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Convergent Evolution of Claw Shape in a Transcontinental Lizard Radiation

Simon Baeckens ,[1,*,†] Charlotte Goeyers[*] and Raoul Van Damme[*]

[*]Functional Morphology Lab, Department of Biology, University of Antwerp, Wilrijk, Belgium; [†]Department of Biological Sciences, Macquarie University, Sydney, Australia

[1]E-mail: simon.baeckens@uantwerp.be

Synopsis Species occupying similar selective environments often share similar phenotypes as the result of natural selection. Recent discoveries, however, have led to the understanding that phenotypes may also converge for other reasons than recurring selection. We argue that the vertebrate claw system constitutes a promising but understudied model system for testing the adaptive nature of phenotypic, functional, and genetic convergence. In this study, we combine basic morphometrics and advanced techniques in form analysis to examine claw shape divergence in a transcontinental lizard radiation (Lacertidae). We find substantial interspecific variation in claw morphology and phylogenetic comparative statistics reveal a strong correlation with structural habitat use: ground-dwelling species living in open areas are equipped with long, thick, weakly curved, slender-bodied claws, whereas climbing species carry high, short, strongly curved, full-bodied claws. Species occupying densely vegetated habitats tend to carry intermediately shaped claws. Evolutionary models suggest that claw shape evolves toward multiple adaptive peaks, with structural habitat use pulling species toward a specific selective optimum. Contrary to findings in several other vertebrate taxa, our analyses indicate that environmental pressures, not phylogenetic relatedness, drive convergent evolution of similarly shaped claws in lacertids. Overall, our study suggests that lacertids independently evolved similarly shaped claws as an adaptation to similar structural environments in order to cope with the specific locomotory challenges posed by the habitat. Future biomechanical studies that link form and function in combination with genomic and development research will prove valuable in better understanding the adaptive significance of claw shape divergence.

Introduction

The observation that distantly related species living in similar environmental conditions often share phenotypic features suggests that evolution is predictable and that natural selection will often follow the same path toward trait optimization (Conway Morris 2003, 2015). Recently, however, several authors have cautioned that external resemblance can arise for other reasons than recurring selection (Losos 2011; Blount et al. 2018). Phenotypes may converge purely by chance (Stayton 2008, 2015), through shared developmental biases, genetic correlations or pleiotropy (Wake 1991; Leroi et al. 1994a, 1994b; Jaekel and Wake 2007), or as a correlated response to selection on another trait (Losos 2011). Also, resemblance at the phenotypical level may mask divergence at the functional level, if the same phenotype optimizes multiple functions (Losos 2011). Conversely, convergence at the functional level does not guarantee phenotypic resemblance (many-to-one mapping; Wainwright et al. 2005; Wainwright 2007). The advent of genomic techniques has revealed that phenotypic convergence can reflect repetitive mutations in the same genes (Gompel and Prud'homme 2009), but may also arise from very different genetic changes (Stern 2013; Thurber et al. 2013). These new insights have revived and deepened the study of convergence; it is now recognized that testing the adaptive nature of convergence may require phylogenetic analyses, assessing the functional significance of the trait and its fitness value in relevant conditions, as well as examining variation in its genomic substrate (Losos 2017; Blount et al. 2018).

The vertebrate claw system constitutes a promising but understudied model system for the study of phenotypic, functional, and genetic convergence. Claws vary considerably in form and function among species, but similar shapes tend to turn up in

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different taxa, such as mammals (e.g., Hamrick 2001; Tulli et al. 2016), birds (e.g., Feduccia 1993; Burnham et al. 2011; Tinius and Russell 2017), and reptiles (e.g., Zani 2000; Birn-Jeffery et al. 2012; Crandell et al. 2014). Biomechanical considerations have led to a number of straightforward predictions on how claw architecture could be optimized for different functional or environmental requirements (Dai et al. 2002; Manning et al. 2006, 2009; Stephan 2014). Short, high, sharp, and strongly curved claws should enhance gripping performance and are therefore expected in species with an arboreal or saxicolous lifestyle (Cartmill 1985; Manning et al. 2006; Burnham et al. 2011; Biewener and Patek 2018). Long, straight claws, by extending effective limb length, should increase running speed and are therefore anticipated in species with cursorial locomotor habits (Van Damme et al. 2003; Tulli et al. 2012; Higham 2015; Vanhooydonck et al. 2015). Experimental work on lizards corroborates the idea that higher claws improve clinging capacity (Zani 2000; Tulli et al. 2011), and arboreal and rock-climbing species indeed tend to have higher claws than cursorial species (Zani 2000; Tulli et al. 2009; Muñoz et al. 2015; D'Amore et al. 2018). The actual effect of claw curvature on attachment strength is less clear (Zani 2000), and while several studies have found that arboreal species of lizards and birds tend to have more strongly curved claws (Cartmill 1974; Tulli et al. 2009; Crandell et al. 2014; D'Amore et al. 2018; Yuan et al. 2018), others have not (Pike and Maitland 2004). The effect of claw sharpness on attachment strength and locomotion is strangely understudied in vertebrates (but see Dai et al. 2002; Xu et al. 2018); D'Amore et al. (2018) found that claws of arboreal varanids have a distinct pointed tip, but Crandell et al. (2014) found the exact opposite in *Anolis*. Clearly, our understanding of the functional morphology and ecology of claw morphology is incomplete.

In this study, we examined claw shape divergence in a transcontinental lizard radiation (Lacertidae) using traditional and 2D geometric morphometric methods based on elliptic Fourier analysis (EFA). Comprising 43 genera and over 300 species, the lacertid family has radiated into all major habitats of Africa and Eurasia, ranging from tundras over heathlands, grasslands, and Mediterranean shrub to sandy deserts and tropical forests (Arnold 1989a, 1989b; Arnold et al. 2007; Mayer and Pavlicev 2007; Pavlicev and Mayer 2009). Within these habitats, lacertids occupy microhabitats and substrates that vary greatly in structure: some species are typically ground-dwelling in open or densely vegetated areas, whereas others frequently climb on rocks, shrubs, or trees (Arnold 1998; Vanhooydonck and Damme 1999). Functional ecomorphological studies on lacertids have revealed that ground-dwelling species in open habitats are typically equipped with long limbs, short tails, and few vertebrae, and are fast sprinters. Species occupying cluttered areas and vertical elements generally have slender and elongated bodies with short limbs, long tails, and many vertebrae, and excel in climbing performance (Arnold 1998; Van Damme and Vanhooydonck 2002; Vanhooydonck and Van Damme 2003; Edwards et al. 2012). Remarkably, while these findings clearly indicate that lacertids have independently evolved multiple times similar morphological adaptations to cope with similar locomotory challenges imposed by the structural habitat, it is still unknown whether claw shape has evolved in parallel. Here, we test the hypothesis that claw shape of lacertids has evolved convergently in species occupying similar structural habitats.

