Bayesian total-evidence dating revisits sloth phylogeny and biogeography: a cautionary tale on morphological clock analyses

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ABSTRACT

Combining morphological and molecular characters through Bayesian total-evidence dating allows inferring the phylogenetic and timescale framework of both extant and fossil taxa, while accounting for the stochasticity and incompleteness of the fossil record. Such an integrative approach is particularly needed when dealing with clades such as sloths (Mammalia: Folivora), for which developmental and biomechanical studies have shown high levels of morphological convergence whereas molecular data can only account for a limited percentage of their total species richness. Here, we propose an alternative hypothesis of sloth evolution that emphasizes the pervasiveness of morphological convergence and the importance of considering the fossil record and an adequate taxon sampling in both phylogenetic and biogeographic inferences. Regardless of different clock models and morphological datasets, the extant sloth *Bradypus* is consistently recovered as a megatherioid, and *Choloepus* as a mylodontoid, in agreement with molecular-only analyses. The recently extinct Caribbean sloths (Megalocnoidea) are found to be a monophyletic sister-clade of Megatherioidea, in contrast to previous phylogenetic hypotheses. Our results contradict previous morphological analyses and further support the polyphyly of "Megalonychidae", whose members were found in five different clades. Regardless of taxon sampling and clock models, the Caribbean colonization of sloths is compatible with the exhumation of islands along Aves Ridge and its geological time frame. Overall, our total-evidence analysis illustrates the difficulty of positioning highly incomplete fossils, although a robust phylogenetic framework was recovered by an *a posteriori* removal of taxa with high percentages of missing characters. Elimination of these taxa improved topological resolution by reducing polytomies and increasing node support. However, it introduced a systematic and geographic bias because most of these incomplete specimens are from northern South America.

This is evident in biogeographic reconstructions, which suggest Patagonia as the area of origin of many clades when taxa are underrepresented, but Amazonia and/or Central and Southern Andes when all taxa are included. More generally, our analyses demonstrate the instability of topology and divergence time estimates when using different morphological datasets and clock models, and thus caution against making macroevolutionary inferences when node support is weak or when uncertainties in the fossil record are not considered.

Keywords

Fossil sloths, GAARlandia, historical biogeography, total-evidence dating, Xenarthra.

INTRODUCTION

Establishing a phylogenetic framework and timescale that reconciles morphological and molecular data is challenging, yet crucial for addressing a variety of questions in evolutionary biology and biogeography. Indeed, considering that most life on Earth is now extinct and does not preserve molecular data suitable for phylogenetic analyses, as these only survive a few million years (Demarchi et al. 2016), the use of morphological data is a prerequisite to elucidate deep-time evolutionary patterns. In the last decade, the development of methods integrating extant and extinct species in a single evolutionary tree improved significantly (Pyron 2011; Didier et al. 2012; Ronquist et al. 2012; O'Reilly et al. 2015; Donoghue and Yang 2016; Ogilvie et al. 2022) with total-evidence dating emerging as an elegant approach to jointly analyze molecular and morphological data (Zhang et al. 2016; Gavryushkina et al. 2017). Bayesian total-evidence dating makes use of the fossilized birth–death tree model (Heath et al. 2014) and the Markov model of discrete morphological evolution (Lewis 2001) to estimate both divergence times and phylogenetic relationships between fossil and extant taxa. Although this method likely represents the future of macroevolution, it also poses new challenges with respect to taxon sampling (Guillerme and Cooper 2016), tree priors (Matzke and Wright 2016), morphological clocks (Lee 2016), fossil sampling and fossilization processes (O'Reilly et al. 2015), models of morphological evolution (Goloboff et al. 2018), and stratigraphic uncertainty (Barido-Sottani et al. 2019, 2020). Empirical cases applying a Bayesian total-evidence approach to an array of organisms such as penguins (Gavryushkina et al. 2017), gharials (Lee and Yates 2018), and ferns (May et al. 2021), have reconciled molecular-clock divergence estimates with the fossil record, improving estimates of evolutionary rates and divergence times of crown taxa.

Sloths are emblems of a once richer mammalian diversity in South America, encompassing a wide breadth of occupied niches, locomotory modes, feeding strategies, and body sizes (e.g., Bargo 2003; de Muizon et al. 2004; Bargo and Vizcaíno 2008; Tejada et al. 2021). Controversial events in the evolution of sloths include the timing and mode of their colonization of the Caribbean Islands (MacPhee and Iturralde-Vinent 1994; Iturralde-Vinent and MacPhee 1999; Viñola-Lopez et al. 2022) and the extinction of more than 90% of their known taxonomic diversity at the end of the Pleistocene, including all the terrestrial forms (Steadman et al. 2005). To date, there is no consensus on the phylogenetic relationships among extant and extinct sloths and evolutionary hypotheses based on morphological (Gaudin 2004; Varela et al. 2019; Casali et al. 2022) and molecular data, including both ancient DNA (Höss et al. 1996; Greenwood et al. 2001; Slater et al. 2016; Delsuc et al. 2018, 2019) and paleoproteomics (Presslee et al. 2019), differ drastically. Sloths thus represent a combination of low extant diversity (6 species in 2 genera), extremely high levels of extinction, and debated phylogenetic interrelationships between fossil and extant taxa. Topologies inferred from DNA and protein sequences found *Bradypus* (the extant three-fingered sloths) nested within Megatherioidea (the clade including *Megatherium*), while *Choloepus* (the extant two-fingered sloths) was identified as a member of Mylodontoidea (the clade including *Mylodon*; Delsuc et al. 2019; Presslee et al. 2019). In contrast, virtually all morphological phylogenies placed the entire fossil sloth diversity more closely related to *Choloepus* than to *Bradypus*, with *Bradypus* as the sister taxon to all other sloths and *Choloepus* closely related to recently extinct Caribbean sloths (e.g., Gaudin 2004; Rincón et al. 2016; Varela et al. 2019; Casali et al. 2022). The consistency of morphology-based topologies, regardless of the methodology used (e.g., maximum parsimony or Bayesian inference), is rather unsurprising since for the last two decades morphological phylogenies have

been mostly based on variations of the same matrix of craniodental characters (i.e., Gaudin 2004). While the construction of this morphological matrix remains a seminal study, some of the characters it contains are of questionable homology (e.g., those based on caniniforms; Hautier et al. 2016; Delsuc et al. 2019). Furthermore, it is now acknowledged that patterns of morphological evolution are more complex than previously recognized, with recurring overlooked issues such as critical homology assessment, morphological covariation, allometry, and rate heterogeneity among discrete morphological characters (Kearney and Rieppel 2006; Dávalos et al. 2014; Harrison and Larsson 2015; Billet and Bardin 2019; Hallgrímsson et al. 2019; Phillips et al. 2023).

