Are phenotypic disparity and rate of morphological evolution correlated with ecological diversity in Carnivora?

MARGOT MICHAUD[1]*, GÉRALDINE VERON[1], STÉPHANE PEIGNÉ[2,†], AMANDINE BLIN[3] and ANNE-CLAIRE FABRE[4]

[1]*Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, CP 51, 57 rue Cuvier, 75231 Paris Cedex 05, France*
[2]*Centre de recherche sur la paléobiodiversité et les paléoenvironnements, UMR 7207 CNRS/MNHN/UPMC, 8 rue Buffon, Paris, France*
[3]*Outils et Méthodes de la Systématique Intégrative, OMSI – UMS 2700 CNRS MNHN, Muséum national d'Histoire naturelle, CP26, 57 rue Cuvier, 75231 Paris Cedex 05, France*
[4]*Adaptations du Vivant, UMR 7179 MECADEV, CNRS/MNHN, 55 rue Buffon, Paris, France*

In the modern definition of adaptive radiation, a clade rapidly diversifies from a common ancestor to colonize a wide variety of new ecological niches. The idea of multiplication of species related to an adaptive radiation is well accepted. However, the assessment of how ecological and phenotypic diversity is interrelated in the case of adaptive radiation has rarely been studied. This is the background of the present paper, which aimed to test the correlation between phenotypic disparity and the rate of morphological evolution in relationship to ecological diversity in terrestrial Carnivora. To do so, we used geometric morphometrics to investigate skull shape disparity and the rate of morphological evolution at the family level in Carnivora. Our analyses highlight a correlation between ecological diversity and phenotypic disparity and demonstrate that the skull shape is impacted by ecology. On the contrary, our data do not provide any correlation between ecological diversity and the rate of morphological evolution, nor between phenotypic disparity and the rate of morphological evolution. We suggest that this absence of correlation could be explained by a contrasting tempo and a shift in morphological evolutionary rate among families.

ADDITIONAL KEYWORDS: cranial morphology – diet – locomotion – morphological evolution – three-dimensional geometric morphometrics.

INTRODUCTION

Understanding the origin and evolution of the tremendous diversity of organisms is a challenge and drives many questions in evolutionary biology. Radiations are known to be the main driver generating species diversity (Kocher, 2004; Losos & Mahler, 2010; Rabosky & Glor, 2010). Indeed, the theory of adaptive radiation is defined by taxonomic and phenotypic diversification in connection with the exploitation of different ecological niches (see Schluter, 2000). In this context, theory predicts strong morphological diversification in relationship to major ecological diversity. Nevertheless, since the genesis of the theory, many studies have demonstrated cases of non-adaptive radiations, with a multiplication of species without strong morphological differentiation (Gittenberger, 1991; Kozak, Weisrock & Larson, 2006). It is thus pertinent to ask whether great ecological diversity leads to more forms in a family, commonly quantified by phenotypic disparity (Marugán-Lobón & Buscalioni, 2003; Figueirido *et al.*, 2011; Jones, Smaers & Goswami, 2015).

Surprisingly, the relationship between phenotypic disparity and ecological diversity has never been tested

---

*Corresponding author. E-mail: margot.michaud@edu.mnhn.fr
†Deceased 4 December 2017.

explicitly. Many studies have focused on the relationship between disparity and a specific ecological factor, such as locomotor habitat (Rowe *et al.*, 2011; Fabre et al., 2015a, b; Dumont *et al.*, 2016) or diet (Hulsey & Wainwright, 2002; Goswami, Milne & Wroe, 2011; Dumont *et al.*, 2016), whereas others have sought to understand the link between taxonomic diversification and environmental parameters (Losos & Ricklefs, 2009; Burbrink, Ruane & Pyron, 2012) or phenotypic diversity (Ricklefs, 2004, 2006; Slater *et al.*, 2010). Another commonly expected pattern is a correlation between the ecological diversity and the rate of morphological evolution (O'Meara *et al.*, 2006; Beaulieu *et al.*, 2012; Rabosky *et al.*, 2013; Adams, 2014a). It is expected that there is a positive correlation between lifestyle and the rate of morphological evolution during species evolution accompanied by speciation in relationship to ecological parameters (Schluter, 2000; Harmon *et al.*, 2003; Slater *et al.*, 2010; Rowe *et al.*, 2011: Muschick, Indermaur & Salzburger, 2012). Likewise, it would be interesting to question the link between phenotypic disparity and the rate of morphological evolution, which is rarely explored in the literature. Most studies focus on disparity at the present time or evolution rates without testing a possible correlation between these two parameters (Rabosky & Adams, 2012; Zelditch *et al.*, 2015; Evans *et al.*, 2017). Empirical and theoretical studies showed a correlation between disparity and rate of evolution (Ricklefs, 2004, 2006). However, Adams *et al.* (2009) tested whether phenotypic disparity would be a proxy for evolution rate and found no correlation between these two parameters.

Among mammals, Carnivora provide a good model with which to study phenotypic diversity and the relationship to ecology, because they display a wide range of lifestyles within various habitats (Johnson *et al.*, 2006; Diniz-Filho *et al.*, 2009), have a worldwide distribution and have the largest body size range among living mammals (from 25 g for the least weasel to > 650 kg for the polar bear; Wilson & Mittermeier, 2009). Terrestrial Carnivora (i.e. excluding the Pinnipedia) are represented by 13 families, which display an extremely broad range of morphological and dietary diversity, from insectivorous (e.g. aardwolf *Proteles cristata*, Hyaenidae) and hypercarnivorous (Felidae and Hyaenidae) to folivorous (e.g. red panda *Ailurus fulgens*, Ailuridae), along with various types of locomotion, from aquatic (e.g. sea otter *Enhydra lutris*, Mustelidae) to terrestrial (e.g. wolf *Canis lupus*, Canidae) and arboreal (e.g. kinkajou *Potos flavus*, Procyonidae).

For this study, the shape of the skull was used because it is a complex structure, both functionally and ontogenetically (Moore, 1981; Hanken & Hall, 1993; Marroig & Cheverud, 2001), and its morphology is under strong selection pressure (Hampton, 2011).

Moreover, several factors linked to lifestyle have been proved to drive the evolution of skull morphology (Kunz & Fenton, 2005; Herrel *et al.*, 2008; Dumont *et al.*, 2016). In this study, we test, at the family level, the correlation between: (1) ecological diversity and both the rate of morphological evolution and the skull shape disparity; (2) specific richness and ecological diversity of families; and (3) the skull shape disparity and the rate of morphological evolution. We make the assumptions that, in the case of a suggested adaptive radiation, there will be a positive correlation between: (1) the ecological diversity and both the rate of morphological evolution and the skull shape disparity; (2) specific richness and ecological diversity; and (3) skull shape disparity and the rate of morphological evolution.

MATERIAL AND METHODS

All analyses were performed in R version 3.4.0 (R Core Team, 2017), with a significance threshold of 5% for all statistical tests used in this study.

MATERIAL

Our sample comprised 277 skulls belonging to 154 species that represent all the 13 families of terrestrial Carnivora, corresponding to 89% of all the genera and to 61% of the terrestrial species of Carnivora (and 100% of species for Hyaenidae and Ursidae). The number of specimens for each species was between one and three. The specimens chosen were adult and preferably wild caught. Specimens were obtained from the mammal collections of the Muséum National d'Histoire Naturelle (Paris, France); Anatomical Museum of Valladolid University (Valladolid, Spain); Museum of Comparative Zoology, Harvard University (Boston, MA, USA); Smithsonian National Museum of Natural History (Washington, DC, USA); Naturhistorisches Museum Basel (Basel, Switzerland); and the American Museum of Natural History (New York, NY, USA). The complete list of specimens used in the analyses are in the Supporting Information (Table S1).

