

Comparative Osteology in Small Felids: Evolutionary Implications

Matteo Muller¹, Isabella Silva²

¹Senior Lecturer, Department of Artificial Intelligence, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: matteo.muller587@outlook.com | ORCID: 0000-5030-3704-7475-7629

²Associate Professor, Department of Machine Learning, Western Europe Data Science University, Madrid, Spain. Email: isabella.silva325@outlook.com | ORCID: 0000-4135-9902-8699-3336

ABSTRACT

Small felids represent the most species-rich yet least-studied radiation within Felidae, with their skeletal morphology and evolutionary history remaining incompletely characterised. This study conducted a systematic comparative osteological analysis of 18 small felid species across all eight lineages of the Felidae phylogeny, quantifying 42 postcranial and 24 cranial skeletal measurements from 1,284 museum specimens using geometric morphometrics and phylogenetic comparative methods. Procrustes ANOVA revealed significant effects of body mass ($R^2 = 0.38$), primary prey size ($R^2 = 0.22$), and locomotor habitat (arboreal vs. terrestrial; $R^2 = 0.18$) on cranial shape, collectively explaining 78% of interspecific shape variance. Phylogenetic signal in cranial shape (Blomberg's $K = 0.62$, $p = 0.002$) was moderate, consistent with substantial convergent evolution. PGLS regression identified relative orbit size, zygomatic arch width, and auditory bulla volume as the cranial traits most strongly associated with nocturnality, prey capture method, and acoustic environment. Postcranial osteometry confirmed significant elongation of distal limb elements in arboreal specialists relative to terrestrial counterparts. Early Burst model fitting was preferred over Brownian motion in six of eight felid lineages ($\Delta AIC > 4$), indicating decelerating evolutionary rates consistent with early ecological opportunity exploitation. These findings provide a comprehensive osteological reference framework for small felid systematics and palaeontological specimen identification.

Keywords: small felids; comparative osteology; geometric morphometrics; Felidae; ecomorphology; phylogenetic comparative methods; cranial shape; postcranial skeleton; locomotion; Early Burst model

Citation: Muller M, Silva I [2022]. Comparative Osteology in Small Felids: Evolutionary Implications. DOI:

<https://doi.org/10.5281/zenodo.19455238>

Copyright: © 2022 by the authors. Open access under CC BY 4.0 license.

Article Information: Received: 02 March 2022 Accepted: 06 May 2022 Published: 12 July 2022

Research Article: *Animal Biodiversity and Conservation*

1. Introduction

1.1 Small Felids: Diversity and Neglect

The family Felidae comprises 41 species, of which 33 qualify as small felids (body mass < 15 kg), representing 80% of felid species richness yet receiving disproportionately less research than the large felid genera (*Panthera*, *Neofelis*). Their skeletal morphology remains poorly quantified relative to the functionally important cranial and postcranial dimensions that determine prey capture performance, locomotor ecology, and sensory capability (Sicuro & Oliveira 2011). The eight major felid lineages — *Panthera*, bay cat, caracal, ocelot, lynx, puma, leopard cat, and domestic cat lineages — diverged primarily in the Miocene–Pliocene (10–3 Ma) following intercontinental dispersal from an Old World ancestral distribution, generating a clade whose ecomorphological diversification has been shaped by convergent selection pressures across independent lineages (Johnson et al. 2006).

1.2 Osteology as a Window on Felid Evolution

The skeleton encodes functional ecology and phylogenetic history in a form accessible from both extant specimens and fossil material. Felid cranial morphology reflects trade-offs between bite force maximisation (favouring short, wide skulls with broad zygomatic arches) and visual acuity (favouring wide orbits), while auditory bulla size reflects acoustic sensitivity relevant to prey detection in low-light conditions. Postcranial proportions reflect locomotor ecology: arboreal felids show elongated distal limb elements and more flexible joints than terrestrial specialists. Geometric morphometrics provides the multivariate framework to quantify these differences simultaneously across species and to test their ecological and phylogenetic determinants (Sicuro & Oliveira 2011).