The oldest undisputed records of fossil sloths come from the late Oligocene of South America (Deseadan SALMA), with at least eight identified genera (Shockey and Anaya 2011; Pujos et al. 2021). Because most of this ancient sloth evidence comes from Patagonia, the southern cone of the continent has been considered the region where sloth evolution took place and from which dispersal to other parts of the continent would have occurred (e.g., Pascual 1984; Varela et al. 2019). In contrast, historical biogeography inference using molecular dating phylogenies of extant xenarthrans suggested a pan-Amazonian origin, as extant sloths (and other folivorans) are now restricted to the tropical Americas (Gibb et al. 2016). Fossil remains of Oligocene (or older) putative sloths in tropical localities are currently limited to one tooth and a proximal femur from the early Oligocene of Peruvian Amazonia (Antoine et al. 2021) and Puerto Rico (MacPhee and Iturralde-Vinent 1995), respectively. The dearth of evidence for early fossil sloths in the tropics, however, might result from the understudied nature of tropical localities, the comparatively fewer number of fossiliferous outcrops, and the scarcity of xenarthran remains throughout most of the Paleogene in general (Gaudin and Croft 2015), rather than being

reflective of a true absence, as attested by the increasing records of fossil mammals found at lower latitudes over the past decade (Carlini et al. 2014; Tejada-Lara et al. 2015; Antoine et al. 2016, 2017, 2021; Marivaux et al. 2016; Boivin et al. 2017).

In the Caribbean, sloths are now completely extinct but they were likely present since the early Oligocene (~31 Ma), as suggested by a partial sloth femur from Puerto Rico (MacPhee and Iturralde-Vinent 1994) and by molecular phylogenies dating the divergence time of extinct Caribbean sloths around the Eocene-Oligocene transition (Delsuc et al. 2019; Presslee et al. 2019). Based on molecular data, the proposed age of the divergence between Caribbean and South American sloths (~34 Ma; Delsuc et al. 2019; Presslee et al. 2019) is temporally compatible with the hypothetical existence of the Greater Antilles Aves Ridge landbridge (GAARlandia; Iturralde-Vinent and MacPhee 1999). Originally conceived as a short-lived but continuous subaerial structure, it would have rather been a series of islands that may have served as stepping stones connecting South America to the Greater Antilles between 35 and 33 Ma (see Philippon et al. 2020; Cornée et al. 2021; Garrocq et al. 2021). Molecular phylogenetic studies, however, are limited in the number of fossil taxa for which ancient DNA or paleoproteins can be obtained, and so the influence of the highly diverse fossil record on macroevolutionary dynamics is yet to be evaluated. Tempo and mode of sloth arrival to the Caribbean islands are important for understanding patterns of biodiversity distribution in the Caribbean region through time. For instance, colonization mode (vicariance or dispersal) and the timing of niche occupation might explain the selective nature of the colonization and why only certain terrestrial clades, and not others, became constituents of the Caribbean biota.

By applying a Bayesian total-evidence dating approach to a fossil-rich dataset of extant and extinct sloths (Xenarthra: Folivora), we aim to improve phylogenetic inferences while time-

calibrating key divergences in sloth evolution (e.g., Antillean colonization) and reassessing

biogeographical patterns previously proposed solely on the basis of morphological (e.g., Varela

et al. 2019) or molecular (Delsuc et al. 2019; Presslee et al. 2019) data. In addition, through a

series of sensitivity analyses, we evaluated the impact of taxon and character sampling on tree

topology and historical biogeography, while critically reassessing macroevolutionary inferences

based solely on morphological data (Varela et al. 2019; Casali et al. 2022, 2023). Our results

incorporating molecular data highlight the pervasiveness of morphological character

convergence in sloths, but also underscore the importance of considering the fossil record and an

adequate taxon sampling for phylogenetic and biogeographic reconstructions.

MATERIALS and METHODS

Taxon sampling, molecular and morphological data

We sampled 89 xenarthran taxa (64 fossil genera and 25 extant species). Among these, 65 are

sloths (the six extant sloth species and 59 fossil sloths), while the remaining 24 taxa are extant

and extinct cingulates and anteaters. The molecular matrix is based on mitogenomic data (15,157

characters in total) and was obtained from two previous studies (Gibb et al. 2016; Delsuc et al.

2019). Molecular sequence data are from 25 extant and seven fossil xenarthrans. The

morphological matrix is composed of 361 characters (synthetic matrix of Varela et al., 2019), of

which 286 characters are craniodental and come from Gaudin (2004). Fourteen species had both

molecular and morphological data (Supplementary Information on Dryad,

https://doi.org/10.5061/dryad.m0cfxpp82).

This initial 89-taxa dataset included a considerable number of fossil taxa represented by only a few coded morphological characters, subsequently yielding phylogenies with high proportion of poorly supported nodes and polytomies (see Results). To assess the impact of missing data on Bayesian phylogenetic inference and global node support, we implemented RoguePlots (Klopfstein and Spasojevic 2019) as a criterion to identify taxa leading to a lack of resolution. Using the results from RoguePlots (Figs. S18-S142) and analyzing them on a case-by-case basis, we sequentially reduced the initial 89-taxa dataset until we obtained a stable tree with an acceptable degree of resolution (~80% of nodes with PP≥0.9). The final dataset corresponds to 64 xenarthran species: 41 sloth taxa including 6 extant sloth species and 35 fossil sloth genera, with morphological data from 46 xenarthran species (extant and extinct). All taxa excluded have more than 40% of missing morphological characters (except for *Analcimorphus* with 34% of missing data). However, not all taxa with more than 40% of missing characters were excluded. Namely, *Neonematherium, Proscelidodon, Valgipes, Pleurolestodon, Parocnus, Megathericulus, Anisodontherium, Australonyx, Ahytherium,* and *Prepoplanops*, all have more than 40% of missing characters (between 42% and 86%) but were retained in the final dataset because they did not contribute to the lack of resolution (See Supplemental Section 1.2). Node support with a posterior probability (PP)≥ 0.9 was considered as high. We only discuss nodes with PP≥ 0.9 from the initial (89 taxa) or final (64 taxa) topologies.

Additionally, we evaluated the specific role of 18 morphological characters on topological structure and node support values. We deemed these 18 morphological characters to be either redundant, incorrectly defined, or of questionable homology (i.e., relying too heavily on caniniform traits, see Hautier et al. 2016). Detailed explanation on the rationale behind the exclusion or coding modification of these characters (as well as other analyses for problematic

character identification) is provided in Figure S1. Analyses were thus conducted using a morphological matrix containing 361 morphological characters, and a reduced matrix with 343 morphological characters (i.e., without the 18 aforementioned dental characters) for both the 89- and 64-taxa datasets (Figs. 2-3, Figs. S2-S17).

Phylogeny and divergence time estimations

Phylogenetic inferences and estimations of divergence times were carried out under a Bayesian total-evidence dating approach with the fossilized birth-death model (FBD) that explicitly models the speciation, extinction, fossilization, and sampling processes (Heath et al. 2014; Zhang et al. 2016; Gavryushkina et al. 2017). Analyses were performed with MrBayes 3.2.7a, with molecular partitions set to have their own evolutionary model: three for protein-coding genes (one per codon position) and one for the ribosomal RNAs 12S and 16S RNAs following previous works (Gibb et al. 2016). Models of sequence evolution were sampled with the reversible-jump Markov Chain Monte Carlo (MCMC) with gamma-distributed site rates and the default parameter of four gamma rate categories for rate heterogeneity (Huelsenbeck et al. 2004). One partition was set for all the morphological characters. Morphological evolution was computed under the Mk model (Lewis 2001) with a gamma rate variation across characters. Additionally, we performed analyses with an eight-category lognormal rate distribution which resulted in the same topologies, similar age divergences, and slightly better node supports (Figs. S6 and S11). Within-partition rate variation was modelled with variable gamma rates, as studies have shown that rates are frequently unequal (heterogeneous) among morphological characters (Wright and Hillis 2014; Harrison and Larsson 2015; Brocklehurst and Benevento 2020).

