# Uncovering the mosaic evolution of carnivoran skeletal systems

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**Abstract**

The diversity of vertebrate skeletal forms is often attributed to adaptations to distinct ecological factors such as diet, locomotion, and sensory environment. Although the adaptive evolution of cranial, appendicular, and vertebral skeletal systems is well studied in vertebrates, comprehensive investigations of all skeletal components are rarely performed simultaneously. Consequently, we know little of how modes of evolution differ among skeletal components. We collected 103 linear measurements from 208 osteological museum specimens to capture skeletal variation across the major components of the skeletal systems of 119 extant carnivores. With these data, we tested if ecological and phylogenetic effects led to distinct modes of evolution among the cranial, appendicular, and vertebral skeletal regions by fitting multivariate evolutionary models. We found mosaic evolution in which only the mandible, hindlimb, and posterior region of the vertebral column showed evidence of adaptation towards ecological regimes whereas the remaining skeletal components followed clade-specific evolutionary shifts. We hypothesize that the decoupled evolution of individual skeletal components may have led to

the origination of distinct adaptive zones and morphologies among extant carnivoran families that reflect phylogenetic hierarchies. Overall, our work highlights the importance of examining multiple skeletal components simultaneously in ecomorphological analyses. Ongoing work integrating the fossil and paleoenvironmental record will further govern carnivoran diversity we see today and reveal the complexity of evolutionary processes in multicomponent systems.

Key words: adaptive landscape; Carnivora; ecomorphology; macroevolution; Ornstein-Uhlenbeck modeling; phylogenetic comparative methods

## Introduction

The diversity of animal forms is one of the most salient patterns across the tree of life. For example, within mammals, morphological innovations in the cranial, appendicular, and axial skeletal systems facilitate the incredible diversity found today, ranging from flying bats with winged forelimbs to the biggest animals to have ever lived on earth. Many researchers have examined how variation in the skull [1–6], limbs [7–10], or vertebrae [11–15] serve as crucial adaptations to their evolution. These skeletal systems (skull, limbs, and vertebrae) are traditionally independently examined and have rarely been investigated simultaneously even though these anatomical regions comprise a single, functionally integrated system to support movement, sensation, and other life functions. When considered wholistically, the observed variation across the different components of organismal anatomy are generally explained by multitudinous factors, some that are potentially incongruous. While this evolutionary push-and-pull between anatomical regions may characterize the process of evolution, the hypothesis can only be tested when the different components of the skeleton are explored simultaneously rather

than piecemeal. Such anatomically integrated studies are critical to our understanding of the role of developmental and/or functional integration in canalizing macroevolutionary trajectories [16–18].

Here, we use carnivorans as a model to investigate how ecological and phylogenetic factors correspond with evolutionary changes in the cranial, appendicular, and axial skeletal systems simultaneously. Carnivorans (bears, cats, dogs, seals, weasels, and their relatives) are an especially productive model system to examine skeletal evolution because of their high species richness and vast geographic distribution across most biomes in all continents and oceans, factors that have led to consequently broad ecological diversity in locomotor traits (e.g., arboreal, cursorial, fossorial, aquatic) and feeding adaptations ranging from herbivory to generalists to hypercarnivory.

Components of carnivoran skeletal systems are well studied individually. In the skull, craniomandibular diversity is influenced by several ecological factors and phylogeny [19–23]. Recently, decoupled modes of evolution were found within the skull: cranial shape follows clade-specific evolutionary shifts suggesting phylogenetic constraints, whereas mandibular shape evolution is linked to broad dietary regimes [6]. In the appendicular skeleton, researchers examined ecomorphological divergence between the hindlimbs, which are adapted primarily for locomotion, and the forelimb, which are adapted for multiple functions ranging from running to grappling prey to manipulating objects [24–27]. Additionally, more recent work using phylogenetic comparative methods found that scaling and phylogeny exhibit stronger effects on limb skeletal evolution than do ecological parameters [28–30]. In contrast to craniomandibular and appendicular ecomorphology, research on the axial skeleton is in nascent stages. Initial research has found that distinct regions of the vertebral column are under different evolutionary

pressures. For example, the anterior region exhibits low disparity due to phylogenetic constraints or ecological conservatism, whereas the posterior region exhibits higher disparity that may be due to adaptations to various locomotor ecologies [12,31]. In contrast to these anatomically-localized studies, researchers examining proxies of the overall body plan report that the evolution of traits like body mass, skeletal size, and body shape often follow a Brownian motion model or clade-based shift model rather than being associated with ecological regimes [23,32,33].

