

## Getting a grip on the evolution of grasping in musteloid carnivorans: a three-dimensional analysis of forelimb shape

A.-C. FABRE\*†‡, R. CORNETTE§, G. SLATER¶, C. ARGOT\*, S. PEIGNÉ\*, A. GOSWAMI‡ & E. POUYDEBAT\*\*

\*Centre de recherche sur la paléobiodiversité et les paléoenvironnements – UMR 7207 Centre National de Recherche Scientifique, Muséum National d'Histoire Naturelle, Univ Paris 06, Paris, France

†Univ Paris Diderot, Paris, France

‡Department of Genetics, Evolution, and Environment and Department of Earth Sciences, University College London, London, UK

§Origine Structure et Evolution de la Biodiversité - UMR 7205 Centre National de Recherche Scientifique, Muséum National d'Histoire Naturelle, Paris, France

¶Department of Paleobiology, National Museum of Natural History, The Smithsonian Institution [NHB MRC 121], Washington, DC, USA

\*\*Département d'Ecologie et de Gestion de la Biodiversité, UMR 7179 Centre National de Recherche Scientifique, Muséum National d'Histoire Naturelle, Paris Cedex 5, France

### Keywords:

ecomorphology;  
geometric morphometrics;  
grasping;  
musteloids.

### Abstract

The ability to grasp and manipulate is often considered a hallmark of hominins and associated with the evolution of their bipedal locomotion and tool use. Yet, many other mammals use their forelimbs to grasp and manipulate objects. Previous investigations have suggested that grasping may be derived from digging behaviour, arboreal locomotion or hunting behaviour. Here, we test the arboreal origin of grasping and investigate whether an arboreal lifestyle could confer a greater grasping ability in musteloid carnivorans. Moreover, we investigate the morphological adaptations related to grasping and the differences between arboreal species with different grasping abilities. We predict that if grasping is derived from an arboreal lifestyle, then the anatomical specializations of the forelimb for arboreality must be similar to those involved in grasping. We further predict that arboreal species with a well-developed manipulation ability will have articulations that facilitate radio-ulnar rotation. We use ancestral character state reconstructions of lifestyle and grasping ability to understand the evolution of both traits. Finally, we use a surface sliding semi-landmark approach capable of quantifying the articulations in their full complexity. Our results largely confirm our predictions, demonstrating that musteloids with greater grasping skills differ markedly from others in the shape of their forelimb bones. These analyses further suggest that the evolution of an arboreal lifestyle likely preceded the development of enhanced grasping ability.

### Introduction

The use of the forelimbs in grasping is common to a large number of vertebrates ranging from amphibians to mammals (Grzimek, 1990; Iwaniuk & Whishaw, 2000; Sustaita *et al.*, 2013). Although the ability to grab food, to hold it and to manipulate it has been observed

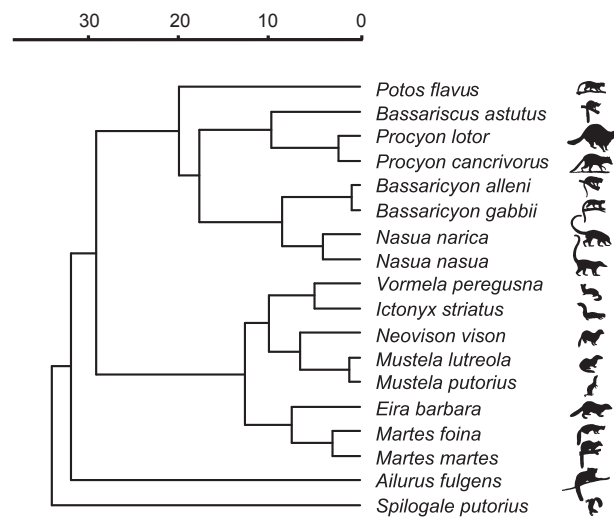
in a variety of aquatic and arboreal frogs (Gray *et al.*, 1997; Manzano *et al.*, 2008), this ability is often thought to be an essentially mammalian trait (Ivanco *et al.*, 1996; Iwaniuk *et al.*, 1999, 2000; Endo *et al.*, 2007; Sacrey *et al.*, 2009). In eutherians, behaviours associated with grasping are widespread and have been observed in species belonging at least to six orders (Ptilosa, Chiroptera, Rodentia, Carnivora, Scandentia and Primates). Previous investigations of prehension have suggested that the ability to grasp with the forelimbs might be derived from locomotor behaviours such as digging (Brácha *et al.*, 1990), arboreal thin-branch climbing (Grillner & Wallén, 1985; Godinot, 1991,

Correspondence: Anne-Claire Fabre, Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements UMR 7207, Muséum Nationale d'Histoire Naturelle, 8 rue Buffon, CP 38, 75005 Paris, France.  
Tel.: +33 140793025; fax: +33 140793580;  
e-mail: acfabre@mnhn.fr

2007; Antón *et al.*, 2006; Salesa *et al.*, 2006; Manzano *et al.*, 2008; Reghem *et al.*, 2012) or the need to manipulate prey (Gray *et al.*, 1997; Iwaniuk & Whishaw, 2000). In spite of data accumulated on different taxa, particularly within Primates (Christel, 1993; Byrne *et al.*, 2001; Corp & Byrne, 2002; Pouydebat *et al.*, 2008, 2009, 2011; Crast *et al.*, 2009; Reghem *et al.*, 2011), the evolution of grasping behaviour has received relatively little attention, and our understanding of this behaviour and the underlying anatomical traits facilitating its evolution remains consequently limited (see Sustaita *et al.*, 2013).

The morphology of the forelimb has often been suggested to be a good indicator of locomotor ecology (Ewer, 1973; Gonyea, 1978; Argot, 2001; Andersson, 2003, 2004, 2005; Flores & Díaz, 2009; Halenar, 2011) with previous studies mainly focusing on the relationship between elbow morphology (Andersson, 2003, 2004; Schutz & Guralnick, 2007; Halenar, 2011) and locomotor mode. Furthermore, in these studies, the focus has been mainly on the humerus, whereas the other long bones of the forelimb (ulna and radius) remain largely unstudied. Yet, all of these elements are crucial to ensure effective movement of the forelimb, especially in tasks requiring fine motor control such as arboreal locomotion or grasping. Thus, a better understanding of the anatomy of these elements in taxa specialized for different locomotor behaviours, in comparison with the morphology observed in grasping taxa, may shed light on the ecological context and the evolutionary origins of grasping ability.

To investigate the evolution of morphological adaptations of the forelimb related to grasping, we here present a quantitative morphological analysis of the three long bones of the forelimb in musteloid carnivorans. The Musteloidea (Mephitidae, Ailuridae, Procyonidae and Mustelidae) are a good model system for this kind of study for a number of reasons. First, they are ecologically diverse, containing a remarkable diversity of lifestyles that ranges from arboreal species, such as the kinkajou and the red panda, to aquatic species, such as the sea otter. Second, the diversity of lifestyles observed in each clade suggests that they have colonized the same type of habitats and acquired the behavioural traits of interest independently. Among the musteloids, three families contain species able to grasp and manipulate objects, providing a unique opportunity to examine the variation in forelimb shape in a group of closely related species differing in their lifestyle and grasping ability. Third, the phylogenetic relationships among musteloids are well resolved (Sato *et al.*, 2009, 2012; Eizirik *et al.*, 2010): the mustelids (weasels, badgers, otters and their relatives) and the procyonids (coatis, raccoons, the kinkajou and their relatives) are sister taxa, whereas the ailurids (which is represented by the unique living representative, the red panda) and the mephitids (skunks) form successive sister lineages to this clade (Fig. 1).



**Fig. 1** The phylogenetic relationships of the musteloid species used in this study, derived from Slater *et al.* (2012). The time scale is in million years.

In this study, we use 3D geometric morphometric methods to quantitatively compare the anatomy of the long bones of the forelimb in musteloids with different lifestyles and grasping ability. Within each lifestyle (arboreal, semi-arboreal and terrestrial), we compare the forelimb morphology of species with different grasping ability (well developed, intermediately developed and poorly developed) where possible. This allows us to (i) test whether arboreal lifestyle precedes grasping ability, (ii) investigate the morphological adaptations related to grasping ability and the differences and/or similarities between arboreal species with different grasping abilities. We predict that if grasping is derived from an arboreal lifestyle as has been suggested previously, then the anatomical specializations of the forelimb for an arboreal lifestyle must be similar to those involved in grasping. Moreover, we predict that arboreal species with a well-developed grasping ability will have articulations that will provide an increase in the range of pronation and supination to facilitate rotation at the wrist and thus allowing more complex movements (Gray *et al.*, 1997).

