

1 **Uncovering the mosaic evolution of carnivoran skeletal systems**

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3 Chris J. Law^{1,2}, Leslea J. Hlusko³, Z. Jack Tseng⁴

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5 ¹Department of Integrative Biology, University of Texas

6 ²Burke Museum and Department of Biology, University of Washington

7 ³National Research Center on Human Evolution (CENIEH), Burgos, Spain

8 ⁴Department of Integrative Biology, University of California Berkeley

9

10 **Abstract**

11 The diversity of vertebrate skeletons is often attributed to adaptations to distinct ecological

12 factors such as diet, locomotion, and sensory environment. Although the adaptive evolution of

13 cranial, appendicular, and vertebral skeletal systems is well studied in vertebrates,

14 comprehensive investigations of all skeletal components simultaneously are rarely performed.

15 Consequently, we know little of how modes of evolution differ among skeletal components.

16 Here, we tested if ecological and phylogenetic effects led to distinct modes of evolution among

17 the cranial, appendicular, and vertebral regions in extant carnivoran skeletons. Using multivariate

18 evolutionary models, we found mosaic evolution in which only the mandible, hindlimb, and

19 posterior region of the vertebral column showed evidence of adaptation towards ecological

20 regimes whereas the remaining skeletal components reflect clade-specific evolutionary shifts.

21 We hypothesize that the decoupled evolution of individual skeletal components may have led to

22 the origination of distinct adaptive zones and morphologies among extant carnivoran families

23 that reflect phylogenetic hierarchies. Overall, our work highlights the importance of examining

24 multiple skeletal components simultaneously in ecomorphological analyses. Ongoing work
25 integrating the fossil and paleoenvironmental record will further clarify deep-time drivers that
26 govern carnivoran diversity we see today and reveal the complexity of evolutionary processes in
27 multicomponent systems.

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

31

32 **Introduction**

33 The diversity of animal forms is one of the most salient patterns across the tree of life. In
34 mammals, morphological innovations in the cranial, appendicular, and axial skeletal systems
35 facilitate the incredible diversity found today, ranging from bats with winged forelimbs to the
36 biggest animals to have ever lived on earth. Many researchers have examined how variation in
37 the skull [1–6], limbs [7–10], or vertebrae [11–15] serve as crucial adaptations to their evolution.
38 These skeletal systems are traditionally examined independently and are rarely investigated
39 simultaneously even though these anatomical regions comprise a single, functionally integrated
40 system to support movement, sensation, and other life functions. When considered holistically,
41 the observed variation across the different components of organismal anatomy is generally
42 explained by multitudinous factors, some that are potentially incongruous [16–18]. While this
43 evolutionary push-and-pull between anatomical regions may characterize the process of
44 evolution, the hypothesis can only be tested when the different skeletal components are explored
45 simultaneously rather than piecemeal. Simultaneous investigation of integrated components is
46 critical to our understanding of the role of developmental and/or functional integration in

47 canalizing macroevolutionary trajectories [19–21]. Here, we use carnivorans to investigate how
48 ecological and phylogenetic factors correspond to evolutionary changes in the cranial,
49 appendicular, and axial skeletal systems. Carnivorans (bears, cats, dogs, seals, and their relatives)
50 are a productive model system to examine skeletal evolution because of their high species
51 richness and vast distribution across most biomes in all continents and oceans, along with broad
52 ecological diversity in locomotor traits and feeding adaptations.

