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Decoupled evolution of the cranium and mandible in carnivoran mammals

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The relationship between skull morphology and diet is a prime example of adaptive evolution. In mammals, the skull consists of the cranium and the mandible. Although the mandible is expected to evolve more directly in response to dietary changes, dietary regimes may have less influence on the cranium because additional sensory and brain-protection functions may impose constraints on its morphological evolution. Here, we tested this hypothesis by comparing the evolutionary patterns of cranium and mandible shape and size across 100+ species of carnivoran mammals with distinct feeding ecologies. Our results show decoupled modes of evolution in cranial and mandibular shape; cranial shape follows clade-based evolutionary shifts, whereas mandibular shape evolution is linked to broad dietary regimes. These results are consistent with previous hypotheses regarding hierarchical morphological evolution in carnivorans and greater evolutionary lability of the mandible with respect to diet. Furthermore, in hypercarnivores, the evolution of both cranial and mandibular size is associated with relative prey size. This demonstrates that dietary diversity can be loosely structured by craniomandibular size within some guilds. Our results suggest that mammal skull morphological evolution is shaped by mechanisms beyond dietary adaptation alone.

KEY WORDS: Adaptive evolution, craniomandibular, geometric morphometrics, Ornstein-Uhlenbeck modeling, phylogenetic comparative methods, skull ecomorphology.

The tight relationship between craniodental morphology and dietary ecology in many vertebrate clades is often used to illustrate adaptive evolution. Form-function studies further provide insights into the mechanisms involved in the evolution of adaptive morphologies in the context of prey acquisition and processing, such as suction feeding (Westneat 2005; Wainwright 2007), lingual feeding (Schwenk and Throckmorton 1989; Wake and Deban 2000), and biting (Herrel et al. 2005; Mehta and Wainwright 2007). For example, species that specialize on small, fast prey often exhibit elongate jaws or increased jaw protrusion for fast biting or suction (Slater et al. 2009; Hulsey and León 2015; Ballell et al. 2019); conversely, species that specialize on hard food items often exhibit blunt skulls with large jaw muscles and bunodont teeth for high bite forces (Darwin 1859; Collar et al. 2014a; Law et al. 2016). These studies also highlight the morphological complexity of the skull, which consists of multiple structures that are functionally integrated with one another to enable cohesive feeding behaviors (Wainwright et al. 2005; Westneat 2005; Nogueira et al. 2009; McCurry et al. 2015; Gidmark et al. 2019; Michaud et al. 2020; Rhoda et al. 2020; but see Collar et al. 2014b). Although previous studies identified patterns of evolutionary and developmental integration within skull components (Goswami 2006; Piras et al. 2014; Bardua et al. 2020; Conith et al. 2020; Michaud et al. 2020; Rhoda et al. 2020; Arbour et al. 2021), less is known about whether and how different skull structures respond differently to selective pressures associated with ecological shifts.

In mammals, the skull consists of two primary structures: the cranium and the mandible. The mammalian cranium is a multifunctional structure that, in addition to feeding, takes part in sensory functions, respiration, and brain protection. In contrast, the mammalian mandible is involved primarily in feeding. Therefore, despite strong integration between the cranium and mandible (Hautier et al. 2012; Figueirido et al. 2013; McLean et al. 2018; Michaud et al. 2020), the cranium may experience more structural, functional, or phylogenetic constraints on its evolution, whereas the mandible may evolve more directly in response to dietary changes. Decoupled adaptive shifts between the cranium and mandible are known in some mammal clades (McLean et al. 2018; Arbour et al. 2019; Michaud et al. 2020; Cassini and Toledo 2021; Meloro and Tamagnini 2021). For example, in bats, sensory functions (i.e., echolocation and vision) are the most influential factors shaping cranial evolution, whereas diet has a stronger influence on mandibular evolution (Arbour et al. 2019).

In this study, we test hypotheses pertaining to decoupled adaptive shifts between the cranium and mandible and examine how phylogenetic history and dietary shifts influenced the evolution of these skull components in terrestrial carnivoran mammals. Carnivora is an ideal clade to examine these patterns because of its high species richness (296 species), well-resolved phylogeny, and diverse dietary ecologies and hunting behaviors (Wilson and Mittermeier 2009). Although relationships between dietary ecology and skull morphology are well understood within some carnivoran families (e.g., Figueirido et al. 2009; Slater 2015; Law et al. 2018), evidence of craniomandibular morphological convergence linked to dietary ecology has been inconsistent across the order (Figueirido et al. 2013; Meloro et al. 2015; Tseng and Flynn 2018; Tamagnini et al. 2021). In fact, the most recent analysis found no evidence of convergent morphological evolution among 188 extant carnivorans (Tamagnini et al. 2021). Early work by Radinsky (Radinsky 1981a,b, 1982) hinted that major carnivoran clades evolved toward distinct adaptive zones, consistent with findings that carnivoran families are discrete phylogenetic clusters (dubbed ‘higher evolutionary significant units’ by Humphreys and Barraclough 2014). This body of work led Slater and Friscia (2019) to hypothesize that carnivoran morphological evolution is *hierarchical* (Simpson 1944, 1955); that is, divergence of skull morphology into partitioned familial levels occurred early in carnivoran evolution, and subsequent adaptive evolution within each family facilitated secondary variation in skull morphologies.

We therefore examine the evolutionary decoupling between components of the skull in the context of the hierarchical morphological evolution hypothesis in carnivorans by (1) evaluating macroevolutionary patterns of skull shape and size across all terrestrial carnivoran clades, (2) testing how dietary ecology, hunting behavior, and prey size influence skull shape and size evolution, and (3) investigating whether adaptive patterns in the cranium and mandible are decoupled. Because of functional differences between the cranium and the mandible, we predict that the macroevolutionary processes driving morphological evolution will be decoupled between these two structures. Specifically, we predict that cranial evolution is clade specific and will primarily follow patterns matching familial branches, whereas mandibular evolution will mirror dietary evolution, leading to adaptive shifts toward similar mandibular morphologies among clades within similar dietary ecologies.

Methods

MORPHOLOGICAL DATA

Our dataset consists of 389 crania across 149 carnivorans and 153 mandibles across 100 carnivorans. Three-dimensional scans were obtained from surface scanning with Next Engine 3D Ultra HD, David SLS-3, HDI 120A-B, or Faro ScanArm 3D-scanner systems; computed tomography (CT) scanning with Skyscan 1172 μCT, Nikon XTH 225 ST μCT, or X5000 Computer Tomography systems; and previously published scans (Law and Mehta 2018; Michaud et al. 2020; Rovinsky et al. 2021) archived on MorphoSource (see Table S1 for list of specimens and museums). All specimens were fully mature, determined by the closure of exoccipital-basioccipital and basisphenoid-basioccipital sutures on the cranium and full tooth eruption.

We quantified cranial and mandibular morphology using three-dimensional geometric morphometrics (Rohlf and Slice 1990; Zelditch et al. 2012). We used 35 landmarks and seven curves with 134 semilandmarks for the cranium and 21 landmarks and four curves with 24 semilandmarks for the mandible (Fig. S1). Landmarks were digitized using Checkpoint

(Stratovan Corporation, Davis, CA, USA), and curves were digitized by oversampling semilandmarks in Checkpoint and resampling them by length in the R package geomorph 4.0.1 (Adams and Otárola-Castillo 2013). Landmarks were superimposed by Generalized Procrustes analysis (Rohlf and Slice 1990), and semilandmarks on the curves were allowed to slide along their tangent vectors until their positions minimized bending energy (Bookstein 1997; Zelditch et al. 2012). As part of the superimposition procedure, bilaterally homologous landmarks and semilandmarks were reflected across the median plane and averaged using the geomorph function bilat.symmetry. All Procrustes superimpositions were performed in the R package geomorph 4.0.1 (Adams and Otárola-Castillo 2013). We used centroid size as our metric of cranial and mandibular size.

