

Does the Morphology of the Forelimb Flexor Muscles Differ Between Lizards Using Different Habitats?

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ABSTRACT

Lizards are an interesting group to study how habitat use impacts the morphology of the forelimb because they occupy a great diversity of ecological niches. In this study, we specifically investigated whether habitat use impacts the morphology of the forelimb flexor muscles in lizards. To do so, we performed dissections and quantified the physiological cross sectional area (PCSA), the fiber length, and the mass of four flexor muscles in 21 different species of lizards. Our results show that only the PCSA of the *m. flexor carpi radialis* is different among lizards with different ecologies (arboreal versus non-arboreal). This difference disappeared, however, when taking phylogeny into account. Arboreal species have a higher *m. flexor carpi radialis* cross sectional area likely allowing them to flex the wrist more forcefully which may allow them climb and hold on to branches better. In contrast, other muscles are not different between arboreal and non-arboreal species. Further studies focusing on additional anatomical features of the lizard forelimb as well as studies documenting how lizards use the arboreal niche are needed to fully understand how an arboreal life style may constrain limb morphology in lizards. *Anat Rec*, 301:424–433, 2018. © 2018 Wiley Periodicals, Inc.

Key words: adaptation; locomotion; ecomorphology; myology; functional morphology

INTRODUCTION

Adaptive divergence in morphology driven by natural selection is often illustrated by Darwin's finch beak morphology (Lack, 1947; Grant & Grant, 2006). However, not only the cranial system but also the locomotor system is subject to strong natural selection, thus driving variation in limb anatomy in relation to variation in habitat use (Losos, 1990a, 1990b; Losos et al., 1994; Payne et al., 2006; Williams et al., 2007; Abdala et al., 2008; Pinto et al., 2008; Tulli et al., 2012; Fabre et al., 2015, 2017b). These differences in the morphology of the locomotor apparatus observed in different ecological contexts are driven by selection on the ability of animals to move effectively in these different habitats, with

selection acting on locomotor performance rather than on the anatomy itself (Aerts et al., 2000). Indeed, it has been shown that increases in hind limb length in *Anolis* lizards are associated with increases in sprinting and jumping capability (Losos, 1990a) of species living on

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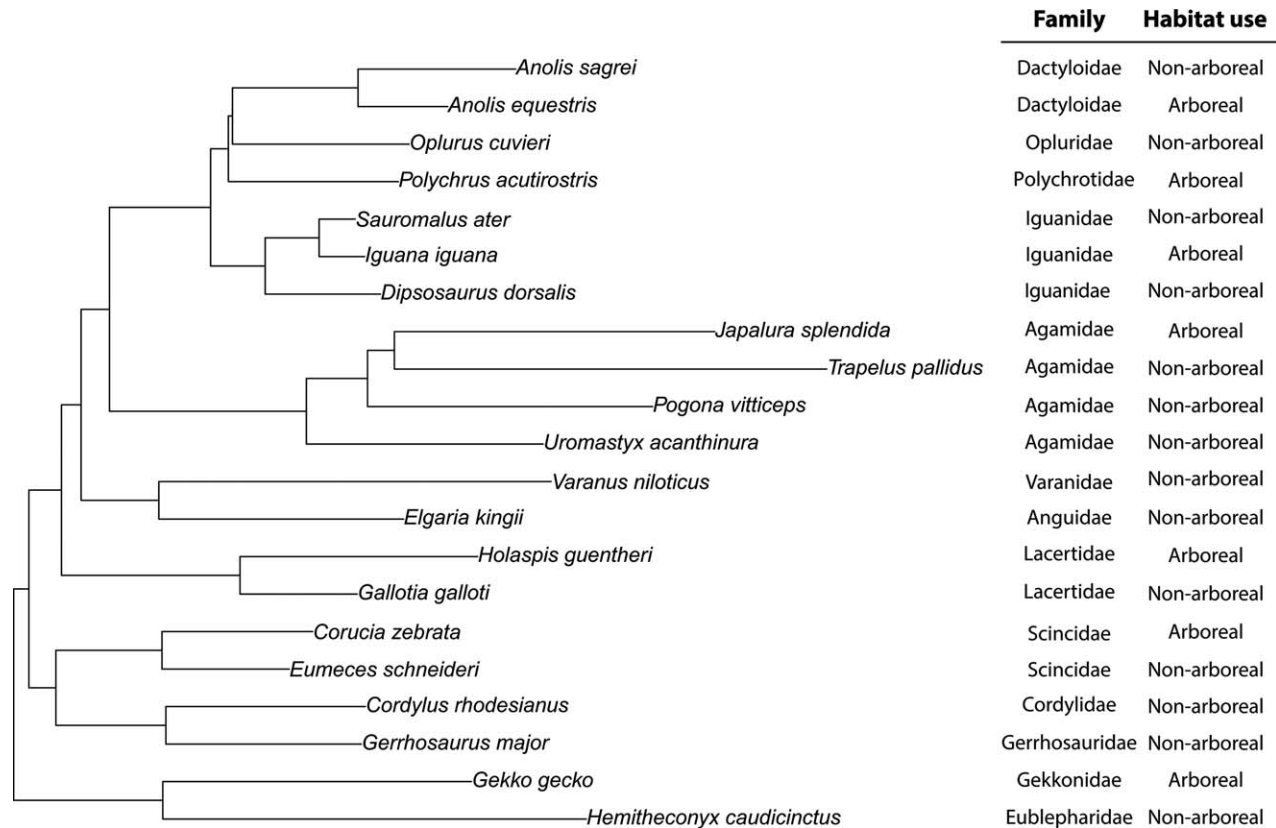


Fig. 1. Pruned phylogenetic tree of Pyron et al. (2013) representing the relationship between the 21 species included in this study. The habitat use and the family of the species are indicated.

broader substrates. Conversely, species with shorter forelimbs jump more frequently and are more stable on narrow substrates (Losos, 1990b). The maximum jump distance is also correlated with limb length and body size (Losos, 1990b; Toro et al., 2003, 2004).

Lizards are an interesting group to study the anatomy of the locomotor system in relation to their environment because they are speciose and morphologically diverse (Pyron et al., 2013; Uetz, 2016) and occupy a multitude of ecological niches (Vitt & Caldwell, 2014). For example, many lizards have radiated independently into an arboreal environment (Fontanarrosa & Abdala, 2016). The main advantages of being arboreal are generally thought to be related to reduced competition and predation (Cartmill, 1985; Preuschoft, 2002). Climbing in trees implies moving against gravity, which requires an increased contribution of the forelimbs to locomotion (Cartmill, 1974, 1985) and involves risks associated with falling (Sinervo & Losos, 1991). Moreover, the arboreal environment is discontinuous and branches are variable in width, orientation, and compliance, creating a highly complex three-dimensional habitat (Cartmill, 1974; Kimura, 2002). To avoid falling in this habitat, many organisms have developed a number of morphological specializations including a prehensile tail, prehensile hands and feet, claws, adhesive pads, long muscular forearms, and relatively long forelimbs relative to the hind limbs (Cartmill, 1974; Hildebrand & Goslow, 2001; Preuschoft, 2002; Sustaita et al., 2013).