## Materials and methods

### Sample

Long bones of the forelimb (humerus, ulna and radius) of 49 individuals belonging to 8 species of procyonids, 1 species of ailurid, 1 of mephitid and 8 of mustelids were used in our study. The number of specimens of each species ranged from 1 to 7 individuals per species (Table 1). All specimens were adults and predominantly of wild-caught origin. Equal numbers of males and

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

Species	Common name	<i>N</i>	Family	Lifestyle	Grasping ability
<i>Spilogale putorius</i>	Eastern spotted skunk	1	Mephitidae	Terrestrial	Poorly developed
<i>Ailurus fulgens</i>	Red panda	5	Ailuridae	Arboreal	Intermediately developed
<i>Eira barbara</i>	Tayra	1	Mustelidae	Semi-arboreal	Poorly developed
<i>Ictonyx striatus</i>	Zorilla	1	Mustelidae	Terrestrial	Poorly developed
<i>Martes foina</i>	Stone marten	2	Mustelidae	Semi-arboreal	Poorly developed
<i>Martes martes</i>	Pine marten	2	Mustelidae	Semi-arboreal	Poorly developed
<i>Mustela lutreola</i>	European mink	2	Mustelidae	Terrestrial	Poorly developed
<i>Mustela putorius</i>	European polecat	2	Mustelidae	Terrestrial	Poorly developed
<i>Neovison vison</i>	American mink	1	Mustelidae	Terrestrial	Poorly developed
<i>Vormela peregusna</i>	Marbled polecat	2	Mustelidae	Terrestrial	Poorly developed
<i>Potos flavus</i>	Kinkajou	4	Procyonidae	Arboreal	Well developed
<i>Procyon cancrivorus</i>	Crab-eating raccoon	2	Procyonidae	Semi-arboreal	Intermediately developed
<i>Procyon lotor</i>	Northern raccoon	4	Procyonidae	Semi-arboreal	Intermediately developed
<i>Nasua narica</i>	White-nosed coati	4	Procyonidae	Semi-arboreal	Poorly developed
<i>Nasua nasua</i>	South American coati	3	Procyonidae	Semi-arboreal	Poorly developed
<i>Bassaricyon alleni</i>	Allen's olingo	3	Procyonidae	Arboreal	Well developed
<i>Bassaricyon gabbii</i>	Bushy-tailed olingo	3	Procyonidae	Arboreal	Well developed
<i>Bassariscus astutus</i>	Ringtail	7	Procyonidae	Semi-arboreal	Poorly developed

females were included where possible. Forelimb bones 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 Data S1 for a list of the specimens used in the analyses. All the bones of the forelimb were digitized using a Breuckmann 3D surface scanner at the Muséum National d'Histoire Naturelle, Paris (white light fringe StereoSCAN<sup>3D</sup> model with a camera resolution of 1.4 megapixels).

### Ancestral character state reconstruction

To test whether the evolution of an arboreal lifestyle preceded the evolution of grasping ability, an ancestral state reconstruction of lifestyle and food-handling behaviour was conducted as follows (Table 1). Three categories of lifestyles were defined following Nowak (2005) and Wilson & Mittermeier (2009): an arboreal lifestyle defines species that spend the majority of their time in the trees; a semi-arboreal lifestyle represents species that spend time both in trees and on the ground without a clear preference for either, and a terrestrial lifestyle defines species that spend the majority of their time on the ground. Three categories of grasping ability are also defined following the descriptions in Iwaniuk & Whishaw (1999) and Antón *et al.* (2006) for procyonids and ailurids, and the descriptions in Nowak (2005) and Wilson & Mittermeier (2009) for all other species. These categories are species with a well-developed

grasping ability, an intermediately developed grasping ability and a poorly developed grasping ability.

The ancestral state reconstructions were performed using the parsimony reconstruction method in Mesquite (Maddison & Maddison, 2011). This method summarizes state change of characters (lifestyle or grasping ability) over the tree by minimizing the number of steps of character change. The unordered states assumption was used as model of evolution, which means that each change of character along the tree is counted as a change. We used the time-calibrated phylogeny of caniform carnivorans from Slater *et al.* (2012) as the framework for our analyses. The tree uses the family-level phylogeny of Carnivora from Eizirik *et al.* (2010) as a backbone, with time-calibrated molecular phylogenies for each family appended to it. Full details of the phylogenetic reconstruction are provided in the supplementary information of Slater *et al.* (2012). For our analyses, we pruned the tree so that only species represented in our data set remained (Fig. 1).

### Quantification of shape variation using 3D geometric morphometrics

Because of the complex shape of the elbow articulation, it cannot be correctly represented using traditional landmarks. Thus, a 3D sliding semi-landmark procedure was used to quantify forelimb morphology based on scanned specimens (Bookstein, 1997; Gunz *et al.*, 2005). With this procedure, sliding semi-landmarks on surfaces and curves are transformed into spatially homologous landmarks (Parr *et al.*, 2012) that can be used to compare shapes. Sliding semi-landmarks are

allowed to slide along the curves and surfaces that are predefined on each surface while minimizing the bending energy. Morphometric data (landmarks, curves) were obtained using the software package Idav Landmarks (Wiley *et al.*, 2005), whereas Edgewarp3D 3.31 (Bookstein & Green, 2002) was used to obtain the sliding semi-landmarks. To do so, we first created a template representing the entire variation of the musteloid data set.

Each specimen is defined by its homologous anatomical landmark coordinates, which are comprised of twenty-one landmarks for the humerus (Fig. 2, Table 2), nineteen landmarks for the ulna (Fig. 2, Table 3) and thirteen landmarks for the radius (Fig. 2, Table 4). Based on the homologous landmarks, the sliding semi-landmarks of the template are warped onto the new specimen while minimizing the bending energy. Next, the warped sliding semi-landmarks are projected onto the predefined curves and surfaces of the new specimen. The curves consist of the distal surface of the articulation of the humerus and the proximal and distal articulations surface of the radius and ulna (Fig. 2). Finally, spline relaxation must be performed allowing sliding semi-landmarks to slide along the curves and surfaces' tangent structures (Gunz *et al.*, 2005). During the relaxation step, sliding semi-landmarks are projected onto the nearest curves and surfaces. Both sliding and relaxation are repeated iteratively until the bending energy is minimized. At the end of this procedure, 306 landmarks (21 homologous landmarks and 285 sliding semi-landmarks) for the humerus, 165 landmarks (13 homologous landmarks and 152 sliding semi-landmarks) for the radius and 330 landmarks (19 homologous landmarks and 311 sliding semi-landmarks) for the ulna describe the shape of each bone and their articulations. After this operation has been performed for each data set, the landmarks of all specimens can be compared using traditional morphometric methods.

Once all landmark data were obtained, a generalized Procrustes superimposition (Rohlf & Slice, 1990) was performed on the point coordinates using the package Rmorph (Baylac, 2012) in R (R Development Core Team, 2011). A principal component analysis (PCA) on the shape data was performed to evaluate the distribution of species in morphospace. The visualizations of shapes change (conformation) at the extreme of each axis were performed in two ways: first, the Evan toolbox (<http://www.evan.at>) package was used to generate 3D thin-plate spline visualizations; and second, a visualization of conformation change using shapes coordinates at the extreme of each axis was obtained with the package Rmorph in R and reconstructed in Geomagic Studio (<http://www.geomagic.com>). A mean conformation was calculated separately for arboreal species having either well-developed or poorly developed grasping ability, as well as for all arboreal species,

allowing visualization of the shape differences between these groups.

