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ORIGINAL PAPER

Quantitative inferences on the locomotor behaviour of extinct species applied to *Simocyon batalleri* (Ailuridae, Late Miocene, Spain)

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Abstract Inferences of function and ecology in extinct taxa have long been a subject of interest because it is fundamental to understand the evolutionary history of species. In this study, we use a quantitative approach to investigate the locomotor behaviour of *Simocyon batalleri*, a key taxon related to the ailurid family. To do so, we use 3D surface geometric morphometric approaches on the three long bones of the forelimb of an extant reference sample. Next, we test the locomotor strategy of *S. batalleri* using a leave-one-out cross-validated linear discriminant analysis. Our results show that *S. batalleri* is included in the morphospace of the living species of musteloids. However, each bone of the forelimb appears to show a different functional signal suggesting that inferring the lifestyle or locomotor behaviour of fossils can be difficult and dependent on the bone investigated. This highlights the importance of studying, where possible, a maximum of skeletal elements to be able to make robust inferences on the lifestyle of extinct species. Finally, our results suggest that *S. batalleri* may be more arboreal than previously suggested.

Keywords Ecomorphology · Locomotion · 3D geometric morphometrics · Palaeobiological inference · Forelimb

Introduction

The reconstruction of the ecology, behaviour and lifestyle of extinct species of mammals is a subject that has been of interest to many evolutionary biologists and palaeontologists (Bock and von Wahlert 1965; Gonyea 1978; Damuth 1981; Gould and Vrba 1982; Van Valkenburgh 1984, 1985, 1987, 1988; Ewer 1973; Taylor 1989; Damuth and MacFadden 1990; Vrba 1992; Janis and Wilhelm 1993; Jones and Stoddart 1998; Iwaniuk et al. 1999, 2000; Yalden 1999; Ruff 2000; Argot 2001, 2003a, b, 2004; Andersson 2003, 2004a, b, 2005; Schmitt 2003; Salesa et al. 2005, 2010; Schutz and Guralnick 2007; Webb and Sparrow 2007; Boyer and Bloch 2008; Boyer et al. 2010a; b; Polly 2008; Polly and Macleod 2008; Samuels and Van Valkenburgh 2008; Flores and Díaz 2009; Meachen-Samuels and Van Valkenburgh 2009; Figueirido et al. 2011; Figueirido and Janis 2011; Halenar 2011; Ercoli et al. 2012; Samuels et al. 2013; Meachen-Samuels 2012; Walmsley et al. 2012; Meloro et al. 2013; Janis and Figueirido 2014; Martín-Serra et al. 2014). Indeed, the investigation of fossil organisms is fundamental to understanding the evolutionary history of species (Simpson 1953; Slater et al. 2012). Unfortunately, a fossil is rarely well preserved with all its soft and hard tissues, and thus teeth, bones or parts of bones are the main material with which palaeontologists work. The reconstruction of the

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palaeobiology of an extinct species with its skeleton as principal evidence is a difficult exercise. As such, one first needs to understand the adaptive nature of the morphology of the skeleton in living species and its relation to ecology, locomotion or behaviour, while taking into account potential effects of shared ancestry.

The main methods used for palaeobiological reconstructions are ecomorphological ones (Wainwright 2007). Although the relationships between form and function are intuitively appealing, they are often not straightforward due to behavioural filters and processes such as many-to-one mapping (Alfaro et al. 2005; Wainwright et al. 2005; Polly 2008). Form and function are, however, linked at a fundamental level, and bones are functionally important (Bock and von Wahlert 1965). They allow movement and, whilst supporting loads, also need to respond and resist to muscular forces (Hildebrand 1985; Bryant and Seymour 1990; Bryant and Russell 1992; Demes et al. 1994; Witmer 1995; Jungers et al. 1998; Biknevicius et al. 2004; Alexander 2006; Polly 2008; Fabre et al. 2014). As bones are shaped by force and motion, they are intimately related to the movements executed and, by inference, also the lifestyle of a species. Following these principles, different approaches can be used to reconstruct the palaeobiology of a species. Most commonly, qualitative approaches consisting of the anatomical comparison of a fossil with living relatives or analogous species are used. The main problem of this approach is the impossibility to test the hypotheses of the inferences that are made. On the other hand, quantitative approaches including morphometrics (e.g. Van Valkenburgh 1984, 1985, 1987, 1988; Andersson 2003, 2004a, b, 2005; Polly 2008; Polly and Macleod 2008; Samuels and Van Valkenburgh 2008; Ercoli et al. 2012; Janis and Figueirido 2014), functional morphology (e.g. Argot 2001, 2003a, b, 2004; Salesa et al. 2005, 2010) and biomechanics (e.g. Schmitt and Lemelin 2002; Hutchinson 2004, 2011; Alexander 2006; Hutchinson and Gatesy 2006; Hutchinson et al. 2007) can be used to reconstruct the locomotor modes of fossils. However, reducing the shape of a bone to linear and angular measurement may lead to a loss of information and a lack of precision. Geometric morphometric approaches allow for a detailed description of the shape of a bone and accurate tests and comparisons of the shape of a fossil to its living relatives and analogues.

