



Do functional demands associated with locomotor habitat, diet, and activity pattern drive skull shape evolution in musteloid carnivorans?

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A major goal of evolutionary studies is to better understand how complex morphologies are related to the different functions and behaviours in which they are involved. For example, during locomotion and hunting behaviour, the head and the eyes have to stay at an appropriate level in order to reliably judge distance as well as to provide postural information. The morphology and orientation of the orbits and cranial base will have an impact on eye orientation. Consequently, variation in orbital and cranial base morphology is expected to be correlated with aspects of an animal's lifestyle. In this study, we investigate whether the shape of the skull evolves in response to the functional demands imposed by ecology and behaviour using geometric morphometric methods. We test if locomotor habitats, diet, and activity pattern influence the shape of the skull in musteloid carnivorans using (M)ANOVAs and phylogenetic (M)ANOVAs, and explore the functional correlates of morphological features in relation to locomotor habitats, diet, and activity pattern. Our results show that phylogeny, locomotion and, diet strongly influence the shape of the skull, whereas the activity pattern seems to have a weakest influence. We also show that the locomotor environment is highly integrated with foraging and feeding, which can lead to similar selective pressures and drive the evolution of skull shape in the same direction. Finally, we show similar responses to functional demands in musteloids, a super family of close related species, as are typically observed across all mammals suggesting the pervasiveness of these functional demands. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **00**, 000–000.

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INTRODUCTION

The skull is ontogenetically and functionally extremely complex (Moore, 1981; Hanken & Hall, 1993). It protects and houses the principal sensory organs (sense of smell, sight, taste, and hearing) and protects the brain which processes the input of these sensory organs (Wake & Roth, 1989; Hanken & Hall, 1993; Lieberman, Ross & Ravosa, 2000; Marroig & Cheverud, 2001, 2004; Van Valkenburg *et al.*, 2014).

It also has important functional roles in food gathering and processing, drinking, vocalization, and breathing (Wake & Roth, 1989; Russell & Thomason, 1993; Lieberman *et al.*, 2000; Marroig & Cheverud, 2001, 2004). Thus, its shape may be constrained by development and phylogeny while also being constrained by the mechanical demands imposed by its different functional roles (Van Valkenburg *et al.*, 2014). Previous studies have shown that locomotor habitat and behaviour such as the activity pattern of an animal (Cartmill, 1970, 1972, 1992; Heesy, 2004,

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2007, 2009; Harmon *et al.*, 2005; Baab *et al.*, 2014), its diet (Goswami, 2006; Cox, 2008; Kulemeyer *et al.*, 2009; Slater & Van Vakenburg, 2009; Baab *et al.*, 2014), and also phylogeny (Lieberman *et al.*, 2000; Baab *et al.*, 2014) play an important role in driving the evolution of skull shape.

In this study, we investigate the influence of locomotor habitat, diet, and activity pattern on skull shape evolution using the Musteloidea as a model group. This group displays a great species diversity, encompassing over 82 species, more than one-third of all living carnivorans (Wilson & Mittermeier, 2009). Musteloids are also ecologically diverse (Ewer, 1973; Nowak, 2005; Wilson & Mittermeier, 2009) and show a remarkable diversity of locomotor habitats (ranging from arboreal species such as the kinkajou and the red panda that climb, to specialized swimmers species such as the sea otter; Ewer, 1973; Nowak, 2005; Wilson & Mittermeier, 2009; Fabre *et al.*, 2013a, 2014b, 2015a, b). Musteloids also show highly diverse diets ranging from strictly herbivorous species such as the red panda to strictly carnivorous species such as the wolverine (Ewer, 1973; Nowak, 2005; Wilson & Mittermeier, 2009). Moreover, musteloids are geographically widespread and occupy a wide range of habitats (Ewer, 1973; Nowak, 2005; Wilson & Mittermeier, 2009). As a consequence of their adaptation to these different kinds of habitats over geological time, they display an exceptional disparity and diversity of form and function. For example, they show variation in size spanning three orders of magnitude (from 45 g for the least weasel to 45 kg for the sea otter), with little or no change in limb posture (Fabre *et al.*, 2013b). Musteloids show also a wide variety of activity patterns from diurnal to nocturnal (Ewer, 1973; Nowak, 2005; Wilson & Mittermeier, 2009). The grison has, for example, a crepuscular activity while others like the coati, the tayra, or the sea otter are diurnal, and yet others change their activity patterns during the year (arrhythmic; e.g. the wolverine). Finally, their phylogeny is well-studied and well resolved (Flynn *et al.*, 2005; Koepfli *et al.*, 2007, 2008; Sato *et al.*, 2009, 2012; Eizirik *et al.*, 2010; Slater, Harmon & Alfaro, 2012). The Musteloidea includes four families: Mephitidae (including skunks and stink badgers; 4 genera, 12 species), Mustelidae (including badgers, otters, weasels, and their relatives; 22 genera, 57 species), Procyonidae (including coatis, raccoons, the kinkajou and their relatives; 6 genera, 12 species), and Ailuridae (which is represented by a sole living representative, the red panda).

Here, we aim to test if locomotor habitat, diet, and activity pattern influence the shape of the skull in musteloids. Previous studies on this group have investigated the morphology of some mustelids (Lee

& Mill, 2004), the relationship between diet and skull morphology in three species of mustelids (Riley, 1985), and in ferrets (He & Kiliaridis, 2004), the sexual dimorphisms in two species of marten (Loy, Spinosi & Carlini, 2004), and the systematics and phylogeny of musteloids with a comparison of results obtained using molecular and the geometric morphometrics datasets (Catalano, Ercoli & Prevosti, 2015). So far, however, no macroevolutionary study examining the influence of functional factors on the skull shape of musteloids has been performed. In this study, we use 3D surface geometric morphometric methods (GMM) to investigate the shape of the skull. This allows us to test if the functional demands of locomotor habitat, diet, and activity pattern influence the evolution of skull shape in musteloids. Moreover, GMM allows us to investigate the morphological adaptations related to locomotor habitat, diet, and activity pattern.

During locomotion and hunting an animal has to maintain its head and the forward-facing eyes at an appropriate level to maintain balance, crucial during locomotion and prey capture (Hilderbrand, 1959; Argot, 2003; Schubert *et al.*, 2003; Stevens & Heesy, 2013). We predict that the locomotor habitat will have an impact on head posture and the shape of the cranial base. Specifically, we predict a shorter skull, with a cranial base oriented more ventrally and a convergence in orbit position for more arboreal species; a cranial base that is more caudally oriented with the orbits laterally oriented for the semi-fossorial and terrestrial species; an anteriorly positioned orbit in aquatic species.

The skull and jaws are also crucial in the context of food acquisition and feeding. To perform these behaviours the muscles that connect the skull to the mandible are activated in order to allow the opening and closing of the mouth as well to generate bite forces (Herrel *et al.*, 2008; Fabre *et al.*, 2014a; Cornette, Tresset & Herrel, 2015). We predict that diet will mainly influence the parts of the skull that are related to mastication and thus we predict the strongest changes in the muscle attachment areas (Cox, 2008; Herrel *et al.*, 2008; Fabre *et al.*, 2014a). We specifically predict that herbivorous species will have a skull shape mainly characterized by a larger masseter muscle with a larger zygomatic arch for its insertion. In contrast, we predict for carnivorous species to have a skull with a well developed sagittal crest providing an enlarged attachment area for the temporalis muscle (Maynard Smith & Savage, 1959). Omnivores are predicted to be intermediate due to the fact that they eat a large variety of foods (more generalist).

Finally, we predict that activity pattern will mostly influenced the position and shape of the orbit.

We predict differences in orbit position in diurnal vs. nocturnal species, with the orbit oriented more convergently in nocturnal species than in diurnal ones.

MATERIAL AND METHODS

MATERIAL

The sample is composed of the skulls of 81 individuals belonging to 19 species of mustelids, one species of ailurid, eight species of procyonids, and three species of mephitids, covering a broad range of genera and species with different ecologies within the clade. The number of specimens ranged from 1 to 7 per species (Table 1). All specimens were adults and predominantly of wild caught origin. Equal numbers of males and females were included where possible. Specimens were obtained from the following collections: Mammifères et Oiseaux, Muséum national d'histoire naturelle, Paris, France; the Naturhistorisches Museum, Basel, Switzerland; the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts, and the Smithsonian National Museum of Natural History, Washington, District of Columbia, USA (see Supporting Information, Table S1 for a complete list of the specimens used in the analyses). Bones were digitized using a Breuckmann 3D surface scanner at the Muséum national d'histoire naturelle, Paris (white light fringe StereoSCAN^{3D} model with a camera resolution of 5 megapixels).

