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Convergence in the functional properties of forelimb muscles in carnivorans: adaptations to an arboreal lifestyle?

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The arboreal environment is complex and irregular and imposes significant constraints on the locomotor ability of vertebrates, resulting in morphological adaptations. Carnivorans are of particular interest because they radiated several times independently into the arboreal milieu, leading to convergence in long bone anatomy. We investigated whether the forelimb muscles show differences in arboreal vs. terrestrial species and tested for convergence in muscle architecture. To do so, we studied the forelimb muscles in 17 species of carnivorans with different locomotor modes (arboreal and terrestrial). Our results showed that the forelimb musculature evolved in a convergent manner in arboreal species, resulting in more forceful and heavier wrist rotators and elbow flexors, even when accounting for phylogeny. This suggests that selective forces imposed by the environment drive the evolution of the muscular system towards a convergent phenotype that provides a functional advantage for locomotion in the complex three-dimensional arboreal habitat.

ADDITIONAL KEYWORDS: arboreality – climbing – evolution – habitat – locomotion – mammals – musculature.

INTRODUCTION

The arboreal habitat is complex and discontinuous. Consequently, it constrains the movements of an organism and impacts its predation strategies and social interactions. Vertebrates have adapted to the constraints imposed by this habitat and show specializations allowing them to exploit this environment (Badoux *et al.*, 1974; Astley & Jayne, 2007; Manzano *et al.*, 2008; Schmidt & Fischer, 2011; Fabre *et al.*, 2015a, 2017). Locomotion is a major challenge, because the three-dimensional nature of the arboreal habitat forces organisms to move on unstable substrates of variable size and orientation (Cartmill, 1985), thus imposing very different functional constraints compared with a terrestrial habitat, where the locomotor environment is relatively homogeneous (Grand, 1990). Specifically, arboreal animals need to climb, maintain balance on narrow substrates, and reach across discontinuities.

Locomotion is a trait that can be considered to be under strong selection given its importance in prey capture and foraging, social interactions and predator escape (Marchisin & Anderson, 1978). The functional constraints associated with locomotion in an arboreal habitat can lead to morphological adaptations. This has been demonstrated in many taxa, including squamates (e.g. Sinervo & Losos, 1991; Lowie *et al.*, 2018), frogs (e.g. Manzano *et al.*, 2008) and mammals (e.g. Anapol & Barry, 1996; Ercoli *et al.*, 2012; Fabre *et al.*, 2015a, 2017; Ercoli & Youlatos, 2016; Böhmer *et al.*, 2018). Many species of mammals have adapted to an arboreal habitat, and several independent origins of arboreality can be observed among marsupials, rodents, primates and carnivores (Dublin, 1903). Most attention has been paid to postcranial osteological features related to primate

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arboreal behaviour (Meldrum *et al.*, 1997; Runestad, 1997), often in an attempt to make better inferences of locomotion in fossils. More recently, several papers have been devoted to the study of the muscular anatomy of arboreal primates (Marchi *et al.*, 2018) and carnivorans (Leischner *et al.*, 2018; Morales *et al.*, 2018).

Carnivora are of particular interest, because an arboreal lifestyle has originated several times independently in this order (Taylor, 1974; McClearn, 1992; Fabre *et al.*, 2013, 2015a). It has previously been shown that the forelimb of carnivorans is a good indicator of locomotor mode (Iwaniuk *et al.*, 1999; Fabre *et al.*, 2013, 2015a, b) and other behaviours, such as prey capture and feeding. Although several authors have investigated differences in limb bone morphology (e.g. Iwaniuk *et al.*, 1999; Samuels *et al.*, 2013; Martín-Serra *et al.*, 2014; Fabre *et al.*, 2015b) and the kinematics of locomotion in arboreal species (Larson *et al.*, 2000; Schmitt & Lemelin, 2002; Gálvez-López *et al.*, 2011), relatively few studies have focused on the forelimb musculature (but see McClearn, 1985; Antón *et al.*, 2006; Hudson *et al.*, 2011; Viranta *et al.*, 2016). Yet, the forelimb muscles are crucial in allowing animals to move in an arboreal habitat, because they provide a major component of the propulsive forces during climbing (Zaaf *et al.*, 1999; Autumn *et al.*, 2006; Hanna *et al.*, 2017). Moreover, arboreal species need to adduct and rotate the forelimbs forcefully to maintain balance (e.g. Argot, 2001; Preuschoft, 2002; Larson & Stern, 2006), but also need limbs excursive enough to reach across discontinuities (Hildebrand & Goslow, 2001).

Here, we investigate the adaptations of the forelimb muscles to the functional constraints imposed by arboreal locomotion in carnivorans. To do so, we make a quantitative comparison of the forelimb musculature in arboreal and terrestrial species. Previous studies have mostly focused on a single species (e.g. Spoor & Badoux, 1986; Hudson *et al.*, 2011; Ercoli *et al.*, 2015; Viranta *et al.*, 2016) or a limited number of species (e.g. Julik *et al.*, 2012). Although some comparative studies have been conducted, they have typically focused on a single family (e.g. Procyonidae by McClearn, 1985; Felidae by Cuff *et al.*, 2016). Thus, it remains unclear whether general trends exist in the adaptation of the muscular system to an arboreal locomotor mode in the Carnivora.