In the present study, we aim to quantitatively infer the locomotor strategy of an extinct carnivoran, the ailurid *Simocyon batalleri*, from the Late Miocene of Spain. The nearly complete skeleton of the extinct species *S. batalleri* was previously described by Salesa et al. (2008) as a generalist terrestrial carnivore able to climb trees: 'Such locomotor abilities are consistent with a palaeobiological model of a generalised carnivore that foraged mainly on the ground but could readily climb to trees for safety if faced with the threat of larger competing carnivore'. Several anatomical features of the postcranial skeleton of *S. batalleri* points towards this lifestyle: for example, this species had an enlarged radial sesamoid ('false thumb') that likely allowed for considerable climbing ability; the lumbar region was likely adapted to produce strong vertical forces whilst climbing; the hand showed a higher degree of pronation–supination capability than other carnivorans; the scapula had an increased attachment areas for those muscles involved in producing strong adduction–abduction forces at the shoulder (Antón et al. 2006; Salesa et al. 2008).

In order to quantitatively test the hypothesis that *S. batalleri* was semi-arboreal, we used 3D surface geometric morphometric approaches performed on the three long bones of the forelimb for a large sample of musteloids and explored the position of *S. batalleri* in the morphospace of the living species. Moreover, we compare the morphology of *S. batalleri* to the mean morphologies of extant species with different types of locomotion. Finally, we test the locomotor strategy of *S. batalleri* using a leave-one-out cross-validated linear discriminant analysis. Our predictions follow those of Salesa et al. (2008), and we predict that *S. batalleri* will fall in the morphospace of the living species that have a generalist terrestrial or semi-arboreal locomotor style.

Materials and methods

Materials

The sample is composed of the three long bones of the forelimb of 77 individuals belonging to 20 extant species of mustelids, one extant species and one extinct species of ailurid, eight extant species of procyonids and four extant species of mephitids. For each species, the number of specimens ranged from 1 to 7 (Table 1; Supplementary Table S1). 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; the Smithsonian National Museum of Natural History, Washington, District of Columbia, USA; the MNCN, Museo Nacional de Ciencias Naturales—CSIC, Madrid. See Supplementary Table S1 for a complete list of the specimens used in the analyses.

Bones of extant specimens were scanned 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 1.4 megapixels). Bones of the fossil were scanned using a Philips Brilliance 64 CT Scan at the Hospital Nuestra Señora de América (Madrid, Spain; Fig. 1).

Table 1 Details of living specimens used in analyses with species name, common name, family, number of individuals included (*N*), lifestyle (*A* arboreal, *SF* semi-fossorial, *SA* semi-arboreal, *AQ* aquatic, *T* terrestrial) and abbreviation of the species name

Family	Species	Common name	*N*	Lifestyle	Literature sources	Abbreviation
Ailuridae	*Ailurus fulgens*	Red panda	5	A	Roberts and Gittleman (1984); Nowak (2005); Wilson and Mittermeier (2009); Heath and Platnick (2008); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Af*
Mephitidae	*Conepatus chinga*	Molina's hog-nosed skunk	1	SF	Afflerbaugh (2002); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Cc*
	Mephitis mephitis	Striped skunk	3	SF	Wade-Smith and Verts (1982); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a); Kiiskila (2014)	*Mh*
	Mydaus javanensis	Sunda stink badger	2	SF	Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Mj*
	Spilogale putorius	Eastern spotted skunk	1	SF	Pennington (2002); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Sp*
Mustelidae	*Eira barbara*	Tayra	1	SA	Schreffler (2003); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Eb*
	Enhydra lutris	Sea otter	2	AQ	Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Allegra et al. (2012); Fabre et al. (2013a, 2015)	*El*
	Galictis vittata	Greater grison	1	T	Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015), Gregg (2013)	*Gv*
	Gulo gulo	Wolverine	2	T	Nowak (2005); Patsy and Sygo (2009); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Gg*
	Ictonyx striatus	Zorilla	1	SF	Larivière (2002); Aguilar (2003); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Is*
	Lontra felina	Marine otter	1	AQ	Savage (2000); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Lf*
	Lutra lutra	European otter	1	AQ	Kennedy (2003); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Ll*
	Martes foina	Stone marten	3	SA	Carter (2004); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Mf*
	Martes martes	Pine marten	2	SA	Schwanz (2000); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Mm*
	Meles meles	Eurasian badger	3	SF	Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Wang (2011); Fabre et al. (2013a, 2015)	*Ms*
	Mellivora capensis	Honey badger	2	SF	Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015); Hoffman (2014)	*Mc*
	Melogale moschata	Chinese ferret-badger	1	SF	Seefeldt (2003); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Ma*
	Mustela eversmanii	Steppe polecat	1	T	Nowak (2005); Wilson and Mittermeier (2009); Dubbelde (2011); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Me*
	Mustela lutreola	European mink	2	T	Shalu (2001); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Ml*
	Mustela putorius	European polecat	2	T	Lundrigan and Conley (2001); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Mp*
	Neovison vison	American mink	1	T	Williams (1955); Schlimme (2003); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Nv*

