Long-fuse evolution of carnivoran skeletal phenomes through the Cenozoic

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Abstract

Climatic change is hypothesized to promote phenotypic diversification. While neontological analyses are often used to test this hypothesis, extant data only captures the time-averaged signal of surviving lineages. More nuanced tests require paired and longitudinal climatic and organismal data from the fossil record. Here, we developed the most comprehensive phenomic dataset of pan-carnivorans incorporating fossil and extant data (118 extant and 81 extinct species) to test hypotheses that Cenozoic climatic change influenced the tempo and mode of the cranial, appendicular, and axial skeleton. We found equal support for two release and radiate models, where skeletal evolution transitioned from an Ornstein–Uhlenbeck process to Brownian motion at the Eocene-Oligocene Transition (EOT) and the Mid-Miocene Climate Transition (MMCT). Disparity-through-time analyses reveal that the EOT led to decreased subclade disparity whereas the MCCT led to increased disparity. Our results suggest that climate transitions facilitated the diversification of skeletal phenomes under a long-fuse model. Specifically, EOT-induced extinction of coeval stem pan-carnivorans released crown carnivorans from a constrained adaptive zone, resulting in phenotypic diversification among families from the Early Oligocene to Mid-Miocene. Intrafamilial skeletal phenome diversification did not occur for another 20 million years until after the MMCT. Overall, the hierarchical progression of ecological diversification across the Cenozoic significantly influenced the establishment of modern carnivorans. Our work demonstrates the essential role of macroevolutionary data from the fossil record for revealing how major global climatic events steered the evolutionary trajectories of modern skeletal phenomes.

Introduction

Ecological opportunities arising from climatic and environmental changes are often hypothesized to promote phenotypic diversification across macroevolutionary time scales (1–3). After the Early Eocene Climate Optimum, trends towards decreased global temperatures (4) and consequent environmental transitions from closed forest habitats to open grassland habitats (5, 6) have facilitated the increase in phenotypic diversity and evolution of novel phenotypes in several mammalian clades. For example, rodents, lagomorphs, and ungulates all independently evolved hypsodont dentitions in association with open habitats along with the lengthening of limbs for more efficient cursoriality (7–10). Similarly, phenotypic diversity in carnivores increased (11–13), enabling them to exploit diverse habitats through a range of hunting behaviors from ambush to cursorial or subterranean pursuit specialization (14–16). However, the question of how these environmental changes influence the rate at which phenotypic disparity accumulates (i.e., tempo) and the pattern of phenotypic change across the phylogeny (i.e., mode) remains difficult to resolve due to the absence of time-sequence data (i.e., paleontological data) considered under a phylogenetic framework. The few studies that have successfully integrated the fossil record into neontological analyses demonstrated that fossils are essential for accurate model selection in phenotypic macroevolution analyses (17–21), thus providing a more informed understanding of phenotypic variation through phylogenetic time (e.g., (15, 19, 22–25). To-date, these studies have primarily focused only on single phenotypic traits like body size or the skull. No study has yet to simultaneously test how major environmental shifts may have facilitated the evolution of the skull, appendicular skeleton, and axial skeleton in both extant and extinct species.

In this study, we take advantage of the rich fossil record of pan-carnivorans (i.e., Carnivoramorpha, which includes Carnivora; Hyaenodonta; and Oxyaenodonta) to test hypotheses that climatic and environmental changes during the past 66 million years influenced the tempo and mode of the cranial, appendicular, and axial skeletal systems. Pan-carnivorans represent one of the best characterized crown mammal groups from the Cenozoic, with a crown-group fossil record going back more than 55 million years and stem taxa being traced back to the early Paleocene. With the extinction of non-avian dinosaurs, early pan-carnivorans became the first large carnivorous mammals (26). Although crown carnivoran lineages co-existed with their extinct sister clades during much of the Eocene, most early carnivorans were small, generalized predators serving as secondary consumers. It was not until later in the Oligocene and Miocene that they expanded to large, specialized top predator niches (11–13, 27, 28). Since their first appearance as small mongoose-like forms (11, 13, 17), carnivorans have diversified into the numerous body forms we see today, ranging from small, elongate weasels to big robust bears to fully aquatic, streamlined seals (29). Here, we address the as-yet unanswered question of what drove the exceptional diversification of carnivoran body plans from a single blueprint.

The two leading hypotheses for the major influences on carnivoran morphological diversification are ecological opportunity facilitated by climate change and the extinction of coeval stem pan-carnivorans. Global cooling, increased aridity, and habitat shift from forest to grasslands have led to several rises and falls of carnivoran and stem pan-carnivoran clades (11). Carnivorans became increasingly more adaptable to these environmental and climatic changes, as dental records suggest that crown carnivorans maintained their morphological diversity even during periods of extinction whereas morphological diversity in stem carnivorans continued to decline (12). Furthermore, stem pan-carnivorans exhibited steeper declines in species richness

than carnivorans, and the overall percentage of stem pan-carnivoran taxa declined as those of carnivoran taxa increased (11–13). These patterns have been attributed to competition between carnivorans and stem pan-carnivorans in which declining stem pan-carnivorans are replaced and excluded by phylogenetically distinct but functionally similar crown carnivorans (11–13, 27). Although analyses based on dental traits have partially supported this hypothesis (11, 12), no quantitative evidence has been explicitly tested for this hypothesized link between paleoenvironmental changes and the diversification of the remaining skeletal phenome.

Here, we tested if periods of rapid climate change facilitated carnivoran skeletal diversity by removing ecological competitors and releasing previously occupied niches, or alternatively, if carnivorans evolved independently from environmental factors. We predicted that the Eocene Oligocene Transition and Mid-Miocene Climate Transition facilitated skeletal diversification within carnivorans, enabling species to exploit new resources during these periods of novel ecological opportunity. We leveraged the vast pan-carnivoran fossil record to quantify skeletal phenomes by incorporating traits from the skull, appendicular skeleton, and axial skeleton of extinct and extant species. We then used phylogenetic comparative framework to examine the tempo and mode of skeletal evolution utilizing a total evidence phylogeny that contains almost all known extant and extinct carnivorans and their stem relatives (21)

Results

Skeletal trait imputation

We quantified the skeletal phenome of 118 extant species and 81 extinct species using 103 linear measurements obtained from 854 specimens held at 17 natural history museums (Table S1). Together, this 192 species dataset includes seven traits in the cranium; seven traits in

the mandible; 13 traits in the forelimb; 13 traits in the hindlimb; and seven traits each in third cervical, fifth cervical, first thoracic, middle thoracic, diaphragmatic thoracic, last thoracic, first lumbar, middle lumbar, and last lumbar vertebrae (Fig. S1). We imputed missing trait measurements (25.2% of trait measurements in the full dataset; 0% in extant dataset; 61.9% in extinct dataset) using multiple imputation with PCA (MIPCA) under a Bayesian framework (30, 31). Our assessment of the quality of the trait imputations revealed one-to-one relationships (i.e., slopes are not significantly different from 1) between imputed and empirical values of each trait regardless of the amount of missing data (Fig. S2), indicating that our phenome dataset can reliably estimate missing trait data.

We performed a principal component analysis (PCA) incorporating all trait measurements with size removed. Seven PC axes were found meaningful following procedures by (32); these were subsequently used as our proxy of the skeletal phenome (76.3% of explained variance; Fig. 1; see Table S2 for trait loadings). The geometric mean of all trait measurements was used as our proxy for skeletal size. We similarly performed PCAs to reduce the dimensions of each skeletal component (i.e., cranium, mandible, forelimb, hindlimb, and each of the nine vertebrae).

Evolution of carnivoran skeletal phenome and size

Phylogenetic signal in carnivoran skeletal phenome was moderate (Pagel's $\lambda = 0.60$, $p = 0.001$; Blomberg's $K = 0.58$, $p = 0.001$), suggesting that disparity in skeletal phenome deviated from Brownian motion (BM) and primarily occurs within clades as opposed to among clades. Disparity through time (DTT) analyses further revealed that disparity in skeletal phenome deviated from Brownian motion near the Eocene-Oligocene Transition (EOT) and Mid-Miocene

Climate Transition (MMCT) (Fig. 2A–C). Subclade disparity increased just prior to the EOT (~37 Ma; morphological disparity index (MDI) = 0.534, P = 0.012) and just after the MMCT (~14 Ma; MDI = 0.238, P = 0.018). These two time points deviated from a general positive relationship between subclade disparity and temperature during the past 66 million years (generalized additive model: EDF = 8.9, $R^2 = 0.77$, $P < 0.001$; Fig. 3). In contrast, high phylogenetic signal (Pagel's $\lambda = 0.91$, p = 0.001; Blomberg's K = 0.56, p = 0.001) and DTT analyses were united in showing that disparity in skeletal size did not significantly deviate from BM and tends to occur within clades (Fig. 2D–F).

We tested 12 alternative hypotheses that could explain the disparity of carnivoran skeletal phenome and size by fitting a series of macroevolutionary models (Fig. 4). For skeletal phenome, we found nearly equal support for two release and radiate models (Table 1), where the evolution of skeletal phenomes transitions from an Ornstein–Uhlenbeck (OU) process to BM at the EOT 34 million years ago ($OUBMi_{EOT}$: AICcW = 0.45) and at the MCCT 17 million years ago ($OUBMi_{MMCT}$: ΔAICc = 0.13, AICcW = 0.42). These models indicated that evolutionary rates slowed after both the EOT (mean $\sigma^2_{pre\text{-}EOT} = 0.097$; mean $\sigma^2_{post\text{-}EOT} = 0.018$) and the MCCT (mean $\sigma^2_{pre\text{-}MCCT} = 0.047$; mean $\sigma^2_{post\text{-}MCCT} = 0.018$). Mean stationary variances ($\sigma^2/2\alpha$) for the OU portion of the $OUBMi_{EOT}$ and $OUBMi_{MMCT}$ models was 0.087 ($\alpha = 0.55$) and 0.269 ($\alpha = 0.09$), respectively. In contrast, models with distinct optima (i.e., sOU and cOU models) for pan-carnivoran groups were poorer fits (ΔAICc = 9.31–29.44). The single-optimum model (OU1) also received moderate support (ΔAICc = 2.67, AICcW = 0.12); however, other single regime models based on BM (single rate BM, BM with a directional trend, and early burst) were poorer fits (ΔAICc > 23). Simulations under the parameters of the $OUBMi_{EOT}$ model indicated that there was substantial power to distinguish this model from BM and alterative models (AICcW >

0.99; Table S3; Fig. 5A). Simulations under the parameters of the $OUBMi_{MMCT}$ model also indicated that there was substantial power to distinguish this model from all alterative models (AICcW = 0.56; Table S3; Fig. 5B) except BM (ΔAICc = 0.61, AICcW = 0.41; Table S3). These simulations thus suggest that the EOT rather than the MMCT may have a stronger effect on the evolution of skeletal phenome.

For skeletal size, the $OUBMi_{MMCT}$ model was the best supported model (AICcW = 0.76), suggesting that the evolution of skeletal size transitions from an OU process ($\alpha = 0.05$; $\sigma^2_{pre\text{-}MCCT} = 0.019$) to BM ($\sigma^2_{post\text{-}MCCT} = 0.008$) during the MMCT 17 million years ago (Table 1). However, simulations were not able to distinguish this best supported model from BM (AICcW = 0.24) and the $OUBMi_{EOT}$ (AICcW = 0.22) models (Table S3). Thus, consistent with the DTT analyses, climatic changes may have had less of an impact on the evolution of skeletal size than suggested by macroevolutionary models.

Evolution of carnivoran skeletal components

Phylogenetic signal of the skeletal components ranged from moderate to high (Pagel's $\lambda = 0.44–0.94$, all $p = 0.001$; Blomberg's $K = 0.38–0.45$, all $p = 0.001$; Table S4), suggesting that variance in skeletal components tended to follow BM and primarily occurred within clades as opposed to among clades. DTT analyses revealed three general patterns in the evolution of these skeletal components (Fig. S3). First, all vertebrae largely followed BM expectations except during last 20 Ma. Second, the cranium and limbs exhibited elevated subclade disparity compared to BM during the Paleocene to Mid-Eocene and Oligocene and from the Early Miocene to present. Third, the mandible exhibited elevated subclade disparity throughout the

majority of pan-carnivoran history. In all cases, subclade disparity tended to increase with increasing temperature change during the past 66 million years (Fig. S4).

The OU1 model was best supported for most skeletal components including the cranium, forelimb, and most vertebrae (AICcW = 0.80–1.00; Table S5). The cOU3 model was best supported for the mandible (AICcW = 1.00) and diaphragmatic vertebrae (AICcW = 0.91); the sOU2 (AICcW = 0.54), OU1 (ΔAICc = 0.44, AICcW = 0.35), and cOU3 (ΔAICc = 1.71, AICcW = 0.19) models were equally supported for the first lumbar vertebra; and the $OUBMi_{MMCT}$ model was best supported for the hindlimb (AICcW = 1.00), first thoracic (AICcW = 0.99), and middle thoracic (AICcW = 0.99) vertebrae (Table S5; see Table S6 for parameter estimates from best model).

Discussion

The global cooling, increased aridity, and habitat shift from forests to grasslands during the past 56 Myr has spurred phenotypic diversification in many mammalian clades (7–10, 14, 15). Here, we found that climatic and environmental changes from the Eocene-Oligocene Transition (EOT) and Mid-Miocene Climate Transition (MCCT) significantly facilitated the diversification of crown carnivoran skeletal phenomes across two distinct phases.

In the initial phase, EOT-induced climatic and environmental changes along with the decline of coeval stem pan-carnivorans released crown carnivorans from a constrained adaptive zone to radiation under Brownian motion, albeit at a slower evolutionary rate (Fig. 5A). With the onset of the EOT, global temperatures plummeted and the first Antarctic ice sheets appeared, transitioning Earth's climate from a warm, equable "greenhouse" to a cooler, temperate "icehouse" with increased seasonality (33–35). This period of climate change led to habitat

transitions from warm-humid forest to dry-temperate forest-steppe and grasslands, which in turn led to massive faunal turnover (34–39). Among pan-carnivorans, the EOT led to tremendous taxonomic turnover, resulting in the decline of Hyaenodonta and Oxyaenodonta and giving opportunities for carnivoran to radiate (11, 40) under a Brownian motion pattern (Fig. 5A). Lower average subclade disparity from the EOT to Mid-Miocene further indicated that diversification of skeletal phenomes occurred primarily among carnivoran families rather than within (Fig. 2). Our analyses suggesting EOT-induced interfamilial diversification is consistent with paleontological records indicating that early carnivorans exhibited generalized, small-bodied forms and did not exhibit major lineage and phenotypic diversification until after the EOT (11, 12, 27). Niche competition from stem pan-carnivorans may have initially constrained early carnivoran diversification prior to the EOT (11–13, 27). However, the EOT marked the decline of stem pan-carnivorans (11, 40), possibly because they had become too specialized (i.e., macroevolutionary ratchet) to adapt to the climatic and environmental changes brought by the EOT (11, 12). Thus, although both stem pan-carnivorans and early carnivorans exhibited a macroevolutionary ratchet towards large body size and hypercarnivory during this time, only carnivorans retained and increased their phenotypic diversity, giving them the opportunity to exploit habitats of the Oligocene (12, 13). This may have further excluded stem pan-carnivorans from novel ecological opportunities (11–13, 27, 28), facilitating stem pan-carnivoran decline but carnivoran diversification and the appearance of all modern carnivoran families from the Early Oligocene to the Mid-Miocene (11).

Further intrafamilial diversification of carnivoran skeletal phenomes did not occur for another 20 million years until after the MMCT. During this second phase, another major period of rapid temperature decline, increased aridity, and enhanced seasonality facilitated further

trends towards grasslands from forest habitats (6, 41–43). Our results suggested that these rapid climatic and environmental changes along with few competing clades of carnivorous mammals enabled crown carnivorans to exploit the new ecological niches from the late Miocene to Pleistocene (11–13, 28). Specifically, intrafamilial diversification of skeletal phenomes may have facilitated resource partitioning among ecologically similar taxa by increasing ecomorphological diversity or innovations in locomotor mode, hunting behavior, and dietary ecology (15, 44–46). For example, elbow-joint morphologies indicative of pounce-pursuit behaviors evolved by the late Miocene within canids (15), presumably in response to the Mid-Miocene diversification of grazing ungulates in open habitats (47, 48). Similarly, small, elongate body plans with short legs evolved within mustelids (16, 46), presumably to exploit the Mid-Miocene diversification of rodents in open habitats, both above and subterranean (7, 49). More recent work indicated that specific skeletal components exhibited strong selection towards these distinct ecological peaks, and functional trade-offs and covariance among and within skeletal components further explain their distribution across the adaptive landscape (45, 50, 51). Interestingly, we found that the OU1 model was best supported for most skeletal components in this current study (Table S5), suggesting that skeletal diversification is constrained towards a single optimum. However, moderate phylogenetic half-lives relative to the age of the clade (mean half-life = 10.4 Ma; Table S6), low phylogenetic signals in all skeletal components (mean Blomberg's K = 0.40; Table S2), and subclade disparity higher than expected under BM (Fig. S3) suggest that the skeletal components exhibit complex macroevolutionary dynamics rather than being constrained to a single optimum. Although multi-optima OU models with distinct ecological peaks may better capture the evolutionary mode of these skeletal components, we are unable to test these models without ecological data from extinct species. Unfortunately,

ecological classifications are typically inferred using the same data (i.e., skeletal traits) used in our analyses, which may lead to biased results if the inferred ecologies of extinct species are used to test for ecological peaks. Nevertheless, previous evolutionary modeling with extant species revealed that OU1 models are the best supported models when multi-optima OU models are not considered (45, 52), providing some evidence that heterogeneous selective pressures will also influence skeletal diversification in macroevolutionary datasets informed by fossil phenomes. Convergence in skeletal components may also explain strong support for OU1 models. However, this explanation may be less likely as subclade disparity was not lower than expected under BM simulations (Fig. S3). Furthermore, there is no evidence of convergence in skull morphology among shared dietary ecologies (50, 53), albeit convergence of appendicular or axial components have yet to be tested.