ECOLOGICAL DATA

We classified carnivoran species using four categorical schemes to capture dietary variation and inform our diet-based selective regime analyses (Table S2). First, we used a traditional dietary categorical scheme (Van Valkenburgh 2007) based on five dietary regimes: hypercarnivory (diets consist of >70% terrestrial vertebrates), omnivory (diets consist of >50% terrestrial vertebrates), insectivory (diets consisting of >70% invertebrates), aquatic carnivory (diets consist of >90% aquatic prey), and herbivory (diets consist of >90% plant material). Second, we used a seven-regime categorical scheme where we divided the carnivory category based on the relative size of the predator to the size of its most common prey (Tamagnini et al. 2021): large (exceeding the predator's own body mass), medium (up to the predator's own body mass), and small (20% of the predator's own body mass) prey hunters. The remaining dietary regimes were kept the same. Third, we categorized carnivorans into five regimes based on physical properties of their main food source: vertebrate muscle (diets consist of >50% muscular flesh of terrestrial vertebrates), invertebrates (diets consist of >70% terrestrial invertebrates), tough (diets consist of tough items such as bones, shells, or bamboo), soft (diets consist of soft fruits), and generalist (diets consist of a variety of prey items). Information to classify species into these dietary ecologies was largely obtained from the Handbook of the Mammals of the World (Wilson and Mittermeier 2009), a thorough secondary source chosen for the editorial consistency of its literature inclusion. Finally, we classified species into one of six hunting behavior categories: ambush (species that stalk and kill prey within a short distance), pounce (species that conduct a moving search ending with a pounce or short chase), pursuit (species that chase prey over long distances), occasional (species that rarely hunt), semifossorial (species that dig for prey), and aquatic (species that hunt in aquatic/marine habitats) following Law (2021).

PHYLOGENETIC COMPARATIVE METHODS

Craniomandibular shape allometry and morphospace

To account for the possible effect of size differences on skull shape variation (Klingenberg 2016), we first tested for evolutionary allometry on cranial and mandibular shape by performing a phylogenetic Procrustes regression (Adams 2014) with a random residual permutation procedure (1000 iterations) in geomorph version 4.0.1 (Adams and Otárola-Castillo 2013). Because both cranial shape ($SS = 0.01$, $MS = 0.\ 01$, $R^2 = 0.09$, $F = 14.75$, $Z = 4.89$, $P = 0.001$) and mandibular shape ($SS = 0.03$, $MS = 0.03$, $R^2 = 0.18$, $F = 22.58$, $Z = 6.1$, $P < 0.001$) exhibited significant evolutionary allometry (Fig. S2), we used both allometry-free shape and uncorrected shape variables in all analyses to examine if and how size influences the distribution of the adaptive shifts and selective regimes in our dataset. We decided to analyze both allometry-free and uncorrected shape data because allometry has been shown to facilitate or constrain skull shape evolution, such as the relative size of the rostrum to braincase in carnivorans, bats, and other mammals (e.g., Slater and Valkenburgh 2009; Cardini and Polly 2013; Santana and Cheung 2016; Arbour et al. 2021). Allometry-free shape was extracted as the shape residuals from the phylogenetic Procrustes regressions. We visualized the phylomorphospace of cranial and mandibular shape by performing principal component analyses (PCA) in the R package geomorph version 4.0.1 (Adams and Otárola-Castillo 2013). We performed all analyses under a phylogenetic framework using the most recent phylogeny of mammals pruned to include just carnivorans (Upham et al. 2019). All analyses were performed in R 4.1.1 (R Core Team 2021).

Phylogenetic effects on craniomandibular shape diversity

To compare patterns between phylogenetic relationships and morphological diversity of the cranium and mandible, we first created cranial and mandibular phenograms using Unweighted Pair Group Method with Arithmetic mean (UPGMA) hierarchical cluster analyses on the allometry-free Procrustes shape datasets with the R function hclust. We then created tanglegrams using the cophylo function in the R package phytools version 0.7 (Revell 2011), which optimized the vertical matching of tips on the phylogeny and each phenogram, and connected the phylogenetic and phenotypic position of each species. Parallel lines linking the same species in the phylogeny and phenograms suggest similarities between evolutionary history and cranial/mandibular diversity, whereas steep lines suggest mismatches that may be due to adaptive evolution. Following Arbour et al. (2019), we quantified whether the vertical displacement between evolutionary history and morphological variation was significantly different from expectations under Brownian motion. We simulated 1000 landmark datasets using the R package geiger

(Pennell et al. 2014), calculated the average of all tip displacements for each simulated tanglegram, and determined whether the observed displacement significantly differed from the distribution of simulated displacements.

Craniomandibular shape evolution

We tested the hypothesis that dietary ecologies and hunting behaviors influenced the evolution of allometry-free cranial shape and allometry-free mandibular shape using multivariate generalized evolutionary models (Hansen 1997; Butler and King 2004; Clavel et al. 2015). We fit six multivariate evolutionary models to the first five PCs of the cranial shape dataset (79.7% of total cranial shape variation) and mandibular shape dataset (86.1% of total mandibular shape variation) using the R package mvMORPH version 1.1.4 (Clavel et al. 2015) to incorporate covariances between axes. We first fit a single-rate multivariate Brownian motion model (mvBM1), which assumes trait variance accumulates stochastically but proportionally to evolutionary time, and a single-optimum Ornstein-Uhlenbeck model (mvOU1), which constrains each PC to evolve toward a single optimum. Support for either of these models would indicate that dietary and hunting behavior regimes do not strongly influence the evolution of cranial or mandibular shape. We then fit four multi-optima Ornstein-Uhlenbeck models (i.e., $\mathrm{mvOUM_{diet}}$, $\mathrm{mvOUM_{rel\ prey\ size}}$, $\mathrm{mvOUM_{prey\ properties}}$, and $\mathrm{mvOUM_{hunting}}$) to test if dietary and hunting behavior regimes influenced the evolution of cranial and mandibular shape. These four models allowed dietary and hunting behavior regimes to exhibit different trait optima (Θ). All six models were fit across 500 stochastically mapped trees to account for uncertainty in phylogenetic topology and the ancestral character states. We inferred the evolution of dietary and hunting behavior regimes by performing stochastic character mapping with symmetric transition rates between regimes (Nielsen 2002; Huelsenbeck et al. 2003; Bollback 2006) in phytools (Revell 2011). We simulated 10 stochastic character maps across 1000 tree topologies randomly drawn from the posterior distribution of trees (Upham et al. 2019), resulting in 10,000-character maps for each set of diet, diet based on relative prey size, diet based on prey properties, and hunting behavior regimes. We randomly sampled 500 trees for subsequent analyses. We also fit a seventh model consisting of a multi-optima OU model ($\mathrm{mvOUM_{phyloEM}}$) without a priori ecological groupings with the R package PhylogeneticEM version 1.4.0 (Bastide et al. 2018). This data-driven approach can detect evolutionary shifts toward different optima without influences of a priori groupings on the tree. We used a scalar OU model that infers the full evolutionary rate matrix and accounts for correlations within multivariate datasets (i.e., PC1–PC5). Relative support for each of the seven models was assessed through computation of small sample-corrected Akaike weights (AICcW). All models with $\Delta\mathrm{AICc} < 2$ were considered to be supported by the data (Burnham and Anderson 2002). Finally, we tested whether carnivorans within each dietary or hunting regime exhibited convergence toward similar crania and mandibles using the convevol package (Stayton 2015).