GEOMETRIC MORPHOMETRICS

A total of 64 anatomical landmarks was taken on the surface of the skull to describe the overall shape (Fig. 1, Table 1). First, all 64 landmarks were manually recorded using Idav Landmark software (Wiley *et al.*, 2005). Then, a generalized Procrustes superimposition (Gower, 1975; Rohlf & Slice, 1990) was performed using the R library 'Geomorph' (Adams & Otárola-Castillo, 2013). A mean shape was calculated for each species.
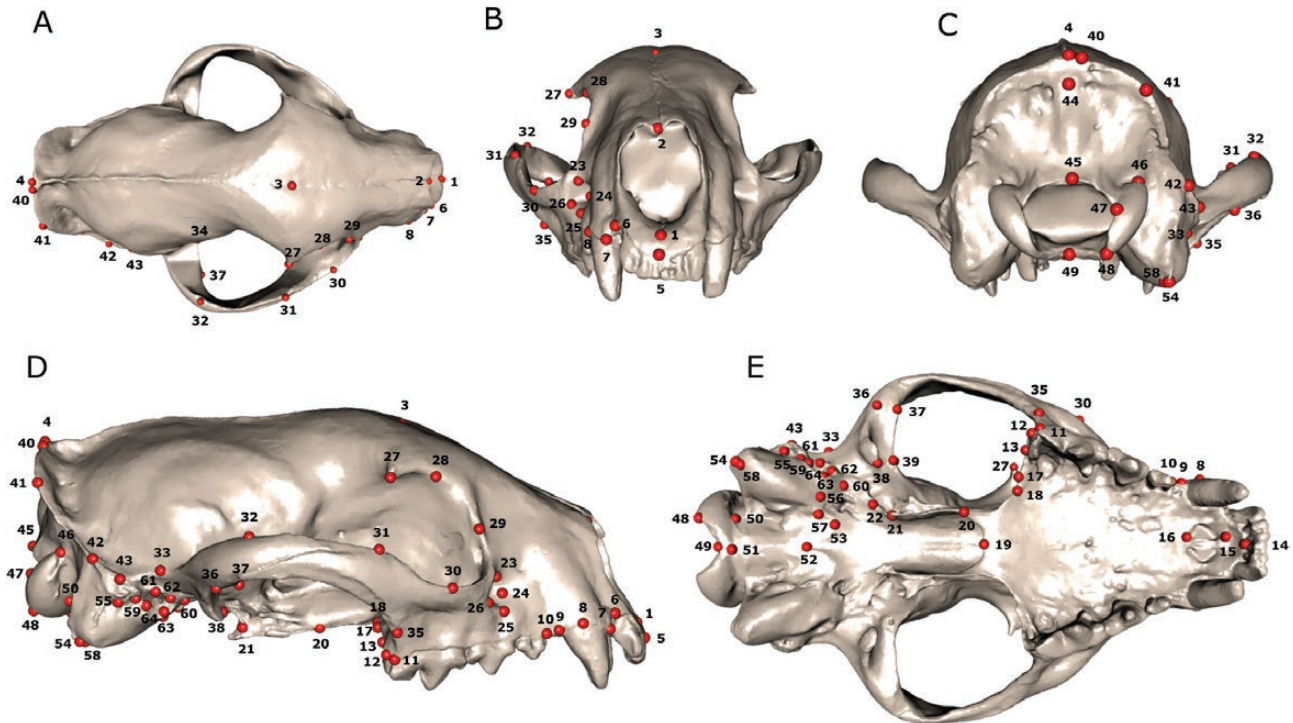
Figure 1. Position of the landmarks taken on the skull and used in our analyses (64 landmarks represented by the red dots) to quantify variation in shape of the skull. A, dorsal view. B, anterior view. C, posterior view. D, lateral view. E, ventral view. The skull used for this representation is a fosa (*Cryptoprocta ferox* MNHN-ZM-MO-1992-1668, Eupleridae).

PHYLOGENETIC SIGNAL

We used the phylogeny of Carnivora of Nyakatura & Bininda-Emonds (2012), which is complete at the specific level, as a basis for all phylogenetically based analyses. We pruned the tree using the R library 'ape' (Paradis, Claude & Strimmer, 2004). A multivariate K-value (K_{mult}) (Adams, 2014b) of the R library 'Geomorph' was used to assess the degree to which closely related Carnivora species display similar trait values. This method is based on 1000 random permutations to assess how well the morphometric data fit a phylogenetic tree. A K-value of zero corresponds to absence of phylogenetic signal, whereas a K-value greater than one indicates a strong phylogenetic signal, implying that morphological traits are conserved within the phylogeny.

PHYLOGENETIC GENERALIZED LEAST SQUARES

Phylogenetic generalized least squares (PGLS) analysis (Rohlf, 2001) was applied to account for both phylogeny and size on skull shape with the 'procD.pgls' function using the R library 'Geomorph' (Adams *et al.*, 2015; Collyer, Sekora & Adams, 2015). This approach allowed us to test whether there was a relationship between skull shape and size while accounting for phylogeny. Assuming a Brownian motion model of evolution (Adams, 2014a), the expected covariance is directly proportional to the amount of shared evolutionary history. Procrustes residuals of the phylogenetic regression can thus be used to conduct analyses with shape data, taking into account phylogeny and allometry effects. The average body mass of males and females was extracted from Hunter & Barrett (2011) and $\log_{10}$-transformed (Gould, 1966). All further analyses were performed on corrected data sets for phylogeny and allometry (PGLS Procrustes residuals).

PHENOTYPIC DISPARITY

Principal component analyses

Principal component analyses (PCAs) were performed to evaluate the distribution of species in morphospace. In order to visualize the phylogenetic relationships of species in the morphospace, the phylogeny (Nyakatura & Bininda-Emonds, 2012) was mapped onto the morphospace with the 'plotGMPhyloMorphoSpace' function using the R library 'Geomorph'.

Disparity

The phenotypic disparity was assessed by a calculation of the variance of Procrustes distances, i.e. square

Table 1. Definition of the anatomical landmarks on the skull used in the geometric morphometrics analysis

Landmark	Definition
1	Most cranio-dorsal point of the premaxilla
2	Tip of the nasal
3	Point of inter-frontal suture
4	Most prominent point of the postparietal
5	Most cranial point in the middle of the incisor row in the premaxilla
6	Most lateral point of the incisors row end
7	Most cranial contact point of the canine and the maxillary
8	Most lateral contact point of the canine and the maxillary
9	Most caudal contact point of the canine and the maxillary
10	Most cranio-lateral contact point of the first premolar and the maxillary
11	Most caudo-lateral contact point of the last premolar and the maxillary
12	Most cranio-lateral contact point of the first molar and the maxillary
13	Most caudo-lateral contact point of the last molar and the maxillary
14	Most caudal point in the middle of the incisive row
15	Most cranial point of the incisive foramen
16	Most caudal point of the incisive foramen
17	Most caudal point between the maxillary and the palatine
18	Point of maximum of curvature of the palatine
19	Caudo-ventral tip of the palatine
20	Most ventral point between the palatine and the pterygoid
21	Insertion point of the pterygoid process in the basisphenoid
22	Contact point between the pterygoid and the oval foramen
23	Most cranio-dorsal point of the infraorbital foramen
24	Most cranio-medial point of the infraorbital foramen
25	Most cranio-ventral point of the infraorbital foramen
26	Most cranio-lateral point of the infraorbital foramen
27	Tip of the post-orbital process
28	Point of maximum of curvature between the post-orbital process and the lachrymal foramen
29	Dorsal tip of the lachrymal foramen
30	Point of the maximum of concavity between the zygomatic process and the jugal
31	Most dorsal contact point between the jugal and the squamosal
32	Most dorsal point of the maximum of convexity of the squamosal
33	Most caudal point of insertion of the zygomatic process on the brain case
34	Most cranial point of insertion of the zygomatic process on the brain case
35	Most caudal point of contact between the jugal and the maxillary
36	Caudo-lateral tip of the glenoid cavity
37	Cranio-lateral tip of the glenoid cavity
38	Cranio-medial tip of the glenoid cavity
39	Caudo-medial tip of the glenoid cavity
40	Contact point between temporal line and the nuchal crest
41	Dorso-lateral point of the maximum of convexity of the nuchal crest
42	Contact point between the occipital and the temporal on the nuchal crest
43	Most dorso-lateral point of the mastoid process
44	Most dorsal point of the occipital protuberance
45	Most dorsal point of the foramen magnum
46	Latero-caudal tip of the occipital condyle
47	Most dorsal point of contact between the occipital condyle and the foramen magnum
48	Most medial point of maximal curvature of the occipital condyle
49	Most ventral point of the foramen magnum
50	Most lateral point of maximal curvature of the occipital condyle
51	Most caudal point of the pharyngeal tubercle
52	Point of contact between the basioccipital and the basisphenoid, middle
53	Point of maximal curvature of the basioccipital–basisphenoid structure

