ORIGINAL ARTICLE

doi:10.1111/evo.14143

SSE 75th anniversary
SOCIETY for the STUDY of EVOLUTION

Evolutionary and morphological patterns underlying carnivoran body shape diversity

Chris J. Law[1,2,3]

[1] Department of Mammalogy and Division of Paleontology, American Museum of Natural History, 200 Central Park West, New York, NY 10024

[2] Department of Biology, University of Washington, Seattle, WA 98105

[3] E-mail: claw@amnh.org

Received May 21, 2020
Accepted November 22, 2020

The diversity of body shapes is one of the most prominent features of phenotypic variation in vertebrates. Biologists, however, still lack a full understanding of the underlying morphological components that contribute to its diversity, particularly in endothermic vertebrates such as mammals. In this study, hypotheses pertaining to the evolution of the cranial and axial components that contribute to the diversity of carnivoran body shapes were tested. Three trends were found in the evolution of carnivoran body shapes: (1) carnivorans exhibit diverse body shapes with intrafamilial variation predicted best by family clade age, (2) body shape is driven by strong allometric effects of body size where species become more elongate with decreasing size, and (3) the thoracic and lumbar regions and rib length contribute the most to body shape variation, albeit pathways differ between different families. These results reveal the morphological patterns that led to increased diversity in carnivoran body shapes and elucidate the similarities and dissimilarities that govern body shape diversity across vertebrates.

KEY WORDS: Axial skeleton, body elongation, evolutionary allometry, phylogenetic comparative methods, thoracolumbar vertebrae.

EVOLUTION
INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Understanding the major patterns of phenotypic variation is a central goal of evolutionary biology. In vertebrates, body shape is one of the most prominent features of morphology, with important consequences to the physiology, performance, and ecology of organisms. Researchers have quantified the major patterns of body shape variation primarily in squamates and fishes, finding that body elongation is often one of the primary axes of body shape diversity and that elongate bodies have evolved repeatedly within many clades (Wiens and Slingluff 2001; Ward and Mehta 2010; Bergmann and Irschick 2012; Claverie and Wainwright 2014; Price et al. 2019). Elongate body shapes further allow clades to generate morphological, functional, and ecological innovations that can lead to increased diversification and niche specialization (Gans 1975; Wiens et al. 2006; Claverie and Wainwright 2014; Sharpe et al. 2015; Collar et al. 2016).

Although the patterns of body shape diversity have been documented across several major ectothermic vertebrate clades, much work is still needed to quantify body shapes in endothermic vertebrates such as mammals. Scientists and public audiences alike have qualitatively described the diversity of mammalian body shapes ranging from robust, tank-like elephants and rhinoceros to elongate weasels and squirrels to streamlined whales and dolphins. Unfortunately, the quantitative evidence to go along with these qualitative descriptions of mammalian body shapes is often absent. Recent work, however, demonstrated that quantifying body shape variation can reveal patterns of diversification in some mammalian clades. For example, mustelids were found to exhibit significant evolutionary shifts towards smaller, more elongate bodies with reduced limb lengths that in turn led to their increased species richness (Law et al. 2018b; Law et al. 2019; Law 2019). Therefore, whether these evolutionary patterns in body plans are unique to musteloids or occur in broader clades of mammals is unknown because of the lack of mammalian body shape datasets.

Similarly, the morphological components that contribute to the diversity of mammalian body shapes also remain unknown.

Evolution 75-2: 365–375

In ectothermic vertebrates, the evolutionary pathways underlying converging body shapes vary. Ectothermic vertebrates can evolve more elongate bodies through multiple pathways including the reduction of body depth, elongation of the head, and lengthening of the body axis by increasing individual vertebral lengths or adding additional vertebrae to the body (Parra-Olea and Wake 2001; Ward and Brainerd 2007; Ward and Mehta 2010; Collar et al. 2013). Elongation of the body in ectothermic vertebrates often arises through increases in the number of vertebrae in a particular region of the axial skeleton (Richardson et al. 1998; Polly et al. 2001; Ward and Brainerd 2007; Ward and Mehta 2010; Mehta et al. 2010) with some clades (e.g., snakes) reaching over 100 vertebrae (Polly et al. 2001; Ward and Mehta 2014). The majority of mammalian lineages, however, are constrained to only 27−32 precaudal vertebrae (Narita and Kuratani 2005); therefore, increased body elongation in mammals is usually not attained by increasing the total number of vertebrae. Instead, evolution toward more elongate bodies must occur through reduction of body depth, elongation of the head, and/or elongation of the individual vertebrae. Previous work has shown that changes in vertebral shape can generate diverse body shapes from long-necked giraffes with elongate cervical vertebrae to fusiform dolphins with shortened and fused cervical vertebrae (Buchholtz 2001; Buchholtz and Schur 2004; Arnold et al. 2017; Vander Linden et al. 2019). Furthermore, more recent work has investigated the evolutionary processes that led to increase in the complexity and regionalization of the mammalian vertebral column (Jones et al. 2018a, b; Jones et al. 2019). Despite these advances, the contribution of different regions of the axial skeleton to the diversity of mammalian body shapes remains largely unexamined (Collar et al. 2013).

In this study, a quantitative dataset of body shapes across 207 carnivorans (∼74% of species) was generated to quantify the evolutionary patterns of body shape variation and the underlying morphological components that contribute to body shape variation between families of the mammalian order Carnivora. Carnivora is an ideal clade because of its high species richness (>280 species; fourth largest mammalian order), large range of body sizes from the 200 g least weasel to the 4000 kg southern elephant seal, and the qualitatively diverse range of body shapes from robust bears to streamlined seals and elongate weasels. Carnivoran families serve as evolutionarily significant units (Humphreys and Barraclough 2014), and disparate evolutionary processes drive differences in morphological variation between individual carnivoran families (Slater and Friscia 2019), particularly in the skull (Radinsky 1981; Christiansen and Wroe 2007; Finarelli and Flynn 2009; Figueirido et al. 2011). Whether the postcranial system similarly exhibits interfamilial differences remains rarely investigated. Therefore, I tested three sets of predictions pertaining to the evolutionary and morphological patterns that underlie the variation of body shape for each individual carnivoran family. First, the evolutionary patterns of body shape between carnivoran families were examined by testing whether familial body shape variation accumulates proportionally to time and increased rate of body shape evolution as predicted under Brownian motion (O'Meara et al. 2006) as well as with increased species richness as often hypothesized (Wiens 2011; Rabosky and Adams 2012; Zelditch et al. 2015). Second, allometric effects of body size were tested on body shape with the prediction that larger species exhibit more robust bodies within each carnivoran family. Several ecological, physiological, and morphological traits scale with size including cranial and body shapes (Jones 2015a; Klingenberg and Zimmermann 1992; Zelditch et al. 2017; Sherratt et al. 2019), and in mammals, larger species are often hypothesized to have more robust bodies to combat the effects of gravity (Jones 2015a, b; McMahon 1975; Prothero and Sereno 1982; Biewener 1983). Third, which components of the cranial-axial skeleton contributed the most to overall body shape variation across all carnivorans and within each carnivoran family were determined. Because the thoracic and lumbar regions of the vertebral column are the primary structures used to support the body against gravity (Kardong 2014), it is predicted that evolutionary changes in body shape will be primary driven through thoracolumbar elongation or shortening.