We acknowledge that using a subset of PC axes instead of the full dataset may lead to inaccurate results (Uyeda et al. 2015; Adams and Collyer 2018), but we were computationally limited to run the full 507 trait dataset. To address this, we used simulations to assess whether we had adequate power to accurately distinguish between complex mvOU models from Brownian motion (Boettiger et al. 2012). We performed 500 simulations for the cranial and mandibular shape datasets using the parameter estimates of the best-fit model in the empirical dataset. These simulated datasets were generated using the *mvSIM* function. We then ran the simulated data through all six models using the *mvBM* and *mvOU* functions to determine whether the simulated model could be accurately recovered (Boettiger et al. 2012). Our simulations under the best-fit models indicated that there was substantial power to distinguish between all models for both cranial and mandibular shape analyses ($\mathrm{AICcW} > 0.99$; Table S4). Lastly, we reran our models using only PCs 1−3 (69.6% of the variance in cranial shape and 74.5% of the variance in mandibular shape) to examine if different subsets of PC axes changed our results.

Because the multi-peak $\mathrm{OUM_{diet}}$ model was the best-fitting model for mandibular shape (see *Results*), we tested whether mandibular shapes differed between the five dietary regimes using a Procrustes phylogenetic analysis of variance (pANOVA) with 1000 iterations and post hoc pairwise permutation tests in the R package RRPP version 1.0.0 (Collyer and Adams 2018). We also tested whether the Procrustes variance of mandibular shapes differed between the five dietary regimes using the morphol.disparity function in geomorph. Further, we determined how well the five dietary regimes can distinguish between mandibular shapes by performing a canonical variate analysis (CVA) with a jackknife cross-validation procedure in the R package Morpho version 2.8 (Schlager 2016).

CRANIOMANDIBULAR SIZE EVOLUTION

We used the same set of procedures described above to test the hypothesis that dietary ecologies and hunting behaviors influenced the evolution of cranial size and mandibular size. For evolutionary modeling, we used the univariate equivalent set of evolutionary models (i.e., BM1, OU1, $\mathrm{mvOUM_{diet}}$, $\mathrm{mvOUM_{rel\ prey\ size}}$, $\mathrm{mvOUM_{prey\ properties}}$, and $\mathrm{mvOUM_{hunting}}$) with the R package OUwie version 2.6 (Beaulieu et al. 2012). Because the multi-peak $\mathrm{OUM_{preysize}}$ model was the best-fitting model for both cranial and mandibular size (see *Results*), we used Procrustes pANOVAs and pairwise post hoc tests to determine whether cranial and mandibular size differed between the seven dietary regimes in RRPP (Collyer and Adams 2018).

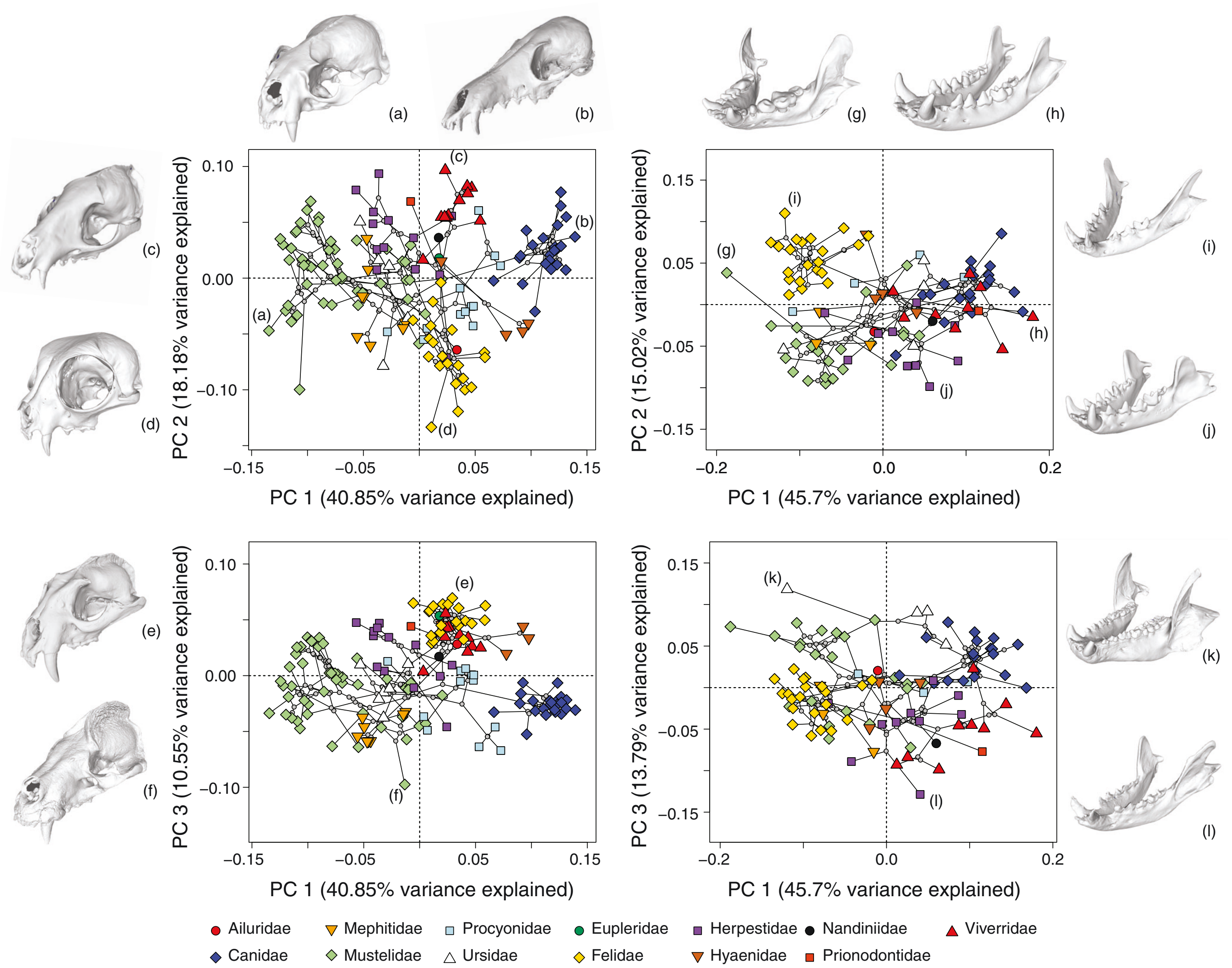

Figure 1. **Morphospace of allometry-free cranial and mandibular shape defined by principal component (PC) axes 1–3. Taxa illustrated for the cranial morphospace: (a) African clawless otter (*Aonyx capensis*), –PC1; (b) kit fox (*Vulpes macrotis*), +PC1; (c) small Indian civet (*Viverricula indica*), +PC2; (d) Pallas's cat (*Otocolobus manul*), –PC2; (e) clouded leopard (*Neofelis nebulosa*), +PC3; and (f) hog badger (*Arctonyx collaris*), –PC3. Taxa illustrated for the mandibular morphospace: (g) sea otter (*Enhydra lutris*), –PC1; (h) African civet (*Civettictis civetta*), +PC1; (i) sand cat (*Felis margarita*), +PC2; (j) Egyptian mongoose (*Herpestes ichneumon*), –PC2; (k) panda (*Ailuropoda melanoleuca*), +PC3; and (l) common kusimanse (*Crossarchus obscurus*), –PC3.**

Results

Results based on allometry-free shape and uncorrected shape data are similar; therefore, we present results on allometry-free shape below. Results of analyses based on the uncorrected shape data are in the Supporting Information (Figs. S3–S6; Table S3).