Most studies dealing with limb function and locomotion in lizards have focused on quadrupedal locomotion and the role of the hind limbs (Snyder, 1954, 1962, Losos, 1990a, 1990b, 1990c; Losos et al., 1994; Irschick & Jayne, 1999; Irschick & Garland, 2001) with only a handful of studies focusing on the forelimbs (Zaaf et al., 1999, 2001b; Zani, 2000; Herrel et al., 2008; Abdala et al., 2009; Tulli et al., 2011; Foster & Higham, 2012, 2014). However, the forelimbs do not have the same functional role during terrestrial locomotion compared to climbing (Zaaf et al., 2001a, 2001b). During terrestrial locomotion the forelimbs mostly support body weight, whereas during climbing they act to pull the body toward the substrate in addition to providing propulsion (Zaaf et al., 2001b). Goodman et al. (2008) moreover showed that climbing speed and clinging ability are positively correlated to forelimb length. These results show that the forelimbs plays a crucial role in the arboreal environment. Yet, our understanding of the morphology and function of the limb muscles in relation to the specific constraints imposed by living in an arboreal milieu remain poorly understood. Indeed, only a handful of studies have provided quantitative data on the limb muscles in lizards occupying different microhabitats or in climbing versus terrestrial lizards (Zaaf et al., 1999; Herrel et al., 2008) and no broad comparative studies exist to date testing whether or not arboreal species are different in the functional properties of the forelimb muscles that would allow them to utilize the complex three-dimensional arboreal environment more effectively.

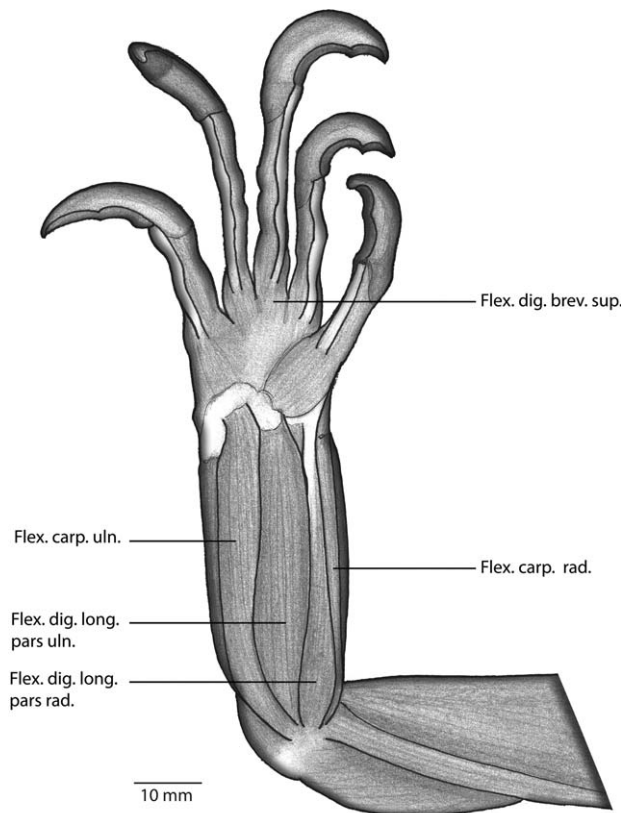


Fig. 2. Superficial view of the flexor muscles of the forearm of *Iguana iguana*. Legend: Flex. dig. brev. sup.: *m. flexores digiti brevis superficialis*; Flex. carp. uln.: *m. flexor carpi ulnaris*; Flex. carp. rad.: *m. flexor carpi radialis*; Flex. dig. long. pars uln.: *m. flexor digitorum longus pars ulnaris*; Flex. dig. long. pars rad.: *m. flexor digitorum longus pars radialis*.

In this study we investigate morphological differences in four flexor muscles in 21 species of lizards that differ in habitat use (arboreal versus non-arboreal, Figs. 1 and 2). Specifically we focus on the force generating capacity and excursion range of the forelimb flexors. Being able to generate larger forces may allow arboreal lizards to grasp a diversity of substrates differing in diameter and orientation, thus increasing stability and reducing the risk of falling (Abdala et al., 2009). Having longer muscles and muscles fibers may be advantageous for climbing in enabling a greater reach of the limb and in maintaining force over a large range of muscle length (Böhmer et al., in press). The architectural features of a muscle including fiber length and physiological cross sectional area define its functional properties (Hildebrand & Goslow, 2001). Indeed, the physiological cross sectional area of a muscle is directly related to the force generating capacity of a muscle, while the length of the muscle fibers is correlated with contractile range (e.g., Zaaf et al., 1999; Herrel et al., 2008; Van Daele et al., 2009; Watson et al., 2014; Ferguson et al., 2015). Given the different role of the forelimbs in species occupying an arboreal habitat, we predict that arboreal lizards will have: (1) a greater physiological cross sectional area of the flexor muscles allowing them to grip the substrate more firmly and (2) longer fibers of the long digital flexors

allowing a greater contractile range providing for an enhanced reach and grasping ability.

MATERIALS AND METHODS

Specimens and Dissections

All specimens used in this study (42 individuals of 21 species; see Table 1) were fixed in a 30% aqueous formalin solution and preserved in 70% ethanol before dissection. All of the specimens belong to the personal collection of Anthony Herrel (Muséum National d'Histoire Naturelle, MNHN). Before dissection the snout-vent length was measured for each individual using digital calipers (Mitutoyo Absolute IP 67). Flexor muscles of the left forelimb were then removed unilaterally on each specimen using a binocular microscope (Leica M3Z) and stored in 70% ethanol. Muscles were blotted dry and weighed on an electronic balance (Mettler AE100; ± 0.01 mg). We dissected four flexor muscles (*m. flexor carpi radialis*, *m. flexor carpi ulnaris*, *m. flexor digitorum longus* and *m. flexores digiti brevis superficialis*). The nomenclature of the muscles follows Abdala and Moro (2006).

The species were divided into two groups: arboreal and non-arboreal (including saxicolous, generalist, burrowers, and terrestrial species) based on published sources. As arboreal we classified *Anolis equestris* (Schwartz & Henderson, 1991), *Polychrus acutirostris* (Avila-Pires, 1995), *Iguana iguana* (Avila-Pires, 1995), *Japalura splendida* (Das, 2010), *Holaspis guentheri* (Spawls et al., 2002), *Corucia zebrata* (Parker, 1970), *Gekko gecko* (Das, 2010); as non-arboreal we classified *Anolis sagrei* (Schwartz & Henderson, 1991), *Oplurus cuvieri* (Glaw & Vences, 2007), *Sauromalus ater* (Stebbins, 2003), *Dipsosaurus dorsalis* (Stebbins, 2003), *Trapelus pallidus* (Schleich et al., 1996), *Pogona vitticeps* (Cogger, 2000), *Uromastix acanthinura* (Schleich et al., 1996), *Varanus niloticus* (Spawls et al., 2002), *Elgaria kingii* (Stebbins, 2003), *Gallotia galloti* (Arnold et al., 1978), *Eumeces schneideri* (Schleich et al., 1996), *Cordylus rhodesianus* (Branch, 1998), *Hemitheconyx caudicinctus* (Chirio & LeBreton, 2007).

