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Different Evolutionary Pathways Lead to Incomplete Convergence of Elongate Body Shapes in Carnivoran Mammals

CHRIS J. LAW[1,2,3,*]

[1]*Department of Integrative Biology, University of Texas, 2415 Speedway #C0930, Austin, TX 78712, USA;* [2]*Department of Biology University of Washington, Box 351800, Seattle, WA 98105, USA; and* [3]*Richard Gilder Graduate School, Department of Mammalogy, and Division of Paleontology, American Museum of Natural History, 200 Central Park West, New York, NY 10024, USA*

[*]*Correspondence to be sent to: Department of Integrative Biology, University of Texas, 2415 Speedway #C0930, Austin, TX 78712, USA; E-mail: chrislaw@utexas.edu*

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Abstract.—Although convergence is often recognized as a ubiquitous feature across the Tree of Life, whether the underlying traits also exhibit similar evolutionary pathways towards convergent forms puzzles biologists. In carnivoran mammals, "elongate," "slender," and "long" are often used to describe and even to categorize mustelids (martens, polecats, and weasels), herpestids (mongooses), viverrids (civets and genets), and other carnivorans together. But just how similar these carnivorans are and whether there is convergence in the morphological component that contribute to elongation has never been assessed. Here, I found that these qualitatively described elongate carnivorans exhibited incomplete convergence towards elongate bodies compared to other terrestrial carnivorans. In contrast, the morphological components underlying body shape variation do not exhibit convergence despite evidence that these components are more elongate in elongate carnivorans compared to nonelongate carnivorans. Furthermore, these components also exhibited shorter but different phylogenetic half-lives towards more elongate adaptive peaks, indicating that different selective pressures can create multiple pathways to elongation. Incorporating the fossil record will facilitate further investigation of whether body elongation evolved adaptively or if it is simply a retained ancestral trait.[Axial skeleton; body elongation; convergent evolution; macroevolution; phylogenetic comparative methods; thoracolumbar vertebrae.]

The independent evolution of similar forms is one of the most striking patterns across the Tree of Life. Lineages that have evolved to be more similar to each other rather than between their ancestors have been defined as convergent (Stayton 2015). Textbook examples of convergence include the evolution of fusiform body plans in aquatic vertebrates (Rubie et al. 2004; Lingham-Soliar 2016), wing membranes in gliding squirrels and marsupials (Grossnickle et al. 2020), and snake-like body plans in multiple clades of squamates (Brandley et al. 2008; Morinaga and Bergmann 2017; Bergmann and Morinaga 2019). However, these convergent forms can evolve through multiple pathways (Ward and Mehta 2010; Wake et al. 2011; Ward and Mehta 2014; Morinaga and Bergmann 2017; Bergmann and Morinaga 2019), leading to questions about the extent to which "convergent" taxa exhibit complete convergence. Many examples of convergence should be considered as incomplete convergence, where "converging" taxa do not occupy overlapping regions of morphospace but are still more similar to one another than their relatives (Herrel et al. 2004; Stayton 2006). Although incomplete convergence is found among many taxa including herbivorous lizards (Stayton 2006), frogs (Moen et al. 2015), gliding mammals (Grossnickle et al. 2020), and saber-toothed "cats" (Castiglione et al. 2019; Janis et al. 2020), it is unclear how factors like different evolutionary pathways, selective pressures, adaptive slopes, and evolutionary time contribute to incomplete convergence. The term "imperfect convergence" has also been used to describe "converging" taxa that evolved towards a broad adaptive peak within a distinct region of morphospace compared to their relatives (Collar et al. 2014). These patterns highlight how underlying morphologies do not necessarily follow the same pathways yet can still lead to the convergence of a trait of interest.

The evolution of body elongation is an exemplary system in which to examine patterns of convergence and the underlying components that contribute to elongate body shapes. Body elongation has independently evolved multiple times within several vertebrate clades (reviewed in Bergmann et al. 2020). Body elongation can also evolve through multiple pathways including the reduction of body depth, elongation of the head, and lengthening of the body axis (Parra-Olea and Wake 2001; Ward and Brainerd 2007; Ward and Mehta 2010; Collar et al. 2013; Bergmann and Morinaga 2019). These different pathways toward elongate body shapes can occur even between closely related clades, providing support that historical contingency can lead to convergence in elongate bodies (Morinaga and Bergmann 2017; Bergmann and Morinaga 2019). Although these pathways have been found in fishes, amphibians, and squamate reptiles (Parra-Olea and Wake 2001; Mehta et al. 2010; Morinaga and Bergmann 2017; Bergmann and Morinaga 2019), investigations of convergence towards similar elongate body plans in mammals are rare. Law (2021a) found that evolutionary pathways to body shape variation in carnivoran mammals are clade specific, but whether body elongation and its underlying morphological components exhibit patterns of convergence remain to be tested.