Table 1. *Continued*

Landmark	Definition
54	Ventral tip of the jugular process
55	Ventral tip of the mastoid process
56	Cranial tip of the tympanic bulla
57	Point of contact between the tympanic bulla and the basioccipital
58	Caudal tip of the tympanic bulla
59	Most caudo-dorsal point of the tympanic bulla narrowing
60	Most cranio-dorsal point of the tympanic bulla narrowing
61	Dorsal tip of the external acoustic meatus
62	Cranial tip of the external acoustic meatus
63	Ventral tip of the external acoustic meatus
64	Caudal tip of the external meatus

distance between the mean conformation for each species (species centroid) and the average conformation of the family (family centroid) as described by Zelditch (2012). The skull shape disparity has not been calculated for monogeneric and monospecific families (Ailuridae, Prionodontidae and Nandiniidae) because there is no morphological variation in these families in our sample. Variance-based disparity metrics include information about the spread of species within the morphospace and are preferentially used to avoid sampling bias and taxonomic differences between group errors (Foote, 1993, 1997; Zelditch, 2012). These metrics were calculated using the R library 'Geomorph' in PGLS Procrustes residuals.

RATE OF MORPHOLOGICAL EVOLUTION

To quantify the rate of morphological evolution in Carnivora at the family level, we used the function 'compare.evol.rates' of the R library 'Geomorph' (Adams, 2014a). This approach uses the aligned specimen coordinates to estimate the net multivariate rate of phenotypic change (σ_{2mult}) along a given phylogeny for each family based on a Brownian motion model. As methods for estimating rates of morphological evolution were based on comparisons among clades, we consider only clades with four or more species in order to avoid problems of morphological evolution rate estimation as recommended by Adams *et al.* (2009). Moreover, there is no phenotypic disparity for monospecific and monogeneric families, hence no possible comparison between skull shape disparity and the rate of morphological evolution for these (Ailuridae, Prionodontidae and Nandiniidae).

ECOLOGICAL DIVERSITY

A species-level presence/absence matrix of ecological dissimilarity was created by assigning several categories of diet and types of locomotion to each

species. The information was taken from Wilson & Mittermeier (2009).

The wide variety of diets of Carnivora were divided into height categories (Table 2). For the majority of species, diet is not composed 100% of a single food category, and the proportion of different types of foods may change depending on the availability of resources (Macdonald & Courtenay, 1996; Grassman, 1997; Lanszki *et al.*, 1999; Bianchi *et al.*, 2014). We considered only categories representing a significant portion of the diet, regardless of the season or geographical region (adapted from Goillot, Blondel & Peigné, 2009). We divided types of locomotion behaviours into six categories adapted from the literature (adapted from Fabre et al., 2015a, b; Table 3). The ecological diversity was calculated corresponding to the average Gower distance (Gower, 1971) of each family using the function 'daisy' of the R library 'Cluster' (Maechler *et al.*, 2017). Information on ecological categories for each species is provided in the Supporting Information (Table S2).

CORRELATION TESTS

To investigate the link between: (1) ecological diversity and both phenotypic disparity and the rate of morphological evolution; (2) specific richness and ecological diversity of families; and (3) phenotypic disparity and the rate of morphological evolution, we performed a non-parametric test using Kendall's τ rank correlation coefficient.

RESULTS

PHYLOGENETIC SIGNAL

Our results show a significant phylogenetic signal in the skull shape (K_{mult} = 0.38; P = 0.001) and highlight the importance of taking into account the phylogeny in further analyses.

Table 2. Definitions of diet categories used in this study (adapted from Goillot *et al.*, 2009)

Diet	Definition
Carnivorous	Diet including a significant portion of vertebrates
Piscivorous	Diet including a significant portion of fish
Malacophagous	Diet including a significant portion of shellfish and crabs
Insectivorous	Diet including a significant portion of arthropods and worms
Frugivorous	Diet including a significant portion of fruits
Folivorous/herbivorous	Diet including a significant portion of leaves and/or grass
Durophagous	Diet including a significant portion of meat and bone marrow
Omnivorous	Diet consists of animal prey, in addition to a variety of fruits or other vegetable matter

Table 3. Definitions of types of locomotion categories used in this study (adapted from Abella *et al.*, 2015; Fabre *et al.*, 2015a, b)

Lifestyle	Definition
Terrestrial	Spend a significant part of their time on the ground, but occasionally climb, swim or dig
Semi-fossorial	Spend a significant part of their time on the ground and often dig to make a burrow or find food
Arboreal	Spend more time in the trees than on the ground; forage actively in trees
Semi-arboreal	Spend a significant part of their time in the trees; do not forage in trees
Aquatic	Spend more time in the water than on the ground and can even sleep in water
Semi-aquatic	Spend a significant part of their time in water

PHYLOGENETIC GENERALIZED LEAST SQUARES

There was a significant effect of the $\log_{10}$-tranformed body mass on the shape of the skull when phylogeny was considered ($R^2 = 0.047$; $P = 0.001$). The following analyses were therefore performed on both skull shape (Procrustes coordinates) and corrected data sets for phylogeny and allometry (PGLS Procrustes residuals).

PRINCIPAL COMPONENT ANALYSES

The first three principal components (PCs) accounted for 61% of the overall variance of skull. The distribution defined by the scatterplot of the first axis tends to separate the Mustelidae from the Canidae (Fig. 2). Morphological conformations associated with the first axis show, at the negative part of the axis, species with a relatively short rostrum and a proportionally small and round orbit (such as the Mustelidae), whereas the positive side of the axis is associated with species showing a proportionally elongated rostrum and orbit on the cranio-caudal axis (such as the Canidae).

The second axis tends to separate the Felidae from the other families of Carnivora. Morphological conformations associated with the second axis show deformation of the skull along the dorso-ventral axis. The minimum of the axis corresponds to an elongated skull on the cranio-caudal axis, with a relatively elongated braincase and a proportionally medium-sized rostrum (such as the Herpestidae), whereas the maximum corresponds to a very rounded braincase, with a proportionally large, forward-facing round orbit and a relatively short rostrum (such as the Felidae).