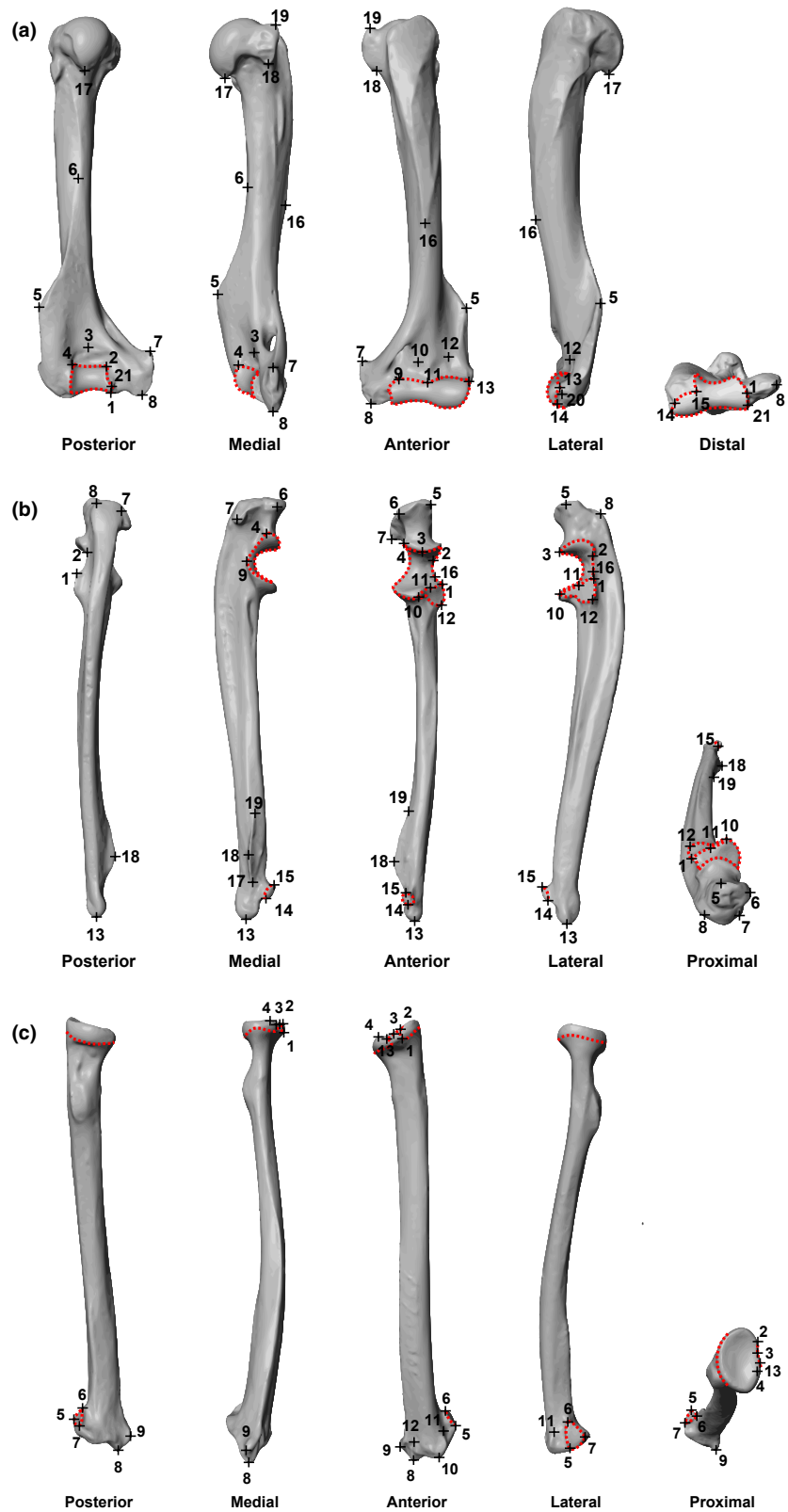
### Statistical analyses

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 recently published phylogeny described above (Fig. 1) and with branch lengths proportional to time. To test whether grasping ability or lifestyle influences forelimb shape, we performed a phylogenetic MANOVA and ANOVAS (Garland *et al.*, 1993) on the principal components that explain a significant proportion of the shape variation for each bone: the first four principal components of the humerus data set and the first three principal components of the ulna and radius data sets. We used the `phy.manova` and the `phy.anova` function in the R package 'geiger' (Harmon *et al.*, 2008) for our analysis. To test whether animals with different lifestyles and grasping abilities differed in shape, simulation of new shapes variables on the tree was performed. 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' statistic as a multivariate test. This gives an approximation of the *F* distribution by a transformation of the test statistic. Finally, standard Bonferroni corrected *post hoc* tests were calculated using the `phyANOVA` function in the R package 'phytools' (Revell, 2012). These corrected *post hoc* tests allow us to test for differences between each lifestyle and grasping ability of group and consist of a comparison of the means of each category in each group.

## Results

### Ancestral character state reconstructions

The ancestral state reconstruction of lifestyle (Fig. 3) suggests that the character state of the common ancestor of musteloids and of the clade containing ailurids + procyonids + mustelids was equivocal. The basal node of the mustelids was either terrestrial or semi-arboreal, whereas procyonids were reconstructed as having an arboreal ancestor. Furthermore, our reconstructions suggest that a specialized arboreal lifestyle evolved on at least two separate occasions: once in the ailurids (*Ailurus fulgens*) and once in procyonids (*Potos flavus*, *Bassariscus astutus*, *Bassaricyon alleni*, *Bassaricyon gabpii*). Semi-arboreality evolved on three separate occasions: once in mustelids (*Martes* and *Eira* clades) and twice



**Fig. 2** Landmarks used in analyses to quantify shape variation on the forelimb bones. (a) humerus; (b) ulna; (c) radius. Black crosses represent landmarks; red dashed lines represent outlines used for the surface analyses of the articulations of each bone.

**Table 2** Definition of the landmarks on the humerus used for geometric morphometric analyses.

Landmark	Definition
1	Most medio-distal point of the caudal part of the trochlea
2	Most medio-proximal point of the caudal side of the trochlea
3	Point of maximum of curvature of the olecranon fossa
4	Most latero-proximal point of the caudal side of the trochlea
5	Point of maximum of convexity of the lateral epicondylar crest
6	Point of insertion of the lateral epicondylar crest on the diaphyse
7	Most proximal tip of the medial epicondyle
8	Most distal tip of the medial epicondyle
9	Most medio-proximal point of the cranial side of the trochlea
10	Point of maximum of curvature of the coronoid fossa
11	Most proximo-anterior point of contact between the trochlea and the capitulum
12	Point of maximum of curvature of the radial fossa
13	Most latero-proximal point of the cranial side of the capitulum
14	Most disto-lateral point of the capitulum
15	Most distal point of contact between the trochlea and the capitulum
16	Most distal point of the deltopectoral crest
17	Tip of the lesser tuberosity
18	Most proximo-medial point of the greater tuberosity
19	Most disto-medial point of the greater tuberosity
20	Most latero-distal point of the cranial side of the capitulum
21	Point of maximum of concavity of the caudo-medio-distal part of the trochlea

independently in procyonids (*Procyon* clade and *Nasua* clade).

The ancestral state reconstruction of grasping ability (Fig. 3) suggests that the common ancestor of musteloids had a poorly developed prehensile ability. The common ancestor of the ailurid, procyonid and mustelid clades was also reconstructed as having poorly developed prehensile abilities. The base of procyonid node was also reconstructed as having a poorly developed prehensile ability. This reconstruction suggests that the character of intermediately developed grasping appeared independently twice: once in the ailurid clade and once in the *Procyon* clade. A well-developed grasping ability evolved on two separate occasions among procyonids: once in the *Potos* lineage and once at the base of the *Bassaricyon* clade.

### Shape variation using 3D geometric morphometrics

Only axes and the associated conformations that were significantly different among groups, as determined by regular or phylogenetic ANOVAS (Table 5), are described below.

#### *Influence of locomotion and grasping ability on humerus shape*

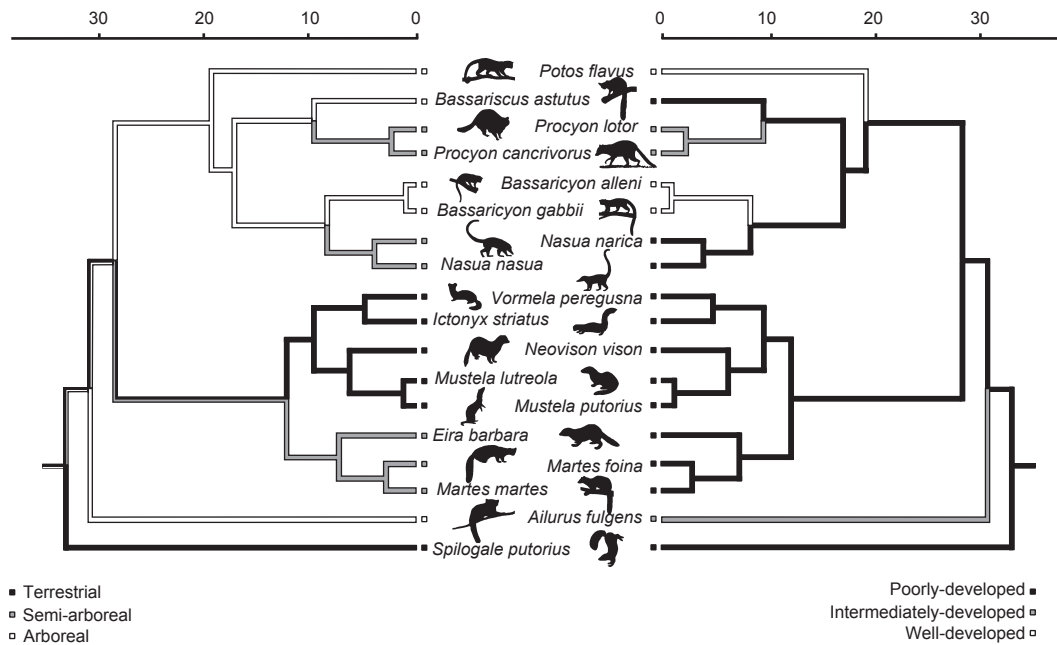
A standard and phylogenetic MANOVA and ANOVA were performed on the first four principal components

**Table 3** Definition of the landmarks on the ulna used for geometric morphometric analyses.

Landmark	Definition
1	Most lateral point of contact between the trochlear notch and the radial notch
2	Most proximo-lateral point of the incisure of the trochlear notch
3	Point of maximum of concavity of the proximal part of the trochlear notch
4	Most proximo-medial point of the incisure of the trochlear notch
5	Most palmar-lateral point of olecranon process
6	Most palmar-medial point of olecranon process
7	Most dorsal-medial point of olecranon process
8	Most dorsal-lateral point of olecranon process
9	Point where the most medial part of the coronoid process meets the most medio-distal part of the trochlear notch
10	Most anterior point of contact between the trochlear notch and the radial notch
11	Point of maximum of concavity between the radial notch and the trochlear notch
12	Most latero-distal point of insertion of the radial notch
13	Tip of the styloid process
14	Most distal point of the articular facet that articulates with the radius
15	Most proximal point of the articular facet that articulates with the radius
16	Point where the proximo-lateral part of the coronoid process meets the lateral part of the trochlear notch
17	Most distal point of insertion of the medial epicondylar crest on the diaphysis
18	Point of maximum of curvature of the medial epicondylar crest
19	Most proximal point of insertion of the medial epicondylar crest on the diaphysis

**Table 4** Definition of the landmarks on the radius used for geometric morphometric analyses.

Landmark	Definition
1	Most disto-lateral point of anterior side of the ulnar facet
2	Most proximo-lateral point of anterior side of the ulnar facet
3	Point of maximum of concavity of the anterior part of the fovea
4	Tip of the fovea
5	Most disto-medial point of the distal articular facet with the ulna
6	Most proximal point of curvature of the distal articular facet with the ulna
7	Most disto-lateral point of the distal articular facet with the ulna
8	Distal tip of the styloid process
9	Medial tip of the styloid process
10	Most disto-lateral point of the dorsal side of the radius
11	Most proximal point of the groove for extensor digitorum and extensor indicis
12	Most proximo point of groove for extensor carpi radialis longus and brevis
13	Most disto-medial point of the anterior side of the ulnar facet



**Fig. 3** Ancestral character state reconstructions for lifestyles on the left and grasping ability on the right.

**Table 5** Results of ANOVAs ( $F$  and  $P$ -values) and Phylogenetic ANOVAs (Phyl  $P$ -value) for the first four principal shape components of the humerus, the first three principal shape components of the ulna and the first three principal shape components of the radius. Principal components showing significant differences are indicated in bold.