In this study, I assessed whether carnivoran clades exhibited evolutionary shifts towards similar elongate bodies. Carnivora is an ideal clade to test this because of its high species richness and diverse body shapes from robust bears to elongate weasels. Weasels and polecats have been qualitatively described as elongate for centuries (Shaw 1800; Griffith 1827; Gray 1865; Brown and Lasiewski 1972; Gliwicz 1988; King 1989). These descriptions were confirmed with quantitative data, which showed that mustelid body elongation may have facilitated increased species richness (Law et al. 2018b, 2019; Law 2019). However, mustelids are not the only terrestrial carnivorans to be qualitatively described as elongate. Civets, genets, and mongooses within the families Eupleridae, Herpestida, Nandiniidae, Prionodontidae, and Viverridae are often described as "elongate," "slender," and "long" (Shaw 1800; Gray 1864; Allen 1924; Nowak and Walker 1999; Wilson and Mittermeier 2009). In fact, many of these species were originally taxonomically categorized together or even with some mustelids (Shaw 1800; Gray 1864; Allen 1924). Although these taxonomic groupings suggested similar morphologies, whether these clades exhibit convergence towards elongate bodies has not been tested. If body elongation convergently evolved, I predict that elongate carnivorans will exhibit i) lower trait disparity compared to nonelongate carnivorans, ii) shared adaptive peaks across the body shape landscape, and iii) more similar morphologies in phylomorphospace than between their ancestral nodes.

Because multiple morphological pathways contribute to carnivoran body shape variation (Law 2021a), I also tested the same predictions on whether elongate carnivorans exhibit similar morphological components including elongation/shortening of the head, elongation/shortening of the vertebral regions, and reduction/increase of body depth. Examining the degree of convergence in these components will clarify whether convergence in body elongation evolved through similar pathways. If convergent elongation evolved through similar pathways, these components should also exhibit convergence. Alternatively, divergence in components would suggest convergence in body elongation evolved through different pathways.

Methods

Body Shape Data

I obtained data on body shape and its underlying morphological components from 176 terrestrial carnivorans (~71% of diversity) from Law (2021a). The components consist of head elongation ratio (head ER), the axial elongation index (AEI_V) of each vertebral region (i.e., cervical, thoracic, lumbar, and sacral), and size-corrected rib length as a proxy for relative body depth (see Appendix 1 of the Supplementary material available on Dryad at https://doi.org/10.5061/dryad.bg79cnpc4.

I classified the 176 carnivorans into "elongate" and "nonelongate" categories (Table S1 of the Supplementary material available on Dryad). Carnivorans described as "elongate," "slender," and "long" in the literature were classified as elongate and the remaining as nonelongate (Shaw 1800; Gray 1864; Allen 1924; Nowak and Walker 1999; Wilson and Mittermeier 2009). Elongate carnivorans have been described in eight clades: Nandiniidae (palm civets), Prionodontidae (linsangs), Viverridae (civets, genets, and oyans except the binturong), Eupleridae (civets, falanoucs, mongooses, and vontsiras except the fossa), Herpestidae (mongooses), Guloninae (martens except the wolverine), Ictonychinae (grisons, polecats, and weasels), and Mustelinae (minks, polecats, and weasels). Therefore, I classified the elongate carnivorans into seven clades (Fig. 1). I used only seven clades instead of all eight because Nandiniidae and Prionodontidae each contain one species. Although otters have been also described as "elongate," I did not categorize them as elongate because previous work indicated that they shifted towards more robust bodies relative to their ancestors (Law 2021b).

Statistical Analyses

All statistical tests were performed in R 3.5.1 (R Core Team 2021), and all phylogenetic comparative methods were performed using the most recent phylogeny of mammals based on molecular data pruned to include just carnivorans (Upham et al. 2019). See Appendix 1 of the Supplementary material available on Dryad for detailed procedures.

Body shape (hbER).—I tested Prediction 1 on whether elongate carnivorans exhibited less disparity in body shape than nonelongate carnivorans using the *morphol.disparity* function in geomorph (Adams and Otárola-Castillo 2013). I also tested whether hbER differed between the seven elongate clades and nonelongate carnivorans using a phylogenetic analysis of variance (pANOVA) and pairwise post hoc tests in RRPP (Collyer and Adams 2018).

