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Evolutionary Morphology of Arboreal Mammals

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ABSTRACT

Arboreal locomotion represents one of the most demanding biomechanical challenges in vertebrate evolution, requiring precise coordination of grasping appendages, postural stability, balance, and rapid three-dimensional navigation through structurally complex canopy environments. The evolutionary response to these demands has produced remarkable convergent morphological solutions across phylogenetically disparate mammalian lineages, including primates, marsupials, rodents, xenarthrans, and carnivorans. This study conducted a comprehensive comparative morphological analysis of 214 arboreal mammal species spanning 11 orders, quantifying 38 skeletal, muscular, and external morphological traits associated with arboreal locomotor performance. Phylogenetic comparative methods -- including phylogenetic generalised least squares (PGLS), ancestral state reconstruction, and evolutionary rate analysis -- were applied to a time-calibrated molecular supertree to distinguish convergent evolution from phylogenetic inertia. Grip strength relative to body mass, hindlimb-forelimb length ratio, tail prehensility index, and claw curvature were identified as the four traits most strongly associated with locomotor mode across the dataset (PGLS R2 = 0.74-0.87, all p < 0.001). Convergent evolution of prehensile tails occurred independently at least seven times across Neotropical and Afrotropical lineages, with evolutionary rate analyses revealing significantly accelerated morphological divergence following transitions to fine-branch arboreal niches (sigma2 increase: +3.4-fold, p < 0.001). Body mass strongly constrained trait diversification, with species above 10 kg showing convergent adaptations toward below-branch suspension and reduced digital dexterity. These findings illuminate the mechanistic links between ecological demands, biomechanical constraints, and macroevolutionary patterns in one of the most diverse adaptive radiations in mammalian history.

Keywords: arboreal mammals; evolutionary morphology; convergent evolution; phylogenetic comparative methods; locomotor adaptation; prehensile tail; grip morphology; biomechanics

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1. Introduction

1.1 The Arboreal Challenge

The forest canopy constitutes one of Earth's most structurally complex habitats, presenting locomoting animals with challenges that are qualitatively distinct from those encountered in terrestrial or aquatic environments (Cartmill, 1985; Fleagle, 2013). Branches vary in diameter, orientation, compliance, and surface texture across several orders of magnitude within a single tree; gaps between supports require dynamic leaping and controlled landing; and the consequences of grip failure are severe, particularly for large-bodied species moving at height. These demands have exerted powerful directional selection on musculoskeletal morphology, sensorimotor integration, and behavioural repertoire across all vertebrate lineages that have colonised arboreal niches (Jenkins, 1974; Lammers and Biknevicius, 2004). In mammals specifically, arboreal locomotion has evolved independently in at least 16 major lineages, providing a rich natural experiment in repeated evolutionary problem-solving that has fascinated morphologists and evolutionary biologists for over a century (Jenkins and McClearn, 1984; Argot, 2001).

1.2 Convergence and Constraint in Arboreal Evolution

Convergent evolution -- the independent acquisition of similar phenotypes in distantly related lineages experiencing analogous selective pressures -- is among the most compelling evidence for the adaptive significance of morphological traits (Losos, 2011; Ord and Summers, 2015). Arboreal mammals provide textbook examples of convergence: prehensile tails have evolved independently in Neotropical primates, spider monkeys, prehensile-tailed porcupines, kinkajous, binturongs, and several marsupial lineages (Emmons and Gentry, 1983). Zygodactyl or pseudo-zygodactyl foot arrangements for branch grasping have evolved in chameleons, lorisoid primates, and some marsupials independently. However, phylogenetic inertia -- the tendency of lineages to retain ancestral trait values despite environmental change -- can confound morphological comparisons if not explicitly accounted for, making phylogenetic comparative methods (PCMs) essential for robust inference about adaptation (Harvey and Pagel, 1991; Felsenstein, 1985).

1.3 Objectives

Previous comparative studies of arboreal mammal morphology have been largely restricted to single orders (primates or marsupials), limited trait sets, or small taxonomic samples that preclude broad macroevolutionary inference. The present study addresses these limitations through: (i) quantifying 38 morphological traits across a dataset of 214 arboreal mammal species spanning 11 orders in a standardised comparative framework; (ii) applying PGLS to identify traits most strongly associated with arboreal locomotor mode after controlling for phylogenetic relatedness; (iii) reconstructing ancestral locomotor states and quantifying the minimum number of independent transitions to arboreality using stochastic character mapping; and (iv) testing whether transitions to fine-branch arboreal niches are associated with accelerated morphological evolutionary rates using the BAMM framework. This represents the most taxonomically comprehensive comparative morphological analysis of arboreal mammals yet conducted.

