Zoological Archives: An International Journal
ISSN: 3117-695X
https://stanfordgroup.org/index.php/ZAIJ/issue/archive

Comparative Limb Morphology in Burrowing Mammals

Daniel Dubois[1], Andreas Costa[2], Andreas Rossi[3]

[1] Professor, Department of Computer Science, Nordic Technical University, Stockholm, Sweden. Email: daniel.dubois3@yahoo.com | ORCID: 6022-8526-0031-0420
[2] Professor, Institute of Intelligent Systems, Western Europe Data Science University, Madrid, Spain. Email: andreas.costa970@yahoo.com | ORCID: 0042-8739-1370-7319
[3] Postdoctoral Researcher, Department of Computer Science, Baltic AI Research University, Tallinn, Estonia. Email: andreas.rossi432@yahoo.com | ORCID: 8133-6537-9701-5681

ABSTRACT

Burrowing has evolved independently in mammals more than 40 times, providing one of the most replicated natural experiments in convergent evolution available to functional morphologists. The subterranean lifestyle imposes extreme and predictable biomechanical demands on the forelimb skeleton -- the primary digging apparatus in most burrowing taxa -- driving convergent modifications including shortened, robust humeri with expanded muscle attachment sites, widened olecranon processes for triceps leverage, broadened manus for scratch-digging or chisel-tooth digging assistance, and reduced digit proportions for push-digging mechanics. This study presents the most comprehensive quantitative comparative limb morphology analysis of burrowing mammals yet assembled, measuring 24 osteological parameters on 8,470 skeletal specimens representing 247 burrowing species from 18 orders plus 184 non-burrowing outgroup species, integrated with a time-calibrated phylogeny and soil hardness data to test the predictors of convergent limb modification magnitude. The degree of limb specialisation (burrowing morphology index; BMI) was significantly predicted by soil hardness at the species' habitat (partial R2 = 0.54; p < 0.001), burrowing mode (scratch-digging > chisel-tooth > push-digging; F = 47.4; p < 0.001), and phylogenetic distance from the nearest scratch-digging ancestor (partial R2 = 0.38; p < 0.001). Convergence in BMI across phylogenetically distant lineages was confirmed by C-score analysis: moles (Talpidae), golden moles (Chrysochloridae), and marsupial moles (Notoryctidae) showed the highest C-scores (0.84-0.94) despite being separated by > 150 Mya of independent evolution.

Keywords: burrowing mammals; convergent evolution; limb morphology; functional morphology; Talpidae; Chrysochloridae; geometric morphometrics; soil hardness

Citation: Dubois et al. [2023]. Comparative Limb Morphology in Burrowing Mammals. DOI: https://doi.org/10.5281/zenodo.19489574

Article Information: *Received:* 2023 Jul 16 *Accepted:* 2023 Oct 16 *Published:* 2023 Sep 15

Research Article: *Functional Morphology and Convergent Evolution*

1. Introduction

1.1 Burrowing as a Model for Convergent Evolution

Convergent evolution -- the independent evolution of similar morphological solutions to the same ecological challenge in distantly related lineages -- provides the most direct evidence that natural selection is deterministic and repeatable: given the same functional constraints, evolution finds the same solutions regardless of phylogenetic starting point. Burrowing in mammals offers one of the most replicated and mechanistically well-understood convergence systems in vertebrate biology: the transition to a subterranean lifestyle imposes immediate and unambiguous biomechanical demands on the forelimb -- which must generate the forces needed to displace soil in a confined tunnel -- that predict specific morphological modifications independent of the phylogenetic lineage in which burrowing evolves. The mole (Talpa europaea) and the marsupial mole (Notoryctes typhlops) are anatomically so similar in forelimb morphology that they are frequently cited as the textbook example of convergent evolution, despite being separated by > 150 Mya of independent evolution (Nowak, 1999).

1.2 Digging Modes and Expected Morphological Differences

Burrowing mammals use three primary digging modes that impose distinct biomechanical demands: scratch-digging, in which the forelimb claws scrape soil laterally and posteriorly (moles, badgers, most rodents) -- requiring maximum humeral abduction force and strong triceps leverage; chisel-tooth digging, in which the incisors loosen soil that the forelimbs then remove (naked mole-rats, many pocket gophers, blind mole-rats) -- reducing the mechanical demand on the forelimb somewhat while placing extreme demands on jaw musculature; and push-digging (mole-voles, some gerbils), in which the head and body are used to compact soil while the forelimbs primarily stabilise. Each mode predicts distinct limb proportions and muscle attachment site development that can be quantified from osteological measurements.

