Biological Journal of the Linnean Society, 2019, **XX**, 1–20. With 3 figures.

Functional relationship between myology and ecology in carnivores: do forelimb muscles reflect adaptations to prehension?

CHRISTINE BÖHMER[1*], ANNE-CLAIRE FABRE[2], MAXIME TAVERNE[1], MARC HERBIN[1], STÉPHANE PEIGNÉ[3†] and ANTHONY HERREL[1]

[1] *UMR 7179 CNRS/MNHN, Bâtiment d'Anatomie Comparée, Muséum National d'Histoire Naturelle, 55 rue Buffon, 75005 Paris, France*
[2] *Life Sciences Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[3] *UMR 7207 CR 2P, MNHN/CNRS/UPMC, Muséum National d'Histoire Naturelle, CP38, 8 rue Buffon, 75005 Paris, France*

Received 15 October 2018; revised 29 January 2019; accepted for publication 26 February 2019

Prehension involves the ability to reach, grasp and transport an object. It is a fitness-relevant behaviour with an important role in food acquisition and locomotion. Grasping an item requires the coordinated action of several muscles and, consequently, the muscular anatomy can be expected to be a good indicator of grasping ability. Here, we quantitatively analyse the myology of the forelimb in Carnivora in relation to their grasping ability, arboreality and locomotor specializations. Carnivorans are a monophyletic group and a good model due to the fact that they vary in ecology and prehensile capabilities. We find that non-prehensile taxa differ in their muscle properties from poorly prehensile taxa and from intermediately to strongly prehensile taxa when taking into account variation in body size and phylogeny. Species with strong prehensile capabilities are characterized by a high force-producing capacity in the forelimb rotators. A strong grasp is not only advantageous for prehension, but also for climbing. Species with poor prehensile capabilities but an intermediate to high degree of arboreality display well-developed flexor muscles contributing to a strong grasp. Although anatomical adaptations for prehensility and arboreality are similar, the present study revealed differences in the muscle specializations of the forelimb in Carnivora.

ADDITIONAL KEYWORDS: arboreality – Carnivora – ecology – musculature – prehensility – quantitative anatomy.

INTRODUCTION

The primary function of the appendicular apparatus is locomotion, but mammals use their forelimbs in several different and highly demanding tasks associated with feeding and social behaviour (Gambaryan, 1974; Hall, 2007; Peckre *et al.*, 2016). In contrast to ungulates or primates that appear relatively homogeneous in their functional adaptations of the limbs (e.g. Smith & Savage, 1955; Myatt *et al.*, 2012), carnivores in particular display a huge variety of functional specializations in their forelimbs in terms of locomotor mode (ranging from cursorial to scansorial taxa) and ability to manually grasp food (ranging from no to well-developed prehensility) (e.g. Ewer, 1977; Holmes, 1980; Van Valkenburgh, 1987; Iwaniuk*et al.*, 1999; Meachen-Samuels & Van Valkenburgh, 2009; Wilson & Mittermeier, 2009; Goswami & Friscia, 2010; Fabre *et al.*, 2013; Sustaita *et al.*, 2013; Martin-Serra *et al.*, 2014; Fabre *et al.*, 2015; Kilbourne, 2017). Manual grasping ability plays an important role in the context of food acquisition and consequently diet, but is also related to arboreal locomotion because a climbing animal has to make secure contact with the discontinuous substrate. Yet, the relationship between arboreality and prehension is not obligatory, as exemplified by the coati (*Nasua nasua*) which is an agile climber but has poorly developed prehensility (Gompper & Decker, 1998; McClearn, 1992). Carnivores use their limbs to

---

*Corresponding author. E-mail: boehmer@vertevo.de
†Deceased

remain attached to the substrate they climb upon, but apply different attachment mechanisms. This includes gripping claws that interlock with surface irregularities or prehensile hands/feet that grasp the substrate (McNeill, 1983; Biewener, 2003; Hildebrand & Goslow, 2004). Morphofunctional attributes that promote grasping strength, however, may conflict with those that promote digital speed (e.g. Sustaita, 2008). This may indicate a possible trade-off between maximizing prehensility and arboreal locomotor speed, and highlights the importance of understanding the functional relationship between forelimb anatomy, ecology and behaviour. Equivalent performance trade-offs have been reported for other arboreal vertebrates, such as chameleons (Losos *et al.*, 1993), with faster species generally being poorer clingers (but see also Herrel *et al.*, 2013).

Previous studies have demonstrated a link between forelimb muscle anatomy and locomotor mode in carnivores (Williams *et al.*, 2008; Hudson *et al.*, 2011; Julik *et al.*, 2012; Junior *et al.*, 2015; Böhmer *et al.*, 2018; Taverne *et al.*, 2018). Put simply, limb retractor and flexor muscles have a higher force-producing capacity in arboreal taxa compared to terrestrial taxa, reflecting the differences in climbing ability. The possible differences in forelimb muscles in relation to prehensility have, however, received less attention in non-primate mammals. Although a growing number of studies that have evaluated forelimb behaviour in rodents, scandentians and marsupials during grasping (e.g. Hyland & Reynolds, 1993; Ivanco *et al.*, 1996; McKenna & Whishaw, 1999; Sargis, 2001; Whishaw *et al.*, 2017), only a few studies have quantified prehensile capabilities in carnivores (McClearn, 1992; Iwaniuk & Whishaw, 1999). To date, it is unknown if and how forelimb muscle anatomy differs in relation to prehensility in carnivores.

Prehension using the forelimb (i.e. the reach, grasp and transport of a food item) involves motion of the shoulder, elbow, wrist and finger joints and, thus, requires the coordinated activation of numerous muscles (Georgopoulos, 1986; Hyland & Reynolds, 1993; Flatt, 2000). Here, we focus on the intrinsic forelimb muscles because we expect them to give a more detailed functional signal in the context of prehensility in carnivores. Neurophysiology analyses and electromyography studies have shown that the activity of the proximal intrinsic forelimb muscles is important during reaching (Hyland & Reynolds, 1993; Tokuda *et al.*, 2016; Geed & van Kan, 2017). In particular, the protractor and extensor muscles are activated to protract the limb, to extend the wrist and to open the hand. Once the food item is reached, activity of the distal intrinsic forelimb muscles contributes to grasping (Jeannerod *et al.*, 1995; Tokuda *et al.*, 2016; Geed & van Kan, 2017). The flexor muscles are activated to close the hand and to provide a firm grasp. Activity of both the proximal and the distal intrinsic forelimb muscles enables transport of the food item (Amundsen Huffmaster *et al.*, 2017). In particular, the adductor and rotator muscles are active in bringing the hand towards the body and mouth, respectively.

The aim of the present study was to identify possible functional correlates of muscle properties in the forelimb of carnivores associated with their prehensile capabilities. This is of particular interest because it will allow us to investigate how these muscle features are manifested in bone morphology and, ultimately, to improve our inferences of prehensility in extinct species known only from fossils. Muscle architecture (i.e. the cross-sectional area of a muscle) is an established proxy for its force-producing capacity (Close, 1972). Consequently, based on the aforementioned observations on limb movement patterns and muscle activation patterns, we predict that intrinsic forelimb muscles promoting efficient forelimb prehension in carnivores should display a relatively larger cross-sectional area in taxa with well-developed prehensility. Furthermore, we explore possible functional adaptations of the forelimb muscles in relation to other ecological aspects such as arboreality.

MATERIAL AND METHODS

STUDY SPECIMENS AND PHYLOGENY

The forelimbs of 18 carnivore taxa were dissected for the present study (one individual per species, except for *Cuon alpinus* for which two individuals were dissected) (Fig. 1). Cadavers were obtained through the Faculty of Veterinary Medicine of Ludwig-Maximilians-Universität in Munich, the INRAP Centre de Recherches Archéologiques de l'Oise in Compiègne, the taxidermy facility and the collection of Comparative Anatomy of the Muséum National d'Histoire Naturelle in Paris, the Parc des Félins in Lumigny and the animal park of La Haute Touche in Obterre. Specimens did not display any pathologies.

Taxa and number of individuals were chosen to provide a sample that includes a large range in body mass, a wide phylogenetic scope, and a broad spectrum of lifestyles within the limits of the availability of specimens for dissection (generally one, except for *C. alpinus*). The phylogeny used in this study is based on the molecular tree presented by Nyakatura & Bininda-Emonds (2012). The tree has been pruned to include only the taxa analysed in the present study.

ECOLOGICAL DATA

Based on information collected from the literature, each taxon in the present study was assigned to a

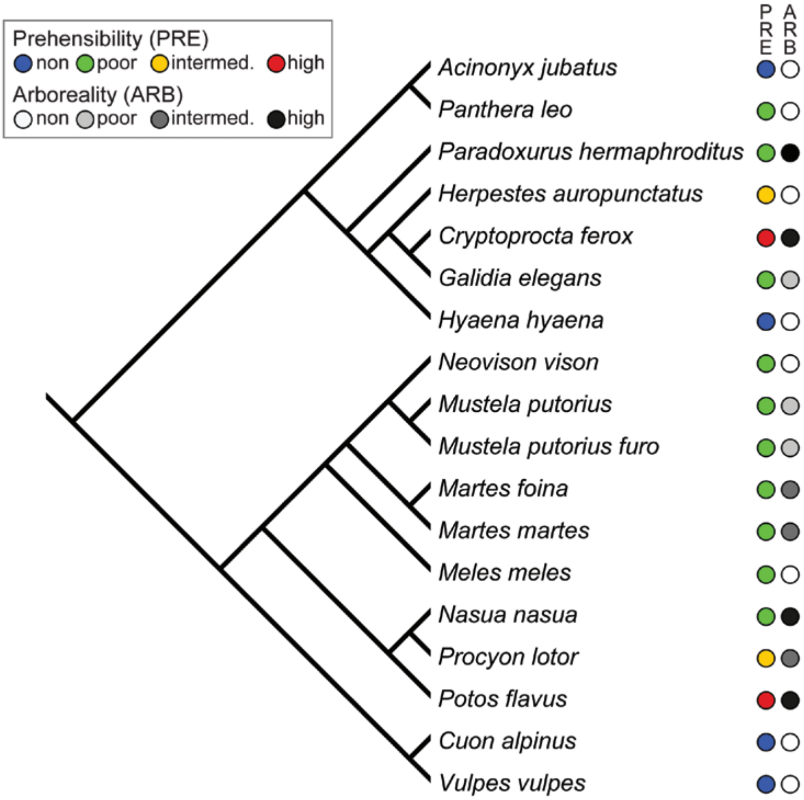

Figure 1. Overview of the sampled taxa. The phylogeny is based on the molecular tree presented by Nyakatura & Bininda-Emonds (2012). The tree has been pruned to include only the taxa analysed in the present study. Refer to Table 1 for further details.

group based on variation in prehensility, arboreality and locomotor specializations (Table 1). Because most of the specimens were not entirely preserved (e.g. the internal organs had been removed during autopsy) and, thus, we were not able to directly obtain body mass data, published mean body masses were taken from the literature as well (Table 1).