GEOMETRIC MORPHOMETRICS

The shape of the skull is complex and cannot be adequately represented using a traditional landmark-based approach (Cornette *et al.*, 2013, 2015). Consequently, a 3D sliding semilandmark procedure (Bookstein, 1997; Gunz, Mitteroecker & Bookstein, 2005) was used to better quantify the morphology of the skull, and especially the orbits and cranial base (occipital, the foramen magnum, and the occipital condyle). Through this procedure, sliding-semilandmarks on surfaces and curves are transformed into geometrically (i.e. spatially) homologous landmarks that can be used to compare shapes (Parr *et al.*, 2012). Semilandmarks are allowed to slide along the curves and surfaces that are predefined while minimizing the bending energy. Landmarks were digitized on the right side of the skull. Landmarks and curves were obtained using the software package Idav Landmark (Wiley *et al.*, 2005), while the library 'Morpho' (Schlager, 2013) in R (R Core Team, 2014) was used to perform the sliding semilandmark procedure. To do so, we first created a template following the method of Cornette *et al.* (2013) with 61 anatomical landmarks, 880

sliding-semilandmarks on curves and 225 sliding-semilandmarks on the surface. In this procedure each specimen is first defined by homologous landmark coordinates (Fig. 1, Table 2).

One hundred and four curves were defined at the margin of the orbital and occipital bones, following suture lines, the temporal line (which defines the medial most edge of the insertion of the temporalis muscle), the occipital and sagittal crests, the auditory bulla, around articulations (glenoid cavity and occipital condyle) and the dental row (see Fig. 1). All these curves are constrained by homologous landmarks (Gunz *et al.*, 2005). Based on the homologous landmarks and curves the sliding semilandmarks (curve and surface sliding-semilandmarks) of the template are projected onto the new specimen using a thin-plate spline deformation (Gunz & Mitteroecker, 2013). Finally, the spline relaxation algorithm associated with the sliding of the semilandmarks must be performed (Gunz *et al.*, 2005). Both sliding and projection phases are repeated iteratively until the bending energy of the thin-plate spline is minimized (Gunz *et al.*, 2005). This has been shown to be the most appropriate method to slide semilandmarks on curves and surfaces according Bookstein (2015). These steps were performed using the library 'Morpho' (Schlager, 2013) that follows the algorithm of Gunz *et al.* (2005) and which is implemented in R (R Core Team, 2014). At the end, four thin-plate spline relaxations were performed, the first relaxation was performed against the template and the three others against the Procrustes consensus calculated using the data from the previous iteration. Both sliding and relaxation are repeated iteratively until the bending energy is minimized (Schlager, 2013). After this operation has been performed, the landmarks of all specimens can be compared using traditional GMMs.

Once all landmark data were obtained a generalised Procrustes superimposition (Gower, 1975; Rohlf & Slice, 1990) was performed using the library 'Geomorph' (Adams & Otárola-Castillo, 2013) in R (R Core Team, 2014). The mean of the Procrustes coordinates of each species was calculated to eliminate intra-specific variation and to allow phylogenetic comparative analyses. In our study we did not take in account the sexual dimorphism. Indeed, even if it was previously shown that sexual dimorphism may have an influence in skull shape (e.g. Loy *et al.*, 2004; Christiansen & Harris, 2012), the interspecific variation is much larger than the intra-specific one (Lee & Mill, 2004; Suzuki, Abe & Motokawa, 2011). Previously studies have also demonstrate that sexual dimorphism is related to reproductive demands rather than diet, habitat, or activity pattern (Gittleman & Van Valkenburgh, 1997; Christiansen

Table 1. Details of specimens used in analyses with family, species name, common name, number of individuals included (*N*) and literature sources

Family	Species	Common name	<i>N</i>	Literature sources
Ailuridae	<i>Ailurus fulgens</i>	Red panda	4	Roberts & Gittleman (1984); Nowak (2005); Wilson & Mittermeier (2009); Heath & Platnick (2008); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
Mephitidae	<i>Conepatus chinga</i>	Molina's hog-nosed skunk	1	Afflerbaugh (2002); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Mephitis mephitis</i>	Striped skunk	2	Wade-Smith & Verts (1982); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Kiiskila (2014); Fabre <i>et al.</i> (2015a, b)
	<i>Spilogale putorius</i>	Eastern spotted skunk	1	Pennington (2002); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
Mustelidae	<i>Eira barbara</i>	Tayra	1	Schreffler (2003); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Galictis vittata</i>	Greater grison	1	Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2013a), Gregg (2013)
	<i>Gulo gulo</i>	Wolverine	2	Nowak (2005); Patsy & Sygo (2009); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Ictonyx striatus</i>	Zorilla	1	Larivière (2002); Aguilar (2003); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Lontra felina</i>	Marine otter	1	Savage (2000); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Lutra lutra</i>	European otter	1	Kennedy (2003); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Martes foina</i>	Stone marten	2	Carter (2004); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Martes martes</i>	Pine marten	2	Schwanz (2000); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Meles meles</i>	Eurasian badger	4	Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Wang (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Mellivora capensis</i>	Honey badger	1	Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2013a); Hoffman (2014)
	<i>Melogale moschata</i>	Chinese ferret-badger	1	Seefeldt (2003); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Mustela eversmannii</i>	Steppe polecat	1	Nowak (2005); Wilson & Mittermeier (2009); Dubbelde (2011); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Mustela lutreola</i>	European mink	2	Shalu (2001); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Mustela putorius</i>	European polecat	3	Lundrigan & Conley (2001); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Neovison vison</i>	American mink	1	Williams (1955); Schlimme (2003); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Poecilogale albinucha</i>	African striped weasel	1	Brilliant (2000); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
<i>Pteronura brasiliensis</i>	Giant otter	1	Bender (2001); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)	
<i>Taxidea taxus</i>	American badger	2	Shefferly (1999); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)	
<i>Vormela peregusna</i>	Marbled polecat	2	Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Petroelje (2011); Fabre <i>et al.</i> (2015a, b)	

Table 1. Continued

Family	Species	Common name	<i>N</i>	Literature sources
Procyonidae	<i>Bassaricyon alleni</i>	Allen's olingo	3	McClearn (1992); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Bassaricyon gabbii</i>	Bushy-tailed olingo	3	McClearn (1992); Berger (2004); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Bassariscus astutus</i>	Ringtail	6	Trapp (1972); McClearn (1992); Goldberg (2003); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Nasua narica</i>	White-nosed coati	7	McClearn (1992); Marceau (2001); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Nasua nasua</i>	South American coati	4	McClearn (1992); Braddy (2003); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Potos flavus</i>	Kinkajou	11	McClearn (1992); Nowak (2005); Rehder (2007); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Procyon cancrivorus</i>	Crab-eating raccoon	4	McClearn (1992); Nowak (2005); Phillips (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)
	<i>Procyon lotor</i>	Northern raccoon	7	McClearn (1992); Fox (2001); Nowak (2005); Wilson & Mittermeier (2009); Hunter & Barrett (2011); Fabre <i>et al.</i> (2015a, b)