53 Components of carnivoran skeletal systems are well studied individually. In the skull,
54 craniomandibular diversity is influenced by several ecological factors and phylogeny [22–26].
55 The skull exhibits decoupled evolutionary modes: cranial shape follows clade-specific
56 evolutionary shifts, whereas mandibular shape evolution is linked to broad dietary regimes
57 [6,27]. In the appendicular skeleton, ecomorphological divergence exists between the hindlimbs,
58 which are adapted primarily for locomotion, and the forelimb, which are adapted for multiple
59 functions ranging from running to grappling prey to manipulating objects [28–31]. Additionally,
60 more recent work using phylogenetic comparative methods found that scaling and phylogeny
61 exhibit stronger effects on limb evolution than do ecological parameters [32–34]. In contrast to
62 craniomandibular and appendicular ecomorphology, research on the axial skeleton is in nascent
63 stages. Initial research indicates that distinct regions of the vertebral column are under different
64 evolutionary pressures. The anterior region exhibits low disparity due to phylogenetic constraints
65 or ecological conservatism, whereas the posterior region exhibits higher disparity that may be
66 due to adaptations to various locomotor ecologies [12,35]. In contrast to these morphologically-
67 localized studies, analyses of the evolution of whole-body traits like body mass, skeletal size,
68 and body shape often follow a Brownian motion model or clade-based shift model rather than
69 being associated with ecological regimes [26,36,37].

70 Compared to skeletal system-specific findings, simultaneous investigation of skulls,
71 limbs, vertebrae, and overall body plan are rarely conducted, likely because of the enormous
72 amount of data that would need to be collected and the complexity of the multivariate analyses
73 required. However, a more comprehensive approach to quantifying skeletal evolution is essential
74 to elucidate its complexity more fully. The search for system-level trends and variations is
75 further obscured by the disparate methods employed to test the effects of ecology and phylogeny
76 on different skeletal systems by different researchers. In this study, we address both issues in our
77 investigation of the mosaic evolution of carnivoran skeletons by creating a new phenomic dataset
78 that encompasses all major components of the skeletal system and using a unified set of
79 multivariate evolutionary models to test the ecological and phylogenetic effects influencing the
80 modes of evolution of these skeletal components.

81

82 **Methods**

83 *Skeletal and ecological traits*

84 We collected 103 linear measurements to capture the skeletal morphology of 119
85 carnivoran species (208 osteological specimens; Fig. S1; Table S1). This dataset includes seven
86 cranial traits, seven mandibular traits, 13 forelimb traits, 13 hindlimb traits, and seven traits in
87 third cervical, fifth cervical, first thoracic, middle thoracic, diaphragmatic thoracic, last thoracic,
88 first lumbar, middle lumbar, and last lumbar vertebrae. Because carnivorans exhibit differing
89 degrees of sexual dimorphism [38,39], we use only male specimens. To remove size effects, we
90 calculated log shape ratios by dividing each skeletal trait by the geometric mean of all 103 traits
91 [40,41]. We then used principal component analyses (PCAs) to reduce the dimension of each
92 skeletal component (i.e., cranium, mandible, forelimb, hindlimb, and each of the nine vertebrae)

93 and retained a number of PC axes that corresponded to >90% of the explained variance. We also
94 conducted a PCA on the entire dataset as our proxy of the whole-skeleton phenome and retained
95 the first six PC axes (~75% of explained variance) for subsequent analyses. We classified the
96 119 carnivoran species into distinct locomotor modes, hunting behaviors, and dietary regimes
97 following [37].

98

99 *Phylogenetic comparative methods*

100 We tested whether each skeletal component evolved as adaptation to specific ecological
101 regimes or exhibited clade-specific evolutionary shifts by fitting multivariate evolutionary
102 models on the retained PC axes of each skeletal component [42–44]. For the adaptive ecological
103 models, we fit three multivariate multi-optima Ornstein-Uhlenbeck models (i.e., $mvOUM_{\text{diet}}$,
104 $mvOUM_{\text{hunting}}$, and $mvOUM_{\text{locomotion}}$) to test if dietary, hunting behavioral, or locomotor regimes
105 influenced the evolution of each skeletal component using mvMORPH [44]. The models were fit
106 across 500 stochastically mapped trees to account for uncertainty in phylogenetic topology and
107 ancestral character states (see electronic supplementary materials). We also calculated the
108 phylogenetic half-lives of the best supported adaptive ecological model [42]. A short
109 phylogenetic half-life relative to the age of Carnivora (48.2 myr) would suggest that skeletal
110 traits are strongly pulled toward distinct ecological optima across the adaptive landscape. For the
111 clade-based model, we fit a multi-optima OU model ($mvOUM_{\text{phyloEM}}$) without *a priori* ecological
112 regimes with PhylogeneticEM [45]. We also fit a single-rate multivariate Brownian motion
113 model (mvBM1) and a single-optimum OU model (mvOU1). We assessed the relative support of
114 models using small sample-corrected Akaike weights (AICcW). Lastly, we assessed the
115 covariation among skeletal components using partial least squares with geomorph [46].