Multi-phasic evolution driven by climatic and environmental changes and coupled with taxonomic turnover appears to characterize the evolution of placental mammals. The delayed intrafamilial diversification in carnivorans is reminiscent of the long fuse model used to describe the diversification of placental mammals, which posits that the initial interordinal diversification of placental mammals occurred in the Cretaceous whereas the majority of intraordinal diversification took place after the K-Pg mass extinction event in response to newly available niche (54–56). The Paleocene–Eocene Thermal Maximum (PETM) may have also facilitated distinct phases of mammalian evolution, albeit this has yet to be quantitatively tested. The rise of forested environments and warmer climates after the PETM resulted in the replacement of stem lineages of the early Paleocene such as multituberculates, pantodonts, and condylarths by crown mammals such as primates, perissodactyls, and artiodactyls (57–59). This turnover led to the evolution of crown mammalian orders that dominated the Cenozoic and today's ecosystems (58).

Together, this body of work suggests that sequential evolutionary phases triggered by climatic and environment changes were largely hierarchical. For carnivorans, the hierarchical progression of ecological diversification across the Cenozoic led to the establishment of modern species. Specifically, climatic and environmental changes from the K-Pg, PETM, EOT, and MMCT facilitated diversification of infraclass Placentalia, mirorder Pan-Carnivora, families within Carnivora, and genera within carnivoran families, respectively. Thus, our results suggest that the long-fuse EOT/MMCT pattern we report here is as consequential for establishing modern-day carnivore guilds as the PETM were for establishing the modern orders of mammals. Overall, this work highlights the importance of analyzing data from extant and extinct species under a phylogenetic comparative framework to disentangle the multiple climatic events that contributed to the tiered evolution and diversity of carnivoran skeletal phenomes. Genetic analyses that improve our assessment methods of skeletal variation will bring even more insight (60–62). We posit that quantification of skeletal phenomes in other crown mammals and their extinct relatives will similarly reveal the effect of Cenozoic climatic change on the multi-phasal, hierarchical establishment of modern-day mammalian biodiversity.

Methods

Morphological data

We quantified the skeletal phenome of 118 extant species and 81 extinct species using 103 linear trait measurements obtained from 208 extant specimens and 646 fossils (see Table S1 for list of specimens and museums). Together, this dataset includes seven traits in the cranium; seven traits in the mandible; 13 traits in the forelimb (scapula, humerus, ulna, radius, third metacarpal); 13 traits in the hindlimb (pelvis, femur, tibia, fibula, calcarean, and third

metatarsal); and seven traits in third cervical, fifth cervical, first thoracic, middle thoracic (the sixth thoracic if the species has 13 or 14 thoracic vertebrae or the seventh thoracic if the species has 15 or 16 thoracic vertebrae), diaphragmatic thoracic, last thoracic, first lumbar, middle lumbar (the third lumbar if the species has four, five, or six lumbar vertebrae or the fourth lumbar if the species has seven lumbar vertebrae), and last lumbar vertebrae (Fig. S1). These measurements were chosen based on previous investigations of distinct ecomorphology among carnivorans (23, 63–66). All measurements were taken using Mitutoyo digital calipers or a tape measure. All specimens were fully mature, determined by the closure of exoccipital-basioccipital and basisphenoid-basioccipital sutures on the cranium, full tooth eruption, or closure of sutures on the limb bones or vertebrae. In our extant dataset, we obtained representatives from 14 of the 16 carnivoran families. We were unable to collect data from Prionodontidae, which contains two extant species of Asiatic linsangs, and Odobenidae, which contains a single extant species, the walrus. We only used male specimens to limit the differing degrees of sexual dimorphism that carnivorans exhibit (67, 68). In our extinct dataset, we obtained representatives from seven extant carnivoran families, seven extinct carnivoran families, stem carnivoramorphs, and stem pan-carnivorans (Hyaenodontidae and Oxyaenidae). We were limited by the availability of fossils that were formally described, placed in a phylogenetic context, free from taphonomic or other deformation.

Due to the fragmented nature of the fossil record, 73 extinct species were missing trait measurements, resulting in 25.2% missing data in the full dataset (61.9% in extinct dataset). We, therefore, imputed missing trait measurements using MIPCA (multiple imputation with PCA) in the R package missMDA v1.19 (30). MIPCA predicts missing trait measurements using an iterative PCA algorithm with a predefined number of dimensions. The number of dimensions

was estimated by generalized cross-validation criterion, and the iterative algorithm was performed under a Bayesian framework that alternates imputation of the data set and draw of the PCA parameters in a posterior distribution (31).

We assessed the quality of the trait imputations by comparing imputed and empirical data using a subset of species (n = 124) that contain all 103 measured traits. Specifically, we generated four datasets with different percentages (10%, 30%, 60%, and 80%) of randomly removed trait measurements and used MIPCA to impute these removed traits. We then assessed the accuracy of MIPCA by plotting the imputed traits against the empirical average traits and conducting reduced major axis regressions to test if the slope significantly differs from 1. We found strong relationships between imputed traits and empirical traits where the slope is not significantly different from 1 for all datasets with different percentages of removed traits (see Fig. S2 for two trait examples).

Using the imputed dataset, we removed the effects of size by dividing each skeletal trait by the geometric mean of all 103 traits (i.e., log shape ratio: ln(trait/geometric mean) (69, 70). We then conducted a principal component analysis (PCA) on the entire dataset retained the first seven PC axes (76.3% of explained variance) as our proxy of skeletal phenome. The number of PC axes to retain was determined using the getMeaningfulPCs function in the R package Morpho v2.11 (71). We also used individual PCAs to reduce the dimension of each skeletal component (i.e., cranium, mandible, forelimb, hindlimb, and each of the nine vertebrae) and retained meaningful PC axes for subsequent analyses.

Phylogenetic data

We used a modified species-level phylogeny containing almost all known extant and extinct carnivorans and stem relatives for our phylogenetic comparative methods (21). After pruning, the phylogeny contained all 118 extant species and 73 of the 81 extinct species in our dataset. We manually added the following extinct species: *Crassidia intermedia* was placed as basal caniform and sister to the genus *Daphoenus* (72); *Corumictis wolsani* was placed as stem to Mustelidae and sister to the genus *Promartes* (73); *Cyonasua brevirostris* was placed as sister to genus *Nasua* (74); *Eoarctos vorax* was placed as sister to Ursidae (75); *Puma pardoides* was placed as sister to *Puma concolor* (76); *Satherium ingens* was placed as sister to sister to genus *Pteronura* (77); *Neovulpavus mccarrolli* was placed as a stem carnivoramorphan and sister to *Miacis washakius* (78); and *Promartes olcotti* was placed as a stem to Mustelidae and sister to the genus *Corumictis* (79) (Table S8).

Phylogenetic Comparative Methods

We first measured phylogenetic signal in skeletal phenome, skeletal size, and each skeletal component using the R package geomorph v4.0.6 (80). We then examined subclade disparity in each dataset by performing disparity through time (DTT) analyses (81) using fdtt (22), a modified version of the dtt function in the R package geiger v2.0.11 (82). We compared carnivoran DTT to a null, constant-rates distribution derived from 10,000 Brownian motion simulations, and computed the morphological disparity index (MDI) as the area between the empirical DTT curve and the median of these simulations. We also examined the relationship between subclade disparity and temperature change. We interpolated missing subclade disparity and temperature change data based on the time scale using linear interpolation in the R package zoo v1.8-12 (83). We then fit a linear model and generalized additive model to test the

relationship between subclade disparity and temperature change and used AIC to determine the best fit model. We repeated these analyses for skeletal size and each skeletal component.

We then tested 12 alternative hypotheses that could explain carnivoran skeletal evolution by fitting a series of macroevolutionary models (Fig. 4):

1. Brownian motion model (BM): Suggests that disparity in skeletal phenome accumulates proportionally to evolutionary time under a random walk.
2. Trend model: Suggests that disparity in skeletal phenome accumulates under BM with a directional drift.
3. Early burst model (EB): Suggests that disparity in skeletal phenome initially accumulates rapidly but declines over time.
4. Single optimum Ornstein-Uhlenbeck process model (OU1): Suggests that disparity in skeletal phenome is constrained or under selection to a single optimum over time.
5. Rate shift after the Eocene Oligocene Transition model ($BMBM_{EOT}$). Suggests that skeletal phenome exhibits two distinct evolutionary rates before and after the EOT 34 million years ago.
6. Rate shift after the Eocene Oligocene Transition model ($BMBM_{MMCT}$). Suggests that skeletal phenome exhibits two distinct evolutionary rates before and after the MMCT 17 million years ago.
7. Release and radiate after the Eocene Oligocene Transition model ($OUBMi_{EOT}$). Suggests that skeletal phenomes are constricted in ancestral carnivorans via an OU model due to extrinsic factors associated with the EOT 34 million years ago, followed by the increased skeletal disparity after the release from these factors via BM.

8. Release and radiate after the Mid-Miocene Climate Transition ($OUBMi_{MCCT}$). Similar as above. 17 Ma was used as the time point that OU shifts to BM.
9. Stepwise optimal shift model (sOU2): Suggests that carnivorans and its stem relatives exhibit separate skeletal phenomic optima via a two-peak OU model.
10. Stepwise optimal shift model (sOU3): Suggests that carnivorans, stem carnivoramorph relatives, and stem pan-carnivoran relatives exhibit separate skeletal phenomic optima via a three-peak OU model.
11. Clade optimal shift model (cOU3): Suggests that feliforms and caniforms exhibit separate skeletal phenomic optima after an initial optimal shift from stem relatives via a three-peak OU model.
12. Clade optimal shift model (cOU4): Suggests that feliforms and caniforms exhibit separate skeletal phenomic optima after initial optimal shifts from stem carnivoramorph relatives and stem pan-carnivoran via a four-peak OU model.

All models were fit to skeletal phenome, skeletal size, and each skeletal component datasets using the R package mvMORPH v1.1.7 (84). Optimal shifts in the sOU and cOU models were specified on the phylogeny using the paintSubTree function in the R package phytools v2.4.4 (85). Relative support for each of the 12 models was assessed through computation of small sample-corrected Akaike weights (AICcW).

Lastly, we assessed whether we had adequate power to accurately distinguish between complex models from Brownian motion using simulations (86). We generated 500 simulations for all datasets using the parameter estimates of the best-supported model(s) from the empirical datasets. We then ran each set of simulated data through all 12 models to determine whether the simulated model could be accurately recovered.

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Declaration of interests

The authors declare no competing interests

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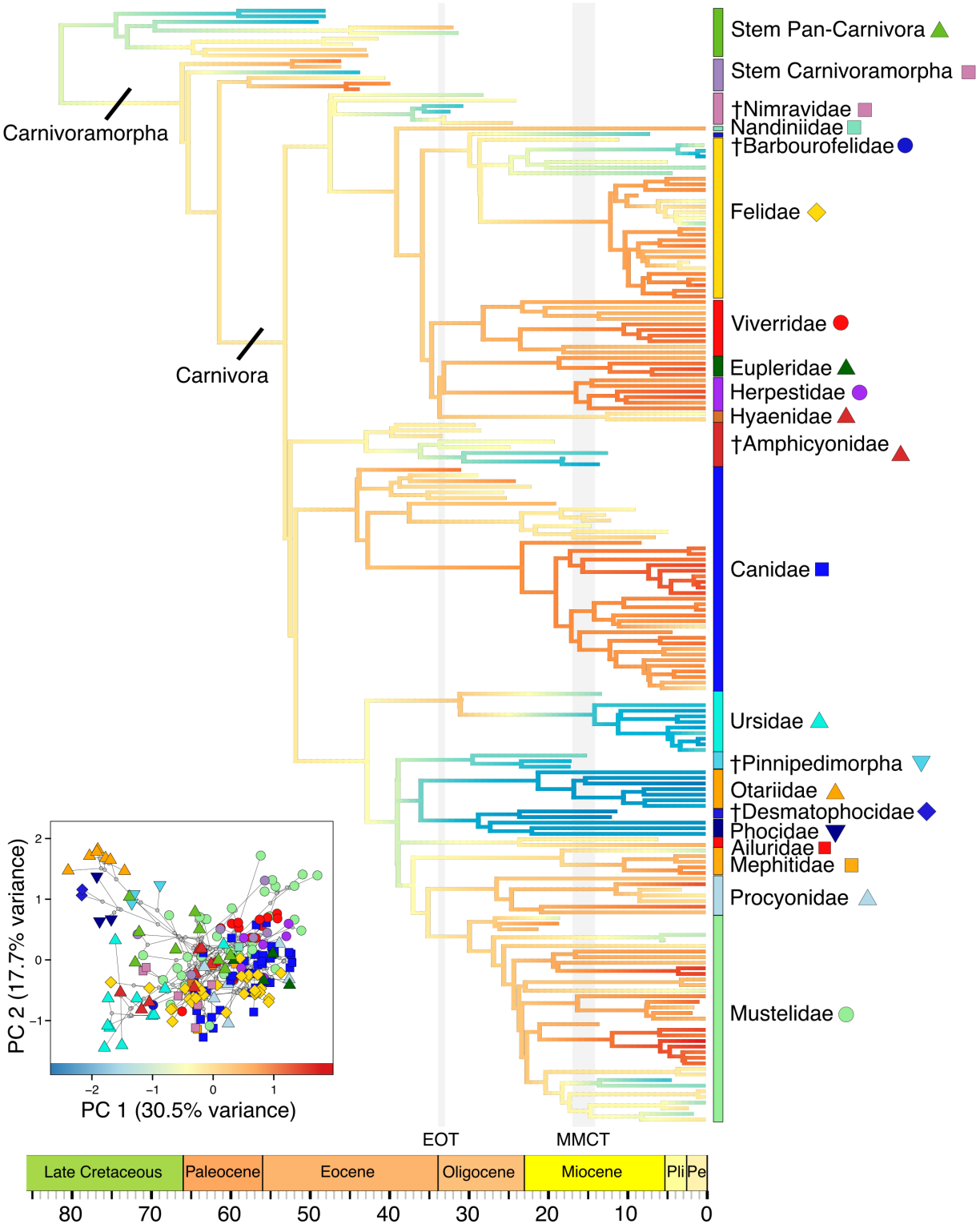

Fig. 1. Pruned pan-carnivoran phylogeny with ancestral reconstruction of PC 1 of skeletal phenome, calculated from all 103 size-corrected skeletal traits.

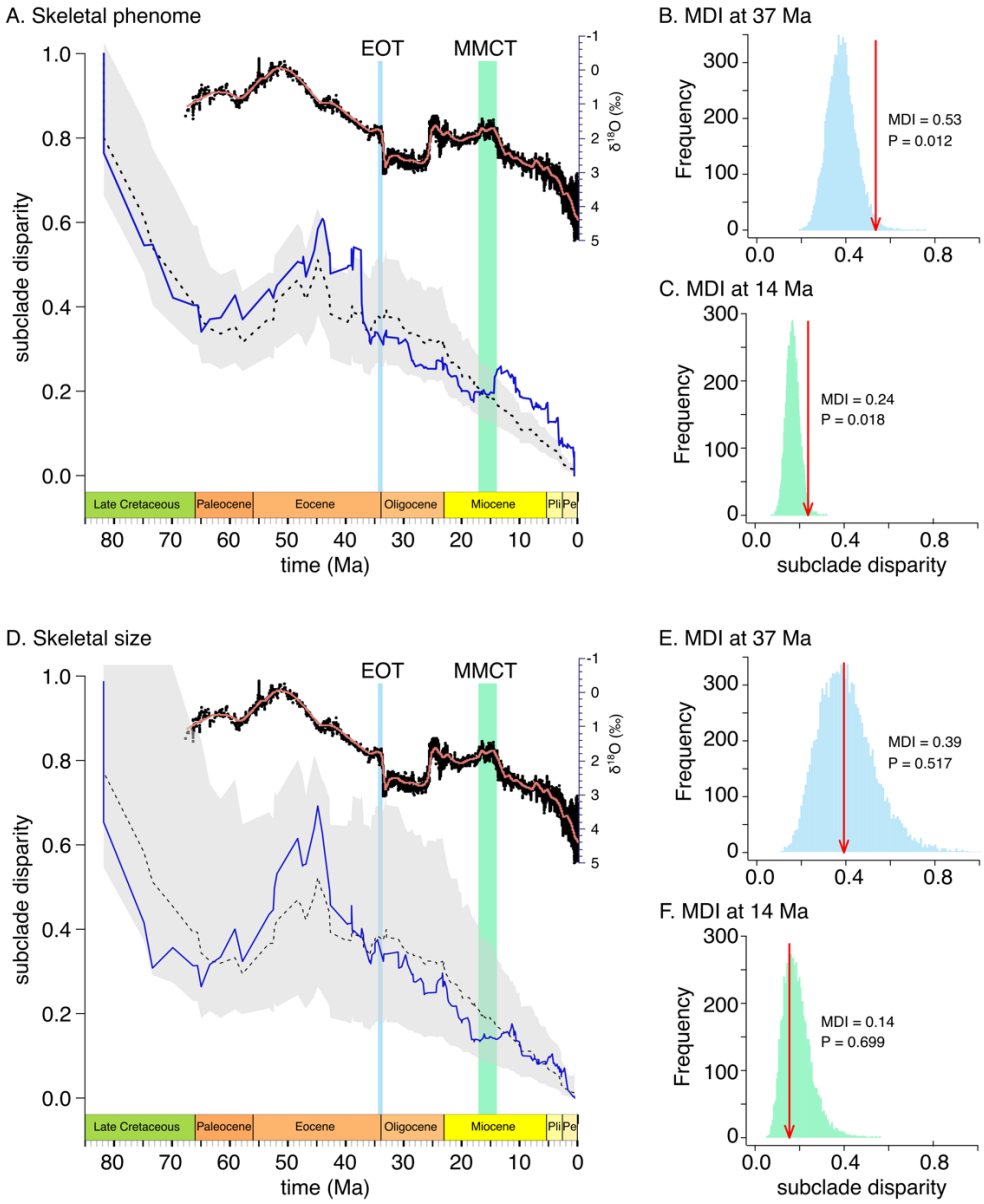

Fig. 2. Disparity-through-time plots of carnivoran skeletal phenome and size. (A) Skeletal phenome deviates from Brownian motion near the Eocene-Oligocene Transition (EOT) and Mid-Miocene Climate Transition (MMCT). Blue solid line indicates the empirical subclade DTT, and the dashed black line indicates the median DTT based on 10,000 simulations of trait evolution under Brownian motion. The grey shaded area indicates the 95% DTT range for the simulated data. Above the DTT is the global deep-sea oxygen isotope records as a proxy for global temperature change (modified from (4)). DTT suggests increased subclade disparity at two time points: (B) just prior to the EOT (~37 Ma; MDI = 0.534, P = 0.012) and (C) just after the MMCT (~14 Ma; MDI = 0.238, P = 0.018). For B. and C., histograms show the distribution of simulated subclade disparities and red arrows signify the empirical subclade disparities at time 37 Ma and

14 Ma, respectively. (D) Skeletal size does not deviate from Brownian motion across time and at (E) ~37 Ma and (F) ~14 Ma.