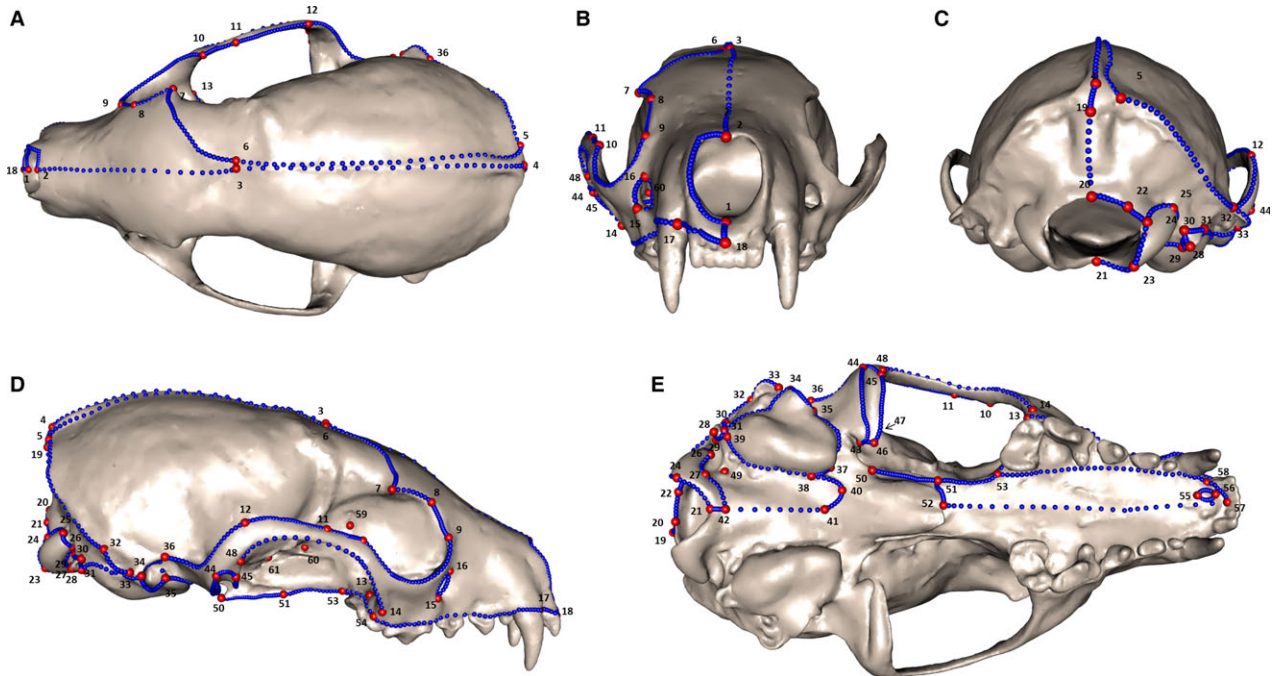


Figure 1. Landmarks used in our analyses to quantify shape variation of the skull. (A) dorsal view; (B) anterior view; (C) caudal view; (D) lateral view, (E) ventral view. Red dots represent landmarks; blue dots represent sliding semilandmarks on curves.

Table 2. Definition of the landmarks of the skull used in the geometric morphometrics analysis

Landmark	Definition
1	Most cranio-dorsal point of the premaxilla, middle
2	Tip of the nasal, middle
3	Most cranio-dorsal point of the braincase, middle
4	Most prominent point of the postparietal, middle
5	Most medial point of the temporal line/sagittal crest
6	Point of constriction of the temporal line
7	Tip of the postorbital process
8	Point of maximum of curvature between the tip of the postorbital process and the lacrimal foramen
9	Point at the top of the lacrimal foramen
10	Tip of the postorbital process on the jugal
11	Dorsal point at the jugal-squamosal suture
12	Point at the maximum of convexity at the dorsal part of the squamosal
13	Most medial point of insertion of the jugal on the maxilla
14	Most lateral point of insertion of the jugal on the maxilla
15	Most ventral point of the infraorbital foramen
16	Most dorsal point of the infraorbital foramen
17	Most laterocranial point of suture between the premaxillar and the maxillar
18	Most cranial point in the middle of the incisors row in the premaxilla, middle
19	Most ventral point of the occipital protuberance, middle
20	Most dorsal point on the foramen magnum, middle
21	Most ventral point on the foramen magnum, middle
22	Point of maximum of curvature between the most dorsal point of the foramen magnum and the occipital condyle
23	Most ventral point of the junction of the occipital condyle and the foramen magnum
24	Most dorsal point of the junction of the occipital condyle and the foramen magnum
25	Most laterodorsal point of the occipital condyle
26	Point at equidistance between the most laterodorsal and the most lateroventral point of the occipital condyle
27	Most lateroventral point of the occipital condyle
28	Tip of the paracondylar process
29	Most cranial point of the paracondylar process

Table 2. *Continued*

Landmark	Definition
30	Most mediadorsal point of the paracondylar process
31	Most mediolateral point of the paracondylar process
32	Point of the junction of parietal and squamosal on the nuchal crest
33	Most ventral point of the mastoid process
34	Most caudal point of the external auditory meatus
35	Most cranial point of the external auditory meatus
36	Point of insertion of the zygomatic arch on the braincase
37	Most cranial point of the tympanic bulla on the basisphenoid
38	Point at the junction between the tympanic bulla and the suture of the basioccipital
39	Most caudal point of the tympanic bulla on the basioccipital
40	Most craniolateral point at the maximum of curvature at the basioccipital-basisphenoid suture
41	Point of contact at the basioccipital-basisphenoid suture, middle
42	Most cranial point of the pharyngeal tubercle, middle
43	Most mediocaudal point of the glenoid cavity
44	Most laterocaudal point of the glenoid cavity
45	Most laterocranial point of the glenoid cavity
46	Most mediocranial point of the glenoid cavity
47	Point of insertion of the zygomatic arch on the braincase
48	Most ventral point at the jugal-squamosal suture
49	Point at the hypoglossal canal
50	Tip of the pterygoid process
51	Point at the palatine-ptyerygoid suture
52	Most posterior point in the middle of the palatine, middle
53	Most mediocaudal point at the palatine-maxillar suture
54	Most laterocaudal point of the maxilla
55	Most caudal point of the incisive foramen
56	Most cranial point of the incisive foramen
57	Most ventrocranial point in the middle of the incisive row
58	Most ventrocaudal point behind the last incisor alveoli
59	Point at the top of the optical foramen
60	Point at the top of the cranial lacerate foramen
61	Point at the top of the rotundum foramen

& Harris, 2012). Furthermore, only species means can be used in phylogenetic comparative analyses.

Next, a Principal Component Analysis (PCA) was performed on the mean of the Procrustes coordinates for each species to evaluate the distribution of species in morphospace. Finally, a multivariate mean shape was calculated separately for each kind of diet, habitat, and activity pattern using the tangent coordinates. This allows a multivariate visualization of the shape differences between the groups. The three-dimensional visualization of the mean shapes were obtained in R and reconstructed in Geomagic Studio (<http://www.geomagic.com>). The three-dimensional visualization of the mean conformation was performed using the 'rgl' (Adler & Murdoch, 2012) and 'Morpho' (Schlager, 2013) libraries and the software Geomagic Studio (<http://www.geomagic.com>).

PHYLOGENY

The phylogenetic tree used in our analyses is based on the family-level phylogeny of Carnivora from Eizirik *et al.* (2010) as a backbone upon which time-calibrated molecular phylogenies for each family are appended (Slater *et al.*, 2012). Full details of the phylogenetic reconstruction and the tree are provided in the supplementary information of Slater *et al.* (2012). For our analyses, we pruned the tree using the library 'ape' (Paradis, Claude & Strimmer, 2004) in R (R Core Team, 2014) so that only species represented in our dataset remained (Fig. 2). This tree was used in all comparative analyses, and branch lengths are proportional to geological time.