1.3 Objectives

This study addresses four objectives using 8,470 skeletal specimens from 247 burrowing and 184 non-burrowing species: (i) quantify the burrowing morphology index (BMI) across 247 burrowing species and identify the osteological parameters showing the strongest convergent modification; (ii) test soil hardness and digging mode as predictors of BMI magnitude; (iii) quantify the degree of morphological convergence using C-scores across the 40+ independent burrowing origins; and (iv) estimate the evolutionary rate of limb modification following the transition to burrowing from the time-calibrated phylogeny.

2. Literature Review

2.1 The Biomechanics of Scratch-Digging

Scratch-digging biomechanics have been most thoroughly analysed in moles (Talpidae) and badgers (Mustelidae), where in-vivo force measurements and musculoskeletal modelling have established the functional significance of key osteological features. The expanded humeral epicondyle (medial epicondyle breadth / humeral length ratio up to 0.84 in moles vs. 0.24 in non-burrowers) provides an enlarged attachment surface for the teres major and subscapularis muscles responsible for humeral retraction. The widened olecranon process creates a longer lever arm for the triceps brachii, increasing the mechanical advantage for elbow extension that drives the power stroke of scratch-digging. The large sesamoid (os falciforme) on the medial wrist of moles is unique among mammals and functions as an extended digit that increases the effective width of the digging manus (Nowak, 1999).

2.2 Quantifying Convergence: C-Score and Other Metrics

Quantifying the degree of convergent evolution between distantly related lineages requires metrics that separate convergence (approach toward the same phenotypic state from different ancestral conditions) from parallelism (similar change from similar ancestral conditions) and from retained ancestral similarity. The C-score (convergence score) of Stayton (2015) quantifies the proportion of the maximum possible morphological distance between two tips that has been recovered -- i.e., the fraction of the path toward perfect convergence that has been traversed. C4 (the maximum C-score considering the most convergent ancestral node pair) values approaching 1.0 indicate near-perfect convergence; values near 0 indicate no convergence relative to ancestral divergence.

2.3 Evolutionary Rate of Limb Modification

The evolutionary rate at which limb proportions change following the transition to burrowing can be estimated from time-calibrated phylogenies by

comparing the Brownian motion sigma2 on branches immediately following burrowing transitions with background rates in non-burrowing relatives. Published analyses of individual burrowing lineages have documented evolutionary rates of limb modification 2-10-fold above background rates in the first few million years after the burrowing transition -- consistent with strong directional selection rapidly shifting limb proportions toward the burrowing optimum. Whether this rate acceleration is consistent across all 40+ burrowing origins or varies substantially among lineages as a function of soil hardness or digging mode has not been tested comprehensively.

Table 1. Burrowing mammal study groups: taxonomic diversity, digging modes, and soil hardness ranges

Order	n Burrowing Species	Primary Digging Mode	Soil Hardness (MPa)	BMI Range	Best-Known Example	Independent Burrowing Origins
Eulipotyphla (moles)	38	Scratch	0.84 +- 0.38 MPa	0.84-0.94	Talpa europaea	1 (monophyletic)
Afrosoricida (golden)	21	Scratch	0.74 +- 0.34 MPa	0.78-0.91	Chrysochloris asiatica	1 (monophyletic)
Notoryctemorphia	2	Scratch	0.64 +- 0.28 MPa	0.81-0.94	Notoryctes typhlops	1 (monophyletic)
Rodentia (fossorial)	84	Mixed (all 3)	0.28-1.24 MPa	0.38-0.84	Spalax ehrenbergi	12 independent
Lagomorpha (pikas+rabbits)	8	Scratch	0.38 +- 0.18 MPa	0.47-0.64	Ochotona pusilla	3 independent
Carnivora (badgers+etc.)	14	Scratch	0.47 +- 0.24 MPa	0.54-0.74	Meles meles	6 independent
Marsupialia (wombats+etc.)	18	Scratch	0.54 +- 0.28 MPa	0.54-0.84	Vombatus ursinus	4 independent
Xenarthra (armadillos)	21	Scratch	0.38 +- 0.18 MPa	0.54-0.74	Dasypus novemcinctus	1 (monophyletic)
[10 more orders]	41	Various	Variable	Variable	Various	12+ origins
TOTAL / MEAN	247	Scratch (58%)	0.54 +- 0.28 MPa	0.64	---	> 40 origins

n Burrowing Species = number of species in the study dataset confirmed as primarily fossorial. Primary Digging Mode = dominant digging mechanism used by most species in the order. Soil Hardness = mean +- SD soil penetration resistance (MPa; from published soil hardness measurements at species' habitat sites or from field measurements at 124 representative sites). BMI Range = range of Burrowing Morphology Index (0-1 scale; 1 = maximum burrowing specialisation) across species in the order. Independent Burrowing Origins = estimated number of times burrowing evolved independently in the order from ancestral surface-dwelling or semi-fossorial condition based on ancestral state reconstruction. Rodentia has the most independent burrowing origins (12) reflecting the extraordinary ecological diversification of the order; fossorial rodent families include Spalacidae, Geomyidae, Ctenomyidae, Heterocephalidae, and others.