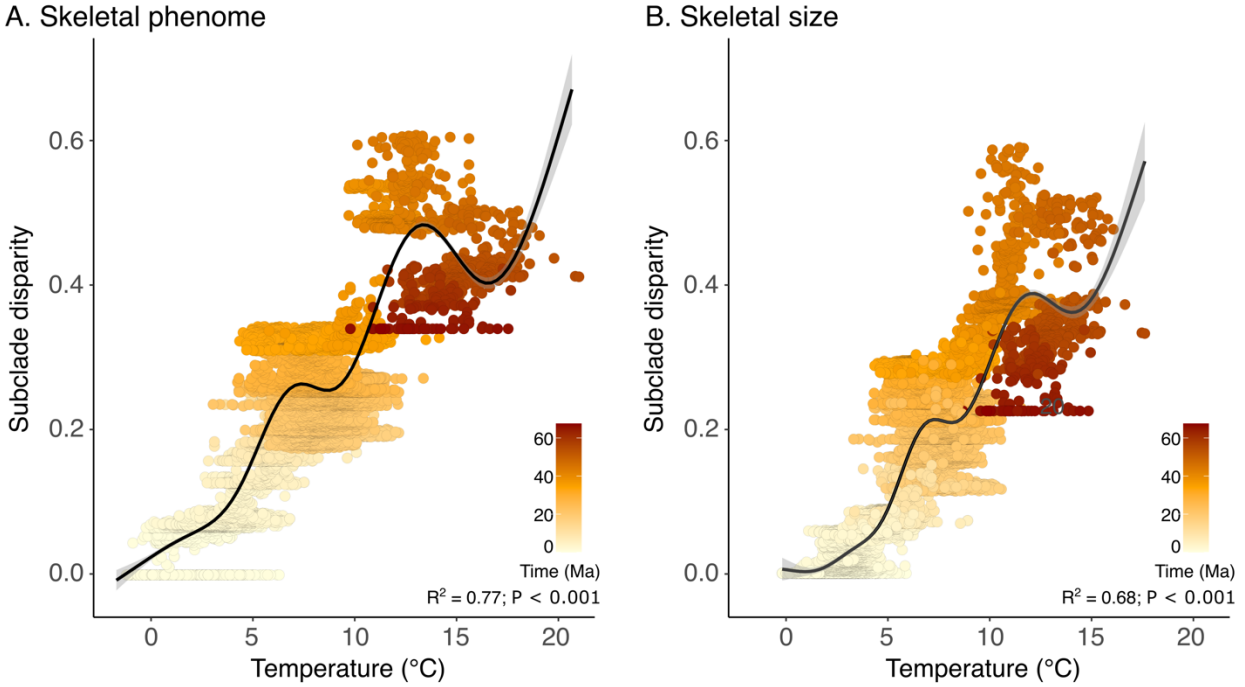

Fig 3. Subclade disparity in skeletal phenome and size tend to increase with higher temperatures during the past 65 million years. Black lines depict the smooth components produced by a generalized additive model (skeletal phoneme: EDF = 8.9; $R^2 = 0.77$; $P < 0.001$; skeletal size: EDF = 8.9; $R^2 = 0.68$; $P < 0.001$).

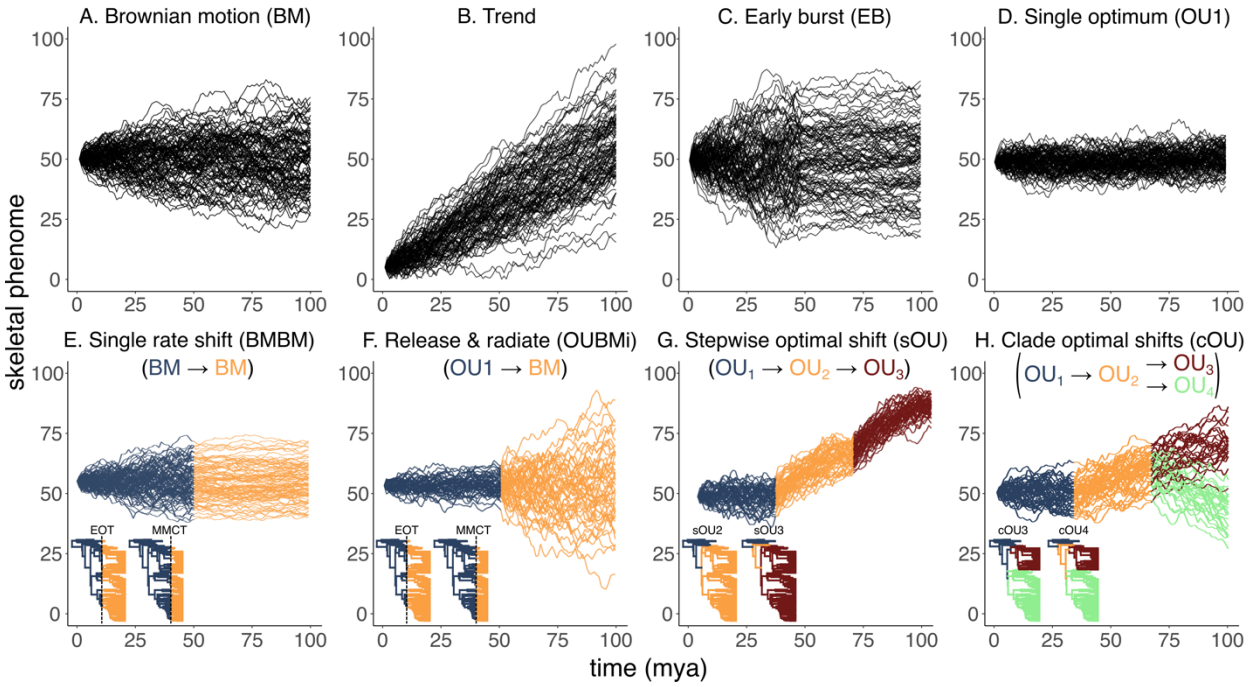

Fig. 4. Alternative hypotheses for the evolution of carnivoran skeletal phenomes. (A) Brownian motion. (B) Brownian motion with a directional drift. (C) Brownian motion with an evolutionary rate that increases or decreases exponentially through time. (D) Single optimum under an Ornstein-Uhlenbeck process. (E) Single rate shift after the Eocene-Oligocene Transition (EOT) or Mid-Miocene Climate Transition (MMCT). (F) Constrained evolution followed by unconstrained evolution after the EOT or MMCT. (G) Stepwise optimal shifts between carnivorans and its stem relatives (sOU2) or among carnivorans, stem carnivoramorphs, and stem pan-carnivorans (sOU3). (H) Stepwise optimal shifts followed by clade optimal shifts among caniforms, feliforms, and its stem relatives (cOU3) or among caniforms, feliforms, stem carnivoramorphs, and stem pan-carnivorans (cOU4).

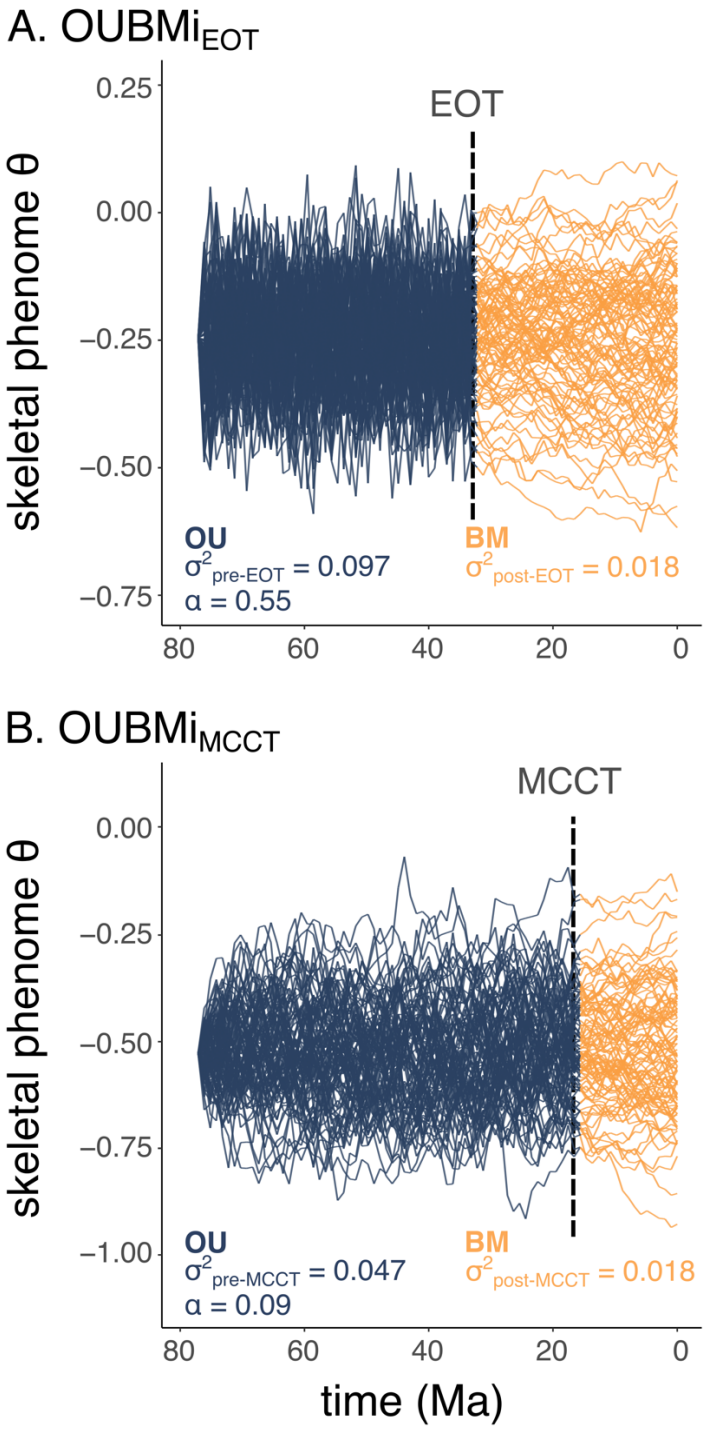

Fig. 5. Simulations of the parameter estimates of the best supported models for skeletal phenome. 100 simulations were used for visualization.

Table 1. Comparisons of the best-fitting evolutionary models for skeletal phenome and skeletal size. Rows in boldface type represent the best-fit model as indicated by the lowest ΔAICc score. ΔAICc = AICc minus the minimum AICc between models.

Trait	Model	AICc	ΔAICc	AICcW
skeletal phenome	BM1	983.37	26.39	0.00
	trend	980.33	23.34	0.00
	EB	985.48	28.50	0.00
	OU1	959.66	2.67	0.12
	$BMBMi_{EOT}$	979.31	22.32	0.00
	$BMBMi_{MMCT}$	980.06	23.07	0.00
	$OUBMi_{EOT}$	**956.98**	**0.00**	**0.45**
	$OUBMi_{MMCT}$	**957.11**	**0.13**	**0.42**
	sOU2	966.30	9.31	0.00
	sOU3	982.31	25.33	0.00
	cOU3	971.46	14.48	0.00
	cOU4	986.42	29.44	0.00
skeletal size	BM1	169.55	6.85	0.02
	trend	167.45	4.75	0.07
	EB	171.61	8.91	0.01
	OU1	171.17	8.47	0.01
	$BMBMi_{EOT}$	168.31	5.61	0.05
	$BMBMi_{MMCT}$	171.14	8.44	0.01
	$OUBMi_{EOT}$	167.92	5.22	0.06
	$OUBMi_{MMCT}$	**162.70**	**0.00**	**0.76**
	sOU2	171.96	9.26	0.01
	sOU3	173.90	11.20	0.00
	cOU3	173.77	11.07	0.00
	cOU4	175.85	13.15	0.00

Supporting Information for

Long-fuse evolution of carnivoran skeletal phenomes through the Cenozoic

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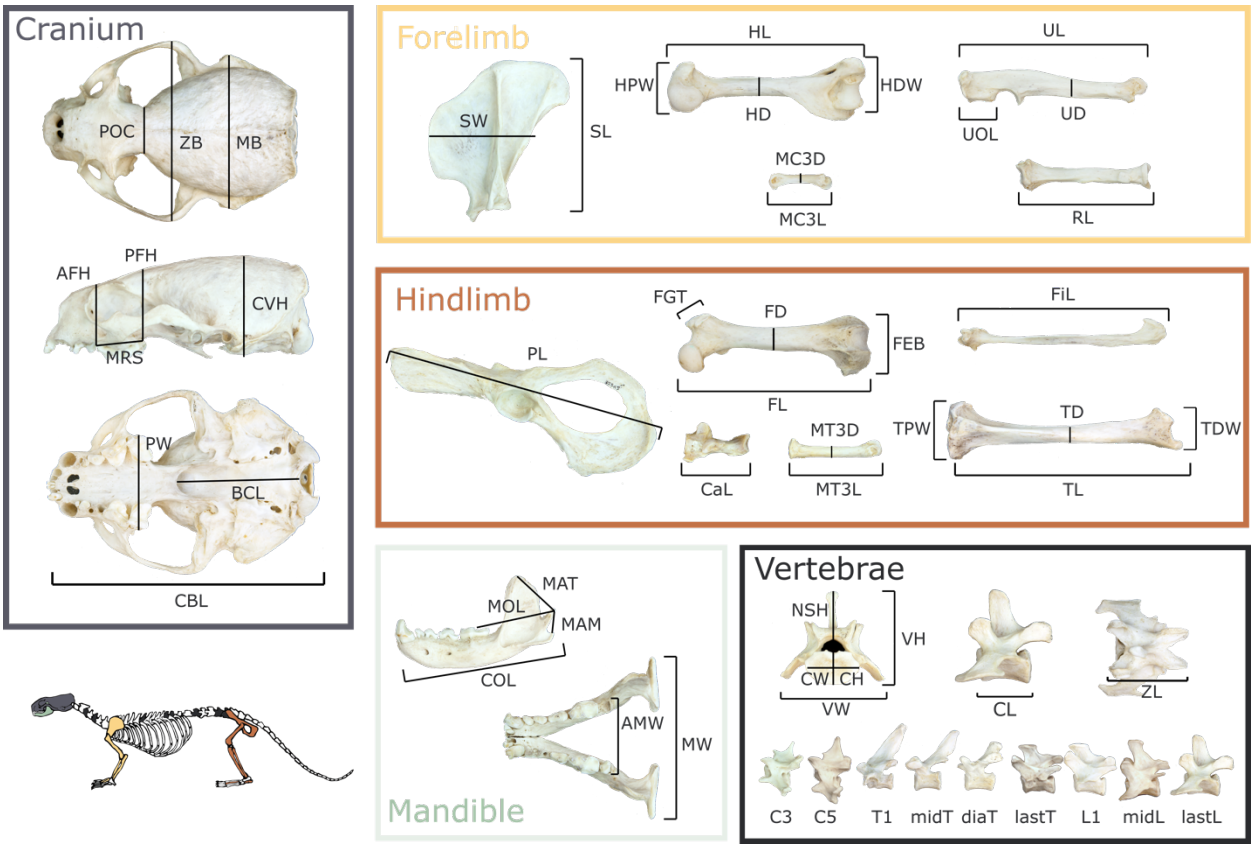

Fig. S1. Skeletal trait measurements used in this study. *Cranium*: CBL = condylobasal length, POC = postorbital constriction breadth, ZB = zygomatic breadth, MB = mastoid breadth, AFH = anterior facial height, PFH = posterior facial height, CVH = cranial vault height, PW = palate width, BCL = basicranial length. *Mandible*: MAT = moment arm of temporalis, MAM = moment arm of masseter, MAM2 = moment arm of masseter; MOL = molar out-lever; COL = canine out-lever; MW = mandibular width; AMW = anterior mandibular width. *Forelimb*: SL = scapula length; SW = scapula width; HL = humerus length; HD = humerus mid-shaft width; HPW = humerus proximal width; HDW = humerus distal width; UL = ulna length; UD = ulna mid-shaft width; UOL = ulnar olecranon length; RL = radius length; RD = radius mid-shaft width; MC3L = third metacarpel length; MC3W = third metacarpel width. *Hindlimb*: PL = pelvis length; FL = femur length; FD = femur mid-shaft width; FEB = femur distal width; FGT = height of the greater trochanter of the femur; TL = tibia length; TD = tibia mid-shaft width; TPW = tibia proximal width; TDW = tibia distal width; FiL = fibula length; CaL = calcaneus length; MT3L = third metatarsal length; MT3D = third metatarsal width. *Vertebrae*: VW = vertebrae width; VH = vertebrae height; CL = centrum length; CW = centrum width (posterior); CH = centrum height (posterior); ZL = inter-zygapophyseal length; NSH = neural spine height.