	Lifestyle	Lifestyle			Grasping ability		
		$F$ -value	$P$ -value	Phyl $P$ -value	$F$ -value	$P$ -value	Phyl $P$ -value
Humerus	PC1	<b>8.35</b>	<b>0.0037**</b>	0.073	<b>7.72</b>	<b>0.0049**</b>	0.063
	PC2	<b>3.78</b>	<b>0.047*</b>	0.27	<b>9.63</b>	<b>0.002**</b>	<b>0.028*</b>
	PC3	2.28	0.14	0.48	0.68	0.52	0.78
	PC4	3.4	0.06	0.326	1.02	0.38	0.70
Ulna	PC1	<b>13.63</b>	<b>0.00042***</b>	<b>0.025*</b>	<b>14.06</b>	<b>0.00036***</b>	<b>0.006**</b>
	PC2	0.58	0.57	0.81	0.59	0.56	0.8
	PC3	3.05	0.077	0.36	1.68	0.21	0.56
Radius	PC1	<b>11.70</b>	<b>0.00087***</b>	<b>0.033*</b>	<b>8.445</b>	<b>0.0035**</b>	<b>0.048*</b>
	PC2	0.80	0.46	0.735	1.82	0.196	0.48
	PC3	3.48	0.057	0.313	<b>4.78</b>	<b>0.025*</b>	0.18

\*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$ .

representing 65% of the variation in humerus shape (Table 5). Results of the MANOVA and phylogenetic MANOVA were significant for lifestyle (MANOVA: Wilks  $\lambda = 0.090$ ,  $F_{2,15} = 7.01$ ,  $P < 0.001$ ; MANOVA  $P_{\text{phyl}} = 0.021$ ) and grasping ability (MANOVA: Wilks  $\lambda = 0.1269$ ,  $F_{2,15} = 5.42$ ,  $P < 0.001$ ; MANOVA  $P_{\text{phyl}} = 0.053$ ). Results of the ANOVAs were significant for the first two axes for lifestyle (PC1  $P = 0.0037$ , PC2  $P = 0.047$ ) and the first two axes for grasping ability (PC1  $P = 0.0049$  and PC2  $P = 0.002$ ). Results were not significant for other axes. Results of the phylogenetic ANOVA were

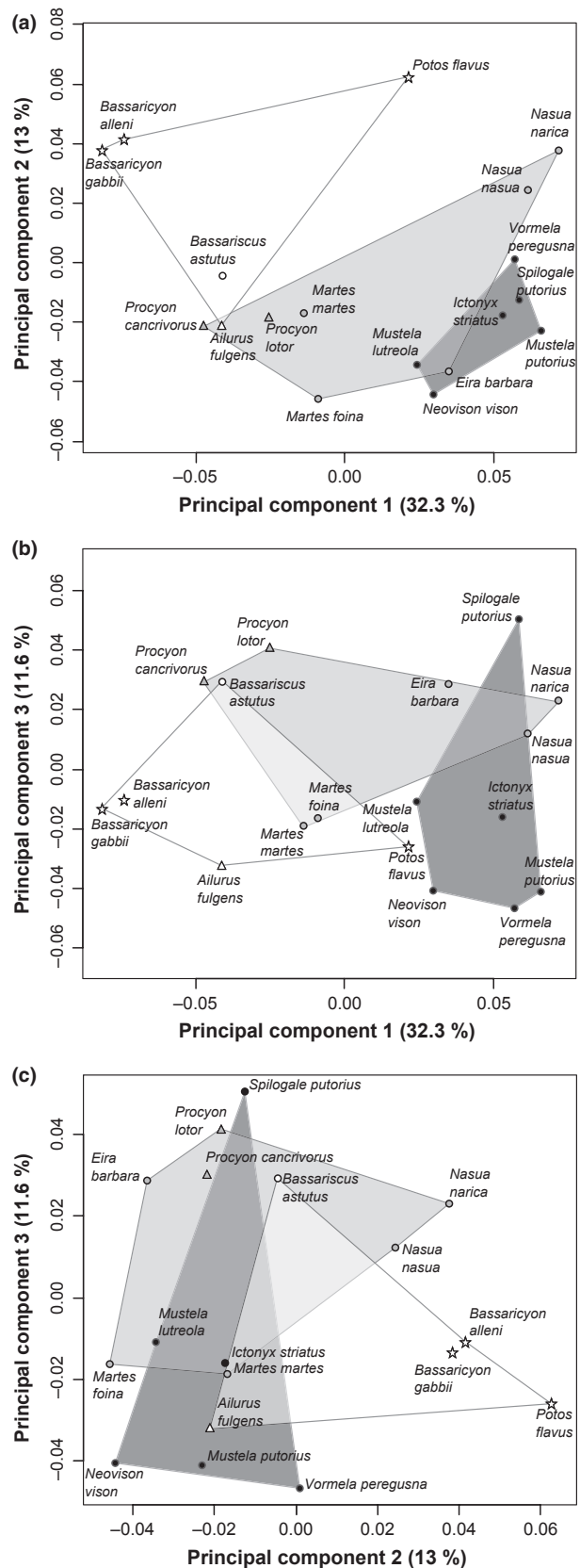
only significant for grasping ability on the second principal component (PC2:  $P_{\text{phyl}} = 0.028$ ). These results indicate a strong influence of prehensile ability on the shape of the humerus as represented by the second axis when phylogeny is taken into account. The *post hoc* tests showed differences in prehensile ability between species displaying an intermediately developed and well-developed ability (PC2  $P = 0.032$ ) and between species showing well-developed and poorly developed ability (PC2  $P = 0.024$ ) on the second axis.

### Shape variation

The first three principal component (PC) axes accounted for 56.9% of the total shape variation. The overall distribution of the different taxa in the morphospace as defined by the first and second axes (Fig. 4) showed a gradient from terrestrial species to arboreal ones. Principal component 1 (Fig. 4) tended to differentiate arboreal species and semi-arboreal species able to grasp on the negative part of the axis from terrestrial species unable to grasp on the positive part of the axis. Shape changes associated with PC1 (Fig. S1) on the negative part of the axis encompass a more gracile humerus with a relatively small distal articulation with a capitulum that is relatively broader in comparison with the trochlea, a relatively narrow and concave trochlea, a relatively straight medial lip of the trochlea, a relatively short medial epicondyle, a relatively small lateral epicondylar crest and a greater tubercle oriented more vertically relatively to the diaphysis. In contrast, terrestrial and some semi-arboreal species falling on the positive part of the axis show a relatively more robust humerus with a relatively broad distal articulation with a smaller capitulum in comparison with the trochlea, a medial lip of the trochlea that is oriented more medially, a relatively large medial epicondyle, a relatively prominent lateral epicondylar crest and a greater tubercle that is oriented more horizontally relatively to the diaphysis.

The negative end of principal component 2 (Fig. 4) is occupied by terrestrial species, semi-arboreal weasels (*Martes*) and the tayra (*Eira barbara*), which are all unable to grasp, as well as the arboreal red panda (*Ailurus fulgens*) and the semi-arboreal raccoons (*Procyon*), which all display an intermediately developed ability to grasp. Arboreal olingos and kinkajous (*Bassaricyon* and *Potos*) with a well-developed ability to manipulate and semi-arboreal coatis (*Nasua*), which are unable to grasp, are positioned towards the positive part of the axis. Shape changes associated with PC2 (Fig. S1) on the negative part of the axis include characterized by a relatively short distal articulation with a relatively broad trochlea in comparison with the capitulum, a relatively narrow and concave trochlea, a relatively narrow and asymmetrical posterior part of the trochlea with a

**Fig. 4** Results of a principal component analysis performed on the morphometric data for the humerus. (a) scatter plot illustrating the position of different species on the first two principal components; (b) scatter plot illustrating the position of different species on axes one and three; (c) scatter plot illustrating the position of different species on the axes two and three. Shaded polygons represent lifestyles; black: terrestrial lifestyle, grey: semi-arboreal, white: arboreal. The prehensile ability of each species is represented by a dot for poorly developed, a triangle for intermediately developed and a star for a well-developed prehensile ability.



higher and asymmetrical olecranon fossa and a relatively smaller coronoid fossa in comparison with the radial fossa. In contrast, species falling on the positive part of the axis display the opposite morphology.