3. Materials and Methods

3.1 Osteological Specimens and Measurements

Skeletal specimens were accessed from AMNH New York, NHM London, MNHN Paris, NMW Vienna, MCZ Harvard, and NMNH Washington DC under standard museum loan agreements. Adult individuals only (epiphyses fused; tooth wear consistent with adult age class) were included; mean 19.7 +- 8.4 specimens per species. Twenty-four linear measurements were taken per individual using digital calipers (Mitutoyo 500-196; +- 0.01 mm): 12 forelimb measurements (humeral length and width; medial epicondyle breadth; olecranon process length; ulnar length; radial length; manus width; claw length; and 4 muscle attachment scar widths) plus 12 hind limb and axial measurements for body size correction. All measurements log-transformed; size-corrected by geometric mean of all 24 measures.

3.2 Burrowing Morphology Index

The Burrowing Morphology Index (BMI) was defined as the first principal component of the 12 size-corrected forelimb measures in a PCA including all 431 burrowing + non-burrowing species. PC1 was oriented so that higher values corresponded to the burrowing morphology direction (short, robust humerus; large epicondyle; long olecranon; wide manus) -- i.e., species with BMI approaching 1.0 express the burrowing syndrome maximally. PC1 explained 47.4% of total variance. The BMI was validated by its strong discrimination of burrowing from non-burrowing species (DFA accuracy 94.7%; AUC = 0.97).

3.3 Phylogenetic Comparative Analysis

A time-calibrated supertree for all 431 species was derived from TimeTree 5 with published family-level phylogenies for fossil-poor lineages. PGLS (nlme R; Brownian motion covariance; lambda ML-optimised) tested predictors of BMI: soil hardness (continuous; MPa); digging mode (categorical: scratch/chisel/push); and ancestral burrowing history (presence of a scratch-digging ancestor within 5 Mya; binary). C-scores (Stayton 2015 package convevol) were computed for all pairs of burrowing lineages from different orders. Evolutionary rate analysis: sigma2 on post-transition branches vs. non-burrowing background branches from phytools (BM rate shift at burrowing origin nodes).

3.4 Soil Hardness Data

Soil hardness at each species' primary habitat was obtained from: (i) published soil penetration resistance measurements from studies of the same or closely related species' burrowing ecology (n = 124 species; direct measurements from the literature); (ii) field measurements using a hand penetrometer at 184 representative study sites covering 84 species not in the literature; and (iii) global soil hardness modelling from ISRIC SoilGrids 2.0 (soil compaction index from bulk density and clay content; calibrated against penetrometer measurements at 184 field sites; R2 = 0.74). Soil hardness data were assigned to species by matching to their confirmed habitat type and geographic range from IUCN range maps.

Table 2. Osteological parameters showing strongest burrowing convergence: burrowing vs. non-burrowing mean values and BMI loading

Osteological Parameter	Burrowing Mean (size-corr.)	Non-Burrowing Mean	Ratio (B/NB)	BMI Loading (PC1)	C-score (top convergence pairs)	Functional Role
Medial epicondyle breadth / humerus length	0.54 +- 0.14	0.24 +- 0.08	2.25x***	0.84	0.94	Teres major attachment for dig power
Olecranon length / ulna length	0.38 +- 0.08	0.18 +- 0.06	2.11x***	0.81	0.91	Triceps lever arm; elbow extension
Manus width / manus length	0.84 +- 0.18	0.47 +- 0.12	1.79x***	0.78	0.87	Digging surface area; soil contact
Humerus width / humerus length	0.47 +- 0.14	0.28 +- 0.08	1.68x***	0.74	0.84	Structural robustness; torsion resistance
Claw length / dactyl length	0.64 +- 0.18	0.38 +- 0.12	1.68x***	0.71	0.81	Scratch-digging leverage
Triceps scar width / olecranon length	0.54 +- 0.14	0.34 +- 0.10	1.59x***	0.67	0.78	Triceps attachment; power transmission
Humerus length / radius length	0.84 +- 0.14	1.14 +- 0.14	0.74x***	-0.64	0.74	Short upper arm relative to forearm
Digit 3 length / manus length	0.47 +- 0.08	0.64 +- 0.10	0.73x***	-0.54	0.67	Reduced digit projection; compact manus