Iwaniuk *et al.* (1999) argued that it is necessary to grade behaviours along a continuum or in an ordered series of categories, because either one of these is more likely to be representative of behavioural variation than are unordered categories. Thus, both prehensility and arboreality were coded as multistate, ordered characters. Prehensility was described in terms of the amount and frequency of occurrence of prehension following Napier (1961), Fabre *et al.* (2013) and Tarquini *et al.* (2017): 0 = non-developed (species with no grasping ability), 1 = poorly developed (species with little or no manipulation of food with their forelimb alone; they frequently use their paws in combination with the ground for manipulation and grasp is mainly used for climbing), 2 = intermediate (species that are able to grasp objects only by using both forelimbs at once and with fine control of digit movements), 3 = well-developed (species that grasp objects using only one hand). The degree of arboreality of a species was divided into the following four categories: 0 = never climbs, 1 = climbs occasionally, 2 = climbs frequently (semi-arboreal), and 3 = nests and/or feeds primarily in trees, climbs well and is often capable of controlled head-first descent (arboreal) (Iwaniuk *et al.*, 1999).

In addition to the degree of arboreality, the species were also assigned to the following locomotor specializations in order to account for possible non-arboreal adaptations: cursorial, fossorial, generalized, natatorial and scansorial. This differentiates, for example, two non-arboreal carnivores: the highly cursorial cheetah from the generalist hyena.

ANCESTRAL CHARACTER STATE RECONSTRUCTION

An ancestral character state reconstruction of arboreality and prehensility was performed to explore whether the evolution of arboreal locomotion preceded the evolution of grasping ability (following Fabre *et al.*, 2013). This analysis was executed using the parsimony reconstruction method in the Mesquite

Table 1. Taxa analysed in the present study with rankings for the two behavioural traits prehensility (predation) and arboreality (locomotion), information on locomotor specialization and mean body mas (mBM) from the literature

Taxonomic group	Species	PRE	ARB	SPE	mBM (kg)	Reference(s)
Canidae						
	Cuon alpinus	0	0	Cu	16.0	Sillero-Zubiri *et al.* (2004); Van Valkenburgh (1985)
	Vulpes vulpes	0	0	Cu	8.5	Sillero-Zubiri *et al.* (2004)
Eupleridae						
	Cryptoprocta ferox	3	3	Sc	6.8	Hawkins & Racey (2005); Iwaniuk *et al.* (2000)
	Galidia elegans	1	1	Sc	0.8	Wilson & Mittermeier (2009)
Felidae						
	Acinonyx jubatus	0	0	Cu	40.2	Krausman & Morales (2005); Macdonald & Loveridge (2010); Wilson & Mittermeier (2009)
	Panthera leo	1	1	Ge	190.0	Iwaniuk *et al.* (2000); Kleiman *et al.* (2004); Macdonald and Loveridge (2010)
Herpestidae						
	Herpestes auropunctatus	2	0	Ge	0.5	Nellis (1989); Nellis & Everard (1983); Wilson & Mittermeier (2009)
Hyaenidae						
	Hyaena hyaena	0	0	Ge	35.0	Wilson & Mittermeier (2009)
Mustelidae						
	Martes foina	1	2	Sc	1.4	Wereszczuk & Zalewski (2015)
	Martes martes	1	2	Sc	1.1	Wereszczuk & Zalewski (2015)
	Meles meles	1	0	Fo	11.7	Wilson & Mittermeier (2009)
	Mustela putorius	1	1	Ge	1.1	Baghli & Verhagen (2004)
	Mustela putorius furo	1	1	Ge	1.2	Thornton *et al.* (1979)
	Neovison vison	1	0	Na	1.2	Chapman & Feldhamer (1982)
Procyonidae						
	Nasua nasua	1	3	Sc	4.3	Gompper & Decker (1998)
	Potos flavus	3	3	Sc	3.0	Ford & Hoffmann (1988)
	Procyon lotor	2	2	Sc	6.4	Iwaniuk & Whishaw (1999); Jones *et al.* (2009); McClearn (1992)
Viverridae						
	Paradoxurus hermaphroditus	1	3	Sc	3.2	Kleiman *et al.* (2004); Nakabayashi *et al.* (2016)

Character coding for prehensility (PRE): 0 = non-developed; 1 = poorly developed, 2 = intermediate, 3 = well developed (Fabre *et al.*, 2013; Tarquini *et al.*, 2017). Character coding for arboreality (ARB): 0 = never/extremely rarely climbs, 1 = climbs occasionally, 2 = climbs frequently (semi-arboreal), 3 = nests and/or feeds primarily in trees, climbs well and is often capable of controlled head-first descent (arboreal) (Iwaniuk *et al.*, 1999). Abbreviations for locomotor specialization (SPE): Ge = generalized, Cu = cursorial, Fo = fossorial, Na = natatorial, Sc = scansorial.

Table 2. Intrinsic muscles of the forelimb in carnivores from proximal to distal (ordered by function). The general muscle topography is identical in all studied species. Muscles are assigned to main functional categories. Because some muscles may perform dual functions, an additional function is indicated as well

Number	Muscle	Acronym	Origin	Insertion	Main and additional function
Shoulder and elbow					
1	M. supraspinatus	SSP	Supraspinate fossa of scapula	Greater tubercle of humerus	Humeral protractor, scapular protractor
2	M. teres major	TMJ	Caudoventral border of scapula	Craniomedial proximal part of humeral diaphysis	Humeral retractor
3	M. spinodeltoideus	DS	Middle 1/3 of scapular spine	Deltoid tuberosity of humerus	Humeral retractor, humeral abductor
4	M. acromiodeltoideus	DA	Acromion	Deltoid tuberosity of humerus	Humeral rectractor, humeral abductor
5	M. infraspinatus	ISP	Infraspinate fossa of scapula	Greater tubercle of humerus	Humeral abductor
6	M. teres minor	TMN	Ventral border of scapula	Greater tubercle of humerus	Humeral abductor
7	M. arcticularis humeri	AH	Coracoid process of scapula	Medial side of olecranon	Humeral adductor
8	M. subscapularis	SUB	Subscapular fossa of scapula	Lesser tubercle of humerus	Humeral adductor
9	M. epitrochlearis	EPI	Caudoventral border of scapula	Caudal side of olecranon	Elbow extensor, humeral retractor
10	M. triceps caput laterale	TBLA	Deltoid ridge of humerus	Lateral side of olecranon	Elbow extensor, humeral retractor
11	M. triceps caput longum	TBLO	Ventral border of scapula (near glenoid cavity)	Olecranon	Elbow extensor, humeral retractor
12	M. triceps brachii caput mediale (short, intermediate and long portion)	TBM	Medial humeral diaphysis	Medial side of olecranon	Elbow extensor
13	M. anconeus	ANC	Caudal on lateral epicondylar crest of humerus	Lateral side of olecranon	Elbow extensor
14	M. triceps brachii caput accessorium	TBA	Caudal medial epicondylar crest of humerus	Medial side of olecranon	Elbow extensor

Table 2. *Continued*

Number	Muscle	Acronym	Origin	Insertion	Main and additional function
15	M. biceps brachii	BB	Coracoid process of scapula	Proximal ulnar diaphysis (distal to trochlear notch)	Elbow flexor, humeral protractor
16	M. brachialis	BCH	Lateral proximal umeral diaphysis	Proximal ulnar diaphysis (distal to BB)	Elbow flexor
Wrist and digits					
17	M. brachioradialis	BCR	Cranial on lateral epicondylar crest of humerus	Styloid process of radius	Wrist rotator
18	M. supinator	SUP	Lateral side of radius	Medial until distal 1/3 of radius	Wrist rotator
19	M. pronator teres	PT	Medial epicondyle of humerus	Radial diaphysis	Wrist rotator
20	M. pronator quadratus	PQ	Distal 1/3 of ventral surface of radius and ulna	Distal end of ventral surface of radius and ulna	Wrist rotator
21	M. extensor carpi radialis longus	ECRL	Lateral epicondylar crest of humerus	Base of MC 2	Wrist extensor, elbow flexor
22	M. extensor carpi radialis brevis	ECRB	Lateral epicondylar crest of humerus	Base of MC 3	Wrist extensor, elbow flexor
23	M. extensor carpi ulnaris	ECU	Cranial on lateral epicondylar crest of humerus	Base of MC 5	Wrist extensor, elbow flexor
24	M. extensor digitorum communis	EDC	Cranial on lateral epicondylar crest of humerus	Phalanges of digits 2, 3, 4, 5	Digit extensor, elbow flexor
25	M. extensor digitorum lateralis	EDL	Cranial on lateral epicondylar crest of humerus	Phalanges of digits 4 and 5	Digit extensor, elbow flexor
26	M. extensor digiti I and II	EI	Lateral side of ulnar diaphysis	Phalanges of digits 1 and 2	Digit extensor
27	M. abductor digiti I longus	EP	Ulnar and radial diaphysis	Base of MC 1 (and radial sesamoid)	Digit extensor (supinator)
28	M. flexor carpi ulnaris, ulnar head	FCUU	Medial side of olecranon	Pisiform	Wrist flexor, elbow extensor

Table 2. *Continued*

Number	Muscle	Acronym	Origin	Insertion	Main and additional function
29	M. flexor carpi ulnaris, humeral head	FCUH	Medial epicondyle of humerus	Pisiform	Wrist flexor, elbow extensor
30	M. flexor carpi radialis	FCR	Medial epicondyle of humerus	Base of MC 2	Wrist flexor, elbow extensor
31	M. palmaris longus	PL	Medial epicondyle of humerus	Palmar fascia (5 tendons)	Digit flexor, elbow extensor
32	M. flexor digitorum profundus (4 heads)	FDP	Medial epicondyle of humerus and medial side of olecranon	Palmar fascia (5 tendons)	Digit flexor, elbow extensor

MC = metacarpal.

software package (Maddison & Maddison, 2011). The method finds the ancestral states that minimize the number of character change steps given the tree and observed character distribution (Swofford & Maddison, 1987). Maximum parsimony is intuitively appealing and highly efficient and, thus, a popular technique for phylogenetic reconstruction (Joy *et al.*, 2016). No reconstruction method can be designated a priori as best because the results of alternative methods are quite similar to one another (Steel & Penny, 2000; Royer-Carenzi *et al.*, 2013).

MUSCLE DATA

There are 32 intrinsic muscles involved in movement of the forelimb (Table 2). Sixteen of these muscles mainly act on the shoulder and elbow. The remaining 16 muscles are primarily responsible for movement of the wrist and digits. These muscles generally function as adductors and abductors, flexors/retractors and extensors/protractors, as well as rotators. Each muscle was assigned to a main function (Table 2). Because some muscles may perform dual functions, an additional function is indicated as well. The assignment of muscles to functional groups is based on their topology and on the manipulation of dissected specimens. We are aware that muscles are versatile because they need to contribute to more than one functional role, but consideration of the muscle's main function facilitates interpretation. Anatomical terminology primarily followed Reighard and Jennings (1902) and the *Nomina Anatomica Veterinaria* (World Association of Veterinary Anatomists, 2012).