Methods

QUANTIFYING BODY SHAPE AND BODY SIZE

I quantified body shape and body size using osteological specimens held at 10 natural history museum collections. My dataset consisted of 207 carnivoran species (∼74% of total species diversity), sampling between one and ten individuals per species (N = 685 individuals; median = 3 individuals per species; dataset in dryad). All specimens were fully mature, determined by the closure of exoccipital–basioccipital and basisphenoid–basioccipital sutures on the cranium and ossification of all vertebrae and limb bones. A combination of females, males, and sex unknown individuals was used because just one sex cannot be used without compromising sample sizes both in terms of the number of species and the number of individuals per species used.

Carnivoran body shape was quantified by calculating the head-body elongation ratio (hbER) as the sum of head length (L_H) and body length (L_B) divided by the body depth (L_R): hbER $= \frac{L_H+L_B}{L_R}$. Head length was measured as the condylobasal length of the cranium. Body length was estimated by summing the centrum lengths (measured along the ventral surface of the vertebral centrum) of each cervical, thoracic, lumbar, and sacral vertebrae, and body depth was estimated as the average length of the four longest ribs. Each rib was measured as a curve from the end of the capitulum to the point of articulation with the costal cartilage. The measurements of the caudal region were omitted in calculations of body length because the number of caudal vertebrae in most species is unknown and there was no way to determine whether the osteological specimens that were used contained all caudal vertebrae.

The head elongation ratio (head ER) and axial elongation index (AEI) (Ward and Brainerd 2007; Law et al. 2019) of each precaudal vertebral region (i.e. cervical, thoracic, lumbar, and sacral) were also quantified to examine how the various regions of the cranial and axial skeletons contribute to body shape variation. The head elongation ratio (head ER) was quantified by dividing cranial length (L_H) by cranial height (H_H). A modified version of the axial elongation index (AEI) (Ward and Brainerd 2007; Law et al. 2019) was then used to examine how each vertebral region (i.e., cervical, thoracic, lumbar, and sacral) contributes to elongation. For each region (V), AEI_V was calculated as the total sum of vertebral lengths (L_V measured along the ventral surface of the vertebral centrum) divided by the average vertebral height (H_V measured from the ventral surface of the centrum to the tip of the neural spine): $AEI_V = \frac{\Sigma L_V}{mean(H_V)}$.

Body size was quantified as the geometric mean of linear measurements taken from the cranium, vertebrae, and ribs (i.e., cranial length and height, curved rib length, and length and height of each vertebrae). The geometric mean was derived from the Nth root of the product of N (N = 11) linear measurements, a widely used as a predictor of the size of an individual (Mosimann 1970; Jungers et al. 1995). All measurements were taken to the nearest 0.01 mm with digital calipers. Species means were calculated prior to statistical analyses.

PHYLOGENETIC COMPARATIVE METHODS

Where applicable, analyses were performed under a phylogenetic framework using the most recent phylogeny of mammals pruned to include just carnivorans (Upham et al. 2019).

Linear regressions were performed to test if clade age, rate of body shape evolution, and species richness influenced body shape variation between carnivoran families. For each family, (1) body shape variation as the variance of hbER, (2) clade age using the cladeage R function written by Sam Price (evovert.com), (3) evolutionary rate (σ^2) of body shape under a Brownian motion model using the fitContinuous function in the R package geiger (Pennell et al. 2014), and (4) species richness as the total number of species were calculated. Nandiniidae, Prionodontidae, Odobenidae, and Ailuridae were excluded in the above analyses because these are single species families.

The allometric effects of body size on body shape (hbER) were tested across carnivorans and within each carnivoran family using phylogenetic generalized least-squares (PGLS) regressions using the R package phylolm (Tung Ho and Ané 2014). Whether each body size-shape slopes significantly deviated from an isometric slope of 0 using 95% bootstrap confidence intervals was tested. Predicted slopes significantly greater or less than the 95% confidence intervals of the observed regression slopes were interpreted as positive or negative allometry, respectively. The isometric slope was set as 0 because hbER is a dimensionless ratio. I also examined the relationships of body shape variation with mean body size and body size variation between families using linear regressions.

Which skeletal components (head elongation, rib cage reduction, and/or elongation of individual vertebral regions) contributed the most to overall body shape variation within each carnivoran family by performing a phylogenetic multiple regression were determined. The statistical significance of the PGLS models was evaluated using the random residual permutation procedure (RRPP) (Adams and Collyer 2018) with 1000 iterations in the R package RRPP version 0.3.0 (Collyer and Adams 2018). The effect sizes were also estimated by calculating the *Z* score as the standard deviation of the observed *F*-value in the distribution of RRPP-generated values (Adams and Collyer 2016). The same phylogenetic multiple regression models were run within each family that contained at least eight species.

Results

BODY SHAPE EVOLUTION AND VARIATION

Carnivorans exhibit great variation in body shapes ranging from robust bears (Ursidae, mean hbER = 3.45), hyaenas (Hyaenidae, mean hbER = 3.64), and the walrus (Odobenidae, hbER = 3.68) to elongate mustelids (mean hbER = 6.20), viverrids (mean hbER = 6.17), and the linsang (Prionodontidae, hbER = 7.48). Mustelids exhibited the greatest body shape variation (hbER variation = 1.059) whereas ursids (hbER variation = 0.045) and otariids (hbER variation = 0.057) exhibited the lowest body shape variation. Linear regressions revealed that body shape variation across carnivoran families exhibited significant positive relationships with family clade age ($R^2 = 0.43$; $P = 0.022$) as predicted under Brownian motion but neither with body shape evolutionary rates ($R^2 = 0.00$; $P = 0.312$) nor species richness ($R^2 = 0.22$; $P = 0.124$; Fig. 1C–E).