Muscle Properties

The muscle bundles were transferred to a 30% aqueous nitric acid (HNO_3 30%) solution for 24 hr to dissolve the connective tissue. Next, the nitric acid was removed and muscles were covered with a 50% aqueous glycerol solution. Fibers were then gently teased apart using blunt-tipped needles. The average fiber length was determined by drawing at least ten fibers for every muscle using a dissecting microscope with *camera lucida* (Leica M3Z). Drawings were scanned and fiber lengths were quantified using ImageJ 1.50i (Wayne Rasband, National Institutes of Health, USA). Finally, the physiological cross-sectional area (PCSA) of each muscle was calculated as follows:

$$\text{PCSA} = \frac{\text{mass (g)}}{\text{muscular density (g.cm}^{-3}) \times \text{fiber length (cm)}}$$

A muscular density of 1.06 g cm^{-3} (Mendez & Keys, 1960) was used.

TABLE 1. Sample size and means \pm SDs of the measurements performed on the 21 species of lizards

Species	N	svl (mm)	PCSA fcr (cm ²)	PCSA _{fcr} (cm ²)	PCSA _{fcr} fcr (cm ²)	PCSA _{fdl} (cm ²)	PCSA _{fdl} fdl (cm ²)	PCSA _{fdl} fdl (cm ²)	fcr mass (mg)	fcr length (mm)	fdl mass (mg)	fdl length (mm)	fdu length (mm)	fdu length (mm)	lfd length (mm)	lfd length (mm)
<i>Anolis aeneus</i>	2	159 \pm 6	0.062 \pm 0.016	0.058 \pm 0.01	0.074 \pm 0.024	0.027 \pm 0.009	0.027 \pm 0.009	41 \pm 13	26 \pm 14	39 \pm 5	6 \pm 2	62.1 \pm 3.3	40.9 \pm 14.8	51.8 \pm 10.2	22.1 \pm 1	22.1 \pm 1
<i>Anolis sagrei</i>	2	57 \pm 1	0.007 \pm 0.002	0.01 \pm 0.001	0.008 \pm 0.002	0.005 \pm 0.002	0.005 \pm 0.002	2 \pm 1	3 \pm 0	2 \pm 0	1 \pm 0	25.4 \pm 1.6	26.1 \pm 3.7	29.7 \pm 8.3	11.9 \pm 2.2	11.9 \pm 2.2
<i>Cordylus rhodestanus</i>	2	81 \pm 5	0.006 \pm 0.000	0.007 \pm 0.000	0.012 \pm 0.004	0.003 \pm 0.001	0.003 \pm 0.001	2 \pm 1	2 \pm 1	4 \pm 3	0 \pm 0	38.7 \pm 16.3	20.9 \pm 10.3	27.3 \pm 11.5	9.8 \pm 0.3	9.8 \pm 0.3
<i>Corucia zebrata</i>	2	210 \pm 0	0.206 \pm 0.029	0.147 \pm 0.054	0.311 \pm 0.122	0.325 \pm 0.063	0.325 \pm 0.063	154 \pm 74	59 \pm 9	279 \pm 41	132 \pm 15	73.5 \pm 44.3	39.6 \pm 8.7	89.2 \pm 22.6	38.6 \pm 3.1	38.6 \pm 3.1
<i>Dipsosaurus dorsalis</i>	2	89 \pm 23	0.008 \pm 0.002	0.024 \pm 0.016	0.012 \pm 0.012	0.019 \pm 0.021	0.019 \pm 0.021	3 \pm 2	7 \pm 5	8 \pm 8	4 \pm 4	41.1 \pm 14.7	24.7 \pm 3.3	39.9 \pm 15.8	17 \pm 3.7	17 \pm 3.7
<i>Elgaria kingii</i>	2	104 \pm 0	0.004 \pm 0.001	0.009 \pm 0.001	0.012 \pm 0.000	0.005 \pm 0.000	0.005 \pm 0.000	1 \pm 0	1 \pm 0	1 \pm 0	0 \pm 0	17 \pm 5.1	11.5 \pm 0.8	11.3 \pm 0.3	5.7 \pm 0.1	5.7 \pm 0.1
<i>Eumeces schneideri</i>	2	126 \pm 5	0.01 \pm 0.002	0.014 \pm 0.001	0.021 \pm 0.005	0.017 \pm 0.000	0.017 \pm 0.000	5 \pm 2	4 \pm 0	10 \pm 4	5 \pm 1	49.5 \pm 11.2	28.8 \pm 2.4	45.2 \pm 8.5	30.1 \pm 4.3	30.1 \pm 4.3
<i>Gallotia galloti</i>	2	106 \pm 7	0.011 \pm 0.007	0.024 \pm 0.008	0.029 \pm 0.021	0.011 \pm 0.001	0.011 \pm 0.001	8 \pm 3	10 \pm 3	11 \pm 3	2 \pm 0	73.9 \pm 17.2	41.4 \pm 1.9	45.2 \pm 22.2	21.2 \pm 0.6	21.2 \pm 0.6
<i>Gekko gekko</i>	2	139 \pm 0	0.04 \pm 0.023	0.035 \pm 0.024	0.025 \pm 0.021	0.011 \pm 0.005	0.011 \pm 0.005	23 \pm 7	9 \pm 2	14 \pm 6	2 \pm 0	58.9 \pm 17.3	30.6 \pm 16.3	67.1 \pm 34.7	14.4 \pm 4.9	14.4 \pm 4.9
<i>Gerrhonotus major</i>	2	174 \pm 5	0.02 \pm 0.003	0.04 \pm 0.005	0.052 \pm 0.002	0.043 \pm 0.000	0.043 \pm 0.000	13 \pm 1	12 \pm 9	24 \pm 7	9 \pm 3	60.4 \pm 3.9	27.6 \pm 16.5	43.7 \pm 15.6	19.8 \pm 5.7	19.8 \pm 5.7
<i>Hemidactylus caudicinctus</i>	2	121 \pm 6	0.016 \pm 0.004	0.034 \pm 0.015	0.018 \pm 0.017	0.005 \pm 0.002	0.005 \pm 0.002	5 \pm 1	10 \pm 3	8 \pm 7	1 \pm 0	32.4 \pm 1.7	29.3 \pm 4.8	46.2 \pm 9.1	17.6 \pm 0.9	17.6 \pm 0.9
<i>Holaspis guentheri</i>	2	49 \pm 1	0.001 \pm 0.001	0.002 \pm 0.000	0.004 \pm 0.000	0.0005 \pm 0.000	0.0005 \pm 0.000	0.5 \pm 0.2	1 \pm 0	1 \pm 0	0.05 \pm 0	31.4 \pm 0	24.8 \pm 3.4	26.7 \pm 0	9.5 \pm 0.1	9.5 \pm 0.1
<i>Iguana iguana</i>	2	330 \pm 42	0.264 \pm 0.079	0.819 \pm 0.155	1.335 \pm 0.098	0.857 \pm 0.118	0.857 \pm 0.118	358 \pm 118	728 \pm 195	1249 \pm 22	449 \pm 24	130 \pm 5.9	87.5 \pm 39.2	113.6 \pm 7.6	49.7 \pm 4.2	49.7 \pm 4.2
<i>Japalura splendida</i>	2	71 \pm 0	0.009 \pm 0.003	0.011 \pm 0.003	0.016 \pm 0.004	0.008 \pm 0.001	0.008 \pm 0.001	2 \pm 0	4 \pm 0	7 \pm 0	1 \pm 0	25.9 \pm 7.2	36.4 \pm 9.2	40.5 \pm 9.8	14.7 \pm 0.1	14.7 \pm 0.1
<i>Oplarus cuvieri</i>	2	118 \pm 5	0.016 \pm 0.006	0.058 \pm 0.029	0.043 \pm 0.025	0.015 \pm 0.002	0.015 \pm 0.002	7 \pm 1	21 \pm 9	21 \pm 10	3 \pm 0	43 \pm 7	34.5 \pm 2.4	47.4 \pm 6.5	22 \pm 4.1	22 \pm 4.1
<i>Pogona vitticeps</i>	2	177 \pm 0	0.046 \pm 0.05	0.181 \pm 0.047	0.19 \pm 0.018	0.106 \pm 0.004	0.106 \pm 0.004	25 \pm 28	92 \pm 38	121 \pm 37	27 \pm 1	49 \pm 3.7	46.8 \pm 7.8	59.8 \pm 12.7	23.8 \pm 0.3	23.8 \pm 0.3
<i>Polychrus acutirostris</i>	2	103 \pm 3	0.015 \pm 0.006	0.015 \pm 0.001	0.033 \pm 0.005	0.008 \pm 0.000	0.008 \pm 0.000	4 \pm 1	5 \pm 0	11 \pm 2	2 \pm 0	25.6 \pm 2.5	33.5 \pm 2.7	32.5 \pm 1.8	19.5 \pm 4	19.5 \pm 4
<i>Sauromalus ater</i>	2	162 \pm 0	0.038 \pm 0.004	0.29 \pm 0.212	0.229 \pm 0.266	0.15 \pm 0.134	0.15 \pm 0.134	39 \pm 8	140 \pm 76	97 \pm 95	37 \pm 31	97.2 \pm 28	49.9 \pm 11.8	51.9 \pm 21	24.9 \pm 2.8	24.9 \pm 2.8
<i>Trapelus pallidus</i>	2	76 \pm 2	0.004 \pm 0.001	0.01 \pm 0.004	0.019 \pm 0.012	0.005 \pm 0.004	0.005 \pm 0.004	2 \pm 1	3 \pm 1	5 \pm 2	1 \pm 0	38.8 \pm 9.9	25.3 \pm 5.8	29.8 \pm 9.1	13.7 \pm 1.7	13.7 \pm 1.7
<i>Uromastyx acanthinura</i>	2	183 \pm 0	0.101 \pm 0.007	0.142 \pm 0.014	0.2 \pm 0.009	0.053 \pm 0.018	0.053 \pm 0.018	80 \pm 16	83 \pm 4	140 \pm 29	23 \pm 12	74.8 \pm 9.9	55.5 \pm 2.7	65.8 \pm 11	40.4 \pm 7.2	40.4 \pm 7.2
<i>Varanus niloticus</i>	2	173 \pm 0	0.032 \pm 0.012	0.035 \pm 0.015	0.058 \pm 0.009	0.044 \pm 0.024	0.044 \pm 0.024	20 \pm 6	18 \pm 9	41 \pm 11	17 \pm 8	59.2 \pm 3.6	47.9 \pm 2.5	66.2 \pm 7.4	36.9 \pm 2.5	36.9 \pm 2.5