Table 1 (continued)

Family	Species	Common name	*N*	Lifestyle	Literature sources	Abbreviation
	Poecilogale albinucha	African striped weasel	1	T	Brilliant (2000); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Pa*
	Pteronura brasiliensis	Giant otter	1	AQ	Bender (2001); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Pb*
	Taxidea taxus	American badger	2	SF	Shefferly (1999); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Tt*
	Vormela peregusna	Marbled polecat	2	T	Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Petroelje (2011); Fabre et al. (2013a, 2015)	*Vp*
Procyonidae	*Bassaricyon alleni*	Allen's olingo	3	A	McClearn (1992); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Ba*
	Bassaricyon gabbii	Bushy-tailed olingo	3	A	McClearn (1992); Berger (2004); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Bg*
	Bassariscus astutus	Ringtail	7	SA	Trapp (1972); McClearn (1992); Goldberg (2003); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Bs*
	Nasua narica	White-nosed coati	4	SA	McClearn (1992); Marceau (2001); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Nr*
	Nasua nasua	South American coati	4	SA	McClearn (1992); Braddy (2003); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Ns*
	Potos flavus	Kinkajou	5	A	McClearn (1992); Nowak (2005); Rehder (2007); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Pf*
	Procyon cancrivorus	Crab-eating raccoon	3	SA	McClearn (1992); Nowak (2005); Phillips (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Pc*
	Procyon lotor	Northern raccoon	5	SA	McClearn (1992); Fox (2001); Nowak (2005); Wilson and Mittermeier (2009); Hunter and Barrett (2011a); Fabre et al. (2013a, 2015)	*Pl*

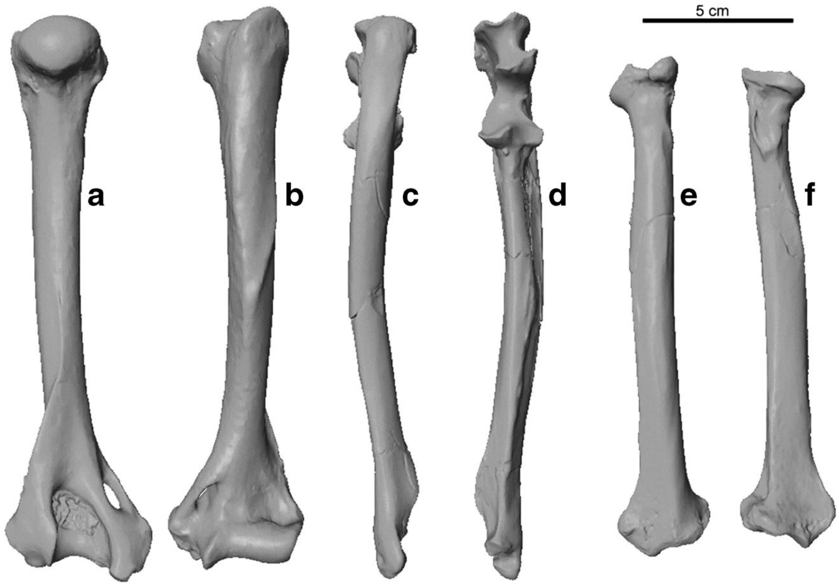

Fig. 1 Long bones of the forelimb of *Simocyon batalleri*: B-2390, right humerus in caudal (**a**) and cranial (**b**) views; B-438, left ulna in caudal (**c**) and cranial (**d**) views; B-430, left radius in cranial (**e**) and caudal (**f**) views