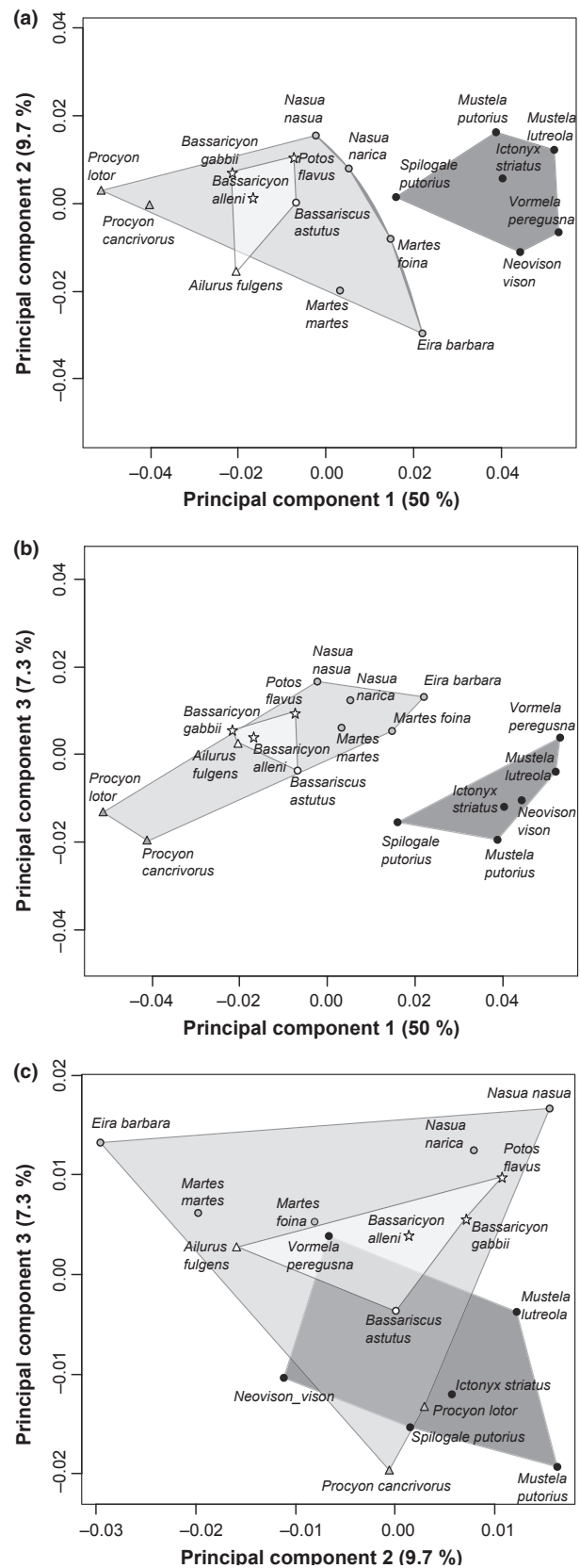
#### *Influence of locomotion and grasping ability on the shape of the ulna*

Results of the MANOVA and phylogenetic MANOVA performed on the first three principal components of the ulna shape were significant for lifestyle (MANOVA: Wilks  $\lambda = 0.081$ ,  $F_{2,15} = 10.81$ ,  $P < 0.001$ ; MANOVA  $P_{\text{phyl}} = 0.004$ ). Results of the MANOVA of the ulna shape were significant for grasping ability, but the phylogenetic MANOVA was not significant (MANOVA: Wilks  $\lambda = 0.21$ ,  $F_{2,15} = 5.02$ ,  $P < 0.001$ ; MANOVA  $P_{\text{phyl}} = 0.07$ ). An ANOVA performed on the first three principal components of the ulna shape (Table 5) showed significant results on the first axis for both lifestyle (PC1  $P < 0.001$ ) and grasping ability (PC1  $P < 0.001$ ). Results of the phylogenetic ANOVA were also significant on the first principal component for lifestyle ( $P_{\text{phyl}} = 0.025$ ) and grasping ability ( $P_{\text{phyl}} = 0.006$ ). Results were not significant for all others axes. Results of the corrected *post hoc* tests show differences in prehensile ability between species with poorly and intermediately developed abilities (PC1  $P = 0.012$ ), and in lifestyle between arboreal and terrestrial species (PC1  $P = 0.048$ ) and between terrestrial and semi-arboreal species (PC1  $P = 0.048$ ).

#### *Shape variation*

The first three PC axes (Fig. 5) accounted for 67% of the overall shape variation. The morphospace as defined by the scatter plots of the first and second and of the first and third axes tended to separate terrestrial species from semi-arboreal and arboreal species. Furthermore, a gradient of prehensile ability can be observed along the first axis from intermediately developed to poorly developed ability.

Principal component 1 (Fig. 5) tended to differentiate semi-arboreal and arboreal species (with the exception of *Martes foina* and *Eira barbara*) from terrestrial species. Species that display an intermediately developed to a well-developed prehensile ability fall on the negative end of the axis. In contrast, more terrestrial species



**Fig. 5** Results of a principal component analysis performed on the morphometric data for the ulna. (a) scatter plot illustrating the position of different species on the first two principal components; (b) scatter plot illustrating the position of different species on axes one and three; (c) scatter plot illustrating the position of different species on axes two and three. Shaded polygons represent lifestyles; black: terrestrial lifestyle, grey: semi-arboreal, white: arboreal. The prehensile ability of each species is represented by a dot for poorly developed, a triangle for intermediately developed and a star for a well-developed prehensile ability.

occupy the positive part of the axis. Shape changes associated with the negative end of PC1 (Fig. S2) describe a relatively gracile and straight ulna with a relatively small proximal and distal articulations, an olecranon process that is relatively short and straight, a radial notch with a double and concave surface, a relatively narrow angle between radial notch and the coronoid process, a relatively short and flat medial epicondylar crest with a more proximal insertion on the diaphysis that is higher than the distal radial facet and a relatively narrow and concave anconeal process. Shape change associated with the positive part of PC1 displays a relatively robust ulna with the opposite morphology to that described above for the negative end of the axis.

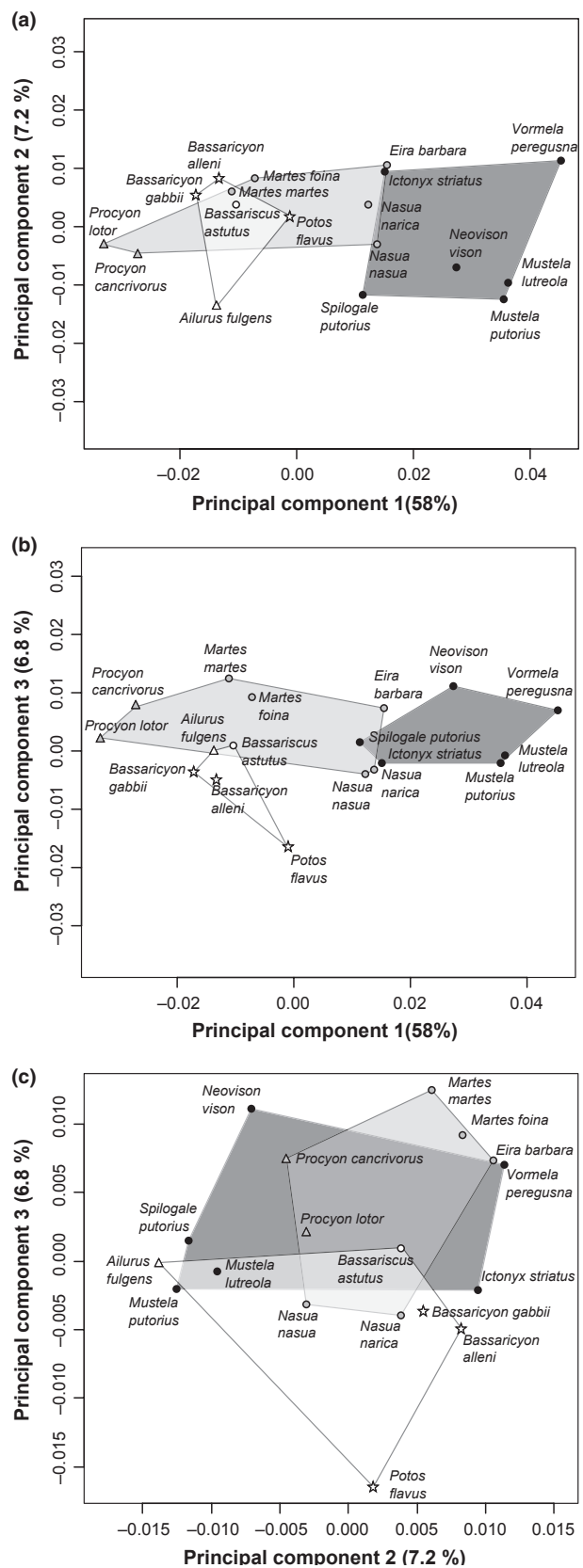
#### *Influence of locomotion and grasping ability on the shape of the radius*

Results of the MANOVA performed on the first three principal components of the radial shape were significant for both lifestyle (MANOVA: Wilks  $\lambda = 0.21$ ,  $F_{2,15} = 5.12$ ,  $P < 0.001$ ) and grasping ability (MANOVA: Wilks  $\lambda = 0.169$ ,  $F_{2,15} = 6.19$ ,  $P < 0.001$ ). However, the results of the phylogenetic MANOVA were only significant for the grasping ability (MANOVA  $P_{\text{phyl}} = 0.025$ ) and not for the influence of the lifestyle (MANOVA  $P_{\text{phyl}} = 0.086$ ). Both a traditional and a phylogenetic ANOVA were performed on the first three principal components of the radius shape (Table 5) and revealed significant differences among groups on the first axis for lifestyle (PC1  $P < 0.001$ ;  $P_{\text{phyl}} = 0.033$ ) and on the first and third axes for grasping ability with results of the phylogenetic ANOVA being significant only on the third axis (PC1  $P = 0.0035$ ,  $P_{\text{phyl}} > 0.05$ ; PC3  $P = 0.025$ ,  $P_{\text{phyl}} = 0.048$ ). Results were not significant for all other axes. Results of the *post hoc* tests were not significant.

