BIOLOGY LETTERS

royalsocietypublishing.org/journal/rsbl

Research

Cite this article: Law CJ, Hlusko LJ, Tseng ZJ. 2024 Uncovering the mosaic evolution of the carnivoran skeletal system. *Biol. Lett.* **20**: 20230526.
https://doi.org/10.1098/rsbl.2023.0526

Received: 9 November 2023
Accepted: 21 December 2023

Subject Category:
Evolutionary biology

Subject Areas:
evolution

Keywords:
adaptive landscape, Carnivora, ecomorphology, macroevolution, Ornstein–Uhlenbeck modelling, phylogenetic comparative methods

Author for correspondence:
Chris J. Law
e-mail: cjlaw@uw.edu

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.7020976.

THE ROYAL SOCIETY PUBLISHING

Uncovering the mosaic evolution of the carnivoran skeletal system

Chris J. Law[1,2,3], Leslea J. Hlusko[4] and Z. Jack Tseng[3]

[1]Department of Integrative Biology, University of Texas, Austin, TX, USA
[2]Burke Museum and Department of Biology, University of Washington, Seattle, WA, USA
[3]Department of Integrative Biology, University of California, Berkeley, CA, USA
[4]National Research Center on Human Evolution (CENIEH), Burgos, Spain

CJL, 0000-0003-1575-7746; ZJT, 0000-0001-5335-4230

The diversity of vertebrate skeletons is often attributed to adaptations to distinct ecological factors such as diet, locomotion, and sensory environment. Although the adaptive evolution of skull, appendicular skeleton, and vertebral column is well studied in vertebrates, comprehensive investigations of all skeletal components simultaneously are rarely performed. Consequently, we know little of how modes of evolution differ among skeletal components. Here, we tested if ecological and phylogenetic effects led to distinct modes of evolution among the cranial, appendicular and vertebral regions in extant carnivoran skeletons. Using multivariate evolutionary models, we found mosaic evolution in which only the mandible, hindlimb and posterior (i.e. last thoracic and lumbar) vertebrae showed evidence of adaptation towards ecological regimes whereas the remaining skeletal components reflect 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 palaeoenvironmental record will further clarify deep-time drivers that govern the carnivoran diversity we see today and reveal the complexity of evolutionary processes in multicomponent systems.

1. Introduction

The diversity of animal forms is one of the most salient patterns across the tree of life. In mammals, morphological innovations in the skull, appendicular skeleton and vertebral column facilitate the incredible diversity found today, ranging from bats with winged forelimbs to the biggest animals to have ever lived on Earth. Many researchers have examined how variation in the skull [1–7], limbs [8–11] or vertebrae [12–16] serve as crucial adaptations to their evolution. These skeletal systems are traditionally examined independently and are rarely investigated simultaneously even though these anatomical regions comprise a single, functionally integrated system that serves as structural support for movement, locomotion, and other life functions. When considered wholistically, the observed variation across the different components of organismal anatomy is generally explained by multitudinous factors, some that are potentially incongruous [17–20]. While this evolutionary push-and-pull between anatomical regions may characterize the process of evolution, the hypothesis can only be tested when the different skeletal components are explored simultaneously rather than piecemeal. Simultaneous investigation of integrated components is critical to our understanding of the role of developmental and/or functional integration in canalizing macroevolutionary trajectories [21–23]. Here, we use carnivorans to investigate how ecological and phylogenetic factors correspond to evolutionary changes in the cranial, appendicular,

and axial skeletal systems. Carnivorans (bears, cats, dogs, seals, and their relatives) are a productive model system to examine skeletal evolution because of their high species richness and vast distribution across most biomes in all continents and oceans, along with broad ecological diversity in locomotor traits and feeding adaptations.

Components of carnivoran skeletal systems are well studied individually. In the skull, craniomandibular diversity is influenced by several ecological factors and phylogeny [24–28]. The skull exhibits decoupled evolutionary modes: cranial shape follows clade-specific evolutionary shifts, whereas mandibular shape evolution is linked to broad dietary regimes [6,29]. In the appendicular skeleton, ecomorphological divergence exists 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 [30–33]. Additionally, more recent work using phylogenetic comparative methods found that scaling and phylogeny exhibit stronger effects on limb evolution than do ecological parameters [34–36]. In contrast to craniomandibular and appendicular ecomorphology, research on the axial skeleton is in nascent stages. Initial research indicates that distinct regions of the vertebral column are under different evolutionary pressures. Anterior (i.e. more cranial) vertebrae exhibit low disparity due to phylogenetic constraints or ecological conservatism, whereas posterior (i.e. more caudal) vertebrae exhibit higher disparity that may be due to adaptations to various locomotor ecologies [13,37]. In contrast to these morphologically localized studies, analyses of the evolution of whole-body 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 [28,38,39].