EFFECTS OF BODY SIZE ON BODY SHAPE DIVERSITY

PGLS regressions indicated that the majority of carnivoran families as well as the overall order exhibited a significant relationship between body shape and body size, where smaller species exhibit more elongate bodies ($P < 0.001$; Fig. 2A; Table 1). However, phocid seals exhibited an opposite relationship between body shape and size where larger phocids exhibited more elongate bodies. In contrast, euplerids, ursids, and otariids did not exhibit a

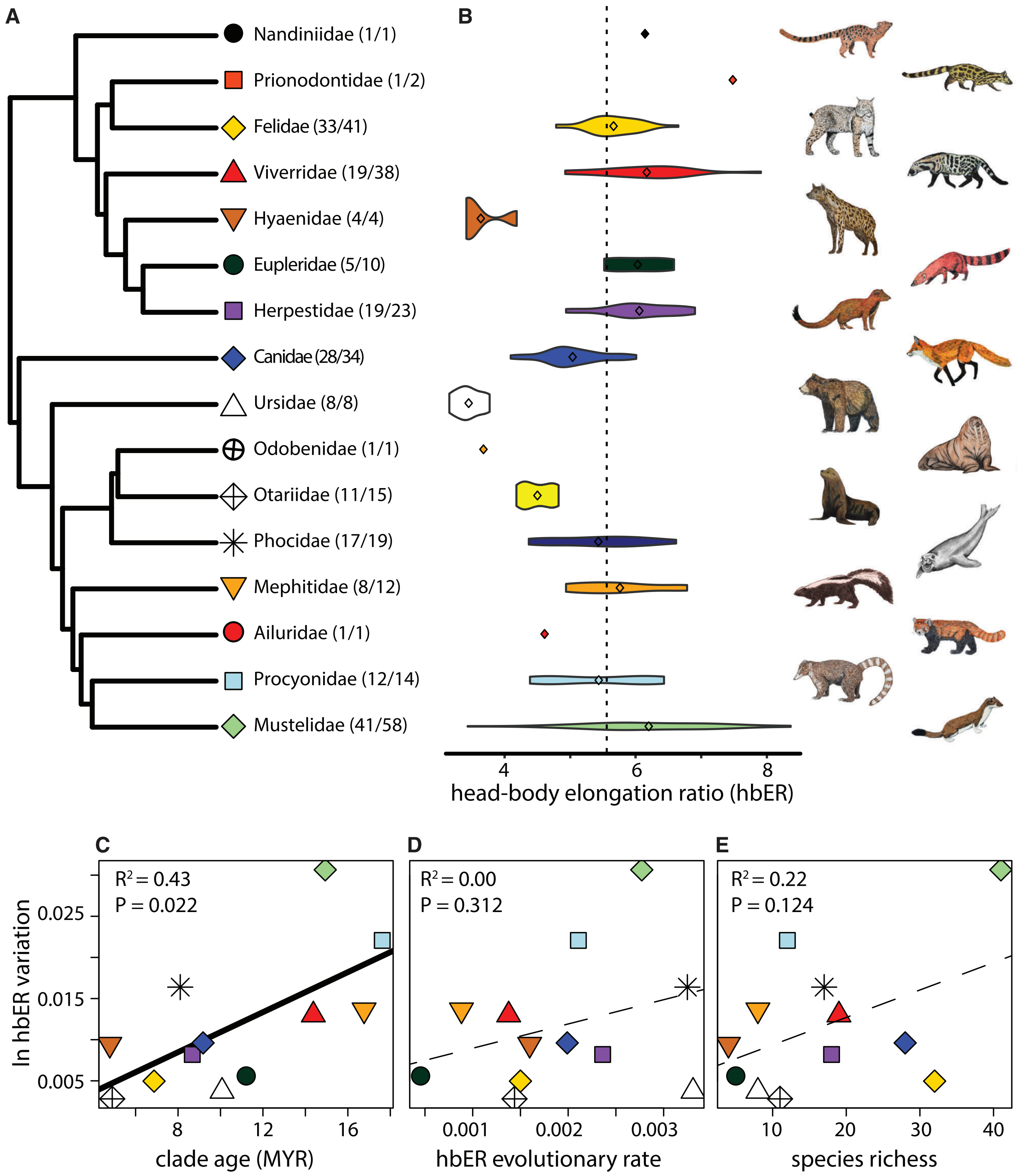

Figure 1. (A) Phylogenetic relationship between all 16 carnivoran families. Numbers represent number of species sampled out of total number of species within each family. (B) Violin plots of body shape as defined by head-body elongation ratio (hbER). Higher hbER values indicate more elongate species. Linear regressions of body shape variation with (C) clade age, (D) hbER evolutionary rates, and (E) species richness.

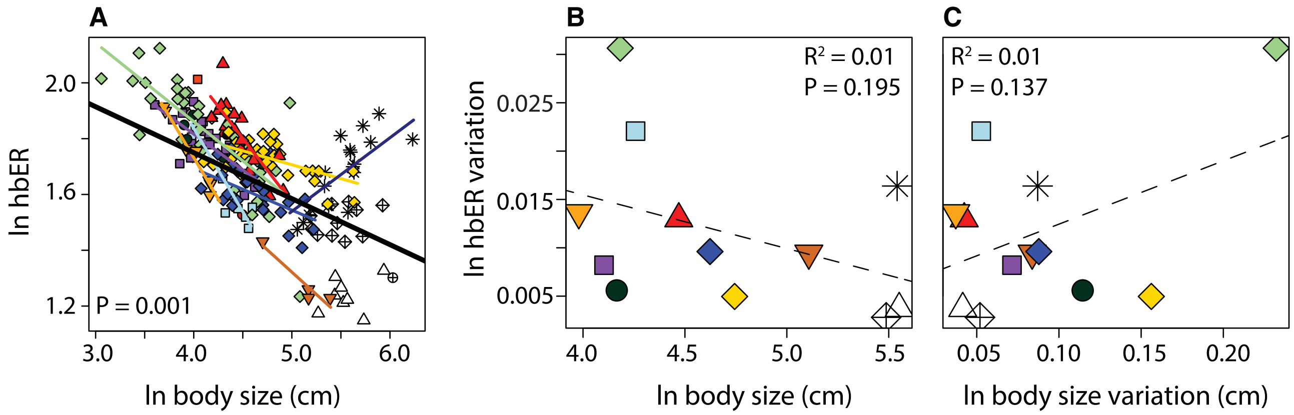

Figure 2. **(A) PGLS regression of body size versus body shape and linear regression of (B) body size versus body shape variation and (C) body size variation versus body shape variation. hbER = head-body elongation ratio. The bold black line indicates significant relationship across all carnivorans. Dashed black lines indicate non-significant relationships. Colored lines indicate significant relationships within specific carnivoran family; colors and symbols are the same as in Figure 1.**

significant body shape-size relationship (Fig. 2A; Table 1). Allometric tests reveal that most families exhibited significantly negative allometric relationships (slopes = −0.105 to −0.598) with the exception of isometry in Canidae, Otariidae, and Ursidae, and positive allometry in Phocidae (Table 1). Body shape variation did not exhibit a significant relationship with either mean body size (P = 0.195) or body size variation (P = 0.137) across the carnivoran families (Fig. 2).