Geometric morphometrics

The shape of the long bones of the forelimb is complex and cannot be adequately represented using a traditional landmark-based approach. Consequently, a 3D sliding-landmark procedure (Bookstein 1997; Gunz et al. 2005; Gunz and Mitteroecker 2013) was used to better describe and quantify the morphology of these long bones, and especially their articulations given the importance of the articulations in determining limb segment excursions important during locomotion. The acquisition of the morphometric data was done using the software Idav Landmarks (Wiley et al. 2005), while Edgewarp3D 3.31 (Bookstein and Green 2002) was used to obtain the sliding landmarks (Supplementary Fig. S1 and Supplementary Tables S2, S3 and S4). Once all landmark data were obtained, a generalised Procrustes superimposition (Rohlf and Slice 1990) was performed using the package Rmorph (Baylac 2012) in R (R Development Core 2011). Finally, a principal component analysis (PCA) was performed on the shape data to evaluate the distribution of the specimens in morphospace. A PCA was also performed on the combined shape data of the forelimb using the whole tangent dataset derived from the Procrustes analyses for each long bone. For more information concerning the protocol and methods of 3D surface geometric morphometric approaches used in this paper, we refer to Fabre et al. (2013a, b; 2014, 2015).

Locomotor category attribution of *S. batalleri*

A leave-one-out cross-validated linear discriminant analysis (LDA) was performed on each long bone of the forelimb as well as on the combined shape data of the entire forelimb. The LDA was performed using the 'lda' function from the 'MASS' package in the software R, performed on the principal components of the Generalised Procrustes Superimposition (GPA) for each bone and for the whole forelimb of the living specimens. The leave-one-out cross-validation procedure removes one specimen at a time and predicts its classification using LDA function computed on all the remaining specimens. At the end, a classification accuracy of the locomotor category of each living specimen is given by the percentage of specimens correctly assigned by the cross-validated LDA. Finally, the fossil is

Table 2 Definitions of lifestyle categories used in this study

Lifestyle	Definition
Terrestrial	Species that spend the most part of their time on the ground, but occasionally climb, swim or dig
Semi-arboreal	Species that spend both time in trees and on the ground without a clear preference for either
Arboreal	Species that spend the majority of their time in trees
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

added to the analysis and assigned to a locomotor category. We defined five categories of locomotion (Table 2) following Nowak (2005), Wilson and Mittermeier (2009), Hunter and Barrett (2011b), Samuels et al. (2013) and Fabre et al. (2013a, 2015) (Tables 1 and 2): arboreal, semi-arboreal, terrestrial, aquatic and semi-fossorial. Note, however, that while animals were classified as belonging to a single lifestyle, they may occasionally also show other locomotor behaviours. For example, most musteloids will swim when needed, and many will dig in the leaf litter and top soil to find food.

Results

Geometric morphometrics

The first two principal component axes of the analysis on the shape of the humerus account for 61.1 % of the total shape variation (Fig. 2a, Supplementary Fig. S2). The overall distribution of the different taxa in the morphospace shows the arboreal and semi-arboreal species clustering together, which tend to overlap with the terrestrial species on these axes. Semi-fossorial and aquatic species are at the opposite side of the