Compared to skeletal system-specific findings, 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, a more comprehensive approach to quantifying skeletal evolution is essential to elucidate its complexity more fully. 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 issues in our investigation of the mosaic evolution of carnivoran skeletons by creating a new phenomic dataset that encompasses all major components of the skeletal system and using a unified set of multivariate evolutionary models to test the ecological and phylogenetic effects influencing the modes of evolution of these skeletal components.

2. Methods

(a) Skeletal and ecological traits

We collected 103 linear measurements to capture the skeletal morphology of 119 carnivoran species (208 osteological specimens; electronic supplementary material, figure S1; electronic supplementary material, table S1). This dataset 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. Because carnivorans exhibit differing degrees of sexual dimorphism [40,41], we use only male specimens. To remove size effects, we calculated log shape ratios by dividing each skeletal trait by the geometric mean of all 103 traits [42,43]. We then used 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 greater than 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 (approx. 75% of explained variance) for subsequent analyses. We classified the 119 carnivoran species into distinct locomotor modes, hunting behaviours and dietary regimes following [39].

(b) Phylogenetic comparative methods

We tested whether each skeletal component evolved as adaptation to specific ecological regimes or exhibited clade-specific evolutionary shifts by fitting multivariate evolutionary models on the retained PC axes of each skeletal component [44–46]. For the adaptive ecological models, we fit three multivariate multi-optima Ornstein–Uhlenbeck (OU) models (i.e. $mvOUM_{diet}$, $mvOUM_{hunting}$ and $mvOUM_{locomotion}$) to test if dietary, hunting behavioural, or locomotor regimes influenced the evolution of each skeletal component using mvMORPH [46]. The models were fit across 500 stochastically mapped trees to account for uncertainty in phylogenetic topology and ancestral character states (see electronic supplementary material). We also calculated the phylogenetic half-lives of the best supported adaptive ecological model [44]. A short phylogenetic half-life relative to the age of Carnivora (48.2 myr) would suggest that skeletal traits are strongly pulled towards distinct ecological optima across the adaptive landscape. For the clade-based model, we fit a multi-optima OU model ($mvOUM_{phyloEM}$) without *a priori* ecological regimes with PhylogeneticEM [47]. We also fit a single-rate multivariate Brownian motion model (mvBM1) and a single-optimum OU model (mvOU1). We assessed the relative support of models using small sample-corrected Akaike weights (AICcW). Lastly, we assessed the covariation among skeletal components using partial least squares with geomorph [48].

Preliminary results revealed that phenotypic differences between pinnipeds (i.e. seals, sea lions, and the walrus) 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 our analyses using a reduced dataset with no pinnipeds. Results of the full dataset with pinnipeds are presented in the electronic supplementary material.

3. 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 [6,29], the cranium and mandible exhibited decoupled evolutionary modes. In the cranium, the clade-specific shift model exhibited overwhelmingly greater support ($mvOUM_{phyloEM}$; AICcW > 0.99) compared to adaptive ecological models (figure 1; electronic supplementary material, table S2). We found eight evolutionary shifts in cranial morphology that correspond to carnivoran clades (figure 2*a*). By contrast, the adaptive dietary model was the best supported model ($mvOUM_{diet}$; AICcW = 0.96) for the mandible with a short phylogenetic half-life of 2.52 myr