PREDICTORS OF BODY SHAPE VARIATION

Phylogenetic multiple regression revealed that elongation/shortening of the lumbar region (R^2 = 0.41; Z = 3.92; P = 0.001), relative shortening/lengthening of the ribs (R^2 = 0.21; Z = 4.17; P = 0.001), and elongation/shortening of the thoracic region (R^2 = 0.14; Z = 3.46; P = 0.001) contributed the most to overall body shape variation across carnivorans (Table 2; Fig. 3). Although the remaining skeletal components also exhibited significant relationships with body shape, only 3−9% of body shape variation can be explained by any one of these components (R^2 = 0.03−0.09; Z = 2.90−3.37; Table 2). Only 6% of the variance in body shape was unexplained by skeletal components. However, relationships between skeletal components and body shape are not consistent within each carnivoran families (Table S1). The best predictor of body shape varied between families including elongation of the head (Mustelidae [R^2 = 0.59; Z = 3.69; P = 0.001]), elongation of the cervical region (Phocidae [R^2 = 0.34; Z = 2.126; P = 0.001], Mephitidae [R^2 = 0.66; Z = 3.77; P = 0.001], and Procyonidae [R^2 = 0.87; Z = 2.81; P = 0.001]), elongation of the lumbar region (Viverridae [R^2 = 0.40; Z = 2.48; P = 0.001] and Herpestidae [R^2 = 0.42; Z = 1.56; P = 0.008]), and relative shortening of rib length (Felidae [R^2 = 0.37; Z = 3.06; P = 0.001], Canidae [R^2 = 0.45; Z = 3.97; P = 0.001], Otariidae [R^2 = 0.86; Z = 2.54; P = 0.001]). None of the skeletal components were significant predictors of hbER in ursids.

Discussion

BODY SHAPE EVOLUTION AND VARIATION

Body shape is one of the most prominent features of trait variation in vertebrates and has been well documented in several ectothermic vertebrate clades but not in endothermic vertebrates. In this study, a quantitative dataset of carnivoran body shapes was created and previously undocumented variation of body shapes between families was found. Clade age, but not rates of body shape evolution or species richness, predicted the variation of body shapes across carnivoran families (Fig. 1), indicating that older families simply had more evolutionary time to accumulate more disparate body shapes than younger families. Although my results somewhat follow predictions of a Brownian motion model (O'Meara et al. 2006), previous empirical studies have found inconsistent relationships between phenotypic variation, clade age, phenotypic evolutionary rates, and species richness (e.g., Rabosky and Adams 2012; Sherratt et al. 2014; Zelditch et al. 2015; Friedman et al. 2019). Together, these findings contribute to the continual discovery of the discrepancy between the variation of phenotypic traits and diversity of species (Martin and Richards 2019).

Mustelidae exhibits the highest variation of body shapes, which may be unsurprising considering they are the most ecomorphologically disparate carnivoran family; members range from insectivorous, fossorial badgers to hypercarnivorous, cursorial weasels to piscivorous, aquatic otters (Law et al. 2018a; Fabre et al. 2015; Kitchener et al. 2018; Parsi-Pour and Kilbourne 2020). Mustelidae also includes the most elongate carnivorans, weasels, and polecats (Law et al. 2019; Law 2019). Interestingly,

Table 1. Results of the PGLS regressions of body size versus body shape across Carnivora and within carnivoran clades. 95% bootstrap confidence intervals were used to determine if body size-shape relationships were allometric.

All Carnivora	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	2.394 [2.145, 2.606]	–	17.748	<0.001
Slope	−0.161 [−0.204, −0.110]	negative	−6.868	<0.001
Felidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	2.230 [1.988, 2.493]	–	17.820	<0.001
Slope	−0.105 [−0.157, −0.053]	negative	−3.998	<0.001
Viverridae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	3.823 [3.268, 4.493]	–	10.878	<0.001
Slope	−0.450 [−0.598, −0.326]	negative	−5.724	<0.001
Hyaenidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	2.882 [2.353, 3.395]	–	8.297	0.014
Slope	−0.312 [−0.412, −0.208]	negative	−4.582	0.044
Eupleridae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	2.572 [2.156, 2.873]	–	8.958	<0.001
Slope	−0.187 [−0.258, −0.089]	negative	−2.715	0.073
Herpestidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	2.773 [2.317, 3.200]	–	11.223	<0.001
Slope	−0.239 [−0.342, −0.131]	negative	−3.972	0.001
Canidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	2.210 [1.596, 2.884]	–	7.674	<0.001
Slope	−0.133 [−0.278, 0.001]	isometry	−2.114	0.044
Ursidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	0.697 [−0.395, 1.733]	–	1.084	0.320
Slope	0.097 [−0.091, 0.290]	isometry	0.840	0.433
Otariidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	1.146 [0.418, 1.820]	–	2.806	0.021
Slope	0.065 [−0.059, 0.195]	isometry	0.873	0.405
Phocidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	0.224 [−0.609, 1.035]	–	0.524	0.608
Slope	0.264 [0.116, 0.412]	positive	3.467	0.003
Mephitidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	4.106 [3.832, 4.459]	–	21.653	<0.001
Slope	−0.593 [−0.680, −0.523]	negative	−12.465	<0.001
Procyonidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	4.229 [3.629, 4.786]	–	12.712	<0.001
Slope	−0.598 [−0.728, −0.460]	negative	−7.663	<0.001
Mustelidae	Estimate [95% bootstrap CI]	Allometry	*t* Value	*P* value
Intercept	2.988 [2.715, 3.278]	–	19.310	<0.001
Slope	−0.282 [−0.353, −0.218]	negative	−7.662	<0.001

other qualitatively elongate groups such as civets (Viverridae) and mongooses (Herpestidae) do not appear to exhibit as elongate of bodies as usually perceived. Further analyses are required to determine if there is true convergence in body elongation between these groups of carnivorans. Bears are on the other side of the spectrum of body shape variation; the low variation of ursid body shapes indicates that the classic "bear-shape" remains consistent across all ursids despite the ecomorphological diversity from the herbivorous panda to hypercarnivorous polar bear (Wilson and Mittermeier 2009). Although ursids exhibit craniomandibular adaptations to these various ecologies (Sacco and Van Valkenburgh 1999; Figueirido et al. 2009), the extent to which ursid body shapes are similarly adapted to different ecologies has yet to be tested.

EFFECTS OF BODY SIZE ON BODY SHAPE DIVERSITY

Body size often contributes to the evolution of cranial and body shapes in various taxa (Jones 2015a; Klingenberg and Zimmermann 1992; Zelditch et al. 2017; Sherratt et al. 2019) by either driving or constraining it (Gould 1966; Cheverud 1982) as

Table 2. Results of the phylogenetic multiple regression with the random residual permutation procedure (RRPP) to determine which skeletal components contributed to most to body shape variation.