Although well studied individually, simultaneous investigation of skulls, limbs, vertebrae, and overall body plan are rarely conducted, likely because of the enormous amount of data that would need to be collected and the complexity of the multivariate analyses required. However, most researchers would likely agree that a more comprehensive approach to skeletal evolution is essential to elucidate the complexity of skeletal evolution. The search for system-level trends and variations is further obscured by the disparate methods employed to test the effects of ecology and phylogeny on different skeletal systems by different researchers. In this study, we address both of these issues, combining anatomical data from across the entire skeleton and applying the same analytical methods. Here, we investigate the mosaic evolution of carnivoran skeletons by creating a new skeletal trait dataset that encompasses all major components of the skeletal system. We then tested the ecological and phylogenetic effects influencing the modes of evolution of the various skeletal components using multivariate generalized evolutionary models.

## Methods

### *Skeletal and ecological traits*

We collected 103 linear measurements from 208 osteological specimens to capture the skeletal morphology of 119 extant carnivorans (Fig. S1; Table S1). This data set includes seven cranial traits, seven mandibular traits, 13 forelimb traits, 13 hindlimb traits, and seven traits in third cervical, fifth cervical, first thoracic, middle thoracic, diaphragmatic thoracic, last thoracic, first lumbar, middle lumbar, and last lumbar vertebrae. For these analyses, we focus only on e male specimens in order to remove the complicating factor of sexual dimorphism as carnivorans exhibit differing degrees of sexual dimorphism [34,35]. To remove the effects of scaling, we calculated log shape ratios by dividing each skeletal trait by the geometric mean of all 103 traits as our metric of size. We then used individual principal component analyses (PCAs) to reduce the dimension of each skeletal component (i.e., cranium, mandible, forelimb, hindlimb, and each of the nine vertebrae) and retained a number of PC axes that corresponded to at least 90% of the explained variance. We also conducted a PCA on the entire dataset as our proxy of the whole-skeleton phenome and retained the first six PC axes (~75% of explained variance) for subsequent analyses. We classified the 119 carnivoran species into distinct locomotor modes, hunting behaviors, and dietary regimes following (Law 2021).

*Phylogenetic comparative methods*

We tested whether each skeletal component evolved as adaptation to diet, hunting behavior, or locomotor mode or exhibited clade-specific evolutionary shifts by fitting multivariate generalized evolutionary models on the retained PC axes of each individual skeletal component [36–38]. For the adaptive ecological models, we fit three multivariate multi-optima Ornstein-Uhlenbeck models (i.e., $mvOUM_{diet}$ , $mvOUM_{hunting\ behavior,}$ and $mvOUM_{locomotion}$) to test if dietary, hunting behavioral, or locomotor regimes influenced the evolution of each set of PC

axes using mvMORPH v1.1.4 [38]. All three models were fit across 500 stochastically mapped trees to account for uncertainty in phylogenetic topology and ancestral character states (see electronic supplementary materials for full methods). We also calculated the phylogenetic half-lives (ln(2)/alpha) of the best supported adaptive ecological model, defined as the time it takes for a trait to evolve halfway toward its new expected optimum after a regime shift [36]. A short phylogenetic half-life relative to the age of Carnivora (48.2 myr) would suggest that skeletal traits are strongly pulled toward distinct ecological peaks across the adaptive landscape. For the clade-based model, we fit a multi-optima OU model ($mvOUM_{phyloEM}$) without *a priori* ecological groupings with the PhylogeneticEM v1.4.0 [39]. We also fit a single-rate multivariate Brownian motion model (mvBM1) and a single-optimum OU model (mvOU1) as null models. Relative support of models was assessed through computation of small sample-corrected Akaike weights (AICcW).

Preliminary results revealed that phenotypic differences between pinnipeds (i.e., seals and sea lions) and terrestrial carnivorans are often the greatest source of variation for most skeletal components. These results are unsurprising considering pinnipeds exhibit derived morphologies that enable them to be fully aquatic. Therefore, we repeated the above model fitting using a reduced dataset with no pinnipeds. Results of the full dataset that includes pinnipeds are presented in the electronic supplementary material.