Materials and methods

Animals

We examined claw morphology of ethanol-preserved lizard specimens stored in the museum collection of the Forschungsmuseum Alexander Koenig (Bonn, Germany). We took measurements of 230 individuals from 58 species belonging to 33 lacertid genera; all species are represented in the time-calibrated squamate phylogeny of Zheng and Wiens (2016). Per species, we sampled on average four large adult male individuals (mean = 4.0; range = 2–5). Lacertid species were categorized into one of three ecological classes based on the structural habitat they utilize (Van Damme and Vanhooydonck 2002): (1) ground-dwelling species living in open, sparsely vegetated terrain, typically desert or semi-desert areas (number of species in our dataset, $N = 13$), (2) ground-dwelling species that occupy densely vegetated habitats, such as meadows, heathlands, and maquis ($N = 22$), and (3) climbing species primarily occupying vertical elements, such as the trunk of trees or steep rocky walls and boulders ($N = 23$). Information on habitat use was gathered from the literature (Arnold 1998; Vanhooydonck and Damme 1999; Van Damme and Vanhooydonck 2002; Arnold and Ovenden 2004; Orriols 2011; Baeckens et al. 2015).

Morphological measurements

We measured snout–vent length (SVL) of each specimen using digital calipers (Mitutoyo, CD-15CPX, precision = 0.01 mm) and used SVL as a proxy for body size. We then took high-resolution digital images of the claws of the fourth digit on the left forefeet and hindfeet using a Nikon D7000 camera (with a Tamron SP 90 mm F/2.8 Macro VC-lens) mounted on a tripod. The claws were positioned lateral-side up and pictures were made with the lens fixed perpendicularly at a fixed distance. From the claw images, we measured claw height, claw length, and claw curvature using the software ImageJ (Abràmof et al. 2005; Fig. 1). Claw height was measured at the base of the claw (i.e., near the most distal skin scales of the digit) as the vertical distance between the most dorsal and most ventral end of the claw, and claw length was measured as the linear distance between its ventral base and the tip (following Zani 2000; Tulli et al. 2009; Yuan et al. 2018; Fig. 1a). Claw curvature was estimated as the diameter of the best-fitting circle applied to the ventral arc of the claw (following Petie and Muller 2007; Goyens et al. 2015; Fig. 1a), which is recommended when claw arcs represent part of a circle (Tinius and Russell 2017). Lizards with a highly curved claw will, thus, have a low value for circle diameter, while lizards with a weakly curved claw will be represented by a high value. The thickness of the claw (at its base; Fig. 1b) was measured using a digital caliper (Mitutoyo, CD-15CPX, precision = 0.01 mm), because it could not be measured from the 2D claw images.

Because univariate data fail to fully capture the complex shape information of the claw (Tinius and Russell 2017), we also characterized shape using EFA (Giardina and Kuhl 1977; Kuhl and Giardina 1982). This method of form analysis is used to describe the shape of 2D outlines that do not possess clearly defined homologous landmarks by mapping the distance from the geometric center of the outline to each point on the contour with a polar (x; y) coordinate function (e.g., Potier et al. 2018; Smith and Kriebel 2018; Baeckens et al. 2019). This function can then be described in terms of a Fourier series with a series of harmonics; the lower harmonics approximate the coarse-scale features of outlines, whereas the higher harmonics capture more subtle variation (Shen et al. 2009). From the 2D photographs of lacertid claws, we first converted the claw images into claw silhouettes (Fig. 1a) in Adobe Illustrator (San Jose, CA) and, subsequently, we transformed the silhouettes into outlines using the R package *Momocs* (Bonhomme et al. 2015; Supplementary Fig. S1). We constructed outlines of the fore and hind claw of one individual per species. We used the "calibrate_harmonics" function to evaluate the number of harmonics needed to effectively describe claw shape, without overparameterization (Claude 2008, 2013), and found that 95% of the power was captured when the number of harmonics was set at five (nb.h = 5; Supplementary Fig. S2). As there are four coefficients associated with each harmonic (i.e., amplitude and phase for x and the same for y), EFA described the shape of each claw with a total set of 20 coefficients, which we summarized by means of a phylogenetic principal component analysis (pPCA) using the function "phyl.pca" in the *phytools* package (Revell 2012). A first pPCA captured 63.9% of the variation in claw shape of the hindfeet in the first component (pPC1) and 21.0% in the second (pPC2). A second pPCA, now on the claws of the forefeet, explained 49.7% of the shape variation in pPC1, and 25.7% in pPC2. Subsequently, we used the respective species scores of pPC1 (now "$\mathrm{pPC1}_{\mathrm{shape}}$") and pPC2 (now "$\mathrm{pPC2}_{\mathrm{shape}}$"), for both the fore- and hindfeet, as a proxy for claw shape in all future statistical analyses.

Data analysis

Prior to analysis, we $\log_{10}$-transformed individual univariate measurements (claw height, claw length, claw thickness, claw curvature, and SVL) and averaged these values for each species in order to obtain species-level trait variables. Since we want to differentiate between the effect of evolutionary convergence and shared ancestry on patterns of claw shape divergence in lacertids, we conducted all statistical analyses in a strict phylogenetic framework. In order to do so, we pruned the phylogenetic tree proposed by Zheng and Wiens (2016) to include only the 58 species implemented in this study (Supplementary Fig. S3). All analyses were performed in R, version 3.3.1 (R Core Team 2013).