The third axis tends to separate the Ursidae, on the positive part of the PC, from the Viverridae and Herpestidae, on the negative part of the PC. Nevertheless, there is no clear distinction between families in the morphospace for this axis (Supporting Information, Fig. S1). For the positive part of the axis, the morphological conformation corresponds to a skull with a rounded cranium and a proportionally medium-sized rostrum, whereas the negative part corresponds to a skull with a flattened braincase and a proportionally medium-sized rostrum.
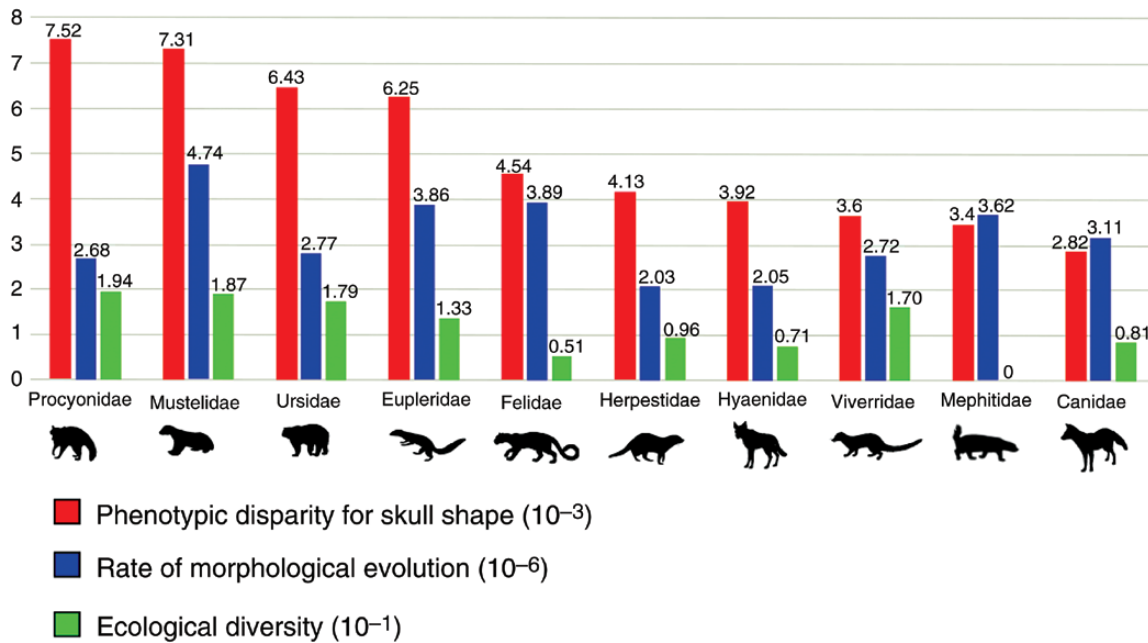
DISPARITY

The Procyonidae family was the most disparate, followed by the Mustelidae (Figs 3, 4). The Eupleridae and Ursidae also had a significant phenotypic disparity despite their small number of species and were respectively in third and fourth position in terms of disparity. The Viverridae, Mephitidae and Canidae had the smallest disparities and were respectively in eighth, ninth and last position.

RATES OF MORPHOLOGICAL EVOLUTION

The rates of morphological evolution were high for the Mustelidae, Felidae and Eupleridae and very low for the Hyaenidae and Herpestidae (Fig. 3).
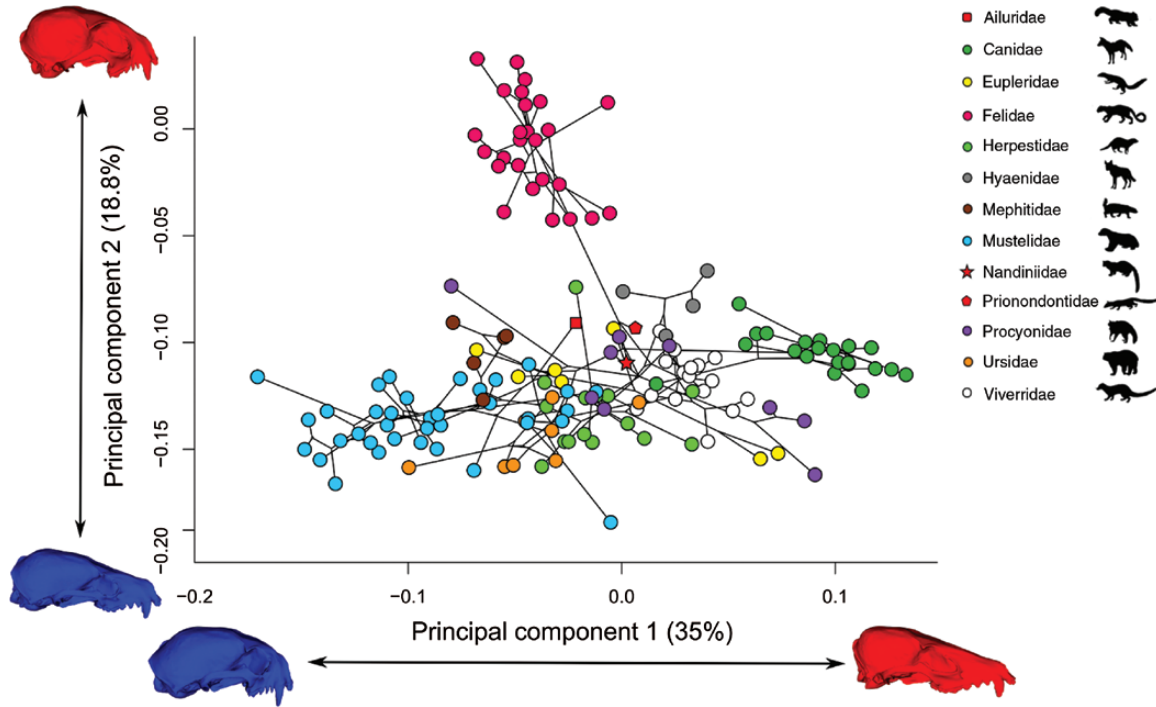
Figure 2. Results of the principal component analyses performed on the morphometric data of the skull. The phylogeny from Nyakatura & Bininda-Emonds (2012) is plotted in the shape space. Scatter plot illustrating the position of different species on the first and second principal components for the skull shape.

Figure 3. Histogram of skull phenotypic disparity, rate of morphological evolution and ecological diversity for the different families of terrestrial Carnivora.

© 2018 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2018, **XX**, 1–14

ECOLOGICAL DIVERSITY

The Procyonidae family was the most ecologically diverse (Figs 3, 4), then the Mustelidae and Ursidae. The Viverridae were fourth, followed by the Eupleridae. Conversely, the Mephitidae were ranked last, with an ecological diversity score of zero (corresponding to a similar ecology in our coding for all species sampled).

CORRELATION TEST

We find a positive significant correlation between phenotypic disparity and ecological diversity (one-tailed test for positive association: $\tau = 0.6$, $P = 0.008$). There was no significant correlation between specific richness and ecological diversity ($\tau = 0.15$, $P = 0.60$). Likewise, there was no significant correlation between the rate of morphological evolution and ecological diversity ($\tau = -0.07$, $P = 0.86$). Finally, there was no significant correlation between skull shape disparity and the rate of morphological evolution ($\tau = 0.06$, $P = 0.86$).

DISCUSSION

CORRELATION BETWEEN SKULL SHAPE DISPARITY AND ECOLOGICAL DIVERSITY IN CARNIVORA

The order Carnivora displays a wide range of diets (Nowak, 2005; Christiansen & Wroe, 2007; Van Valkenburgh, 2007) and shows an amazing diversity of modes of locomotion (Van Valkenburgh, 1985, 1987; Andersson *et al.*, 2003; Samuels, Meachen & Sakai, 2013; Martín-Serra, Figueirido & Palmqvist, 2014). Ecological traits and behaviour are suggested to drive the evolution of the morphology of species (Miles & Ricklefs, 1984; Norberg & Rayner, 1987; Ross & Kirk, 2007; Goodman, Miles & Schwarzkopf, 2008), and thereby a specific morphology can often be associated with a particular lifestyle (Wainwright, 1991; Argot, 2001; Sacco & Van Valkenburgh, 2004; Lewis, 2008; Polly & MacLeod, 2008; Milne *et al.*, 2009; Samuels *et al.*, 2013; Fabre et al., 2015a, b; Dumont *et al.*, 2016). For Carnivora, several studies have already highlighted the link between some morphological traits and lifestyle for extant species (Polly, 2008; Slater, Dumont & Van Valkenburgh, 2009; Fabre et al., 2013, 2014, 2015a, b; Botton-Divet *et al.*, 2016; Dumont *et al.*, 2016). However, the link between phenotypic disparity and ecological diversity among all Carnivora had never been tested before.