## Results and Discussion

We found mosaic evolution of the carnivoran skeleton in which ecology and phylogeny have differing influences on the evolutionary mode of the various skeletal components. Consistent with recent results, the carnivoran skull exhibited decoupled modes of evolution

between the cranium and mandible. In the cranium, the clade-specific shift model exhibited overwhelmingly greater support ($mvOUM_{phyloEM}$; AICcW > 0.99) compared to adaptive ecological models based on diet, hunting behavior, and locomotion (Fig. 1; Table S2). We found eight evolutionary shifts in cranial morphology that correspond to carnivoran clades (Fig. S2A). In contrast, the adaptive ecological model based on diet was the best supported model ($mvOUM_{diet}$; AICcW = 0.96) for the mandible with a short phylogenetic half-life of 2.52 myr (Fig. 1; Table S2). These results are congruent with previous findings revealing that mandibular shape is evolutionarily labile with respect to dietary evolution whereas cranial shape is partitioned between families rather than between dietary groups [6]. Decoupling between the cranium and mandible may be explained by their functions. Diet is often found to have had a strong influence on the evolution of the mandible because of its direct mechanical role in feeding [3,40–44]. However, in addition to feeding, the multiple sensory functions that the cranium also performs also influence its evolution [45–47]; therefore, cranial shape may be more constrained in its ability to evolve to match dietary demands alone.

The appendicular system exhibited decoupled modes of evolution between forelimbs and hindlimbs. The clade-specific shift model ($mvOUM_{phyloEM}$; AICcW > 0.99) was best supported in the forelimb (Fig. 1; Table S2). Seven evolutionary shifts in forelimb evolution occur primarily along familial branches (Fig. S2B), indicating that the complexity and variation of carnivoran forelimb adaptations cannot be captured effectively by dietary, hunting behavioral, or locomotor categories. Instead, these shifts suggest that clade-specific adaptations enabled the diversity of forelimb skeletons for tasks such as grappling or manipulating prey, swimming, or digging [24–27,30,48,49]. For example, most felids use their prehensile forelimbs to ambush and subdue prey, most canids and hyaenids pounce and pursue prey, and some mustelids use their

161 powerful forelimbs to dig out prey while other, more derived mustelids (i.e., weasels and
162 polecats) pursue prey in tight crevices and burrows [50]. In contrast, the adaptive ecological
163 model based on locomotor mode was the best supported model ($mvOUM_{locomotion}$; AICcW =
164 0.83) in the hindlimb with a short phylogenetic half-life of 5.05 myr (Fig. 1; Table S2),
165 supporting hypotheses that the hindlimb is adapted primarily for locomotion as typically found in
166 quadrupedal mammals [51]. Together, this body of work is in line with findings that non-
167 cursorial carnivorans exhibit weaker integration between the limbs [30] and supports the
168 hypothesis of functional divergence between the forelimbs and hindlimbs of carnivorans.
169 The axial skeleton exhibits distinct modes of evolution between the anterior and posterior
170 regions of the vertebral column: clade-specific shift or single-peak OU models tended to be the
171 best supported model for cervical and most thoracic vertebrae, whereas adaptive ecological
172 models based on hunting behavior or locomotor mode were the best supported model for the last
173 thoracic and all lumbar vertebrae (Fig. 1; Fig. S2C–F; Table S2). Our findings strengthen the
174 coalescing hypothesis that anterior vertebrae exhibit lower disparity, higher evolutionary
175 constraints, and more subtle adaptations to locomotion whereas posterior vertebrae exhibit the
176 opposite pattern in carnivorans [31] and broadly across mammals [13]. We posit that high
177 evolutionary constraints of the anterior vertebrae are associated with clade-specific shifts in the
178 cervical and most thoracic vertebrae. In contrast, relaxed evolutionary constraints of the posterior
179 vertebrae facilitate the evolution of disparate lumbar vertebrae across the entire carnivoran order.
180 These disparate vertebrae serve as adaptations to diverse locomotor modes or hunting behaviors
181 based on the mobility of the posterior backbone and irrespective of clade origins. The short
182 phylogenetic half-lives (1.47–5.12 myr; Fig. 1) further suggests strong pulls towards these
183 different adaptive optima. More broadly, this increased mobility of the lumbar region over

evolutionary time is hypothesized to be an evolutionary innovation for the evolution of extant mammals [13,52,53].