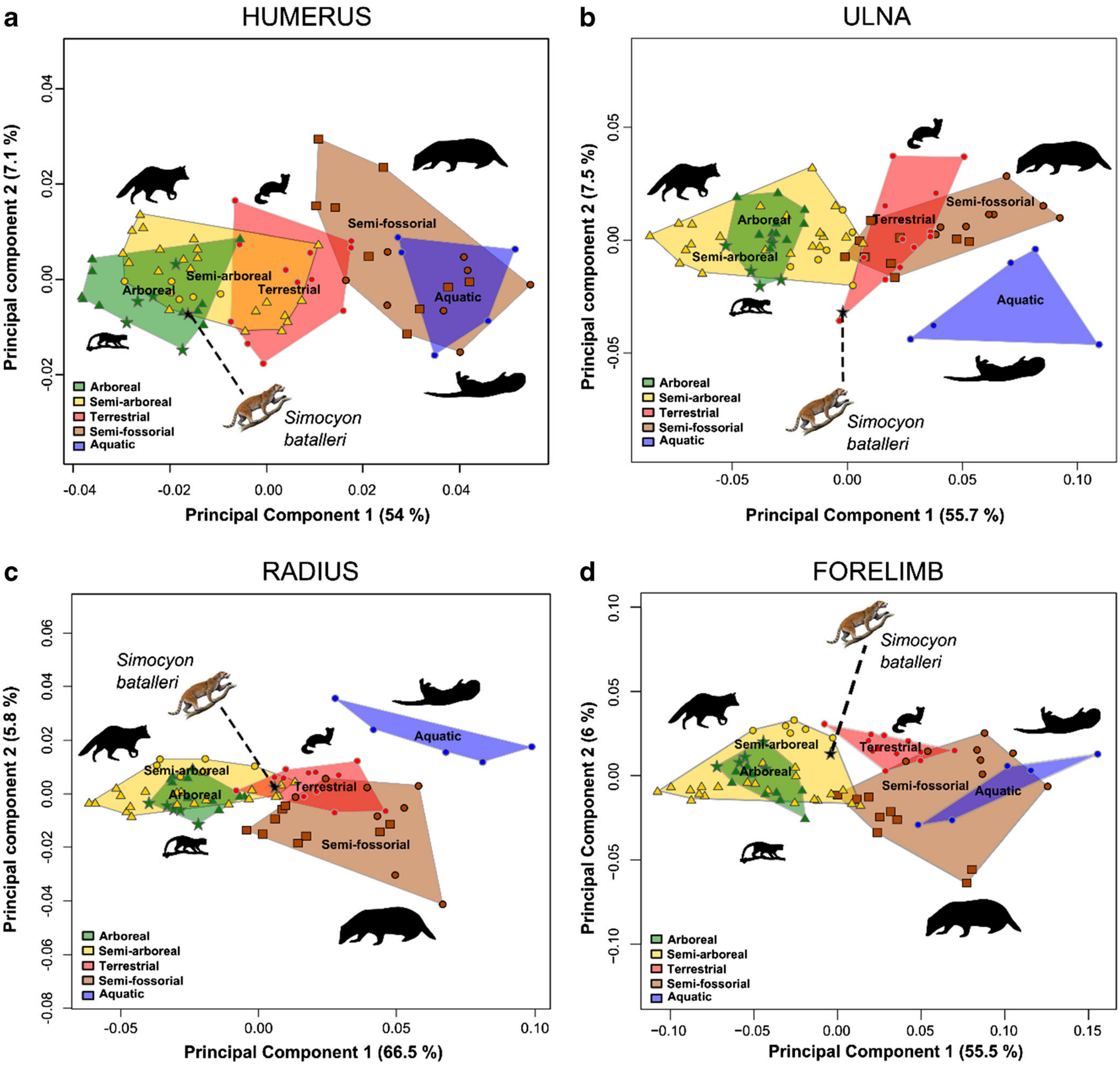

Fig. 2 Results of the principal components analyses performed on the morphometric data of **a** the humerus, **b** the ulna, **c** the radius and **d** the forelimb. Symbols are as follows: *green circles* and *polygon* indicate arboreal species; *yellow circles* and *polygon* indicate semi-arboreal species; *red circles* and *polygon* indicate terrestrial species; *brown circles* and *polygon* indicate semi-fossorial species; *blue circles* and *polygon* indicate aquatic species; *black circle* indicates *Simocyon batalleri*

arboreal and semi-arboreal species, and semi-fossorial species tend also to overlap with the terrestrial species on these axes. In this scatter plot, *S. batalleri* falls in the morphospace of the arboreal and semi-arboreal species. This suggests that the shape of the humerus of *S. batalleri* is similar to that of arboreal and semi-arboreal musteloids. Indeed, *S. batalleri* falls in the morphospace of extant species (Supplementary Fig. S2) close to the arboreal red panda (*Ailurus fulgens*), kinkajou (*Potos flavus*), the semi-arboreal stone marten (*Martes foina*) and the pine marten (*Martes martes*).

The first two principal components axes accounted for 63.2 % of the total shape variation of the ulna (Fig. 2b, Supplementary Fig. S3). The overall distribution of the locomotor categories shows that the arboreal species are included within the morphospace of the semi-arboreal species when considering these two axes. Both of them tend to be separated from terrestrial, semi-fossorial and aquatic species which fall in the opposite part of the morphospace. Aquatic species tend to be separated from all the other locomotor styles. In this scatter plot, *S. batalleri* falls in the morphospace of the terrestrial species, not so far of the semi-arboreal and semi-fossorial ones. This suggests that the ulna of *S. batalleri* is morphologically similar to some terrestrial, semi-arboreal and semi-fossorial musteloids. More specially, *S. batalleri* tends to cluster with the generalist terrestrial wolverine (*Gulo gulo*) and the semi-arboreal tayra (*Eira barbara*).