Skeletal components	DF	SS	MS	R^2	F	Z	P
ln head elongation ratio	1	0.336	0.336	0.05	168.11	2.8989	**0.001**
ln AEI cervical	1	0.649	0.648	0.09	324.16	3.1654	**0.001**
ln AEI thoracic	1	1.024	1.024	0.14	511.91	3.4604	**0.001**
ln AEI lumbar	1	2.937	2.937	0.41	1468	3.9264	**0.001**
ln AEI sacral	1	0.224	0.224	0.03	112.16	3.3722	**0.001**
ln size-corrected rib length	1	1.515	1.515	0.21	757.09	4.1698	**0.001**
Residuals	200	0.4	0.002	0.06			
Total	206	7.085					

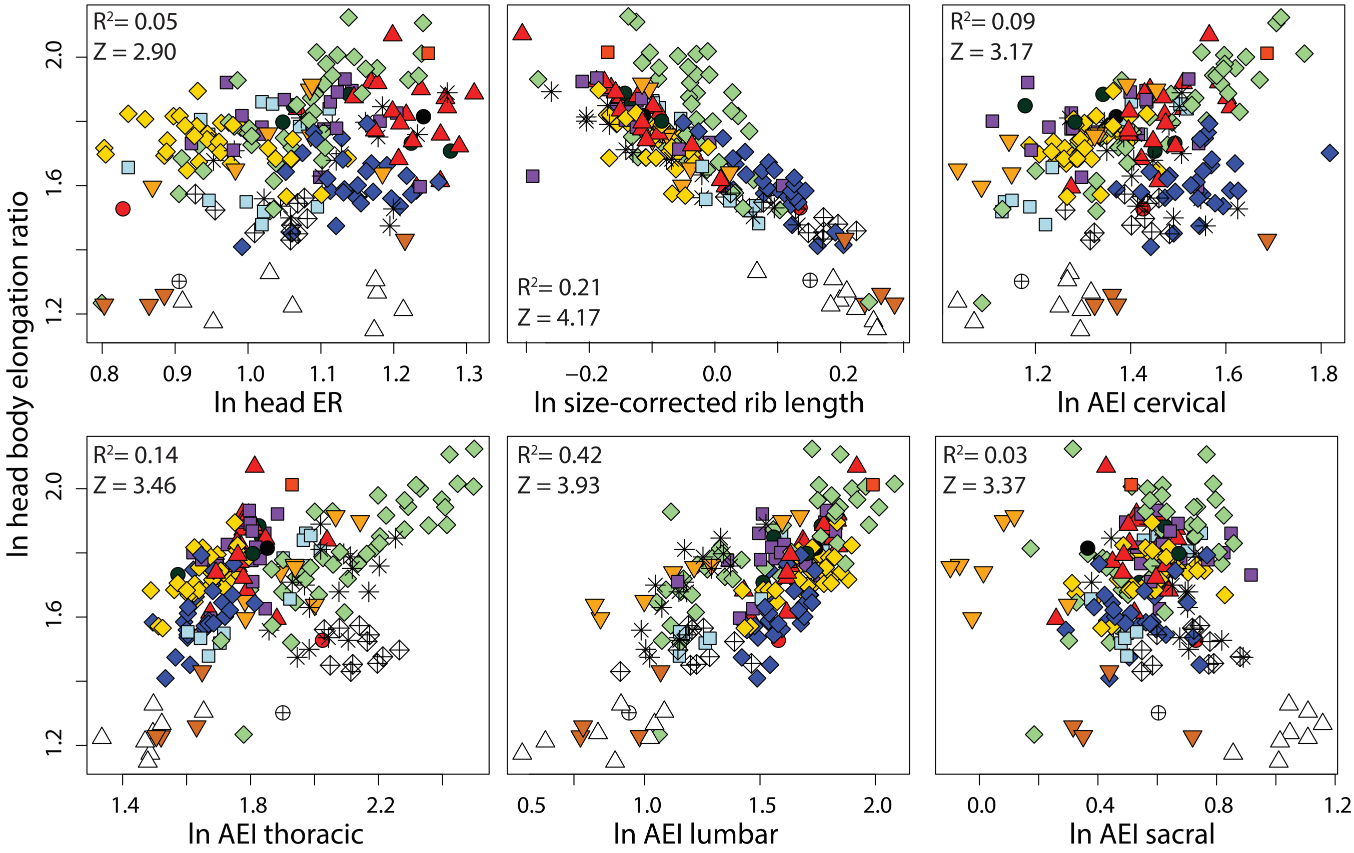

Figure 3. Scatterplots of head-body elongation ratio (hbER) versus skeletal components underlying body shape diversity. R^2 and Z scores were obtained from phylogenetic multiple regression with the random residual permutation procedure (RRPP). See Table 2 for full results. Colors and symbols are the same as in Figure 1.

a result of multiple selective pressures including interactions between biomechanical constraints, ecological factors, physiological, and phylogenetic effects. Consistent with these trends, it was found that body size influenced overall body shape across Carnivora ($R^2 = 0.42$) as well as within most terrestrial families ($R^2 = 0.34–0.96$), where smaller species exhibit more elongate bodies and larger species exhibit more robust bodies (Fig. 2A). This trend follows previous findings that thoracolumbar centra become more robust with increasing body size (Jones 2015a, b).

The mechanical demands of terrestrial locomotion may contribute to the allometric trend on body shape. Smaller, more elongate and flexible bodies enable carnivorans such as weasels to exploit prey in crevices, burrows, and other small constricted spaces (Horner and Biknevicius 2010; Horner et al. 2016). Furthermore, arguments can be made that elongation of the body may compensate for body size reduction, which would limit problems associated with smaller body sizes such as overpowering and killing larger prey (King and Powell 2006). However, increased body elongation constrains these carnivorans during above ground locomotion by requiring them to use a half-bound or bound gait for rapid locomotion (Williams 1983). Therefore, less elongate bodies of mid-sized carnivorans such as most canids and felids may facilitate more efficient cursorial gaits while still maintaining dorsomobile flexibility for locomotion (Jones 2015a). In contrast, large animals require robust body shapes to support their heavier bodies (Kardong 2014) and favor more dorsostability of the vertebral column (Jones 2015a; Halpert et al. 1987); thus, the largest terrestrial carnivorans (i.e., bears) exhibit stout, robust bodies. As the clade with the least disparate body sizes and shapes, ursids do not exhibit a significant relationship between body size and shape. Whether they are constrained due to their larger body sizes and have remained unchanged throughout their evolutionary history requires additional investigation with the ursid fossil record.