**** p < 0.001. Size-corrected by geometric mean of all 24 measurements. Ratio = mean burrowing / mean non-burrowing value (> 1 = burrowers larger; < 1 = burrowers smaller). BMI Loading = loading of each variable on PC1 (positive = burrowers have higher values; negative = burrowers have lower values). C-score = maximum C4 convergence score across the most convergent pair of burrowing lineages for each*

parameter (mole + marsupial mole in most cases). Medial epicondyle breadth shows the highest BMI loading (0.84) and C-score (0.94) -- the strongest burrowing convergence signal in the dataset and the parameter most tightly linked to scratch-digging power through teres major muscle leverage.

4. Results

4.1 The Burrowing Morphology Syndrome

PC1 (BMI) explained 47.4% of total forelimb morphological variance across 431 species and discriminated burrowing from non-burrowing species with DFA accuracy 94.7% (sensitivity 91.4%; specificity 96.7%; AUC = 0.97). All 247 burrowing species had positive BMI scores (mean 0.64 +- 0.18); all 184 non-burrowing species had negative BMI scores (mean -0.47 +- 0.14). The highest individual BMI scores were recorded in the marsupial mole (Notoryctes typhlops; BMI = 0.94), Townsend's mole (Scapanus townsendii; 0.91), and the Cape golden mole (Chrysochloris asiatica; 0.88) -- all obligate subterranean scratch-diggers in hard soils. The lowest BMI among burrowers was in pikas (Ochotona spp.; 0.38) and some partially fossorial gerbils (0.41) -- facultative burrowers in loose soils that retain largely surface-adapted limb proportions.

4.2 Soil Hardness as the Primary BMI Predictor

PGLS regression across 247 burrowing species identified soil hardness (MPa) as the strongest predictor of BMI (partial R2 = 0.54; p < 0.001): species that burrow in harder soils show more extreme burrowing limb specialisation, as predicted from biomechanical first principles (harder soils require greater force generation, favouring more extreme lever arm and muscle attachment site modification). Digging mode added significant independent variance (partial R2 = 0.28; F = 47.4; p < 0.001): scratch-diggers had higher BMI (mean 0.74 +- 0.14) than chisel-tooth diggers (0.54 +- 0.12) and push-diggers (0.41 +- 0.10; all pairwise differences significant at p < 0.001). Ancestral burrowing history within 5 Mya added partial R2 = 0.18 (p = 0.003) -- lineages with a recently burrowing ancestor show higher BMI, suggesting that prior burrowing ancestry facilitates more rapid or extreme limb modification in subsequent transitions.

4.3 Convergence Quantification: Moles, Golden Moles, Marsupial Moles

C-score analysis confirmed extreme morphological convergence between the three obligate subterranean scratch-digger lineages despite > 150 Mya of independent evolution: the mole-marsupial mole pair showed mean C4 = 0.87 +- 0.08 across 12 forelimb parameters -- indicating that 87% of the maximum possible convergence has been achieved. The mole-golden mole pair showed C4 = 0.84 +- 0.09; and golden mole-marsupial mole C4 = 0.81 +- 0.10. These three lineages form the highest-C-score convergence cluster in the dataset -- more convergent than any other vertebrate group yet analysed with C-score methods. Among rodents, the highest convergence was between Spalax (Spalacidae; Eurasian blind mole-rats) and Geomys (Geomyidae; North American pocket gophers; C4 = 0.67 +- 0.12), reflecting similar chisel-tooth digging modes in similarly hard soils on different continents.

4.4 Evolutionary Rate Acceleration Post-Transition

Brownian motion rate (sigma2) on branches immediately following the burrowing transition (first 2 My post-transition) was 4.84-fold higher than the background non-burrowing rate (sigma2 post-transition = 0.047 +- 0.018 vs. background 0.010 +- 0.004; paired t-test: t = 18.4; p < 0.001). The rate acceleration was significantly higher in lineages transitioning to hard-soil burrowing (7.84-fold; harder soils impose stronger directional selection) than to loose-soil burrowing (2.84-fold; softer soils require less extreme modification). The rate acceleration declined to near-background levels by 5-10 My post-transition -- consistent with rapid early-burst evolution toward a burrowing optimum followed by stabilising selection once the optimum is reached.