The first two principal component axes represent 71.8 % of the total shape variation of the radius (Fig. 2c, Supplementary Fig. S4). This scatter plot displays the arboreal and semi-arboreal species in the same part of the morphospace. They tend to overlap with a few of the species on these first two axes. The terrestrial species tend to overlap with the semi-fossorial species on these axes. Aquatic species are in the same part of the morphospace as semi-fossorial and terrestrial species, but they are completely separated from other kinds of locomotor types. In this scatter plot, *S. batalleri* falls in the morphospace of semi-arboreal and terrestrial species. This suggests that *S. batalleri* has a radius that is morphologically similar to semi-arboreal and terrestrial musteloids. In this scatter plot, *S. batalleri* tends to be similar to the semi-arboreal coatis (*Nasua nasua* and *Nasua narica*), the terrestrial wolverine (*Gulo gulo*) and the American mink (*Neovison vison*).

The first two principal components axes represent 61.5 % of the overall shape variation of the combined data set for the forelimb (Fig. 2d, Supplementary Fig. S5). This scatter plot shows the arboreal species are included in the morphospace of the semi-arboreal species on the plot defined by the first two PC axes. The terrestrial species are in the middle of the morphospace and overlap with some semi-arboreal species and some semi-fossorial species on these axes. The semi-fossorial species have a large distribution and they overlap with a large part of the aquatic species on the first two PC axes. Both of them are located at the opposite side of the arboreal and semi-arboreal species. In this scatter plot, *S. batalleri* is included within the morphospace of the semi-arboreal living species of musteloids which means that *S. batalleri* display an overall morphology of the long bones of the forelimb similar to that of semi-arboreal musteloids. In this scatter plot, *S. batalleri* tends to group with the semi-arboreal coatis (*N. nasua* and *N. narica*), the tayra (*Eira barbara*) and the ringtail (*Bassariscus astutus*).

Locomotor categories discrimination and attribution of *S. batalleri*

The results obtained after the LDA for the humerus shows that 80 % of the aquatic specimens are well classified and 20 % is classified as semi-fossorial (Table 3). Concerning the arboreal specimens, 86.7 % are well classified and 13.3 % of them are classified as semi-arboreal. For the semi-arboreal group, 88.9 % specimens are well classified and 7.4 % of them are classified as arboreal, and 3.7 % of them as terrestrial. One hundred percent of the semi-fossorial specimens are well classified. Finally, 75 % of the terrestrial specimens are well classified and 16.7 % is attributed to the semi-arboreal group and 8.3 % to the semi-fossorial group. The results of the leave-one-out cross-validated linear discriminant analysis performed on the shape data of the humerus attribute *S. batalleri* to the arboreal category at 97.5 %. The shape of the humerus of *S. batalleri* appears similar to that of the arboreal musteloids.

For the ulna, the LDA classified 80 % of the aquatic specimens correctly and misclassified 20 % as terrestrial species (Table 3). Eighty six percent (86.7 %) of the arboreal specimens are correctly attributed; thirty percent (13.3 %) of them are attributed to the semi-arboreal group. Concerning the semi-arboreal category, 18 specimens are well attributed, and three are classified as arboreal. For the semi-fossorial category, 14 specimens are well classified whereas two are attributed to the semi-arboreal group. Finally, all the specimens of the terrestrial category are well classified. The results of the LDA performed on the ulnar shape data attribute *S. batalleri* to the semi-arboreal category at 48 % to semi-fossorial at 23.4 % and to the terrestrial one at 19.8 %. This suggests that the ulna of *S. batalleri* is morphologically similar to that of semi-arboreal species and some semi-fossorial and terrestrial ones.

For the radius, the result of the classification for the aquatic specimens after an LDA resulted in 40 % being classified correctly, 40 % attributed to the terrestrial group and 20 % attributed to the semi-fossorial group (Table 3). Ninety three percent (93.3 %) of the arboreal specimens are well classified and 6.7 % of them are attributed to the semi-arboreal group. Concerning the semi-arboreal specimens, 88.9 % of them are well attributed whereas 3.7 % of them are attributed to the arboreal specimens and 7.4 % of them to the semi-fossorial

Table 3 The cross-classification table of predicted and actual specimens assignments to each locomotor category given by the linear discriminant analysis

		Aquatic	Arboreal	Semi-arboreal	Semi-fossorial	Terrestrial
Predictions for the humerus according to the discriminant	Aquatic	4	0	0	0	0
	Arboreal	0	13	2	0	0
	Semi-arboreal	0	2	24	0	2
	Semi-fossorial	1	0	0	17	1
	Terrestrial	0	0	1	0	9
	Sum	5	15	27	17	12
Predictions for the ulna according to the discriminant	Aquatic	4	0	0	0	0
	Arboreal	0	13	4	0	0
	Semi-arboreal	0	2	23	0	2
	Semi-fossorial	1	0	0	16	1
	Terrestrial	0	0	0	1	9
	SUM	5	15	27	17	12
Predictions for the radius according to the discriminant	Aquatic	2	0	0	0	0
	Arboreal	0	14	1	0	0
	Semi-arboreal	0	1	24	3	2
	Semi-fossorial	1	0	2	13	2
	Terrestrial	2	0	0	1	8
	SUM	5	15	27	17	12
Predictions for the forelimb according to the discriminant	Aquatic	5	0	0	0	0
	Arboreal	0	14	0	0	1
	Semi-arboreal	0	0	27	0	1
	Semi-fossorial	0	0	0	15	2
	Terrestrial	0	1	0	2	8
	SUM	5	15	27	17	12