First, we examined the link between species' structural habitat use and claw morphology by testing whether the relationship (slope and intercept) between SVL and the claw variable of interest differed among species that occupy different structural habitats. To do so, we performed phylogenetic generalized least square (PGLS; "pgls" function in *caper*; Orme 2012) regressions with SVL as a predictor variable, claw morphology as response variable (i.e., claw height, claw length, claw thickness, claw curvature, $\mathrm{pPC1}_{\mathrm{shape}}$, and $\mathrm{pPC2}_{\mathrm{shape}}$), and habitat class as factor. We controlled the structure of the phylogenetic signal in the PGLS analyses by optimizing the branch length transformations using maximum-likelihood (λ = ML, κ = ML, δ = ML).

Second, we performed phylogenetic multivariate analysis of variance (MANOVAs) to test whether the whole multivariate claw morphology of lacertids

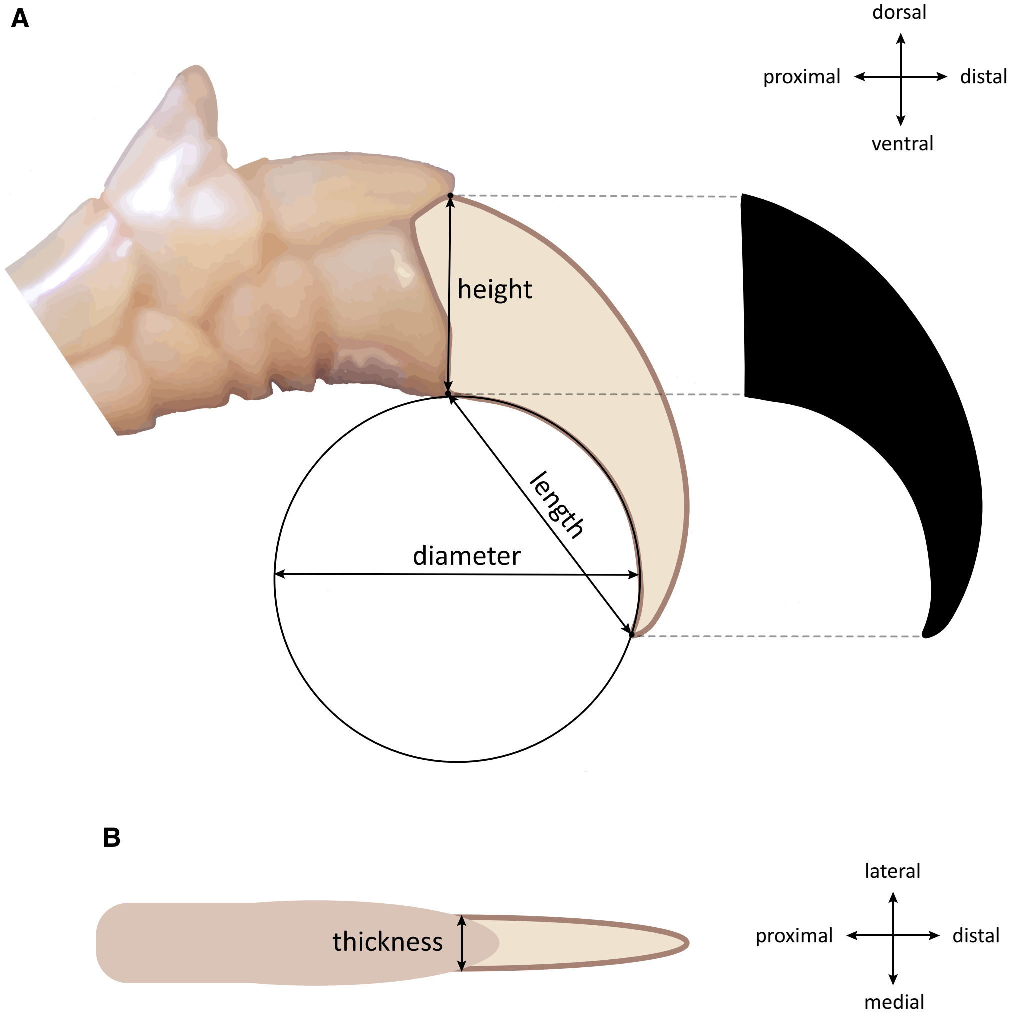

Fig. 1 Claw morphometrics. Schematic representation of a lizard claw with annotations on the different claw morphometrics measured in this study: claw height, length, thickness, and curvature (as the diameter of the best fitting circle inside the claw). Claw silhouettes were used for geometric morphometrics analyses of claw shape.

(i.e., matrix of claw curvature, height, length, thickness, $\mathrm{pPC1}_{\mathrm{shape}}$, and $\mathrm{pPC2}_{\mathrm{shape}}$) differs among species occupying different structural habitats. Because all nongeometric measurements of claw morphology were strongly body size-dependent (Table 1), we used size-adjusted values for the different claw variables in the MANOVAs; that is, the phylogenetic residual values calculated from a phylogenetic regression analysis of the univariate claw variable (claw curvature, height, length, or thickness) as response variable and SVL as predictor variable ("phyl.resid" function of *phytools*; Revell 2009). In sum, input variables for the multivariate analyses were residual claw curvature, residual height, residual length, residual thickness, $\mathrm{pPC1}_{\mathrm{shape}}$, and $\mathrm{pPC2}_{\mathrm{shape}}$; the test was conducted for the hind- and forefeet separately.

Thirdly, to estimate phylogenetic signal of the multivariate claw, we calculated $\mathrm{K}_{\mathrm{mult}}$, which is a modification of Blomberg's *K*-statistics suited for high-dimensional and multivariate data (Blomberg et al. 2003; Adams 2014). We used the "K.mult" function of the *phylocurve* package (Goolsby 2016), with phylogenetic permutation set at 9999 iterations. As for the MANOVAs, we used the size-adjusted claw values for the $\mathrm{K}_{\mathrm{mult}}$ analyses, that is, residual claw curvature, residual height, residual length, residual thickness, $\mathrm{pPC1}_{\mathrm{shape}}$, and $\mathrm{pPC2}_{\mathrm{shape}}$.