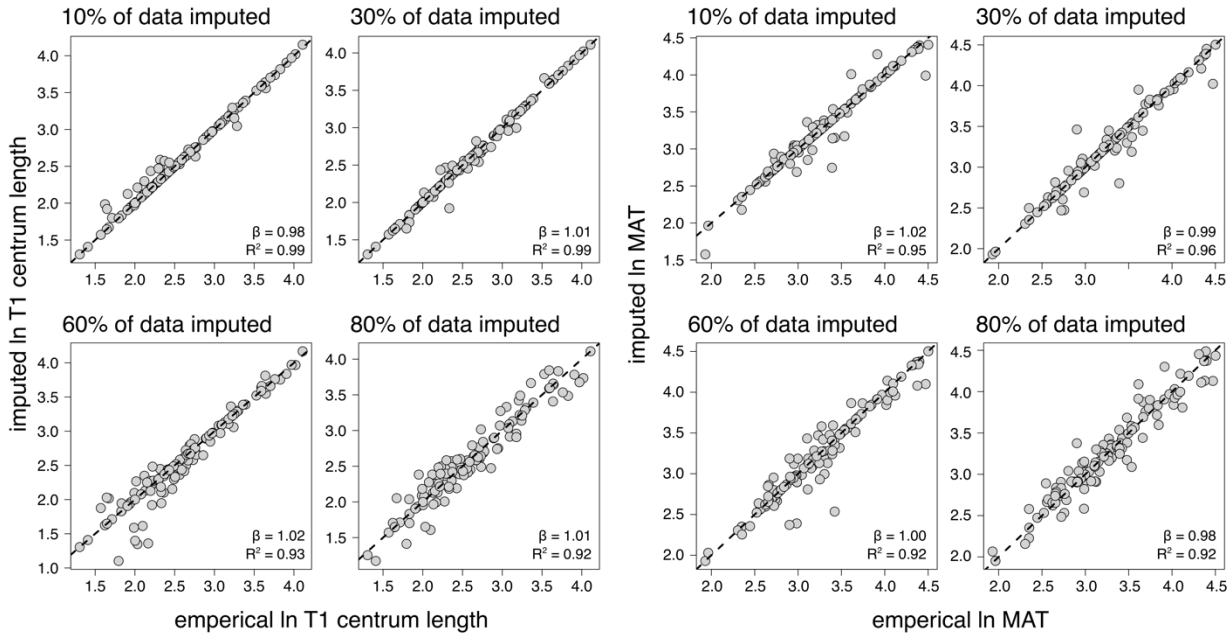

Fig. S2. Relationships between imputed and empirical trait values to assess the quality of trait MIPCA imputation. Assessments were performed using a subset of species (n = 192) that contain all 103 measured traits and randomly removing different percentages (10%, 30%, 60%, and 80%) of trait measurements. MIPCA was used to impute these removed traits, and reduced major axis regression models were used to test the relationship between imputed traits and empirical traits. Black dashed line indicates the 1:1 line. β = slope obtained from RMA models. T1 = first thoracic vertebrae. MAT = moment arm of the temporalis muscle.

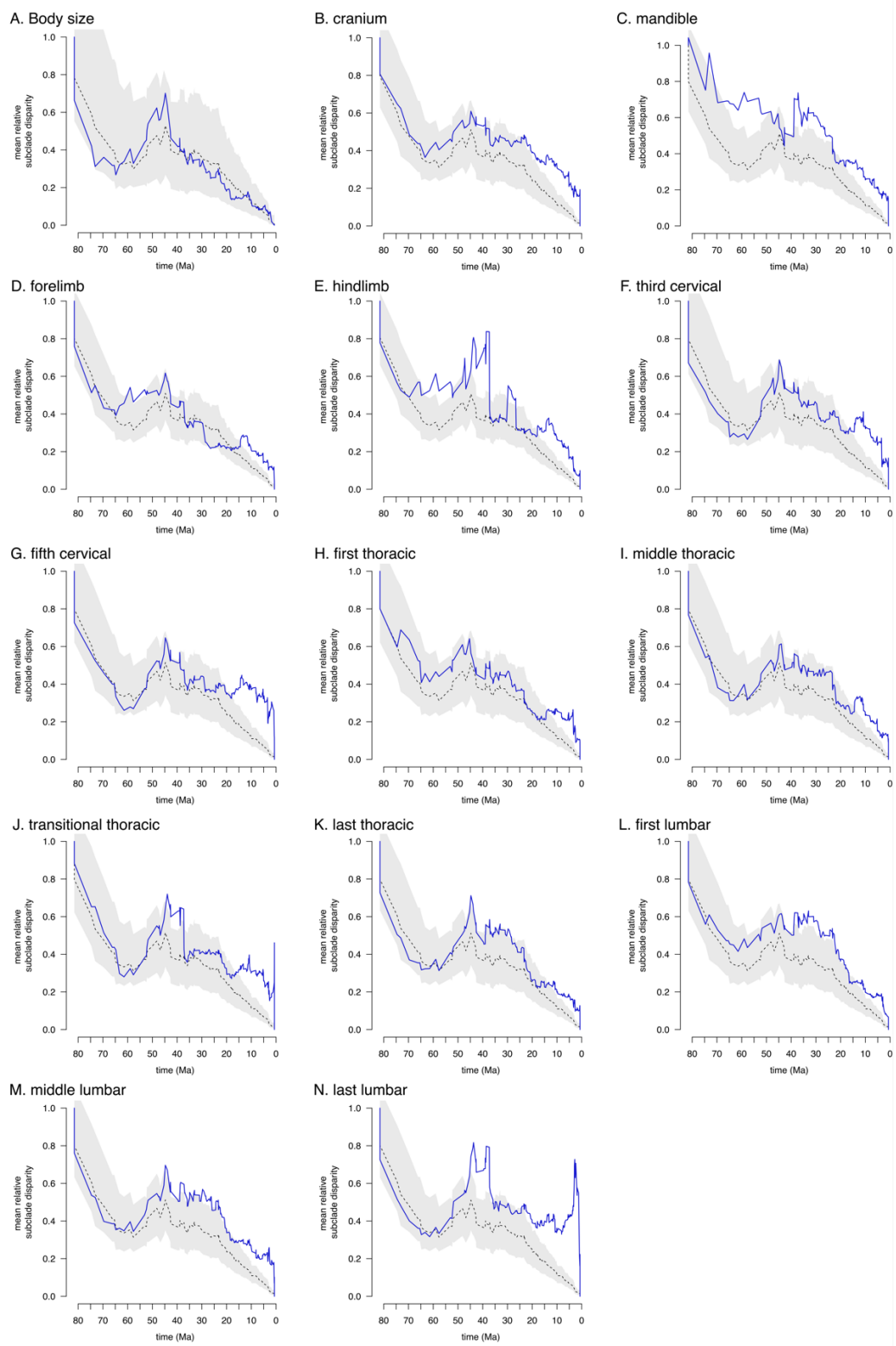

Fig. S3. Disparity through time plots of skeletal components. Blue solid line indicates the empirical subclade DTT, and the dashed black line indicates the median DTT based on 10,000 simulations of trait evolution under Brownian motion. The grey shaded area indicates the 95% DTT range for the simulated data.

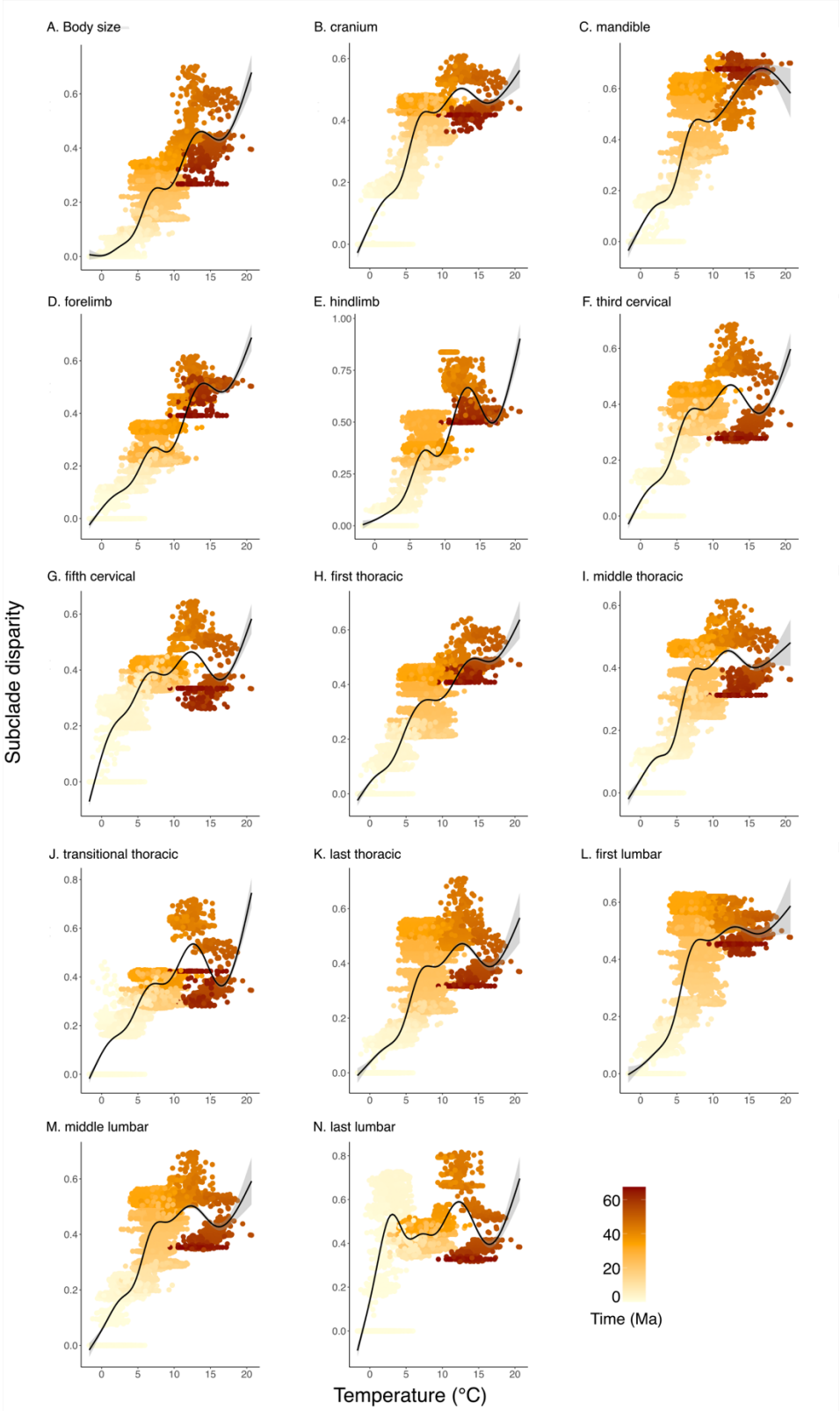

Fig. S4. Relationships between subclade disparity in skeletal components and temperatures during the past 65 million years. Black lines depict the smooth components produced by generalized additive models.

Table S1. Specimens and museum catalog numbers used in this study. AMNH = American Museum of Natural History; CAS = California Academy of Sciences; FMNH = Field Museum of Natural History; JODA = John Day Fossil Beds National Monument; LACM = Natural History Museum of Los Angeles County; MVZ = Museum of Vertebrate Zoology; NHMUK = Natural History Museum, London; SDNHM = San Diego Natural History Museum; TxVP = Texas Vertebrate Paleontology Collection; UCMP = UC Berkeley Museum of Palenotology; UNSM = University of Nebraska State Museum; USNM = National Museum of Natural History; UWBM = Burke Museum of Natural History and Culture; YPM = Yale Peabody Museum

clade	family	species	status	catalog
Carnivora	Nandiniidae	*Nandinia_binotata*	extant	AMNH239582
Carnivora	Nandiniidae	*Nandinia_binotata*	extant	FMNH161266
Carnivora	Nandiniidae	*Nandinia_binotata*	extant	FMNH224514
Carnivora	Felidae	*Acinonyx_jubatus*	extant	AMNH119654
Carnivora	Felidae	*Caracal_aurata*	extant	AMNH51994
Carnivora	Felidae	*Caracal_caracal*	extant	USNM520686
Carnivora	Felidae	*Felis_chaus*	extant	AMNH238649
Carnivora	Felidae	*Felis_chaus*	extant	FMNH97867
Carnivora	Felidae	*Felis_silvestris*	extant	NHMUK1953.6.11.1
Carnivora	Felidae	*Herpailurus_yagouaroundi*	extant	AMNH215137
Carnivora	Felidae	*Herpailurus_yagouaroundi*	extant	FMNH69647
Carnivora	Felidae	*Leopardus_geoffroyi*	extant	AMNH205910
Carnivora	Felidae	*Leopardus_geoffroyi*	extant	AMNH205911
Carnivora	Felidae	*Leopardus_pardalis*	extant	AMNH133959
Carnivora	Felidae	*Leptailurus_serval*	extant	FMNH127843
Carnivora	Felidae	*Lynx_canadensis*	extant	MVZ184071
Carnivora	Felidae	*Lynx_canadensis*	extant	UWBM80612
Carnivora	Felidae	*Lynx_canadensis*	extant	UWBM82238

Carnivora	Felidae	*Lynx_rufus*	extant	UWBM32042
Carnivora	Felidae	*Lynx_rufus*	extant	UWBM32046
Carnivora	Felidae	*Lynx_rufus*	extant	UWBM75808
Carnivora	Felidae	*Otocolobus_manul*	extant	UWBM35449
Carnivora	Felidae	*Panthera_leo*	extant	AMNH52078
Carnivora	Felidae	*Panthera_onca*	extant	AMNH139959
Carnivora	Felidae	*Panthera_onca*	extant	FMNH70566
Carnivora	Felidae	*Panthera_pardus*	extant	AMNH113745
Carnivora	Felidae	*Panthera_tigris*	extant	AMNH54460
Carnivora	Felidae	*Prionailurus_bengalensis*	extant	FMNH62888
Carnivora	Felidae	*Prionailurus_bengalensis*	extant	USNM196601
Carnivora	Felidae	*Prionailurus_viverrinus*	extant	AMNH70128
Carnivora	Felidae	*Puma_concolor*	extant	UWBM32105
Carnivora	Felidae	*Puma_concolor*	extant	UWBM35217
Carnivora	Viverridae	*Arctictis_binturong*	extant	FMNH98270
Carnivora	Viverridae	*Arctictis_binturong*	extant	UWBM81977
Carnivora	Viverridae	*Arctogalidia_trivirgata*	extant	NHMUK1971.3072
Carnivora	Viverridae	*Civettictis_civetta*	extant	AMNH51797
Carnivora	Viverridae	*Genetta_genetta*	extant	AMNH187721
Carnivora	Viverridae	*Genetta_genetta*	extant	AMNH187725
Carnivora	Viverridae	*Genetta_genetta*	extant	AMNH187740
Carnivora	Viverridae	*Genetta_maculata*	extant	AMNH216345
Carnivora	Viverridae	*Genetta_maculata*	extant	FMNH17550