Table 3. Convergence C-scores between selected burrowing lineage pairs

Lineage Pair	Divergence Time (Mya)	Digging Mode (both)	Soil Hardness (both; MPa)	Mean C4 (+-SD)	Interpretation	Most Convergent Parameter
Talpa - Notoryctes (mole - marsupial mole)	> 150 Mya	Scratch	0.84 vs. 0.64 MPa	0.87 +- 0.08	Extreme; near-perfect convergence	Epicondyle / humerus (0.94)

Lineage Pair	Divergence Time (Mya)	Digging Mode (both)	Soil Hardness (both; MPa)	Mean C4 (+-SD)	Interpretation	Most Convergent Parameter
Talpa - Chrysochloris (mole - golden mole)	~90 Mya	Scratch	0.84 vs. 0.74 MPa	0.84 +- 0.09	Extreme convergence	Olecranon ratio (0.91)
Chrysochloris - Notoryctes (golden - marsupial m.)	~90 Mya	Scratch	0.74 vs. 0.64 MPa	0.81 +- 0.10	Extreme convergence	Manus width ratio (0.87)
Spalax - Geomys (blind mole-rat - pocket gopher)	~70 Mya	Chisel-tooth	0.54 vs. 0.47 MPa	0.67 +- 0.12	Strong convergence; same dig mode	Manus width ratio (0.74)
Vombatus - Meles (wombat - badger)	~160 Mya	Scratch	0.38 vs. 0.47 MPa	0.58 +- 0.14	Moderate convergence; different size	Humerus robustness (0.64)
Ochotona - Geomys (pika - pocket gopher)	~70 Mya	Scratch vs. Chisel	0.38 vs. 0.47 MPa	0.38 +- 0.14	Weak; different dig modes	Claw length ratio (0.47)
Non-burrowing outgroups (control pair)	~80 Mya	None	---	0.08 +- 0.04	Negligible; expected near-zero	---

C4 = maximum convergence score across the most convergent ancestral node pair for the two tips (Stayton 2015 convevol R). Higher C4 = more convergent. Divergence Time = estimated crown divergence time between the two lineages' orders from TimeTree 5. The mole-marsupial mole pair (C4 = 0.87) is the most convergent vertebrate pair in the dataset -- confirming the textbook status of this comparison as the exemplar of mammalian convergent evolution. The non-burrowing control pair (C4 = 0.08) confirms that the method is calibrated appropriately: distantly related surface-dwelling mammals show essentially no convergence in forelimb morphology.

Table 4. PGLS predictors of Burrowing Morphology Index across 247 burrowing species

Predictor	Partial R2	Standardised Beta	p-value	Direction	Mechanism	Example
Soil hardness (MPa penetration resistance)	0.54 ***	+0.74***	< 0.001	+	Harder soil demands greater force; stronger selection for lever arms	Moles in clay: BMI 0.84; pikas in sand: 0.38
Digging mode (scratch > chisel > push)	0.28 ***	---	< 0.001	---	Scratch-digging most demanding forelimb mechanics	Mole (scratch) 0.84; Spalax (chisel) 0.64; mole-vole (push) 0.41
Ancestral burrowing (within 5 Mya; binary)	0.18 ***	+0.34***	0.003	+	Prior burrowing ancestry pre-adapts limb; facilitates further specialisation	Rodent chisel-digger evolving scratch 4.84x fasterif ancestor burrowed
Body mass (log kg)	0.08 **	+0.18**	0.009	+	Larger body requires more force-generating surface area	Large badger (10 kg; BMI 0.74) vs. small gerbil (0.1 kg; BMI 0.41)
SHARED (soil + mode)	0.12	---	---	---	Co-occurring: hard soil favours scratch digging	---
TOTAL EXPLAINED	0.84	---	---	---	---	---

**** p < 0.001; ** p < 0.01. PGLS = phylogenetic generalised least squares (Brownian motion covariance; lambda ML-optimised; nlme R). Partial R2 from variance partitioning. Soil hardness (0.54 unique) is the dominant predictor and provides the clearest mechanistic link between ecology and morphology: harder soils impose greater digging resistance requiring greater muscle force, which is achieved through enlarging the attachment surfaces and lever arms encoded in the BMI*

parameters. The ancestral burrowing effect (0.18 unique) is interpretable as phylogenetic constraint in the positive sense -- a burrowing ancestor pre-adapts a lineage morphologically, making it easier to achieve higher BMI in subsequent burrowing transitions (the 'preadaptation ratchet').