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

122

123 **Results and Discussion**

124 We found mosaic evolution of the carnivoran skeleton in which ecology and phylogeny
125 have differing influences on the evolutionary mode of the various skeletal components.
126 Consistent with [6,27], the cranium and mandible exhibited decoupled evolutionary modes. In
127 the cranium, the clade-specific shift model exhibited overwhelmingly greater support
128 ($mvOUM_{phyloEM}$; $AICcW > 0.99$) compared to adaptive ecological models (Fig. 1; Table S2). We
129 found eight evolutionary shifts in cranial morphology that correspond to carnivoran clades (Fig.
130 2A). In contrast, the adaptive dietary model was the best supported model ($mvOUM_{diet}$;
131 $AICcW = 0.96$) for the mandible with a short phylogenetic half-life of 2.52 myr (Fig. 1; Fig. S2B;
132 Table S2; see Supplementary Results for optima distribution in phylomorphospace). These
133 results are congruent with findings revealing that mandibular shape is evolutionarily labile with
134 respect to dietary evolution whereas cranial shape is partitioned among families rather than
135 among dietary groups [6]. Despite their covariation ($r = 0.73$; Table S3), decoupled evolutionary
136 modes between the cranium and mandible may be explained by their functions. Diet is often
137 found to have had a strong influence on mandibular evolution because of its direct role in feeding
138 [3,47–51]. In contrast, the cranium has multiple sensory functions in addition to feeding that

139 influence its evolution [52–54], and therefore, the signal from dietary adaptations in its
140 morphology may be obscured.

141 The appendicular system exhibited decoupled evolutionary modes between forelimbs and
142 hindlimbs. The forelimb was best supported by the $mvOUM_{phyloEM}$ model ($AICcW > 0.99$; Fig. 1;
143 Table S2). Seven shifts in forelimb evolution occur primarily along familial branches (Fig. 2B),
144 indicating that the complexity and variation of carnivoran forelimb morphology cannot be
145 captured effectively by dietary, hunting behavioral, or locomotor categories. Instead, these shifts
146 suggest that clade-specific adaptations enabled the diversity of forelimb skeletons for tasks such
147 as grappling or manipulating prey, swimming, or digging [28–31,34,55,56]. For example, most
148 felids use their prehensile forelimbs to ambush and subdue prey, most canids and hyaenids
149 pounce and pursue prey, and some mustelids use their powerful forelimbs to dig out prey while
150 other more derived mustelids (i.e., weasels) pursue prey in tight crevices and burrows [57]. In
151 contrast, the hindlimb was best supported by the $mvOUM_{locomotion}$ model ($AICcW = 0.83$) in the
152 hindlimb with a short phylogenetic half-life of 5.05 myr (Fig. 1; Table S2), supporting
153 hypotheses that the hindlimb is adapted primarily for locomotion as typically found in
154 quadrupedal mammals [58]. Although the forelimb and hindlimb covaries ($r = 0.87$; Table S3),
155 previous work found that this integration is weaker than expected in carnivorans that do not
156 specialize in cursoriality [34]. This work together supports the hypothesis of functional
157 divergence between the forelimbs and hindlimbs of carnivorans.

158 The axial skeleton exhibits distinct evolutionary modes between the anterior and
159 posterior regions of the vertebral column: cervical and most thoracic vertebrae tended to be best
160 supported by clade-specific shift or single-peak OU models, whereas the last thoracic and all
161 lumbar vertebrae were best supported by $mvOUM_{hunting}$ or $mvOUM_{locomotion}$ models (Fig. 1; Fig.