Lastly, we used a model selection framework to investigate whether and how changes in structural habitat use may have influenced claw shape evolution. We tested three different models of the evolution using the methods and codes (*ouch* package) developed by Butler and King (2004). For the fore- and hind claw separately, models were fit to $\mathrm{pPC1}_{\mathrm{shape}}$. Out of the three models, the first model tested whether claw shape varies at random following

Table 1 Results (*F*- and *P*-values) of the PGLS analyses testing for the effect of two predictors, that is, structural habitat use and SVL, on the individual claw measurements (response variables)

	Fore claw						Hind claw					
	SVL		Habitat		SVL: habitat		SVL		Habitat		SVL: habitat	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Basic claw morphometrics												
Thickness	**129.54**	**<0.001**	**4.20**	**0.020**	2.04	0.139	**175.80**	**<0.001**	**5.95**	**0.005**	0.31	0.737
Curvature	**42.40**	**<0.001**	**26.75**	**<0.001**	0.78	0.462	**21.64**	**<0.001**	**20.46**	**<0.001**	0.49	0.614
Length	**195.15**	**<0.001**	**11.23**	**<0.001**	1.52	0.223	**248.37**	**<0.001**	**18.62**	**<0.001**	1.91	0.160
Height	**494.82**	**<0.001**	**4.13**	**0.022**	0.31	0.727	**562.57**	**<0.001**	2.62	0.083	0.77	0.467
Geometric morphometrics of claw shape												
$pPC1_{shape}$	0.67	0.417	**14.99**	**<0.001**	0.60	0.551	1.45	0.233	**15.60**	**<0.001**	0.51	0.603
$pPC2_{shape}$	0.04	0.843	1.95	0.152	0.66	0.520	0.06	0.815	**3.95**	**0.025**	0.41	0.665

Statistically significant results ($P < 0.05$) are shown in bold.

a Brownian motion (BM) process, where phenotypic variation accumulates with time. A rejection of the BM model implies that phenotypic evolution has not followed a random evolutionary trajectory (neutral drift). The two other models followed an Ornstein–Uhlenbeck (OU) process (Lande 1976; Hansen 1997), with the simplest model ("OU1") having a single (global) optimum for all species regardless of selective regime. The third model ("OU3") adds additional optima for each selective regime so that we have separate optima for the three different habitat types. Model "OU3" estimates an ancestral regime optimum for all internal branches (based on maximum-likelihood). To determine the goodness of fit of candidate evolutionary models, we compared all models by means of the second-order Akaike information criteria (AICc) (Burnham and Anderson 2002). For the best-fit model, optimum values (θ) were extracted and confidence intervals were estimated using parametric bootstraps (number of bootstraps = 500). Additional analysis of variance were conducted to test for significant differences in average optimal values among selective regimes.

Results

Simple claw dimensions and derived shape scores vary greatly among species of Lacertidae (Table 1; Supplementary Table S1). The results of the PGLS analyses indicate that the relationship (i.e., slope) between body size and all basic claw morphometrics is similar for lizards occupying different structural habitats (Table 1; Supplementary Fig. S4). However, the intercepts of these body size-claw morphology relationships differ significantly among species using dissimilar habitat structures (Table 1; Fig. S4). Relative to their size, ground-dwelling species living in open areas have significantly longer, thicker, and less curved claws (both front and hind) than species occupying other habitat types (Supplementary Table S2). Relative claw length, thickness, and curvature do not differ between species occupying vertical elements and species inhabiting densely vegetated areas. Relative claw height of ground-dwelling species is significantly larger than species occupying other structural habitats (Supplementary Table S2), but this is only true for claws on the forefeet (Table 1).

For all univariate claw measurements, we found a strong association between species' fore and hind claw morphology (Supplementary Table S3 and Fig. S5). The positive relationship (slope and intercept) between fore- and hind claw length and height is similar for all species regardless of their habitat use, but this is not the case for claw thickness and claw curvature (Table S3). Ground-dwelling species in open environments have significantly weaker curved hind claws relative to their fore claws in comparison to climbing species (PGLS; $t_{2,52} = -3.31$, $P = 0.002$) and species inhabiting densely vegetated areas ($t_{2,52} = -2.87$, $P = 0.006$; Supplementary Fig. S4); there is no significant intercept difference between climbing species and species inhabiting densely vegetated areas ($t_{2,52} = -0.72$, $P = 0.473$). In contrast to claw curvature, the slope of hind claw thickness over fore claw thickness differs significantly among species occupying dissimilar habitats (Supplementary Table S3), with ground-dwelling species in open habitats having a lower slope than climbing species ($t_{2,52} = 3.65$, $P < 0.001$) and species inhabiting densely vegetated areas ($t_{2,52} = 3.59$, $P = 0.001$; Supplementary Fig. S4); species of the

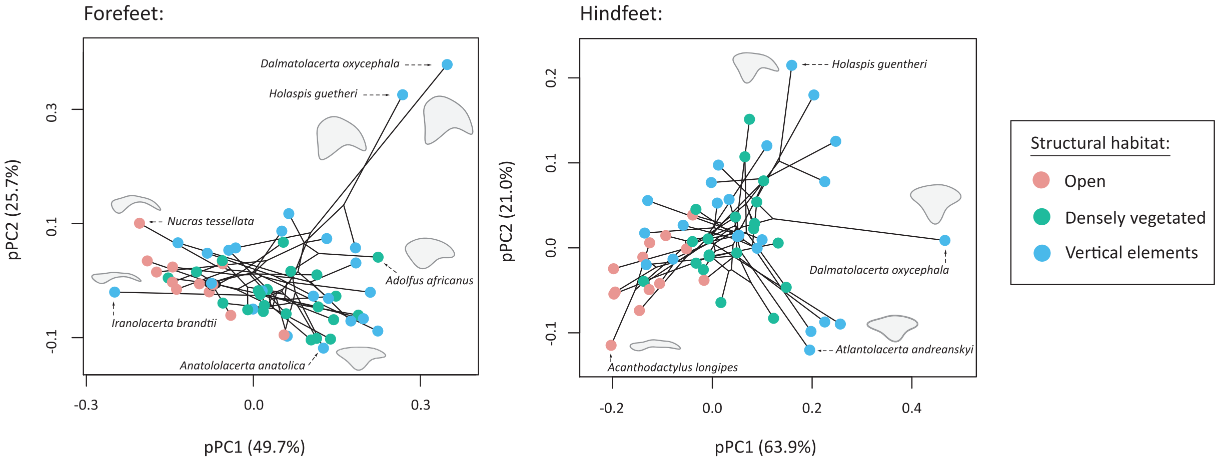

Fig. 2 Phylomorphospace of claw shape in lacertid lizards. Scatterplots of $\mathrm{pPC2}_{\mathrm{shape}}$ over $\mathrm{pPC1}_{\mathrm{shape}}$ for claws on the fore- and hindfeet; colors indicate species' structural habitat use. Claw outlines are shown for species with the most diverged claw shape in morphological space.

latter two habitat types had a similar slope ($t_{2,52} = -0.65$, $P = 0.512$).