The dissection protocol follows that described by Böhmer *et al.* (2018). In brief, each muscle was identified and systematically dissected. The following architectural features were quantified. First, the blotted dry muscles were weighed on a digital precision balance (Mettler) (±0.1 mg). Next, the fibre length (as the mean of 15 randomly selected fibres) of each excised muscle was recorded. The length parameter was measured directly on the muscle using a standard ruler for very large specimens such as the cheetah or the lion because muscle fibres were clearly visible with the naked eye. To do so, we cut the respective muscle parallel to its fibre orientation, which allowed us to clearly identify individual fibres. For small specimens such as the fossa or the ferret, muscle fibres were separated by digesting the muscles in a 30% aqueous nitric acid solution for about 24 h, after which they were transferred to a 50% aqueous glycerin solution (Antón, 1999; Herrel *et al.*, 2008). For each muscle, individual fibres were teased apart and documented by taking scaled digital photographs. The length of 15 randomly selected fibres was measured using the software ImageJ v.1.48 (Schneider *et al.*, 2012) and mean fibre length was then calculated.

The recorded parameters (muscle mass and fibre length) allow us to determine the following variables.

Muscle volume (*V*) was calculated by dividing muscle mass (*m*) by a standard muscle density (ρ) of 1.06 g/cm³ (Mendez and Keys, 1960):

$$\mathrm{V}\ \left[\mathrm{cm}^3\right]\ =\ \mathrm{m}\ [\mathrm{g}]\,/\,\rho\,\left[\mathrm{g/cm}^3\right] \tag{1}$$

Anatomical cross-sectional area (ACSA) is a function of muscle volume and fibre length (l_f) (Powell *et al.*, 1984; Sacks & Roy, 1982). It was calculated using the following equation:

$$\mathrm{ACSA}\ \left[\mathrm{cm}^2\right]\ =\ \left(\mathrm{V}\ \left[\mathrm{cm}^3\right]/\left(\mathrm{l_f}\,[\mathrm{cm}]\right)\right) \tag{2}$$

In contrast to physiological cross-sectional area (e.g. Kupczik *et al.*, 2015; Nyakatura & Stark, 2015; Rupert *et al.*, 2015; Rosin & Nyakatura, 2017; Böhmer *et al.*, 2018), ACSA does not take the pennation angle of the muscle fibres into account. In increasingly pennate muscles, the ASCA may be less accurate in predicting the force-producing capacity per muscle volume (e.g. Lieber & Friden, 2001). However, muscle force output is related to the cosine of pennation and, thus, neglecting small angles may cause only a small percentage of error in force estimates (Scott & Winter, 1991). Because pennation angles appear to be typically rather small in carnivoran forelimb muscles (e.g. Williams *et al.*, 2008; Moore *et al.*, 2013; Böhmer *et al.*, 2018), we excluded this measure in order to obtain a larger comparative data set. Furthermore, the surface pennation angle of a muscle may vary significantly from its deep pennation angle (Sopher *et al.*, 2017) and consequently only micro-dissection or micro-computed tomography analyses may allow accurate study of the pennation of all fascicles that make up the muscle (e.g. Kupczik *et al.*, 2015; Nyakatura & Stark, 2015; Rosin & Nyakatura, 2017; Dickinson *et al.*, 2018).

STATISTICAL ANALYSES

Analyses were performed using the software R v.3.5.1 (respective packages are indicated below) (R Development Core Team, 2017) and PAST v.3.21 (Hammer *et al.*, 2001).

Size corrections

The body mass of the dissected taxa ranged from around 800 g (e.g. the ring-tailed mongoose *Galidia elegans*) to about 200 kg (e.g. the lion *Panthera leo*) (Table 1). Because morphological traits typically scale with overall body size, meaningful comparisons of trait values among specimens that differ significantly in size require size correction (e.g. Allen *et al.*, 2010, 2014; Cuff *et al.*, 2016; Dick & Clemente, 2016). Two methods were used to account for body mass differences between the analysed taxa. In the first method, the muscle variables (ACSA) were logarithmically ($\log_{10}$) transformed. The $\log_{10}$-transformed muscle data were then regressed against $\log_{10}$-transformed body mass for each taxon. The resulting residuals were used for subsequent statistical analyses. The same procedure was applied when performing the second method, but with respect to an overall reference metric. This reference metric is the average body mass of all taxa. The second method was performed using the 'remove size from distances' tool with the 'allometric vs. standard' option in the software PAST.

Principal component analysis

The raw data and the data set resulting from the aforementioned size corrections were subjected to a principal component analysis (PCA) in order to reduce the dimensionality. We performed the PCA on the correlation matrix (e.g. Parsons *et al.*, 2009). Accordingly, PCA was performed using the 'prcomp' function in the R package 'stats', and the R package 'factoextra' was used to extract and visualize the results of the multivariate data analysis (Kassambara & Mundt, 2017). The 'phylomorphospace' function in the R package 'phytools' (Revell, 2012) was used to project the phylogenetic tree into the morphospace resulting from the PCA (Sidlauskas, 2008). The cos2 values (squared loading matrix of the variables) were used to determine the contribution of the variables to the principal component (PC) and given as a percentage in relation to all PCs (Kassambara, 2017).

We performed a *K*-means cluster analysis on the total number of PCs (explaining 100% of the detected variation) (Horn & Friedman, 2003; Ding & He, 2004) in order to reveal the grouping of the studied taxa based on the muscle data. The number of clusters (*K*) was specified as four (corresponding to the number of prehensility and arboreality categories). The non-hierarchical method defines clusters based on a centroid (centre point) and assigns each data point to the cluster with the closest centroid. The ratio of the sum of squares (SS) between and within the groups indicates the quality of the classification, ideally being 100% (or 1). This analysis was performed using the 'kmeans' function in the R package 'stats' and was visualized using the 'clusplot' function in the R package 'cluster' (Maechler *et al.*, 2018).

Phylogenetic signal

Because closely related species (descended from a relatively recent common ancestor) share a common

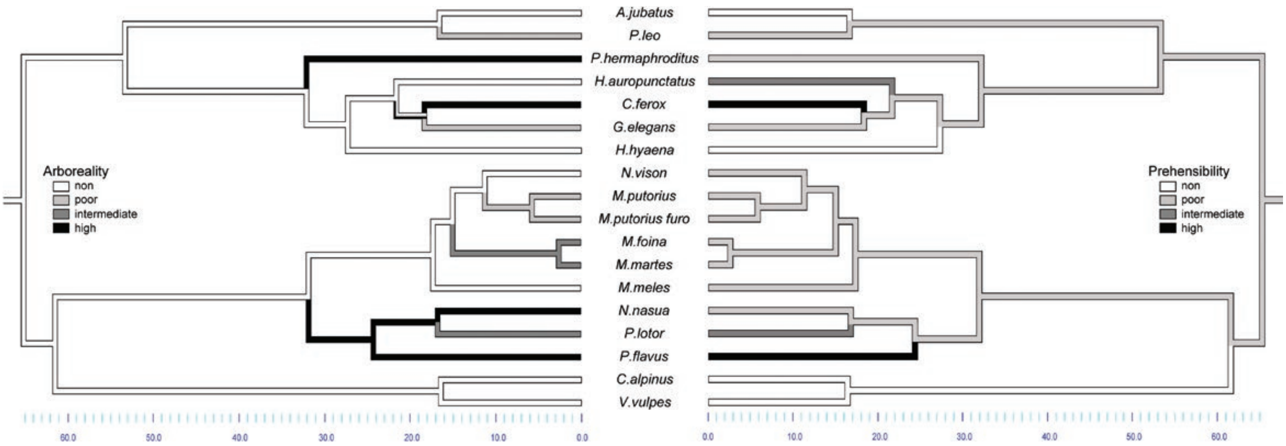

Figure 2. Ancestral character state reconstruction for arboreality and prehensility in the taxa analysed.

history, the data cannot be considered as independent (Harvey & Pagel, 1991). The phylogenetic signal was estimated using a Blomberg's *K* (Blomberg *et al.*, 2003) with the function 'phylosig' in the R package 'phytools' (Revell, 2012). Blomberg's *K* allowed us to test whether the same muscle properties are present in related taxa more frequently than expected by Brownian motion (Blomberg *et al.*, 2003). A value of $K > 1$ indicates a strong phylogenetic signal, while a value of *K* close to zero indicates a weak phylogenetic signal. Note, however, that other evolutionary models (e.g. Ornstein–Uhlenbeck) may provide a better fit of the data distribution across the phylogeny if adaptive peaks are present in the data (Butler & King, 2004; Beaulieu *et al.*, 2012).

(M)ANOVAs and phylogenetic (M)ANOVAs

To test if the muscle parameters differ depending on the ecological categories (prehensility and arboreality), we performed a phylogenetic MANOVA on the PCs that explain about 10% or more of the total variance using the 'aov.phylo' function in the R package 'geiger' (Pennell *et al.*, 2014). For each muscle we next tested whether differences were observed between ecological groups using phylogenetic ANOVAs coupled to Bonferroni post-hoc tests in R using 'geiger'.

RESULTS

ANCESTRAL CHARACTER STATE RECONSTRUCTION

The ancestral state reconstructions of arboreality and prehensility suggest that the character state of the common ancestor of the carnivores in our sample was non-arboreal and poorly prehensile (Fig. 2). The analysis further indicated that a high degree of arboreality evolved at least twice in the suborder Feliformia (*Paradoxurus hermaphroditus*, *Cryptoprocta ferox*) and at least once in the suborder Caniformia (*Potos flavus*). Strong prehensility appears to have evolved at least once in both suborders (Feliformia: *Cryptoprocta ferox*, Caniformia: *Potos flavus*). The results also suggest that the loss of all prehensile capability appeared twice among Feliformia (*Acinonyx jubatus*, *Hyaena hyaena*) and once in Canidae (*Cuon alpinus*, *Vulpes vulpes*).

PRINCIPAL COMPONENT ANALYSIS

The PCA on the raw data (Table 3) displayed a strong separation of the analysed taxa based on differences in body mass. The PCA on the scaled data revealed the same pattern for both size-normalized datasets. Moreover, regression analysis of the PCs against $\log_{10}$-transformed mean body mass showed no significant correlation. In the following, we solely refer to the results obtained from the first scaling method as both provided similar results.