Abbreviations: fcr = m. flexor carpi radialis; fcu = m. flexor carpi ulnaris; fdl = m. flexor digitorum longus; fdb = m. flexores digiti brevis superficialis.

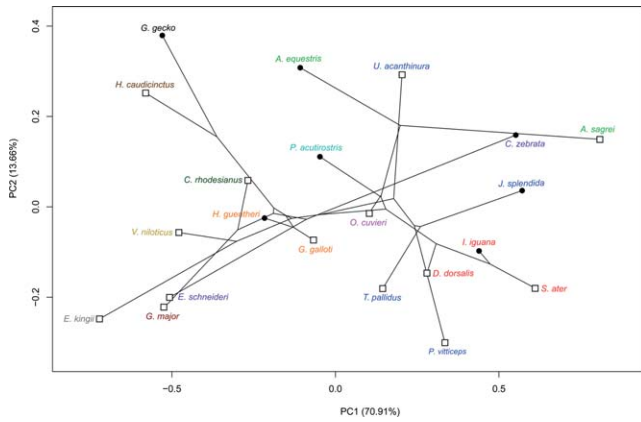


Fig. 3. Scatterplot representing the results of a principal component analysis performed on the PCSA of the flexor muscles. The phylogeny is plotted on the morphospace to assess how phylogeny structures species differences. Legend: black filled circles: arboreal species; open squares: non-arboreal species. Species names are color-coded by family.

Table 1 provides the sample size and the means \pm SD for the 13 variables (i.e., the length, mass, and PCSA of the four flexor muscles in addition to the snout-vent length) for the 21 species of lizards included in our data set.

Statistical Analyses

For each species, means were calculated and Log_{10} -transformed before analyses to fulfill the assumption of normality and homoscedasticity. All analyses were performed in R (R Core Team, 2016). The significance threshold was set at $\alpha = 0.05$.

Phylogeny

The phylogenetic tree used in our analyses is based on Pyron et al. (2013). Full details of the phylogenetic reconstruction can be found in this article. This tree was pruned to include only the species included in our study.

Linear Regressions

In order to assess the effect of the snout-vent length (svl) on the muscle traits, a regression of the Log_{10} -transformed snout-vent length on the Log_{10} -transformed muscle traits was performed. The results of this regression was significant for all variables (all $P < 0.001$). Snout-vent length was consequently used as a co-variate in all subsequent analyses and residuals were calculated to be used as input for our principal component analyses.

Phylomorphospace

A principal component analysis was performed on the residuals of the linear regressions of muscle PCSA and fiber length on snout-vent length. The phylogeny of Pyron et al. (2013) was then plotted on the morphospace composed of the first two axes using the “phylomorphospace” function of the “phytools” library (Revell, 2012).