We predict that arboreal species will have larger flexor muscles and humeral retractors to assist them during climbing on vertical substrates, such as tree trunks (Youlatos, 2000). We also predict longer muscular fibres, allowing for an increase in movement amplitude, which is important during gap bridging (Hildebrand & Goslow, 2001; Foster & Higham, 2012), and more robust adductors to provide stability when walking on narrow branches (Anzai *et al.*, 2014) in a crouched posture (Schmidt & Fischer, 2000). Finally, we predict that the wrist flexors and rotators will be better developed, because they allow wrist flexion and rotation, which is likely to be important during both climbing and locomotion on narrow substrates (e.g. Larson & Stern, 2006; Fabre *et al.*, 2015a).

MATERIAL AND METHODS

Specimens and dissections

In total, 32 limbs from 22 specimens were dissected (Supporting Information Table S1), representing 17 species of carnivorans (Fig. 1). The species were selected to obtain a broad phylogenetic distribution. Muscles were dissected from the right forelimb unless muscles were damaged, in which case the left limb was dissected. For some specimens, both limbs were dissected to evaluate intra-individual variability in muscle size and architecture. Most of the specimens were preserved in formaldehyde (4–10%) and stored in an aqueous solution of ethanol (70%). Owing to their body size, it was not feasible to fix the large specimens; consequently, they were dissected fresh. None of the dissected animals was damaged or in bad physical condition. Some cadavers were obtained from animal parks where the animals had lived in large outdoor enclosures (Supporting Information Table S1). No animal was killed for the present study.

Phylogeny

The phylogenetic framework used in the present study was based on the time-calibrated molecular phylogeny presented by Nyakatura & Bininda-Emonds (2012). For all our comparative analyses, we pruned the phylogeny to include only species for which muscle data were available (Fig. 1).

Locomotor classification

All species were classified as either arboreal or terrestrial based on literature data as listed in Table 1.

Dissection of the forelimb muscles

After removal of the skin and the fasciae surrounding the muscles of the shoulder and the limb, each muscle was identified and detached from its origin to its insertion. The qualitative orientation of the muscle fibres and the origin and insertion sites of the muscles were recorded, but not included in the analyses because data were lacking for some species. Forty-eight muscles were extracted from each limb (the number differs in the case of fused muscles), including the extrinsic and intrinsic muscles of the forelimb. We used the muscle terminology proposed by Reighard & Jennings (1901) (Supporting Information Table S2). The muscles were classified into 13 functional groups based on Dyce *et al.* (2009) and personal observations by C.B., A.H., and M.T. (Table 2). In

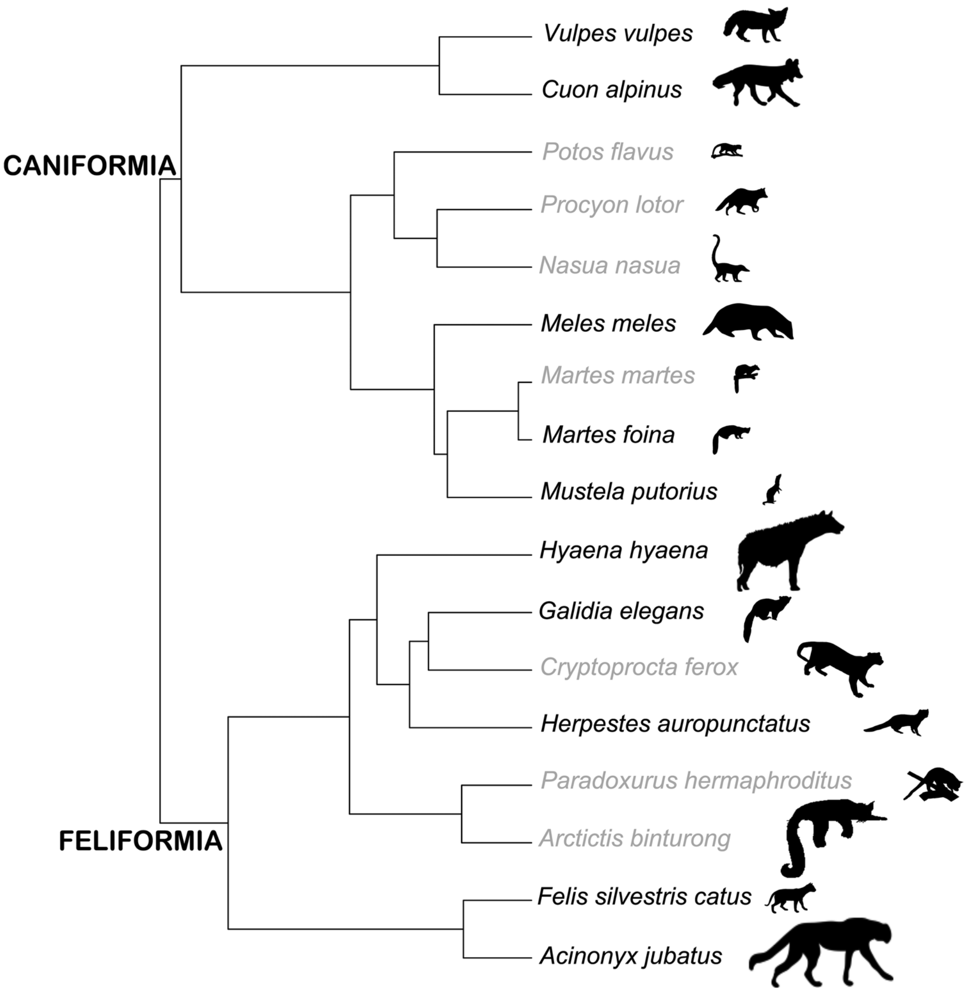

Figure 1. Phylogeny from Nyakatura & Bininda-Emonds (2012) pruned down to include only the species included in our analyses. Black text represents terrestrial species and grey text arboreal species.

the event that a muscle was involved in several movements, it was assigned to all the corresponding functional groups (Fig. 2).