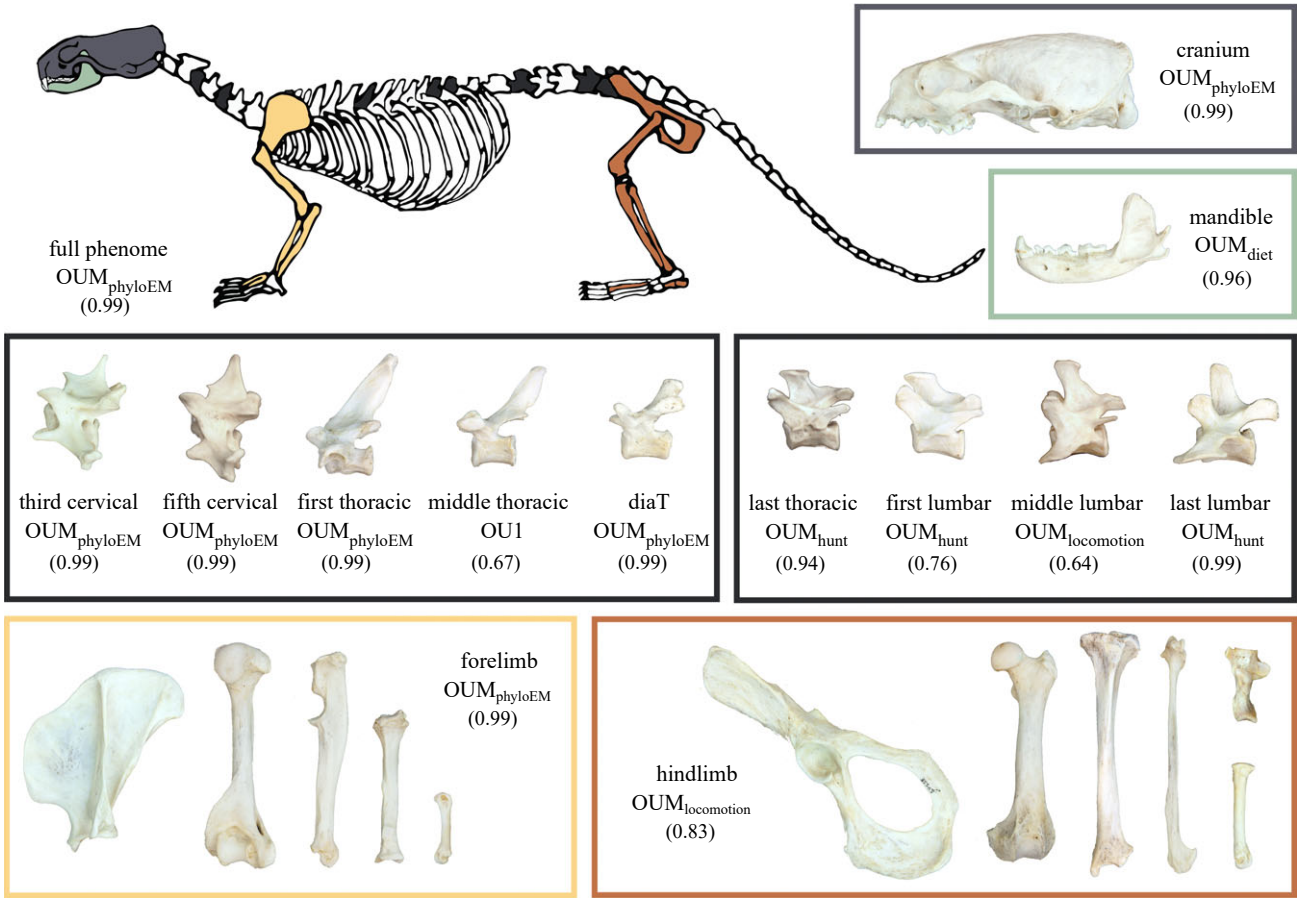

Figure 1. Diagram of the skeletal components and their best-fitting evolutionary model on *Lontra canadensis*. AICcW are in parentheses. See electronic supplementary material, table S2 for full AICc table. diaT = diaphragmatic thoracic vertebrae.

(figure 1; electronic supplementary material, figure S2*b*; electronic supplementary material, table S2; see electronic supplementary material, Supplementary Results for optima distribution in phylomorphospace). These results are congruent with findings revealing that mandibular shape is evolutionarily labile with respect to dietary evolution whereas cranial shape is partitioned among families rather than among dietary groups [6]. Despite their covariation ($r = 0.73$; electronic supplementary material, table S3), decoupled evolutionary modes between the cranium and mandible may be explained by their functions. Diet is often found to have had a strong influence on mandibular evolution because of its direct role in feeding [3,49–53]. By contrast, the cranium has multiple sensory functions in addition to feeding that influence its evolution [54–56], and therefore, the signal from dietary adaptations in its morphology may be obscured.

The appendicular system exhibited decoupled evolutionary modes between forelimbs and hindlimbs. The forelimb was best supported by the mvOUM$_{phyloEM}$ model (AICcW > 0.99; figure 1; electronic supplementary material, table S2). Seven shifts in forelimb evolution occur primarily along familial branches (figure 2*b*), indicating that the complexity and variation of carnivoran forelimb morphology cannot be captured effectively by dietary, hunting behavioural 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 [30–33,36,57,58]. 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 powerful forelimbs to dig out prey while other more derived mustelids (i.e. weasels) pursue prey in tight crevices and burrows [59]. By contrast, the hindlimb was best supported by the mvOUM$_{locomotion}$ model (AICcW = 0.83) in the hindlimb with a short phylogenetic half-life of 5.05 myr (figure 1; electronic supplementary material, table S2), supporting hypotheses that the hindlimb is adapted primarily for locomotion as typically found in quadrupedal mammals [60]. Although the forelimb and hindlimb covary ($r = 0.87$; electronic supplementary material, table S3), previous work found that this integration is weaker than expected in carnivorans that do not specialize in cursoriality [36]. This work together supports the hypothesis of functional divergence between the forelimbs and hindlimbs of carnivorans.