I tested Prediction 2 on whether elongate groups exhibited evolutionary shifts towards similar body shapes by fitting seven evolutionary models (Hansen 1997; Butler and King 2004): i) single-rate Brownian motion model (BM1), ii) single-peak Ornstein–Uhlenbeck model (OU1), iii) eight-peak Ornstein–Uhlenbeck model ($OUM_{elongate\_clades}$) that assigned different optima for each of the seven elongate clades and the nonelongate carnivorans, and iv) two-peak Ornstein–Uhlenbeck model ($OUM_{elongate}$) that assigned one optimum to all seven clades and a second optimum to all nonelongate carnivorans. Because Mustelinae and Guloninae were the only clades that exhibited significantly more elongate bodies compared to nonelongate carnivorans (see pANOVA Results), I also tested a v) two-peak OUM model ($OUM_{gul+mus}$) that assigned one optimum to Mustelinae and Gulonina and a second optimum to the remaining carnivorans and vi and vii) two additional two-peak OUM models (OUM_{mus} and OUM_{gul}) that allowed Mustelinae and Guloninae, respectively, to exhibit a different optimum compared to the remaining carnivorans. I fit

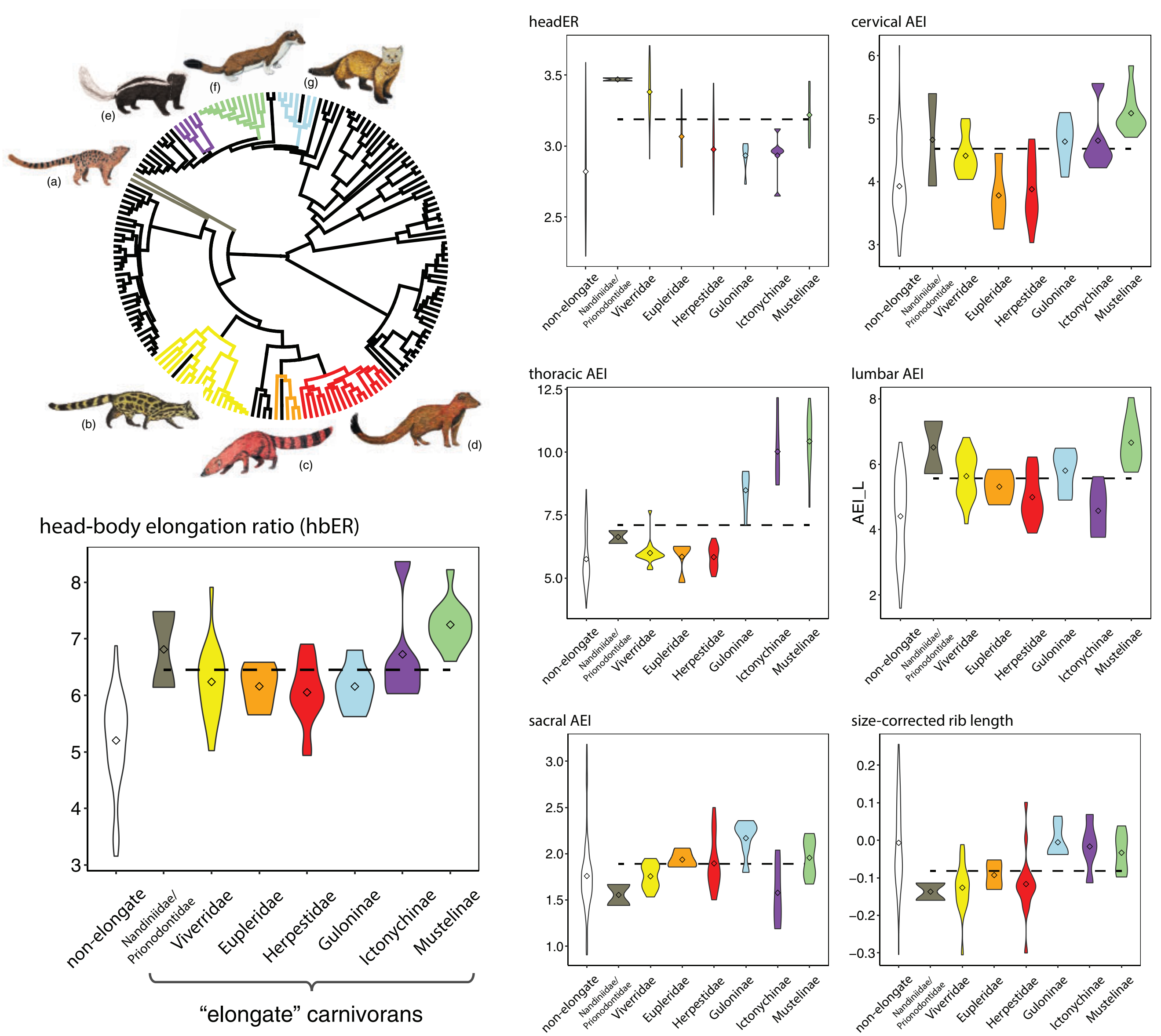

FIGURE 1. Groups of qualitatively described elongate carnivorans mapped on the carnivoran phylogeny and violin plots of head–body elongation ratio (hbER) and underlying morphological components. Dashed black line indicates mean hbER across elongate carnivorans. a) banded linsang, *Prionodon linsang*; b) common genet, *Genetta genetta*; c) ring-tailed mongoose, *Galidia elegans*; d) slender mongoose, *Galerella sanguinea*; e) African striped weasel, *Poecilogale albinucha*; f) short-tailed weasel, *Mustela erminea*; and g) American marten, *Martes americana*.