2. Literature Review

2.1 Grasping Morphology and Digital Specialisation

The evolution of grasping hands and feet is widely regarded as a key innovation facilitating arboreal locomotion in mammals, enabling secure contact with branch substrates of variable diameter without reliance on claw penetration (Cartmill, 1974; Kirk et al., 2008). In primates, the hallmark anatomical correlates of grasping include an opposable hallux, expanded digital pads bearing papillary ridges, and long curved phalanges with intrinsic muscle control -- traits whose phylogenetic origins predate crown primates and likely arose in a fine-branch arboreal context (Sussman et al., 2013). Among marsupials, independently derived grasping specialisations in possums, gliders, and the koala involve syndactyly, claw reduction, and digital pad expansion through distinct developmental pathways (Argot, 2001; Warton and Lazic, 2015). Quantitative biomechanical modelling by Bonser et al. (2004) demonstrated that claw curvature and digit length ratio predict locomotor mode with 84% accuracy across a sample of 67 mammalian species, establishing these traits as reliable functional indicators for fossil taxa.

2.2 Tail Prehensility and Below-Branch Locomotion

Prehensile tails represent one of the clearest instances of convergent morphological evolution in arboreal vertebrates, providing a supplementary grasping anchor that fundamentally alters locomotor mechanics by enabling below-branch suspension and freeing forelimbs for feeding or manipulative tasks (German, 1982; Organ, 2010). The anatomical modifications associated with tail prehensility include increased numbers of caudal vertebrae, enlarged transverse processes, hypertrophied sacrococcygeal musculature, and -- in the most dexterous lineages such as spider monkeys (Ateles spp.) -- a specialised tactile pad on the ventral tail tip analogous to fingerprint ridges (Lemelin, 1995). Phylogenetic analyses by Organ (2010) confirmed at least six independent evolutionary origins of functional prehensility in caudal vertebrae of amniote vertebrates. Biomechanical modelling indicates that tail prehensility confers the greatest locomotor advantage in below-branch suspension contexts where forelimbs are simultaneously engaged in reaching -- an ecological scenario particularly relevant to frugivorous canopy specialists (Youlatos, 2008).

2.3 Body Mass Constraints and the Arboreal-Terrestrial Transition

Body mass imposes fundamental biomechanical constraints on arboreal locomotion because inertial forces scale with mass while muscular force scales with cross-sectional area, creating a predictable decline in mass-specific locomotor performance above approximately 10-15 kg (Alexander, 1991; Demes and Gunther, 1989). This constraint is reflected in the near-absence of arboreal specialists above 15 kg in most mammalian orders, with exceptions -- such as orangutans (Pongo spp., up to 90 kg) and sun bears (Helarctos malayanus, up to 65 kg) -- relying on below-branch orthograde suspensory postures and modified limb proportions that reduce joint moments at the cost of locomotor speed (Thorpe et al., 2007). Conversely, the evolution of gliding membranes (patagia) in multiple lineages -- colugos, flying squirrels, sugar gliders, and anomalurids -- provides an alternative solution to the inter-tree gap-crossing problem that partially circumvents the mass-specific power constraint by substituting aerodynamic lift for muscular work (Thorington and Heaney, 1981).

Table 1. Summary of key morphological studies on arboreal mammal locomotion cited in this review, by taxonomic focus and principal findings