Each MrBayes analysis consisted of two runs with eight incrementally heated MCMC starting from a random tree. MCMC were run for 20 million generations with trees and associated model parameters sampled every 2,000 generations. Morphological and molecular data were modelled using the same relaxed clock model to remain consistent with previous molecular dating analyses of the clade (Delsuc et al. 2004; Gibb et al. 2016; Delsuc et al. 2019; Presslee et al. 2019). However, analyses were carried out using both an uncorrelated gamma rate model (IGR model, Lepage et al. 2007), in which tree branches have their own evolutionary rates that follow a gamma distribution, and an autocorrelated lognormal rate model (TK02 model; Thorne and Kishino 2002) in which branch rates follow a lognormal distribution and the evolutionary rate in a descendant branch is influenced by that of its ancestral branch. Unless noted, the results and discussion are based on the phylogenies obtained using the TK02 autocorrelated relaxed clock model. Indeed, previous knowledge and results on the same dataset showed that the TK02 model better fits the xenarthran molecular data through a Bayesian cross-validation procedure (Delsuc et al. 2019). However, the results for all dating analyses are presented and discussed in the main text and Figures S2-S11.

The sampling strategy of taxa was set to diversity (*prset samplestrat=diversity*) wherein extant taxa are sampled to maximize the clade diversity, while fossils are sampled randomly and can be tips or ancestors. The fossilization prior was set to a beta distribution: *prset fossilizationpr=beta(1, 1)*. An exponential prior and a beta prior were used for the net speciation rate and the relative extinction rate, respectively: *prset speciationpr=exp(10)*; *prset extinctionpr=beta(1, 1)*, while the node age prior was set to 'calibrated' (*prset nodeagepr=calibrated*). Topological hard constraints were set for all *Bradypus* species because we observed a rogue placement of *B. torquatus* in preliminary analyses (as also observed in a

concatenated analysis of genomic and proteomic data, Presslee et al. 2019), and for Pilosa

(excluding *Pseudoglyptodon*, although an analysis free of constraints is shown in Fig. S5). Our

discussion is mostly based on our reduced dataset of 64 taxa, and therefore our conclusions do

not change even if we consider *Pseudoglyptodon a priori* as Pilosa.

Dates of fossil occurrence (fixed, for radiometrically-dated Quaternary sloths; uniform

intervals for all pre-Quaternary sloths) were used to estimate divergence dates (Table S2). The

FBD model requires a prior for the root age, which was set between 72-51 Ma (*prset

treeagepr=unif(51, 72)*) based on previous studies (Meredith et al. 2011; Gibb et al. 2016;

Delsuc et al. 2019) and the most ancient xenarthran fossil (†*Riostegotherium yanei* Oliveira and

Bergqvist 1998, from the Itaboraí Formation [50-53 Ma]). For the reduced matrix of 64 taxa, an

age prior was also set on the Mylodontoidea node (45-33.2 Ma) based on the record from

Antoine et al (2021), a small early Oligocene mylodontid molariform from the TAR-22 locality

in Peruvian Amazonia. Due to its fragmentary nature, total-evidence dating analyses without this

internal calibration were also performed to evaluate its effect on divergence age estimations

(Figs. S7-S10). Convergence diagnostics were checked for each analysis with average standard

deviation of split frequencies (ASDF) <0.01, potential scale reduction factor (PSRF) close to 1.0,

and effective sample size (ESS) >200 in Tracer 1.7.1 (Rambaut et al. 2018).

Biogeographic estimations

To test hypotheses of Caribbean colonization by sloths, we estimated ancestral ranges on the

total-evidence time-calibrated phylogenies using the Dispersal-Extinction-Cladogenesis (DEC)

model (Ree and Smith 2008) as implemented in DECX (Beeravolu and Condamine 2016).

Twelve geographic areas (seven areas in the Americas and five in the Caribbean region, Fig. 1)

were considered based on recent advances in geologic history, modern biome configurations, and

extant and extinct xenarthran distribution patterns: (1) northern South America, including northern Andes in Ecuador, Colombia and Venezuela, and Venezuelan coastal and Llanos areas, (2) central and southern Andes in Peru, Bolivia, Chile, and Argentina; (3) Amazonia, encompassing all Amazon basin and the Guiana Shield; (4) Dry Diagonal, including Chaco, Cerrado, and Caatinga regions; (5) Atlantic Forest; (6) southern South America, including the steppes, grasslands, and deserts of Argentina, Uruguay, and southern Brazil; (7) Central and North America; (8) Cuba and Hispaniola; (9) Puerto Rico; (10) islands along the currently submerged Aves Ridge; (11) northern Lesser Antilles (including Anguilla, Antigua, St Martin, St Bartholomew, Barbuda, and other small islands north of Guadeloupe); and (12) southern Lesser Antilles, islands of Miocene or younger volcanic origin south of Guadeloupe. Species ranges were defined as presence-absence in the defined geographic areas (Table S3). We allowed a maximum range size of five areas, based on the maximum observed distribution of the studied taxa. We defined a time-stratified model with eight-time intervals reflecting major changes that affected the connectivity of the geographic areas considered, as follows:

I.   70 to 45 Ma: The Caribbean plate was located more to the west, relatively to South and North America, than at present (Escalona and Mann 2011), and so northwestern islands of Greater Antilles (e.g., Cuba, Jamaica, Cayman Islands) were contiguous to Central America. Lesser Antilles were not yet existent. Aves Ridge could have been aerial during this time interval (Bouysse et al. 1985; Garrocq et al. 2021). In the absence of the northern Andes and other major modern biomes, such as the Dry Diagonal, Pan-Amazonia was connected to southern and central Andes, the Atlantic Forest, and southern South America (Fig. 1d). This time interval was also

characterized by warm global temperature (Westerhold et al. 2020) and high global mean sea level between 56 and 48 Ma (Miller et al. 2020).

II.   45 to 37 Ma: The Caribbean plate migrates NE toward North America, and therefore the Greater Antilles started to become increasingly separated from Central America as the Cayman Trench starts opening (Doubrovine et al. 2012). Although some aerial reliefs existed (e.g., profile BOL30 in Garrocq et al. 2021), shallow, reefal carbonate platforms provide evidence that some parts of the Aves Ridge were submerged at this time interval (Fox et al. 1971; Marlowe 1971; Bouysse et al. 1985; Garrocq et al. 2021). The Pozo System, precursor of the Pebas System, became established (Roddaz et al. 2010; Andriolli et al. 2023). Biome configuration in South America is considered the same as in the precedent time interval. Global trend toward cooler climate conditions ("cool greenhouse", Westerhold et al. 2020) and the appearance of small ephemeral ice sheets produced a 10-30 m decrease in the global sea level (Miller et al. 2020).