The axial skeleton exhibits distinct evolutionary modes between the anterior and posterior regions of the vertebral column: cervical and most thoracic vertebrae tended to be best supported by clade-specific shift or single-peak OU models, whereas the last thoracic and all lumbar vertebrae were best supported by mvOUM$_{hunting}$ or mvOUM$_{locomotion}$ models (figure 1; figure 2*c–f*; electronic supplementary material, table S2). Our findings strengthen the coalescing hypothesis that anterior vertebrae exhibit lower disparity, higher evolutionary constraints, and more subtle adaptations to locomotion whereas posterior vertebrae exhibit the opposite patterns in carnivorans [37] and broadly across mammals [14]. We posit that high evolutionary constraints of the anterior vertebrae are associated with clade-specific

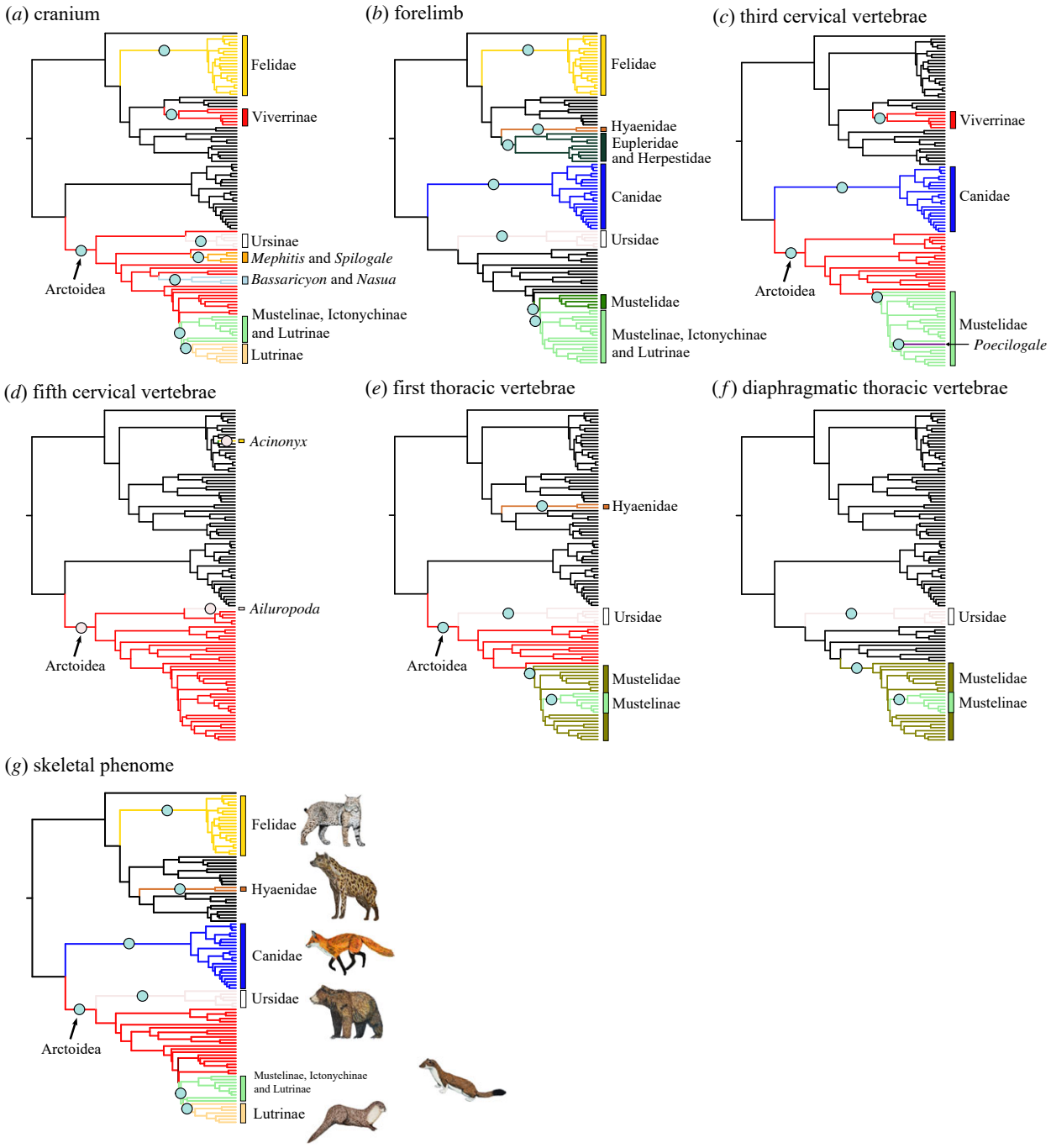

Figure 2. Clade-specific evolutionary shifts in skeletal components across terrestrial carnivorans identified by PhylogeneticEM. Shifts are represented as pink circles, and branches on the phylogenies are coloured according to each regime.

shifts in the cervical and most thoracic vertebrae. Importantly, subtle adaptations in these anterior vertebrae could be masked by many-to-one or one-to-many mappings, making it difficult to uncover the form–function associations with evolutionary models [61]. By contrast, relaxed evolutionary constraints of the posterior vertebrae facilitate the evolution of disparate lumbar vertebrae across the entire carnivoran order. These disparate vertebrae adapt to diverse locomotor modes or hunting behaviors based on the mobility of the posterior vertebrae and irrespective of clade origins. The short phylogenetic half-lives (1.47–5.12 myr) further suggests strong pulls towards these different adaptive optima. More broadly, this increased mobility of the lumbar region over evolutionary time is hypothesized to be an innovation characterizing crown mammals [14,62,63]. Correspondingly, the posterior vertebrae are tightly integrated ($r = 0.84$–0.96; electronic supplementary material, table S3).