Geometric morphometric analyses indicate that the majority of the interspecific variation in claw shape (fore claws: 75.4%; hind claws: 85.0%) can be reduced to two axes of variance (Fig. 2). In both manus and pes, the first axis ($\mathrm{pPC1}_{\mathrm{shape}}$) predominantly describes variation in the distance between the dorsal and ventral arcs of the claw across its complete length, from base to tip (fore claw $\mathrm{pPC1}_{\mathrm{shape}}$: 49.7%; hind claw $\mathrm{pPC1}_{\mathrm{shape}}$: 63.9%), with robust and full-bodied claws having high values for $\mathrm{pPC1}_{\mathrm{shape}}$ (e.g., *Dalmatolacerta oxycephala*), and slim and slender-bodied claws having low values for $\mathrm{pPC1}_{\mathrm{shape}}$ (e.g., *Acanthodactylus longipes*). The second axis ($\mathrm{pPC2}_{\mathrm{shape}}$) mainly explains variation in the curvature of the claw arc (fore claw $\mathrm{pPC2}_{\mathrm{shape}}$: 25.7%; hind claw $\mathrm{pPC2}_{\mathrm{shape}}$: 21.0%), with strongly arched claws having high values for $\mathrm{pPC2}_{\mathrm{shape}}$ (e.g., *Holaspis guentheri*), and weakly arched claws having low values for $\mathrm{pPC2}_{\mathrm{shape}}$ (e.g., *Atlantolacerta andreanskyi*).

Unlike the basic claw morphometrics, claw shape ($\mathrm{pPC1}_{\mathrm{shape}}$ and $\mathrm{pPC2}_{\mathrm{shape}}$) does not significantly change with body size (Table 1). However, species occupying different structural habitats strongly differ in the shape of their claws (Table 1). Ground-dwelling species inhabiting open areas have a significantly lower value for $\mathrm{pPC1}_{\mathrm{shape}}$ and $\mathrm{pPC2}_{\mathrm{shape}}$ than species occupying other structural habitats, meaning that ground-dwelling species are equipped with more slender-formed ($\mathrm{pPC1}_{\mathrm{shape}}$) and weakly curved ($\mathrm{pPC2}_{\mathrm{shape}}$) claws than others lacertid species (Supplementary Table S3; Fig. 3). This is, however, not true for $\mathrm{pPC2}_{\mathrm{shape}}$ of the fore claws (Supplementary Table S3; Fig. 3). Although climbing species tend to have fuller-bodied (higher values for $\mathrm{pPC1}_{\mathrm{shape}}$) and stronger curved claws (higher values for $\mathrm{pPC2}_{\mathrm{shape}}$) than species from densely vegetated areas, the difference is not statistically significant at the 0.05 level (Supplementary Table S3; Fig. 3).

Like the PGLS analyses on individual claw variables, phylogenetic MANOVAs show significant differences in the multivariate claw morphology among species occupying dissimilar structural habitats; this is true both for the fore claw (Wilks' $\lambda = 0.32$, approximately $F_{16,96} = 4.57$, $P = 0.008$) and hind claw (Wilks' $\lambda = 0.36$, approximately $F_{16,96} = 4.57$, $P = 0.004$).

Tests for phylogenetic signal in claw morphology reveal that both hind and fore claws show significant signal in their multivariate phenotype (hind: $K_{\mathrm{mult}} = 0.94$, $P < 0.001$; fore: $K_{\mathrm{mult}} = 0.75$, $P < 0.001$). The amount of phylogenetic signal is <1, indicating that species resemble each other less than is expected under BM. This is reflected in the dispersion of the species in phylomorphospace, where there are many overlapping branches and where closely related species are not adjacent in shape morphospace (Fig. 2).

When fitting models of trait evolution, the BM model receives less support than the OU models of claw shape evolution (Table 2), suggesting that the evolution of claw shape oscillates, at least in part, around one or more phenotypic optima. More specifically, the OU model with multiple optima ("OU3"), that is, one for each of the different selective regimes, is for both fore- and hind claws the absolute best-fitting model (Table 2). The estimated