CRANIOMANDIBULAR MORPHOSPACE

PCs 1−3 explain 69.6% of the cranial shape variation (Fig. 1). Positive PC 1 scores are associated with elongation of the rostrum and reduction of the braincase through narrowing of the nuchal crests; positive PC 2 describes lateral narrowing of the cranium at the zygomatic arches and slight dorsoventral rostral flexure; and positive PC describes slight broadening of the cranium at the zygomatic arches and braincase. PCs 1−3 explain 74.5% of the mandibular shape variation (Fig. 1). Positive PC 1 describes anteroposterior elongation of the mandibular body and lateral compression of the coronoid processes; positive PC 2 describes dorsoventral mandibular flexure and lateral broadening of the coronoid processes; and positive PC 3 describes increases in coronoid height.

PHYLOGENETIC EFFECTS ON CRANIOMANDIBULAR SHAPE DIVERSITY

Both morphology-phylogeny tanglegrams and evolutionary models revealed different patterns of adaptive evolution in the

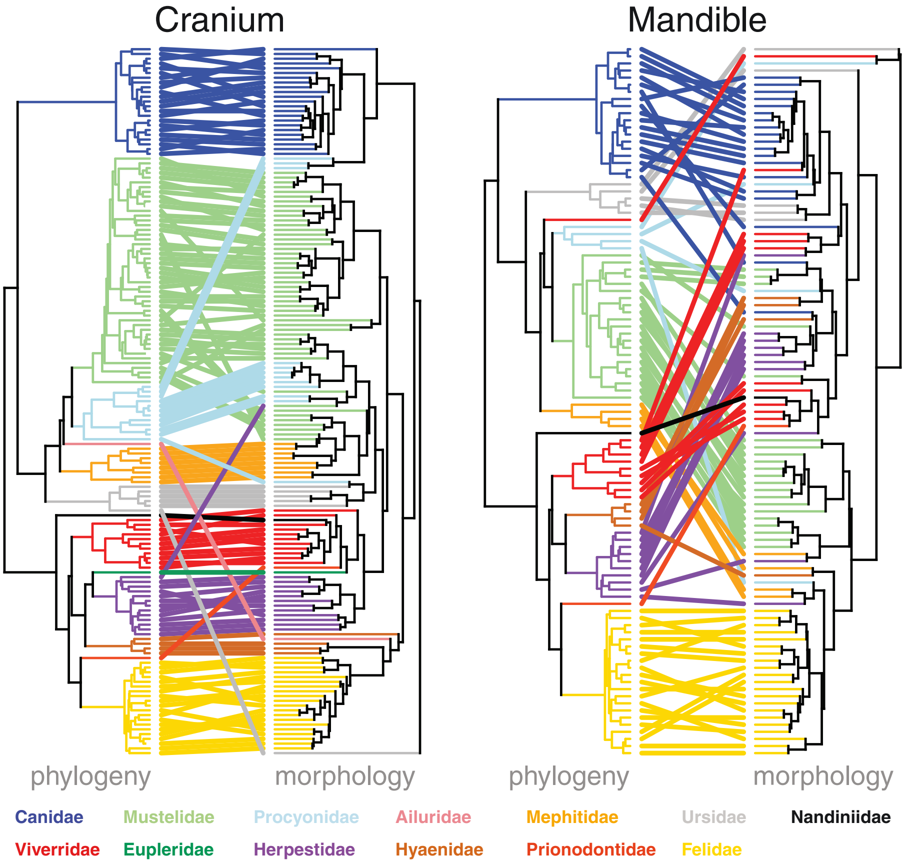

Figure 2. **Morphology-phylogeny tanglegrams showed stronger correspondence between cranial shape diversity and phylogenetic relationships than between mandibular shape diversity and phylogenetic relationships. The observed taxon displacement between the phylogeny and cranial phenogram was significantly lower than expected under a multivariate BM process (tip displacement value = 7.2, simulated displacement value = 8.1, $P = 0.017$), whereas the observed taxon displacement between the phylogeny and mandibular phenogram was significantly greater than expected under a multivariate BM process (tip displacement value = 13.4, simulated displacement value = 5.2, $P < 0.001$). Lines link the same species between phylogenies and phenograms. Parallel lines suggest similarities between evolutionary history and cranial/mandibular diversity, whereas steep lines suggest mismatches that may be due to adaptive evolution.**

and mandible. The tanglegrams showed stronger correspondence (i.e., more parallel lines) between phylogenetic relationships with cranial shape disparity than with mandibular shape disparity (Fig. 2). The observed taxon displacement between the phylogeny and cranial phenogram was significantly lower than expected under a multivariate BM process (tip displacement value = 7.2, simulated displacement value = 8.1, $P = 0.017$), whereas the observed taxon displacement between the phylogeny and mandibular phenogram was significantly greater than expected under a multivariate BM process (tip displacement value = 13.4, simulated displacement value = 5.2, $P < 0.001$). Mismatches between mandibular shape and phylogenetic relationships suggest that additional factors aside from phylogenetic history influence mandibular shape evolution in Carnivora.

CRANIOMANDIBULAR SHAPE EVOLUTION

The morphology-phylogeny patterns described above were confirmed by evolutionary models. In the cranium, the PhylogeneticEM model ($\text{mvOUM}_{\text{phyloEM}}$) exhibited overwhelmingly greater support compared to a priori dietary and hunting behavior based OUM models (AICcW = 1.00; Table 1). PhylogeneticEM revealed 13 adaptive zone shifts in cranial shape that occur along the branches of named clades (Fig. 3). In feliforms, evolutionary shifts occurred along the entire feliform clade except Nandiniidae, the two subfamilies (Pantherinae and Felinae) of Felidae (cats), Viverridae (civets and genets), and Hyaenidae (hyenas). Within caniforms, evolutionary shifts occurred along Canidae (dogs), Ursidae (bears), and Musteloidea. Further shifts occur within musteloids including Mephitidae (skunks), the procyonid