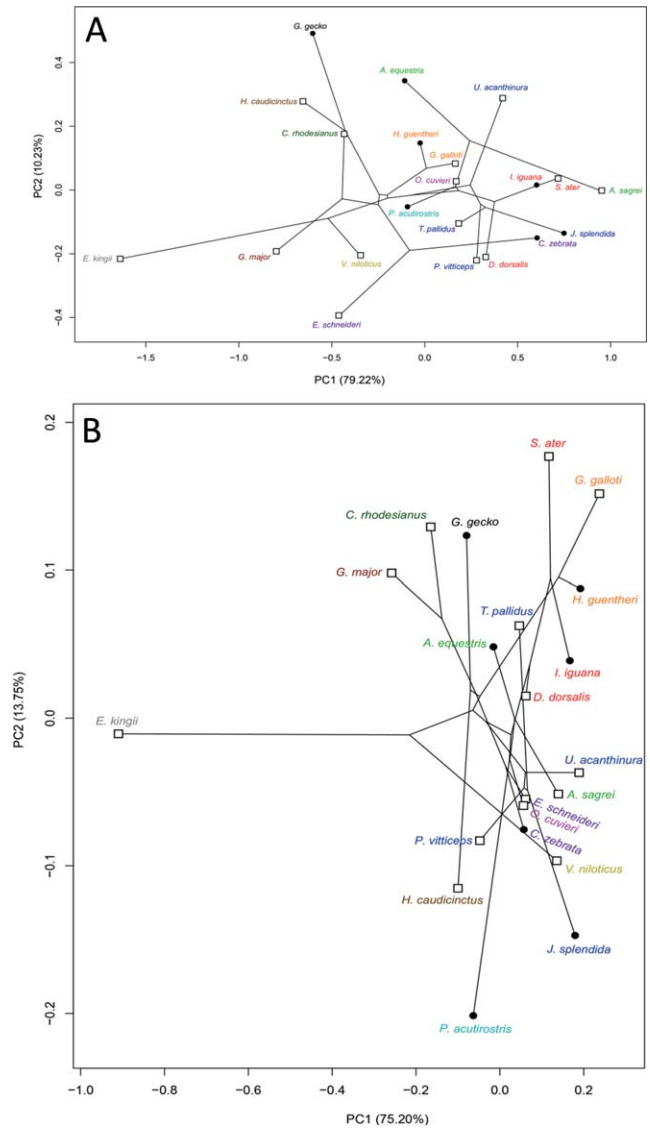


Fig. 4. (A) Scatterplot representing the results of a principal component analysis performed on the residual fiber lengths of the flexor muscles. (B) Scatterplot representing the results of a principal component analysis performed on the residual mass of the flexor muscles. The phylogeny is plotted onto the morphospace to assess how phylogeny structures species differences. Legend: black filled circles: arboreal species; open squares: non-arboreal species. Species names are color-coded by family.

Phylogenetic Signal

To estimate the phylogenetic signal in the residual data, a multivariate version of the K -statistic was used using the “physignal” function from the “geomorph” library (Adams & Otárola-Castillo, 2013; Adams, 2014). The higher the K -value is, the stronger the phylogenetic signal. The phylogenetic signal was also tested for each variable separately using a univariate Pagel’s λ with the function “phylosig” in the “phytools” library (Revell, 2012). The higher the λ , the stronger the phylogenetic signal is.

TABLE 2. Loadings of the residual PCSA of the flexor muscles on the first four principal components

	PC1	PC2	PC3	PC4
PCSA fcr	0.36	0.89	0.27	0.1
PCSA fcu	0.5	0.03	-0.83	0.23
PCSA fdl	0.49	-0.11	0.06	-0.86
PCSA fdb	0.61	-0.45	0.48	0.44
Proportion of variance	0.71	0.14	0.09	0.06
Cumulative proportion	0.71	0.85	0.94	1
Mass fcr	0.39	0.63	-0.61	-0.27
Mass fcu	0.52	0.28	0.75	-0.29
Mass fdl	0.50	0.03	-0.03	0.86
Mass fdb	0.57	-0.72	-0.25	-0.31
Proportion of variance	0.80	0.10	0.07	0.03
Cumulative proportion	0.80	0.90	0.97	1
Length fcr	0.42	0.88	-0.14	-0.14
Length fcu	0.52	-0.16	-0.26	0.80
Length fdl	0.52	-0.13	0.83	-0.09
Length fdb	0.53	-0.42	-0.46	-0.57
Proportion of variance	0.75	0.14	0.06	0.05
Cumulative proportion	0.75	0.89	0.95	1

Abbreviations: fcr = *m. flexor carpi radialis*; fcu = *m. flexor carpi ulnaris*; fdl = *m. flexor digitorum longus*; fdb = *m. flexores digiti brevis superficialis*. Bolded variables are those showing loadings >0.7.

Analysis of Covariance

First, multivariate analyses of covariance (MANCOVA) were performed on the Log₁₀-transformed PCSA, the mass, and the fiber length of the four muscles with Log₁₀-transformed snout-vent length as covariate to test for differences in muscle properties between arboreal and non-arboreal lizards. Next, each variable was tested one by one using analyses of covariance (ANCOVA) with habitat use (arboreal versus non-arboreal) as the independent variable. These analyses were performed using the 3.3.2 version of the R “stats” package (R Core Team, 2016). Finally, the phylogeny of Pyron et al. (2013) was taken into account in the analyses to perform phylogenetic MANCOVAs and ANCOVAs using the “procD.pgls” function of the “geomorph” library in R (Adams & Otárola-Castillo, 2013).

RESULTS

Phylomorphospace

A principal components analysis performed on the residuals of the PCSA and the fiber length of the four muscles (Figs. 3 and 4) showed that all variables loaded similarly on the first axis. However, the second axis mainly represents the PCSA of the *m. flexor carpi radialis* (Table 2). Arboreal species are situated towards the positive side of the axis together with a few non-arboreal species such as *Hemitheconyx caudicinctus*, *Uromastix acanthinura* and *Anolis sagrei* (Fig. 3). When the phylogeny is plotted in the morphospace it becomes clear that related species are generally found in the same area of the morphospace (Fig. 3). The principal components analysis performed on the fiber length and the mass data show little structure except for the extreme position of *Elgaria kingii* (Fig. 4A,B). Moreover, species do not appear to cluster by phylogenetic affinity on the scatter plot of the first two axes (Fig. 4A).

TABLE 3. Summary of the Pagel's λ calculated on the residual data

	λ	P value
PCSA fcr	>0.001	1
PCSA fcu	0.6	0.04
PCSA fdl	0.8	0.04
PCSA fdb	0.48	0.3
Mass fcr	>0.001	1
Mass fcu	0.8	0.02
Mass fdl	0.77	0.12
Mass fdb	0.74	0.15
Length fcr	0.8	1
Length fcu	0.99	0.03
Length fdl	0.89	0.77
Length fdb	0.99	0.14

Abbreviations: fcr = *m. flexor carpi radialis*; fcu = *m. flexor carpi ulnaris*; fdl = *m. flexor digitorum longus*; fdb = *m. flexores digiti brevis superficialis*. Significant results are indicated in bold.

TABLE 4. Summary of the MANCOVA results

		$F_{1,17}$	P value
PCSA	Size	29.69	>0.001
	Habitat use	2.78	0.07
	Size \times habitat use	0.58	0.68
Mass	Size	25.74	>0.001
	Habitat use	2.78	0.07
	Size \times habitat use	0.42	0.79
Length	Size	7.75	0.002
	Habitat use	1.56	0.24
	Size \times habitat use	0.21	0.93

Significant results are indicated in bold. Habitat use = arboreal versus non-arboreal.

Phylogenetic Signal

The multivariate phylogenetic signal calculated on the residuals was significant for the PCSA and the mass but not for the length of the four muscles (PCSA: $K_{\text{mult}} = 0.84$, $P = 0.005$; mass $K_{\text{mult}} = 0.92$, $P = 0.001$; length: $K_{\text{mult}} = 0.77$, $P = 0.097$). The Pagel's λ calculated showed significant signal only for the PCSA of the *m. flexor carpi ulnaris* ($\lambda = 0.6$, $P = 0.04$) and the *m. flexor digitorum longus* ($\lambda = 0.8$, $P = 0.04$), for the mass of the *m. flexor carpi ulnaris* ($\lambda = 0.8$, $P = 0.02$), and for the length of the *m. flexor carpi ulnaris* ($\lambda = 0.99$, $P = 0.03$; Table 3).