III.   37 to 28 Ma: Although the Aves Ridge was experiencing an almost continuous subsidence since at least the middle Eocene (Garrocq et al. 2021), aerial exposures can be expected during this time frame based on the occurrence of two major erosional unconformities (Garrocq et al. 2021) and the presence of Oligocene conglomerates thought to be continental (Iturralde-Vinent and MacPhee 1999, Fig. 1h). Indeed, major erosional unconformities have been documented, but only on highs of the Aves Ridge (Garrocq et al. 2021) suggesting that numerous islands, and not a continuous continental bridge, were present. To the north of the Aves Ridge, sequences of uplift and emergence of areas of hundreds of square kilometers

connecting Puerto Rico and northern Lesser Antilles have also been evidenced (i.e.,
GrANoLA *sensu* Philippon et al. 2020; Cornée et al. 2021). Subduction of the
buoyant Bahamas bank drove uplifting of Cuba and Hispaniola and would have also
led to the uplifting of some islands of the northernmost Aves Ridge (Philippon et al.
2020). Further decrease in global temperature and the appearance of continental-scale
ice sheets ("Icehouse Earth", Westerhold et al. 2020) led to a sea-level drop of more
than 50 m (Miller et al. 2020), which might have contributed to the exposure of some
islands in the Caribbean region. Major marine incursions in the Andean foreland
basins (Pozo embayment) would have occupied the western part of modern Amazonia
(Wesselingh and Hoorn 2011)

IV.   28 to 20.4 Ma: Shallow platforms and reef structures evidence that the Aves Ridge
was submerged at shallow depth until the end of the Aquitanian (~20.4 Ma, earliest
Miocene; Fox et al. 1971; Bouysse et al. 1985; Garrocq et al. 2021), although some
parts were emerged or at least close to the sea level. The Pebas wetland system was
becoming established and about to isolate eastern proto-Amazonia from the Andes at
the end of this time interval (Hoorn et al. 2010).

V.   20.4 to 13.8 Ma: Full extension of Pan-Amazonia encompassing most of northern
South America (Fig. 1c). No evidence for existence of the Dry Diagonal at this or
older time bins (Werneck 2011). Pan-Amazonian forested areas would have covered
most of Brazil, reaching northern Argentina and the Atlantic Forest area. The
occurrence of an erosional unconformity on the highs of the Aves Ridge (Garrocq et
al. 2021) suggests that these highs would have been aerial at this time frame and at
least until the beginning of the Serravallian when the drowning of the Aves Ridge

started (Garrocq et al. 2021, Fig. 1g). Permanent ice sheets formed in East Antarctica (Miller et al. 2020).

VI.   13.8 to 9 Ma: The Lesser Antilles Arc grows enough to become emergent in some points. The Aves Ridge subsided rapidly and became completely and permanently submerged (Garrocq et al. 2021). Transition from the Pebas (mega-wetland) to the Acre (fluvial) System marked a major transition in tropical South America (Fig. 1b). Pulses of uplift of central and northern Andes are recorded, as well as the uplift of Vaupes Arch and onset of the Orinoco-Amazon divide (Wesselingh and Hoorn 2011).

VII.   9 to 4 Ma: Most present-day Lesser Antilles islands became emergent during this time frame (Fig. 1f). Strong uplift along the entire Andes. Development of modern Amazonia fluvial system. All modern-day geographic regions were present, the sole difference being the disconnection between South and Central America. Geographic configuration of the Caribbean region is similar to that of the present (Philippon et al. 2020).

VIII.   4 Ma to Present: Modern day geographic configuration of the Americas and the Caribbean is fully acquired (Fig. 1a, e). Lower limit is marked by the full establishment of the Isthmus of Panama allowing the interchange of terrestrial faunas between South and Central/North America.

RESULTS AND DISCUSSION

A new phylogenetic hypothesis for sloth evolution and the effects of taxon sampling

Our phylogenetic analyses combining mitogenomic and morphological data through Bayesian total-evidence dating propose an alternative hypothesis of sloth evolution that highlights the pervasiveness of morphological convergence (Table S4) and the key role of both the fossil record and taxon sampling in phylogenetic and biogeographic reconstructions.

Two major well-supported clades were identified within sloths: (1) Mylodontoidea (PP > 0.99), here defined as the least inclusive clade including *Mylodon* and *Choloepus*, and (2) Megatherioidea + Megalocnoidea (PP > 0.98), the former clade including *Bradypus* and *Megatherium* (PP = 1)*,* and the latter, Caribbean sloths (PP = 1, Figs. 2-3). Our phylogenetic analyses are consistent with previous molecular-based hypotheses (Höss et al. 1996; Greenwood et al. 2001; Delsuc et al. 2018, 2019; Presslee et al. 2019) in the placement of modern sloths — *Choloepus* as a mylodontoid and *Bradypus* as a megatherioid— the latter also suggested by early anatomical studies of the ear region (Guth 1962; Patterson et al. 1992). These unambiguously supported results (PP > 0.99) were obtained with both types of morphological partitions (361 and 343 characters), taxon sampling (Figs. 2-3), and under both IGR and TK02 clock models (Figs. S2-S11).

Another major departure from morphological-only analyses concerns the placement of Caribbean sloths (megalocnoids), which we found to be the sister-group of the megatherioid lineage. Caribbean sloths are thus more closely related to *Bradypus* than to *Choloepus* (Figs. 2-3), which stands in sharp contrast to the traditional view based on morphology that considered them as recently-extinct "megalonychids" (Gaudin 2004). This topology also differs from their proposed position as sister to all other folivoran clades suggested by molecular-only analyses

(Delsuc et al. 2019; Presslee et al. 2019), although this placement was only weakly supported by

mitogenomes (Delsuc et al. 2019). In this new scenario, the divergence of Caribbean sloths

would have occurred only a few million years after the divergence of mylodontoids and

megatherioids + megalocnoids (~34 Ma), which corresponds in time to the proposed existence of

GAARlandia (as discussed below). Biogeographically, this implies that sloths were widely

distributed across the continent by the late Eocene. Within Megalocnoidea, the clade of

Caribbean sloths, two unambiguously supported (PP = 1) clades were identified: (1) *Parocnus* +

Megalocnus and (2) *Neocnus* + *Acratocnus* (Fig. 3).

The so-called "Megalonychidae" family (formerly grouping the two-fingered sloths

Choloepus spp., Caribbean sloths, Pleistocene forms such as *Megalonyx*, and early Miocene

sloths such as *Hapalops)* is polyphyletic in our total-evidence phylogenetic framework, which is

in line with previous molecular analyses based on mitogenomes (Delsuc et al. 2019) and

paleoproteins (Presslee et al. 2019). Former megalonychid members are now placed in at least

four distinct clades (Fig. 2). From a morphological perspective, 18 craniodental characters have

been proposed as unambiguous synapomorphies supporting "Megalonychidae" (Gaudin 2004);

nine of these are related to caniniform characters. Interestingly, none of our resulting total-

evidence phylogenies (even those including caniniform-related characters) support such a

relationship, implying a very high degree of homoplasy in these dental characters, as previously

reported (Hautier et al. 2016; Delsuc et al. 2019).