In total, the PCA revealed 19 PCs. The *k*-means cluster analysis (SS ratio = 48.9%) assigned the studied animals to four clusters that correspond to about 74% (14 out of 19 taxa) of the a priori defined prehensility categories (Table 4). The first cluster includes all non-prehensile taxa except the cheetah (*Acinonyx jubatus*). In the second cluster, all poorly prehensile taxa are grouped together except the ring-tailed mongoose (*Galidia elegans*), the ferret (*Mustela putorius furo*) and the mink (*Neovison vison*). The third cluster is a mixed group encompassing the intermediately prehensile small Indian mongoose (*Herpestes auropunctatus*) as well as the non-prehensile cheetah and the poorly prehensile ring-tailed mongoose. The fourth cluster includes the strongly prehensile taxa including the

Table 3. Estimates of anatomical cross-sectional area (cm^2) of named forelimb muscles in the analysed carnivores. Refer to Table 2 for muscle acronyms

Muscle	*Cuon alpinus 1*	*Cuon alpinus 2*	*Vulpes vulpes*	*Cryptoprocta ferox*	*Galidia elegans*	*Acinonyx jubatus*	*Panthera leo*	*Herpestes auropunctatus*	*Hyaena hyaena*	*Martes foina*
SSP	10.25	11.14	7.53	2.15	0.91	13.55	28.58	0.44	12.85	1.17
TMJ	1.73	1.66	1.41	0.74	0.23	4.90	10.83	0.30	3.98	0.35
DS	1.28	0.86	0.50	0.34	0.09	2.82	4.48	0.10	2.35	0.27
DA	1.69	1.61	0.73	0.98	0.20	3.01	6.04	0.17	2.06	0.48
ISP	13.72	12.43	6.93	1.70	0.82	22.79	24.48	0.60	22.53	1.14
TMN	0.48	0.33	0.29	0.21	0.06	1.73	2.94	0.06	0.90	0.11
AH	0.58	0.70	0.75	0.29	0.05	0.31	0.86	0.01	0.61	0.22
SUB	18.52	22.01	9.77	2.70	1.25	34.66	94.48	0.80	21.97	1.84
EPI	0.0	0.0	0.0	0.0	0.0	0.0	1.14	0.0	0.0	0.23
TBLA	4.24	3.83	1.24	2.60	0.37	6.75	10.61	0.24	7.15	0.99
TBLO	9.30	8.07	3.80	4.44	1.37	17.16	19.40	0.94	14.04	2.13
TBM	4.01	3.45	2.92	2.07	0.38	3.24	11.80	0.29	3.34	1.06
ANC	0.54	0.80	0.68	0.40	0.12	0.84	4.13	0.06	1.17	0.11
TBA	0.0	0.0	0.0	0.38	0.09	0.24	3.69	0.04	0.0	0.15
BB	2.27	2.00	0.71	1.02	0.28	6.35	10.81	0.15	4.17	0.82
BCH	1.13	0.85	0.83	0.78	0.15	1.22	11.03	0.13	2.76	0.35
BCR	0.0	0.0	0.0	0.22	0.02	0.0	1.00	0.08	0.0	0.13
SUP	0.31	0.34	0.09	0.59	0.14	0.70	3.90	0.13	0.69	0.32
PT	0.63	0.57	0.18	0.69	0.19	1.57	3.75	0.12	0.80	0.69
PQ	3.77	2.95	0.61	0.45	0.24	1.87	5.13	0.07	1.89	0.26
ECRL	0.61	0.55	1.07	0.21	0.16	2.02	5.53	0.16	1.54	0.27
ECRB	1.44	1.28	1.00	0.32	0.06	2.02	9.15	0.16	1.77	0.36
ECU	2.55	1.72	5.08	1.11	0.30	1.10	3.65	0.27	3.42	0.79
EDC	2.25	2.16	1.16	0.37	0.13	2.97	10.23	0.09	4.12	0.36
EDL	1.68	1.89	0.96	0.46	0.16	1.03	6.92	0.11	1.97	0.26
EI	1.63	2.31	0.10	0.14	0.05	0.36	2.58	0.01	4.35	0.14
EP	1.99	0.81	1.99	1.04	0.33	1.54	9.04	0.24	2.36	0.41
FCUU	0.55	0.63	1.03	0.90	0.23	1.5	4.69	0.06	0.89	0.66
FCUH	1.79	2.67	1.89	0.47	0.23	1.5	9.06	0.06	2.78	0.57
FCR	1.20	1.99	0.73	0.73	0.18	2.04	5.13	0.18	3.33	0.44
PL	2.80	2.66	4.37	0.37	0.32	2.01	6.51	0.55	2.32	0.73
FDP	7.08	9.68	5.64	2.72	0.94	15.02	47.71	0.91	23.00	1.61

Table 3. *Continued*

Muscle	*Martes martes*	*Meles meles*	*Mustela putorius*	*Mustela putorius furo*	*Neovison vison*	*Nasua nasua*	*Potos flavus*	*Procyon lotor*	*Paradoxurus herm-aphroditus*
SSP	1.62	7.35	1.57	0.63	1.37	1.94	1.56	2.03	4.18
TMJ	0.45	0.94	0.34	0.22	0.19	1.79	0.59	0.68	2.03
DS	0.33	0.83	0.35	0.17	0.12	0.49	0.22	0.24	1.19
DA	0.61	1.15	0.24	0.09	0.28	1.86	0.75	0.56	3.07
ISP	1.63	5.12	1.09	0.49	0.75	3.67	1.38	2.29	4.39
TMN	0.09	0.43	0.06	0.12	0.22	0.17	0.10	0.26	0.68
AH	0.23	0.19	0.0	0.10	0.07	0.12	0.13	0.11	0.34
SUB	2.41	10.15	2.02	1.26	1.33	4.47	2.70	3.97	3.79
EPI	0.40	1.38	0.34	0.27	0.27	0.34	0.43	0.39	0.0
TBLA	1.57	3.94	0.88	0.65	0.63	0.69	0.93	1.18	1.19
TBLO	3.00	8.47	1.97	0.96	1.45	2.28	1.41	2.25	3.66
TBM	1.51	3.32	0.99	0.40	0.51	0.78	0.84	0.77	2.30
ANC	0.16	0.67	0.27	0.08	0.13	0.59	0.33	0.26	0.40
TBA	0.15	0.58	0.14	0.0	0.08	0.29	0.15	0.16	0.24
BB	1.29	2.02	0.64	0.31	0.68	2.33	0.89	0.89	1.98
BCH	0.51	0.99	0.38	0.17	0.27	1.74	0.77	0.64	1.06
BCR	0.14	0.85	0.11	0.06	0.11	0.42	0.20	0.25	0.56
SUP	0.42	0.70	0.51	0.18	0.17	0.96	0.41	0.41	1.39
PT	1.05	1.88	0.53	0.25	0.20	1.26	0.78	0.75	1.72
PQ	0.34	0.59	0.29	0.15	0.11	0.66	0.31	0.41	1.07
ECRL	0.23	0.43	0.15	0.08	0.09	0.33	0.26	0.28	0.43
ECRB	0.42	0.56	0.27	0.14	0.09	0.53	0.32	0.27	0.37
ECU	1.11	3.28	0.49	0.29	0.35	0.89	0.64	0.64	2.60
EDC	0.38	0.91	0.33	0.15	0.14	0.35	0.29	0.32	0.65
EDL	0.33	0.91	0.40	0.15	0.10	0.31	0.21	0.40	0.66
EI	0.10	0.20	0.15	0.08	0.0	0.22	0.08	0.16	0.23
EP	0.54	1.37	0.42	0.26	0.26	0.97	0.56	0.63	2.76
FCUU	1.05	1.25	0.92	0.18	0.09	0.14	0.29	0.59	1.56
FCUH	0.92	2.57	0.21	0.28	0.16	1.38	0.72	0.42	1.11
FCR	0.58	0.62	0.37	0.20	0.10	0.82	0.52	0.49	1.64
PL	1.45	3.96	0.95	0.42	0.80	0.45	0.23	1.09	1.15
FDP	2.36	9.89	1.66	0.75	0.94	5.50	3.29	1.79	5.15

Table 4. The *k*-means clustering results on all 19 principal components (explaining 100% of the detected variation)

Species	*k*-means cluster
Cuon alpinus 1	1
Cuon alpinus 2	1
Vulpes vulpes	1
Hyaena hyaena	1
Panthera leo	2
Martes foina	2
Martes martes	2
Meles meles	2
Mustela putorius	2
Nasua nasua	2
Paradoxurus hermaphroditus	2
Galidia elegans	3
Acinonyx jubatus	3
Herpestes auropunctatus	3
Cryptoprocta ferox	4
Mustela putorius furo	4
Neovison vison	4
Potos flavus	4
Procyon lotor	4

fossa (*Cryptoprocta ferox*) and the kinkajou (*Potos flavus*), but also the intermediately prehensile raccoon (*Procyon lotor*), and the poorly prehensile ferret and mink. In summary, the five taxa that differ from the a priori prehensility categories are: the cheetah, the ring-tailed mongoose, the raccoon, the ferret and the mink.

PHYLOMORPHOSPACE

The first three PC axes explain 63.5% of the total detected variation in the sample (PC1 = 39.0%, PC2 = 15.4%, PC3 = 9.1%). All Blomberg's K values were <1, indicating that related species resemble each other less than expected under the Brownian motion model of trait evolution. Whereas PC1 ($K = 0.24$, $P = 0.65$) and PC3 ($K = 0.47$, $P = 0.06$) showed no phylogenetic signal, this was significant for the second PC ($K = 0.77$, $P < 0.005$).

The five muscles contributing most along PC1 are the M. spinodeltoideus (DS), M. extensor digitorum communis (EDC), M. triceps brachii caput mediale (TBM), M. flexor digitorum profundus (FDP) and M. flexor carpi radialis (FCR) (Fig. 3A; Table 5). In total, they account for about 27% of the variation along the first PC axis. All five muscles have negative loadings on PC1 (Table 5) indicating that the taxa on the negative side of the first PC axis have larger ASCAs in these muscles.

The five muscles contributing most along PC2 are the M. supinator (SUP), M. brachioradialis (BCR), M. pronator teres (PT), M. brachialis (BCH) and M. triceps brachii caput accessorium (TBA) (Fig. 3C; Table 5). In total, they account for almost 50% of the variation along the second PC axis. All five muscles have negative loadings on PC2 (Table 5). The taxa on the negative side of PC2 have larger ASCAs in these muscles.

The overall pattern in terms of prehensility appears unclear at first glance. However, when considering the extremes in our sample, i.e. non-prehensile vs. strongly prehensile animals, taxa are largely separated by PC1 and PC2 (Fig. 3B). All non-prehensile animals in our sample, such as the cheetah (*Acinonyx jubatus*), the hyena (*Hyaena hyaena*), the dhole (*Cuon alpinus*) and the fox (*V. vulpes*), are associated with PC1 scores close to zero and positive PC2 scores. Taxa with the strongest prehensility, namely the fossa (*Cryptoprocta ferox*) and the kinkajou (*Potos flavus*), are characterized by positive PC1 and negative PC2 scores. Poorly and intermediately prehensile animals are scattered between these extremes with the intermediately prehensile taxa, the small Indian mongoose (*Herpestes auropunctatus*) and the raccoon (*Procyon lotor*) being associated with positive PC1 scores.