PHYLOGENETIC SIGNAL

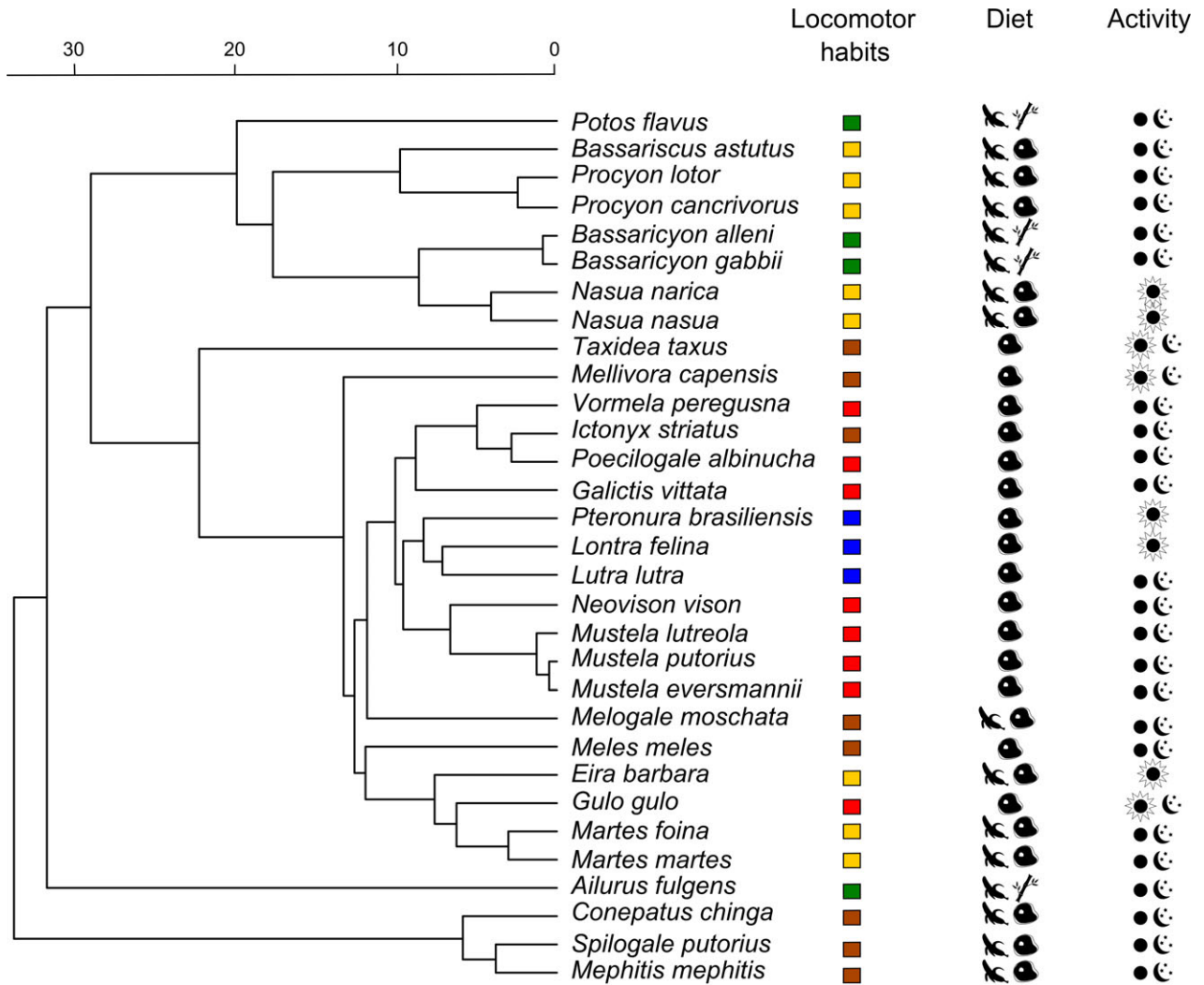
To estimate the phylogenetic signal in skull shape, we used a randomization test following the method of Blomberg, Garland & Ives (2003) and the extended methods of Adams (2014). A multivariate K -statistic (Adams, 2014) was calculated based on the Procrustes coordinates using the 'geomorph' library (Adams & Otarola-Castillo, 2013) in R (R Core Team, 2014). Next, a univariate K -statistic was calculated for the first five principal components of the skull using the 'picante' library in R (Kembel *et al.*, 2010). The higher the K -value is, the stronger the phylogenetic signal. A K -value of one corresponds to character evolution under Brownian motion. A K -value greater than one indicates a strong phylogenetic signal, implying that traits are conserved within the phylogeny. Conversely, a K -value close to zero means that phylogenetic signal is weak. We finally also mapped the phylogeny onto the morphospace using the polymorphospace function in R (R Core Team, 2014) implemented in the 'phytools' library (Revell,

2012) to compare phylogenetic and morphometric structure.

STATISTICAL ANALYSES

As species share some part of their evolutionary history, they cannot be treated as independent data points. Thus, we conducted these analyses in a phylogenetic framework (Felsenstein, 1985; Harvey & Pagel, 1991) using the phylogeny described above (Fig. 2). To test whether diet or locomotor habitat influence skull shape, we performed a phylogenetic MANOVA and ANOVAs (Garland *et al.*, 1993) on the first five principal components that together explain a significant proportion of the skull shape variation (> 77% of the shape variation). We used the `aov.phylo` function in the R package 'geiger' (Harmon *et al.*, 2008) for our analysis. To test whether animals with different locomotor habitat, diet, and activity differed in shape (Fig. 2, Table 2 for the literature concerning the different groups), simulations of shape variables on the tree were performed. Locomotor habitats were defined as in Fabre *et al.* (2015a, b; see Table 1 for the literature concerning the different groups) as follows: terrestrial, species that spend the most part of their time on the ground, but occasionally climb, swim, or dig; arboreal, species that spend the majority of their time in trees; semi-arboreal, species that spend both time in trees and on the ground without a clear preference for either; aquatic, species that spend the most of their time in water to forage, escape, disperse; semi-fossorial, species that spend the majority of time on the ground, but regularly dig burrows or dig to find food (see Table 1 for references). Definitions of diet categories were defined as follows: herbivorous, species that mainly eat plants (Macdonald, 2006); carnivorous, species that mainly eat vertebrate prey; omnivorous, species that eat vertebrate and invertebrate prey in addition to feeding on a variety of fruits, eggs, and other foods (Soley & Alvarado-Díaz, 2011). Activity patterns categories were defined as follows: nocturnal-crepuscular, species are mainly active during the beginning of the night; diurnal, species that are mainly active during the day; arrhythmic, species that are active at any time during the day (see Table 1 for references).

We used Brownian motion as our model for evolutionary change and ran 1000 simulations to create an empirical null distribution against which the F -value from the original data could be compared. We considered differences among categories significant if the original P -value was higher than the P_{95} -value derived from the empirical, simulated distribution. For the MANOVA, we used a Wilks' lambda as our multivariate test. This gives an approximation of the



Legends:

Locomotor habits	Diet	Activity
■ Aquatic	● Carnivorous	☀ Diurnal
■ Terrestrial	🐿 Herbivorous	☾ Nocturnal/crepuscular
■ Arboreal	🐿 Omnivorous	☀☾ Arrhythmic
■ Semi-fossorial		
■ Semi-arboreal		

Figure 2. The phylogenetic relationships of the musteloid species used in this study (based on Slater *et al.*, 2012). The time scale is in millions of years. The different life styles, diets, and activity patterns are also indicated.

F distribution by a transformation of the test statistic. Finally, Bonferroni corrected post-hoc tests were calculated using the phylANOVA function in the R package ‘phytools’ (Revell, 2012). These corrected

post-hoc tests allow us to test for differences between each locomotor habitat and diet group and consist of a comparison of the means of each category in each group.

RESULTS

PHYLOGENETIC SIGNAL

The result of the multivariate K -statistic calculated on the shape data is significant ($K_{\text{mult}} = 0.35$, $P = 0.01$). The K -statistic calculated for the first principal component describing skull shape is higher than one (PC1, $K = 1.57$, $P = 0.001$), which indicates a strong phylogenetic signal in the shape of the skull of musteloids. The K -statistic calculated for the second, third, and fourth axes is lower than one, but the randomization tests showed a significant phylogenetic signal for the second and third principal components (PC2, $K = 0.7$, $P = 0.001$; PC3, $K = 0.29$, $P = 0.001$; PC4, $K = 0.29$, $P = 0.13$). The K -statistic calculated on the fifth axis is lower than one and non-significant. These results show significant phylogenetic signal in the shape of the skull and highlight the importance of taking phylogeny into account.

INFLUENCE OF DIET, LOCOMOTION AND ACTIVITY ON THE SHAPE OF THE SKULL

The MANOVA and phylogenetic MANOVA performed on the first five principal components of the skull shape were significant for both diet (MANOVA: Wilks $\lambda = 0.12$, $F_{2,28} = 8.75$, $P < 0.0001$; phylogenetic MANOVA: Wilks $\lambda = 0.12$, $F_{2,28} = 8.7$, $P_{\text{phyl}} = 0.01$) and locomotion (MANOVA: Wilks $\lambda = 0.49$, $F_{4,26} = 2$, $P = 0.0001$; phylogenetic MANOVA: Wilks $\lambda = 0.03$, $F_{4,26} = 6.8$, $P_{\text{phyl}} = 0.002$). Activity pattern was not significant, however (MANOVA: Wilks $\lambda = 0.49$, $F_{2,28} = 2$, $P = 0.05$; phylogenetic MANOVA: Wilks $\lambda = 0.49$, $F_{2,28} = 2$, $P_{\text{phyl}} = 0.11$).