Ecological factors can also influence body shape allometry. For example, euplerids, small to mid-sized carnivorans of Madagascar, do not exhibit a significant relationship between body size and shape. Few morphological characteristics can be used to define this eight-species clade, as members of this group occupy niches normally divided up by several families around the world and therefore exhibit extraordinary morphological convergence to felids, civets, and mongoose (Wilson and Mittermeier 2009). Although these convergences have yet to be quantified, the disparate body shapes suggest that ecological factors rather than body size may be more important in influencing the evolution of body shapes across Eupleridae.

Pinnipeds exhibited the opposite trend of terrestrial carnivorans, in which larger species were more elongate compared to smaller species (significant relationship for phocids but not otariids). A possible explanation for this positive trend is the balance between drag reduction and thermoregulation that pinnipeds must manage within the aquatic environment. The optimal fineness ratio (body length to thickness ratio) that reduces total body drag ranges between 3.3 and 7.0 (Fish 1993; 1996). Body shapes of phocids, as quantified by hbER, range from 4.4 to 6.6 within the optimal fineness ratio limits, albeit relationships between hbER and fineness ratio requires further examination. However, body shapes must also be optimized to prevent heat loss in the water, particularly in smaller species. Having a more rotund body (lower hbER) would reduce heat loss by reducing surface area in smaller species with only a small drag decrease (Ahlborn 2004). In contrast, larger phocids retain relatively greater amounts of heat due to their relatively lower surface area to volume ratio and therefore may have the luxury of exhibiting a more elongate body that is closer to the optimal fineness ratio without compensating thermoregulatory needs or drag reduction (Ahlborn 2004). It is important to note that hbER and fineness ratio are very crude proxies for streamlining; interactions between locomotion, habitat, flipper morphology, and a variety of ecomorphological factors may provide better insight into the evolution of body shapes within phocids. Further evidence that aquatic lifestyles can influence the allometric patterns of body shape is exemplified in fishes. Although larger fish tend to have more elongate bodies, body size only explained 2.9% of body shape variation in Indo-Pacific shore fishes (Friedman et al. 2019). Fishes are free of the constraints of gravity and can take advantage of the buoyancy of water. Therefore, the primary function of fish body shapes may not necessarily be to support the body as needed in terrestrial animals against the force of gravity (Kardong 2014). Instead, dietary, locomotor, and other ecological factors are able to overcome biomechanical constraints reflected in allometry on body shapes and may be the primary drivers in the evolution of different fish body shapes (Friedman et al. 2019).

PREDICTORS OF BODY SHAPE VARIATION

Across all carnivorans, it was found that the lumbar region ($R^2 = 0.41$) followed by relative rib length ($R^2 = 0.21$) and the thoracic region ($R^2 = 0.14$) contributed the most to body shape variation. This indicates that evolutionary changes in body shapes in carnivorans were primarily achieved through elongation/shortening of the thoracolumbar regions. The thoracic and lumbar regions of the vertebral column and ribcage are the primary structures used to support the body against gravity and transmit and receive propulsive forces to/from the limbs to generate locomotion (Kardong 2014). Therefore, changes in the thoracic and lumbar regions and ribcage can directly facilitate the locomotory efficiency: elongation of these vertebral regions facilitates increased dorsoventral flexibility and maneuverability during locomotion whereas shortening facilitates dorsostability (Jones 2015a, b; Boszczyk et al. 2001).

However, changes in the thoracic and lumbar regions were not the greatest contributors to body shape variation within each carnivoran family. Instead, the best contributors to body shape variation include elongation/shortening of the head, cervical, and/or lumbar regions as well as relative shortening/lengthening of the ribs, indicating that multiple pathways can lead to the evolution of different body shapes between and within carnivoran families. It is important to note that this present study examined relationships between skeletal components and body shape based on taxonomic rank (i.e., families) when in fact locomotion, habitat use, or other biomechanical interactions with the environment may be more important forces that drive these relationships. Previous work has demonstrated that ecology and locomotory mode influences the evolution of various aspects of the axial skeleton (Jones et al. 2018b; Boszczyk et al. 2001; Galis et al. 2014; Randau et al. 2017; Williams et al. 2019). For example, the variability in the number of presacral vertebrae significantly differs between fast and slow running carnivorans, where fast, agile carnivorans exhibit no variation in presacral vertebral counts whereas slow carnivorans exhibit ~25% abnormal counts (Galis et al. 2014 but see Williams et al. 2019). Whether ecological, biomechanical, and locomotory interactions similarly influence the relationship between body shape and its underlying skeletal components requires further investigation.

Conclusions

In this study, the diversity of body shapes was quantified both between and within carnivoran clades. It was found that older carnivoran clades exhibited higher body shape variation. Body size has strong allometric effects on body shape, in which carnivorans become more robust with increasing size. Lastly, it was found that evolutionary changes in body shape was primarily driven through changes of the thoracic and lumbar regions. Altogether, these results fill a critical gap in our understanding of the evolution of vertebrate body shapes and provide a strong morphological foundation for future research investigating the evo-devo and evolutionary ecology of mammalian body shapes.

AUTHOR CONTRIBUTIONS

C.J.L. conceived the study, performed analyses, and wrote the manuscript.

ACKNOWLEDGMENTS

The author is grateful to the collections and its staff of the American Museum of Natural History, Burke Museum, California Academy of Sciences, Field Museum of Natural History, University of Kansas Natural History Museum, Natural History Museum of Los Angeles County, Museum of Southwestern Biology, Museum of Vertebrate Zoology, Florida Museum of Natural History, Smithsonian National Museum of Natural History, and Yale Peabody Museum of Natural History. The author also thanks Sharlene Santana for feedback on earlier versions of this manuscript and John Flynn and Frank Fish for helpful discussions. This work was supported a NSF Postdoctoral Fellowship (DBI−1906248); a Gerstner Scholars Postdoctoral Fellowship, the Gerstner Family Foundation, the Richard Gilder Graduate School, and the Department of Mammalogy at the American Museum of Natural History; and the ARCS Foundation.

DATA ARCHIVING

Dataset is uploaded on Dryad Digital Repository: https://doi.org/10.5061/dryad.pnvx0k6kj

CONFLICT OF INTEREST

The author has no conflict of interest to declare.

LITERATURE CITED

Adams, D. C., and M. L. Collyer. 2016. On the comparison of the strength of morphological integration across morphometric datasets. Evolution 70:2623–2631.

Adams, D. C., and M. L. Collyer. 2018. Phylogenetic ANOVA: Group-clade aggregation, biological challenges, and a refined permutation procedure. Evolution 72:1204–1215.

Ahlborn, B. K. 2004. Zoological Physics. Springer Science & Business Media, Berlin, Germany.

Arnold, P., E. Amson, and M. S. Fischer. 2017. Differential scaling patterns of vertebrae and the evolution of neck length in mammals. Evolution 85:2706–2713.