Our results show a significant correlation between skull shape disparity and ecological diversity among Carnivora families. This suggests that skull morphology is adaptive and is partly driven by constraints imposed by the different ecological niches, such as diet and locomotion, and that ecological opportunities could be the origin of phenotypic diversity. These results are consistent with previous studies showing that
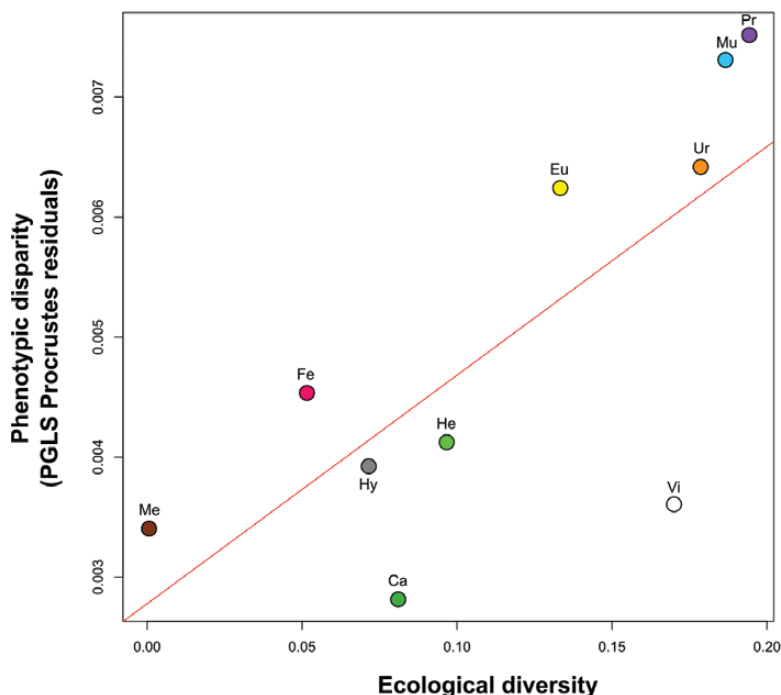
Figure 4. Correlation between phenotypic disparity and ecological diversity (Ca: Canidae, Eu: Eupleridae, Fe: Felidae, He: Herpestidae, Hy: Hyaenidae, Me: Mephitidae, Mu: Mustelidae, Pr: Procyonidae, Ur: Ursidae, Vi: Viverridae).

the diversity of forms generally increases with the diversity of ecological niches (Simpson, 1955; Collar, Near & Wainwright, 2005). The most striking example can be illustrated by the Mustelidae family, which shows a high skull shape disparity associated with an important ecological diversity. We also observe contrasting skull conformations related to ecological niches. Semi-aquatic or aquatic piscivorous and malacophagous species, such as otters, have particular cranial characteristics, with a very short rostrum and an elongated skull on the cranio-caudal axis associated with strong zygomatic arches. Semi-fossorial carnivorous and omnivorous species are characterized by a skull with a relatively elongated rostrum and proportionally elongated and round braincase. Semi-arboreal omnivorous and carnivorous species, such as *Martes* species, are distinguished by a proportionally medium-sized rostrum and elongated braincase. High diversity of form associated with a variety of ecological niches is one of the characteristics of adaptive radiation (see Schluter, 2000). Although the number of bursts in diversification of Mustelidae and palaeoenvironmental influences for speciation are debated (Koepfli *et al.*, 2008; Law, Slater & Mehta, 2018), our results highlight a link between the phenotypic diversification and the occupation of new ecological niches for this family. On the contrary, the Canidae present both a low phenotypic disparity and a low ecological diversity, and exhibit a single skull conformation characterized by a proportionally very long rostrum and an elongated skull on the cranio-caudal axis.

Although the assumption of a correlation between skull shape disparity and ecological diversity appears to be reasonably intuitive, testing this correlation is a necessity because many studies show that this correlation is not universal. For example, 'many-to-one mapping' of form and function suggests that several morphologies and physiologies can yield equivalent function in the same ecological environment (Alfaro, Bolnick & Wainwright, 2005; Wainwright *et al.*, 2005; Dean, Bizzarro & Summers, 2007; Khatri, McLeish & Sear, 2009). From this definition, a high disparity should be related to a low ecological diversity. Such a pattern is found in the Felidae. Indeed, the high phenotypic skull disparity that we found in this family goes against the hypotheses that highly specialized families, such as hypercarnivorous families, present a lower phenotypic disparity than families with a wide range of diets. Previous studies on phenotypic disparity among Felidae focused only on the dentition and mandible (Holliday & Steppan, 2004) or had only a small sample of extant species (Goswami *et al.*, 2011). All Felidae could be characterized by a rounded braincase, a large, round orbit and a proportionally medium to short rostrum. But despite these common features, there is a high skull shape disparity within

this family; for example, *Octolobus manul* has a very spherical skull with an extremely wide orbit, whereas *Panthera leo* displays a relatively medium-sized rostrum with an elongated sagittal crest. On the contrary, other studies have shown that different ecological pressures can lead to very similar morphological and physiological traits (Landmann, 1995; Marino, 2002; Taylor, Nudds & Thomas, 2003; Gleiss *et al.*, 2011), and some morphologies are more generalist and allow the exploitation of different ecological niches (Yamada & Boulding, 1998; Scott *et al.*, 2003; Tulli *et al.*, 2016). Thus, even though our data show a positive correlation between skull shape disparity and ecological diversity, we note that some families, such as Viverridae, have a very high ecological diversity but a low phenotypic disparity. Also, the different ecological categories are not equal in terms of selective pressure on morphology (Schmidt-Nielsen, 1972; Landmann, 1995; Skrovan *et al.*, 1999), which can affect the disparity.

Finally, it should be emphasized that ecological diversity was calculated using a matrix of diet and type of locomotion categories taken from the literature. Also, data often remain partial or anecdotal, especially for species that are difficult to observe in the wild. Information is also very often generalized for a genus or taxon, without precise quantification of the composition of the diet or the time spent in the various locomotor habitats. Moreover, the way of coding has a significant influence on the analyses. Likewise, it is important to note that Carnivora are represented by only ten families (once monogeneric families have been removed). The robustness of the statistical tests used in the present study could thus be improved by using a wider sampling among mammals. The analysis of several large orders of mammals could improve the statistical robustness of our tests and would be useful to check whether this correlation is found in other orders of mammals.

ABSENCE OF SIGNIFICANT CORRELATION BETWEEN RATE OF MORPHOLOGICAL EVOLUTION AND ECOLOGICAL DIVERSITY

Our study does not reveal a significant correlation between the rate of morphological evolution and ecological diversity. It seems that only some Carnivora families have undergone a high rate of change of skull shape linked to ecological opportunities. For example, the Mustelidae show both a high rate of morphological evolution and a high ecological diversity. Moreover, the fact that this family has a great phenotypic disparity is congruent with the assumed hypothesis of adaptive radiation for the Mustelidae (see Koepfli *et al.*, 2008). It is interesting to note that the same pattern can be found in the Eupleridae, a family endemic to Madagascar, which has diversified in the absence of other carnivores (Yoder *et al.*, 2003).