all models using OUwie (Beaulieu et al. 2012) across 100 mapped trees to take into account uncertainty in phylogenetic topology and stochastic character maps of the elongate and nonelongate group designations. Models were assessed with small sample corrected Akaike weights (AICcW). I generated 95% bootstrapped confidence intervals for best-fitting model parameters and determined whether I had adequate power to distinguish between models using simulations. I used phylogenetic half-lives ($\ln(2)/\alpha$) to assess the responsiveness of elongate clades to adaptive peaks.

I tested Prediction 3 on whether elongate clades exhibited more similar morphologies in phylomorphspace than between their ancestral nodes using distance-based and frequency-based metrics of convergence (C-metrics) in convevol (Stayton 2015). I also measured the strength of convergent evolution using the Wheatsheaf index in windex (Arbuckle and Minter 2015).

Morphological components underlying body shape.—I used the same set of procedures as described above to test predictions on whether elongate carnivorans exhibit convergence in the six morphological components (i.e., headER, AEI of each vertebral region, and relative rib length). For evolutionary modeling, I used the multivariate models (mvBM1, mvOU1, $\mathrm{mvOUM_{elongate\_clades}}$, $\mathrm{mvOUM_{elongate}}$, $\mathrm{mvOUM_{mus}}$,

$mvOUM_{gul}$, and $mvOUM_{mus+gul}$) with mvMORPH (Clavel et al. 2015). Because multivariate models may be unreliable (Adams and Collyer 2018), I also fit the seven univariate models to each of the six morphological components using OUwie.

I examined the phylomorphospace of morphological components using a phylogenetic principal component analysis (pPCA) with the correlation matrix and accounted for phylogenetic signal using Pagel's λ (Pagel 1999) in phytools (Revell 2009). To visualize the morphospace with respect to ancestral nodes, I projected pPC axes in phylomorphospace (Sidlauskas 2008) and created phenograms (Evans et al. 2009) using phytools.

To compare pathways towards elongate body plans between elongate clades, I used multiple regressions to test which morphological component(s) (i.e., headER, AEI of each vertebral region, and relative rib length) contributed the most to body shape variation (hbER) within each elongate clade with >12 species. Multiple regressions were performed in RRPP.

Results

Convergence in Body Shape (hbER)

Prediction 1.—Qualitatively described elongate carnivorans exhibit more elongate bodies (greater hbER) compared to nonelongate carnivorans (pANOVA: $R^2 = 0.09$, $F_{6,169} = 16.53, P < 0.001$). Post hoc pairwise comparison tests revealed Mustelinae and Guloninae were the only clades to exhibit significantly more elongate bodies compared to other elongate clades (Table S2 of the Supplementary material available on Dryad). Elongate carnivorans (Procrustes variance $= 0.018$) exhibited less disparate body shapes compared to nonelongate carnivorans (Procrustes variance $= 0.032$) ($P = 0.008$).

Prediction 2.—The best-fitting model for hbER was the $OUM_{elongate}$ model (AICcW $= 0.95$; Table S3 of the Supplementary material available on Dryad) with a phylogenetic half-life of 15.1 myr. Parametric bootstrapping revealed that elongate carnivorans exhibited a more elongate body optimum (hbER $\Theta_{elongate}$ [95% CI] $= 7.3$ [5.9–8.9]) compared to nonelongate carnivorans (hbER $\Theta_{nonelongate} = 4.5$ [4.0–5.0]). Simulations under the $OUM_{elongate}$ model indicated that there was substantial power to distinguish between all seven models (AICcW > 0.99; Table S4 of the Supplementary material available on Dryad).

Prediction 3.—The distance-based metric of convergence revealed a 50% reduction in the distances between all seven elongate clades relative to the maximum spread of their ancestors ($C_1 = 0.50, P < 0.001$). This represents 23% of the total evolution between clades and 1% of the total evolution of carnivorans ($C_3 = 0.23, P < 0.001; C_4 = 0.01, P = 0.029$). Similarly, the Wheatsheaf index indicated significantly greater convergence towards elongate body morphologies than expected ($w = 1.28, P = 0.001$). In contrast, the frequency-based metric of convergence indicated that the number of transitions into phylomorphospace of elongate carnivorans was not significantly greater than expected ($C_5 = 2, P = 0.380$).