Carnivora	Viverridae	*Genetta_servalina*	extant	AMNH150447
Carnivora	Viverridae	*Genetta_servalina*	extant	FMNH145228
Carnivora	Viverridae	*Genetta_servalina*	extant	FMNH145230
Carnivora	Viverridae	*Genetta_victoriae*	extant	AMNH51406
Carnivora	Viverridae	*Paguma_larvata*	extant	UWBM73281
Carnivora	Viverridae	*Paguma_larvata*	extant	NHMUK1980.867
Carnivora	Viverridae	*Paradoxurus_hermaphroditus*	extant	MVZ186573
Carnivora	Viverridae	*Viverra_zibetha*	extant	AMNH113482
Carnivora	Viverridae	*Viverra_zibetha*	extant	FMNH104395
Carnivora	Hyaenidae	*Crocuta_crocuta*	extant	AMNH147880
Carnivora	Hyaenidae	*Crocuta_crocuta*	extant	AMNH187769
Carnivora	Hyaenidae	*Hyaena_hyaena*	extant	USNM329351
Carnivora	Eupleridae	*Cryptoprocta_ferox*	extant	NHMU1938.11.16.1
Carnivora	Eupleridae	*Galidia_elegans*	extant	FMNH151925
Carnivora	Eupleridae	*Galidia_elegans*	extant	FMNH156651
Carnivora	Eupleridae	*Galidictis_fasciata*	extant	FMNH162111
Carnivora	Eupleridae	*Mungotictis_decemlineata*	extant	FMNH176128
Carnivora	Herpestidae	*Atilax_paludinosus*	extant	LACM053753
Carnivora	Herpestidae	*Galerella_pulverulenta*	extant	CAS28740
Carnivora	Herpestidae	*Herpestes_edwardsii*	extant	USNM329348
Carnivora	Herpestidae	*Herpestes_ichneumon*	extant	AMNH187746
Carnivora	Herpestidae	*Herpestes_sanguineus*	extant	AMNH51019
Carnivora	Herpestidae	*Ichneumia_albicauda*	extant	AMNH216353

Carnivora	Herpestidae	*Ichneumia_albicauda*	extant	AMNH51594
Carnivora	Herpestidae	*Ichneumia_albicauda*	extant	TxVP12616
Carnivora	Canidae	*Canis_adustus*	extant	AMNH216344
Carnivora	Canidae	*Canis_aureus*	extant	AMNH54516
Carnivora	Canidae	*Canis_latrans*	extant	MVZ25553
Carnivora	Canidae	*Canis_latrans*	extant	MVZ83446
Carnivora	Canidae	*Canis_latrans*	extant	MVZ83447
Carnivora	Canidae	*Canis_lupus*	extant	MVZ44166
Carnivora	Canidae	*Canis_lupus*	extant	MVZ88225
Carnivora	Canidae	*Canis_mesomelas*	extant	AMNH34734
Carnivora	Canidae	*Canis_simensis*	extant	AMNH81001
Carnivora	Canidae	*Cerdocyon_thous*	extant	AMNH205807
Carnivora	Canidae	*Cerdocyon_thous*	extant	AMNH205811
Carnivora	Canidae	*Chrysocyon_brachyurus*	extant	AMNH133941
Carnivora	Canidae	*Cuon_alpinus*	extant	AMNH54984
Carnivora	Canidae	*Lycaon_pictus*	extant	AMNH82083
Carnivora	Canidae	*Lycaon_pictus*	extant	AMNH82085
Carnivora	Canidae	*Lycaon_pictus*	extant	FMNH127812
Carnivora	Canidae	*Otocyon_megalotis*	extant	LACM041790
Carnivora	Canidae	*Otocyon_megalotis*	extant	LACM041792
Carnivora	Canidae	*Pseudalopex_culpaeus*	extant	AMNH262663
Carnivora	Canidae	*Pseudalopex_gymnocercus*	extant	AMNH205777
Carnivora	Canidae	*Pseudalopex_gymnocercus*	extant	AMNH205778

Carnivora	Canidae	*Speothos_venaticus*	extant	FMNH125402
Carnivora	Canidae	*Urocyon_cinereoargenteus*	extant	MVZ225296
Carnivora	Canidae	*Urocyon_cinereoargenteus*	extant	MVZ236230
Carnivora	Canidae	*Urocyon_cinereoargenteus*	extant	UWBM13640
Carnivora	Canidae	*Urocyon_littoralis*	extant	LACM6391
Carnivora	Canidae	*Urocyon_littoralis*	extant	LACM6397
Carnivora	Canidae	*Urocyon_littoralis*	extant	SDNHM233389
Carnivora	Canidae	*Vulpes_chama*	extant	LACM041795
Carnivora	Canidae	*Vulpes_lagopus*	extant	MVZ206554
Carnivora	Canidae	*Vulpes_lagopus*	extant	UWBM82184
Carnivora	Canidae	*Vulpes_lagopus*	extant	UWBM82638
Carnivora	Canidae	*Vulpes_macrotis*	extant	MVZ206981
Carnivora	Canidae	*Vulpes_macrotis*	extant	MVZ224411
Carnivora	Canidae	*Vulpes_macrotis*	extant	MVZ224412
Carnivora	Canidae	*Vulpes_velox*	extant	LACM86858
Carnivora	Canidae	*Vulpes_velox*	extant	LACM86859
Carnivora	Canidae	*Vulpes_velox*	extant	LACM86862
Carnivora	Canidae	*Vulpes_vulpes*	extant	UWBM32532
Carnivora	Canidae	*Vulpes_vulpes*	extant	UWBM32533
Carnivora	Canidae	*Vulpes_vulpes*	extant	UWBM32534
Carnivora	Canidae	*Vulpes_zerda*	extant	FMNH89716
Carnivora	Ursidae	*Ailuropoda_melanoleuca*	extant	AMNH89028
Carnivora	Ursidae	*Helarctos_malayanus*	extant	USNM198713

Carnivora	Ursidae	*Melursus_ursinus*	extant	AMNH54467
Carnivora	Ursidae	*Ursus_americanus*	extant	UWBM33259
Carnivora	Ursidae	*Ursus_americanus*	extant	UWBM39060
Carnivora	Ursidae	*Ursus_arctos*	extant	MVZ4385
Carnivora	Ursidae	*Ursus_arctos*	extant	MVZ970
Carnivora	Ursidae	*Ursus_maritimus*	extant	AMNH100039
Carnivora	Otariidae	*Arctocephalus_galapagoensis*	extant	AMNH100341
Carnivora	Otariidae	*Arctocephalus_pusillus*	extant	AMNH81701
Carnivora	Otariidae	*Callorhinus_ursinus*	extant	USNM258588
Carnivora	Otariidae	*Eumetopias_jubatus*	extant	AMNH38400
Carnivora	Otariidae	*Otaria_byronia*	extant	USNM484912
Carnivora	Otariidae	*Phocarctos_hookeri*	extant	USNM484526
Carnivora	Otariidae	*Zalophus_californianus*	extant	UWBM32518
Carnivora	Phocidae	*Erignathus_barbatus*	extant	USNM500251
Carnivora	Phocidae	*Monachus_schauinslandi*	extant	USNM606271
Carnivora	Phocidae	*Pusa_hispida*	extant	SDNHM12214
Carnivora	Mephitidae	*Conepatus_leuconotus*	extant	AMNH136415
Carnivora	Mephitidae	*Conepatus_leuconotus*	extant	MVZ85319
Carnivora	Mephitidae	*Conepatus_leuconotus*	extant	TxVP10785
Carnivora	Mephitidae	*Mephitis_macroura*	extant	MVZ41133
Carnivora	Mephitidae	*Mephitis_macroura*	extant	MVZ85324
Carnivora	Mephitidae	*Mephitis_mephitis*	extant	MVZ198469
Carnivora	Mephitidae	*Mephitis_mephitis*	extant	MVZ38300

Carnivora	Mephitidae	*Mephitis_mephitis*	extant	UWBM26340
Carnivora	Mephitidae	*Spilogale_gracilis*	extant	MVZ39890
Carnivora	Mephitidae	*Spilogale_gracilis*	extant	MVZ90009
Carnivora	Mephitidae	*Spilogale_gracilis*	extant	UWBM38625
Carnivora	Mephitidae	*Spilogale_putorius*	extant	MVZ41127
Carnivora	Mephitidae	*Spilogale_putorius*	extant	MVZ41130
Carnivora	Mephitidae	*Spilogale_putorius*	extant	MVZ99980
Carnivora	Ailuridae	*Ailurus_fulgens*	extant	UWBM39029
Carnivora	Ailuridae	*Ailurus_fulgens*	extant	UWBM76122
Carnivora	Procyonidae	*Bassaricyon_neblina*	extant	FMNH70726
Carnivora	Procyonidae	*Bassariscus_astutus*	extant	MVZ191007
Carnivora	Procyonidae	*Bassariscus_astutus*	extant	MVZ44099
Carnivora	Procyonidae	*Bassariscus_astutus*	extant	UWBM34131
Carnivora	Procyonidae	*Nasua_narica*	extant	FMNH129310
Carnivora	Procyonidae	*Nasua_nasua*	extant	AMNH214716
Carnivora	Procyonidae	*Nasua_nasua*	extant	AMNH214718
Carnivora	Procyonidae	*Nasua_nasua*	extant	AMNH255871
Carnivora	Procyonidae	*Potos_flavus*	extant	USNM449468
Carnivora	Procyonidae	*Procyon_lotor*	extant	CAS703
Carnivora	Procyonidae	*Procyon_lotor*	extant	LACM052204
Carnivora	Procyonidae	*Procyon_lotor*	extant	UWBM35531
Carnivora	Mustelidae	*Aonyx_capensis*	extant	MVZ226937
Carnivora	Mustelidae	*Aonyx_congicus*	extant	MVZ19210

Carnivora	Mustelidae	*Eira_barbara*	extant	FMNH69585
Carnivora	Mustelidae	*Eira_barbara*	extant	FMNH69586
Carnivora	Mustelidae	*Eira_barbara*	extant	MVZ153647
Carnivora	Mustelidae	*Enhydra_lutris*	extant	MVZ140630
Carnivora	Mustelidae	*Enhydra_lutris*	extant	MVZ486320
Carnivora	Mustelidae	*Enhydra_lutris*	extant	UWBM34543
Carnivora	Mustelidae	*Galictis_vittata*	extant	USNM395079
Carnivora	Mustelidae	*Gulo_gulo*	extant	FMNH57196
Carnivora	Mustelidae	*Gulo_gulo*	extant	MVZ184099
Carnivora	Mustelidae	*Gulo_gulo*	extant	MVZ22121
Carnivora	Mustelidae	*Lontra_canadensis*	extant	UWBM32230
Carnivora	Mustelidae	*Lontra_canadensis*	extant	UWBM32242
Carnivora	Mustelidae	*Lontra_canadensis*	extant	UWBM81969
Carnivora	Mustelidae	*Lontra_felina*	extant	MVZ141632
Carnivora	Mustelidae	*Lutra_lutra*	extant	FMNH99384
Carnivora	Mustelidae	*Martes_americana*	extant	UWBM33272
Carnivora	Mustelidae	*Martes_americana*	extant	UWBM33278
Carnivora	Mustelidae	*Martes_americana*	extant	UWBM33279
Carnivora	Mustelidae	*Martes_martes*	extant	AMNH183359
Carnivora	Mustelidae	*Meles_meles*	extant	AMNH70604
Carnivora	Mustelidae	*Meles_meles*	extant	NHMUK2002.476
Carnivora	Mustelidae	*Meles_meles*	extant	NHMUK2006.551
Carnivora	Mustelidae	*Mellivora_capensis*	extant	USNM96107

Carnivora	Mustelidae	*Melogale_moschata*	extant	NHMUK2004.20
Carnivora	Mustelidae	*Melogale_personata*	extant	USNM357537
Carnivora	Mustelidae	*Mustela_erminea*	extant	UWBM33273
Carnivora	Mustelidae	*Mustela_erminea*	extant	UWBM56648
Carnivora	Mustelidae	*Mustela_erminea*	extant	UWBM57518
Carnivora	Mustelidae	*Mustela_frenata*	extant	UWBM31872
Carnivora	Mustelidae	*Mustela_frenata*	extant	UWBM39154
Carnivora	Mustelidae	*Mustela_frenata*	extant	UWBM82713
Carnivora	Mustelidae	*Mustela_nigripes*	extant	FMNH88607
Carnivora	Mustelidae	*Mustela_nigripes*	extant	MVZ78134
Carnivora	Mustelidae	*Mustela_nivalis*	extant	MVZ143796
Carnivora	Mustelidae	*Mustela_nivalis*	extant	UWBM30001
Carnivora	Mustelidae	*Mustela_putorius*	extant	LACM31087
Carnivora	Mustelidae	*Mustela_sibirica*	extant	USNM239584
Carnivora	Mustelidae	*Mustela_vison*	extant	UWBM41783
Carnivora	Mustelidae	*Mustela_vison*	extant	UWBM41784
Carnivora	Mustelidae	*Mustela_vison*	extant	UWBM41791
Carnivora	Mustelidae	*Pekania_pennanti*	extant	UWBM34568
Carnivora	Mustelidae	*Pekania_pennanti*	extant	UWBM77855
Carnivora	Mustelidae	*Pekania_pennanti*	extant	UWBM81034
Carnivora	Mustelidae	*Poecilogale_albinucha*	extant	FMNH177235
Carnivora	Mustelidae	*Poecilogale_albinucha*	extant	FMNH177236
Carnivora	Mustelidae	*Pteronura_brasiliensis*	extant	NHMUK1939.3.4.1

Carnivora	Mustelidae	*Pteronura_brasiliensis*	extant	AMNH30190
Carnivora	Mustelidae	*Taxidea_taxus*	extant	MVZ218236
Carnivora	Mustelidae	*Taxidea_taxus*	extant	MVZ41454
Carnivora	Mustelidae	*Taxidea_taxus*	extant	UWBM34281
Carnivora	Felidae	*Amphimachairodus_coloradensis*	extinct	TxVP41261-8
Carnivora	Felidae	*Puma_pardoides*	extinct	YPM031526
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec

Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP_unspec
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP933-1
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP933-3444
Carnivora	Felidae	*Homotherium_serum*	extinct	TxVP933-3582
Carnivora	Felidae	*Hyperailurictis_marshi*	extinct	YPM012865
Carnivora	Felidae	*Lynx_longignathus*	extinct	SDNHM68691
Carnivora	Felidae	*Nimravides_catacopsis*	extinct	AMNH104044
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec

Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec

Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
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Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec

Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
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Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
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Carnivora	Felidae	*Panthera_atrox*	extinct	LACM_unspec
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Carnivora	Felidae	*Panthera_atrox*	extinct	LACM2900-8
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM2900-9
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM599
Carnivora	Felidae	*Panthera_atrox*	extinct	LACM65
Carnivora	Felidae	*Panthera_atrox*	extinct	LACMcompile
Carnivora	Felidae	*Smilodon_fatalis*	extinct	LACM_unspec
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Carnivora	Felidae	*Smilodon_fatalis*	extinct	LACM_unspec
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Carnivora	Felidae	*Smilodon_fatalis*	extinct	LACM1359
Carnivora	Felidae	*Smilodon_fatalis*	extinct	LACM186
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF226962
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF226963
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF226991
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF226994
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF80088
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF80162
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF81154
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF81294
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF81724
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF84411
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF86330
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF87239
Carnivora	Felidae	*Smilodon_gracilis*	extinct	UF_unspecified
Carnivora	Felidae	*Smilodon_populator*	extinct	FMNH-P14271
Carnivora	Felidae	*Smilodon_populator*	extinct	FMNH-P14294
Carnivora	Canidae	*Aelurodon_ferox*	extinct	AMNH_unspec
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM46630
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM76624
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM76625

Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM76631
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM83898
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM83910
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM83916
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM83917
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM83923
Carnivora	Canidae	*Aelurodon_ferox*	extinct	UNSM83929
Carnivora	Canidae	*Aelurodon_ferox*	extinct	USNM539
Carnivora	Canidae	*Aelurodon_ferox*	extinct	YPM010057
Carnivora	Canidae	*Aelurodon_mcgrewi*	extinct	AMNH22410
Carnivora	Canidae	*Aelurodon_stirtoni*	extinct	UNSM25789
Carnivora	Canidae	*Aenocyon_dirus*	extinct	LACM_unspec
Carnivora	Canidae	*Aenocyon_dirus*	extinct	LACM_unspec
Carnivora	Canidae	*Aenocyon_dirus*	extinct	LACM_unspec
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Carnivora	Canidae	*Aenocyon_dirus*	extinct	LACM_unspec
Carnivora	Canidae	*Aenocyon_dirus*	extinct	LACM_unspec
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Carnivora	Canidae	*Aenocyon_dirus*	extinct	LACM_unspec
Carnivora	Canidae	*Aenocyon_dirus*	extinct	LACMcompile
Carnivora	Canidae	*Canis_edwardii*	extinct	AMNH63100
Carnivora	Canidae	*Enhydrocyon_stenocephalus*	extinct	JODA6222
Carnivora	Canidae	*Epicyon_haydeni*	extinct	UCMP29638
Carnivora	Canidae	*Epicyon_saevus*	extinct	AMNH8305
Carnivora	Canidae	*Eucyon_davisi*	extinct	UO3241

Carnivora	Canidae	*Hesperocyon_gregarius*	extinct	FMNH-UC1405
Carnivora	Canidae	*Hesperocyon_gregarius*	extinct	FMNH-UC1417
Carnivora	Canidae	*Hesperocyon_gregarius*	extinct	FMNH-UC495
Carnivora	Canidae	*Hesperocyon_gregarius*	extinct	UNSM133290
Carnivora	Canidae	*Hesperocyon_gregarius*	extinct	UNSM25701
Carnivora	Canidae	*Hesperocyon_gregarius*	extinct	YPM010068
Carnivora	Canidae	*Leptocyon_vafer*	extinct	UNSM51949
Carnivora	Canidae	*Leptocyon_vafer*	extinct	UNSM51950
Carnivora	Canidae	*Mesocyon_brachyops*	extinct	UO4351
Carnivora	Canidae	*Mesocyon_coryphaeus*	extinct	USNM552
Carnivora	Canidae	*Mesocyon_coryphaeus*	extinct	YPM011163
Carnivora	Canidae	*Mesocyon_coryphaeus*	extinct	
Carnivora	Canidae	*Paraenhydrocyon_josephi*	extinct	JODA761
Carnivora	Canidae	*Paraenhydrocyon_josephi*	extinct	YPM012702
Carnivora	Canidae	*Phlaocyon_multicuspus*	extinct	
Carnivora	Canidae	*Protocyon_troglodytes*	extinct	UF27889
Carnivora	Canidae	*Sunkahetanka_geringensis*	extinct	YPM013602
Carnivora	Canidae	*Tephrocyon_rurestris*	extinct	UO24191
Carnivora	Ursidae	*Arctodus_pristinus*	extinct	UF322971
Carnivora	Ursidae	*Arctodus_pristinus*	extinct	UF40089
Carnivora	Ursidae	*Arctodus_simus*	extinct	USNM521336
Carnivora	Ursidae	*Arctodus_simus*	extinct	YPM055748
Carnivora	Ursidae	*Plithocyon_ursinus*	extinct	AMNH21101