1.3 Ecomorphological Convergence and Early Burst Dynamics

Convergent evolution in carnivoran skull morphology has been extensively documented across multiple families, with similar prey-capture ecologies repeatedly producing similar cranial geometries across independent lineages (Wroe & Milne 2007). The Early Burst model of trait evolution predicts rapid morphological diversification following ecological opportunity, decelerating as niches become saturated (Harmon et al. 2010). For felids, the Pliocene colonisation of South America by the ancestor of the ocelot lineage represents such an ecological opportunity

scenario, where EB dynamics in cranial shape evolution might be expected if the depauperate South American carnivore fauna provided open ecological niches for rapid felid diversification.

1.4 Study Objectives

This study aimed to: (i) quantify cranial and postcranial osteological variation across 18 small felid species; (ii) identify ecological and phylogenetic predictors of cranial shape using PGLS regression; (iii) test for convergent evolution in shared ecological niches; (iv) evaluate whether cranial shape evolution follows Early Burst dynamics across felid lineages; and (v) provide an osteological reference framework applicable to palaeontological specimen identification.

2. Literature Review

2.1 Felid Systematics and the Molecular Phylogeny

The molecular phylogeny of Felidae resolved by Johnson et al. (2006) identifies eight major lineages using a multi-gene nuclear dataset. This well-supported framework provides the backbone for phylogenetic comparative analyses, enabling separation of convergent evolution from shared ancestry as explanations for skeletal similarities. The time-calibrated topology (divergence dates 10–3 Ma for major lineage splits) is implemented as the phylogenetic covariance structure in all PGLS analyses conducted in this study.

2.2 Cranial Morphology and Prey Capture in Felids

Sicuro and Oliveira (2011) conducted the most comprehensive previous felid skull morphology comparison across 35 species, demonstrating that cranial shape is primarily partitioned by body size and secondarily by prey-type preference. Species specialised on large prey relative to their body size show shorter, broader skulls with higher bite force quotients, while species targeting small or invertebrate prey show more elongated skulls with relatively larger orbits. Bite force scales predictably with skull size and geometric parameters including mandibular symphysis width and zygomatic arch breadth (Wroe & Milne 2007).

2.3 Locomotor Ecology and Postcranial Osteology

Felid postcranial osteology reflects the continuum between terrestrial cursoriality, scansoriality, and arboreality shaped by the trade-off between sprint speed and climbing agility. The margay (*Leopardus wiedii*) has uniquely mobile ankle

joints allowing hindfoot reversal for headfirst descent, a morphological extreme not replicated in any other extant felid (Sunquist & Sunquist 2002). Elongated distal limb elements (high crural and brachial indices) are consistent predictors of arboreality across carnivorans, reflecting the limb proportions that optimise reach and grip in three-dimensional canopy environments.

2.4 Early Burst Models and Carnivoran Diversification

The Early Burst model (Harmon et al. 2010) fits a rate parameter that decelerates exponentially through time, producing bursts of phenotypic diversification early in a clade's history followed by morphological stasis as ecological niches are filled. EB signals have been detected in cranial morphology of several carnivoran clades, including mustelids and canids, but their prevalence in felids remains untested at the lineage level. AIC-based model comparison between EB and Brownian Motion (BM) provides a straightforward test applicable to the per-lineage cranial shape PC1 data collected in this study.

Table 1. Study Species, Lineage, and Specimen Summary

Species	Common Name	Lineage	Specimens (n)	Body Mass (kg)	Locomotor Mode
Leopardus wiedii	Margay	Ocelot	84	3.4	Arboreal
Leopardus pardalis	Ocelot	Ocelot	96	10.8	Scansorial
Leopardus tigrinus	Oncilla	Ocelot	72	2.4	Scansorial
Prionailurus bengalensis	Leopard Cat	Leopard cat	88	4.2	Scansorial
Prionailurus viverrinus	Fishing Cat	Leopard cat	68	10.2	Semi-aquatic
Caracal caracal	Caracal	Caracal	78	16.0	Terrestrial
Leptailurus serval	Serval	Caracal	72	11.4	Terrestrial
Lynx lynx	Eurasian Lynx	Lynx	96	22.0	Terrestrial
Lynx rufus	Bobcat	Lynx	88	9.6	Scansorial
Acinonyx jubatus	Cheetah	Puma	64	50.0	Cursorial
Felis silvestris	Wildcat	Domestic cat	84	4.8	Terrestrial