No Convergence in Morphological Components

Prediction 1.—Compared to nonelongate carnivorans, qualitatively described elongate carnivorans exhibited more elongate cervical, thoracic, and lumbar vertebrae (pANOVA, $P = 0.001 - 0.015$; Table S5 of the Supplementary material available on Dryad). Post hoc pairwise comparisons revealed that mustelines and gulonines exhibited increased elongation in the cervical region; mustelines and ictonychines exhibited increased elongation in the thoracic region; and mustelines, gulonines, and herpestids exhibited increased elongation in the lumbar region (Table S6 of the Supplementary material available on Dryad). Elongate carnivorans (Procrustes variance $= 0.167$) exhibited less disparate body components compared to nonelongate carnivorans (Procrustes variance $= 0.236$) ($P = 0.005$).

Prediction 2.—The best-fitting multivariate model for the morphological components was the $mvOUM_{elongate}$ model (AICcW > 0.99), indicating that elongate carnivorans exhibited more elongate crania and vertebrae and relatively reduced body depth (Table 1). Phylogenetic half-lives ranged from 0.34 myr to 4.16 myr (Table 1). Univariate models largely confirmed that elongate carnivorans exhibit elongate morphologies with some slight differences. The $OUM_{elongate}$ model was the best-fitting model for headER (AICcW $= 0.66$), the lumbar region (AICcW $= 0.52$), and size-corrected rib length (AICcW $= 0.96$). Parametric bootstrapping revealed that elongate carnivorans exhibited more elongate crania and lumbar vertebrae, and relatively reduced body depths (Table S7 of the Supplementary material available on Dryad). The $OUM_{elongate\_clades}$ model was the best-fitting model for the cervical (AICcW $= 0.82$) and thoracic regions (AICcW $= 0.91$), and parametric bootstrapping revealed that mustelids (i.e., Mustelinae, Guloninae, and Ictonychinae) exhibited more elongate cervical and thoracic vertebrae compared to elongate feliforms (i.e., Nandiniidae, Prionodontidae, Viverridae, Eupleridae, and Herpestidae) and nonelongate carnivorans (Table S7 of the Supplementary material available on Dryad). Lastly, the $OUM_{mus+gul}$ model was the best-fitting model for the sacral region (AICcW $= 0.63$; Table S7 of the Supplementary material available on Dryad), and parametric bootstrapping indicated that mustelines and gulonines exhibited more elongate sacral vertebrae compared to all other carnivorans (Table S7 of the Supplementary material available on Dryad). Simulations under the best-fit models indicated that there was substantial power to distinguish between all models (AICcW > 0.99; Table S4 of the Supplementary material available on Dryad).

Prediction 3.—Despite the shared adaptive peaks, the distance-based metrics revealed no significant convergence in the morphological components between all

TABLE 1. Comparisons of the best fitting evolutionary models in body shape components

Model	AICc	ΔAICc	AICcW	Components	Phylo 1/2 life (myr)	$\Theta_{elongate}$	$\Theta_{nonelongate}$
mvBM1	−1203.25	325.76	0.00	—	—	—	—
mvOU1	−1507.32	21.69	0.00	—	—	—	—
mvOUM$_{elongate}$	−1529.01	0.00	1.00	headER	0.34	3.1	2.8
				Cervical AEI	0.38	4.6	3.9
				Thoracic AEI	4.16	8.1	7.2
				Lumbar AEI	2.54	8.6	4.3
				Sacral AEI	0.84	1.2	1.4
				sc rib length	0.47	−0.3	−0.1
mvOUM$_{elongate_clades}$	−1406.56	122.45	0.00	—	—	—	—
mvOUM$_{Gul+Mus}$	−1437.90	91.11	0.00	—	—	—	—
mvOUM$_{Guloninae}$	−1483.71	45.30	0.00	—	—	—	—
mvOUM$_{Mustelinae}$	−1484.88	44.13	0.00	—	—	—	—

Note: Akaike information criterion weights (AICcW) were calculated for each of the 100 replications to account for uncertainty in phylogenetic topology and stochastic character mapping.
ΔAICc = the mean of AICc minus the minimum AICc between models. Bolded rows represent the best-fit model as indicated by the lowest ΔAICc score. Θ = mean evolutionary optima for elongate and nonelongate groups of best model.

seven elongate clades ($C_1 = 0.15, P = 0.090$; $C_3 = 0.06, P = 0.104$; $C_4 = 0.01, P = 0.073$; $w = 0.80, P = 0.758$). In contrast, the frequency-based metric indicated that the number of transitions into morphospace of elongate carnivorans was significantly greater than expected ($C_5 = 5, P < 0.001$).