Bergmann, P. J., and D. J. Irschick. 2012. Vertebral evolution and the diversification of squamate reptiles. Evolution 66:1044–1058.

Biewener, A. A. 1983. Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size. J Exp Biol 105:147–171.

Boszczyk, B. M., A. A. Boszczyk, and R. Putz. 2001. Comparative and functional anatomy of the mammalian lumbar spine. Anat. Rec 264:157–168.

Buchholtz, E. A. 2001. Vertebral osteology and swimming style in living and fossil whales (Order: Cetacea). J Zool 253:175–190.

Buchholtz, E. A., and S. A. Schur. 2004. Vertebral osteology in Delphinidae (Cetacea). Zool J Linn Soc 140:383–401.

Cheverud, J. M. 1982. Relationships among ontogenetic, static, and evolutionary allometry. Am. J. Phys. Anthropol 59:139–149.

Christiansen, P., and S. Wroe. 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivores. Ecology 88:347–358.

Claverie, T., and P. C. Wainwright. 2014. A morphospace for reef fishes: elongation is the dominant axis of body shape evolution. PLoS ONE 9:e112732–11.

Collar, D. C., C. M. Reynaga, A. B. Ward, and R. S. Mehta. 2013. A revised metric for quantifying body shape in vertebrates. Zool 116:246–257.

Collar, D. C., M. Quintero, B. Buttler, A. B. Ward, and R. S. Mehta. 2016. Body shape transformation along a shared axis of anatomical evolution in labyrinth fishes (Anabantoidei). Evolution 70:555–567.

Collyer, M. L., and D. C. Adams. 2018. RRPP: An rpackage for fitting linear models to high-dimensional data using residual randomization. Methods Ecol Evol 9:1772–1779.

Fabre, A.-C., R. Cornette, A. Goswami, and S. Peigné. 2015. Do constraints associated with the locomotor habitat drive the evolution of forelimb shape? A case study in musteloid carnivorans. J Anatomy 226:596–610.

Figueirido, B., B. Figueirido, P. Palmqvist, P. Palmqvist, J. A. Pérez-Claros, and J. A. Pérez Claros. 2009. Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics. J Zool 277:70–80.

Figueirido, B., N. MacLeod, J. Krieger, M. De Renzi, J. A. Pérez-Claros, and P. Palmqvist. 2011. Constraint and adaptation in the evolution of carnivoran skull shape. Paleobiology 37:490–518.

Finarelli, J. A., and J. J. Flynn. 2009. Brain-size evolution and sociality in Carnivora. Proc Natl Acad Sci USA 106:9345–9349.

Fish, F. E. 1993. Influence of Hydrodynamic-Design and Propulsive Mode on Mammalian Swimming Energetics. Australian Journal of Zoology 42:79–101.

Fish, F. E. 1996. Transitions from drag-based to lift-based propulsion in mammalian swimming. Amer. Zool 36:628–641.

Friedman, S. T., C. M. Martinez, S. A. Price, and P. C. Wainwright. 2019. The influence of size on body shape diversification across Indo-Pacific shore fishes. Evolution 63:1873–1884.

Galis, F., D. R. Carrier, J. van Alphen, S. D. van der Mije, T. J. M. Van Dooren, J. A. J. Metz, and C. M. A. ten Broek. 2014. Fast running restricts evolutionary change of the vertebral column in mammals. Proc. Natl. Acad. Sci. U.S.A 111:11401–11406.

Gans, C. 1975. Tetrapod limblessness: evolution and functional corollaries. Amer. Zool 15:455–467.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biol Rev.

Halpert, A. P., F. A. Jenkins, and H. Franks. 1987. Structure and scaling of the lumbar vertebrae in African bovids (Mammalia: Artiodactyla). J Zool 211:239–258.

Horner, A. M., and A. R. Biknevicius. 2010. A comparison of epigean and subterranean locomotion in the domestic ferret (*Mustela putorius furo*: Mustelidae: Carnivora). Zool 113:189–197. .

Horner, A. M., J. B. Hanna, and A. R. Biknevicius. 2016. Crouching to fit in: the energetic cost of locomotion in tunnels. J. Exp. Biol 219:3420–3427.

Humphreys, A. M., and T. G. Barraclough. 2014. The evolutionary reality of higher taxa in mammals. Proc R Soc B 281:20132750–10.

Jones, K. E. 2015a. Evolutionary allometry of lumbar shape in Felidae and Bovidae. Biol J Linn Soc 116:721–740.

———. 2015b. Evolutionary allometry of the thoracolumbar centra in felids and bovids. J Morpho 276:818–831.

Jones, K. E., K. D. Angielczyk, and S. E. Pierce. 2019. Stepwise shifts underlie evolutionary trends in morphological complexity of the mammalian vertebral column. Nature Communications 10:1–13.

Jones, K. E., K. D. Angielczyk, P. D. Polly, J. J. Head, V. Fernandez, J. K. Lungmus, S. Tulga, and S. E. Pierce. 2018a. Fossils reveal the complex evolutionary history of the mammalian regionalized spine. Science 361:1249–1252.

Jones, K. E., L. Benitez, K. D. Angielczyk, and S. E. Pierce. 2018b. Adaptation and constraint in the evolution of the mammalian backbone. BMC Evol Biol 18:1–13.

Jungers, W. L., A. B. Falsetti, and C. E. Wall. 1995. Shape, relative size, and size-adjustments in morphometrics. Am. J. Phys. Anthropol 38:137–161.

Kardong, K. V. 2014. Vertebrates: comparative anatomy, function, evolution. McGraw-Hill Education, Boston.

King, C. M., and R. A. Powell. 2006. Hunting Behavior. Pp. 113–136 *in* C. M. King and R. A. Powell, eds. The Natural History of Weasels and Stoats Ecology, Behavior, and Management.

Kitchener, A. C., C. Meloro, and T. M. Williams. 2018. Form and function of the musteloids. *in* Biology and Conservation of Musteloids. Oxford University Press.

Klingenberg, C. P., and M. Zimmermann. 1992. Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. Am Nat 140:601–620.

Law, C. J. 2019. Evolutionary shifts in extant mustelid (Mustelidae: Carnivora) cranial shape, body size and body shape coincide with the Mid-Miocene Climate Transition. Biol. Lett 15:20190155–6.

Law, C. J., E. Duran, N. Hung, E. Richards, I. Santillan, and R. S. Mehta. 2018a. Effects of diet on cranial morphology and biting ability in musteloid mammals. J. Evol. Biol 31:1918–1931.

Law, C. J., G. J. Slater, and R. S. Mehta. 2018b. Lineage diversity and size disparity in Musteloidea: testing patterns of adaptive radiation using molecular and fossil-based methods. Syst. Biol 67:127–144.

———. 2019. Shared extremes by ectotherms and endotherms: body elongation in mustelids is associated with small size and reduced limbs. Evolution 73:735–749.