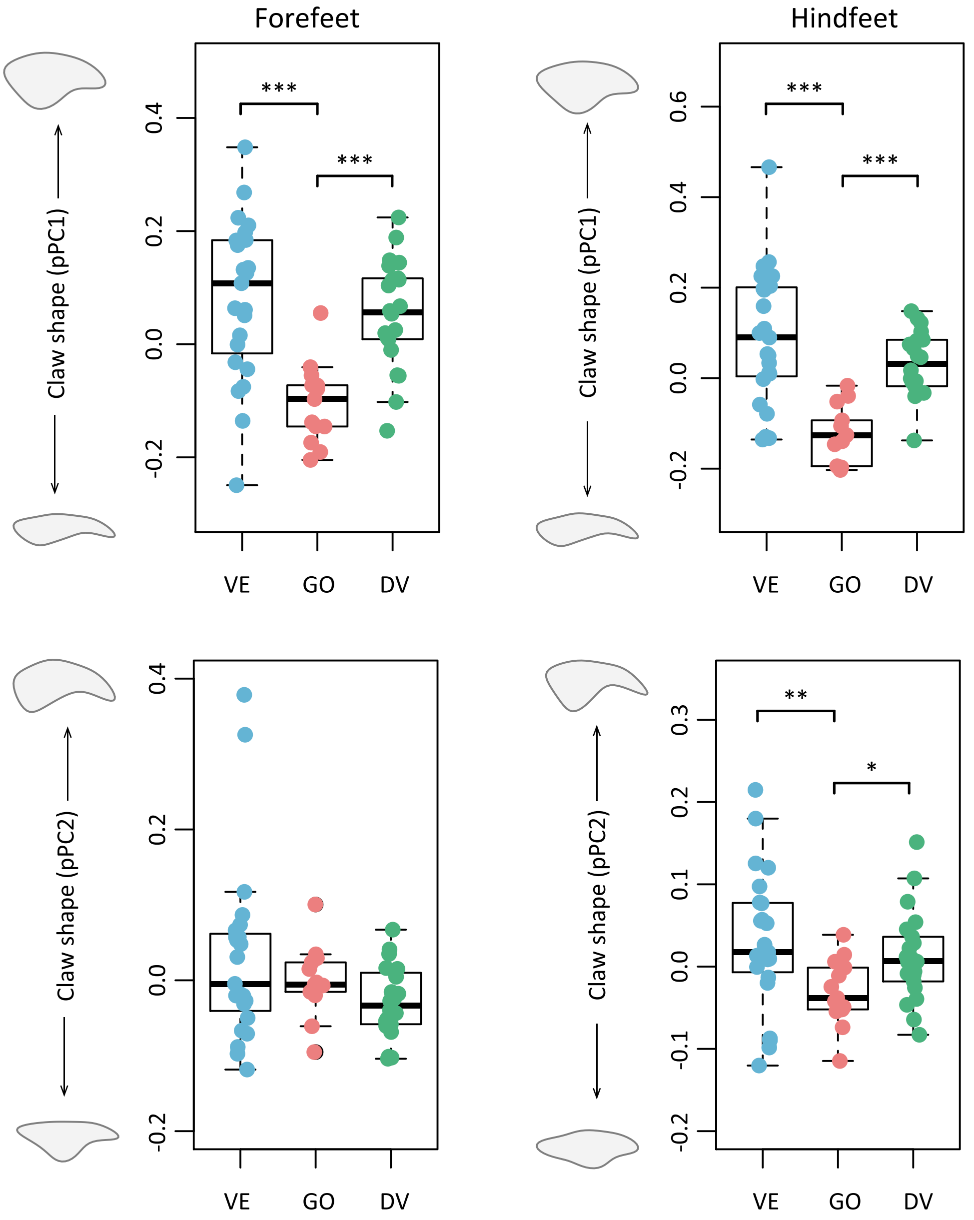

Fig. 3 Claw shape of species occupying different structural habitats. The black lines in the boxplots depict the median claw shape ($pPC1_{shape}$ and $pPC2_{shape}$) per structural habitat type, with boxes and whiskers indicating the quartiles. Significant differences (represented by the asterisks) among species occupying different habitat types were revealed by PGLS analyses ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$). GO, ground-dwelling in open areas; DV, inhabiting densely vegetated areas; VE, occupying vertical elements.

Table 2 Performance of models for claw shape evolution ($pPC1_{shape}$)

	Fore claw			Hind claw		
Model	**BM**	**OU1**	**OU3**	**BM**	**OU1**	**OU3**
LogL	37.11	37.68	46.96	36.10	36.85	47.98
AICc	−69.99	−68.95	−81.33	−67.98	−67.25	−84.81
ΔAICc	11.34	12.38	0	16.84	17.57	0

For each model, the likelihood values (LogL), and (delta) bias-corrected AICc are given. For OU with (1) or (3) optima, see text for more details.

selective optima (θ) are found within the observed values for $pPC1_{shape}$ (Supplementary Table S4), suggesting that the models are a realistic assessment of current phenotypic patterns. Optima estimates differ statistically significantly among selective regimes (Supplementary Table S4 and Fig. S6), with each selective regime experiencing its own optimal value (fore: $F_{2,1497} = 7388$; $P < 0.001$; hind: $F_{2,1497} = 9942$; $P < 0.001$). A qualitative visual inspection of the optima landscape (Supplementary Fig. S6) shows that the landscape is largely divided into two optima