Phylomorphospace of Morphological Components

The phylomorphospace and phenogram revealed great variation of the six morphological components between the seven elongate clades (Fig. 2). The first two pPC axes accounted for 54.7% of the variation of the components (phylogenetic signal $\lambda = 0.92$). Carnivorans with low pPC1 scores exhibited relatively elongate vertebrae, particularly for the lumbar (loading $= -0.83$), cervical (-0.76), and thoracic (-0.70) regions, and reduced body depths whereas those with high pPC1 scores are relatively short and stout (relative rib length loading $= 0.372$) (Fig. 2a; Table S8 of the Supplementary material available on Dryad). pPC2 describes shape variation associated with the anterior part of the body where carnivorans with high pPC2 scores exhibit relatively elongate crania (0.763) (Fig. 2a; Table S8 of the Supplementary material available on Dryad). All elongate clades tend to exhibit low pPC1 values whereas they are more broadly distributed across the full range of pPC2 (Fig. 2b).

Different Pathways Lead to Body Elongation

Multiple regressions indicated that the best predictor(s) of body shape varied between the three elongate clades with sufficient species sample sizes. In Mustelinae, relative rib length ($R^2 = 0.54, P = 0.003$), thoracic elongation $R^2 = 0.20, P = 0.012$), and cervical elongation ($R^2 = 0.28, P = 0.012$) were the best predictors of body elongation (Table S9 of the Supplementary material available on Dryad). In Viverridae, lumbar elongation ($R^2 = 0.49, P = 0.001$) and cervical elongation ($R^2 = 0.23, P = 0.001$) were the best predictors of body elongation; the remaining components exhibited low R^2 ($R^2 < 0.10$; Table S9 of the Supplementary material available on Dryad). In Herpestidae, lumbar elongation ($R^2 = 0.39, P = 0.022$) was the only predictor of body elongation (Table S9 of the Supplementary material available on Dryad).

DISCUSSION

That elongate carnivorans exhibit convergence in body shape is supported by three lines of evidence, matching my predictions. First, qualitatively described elongate carnivorans have more elongate bodies that are less disparate than nonelongate carnivorans. Second, OU modeling demonstrated that elongate and nonelongate carnivorans exhibited separate body shape optima that are biologically realistic and within the limits of the empirical data (hbER $\Theta_{elongate} = 7.3$ [5.9−8.9]; hbER $\Theta_{nonelongate} = 4.5$ [4.0−5.0]). Third, elongate carnivorans exhibited a 50% reduction in the morphological distances between clades relative to their ancestors. Given these three lines of evidence, it is tempting to propose that strong selection is leading to the convergence of increased body elongation. However, the two-peak OUM$_{elongate}$ model's phylogenetic half-life (16.8 myr, close to half of the age of Carnivora itself [48.2 myr]) along with high phylogenetic signal in hbER ($\lambda = 0.96, P < 0.001$) indicated weaker selection towards a more elongate body optimum than expected under an OU process (Cooper et al. 2016). Weaker selection is suggestive that the body shape landscape contains broader adaptive slopes rather than distinct adaptive peaks with steep slopes (Phillips and Arnold 1989; Polly 2004), and converging elongate clades are only weakly "pulled" towards an elongate body optimum. A broadly sloped selective landscape may also explain why elongate carnivorans exhibit only a 50% reduction in the distances between all seven elongate clades and not complete convergence in body shape. Similarly, the