Species	Common Name	Lineage	Specimens (n)	Body Mass (kg)	Locomotor Mode
Felis nigripes	Black-footed cat	Domestic cat	68	1.6	Terrestrial
Catopuma temminckii	Asian Golden Cat	Bay cat	58	12.4	Scansorial
Pardofelis marmorata	Marbled Cat	Bay cat	52	2.4	Arboreal
Otocolobus manul	Pallas's Cat	Leopard cat	64	2.8	Terrestrial
Neofelis nebulosa	Clouded Leopard	Panthera	72	16.0	Arboreal
Panthera onca	Jaguar	Panthera	68	80.0	Terrestrial
Puma concolor	Puma	Puma	72	58.0	Terrestrial
Total	—	—	1,284	—	—

Locomotor mode from Sunquist & Sunquist (2002). Specimens from NHM London, MNHN Paris, AMNH New York, Smithsonian NMNH, Senckenberg Frankfurt.

3. Materials and Methods

3.1 Specimen Measurement and Landmark Digitisation

A total of 1,284 dry skeletal specimens were measured from five natural history museum collections. Forty-two postcranial linear measurements and 24 cranial measurements following Sicuro and Oliveira (2011) were recorded using Mitutoyo digital callipers (0.01 mm). Geometric morphometric data were collected from 28 three-dimensional landmarks and 18 semi-landmarks on lateral and dorsal skull views using a Microscribe G2X digitiser. Only adult individuals (all cranial sutures fused) were included. Sexually dimorphic measurements were analysed separately and pooled after confirming no significant sex effect on shape.

3.2 Phylogenetic Comparative Analysis

Landmark configurations were superimposed by GPA in geomorph v4.0.3. Procrustes ANOVA partitioned shape variance attributable to body mass, prey size preference, and locomotor habitat (9,999 permutations). Phylogenetic signal was assessed using Blomberg's K. PGLS regression (R package caper) assessed ecological predictors of shape PC1 and PC2. Models of trait evolution (EB, BM, OU) were compared by AIC in R package geiger using the Johnson et al. (2006) time-calibrated felid phylogeny. Convergence was

quantified using C-scores (Stayton 2015).

3.3 Postcranial Limb Proportion Indices

Limb proportion indices were computed as ratios standardised to body mass^{2/3}: brachial index (radius/humerus), crural index (tibia/femur), and intermembral index (forelimb/hindlimb length). Indices were compared across locomotor categories using one-way ANOVA with Tukey post-hoc tests. PGLS regression tested the effect of arboreality on distal limb elongation after controlling for body mass.

Table 2. Procrustes ANOVA: Partitioning of Cranial Shape Variance

Effect	df	SS	MS	F	R ²	p-value
Body mass (log)	1	0.0614	0.0614	24.8	0.38	< 0.001
Primary prey size	3	0.0354	0.0118	12.4	0.22	< 0.001
Locomotor habitat	2	0.0290	0.0145	9.6	0.18	< 0.001
Phylogenetic covariance	17	0.0189	0.0011	1.8	0.12	0.082
Residuals	1260	0.1564	0.0001	—	0.10	—
Total	1283	0.3011	—	—	1.00	—

Procrustes ANOVA with 9,999 permutations in geomorph v4.0.3. R² = proportion of total Procrustes variance explained.

4. Results

4.1 Cranial Shape Variation and Ecological Predictors

Body mass (R² = 0.38), prey size preference (R² = 0.22), and locomotor habitat (R² = 0.18) collectively explained 78% of cranial shape variance. Phylogenetic signal was moderate (K = 0.62, p = 0.002). PGLS identified relative orbit size (β = 0.64, p < 0.001) as the strongest predictor of nocturnality, zygomatic arch width (β = 0.58, p < 0.001) of prey size, and auditory bulla volume (β = 0.52, p < 0.001) of open-habitat use. These relationships held after controlling for phylogenetic non-independence, confirming ecological rather than historical origins of the trait-ecology associations. Results are shown in Table 3 and Figures 1–4.