Overall, we elucidate the mosaic evolution of the carnivoran skeleton, finding that different skeletal components exhibit distinct modes of evolution. Our results suggest that different methodologies and taxonomic samples do not necessarily explain previously reported region-specific macroevolutionary patterns; rather, complexity in explanatory factors of skeletal diversity is a key feature of Carnivora. The ability of individual skeletal components to adapt to specific ecological factors independently from each other may have contributed to the clade's *hierarchical* [54,55] evolution. As previously hypothesized [23,32], the restriction of carnassial shear to the P4/m1 pair may have been the key innovation that facilitated the initial carnivoran diversification early in the clade's evolutionary history. Subsequent evolution led to the continual partitioning between clades, resulting in the origination of extant carnivoran families as discrete phylogenetic clusters that occupy different adaptive zones [56] with distinct morphologies including body size and shape [33,57], various components of the skeleton [e.g., skull 6]; Fig. 1), as well as the overall skeletal phenome (Fig. 2). Within-clade variation then arises to reflect resource partitioning among ecologically similar taxa, leading to adaptations in morphologies such as the mandible, hindlimb, and posterior region of the vertebral column (Fig. 1). These traits were strongly pulled toward distinct ecological peaks across the adaptive landscape as revealed by their short phylogenetic half-lives (1.47–5.12 myr) relative to the age of Carnivora itself (48.2 myr).

Our research statistically revealed the mosaic evolution of carnivoran skeletons. These distinct evolutionary modes demonstrate the importance of examining multiple skeletal components in ecomorphological analyses. Nevertheless, key questions remain: 1) what spurred

the evolutionary transitions towards the evolutionary shifts or adaptations of the various skeletal components? 2) when in the 55 million years of carnivoran evolutionary history did these evolutionary events occur? And lastly, 3) what developmental and genetic phenomena underlie the dissociation of various skeletal elements? Ongoing work integrating the fossil and paleoenvironmental record will further elucidate the carnivoran diversity we see today and reveal the complexity of evolutionary processes in multicomponent systems.

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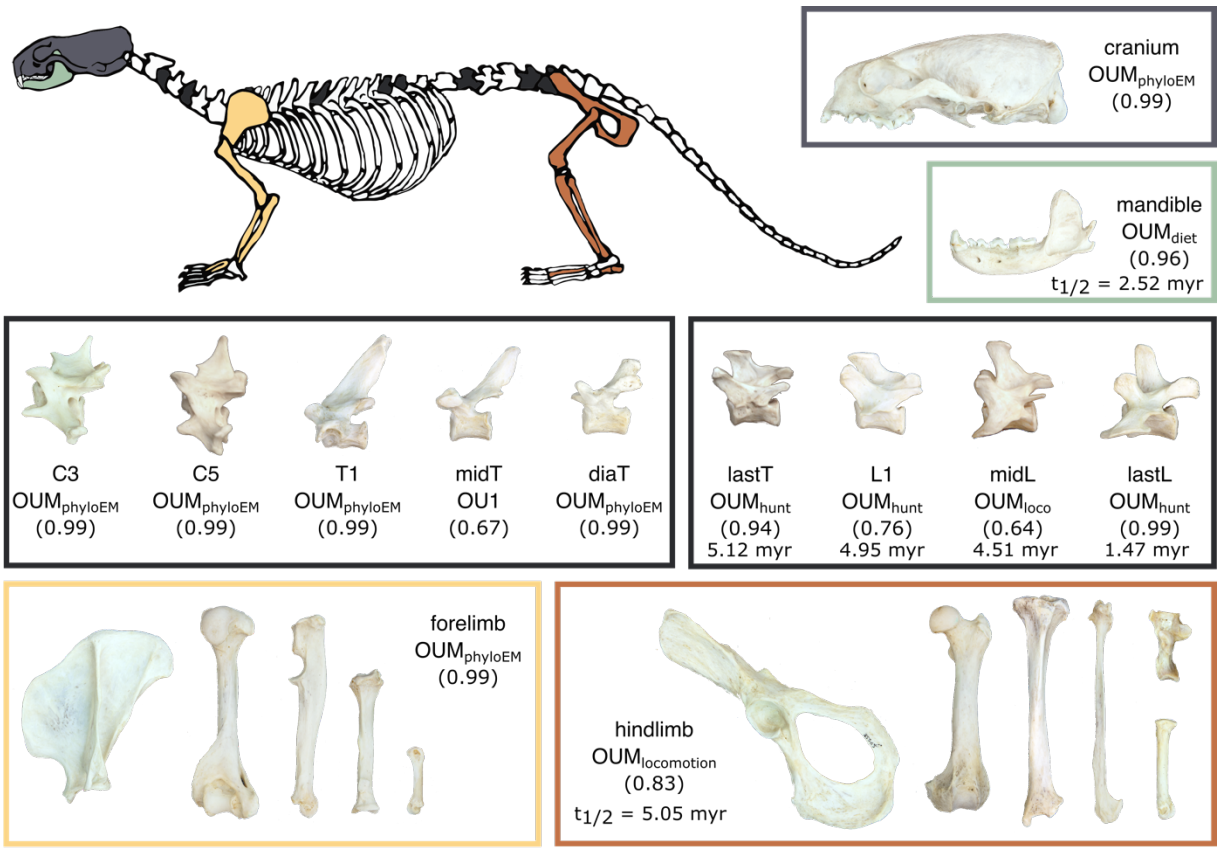