Differences in Muscle Morphology between Species with Different Ecologies

The MANCOVA analyses showed a tendency towards significance for the PCSA and the mass of the flexor muscles (PCSA: $F_{1,17} = 2.78$, $P = 0.07$; mass: $F_{1,17} = 2.78$, $P = 0.07$; Table 4). The subsequent univariate analyses of covariance showed that only the PCSA of the *m. flexor carpi radialis* differed between arboreal and non-arboreal species ($F_{1,18} = 5.55$, $P = 0.03$; Table 5). An inspection of the means of the PCSA of the *m. flexor carpi radialis* shows that arboreal species have a higher PCSA for a given size (Fig. 5). However, when taking into account the phylogenetic relatedness among species the differences between arboreal and non-arboreal species were no longer significant (PCSA: $F_{1,17} = 2.15$, $P = 0.39$;

TABLE 5. Summary of the ANCOVA results

		$F_{1,17}$	P value	Variables		$F_{1,17}$	P value
PCSA fcr	Size	111.08	>0.01	Mass fdl	Size	89.73	>0.01
	Habitat use	5.55	0.03		Habitat use	2.06	0.17
	Size \times habitat use	2.07	0.17		Size \times habitat use	0.18	0.68
PCSA fcu	Size	74.74	>0.01	Mass fdb	Size	82.19	>0.01
	Habitat use	0.1	0.76		Habitat use	0.04	0.85
	Size \times habitat use	0.66	0.43		Size \times habitat use	0.52	0.48
PCSA fdl	Size	88.29	>0.01	Length fcr	Size	23.55	>0.01
	Habitat use	1.06	0.32		Habitat use	>0.01	0.97
	Size \times habitat use	0.32	0.57		Size \times habitat use	0.02	0.9
PCSA fdb	Size	86.4	>0.01	Length fcu	Size	13.18	>0.01
	Habitat use	0.03	0.87		Habitat use	1.07	0.31
	Size \times habitat use	1.29	0.27		Size \times habitat use	0.38	0.54
Mass fcr	Size	105.76	>0.01	Length fdl	Size	24.31	>0.01
	Habitat use	3.11	0.1		Habitat use	2.17	0.16
	Size \times ecolo habitat use	1.28	0.27		Size \times habitat use	>0.01	0.96
Mass fcu	Size	57.31	>0.01	Length fdb	Size	26.19	>0.01
	Habitat use	0.02	0.88		Habitat use	0.03	0.87
	Size \times habitat use	0.13	0.72		Size \times habitat use	0.17	0.68

Abbreviations: fcr = *m. flexor carpi radialis*; fcu = *m. flexor carpi ulnaris*; fdl = *m. flexor digitorum longus*; fdb = *m. flexores digiti brevis superficialis*. Habitat use = arboreal versus non-arboreal. Significant results are indicated in bold.

mass: $F_{1,17} = 0.99$, $P = 0.639$, length: $F_{1,17} = 1.21$, $P = 0.57$).

DISCUSSION

Links between Phylogeny and Morphology

The multivariate phylogenetic signal calculated shows significant results for the PCSA and the mass of the muscles. Species that are closely related appear to have a similar PCSA and muscle mass, at least for the species included in our study. Moreover, when the phylogeny is taken into account in our multivariate analyses the difference between arboreal and non-arboreal animals disappears. Tulli et al. (2012) found similar results for the length of the *m. flexor carpi ulnaris* and observed no significant differences between 50 species with different ecologies when the phylogeny was included in the analyses.

Distribution of the Species on the Phylomorphospace

Arboreal species are positioned in the same area of the scatter plot of the PCA and are thus characterized by a higher relative *m. flexor carpi radialis* PCSA (Fig. 3) suggesting that a stronger *m. flexor carpi radialis* may be beneficial to arboreal lizards. However, some non-arboreal species can also be found in this area of the scatter plot. The most noticeable is *U. acanthinura*. This non-arboreal species uses burrows extensive tunnel systems using its forelimbs (Wilms & Böhme, 2007; Wilms et al., 2010). The digging behavior of this species may explain its position in the morphospace if indeed the *m. flexor carpi radialis* is involved in digging. Given that digging involves the flexion of the hand in many animals, the flexor muscle may indeed play an important role (Lagaria & Youtatos, 2006; Warburton, 2006). Although no quantitative data exist for lizards, in digging mammals the carpal flexors are indeed strongly developed (Windle & Parsons, 1899; Gasc et al., 1986; Lessa & Stein, 1992; Lagaria & Youtatos, 2006; Warburton, 2006), suggesting that this may also be the case for

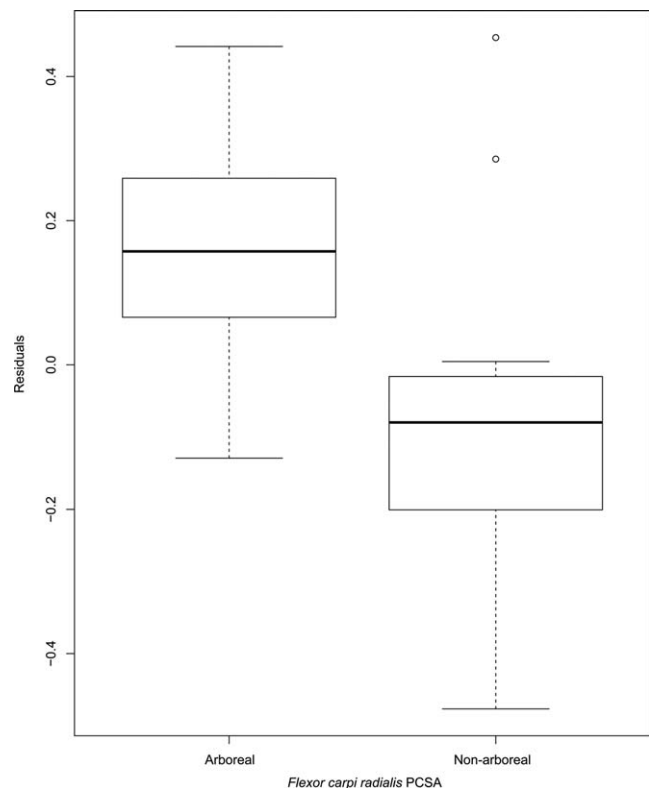


Fig. 5. Boxplot representing the residuals of the PCSA of the *m. flexor carpi radialis* for arboreal and non-arboreal species.

Uromastyx. The non-arboreal species *H. caudicinctus* also shows a relatively high *m. flexor carpi radialis* PCSA. The large *m. flexor carpi radialis* PCSA in this species may have been inherited from a common ancestor as other geckoes similarly have large *m. flexor carpi radialis* PCSAs. *Anolis sagrei* and *O. cuvieri* are both also scattered among the arboreal species in the graph.

Given that these two are semi-arboreal species also occasionally climb, this may drive the development of stronger flexor muscles. Finally the position of the non-arboreal *C. rhodesianus* might similarly be explained by the fact that it is a good rock climber (Branch, 1998; Vitt & Caldwell, 2014) and thus needs forceful flexors to climb rocks. The phylomorphospace of the residuals of the mass of the flexor muscles does not appear to discriminate between species with different ecologies. However, species do cluster by phylogenetic affinity (Fig. 4A). The phylomorphospace of the residuals of the fiber length of the flexor muscles also does not appear to discriminate between species with different ecologies (Fig. 4B). However, *E. kingii* appears to be an outlier which may be explained by the fact that this lizard has an elongated body with very small forelimbs.