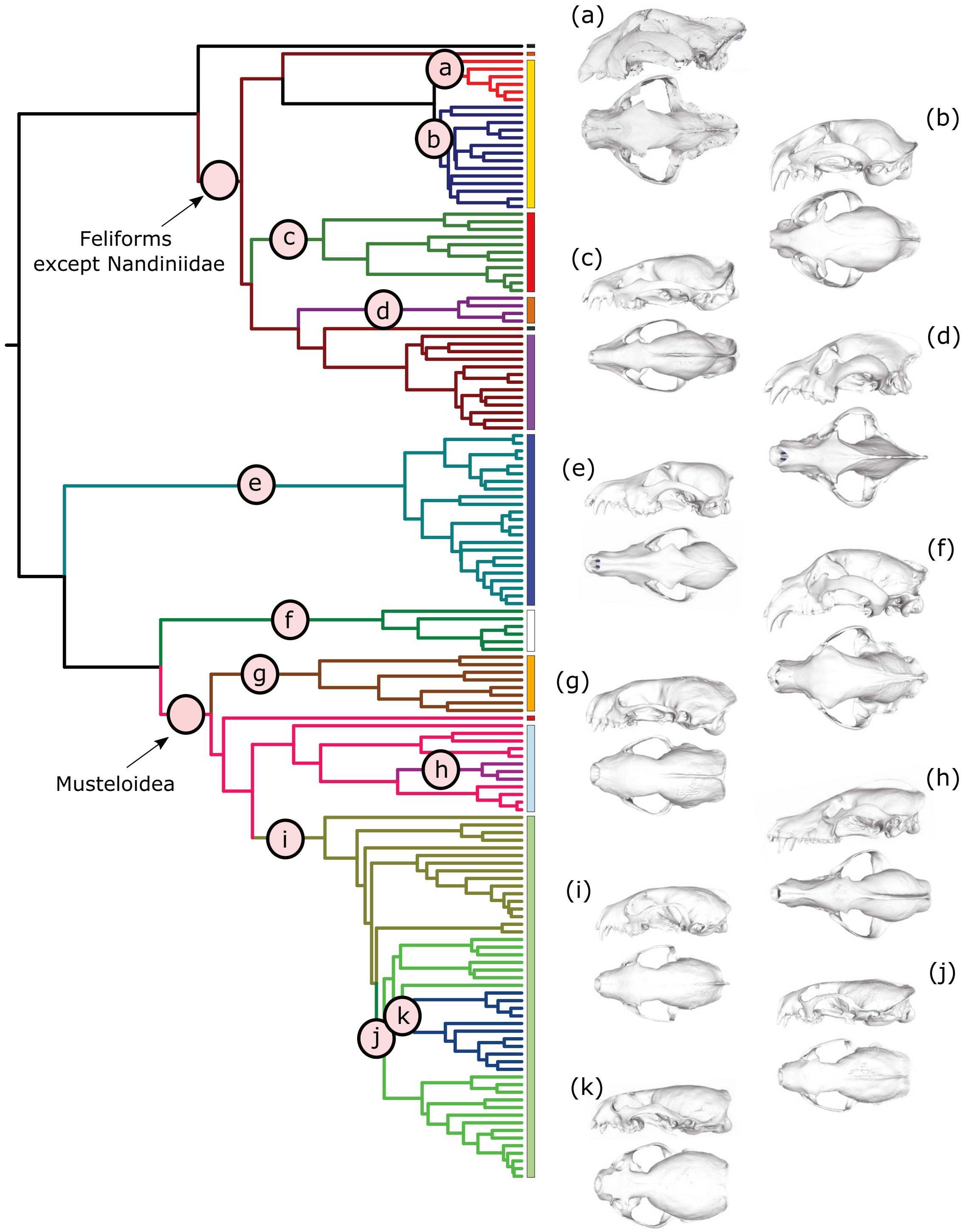

Figure 3. Adaptive shifts in allometry-free cranial shape (PCs 1–5) largely occurred on branches leading to carnivoran families. PhylogeneticEM found 13 evolutionary shifts, each represented as pink circles. Branches on the phylogenies are colored according to each regime. Cranial images show the species that most closely resemble the mean shape of each regime: (a) tiger (*Panthera tigris*) representing Pantherinae, (b) leopard cat (*Prionailurus bengalensis*) representing Felinae, (c) masked palm civet (*Paguma larvata*) representing Viverridae, (d) striped hyaena (*Hyaena hyaena*) representing Hyaenidae, (e) golden jackal (*Canis aureus*) representing Canidae, (f) American black bear (*Ursus americanus*) representing Ursidae, (g) Molina's hog-nosed skunk (*Conepatus chinga*) representing Mephitidae, (h) South American coati (*Nasua nasua*) representing Nasuina, (i) European pine marten (*Martes martes*) representing Mustelidae, (j) American mink (*Mustela vison*) representing a mustelid subclade consisting of Mustelinae, Lutrinae, and Ictonychinae, and (k) North American river otter (*Lontra canadensis*) representing Lutrinae.

Table 1. Comparisons of the best-fitting evolutionary models in allometry-free shape and size of the cranium and mandible. Small sample-corrected Akaike weights (AICcW) were calculated for each of the 500 replications to account for uncertainty in phylogenetic topology and the ancestral character states. Rows in boldface type represent the best-fit model as indicated by the lowest ΔAICc score. ΔAICc = the mean of AICc minus the minimum AICc between models.

Structure	Model	AICc	ΔAICc	AICcW
Cranial shape	mvBM1	−3501.23	185.54	0.00
	mvOU1	−3532.76	154.01	0.00
	$\mathrm{mvOUM}_{\mathrm{diet}}$	−3532.99	153.77	0.00
	$\mathrm{mvOUM}_{\mathrm{prey\_properties}}$	−3559.55	127.22	0.00
	$\mathrm{mvOUM}_{\mathrm{hunting}}$	−3539.3	147.46	0.00
	$\mathrm{mvOUM}_{\mathrm{rel\_prey\_size}}$	−3524.27	162.50	0.00
	$\mathbf{mvOUM}_{\mathbf{phyloEM}}$	**−3686.76**	**0.00**	**1.00**
Mandibular shape	mvBM1	−1814.24	78.38	0.00
	mvOU1	−1873.06	19.56	0.00
	$\mathbf{mvOUM}_{\mathbf{diet}}$	**−1892.62**	**0.00**	**0.97**
	$\mathrm{mvOUM}_{\mathrm{prey\_properties}}$	−1882.24	10.38	0.01
	$\mathrm{mvOUM}_{\mathrm{hunting}}$	−1862.56	30.06	0.00
	$\mathrm{mvOUM}_{\mathrm{rel\_prey\_size}}$	−1885.07	7.55	0.02
	$\mathrm{mvOUM}_{\mathrm{phyloEM}}$	No shifts		
Cranial size	mvBM1	74.36	14.43	0.00
	mvOU1	65.59	5.66	0.05
	$\mathrm{mvOUM}_{\mathrm{diet}}$	69.29	9.36	0.01
	$\mathrm{mvOUM}_{\mathrm{prey\_properties}}$	69.94	10.01	0.01
	$\mathrm{mvOUM}_{\mathrm{hunting}}$	66.44	6.51	0.03
	$\mathbf{mvOUM}_{\mathbf{rel\_prey\_size}}$	**59.93**	**0.00**	**0.90**
	$\mathrm{mvOUM}_{\mathrm{phyloEM}}$	No shifts		
Mandibular size	mvBM1	118.48	23.69	0.00
	mvOU1	99.63	4.84	0.08
	$\mathrm{mvOUM}_{\mathrm{diet}}$	104.37	9.57	0.01
	$\mathrm{mvOUM}_{\mathrm{prey\_properties}}$	104.39	9.60	0.01
	$\mathrm{mvOUM}_{\mathrm{hunting}}$	106.38	11.58	0.00
	$\mathbf{mvOUM}_{\mathbf{rel\_prey\_size}}$	**94.79**	**0.00**	**0.90**
	$\mathrm{mvOUM}_{\mathrm{phyloEM}}$	No shifts		

clade Nasuina (coatis), and Mustelidae. Mustelids exhibit further evolutionary shifts along a subclade consisting of Mustelinae (minks, polecats, and weasels) + Lutrinae (otters) + Ictonychinae (polecats and weasels) and again within Lutrinae alone. Simulations under the best-fitting model confirm there was substantial statistical power to distinguish complex OUMs from the BM1 and OU1 models (Table S4). Furthermore, we largely found no evidence of cranial convergence within each dietary regime except for insectivores ($C1 = 0.19$; $P = 0.021$) and pursuit hunters ($C1 = 0.25$; $P = 0.026$) (Table S7).