Within Mylodontoidea, *Choloepus* is found as the earliest offshoot, implying an earlier

divergence (late Eocene) than suggested by molecular-only analyses (*ca*. 29 and 21 Ma,

respectively, Slater et al. 2016; Delsuc et al. 2019; Presslee et al. 2019). This finding also implies

a more than 30 Myr gap in the fossil record, as neither of the two extant tree sloth genera has a

pre-Quaternary fossil record. Inferred relationships within Megatherioidea are slightly less resolved (i.e., lower node support) than for mylodontoids and vary depending on the taxa included in the analyses and the clock model chosen (Figs. 2-3). For instance, in the reduced dataset of 64 taxa, Santacrucian taxa (e.g., *Hapalops, Eucholoeops, Schismotherium,* or *Pelecyodon*) are recovered as closely related to extant three-fingered sloths *Bradypus* (Figs. S7-S11), but their position is not resolved in our full dataset (Fig. 2, Figs. S2-S6). Pleistocene taxa *Megalonyx, Australonyx*, and *Ahytherium* formed a strongly supported clade (PP = 1), but how they are related to other megatherioids remains uncertain (Fig. 2).

The position of *Pseudoglyptodon* within cingulates —as opposed to within Folivora— is unambiguously supported (PP ≥ 0.9) with the reduced matrix of 343 characters and the TK02 clock model scenario (Fig. 2). The position of *Pseudoglyptodon* as a cingulate was also found with the IGR model, the full character dataset (i.e., including caniniforms, Figs. S2-S4, S72), and in a constraint-free analysis (Figs. S5, S132), although support was not strong (PP < 0.6-0.87). This alternative phylogenetic hypothesis, if corroborated, would have important implications for character polarization and macroevolutionary analyses, including biogeographic reconstructions, because *Pseudoglyptodon* is commonly considered to represent the earliest fossil sloth (McKenna et al. 2006). Admittedly, the phylogenetic position of *Pseudoglyptodon* is likely to remain controversial until more and better-preserved material is found (providing information of the ancestral morphological traits of early sloths), but also when early-diverging cingulates that could affect the inferred morphology at ancestral nodes (e.g., *Peltephilus*) are placed in a phylogenetic context.

Overall, our total-evidence analyses illustrate the difficulty of positioning highly incomplete fossils (Fig. 2), although a more robust phylogenetic framework was obtained when

fossils with a high proportion of missing characters were excluded (> 40% overall, Fig. 3).

Indeed, only 50% of nodes had a PP > 0.9 in our analysis including 89 taxa (Fig. 2), while the

average node support obtained with the 64-taxa dataset improved significantly (79-84% of nodes

had PP ≥ 0.9, Table S1). Removing highly incomplete taxa improved topological resolution by

reducing polytomies and increasing node support. However, it also introduced a systematic bias

because most of these incomplete specimens come from northern South America. This is

particularly true for Mylodontoidea, where 35% of tropical taxa were excluded based on

character completeness preventing resolution. This in turn affected biogeographic

reconstructions within and outside Mylodontoidea, as several of these taxa come from rocks

older than the remaining species. For instance, Patagonia was found to be the area of origin for

Mylodontoidea in the 64-taxa tree, whereas the Central and Southern Andes were recovered as

the most likely ancestral area for this clade in the 89-taxa tree. The origin of the extant genus

Bradypus also illustrates the influence of taxon sampling in biogeographic reconstructions, with

conflicting results obtained when using topologies inferred from the full dataset (Amazonia and

Atlantic Forest; Fig. 2), the reduced dataset (southern South America; Fig. 3), or data from extant

species only (Amazonia and northern Andes; Gibb et al. 2016). Although the true ancestral areas

for these clades are unknown, these results demonstrate the limitations of using only subsets of

the known diversity, whether by using data from extant species only, or by excluding fossils

from biogeographic analyses, as also demonstrated in other taxonomic systems (e.g., Mayr 2017;

Wisniewski et al. 2022).

Finally, the numerous ghost lineages implied by our results (Fig. 3) underscore the extent

of our yet-to-be-discovered knowledge, particularly in tropical regions that are prominent in our

biogeographic reconstructions. Within Mylodontoidea, for instance, it is observed in the early

divergence of *Choloepus* from other mylodontoids and later in that of *Mylodon*. In turn, the large

ghost lineage implied by previous morphological analyses for *Bradypus* is no longer observed.

Other notable ghost lineages are evidenced in the divergence of (and within) Megalocnidae— a

~14 Myr separation between *Parocnus* + *Megalocnus* and *Neocnus* + *Acratocnus*— and the

divergence of Megatheriidae.

A cautionary tale on morphological clock analyses

Morphology is crucial for phylogenetic reconstructions because it allows the inclusion of fossils,

which are essential for deciphering the evolution of modern and extinct organisms, and for

constraining the rate and timing of macroevolutionary processes (Jenner 2004; Wiens 2004;

Smith and Turner 2005; Mongiardino Koch et al. 2021). However, decisions about the

phylogenetic relevance of morphological characters can be highly subjective, especially in the

absence of developmental and population variability data (Kearney and Rieppel 2006; McAfee

2015; Hautier et al. 2016). Overlooked biological correlations among characters —e.g.,

allometry, which underlies much of the rostral shape variation in placentals, including

xenarthrans (Cardini 2019; Le Verger et al. 2020)— and cases of unevaluated intraspecific

variations coded as evolutionarily meaningful characters, are expected to introduce noise and to

affect topology reconstructions (Garamszegi and Moller 2010; Billet and Bardin 2019). For

example, the length and robustness of bony elements, as well as the density and degree of bone

sutural fusion (particularly variable in xenarthrans), might be correlated with age rather than

specific differences (Naples 1985; Rager et al. 2014). Some of these traits are coded as

phylogenetically informative characters in sloth morphological matrices (e.g., Char. 61 and 67 in

Gaudin 2004, Char. 293 in Varela et al. 2019 from Miño-Boilini 2012, Char. 15 in Pujos 2006).

An even more fundamental, but unfortunately often overlooked issue, is the assumption of character homology (i.e., primary homology, de Pinna 1991). In sloths, identification of dental homologies is challenging. Neontological studies of dental developmental sequences showed that the upper caniniforms of the two extant sloth genera are likely not homologous (Hautier et al. 2016), yet dental characters make up an important part of sloth morphological matrices (e.g., 18% in Gaudin 2004). In our analyses, removal of caniniform characters altered both topology and node support (Figs. S2-S11).

Ignoring these issues is likely to result in unreliable topologies leading to flawed divergence time estimates, which in turn will negatively affect downstream analyses of diversification, phenotypic evolution, disparity through time, and biogeographic inferences, regardless of the type of phylogenetic reconstruction methodology (i.e., maximum parsimony, Bayesian, or maximum likelihood). For instance, by implementing a Bayesian clock approach using tip dating on a matrix of craniodental characters, Varela et al. (2019) failed to recover a topology in agreement with that proposed by molecular analyses (Delsuc et al. 2019; Presslee et al. 2019). The robust molecular framework, obtained independently on both ancient mitogenomes (Delsuc et al. 2019) and paleoproteins (Presslee et al. 2019), is currently considered to represent the most likely evolutionary history for sloths. Therefore, results obtained from phylogenies that disregard molecular data and rely exclusively on morphology to conduct taxonomic status updates, and their integration to analyses of morphological disparity and character evolution are likely to be fundamentally flawed (e.g., Varela et al. 2019; Casali et al. 2022). Similarly, reconstructions of ancestral states based on poorly supported nodes are unreliable (Casali et al. 2023).