Does Habitat Use Impact Flexor Muscle Morphology and Function

Of all our variables, only the PCSA of the *m. flexor carpi radialis* showed significant differences between arboreal and non-arboreal species. Arboreal species tends to have a higher PCSA for the *m. flexor carpi radialis*, confirming the results of Abdala et al. (2009) that suggested that wrist flexion is important when grasping narrow substrate such as branches. Moreover, the *m. flexor carpi radialis* has a slight action of pronating the forearm which may help securing a grip on narrow substrates like branches (Abdala et al., 2009). Yet, none of the other flexor muscles showed differences between arboreal and non-arboreal lizards. This suggests that either the functional constraints imposed by an arboreal life style are not as strong for lizards, or alternatively, that functional trade-offs prevent a stronger development of the other muscles due to the use of the forearm in other functions (e.g., weight support, impact reduction after jumping). Moreover, the individualization of the different muscles and tendons may in fact play a bigger role in the ability to grasp in lizards as suggested previously (Abdala et al., 2009). Finally, other anatomical features may also be better indicators of an arboreal life-style including the anatomy of other functionally important muscles (other flexor muscles such as elbow or shoulder flexors, as well as wrist extensors or rotators) as well bone shape (e.g., Fabre et al., 2018a). Future studies exploring the anatomy of the forelimb more broadly, especially in relationship to *in vivo* measures of gripping performance would be particularly insightful to better understand the relationships between forelimb muscle anatomy and habitat use.

In conclusion, our results on a broad comparative sample of lizards show that the force generation capacity of one of the flexor muscles is greater in arboreal species possibly allowing a stronger flexion of the wrist allowing a firm grasp of narrow substrates. However, no differences in fiber length were observed between arboreal and non-arboreal species, suggesting that longer fibers potentially allowing for a greater range of excursion are not selected for in arboreal lizards. Future studies would benefit from investigating other features of the forelimb in order to fully understand how arboreality and habitat use more generally may drive the morphology of the lizard forelimb.

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LITERATURE CITED

- Abdala V, Moro S. 2006. Comparative myology of the forelimb of *Liolaemus* sand lizards (Liolaemidae). *Acta Zool* 87:1–12.
- Abdala V, Manzano AS, Herrel A. 2008. The distal forelimb musculature in aquatic and terrestrial turtles: Phylogeny or environmental constraints?. *J Anat* 213:159–172.
- Abdala V, Manzano AS, Tulli MJ, Herrel A. 2009. The tendinous patterns in the palmar surface of the lizard manus: Functional consequences for grasping ability. *Anat Rec* 292:842–853.
- Adams DC, Otárola-Castillo E, Paradis E. 2013. Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol Evol* 4:393–399.
- Adams DC, Otárola-Castillo E. 2013. Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol Evol* 4:393–399.
- Adams DC. 2014. A generalized K statistic for estimating phylogenetic signal from shape and other high dimensional multivariate data. *Syst Biol* 63:685–697.
- Aerts P, Van Damme R, Vanhooydonck B, Zaaf A, Herrel A. 2000. Lizard Locomotion: How morphology meets ecology. *Netherlands J Zool* 50:261–277.
- Arnold, E.N., Burton, J.A. & Oviden, O. (1978). *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. United Kingdom: Collins.
- Avila-Pires TCS. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zool Verh (Leiden)* 299:1–706.
- Branch, B. 1998. *Field guide to the snakes and other reptiles of Southern Africa*. 3rd ed. Cape Town: Struik.
- Böhmer C, Fabre A-C, 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*. *Anat. Rec* 301:449–472.
- Branch, B. (1998). *Field Guide to the Snakes and Other Reptiles of Southern Africa*. 3rd ed. Sanibel.
- Cartmill, M. 1974. Pads and claws in arboreal locomotion. In Farish, A & Jenkins, J, editors. *Primate locomotion*. New York: Academic Press.
- Cartmill, M. (1985). Climbing. In *Functional Vertebrate Morphology*. In: Hildebrand, M., Bramble, D.M., Liem, K.F. & Wake, D.B., editors. Cambridge: Belknap Press. p 73–85.
- Chirio, L, LeBreton, M. 2007. *Atlas des reptiles du Cameroun*. Paris: Muséum national d'Histoire naturelle, IRD (Patrimoine naturels, 67).
- Cogger, H.G. (2000). *Reptiles & Amphibians of Australia*. 6th ed. Australia: Reed New Holland.
- Das, I. (2010). *A Field Guide to the Reptiles of South-East Asia*. United Kingdom: New Holland Publisher.
- Fabre A, 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. *J Anat* 226: 596–610.
- Fabre A-C, Perry J, Hartstone-Rose A, Lowie A, Dumont M. 2018a. Do muscles constrain skull shape evolution in Strepsirrhines? *Anat Rec* 301:291–310.
- Fabre A, Marigó J, Granatosky MC, Schmitt D. 2017b. Functional associations between support use and forelimb shape in strepsirrhines and their relevance to inferring locomotor behavior in early primates. *J Hum Evol* 108:11–30.
- Ferguson AR, Huber DR, Lajeunesse MJ, Motta PJ. 2015. Feeding performance of King Mackerel, *Scomberomorus Cavalla*. *J Exp Zool* 323:399–413.