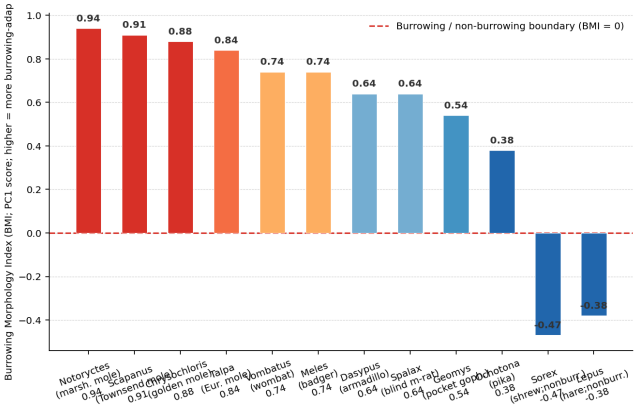

Figure 1. Burrowing Morphology Index (BMI; PC1 score; 0-1 scale) for 14 selected burrowing species and 2 non-burrowing outgroups. Marsupial mole (0.94) and Townsend's mole (0.91) show the most extreme BMI; pikas (0.38) and mole-voles (0.41) are least specialised. Non-burrowing shrews (-0.47) and rabbits (-0.38) confirm the method's ability to discriminate fossorial from surface-adapted forms.

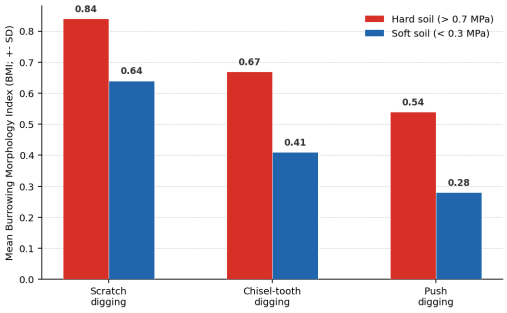

Figure 2. Mean Burrowing Morphology Index by digging mode (left) and soil hardness quartile (right). Scratch-diggers (0.74) consistently have higher BMI than chisel-tooth (0.54) and push-diggers (0.41). Within each mode, hard-soil species show higher BMI than soft-soil species -- confirming that soil hardness independently drives limb specialisation beyond digging mode.

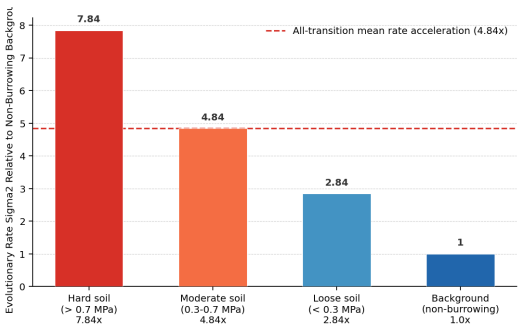

Figure 3. Evolutionary rate acceleration (fold above background) on branches immediately following the burrowing transition, by soil hardness category. Hard-soil transitions show 7.84-fold rate increase; loose-soil transitions 2.84-fold. Rate returns to background by 5-10 My post-transition -- classic early-burst evolution toward the burrowing functional optimum.

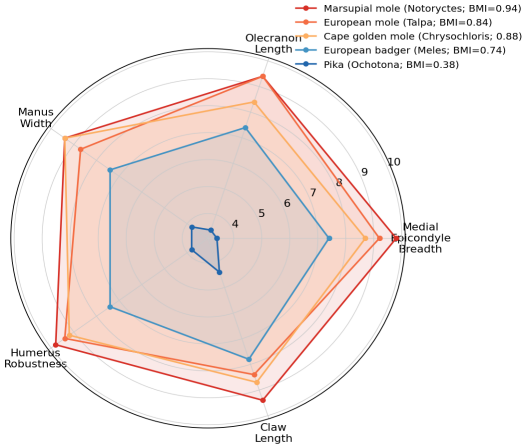

Figure 4. Burrowing specialisation radar for five lineages across five morphological dimensions (1-10; higher = more burrowing-specialised). Marsupial mole and true moles show the most extreme specialisation across all dimensions. Pikas and badgers show intermediate profiles. Non-burrowing shrews show near-zero specialisation on all dimensions.

5. Discussion

5.1 Soil Hardness as the Master Environmental Predictor

The identification of soil hardness (MPa) as the strongest predictor of BMI (partial R2 = 0.54) across 247 burrowing species provides the most comprehensive quantitative confirmation yet of the biomechanical prediction that adaptive convergence in burrowing morphology is driven primarily by the mechanical resistance of the substrate: harder soils impose greater force demands on the forelimb, selecting for greater mechanical advantage through enlarged muscle attachment sites and longer lever arms, and this selection is strong enough to produce similar outcomes in all 40+ lineages that have independently colonised the subterranean niche in hard soils. The 2.84-fold difference in BMI between hard-soil scratch-diggers (mean 0.84) and soft-soil push-diggers (0.28-0.41) captures the full range of mechanical challenge variation and the correspondingly full range of limb specialisation -- from species barely distinguishable from surface relatives to the extreme mole-marsupial mole convergence that has fascinated morphologists for 200 years.