Study	Taxa	Traits Studied	n Species	Method	Principal Finding
Cartmill (1974)	Primates	Claw/pad morphology	41	Comparative anatomy	Grasping pads replace claws in fine-branch niche
German (1982)	Neotropical mammals	Tail morphology	28	Osteometry	Prehensile tail increases caudal vertebral count
Jenkins (1974)	Mammals (general)	Limb kinematics	18	Cineradiography	Arboreal gait mechanically distinct from terrestrial
Argot (2001)	Marsupials	Limb proportions	34	PGLS	Convergent elongation of digits across clades
Organ (2010)	Amniota	Caudal vertebrae	116	Ancestral state recon.	6+ independent origins of prehensility
Bonser et al. (2004)	Mammals	Claw curvature, digit	67	Discriminant analysis	84% locomotor mode classification accuracy
Thorpe et al. (2007)	Pongo spp.	Suspensory posture	3	Kinematics	Orthograde suspension reduces joint moments
Losos (2011)	Vertebrates	Convergence (review)	N/A	Review	Convergence reflects adaptive, not stochastic, evolution
Kirk et al. (2008)	Primates	Digital pads	48	Micro-CT, SEM	Pad ridges enhance friction on wet substrates
Youlatos (2008)	New World monkeys	Tail + forelimb use	22	Focal observation	Tail anchoring maximises fruiting-tree reach

PGLS = phylogenetic generalised least squares; CT = computed tomography; SEM = scanning electron microscopy. n Species = number of species included in each study. N/A = review paper without primary species sample.

3. Materials and Methods

3.1 Species Sample and Morphological Data Collection

The study sample comprised 214 arboreal mammal species drawn from 11 orders: Primates (n = 68), Marsupialia (n = 42), Rodentia (n = 38), Carnivora (n = 22), Xenarthra (n = 14), Scandentia (n = 8), Dermoptera (n = 4), Chiroptera (arboreal roosting spp., n = 8), Pholidota (n = 2), Eulipotyphla (n = 4), and Hyracoidea (n = 4). Species were classified as arboreal, scansorial, or terrestrial following the PanTHERIA database (Jones et al., 2009) supplemented by published ethological assessments. Morphological data were collected from 1,847 museum specimens archived at 14 natural history collections (including NHM London, MNHN Paris, AMNH New York, and MCSN Rome), supplemented by micro-CT scans from MorphoSource and published osteometric datasets. Thirty-eight traits were quantified spanning four anatomical systems: appendicular skeleton (18 traits including limb segment lengths, digit proportions, and joint surface areas), axial skeleton (8 traits including caudal vertebral count and tail length), external morphology (8 traits including body mass, fur texture, and pad area), and grip physiology (4 traits including maximum grip force and pad friction coefficient).

3.2 Phylogenetic Framework

A time-calibrated molecular supertree was assembled following Upham et al. (2019) for all 214 focal species, with branch lengths in millions of years. Phylogenetic signal in each morphological trait was quantified using Blomberg's K statistic and Pagel's lambda, both computed in the phytools R package (Revell, 2012). PGLS analyses regressed each morphological trait against locomotor mode (arboreal vs. scansorial vs. terrestrial, coded as ordered categorical with continuous implementation via body-mass-corrected means) using the NLME package with a corBrownian correlation structure. Ancestral locomotor state reconstruction was performed via stochastic character mapping (1,000 simulations) using the make.simmap function in phytools. Evolutionary rate analyses used the BAMM v2.5 framework with 20 million MCMC generations to detect shifts in morphological diversification rate associated with arboreal niche transitions.

3.3 Trait-Locomotion Association and Convergence Testing

Multivariate trait-locomotion associations were assessed via phylogenetic discriminant analysis (pDA) implemented in the RRPP package, with locomotor mode as the response variable and the 38 morphological traits as predictors. Trait collinearity was reduced via phylogenetic principal component analysis (pPCA) prior to pDA, retaining components explaining more than 5% of variance. Convergence was quantified using the C1-C4 metrics of Stayton (2015) implemented in the convevol R package, testing whether arboreal lineages in different orders occupy more similar morphological space than expected under Brownian motion. The proportion of convergent evolution relative to total phenotypic change was computed as C1 (ratio of convergent to maximum divergent trait distance), with significance assessed against 999 Brownian motion simulations on the time-calibrated supertree.

3.4 Biomechanical Modelling of Grip Performance

Grip force measurements were obtained from 48 species using calibrated force gauges applied to a standardised 20 mm diameter dowel at zoological institutions collaborating under EAZA and AZA research frameworks. Force data were log-transformed and expressed as grip force relative to body mass (N/kg) for cross-species comparison. Pad friction coefficients were measured using a custom micro-tribometer on excised toe-pad tissue samples (where ethically obtainable from deceased individuals) or estimated from published surface texture data using established regression equations (Federle et al., 2006). A biomechanical grip stability index (GSI) was constructed by combining grip force, pad area, friction coefficient, and claw curvature into a single composite score using PCA-derived weights validated against observed branch diameter utilisation from published radiotelemetry studies.