162 2C–F; Table S2). Our findings strengthen the coalescing hypothesis that anterior vertebrae
163 exhibit lower disparity, higher evolutionary constraints, and more subtle adaptations to
164 locomotion whereas posterior vertebrae exhibit the opposite patterns in carnivorans [35] and
165 broadly across mammals [13]. We posit that high evolutionary constraints of the anterior
166 vertebrae are associated with clade-specific shifts in the cervical and most thoracic vertebrae.
167 Importantly, subtle adaptations in these anterior vertebrae could be masked by many-to-one or
168 one-to-many mappings, making it difficult to uncover the form-function associations with
169 evolutionary models [59]. In contrast, relaxed evolutionary constraints of the posterior vertebrae
170 facilitate the evolution of disparate lumbar vertebrae across the entire carnivoran order. These
171 disparate vertebrae adapt to diverse locomotor modes or hunting behaviors based on the mobility
172 of the posterior backbone and irrespective of clade origins. The short phylogenetic half-lives
173 (1.47–5.12 myr) further suggests strong pulls towards these different adaptive optima. More
174 broadly, this increased mobility of the lumbar region over evolutionary time is hypothesized to
175 be an innovation characterizing crown mammals [13,60,61]. Correspondingly, the posterior
176 vertebrae are tightly integrated ($r = 0.84\text{--}0.96$; Table S3).

177 Lastly, we found that the clade-specific shift model ($\text{mvOUM}_{\text{phyloEM}}$; $\text{AICcW} > 0.99$) best
178 described the overall skeletal phenome (Table S2), a pattern that is consistent with previous
179 investigations of whole-body proxies such as body size and body shape [26,36,37]. The
180 mammalian body plan is comprised of cranial, axial, and appendicular components; therefore, its
181 multidimensionality transcends one-to-one mapping relationships between morphology and
182 ecological function. Instead, individual skeletal components within distinct body plans can adapt
183 to specific ecological factors independently from each other, enabling species with distinct body
184 plans to exhibit similar ecological or functional regimes and vice versa.

185 Overall, we elucidate the mosaic evolution of the carnivoran skeleton, finding that
186 different skeletal components exhibit distinct modes of evolution. Our results suggest that
187 different methodologies and taxonomic samples do not necessarily explain previously reported
188 region-specific macroevolutionary patterns; rather, complexity in explanatory factors of skeletal
189 diversity is a key feature of Carnivora. The ability of individual skeletal components to adapt to
190 specific ecological factors independently from each other may have contributed to the clade's
191 *hierarchical* [62,63] evolution. As previously hypothesized [26,36], the restriction of carnassial
192 shear to the P4/m1 pair may have been the key innovation that facilitated the initial carnivoran
193 diversification early in the clade's evolutionary history. Subsequent evolution led to the
194 continual partitioning between clades, resulting in the origination of extant carnivoran families as
195 discrete phylogenetic clusters that occupy different adaptive zones [64] with distinct
196 morphologies including body size and shape [37,65] and various components of the skeleton
197 ([6]; Fig. 2). Within-clade variation then arises to reflect resource partitioning among
198 ecologically similar taxa, leading to adaptations in morphologies such as the mandible, hindlimb,
199 and posterior region of the vertebral column (Fig. 1). These traits were strongly pulled toward
200 distinct ecological peaks across the adaptive landscape as revealed by their short phylogenetic
201 half-lives (1.47–5.12 myr) relative to the clade's age (48.2 myr).

202 Our research statistically revealed the mosaic evolution of carnivoran skeletons. These
203 distinct evolutionary modes demonstrate the importance of examining multiple skeletal
204 components in ecomorphological analyses. Nevertheless, key questions remain: What spurred
205 the evolutionary transitions towards the evolutionary shifts or adaptations of the various skeletal
206 components? When in the 55 million years of carnivoran evolutionary history did these
207 evolutionary events occur? And what developmental and genetic phenomena underlie the

208 evolutionary dissociation of various skeletal elements? Ongoing work integrating the fossil and
209 paleoenvironmental record will further elucidate the carnivoran diversity we see today and reveal
210 the complexity of evolutionary processes in multicomponent systems.