In contrast, the multi-peak $\mathrm{mvOUM}_{\mathrm{diet}}$ model with broad dietary regimes was the best-fitting model for mandibular shape (AICcW = 0.97; Table 1) and exhibited a mean phylogenetic half-life of 3.78 Myr. The other multi-peak models with more specific regime schemes based on hunting behavior, physical properties of prey, or relative prey size were all poorer fits (all $\Delta\mathrm{AICc} > 7.55$), and the PhylogeneticEM model did not find any evolutionary shifts in mandibular shape. Further Procrustes phylogenetic ANOVA indicated significant differences in mandibular shape between these broad dietary regimes ($SS = 0.01$, $MS = 0.00$, $R^2 = 0.10$, $F = 2.79$, $Z = 3.57$, $P < 0.001$). Relative to the mean mandibular shape, omnivores exhibited relatively elongate, narrow mandibles; herbivores exhibited relatively blunt, narrow mandibles with broader rami; insectivores exhibited slightly longer mandibles with shorter rami; and piscivores exhibited relatively blunt mandibles with broader mandibular rami (Fig. 4a). Hypercarnivores exhibited mandibles that most closely resemble the mean mandibular shape. However, the Procrustes phylogenetic ANOVA model indicated that diet accounted for only 10% of the mandibular shape variation, and pairwise tests revealed that mandibular shapes are not statistically different between all dietary regimes: significantly different mandibular shapes were found between piscivorous and all other dietary groups except insectivores, between hypercarnivores and

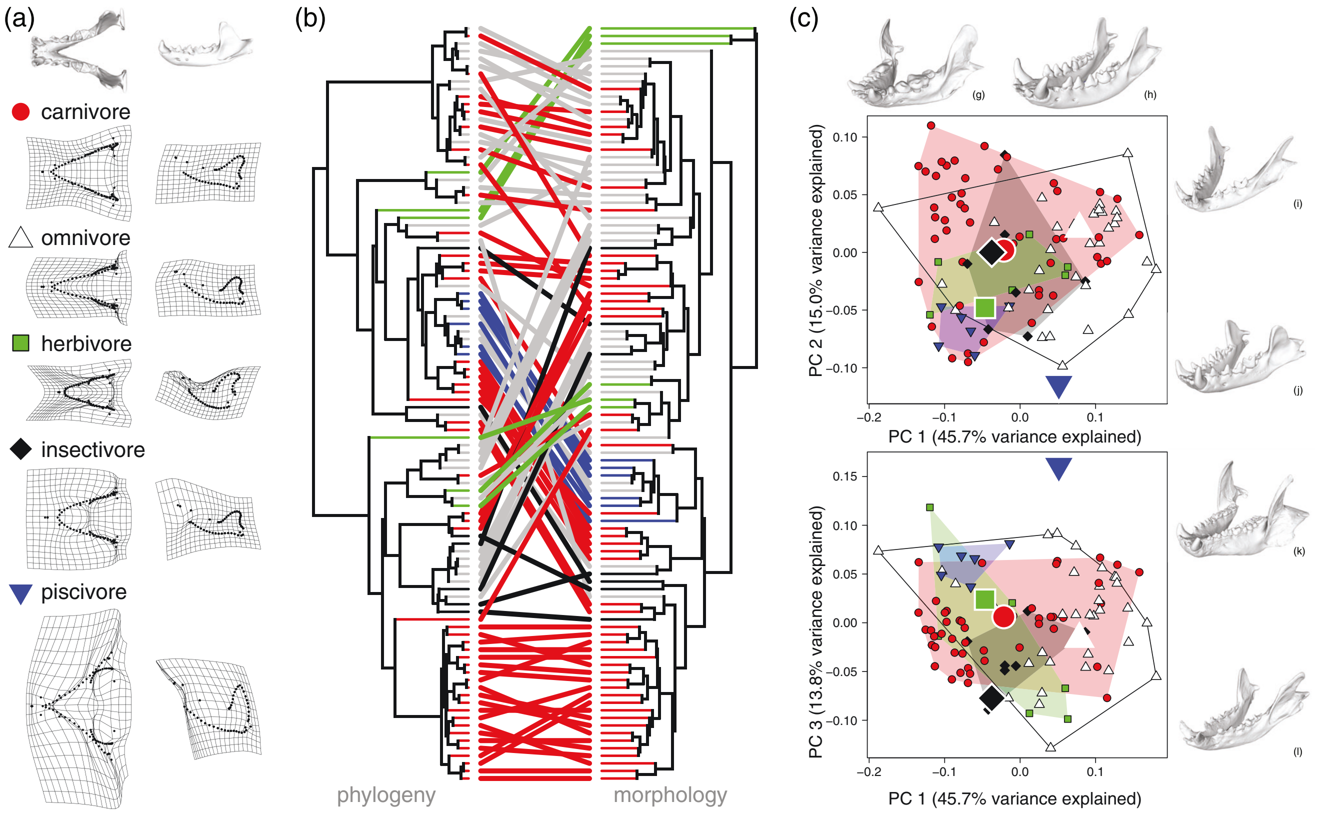

Figure 4. **Depiction of relationships between mandibular shape variation and diet in carnivorans. (a) Mandibular shape differences between mean carnivoran mandible and each dietary regime. Shape differences were magnified by a factor of 2. (b) Morphology-phylogeny tanglegrams depicting correspondence between mandibular shape diversity and phylogenetic relationships overlayed with the five dietary regimes. (c) Morphospace of allometry-free mandibular shape defined by principal component (PC) axes 1–3 overlayed with the five dietary regimes. Larger symbols in panel (c) represent adaptive optima of each dietary regime from the multi-peak OUMd$_{\text{iet}}$ model. Taxa illustrated for the mandibular morphospace are the same as Figure 1.**

omnivores, and between insectivores and herbivores (Table S5). Furthermore, a CVA with Jackknife cross-validation reclassified mandibular shapes in their correct dietary regime with 58% accuracy (Table S6; Fig. S7), suggesting that dietary categories cannot be reliably sorted using mandibular shape. The Procrustes variances of herbivores (0.020, $n = 6$), hypercarnivores (0.015, $n = 48$), and omnivores (0.013, $n = 33$) were significantly greater than insectivores (0.007, $n = 7$) and piscivores (0.004, $n = 6$). The mandible-phylogeny tanglegram (Fig. 2) and mandibular PCA overlayed with the five dietary regimes are consistent with pairwise tests and the CVA, showing varying correspondences between species and mandibular shape with shared dietary regimes (Fig. 4b) and overlapping regions of mandibular shape space between many dietary regimes (Fig. 4c), respectively. The cranial PCA overlayed with the five dietary regimes also show overlapping regions of cranial shape space (Fig. S8). Consistently, we found no evidence of mandibular convergence within each dietary regime (Table S7).