The traditional ANOVAs were significant on the first three axes for diet (PC1: $F_{2,28} = 14.24$, $P = 0.0001$; PC2: $F_{2,28} = 6.17$, $P = 0.006$; PC3: $F_{2,28} = 4.8$, $P = 0.01$), on the first four axes for locomotion (PC1: $F_{4,26} = 12.8$, $P = 0.0001$; PC2: $F_{4,26} = 6.18$, $P = 0.001$; PC3: $F_{4,26} = 3.19$, $P = 0.02$; PC4: $F_{4,26} = 7.8$, $P = 0.0001$), and on the third and fourth axis for activity pattern (PC3: $F_{2,28} = 4.5$, $P = 0.01$; PC4: $F_{2,28} = 3.5$, $P = 0.04$). The results of the phylogenetic ANOVAs were also significant on the first axis for locomotion (PC1: $F_{4,26} = 12.7$, $P_{\text{phyl}} = 0.01$) and on the third axis for activity pattern (PC3: $F_{2,28} = 4.4$, $P_{\text{phyl}} = 0.02$). Results were not significant for the other axes.

SHAPE VARIATION

The first three principal components accounted for 65.4% of the overall variance in skull shape. The distribution defined by the scatterplot of the first two axes (Fig. 3) tends to separate semi-arboreal and arboreal species from aquatic, terrestrial, and

semi-fossorial species. Arboreal species are well separated from semi-arboreal species, and aquatic from terrestrial species on the second axis. The distribution of the species on the first and third axes (Fig. S1B) is similar with terrestrial and semi-fossorial on the one hand and semi-arboreal and arboreal species on the other hand tending to overlap more. The aquatic species form the only distinct group. The distribution of the species on the second and third axes is less clear (Fig. S1C) as groups overlap more.

The mean shapes associated with each type of locomotion (Fig. 3) show that arboreal species have a rounder braincase than the aquatic, semi-arboreal, semi-fossorial, and terrestrial ones where it is more elongated. Arboreal species display a temporal line which is more laterally expanded than the other groups. There is also a gradient of shape concerning the orientation of the cranial base which is oriented more ventrally in arboreal species than in aquatic, terrestrial, and semi-fossorial species where it is oriented more caudally; in semi-arboreal species the cranial base has an intermediate orientation. The occipital condyles are proportionally larger and oriented more caudo-dorsally in aquatic species. The snout of the aquatic and terrestrial species is shorter, whereas it is longer in semi-arboreal ones and intermediate in arboreal and semi-fossorial ones. The dental row is proportionally shorter in aquatic and terrestrial species than in arboreal, semi-arboreal, and semi-fossorial ones where it is more elongated proximo-distally. The orbit is larger and oriented more anteriorly in arboreal and semi-arboreal species than in terrestrial and semi-fossorial ones where it is smaller and oriented more laterally; aquatic species display the smallest orbits, which are also oriented more dorsally. The auditory bulla is proportionally larger in terrestrial species than in aquatic ones, where it is smaller; arboreal, semi-arboreal, and semi-fossorial species display an intermediate shape. The palatine bone is proportionally longer in arboreal and semi-arboreal species than in terrestrial and aquatic species where it is shorter; it is intermediate in length in semi-fossorial species.

The overall distribution defined by the scatterplot of the first two axes also allows for differentiation of species based on their diet (Fig. 4, Fig. S2). The first axis tends to separate the carnivorous from the herbivorous and omnivorous species, whereas the second axis tends to separate the herbivorous and from carnivorous species. The distribution defined by the scatterplot of the first and third axes (Fig. S2B) clearly differentiates herbivorous from carnivorous species. Omnivorous and herbivorous species overlap whereas part of the carnivorous species tends to overlap with part of the omnivorous species.

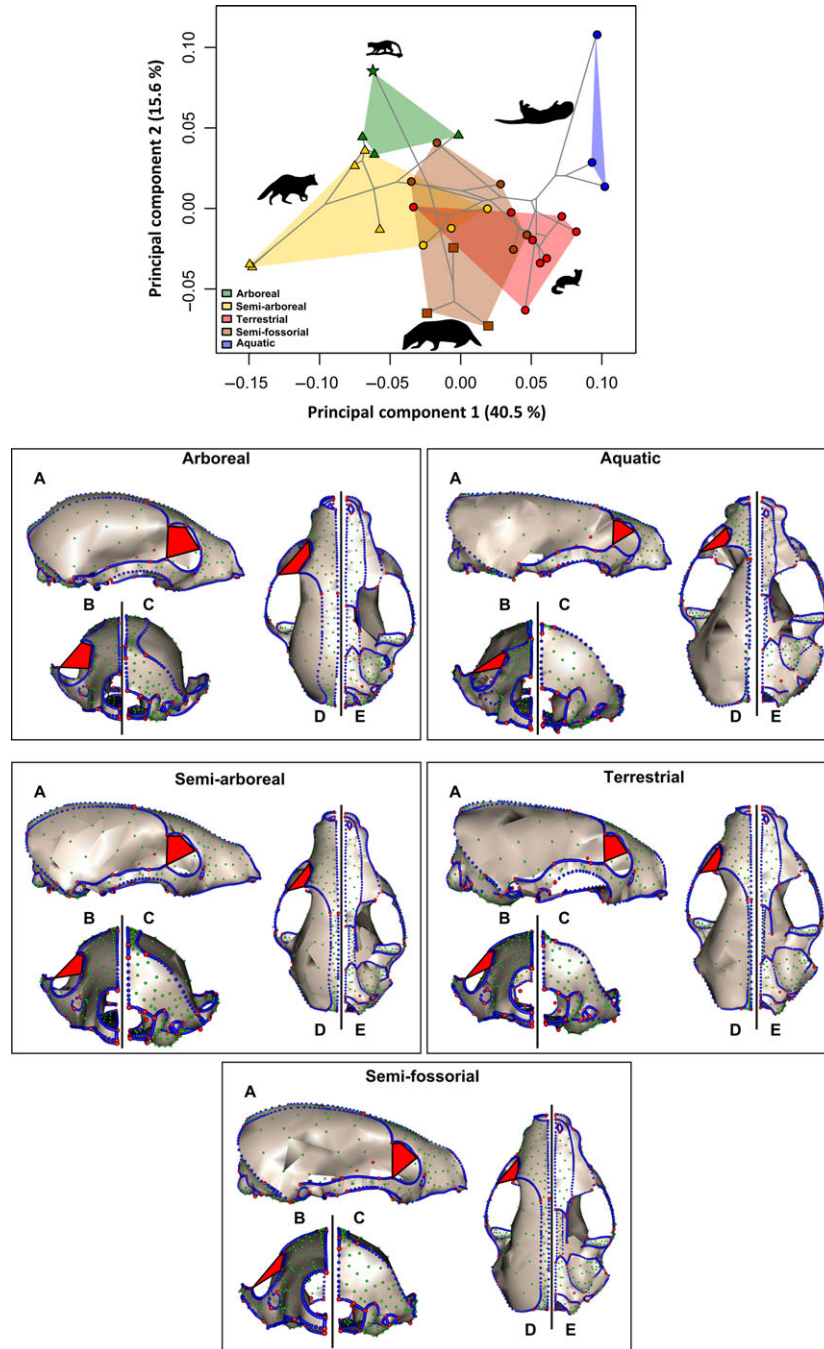


Figure 3. Results of the principal components analyses performed on the morphometric data of the skull. Scatter plot illustrating the position of different species on the first two principal components for each locomotor category. The family of each species is represented by a circle for mustelids, a triangle for procyonids, a square for mephitids, and a star for ailurids. The mean shapes of the skulls corresponding to each locomotor category are represented below the scatter-plot: (A) lateral view; (B) cranial view; (C) caudal view; (D) dorsal view; (E) ventral view. Red dots represent homologous landmark, blue dots represent sliding-semilandmark on curves and green dots represent sliding-semilandmark on surfaces; the red polygon provides a schematic representation of the orientation of the orbit.