- Fontanarrosa G, Abdala V. 2016. Bone indicators of grasping hands in lizards. *Peer J* 4:e1978.
- Foster KL, Higham TE. 2012. How forelimb and hindlimb function changes with incline and perch diameter in the green anole, *Anolis carolinensis*. *J Exp Biol* 215:2288–2300.
- Foster KL, Higham TE. 2014. Context-dependent changes in motor control and kinematics during locomotion: Modulation and decoupling. *Proc Biol Sci* 281:2013331.
- Gasc JP, Jouffroy FK, Renous S, Von Blottnitz F. 1986. Morphofunctional study of the digging system of the Namib Desert golden mole (*Erimitalpa granti nambiensis*): cinefluorographical and anatomical analysis. *J Zool* 208:9–35.
- Gasc JP, Jouffroy FK, Renous S, Von Blottnitz F. 2009. Morphofunctional study of the digging system of the Namib Desert golden mole (*Erimitalpa granti nambiensis*): Cinefluorographical and anatomical analysis. *J Zool* 208:9–35.
- Glaw, F, Vences M. (2007). A Field Guide to the Amphibians and Reptiles of Madagascar. 3rd ed. Cologne: Vences & Glaw Verlag.
- Goodman BA, Miles DB, Schwarzkopf L. 2008. Life on the rocks: Habitat use drives morphological and performance evolution in lizards. *Ecology* 89:3462–3471.
- Grant PR, Grant BR. 2006. Evolution of character displacement in Darwin's finches. *Science* 313:224–226.
- Herrel A, Vanhooydonck B, Porck J, Irschick D. 2008. Anatomical basis of differences in locomotor behavior in *Anolis* lizards: A comparison between two ecomorphs. *Bull Museum Comp Zool* 159:213–238.
- Hildebrand, M, Goslow, G. 2001. In McFadden, P, editor. Analysis of vertebrate structure. 5th ed. New York, NY: Wiley.
- Irschick D, Jayne B. 1999. Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J Exp Biol* 202:1047–1065.
- Irschick DJ, Garland T. Jr. 2001. Integrating function and ecology in studies of adaptation: Investigations of locomotor capacity as a model system. *Ann Rev Ecol Syst* 32:367–396.
- IUCN. (2017). The IUCN Red List of Threatened Species. Viewed 29 June 2017, <http://www.iucnredlist.org/>.
- Kimura T. 2002. Primate limb bones and locomotor types in arboreal or terrestrial environments. *Z Morphol Anthropol* 83:201–219.
- Lack, D. (1947). Darwin's Finches. Cambridge: Cambridge University Press.
- Lagaria A, Youlatos D. 2006. Anatomical correlates to scratch digging in the forelimb of European ground squirrels (*Spermophilus citellus*). *J Mammal* 87:563–570.
- Lessa EP, Stein BR. 1992. Morphological constraints in the digging apparatus of pocket gophers (Mammalia: Geomyidae). *Biol J Linn Soc* 47:439–453.
- Losos JB, Irschick DJ, Schoener TW. 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Proc Biol Sci* 48:1786–1798.
- Losos JB. 1990. The evolution of form and function: Morphology and locomotor performance in west indian *Anolis* lizards. *Evolution* 44:1189–1203.
- Losos JB. 1990a. The evolution of form and function: Morphology and locomotor performance in West indian *Anolis* lizards. *Evolution* 44:1189–1203.
- Losos JB. 1990b. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. *Anim Behav* 39:879–890.
- Losos JB. 1990c. Ecomorphology, performance capability, and scaling of west indian *Anolis* lizards: An evolution analysis. *Ecol Monogr* 60:369–388.
- Mendez J, Keys A. 1960. Density and composition of mammalian muscle. *Metabolism* 9:184–188.
- Parker F. 1970. Collecting reptiles and amphibians in New Guinea. *Aust Nat Hist* 16:309–314.
- Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunther MM, Thorpe SKS, D'Aut K. 2006. Morphological analysis of the hindlimb in apes and humans. II. Moment Arms *J Anat* 208:725–742.
- Pinto G, Mahler DL, Harmon LJ, Losos JB. 2008. Testing the island effect in adaptive radiation: Rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proc R Soc B Biol Sci* 275:2749–2757.
- Preuschoft H. 2002. What does “arboreal locomotion” mean exactly and what are the relationships between “climbing”, environment and morphology? *Z Morphol Anthropol* 83:171–188.
- Pyron RA, Burbrink FT, Wiens JJ. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol Biol* 13:93.
- R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Revell LJ. 2012. Phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol* 3:217–223.
- Schleich, HH, Kastle, W, Kabisch, K. (1996). Amphibians and Reptiles of North Africa. Koenigstein: Koeltz Scientific Books.
- Schwartz, A, Henderson, RW. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. Gainesville: University of Florida Press.
- Sinervo B, Losos JB. 1991. Walking the tight rope: Arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* 72:1225–1233.
- Snyder RC. 1954. The anatomy and function of the pelvic girdle and hindlimbs in lizard locomotion. *Am J Anat* 95:1–45.
- Snyder RC. 1962. Adaptations for bipedal locomotion of lizards. *Am Zool* 2:191–203.
- Spawls, S, Howell, K, Drewes, R, Ashe, J. (2002). A Field Guide to the Reptiles of East Africa. San Diego: Academic Press.
- Stebbins, R.C. (2003). Western Reptiles and Amphibians. 3rd ed. Boston: Houghton Mifflin Harcourt.
- Sustaita D, Pouydebat E, Manzano A, Abdala V, Hertel F, Herrel A. 2013. Getting a grip on tetrapod grasping: Form, function, and evolution. *Biol Rev* 88:380–405.
- Toro E, Herrel A, Irschick DJ. 2004. The evolution of jumping performance in Caribbean *Anolis* Lizards: Solutions to biomechanical trade-offs. *Am Nat* 163:844–856.
- Toro E, Herrel A, Vanhooydonck B, Irschick DJ. 2003. A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards. *J Exp Biol* 206:2641–2652.
- Tulli MJ, Abdala V, Cruz FB. 2011. Relationships among morphology, clinging performance and habitat use in Liolaemini lizards. *J Evol Biol* 24:843–855.
- Tulli MJ, Herrel A, Vanhooydonck B, Abdala V. 2012. Is phylogeny driving tendon length in lizards? *Acta Zool* 93:319–329.
- Uetz, P. (2016). The Reptile Database. Viewed 22 June 2017, <http://www.reptile-database.org/>.
- Van Daele PAAG, Herrel A, Adriaens D. 2009. Biting performance in teeth-digging African mole-rats (*Fukomys*, Bathyergidae, Rodentia). *Physiol Biochem Zool* 82:40–50.
- Vitt, LJ, Caldwell, JP. 2014. Herpetology: an introductory biology of amphibians and reptiles. 4th ed. London, Waltham, San Diego: Academic Press.
- Warburton, N. M. (2006). Functional morphology of marsupial moles (Marsupialia: Notoryctidae). *Verh Naturwiss Ver Hamburg* 42, 39–149.
- Watson PJ, Gröning F, Curtis N, Fitton LC, Herrel A, McCormack SW, Fagan MJ. 2014. Masticatory biomechanics in the rabbit: A multi-body dynamics analysis. *J R Soc Interface* 11:20140564.
- Williams SB, Wilson AM, Payne RC. 2007. Functional specialisation of the thoracic limb of the hare (*Lepus europeus*). *J Anat* 210:491–505.
- Wilms TM, Böhme W. 2007. Review of the taxonomy of the spiny-tailed lizards of Arabia (Reptilia: Agamidae: Leiolepidinae: *Uromastyx*). *Fauna Arab* 23:435–468.
- Wilms, T.M., Wagner, P., Shobrak, M., Lutzman, N. & Böhme, W. (2010). Aspects of the ecology of the Arabian spiny-tailed lizard (*Uromastyx aegyptia microlepis* Blanford, 1875) at Mahazat as-Sayd protected area, Saudi Arabia. *Salamandra* 46, 131–140.
- Windle B, Parsons F. 1899. On the myology of the Edentata. *Proc Zool Soc* 1899:314–399.

- Zaaf A, Van Damme R, Herrel A, Aerts P. 2001a. Limb joint kinematics during vertical climbing and level running in a specialist climber: *Gekko gecko* Linneus, 1758 (Lacertilia: Gekkonidae). *Belg J Zool* 131: 173–182.
- Zaaf A, Van Damme R, Herrel A, Aerts P. 2001b. Spatio-temporal gait characteristics of level and vertical locomotion in a ground-dwelling and a climbing gecko. *J Exp Biol* 204:1233–1246.
- Zaaf A, Herrel A, Aerts P, De Vree F. 1999. Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habits (Lepidosauria). *Zoomorphology* 119: 9–22.
- Zani PA. 2000. The comparative evolution of lizard claw and toe morphology and clinging performance. *J Evol Biol* 13:316–325.