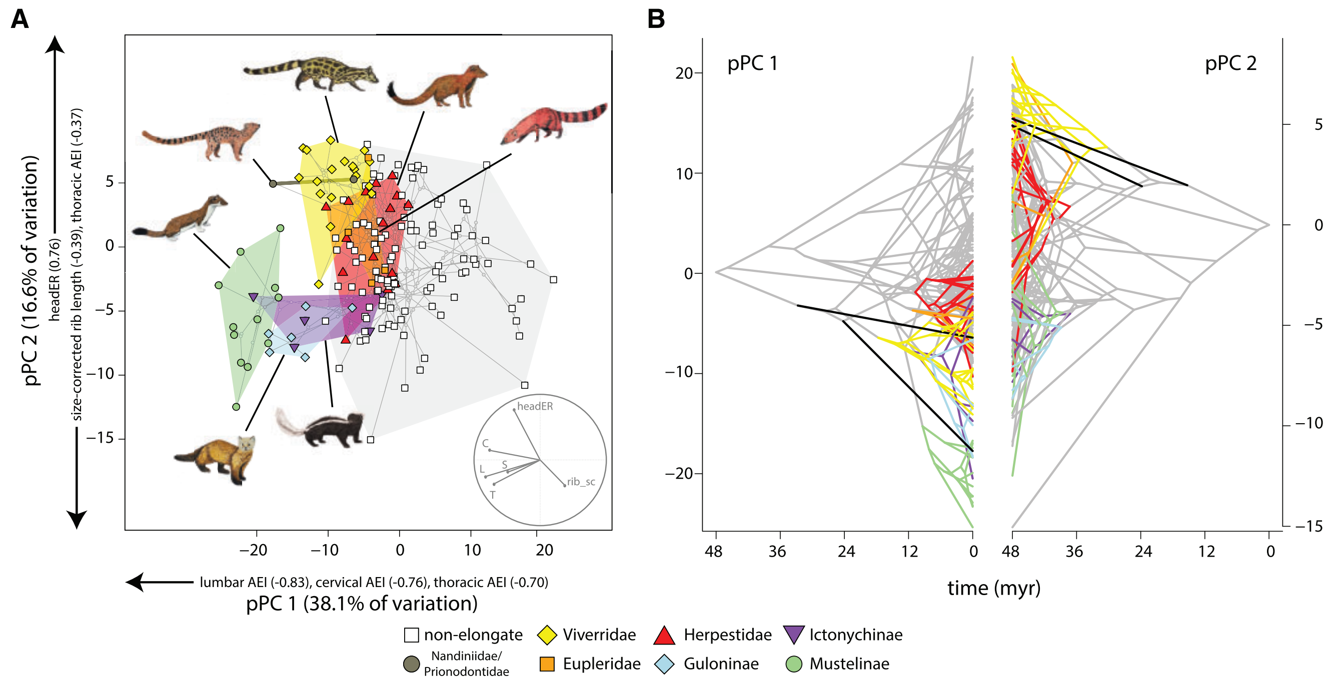

FIGURE 2. a) Morphospace of the morphological components underlying body shape variation based on phylogenetic principal components (pPC) 1 and 2. Loadings of major components are in parentheses. Loadings are also shown in the insert (see Table S8 of the Supplementary material available on Dryad for loadings of all pPC axes). b) Phenograms of pPCs 1 and 2. AEI = axial elongation index; C = cervical; T = thoracic; L = lumbar; S = sacral; rib_sc = size-corrected rib length.

C_3 results indicate that convergence accounts for only 23% of the overall evolutionary change between elongate clades. Overall, these results suggest that elongate carnivorans exhibit incomplete convergence with weak selection towards more elongate bodies.

In contrast, the morphological components underlying body shape variation do not exhibit convergence despite evidence that some of these components share adaptive optima between the seven clades and are more elongate in elongate carnivorans than in nonelongate carnivorans. Multivariate modeling indicated that elongate carnivorans exhibited more elongate cranial and vertebral optima and relatively reduced body depth optima (Table 1). Additional univariate modeling revealed that mustelids exhibited further elongation of the cervical and thoracic vertebrae compared to elongate feliforms and nonelongate carnivorans, whereas mustelines and gulonines exhibited further elongation of the sacral vertebrae compared to all other carnivorans (Table S7 of the Supplementary material available on Dryad). The differences in the degree of elongation in body components between the seven elongate clades may be due to different clade-specific selective pressures. Short but different phylogenetic half-lives of the best models associated with each of the six body components (0.34–4.16 myr; Table 1) indicated that the components are strongly pulled towards distinct elongate peaks either over different adaptive slopes or at different rates. The different natural histories of each clade support distinct adaptive landscapes (see below). Interestingly, these phylogenetic half-lives were much shorter than the phylogenetic half-life for overall body shape (16.8 myr), providing support that different selective pressures act on the individual body components rather than overall body shape. This hypothesis is further supported by findings that multiple pathways can lead to the evolution of different body shapes between and within carnivoran families (Law 2021a) and between elongate clade. Elongation of the thoracic region via reduction of relative rib length and elongation of the thoracic vertebrae was the best predictor of body shape evolution in musteline weasels whereas elongation of the lumbar region was the best predictor in viverrids and herpestids (Table S9 of the Supplementary material available on Dryad). Like body size, body shape is a prominent feature of vertebrate morphology (Bergmann et al. 2020) that may transcend one-to-one relationships between morphology and function across macroevolutionary scales (Law 2021b). Therefore, the multidimensionality of an all-encompassing trait such as body shape may conceal evidence of adaptive evolution (Wainwright et al. 2005; Alfaro et al. 2005; Bergmann and McElroy 2014; Zelditch et al. 2017). Instead, stronger signals of selection are usually found in individual traits with more direct for–function relationships such as craniodental measurements, vertebral shape, or limb bone compactness (e.g., Tseng 2018; Jones et al. 2018; Law et al. 2018a; Slater and Friscia 2019; Vander Linden et al. 2019; Michaud et al. 2020; Amson and Bibi 2021). This present study lends further support that the body components are under different selective pressures that can nevertheless lead to a converging body plan.