Lastly, we found that the clade-specific shift model ($\text{mvOUM}_{\text{phyloEM}}$; AICcW > 0.99) best described the overall skeletal phenome (electronic supplementary material, table S2), a pattern that is consistent with previous investigations of whole-body proxies such as body size and body shape [28,38,39]. The mammalian body plan is comprised of cranial, axial and appendicular components; therefore, its multidimensionality transcends one-to-one mapping relationships between morphology and ecological function. Instead, individual skeletal components within distinct body plans can adapt to specific ecological factors independently from each other, enabling species with distinct body plans to exhibit similar ecological or functional regimes and vice versa.

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* [64,65] evolution. As previously hypothesized [28,38], 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 [66] with distinct morphologies including body size and shape [39,67] and various components of the skeleton ([6]; figure 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 (figure 1). These traits were strongly pulled towards distinct ecological peaks across the adaptive landscape as revealed by their short phylogenetic half-lives (1.47–5.12 myr) relative to the clade's age (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: what spurred the evolutionary transitions towards the evolutionary shifts or adaptations of the various skeletal components? When in the 55 million years of carnivoran evolutionary history did these evolutionary events occur? And what developmental and genetic phenomena underlie the evolutionary dissociation of various skeletal elements? Ongoing work integrating the fossil and palaeoenvironmental record will further elucidate the carnivoran diversity we see today and reveal the complexity of evolutionary processes in multicomponent systems.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data and original code are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c2fqz61gf [68].

The data are provided in the electronic supplementary material [69].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.J.L.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, validation, visualization, writing—original draft, writing—review and editing; L.J.H.: funding acquisition, investigation, writing—review and editing; Z.J.T.: funding acquisition, investigation, project administration, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Funding was supported by the National Science Foundation (grant no. DBI-2128146) to C.J.L., L.J.H., and Z.J.T.; a University of Texas Early Career Provost Fellowship and Stengl-Wyer Endowment Grant (grant no. SWG-22-02) to C.J.L.; and the European Research Council (Tied2Teeth, grant no. 101054659) to L.J.H.

Acknowledgements. We are grateful to the staff and collections at the American Museum of Natural History, California Academy of Sciences, Field Museum of Natural History, Natural History Museum of Los Angeles County, Museum of Vertebrate Zoology, Natural History Museum London, San Diego Natural History Museum, Texas Vertebrate Paleontology Collection, National Museum of Natural History, and Burke Museum of Natural History and Culture. We thank Vera Weisbecker and three anonymous reviewers for their feedback.

References

1. Dumont ER, Davalos LM, Goldberg A, Santana SE, Rex K, Voigt CC. 2012 Morphological innovation, diversification and invasion of a new adaptive zone. *Proc. R. Soc. B* **279**, 1797–1805. (doi:10.1098/rspb.2011.2005)
2. Zelditch ML, Ye J, Mitchell JS, Swiderski DL. 2017 Rare ecomorphological convergence on a complex adaptive landscape: body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* **71**, 633–649. (doi:10.1111/evo.13168)
3. Grossnickle DM. 2020 Feeding ecology has a stronger evolutionary influence on functional morphology than on body mass in mammals. *Evolution* **74**, 610–628. (doi:10.1111/evo.13929)
4. Arbour JH, Curtis AA, Santana SE. 2019 Signatures of echolocation and dietary ecology in the adaptive evolution of skull shape in bats. *Nat. Commun.* **10**, 2036. (doi:10.1038/s41467-019-09951-y)
5. Goswami A *et al.* 2022 Attenuated evolution of mammals through the Cenozoic. *Science* **378**, 377–383. (doi:10.1126/science.abm7525)
6. Law CJ, Blackwell EA, Curtis AA, Dickinson E, Hartstone-Rose A, Santana SE. 2022 Decoupled evolution of the cranium and mandible in carnivoran mammals. *Evolution* **76**, 2959–2974. (doi:10.1111/evo.14578)
7. Weisbecker V, Beck RMD, Guillerme T, Harrington AR, Lange-Hodgson L, Lee MSY, Mardon K, Phillips MJ. 2023 Multiple modes of inference reveal less phylogenetic signal in marsupial basicranial shape compared with the rest of the cranium. *Phil. Trans. R. Soc. B* **378**, 20220085. (doi:10.1098/rstb.2022.0085)
8. Patel BA. 2010 Functional morphology of cercopithecoid primate metacarpals. *J. Hum. Evol.* **58**, 320–337. (doi:10.1016/j.jhevol.2010.01.001)
9. Kilbourne BM. 2017 Selective regimes and functional anatomy in the mustelid forelimb: diversification toward specializations for climbing, digging, and swimming. *Ecol. Evol.* **66**, 2369–2312. (doi:10.1002/ece3.3407)
10. Grossnickle DM, Chen M, Wauer JGA, Pevsner SK, Weaver LN, Meng QJ, Liu D, Zhang YG, Luo ZX. 2020 Incomplete convergence of gliding-mammal skeletons. *Evolution* **74**, 2662–2680. (doi:10.1111/evo.14094)
11. Rickman J, Burtner AE, Linden TJ, Santana SE, Law CJ. 2023 Size and locomotor ecology have differing effects on the external and internal morphologies of squirrel (Rodentia: Sciuridae) limb bones. *Integr. Org. Biol.* **5**, obad017. (doi:10.1093/iob/obad017)
12. Pierce SE, Clack JA, Hutchinson JR. 2011 Comparative axial morphology in pinnipeds and its correlation with aquatic locomotory behaviour. *J. Anat.* **219**, 502–514. (doi:10.1111/j.1469-7580.2011.01406.x)
13. Randau M, Cuff AR, Hutchinson JR, Pierce SE, Goswami A. 2017 Regional differentiation of felid vertebral column evolution: a study of 3D shape trajectories. *Org. Divers. Evol.* **17**, 1–15. (doi:10.1007/s13127-016-0304-4)
14. Jones KE, Benitez L, Angielczyk KD, Pierce SE. 2018 Adaptation and constraint in the evolution of the mammalian backbone. *BMC Evol. Biol.* **18**, 172. (doi:10.1186/s12862-018-1282-2)
15. Martín-Serra A, Pérez-Ramos A, Pastor FJ, Velasco D, Figueirido B. 2021 Phenotypic integration in the carnivoran backbone and the evolution of functional