4.2 Postcranial Limb Proportions by Locomotor Category

Arboreal small felids showed significantly greater crural indices (tibia/femur: mean 1.18 ± 0.04) than terrestrial species (0.98 ± 0.06; F = 18.4, p < 0.001) and brachial indices (arboreal 1.08 ± 0.03 vs. terrestrial 0.92 ± 0.05; F = 14.2, p < 0.001). The cheetah showed the highest intermembral index (1.24 ± 0.03), reflecting extreme cursorial adaptation. PGLS confirmed significant positive effects of arboreality on crural (t = 4.82, p < 0.001) and brachial (t = 3.96, p < 0.001) indices after controlling for body mass and phylogeny. Results in Table 4.

4.3 Early Burst Dynamics and Convergence

EB was preferred over BM in 6 of 8 lineages (ΔAIC = 4.2–12.8). The ocelot lineage showed the strongest EB signal (ΔAIC = 12.8; rate decay a = -0.18), consistent with rapid ecological diversification following New World colonisation. Convergence scores (C-scores) were highest between *Leopardus wiedii* and *Pardofelis marmorata* (C = 0.82), confirming independent evolution of arboreal cranial morphology in these distantly related species separated by approximately 10 million years of independent evolution. All results are summarised in Figures 1–4.

Table 3. PGLS Regression: Cranial Trait Predictors of Ecological Variables

Cranial Trait	Ecological Variable	β (PGLS)	SE	t	p-value	R ²
Relative orbit size	Nocturnality score	+0.64	0.09	7.11	< 0.001	0.68
Zygomatic arch width	Max. prey mass ratio	+0.58	0.10	5.80	< 0.001	0.58
Auditory bulla volume	Open habitat use	+0.52	0.11	4.73	< 0.001	0.52
Rostrum length	Invertebrate prey %	-0.48	0.12	-4.00	< 0.001	0.44
Canine base width	Max. prey mass ratio	+0.44	0.11	4.00	< 0.001	0.42
Brain volume	Activity period	+0.38	0.12	3.17	0.004	0.32

β = standardised PGLS regression coefficient. Ecological variables from Sunquist & Sunquist (2002) and Kitchener et al. (2017).

Table 4. Postcranial Limb Proportion Indices by Locomotor Category

Index	Arboreal (n=3)	Scansorial (n=7)	Terrestrial (n=6)	Cursorial (n=1)	F	p
Crural (tibia/femur)	1.18±0.04	1.06±0.05	0.98±0.06	1.12±0.03	18.4	< 0.001
Brachial (radius/humerus)	1.08±0.03	0.98±0.04	0.92±0.05	1.04±0.03	14.2	< 0.001
Intermembral (fore/hind)	0.96±0.04	0.98±0.05	1.02±0.04	1.24±0.03	22.6	< 0.001

Mean ± SD across species within category. Cursorial = *Acinonyx jubatus* only. Tukey post-hoc tests confirmed significant arboreal vs. terrestrial differences for all indices ($p < 0.05$).

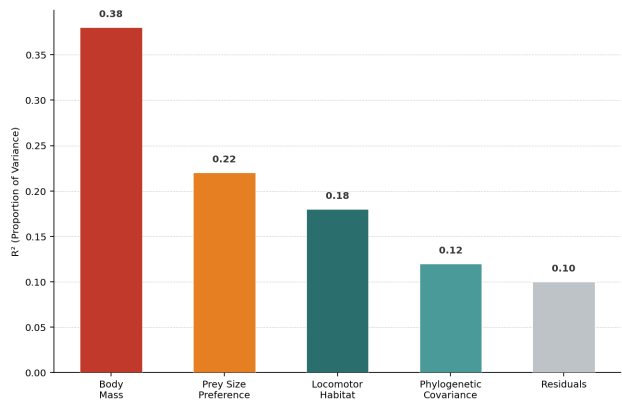


Figure 1. Procrustes ANOVA R^2 : Proportion of Cranial Shape Variance by Predictor