Muscle measurements

Each muscle of the preserved specimens was stored in an aqueous ethanol solution (70°) after being removed. Muscles were weighed using a Mettler digital scale (± 0.1 mg) for the smaller muscles (≤ 20 g) or an HK digital scale (± 1 g) for the bigger muscles. For the large fresh specimens, the muscles were weighed immediately after being removed. The muscle volume was computed using a muscle density of 1.06 g cm^{-3} (Mendez & Keys, 1960). Although some authors previously have highlighted that tissue preservation in formalin may lead to a decrease in muscle weight (Kikuchi & Kuraoka, 2014), no correction for preservation was applied to our data because a regression of total muscle mass on body mass did not reveal any outliers and showed a very tight relationship between the two variables ($R = 0.964$). The mean length of each muscle was calculated based on the maximal and minimal length of the muscle measured using a graduated ruler (± 1 mm). No correction subsequent to the measurement of fixed muscle length was used (see Cutts, 1988).

Next, muscles were immersed in an aqueous solution of nitric acid (30%) for 15–20 h in order to digest the connective tissue and to separate the fibres (Loeb & Gans, 1986). Approximately ten haphazardly selected fibres were then isolated and photographed using a Panasonic Lumix camera (DMC-MZ200). A scale bar was included in each photograph. Fibre lengths were subsequently measured using ImageJ (v. 1.48; National Institutes of Health, USA).

For large specimens dissected fresh, fibre length was measured directly on ten haphazardly selected fibre bundles using a graduated ruler (± 1 mm). The muscle cross-sectional area (CSA) was calculated as the muscle

Table 1. Attribution of the species to a locomotor category

Species	Locomotor category	References
Acinonyx jubatus	t	Van Valkenburgh (1985)
Arctictis binturong	a	Wemmer & Murtaugh (1981)
Cryptoprocta ferox	a	Iwaniuk *et al.* (2000)
Cuon alpinus	t	Van Valkenburgh (1985)
Felis silvestris catus	t	Iwaniuk *et al.* (2000)
Galidia elegans	t	Galvez-Lopez (2014)
Herpestes auropunctatus	t	Taylor (1974)
Hyaena hyaena	t	Van Valkenburgh (1985)
Martes foina	t	Fabre *et al.* (2015a)
Martes martes	a	Iwaniuk *et al.* (2000)
Meles meles	t	Fabre *et al.* (2015a)
Mustela putorius	t	Fabre *et al.* (2015a)
Nasua nasua	a	McClearn (1990)
Paradoxurus hermaphroditus	a	Kirk *et al.* (2008)
Potos flavus	a	McClearn (1990)
Procyon lotor	a	McClearn (1990, 1992)
Vulpes vulpes	t	Ables (1975)

Abbreviations: a, arboreal; t, terrestrial.

volume divided by its length; the muscle physiological cross-sectional area (PCSA; an estimator of the force-producing capacity of a muscle) was calculated as the muscle volume divided by the mean fibre length. No correction for pennation angle was included in the analysis because pennation angles are typically small in the forelimb muscles, consequently having only a minor impact on the overall PCSA (Hartstone-Rose *et al.*, 2012).

PRINCIPAL COMPONENTS ANALYSES

The four measures of interest (muscle volume, CSA, PCSA and fibre length) were $\log_{10}$ transformed in order to render them normal and homoscedastic as required for parametric analyses. Given that the animals differed in size, the effect of size was removed from the data by regressing all variables against the weight of the forelimb, which was calculated as the sum of all muscle weights. The resulting residuals from the four variables helped us to build four datasets that were used in further statistical analyses Table S4a–d.

Principal components analyses (PCAs) were performed on each dataset to reduce its dimensionality. The phylogeny was projected into the morphospace constructed based on the first two principal component (PC) axes using the 'phylomorphospace' function of the 'phytools' library (Revell, 2012) in R (R Core Team, 2014). We next explored how the variability in the dataset was influenced by phylogeny by estimating the multivariate *K* statistic (Adams, 2014) using the 'physignal' function

Table 2. Attribution of the muscles of the forelimb functional groups

Function	Muscles
Humeral abductor	Clavotrapezius, teres minor, acromiodeltoideus, spinodeltoideus, infraspinatus
Humeral adductor	Articularis humeri, subscapularis, pectoantebrachialis, pectoralis major, pectoralis minor, xiphihumeralis
Humeral protractor	Clavotrapezius, cleidomastoideus, clavobrachialis, biceps brachii, supraspinatus
Humeral retractor	Latissimus dorsi, epitrochlearis, triceps laterale, triceps longum, pectoralis minor, teres major
Scapular abductor	Acromiotrapezius, spinotrapezius
Scapular adductor	Rhomboideus capitis, rhomboideus profundus, rhomboideus cervicis, rhomboideus thoracis
Scapular protractor	Omotransversarius, rhomboideus capitis, rhomboideus profundus, rhomboideus cervicis, supraspinatus
Scapular retractor	Spinotrapezius, rhomboideus thoracis
Elbow extensor	Triceps mediale short portion, triceps mediale long and intermediate portions, epitrochlearis, triceps laterale, triceps longum, anconeus, triceps accessorium, flexor carpi ulnaris ulnar head, humeral head, palmaris longus, flexor carpi radialis, flexor digitorum profundus
Elbow flexor	Extensor carpi ulnaris, extensor digitorum lateralis, extensor digitorum communis, extensor carpi radialis longus, extensor carpi radialis brevis, biceps brachii, brachialis
Wrist extensor	Extensor carpi ulnaris, extensor indicis, extensor pollicis, extensor digitorum lateralis, extensor digitorum communis, extensor carpi radialis longus, extensor carpi radialis brevis
Wrist flexor	Palmaris longus, flexor carpi ulnaris ulnar head, flexor carpi ulnaris humeral head, flexor carpi radialis, flexor digitorum profundus
Wrist rotator	Brachioradialis, pronator teres, pronator quadratus, supinator

Note that the wrist rotators include all the muscles that allow pronation–supination movements by rotating the forearm relative to the elbow joint.