#### *Shape variation*

The first three PC axes accounted for 72% of the total shape variation. The overall distribution of taxa on the first and second axes and the first and third axes (Fig. 6) showed a cluster of terrestrial species that was generally differentiated from semi-arboreal and arboreal species. Species that display a well-developed prehensile

**Fig. 6** Results of a principal component analysis performed on the morphometric data for the radius. (a) scatter plot illustrating the position of different species on the first two principal component; (b) scatter plot illustrating the position of different species on axes one and three; (c) scatter plot illustrating the position of different species on axes two and three. Shaded polygons represent lifestyles; black: terrestrial lifestyle, grey: semi-arboreal, white: arboreal. The prehensile ability of each species is represented by a dot for poorly developed, a triangle for intermediately developed and a star for a well-developed prehensile ability.



ability tend to cluster in morphospace. Arboreal species with a degree of grasping ability tend to be separate from semi-arboreal and terrestrial species in the morphospace defined by the first and third axes.

The negative end of principal component 1 (Fig. 6) was occupied by arboreal species and semi-arboreal species with intermediately developed ability of grasping, as well as weasels (*Martes*) that have poorly developed ability to grasp, whereas terrestrial species and some semi-arboreal species that are unable to grasp fell along the positive part of the axis. The negative part of the PC1 (Fig. S3) was defined by a relatively gracile radius with a relatively small proximal and distal articulation, a circular proximal articular surface, a relatively flatter than convex fovea with a relatively flat tip, a posterior border of the proximal surface contacting the radial notch of the ulna which is circular and an anterior border which is round with a relatively narrow interruption of its rim, an antero-medial part of the proximal surface contacting the radial notch of the ulna which is relatively thin and a relatively narrow and asymmetrical distal epiphysis with a relatively small medial styloid process. Shape change associated with the positive part of the PC1 displays a relatively robust radius with a radial head that is oval-shaped, a relatively more concave anterior part of the fovea with a relatively prominent tip, a posterior border of the proximal ulnar facet which is oval, but an anterior border that is relatively concave with a relatively broad interruption of its rim, an antero-medial part of the proximal ulnar facet which is relatively broad, a distal articulation which is relatively broad, and a relatively large and symmetric distal epiphysis with a prominent medial styloid process.

Principal component 3 (Fig. 6) tends to separate the kinkajou (*Potos flavus*) on the negative part of the axis from all other species. Radial morphology associated with species on the negative part of PC3 (Fig. S3) consists of a rounded radial head, which is oriented postero-distally, a relatively broader posterior rim of the proximal ulnar facet, a tip of the fovea that is relatively flat, a relatively round and concave fovea, a proximal ulnar facet with a relatively equal antero-lateral surface in comparison with the antero-medial one, an antero-medial surface of the proximal ulnar facet that is relatively large and flat, a relatively low tip on the styloid process and a relatively convergent orientation of the groove of the extensor digitorum and extensor indicis to the groove of the extensor carpi radialis longus and brevis. Shape changes associated with species on the positive part of the axis involve the opposite morphology.

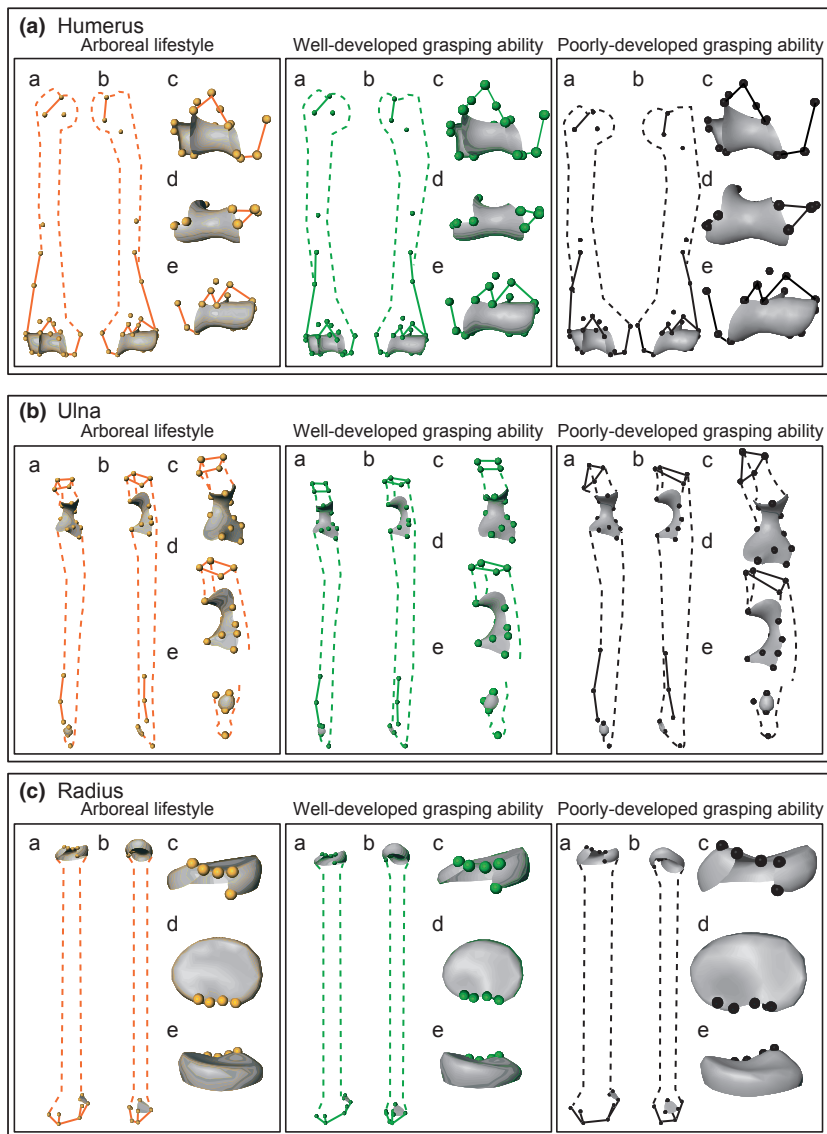
## Discussion

Our analyses of humerus shape (Fig. 4, Table 5) show that arboreal species tend to fall in the same part of morphospace as species having a well-developed grasping ability. Shapes associated with the humerus (Fig. 7,

Fig. S1) of arboreal species and species displaying a well-developed grasping ability show mainly a narrow trochlea relative to the capitulum, which is broad and well-developed distally where the fovea of the radial head articulates. This kind of conformation has been suggested to facilitate forearm movements during pronation–supination, which is important during both arboreal locomotion and grasping (Sargis, 2002; Antón *et al.*, 2006; Candela & Picasso, 2008; Flores & Díaz, 2009). The trochlea of arboreal species is relatively narrow with a shallow trochlear groove. It reflects the trochlear notch on the ulna, which is also small and narrow. Terrestrial species unable to grasp display the opposite morphology, and this pattern of form likely restricts movement and stabilizes the elbow joint. As such, it is likely efficient for load bearing and may help dissipate the load of the anterior part of the animal transferred to the front limbs during locomotion (Szalay & Sargis, 2001).

The analyses of the shape of the ulna (Fig. 5, Table 5, and Fig. S2) and radius (Fig. 6, Table 5, and Fig. S3) show that arboreal and semi-arboreal species again fall in the same area of morphospace as do species able to grasp. Moreover, morphological differences between species with different degrees of grasping behaviour are evident in the distribution of taxa in the ulnar and radial morphospaces. Indeed, a cluster of species having a well-developed grasping ability is clearly differentiated from another cluster of semi-arboreal species having an intermediately developed grasping ability for both the ulna (Fig. 5A, Fig. S2) and the radius (Fig. 6A, Fig. S3). The ulnar and radial morphologies (Fig. 7, Fig. S2) of species with a well-developed grasping ability, as well as of arboreal species, correspond to gracile bones with a less developed medial epicondylar crest on the diaphysis of the ulna and a narrow and poorly developed distal end of the radius. The ulnae of arboreal species display a short olecranon process. This character has biomechanical consequences as it decreases the lever arm and consequently decreases the force during flexion–extension movements. However, this character appears to be related to an increase in the speed of movement (Rose, 1993; Argot, 2001) and was previously interpreted as an adaptation to arboreality observed in species able to perform rapid locomotion on thin branches (Rose, 1993; Argot, 2001). The ulnae of arboreal species display a straight diaphysis and olecranon process (Fig. 7, Fig. S2). This character is thought to facilitate the transmission of compressive loading (Lanyon, 1980; Flores & Díaz, 2009) and likely relates to the importance of this bone in load transfer and stability of the forelimb.