In terms of arboreality, the extremes in our sample (i.e. non-arboreal vs. highly arboreal animals) tend to lie on the opposite sides of the graph. Except for the lion (*Panthera leo*) and the badger (*Meles meles*), the non-arboreal animals in our sample are associated with positive PC2 scores (Fig. 3B, D). Taxa with the highest arboreality, namely the palm civet (*Paradoxurus hermaphroditus*), the fossa (*Cryptoprocta ferox*), and the coati (*Nasua nasua*), are characterized by negative PC2 scores. Poorly and intermediately arboreal animals are scattered between these extremes.

Our quantitative analyses revealed no significant signal of arboreality (Wilks' lambda = 0.22; $F = 1.67$; $P = 0.13$; Pphyl = 0.12) nor of prehensile capability (Wilks' lambda = 0.23; $F = 1.61$; $P = 0.15$; Pphyl = 0.28) on muscle anatomy when using the first four principal components and irrespective of whether phylogeny was taken into account. This suggests not global trends exist. Univariate analyses of variance taking phylogeny into account suggested, however, differences in muscle ACSA between species differing in prehensility. Specifically, differences were detected in the M. supraspinatus ($F = 5.80$; $P = 0.009$; Pphyl = 0.01), the M. infraspinatus ($F = 5.60$; $P = 0.01$; Pphyl = 0.02), the M. subscapularis ($F = 5.60$; $P = 0.01$; Pphyl = 0.02), the M. triceps brachii caput laterale ($F = 5.60$; $P = 0.01$; Pphyl = 0.02), the M. brachioradialis ($F = 11.10$; $P < 0.001$; Pphyl < 0.001) and the M. pronator teres ($F = 4.40$; $P = 0.02$; Pphyl = 0.04). However, after Bonferroni correction

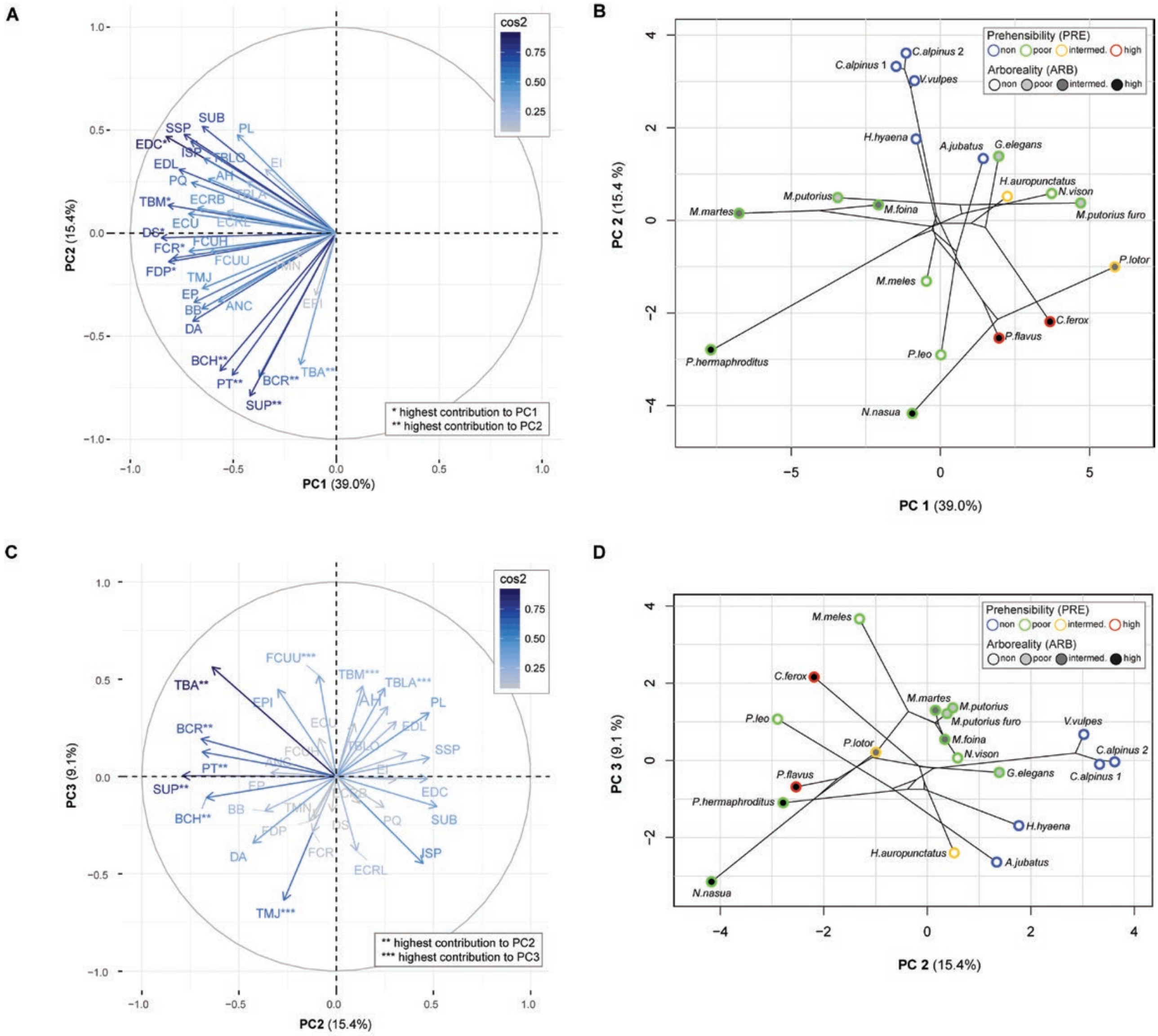

Figure 3. Results of the principal components (PC) analysis of the muscle data. (A,C) Contribution of the variables. (B,D) Scatterplot and projected phylogeny illustrating the distribution of the sampled taxa in morphospace.

for multiple testing only the M. brachioradialis showed differences in ACSA. Post-hoc tests showed that differences in the brachioradialis ACSA were significant between species that have no grasping ability and those that show either poorly developed (t = 5.56; P = 0.006) or well-developed grasping abilities (t = 3.97; P = 0.036). When testing for effects of arboreality, differences in muscle ACSA were significant for the M. acromiodeltoideus (F = 3.77; P = 0.04; Pphyl = 0.03), the M. supinator (F = 3.78; P = 0.03; Pphyl = 0.02) and the M. pronator teres (F = 3.99; P = 0.03; Pphyl = 0.02). Although none of these differences was significant after Bonferroni correction for multiple testing, post-hoc tests suggested that the differences were mainly between primarily arboreal vs. non-arboreal species (P = 0.04).

DISCUSSION

Although basal Carnivoraformes have been reconstructed as being ambiguous, the most conservative assessment of currently available information supports the hypothesis of primitive arboreal locomotion in carnivoraforms (Spaulding & Flynn, 2009; Goswami & Friscia, 2010). Our results

Table 5. Contribution of the variables (%) to the first three principal components (PC1 to PC3) and loadings of the variables. The five variables that contribute most for each PC are indicated in bold and with asterisks (*)

Variable	PC1		PC2		PC3	
	Contribution	Loading	Contribution	Loading	Contribution	Loading
SSP	4.38	−0.21	4.68	0.22	0.32	0.06
TMJ	3.39	−0.18	1.47	−0.12	**13.92***	**−0.37***
DS	**5.78***	**−0.24***	0.01	−0.01	1.12	−0.11
DA	3.89	−0.20	3.73	−0.19	4.04	−0.20
ISP	4.00	−0.20	4.06	0.20	6.87	−0.26
TMN	0.31	−0.06	0.26	−0.05	1.55	−0.12
AH	3.09	−0.18	1.43	0.12	4.43	0.21
SUB	3.39	−0.18	5.45	0.23	0.82	−0.09
EPI	0.08	−0.03	1.83	−0.14	6.91	0.26
TBLA	1.50	−0.12	1.27	0.11	**7.10***	**0.27***
TBLO	3.31	−0.18	2.69	0.16	0.49	0.07
TBM	**5.35***	**−0.23***	0.37	0.06	**7.41***	**0.27***
ANC	2.62	−0.16	2.27	−0.15	0.01	0.01
TBA	0.24	−0.05	**8.27***	**−0.29***	**10.89***	**0.33***
BB	3.41	−0.18	2.74	−0.17	1.09	−0.10
BCH	2.55	−0.16	**9.07***	**−0.30***	0.41	−0.06
BCR	1.12	−0.11	**9.81***	**−0.31***	1.28	0.11
SUP	1.41	−0.12	**12.70***	**−0.36***	0.00	0.00
PT	2.04	−0.14	**9.66***	**−0.31***	0.55	0.07
PQ	3.96	−0.20	1.23	0.11	0.87	−0.09
ECRL	2.25	−0.15	0.23	0.05	5.02	−0.22
ECRB	3.63	−0.19	0.30	0.05	0.66	−0.08
ECU	4.12	−0.20	0.18	0.04	2.56	0.16
EDC	**5.47***	**−0.23***	4.47	0.21	0.00	−0.01
EDL	4.67	−0.22	1.94	0.14	2.73	0.17
EI	0.94	−0.10	1.95	0.14	0.01	−0.01
EP	3.82	−0.20	2.30	−0.15	0.01	0.01
FCUU	2.98	−0.17	0.16	−0.04	**9.28***	**0.30***
FCUH	4.10	−0.20	0.16	−0.04	1.33	0.12
FCR	**5.05***	**−0.22***	0.30	−0.05	2.80	−0.17
PL	1.85	−0.14	4.64	0.22	3.69	0.19
FDP	**5.32***	**−0.23***	0.39	−0.06	1.84	−0.14

suggest that the ancestral modern carnivore was probably non-arboreal and had poor prehensility based on the species included in our study. However, it is important to note that our ancestral reconstruction is based on a limited sample and includes only representative members of the crown-clade Carnivora. This is in accordance with a previous study that indicated that the common ancestor of the ailurid, procyonid and mustelid clades was terrestrial or semi-arboreal and had poorly developed prehensile capabilities (Fabre *et al.*, 2013). The loss of any prehensile capability occurred convergently in Feliformia (*Acinonyx jubatus*, *Hyaena hyaena*) and Caniformia (Canidae) (Fig. 2). Forelimb bone morphology and in particular elbow joint morphology supports this observation (Ewer, 1977; Iwaniuk *et al.*, 1999; Andersson & Werdelin, 2003). Some carnivores retained supinatory ability allowing them to manipulate food items, whereas other carnivores lost the ability to supinate and became strictly cursorial (Ewer, 1977; Andersson & Werdelin, 2003).