**Fig. 1.** Diagram of the skeletal components and their best-fitting evolutionary model. AICcW are in parentheses. See Table S2 for full AICc table. $t_{1/2}$ = phylogenetic half-life calculated as ln(2)/ α for adaptive ecological models. Myr = million years. C3 = third cervical vertebrae; C5 = fifth cervical vertebrae; T1 = first thoracic vertebrae; midT = middle thoracic vertebrae; diaT = diaphragmatic thoracic vertebrae; lastT = last thoracic vertebrae; L1 = first lumbar vertebrae; midL = middle lumbar vertebrae; lastL = last lumbar vertebrae.

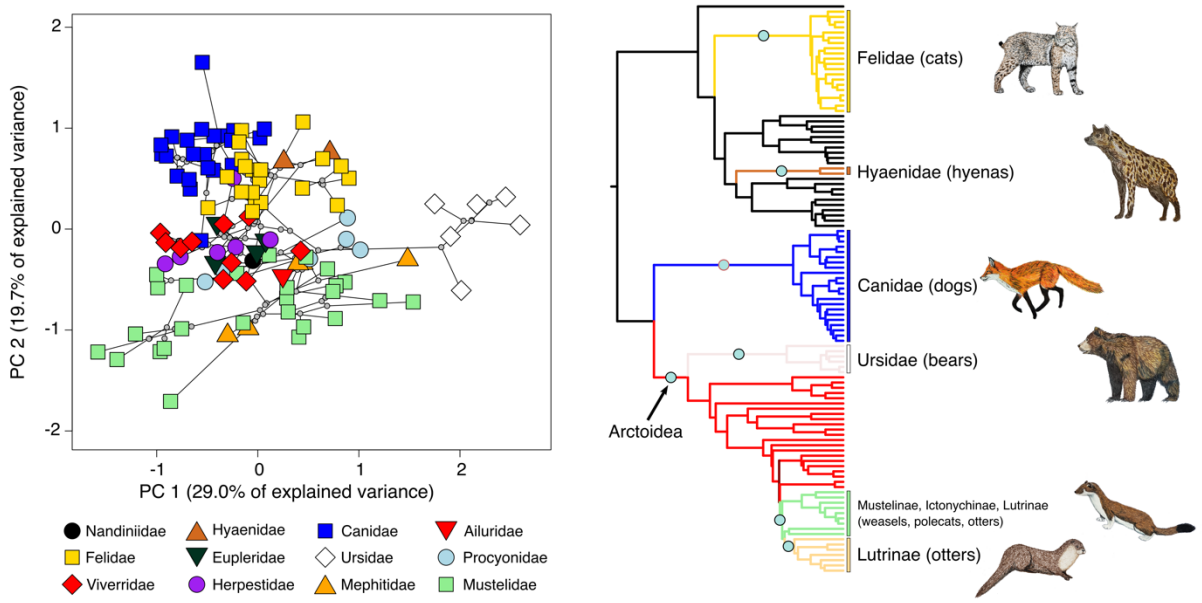


**Fig. 2.** A) Phylomorphospace and B) clade-specific evolutionary shifts of the full skeletal dataset across terrestrial carnivorans identified by PhylogeneticEM. Shifts are calculated from PCs 1-6 (74.7% of explained variance) and are represented as pink circles. Branches on the phylogenies are colored according to each regime.

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