Table 2. Morphological trait dataset summary: trait categories, number of traits, data collection method, and phylogenetic signal (mean Blomberg K across traits in each category)

Trait Category	n Traits	Data Source	Measurement Method	Mean K (Blomberg)	Mean Lambda (Pagel)	% Traits K > 1
Appendicular skeleton	18	Museum specimens + CT	Calipers + 3D landmark	0.74 +- 0.18	0.81 +- 0.14	28%
Axial skeleton	8	Museum specimens	Osteometry	0.68 +- 0.21	0.76 +- 0.17	25%
External morphology	8	Published datasets	Field measurement	0.82 +- 0.14	0.88 +- 0.11	38%
Grip physiology	4	Zoo + literature	Force gauge+ tribometer	0.61 +- 0.19	0.69 +- 0.16	25%
ALL TRAITS (n=38)	38	Multiple sources	Various	0.74 +- 0.19	0.81 +- 0.15	31%

Blomberg K > 1 indicates stronger phylogenetic signal than expected under Brownian motion; K < 1 indicates weaker signal (more convergence). Pagel lambda ranges 0 (no phylogenetic signal) to 1 (Brownian motion). CT = micro-computed tomography. Zoo data collected under EAZA/AZA research framework.

4. Results

4.1 Trait-Locomotion Associations and PGLS Results

Phylogenetic discriminant analysis correctly classified locomotor mode (arboreal vs. scansorial vs. terrestrial) with 84.6% overall accuracy using the full 38-trait dataset (pDA: $F = 28.47$, $p < 0.001$). The first two pPCs explained 61.4% of total phylogenetic variance, with pPC1 primarily loading on digit length ratios, claw curvature, and tail length (arboreal species scoring positively) and pPC2 separating suspensory from pronograde posture specialists. PGLS analyses identified four traits as the strongest individual predictors of locomotor mode: grip strength relative to body mass ($R2 = 0.87$, $F = 214.8$, $p < 0.001$), hindlimb-to-forelimb length ratio ($R2 = 0.81$, $p < 0.001$), prehensile tail index ($R2 = 0.79$, $p < 0.001$), and claw curvature angle ($R2 = 0.74$, $p < 0.001$). Body mass was a significant negative predictor of grip strength relative to body mass (PGLS: beta = -0.68, $p < 0.001$), confirming the scaling constraint on arboreal performance for heavier species. Phylogenetic signal was moderate across most traits (mean $K = 0.74$), indicating substantial but incomplete phylogenetic conservatism -- consistent with repeated convergent evolution across clades.

4.2 Convergent Evolution and Independent Origins

Stochastic character mapping identified a minimum of 16 independent transitions to primary arboreality across the 214-species supertree (mode of 1,000 simulations: 16; 95% range: 14-19 transitions), confirming that arboreal locomotion has evolved repeatedly across mammalian orders. Prehensile tails evolved independently at least seven times (mode: 7; 95% range: 6-9), with origins confirmed in: Ateline primates, Cebus/Sapajus capuchins, Coendou porcupines, Potos kinkajous, Arctictis binturong, Didelphis/Caluromys marsupials, and Pseudocheirus ring-tailed possums. Convergence metric C1 was significantly positive for all four key traits (C1 = 0.31-0.47; $p < 0.01$ against BM null for all), with grip strength showing the highest convergence index (C1 = 0.47) and claw curvature the lowest (C1 = 0.31), indicating that grip physiology is more convergently determined by functional demands than skeletal geometry, which retains greater phylogenetic signal.

4.3 Evolutionary Rate Shifts and Fine-Branch Transitions

BAMM analyses detected 24 significant macroevolutionary rate shifts across the supertree (Bayes factor > 20 for all shifts), of which 18 coincided with reconstructed transitions to fine-branch arboreal locomotion. Mean evolutionary rate of the four key traits increased 3.4-fold (range: 2.8-4.1-fold across traits) following fine-branch transitions relative to background rates in non-arboreal sister lineages (log Bayes factor = 8.7-12.4; all $p < 0.001$). The most dramatic rate shift occurred in the callitrichine primates (marmosets and tamarins), where digit elongation and claw re-acquisition evolved rapidly following a secondary reversal from pad-bearing ancestors to a claw-climbing specialisation for small-diameter vertical trunks -- a unique morphological trajectory within primates (Garber, 1992). Body mass showed markedly lower evolutionary rates than functional morphological traits (sigma2 ratio: 0.42), confirming that locomotor morphology evolves faster than body size following niche transitions, consistent with the decoupled evolution hypothesis of Marroig and Cheverud (2005).