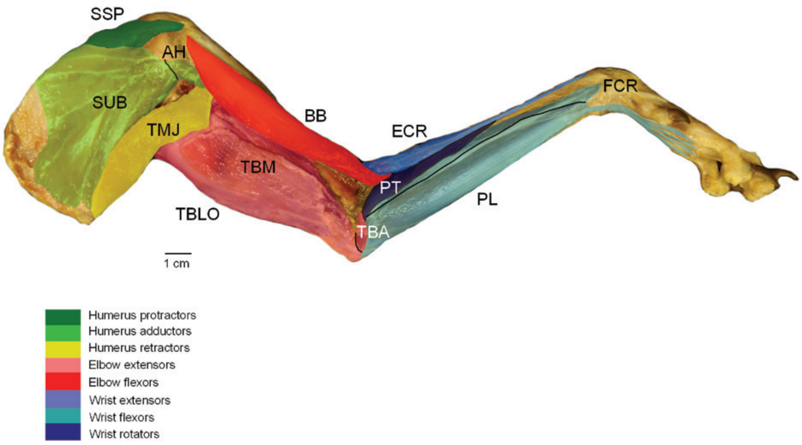

Figure 2. Medial view of the intrinsic muscles of the right forelimb of a red fox (*Vulpes vulpes*), with each muscle assigned to a functional group. Abbreviations: AH, articularis humeri; BB, biceps brachii; ECR, extensor carpi radialis; FCR, flexor carpi radialis; PL, palmaris longus; PT, pronator teres; SSP, supraspinatus; SUB, subscapularis; TBLO, triceps brachii longum; TBM, triceps brachii mediale; TMJ, teres major.

of the 'geomorph' library (Adams *et al.*, 2017) in R. Next, multivariate analyses of the variance (MANOVAs) were run on the PCs of the PCA to test for differences in muscle properties between terrestrial and arboreal species. Phylogenetic MANOVAs ('aov.phylo' using the 'phytools' library; see Garland *et al.*, 1993) coupled to univariate ANOVAs were conducted because species are not independent data points, and similarity between species may be caused by phylogenetic history.

ANALYSES OF CONVERGENCE

We used the '*convevol*' R package (Stayton, 2017) to test for convergence. This provides four distance-based measures (C_1–C_4) that compare the way two tip taxas resemble each other and the way their most phenotypically divergent ancestors differ from one another (Stayton, 2015). The significance of these parameters was tested using 1000 simulations (Stayton, 2017).

RESULTS

PHYLOGENETIC SIGNAL

Muscle mass data showed a moderately high phylogenetic signal ($K_{\text{mult}} = 0.553$; $P = 0.002$), as did muscle cross-sectional area ($K_{\text{mult}} = 0.545$; $P = 0.002$). Physiological cross-sectional area showed a lower, yet significant phylogenetic signal ($K_{\text{mult}} = 0.489$; $P = 0.033$), and fibre length data showed no phylogenetic signal ($K_{\text{mult}} = 0.442$; $P = 0.096$).

DISTRIBUTION OF THE SPECIES IN THE PHYLOMORPHOSPACE

The four first axes of the PCA computed on the muscle volume explained 86.67% of the total variance (PC1 = 45.27%, PC2 = 20.03%, PC3 = 13.23% and PC4 = 8.13%). Arboreal and terrestrial species can be distinguished along the first axis (Supporting Information Fig. S1). The wrist rotators and the wrist flexors loaded strongly on the negative side of this axis, suggesting that arboreal species have heavier wrist rotators and flexors. The humeral adductors and the scapular adductors and protractors loaded positively on the first axis, implying that terrestrial species have heavier humeral adductors and scapular adductors and protractors.

The PCA computed on the CSA dataset retained four axes explaining 86.99% of the total variance (PC1 = 34.81%, PC2 = 28.75%, PC3 = 15.08% and PC4 = 8.35%). The arboreal species are well separated from the terrestrial ones along the first axis (Fig. 3). The wrist rotators, the wrist flexors and the elbow flexors loaded strongly on the positive side of this axis, suggesting that arboreal species have a greater CSA for the wrist flexors and rotators and for the elbow flexors (Supporting Information Table S3). Scapular adductors and protractors load strongly on the negative side of this axis, suggesting that terrestrial species have a greater CSA of the scapular adductors and protractors.

The PCA computed on the PCSA dataset retained four axes explaining 88.36% of the total variance (PC1 = 62.42%, PC2 = 13.49%, PC3 = 8.45% and PC4 = 4.58%). Graphically, the arboreal species can be distinguished from the terrestrial ones by considering both first and second axes (Supporting Information Fig. S1). The position of the arboreal species in the morphospace is determined by the positive values of PC1 and the negative values of PC2. This position in the morphospace was associated with strong scapular retractors, humeral retractors and wrist muscles.