group. Seventy six percent (76.5 %) of the semi-fossorial specimens are well classified; 17.6 % are attributed to the semi-arboreal group and 5.9 % to the terrestrial category. For the terrestrial category, 66.7 % of the species are well classified, 16.65 % are classified as semi-fossorial and 16.65 % as semi-arboreal. The results of the LDA predictions using the radial shape data attribute *S. batalleri* to the arboreal locomotor strategy at 68.2 % and to the terrestrial locomotor strategy at 24.8 %. This result means that the shape of the radius of *S. batalleri* is similar to that of arboreal and some terrestrial specimens of musteloids.

The results of the LDA for the combined data set of the forelimb show a good classification for all the specimens in the aquatic category (Table 3). Ninety three percent (93.3 %) of the specimens of the arboreal category are well attributed whereas only 6.7 % are classified as semi-arboreal. For the semi-arboreal category, all the specimens are well classified. Eighty eight percent (88.2 %) of the specimens are well attributed to the semi-fossorial category, whereas 11.8 % of them are attributed to the terrestrial category. Among the terrestrial category, 66.7 % of the specimens are well classified, 16.7 % are classified among the semi-fossorial category, 8.3 % among the semi-arboreal category and 8.3 % to the arboreal one. Finally, the result of the LDA performed on the discriminant function of the whole forelimb shape attributed *S. batalleri* to the arboreal locomotor group at 99.9 % probability. This suggests that the shape of the long bones of the forelimb in *S. batalleri* is morphologically similar to that of the arboreal species of musteloids.

Discussion

The first interesting result of this analysis is that *S. batalleri* falls within the morphospace of the living species, which means that its forelimb morphology is similar to that of extant musteloids. The PCA performed on the forelimb shape data set showed different results depending on the bone analysed. *S. batalleri* falls in the morphospace of the arboreal and semi-arboreal species when evaluating the humerus shape (Fig. 2a). However, when examining the ulna, *S. batalleri* falls in the morphospace of the terrestrial species (Fig. 2b), and for the radius, *S. batalleri* falls in the morphospace of the terrestrial and semi-arboreal species (Fig. 2c). The results obtained for the humerus, the ulna and the radius are relatively congruent with the locomotor hypothesis of Salesa et al. (2008).

Importantly, these results show that the functional signal can be different from one bone to another. When taking into account the whole forelimb in the shape analysis (Fig. 2d), the results of the PCA show that *S. batalleri* fall in the morphospace of the semi-arboreal musteloids. This result confirms the prediction of Salesa et al. (2008) that *S. batalleri* tends to be a generalist with a semi-arboreal locomotor strategy. This result shows that including the different bones together in the analysis may provide better results than when treating each bone separately.

The results of the cross-validation test of the LDA of the living musteloids for each bone show that the species tend to be generally well assigned to the locomotor categories based on literature data (Table 3). For the humerus, the locomotor assignment is perfect for the semi-fossorial specimens and particularly high for the aquatic, the terrestrial and the semi-fossorial specimens in comparison to those of the other categories. The results are similar for the ulna with good attribution for aquatic and semi-fossorial specimens. However, for the radius, terrestrial specimens appear to be better assigned than those of other categories. Nevertheless, the assignment is better when the three bones are used together, except for the semi-fossorial specimens where the humerus by itself provides better results.

The results of the LDA attribute *S. batalleri* to the arboreal category for the humerus. Yet, when using the ulnar shape, this fossil ailurid is similar to the semi-fossorial species and some terrestrial species. The results of the LDA for the radius suggest that *S. batalleri* is similar to the arboreal and some terrestrial specimens of musteloids. Finally, the result for the whole forelimb suggests very strongly that *S. batalleri* is morphologically similar to arboreal specimens of musteloids. For each bone taken individually, the results are similar to those of the PCA performed on the forelimb data set and highlight the fact that each bone can have a different functional signal. This highlights the difficulty to infer the palaeobiology of an extinct species based on single bones. However, these results tend to be in accordance with the terrestrial and semi-arboreal locomotor category attribution of *S. batalleri* in the study of Salesa et al. (2008). Concerning the result obtained for the whole forelimb, it is somewhat different than the previous results, suggesting that *S. batalleri* is more arboreal than expected. The results, with *S. batalleri* attributed to the arboreal locomotion for the humerus, radius and the total forelimb, whereas it is attributed to semi-arboreal category for the ulna, may reflect the fact that there are multiple morphologic (phenotypic) solutions to the same functional or ecological problem (Alfaro et al. 2005: Wainwright et al. 2005; Wainwright 2007; Losos 2011).