The mvOUM$_{\text{phyloEM}}$ and mvOUM$_{\text{diet}}$ models were the best fitting models for allometry-free cranial shape and allometry-free mandibular shape, respectively, when only PCs 1–3 were analyzed (Table S8).

CRANIOMANDIBULAR SIZE EVOLUTION

The multi-peak OUM$_{\text{preysize}}$ model was the best-fitting model for both cranial size (AICcW = 0.90; phylogenetic half-life = 11.2 Myr) and mandibular size (AICcW = 0.90; phylogenetic half-life = 4.3 Myr; Table 1). The PhylogeneticEM model did not find any evolutionary shifts in either. Procrustes phylogenetic ANOVA indicated significant differences between these seven dietary regimes in cranial size (SS = 0.24, MS = 0.04, $R^2 = 0.15$, $F = 4.19$, $Z = 3.02$, $P = 0.001$) and mandibular size (SS = 0.22, MS = 0.04, $R^2 = 0.13$, $F = 2.31$, $Z = 1.81$, $P = 0.037$). Post hoc pairwise tests revealed that hypercarnivores that specialize on relatively large prey exhibit significantly larger crania and mandibles than small prey hypercarnivores, insectivores, and omnivores ($P = 0.005–0.035$) but not herbivores, piscivores, and medium prey hypercarnivores (Table S9).

Discussion

Our results demonstrate contrasting patterns in the evolution of the cranium and mandible in carnivorans. First, the shapes of the carnivoran cranium and mandible exhibit decoupled modes of evolution; cranial shape follows clade-based evolutionary shifts (Figs. 2, 3), whereas mandibular shape evolution is linked to broad dietary regimes (Figs. 2, 4). Second, the evolution of cranial size and mandibular size was associated with the relative size of prey in hypercarnivores but not carnivorans with other diets. When removing the effects of size, we found that mandibular shape is more evolutionary labile than cranial shape with respect to dietary evolution; the shape of the cranium may be more constrained in its ability to evolve to match dietary demands because it performs multiple functions in addition to feeding.

CRANIAL SHAPE EVOLUTION IS CLADE BASED

Adaptive shifts in cranial shape evolution occur primarily along familial branches; all diet-specific models were poor fits, and there is no evidence of convergence among a priori dietary or hunting regimes. This indicates that the complexity and variation of carnivoran cranial adaptations cannot be captured effectively by these categories, and/or that carnivorans with shared dietary ecologies do not evolve similar cranial shapes—confirming that convergent evolution of cranial morphology is rare among carnivorans (Tamagnini et al. 2021). Our results also support earlier findings that the diversity of the carnivoran skull is partitioned between families rather than between ecological groups (Radinsky 1981a,b, 1982). Disparate evolutionary processes also appear to have shaped morphological diversity within individual carnivoran clades. For instance, dietary ecologies influence cranial shape evolution within clades that exhibit greater dietary variation, such as musteloids (Dumont et al. 2015; Law et al. 2018) and ursids (Figueirido et al. 2009); however, we find that these same dietary regimes weakly influence cranial shape evolution across all carnivorans. These results are consistent with previous analyses of masticatory myology that have found relationships between dietary ecology and jaw muscle architecture in musteloids and ursids but not across the entire carnivoran clade (Hartstone-Rose et al. 2019, 2022).

Similar patterns are also found in other vertebrate clades as well. For example, patterns of cranial shape diversity appear to follow the phylogeny in turtles (Foth et al. 2017) but with clearer relationships between cranial shape and diet within groups such as Testudinoidea (Claude et al. 2004) and sea turtles (Parham and Pyenson 2010). In caecilians, cranial morphospace occupies distinct clusters that closely correspond to major clades but with evidence of morphological convergence within some clades (Sherratt et al. 2014). Clade-specific shifts in cranial shape are also found across birds (Felice et al. 2019); however, like the carnivoran mandible (see next section), beak shape may have a stronger ecological signal in groups such as waterfowl (Olsen 2017), Darwin's finches, and Hawaiian honeycreepers (Tokita et al. 2017).

Clade-specific shifts in carnivoran cranial morphologies extend to their overall body shape; evolutionary shifts in carnivoran body shape also occur along clade branches, whereas locomotor, hunting, and dietary ecologies are poor predictors of body shape variation (Law 2021). Together, these results reiterate that extant carnivoran families are evolutionarily significant units occupying different adaptive zones (Humphreys and Barraclough 2014). The formation of these family-level units may be due to the hierarchical nature of carnivoran evolution, in which ecomorphologies diverged into familial partitions early in carnivoran evolution followed by morphological evolution that reflects resource partitioning among ecologically similar taxa within each clade (Slater and Friscia 2019). Slater and Friscia posited that dental traits associated with 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. Early carnivoran diversification, in turn, led to the partition between clades and resulted in the origination of extant carnivoran families. Subsequent diversification of traits then was clade specific, leading to within-clade variation in body mass (Slater and Friscia 2019), body shape (Law 2021), and cranial shape independently from one another.

Another possible explanation for the lack of dietary signal on cranial shape evolution across carnivorans is one-to-many mapping of form to function (Zelditch et al. 2017), which suggests that the cranium is a versatile structure capable of performing multiple functions. In addition to feeding, the cranium supports sensory structures and protects the brain, and these functions may also have influenced cranial shape evolution. For example, the evolution of different sensory modalities (echolocation, vision) reshaped the evolution and modularity of the bat cranium (Arbour et al. 2019, 2021; Hall et al. 2021) and likely led to nasofacial asymmetry in toothed whale crania (Coombs et al. 2020). Other body elements may also have stronger relationships with dietary ecologies. For example, raptors exhibit significant relationships between foraging behavior and talons on their hind limbs (Ward et al. 2002) rather than cranial or beak morphology (Bright et al. 2016). Furthermore, Tseng and Flynn (2018) found that cranial shape in carnivorans corresponds with not only dietary ecologies but also with traits not related to feeding, such as sexual maturity and precipitation-related arboreality; however, the underlying mechanisms linking these variables remain unknown. Together, these findings highlight the need to investigate the form-function relationships between cranial shape and ecological factors other than diet, and their potential effects on the covariation between dietary ecology, cranial shape, and other morphological traits.

MANDIBULAR SHAPE AS A FUNCTIONALLY RELEVANT MORPHOLOGY?

Diet is often found to have had a strong evolutionary influence on mandibular shape due to the direct mechanical role of the mandible in feeding (Meloro et al. 2008; Figueirido et al. 2010, 2013; Prevosti et al. 2011; Grossnickle 2020; Morales-García et al. 2021). Here, we found that diet, broadly defined, helped shape the evolution of mandibular morphology in carnivorans. Furthermore, the short phylogenetic half-life (3.78 Myr) relative to the age of Carnivora itself (48.2 Myr) indicates that mandibular shape is strongly pulled toward distinct dietary peaks across the adaptive landscape.