The pattern of low ecological diversity associated with a high rate of morphological evolution could be explained by an important phenotypic shift of skull morphology leading to a shared morphotype (low disparity) adapted for one particular lifestyle. For example, the Mephitidae display a very low disparity, a high rate of morphological evolution and a low ecological diversity, which could indicate an important change of skull shape leading to a single semi-fossorial morphotype (elongated skull on the cranio-caudal axis, with relatively elongated braincase and a weak post-orbital process).

Some families have a low rate of evolution and both high ecological diversity and high phenotypic disparity, such as the Procyonidae and Ursidae. This could be explained by the fact that morphological changes, even when driven by ecology, could be made gradually rather than by a fast shift. These two patterns (many progressive morphological changes vs. a small number of significant morphological changes) could lead to a similar phenotypic disparity and ecological diversity, but with a contrasting rate of morphological evolution (Adams *et al.*, 2009).

Of course, some environmental and behavioural parameters known to influence the rate of morphological evolution were not considered in the present study. For example, hunting behaviour and, in particular, solitary vs. pack hunting, might affect the evolution rate in Carnivora, with solitary hunters having slower rates of morphological evolution, as shown by Meloro, Clauss & Raia (2015) for the mandible.

ABSENCE OF SIGNIFICANT CORRELATION BETWEEN PHENOTYPIC DISPARITY AND THE RATE OF MORPHOLOGICAL EVOLUTION

We did not find a significant correlation between skull shape disparity and the rate of morphological evolution for the skull shape in Carnivora. Our initial hypothesis of a correlation between phenotypic disparity and the evolution rate came from the intuitive idea that the higher the rate of morphological evolution is in a family, the greater the diversity of forms would be. This pattern is particularly expected in adaptive radiation (Schluter, 2000; Harmon et al., 2005, 2008; Jones *et al.*, 2015; Esquerré & Keogh, 2016). Interestingly, our results for the Eupleridae, the endemic family of Malagasy Carnivora, show a high rate of morphological evolution and a great phenotypic disparity, which are the expected patterns in an island radiation (Garcia-Porta *et al.*, 2016).

Adams *et al.* (2009) showed that a correlation between phenotypic disparity and the rate of morphological evolution is far from being universal. Regarding our data, several explanations can be given for the mismatch between these two parameters. A low disparity associated with a high rate of evolution could be the result of a major morphological change early in the taxa history, leading to very similar morphologies for the whole family, as already discussed for the Mephitidae. The Felidae could represent a good example of this pattern insofar as they cover a whole specific portion of the Carnivora morphological space and present very specific characteristics (Christiansen, 2008; Sakamoto & Ruta, 2012). But contrary to our expectations, this family has an important skull shape disparity.

On the contrary, a high skull shape disparity associated with a very low evolution rate could be explained by more morphological changes along the phylogenetic tree that lead to more gradual and sparse changes in the morphology of the family. This leads to contrasting morphotypes within a family. This phenomenon is observed in the Procyonidae, in which three morphotypes could be distinguished in the morphospace corresponding to: (1) *Potos* (round braincase, wide orbit and relatively short rostrum); (2) *Bassaricyon*, *Bassariscus* and *Procyon* (relatively flatter braincase and medium rostrum); and (3) *Nasua* and *Nasuella* (proportionally very long rostrum with robust zygomatic arches). Interplay between evolutionary rates and modularity (the tendency of characters to vary in a coordinated way) has also been demonstrated to influence the disparity and evolution rate for Carnivora, which could explain this result (Goswami & Polly, 2010; Goswami *et al.*, 2014). Modularity is acting as a control factor of morphological evolution. Strong modularity could possibly promote phenotypic disparity and the rate of morphological evolution, whereas strong integration might have a tendency to constrain the emergence of new morphologies (Klingenberg, 2008; Goswami & Polly, 2010; Sanger *et al.*, 2012; Goswami *et al.*, 2014). It is also important to note that the calculation of the rates of evolution originates from a topology (O'Meara *et al.*, 2006). We consider only modern taxa that have evolved since the Palaeocene; it is therefore possible that including fossil taxa would bring more different results by adding very different skull morphology to our sample (Goswami *et al.*, 2011).

CONCLUSION

Our study suggests the existence of a significant correlation between ecological diversity (based on diet and type of locomotion) and skull shape disparity in Carnivora. On the contrary, our data did not show any correlation between ecological diversity and the rate of morphological evolution, or between phenotypic disparity and the rate of morphological evolution, which could be explained by a contrasting shift in morphological evolutionary rate among families. This could be explored further using a larger sample within mammals.

ACKNOWLEDGEMENTS

REFERENCES

Abella J, Pérez-Ramos A, Valenciano A, Alba DM, Ercoli MD, Hontecillas D, Montoya P, Morales J. 2015. Tracing the origin of the panda's thumb. *Science of Nature* **102:** 35.

Adams DC. 2014a. Quantifying and comparing phylogenetic evolutionary rates for shape and other high-dimensional phenotypic data. *Systematic Biology* **63:** 166–177.

Adams DC. 2014b. A generalized *K* statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. *Systematic Biology* **63:** 687–697.

Adams DC, Berns CM, Kozak KH, Wiens JJ. 2009. Are rates of species diversification correlated with rates of morphological evolution? *Proceedings of the Royal Society B: Biological Sciences* **276:** 2729–2738.

Adams DC, Collyer ML. 2015. Permutation tests for phylogenetic comparative analyses of high-dimensional shape data: what you shuffle matters. *Evolution* **69:** 823–829.

Adams DC, Otárola-Castillo E. 2013. Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution* **4:** 393–399.

Alfaro ME, Bolnick DI, Wainwright PC. 2005. Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. *The American Naturalist* **165:** 140–154.

Andersson K, Werdelin L. 2003. The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology. *Proceedings of the Royal Society B: Biological Sciences* **270:** S163–S165.

Argot C. 2001. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology* **247:** 51–79.

Beaulieu JM, Jhwueng DC, Boettiger C, O'Meara BC. 2012. Modeling stabilizing selection: expanding the Ornstein–Uhlenbeck model of adaptive evolution. *Evolution* **66:** 2369–2383.

Bianchi CR de C, Campos RC, Xavier-Filho NL, Olifiers N, Gompper ME, Mourão G. 2014. Intraspecific, interspecific, and seasonal differences in the diet of three mid-sized carnivores in a large neotropical wetland. *Acta Theriologica* **59:** 13–23.

Botton-Divet L, Cornette R, Fabre AC, Herrel A, Houssaye A. 2016. Morphological analysis of long bones in semi-aquatic mustelids and their terrestrial relatives. *Integrative and Comparative Biology* **56:** 1298–1309.

Burbrink FT, Ruane S, Pyron RA. 2012. When are adaptive radiations replicated in areas? Ecological opportunity and unexceptional diversification in West Indian dipsadine snakes (Colubridae: Alsophiini). *Journal of Biogeography* **39:** 465–475.

Caumul R, Polly PD. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). *Evolution* **59:** 2460–2472.

Christiansen P. 2008. Evolution of skull and mandible shape in cats (Carnivora: Felidae). *PLoS ONE* **3:** e2807.

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

Collar DC, Near TJ, Wainwright PC. 2005. Comparative analysis of morphological diversity: does disparity accumulate at the same rate in two lineages of centrarchid fishes? *Evolution* **59:** 1783–1794.

Collyer ML, Sekora DJ, Adams DC. 2015. A method for analysis of phenotypic change for phenotypes described by high-dimensional data. *Heredity* **115:** 357–365.

Dean MN, Bizzarro JJ, Summers AP. 2007. The evolution of cranial design, diet, and feeding mechanisms in batoid fishes. *Integrative and Comparative Biology* **47:** 70–81.