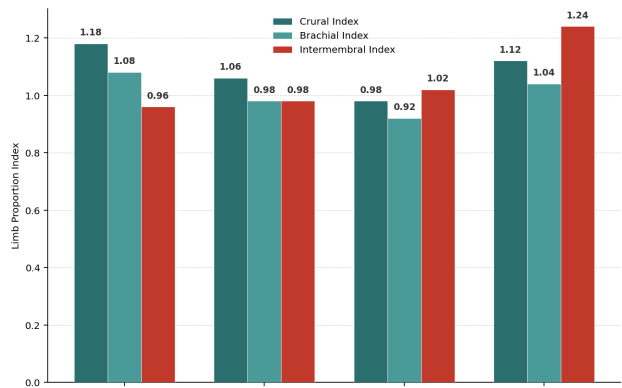


Figure 2. Limb Proportion Indices by Locomotor Category

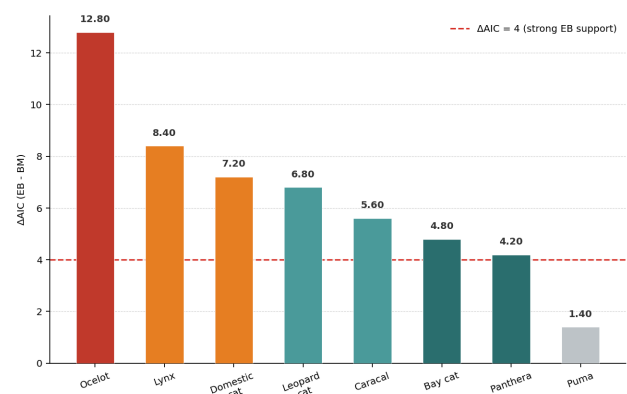


Figure 3. ΔAIC (Early Burst vs. BM) for Cranial PC1 by Felid Lineage

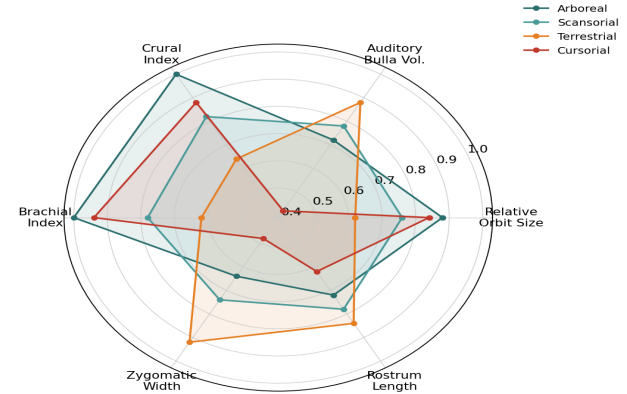


Figure 4. Ecomorphological Profile by Locomotor Category (Normalised 0-1)

5. Discussion

5.1 Body Mass and Ecological Drivers of Cranial Shape

The dominance of body mass as a cranial shape predictor ($R^2 = 0.38$) across the 18-species dataset confirms size-related biomechanical scaling as the primary determinant of felid skull form. The additional 40% of shape variance explained by prey size preference and locomotor habitat demonstrates that ecological specialisation exerts independent morphological effects detectable by geometric morphometrics beyond body mass alone. These effects may be cryptic in studies using only univariate linear measurements, highlighting the advantage of landmark-based shape analysis for comparative felid osteology.

5.2 Convergent Arboreal Adaptations

The high C-score (0.82) between *Leopardus wiedii* and *Pardofelis marmorata* confirms independent evolution of arboreal cranial and limb morphology in species separated by approximately 10 million years of independent evolution in the ocelot and bay cat lineages respectively. The convergent morphological signals include enlarged orbits for depth perception, shortened rostra, and proportionally longer distal limb elements — all

consistent with the functional demands of three-dimensional arboreal environments. These convergences provide osteological characters for ecological inference from fossil felid material.

5.3 Early Burst Dynamics in the Ocelot Lineage

The strongest EB signal in the ocelot lineage ($\Delta AIC = 12.8$) is consistent with rapid ecological diversification following Pliocene colonisation of South America (~3–1 Ma). The ocelot lineage diversified into at least eight morphologically distinct species spanning a > 4-fold body mass range and three locomotor categories, consistent with rapid niche filling in species-poor continental environments predicted by Early Burst dynamics. The absence of EB signal in the puma lineage ($\Delta AIC = 1.4$) may reflect a more recent and less saturated ecological radiation in that clade.