Finally, the PCA computed on the fibre length dataset retained three axes explaining 86.04% of the

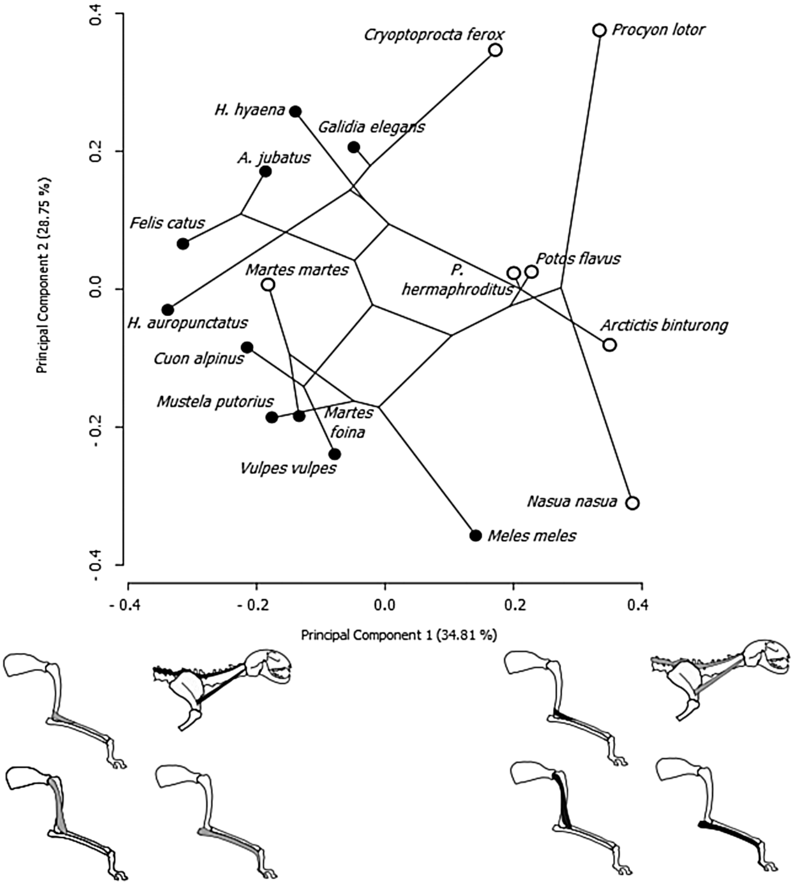

Figure 3. Projection of the phylogeny into the morphospace obtained by the computation of a principal components analysis on the cross-sectional area (CSA) dataset. Principal components 1 and 2 are illustrated. Open symbols represent arboreal species and filled symbols terrestrial species. The illustrations show which functional groups drive the variability along the axes. Muscles represented in light grey and black correspond respectively to lower and higher values of CSA for these functional groups.

overall variance (PC1 = 47.98%, PC2 = 25.89% and PC3 = 12.17%). However, none of these axes indicated differences between arboreal and terrestrial species, because all studied individuals are distributed over the morphospace without revealing any significant pattern (Supporting Information Fig. S1).

ANALYSES OF VARIANCE

The multivariate analyses of variance performed on the PCs of the PCA showed that arboreal and terrestrial species differ significantly in their CSA and muscle volume even when accounting for phylogeny. No differences in PCSA and fibre length were observed between the two locomotor groups, however (Table 3).

The univariate ANOVAs performed on each functional muscle group show differences between arboreal and terrestrial species even when phylogeny is taken into account (Table 4). Arboreal species have the greatest values for the CSA of the wrist rotators ($F_{1,16} = 16.57$; $P = 0.001$; $P_{\text{phy}} = 0.004$) and the elbow flexors ($F_{1,16} = 6.362$; $P = 0.023$; $P_{\text{phy}} = 0.032$), whereas terrestrial species have the highest values for scapular protractors ($F_{1,16} = 19.27$; $P < 0.001$; $P_{\text{phy}} < 0.001$) and humeral retractors ($F_{1,16} = 6.09$; $P = 0.026$; $P_{\text{phy}} = 0.036$; Table 4). Arboreal species also have heavier elbow flexors ($F_{1,16} = 10.08$; $P = 0.006$; $P_{\text{phy}} = 0.012$) and wrist rotators ($F_{1,16} = 18.69$; $P < 0.001$; $P_{phy} = 0.001$), whereas terrestrial species have heavier scapular protractors ($F_{1,16} = 24.83$; $P < 0.001$; $P_{\text{phy}} = 0.001$), humeral retractors ($F_{1,16} = 11.54$; $P = 0.004$; $P_{\text{phy}} = 0.008$) and scapular adductors ($F_{1,16} = 10.09$; $P = 0.006$; $P_{\text{phy}} = 0.009$).

ANALYSES OF CONVERGENCE

Analyses of convergence showed convergence for both terrestrial and arboreal species (Table 5). Physiological cross-sectional area is highly convergent in arboreal species, where 29% of the maximal phenotypic distance between the ancestors has been closed by subsequent evolution. The convergence observed here explains 13% of the total phenotypic evolution of this lineage.

DISCUSSION

The phylogenetic signal is significant for most traits except fibre length. Based on a purely Brownian model of evolution, we found that the traits of interest vary more than predicted. Thus, animals that are more closely related are more similar in terms of their muscular architecture.