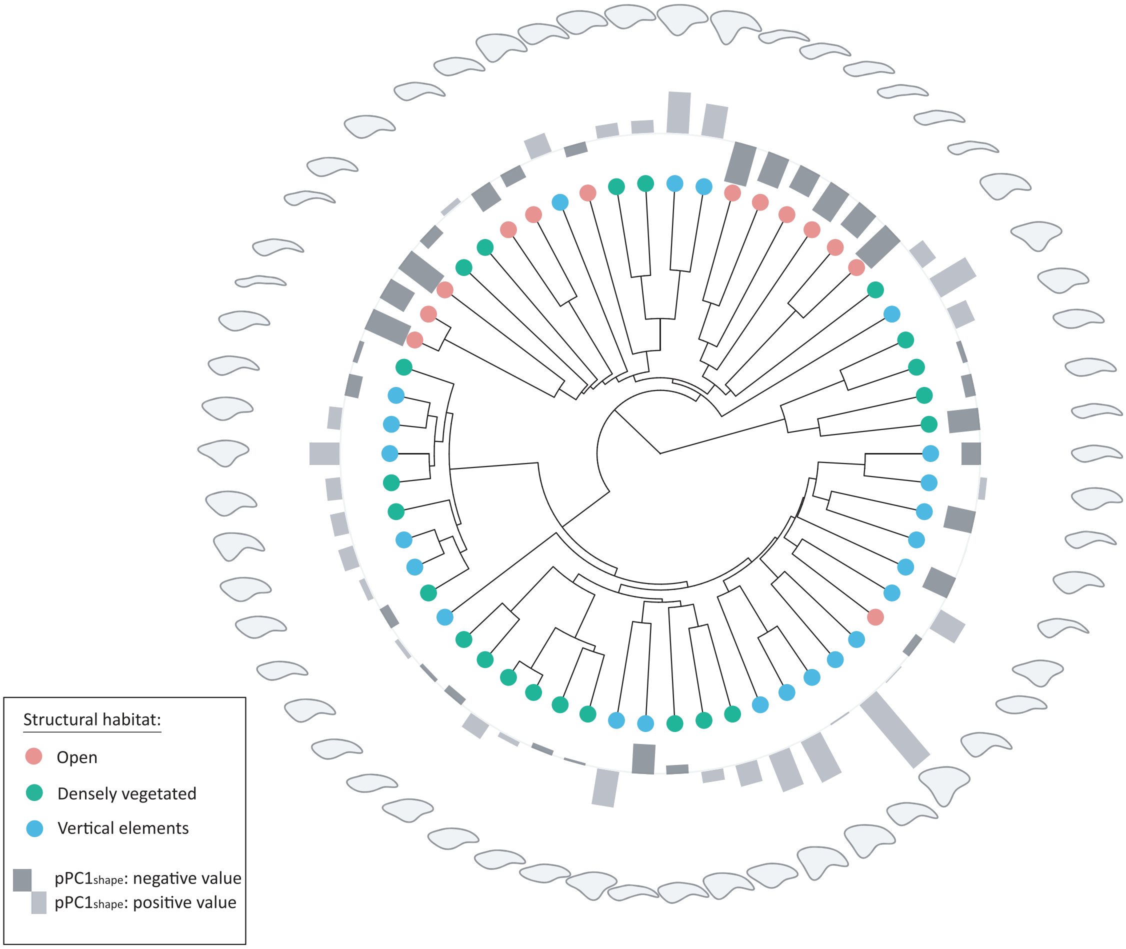

Fig. 4 Claw shape convergence in lacertid lizards. Phylogenetic tree of the 58-lacertid species of study with the colored circles at the tree tips representing species' structural habitat use. Bars at the tree tips denote species' values for $\mathrm{pPC1}_{\mathrm{shape}}$ of the hind claw, with additional silhouettes of their claw shape (after EFA transformation).

clusters, with the selective optimum for ground-dwellers in open areas differing from the partly overlapping optima for the other two habitat types.

Discussion

Over much of the Old World, lacertid lizards have successfully radiated into a variety of ecological niches (Arnold 1989a; Hipsley and Müller 2017). Our analyses suggest that with its radiation lacertids convergently evolved similarly shaped claws as an adaptation to similar structural environments (Fig. 4) in order to cope with the specific locomotory challenges posed by the habitat. It is likely that the adaptive diversification of claw shape may have facilitated the colonization of different structural habitats, offering novel ecological opportunities.

Claw shape adaptations for efficient locomotion on disparate structural habitats

Combining basic morphometrics and advanced techniques in form analysis, our study reveals that lacertid species occupying dissimilar structural habitats are equipped with dissimilarly shaped claws, with ground-dwelling and climbing species bearing the most disparately shaped claws in morphological space.

First, we find that ground-dwelling species that inhabit open terrains, typically desert or semi-desert areas, carry long, weakly curved, slender-bodied claws. Comparable findings have been documented for *Liolaemus* (Tulli et al. 2009) and varanid lizards (D'Amore et al. 2018). Claws of such form are thought to increase effective limb length, and thus, increase stride length and spiriting capacity on horizontal surfaces (Garland and Losos 1994; Van Damme et al. 2003; Higham 2015). As such, carrying long, weakly curved claws is most likely an adaptation for efficient cursorial locomotion, as ground-dwelling species living on the open terrain only have limited shelter opportunities and therefore strongly rely on fast sprinting abilities (high speeds and acceleration) for escaping predators and chasing prey (Ricklefs et al. 1981; Vanhooydonck and Van Damme 2003; Miles et al. 2007). Moreover, our finding that the claws of ground-dwelling species are even less curved on the hindfeet relative to the forefeet supports the hypothesis that these claws are adaptations for fast running in open terrain: burst locomotion in lizards mainly originates from pushing forces of the hind limbs (Vanhooydonck et al. 2001, 2014; Aerts et al. 2003), thus, claws that increase stride lengths of the hind limbs, rather than the fore limbs, will be most advantageous for attaining high running speeds. It might also be that ground-dwellers diverged toward having uncurved claws not strictly to improve sprinting speed on flat terrain, but because curved claws simply impede cursorial locomotion. Manipulation of claw curvature and claw length in future studies of locomotor performance and kinematics in lizards might provide further insight.

Second, our findings largely corroborate earlier observations of claw shape made in other lizard taxa (Zani 2000; D'Amore et al. 2018; Yuan et al. 2018; but Crandell et al. 2014), birds (Birn-Jeffery et al. 2012; but Pike and Maitland 2004), and mammals (Tulli et al. 2016), in that climbing species occupying vertical elements carry short, strongly curved, full-bodied claws. Biomechanical and experimental work showed that claws of such shape have a high mechanical strength and improve clinging performance on rough surfaces by increasing frictional grip (Zani 2000; Dai et al. 2002; Provancher et al. 2005; Tulli et al. 2011; Xu et al. 2016), which suggests that carrying short, strongly curved, full-bodied claws is an adaptation for efficient locomotion on vertical elements (Zani 1999). Interestingly, our data also show that climbing species have less thick claws (relative to body size) than ground-dwelling species. This is somewhat unexpected knowing that claw thickness partly determines the breaking stress of the claw (Dai et al. 2002) and that claws undergo higher external forces while climbing on vertical elements than while running on flat substrata due to gravitational forces. One explanation for this finding lies in line with the idea of economic design (Weibel et al. 1991), in that with a minimum (or limited) amount of biological material (here: β-keratin), maximum claw strength should be achieved; one could imagine that it would be more economic to invest, for instance, in claw height, because an equal material investment in thickness would not gain as much strength as an investment in claw height would. Indeed, climbing species have much higher claws than ground-dwelling species, and claw height strongly determines clinging performance in lizards (Zani 2000; Tulli et al. 2011). Comparably, birds that crush hard seeds are also known to bear short high beaks as such shape limits the risk of beak failure while tolerating high biting forces (e.g., Soons et al. 2010). Clearly, more biomechanical research (e.g., finite-element modelling) is necessary to assess the effect of complex claw shape variation on stress magnitude and distribution, and more experimental studies to understand how variation in specific claw dimensions translates to variation in climbing performance. In addition, genomic and development research is required to gauge the genetic factors that might constrain the co-evolution of certain claw characteristics.