The mean shape shows that herbivorous species (Fig. 4) have a rounder braincase than the omnivorous and carnivorous ones where it is more

elongated. Species display a gradient from a sagittal crest to a temporal line with herbivorous species displaying a temporal line which is lower down on the

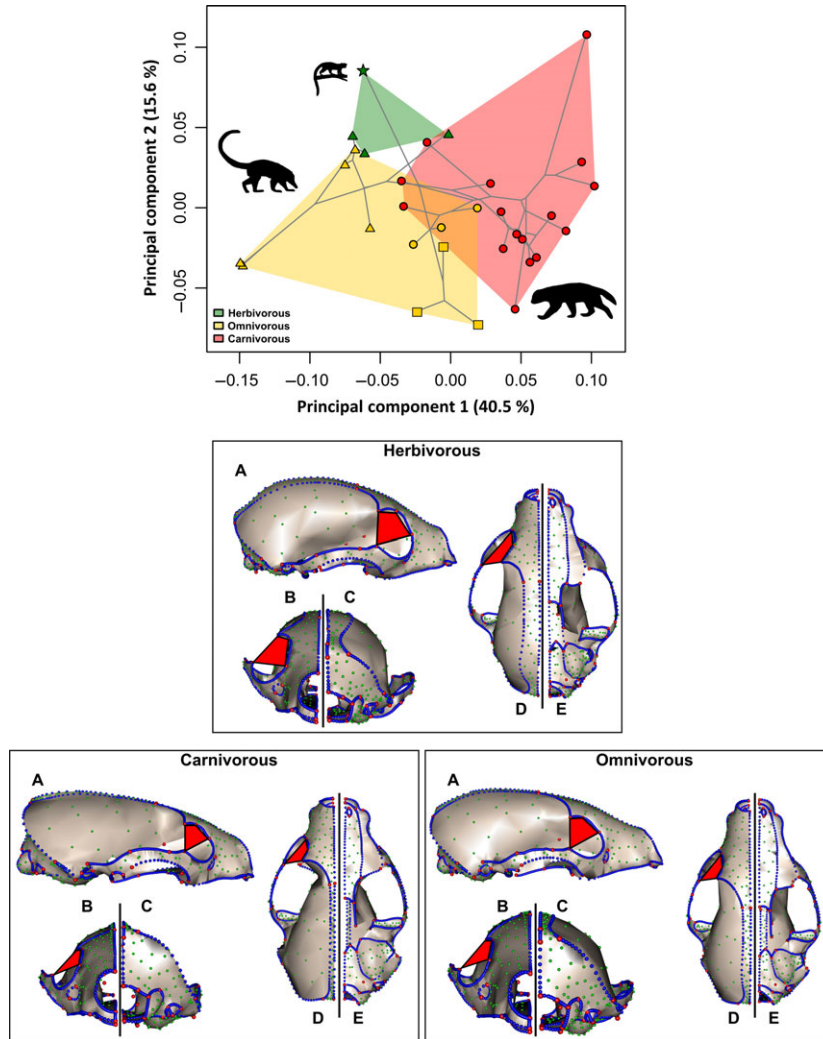


Figure 4. Results of the principal components analyses performed on the morphometric data of the skull. Scatter plot illustrating the position of different species on the first two principal components for each diet category. The family of each species is represented by a circle for mustelids, a triangle for procyonids, a square for mephitids, and a star for ailurids. The mean shape of the skull of each diet category is represented below the scatterplot. (A) lateral view; (B) cranial view; (C) caudal view; (D) dorsal view; (E) ventral view. Red dots represent homologous landmarks, blue dots represent sliding-semilandmarks on curves, and green dots represent sliding-semilandmark on surfaces; the red polygon provides a schematic representation of the orientation of the orbit.

side of the braincase in comparison to omnivorous species where it is closest to the middle of the braincase. A sagittal crest is present only in carnivorous species. The zygomatic arch is dorsally curved in carnivorous species whereas it is straighter in herbivorous and omnivorous species. The anterior root of the zygomatic arch is broad and cranio-ventrally oriented in herbivorous species in comparison to carnivorous and omnivorous species where it is less developed. There is also a shape gradient seen in the cranial base which is oriented more ventrally in herbivorous species than in carnivorous species where it is oriented more caudally; it is intermediate in

omnivorous species. The occipital condyles are proportionally larger and oriented more caudo-dorsally in carnivorous species than in herbivorous ones where they are smaller and oriented more ventro-lateral, omnivorous species display an intermediate shape. The snout of the herbivorous and carnivorous species is shorter whereas it is longer in omnivorous species. The dental row is proportionally shorter in carnivorous species than in herbivorous and omnivorous species where it is longer. The orbit is larger and oriented more frontally in herbivorous species than in carnivorous ones where it is smaller and oriented more laterally; omnivorous species display an

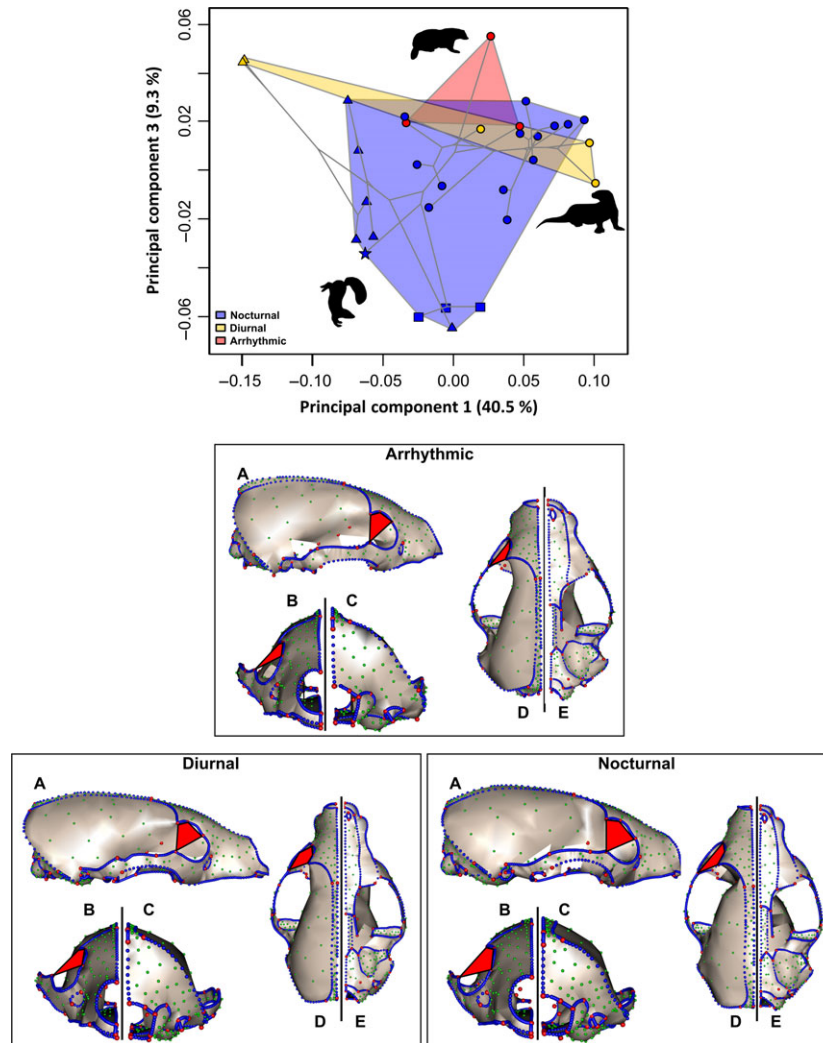


Figure 5. Results of the principal components analyses performed on the morphometric data of the skull. Scatter plot illustrating the position of different species on the first and third principal components for each activity pattern. The family of each species is represented by a circle for mustelids, a triangle for procyonids, a square for mephitids, and a star for ailurids. The mean shape of the skull of each activity pattern is represented below the scatterplot. (A) lateral view; (B) cranial view; (C) caudal view; (D) dorsal view; (E) ventral view. Red dots represent homologous landmarks, blue dots represent sliding-semilandmarks on curves, and green dots represent sliding-semilandmarks on surfaces; the red polygon provides a schematic representation of the orientation of the orbit.

intermediate orbit shape. Herbivorous species have a glenoid cavity that is proportionally larger and more ventrally oriented than carnivorous ones where it is narrower and more frontally oriented. The auditory bulla is proportionally smaller in herbivorous and omnivorous species than in carnivorous ones, where it is larger.

The morphospace defined by the first and third axes (Fig. 5, Fig. S3B) tends to separate the nocturnal species from the diurnal and the arrhythmic ones. Activity patterns overlap broadly on the first axis, but the third axis tends to separate the nocturnal from the diurnal and arrhythmic species.