DISTRIBUTION OF THE SPECIES IN THE MYOLOGICAL SPACE

The PCAs performed on the different functional traits of the forelimb muscles suggested that arboreal species have more strongly developed wrist rotators than terrestrial species. Pronation–supination is the ability to rotate the wrist, allowing an animal to adapt the orientation of the hand and to grasp (Gray *et al.*, 1997; Iwaniuk & Whishaw, 1999; Argot, 2001; Antón *et al.*, 2006). This is likely to be important for arboreal species, because it allows them to adjust hand position to the diversity of substrate sizes and orientations encountered in this environment (Haines, 1958; Hutson, 2010). In contrast, terrestrial species, such as the cheetah (*Acinonyx jubatus* Schreber, 1775) and the red fox (*Vulpes vulpes* Linnaeus, 1758), seem to have less developed wrist rotators. This reduced development of the wrist rotators could be associated with the presence of an interosseous membrane between the radius and ulna that strongly constrains the wrist joint, probably increasing the stability of the forearm and the hand during running (Andersson, 2003; Figueirido *et al.*, 2015; Hudson *et al.*, 2011). Osteological data can also provide insights into this pronation–supination ability, because gracile forearm bones with wide articular surfaces that allow for a greater range of movements were observed in arboreal species of musteloids (Fabre *et al.*, 2017).

We also observed that arboreal species tend to have stronger wrist flexors. These muscles are responsible for wrist and finger flexion, and thus, possibly allow a better grip on the substrate (Preuschoft, 2002; Lammers & Zurcher, 2011). However, during climbing, arboreal species vary in the use of their forelimb. Some grasp branches (such as the kinkajou, *Potos flavus* Schreber, 1774; McClearn, 1992) whereas others use their claws to hook onto the substrate. The ability to grasp has been suggested to aid an animal in gaining stability and to reduce its mediolateral balancing movements (Preuschoft, 2002; Lammers & Biknevicius, 2004; Schmidt, 2008). The position of the badger (*Meles meles* Linnaeus, 1758) close to arboreal species in the morphospace is attributable to its strong elbow and wrist flexors and wrist rotators. The active digging behaviour of the European badger could explain the observed pattern (Moore *et al.*, 2013), with the flexors allowing it to scratch the ground or to pull the soil away from the burrow, and the rotators to adapt the orientation of the hand during digging.

Table 3. Results of the multivariate analyses of variance performed on the four datasets

Dataset	Wilk's λ	$F_{4,12}$	P	P_{Phy}
CSA	0.32	6.50	0.006*	0.006*
Mass	0.25	9.09	0.001*	0.003*
PCSA	0.50	2.97	0.06	0.11
Fibre length	0.78	1.22	0.65	0.73

Abbreviations: CSA, physiological cross-sectional area; PCSA, physiological cross-sectional area; PPhy, *P*-value for phylogenetic test. *Significant result.

Table 4. Results of the univariate ANOVAs performed on the four datasets and for each functional group

Dataset	Statistics	Hab	Had	Hpro	Hret	Sab	Sad	Spro	Sret	Eext	Eflex	Wext	Wflex	Wrot
CSA	Fnum/denum	0.670	0.766	0.767	6.092	1.138	4.275	19.27	0.748	0.014	6.362	2.544	1.767	16.57
	P	0.426	0.396	0.395	0.026*	0.303	0.056	< 0.001*	0.401	0.907	0.023*	0.132	0.204	0.001*
	P_{phy}	0.474	0.437	0.451	0.036*	0.356	0.083	< 0.001*	0.464	0.915	0.032*	0.157	0.260	0.004*
Mass	Fnum/denum	0.133	1.549	1.656	11.54	0.380	10.09	24.83	0.584	0.359	10.08	2.356	2.979	18.69
	P	0.721	0.232	0.218	0.004*	0.547	0.006*	< 0.001*	0.456	0.558	0.006*	0.146	0.105	< 0.001*
	P_{phy}	0.768	0.295	0.236	0.008*	0.604	0.009*	0.001*	0.505	0.602	0.012*	0.210	0.137	0.001*
PCSA	Fnum/denum	0.551	1.033	0.109	0.757	0.216	1.807	1.785	0.494	1.080	1.739	0.006	1.223	5.840
	P	0.470	0.326	0.746	0.398	0.649	0.199	0.201	0.493	0.315	0.207	0.939	0.286	0.029*
	P_{phy}	0.504	0.369	0.767	0.417	0.667	0.245	0.239	0.539	0.394	0.258	0.959	0.335	0.045*
Fibre length	Fnum/denum	0.278	0.185	0.003	0.169	2.893	0.403	0.293	1.501	0.465	0.194	0.249	0.002	1.439
	P	0.606	0.673	0.858	0.687	0.110	0.535	0.596	0.239	0.506	0.666	0.625	0.965	0.249
	P_{phy}	0.638	0.697	0.863	0.696	0.130	0.541	0.634	0.280	0.545	0.692	0.667	0.962	0.297

Abbreviations: CSA, physiological cross-sectional area; Eext, elbow extensors; Eflex, elbow flexors; Hab, humeral abductors; Had, humeral adductors; Hpro, humeral protractors; Hret, humeral retractors; PCSA, physiological cross-sectional area; PPhy, *P*-value for phylogenetic test; Sab, scapular abductors; Sad, scapular adductors; Spro, scapular protractors; Sret, scapular retractors; Wext, wrist extensors; Wflex, wrist flexors; Wrot, wrist rotators. *Significant differences between arboreal and terrestrial species.