Martin, C. H., and E. J. Richards. 2019. The Paradox Behind the Pattern of Rapid Adaptive Radiation: How Can the Speciation Process Sustain Itself Through an Early Burst? Annu. Rev. Ecol. Evol. Syst 50:569–593.

McMahon, T. A. 1975. Using body size to understand the structural design of animals: quadrupedal locomotion. Journal of Applied Physiology 39:619–627.

Mehta, R. S., A. B. Ward, M. E. Alfaro, and P. C. Wainwright. 2010. Elongation of the body in eels. Integr Comp Biol 50:1091–1105.

Mosimann, J. E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. J. Am. Stat. Assoc 65:930–945.

Narita, Y., and S. Kuratani. 2005. Evolution of the vertebral formulae in mammals: A perspective on developmental constraints. J. Exp. Zool 304B:91–106.

O'Meara, B. C., C. Ané, M. J. Sanderson, and P. C. Wainwright. 2006. Testing for different rates of continuous trait evolution using likelihood. Evolution 60:922–913.

Parra-Olea, G., and D. B. Wake. 2001. Extreme morphological and ecological homoplasy in tropical salamanders. Proc Natl Acad Sci USA 98:7888–7891.

Parsi-Pour, P., and B. M. Kilbourne. 2020. Functional Morphology and Morphological Diversification of Hind Limb Cross-Sectional Traits in Mustelid Mammals. Integrative Organismal Biology 2:1204–1221.

Pennell, M. W., J. M. Eastman, G. J. Slater, J. W. Brown, J. C. Uyeda, R. G. FitzJohn, et al. (2014). geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. Bioinformatics 30:2216–2218. http://doi.org/10.1093/bioinformatics/btu181

Polly, P. D., J. J. Head, and M. J. Cohn. 2001. Testing modularity and dissociation: the evolution of regional proportions in snakes. Pp. 305–335 *in* M. L. Zelditch, ed. Beyond Heterochrony The Evolution of Development. the evolution of development Wiley-Liss, New York, NY.

Price, S. A., S. T. Friedman, K. A. Corn, C. M. Martinez, O. Larouche, and P. C. Wainwright. 2019. Building a body shape morphospace of teleostean fishes. Integr Comp Biol 59:716–730.

Prothero, D. R., and P. C. Sereno. 1982. Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. Paleobiology 8:16–30.

Rabosky, D. L., and D. C. Adams. 2012. Rates of morphological evolution are correlated with species richness in salamanders. Evolution 66:1807–1818.

Radinsky, L. B. 1981. Evolution of skull shape in Carnivores .1. Representative modern Carnivores. Biol J Linn Soc 15:369–388.

Randau, M., A. R. Cuff, J. R. Hutchinson, S. E. Pierce, and A. Goswami. 2017. Regional differentiation of felid vertebral column evolution: a study of 3D shape trajectories. Org Divers Evol 17:1–15.

Richardson, M. K., S. P. Allen, G. M. Wright, A. Raynaud, and J. Hanken. 1998. Somite number and vertebrate evolution. Development 125:151–160.

Sacco, T., and B. Van Valkenburgh. 1999. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). J Zool 263:41–54.

Sharpe, S. S., S. A. Koehler, R. M. Kuckuk, M. Serrano, P. A. Vela, J. Mendelson, and D. I. Goldman. 2015. Locomotor benefits of being a slender and slick sand-swimmer. J Exp Biol 218:440–450.

Sherratt, E., D. J. Gower, C. P. Klingenberg, and M. Wilkinson. 2014. Evolution of Cranial Shape in Caecilians (Amphibia: Gymnophiona). Evol Biol 41:528–545.

Sherratt, E., K. L. Sanders, A. Watson, M. N. Hutchinson, M. S. Y. Lee, and A. Palci. 2019. Heterochronic Shifts Mediate Ecomorphological Convergence in Skull Shape of Microcephalic Sea Snakes. Integr Comp Biol 59:616–624.

Slater, G. J., and A. R. Friscia. 2019. Hierarchy in adaptive radiation: A case study using the Carnivora (Mammalia). Evolution 87:S50–16.

Tung Ho, L. S., and C. Ané. 2014. A Linear-Time Algorithm for Gaussian and Non-Gaussian Trait Evolution Models. Syst. Biol 63:397–408.

Upham, N. S., J. A. Esselstyn, and W. Jetz. 2019. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biol 17:e3000494–44.

Vander Linden, A., K. M. Campbell, E. K. Bryar, and S. E. Santana. 2019. Head-turning morphologies: Evolution of shape diversity in the mammalian atlas–axis complex. Evolution 73:2060–2071.

Ward, A. B., and E. L. Brainerd. 2007. Evolution of axial patterning in elongate fishes. Biol J Linn Soc 90:97–116.

Ward, A. B., and R. S. Mehta. 2010. Axial elongation in fishes: using morphological approaches to elucidate developmental mechanisms in studying body shape. Integr Comp Biol 50:1106–1119.

Ward, A. B., and R. S. Mehta. 2014. Differential occupation of axial morphospace. Zool 117:70–76.

Wiens, J. J. 2011. The causes of species richness patterns across space, time, and clades and the role of “ecological limits. The Quarterly Review of Biology 86:75–96.

Wiens, J. J., and J. L. Slingluff. 2001. How lizards turn into snakes: A phylogenetic analysis of body-form evolution in anguid lizards. Evolution 55:2303–2318.

Wiens, J. J., M. C. Brandley, and T. W. Reeder. 2006. Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. Evolution 60:123–141.

Williams, S. A., J. K. Spear, L. Petrullo, D. M. Goldstein, A. B. Lee, A. L. Peterson, D. A. Miano, E. B. Kaczmarek, and M. R. Shattuck. 2019. Increased variation in numbers of presacral vertebrae in suspensory mammals. Nature Ecology & Evolution 107:1–11.

Williams, T. M. 1983. Locomotion in the North American mink, a semiaquatic mammal. II. The effect of an elongate body on running energetics and gait patterns. J Exp Biol 105:283–295.

Wilson, D. E., and R. A. Mittermeier. 2009. Handbook of the Mammals of the World. Lynx Edicions.

Zelditch, M. L., J. Li, L. A. P. Tran, and D. L. Swiderski. 2015. Relationships of diversity, disparity, and their evolutionary rates in squirrels (Sciuridae). Evolution 69:1284–1300.

Zelditch, M. L., J. Ye, J. S. Mitchell, and D. L. Swiderski. 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.

Associate Editor: A. Goswami
Handling Editor: T. Chapman

Supporting Information

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

Table S1. Results of the multiple phylogenetic regression with the random residual permutation procedure (RRPP) to determine which skeletal components contributed to most to body shape variation within carnivoran families with more than 8 species.