differentiation in metameric structures. *Evol. Lett.* **5**, 1–14. (doi:10.1002/evl3.224)

16. Linden TJ, Burtner AE, Rickman J, McFeely A, Santana SE, Law CJ. 2023 Scaling patterns of body plans differ among squirrel ecotypes. *PeerJ* **11**, e14800. (doi:10.7717/peerj.14800)
17. Friedman ST, Price SA, Wainwright PC. 2021 The effect of locomotion mode on body shape evolution in teleost fishes. *Integr. Org. Biol.* **3**, obab016. (doi:10.1093/iob/obab016)
18. Law CJ. 2021 Evolutionary and morphological patterns underlying carnivoran body shape diversity. *Evolution* **75**, 365–375. (doi:10.1111/evo.14143)
19. Bergmann PJ, Irschick DJ. 2009 Alternate pathways of body shape evolution translate into common patterns of locomotor evolution in two clades of lizards. *Evolution* **64**, 1569–1582. (doi:10.1111/j.1558-5646.2011.01491.x)
20. Orkney A, Bjarnason A, Tronrud BC, Benson RBJ. 2021 Patterns of skeletal integration in birds reveal that adaptation of element shapes enables coordinated evolution between anatomical modules. *Nat. Ecol. Evol.* **5**, 1250–1258. (doi:10.1038/s41559-021-01509-w)
21. Goswami A, Randau M, Polly PD, Weisbecker V, Bennett CV, Hautier L, Sánchez-Villagra MR. 2016 Do developmental constraints and high integration limit the evolution of the marsupial oral apparatus? *Integr. Comp. Biol.* **56**, 404–415. (doi:10.1093/icb/icw039)
22. Goswami A, Weisbecker V, Sánchez-Villagra MR. 2009 Developmental modularity and the marsupial–placental dichotomy. *J. Exp. Zoöl. Part B: Mol. Dev. Evol* **312B**, 186–195. (doi:10.1002/jez.b.21283)
23. Goswami A, Smaers JB, Soligo C, Polly PD. 2014 The macroevolutionary consequences of phenotypic integration: from development to deep time. *Phil. Trans. R. Soc. B* **369**, 20130254. (doi:10.1098/rstb.2013.0254)
24. Radinsky LB. 1981 Evolution of skull shape in carnivores. 1. Representative modern carnivores. *Biol. J. Linn. Soc.* **15**, 369–388. (doi:10.1111/j.1095-8312.1981.tb00770.x)
25. Valkenburgh BV. 2007 Deja vu: the evolution of feeding morphologies in the Carnivora. *Amer. Zool.* **47**, 147–163. (doi:10.1093/icb/icm016)
26. Law CJ, Duran E, Hung N, Richards E, Santillan I, Mehta RS. 2018 Effects of diet on cranial morphology and biting ability in musteloid mammals. *J. Evol. Biol.* **31**, 1918–1931. (doi:10.1111/jeb.13385)
27. Tseng ZJ, Flynn JJ. 2018 Structure–function covariation with nonfeeding ecological variables influences evolution of feeding specialization in Carnivora. *Sci. Adv.* **4**, eaao5441. (doi:10.1126/sciadv.aao5441)
28. Slater GJ, Friscia AR. 2019 Hierarchy in adaptive radiation: a case study using the Carnivora (Mammalia). *Evolution* **73**, 524–539. (doi:10.1111/evo.13689)
29. Figueirido B, MacLeod N, Krieger J, Renzi MD, Pérez-Claros JA, Palmqvist P. 2011 Constraint and adaptation in the evolution of carnivoran skull shape. *Paleobiology* **37**, 490–518. (doi:10.1666/09062.1)
30. Valkenburgh BV. 1985 Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* **11**, 406–428. (doi:10.1017/s0094837300011702)
31. Valkenburgh BV. 1987 Skeletal indicators of locomotor behavior in living and extinct carnivores. *J. Vertebr. Paleontol.* **7**, 162–182. (doi:10.1080/02724634.1987.10011651)
32. Iwaniuk AN, Pellis SM, Whishaw IQ. 1999 The relationship between forelimb morphology and behaviour in North American carnivores (Carnivora). *Can. J. Zool.* **77**, 1064–1074. (doi:10.1139/z99-082)
33. Samuels JX, Meachen JA, Sakai SA. 2013 Postcranial morphology and the locomotor habits of living and extinct carnivorans. *J. Morphol.* **274**, 121–146. (doi:10.1002/jmor.20077)
34. Martín-Serra A, Figueirido B, Palmqvist P. 2014 A three-dimensional analysis of morphological evolution and locomotor performance of the carnivoran forelimb. *PloS One* **9**, e85574. (doi:10.1371/journal.pone.0085574)
35. Martín-Serra A, Figueirido B, Palmqvist P. 2014 A three-dimensional analysis of the morphological evolution and locomotor behaviour of the carnivoran hind limb. *BMC Evol. Biol.* **14**, 1–13. (doi:10.1186/1471-2148-14-129)