Carnivora	Ursidae	*Plithocyon_ursinus*	extinct	YPM012915
Carnivora	Ursidae	*Tremarctos_floridanus*	extinct	UF133299
Carnivora	12Phocidae	*Pteronarctos_goedertae*	extinct	UO35536
Carnivora	12Phocidae	*Pteronarctos_piersoni*	extinct	UO35535
Carnivora	14Ailuridae	*Simocyon_primigenius*	extinct	YPM011649
Carnivora	Procyonidae	*Cyonasua_brevirostris*	extinct	FMNH-P14342
Carnivora	Procyonidae	*Cyonasua_brevirostris*	extinct	FMNH-P14537
Carnivora	Mustelidae	*Enhydrictis_ardea*	extinct	YPM031529
Carnivora	Mustelidae	*Enhydritherium_terraenovae*	extinct	UF100000
Carnivora	Mustelidae	*Satherium_ingens*	extinct	UO11837
Carnivora	Mustelidae	*Megalictis_ferox*	extinct	FMNH12154
Carnivora	Mustelidae	*Promartes_olcotti*	extinct	FMNH14055
Carnivora	Mustelidae	*Promartes_olcotti*	extinct	FMNH15178
Carnivora	Mustelidae	*Satherium_piscinarium*	extinct	USNM23266
Carnivora	Mustelidae	*Sthenictis_dolichops*	extinct	AMNH25235
Carnivora	Mustelidae	*Taxidea_mexicana*	extinct	LACM_CIT3532
Carnivora	Mustelidae	*Trigonictis_cookii*	extinct	UO16352
Carnivora	Mustelidae	*Trigonictis_macrodon*	extinct	UF234500
Carnivora	Mustelidae	*Trigonictis_macrodon*	extinct	UO16351
Carnivora	Mustelidae	*Zodiolestes_daimonelixensis*	extinct	FMNH12032
Carnivora	Amphicyonidae	*Amphicyon_ingens*	extinct	AMNH
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec

Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF_unspec
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF162716
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF201000
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF211501
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF254770
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF260014
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF299539
Carnivora	Amphicyonidae	*Crassidia_intermedia*	extinct	UF6501
Carnivora	Amphicyonidae	*Brachyrhynchocyon_dodgei*	extinct	USNM17847
Carnivora	Amphicyonidae	*Brachyrhynchocyon_dodgei*	extinct	YPM024612
Carnivora	Amphicyonidae	*Cynelos_sinapius*	extinct	AMNH9356
Carnivora	Amphicyonidae	*Daphoenus_hartshornianus*	extinct	UF207948
Carnivora	Amphicyonidae	*Daphoenus_hartshornianus*	extinct	UNSM25785
Carnivora	Amphicyonidae	*Daphoenus_hartshornianus*	extinct	YPM011421

Carnivora	Amphicyonidae	*Daphoenus_vetus*	extinct	FMNH-P12021
Carnivora	Amphicyonidae	*Daphoenus_vetus*	extinct	YPM013580
Carnivora	Amphicyonidae	*Daphoenus_vetus*	extinct	YPM013792
Carnivora	Amphicyonidae	*Daphoenus_vetus*	extinct	USNM17842
Carnivora	Amphicyonidae	*Temnocyon_altigenis*	extinct	YPM010065
Carnivora	Amphicyonidae	*Temnocyon_fingeruti*	extinct	UO280161
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec

Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF_unspec
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF24429
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF24447
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF24458
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF30000
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF37000
Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF466168

Carnivora	Barbourofelidae	*Barbourofelis_loveorum*	extinct	UF466174
Carnivora	Desmatophocidae	*Allodesmus_kelloggi*	extinct	AMNH32763
Carnivora	Desmatophocidae	*Allodesmus_kernensis*	extinct	SDNHM143027
Carnivora	Nimravidae	*Dinictis_felina*	extinct	AMNH38805
Carnivora	Nimravidae	*Dinictis_felina*	extinct	UF207947
Carnivora	Nimravidae	*Dinictis_felina*	extinct	USNM18219
Carnivora	Nimravidae	*Dinictis_felina*	extinct	UWBM90773
Carnivora	Nimravidae	*Dinictis_felina*	extinct	YPM010035
Carnivora	Nimravidae	*Dinictis_felina*	extinct	YPM010972
Carnivora	Nimravidae	*Dinictis_felina*	extinct	YPM056858
Carnivora	Nimravidae	*Hoplophoneus_cerebralis*	extinct	JODA7047
Carnivora	Nimravidae	*Hoplophoneus_mentalis*	extinct	YPM013593
Carnivora	Nimravidae	*Hoplophoneus_primaevus*	extinct	AMNH655
Carnivora	Nimravidae	*Hoplophoneus_primaevus*	extinct	UWBM87094
Carnivora	Nimravidae	*Hoplophoneus_sicarius*	extinct	FMNH-PM9467
Carnivora	Nimravidae	*Nimravus_brachyops*	extinct	JODA1312
Carnivora	Nimravidae	*Nimravus_brachyops*	extinct	JODA17778
Carnivora	Nimravidae	*Nimravus_brachyops*	extinct	USNM3957
Carnivora	Nimravidae	*Nimravus_brachyops*	extinct	YPM010517
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec

Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec

Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH_unspec
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNH22520
Carnivora	Semantoridae	*Potamotherium_valletoni*	extinct	AMNHcomp
Carnivora	Subparictidae	*Eoarctos_vorax*	extinct	USNM637259
Carnivoramorpha	Miacidae	*Miacis_washakius*	extinct	FMNH-PM3869
Carnivoramorpha	Miacidae	*Miocyon_vallisrubrae*	extinct	TxVP_unspec
Carnivoramorpha	Miacidae	*Miocyon_vallisrubrae*	extinct	TxVP40165-4
Carnivoramorpha	Miacidae	*Neovulpavus_mccarrolli*	extinct	FMNH3593
Carnivoramorpha	Miacidae	*Tapocyon_robustus*	extinct	SDNHM36000
Carnivoramorpha	Miacidae	*Vulpavus_hargeri*	extinct	YPM011839
Carnivoramorpha		*Vulpavus_profectus*	extinct	USNM538
Pan-Carnivora	Hyaenodontidae	*Arfia_shoshoniensis*	extinct	YPM016141
Pan-Carnivora	Hyaenodontidae	*Hyaenodon_crucians*	extinct	YPM010076
Pan-Carnivora	Hyaenodontidae	*Hyaenodon_crucians*	extinct	YPM012553
Pan-Carnivora	Hyaenodontidae	*Hyaenodon_horridus*	extinct	UNSM1-15-8-33SP
Pan-Carnivora	Hyaenodontidae	*Hyaenodon_horridus*	extinct	YPM010010
Pan-Carnivora	Hyaenodontidae	*Hyaenodon_horridus*	extinct	YPM010074
Pan-Carnivora	Hyaenodontidae	*Limnocyon_potens*	extinct	AMNH13138
Pan-Carnivora	Hyaenodontidae	*Limnocyon_verus*	extinct	AMNH12155

Pan-Carnivora	Hyaenodontidae	*Limnocyon_verus*	extinct	YPM011796
Pan-Carnivora	Hyaenodontidae	*Sinopa_major*	extinct	USNM5341
Pan-Carnivora	Hyaenodontidae	*Tritemnodon_agilis*	extinct	YPM010073
Pan-Carnivora	Oxyaenidae	*Oxyaena_forcipata*	extinct	YPM014551
Pan-Carnivora	Oxyaenidae	*Palaeonictis_occidentalis*	extinct	FMNH-216

Table S2. Trait loadings from PCAs of skeletal phenome and each component. Trait abbreviations are defined in Fig. S1.

A. Skeletal phenome	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	30%	18%	11%	6%	5%	4%	3%
lnCBL_lsr	0.06	0.05	0.02	0.13	0.08	0.05	0.11
lnPOC_lsr	0.20	-0.12	-0.12	0.13	-0.24	0.20	-0.09
lnZB_lsr	0.04	-0.02	-0.04	0.07	0.01	0.11	0.01
lnMB_lsr	-0.01	0.12	-0.21	0.13	-0.07	0.07	-0.03
lnCVH_lsr	0.05	0.04	-0.02	0.10	-0.01	0.10	0.01
lnPW_lsr	0.13	-0.06	-0.04	0.04	0.04	0.01	-0.07
lnBCL_lsr	0.08	0.09	0.01	0.02	0.01	0.05	0.03
lnMAT_lsr	0.05	0.04	-0.04	0.14	0.15	0.15	0.07
lnMAM_lsr	0.01	0.00	0.06	0.02	0.21	0.00	0.39
lnMAM2_lsr	0.01	0.05	0.06	0.03	0.11	0.19	0.09
lnMOL_lsr	0.02	0.05	0.07	0.13	0.15	0.09	0.28
lnCOL_lsr	0.07	0.03	0.11	0.12	0.14	0.05	0.21
lnMW_lsr	0.07	0.05	-0.06	0.02	0.01	0.02	0.00
lnAMW_lsr	0.07	-0.04	-0.06	0.02	0.02	0.06	-0.04
lnscap_L_lsr	-0.05	-0.06	0.14	-0.05	-0.03	0.06	-0.03
lnscap_W_lsr	-0.17	0.03	0.13	-0.06	-0.12	0.17	-0.02
lnhum_L_lsr	0.09	-0.14	0.08	-0.02	-0.01	0.15	0.00
lnhum_D_lsr	-0.16	-0.02	0.13	-0.04	-0.02	0.19	-0.02
lnhum_prox_lsr	-0.10	0.00	0.05	-0.01	-0.07	0.15	-0.06
lnhum_dist_lsr	-0.13	-0.02	-0.05	0.01	0.00	0.21	-0.09
lnul_L_lsr	0.06	-0.13	0.18	-0.04	-0.04	0.13	0.03
lnul_D_lsr	-0.22	-0.04	-0.05	-0.13	0.06	0.29	-0.21
lnul_OL_lsr	-0.14	0.05	0.11	-0.06	0.10	0.21	-0.09
lnrad_L_lsr	0.07	-0.15	0.24	-0.04	-0.07	0.13	0.08
lnrad_D_lsr	-0.24	-0.01	0.27	-0.11	-0.10	0.22	0.06
lnMC3L_lsr	0.18	-0.10	0.26	-0.05	-0.17	-0.03	0.02
lnMC3W_lsr	-0.07	-0.12	0.11	-0.05	-0.01	0.02	-0.17
lnpel_L_lsr	-0.02	-0.06	-0.02	-0.10	-0.01	-0.04	0.05
lnfem_L_lsr	0.17	-0.27	0.05	0.00	-0.03	0.14	-0.01
lnfem_D_lsr	-0.13	-0.10	0.02	-0.23	0.57	-0.12	0.03
lnfem_EB_lsr	-0.06	-0.05	-0.02	-0.06	-0.03	0.04	0.05
lnfem_GT_lsr	-0.08	-0.21	-0.07	0.09	0.12	0.21	0.37
lntib_L_lsr	0.13	-0.04	0.10	-0.13	-0.06	0.02	0.15
lntib_D_lsr	-0.04	-0.09	0.13	-0.14	-0.08	0.01	0.07
lntib_prox_lsr	-0.04	-0.08	0.00	-0.07	-0.06	0.06	0.01

lntib_dist_lsr	-0.05	-0.07	-0.01	-0.05	-0.10	0.07	-0.08
lnfib_L_lsr	0.14	-0.05	0.10	-0.13	-0.04	0.01	0.15
lncal_L_lsr	0.03	-0.09	0.08	-0.10	-0.01	0.02	0.03
lnMT3L_lsr	0.26	-0.07	0.17	-0.18	-0.10	-0.18	0.02
lnMT3D_lsr	0.03	-0.14	0.07	-0.18	-0.07	-0.12	-0.14
lnC3_VW_lsr	-0.06	0.11	-0.03	0.07	-0.04	-0.01	-0.11
lnC3_VH_lsr	0.01	0.15	0.09	0.06	-0.02	-0.01	-0.05
lnC3_CL_lsr	0.03	0.17	0.26	0.02	0.01	-0.07	0.03
lnC3_CW_lsr	-0.08	0.03	0.00	0.01	-0.08	0.05	-0.04
lnC3_CH_lsr	-0.07	0.16	0.11	0.06	-0.05	-0.10	0.03
lnC3_ZL_lsr	0.04	0.16	0.21	0.06	0.02	-0.07	0.00
lnC3_NSH_lsr	0.07	0.12	0.07	0.08	0.00	0.07	-0.10
lnC5_VW_lsr	-0.11	0.05	-0.08	0.04	-0.02	0.07	-0.12
lnC5_VH_lsr	0.00	0.11	0.14	0.07	0.03	-0.04	-0.11
lnC5_CL_lsr	-0.02	0.22	0.19	0.05	0.05	-0.06	0.04
lnC5_CW_lsr	-0.10	0.05	-0.05	0.06	-0.04	0.04	0.00
lnC5_CH_lsr	-0.07	0.14	0.18	0.04	-0.07	-0.10	0.06
lnC5_ZL_lsr	0.00	0.19	0.16	0.08	-0.01	-0.02	0.01
lnC5_NSH_lsr	0.03	0.08	0.11	0.07	0.16	0.00	-0.23
lnT1_VW_lsr	-0.10	0.06	-0.08	0.01	0.00	0.03	0.03
lnT1_VH_lsr	-0.02	0.00	0.16	0.02	0.03	-0.04	-0.11
lnT1_CL_lsr	-0.02	0.19	0.08	-0.04	-0.02	0.00	-0.02
lnT1_CW_lsr	-0.08	-0.01	0.02	0.12	-0.07	0.00	-0.01
lnT1_CH_lsr	-0.18	0.07	0.11	0.03	-0.02	-0.06	0.04
lnT1_ZL_lsr	-0.03	0.20	0.09	-0.02	-0.02	0.01	-0.02
lnT1_NSH_lsr	0.01	-0.03	0.18	0.03	0.06	-0.03	-0.16
lnmidT_VW_lsr	-0.07	0.04	-0.08	-0.01	-0.06	-0.02	0.01
lnmidT_VH_lsr	-0.07	-0.10	0.10	-0.03	0.02	-0.04	-0.12
lnmidT_CL_lsr	-0.01	0.18	-0.03	-0.10	-0.01	0.01	-0.03
lnmidT_CW_lsr	-0.09	0.04	-0.01	-0.04	-0.13	-0.03	0.03
lnmidT_CH_lsr	-0.18	0.00	0.09	-0.02	-0.05	0.00	0.04
lnmidT_ZL_lsr	-0.02	0.13	-0.06	-0.08	0.00	-0.01	-0.01
lnmidT_NSH_lsr	-0.03	-0.15	0.11	-0.03	0.15	-0.06	-0.21
lntranT_VW_lsr	-0.05	0.03	-0.08	0.02	-0.13	-0.04	0.05
lntranT_VH_lsr	-0.13	-0.07	0.01	0.10	0.16	-0.10	-0.05
lntranT_CL_lsr	0.00	0.16	-0.04	-0.17	-0.04	0.00	0.02
lntranT_CW_lsr	-0.08	0.03	-0.02	0.06	-0.12	-0.06	0.04
lntranT_CH_lsr	-0.19	-0.04	0.02	-0.06	-0.01	-0.01	0.06
lntranT_ZL_lsr	-0.06	0.12	-0.06	-0.05	-0.03	-0.02	0.05
lntranT_NSH_lsr	-0.09	-0.08	0.01	0.18	0.22	-0.15	-0.10

lnlastT_VW_lsr	-0.06	0.01	-0.10	0.03	-0.04	-0.03	0.02
lnlastT_VH_lsr	-0.14	-0.08	0.02	0.02	-0.03	-0.08	0.04
lnlastT_CL_lsr	0.04	0.14	-0.05	-0.18	-0.05	-0.01	0.07
lnlastT_CW_lsr	-0.08	-0.01	-0.06	0.02	-0.08	-0.03	0.02
lnlastT_CH_lsr	-0.18	-0.01	-0.03	-0.07	-0.06	0.03	0.10
lnlastT_ZL_lsr	0.01	0.08	-0.06	-0.14	-0.02	-0.02	0.04
lnlastT_NSH_lsr	-0.11	-0.12	0.04	0.07	-0.02	-0.14	0.01
lnL1_VW_lsr	-0.09	-0.02	0.01	0.06	-0.12	-0.21	0.15
lnL1_VH_lsr	-0.13	-0.08	0.01	0.03	-0.07	-0.12	0.04
lnL1_CL_lsr	0.06	0.11	-0.05	-0.21	-0.05	-0.03	0.06
lnL1_CW_lsr	-0.07	-0.04	-0.08	0.03	-0.09	-0.02	0.02
lnL1_CH_lsr	-0.18	0.00	-0.03	-0.09	-0.02	0.01	0.10
lnL1_ZL_lsr	0.03	0.08	-0.06	-0.17	-0.02	-0.01	0.02
lnL1_NSH_lsr	-0.10	-0.12	0.03	0.11	-0.13	-0.18	0.01
lnmidL_VW_lsr	-0.06	-0.08	0.03	0.08	-0.16	-0.20	0.09
lnmidL_VH_lsr	-0.08	-0.10	0.01	-0.03	-0.04	-0.13	0.02
lnmidL_CL_lsr	0.09	0.09	-0.03	-0.27	0.00	-0.01	0.05
lnmidL_CW_lsr	-0.05	-0.04	-0.08	0.02	-0.09	-0.01	0.03
lnmidL_CH_lsr	-0.19	-0.03	-0.02	-0.08	-0.08	0.01	0.11
lnmidL_ZL_lsr	0.07	0.08	-0.06	-0.21	-0.01	0.03	0.01
lnmidL_NSH_lsr	-0.03	-0.15	0.02	-0.01	0.01	-0.19	-0.04
lnlastL_VW_lsr	0.00	-0.09	-0.02	0.08	-0.08	-0.11	0.11
lnlastL_VH_lsr	-0.09	-0.07	-0.06	-0.09	0.03	-0.09	-0.01
lnlastL_CL_lsr	0.05	0.07	-0.09	-0.27	0.06	-0.01	-0.01
lnlastL_CW_lsr	-0.03	-0.06	-0.07	0.02	-0.07	-0.04	0.06
lnlastL_CH_lsr	-0.16	0.00	-0.03	-0.14	-0.02	-0.01	0.11
lnlastL_ZL_lsr	0.04	0.07	-0.11	-0.21	0.08	0.01	-0.02
lnlastL_NSH_lsr	-0.05	-0.12	-0.08	-0.10	0.14	-0.14	-0.09