The effects of these different selective pressures on the seven elongate clades are also apparent in phylomorphospace. Although the frequency-based metric of convergence indicates that five of the seven elongate clades exhibit similar evolutionary trajectories towards a shared region of morphospace ($C_5 = 5, P < 0.001$), they do not completely overlap with each other in a morphospace consisting of pPCs 1 and 2 (Fig. 2a). Herpestids (mongooses) and euplerids (Malagasy carnivorans) are the only elongate clades that fall completely within the boundary of the nonelongate region of morphospace. pPC 1, which describes a continuum from relatively elongate to relatively robust vertebrae, separates out most elongate species from nonelongate carnivorans. Ancestral nodes of herpestids, euplerids, and viverrids (genets and civets) fall within their respective regions of morphospace (Fig. 2b), suggesting that ancestral species previously evolved elongate morphologies and extant descendants simply retained this ancestral trait. In contrast, the ancestral nodes of Mustelinae and Prionodontidae originated within the nonelongate region of morphospace, and their respective descendants extended towards the lower bound of pPC 1 to occupy their own region of morphospace (Fig. 2). For musteline weasels, this evolutionary trajectory fits the working hypothesis that axial elongation serves as an innovation that enabled weasels and other mustelids to pursue subterranean prey with more flexible bodies for greater locomotor efficiency (Law et al. 2018b, 2019; Law 2019). Gulonines (martens) and ictonychines (polecats) also fit within this hypothesis as they also approach the lower bound of pPC 1 and pursue prey in underground or snow burrows. In contrast, the Asiatic linsang (Prionodontidae) exhibits a semiarboreal lifestyle with a largely omnivorous diet and cat-like pouncing behavior (Wilson and Mittermeier 2009).How an elongate body serves as an adaptation awaits additional natural history for this relatively unknown carnivoran. pPC 2, which largely describes a continuum from robust to elongate crania and relative rib length to a certain extent, loosely separates elongate feliforms (i.e., Eupleridae, Herpestidae, Nandiniidae/Prionodontidae, and Viverridae) from elongate mustelids (i.e., Guloninae, Ictonychinae, and Mustelinae). Ancestral nodes of all elongate clades fall within their respective regions of morphospace (Fig. 2b), suggesting that extant descendants of these clades simply retained the ancestral trait of the components associated with pPC 2. pPC 2 also partially separates out viverrids (civets and genets), euplerids (Malagasy carnivorans), and herpestids (mongooses). The transition from viverriids with higher pPC 2 scores to herpestids with lower pPC 2 scores with euplerids scattered in between may be loosely associated with their locomotor and hunting behaviors. Viverrids are primarily semiarboreal with cat-like pouncing behaviors whereas herpestids are primarily terrestrial with rare pouncing behavior (Wilson and Mittermeier 2009). Eupleridae, on the other hand, contains species that are either semiarboreal or terrestrial with hunting behaviors that range from pouncing to insectivorous foraging (Wilson and Mittermeier 2009). These loose associations with locomotor mode and hunting behavior may explain the relative positions of viverrids, euplerids, and herpestids in morphospace. Nevertheless, the complexity and variation of the carnivoran body shape landscape cannot be effectively captured by *a priori* ecological regimes across the macroevolutionary level (Law 2021b). Instead, elongate carnivorans exhibit diverse ecologies that mirror the diversity found across all carnivorans. As a result, each elongate carnivoran clade exhibits overlapping ecologies and behaviors despite converging elongate bodies or similar body components. Therefore, additional biomechanical studies are still needed to examine how the form–function relationships between elongate bodies and ecologies differ between these seven clades.

Overall, this study found incomplete convergence of body elongation in carnivoran clades but with a nuanced interpretation of the evolution of the morphological components that underlie body shape variation. That is, all components were more elongate in elongate carnivorans compared to nonelongate species but do not exhibit convergence. The phylogenetic half-lives of these components were shorter than the half-life in overall body shape and were different from each other, indicating that different selective pressures can act on each component independently and create multiple pathways towards converging body elongation. These results align with research demonstrating that similar or converging body plans can arise through diverging evolutionary pathways (Ward and Mehta 2010; Wake et al. 2011; Ward and Mehta 2014; Morinaga and Bergmann 2017; Bergmann and Morinaga 2019) as a result of different adaptive slopes (Grossnickle et al. 2020). Furthermore, ancestral nodes of many elongate clades fall within their respective regions of body component morphospace, suggesting that extant descendants of these clades simply retained the ancestral trait of elongate morphologies. Incorporating the fossil record to quantify the body shapes of extinct carnivorans and perform its ancestral state reconstructions would facilitate tests between convergence and conservatism of elongate body plans in carnivorans and other mammals.

Supplementary Material

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bg79cnpc4.

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