FORELIMB MUSCULATURE AND PREHENSILITY

Considering the extremes in our sample, comparison of the force-producing capacity of the intrinsic musculature overall reflects the ecology of the carnivores in our sample. Non-prehensile taxa (e.g. the dhole, *Cuon alpinus*, or the hyaena, *Hyaena hyaena*) differ in their muscle properties from poorly prehensile taxa (e.g. the stone marten, *Martes foina*) and from intermediately to strongly prehensile taxa (e.g. the kinkajou, *Potos flavus*). The non-prehensile taxa in our sample include canids and hyaenids as well as the cheetah (*Acinonyx jubatus*) that chase their prey over relatively long distances and that do not use their forelimbs to grab and manipulate prey. The cheetah's morphological features are unique among felids, including an increased cursorial ability that was acquired at the expense of the manipulative capabilities of the forelimb (Russell & Bryant, 2001).This is supported by the observation that these specimens lack or have poorly developed muscles that help to rotate the forelimb (e.g. M. epitrochlearis, M. brachioradialis, M. supinator, M. pronator teres). It is also in accordance with the morphology of the bones and the joints that point to a restriction of movements of the radius and ulna to a sagittal plane (e.g. Gonyea, 1978; Spoor & Badoux, 1986; Martín-Serra *et al.*, 2016). The two distantly related taxa with the strongest prehensility in our sample, the euplerid fossa (*Cryptoprocta ferox*) and the procyonid kinkajou (*Potos flavus*), are significantly different from the non-prehensile taxa and share similar force-producing capacities of the forelimb muscles. In particular, the rotator muscles are well developed, thus enhancing pronation and supination of the forelimb, as has been shown in other prehensile carnivores such as the lynx and the ocelot (Julik *et al.*, 2012; Viranta *et al.*, 2016). More specifically, it is the M. brachioradialis that differs between taxa that differ in grasping ability. This muscle is an important rotator, as demonstrated by the brachioradialis reflex, which causes pronation or supination and slight elbow flexion (Teasdall & Magladery, 1974). In accordance with our study, a greater functional importance for the M. brachioradialis has been reported for mustelids, procyonids and felids when compared to canids (Junior *et al.*, 2015). The soft tissue adaptations go hand in hand with a specialized limb bone morphology allowing for a wide range of rotation in the forelimb (e.g. Andersson, 2004; Ercoli *et al.*, 2012).

PREHENSILITY AND ARBOREALITY

Generally, a single evolutionary origin is proposed for prehension, possibly derived from either digging (e.g. Brácha *et al.*, 1990), climbing on thin branches (e.g. Anton *et al.*, 2006) or capturing prey (e.g. Iwaniuk & Whishaw, 2000). Although the functional signal in the muscles indicating strong prehensility is not clearly distinguishable from that indicating high arboreality, the present results suggest a trend in differences in muscular adaptations for prehensile capabilities and arboreal locomotion. Among the excellent climbers in our sample, differences in the degree of prehensility are reflected in the forelimb musculature (primarily along PC1): the poorly prehensile palm civet (*Paradoxurus hermaphroditus*) and coati (*Nasua nasua*) vs. the strongly prehensile kinkajou (*Potos flavus*) and fossa (*Cryptoprocta ferox*). Thus, a strong prehensile capability in the forelimb is not a prerequisite for climbing in carnivores. There are alternative strategies to make secure contact with the arboreal substrate (Iwaniuk *et al.*, 2000). The palm civet (*Paradoxurus hermaphroditus*) has strongly grasping hindfeet that it uses for arboreal locomotion (Gittleman, 1985). The agile and fast-moving coati (*Nasua nasua*) may represent a possible trade-off between maximizing prehensility and arboreal locomotor speed (e.g. Kleiman *et al.*, 2004). Overall, this supports the observation based on the forelimb bone morphology of musteloids that the evolution of an arboreal lifestyle preceded the development of enhanced grasping ability (Fabre *et al.*, 2013).

Among the taxa with intermediate to strong prehensility, differences in the degree of arboreality are also reflected in the forelimb musculature (primarily along PC2): the non-arboreal small Indian mongoose (*Herpestes auropunctatus*) vs. the intermediately arboreal raccoon (*Procyon lotor*) and the highly arboreal kinkajou (*Potos flavus*) and fossa (*Cryptoprocta ferox*). This suggests that prehensility may have evolved independently from arboreality in some taxa. Interestingly, the prehensile capabilities in the small Indian mongoose (*Herpestes auropunctatus*) and the raccoon (*Procyon lotor*) are strongly associated with a high degree of dexterity (McClearn, 1985, 1992; Iwaniuk & Whishaw, 1999; Estes, 2012). Raccoons find most of their food on the ground and have exquisite fine control of forepaw digits, but do not have the converging grasp of kinkajous (McClearn, 1992). In this context, an important distinction has to be considered: precision vs. power grasping (reviewed by Sustaita *et al.*, 2013). The precision grasp is characterized by high dexterity and sensibility, whereas the power grasp is attributed to high stability and security. Because larger muscle ACSAs are expected to be linked to the power grasp rather than the precision grasp, it is not surprising that the dexterous taxa in our sample differ from the strongly prehensile ones. The power grasp appears to be advantageous for arboreal locomotion, whereas the precision grasp can evolve independently from a climbing lifestyle. To fully assess the role that the muscles of the forelimb may play in determining prehensility in carnivores, it would be interesting to evaluate the musculature responsible for fine control of the digits.

CONCLUSION

The major factors responsible for adaptive modifications in the forelimb morphology of mammals involve food and feeding as well as locomotion. A strong grasp is advantageous for both predation and arboreal locomotion and, thus, prehensility and arboreality are tightly linked to each other (reviewed by Sustaita *et al.*, 2013). The general movements needed to grasp a food item or to grasp a tree trunk or branch are relatively similar. In frogs and primates, for example, the evolution of grasping is thought to be an exaptation of the specialization of the forelimbs for arboreal locomotion (Napier, 1967; Gray *et al.*, 1997; Manzano *et al.*, 2008). Within carnivores, this may also be the case for the red panda (*Ailurus fulgens*) (Anton *et al.*, 2006; Salesa *et al.*, 2006; Endo *et al.*, 2007) and has been reported for mustelids in general (Fabre *et al.*, 2013). In contrast, climbing adaptations in the musculoskeletal system of the forearm and hand in the giant panda (*Ailuropoda melanoleuca*) are interpreted to be an exaptation of the specialization of the forelimbs for the manipulation of bamboo (Davis, 1964; Anton *et al.*, 2006; Salesa *et al.*, 2006).

Acknowledging certain limitations, the present results suggest that strong prehensile capabilities are primarily associated with well-developed rotator muscles favouring the transport phase of prehension, whereas a high degree of arboreality is primarily linked to well-developed flexor muscles contributing to a strong grasp (Fig. 3A). Because the muscle properties characterizing prehensile taxa do not correspond to those characterizing arboreal taxa, the present study suggests a dual origin of prehensility in carnivores. On the one hand, the ability to grasp appears to be derived from arboreal thin-branch climbing (e.g. Grillner & Wallen, 1985) as perhaps for the kinkajou (*Potos flavus*). On the other hand, prehensility may be derived from the need to manipulate food items (e.g. Iwaniuk & Whishaw, 2000) as perhaps for the raccoon (*Procyon lotor*). Thus, the differences in forelimb muscle specialization in carnivores may be explained by evolutionary pressures favouring either prehensility or arboreality. According to the 'Dual Visuomotor Channel Theory', the reach phase and the grasp phase during prehension are of independent origin (Karl & Whishaw, 2013). The two phases depend on two neural pathways that extend from visual cortex to motor cortex via the parietal lobe (Karl & Whishaw, 2013). It would be interesting to investigate the neural pathway that mediates the transport phase as well. If it is independent of the grasp phase, this would support the observed differences in muscle specialization in terms of prehensility and arboreality.

ACKNOWLEDGMENTS

This paper was a contribution to a European Federation for Primatology symposium on 'What an interdisciplinary approach can tell us about the evolution of grasping and manipulation' held on 21–25 August 2017 at the University of Strasbourg in France and organized by Emmanuelle Pouydebat and Ameline Bardo, the proceedings of which have been collated as a Special Issue of the Journal (2019). We would like to thank Grégory Breton and Jérôme Catinaud from the parc des félins and the animal park of la Haute-Touche for providing specimens for study; and Eric Pellé, Zoé Thalaud and Christophe Voisin from the taxidermy facilities for the preparation of these specimens. We are grateful to the collections of the Muséum National d'Histoire Naturelle for access to specimens. We also thank Dr Sven Reese and Dr Estella Böhmer (Faculty of Veterinary Medicine of the Ludwig-Maximilians-Universität in Munich), Opale Robin and Benoît Clavel (INRAP Centre de Recherches Archologiques de l'Oise in Compiegne), Christophe Gottini (taxidermy facility of the MNHN in Paris), Géraldine Veron and Jérôme Fuchs for providing us with specimens for dissection. We would also like to thank two anonymous reviewers for their helpful comments. The present study was financially supported by a Labex BCDiv Postdoc fellowship (C.B.) the Investissement d'Avenir Project Labex BCDiv (ANR-10-LABX-0003), a Labex BCDiv Master fellowship (M.T.) the Investissement d'Avenir Project Labex BCDiv (ANR-10-LABX-0003) and a Marie-Skłodowska Curie fellowship (H2020-EU.1.3.2. EU project 655694 - GETAGRIP) (A.-C.F.).

REFERENCES

Allen V, **Elsey RM**, **Jones N**, **Wright J**, **Hutchinson JR. 2010.** Functional specialization and ontogenetic scaling of limb anatomy in *Alligator mississippiensis*. *Journal of Anatomy* **216:** 423–445.

Allen V, **Molnar J**, **Parker W**, **Pollard A**, **Nolan G**, **Hutchinson JR. 2014.** Comparative architectural properties of limb muscles in Crocodylidae and Alligatoridae and their relevance to divergent use of asymmetrical gaits in extant Crocodylia. *Journal of Anatomy* **225:** 569–582.

Amundsen Huffmaster SL, **Van Acker GM 3rd**, **Luchies CW**, **Cheney PD. 2017.** Muscle synergies obtained from comprehensive mapping of the primary motor cortex forelimb representation using high-frequency, long-duration ICMS. *Journal of Neurophysiology* **118:** 455–470.

Andersson K. 2004. Elbow-joint morphology as a guide to forearm function and foraging behavior in mammalian carnivores. *Zoological Journal of the Linnean Society* **142:** 91–104.

Andersson K, **Werdelin L. 2003.** The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology. *Proceedings of the Royal Society London B* **270:** S163–165.

Antón SC. 1999. Macaque masseter muscle: internal architecture, fiber length and cross-sectional area. *International Journal of Primatology* **20:** 441–462.

Antón M, **Salesa MJ**, **Pastor JF**, **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. *Journal of Anatomy* **209:** 757–764.