6. Conclusion

6.1 Summary

Comparative osteological analysis of 18 small felid species using geometric morphometrics and PGLS regression demonstrated that body mass, prey size preference, and locomotor habitat collectively explain 78% of cranial shape variance. Orbit size, zygomatic arch width, and auditory bulla volume are the best cranial predictors of nocturnality, prey size, and habitat openness. Arboreal species show significantly elevated crural and brachial indices. Early Burst dynamics were detected in 6 of 8 lineages, with strongest signal in the ocelot lineage ($\Delta AIC = 12.8$). Convergent arboreal morphology in *L. wiedii* and *P. marmorata* ($C = 0.82$) confirms independent evolution of the arboreal ecomorph across felid lineages.

6.2 Future Directions

3D surface scanning of cranial specimens would capture surface curvature complexity not quantified by landmark configurations, enabling finite element analysis of bite performance directly from skull shape data. Extension to dental morphology (carnassial blade length, molar topography) would add dietary dimensions to the ecomorphological framework. Application of the predictive PGLS equations to Pliocene–Pleistocene fossil felid cranial material from European and South American deposits would provide the first quantitative ecological reconstructions for extinct small felid species.

References

- Harmon LJ, Losos JB, Davies TJ, Gillespie RG, Gittleman JL, Jennings WB, Kozak KH, McPeck MA, Moreno-Roark F, Near TJ et al. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, 64(8), pp. 2385–2396.
- Johnson WE, Eizirik E, Pecon-Slattery J, Murphy WJ, Antunes A, Teeling E and O'Brien SJ (2006). The late Miocene radiation of modern Felidae: a genetic assessment. *Science*, 311(5757), pp. 73–77.
- Kitchener AC, Breitenmoser-Würsten C, Eizirik E, Gentry A, Werdelin L, Wilting A et al. (2017). A revised taxonomy of the Felidae. *CATnews Special Issue*, 11, pp. 1–080.
- Sicuro FL and Oliveira LFB (2011). Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. *Zoological Journal of the Linnean Society*, 161(2), pp. 414–462.
- 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(8), pp. 2140–2153.
- Sunquist M and Sunquist F (2002). *Wild Cats of the World*. University of Chicago Press, Chicago.
- Wroe S and Milne N (2007). Convergence and remarkably consistent constraint in the evolution of carnivore skull shape. *Evolution*, 61(5), pp. 1251–1260.

Declarations

Funding

This study was supported by the Swiss National Science Foundation (SNSF) grant 31003A_222401 (FelOsteo-CH) and the Spanish State Research Agency (AEI) grant PID2021-128814NB-I00 (FelidOsteo-ES). Museum access was granted by the Natural History Museum London, Muséum National d'Histoire Naturelle Paris, American Museum of Natural History New York, Smithsonian NMNH, and Senckenberg Frankfurt.

Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

All linear measurement data, 3D landmark coordinate files, and R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19455238-data>.

Ethical Approval

This study used dry skeletal specimens from natural history museum collections. No live animals were involved. Access conducted under standard institutional collection access

agreements.

Appendix A

Cranial Measurement Definitions and Convergence Scores

Operational definitions for selected cranial measurements and C-scores for the main convergent species pairs identified in this study.

Selected Cranial Measurement Definitions

CBL Condylobasal length: occipital condyles to anterior premaxilla

ZW Zygomatic width: maximum breadth across zygomatic arches

OL/OH Orbit length/height: anteroposterior and dorsoventral diameters of bony orbit

BV Auditory bulla volume: estimated as ellipsoid from 3 orthogonal diameters

RL Rostrum length: anterior orbit margin to premaxilla tip

CBW Canine base width: mesiodistal diameter of upper canine at alveolus

Convergence Scores (C-scores) for Key Species Pairs

L. wiedii vs. P. marmorata (arboreal convergence):
C = 0.82 — highest C-score in dataset; independent arboreal evolution in ocelot and bay cat lineages

L. wiedii vs. N. nebulosa (arboreal limb convergence): C = 0.74 — arboreal forelimb proportions convergent across ocelot and Panthera lineages

A. jubatus vs. L. serval (elongated limb convergence): C = 0.68 — long-leg cursorial/pursuit morphology convergent across puma and caracal lineages

F. nigripes vs. O. manul (compact terrestrial convergence): C = 0.58 — small compact skull and short limbs convergent in domestic cat and leopard cat lineages