The orientations of the proximal and distal radial notches (Fig. 7, Fig. S2) of arboreal species are clearly different from those of species unable to grasp, which are mainly terrestrial. The proximal radial notch of the ulna is broad and laterally oriented, and the distal



**Fig. 7** Mean shape of forelimb elements of arboreal species (orange) and species having a well (green) and poorly developed grasping ability (black). (a) humerus: (a) posterior view; (b) anterior view; (c) close-up of the distal articulation in posterior view; (d) close-up of the distal articulation in distal view; (e) close-up of the distal articulation in anterior view. (b) ulna: (a) anterior view; (b) lateral view; (c) close-up of the proximal articulation in anterior view; (d) close-up of the proximal articulation in lateral view; (e), close-up of the distal articulation in anterior view. (c) radius: (a) anterior view; (b) lateral view; (c), close-up of the proximal articulation in anterior view; (d), proximal view; (e) close-up of the proximal articulation in posterior view. Dots and grey surfaces represent landmarks; lines represent real links between landmarks; dashed lines represent a schematic representation of the bone.

radial notch is antero-distally oriented. The proximal ulnar notch of the radius is broad around the fovea, and the distal one is broad and proximally oriented relative to the diaphysis. Both of these articular surfaces of the forearm seem to perfectly fit with each other, suggesting a strong degree of co-evolution. These configurations likely also facilitate the rotation of the radius around the ulna given the extent of the articulation and its orientation. Furthermore, the circular shape of the radial head together with a round and slightly concave fovea in arboreal species, and especially in species having a well-developed grasping ability, may allow the rotation of the radius on the ulna and also on the capitulum of the humerus. This configuration likely provides a wide range of pronation–supination movements and consequently a greater mobility to the

forearm and the hand (MacLeod & Rose, 1993; Argot, 2001; Szalay & Sargis, 2001; Flores & Díaz, 2009). In contrast, terrestrial species and species showing poorly developed grasping ability display an oval-shaped radial head complemented by a sharp antero-medial fovea, which likely restricts the range of rotational movements.

Although our results thus show many similarities between arboreal species and those species with a well-developed grasping ability, shape differences do exist (Fig. 7). Species with a well-developed grasping ability appear to exhibit exaggerated arboreal characteristics, rather than novel attributes. In the humerus, they display a distal articulation with a relatively broader capitulum in comparison with the trochlea, a relatively flat trochlear groove and a relatively poorly developed

lateral epicondylar crest. In the ulna, the mean shape of species with a well-developed ability to grasp (Fig. 7) involves a relatively straight olecranon process, a relatively narrow medio-distal trochlear notch, a relatively more distal insertion of the medial epicondylar crest on the diaphysis that is positioned at the same level as the distal radial facet, and a relatively narrow and oval-shaped distal radial facet. The radius of species having a well-developed grasping ability (Fig. 7) is a gracile element with a relatively small radial head, which is circular, a fovea with a skewed orientation relative to the diaphysis, an antero-medial part of the proximal surface contacting the radial notch of the ulna which is relatively thin, a distal ulnar articulation which is oriented more perpendicularly than parallel relative to the diaphysis, and a relatively short, narrow and asymmetrical distal part of the radius. Overall, the forelimb of species with a well-developed ability to grasp appears to provide a greater potential for rotation, yet this remains to be tested empirically.

Thus, our quantitative shape descriptions suggest differences in forelimb shape that reflect both the influences of lifestyle and grasping ability. The results of our MANOVAS show that both lifestyle and grasping behaviour influence the shape of long bones of the forelimb. Nevertheless, our results of our phylogenetic MANOVAS show that grasping behaviour appears to influence the radial shape more, whereas locomotion influences primarily the humeral and ulnar shapes. These results seem to suggest that the ulna plays a greater role in load transfer than mobility *per se*. The results of our ANOVAS and phylogenetic ANOVAS (Table 5) confirm this. Overall, the results of our shape analyses show that species having a well-developed grasping ability tend to fall in the same area of morphospace as do arboreal ones, and this pattern holds for all the long bones of the forelimb. This distribution of species in morphospace can be seen particularly clearly for the more distal elements (radius and ulna). Moreover, the radial and ulnar morphospaces were more similar to one other in comparison with those of the humerus, suggesting that these elements may play a functional role that is distinct from those of the humerus but more similar to each other during grasping and/or arboreal locomotion. Indeed, grasping and manipulation involve pronation–supination movements, which mainly occur at the elbow joint and primarily involve the lower arm bones. Pronation and supination consist of a rotational movement where the radius revolves medio-laterally around the ulna. These movements of rotation occur on the proximal part of the radius where the proximal ulnar notch of the radial head allows the rotational movements around the radial notch of the ulna and at the distal ulnar notch, which is a concave surface that allows rotation of the radius against the ulna. Interestingly, our shape analyses indicate that it is exactly these zones that show the largest differences between groups.

In addition to showing quantitative differences in the shape of the long bones of the forelimb, our ancestral character state reconstruction (Fig. 3) also showed that the evolution of an arboreal lifestyle in musteloids tends to precede the development of specializations for grasping ability. This may explain the observed similarity in shape between arboreal species and species with a well-developed grasping ability (Fig. 7), with the morphology of able graspers being an exaggerated version of that of arboreal species. Moreover, our results show multiple independent origins of a well-developed grasping ability among musteloids. These results suggest that arboreal lifestyle can confer an advantage in the development of complex grasping as suggested previously for ailurid carnivorans (Antón *et al.*, 2006; Salesa *et al.*, 2006) and primates (Godinot, 1991, 2007). Yet, whether these patterns are generally applicable to mammals remains to be seen, and a broader analysis of forelimb shape including taxa with other lifestyles such as aquatic or fossorial species is needed to more fully understand the evolution of grasping and the morphologies that underlie it.

In conclusion, our results confirm our predictions and suggest that the functional signal of grasping ability on forelimb shape is stronger for forelimb bones most implicated in the movement such as the radius. The humerus and ulna, on the other hand, appear to be influenced more by constraints for load bearing. The overall shape of the forelimb of both arboreal species and species showing a well-developed grasping ability suggests a potential wide range of pronation–supination movements that may confer a greater mobility to the forearm and the hand. Our results demonstrate the importance of using 3D surface methods to describe differences in morphology related to functional traits involving complex movements. The addition of quantitative and qualitative behavioural data of species during grasping and manipulation (such as rotational capacity and movement complexity) complemented by detailed information on muscular anatomy would contribute to further improving the ability to characterize forelimb morphology in the context of locomotion and grasping ability. Finally, despite the abundance of research focused on the evolution of grasping ability and forelimb shape in mammals, the complete lack of quantitative data for the majority of taxa prevents broader interpretations of evolutionary patterns. Thus, more quantitative data on shape and behaviour are needed to advance our understanding of the evolution this complex attribute.

## Acknowledgments

We thank Jacques Cuisin, Géraldine Véron, Julie Villemain, Céline Bens and Tarik for access to specimens from the collections Mammifères et Oiseaux, MNHN, Paris. We also thank Loïc Costeur for allowing us to

scan the material from the Naturhistorisches Museum, Basel; Judy Chupasko for allowing us to scan the material from the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts; and Suzanne Peurach for allowing us to scan the material from the Smithsonian National Museum of Natural History, Washington, D.C. We thank the 'plate-forme de morphométrie' of the UMS 2700 (CNRS, MNHN) for access to the surface scanner. ACF thanks the doctoral school FdV, the Fondation Bettencourt-Schueller, and, Andrew Murray and Mary Collins to help her to obtain a UCL IMPACT scholarship for funding. We also thank Andrew Murray, Mary Collins, Anthony Herrel, Livia Bascher, Marcela Randau, Sybille Moulin and Céline Houssin for their helpful discussions and comments on this manuscript.