Diniz-Filho JAF, Rodríguez MÁ, Bini LM, Olalla-Tarraga MA, Cardillo M, Nabout JC, Hortal J, Hawkins BA. 2009. Climate history, human impacts and global body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales. *Journal of Biogeography* **36:** 2222–2236.

Dumont M, Wall CE, Botton-Divet L, Goswami A, Peigné S, Fabre AC. 2016. Do functional demands associated with locomotor habitat, diet, and activity pattern drive skull shape evolution in musteloid carnivorans? *Biological Journal of the Linnean Society* **117:** 858–878.

Esquerré D, Keogh JS. 2016. Parallel selective pressures drive convergent diversification of phenotypes in pythons and boas. *Ecology Letters* **19:** 800–809.

Evans KM, Waltz BT, Tagliacollo VA, Sidlauskas BL, Albert JS. 2017. Fluctuations in evolutionary integration allow for big brains and disparate faces. *Scientific Reports* **7:** 40431.

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

Fabre AC, Cornette R, Peigné S, Goswami A. 2013. Influence of body mass on the shape of forelimb in musteloid carnivorans. *Biological Journal of the Linnean Society* **110:** 91–103.

Fabre AC, Goswami A, Peigné S, Cornette R. 2014. Morphological integration in the forelimb of musteloid carnivorans. *Journal of Anatomy* **225:** 19–30.

Fabre AC, Salesa MJ, Cornette R, Antón M, Morales J, Peigné S. 2015b. Quantitative inferences on the locomotor behaviour of extinct species applied to *Simocyon batalleri* (Ailuridae, Late Miocene, Spain). *Die Naturwissenschaften* **102:** 30.

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

Foote M. 1993. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* **19:** 185–204.

Foote M. 1997. The evolution of morphological diversity. *Annual Review of Ecology and Systematics* **28:** 129–152.

Garcia-Porta J, Šmíd J, Sol D, Fasola M, Carranza S. 2016. Testing the island effect on phenotypic diversification: insights from the *Hemidactylus* geckos of the Socotra Archipelago. *Scientific Reports* **6:** 23729.

Gittenberger E. 1991. What about non-adaptive radiation? *Biological Journal of the Linnean Society* **43:** 263–272.

Gleiss AC, Jorgensen SJ, Liebsch N, Sala JE, Norman B, Hays GC, Quintana F, Grundy E, Campagna C, Trites AW, Block BA, Wilson RP. 2011. Convergent evolution in locomotory patterns of flying and swimming animals. *Nature Communications* **2:** 352.

Goillot C, Blondel C, Peigné S. 2009. Relationships between dental microwear and diet in Carnivora (Mammalia) — implications for the reconstruction of the diet of extinct taxa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **271:** 13–23.

Goodman BA, Miles DB, Schwarzkopf L. 2008. Life on the rocks: habitat use drives morphological and performance evolution in lizards. *Ecology* **89:** 3462–3471.

Goswami A. 2006. Morphological integration in the carnivoran skull. *Evolution* **60:** 169–183.

Goswami A, Milne N, Wroe S. 2011. Biting through constraints: cranial morphology, disparity and convergence across living and fossil carnivorous mammals. *Proceedings of the Royal Society B: Biological Sciences* **278:** 1831–1839.

Goswami A, Polly PD. 2010. The influence of modularity on cranial morphological disparity in Carnivora and Primates (Mammalia). *PLoS One* **5:** e9517.

Goswami A, Smaers JB, Soligo C, Polly PD. 2014. The macroevolutionary consequences of phenotypic integration: from development to deep time. *Philosophical Transactions of the Royal Society B: Biological Sciences* **369:** 20130254.

Gould SJ. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews of the Cambridge Philosophical Society* **41:** 587–640.

Gower, JC. 1971. A general coefficient of similarity and some of its properties. *Biometrics* **27:** 857.

Gower JC. 1975. Generalized procrustes analysis. *Psychometrika* **40:** 33–51.

Grassman LI Jr. 1997. *Ecology and behavior of four sympatric carnivore species (Mammalia: Carnivora) in Kaeng Krachan National Park, Thailand*. Unpublished MSc. Thesis, Bangkok: Kasetsart University.

Hampton PM. 2011. Comparison of cranial form and function in association with diet in natricine snakes. *Journal of Morphology* **272:** 1435–1443.

Hanken J, Hall BK. 1993. *The skull, volume 3: functional and evolutionary mechanisms*. Chicago: University of Chicago Press.

Harmon LJ, Kolbe JJ, Cheverud JM, Losos JB. 2005. Convergence and the multidimensional niche. *Evolution* **59:** 409–421.

Harmon LJ, Melville J, Larson A, Losos JB. 2008. The role of geography and ecological opportunity in the diversification of day geckos (*Phelsuma*). *Systematic Biology* **57:** 562–573.

Harmon LJ, Schulte JA 2nd, Larson A, Losos JB. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* **301:** 961–964.

Hartstone-Rose A, Wahl S. 2008. Using radii-of-curvature for the reconstruction of extinct South African carnivoran masticatory behavior. *Comptes Rendus Palevol* **7:** 629–643.

Herrel A, Holanova V. 2008. Cranial morphology and bite force in *Chamaeleolis* lizards – adaptations to molluscivory? *Zoology* **111:** 467–475.

Holliday JA, Steppan SJ. 2004. Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. *Paleobiology* **30:** 108–128.

Hunter L, Barrett P. 2011. *Carnivores of the world*. Princeton: Princeton University Press.

Hulsey CD, Wainwright PC. 2002. Projecting mechanics into morphospace: disparity in the feeding system of labrid fishes. *Proceedings of the Royal Society B: Biological Sciences* **269:** 317–326.

Johnson WE, Eizirik E, Pecon-Slattery J, Murphy WJ, Antunes A, Teeling E, O'Brien SJ. 2006. The late Miocene radiation of modern Felidae: a genetic assessment. *Science* **311:** 73–77.

Jones KE, Smaers JB, Goswami A. 2015. Impact of the terrestrial-aquatic transition on disparity and rates of evolution in the carnivoran skull. *BMC Evolutionary Biology* **15:** 8.

Khatri BS, McLeish TCB, Sear RP. 2009. Statistical mechanics of convergent evolution in spatial patterning. *Proceedings of the National Academy of Sciences of the United States of America* **106:** 9564–9569.

Klingenberg CP. 2008. Morphological integration and developmental modularity. *Annual Review of Ecology, Evolution, and Systematics* **39:** 115–132.

Kocher TD. 2004. Adaptive evolution and explosive speciation: the cichlid fish model. *Nature Reviews. Genetics* **5:** 288–298.

Koepfli KP, Deere KA, Slater GJ, Begg C, Begg K, Grassman L, Lucherini M, Veron G, Wayne RK. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology* **6:** 10.

Kozak KH, Weisrock DW, Larson A. 2006. Rapid lineage accumulation in a non-adaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (Plethodontidae: Plethodon). *Proceedings of the Royal Society B: Biological Sciences* **273:** 539–546.

Kunz TH, Fenton MB. 2005. *Bat ecology*. Chicago: University of Chicago Press.

Landmann A. 1995. Guild organisation and morphology of high-altitude granivorous and insectivorous birds: convergent evolution in an extreme environment. *Oikos* **73:** 237–250.

Lanszki J, Körmendi S, Hancz C, Zalewski A. 1999. Feeding habits and trophic niche overlap in a Carnivora community of Hungary. *Acta Theriologica* **44:** 429–442.

Law CJ, Slater GJ, Mehta RS. 2018. Lineage diversity and size disparity in Musteloidea: testing patterns of adaptive radiation using molecular and fossil-based methods. *Systematic Biology* **67:** 127–144.

Lewis ME. 2008. The femur of extinct bunodont otters in Africa (Carnivora, Mustelidae, Lutrinae). *Comptes Rendus Palevol* **7:** 607–627.