The mean shape associated with each activity (Fig. 5) shows that arrhythmic species tend to have a braincase that is proportionally rounder than the diurnal and nocturnal ones where it is more elongated. Arrhythmic species also display a cranial base that is caudally oriented in comparison to the diurnal and nocturnal species that have a cranial base that is proportionally more ventrally oriented. The occipital bone is proportionally more laterally expanded in arrhythmic and nocturnal species than in diurnal species. The snout is proportionally shorter in arrhythmic and nocturnal species than it is diurnal ones. Similarly, the dental row is wider in

diurnal species than in arrhythmic and nocturnal ones where it is thinner. The auditory bulla is proportionally larger in nocturnal and arrhythmic species than in diurnal one where it is smaller. There is a gradient concerning the orbit, being proportionally larger and frontally oriented in nocturnal species than in diurnal one. The arrhythmic species have proportionally smaller and more laterally oriented orbits.

DISCUSSION

The results of our analyses of skull shape show that there are significant differences between species with different locomotor habitats, diet, and, to a lesser extent, activity patterns, even when taking into account the effect of phylogeny. This is in accordance with previous studies (Ewer, 1973; Nowak, 2005; Sato *et al.*, 2009, 2012; Wilson & Mittermeier, 2009; Eizirik *et al.*, 2010; Hunter & Barrett, 2011; Fabre *et al.*, 2015a, b). These results suggest that skull shape is adaptive and evolves, at least partly, in association with the functional demands imposed by the different locomotor habitats, diet, and activity of musteloid species.

LOCOMOTOR HABITAT

The PCA performed on the shape of the skull (Fig. 3) separates semi-arboreal and arboreal species from aquatic, terrestrial, and semi-fossorial species. The mean shape conformations show different morphological characters that allow one to discriminate arboreal, aquatic, and terrestrial species based on skull shape. The major shape differences between species with a different locomotor habitats (Fig. 3) follow our predictions and reside in the head posture (orientation of the cranial base and occipital condyles, the braincase shape) and differences in orbit orientation. The difference in the orientation of the cranial base may be explained by the different head postures needed by animals moving in different habitats (Ross & Ravosa, 1993; Lieberman *et al.*, 2000). Indeed, it is important for the animal to maintain the head and the forward-facing eyes at the appropriate level during locomotion and hunting (Hilderbrand, 1959; Argot, 2003; Schubert *et al.*, 2003; Stevens & Heesy, 2013). Furthermore, the locomotor substrate may influence head posture and consequently the alignment of the visual field (Strait & Ross, 1999; Dunbar *et al.*, 2004; Stevens & Heesy, 2013). For example, arboreal species tend to have a cranial base that is oriented more ventrally. Arboreal species move and forage in a complex three-dimensional habitats where they have to accurately judge the distance

between one branch to another (Cartmill, 1970, 1972, 1990, 1992; Crompton, 1995; Bergeson, 1998; Heesy, 2009). Thus, their head posture needs to be adjusted to their visual field during climbing and leaping (Strait & Ross, 1999; Stevens & Heesy, 2013). The head posture differences between species with different locomotor habitats is also reflected in the morphology of the occipital condyles. The occipital condyles in aquatic and terrestrial species are larger than those of arboreal, semi-arboreal, and semi-fossorial species. In the literature, a wide occipital condyle is related to an increase of the lateral stability of the head at the atlanto-occipital joint (Rosenberger, 2010). Small and narrow condyles, on the other hand are related to an increase in head mobility (Rosenberger, 2010).

It is also important to note that the shape of the cranial base may also be linked to relative brain size. In this study, we did not explore the influence of brain size on the skull shape directly, but the cranial base shape variation is reminiscent of that observed for animals with differently sized brains. Relative brain size seems to be an important factor shaping the degree of basicranial flexion (Ross & Ravosa, 1993). This hypothesis was supported for hominids where brain size rather than the head and neck posture is the principal influence on flexion (Ross & Ravosa, 1993; Ross & Hennerberg, 1995; Strait & Ross, 1999). It is difficult to determine based on our results if the brain size of the arboreal species is relatively larger than that of other groups, even if their braincase appears generally rounder on average.

Another anatomical feature related to the locomotor habitat in musteloids is the general morphology and orientation of the orbits. Our results show that, as expected, the arboreal and semi-arboreal species have larger and more anteriorly oriented orbits compared to terrestrial and semi-fossorial ones. Arboreality is suggested as one of the predominant factors that influence orbital convergence (Heesy, 2004, 2009). Indeed, animals engaging in acrobatic and leaping locomotion need visual specializations for depth judgement and have a tendency to develop binocular vision (Cartmill, 1970, 1972, 1992; Martin, 1990; Heesy, 2007, 2009). But this condition is not necessarily reciprocal. There are many arboreal species that have divergent orbits and panoramic visual fields (Cartmill, 1974; Ross, 2000; Heesy, 2009). This confirms that the locomotor environment, and more precisely arboreal locomotion, influences the shape of the skull. It is also important to take into account that orbit position can be affected by relative palate length and relative brain size as suggested by previous studies (Cartmill, 1970; Ross, 1995; Noble, Kowalski & Ravosa, 2000; Finarelli & Goswami, 2009).

Large differences in the auditory bulla are also observed with terrestrial animals showing a relatively larger auditory bulla in comparison to species using other kinds of locomotor habitats. The relation between the size and the function of the bullae remains, however, unclear (e.g. van Kampen, 1905; van der Klaauw, 1931; Hough, 1944, 1948; Savage, 1957). It has been suggested that an increase in auditory sensitivity is associated with an increase in the volume of the middle ear cavity (Hunt, 1974). Moreover, species living in open habitats tend to have larger auditory bullae, which increase sensitivity to low frequency sounds (2 kHz or less; Huang, Rosowski & Ravicz, 2002). Among carnivorans, this correlation has been experimentally demonstrated in the sand cat *Felis margarita* (Huang *et al.*, 2002) and, based on a functional morphology analysis, in herpestids (Kawakami Gishlick, 2008). However, the size of the auditory bulla is still poorly understood and remains to be investigated further to clearly understand the functional effects of variation in bulla size as explained by Coleman & Ross (2004).

DIET

The PCA shows a differentiation of the species depending on their diet (Fig. 4). Previous studies have already shown in other vertebrates that the skull plays an important role during feeding. These studies have shown that mastication and the associated muscles have a direct effect on cranial shape (Cox, 2008; Herrel *et al.*, 2008; Fabre *et al.*, 2014a). The skull and jaws are crucial in the context of prey capture, prey killing, and the subsequent prey processing and mastication (Anderson, McBrayer & Herrel, 2008; Cornette *et al.*, 2015). To perform these behaviours the muscles that connect the skull to the mandible are activated in order to allow the opening and closing of the mouth as well to generate the forces that reduce the food (Herrel *et al.*, 2008; Fabre *et al.*, 2014a; Cornette *et al.*, 2015). In our study, the mean shapes associated with each dietary group show differences in the snout, the dental row length, the braincase morphology, the sagittal crest/temporal line, and in the shape of the zygomatic arch. Both herbivorous and carnivorous species have a shorter snout than do omnivorous species. On other hand, the dental row is shorter in carnivores and longer in herbivorous and omnivorous species. In several studies, the length of the snout has been correlated with bite force (Aguirre *et al.*, 2002, 2003; Van Cakenberghe, Herrel & Aguirre, 2002; Herrel *et al.*, 2007; Santana, Dumont & Davis, 2010; Marshall *et al.*, 2012). This phenomenon is also observed in lizards (e.g. Herrel, De Grauw & Lemos-Espinal, 2001; Verwajen, Van Damme & Herrel, 2002; Kohlsdorf *et al.*,

2008) and in other carnivorans (Figueirido *et al.*, 2010, 2011a, b). Snout length correlates with the jaw outlever and thus a short snout increases the mechanical advantage for biting (i.e. increases the bite force). The shortest snout is observed in carnivorous musteloids. This may be related to the fact that they need to generate high bite forces at the canines during prey capture or the fact that the carnivorous musteloids included in our data set eat relatively hard prey.