211

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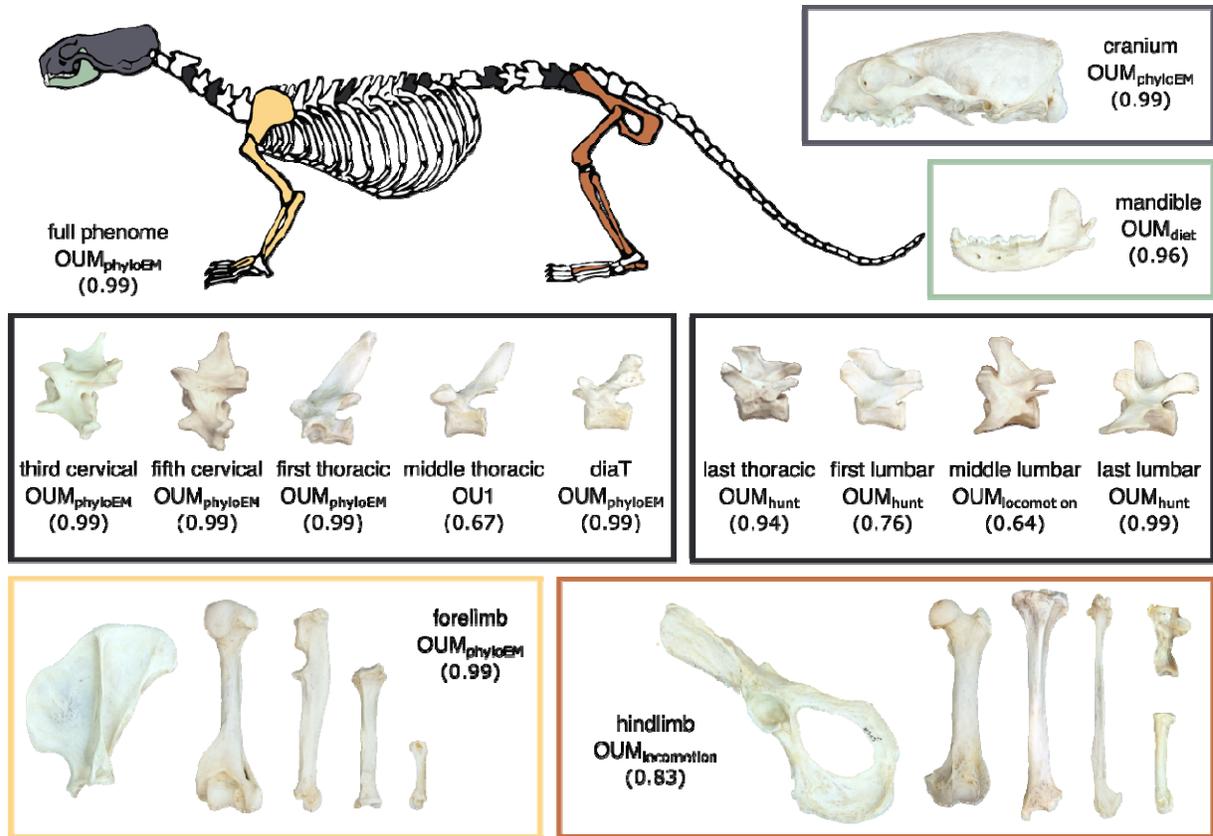
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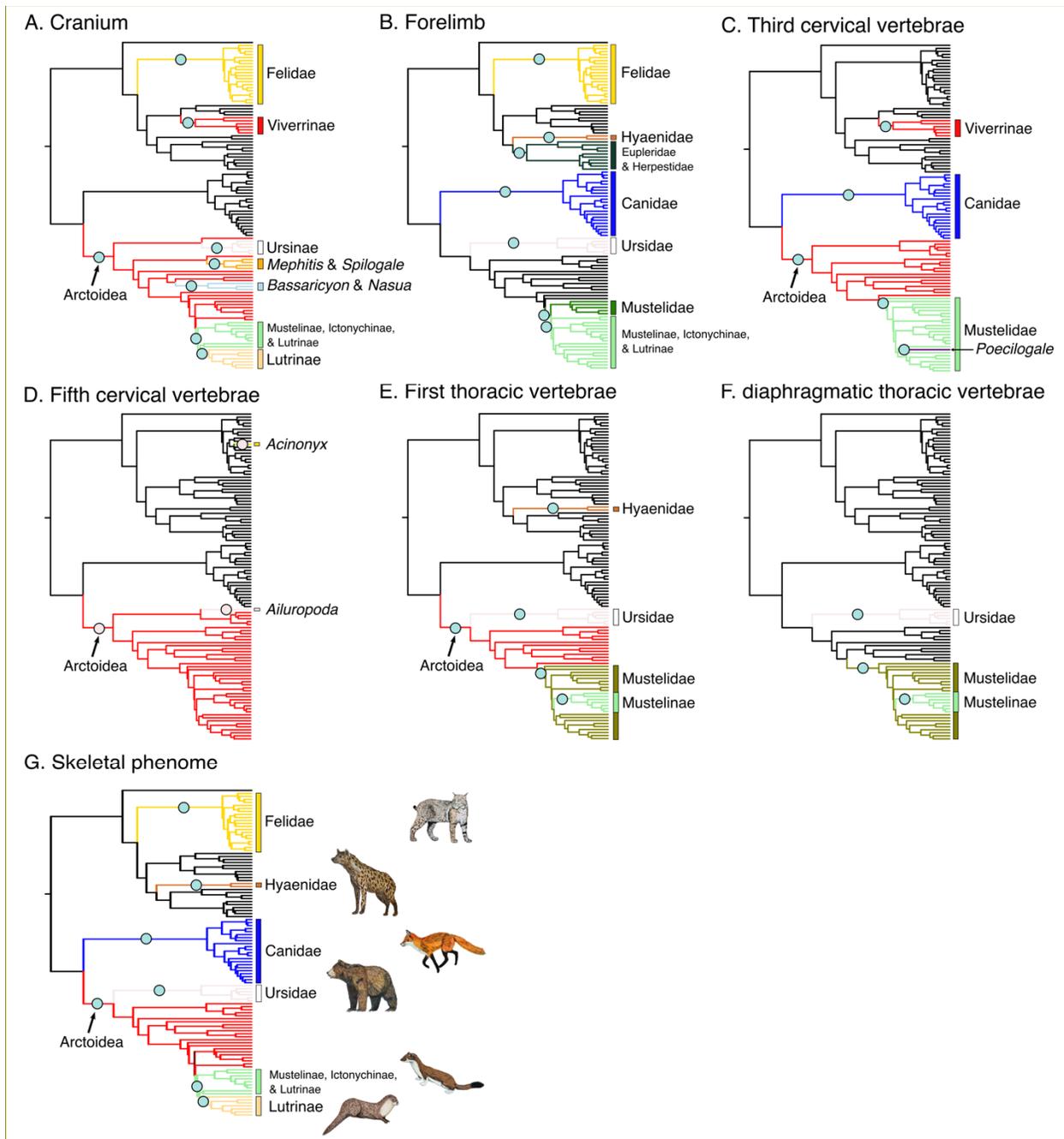


224

225 **Fig. 1.** Diagram of the skeletal components and their best-fitting evolutionary model on *Lontra*

226 *canadensis*. AICcW are in parentheses. See Table S2 for full AICc table. diaT = diaphragmatic

227 thoracic vertebrae



228

229 **Fig. 2.** Clade-specific evolutionary shifts in skeletal components across terrestrial carnivorans

230 identified by PhylogeneticEM. Shifts are represented as pink circles, and branches on the

231 phylogenies are colored according to each regime.

232

233

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