B. Cranium	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	50%	20%	13%	8%	5%	2%	2%
lnCBL_lsr	0.13	0.14	0.48	0.18	0.30	0.73	0.27
lnPOC_lsr	0.86	-0.17	-0.39	0.27	0.02	0.05	0.04
lnZB_lsr	0.17	0.08	0.10	-0.25	0.21	0.20	-0.90
lnMB_lsr	0.16	0.87	-0.21	-0.29	-0.27	0.08	0.12
lnCVH_lsr	0.18	0.25	0.23	-0.07	0.72	-0.56	0.14
lnPW_lsr	0.35	-0.30	0.42	-0.70	-0.27	-0.07	0.20
lnBCL_lsr	0.18	0.20	0.58	0.50	-0.45	-0.32	-0.20

C. Mandible	PC1	PC2	PC3	PC4	PC5	PC6	PC7

Proportion of Variance	47%	21%	14%	8%	6%	3%	3%
lnMAT_lsr	0.41	0.47	0.34	0.59	0.36	0.16	0.06
lnMAM_lsr	0.53	-0.81	0.13	0.19	0.04	-0.05	-0.01
lnMAM2_lsr	0.33	0.21	-0.28	0.29	-0.77	-0.07	-0.30
lnMOL_lsr	0.47	0.20	-0.31	-0.31	0.01	-0.24	0.70
lnCOL_lsr	0.45	0.15	-0.08	-0.57	0.23	0.31	-0.54
lnMW_lsr	0.07	0.13	0.34	-0.13	0.09	-0.87	-0.29
lnAMW_lsr	0.06	0.05	0.76	-0.31	-0.46	0.24	0.23

D. Forelimb	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	49%	27%	7%	5%	3%	3%	2%
lnscap_L_lsr	0.13	0.20	0.01	0.08	0.07	0.05	0.21
lnscap_W_lsr	0.35	0.08	0.20	0.15	-0.30	-0.58	0.51
lnhum_L_lsr	-0.10	0.29	-0.32	0.31	-0.11	0.08	0.00
lnhum_D_lsr	0.33	0.12	0.04	-0.01	-0.10	0.17	-0.05
lnhum_prox_lsr	0.22	0.05	0.04	-0.07	0.01	0.14	-0.46
lnhum_dist_lsr	0.24	-0.08	-0.26	0.11	-0.09	0.02	-0.19
lnul_L_lsr	-0.04	0.40	-0.09	0.30	0.08	0.14	0.02
lnul_D_lsr	0.44	-0.12	-0.58	0.14	-0.06	-0.31	-0.28
lnul_OL_lsr	0.31	0.00	0.13	0.16	0.89	-0.10	0.07
lnrad_L_lsr	-0.06	0.50	-0.03	0.37	-0.04	0.19	0.09
lnrad_D_lsr	0.51	0.28	0.44	-0.21	-0.21	0.24	-0.18
lnMC3L_lsr	-0.25	0.55	0.02	-0.36	0.10	-0.58	-0.36
lnMC3W_lsr	0.15	0.21	-0.48	-0.64	0.10	0.23	0.44

E. Hindlimb	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	37%	24%	14%	7%	5%	4%	3%
lnpel_L_lsr	0.03	0.14	0.04	0.64	0.70	0.23	0.10
lnfem_L_lsr	0.48	0.35	-0.25	-0.02	0.19	-0.55	-0.45
lnfem_D_lsr	-0.26	0.51	0.76	-0.23	0.13	-0.08	-0.13
lnfem_EB_lsr	-0.06	0.15	-0.03	0.19	-0.11	0.08	-0.05
lnfem_GT_lsr	-0.10	0.66	-0.50	-0.33	0.05	0.30	0.32
lntib_L_lsr	0.33	0.01	0.08	-0.08	-0.04	0.39	-0.26
lntib_D_lsr	0.07	0.19	0.08	0.32	-0.47	0.31	-0.09
lntib_prox_lsr	0.00	0.16	-0.03	0.24	-0.16	0.02	-0.10
lntib_dist_lsr	-0.02	0.12	-0.08	0.27	-0.25	-0.10	-0.06
lnfib_L_lsr	0.34	0.01	0.10	-0.13	0.02	0.38	-0.24
lncal_L_lsr	0.16	0.14	0.07	0.16	-0.22	0.09	-0.18
lnMT3L_lsr	0.63	-0.07	0.24	-0.18	0.07	0.07	0.48
lnMT3D_lsr	0.19	0.21	0.16	0.28	-0.28	-0.35	0.51

F. Third cervical	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	62%	17%	12%	5%	3%	1%	0%
lnC3_VW_lsr	0.16	0.54	0.43	0.50	0.43	0.23	0.02
lnC3_VH_lsr	0.37	0.01	0.33	-0.31	-0.01	-0.12	-0.80
lnC3_CL_lsr	0.57	-0.17	-0.38	0.20	-0.21	0.65	-0.07
lnC3_CW_lsr	0.05	0.47	0.06	0.24	-0.82	-0.23	0.00
lnC3_CH_lsr	0.39	0.52	-0.19	-0.63	0.13	-0.05	0.35
lnC3_ZL_lsr	0.51	-0.19	-0.24	0.38	0.21	-0.68	0.08
lnC3_NSH_lsr	0.32	-0.39	0.68	-0.12	-0.20	0.03	0.46

G. Fifth cervical	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	61%	19%	11%	5%	2%	2%	1%
lnC5_VW_lsr	0.06	0.61	0.49	0.03	0.50	0.35	0.11
lnC5_VH_lsr	0.34	-0.19	0.35	-0.32	0.12	-0.10	-0.77
lnC5_CL_lsr	0.59	0.00	-0.23	0.46	-0.23	0.56	-0.14
lnC5_CW_lsr	0.09	0.58	0.19	0.22	-0.57	-0.47	-0.13
lnC5_CH_lsr	0.44	0.26	-0.28	-0.74	-0.14	0.04	0.29
lnC5_ZL_lsr	0.49	-0.04	-0.19	0.29	0.52	-0.58	0.18
lnC5_NSH_lsr	0.28	-0.43	0.66	0.01	-0.25	-0.02	0.48

H. First thoracic	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	50%	23%	19%	3%	3%	1%	0%
lnT1_VW_lsr	0.28	0.43	0.02	0.57	0.64	0.03	0.01
lnT1_VH_lsr	0.19	-0.48	0.29	0.10	0.12	0.07	0.78
lnT1_CL_lsr	0.43	-0.17	-0.51	-0.11	0.08	-0.71	0.05
lnT1_CW_lsr	0.24	0.22	0.35	-0.77	0.41	0.00	-0.02
lnT1_CH_lsr	0.66	0.19	0.41	0.15	-0.56	-0.04	-0.13
lnT1_ZL_lsr	0.45	-0.19	-0.51	-0.12	0.03	0.69	-0.08
lnT1_NSH_lsr	0.07	-0.66	0.32	0.15	0.28	-0.05	-0.60

I. Middle thoracic	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	43%	37%	11%	5%	3%	1%	1%
lnmidT_VW_lsr	0.02	0.35	0.31	0.67	0.57	0.05	0.04
lnmidT_VH_lsr	-0.51	0.11	-0.22	0.07	-0.07	0.06	0.82
lnmidT_CL_lsr	0.40	0.32	-0.59	0.06	-0.02	0.62	-0.01
lnmidT_CW_lsr	-0.03	0.45	0.29	0.30	-0.78	0.01	-0.09
lnmidT_CH_lsr	-0.38	0.67	0.04	-0.54	0.24	-0.01	-0.24
lnmidT_ZL_lsr	0.29	0.28	-0.47	0.10	0.01	-0.78	0.06
lnmidT_NSH_lsr	-0.60	-0.17	-0.45	0.39	-0.04	0.00	-0.51

J. Diaphragmatic	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	51%	29%	10%	7%	2%	2%	0%
lntranT_VW_lsr	0.06	0.30	0.00	0.65	0.56	0.41	0.08
lntranT_VH_lsr	0.58	-0.06	0.13	-0.13	0.00	0.01	0.79
lntranT_CL_lsr	-0.20	0.48	0.53	-0.29	0.42	-0.44	0.06
lntranT_CW_lsr	0.17	0.31	-0.03	0.59	-0.44	-0.58	0.00
lntranT_CH_lsr	0.49	0.46	-0.57	-0.33	0.18	-0.06	-0.28
lntranT_ZL_lsr	0.03	0.53	0.34	-0.13	-0.53	0.55	-0.07
lntranT_NSH_lsr	0.59	-0.31	0.51	0.07	0.09	-0.02	-0.53

K. Last thoracic	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	60%	23%	8%	5%	2%	1%	0%
lnlastT_VW_lsr	0.18	0.27	0.83	0.19	0.41	0.02	0.00
lnlastT_VH_lsr	0.51	0.01	-0.21	0.20	0.10	0.05	-0.80
lnlastT_CL_lsr	-0.28	0.62	-0.22	0.30	-0.02	0.63	0.00
lnlastT_CW_lsr	0.27	0.21	0.31	0.01	-0.89	-0.02	-0.01
lnlastT_CH_lsr	0.54	0.46	-0.22	-0.58	0.18	-0.01	0.28
lnlastT_ZL_lsr	-0.14	0.47	-0.20	0.35	0.02	-0.77	0.01
lnlastT_NSH_lsr	0.50	-0.24	-0.18	0.61	0.03	0.09	0.53

L. First lumbar	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	60%	20%	10%	7%	3%	1%	0%
lnL1_VW_lsr	0.40	0.18	0.61	0.65	0.04	0.09	0.00
lnL1_VH_lsr	0.48	0.03	0.00	-0.30	0.17	-0.08	-0.80
lnL1_CL_lsr	-0.27	0.58	0.38	-0.27	0.08	-0.60	0.03
lnL1_CW_lsr	0.23	0.13	-0.03	-0.08	-0.96	-0.09	-0.02
lnL1_CH_lsr	0.45	0.58	-0.58	0.10	0.19	-0.01	0.30
lnL1_ZL_lsr	-0.18	0.46	0.20	-0.31	-0.04	0.78	-0.05
lnL1_NSH_lsr	0.50	-0.27	0.33	-0.55	0.11	0.01	0.51

M. Middle lumbar	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	54%	18%	14%	9%	3%	1%	0%
lnmidL_VW_lsr	0.39	0.06	0.24	0.86	0.21	0.07	0.04
lnmidL_VH_lsr	0.36	-0.02	0.37	-0.25	0.08	-0.08	-0.81
lnmidL_CL_lsr	-0.45	-0.35	0.53	0.10	0.09	-0.61	0.09
lnmidL_CW_lsr	0.21	-0.19	0.05	0.15	-0.94	-0.11	-0.01
lnmidL_CH_lsr	0.48	-0.77	-0.12	-0.20	0.22	0.02	0.26
lnmidL_ZL_lsr	-0.37	-0.33	0.37	0.05	-0.07	0.78	-0.09
lnmidL_NSH_lsr	0.32	0.37	0.61	-0.36	-0.04	0.09	0.51

N. Last lumbar	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of Variance	39%	29%	16%	10%	4%	1%	1%
lnlastL_VW_lsr	0.22	0.37	0.52	0.66	0.33	0.03	0.07
lnlastL_VH_lsr	0.54	-0.05	0.00	-0.12	0.08	0.07	-0.82
lnlastL_CL_lsr	-0.01	-0.68	0.21	0.25	0.03	-0.65	-0.05
lnlastL_CW_lsr	0.20	0.09	0.04	0.31	-0.92	-0.01	0.00
lnlastL_CH_lsr	0.50	-0.09	-0.71	0.33	0.18	-0.03	0.30
lnlastL_ZL_lsr	-0.02	-0.61	0.14	0.20	0.00	0.75	0.05
lnlastL_NSH_lsr	0.60	-0.08	0.40	-0.50	-0.02	-0.02	0.47

Table S3. Comparisons of the best fitting evolutionary models in simulated datasets of skeletal phenome and size. Simulated datasets were generated using the parameter estimates of the best-fit model(s) in the empirical dataset for skeletal phenome and skeletal size. Rows in boldface type represent the best-fit model as indicated by ΔAICc < 2.

Model	AICc	ΔAICc	AICcW
Skeletal phenome: Simulations under $OUBMi_{MMCT}$			
BM1	-7704.47	35.10	0.00
trend	-7685.17	54.40	0.00
EB	-7698.09	41.48	0.00
OU1	-7604.70	134.87	0.00
$OUBMi_{EOT}$	-7672.84	66.72	0.00
$OUBMi_{MMCT}$	**-7739.57**	**0.00**	**1.00**
OU2	-7606.85	132.71	0.00
OU3	-7594.45	145.12	0.00
Skeletal phenome: Simulations under $OUBMi_{EOT}$			
BM1	**-7664.99**	**0.00**	**0.96**
trend	-7648.42	16.57	0.00
EB	-7658.38	6.61	0.04
OU1	-7598.02	66.98	0.00
$OUBMi_{EOT}$	-7646.95	18.05	0.00
$OUBMi_{MMCT}$	-7621.89	43.11	0.00
OU2	-7552.73	112.26	0.00
OU3	-7530.80	134.20	0.00
Skeletal size: Simulations under $OUBMi_{MMCT}$			
BM1	-1079.55	7.18	0.01
trend	**-1086.73**	**0.00**	**0.46**
EB	-1077.61	9.12	0.01
OU1	-1080.53	6.20	0.02
$OUBMi_{EOT}$	**-1085.44**	**1.29**	**0.24**
$OUBMi_{MMCT}$	**-1085.44**	**1.29**	**0.24**
OU2	-1078.60	8.13	0.01
OU3	-1076.57	10.16	0.00

Table S4. Phylogenetic signal of skeletal components.

Skeletal component	Pagel's λ	P-value	Blomberg's K	P-value
cranium	0.94	0.001	0.38	0.001
mandible	1.00	0.001	0.45	0.001
forelimb	0.44	0.001	0.36	0.001
hindlimb	0.44	0.001	0.36	0.001
third cervical	1.00	0.001	0.42	0.001
fifth cervical	0.97	0.001	0.39	0.001
first thoracic	1.00	0.001	0.42	0.001
middle thoracic	1.00	0.001	0.42	0.001
diaphragmatic	0.97	0.001	0.39	0.001
last thoracic	0.97	0.001	0.39	0.001
first lumbar	0.97	0.001	0.39	0.001
middle lumbar	0.97	0.001	0.39	0.001
last lumbar	0.97	0.001	0.39	0.001

Table S5. Comparisons of the best-fitting evolutionary models in each of the skeletal components. Rows in boldface type represent the best supported model as indicated by ΔAICc < 2.