Carnivorous species have a tendency to reduce their premolar and molar row in favour of canines (Figueirido & Soibelzon, 2009; Figueirido *et al.*, 2011a, b). This is also observed here with the development of a large canine alveola in the carnivorous species (Fig. 4). Herbivorous and omnivorous species tend to lengthen the premolar and molar row (e.g. Van Valkenburg, 2007; Figueirido & Soibelzon, 2009), as is shown here for musteloids. Although herbivorous musteloids have a tendency to shorten their snout, they maintain a long postcanine tooth row; this factor and their short snout have an effect to displace the palate posteriorly. A possible explanation is that the herbivorous musteloids need to increase the bite lever while simultaneously maintaining a large occlusal area. This may allow them to generate high bite forces to reduce tough plant material as is observed in other vertebrates (Aguirre *et al.*, 2002, 2003; Van Cakenberghe *et al.*, 2002; Herrel *et al.*, 2007; Santana *et al.*, 2010). Yet this also allows them to maintain a large surface area to resist high wear and increase occlusal contacts (Kay, 1981; Puech, Prone & Albertini, 1981; Puech, 1986). Moreover, short snouts may be better for resisting high compressive strains (Figueirido *et al.*, 2011a). This is in agreement with the caudal rather than cranial extension of the premolar row observed in these animals (Fig. 4).

The braincase and sagittal crest/temporal line change shape according to the different diets in musteloids, confirming our predictions. The braincase is more rounded in herbivorous species and more elongated in carnivorous species. Furthermore, herbivorous species display a temporal line in contrast to carnivorous species that display a well developed sagittal crest (Fig. 4). Omnivorous species display a temporal line that is closer to the midline of the skull. The development of the sagittal crest in carnivorous species can be explained by the development of a relatively large temporalis muscle, an important muscle that allows carnivorous species to generate bite force at large gapes (Turnbull, 1970; Christiansen, 2008; Figueirido & Soibelzon, 2009; Meachen-Samuels & Van Valkenburgh, 2009; Figueirido *et al.*, 2010, 2011a, b; Meloro & Slater, 2012). Several studies have shown that the development of

a sagittal crest provides an enlarged attachment area for the temporalis muscle (Maynard Smith & Savage, 1959). Given the importance of the temporalis muscle in biting at large gape angles (Turnbull, 1970) these observations suggest that carnivorous musteloids maintain large temporalis muscles in order to feed on relatively large prey that need to be killed by biting.

The zygomatic arch is concave ventrally and is deepest anteriorly in all three groups. However, the arch is notably more robust anteriorly in the herbivorous group. The anterior zygomatic arch is where the fibres of the masseter muscle converge on a strong tendon. *In vivo* bone strain data for macaques shows that this part of the zygomatic arch is more heavily loaded by the masseter muscle than the posterior arch during biting and mastication (Hylander & Johnson, 1997). These observations suggest an increase in the size and the stresses associated with the masseter muscle. This is in agreement with the ventral position of the temporal line in the herbivorous species which suggests a decrease in the surface area of insertion of the temporalis muscle. With the exception of the herbivorous red panda (*Ailurus fulgens*) which eats tough and fibrous food items and which displays a sagittal crest, most of the other herbivores appear to rely on a larger masseter muscle rather than a well developed temporalis. Herbivores typically do not need to generate bite force at large gape and the masseter rather than the temporalis is usually well developed given that it is biomechanically better positioned for generating high bite force at low gape (Maynard Smith & Savage, 1959). Omnivores show slightly less robust development of the anterior zygomatic arch, but a markedly shallower dorsoventral depth to the arch overall in comparison to both the carnivorous and the herbivorous group. These observations suggest that neither the masseter nor the temporalis muscle are differentially developed in the omnivores.

Our mean shapes for animals with different diets also showed that herbivorous species have a glenoid surface that is proportionally larger craniocaudally, more ventrally oriented, and less curved in the postglenoid and preglenoid regions than carnivorous ones, where it is narrower craniocaudally and strongly curved with well developed postglenoid and preglenoid processes. These differences in the shape of the glenoid surface may result from differences in the orientation of the joint reaction forces (i.e. the force induced by the mandible on the skull as a result of biting) and differing amounts of translational motion of the mandibular condyles during mastication. The large, horizontal glenoid surface of herbivores may indicate more vertical joint reaction forces and would permit a greater range of joint motion during the

power stroke of mastication. A greater range of motion may be important for maintaining occlusal contact along the shearing and grinding edges of the postcanine teeth. The small, hinge-like glenoid surface of carnivores may indicate a more anteriorly oriented joint reaction force and would restrict anteroposterior sliding motion during the power stroke of biting. This may be important for preventing condylar dislocation during prey capture. The differences in the shape and orientation of the glenoid surface parallel those observed across mammals in general with herbivores typically having flatter and more horizontally oriented glenoid in contrast to carnivores (von Schumacher, 1961; Turnbull, 1970).

Two other anatomical features can be related to differences in the posture of the head: the orientation of the cranial base and the occipital condyles. They are respectively more caudally and caudo-dorsally oriented in the carnivorous species and more ventrally and ventro-laterally in the herbivorous species. The orbit is larger and more frontally oriented in herbivorous species than in carnivorous ones where it is smaller and oriented more laterally. These morphological characteristics may be due to the fact that the herbivorous species in our sample are all arboreal. The idea that the locomotor environment is highly integrated with foraging and feeding has been suggested in several previous studies (e.g. Altenbach, 1989; Dunbar & Badam, 2000; Domenici, 2001; Wainwright *et al.*, 2001; Higham, 2007) and may explain why we find common anatomical features between the mean shapes of species having a common diet (implying foraging strategy/feeding) and those associated with animals using different locomotor environments. Thus, different selective pressures may drive the evolution of cranial shape in the same direction (Arnold, 1992; Schwenk, 1995; Kohlsdorf *et al.*, 2008).

ACTIVITY PATTERNS

Our results show that activity patterns also has an influence on skull shape, but this effect is restricted to the third axis of the PCA which tends to separate arrhythmic and diurnal species from nocturnal ones. This can be related to vision and orbital aperture size. Indeed Heesy (2007, 2009) showed that the activity pattern, and specifically nocturnality explains most of the variance in orbit convergence. As in his studies on strepsirrhine primates we observed that nocturnal species present proportionally larger and more convergent orbits compared to arrhythmic and diurnal species. However, we also found that among musteloids, the herbivores, all of whom are arboreal, show the strongest differentiation of orbital size and orientation (i.e. more frontally

oriented in opposition to laterally oriented) in comparison to the omnivores and the carnivores. These findings also suggest that nocturnal arboreality is more tightly linked to orbit orientation. The smaller orbit size observed in diurnal species is in accordance with results for anthropoids (Ross, 1995, 1996) and in contrast with the observations of Kirk (2006), who did not report any differences between diurnal and nocturnal species.

CONCLUSION

Our study shows that phylogeny, locomotor habitat, diet, and activity pattern all significantly influence the shape of the skull of musteloids. In particular, locomotor habitat appears to have strong influence on skull shape compared to diet and activity pattern. It is important to note, however, that the locomotor environment is highly integrated with foraging and feeding, which can lead to similar selective pressures that may drive the evolution of skull shape in parallel directions. Nonetheless, locomotor habitat appears to mainly influence the braincase shape, head posture, and the shape of the orbits, whereas, the influence of diet mostly affects the regions of the skull that are related to the biomechanics of chewing and biting (the snout, palate and row length, the zygomatic arches, temporal line/sagittal crest), with a strong effect on muscle attachment sites. Finally, as we predicted, activity pattern has also an influence which is most evident in orbit size and convergence. This study confirms that musteloids are a particularly interesting group for ecomorphological studies as they show the morphological patterns induced by functional demands as they are typically observed only in broader studies across mammals as a whole.

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SUPPORTING INFORMATION

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

Figure S1. Results of the principal components analyses performed on the morphometric data of the skull. Scatter plot illustrating the position of different species on the: (A) first and second principal components, (B) first and third principal components, and (C) second and third principal components for each locomotor habitat. The family of each species is represented by a circle for mustelids, a triangle for procyonids, a square for mephitids, and a star for ailurids.

Figure S2. Results of the principal components analyses performed on the morphometric data of the skull. Scatter plot illustrating the position of different species on the: (A), first and second principal components, (B) first and third principal components, and (C) second and third principal components for each diet. The family of each species is represented by a circle for mustelids, a triangle for procyonids, a square for mephitids, and a star for ailurids.

Figure S3. Results of the principal components analyses performed on the morphometric data of the skull. Scatter plot illustrating the position of different species on the: (A) first and second principal components, (B) first and third principal components, and (C) second and third principal components for each activity pattern. The family of each species is represented by a circle for mustelids, a triangle for procyonids, a square for mephitids, and a star for ailurids.

Table S1. Specimens used in the analyses.