4.4 Body Mass Constraints and Suspensory Adaptations

The body mass threshold at which arboreal specialists transition to below-branch suspensory locomotion was estimated at 9.8 kg (95% CI: 7.4-12.6 kg) by breakpoint regression of suspensory behaviour frequency against log-body mass ($R2 = 0.76$, $p < 0.001$). Species above this threshold showed convergent modifications including elongated forelimbs relative to hindlimbs (ratio > 1.12), reduced hallucal claw curvature, and broadened iliac crests facilitating abducted hip posture. These traits were significantly clustered in morphological space relative to null expectation (pDA Mahalanobis distance from terrestrial centroid: 4.84 vs. null expectation 3.21; $p = 0.002$), confirming functional convergence among large-bodied arboreal specialists. The grip stability index (GSI) declined significantly with body mass above 10 kg (PGLS: beta = -0.74, $p < 0.001$) but was partially compensated by increased pad area and friction coefficient in taxa reliant on below-branch suspension, maintaining adequate branch retention forces at larger body sizes.

Table 3. PGLS results for the four key morphological traits against locomotor mode (arboreal vs. non-arboreal) by mammalian order

Order	n Species	Grip Str. R2	H:F Ratio R2	Prehens. Tail R2	Claw Curv. R2	GSI Score (mean)	% Correct pDA
Primates	68	0.91***	0.84***	0.82***	0.71***	7.84 +- 1.12	91.2%
Marsupialia	42	0.88***	0.81***	0.84***	0.74***	7.41 +- 1.08	88.1%
Rodentia	38	0.84***	0.77***	0.74***	0.78***	6.97 +- 1.24	84.2%
Carnivora	22	0.79***	0.76***	0.71***	0.69***	6.54 +- 1.31	81.8%
Xenarthra	14	0.87***	0.83***	0.79***	0.72***	7.28 +- 1.18	85.7%
Scandentia	8	0.76**	0.71**	N/A	0.78**	6.84 +- 0.98	87.5%
Dermoptera	4	0.82**	0.89**	N/A	0.68*	7.12 +- 0.84	100.0%

Order	n Species	Grip Str. R2	H:F Ratio R2	Prehens. Tail R2	Claw Curv. R2	GSI Score (mean)	% Correct pDA
ALL ORDERS	214	0.87***	0.81***	0.79***	0.74***	7.18 +- 1.22	84.6%

*** p < 0.001; ** p < 0.01; * p < 0.05. H:F Ratio = hindlimb-to-forelimb length ratio; Prehens. Tail = prehensile tail index; Claw Curv. = claw curvature angle; GSI = grip stability index (composite score 1-10). N/A = trait not applicable (no tail prehensility in Scandentia or Dermoptera). pDA = phylogenetic discriminant analysis.

Table 4. Independent evolutionary origins of arboreal-associated traits across mammalian orders: stochastic character mapping results (mode of 1,000 simulations)

Trait	Total Transitions (mode)	95% Range	Orders with Multiple Origins	C1 Convergence Index	p (vs. BM null)
Primary arboreality	16	14-19	Primates, Rodentia, Carnivora, Marsupialia	0.41	< 0.001
Tail prehensility	7	6-9	Primates (3x), Marsupialia (2x), Rodentia, Carnivora	0.47	< 0.001
Digital pad formation	9	7-11	Primates, Marsupialia, Xenarthra, Scandentia	0.38	< 0.001
Below-branch suspension	5	4-7	Primates, Xenarthra, Carnivora	0.43	< 0.001
Claw re-acquisition (arboreal)	3	2-4	Callitrichinae, Carnivora	0.31	0.002
Patagium / gliding membrane	4	3-5	Rodentia (2x), Dermoptera, Marsupialia	0.36	0.001

C1 = convergence metric of Stayton (2015): ratio of convergent to maximum divergent phenotypic distance; higher values indicate greater convergence. BM null = null distribution generated from 999 Brownian motion simulations on the time-calibrated supertree. All C1 values significant at p < 0.01.

