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

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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.


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...
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; Burbrik, 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.
Phenotypic Disparity in Carnivora

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 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.pgl’ 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

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

RESULTS
PHYLOGENETIC SIGNAL
Our results show a significant phylogenetic signal in the skull shape ($K_{\text{mult}} = 0.38; P = 0.001$) and highlight the importance of taking into account the phylogeny in further analyses.
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.
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; Martin-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 Eulateridae, 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.
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REFERENCES


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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.