In our analyses, we did not differentiate between arboreal species that climb on the trunk of trees and saxicolous species that climb on rocky walls and boulders. Yet, bark and stone differ in substrate roughness (Winchell et al. 2018), which potentially affect friction forces while climbing. Dai et al. (2002) reported that not only the dimensions of the claw tip, but also substrate roughness strongly determine friction forces of the claw system. In other words, whether claws succeed in interlocking with the irregularities of the substrate or whether claws fail to hook and slip are partly dependent on the roughness of the substratum (Dai et al. 2002; Tulli et al. 2011). Efficient climbing on bark or stone may, therefore, require slightly different claw adaptations (Cartmill 1985). In the Lacertidae family, however, only a limited number of species (those of the genus *Holaspis* and *Gastropholis*) are truly arboreal (unlike in other lizard taxa, such as iguanians), rendering a portioning of the climbing guild statistically undesirable. At first glance, claws of the only truly arboreal lacertid in our dataset, *H. guentheri*, are positioned close to those of rock climbing species (e.g., *D. oxycehpahala*) in morphospace (Fig. 2), suggesting a general "climbing" claw. However, a closer examination of the differences in morphological claw demands between rock climbing and tree climbing might prove valuable.

In our dataset, ground-dwelling lacertid species that occupy densely vegetated habitats show an intermediate claw shape between climbing species and species that dwell on open terrains. Because of the more generalist lifestyle of lizards occupying such vegetated microhabitats, Ribas et al. (2004) and Teixeira-Filho et al. (2001) postulated that these species might, on the one hand, benefit from long and weakly curved claws that increase contact with the ground, but on the other hand, also benefit from short and strongly curved claws for maneuvering in complex and densely vegetated areas. This would suggest that lacertids that occupy densely vegetated habitats evolved a compromise claw phenotype as the result of the functional trade-offs that emerge by the conflicting design demands of claws for climbing and claws for terrestrial sprinting. As this still remains speculative, future studies should assess the effect of vegetation density on the actual locomotor performance of species equipped with dissimilar claws.

Evolutionary convergence of claw shape

With the aim to examine patterns of claw shape divergence in lacertids, we analyzed our data in a strict phylogenetic framework in order to be able to disentangle the role of evolutionary convergence from that of shared ancestry. Our analyses indicate a significant phylogenetic signal in lacertid claw morphology, inferring that evolutionary history influences, at least part of, the observed patterns of claw morphology in this radiation of lizards. However, the strength of the phylogenetic signal was relatively low, as species resembled each other less than expected under the BM of evolution, which suggests that external selective pressures are in play and responsible for a significant share of the interspecific variation. Indeed, our analyses show that phylogenetic affinity is less strongly correlated with shape that are associations with ecological groups, indicating that species' structural habitat use, not phylogenetic relatedness, drives the independent evolution of similarly shaped claws in lacertids.

The idea that the shape of the claw is a reliable indicator of the ecology of a species (and vice versa) is not particularly novel (e.g., Cartmill 1974; Feduccia 1993), as several studies have provided correlative evidence that particular claw features evolved as an adaptation to the use of a particular structural microhabitat (e.g., Pike and Maitland 2004; Tulli et al. 2009, 2016; Birn-Jeffery et al. 2012; Yuan et al. 2018). Yet, evidence for convergent evolution of claw shape, that is the independent evolution of similar features in different evolutionary lineages, is remarkably rare. For instance, Tulli et al. (2009) showed that while claw morphology (specifically claw length and height) of *Liolaemus* lizards is strongly correlated with habitat use (ground-dwelling vs. climbing), common ancestry is still the main predictor of the observed morphological variation. Comparable findings have been documented in sigmodontinae rodents (Tulli et al. 2016) and birds (Birn-Jeffery et al. 2012): species inhabiting similar environments are equipped with similarly shaped claws, yet, evolutionary history still explains claw shape variation best. This over-arching effect of phylogeny on trait variation in the aforementioned taxa is most likely the result of closely related species occupying similar environments (Wiens and Graham 2005; Losos 2008). If habitat use is heavily clustered on a phylogenetic tree, with members of large clades occupying the same habitat, the statistical power of the phylogenetic comparative analyses weakens due to the low number of habitat transitions that have occurred in the history of the taxa (Garland et al. 1993; Vanhooydonck and Damme 1999). As a result, traditional statistics might reveal significant effects of habitat use on claw shape, while phylogenetically-informed analyses might not (Garland et al. 1993; Vanhooydonck and Damme 1999). Note that the occurrence of phylogenetic clustering does not necessarily reject the possibility of adaptive evolution (Garland et al. 1993; Losos 2008). Based on the simple principle of maximum parsimony (Maddison 1994), the minimum number of observed character-state transitions in our dataset is 15 (*phylo.signal.disc* package; Paleo-López et al. 2016). Due to this relatively high number of evolutionary transitions, our dataset shows only little phylogenetic clustering, indicating that throughout their evolutionary history, lacertids have colonized different structural habitats multiple times (see also Hipsley et al. 2009; Hipsley and Müller 2017). Our phylogenetically-informed analyses suggest that, together with these colonizations, species independently evolved similar claw features to cope with similar locomotory demands posed by the newly established structural environment. Moreover, we provide convincing evidence for evolutionary convergence as our models indicate that claw shape most likely evolves toward multiple adaptive peaks (not at random), with habitat use pulling species toward a specific evolutionary optimum. As a first, this study provides evidence for evolutionary convergence of claw shape in a transcontinental lizard radiation. In a recent study, Yuan et al. (2018) found comparable patterns of claw shape convergence in a neotropical lizard radiation, that is, genus *Anolis*. Anoles adaptively radiated on different islands in the Greater Antilles by vertically partitioning structural habitat (Williams 1972; Losos et al. 1998; Losos 2009). New evidence suggests that the evolution of high and strongly curved claws partly facilitated the colonization of arboreal habitats; an event which happened multiple times in different *Anolis* lineages (Yuan et al. 2018). The discrepancy between studies on the finding of convergent evolution of claw shape calls for a large macroevolutionary comparative approach that examines claw morphology across all amniote lineages. In the era of "big data" with reliable phylogenies of numerous animal groups and extensive digital museum collections at hand (Muñoz and Price 2019), it would be interesting to quantify claw morphology of a large number of amniote species (>1000 species) as it would enable to perform tests of evolutionary innovation and trait-dependent diversification and speciation (which require large phylogenies to achieve reasonable statistical power; Rabosky and Huang 2016; Rabosky 2017).

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Supplementary data

Supplementary data available at *ICB* online.

Author contributions

S.B. conceived and designed the study; S.B. and C.G. collected the data, S.B. analyzed the data and prepared figures with input from R.V.D., and S.B. and R.V.D. wrote the article.

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