The mandible serves as a lever that transmits jaw muscle forces to food items during biting (Smith and Savage 1959; Turnbull 1970); therefore, evolutionary changes in mandibular shape lead to changes in bite performance during prey capture and consumption. In carnivorans, herbivores specializing on tough, fibrous plant material and hypercarnivores specializing on relatively large prey tend to exhibit the strongest bite force relative to body mass (Christiansen and Wroe 2007). Many studies have identified corresponding mandibular traits that increase the mechanical advantage of the jaw adductor muscles to generate these strong bite forces (Radinsky 1981a,b; Christiansen and Wroe 2007; Meloro et al. 2008; Figueirido et al. 2010, 2013; Prevosti et al. 2011). Consistent with these previous studies, we found that both herbivores and hypercarnivores evolved a taller, broader coronoid process, which increases the in-lever of the temporalis muscle during biting (Fig. 4a). We further found that herbivorous carnivorans evolved (1) relatively blunter mandibles (i.e., shorter jaw out-lever); (2) a deeper posterior portion of the mandibular corpus, which may facilitate grinding of tough plant material at the molars; and (3) taller ascending rami, which further increase the in-levers of the temporalis and masseter jaw muscles. In contrast, insectivorous carnivorans tend to exhibit the weakest bite forces relative to body mass (Christiansen and Wroe 2007). Instead of adaptations for forceful bites, insectivores exhibit relatively longer jaws and shorter mandibular rami. These adaptations increase biting speed, which is advantageous for catching small, fast-moving insects.

Although our results demonstrate that mandibular shape evolution reflects adaptations to distinct dietary ecologies in carnivorans, whether mandibular shape can be used as a reliable functional trait to distinguish between dietary regimes in carnivorans remains in question. Despite evidence of strong selection from diet toward distinct mandibular shape peaks, the CVA and PCA poorly discriminated carnivorans between dietary regimes in morphospace (Figs. 4c, S3), and we found no evidence that carnivorans with shared dietary regimes exhibit convergence in overall mandibular shapes. Furthermore, diet accounted for only 10% of mandibular shape variation. A possible explanation is that dietary ecology likely shapes only some aspects of mandibular morphology rather than the shape of the entire mandible; for example, Meloro et al. (Meloro et al. 2008, 2011; Meloro and O'Higgins 2011) previously found that the corpus and ramus of the carnivoran mandible differ considerably in shape among predaceous and non-predaceous species. In our dataset, traits associated with the lever mechanics of jaw closing likely describe the primary shape differences between dietary regimes (Fig. 4a). Single linear traits that quantify the moment arms of the masticatory muscles, outlever of the bite point, or size of the jaw muscle attachment sites have been reliable for distinguishing among dietary regimes in carnivorans (Radinsky 1981a,b, 1982; Friscia et al. 2007) and across mammals (Grossnickle 2020; Morales-García et al. 2021). Dental traits, especially those associated with relative grinding area, are also important discriminators of dietary ecologies in carnivorans (Valkenburgh 1989, 1999; Friscia et al. 2007; Slater and Friscia 2019 but see Hopkins et al. 2021). Therefore, a comparative functional trait approach is likely to yield stronger links between mandible adaptive evolution and dietary shifts.

THE ROLE OF SIZE IN CRANIOMANDIBULAR EVOLUTION

Size is a fundamentally important trait that influences many aspects of organismal form, performance, and ecology (Schmidt-Nielsen 1984). In the context of feeding, bite performance metrics such as bite force scale positively with craniomandibular and body size (van der Meij and Bout 2004; Erickson et al. 2013; Maestri et al. 2016; Santana and Miller 2016; Hartstone-Rose et al. 2022). Therefore, species can adapt to consuming tougher, larger, or more challenging foods simply by evolving larger sizes. Unsurprisingly, size has strong effects on skull shape in many vertebrate clades such as raptors (Bright et al. 2016), crocodylomorphs (Godoy 2020), and frogs (Bardua et al. 2021). Evolution of increased size is seen as a possible path of least resistance that could facilitate diversification of dietary ecologies not only in mammals (Marroig and Cheverud 2005, 2010; Santana and Cheung 2016; Zelditch et al. 2017) but in other vertebrate groups (Bright et al. 2016). However, evolutionary or ecological constraints often limit the evolution of larger sizes (Zelditch et al. 2017) and evolutionary shifts toward higher bite forces often occur through morphological changes that increase the mechanical advantage of the feeding apparatus. Terrestrial carnivorans span five orders of magnitude in body size (~55 g least weasel to 800 kg polar bear). Correspondingly, body size helps facilitate the evolution of dietary ecologies in carnivorans (Carbone et al. 1999; Price and Hopkins 2015). Our results provide further evidence that dietary diversity is loosely structured by craniomandibular size specifically within hypercarnivores. The $\text{OUM}_{\text{preysize}}$ model was the best model for both cranial size and mandibular size, demonstrating an adaptive relationship between dietary ecology and craniomandibular size. Hypercarnivores specializing on relatively large prey exhibit significantly larger mandibles and, to a lesser extent, crania compared to most other dietary regimes (Table S5). These results suggest that selective pressures toward larger heads alone could lead to specialization on larger vertebrate prey. This is consistent with previous findings that carnivoran communities exhibit substantial size-based partitioning of prey resources at lower phylogenetic and niche levels (Dayan et al. 1989; Dayan and Simberloff 1994, 1998). In contrast, we found no differences in craniomandibular size between the remaining dietary regimes. Instead, differences in dietary regimes can be linked to variation in mandibular shape and other mandibular traits associated with the lever mechanics of generating bite force as described above.

Conclusions

This study demonstrates decoupled modes of evolution in the shape and size of the cranium and mandible. We found that cranial shape follows clade-based evolutionary shifts, whereas mandibular shape and craniomandibular size are linked to dietary variation. These results invite future investigation of the functional relationships between cranial and mandibular morphology and additional traits that may serve as adaptations to diverse ecologies. For example, previous work has revealed links between dietary groups and different masticatory muscle properties (Hartstone-Rose et al. 2012, 2019) that may be more informative predictors of dietary adaptation compared to osteological characters (Dickinson et al. 2021). Furthermore, species across dietary groups vary in mandible trabecular bone morphology (Watson et al. 2018; Wysocki and Tseng 2018), which can contribute to specialization not captured by external shape analyses. Therefore, future work integrating the external and internal bone structures with the musculature under a phylogenetic framework could provide a more holistic understanding of the evolution of the skull in carnivorans.

AUTHOR CONTRIBUTIONS

CJL, AHR, and SES designed the study. CJL analyzed the data and drafted the manuscript. CJL, EAB, AAC, ED, AHR, and SES collected and helped interpret the data. All authors read, edited, and approved the final manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

Raw landmark coordinates are available on Dryad (https://doi.org/10.5061/dryad.ht76hdrjk).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Geometric morphometric landmarks and curves
Fig S2. Procrustes regressions between size and shape of the cranium and mandible
Fig. S3. Morphospace of cranial and mandibular shape
Fig. S4. Morphology–phylogeny tanglegrams between cranial/mandibular shape diversity and phylogenetic relationships
Fig. S5. Adaptive shifts in cranial shape
Fig. S6. Depiction of relationships between mandibular shape variation and diet in carnivorans
Fig. S7. Canonical variates of allometry-free cranial shape
Fig. S8. Morphospace of allometry-free cranial shape coded with dietary regimes
Table S1. List of specimens used in the study.
Table S2. Dietary regimes of each species.
Table S3. Comparisons of the best-fitting evolutionary models in cranial shape and mandibular shape.
Table S4. Comparisons of the best fitting evolutionary models in simulated datasets
Table S5. Pairwise comparison tests of allometry-free mandibular shape between dietary regimes
Table S6. Canonical variate analysis of allometry-free cranial shape
Table S7. Convergence metric of cranial and mandibular shape
Table S8. Comparisons of the best-fitting evolutionary models in cranial shape and mandibular shape using PCs 1−3
Table S9. Pairwise comparison tests of cranial size and mandibular size between dietary regimes