Table 5. Results of the convergence tests

	Muscle volume		CSA		Fibre length		PCSA	
		P		*P*		*P*		*P*
Terrestrial								
C_1	0.23	0.03*	0.17	0.01*	0.15	0.12	0.16	0.07
C_2	0.07	0.06	0.44	0.04*	0.06	0.13	0.07	0.03*
C_3	0.12	0.07	0.08	0.09	0.07	0.31	0.08	0.08
C_4	0.00	0.22	0.00	0.09	0.00	0.71	0.00	0.13
Arboreal								
C_1	0.25	0.04*	0.10	0.47	0.11	0.46	0.29	0.00*
C_2	0.10	0.02*	0.03	0.31	0.04	0.35	0.09	0.01*
C_3	0.13	0.09	0.05	0.54	0.05	0.56	0.13	0.01*
C_4	0.00	0.52	0.00	0.56	0.00	0.53	0.00	0.28

The four distance-based parameters are for each of the four datasets. Abbreviations: CSA, physiological cross-sectional area; PCSA, physiological cross-sectional area. *Significant convergence.

QUANTITATIVE ANALYSES

The ANOVAs corroborate the qualitative observations of the myological space, suggesting that some functional groups discriminate arboreal species from terrestrial ones. Although they confirm that arboreal species have greater values of CSA for the wrist rotators, this is not the case for the CSA of the wrist flexors nor for the CSA of the scapular retractors. These analyses reveal that the arboreal lifestyle is associated with better-developed elbow flexors, which is concordant with our predictions. Most importantly, the greater force-producing capacity of the wrist rotators in arboreal species, confirmed here, probably helps animals to overcome the mediolateral oscillations that are associated with moving on narrow substrates (Schmitt, 2003; Lammers & Biknevicius, 2004; Schmidt & Fischer, 2010). Contrary to terrestrial species, joint surfaces between the radius, the ulna and the humerus in arboreal animals are broad and likely to favour a greater pronation–supination ability (Fabre *et al.*, 2013, 2015a). Moreover, four terrestrial species lacked a brachioradialis (the largest supinator muscle of the forelimb; see Junior *et al.*, 2015): the fox, the cheetah, the dhole (*Cuon alpinus* Pallas, 1811) and the hyena (*Hyaena hyaena* Linnaeus, 1758). These are also the most cursorial species in our dataset, and all have lost the ability to supinate their hands fully (Iwaniuk *et al.*, 1999; Polly, 2007; Fabre *et al.*, 2014). Although the cheetah is a very cursorial species, showing poor pronation–supination abilities compared with the other felids (Andersson, 2004), this movement remains essential to the cheetah for prey capture (Gorman & Londei, 2000; Russel & Bryant, 2001). Surprisingly, we did not find a brachioradialis muscle in the cheetah, whereas Hudson *et al.* (2011) identified this muscle in all eight captive cheetah specimens that they dissected. This suggests an unexpected variability in the occurrence of the brachioradialis. The absence of a brachioradialis in these four species may then help to explain the difference in total CSA between the two lifestyles when comparing the wrist rotators. Moreover, our results confirm the suggestion of Argot (2001) and Fabre *et al.* (2015a), who showed that arboreal species possess a larger lateral condylar crest on the humerus and predicted that this was associated with a greater development of the muscles.

Interestingly, it also appears that a terrestrial lifestyle is accompanied by an increase in the volume and CSA of the scapular protractors. These muscles are involved in the translation of the scapula relative to the trunk and may facilitate the forward projection of the forelimb, thus contributing to an increase in stride length. Indeed, the scapula has been shown to be the most propulsive segment of the forelimb (Kuznetsov, 1985; Fischer *et al.*, 2002). Most terrestrial quadrupeds, when running, increase the stride length to accelerate rather than increasing the stride frequency (Pennycuick, 1975; Heglund & Taylor, 1988; Hutchinson *et al.*, 2006). Consequently, having better-developed scapular protractors would be advantageous for terrestrial cursorial species. Several arboreal animals have been suggested preferentially to increase stride frequency when increasing speed (Zaaf *et al.*, 2001; Karantanis *et al.*, 2017). An increase in frequency might help to reduce vertical oscillations of the centre of mass, thus preventing the support from swinging, and could thus be a good strategy for arboreal animals (Delciellos & Vieira, 2007; Gálvez-López *et al.*, 2011). Nevertheless, this remains to be tested for arboreal carnivorans.

Our prediction that longer fibres would be observed in the muscles of the forelimb in arboreal carnivorans was not confirmed by our results. Thus, fibre length appears to be a more evolutionarily constrained parameter, at least across the species included in our dataset. A recent study investigating differences between two sympatric marten species (Böhmer *et al.*, 2018), *Martes martes* (Linnaeus, 1758) and *Martes foina* (Erxleben, 1777), suggested that different locomotor habits could be associated with a difference in fibre length. Longer fibres were detected for two biarticular muscles in the arboreal pine marten compared with the terrestrial stone marten. Our analyses did not reveal such differences. However, this could be the consequence of the attribution of the muscles to functional groups. Indeed, muscles spanning several joints may be subjected to different or even antagonistic functional demands. An alternative strategy for modulating the excursion angle is to vary the position of muscle insertions (McClearn, 1985). If so, selection may no longer act upon fibre length, thus possibly explaining the lack of a significant pattern in our analyses. Additionally, the absence of a signal in fibre length might also originate from differences in the muscle architecture and, specifically, the degree of pennation, which was not quantified in our study. In contrast, fibre length was demonstrated to be correlated with diet and the size of items ingested in a study on primates (Taylor & Vinyard, 2004; Perry *et al.*, 2011). Although fibre length is a crucial variable in mastication in setting the upper limit to contractile velocity, it also plays an important role in jaw opening. Indeed, muscles with shorter fibres and a greater degree of pennantion may resist jaw opening and, as such, animals eating large food items can be expected to have longer muscle fibres (Herring & Herring, 1974; Dumont *et al.*, 2009; Perry *et al.*, 2011). Stretch constraints probably do not play an important role in locomotion and, as such, this might explain the observed difference between jaw and locomotor muscles. Future work should focus on the fibre length and on the complex three-dimensional orientation of muscles in order to unravel the variability of this trait within carnivorans and how it may be correlated with locomotor abilities and lifestyle.