In fact, beyond the evaluation of partition models and other statistical parameters (e.g.,

Casali et al. 2022), to fully exploit morphological data for phylogenetic purposes, character

coding practices –and the typological way of assessing morphological variation– should be

reconsidered. This can be done by carefully analyzing morphological integration, intraspecific

variation, and evaluating developmental sequences to assess character homology and

phylogenetic relevance. Our results show that morphological data are necessary to obtain a more

complete picture of sloth evolution, but only if complementary molecular data are fully

considered. Furthermore, characters that scale allometrically (e.g., Phillips et al. 2023) or that

heavily relate to functional attributes such as diet (teeth) or locomotion (limbs) are often subject

to ecomorphological convergence, making them inadequate for phylogenetic inference at the

mammalian inter-ordinal level (Springer et al. 2007, 2013; Zou and Zhang 2016), at least until

specific models accounting for high homoplasy are developed (Dávalos et al. 2014). In the case

of sloths, the pervasive morphological convergence, lack of knowledge about character

covariation and intraspecific variability, presence of numerous ghost lineages, and high

extinction rates throughout their evolutionary history suggest that current morphological matrices

may only be useful when used in combination with molecular data to help overcome their

limitations, as in other crown mammal clades (Baker et al. 1998; Lee and Camens 2009). Our

results based on a total-evidence approach thus caution against believing that integrated

statistical approaches such as the Bayesian morphological clock will overcome the lack of a

thorough consideration of the complex evolution of morphological characters coupled with the

integration of molecular data.

Total evidence dating, sloth biogeography, and colonization of Caribbean islands

Our results (TK02 model, 343 morphological characters on 64 taxa, Fig. 3) placed the origins of Pilosa in the Paleocene around 63.7 Ma (95% HPD: 57.4-70.1 Ma, Fig. 3), when sloths and anteaters diverged. Nothing is known about sloth evolution for the next 27 million years, and it was not until the late Eocene (~36 Ma, 95% HPD: 34.8-38.1 Ma) that a major cladogenetic event gave rise to the two major clades Mylodontoidea and Megatherioidea + Megalocnoidea. These clades would have started to diversify almost synchronously at the Eocene–Oligocene transition.

As the first offshoot within Mylodontoidea, *Choloepus* spp. would have diverged from all other taxa around 33.8 Ma (95% HPD: 33.2-34.9 Ma) whereas *Mylodon* diverged from other mylodontines around 15.5 Ma. The Caribbean lineage (Megalocnoidea) diverged from its South American megatherioid relatives around 34 Ma (95% HPD: 32.1-36.2 Ma, Fig. 3), and its two constituent clades, *Parocnus* + *Megalocnus* and *Neocnus* + *Acratocnus*, would have separated at ~26 Ma. The divergence of the megatheriids is estimated to have occurred during the mid-Miocene (16.4 Ma, 95% HPD: 22.4-12 Ma). However, these estimates are also dependent on the age of the calibration prior set on the Mylodontoidea node (45-33.2 Ma; Antoine et al. 2021). When this calibration prior was not considered, the inferred divergence times were younger for these branches, as well as for deeper nodes (Table S1, Figs. S7-S11).

The influence of taxon sampling on biogeographic reconstructions is demonstrated by the differences between the 89- and 64-taxa datasets. Nevertheless, because the evolutionary

relationships proposed here depart from previous phylogenetic hypotheses, even the reduced

dataset (biased toward Patagonian species) highlights the role of regions other than Patagonia

(e.g., Amazonia, and Central and Southern Andes) in sloth evolution. Although we refrain from

making conclusive statements about macroevolutionary and biogeographic patterns when node

support is weak (i.e., PP < 0.9), we found some recurrent patterns, particularly regarding the

origin of Megatherioidea and Megalocnoidea. Our results suggest that the Aves Ridge would

have played a critical role in the dispersal of sloths from South America to the Caribbean islands

from as early as the late Eocene (~36 Ma) to as late as the late Oligocene (~25.4 Ma) (Fig. 3,

Table S1). This temporal range is largely consistent with exhumation of islands along Aves

Ridge (Philippon et al. 2020; Cornée et al. 2021; Garrocq et al. 2021).

The concept of GAARlandia and its role in the dispersal of terrestrial organisms from

South America to the Caribbean islands is not without controversy (e.g., Dávalos 2004; Ali and

Hedges 2021). The debate stems from the extent of the land area exposed and the timing and

duration of aerial exposure (as originally defined in MacPhee and Iturralde-Vinent 1994,

GAARlandia was only exhumated for 2 Myr). Although a continuous land bridge linking South

America and Greater Antilles is not supported by the strongly selective nature of the faunal

dispersal, as documented today and in the fossil record, and the overall Antillean species

diversity (Dávalos 2004), there is evidence of island exposure across the Aves Ridge at different

time intervals during the Paleogene and early Neogene times (Philippon et al. 2020; Cornée et al.

2021; Garrocq et al. 2021). The largest extent of aerial exposure is thought to have occurred from

the end Cretaceous until the early Eocene (Garrocq et al. 2021). Since the early Eocene, there is

evidence of a subsidence trend but no compelling evidence supporting a complete submersion

before the middle Miocene. For instance, the position of the erosional unconformity D0 and the

depositional hiatus, i.e., the reduced, and at parts nonexistent accumulation of early Eocene to

Oligocene sediments (line BOL30 of Garrocq et al. 2021) indicate that between the early Eocene

(U1a unit) and the early Miocene (U2b), the southern region of the Aves Ridge was emerged or

at least close to the sea level (Fig. 5e and Fig. S5 of Garrocq et al. 2021). In other parts all along

the Aves Ridge (lines GA21 and GA29 of Garrocq et al. 2021; lines C2, GA11 and GA15 of

Cornée et al. 2021), it sporadically emerged during the middle Miocene. The duration of these

emersions cannot be precisely estimated but emersion lasted from 3 to 6 million years—during

the Langhian (~16-13 Ma) or between the end of the Aquitanian (~20 Ma) to the early

Serravallian (~14 Ma)—to maybe tens of million years (between the late Eocene and early

Miocene).

Post-middle Eocene formation of islands along the Aves Ridge has been challenged by

the average amount and rate of subsidence inferred from the thickness of carbonate platforms

because reef building is assumed to compensate for subsidence (Ali and Hedges 2021).

However, this proxy does not provide unequivocal evidence for emersion/submersion of

landmasses because it does not allow estimation of the amount of emerged and eroded material.

This is relevant because uplift, which could certainly influence the amount of exhumation, is

observed during the late Eocene and much of the Oligocene, resulting in the emergence of the

GrANoLA landmass that connected Puerto Rico and northern Lesser Antilles (Philippon et al.