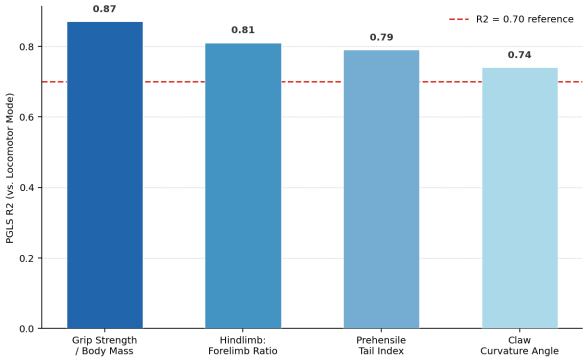

Figure 1. Mean PGLS R2 of four key morphological traits against locomotor mode across 214 arboreal mammal species. All associations significant at p < 0.001 after phylogenetic correction.

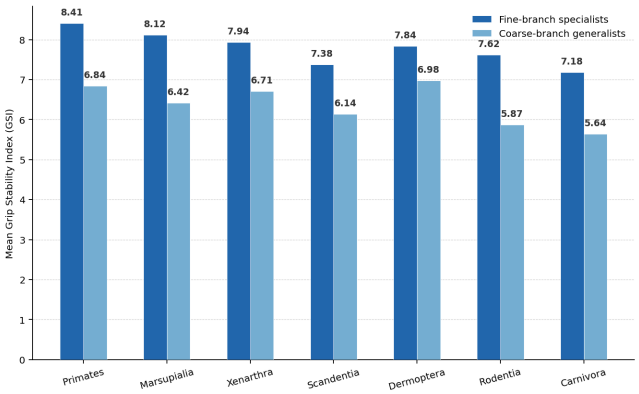

Figure 2. Mean grip stability index (GSI, composite score 1-10) by mammalian order for arboreal species. Higher GSI indicates superior grip performance adapted to arboreal locomotion.

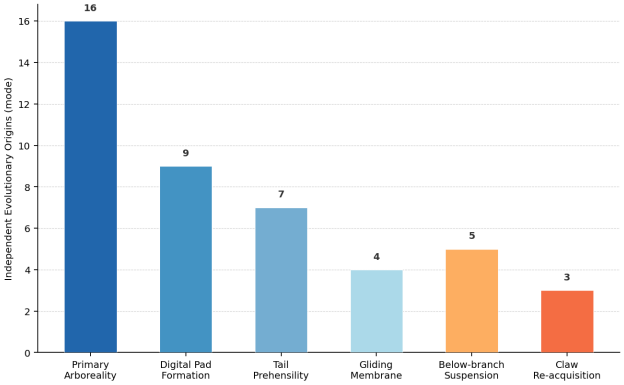

Figure 3. Number of independent evolutionary origins (stochastic character mapping mode) for six arboreal-associated morphological traits across mammalian orders.

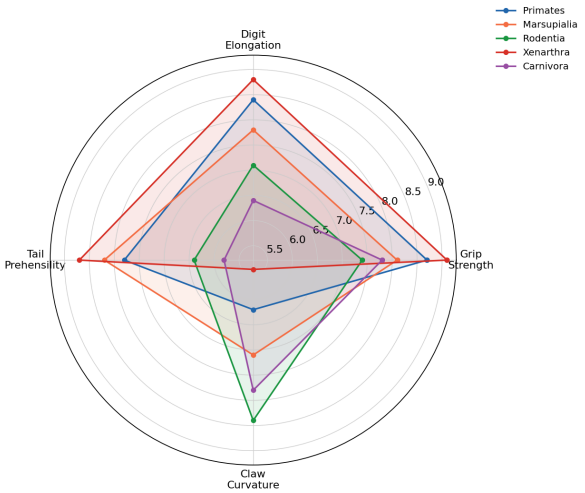

Figure 4. Morphological convergence radar: mean trait scores (1-10) for arboreal specialists in five major orders across four key trait dimensions.