36. Martín-Serra A, Figueirido B, Pérez-Claros JA, Palmqvist P. 2015 Patterns of morphological integration in the appendicular skeleton of mammalian carnivores. *Evolution* **69**, 321–340. (doi:10.1111/evo.12566)
37. Figueirido B, Martín-Serra A, Pérez-Ramos A, Velasco D, Pastor FJ, Benson RJ. 2021 Serial disparity in the carnivoran backbone unveils a complex adaptive role in metameric evolution. *Commun. Biol.* **4**, 1–15. (doi:10.1038/s42003-021-02346-0)
38. Slater GJ. 2022 Topographically distinct adaptive landscapes for teeth, skeletons, and size explain the adaptive radiation of Carnivora (Mammalia). *Evolution* **76**, 2049–2066. (doi:10.1111/evo.14577)
39. Law CJ. 2021 Ecological drivers of carnivoran body shape evolution. *Am. Nat.* **198**, 406–420. (doi:10.5061/dryad.pg4f4qrpm)
40. Law CJ. 2019 Solitary meat-eaters: solitary, carnivorous carnivorans exhibit the highest degree of sexual size dimorphism. *Sci. Rep.* **9**, 15344. (doi:10.1038/s41598-019-51943-x)
41. Morris JS, Carrier DR. 2016 Sexual selection on skeletal shape in Carnivora. *Evolution* **70**, 767–780. (doi:10.1111/evo.12904)
42. Claude J. 2013 Log-shape ratios, Procrustes superimposition, elliptic Fourier analysis: three worked examples in R. *Hystrix It. J. Mamm.* **24**, 94–102.
43. Mosimann JE. 1970 Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *J. Am. Stat. Assoc.* **65**, 930–945. (doi:10.1080/01621459.1970.10481136)
44. Hansen TF. 1997 Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51**, 1341–1351. (doi:10.1111/j.1558-5646.1997.tb01457.x)
45. Butler MA, King AA. 2004 Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**, 683–695. (doi:10.1086/426002)
46. Clavel J, Escarguel G, Merceron G. 2015 mv morph: an R package for fitting multivariate evolutionary models to morphometric data. *Methods Ecol. Evol.* **6**, 1311–1319. (doi:10.1111/2041-210x.12420)
47. Bastide P, Ané C, Robin S, Mariadassou M. 2018 Inference of adaptive shifts for multivariate correlated traits. *Syst. Biol.* **67**, 662–680. (doi:10.1093/sysbio/syy005)
48. Baken EK, Collyer ML, Kaliontzopoulou A, Adams DC. 2021 geomorph v4.0 and gmShiny: enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods Ecol. Evol.* **12**, 2355–2363. (doi:10.1111/2041-210x.13723)
49. Meloro C, Raia P, Piras P, Barbera C, OHiggins P. 2008 The shape of the mandibular corpus in large fissiped carnivores: allometry, function and phylogeny. *Zool. J. Linn. Soc.* **154**, 832–845. (doi:10.1111/j.1096-3642.2008.00429.x)
50. Figueirido B, Serrano-Alarcón FJ, Slater GJ, Palmqvist P. 2010 Shape at the cross-roads: homoplasy and history in the evolution of the carnivoran skull towards herbivory. *J. Evol. Biol.* **23**, 2579–2594. (doi:10.1111/j.1420-9101.2010.02117.x)
51. Figueirido B, Tseng ZJ, Martín-Serra A. 2013 Skull shape evolution in durophagous carnivorans. *Evolution* **67**, 1975–1993. (doi:10.1111/evo.12059)
52. Prevosti FJ, Turazzini GF, Ercoli MD, Hingst-Zaher E. 2011 Mandible shape in marsupial and placental carnivorous mammals: a morphological comparative study using geometric morphometrics. *Zool. J. Linn. Soc.* **164**, 836–855. (doi:10.1111/j.1096-3642.2011.00785.x)
53. Morales-García NM, Gill PG, Janis CM, Rayfield EJ. 2021 Jaw shape and mechanical advantage are indicative of diet in Mesozoic mammals. *Commun. Biol.* **4**, 1–14. (doi:10.1038/s42003-021-01757-3)
54. Finarelli JA, Flynn JJ. 2009 Brain-size evolution and sociality in Carnivora. *Proc. Natl Acad. Sci.* **106**, 9345–9349. (doi:10.1073/pnas.0901780106)
55. Curtis AA, Valkenburgh BV. 2014 Beyond the sniffer: frontal sinuses in Carnivora. *Anat. Rec.* **297**, 2047–2064. (doi:10.1002/ar.23025)
56. Bird DJ, Murphy WJ, Fox-Rosales L, Hamid I, Eagle RA, Valkenburgh BV. 2018 Olfaction written in bone: cribriform plate size parallels olfactory receptor gene repertoires in Mammalia. *Proc. Biol. Sci.* **285**, 20 180 100–20 180 109. (doi:10.1098/rspb.2018.0100)
57. Meachen-Samuels J, Valkenburgh BV. 2009 Forelimb indicators of prey-size preference in the Felidae. *J. Morphol.* **270**, 729–744. (doi:10.1002/jmor.10712)
58. Michaud M, Veron G, Fabre A. 2020 Phenotypic integration in feliform carnivores: covariation patterns and disparity in hypercarnivores versus