These results highlight the importance to study the whole skeleton, at least where possible, and to be careful in inferring lifestyle when studying isolated bones, even when using quantitative methods as was done here. Our results also show that some bones better capture functional signal than others, which implies that some bones can be more informative for inferring locomotor and behavioural strategies in extinct species. For example (Table 3), the humerus appears to be a good indicator of aquatic and semi-fossorial adaptations, the ulna for the arboreal and semi-fossorial adaptations, and the radius for arboreal adaptations based on our LDA analysis. Nevertheless, it is important to note that the discriminant analysis forces the group classification by decreasing the intragroup variability and increasing the intergroup variability which may influence the result that we obtained. To overcome this problem, it would be interesting to use alternative classification methods such as Gaussian Mixture Model that allow one to test the presence of groups without a priori assignments.

These results tend also to corroborate the previous study made on the anatomy of the postcranial skeleton of *S. batalleri*. Indeed, several anatomical features point towards this as an arboreal/semi-arboreal lifestyle: for example, the forearm of *S. batalleri* shows a higher degree of pronation–supination capability compared to other carnivorans as shown by the study of Fabre et al. (2015). The olecranon process of the ulna is short which allows a full extension of the elbow (Samuels and Van Valkenburgh 2008). The radial notch is also oriented laterally in arboreal species and in *S. batalleri*. This has been interpreted in previous studies as increasing the degree of pronation and supination of the forelimb, thus allowing a wider range of rotation at the elbow (Hildebrand 1988; Andersson 2003, 2004b; Peigné et al. 2008; Ercoli et al. 2012; Fabre et al. 2015). Furthermore, several other anatomical features of the postcranial skeleton of *S. batalleri* points towards this lifestyle: for example, this species has an enlarged radial sesamoid (‘false thumb’) that likely allowed for considerable climbing ability, refining the grasping capacity of the hand and allowing this species to reach the highest parts of trees. Moreover, the configuration of the carpals shows adaptations to a semi-arboreal lifestyle: the pisiform, for example, has a strong and ridged articular facet for the transverse carpal ligament (or flexor retinaculum), which is markedly different from that in other musteloids (in which the facet is smooth and lacking ridged borders). This ligament is the attachment surface of the muscles abductor pollicis brevis and opponens pollicis (Davis 1964; Antón et al. 2006), the main flexors of the pollex and the palm. The morphology of the pisiform thus suggests a strong development of this ligament in *S. batalleri*, pointing towards the presence of very strong muscles (Antón et al. 2006; Salesa et al. 2008). Previous studies have also shown that the spinous processes of the lumbar vertebrae of *S. batalleri* are triangular instead of rectangular which is common in other musteloids. This indicates the presence of well-developed interspinal muscles between the spinous processes, typical of carnivorans that bound, but do not trot or gallop. These muscles may play an important role when climbing trees. Finally, the scapula has an increased attachment area for those muscles involved in producing adduction–abduction at the shoulder (Antón et al. 2006; Salesa et al. 2008).

Conclusion

Our results show that *S. batalleri* is included in the morphospace of the living musteloids for each bone of the forelimb. However, our results also show that different bones may show a different functional signal, which indicates that inferring lifestyle of extinct taxa can be difficult. This implies that one has to be careful when reconstructing the palaeobiology of an extinct species when studying only isolated bones. Our results also highlight the importance to study, when possible, a maximum of skeletal elements to infer the lifestyle of an extinct species. Our results suggest that *S. batalleri* may be more arboreal than previously suggested, although the different methods employed provided slightly different results. This fossil ailurid shared its habitat with other larger carnivorans, such as the sabre-toothed felids *Machairodus aphanistus* and *Promegantereon ogygia*, or the lion-sized amphicyonid *Magericyon anceps* (Antón et al. 2004; Peigné et al. 2008; Salesa et al. 2006; Siliceo et al. 2015). In this context, it seems reasonable that a generalised carnivoran such as *S. batalleri*, lacking large canines and being smaller than other large members of the predator guild, developed strong climbing abilities for escape from these larger species, but likely also for some foraging on trees (Salesa et al. 2008). A quantitative assessment of behaviour in extant species rather than qualitative categories may provide better congruence among methods, yet this remains to be tested.

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