CONVERGENT EVOLUTION OF THE FORELIMB MUSCULATURE

Our results on convergence clearly suggest that the musculature of the forelimb responds to the functional demands inherent to the locomotor environment of an animal. Adams (2014) argued that K-values less than one are likely to suggest convergence. The force-producing capacity, estimated by the PCSA, is under strong selection because it is directly related to the performance of the organism. Consequently, it is not surprising that arboreal and terrestrial species differ in this trait specifically. Convergence in function can, however, be achieved in different ways (many-to-one mapping of form to function; see Wainwright *et al.*, 2005): by varying muscle volume, fibre length, muscle physiology or muscle insertions.

Our results show that muscle volume is highly convergent, in contrast to fibre length. This suggests that selection on performance and, consequently, on muscle force primarily impacts muscle volume. Additionally, muscle volume (Lüthi *et al.*, 1986), fibre type (Hather *et al.*, 1991), fibre contractile properties (Trappe *et al.*, 2006) and fibre CSA (Widrick *et al.*, 2002) have all been demonstrated to be plastic and thus capable of changing in response to training or muscle disuse.

Nevertheless, despite this great plasticity of the muscular system (Byron *et al.*, 2011), our results show that interspecific differences attributable to the functional constraints imposed by the locomotor habitat are much greater than the intraspecific variability in muscular characteristics. It is, however, noteworthy that the present study includes specimens maintained in captivity, which could potentially influence the results if muscles were impacted by disuse. Given that the general anatomical trends highlighted here are probably not attributable to this type of plastic response, because cadavers were obtained from animal parks where animals had large enclosures that ensured normal locomotor behaviour, we assume that this bias is limited.

Numerous studies have highlighted the importance of convergence at different levels of organismal integration. Indeed, convergence can occur in behaviour (Johnson *et al.*, 2009), performance (Legreneur *et al.*, 2011) and morphology (Herrel *et al.*, 2008b; Botton-Divet *et al.*, 2017). As shown by our results, the arboreal habitat imposes strong functional constraints that drive the evolution of convergent phenotypes. This has previously been demonstrated for other taxa, including *Anolis* lizards of the Greater Antilles (Losos, 1992). These lizards independently evolved similar morphological traits, resulting in similar levels of performance in the same ecological context. Convergence is often strongest in environmental contexts where resources are limited (e.g. on islands; Cornette *et al.*, 2012; Sagonas *et al.*, 2014; Donihue *et al.*, 2016) or when the functional constraints imposed by the physical environment are strong (Herrel *et al.*, 2008a; Segall *et al.*, 2016). The fact that convergence in muscle architecture was observed in the present study suggests that the functional demands of the arboreal habitat are strong for medium-sized animals, such as carnivorans. The literature gives numerous examples of other traits that are convergent within Carnivora, such as bone morphology (in long bones; see Fabre *et al.*, 2013; Botton-Divet *et al.*, 2017), retraction of the digits and claws (Russel & Bryant, 2001), or skull morphology (Wroe & Milne, 2007; Goswami *et al.*, 2011; Meachen-Samuels, 2012), emphasizing the fact that convergent evolution is common and that habitat use is an important driver of anatomical and morphological diversity within carnivorans.

CONCLUSION

Our results highlight that the muscular system of carnivorans is profoundly impacted by the locomotor habitat. Specifically, we demonstrated convergence in muscle architecture in both arboreal and terrestrial species, with arboreal species showing better-developed wrist rotators and elbow flexors, and terrestrial species showing better-developed scapular protractors and humeral retractors. The present study shows that the locomotor environment imposes strong functional constraints that drive the evolution of functionally relevant muscle properties. Despite the plasticity of the muscular system, these constraints are great enough to drive convergence in muscle architecture. Future studies should investigate how these differences in muscle properties impact bone morphology, thus allowing better inferences on extinct taxa.

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SUPPORTING INFORMATION

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

Figure S1. Projection of the phylogeny into the morphospace obtained by the computation of a principal components analysis on each dataset. Principal components 1 and 2 are illustrated. Open symbols represent arboreal species and filled symbols terrestrial ones.
Table S1. List of the specimens included in the present study, and their origin.
Table S2. List of the different terminologies of the forelimb muscles.
Table S3. Loadings of the principal component analyses for the first six components.
TableS4a. Means of the raw values of the cross-sectional area (in square centimetres) for each functional group in the different species. Loco (locomotor category): a, arboreal; t, terrestrial. LW (limb weight) is given in grams.
Table S4b. Means of the raw values of the muscle volume (in cubic centimetres) for each functional group.
Table S4c. Means of the raw values of the fibre length (in centimetres) for each functional group.
Table S4d. Means of the raw values of the physiological cross-sectional area (in square centimetres) for each functional group.