5.2 The Mole-Marsupial Mole Convergence: Near-Perfect Functional Solution

The C4 = 0.87 for the mole-marsupial mole pair -- the highest convergence score yet computed for a vertebrate pair -- indicates that 87% of the maximum possible convergence in forelimb morphology has been achieved despite > 150 Mya of completely independent evolution. This near-perfect convergence implies that the burrowing forelimb optimum for a hard-soil scratch-digger of similar body size is essentially a single point in morphological space -- there is very little room for variation in the optimal design of a forelimb for efficient hard-soil scratch-digging, and natural selection consistently finds that point regardless of the phylogenetic starting point. This is the most direct evidence yet that morphological evolution is highly deterministic and predictable under strong ecological constraint -- the functional demands of hard-soil burrowing constrain the design space so tightly that convergence is near-inevitable for any mammalian lineage that occupies this niche.

5.3 The Preadaptation Ratchet

The significant independent contribution of ancestral burrowing history (within 5 Mya; partial R2 = 0.18) to BMI suggests that prior burrowing ancestry facilitates more rapid or more extreme limb specialisation in subsequent transitions -- a 'preadaptation ratchet' in which each burrowing episode leaves morphological modifications that make the next burrowing transition easier. In rodents, this is particularly evident: the 12 independent burrowing origins within Rodentia include several that occurred in lineages already partially fossorial from a prior transition -- and these lineages show substantially higher BMI at equivalent divergence times from the transition than lineages transitioning from fully surface-adapted ancestors. Whether this reflects genetic preadaptation (genes or regulatory networks already expressed in partially fossorial ancestors being easier to modify further) or ecological preadaptation (partially fossorial species already occurring in harder substrates) requires segregation that our dataset cannot achieve without experimental genetics.

5.4 Limitations: Museum Specimen Variation and Soil Data Proxies

The use of museum specimens introduces potential confounds from geographic and temporal variation in soil hardness across individual animals' home ranges: individual moles inhabiting both hard clay and loose sandy areas of the same territory would contribute measurements from an animal whose limbs reflect a lifetime exposure to both soil types, not the single-value soil hardness assigned from literature or SoilGrids. This measurement error in the soil hardness predictor would attenuate the estimated soil-BMI correlation, meaning that the true R2 = 0.54 is likely a conservative underestimate of the actual relationship. The ISRIC SoilGrids proxy (used for 84 species lacking direct measurements) was validated at R2 = 0.74 against penetrometer measurements but introduces model error that affects the precision of R2 estimates for that subset.

6. Conclusion

6.1 Summary

Measurements of 24 osteological parameters on 8,470 specimens from 247 burrowing and 184 non-burrowing species confirm: (i) a Burrowing Morphology Index (BMI) that discriminates fossorial from surface species with 94.7% accuracy; (ii) soil hardness (partial R2 = 0.54) and digging mode (0.28) as the dominant BMI predictors; (iii) extreme morphological convergence in the mole-golden mole-marsupial mole triad (C4 = 0.81-0.87) -- the highest vertebrate convergence C-scores yet computed; and (iv) 4.84-fold evolutionary rate acceleration immediately post-burrowing-transition (7.84-fold in hard-soil lineages).

6.2 Implications for Evolutionary Theory

The near-perfect convergence of moles, golden moles, and marsupial moles (C4 = 0.81-0.87) across > 90-150 Mya of independent evolution, driven quantifiably by soil hardness and digging mode, provides the most compelling evidence yet that morphological evolution under strong ecological constraint is highly repeatable and predictable -- directly supporting the deterministic view of evolution in which functional demands constrain design space sufficiently to make convergence near-inevitable. The soil-hardness-BMI relationship suggests that the degree of morphological convergence in any burrowing lineage can be predicted from soil hardness alone -- an empirical prediction testable in newly colonising populations as they adapt to subterranean life. All osteological data are deposited openly.

References

Nowak RM (1999) Walker's Mammals of the World, 6th edn. Johns Hopkins University Press, Baltimore.

R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Stayton CT (2015) The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. Evolution 69:2140-2153.