Baghli A, **Verhagen R. 2004.** Home ranges and movement patterns in a vulnerable polecat *Mustela putorius* population. *Acta Theriologica* **49:** 247–258.

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

Biewener AA. 2003. *Animal locomotion.* Oxford: Oxford University Press.

Blomberg SP, **Garland T Jr**, **Ives AR. 2003.** Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57:** 717–745.

Böhmer C, **Fabre AC**, **Herbin M**, **Peigné S**, **Herrel A. 2018.** Anatomical basis of differences in locomotor behavior in martens: a comparison of the forelimb musculature between two sympatric species of martes. *Anatomical Record* **301:** 449–472.

Brácha V, **Zhuravin IA**, **Bures J. 1990.** The reaching reaction in the rat: a part of the digging pattern? *Behavioural Brain Research* **36:** 53–64.

Butler MA, **King AA. 2004.** Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist* **164:** 683–695.

Chapman JG, **Feldhamer G. 1982.** *Wild mammals of North America.* Baltimore: The Johns Hopkins University Press.

Close RI. 1972. Dynamic properties of mammalian skeletal muscles. *Physiological Reviews* **52:** 129–197.

Cuff AR, **Sparkes EL**, **Randau M**, **Pierce SE**, **Kitchener AC**, **Goswami A**, **Hutchinson JR. 2016.** The scaling of postcranial muscles in cats (Felidae) I: forelimb, cervical, and thoracic muscles. *Journal of Anatomy* **229:** 128–141.

Davis DD. 1964. The giant panda. A morphological study of evolutionary mechanisms. *Fieldiana Zoology Memoirs* **3:** 1–339.

Dick TJ, **Clemente CJ. 2016.** How to build your dragon: scaling of muscle architecture from the world's smallest to the world's largest monitor lizard. *Frontiers in Zoology* **13:** 8.

Dickinson E, **Stark H**, **Kupczik K. 2018.** Non-destructive determination of muscle architectural variables through the use of DiceCT. *Anatomical Record* **301:** 363–377.

Ding C, **He X. 2004.** K-means clustering via principal component analysis. In *Proceedings of the* 21st International Conference on Machine Learning. Banff, Canada, 225–232.

Endo H, **Hama N**, **Niizawa N**, **Kimura J**, **Itou T**, **Koie H**, **Sakai T. 2007.** Three-dimensional analysis of the manipulation system in the lesser panda. *Mammal Study* **32:** 99–103.

Ercoli MD, **Prevosti FJ**, **Álvarez A. 2012.** Form and function within a phylogenetic framework: locomotory habits of extant predators and some Miocene Sparassodonta (Metatheria). *Zoological Journal of the Linnean Society* **165:** 224–251.

Estes RD. 2012. *The behavior guide to African mammals: including hoofed mammals, carnivores, primates.* Berkeley: University of California Press.

Ewer R. 1977. *The Carnivores.* New York: Cornell University Press.

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

Fabre AC, **Cornette R**, **Slater G**, **Argot C**, **Peigné S**, **Goswami A**, **Pouydebat E. 2013.** Getting a grip on the evolution of grasping in musteloid carnivorans: a three-dimensional analysis of forelimb shape. *Journal of Evolutionary Biology* **26:** 1521–1535.

Flatt AE. 2000. Grasp. *Proceedings (Baylor University. Medical Center)* **13:** 343–348.

Ford LS, **Hoffmann RS. 1988.** *Potos flavus*. *Mammalian Species* **321:** 1–9.

Gambaryan PP. 1974. *How mammals run: anatomical adaptations.* New York: John Wiley & Sons.

Geed S, **van Kan PLE. 2017.** Grasp-based functional coupling between reach- and grasp-related components of forelimb muscle activity. *Journal of Motor Behavior* **49:** 312–328.

Georgopoulos AP. 1986. On reaching. *Annual Review of Neuroscience* **9:** 147–170.

Gittleman JL. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia* **67:** 540–554.

Gompper ME, **Decker DM. 1998.** *Nasua nasua. Mammalian Species* **508:** 1–9.

Gonyea WJ. 1978. Functional implications of felid forelimb anatomy. *Acta Anatomica* **102:** 111–121.

Goswami A, Friscia A, eds. 2010. *Carnivoran evolution. New views on phylogeny, form and function.* Cambridge: Cambridge University Press.

Gray LA, **O'Reilly JC**, **Nishikawa KC. 1997.** Evolution of forelimb movement patterns for prey manipulation in anurans. *The Journal of Experimental Zoology* **277:** 417–424.

Grillner S, **Wallén P. 1985.** Central pattern generators for locomotion, with special reference to vertebrates. *Annual Review of Neuroscience* **8:** 233–261.

Hall BK, ed. 2007. *Fins into limbs: evolution, development, and transformation.* Chicago: University of Chicago Press.

Hammer Ø, **Harper DAT**, **Ryan PD. 2001.** PAST: palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4:** 1–9.

Harvey PH, **Pagel MD. 1991.** *The comparative method in evolutionary biology.* Oxford: Oxford University Press.

Hawkins CE, **Racey PA. 2005.** Low population density of a tropical forest carnivore, *Cryptoprocta ferox*: implications for protected area management. *Oryx* **39:** 35–43.

Herrel A, **De Smet A**, **Aguirre LF**, **Aerts P. 2008.** Morphological and mechanical determinants of bite force in bats: do muscles matter? *The Journal of Experimental Biology* **211:** 86–91.

Herrel A, **Tolley KA**, **Measey GJ**, **da Silva JM**, **Potgieter DF**, **Boller E**, **Boistel R**, **Vanhooydonck B. 2013.** Slow but tenacious: an analysis of running and gripping performance in chameleons. *The Journal of Experimental Biology* **216:** 1025–1030.

Hildebrand M, **Goslow GE. 2004.** *Vergleichende und funktionelle Anatomie der Wirbeltiere.* Berlin: Springer.

Holmes T. 1980. *Locomotor adaptations in the limb skeletons of North American mustelids.* Unpublished Dissertation, Humboldt State University.

Horn CC, **Friedman MI. 2003.** Detection of single unit activity from the rat vagus using cluster analysis of principal components. *Journal of Neuroscience Methods* **122:** 141–147.

Hudson PE, **Corr SA**, **Payne-Davis RC**, **Clancy SN**, **Lane E**, **Wilson AM. 2011.** Functional anatomy of the cheetah (*Acinonyx jubatus*) forelimb. *Journal of Anatomy* **218:** 375–385.

Hyland BI, **Reynolds JN. 1993.** Pattern of activity in muscles of shoulder and elbow during forelimb reaching in the rat. *Human Movement Science* **12:** 51–69.

Ivanco TL, **Pellis SM**, **Whishaw IQ. 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. *Behavioural Brain Research* **79:** 163–181.

Iwaniuk AN, **Pellis SM**, **Whishaw IQ. 1999.** The relationship between forelimb morphology and behaviour in North American carnivores (Carnivora). *Canadian Journal of Zoology* **77:** 1064–1074.

Iwaniuk AN, **Pellis SM**, **Whishaw IQ. 2000.** The relative importance of body size, phylogeny, locomotion, and diet in the evolution of forelimb dexterity in fissiped carnivores (Carnivora). *Canadian Journal of Zoology* **78:** 1110–1125.

Iwaniuk AN, **Whishaw IQ. 1999.** How skilled are the skilled limb movements of the raccoon (*Procyon lotor*)? *Behavioural Brain Research* **99:** 35–44.

Iwaniuk AN, **Whishaw IQ. 2000.** On the origin of skilled forelimb movements. *Trends in Neurosciences* **23:** 372–376.

Jeannerod M, **Arbib MA**, **Rizzolatti G**, **Sakata H. 1995.** Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in Neurosciences* **18:** 314–320.

Jones KE, **Bielby J**, **Cardillo M**, **Fritz SA**, **O'Dell J**, **Orme CDL**, **Safi K**, **Sechrest W**, **Boakes EH**, **Carbone C**, **Connolly C**, **Cutts MJ**, **Foster JK**, **Grenyer R**, **Habib M**, **Plaster CA**, **Price SA**, **Rigby EA**, **Rist J**, **Teacher A**, **Bininda-Emonds ORP**, **Gittleman JL**, **Mace GM**, **Purvis A. 2009.** PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90:** 2648–2648.

Joy JB, **Liang RH**, **McCloskey RM**, **Nguyen T**, **Poon AF. 2016.** Ancestral reconstruction. *PLoS Computational Biology* **12:** e1004763.

Julik E, **Zack S**, **Adrian B**, **Maredia S**, **Parsa A**, **Poole M**, **Starbuck A**, **Fisher RE. 2012.** Functional anatomy of the forelimb muscles of the ocelot (*Leopardus pardalis*). *Journal of Mammalian Evolution* **19:** 277–304.

Junior PdS, **Santos LMRPd**, **Nogueira DMP**, **Abidu-Figueiredo M**, **Santos ALQ. 2015.** Occurrence and morphometrics of the brachioradialis muscle in wild carnivorans (Carnivora: Caniformia, Feliformia). *Zoologia* **32:** 23–32.

Karl JM, **Whishaw IQ. 2013.** Different evolutionary origins for the reach and the grasp: an explanation for dual visuomotor channels in primate parietofrontal cortex. *Frontiers in Neurology* **4:** 1–13.

Kassambara A. 2017. *Practical guide to principal component methods in R.* Scotts Valley: CreateSpace Independent Publishing Platform.

Kassambara A, **Mundt F. 2017.** *factoextra. Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.5.* Available at: https://cran.r-project.org/package=factoextra.

Kilbourne BM. 2017. Selective regimes and functional anatomy in the mustelid forelimb: diversification toward specializations for climbing, digging, and swimming. *Ecology and Evolution* **7:** 8852–8863.

Kleiman DG, **Geist V**, **McDade MC. 2004.** *Grzimek's animal life encyclopedia, Vol. 14 Mammals III.* Farmington Hills: Gale Group.

Krausman PR, **Morales SM. 2005.** *Acinonyx jubatus*. *Mammalian Species* **771:** 1–6.

Kupczik K, **Stark H**, **Mundry R**, **Neininger FT**, **Heidlauf T**, **Röhrle O. 2015.** Reconstruction of muscle fascicle architecture from iodine-enhanced microCT images: a combined texture mapping and streamline approach. *Journal of Theoretical Biology* **382:** 34–43.

Lieber RL, **Friden J. 2001.** Clinical significance of skeletal muscle architecture. *Clinical Orthopaedics and Related Research* **383:** 140–151.

Losos JB, **Walton BM**, **Bennett AF. 1993.** Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Functional Ecology* **7:** 281–286.

Macdonald DW, **Loveridge AJ**, **eds. 2010.** *The biology and conservation of wild felids.* Oxford: Oxford University Press.