2020; Cornée et al. 2021). Furthermore, Ali and Hedges (2021) asserted that small carbonate

islands represent unfavorable habitats for vertebrate colonization, and thus, islands along Aves

Ridge could not have served as stepping-stones for terrestrial vertebrates migrating from

mainland toward the Antilles. This notion is inaccurate, as exemplified by the Sombrero Island, a tiny Pleistocene limestone block north of Anguilla. Sombrero Island is 1.2 km long, less than 400 m wide, has an elevation of 6-12 m, no beaches, and is subject to severe ground swells (Ogden et al. 1985). In addition to being home to several number of extant squamates, including at least one endemic teiid lizard (*Ameiva corvina*, Shew et al. 2002), fossil remains of the extinct giant land turtle *Geochelone sombreroensis* (Ogden et al. 1985) evidence not only a successful colonization by terrestrial vertebrates, but also a rapid biotic turnover. Successful colonization of carbonate islands by mammals is also well known, including the persistent Plio-Pleistocene colonization of the bovid *Myotragus* on the Balearic Islands (Bate 1909) and the rich late Miocene to Pleistocene deer-elephant fauna of the Ryukyu Islands (Otsuka and Takahashi 2000). Thus, the notion that atolls and low-elevation carbonate islands cannot support terrestrial vertebrate communities is incorrect.

Indeed, our biogeographic analyses support the hypothesis that islands along the Aves Ridge have played a role in the colonization of the Antilles by sloths (Figs. 2-3), and probably other terrestrial vertebrates (Blackburn et al. 2020; Marivaux et al. 2020). However, considering the intermittency in the extent and duration of exhumation, we see overwater dispersal as a complementary and necessary mechanism for biotic migration from South America to the Antilles. Our biogeographic results could also be interpreted as if an archipelago of long-lived islands in the Aves Ridge (and Puerto Rico under the 89-taxa analyses) were part of the mega-territory where megatherioid + megalocnoid sloth ancestors were distributed. The idea of islands in the Caribbean (including on the Aves Ridge) as potential sources of origin for sloths, however, is questionable given the irregular nature of their existence and the lack of concrete fossil

evidence. Indeed, unequivocal fossil evidence supporting Caribbean islands as sources of

diversity for terrestrial mammals (rather than sinks from the mainland) is not available, but the

idea has been proposed for groups including bats, lizards, birds, and arthropods (Glor et al. 2005;

Nicholson et al. 2005; Sturge et al. 2009; Lewis et al. 2015; Tavares et al. 2018; Crews and

Esposito 2020).

Increased paleontological, geological, and macroevolutionary studies in the Caribbean

are needed to understand extinct and extant Neotropical biogeographic patterns, and the

complexity behind the origin of the Caribbean fauna. Rodents, for instance, long thought to have

all migrated from South America, are now known to have also colonized Caribbean islands from

North America (Marivaux et al. 2021). Furthermore, Caribbean Islands may have played a

crucial role in the first biotic exchange between North and South America during the late

Mesozoic (Goin et al. 2016), as attested by fossil evidence from the Late Cretaceous of Cuba

(Viñola-López et al. 2022). Further analyses that co-infer trees, divergence times, and geographic

distributions (e.g., Landis et al. 2021) would be worth exploring to test the effect of

biogeographic distributions on the phylogenies themselves.

Conclusions

Combining morphological and molecular data to reconstruct phylogenetic relationships is not

straightforward, as each type of data comes with its own limitations and biases. Bayesian total-evidence

dating provides a way to reconcile both data types, allowing more accurate inferences of ancestral states,

diversification dynamics, and historical biogeography. Our case study of extinct and extant sloths

demonstrates the usefulness of integrating these data and their impact on phylogenetic and biogeographic

inferences. However, even Bayesian phylogenetics cannot circumvent the limitations and flaws imposed

by a biased taxonomic sampling and by matrices containing characters of tenuous phylogenetic significance. We stress that caution should be exercised when proposing phylogenetic hypotheses that use only subsets of data. Macroevolutionary interpretations should be avoided when node support is low.

Our new hypothesis of sloth evolution suggests that the two main sloth lineages, Mylodontoidea and Megatherioidea + Megalocnoidea, diverged during the late Eocene (~37 Ma). Our evolutionary scenario is consistent with previous molecular studies in placing *Choloepus* as a mylodontoid and *Bradypus* as a megatherioid, while Caribbean sloths represent the sister lineage to Megatherioidea. Caribbean sloths would have diverged from other megatherioids around 34 Ma, corresponding to the proposed existence of a now-vanished archipelago along the Aves Ridge. Our biogeographic reconstructions support sloth colonization of the Caribbean via the Aves Ridge and highlight the key role of Amazonia and the central and southern Andes, together with southern South America, in the early evolution of sloths.

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Figure legends

Figure 1. Key time periods in the geographic evolution of the Americas (a-d) and the Antilles (e-h). Present day South American (a) and Antillean (e) biome configurations. Geographic reconstructions depicting past biomes in South America (b-d) and the Caribbean region (f-h). Data for paleo reconstructions from (Hernández et al. 2005; Hoorn et al. 2010; Blakey 2016; Philippon et al. 2020; Cornée et al. 2021; Garrocq et al. 2021). Shorelines, mountains, rivers are conjectural approximations.

Figure 2. Bayesian total-evidence (morphological + molecular data) time-calibrated phylogeny and biogeographic estimations for the full xenarthran dataset (i.e., 89 taxa including 64 fossil sloth genera and all 6 extant sloth species). Dating was estimated under an autocorrelated relaxed clock model (TK02). Morphological matrix used for the phylogenetic reconstruction included 343 characters. Values at nodes represent posterior probabilities (PP). Nodes with PP>0.9 are in bold. Purple bars represent 95% highest posterior density intervals (HPD) for divergence age estimations. Colored circles at nodes represent the most likely geographic origin for clades, as indicated in the lower left corner inset. Colored circles on tips represent known distributions for all species included. Percentages at the right of taxa names represent amount of missing morphological data, (-) indicates that taxon has not been coded for morphology. Extant sloths are highlighted in yellow. Vertical grey and white divisions with Roman numerals represent the eight-time bins used for biogeographic estimations, as described in main text.