Skeletal component	Model	AICc	ΔAICc	AICcW
cranium	BM1	-1086.52	106.59	0.00
(PCs 1-5: 95.8% of variance)	trend	-1092.37	100.74	0.00
	EB	-1084.35	108.76	0.00
	OU1	**-1193.11**	**0.00**	**0.80**
	$OUBMi_{EOT}$	-1127.82	65.29	0.00
	$OUBMi_{MMCT}$	-1149.55	43.56	0.00
	OU2	-1190.22	2.90	0.19
	OU3	-1183.56	9.55	0.01
mandible	BM1	-1286.84	120.16	0.00
(PCs 1-5: 94.7% of variance)	trend	-1297.50	109.49	0.00
	EB	-1282.74	124.25	0.00
	OU1	-1392.26	14.73	0.00
	$OUBMi_{EOT}$	-1304.97	102.03	0.00
	$OUBMi_{MMCT}$	-1346.69	60.31	0.00
	OU2	**-1406.99**	**0.00**	**1.00**
	OU3	-1391.31	15.68	0.00
forelimb	BM1	-1011.94	191.06	0.00
(PCs 1-7: 95.8% of variance)	trend	-1006.52	196.48	0.00
	EB	-1009.83	193.17	0.00
	OU1	**-1203.00**	**0.00**	**0.99**
	$OUBMi_{EOT}$	-1035.73	167.27	0.00
	$OUBMi_{MMCT}$	-1082.03	120.97	0.00
	OU2	-1193.50	9.50	0.01
	OU3	-1175.50	27.51	0.00
hindlimb	BM1	-596.78	254.60	0.00
(PCs 1-7: 95.1% of variance)	trend	-600.57	250.82	0.00
	EB	-594.60	256.78	0.00
	OU1	-795.76	55.62	0.00
	$OUBMi_{EOT}$	-702.51	148.87	0.00
	$OUBMi_{MMCT}$	**-851.38**	**0.00**	**1.00**
	OU2	-796.47	54.91	0.00

	OU3	-784.40	66.98	0.00
third cervical vertebrae	BM1	-332.51	69.12	0.00
(PCs 1-3: 90.9% of variance)	trend	-334.14	67.49	0.00
	EB	-330.44	71.19	0.00
	OU1	**-401.63**	**0.00**	**0.89**
	$OUBMi_{EOT}$	-374.92	26.71	0.00
	$OUBMi_{MMCT}$	-381.42	20.21	0.00
	OU2	-397.39	4.24	0.11
	OU3	-391.13	10.50	0.00
fifth cervical vertebrae	BM1	-654.01	161.09	0.00
(PCs 1-4: 95.9% of variance)	trend	-656.76	158.35	0.00
	EB	-651.30	163.81	0.00
	OU1	**-815.11**	**0.00**	**0.95**
	$OUBMi_{EOT}$	-727.12	87.98	0.00
	$OUBMi_{MMCT}$	-771.65	43.46	0.00
	OU2	-809.15	5.96	0.05
	OU3	-800.96	14.15	0.00
first thoracic vertebrae	BM1	-509.05	31.49	0.00
(PCs 1-3: 92.4% of variance)	trend	-507.01	33.53	0.00
	EB	-506.98	33.56	0.00
	OU1	-529.81	10.73	0.01
	$OUBMi_{EOT}$	-525.58	14.96	0.00
	$OUBMi_{MMCT}$	**-540.54**	**0.00**	**0.99**
	OU2	-529.44	11.10	0.00
	OU3	-523.96	16.58	0.00
middle thoracic vertebrae	BM1	-551.60	35.01	0.00
(PCs 1-3: 89.9% of variance)	trend	-549.43	37.18	0.00
	EB	-549.24	37.36	0.00
	OU1	-574.87	11.74	0.00
	$OUBMi_{EOT}$	-577.31	9.29	0.01
	$OUBMi_{MMCT}$	**-586.60**	**0.00**	**0.99**
	OU2	-572.10	14.51	0.00
	OU3	-565.98	20.63	0.00
diaphragmatic vertebrae	BM1	-745.06	141.40	0.00

(PCs 1-4: 96.3% of variance)	trend	-746.47	139.99	0.00
	EB	-742.96	143.50	0.00
	OU1	**-886.46**	**0.00**	**0.98**
	$OUBMi_{EOT}$	-786.69	99.77	0.00
	$OUBMi_{MMCT}$	-823.31	63.15	0.00
	OU2	-878.80	7.66	0.02
	OU3	-866.34	20.12	0.00
last thoracic vertebrae	BM1	-1001.57	143.53	0.00
(PCs 1-4: 96.8% of variance)	trend	-1000.09	145.01	0.00
	EB	-999.41	145.69	0.00
	OU1	**-1145.10**	**0.00**	**0.97**
	$OUBMi_{EOT}$	-1038.72	106.38	0.00
	$OUBMi_{MMCT}$	-1101.69	43.41	0.00
	OU2	-1137.80	7.31	0.03
	OU3	-1130.02	15.09	0.00
first lumbar vertebrae	BM1	-875.29	100.95	0.00
(PCs 1-4: 96.4% of variance)	trend	-874.36	101.88	0.00
	EB	-872.46	103.78	0.00
	OU1	**-975.82**	**0.42**	**0.44**
	$OUBMi_{EOT}$	-921.03	55.21	0.00
	$OUBMi_{MMCT}$	-963.13	13.11	0.00
	OU2	**-976.24**	**0.00**	**0.54**
	OU3	-970.32	5.92	0.03
middle lumbar vertebrae	BM1	-732.32	96.99	0.00
(PCs 1-4: 95.6% of variance)	trend	-729.47	99.84	0.00
	EB	-729.73	99.58	0.00
	OU1	**-829.32**	**0.00**	**0.97**
	$OUBMi_{EOT}$	-760.61	68.71	0.00
	$OUBMi_{MMCT}$	-785.69	43.62	0.00
	OU2	-822.16	7.16	0.03
	OU3	-814.77	14.54	0.00
last lumbar vertebrae	BM1	-480.37	251.06	0.00
(PCs 1-4: 94.9% of variance)	trend	-479.90	251.52	0.00
	EB	-478.29	253.13	0.00
	OU1	**-731.42**	**0.00**	**0.97**

$OUBMi_{EOT}$	-524.66	206.76	0.00
$OUBMi_{MMCT}$	-569.45	161.98	0.00
OU2	-724.40	7.03	0.03
OU3	-717.61	13.81	0.00

Table S6. Parameter estimates from best fitting evolutionary models of skeletal components. Mean parameters were calculated from all PC axes used in each model. θ = theta; σ^2 = evolutionary rate; α = strength of selection; SV = stationary variances ($\sigma^2/2\alpha$); half-life = phylogenetic half-life ($\ln(2)/\alpha$). Where the cOU3 model is the best model, the "mean θ" column shows the mean θ value of stem Pan-Carnivora, and the "parameter" column shows the mean θ values of Caniformia and Feliformia. Where the sOU2 model is the best model, the "mean θ" column shows the mean θ value of stem Pan-Carnivora, and the "parameter" column shows the mean θ value of Carnivora. Where the $OUBMi_{MMCT}$ model is the best model, the "mean σ^2" column shows the mean σ^2 values from before the MMCT, and the "parameter" column shows the mean σ^2 values from after the MMCT.

skeletal component	best model	mean θ	mean σ^2	mean α	SV	half-life	parameter
cranium	OU1	-0.100	0.003	0.044	0.032	15.7	
mandible	cOU3	0.005	0.003	0.065	0.020	10.7	$\theta_{Caniform}$ = -0.020 $\theta_{Feliform}$ = -0.012
forelimb	OU1	0.369	0.004	0.067	0.030	10.3	
hindlimb	$OUBMi_{MMCT}$	-0.146	0.010	0.111	0.046	6.3	$\sigma^2_{post\text{-}MMCT}$ = 0.003
third cervical	OU1	-0.004	0.004	0.049	0.041	14.3	
fifth cervical	OU1	0.066	0.005	0.089	0.027	7.8	
first thoracic	$OUBMi_{MMCT}$	0.203	0.003	0.049	0.026	14.0	$\sigma^2_{post\text{-}MMCT}$ = 0.002
middle thoracic	$OUBMi_{MMCT}$	-0.026	0.003	0.051	0.026	13.6	$\sigma^2_{post\text{-}MMCT}$ = 0.002
diaphragmatic	cOU3	-0.020	0.004	0.090	0.025	7.7	$\theta_{Caniform}$ = -0.021 $\theta_{Feliform}$ = -0.067
last thoracic	OU1	0.151	0.002	0.086	0.014	8.1	
first lumbar	sOU2	-0.156	0.003	0.076	0.019	9.2	$\theta_{Carnivora}$ = 0.030
middle lumbar	OU1	0.104	0.003	0.053	0.030	13.2	
last lumbar	OU1	0.070	0.012	0.298	0.020	2.3	

Table S7. Comparisons of the best fitting evolutionary models in simulated datasets of skeletal components. Simulated data were generated using parameter estimates of the best-fit model in the empirical dataset of each skeletal component. Rows in boldface type represent the best supported model as indicated by ΔAICc < 2.

Skeletal component	Model	AICc	ΔAICc	AICcW
cranium	**BM1**	**-7378.19**	**0.00**	**0.97**
(PCs 1-5: 95.8% of variance)	trend	-7365.73	12.46	0.00
	EB	-7362.84	15.35	0.00
	OU1	-7371.23	6.96	0.03
	$BMBMi_{EOT}$	-7347.55	30.64	0.00
	$BMBMi_{MMCT}$	-7347.16	31.03	0.00
	$OUBMi_{EOT}$	-7348.16	30.03	0.00
	$OUBMi_{MMCT}$	-7364.35	13.84	0.00
	OU2	-7363.37	14.82	0.00
	OU3	-7359.98	18.21	0.00
mandible	BM1	-6226.06	195.93	0.00
(PCs 1-5: 94.7% of variance)	trend	-6047.64	374.35	0.00
	EB	**-6421.99**	**0.00**	**1.00**
	OU1	-5933.32	488.67	0.00
	$BMBMi_{EOT}$	-6194.30	227.69	0.00
	$BMBMi_{MMCT}$	-6365.85	56.14	0.00
	$OUBMi_{EOT}$	-6255.22	166.76	0.00
	$OUBMi_{MMCT}$	-6163.86	258.13	0.00
	OU2	-6015.29	406.70	0.00
	OU3	-6020.34	401.65	0.00
forelimb	BM1	-9692.21	104.26	0.00
(PCs 1-7: 95.8% of variance)	trend	-9672.87	123.61	0.00

	EB	-9677.44	119.04	0.00
	OU1	-9796.48	0.00	0.65
	$BMBMi_{EOT}$	-9632.55	163.93	0.00
	$BMBMi_{MMCT}$	-9632.90	163.58	0.00
	$OUBMi_{EOT}$	-9582.42	214.05	0.00
	$OUBMi_{MMCT}$	-9632.23	164.25	0.00
	OU2	-9794.47	2.01	0.24
	OU3	-9792.90	3.58	0.11
hindlimb	BM1	-9287.40	51.97	0.00
(PCs 1-7: 95.1% of variance)	trend	-9267.00	72.36	0.00
	EB	-9268.83	70.53	0.00
	OU1	-9056.37	282.99	0.00
	$BMBMi_{EOT}$	-9227.84	111.52	0.00
	$BMBMi_{MMCT}$	**-9339.36**	**0.00**	**0.99**
	$OUBMi_{EOT}$	-9179.97	159.39	0.00
	$OUBMi_{MMCT}$	-9330.74	8.62	0.01
	OU2	-9061.64	277.72	0.00
	OU3	-9052.45	286.91	0.00
third cervical vertebrae	BM1	-4108.51	42.29	0.00
(PCs 1-3: 90.9% of variance)	trend	-4100.29	50.51	0.00
	EB	-4106.43	44.37	0.00
	OU1	**-4150.80**	**0.00**	**0.93**
	$BMBMi_{EOT}$	-4096.63	54.17	0.00
	$BMBMi_{MMCT}$	-4099.42	51.38	0.00
	$OUBMi_{EOT}$	-4101.87	48.93	0.00
	$OUBMi_{MMCT}$	-4124.98	25.82	0.00
	OU2	-4145.38	5.42	0.06
	OU3	-4140.97	9.83	0.01
fifth cervical vertebrae	BM1	-5640.77	90.20	0.00
(PCs 1-4: 95.9% of variance)	trend	-5631.28	99.69	0.00
	EB	-5615.36	115.61	0.00
	OU1	**-5730.97**	**0.00**	**0.96**
	$BMBMi_{EOT}$	-5594.24	136.73	0.00
	$BMBMi_{MMCT}$	-5595.16	135.81	0.00
	$OUBMi_{EOT}$	-5624.94	106.03	0.00

	$OUBMi_{MMCT}$	-5654.42	76.55	0.00
	OU2	-5724.75	6.22	0.04
	OU3	-5717.50	13.47	0.00
first thoracic vertebrae	**BM1**	**-4167.15**	**0.00**	**0.72**
(PCs 1-3: 92.4% of variance)	trend	-4154.14	13.01	0.00
	EB	-4165.08	2.07	0.26
	OU1	-4145.60	21.55	0.00
	$BMBMi_{EOT}$	-4155.04	12.11	0.00
	$BMBMi_{MMCT}$	-4158.43	8.72	0.01
	$OUBMi_{EOT}$	-4146.57	20.58	0.00
	$OUBMi_{MMCT}$	-4158.98	8.17	0.01
	OU2	-4148.14	19.01	0.00
	OU3	-4148.25	18.90	0.00
middle thoracic vertebrae	**BM1**	**-4246.21**	**0.00**	**0.71**
(PCs 1-3: 89.9% of variance)	trend	-4237.86	8.35	0.01
	EB	-4244.14	2.07	0.25
	OU1	-4207.90	38.31	0.00
	$BMBMi_{EOT}$	-4234.52	11.68	0.00
	$BMBMi_{MMCT}$	-4234.24	11.97	0.00
	$OUBMi_{EOT}$	-4233.60	12.61	0.00
	$OUBMi_{MMCT}$	-4239.67	6.53	0.03
	OU2	-4203.58	42.63	0.00
	OU3	-4204.52	41.69	0.00
diaphragmatic vertebrae	BM1	-5754.65	41.35	0.00
(PCs 1-4: 96.3% of variance)	trend	-5739.92	56.08	0.00
	EB	-5740.67	55.33	0.00
	OU1	**-5796.00**	**0.00**	**0.90**
	$BMBMi_{EOT}$	-5733.94	62.07	0.00
	$BMBMi_{MMCT}$	-5734.22	61.78	0.00
	$OUBMi_{EOT}$	-5719.95	76.05	0.00
	$OUBMi_{MMCT}$	-5735.74	60.27	0.00
	OU2	-5791.14	4.87	0.08
	OU3	-5788.63	7.38	0.02
last thoracic vertebrae	BM1	-6069.48	17.73	0.00

(PCs 1-4: 96.8% of variance)	trend	-6059.79	27.42	0.00
	EB	-6067.21	20.01	0.00
	OU1	**-6087.21**	**0.00**	**0.96**
	$BMBMi_{EOT}$	-6048.46	38.75	0.00
	$BMBMi_{MMCT}$	-6048.46	38.75	0.00
	$OUBMi_{EOT}$	-6045.40	41.81	0.00
	$OUBMi_{MMCT}$	-6062.20	25.02	0.00
	OU2	-6080.75	6.47	0.04
	OU3	-6073.60	13.61	0.00
first lumbar vertebrae	BM1	-4924.07	276.35	0.00
(PCs 1-4: 96.4% of variance)	trend	-4753.55	446.86	0.00
	EB	-5089.46	110.95	0.00
	OU1	-4741.25	459.17	0.00
	$BMBMi_{EOT}$	-5167.17	33.24	0.00
	$BMBMi_{MMCT}$	-5147.00	53.41	0.00
	$OUBMi_{EOT}$	-5119.43	80.98	0.00
	$OUBMi_{MMCT}$	-5029.46	170.96	0.00
	OU2	**-5196.89**	**3.52**	**0.15**
	OU3	**-5200.41**	**0.00**	**0.85**
middle lumbar vertebrae	BM1	-5726.64	65.45	0.00
(PCs 1-4: 95.6% of variance)	trend	-5717.13	74.95	0.00
	EB	-5716.34	75.75	0.00
	OU1	-5792.09	0.00	0.95
	$BMBMi_{EOT}$	-5705.91	86.18	0.00
	$BMBMi_{MMCT}$	-5707.84	84.24	0.00
	$OUBMi_{EOT}$	-5695.30	96.78	0.00
	$OUBMi_{MMCT}$	-5720.10	71.99	0.00
	OU2	-5785.92	6.17	0.04
	OU3	-5780.76	11.33	0.00
last lumbar vertebrae	BM1	-5560.17	97.63	0.00
(PCs 1-4: 94.9% of variance)	trend	-5550.07	107.74	0.00
	EB	-5557.97	99.83	0.00
	OU1	**-5657.81**	**0.00**	**0.87**
	$BMBMi_{EOT}$	-5539.20	118.61	0.00
	$BMBMi_{MMCT}$	-5542.73	115.08	0.00

$OUBMi_{EOT}$	-5537.64	120.17	0.00
$OUBMi_{MMCT}$	-5585.76	72.05	0.00
OU2	-5653.86	3.94	0.12
OU3	-5647.34	10.47	0.01

Table S8. Extinct species that were added to the phylogeny. PBDB = Paleobiology Database.

Species	Phylogenetic position	Age Range
Crassidia intermedia	Basal caniform (sister to *Daphoenus*) (1)	18 Ma (Florida Museum)
Corumictis wolsani	Stem to Mustelidae (sister to *Promartes*) (2)	30.8-18.5 Ma (PBDB)
Cyonasua brevirostris	Sister to genus *Nasua* (3)	7.24-3 Ma (PBDB)
Eoarctos vorax	Sister to Ursidae (4)	32.0–31.4 Ma (4)
Puma pardoides	Sister to *Puma concolor* (5)	L Plio to E Pleist. (~3-2 Ma) (5)
Satherium ingens	Sister to genus *Pteronura* (6)	4.9-1.8 Ma (PBDB)
Neovulpavus mccarrolli	Stem carnivoramorphan (7)	Early Uintan (Ui1b) NALMA (46.2 - 39.7 Ma) (7)
Promartes olcotti	Stem to Mustelidae (sister to *Corumictis*) (8)	26.3-18.5 Ma (PBDB)

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