Losos JB, Mahler DL. 2010. Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In: Bell MA, Futuyama DJ, Eanes WF, Levinton JS, eds. *Evolution since Darwin: the first 150 years*. Sunderland, MA: Sinauer Associates, 381–420.

Losos JB, Ricklefs RE. 2009. Adaptation and diversification on islands. *Nature* **457:** 830–836.

Macdonald DW, Courtenay O. 1996. Enduring social relationships in a population of crab-eating zorros, *Cerdocyon thous*, in Amazonian Brazil (Carnivora, Canidae). *Journal of Zoology* **239:** 329–355.

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. 2017. *Cluster: cluster analysis basics and extensions*. Available at: https://cran.r-project.org/web/views/Cluster.html

Marino L. 2002. Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution* **59:** 21–32.

Marroig G, Cheverud JM. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of New World monkeys. *Evolution* **55:** 2576–2600.

Martín-Serra A, Figueirido B, Palmqvist P. 2014. A three-dimensional analysis of the morphological evolution and locomotor behaviour of the carnivoran hind limb. *BMC Evolutionary Biology* **14:** 129.

Marugán-Lobón J, Buscalioni AD. 2003. Disparity and geometry of the skull in Archosauria (Reptilia: Diapsida). *Biological Journal of the Linnean Society* **80:** 67–88.

Meloro C, Clauss M, Raia P. 2015. Ecomorphology of Carnivora challenges convergent evolution. *Organisms Diversity and Evolution* **15:** 711–720.

Miles DB, Ricklefs RE. 1984. The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* **65:** 1629–1640.

Milne N, Vizcaíno SF, Fernicola JC. 2009. A 3D geometric morphometric analysis of digging ability in the extant and fossil cingulate humerus. *Journal of Zoology* **278:** 48–56.

Moore WJ. 1981. *The mammalian skull*. Cambridge: Cambridge University Press.

Muschick M, Indermaur A, Salzburger W. 2012. Convergent evolution within an adaptive radiation of cichlid fishes. *Current Biology* **22:** 2362–2368.

Norberg UM, Rayner JMV. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **316:** 335–427.

Nowak RM. 2005. *Walker's carnivores of the world*. Baltimore, MD: JHU Press.

Nyakatura K, Bininda-Emonds OR. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* **10:** 12.

O'Meara BC, Ané C, Sanderson MJ, Wainwright PC. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution* **60:** 922–933.

Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20:** 289–290.

Polly PD, Macleod N. 2008. Characterization and comparison of 3D shapes using eigen surface analysis: locomotion in Tertiary carnivora. *Journal of Vertebrate Paleontology* **11:** 10–13.

R Core Team. 2017. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Rabosky DL, Adams DC. 2012. Rates of morphological evolution are correlated with species richness in salamanders. *Evolution* **66:** 1807–1818.

Rabosky DL, Glor RE. 2010. Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proceedings of the National Academy of Sciences of the United States of America* **107:** 22178–22183.

Rabosky DL, Santini F, Eastman J, Smith SA, Sidlauskas B, Chang J, Alfaro ME. 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications* **4:** 1958.

Revell LJ. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3:** 217–223.

Ricklefs RE. 2004. Cladogenesis and morphological diversification in passerine birds. *Nature* **430:** 338–341.

Ricklefs RE. 2006. Time, species, and the generation of trait variance in clades. *Systematic Biology* **55:** 151–159.

Rohlf FJ. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* **55:** 2143–2160.

Rohlf FJ, Slice D. 1990. Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39:** 40–59.

Ross CF, Kirk EC. 2007. Evolution of eye size and shape in primates. *Journal of Human Evolution* **52:** 294–313.

Rowe KC, Aplin KP, Baverstock PR, Moritz C. 2011. Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. *Systematic Biology* **60:** 188–203.

Sacco T, Van Valkenburgh B. 2004. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). *Journal of Zoology* **263:** 41–54.

Sakamoto M, Ruta M. 2012. Convergence and divergence in the evolution of cat skulls: temporal and spatial patterns of morphological diversity. *PLoS One* **7:** e39752.

Samuels JX, Meachen JA, Sakai SA. 2013. Postcranial morphology and the locomotor habits of living and extinct carnivorans. *Journal of Morphology* **274:** 121–146.

Sanger TJ, Mahler DL, Abzhanov A, Losos JB. 2012. Roles for modularity and constraint in the evolution of cranial diversity among *Anolis* lizards. *Evolution* **66:** 1525–1542.

Schluter D. 2000. *The ecology of adaptive radiation*. Oxford: Oxford University Press.

Schmidt-Nielsen K. 1972. Locomotion: energy cost of swimming, flying, and running. *Science* **177:** 222–228.

Scott SN, Clegg SM, Blomberg SP, Kikkawa J, Owens IP. 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. *Evolution* **57:** 2147–2156.

Simpson GG. 1944. *Tempo and mode in evolution*. New York: Columbia University Press.

Simpson GG. 1955. *Major features of evolution*. New York: Columbia University Press.

Skrovan RC, Williams TM, Berry PS, Moore PW, Davis RW. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. *The Journal of Experimental Biology* **202:** 2749–2761.

Slater GJ, Dumont ER, Van Valkenburgh B. 2009. Implications of predatory specialization for cranial form and function in canids. *Journal of Zoology* **278:** 181–188.

Slater GJ, Price SA, Santini F, Alfaro ME. 2010. Diversity versus disparity and the radiation of modern cetaceans. *Proceedings of the Royal Society B: Biological Sciences* **277:** 3097–3104.

Taylor GK, Nudds RL, Thomas AL. 2003. Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. *Nature* **425:** 707–711.

Tulli MJ, Cruz FB, Kohlsdorf T, Abdala V. 2016. When a general morphology allows many habitat uses. *Integrative Zoology* **11:** 483–499.

Van Valkenburgh B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* **11:** 406–428.

Van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. *Journal of Vertebrate Paleontology* **7:** 162–182.

Van Valkenburgh B. 2007. Deja vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology* **47:** 147–163.

Wainwright PC. 1991. Ecomorphology: experimental functional anatomy for ecological problems. *Integrative and Comparative Biology* **31:** 680–693.

Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD. 2005. Many-to-one mapping of form to function: a general principle in organismal design? *Integrative and Comparative Biology* **45:** 256–262.

Wiley DF, Amenta N, Alcantara DA, Ghosh D, Kil YJ, Delson E, Harcourt-Smith W, Rohlf FJ, St John K, Hammann B. 2005. Evolutionary morphing. In: *Proceedings of the IEEE Visualization Conference*. 55.

Wilson DE, Mittermeier RA. 2009. *Handbook of the mammals of the world. Volume 1. Carnivores*. Barcelona: Lynx Edicions.

Yamada SB, Boulding EG, Yamada SB, Pianka ER. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology* **220:** 191–211.

Yoder AD, Burns MM, Zehr S, Delefosse T, Veron G, Goodman SM, Flynn JJ. 2003. Single origin of Malagasy Carnivora from an African ancestor. *Nature* **421:** 734–737.

Zelditch ML, Li J, Tran LA, Swiderski DL. 2015. Relationships of diversity, disparity, and their evolutionary rates in squirrels (Sciuridae). *Evolution* **69:** 1284–1300.

Zelditch ML, Swiderski DL, Sheets HD, Fink WL. 2012. *Geometric morphometrics for biologists: a primer*. London: Elsevier Academic Press.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Specimens used in this study and all associated information.

Table S2. Ecology and average body mass of sampled species.

Figure S1. Results of the principal component analyses performed on the morphometric data of the skull (phylogenetic generalized least squares Procrustes residuals). The phylogeny from Nyakatura & Bininda-Emonds (2012) is plotted in the shape space. Scatter plot illustrating the position of different species on the first and third principal components for the skull shape.