Figure 3. Bayesian total-evidence time-calibrated phylogeny for the reduced xenarthran dataset (i.e., 64 taxa including 39 fossil sloth genera, 6 extant sloth species, and 343 morphological characters). Dating was estimated with an autocorrelated relaxed clock model (TK02). Values at nodes represent posterior probabilities (PP). Colored circles at nodes and tips, and vertical grey and white divisions with Roman numerals as in Figure 2. Extant sloths are highlighted in yellow. Horizontal purple bars represent 95% HPD intervals. Skull figures and silhouettes are not to scale.
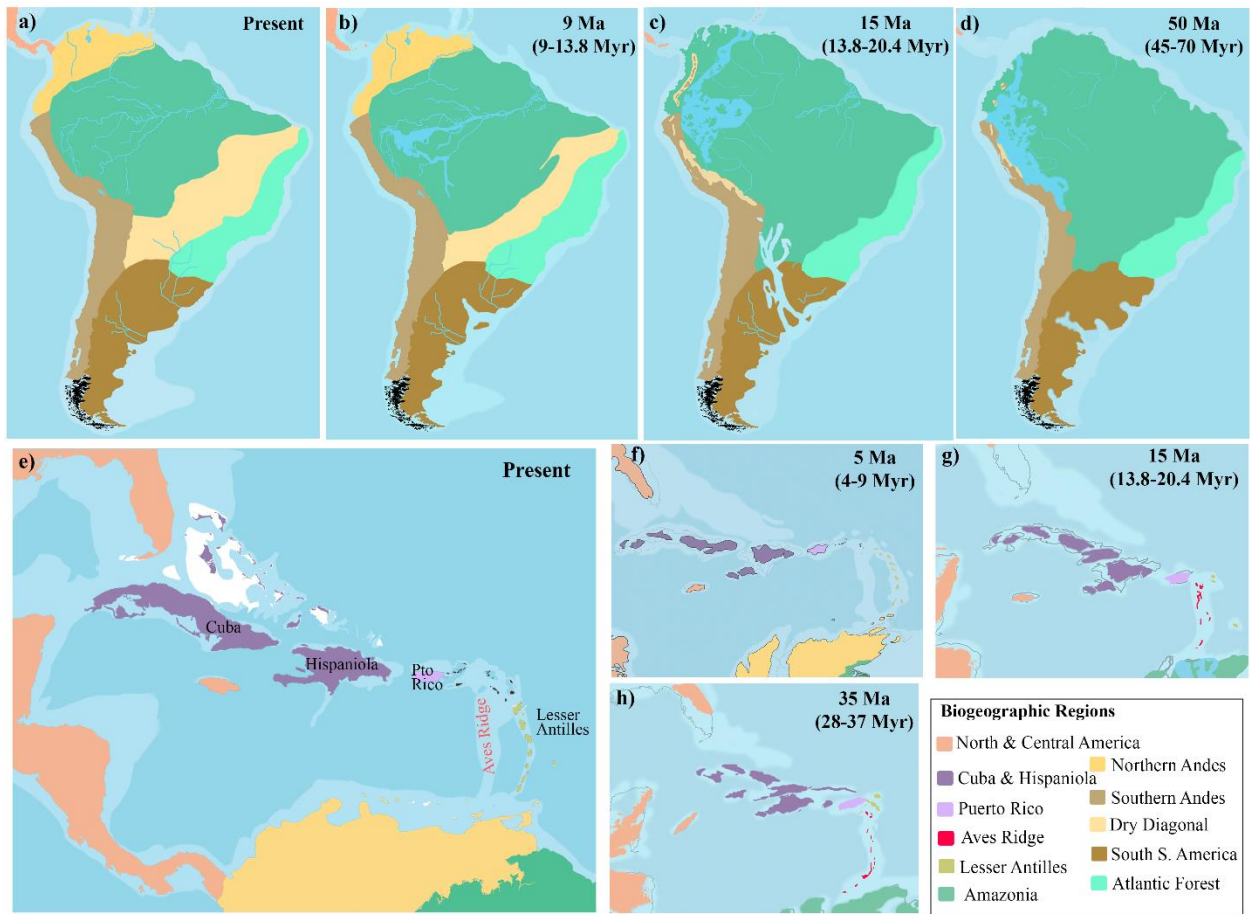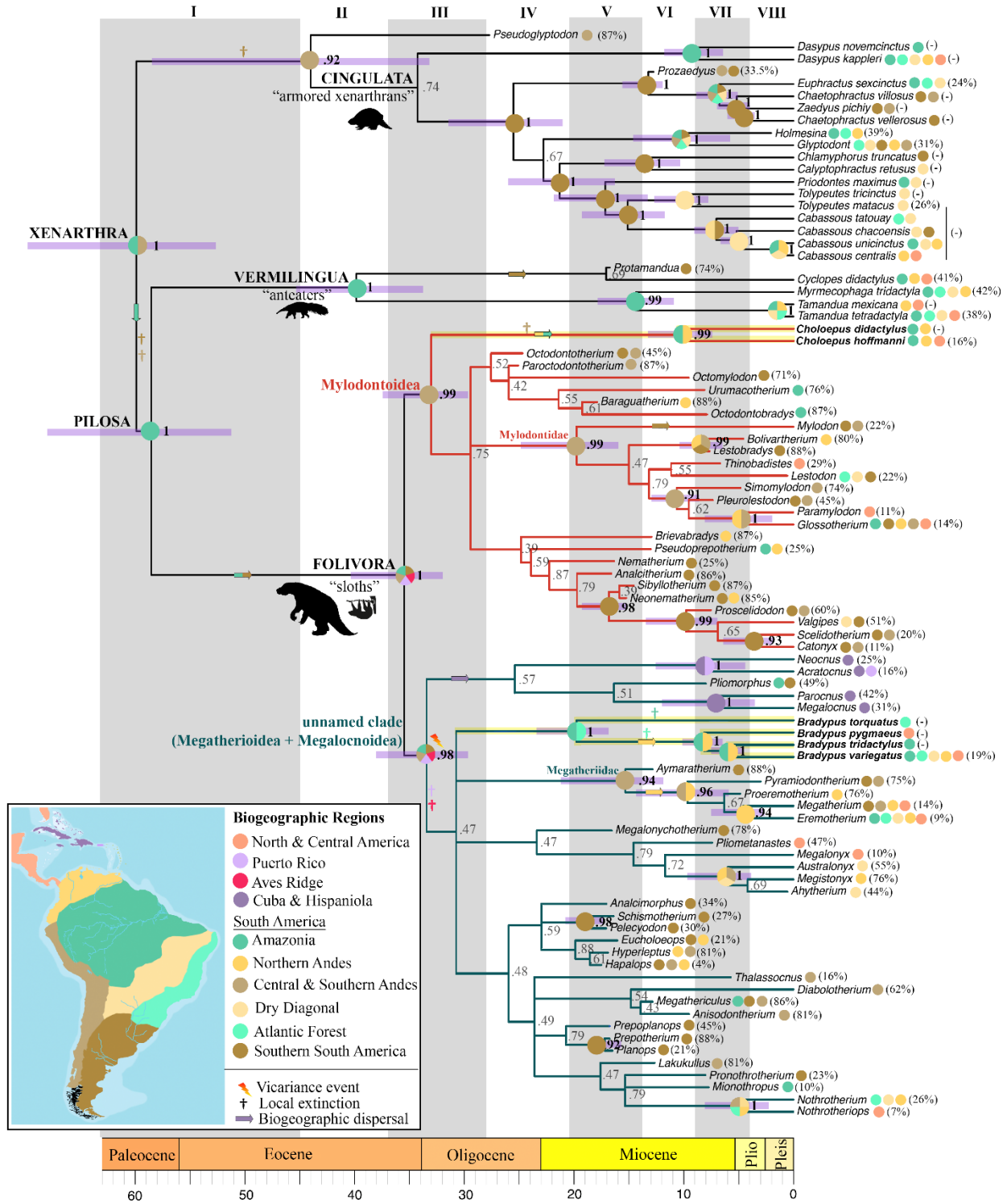
Figure 1

Figure 2

Figure 3