of models applied in ancestral states estimations of diet and locomotion.

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