Maddison WP, **Maddison DR. 2011.** *Mesquite: a modular system for evolutionary analysis, Version 2.75*. Available at: http://mesquiteproject.org/

Maechler M, **Rousseeuw P**, **Struyf A**, **Hubert M**, **Hornik K. 2018.** *cluster: cluster analysis basics and extensions. R package version 2.0.7-1.* Available at: https://cran.r-project.org/package=cluster

Manzano AS, **Abdala V**, **Herrel A. 2008.** Morphology and function of the forelimb in arboreal frogs: specializations for grasping ability? *Journal of Anatomy* **213:** 296–307.

Martín-Serra A, **Figueirido B**, **Palmqvist P. 2014.** A three-dimensional analysis of morphological evolution and locomotor performance of the carnivoran forelimb. *PLoS One* **9:** e85574.

Martín-Serra A, **Figueirido B**, **Palmqvist P. 2016.** In the pursuit of the predatory behavior of Borophagines (Mammalia, Carnivora, Canidae): inferences from forelimb morphology. *Journal of Mammalian Evolution* **23:** 237–249.

McClearn D. 1985. Anatomy of raccoon (*Procyon lotor*) and coati (*Nasua narica* and *N. nasua*) forearm and leg muscles: relations between fiber length, moment-arm length, and joint-angle excursion. *Journal of Morphology* **183:** 87–115.

McClearn D. 1992. Locomotion, posture, and feeding behavior of Kinkajous, Coatis, and Raccoons. *Journal of Mammalogy* **73:** 245–261.

McKenna JE, **Whishaw IQ. 1999.** Complete compensation in skilled reaching success with associated impairments in limb synergies, after dorsal column lesion in the rat. *The Journal of Neuroscience* **19:** 1885–1894.

McNeill AR. 1983. *Animal mechanics.* London: Blackwell Scientific.

Meachen-Samuels J, **Van Valkenburgh B. 2009.** Forelimb indicators of prey-size preference in the Felidae. *Journal of Morphology* **270:** 729–744.

Mendez J, **Keys A. 1960.** Density and composition of mammalian muscle. *Metabolism* **9:** 184–188.

Moore AL, **Budny JE**, **Russell AP**, **Butcher MT. 2013.** Architectural specialization of the intrinsic thoracic limb musculature of the American badger (*Taxidea taxus*). *Journal of Morphology* **274:** 35–48.

Myatt JP, **Crompton RH**, **Payne-Davis RC**, **Vereecke EE**, **Isler K**, **Savage R**, **D'Août K**, **Günther MM**, **Thorpe SK. 2012.** Functional adaptations in the forelimb muscles of non-human great apes. *Journal of Anatomy* **220:** 13–28.

Nakabayashi M, **Ahmad AH**, **Kohshima S. 2016.** Behavioral feeding strategy of frugivorous civets in a Bornean rainforest. *Journal of Mammalogy* **97:** 798–805.

Napier JR. 1961. Prehensility and opposability in the hands of primates. *Symposia of the Zoological Society of London* **5:** 115–132.

Napier JR. 1967. Evolutionary aspects of primate locomotion. *American Journal of Physical Anthropology* **27:** 333–341.

Nellis DW. 1989. *Herpestes auropunctatus*. *Mammalian Species* **342:** 1–6.

Nellis DW, **Everard COR. 1983.** The biology of the mongoose in the Caribbean. *Studies on the Fauna of Curaçao and Other Caribbean Islands* **64:** 1–162.

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

Nyakatura JA, **Stark H. 2015.** Aberrant back muscle function correlates with intramuscular architecture of dorsovertebral muscles in two-toed sloths. *Mammalian Biology - Zeitschrift für Säugetierkunde* **80:** 114–121.

Parsons KJ, **Cooper WJ**, **Albertson RC. 2009.** Limits of principal components analysis for producing a common trait space: implications for inferring selection, contingency, and chance in evolution. *PLoS One* **4:** e7957.

Peckre L, **Fabre AC**, **Wall CE**, **Brewer D**, **Ehmke E**, **Haring D**, **Shaw E**, **Welser K**, **Pouydebat E. 2016.** Holding-on: co-evolution between infant carrying and grasping behaviour in strepsirrhines. *Scientific Reports* **6:** 37729.

Pennell MW, **Eastman JM**, **Slater GJ**, **Brown JW**, **Uyeda JC**, **FitzJohn RG**, **Alfaro ME**, **Harmon LJ. 2014.** geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* **30:** 2216–2218.

Powell PL, **Roy RR**, **Kanim P**, **Bello MA**, **Edgerton VR. 1984.** Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs. *Journal of Applied Physiology* **57:** 1715–1721.

R Development Core Team. **2017.** *R: A language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing.

Reighard J, **Jennings HS. 1902.** *Anatomy of the cat*. New York: Henry Holt and Company.

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

Rosin S, **Nyakatura JA. 2017.** Hind limb extensor muscle architecture reflects locomotor specialisations of a jumping and a striding quadrupedal caviomorph rodent. *Zoomorphology* **136:** 267–277.

Royer-Carenzi M, **Pontarotti P**, **Didier G. 2013.** Choosing the best ancestral character state reconstruction method. *Mathematical Biosciences* **242:** 95–109.

Rupert JE, **Rose JA**, **Organ JM**, **Butcher MT. 2015.** Forelimb muscle architecture and myosin isoform composition in the groundhog (*Marmota monax*). *The Journal of Experimental Biology* **218:** 194–205.

Russell AP, **Bryant HN. 2001.** Claw retraction and protraction in the Carnivora: the cheetah (*Acinonyx jubatus*) as an atypical felid. *Journal of Zoology* **254:** 67–76.

Sacks RD, **Roy RR. 1982.** Architecture of the hind limb muscles of cats: functional significance. *Journal of Morphology* **173:** 185–195.

Salesa MJ, **Anton M**, **Peigne S**, **Morales J. 2006.** Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. *Proceedings of the National Academy of Sciences USA* **103:** 379–382.

Sargis EJ. 2001. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). *Journal of Zoology* **253:** 485–490.

Schneider CA, **Rasband WS**, **Eliceiri KW. 2012.** NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* **9:** 671–675.

Scott SH, **Winter DA. 1991.** A comparison of three muscle pennation assumptions and their effect on isometric and isotonic force. *Journal of Biomechanics* **24:** 163–167.

Sidlauskas B. 2008. Continuous and arrested morphological diversification in sister clades of characiform fishes: a phylomorphospace approach. *Evolution* **62:** 3135–3156.

Sillero-Zubiri C, **Ginsberg JR**, **Macdonald DW. 2004.** *Canids: foxes, wolves, jackals, and dogs. Status Survey and Conservation Action Plan*. Gland: ICUN International Union for Conservation of Nature and Natural Resources.

Smith JM, **Savage RJG. 1955.** Some locomotory adaptations in mammals. *Zoological Journal of the Linnean Society* **42:** 603–622.

Sopher RS, **Amis AA**, **Davies DC**, **Jeffers JR. 2017.** The influence of muscle pennation angle and cross-sectional area on contact forces in the ankle joint. *The Journal of Strain Analysis for Engineering Design* **52:** 12–23.

Spaulding M, **Flynn JJ. 2009.** Anatomy of the postcranial skeleton of "*Miacis*" *uintensis* (Mammalia: Carnivoramorpha). *Journal of Vertebrate Paleontology* **29:** 1212–1223.

Spoor CF, **Badoux DM. 1986.** Descriptive and functional morphology of the neck and forelimb of the striped hyena (*Hyaena hyaena*, L. 1758). *Anatomischer Anzeiger* **161:** 375–387.

Steel M, **Penny D. 2000.** Parsimony, likelihood, and the role of models in molecular phylogenetics. *Molecular Biology and Evolution* **17:** 839–850.

Sustaita D. 2008. Musculoskeletal underpinnings to differences in killing behavior between North American accipiters (Falconiformes: Accipitridae) and falcons (Falconidae). *Journal of Morphology* **269:** 283–301.

Sustaita D, **Pouydebat E**, **Manzano A**, **Abdala V**, **Hertel F**, **Herrel A. 2013.** Getting a grip on tetrapod grasping: form, function, and evolution. *Biological Reviews of the Cambridge Philosophical Society* **88:** 380–405.

Swofford DL, **Maddison WP. 1987.** Reonstructing ancestral character states using Wagner parsimony. *Mathematical Biosciences* **87:** 199–229.

Tarquini J, **Toledo N**, **Morgan CC**, **Soibelzon LH. 2017.** The forelimb of †*Cyonasua* sp. (Procyonidae, Carnivora): ecomorphological interpretation in the context of carnivorans. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **106:** 325–335.

Taverne M, **Fabre A-C**, **Herbin M**, **Herrel A**, **Peigné S**, **Lacroux C**, **Lowie A**, **Pagès F**, **Theil J-C**, **Böhmer C. 2018.** Convergence in the functional properties of forelimb muscles in carnivorans: adaptations to an arboreal lifestyle? *Biological Journal of the Linnean Society* **125:** 250–263.

Teasdall RD, **Magladery JW. 1974.** Brachioradialis reflex and contraction of forearm flexors. An electromyographic study. *Archives of Neurology* **30:** 94–95.

Thornton PC, **Wright PA**, **Sacra PJ**, **Goodier TE. 1979.** The ferret, *Mustela putorius furo*, as a new species in toxicology. *Laboratory Animals* **13:** 119–124.

Tokuda K, **Lee B**, **Shiihara Y**, **Takahashi K**, **Wada N**, **Shirakura K**, **Watanabe H. 2016.** Muscle activation patterns in acceleration-based phases during reach-to-grasp movement. *Journal of Physical Therapy Science* **28:** 3105–3111.

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

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

Viranta S, **Lommi H**, **Holmala K**, **Laakkonen J. 2016.** Musculoskeletal anatomy of the Eurasian lynx, *Lynx lynx* (Carnivora: Felidae) forelimb: adaptations to capture large prey? *Journal of Morphology* **277:** 753–765.

Wereszczuk A, **Zalewski A. 2015.** Spatial niche segregation of sympatric stone marten and pine marten–avoidance of competition or selection of optimal habitat? *PLoS One* **10:** e0139852.

Whishaw IQ, **Faraji J**, **Kuntz JR**, **Mirza Agha B**, **Metz GAS**, **Mohajerani MH. 2017.** The syntactic organization of pasta-eating and the structure of reach movements in the head-fixed mouse. *Scientific Reports* **7:** 10987.

Williams SB, **Wilson AM**, **Daynes J**, **Peckham K**, **Payne RC. 2008.** Functional anatomy and muscle moment arms of the thoracic limb of an elite sprinting athlete: the racing greyhound (*Canis familiaris*). *Journal of Anatomy* **213:** 373–382.

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

World Association of Veterinary Anatomists. **International Committee on Veterinary Anatomical Nomenclature**. **2012.** *Nomina anatomica veterinaria.* Vienna: International Committee on Veterinary Anatomical Nomenclature.