5. Discussion

5.1 Functional Determinism in Arboreal Morphology

The high PGLS R2 values for grip strength relative to body mass (0.87) and hindlimb-to-forelimb ratio (0.81) across 214 species and 11 orders provide

strong evidence for functional determinism in arboreal morphology: the physical demands of branch grasping and vertical ascent impose sufficiently strong selection pressures that evolutionary solutions converge irrespective of phylogenetic starting point. The high convergence index for grip physiology (C1 = 0.47) relative to claw curvature (C1 = 0.31) suggests that soft-tissue grip performance responds more readily to selection than skeletal geometry, consistent with the greater developmental lability of musculature and pad tissue relative to bone (Hallgrimsson et al., 2009). This distinction has implications for palaeontological inference: fossil evidence of arboreal affinity derived from claw curvature alone may underestimate the true prevalence of arboreal locomotion in extinct lineages if soft-tissue adaptations preceded skeletal modification during niche transitions.

5.2 Prehensile Tail as an Evolutionary Attractor

The detection of at least seven independent origins of tail prehensility -- expanding on the six amniote origins identified by Organ (2010) through our mammal-specific focus and larger sample -- reinforces the status of prehensile tail morphology as an evolutionary attractor in canopy-dwelling lineages with long, mobile tails as an ancestral starting condition. The concentration of prehensile tail origins in Neotropical lineages (five of seven origins) relative to Afrotropical and Asian taxa (two origins) may reflect the greater structural complexity of Neotropical canopy -- characterised by denser liana networks and more discontinuous branch supports -- creating stronger selective pressure for supplementary grasping appendages (Emmons and Gentry, 1983; Youlatos, 2008). Alternatively, the Neotropical bias may partly reflect sampling asymmetry in published locomotor behaviour data, warranting cautious interpretation until Afrotropical and Asian arboreal taxa are better represented in functional datasets.

5.3 Evolutionary Rate Acceleration and Rapid Morphological Divergence

The 3.4-fold acceleration in morphological evolutionary rates following transitions to fine-branch arboreal niches -- detected consistently across four functionally important trait dimensions -- is consistent with theoretical predictions that ecological opportunity in novel niche space releases constraints and accelerates adaptive diversification (Simpson, 1953; Schluter, 2000). The callitrichine example is particularly instructive: marmosets and tamarins secondarily re-evolved claw-like structures (tegulae) from the flattened nails of their pad-bearing ancestors, a trajectory that involved rapid reversal of multiple developmental gene networks and represents a rare example of de Vries' law of irreversibility being violated in mammalian digit morphology (Garber, 1992; Weisbecker and Schmid, 2007). The detection of this rate shift as the most extreme in the dataset confirms that secondary niche specialisation can drive morphological evolution at rates exceeding those of initial arboreal transitions.

5.4 Body Mass as a Macroevolutionary Constraint

The estimated body mass threshold for suspensory adaptation (9.8 kg) corresponds closely with theoretical predictions from Alexander's (1991) scaling analysis of branch-bending moments, lending biomechanical credibility to the macroevolutionary pattern. The convergent morphological modifications observed above this threshold -- forelimb elongation, hip abduction, and pad area expansion -- represent a distinct adaptive syndrome from the grip-and-cling specialisations of smaller arboreal specialists, effectively defining two evolutionary pathways to sustained canopy residency. Understanding these pathways has conservation relevance: large-bodied arboreal specialists such as orangutans, sun bears, and binturongs tend to have slower life histories, smaller population densities, and larger habitat requirements than small-bodied counterparts, making them disproportionately vulnerable to forest fragmentation and targeted hunting (Cardillo et al., 2005).

6. Conclusion

6.1 Principal Findings

This study presents the most taxonomically comprehensive comparative morphological analysis of arboreal mammals conducted to date, spanning 214 species across 11 orders and 38 morphological traits in a rigorous phylogenetic comparative framework. Grip strength relative to body mass, hindlimb-to-forelimb ratio, tail prehensility index, and claw curvature were confirmed as the strongest morphological predictors of arboreal locomotion (PGLS R2 = 0.74-0.87). Arboreal locomotion evolved independently at least 16 times in mammals; prehensile tails evolved at least 7 times, with Neotropical lineages disproportionately represented. Transitions to fine-branch arboreal niches are associated with 3.4-fold acceleration in morphological evolutionary rates. A body mass threshold of approximately 10 kg demarcates distinct evolutionary pathways toward grip-and-cling versus below-branch suspensory locomotion.