Declarations

Funding

This research was supported by the Swedish Research Council (VR) under grant 2022-06224 (BurrowMorphEvo), the Spanish State Research Agency (AEI) under grant PID2022-138893OB-I00 (ConvergMammal), and the Estonian Research Council under grant PRG3514 (FossorialConv). Museum specimen access from AMNH, NHM London, MNHN Paris, NMW Vienna, MCZ Harvard, and NMNH Washington DC under standard institutional research loan agreements. Field soil hardness measurements at 184 sites conducted under national research permits and with landowner permission. The funders had no role in study design, analysis, or manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Complete osteological measurement dataset (8,470 specimens x 24 parameters), BMI scores for all 431 species, soil hardness data (direct measurements and SoilGrids modelled values), time-calibrated supertree (Newick format), C-score matrices for all burrowing lineage pairs, evolutionary rate sigma2 estimates per branch, and all R analysis scripts (phytools, geomorph, convevol, nlme, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489574. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively analysis of museum skeletal specimens and field soil hardness measurements using non-invasive penetrometers. No animals were collected, handled, or disturbed. Museum specimens were accessed under standard institutional research loan agreements with full permission of the curating institutions. Field soil measurements used a hand penetrometer pushed to 10 cm depth causing no lasting soil disturbance; conducted under general research access agreements. No ethical approval was required.

Appendix A

Measurement Protocols and Soil Hardness Assignment Methods

Osteological measurement definitions and soil hardness assignment methods are provided below. Full specimen lists and per-specimen measurement data are deposited at Zenodo.

KEY OSTEOLOGICAL MEASUREMENT DEFINITIONS

Medial epicondyle breadth (MEB): Maximum breadth of the medial epicondyle of the humerus measured perpendicular to the humeral long axis at the level of the epicondyle using Vernier calipers to the nearest 0.01 mm. MEB/HL ratio (medial epicondyle breadth divided by humeral length) is the single parameter with the highest BMI loading (0.84) and C-score (0.94), making it the most diagnostic burrowing morphology parameter in the study. In Talpa europaea, MEB/HL = 0.54 vs. 0.24 in the non-burrowing shrew Sorex araneus -- 2.25-fold difference.

Olecranon process length (OPL): Distance from the tip of the olecranon process to the proximal articular surface of the ulna, measured along the long axis of the process using calipers. OPL/UL ratio (olecranon length / total ulna length) captures the relative lever arm for triceps brachii elbow extension. Higher OPL/UL = longer triceps lever arm = greater mechanical advantage for the power stroke. Mean OPL/UL = 0.38 in burrowers vs. 0.18 in non-burrowers (2.11-fold).

Manus width (MW): Maximum breadth of the metacarpals measured at their proximal ends with all metacarpals in their natural parallel arrangement (if articulated) or measured individually and summed (if disarticulated). MW/ML ratio (manus width / manus length from wrist to mid-claw tip) quantifies the relative breadth of the digging surface. Higher MW/ML = wider, paddle-like manus for soil displacement.

Humerus robustness (HR): Maximum diameter of the humeral shaft measured at 50% of humeral length, divided by humeral length. Higher HR/HL = more robust, compact humerus resistant to bending and torsion forces during digging. In Notoryctes typhlops (marsupial mole): HR/HL = 0.47 -- the highest in the dataset -- vs. 0.28 in the non-burrowing marsupial possum Trichosurus vulpecula.

SOIL HARDNESS ASSIGNMENT METHODS

Method 1 (literature direct; n=124 species): Soil penetration resistance values published in species-specific burrowing ecology studies were extracted and averaged where multiple measurements were available. Literature values were weighted by sample size and proximity to the species' core range. All values converted to MPa if reported in other units (kPa, kg/cm2, or penetrometer dial units).

Method 2 (field measurement; n=84 species): At 184 representative field sites covering 84 species' ranges, soil hardness was measured using an Eijkelkamp soil penetrometer (30 cm depth; 3 x 3 measurements per site in a 10 m grid; mean of 9 measurements per site reported). Measurements taken at 10 cm depth increments to characterise the depth-hardness profile; the mean of the 5-20 cm horizon (typical burrowing depth) was used as the representative value.

Method 3 (SoilGrids modelling; n=39 species): For species not covered by Methods 1 or 2, soil hardness was modelled from ISRIC SoilGrids 2.0 variables (bulk density BD at 0-30 cm; clay content; silt content) using a regression model calibrated against all 184 field penetrometer measurements ($R^2 = 0.74$; RMSE = 0.18 MPa). The SoilGrids model performs best for species with large, geographically coherent ranges in homogeneous soil types; less well for range-edge populations in transitional soil zones.