## References

- Andersson, K. 2003. *Locomotor Evolution in the Carnivora (Mammalia): Evidence From the Elbow Joint*. University of Uppsala, Sweden.
- Andersson, K. 2004. Elbow-joint morphology as a guide to forearm function and foraging behaviour in mammalian carnivores. *Zool. J. Linn. Soc.* **142**: 91–104.
- Andersson, K. 2005. Were there pack-hunting canids in the Tertiary, and how can we know? *Paleobiology* **31**: 56–72.
- Antón, M., Salesa, M.J., Pastor, J., Peigné, S. & Morales, J. 2006. Implications of the functional anatomy of the hand and forearm of *Ailurus fulgens* (Carnivora, Ailuridae) for the evolution of the "false-thumb" in pandas. *J. Anat.* **209**: 757–764.
- Argot, C. 2001. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *J. Morphol.* **247**: 51–79.
- Baylac, M. 2012. Rmorph: a R geometric and multivariate morphometrics library. Available from the author: baylac@mnhn.fr.
- Bookstein, F.L. 1997. Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Med. Image Anal.* **1**: 225–243.
- Bookstein, F.L. & Green, W.D.K. 2002. User's Manual, EWSH3.19. URL <http://brainmap.stat.washington.edu/edge-warp>.
- Brácha, V., Zhuravin, I.A. & Bures, J. 1990. The reaching reaction in the rat: a part of the digging pattern? *Behav. Brain Res.* **36**: 53–64.
- Byrne, R.W., Corp, N. & Byrne, J.M. 2001. Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. *Anim. Cogn.* **4**: 347–361.
- Candela, A.M. & Picasso, M.B.J. 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): Indicators of locomotor behavior in Miocene porcupines. *J. Morphol.* **269**: 552–593.
- Christel, M. 1993. Grasping techniques and hand preference in Hominoidea. In: *Hands of Primates* (H. Preuschoft, D.J. Chivers, eds), pp. 91–108. Springer, Wien, New York.
- Corp, N. & Byrne, R.W. 2002. The Ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of Saba Florida. *Behaviour* **139**: 137–168.
- Crast, J., Fragaszy, D., Hayashi, M. & Matsuzawa, T. 2009. Dynamic in-hand movements in adult and young juvenile chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **138**: 274–285.
- Eizirik, E., Murphy, W.J., Koepfli, K.-P., Johnson, W.E., Dragoo, J.W., Wayne, R.K. et al. 2010. Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Mol. Phylogenet. Evol.* **56**: 49–63.
- Endo, H., Hama, N., Niizawa, N., Kimura, J. & Itou, T. 2007. Three-dimensional analysis of the manipulation system in the lesser panda. *Mammal Study* **32**: 99–103.
- Ewer, R.F. 1973. *The Carnivores*. Cornell University Press, Ithaca, New York.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Amer. Nat.* **125**: 1–15.
- Flores, D.A. & Díaz, M.M. 2009. Postcranial skeleton of *Gliro-nia venusta* (Didelphimorphia, Didelphidae, Caluromyinae): Description and Functional Morphology. *Zoosyst. Evol.* **85**: 311–339.
- Garland, T., Dickerman, A.W., Janis, C.M. & Jones, J.A. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**: 265–292.
- Godinot, M. 1991. Approche fonctionnelle des mains des primates paléogènes. *Geobios* **24**: 161–173.
- Godinot, M. 2007. Primate origins: a reappraisal of historical data favoring tupaiid affinities. In: *Primate Origins: Adaptations and Evolution* (M.J. Ravosa, M. Dagosto, eds), pp. 83–133. Springer Press, New York.
- Gonyea, W.J. 1978. Functional implications of felid forelimb morphology. *Acta Anat.* **102**: 111–121.
- Gray, L.A., O'Reilly, J.C. & Nishikawa, K.C. 1997. Evolution of forelimb movement patterns for prey manipulation in anurans. *J. Exp. Zool.* **277**: 417–424.
- Grillner, S. & Wallén, P. 1985. Central pattern generators for locomotion, with special reference to vertebrates. *Annu. Rev. Neurosci.* **8**: 233–261.
- Grzimek, B. 1990. *Grzimek's Encyclopedia of Mammals*. McGraw-Hill Publishing Company, New York.
- Gunz, P., Mitteroecker, P. & Bookstein, F.L. 2005. Semilandmarks in three dimensions. In: *Modern Morphometrics in Physical Anthropology* (D.E. Slice, ed.), pp. 73–98. Kluwer Academic/Plenum Publishers, New York.
- Halenar, L.B. 2011. Reconstructing the locomotor repertoire of *Protopithecus brasiliensis*. II. Forelimb morphology. *Anat. Rec.* **294**: 2048–2063.
- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**: 129–131.
- Harvey, P.H. & Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, UK.
- Ivanco, T.L., Pellis, S.M. & Whishaw, I.Q. 1996. Skilled forelimb movements in prey catching and in reaching by rats (*Rattus norvegicus*) and opossums (*Monodelphis domestica*): relations to anatomical differences in motor systems. *Behav. Brain Res.* **79**: 163–181.
- Iwaniuk, A.N. & Whishaw, I.Q. 1999. How skilled are the skilled limb movements of the raccoon (*Procyon lotor*)? *Behav. Brain Res.* **99**: 35–44.
- Iwaniuk, A.N. & Whishaw, I.Q. 2000. On the origin of skilled forelimb movements. *Trends Neurosci.* **23**: 372–376.

- Iwaniuk, A.N., Pellis, S.M. & Whishaw, I.Q. 1999. The relationship between forelimb morphology and behaviour in North American carnivores (Carnivora). *Can. J. Zool.* **77**: 1064–1074.
- Iwaniuk, A.N., Pellis, S.M. & Whishaw, I.Q. 2000. The relative importance of body size, phylogeny, locomotion, and diet in the evolution of forelimb dexterity in fissiped carnivores (Carnivora). *Can. J. Zool.* **78**: 1110–1125.
- Lanyon, L.E. 1980. The influence of function on the development of bone curvature. An experimental study on the tibia rat. *J. Zool.* **198**: 457–466.
- MacLeod, N. & Rose, K.D. 1993. Inferring locomotor behavior in paleogene mammals via eigenshape analysis. *Am. J. Sci.* **293-A**: 300–355.
- Maddison, W.P. & Maddison, D.R. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. URL <http://mesquiteproject.org>.
- Manzano, A.S., Abdala, V. & Herrel, A. 2008. Morphology and function of the forelimb in arboreal frogs: specializations for grasping ability? *J. Anat.* **213**: 296–307.
- Nowak, R.M. 2005. *Walker's Carnivores of the World*. The Johns Hopkins University Press, Baltimore.
- Parr, W.C.H., Wroe, S., Chamoli, U., Richards, H.S., McCurry, M.R., Clausen, P.D. *et al.* 2012. Toward integration of geometric morphometrics and computational biomechanics: new methods for 3D virtual reconstruction and quantitative analysis of Finite Element Models. *J. Theor. Biol.* **301**: 1–14.
- Pouydebat, E., Laurin, M., Gorce, P. & Bels, V. 2008. Evolution of grasping among anthropoids. *J. Evol. Biol.* **21**: 1732–1743.
- Pouydebat, E., Gorce, P., Coppens, Y. & Bels, V. 2009. Biomechanical study of grasping according to the volume of the object: human versus non-human primates. *J. Biomech.* **42**: 266–272.
- Pouydebat, E., Reghem, E., Borel, A. & Gorce, P. 2011. Diversity of grip in adults and young humans and chimpanzees (*Pan troglodytes*). *Behav. Brain Res.* **218**: 21–28.
- R Development Core Team 2011. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna: R Foundation for Statistical Computing, ISBN 3-900051-07-0. URL <http://www.R-project.org>.
- Reghem, E., Tia, B., Bels, V. & Pouydebat, E. 2011. Food prehension and manipulation in *Microcebus murinus* (Prosimii, Cheirogaleidae). *Folia Primatol.* **82**: 177–188.
- Reghem, E., Byron, C., Bels, V. & Pouydebat, E. 2012. Hand posture in the grey mouse lemur during arboreal locomotion on narrow branches. *J. Zool.* **288**: 76–81.
- Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.
- Rohlf, F.J. & Slice, D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Zool.* **39**: 40–59.
- Rose, M.D. 1993. Functional anatomy of the elbow and forearm in primates. In: *Postcranial Adaptations in non-Human Primates* (D.L. Gebo, ed.), pp. 70–95. Northern Illinois Univ Press, DeKalb.
- Sacrey, L.-A.R., Alaverdashvili, M. & Whishaw, I.Q. 2009. Similar hand shaping in reaching-for-food (skilled reaching) in rats and humans provides evidence of homology in release, collection, and manipulation movements. *Behav. Brain Res.* **204**: 153–161.
- Salesa, M.J., Antón, M., Peigné, S. & Morales, J. 2006. Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. *Proc. Natl. Acad. Sci.* **103**: 379–382.
- Sargis, E.J. 2002. Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *J. Morphol.* **253**: 10–42.
- Sato, J.J., Wolsan, M., Minami, S., Hosoda, T., Sinaga, M.H., Hiyama, K. *et al.* 2009. Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. *Mol. Phylogenet. Evol.* **53**: 907–922.
- Sato, J.J., Wolsan, M., Prevosti, F.J., D'Elía, G., Begg, C., Begg, K. *et al.* 2012. Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). *Mol. Phylogenet. Evol.* **63**: 745–757.
- Schutz, H. & Guralnick, R.P. 2007. Postcranial element shape and function: assessing locomotor mode in extant and extinct mustelid carnivorans. *Zool. J. Linn. Soc.* **150**: 895–914.
- Slater, G.J., Harmon, L.J. & Alfaro, M.E. 2012. Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution* **66**: 3931–3944.
- Sustaita, D., Pouydebat, E., Manzano, A., Abdala, V., Hertel, F. & Herrel, A. 2013. Getting a grip on tetrapod grasping: form, function, and evolution. *Biol. Rev. Camb. Philos. Soc.* **88**: 380–405.
- Szalay, F.S. & Sargis, E.J. 2001. Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria. *Geodiversitas* **23**: 139–302.
- Wiley, D.F., Amenta, N., Alcantara, D.A., Ghosh, D., Kil, Y.J., Delson, E. *et al.* 2005. Evolutionary morphing. In: *Proceedings of IEEE Visualization 2005 (VIS'05), 23–28 October 2005*, pp. 431–438. Minneapolis, MN, USA.
- Wilson, D.E. & Mittermeier, R.A. 2009. In: *Handbook of the Mammals of the World* (D.E. Wilson & R.A. Mittermeier, eds), pp. 1–728. Lynx Edicions, Barcelona.

## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Data S1** Specimens used in analyses.

**Figure S1** Shapes change of the humerus associated with each significant principal component. Shapes correspond to the positive (red) and negative (blue) extremes of each axis.

**Figure S2** Shapes change of the ulna associated with each principal significant component axis. Shapes correspond to the positive (red) and negative (blue) extremes of each axis.

**Figure S3** Shapes change of the radius associated with each principal component axis. Shapes correspond to the positive (red) and negative (blue) extreme of each axis.

Received 26 November 2012; accepted 10 March 2013