generalists. *Evolution* **74**, 2681–2702. (doi:10.1111/evo.14112)
59. Wilson DE, Mittermeier RA. 2014 *Handbook of the mammals of the world: volume 1. Carnivores*. Cerdanyola del Vallès, Spain: Lynx Edicions.
60. Polly PD. 2007 Limbs in mammalian evolution. In *Fins into limbs: evolution, development, and transformation* (ed. BK Hall), pp. 245–268. Chicago, IL: The University of Chicago.
61. Simon MN, Moen DS. 2023 Bridging performance and adaptive landscapes to understand long-term functional evolution. *Physiol. Biochem. Zoöl.* **96**, 304–320. (doi:10.1086/725416)
62. Jones KE, Angielczyk KD, Polly PD, Head JJ, Fernandez V, Lungmus JK, Tulga S, Pierce SE. 2018 Fossils reveal the complex evolutionary history of the mammalian regionalized spine. *Science* **361**, 1249–1252. (doi:10.1126/science.aar3126)
63. Jones KE, Angielczyk KD, Pierce SE. 2019 Stepwise shifts underlie evolutionary trends in morphological complexity of the mammalian vertebral column. *Nat. Commun.* **10**, 5071. (doi:10.1038/s41467-019-13026-3)
64. Simpson GG. 1944 *Tempo and mode in evolution*. New York, NY: Columbia University Press.
65. Simpson GG. 1955 *Major features of evolution*. New York, NY: Columbia University Press.
66. Humphreys AM, Barraclough TG. 2014 The evolutionary reality of higher taxa in mammals. *Proc. R. Soc. B* **281**, 20132750. (doi:10.1098/rspb.2013.2750)
67. Law CJ. 2019 Evolutionary shifts in extant mustelid (Mustelidae: Carnivora) cranial shape, body size and body shape coincide with the Mid-Miocene Climate Transition. *Biol. Lett.* **15**, 20 190 155–20 190 156. (doi:10.1098/rsbl.2019.0155)
68. Law CJ, Hlusko LJ, Tseng ZJ. 2024 Data from: Uncovering the mosaic evolution of the carnivoran skeletal system. Dryad Digital Repository. (doi:10.5061/dryad.c2fqz61gf)
69. Law CJ, Hlusko LJ, Tseng ZJ. 2024 Uncovering the mosaic evolution of the carnivoran skeletal system. Figshare. (doi:10.6084/m9.figshare.c.7020976)