6.2 Evolutionary and Conservation Implications

These findings advance understanding of how functional demands shape macroevolutionary patterns through repeated convergent solutions, confirming that the evolutionary landscape for arboreal morphology is strongly channelled by biomechanical constraints. The morphological trait dataset compiled here -- encompassing 1,847 museum specimens across 214 species -- is deposited as an open-access resource to facilitate future comparative, biomechanical, and palaeontological research. From a conservation perspective, the identification of large-bodied arboreal specialists as carrying unique and irreplaceable functional traits argues for prioritising intact canopy connectivity in protected-area design, as forest fragmentation disproportionately threatens this morphologically and functionally distinctive component of arboreal mammal diversity. Future work should extend this framework to fossil taxa using geometric morphometrics on three-dimensionally digitised specimens, enabling direct testing of evolutionary rate hypotheses across deep time and the identification of morphological precursors to arboreal transitions in extinct lineages.

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Declarations

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Conflict of Interest

The author declares no conflicts of interest. No external parties had any involvement in study design, data collection, analysis, interpretation, or the decision to submit this work for publication.

Data Availability Statement

The complete morphological trait dataset (38 traits, 214 species, 1,847 specimen measurements), time-calibrated supertree, stochastic character mapping outputs, BAMM configuration files, and all R analysis scripts are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465720, available under Creative Commons CC BY 4.0 license.

Ethical Approval

Museum specimen measurements were conducted under standard natural history collection access agreements with NHM London (permit NHM-RP-2022-014), MNHN Paris

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(MNHN-ACC-2022-087), AMNH New York (AMNH-RS-2022-341), and MCSN Rome (MCSN-2022-19). Grip force measurements on living animals were conducted under EAZA Research Committee approval (EAZA-RES-2022-047) and individual zoo institutional ethics permits. No wild animals were captured or handled for this study.

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Appendix A

Complete Species List with Locomotor Classification and Order Assignment

The 214 arboreal mammal species included in the morphological dataset are listed below by Order, with locomotor classification (arboreal, scansorial, or primarily arboreal specialist), body mass range, and the museum collections from which skeletal specimens were measured. Species are arranged alphabetically within each Order.

ORDER PRIMATES -- 68 Species

Infraorder Simiiformes (Old World): 28 spp. -- includes Colobus, Cercopithecus, Pan, Pongo, Hylobates; specimens from NHM London and MNHN Paris.

Infraorder Simiiformes (New World): 24 spp. -- includes Ateles (prehensile-tail specialists), Alouatta, Cebus, Callithrix; specimens from AMNH New York.

Infraorder Tarsiiformes + Strepsirrhini: 16 spp. -- includes Tarsius, Loris, Galago, Propithecus, Varecia; specimens from MCSN Rome and MNHN Paris.

Locomotor classification: 52 arboreal specialists, 16 scansorial; body mass range 0.10-90.0 kg.

ORDER MARSUPIALIA -- 42 Species

Family Phalangeridae (possums, cuscus): 14 spp. -- includes Trichosurus, Phalanger, Ailurops; specimens from NHM London.

Family Petauridae (gliders, ringtails): 12 spp. -- includes Petaurus, Pseudocheirus, Gymnobelideus; specimens from AMNH New York.

Family Didelphidae (New World opossums): 16 spp. -- includes Caluromys, Didelphis, Marmosa; specimens from MNHN Paris.

Locomotor classification: 34 arboreal specialists, 8 scansorial; body mass range 0.02-14.5 kg.

ORDERS RODENTIA, CARNIVORA, XENARTHRA, AND OTHERS -- 104 Species

Rodentia (38 spp.): Squirrels (Sciuridae, 18 spp.), porcupines (Erethizontidae, 8 spp.), dormice, hutias; mass range 0.02-16.0 kg.

Carnivora (22 spp.): Procyonidae (8 spp. incl. Potos, Nasua), Mustelidae (6 spp.), Viverridae (4 spp. incl. Arctictis binturong), Ursidae (4 spp.); mass range 0.3-65.0 kg.

Xenarthra (14 spp.): Bradypodidae (4 spp.), Megalonychidae (2 spp.), Myrmecophagidae (4 spp.), Cyclopedidae (4 spp.); mass range 0.18-8.5 kg.

Scandentia, Dermoptera, Chiroptera, Pholidota, Eulipotyphla, Hyracoidea: 30 spp. total; specialists in arboreal roosting or scansorial foraging.

Total: 214 species; 1,847 museum specimens measured; 38 traits quantified per species (mean 8.6 specimens per species for appendicular skeleton traits).