



Developmental dynamics of ecomorphological convergence in a transcontinental lizard radiation

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Phenotypic convergence has confounded evolutionary biologists for centuries, explained as adaptations to shared selective pressures, or alternatively, the result of limited developmental pathways. We tested the relative roles of adaptation and constraint in generating convergent cranial morphologies across a large lizard radiation, the Lacertidae, whose members inhabit diverse environments throughout the Old World and display high amounts of homoplasy associated with ecological niche. Using 3D X-ray computed tomography, we quantified cranial shape variation associated with ontogeny, allometry, and ecology, covering all lacertid genera and one-third of species diversity. Landmark-based geometric morphometrics showed that cranial shape varied significantly among biomes, with substantial convergence among arid-dwelling lineages. Comparisons of species cranial growth trajectories between biomes revealed that allometric postdisplacement, as evidenced by decreased elevation of a constant ontogenetic slope, drives the convergent paedomorphic appearance of independent arid-dwelling forms. We hypothesize that observed heterochronic changes reflect temporal compression of ancestral life history in response to extreme environments, with associated phenotypes occurring as by-products of adaptive shifts in reproductive investment. Although allometry has long been considered a developmental constraint, our results demonstrate that allometric flexibility during early ontogeny produces convergent ecomorphologies over vast temporal and spatial scales, thus dramatically obscuring underlying phylogenetic signals.

KEY WORDS: Allometry, constraint, convergence, Lacertidae, ontogeny.

Convergent evolution as evidence of adaptation or constraint has constituted a fundamental dichotomy in evolutionary biology for nearly two centuries, predating the Darwinian Revolution (Darwin 1859; Maynard Smith et al. 1985; Gould 2002). Convergence, defined as the evolution of similar features in independent lineages, is widely cited as the outcome of natural selection, generating optimal solutions to shared environmental challenges (Losos 2011). Others see in it limitations on the developmental mechanisms that produce phenotypic variation, leading to the recurrent evolution of analogous types (McGhee 2011).

A central goal of evolutionary biology (and the impetus for evolutionary developmental biology; Brakefield 2006) is to distinguish between these hypotheses (Losos 2011), yet a growing number of studies indicate that these processes are not mutually

exclusive but interact over time to produce adaptive developmental constraints (Klingenberg 2010; Pélabon et al. 2014; Voje et al. 2014). Whether this interaction is maintained over longer evolutionary periods, however, is still unknown, because the majority of investigations focus on ontogenetic variation within a single genus (Klingenberg and Spence 1993; Adams and Nistri 2010; Piras et al. 2011; Sanger et al. 2013) or developmental stage (i.e., adults; Sanger et al. 2012; Klingenberg and Marugán-Lobón 2013; Openshaw and Keogh 2014). Furthermore, it is unclear how specific changes in ontogenetic parameters (e.g., growth rate, timing of on- and offset) affect diversification at higher taxonomic levels, and to what extent those changes contribute to patterns of morphological convergence across broad temporal and spatial scales (Pélabon et al. 2014; Voje et al. 2014).

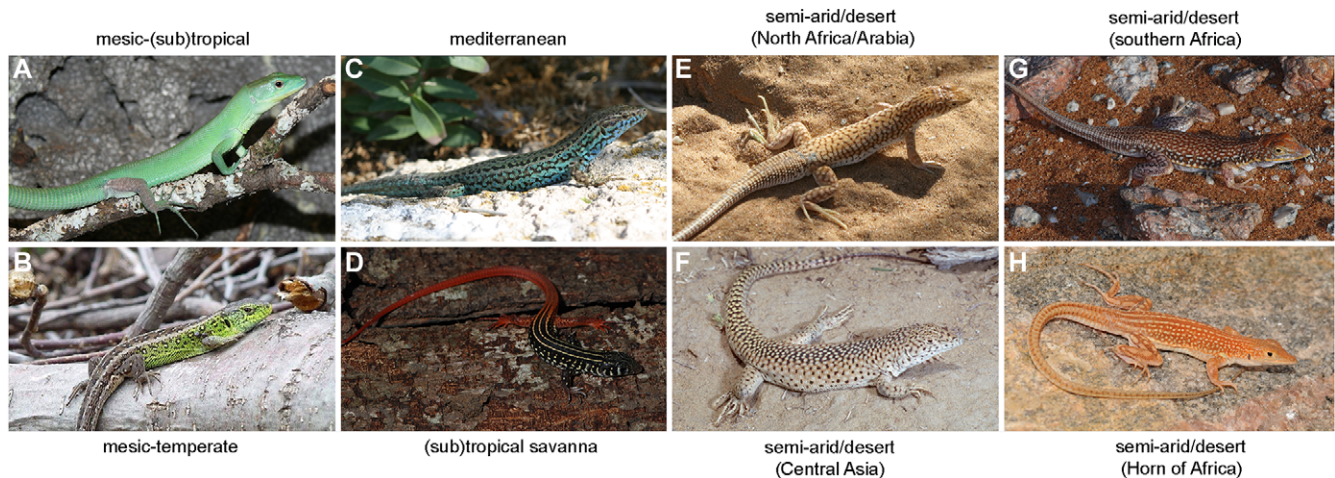


Figure 1. Examples of lacertid phenotypic diversity across different biomes. (A) *Gastropholis prasina*, captive specimen; (B) *Lacerta agilis*, Germany; (C) *Podarcis pityusensis*, Spain; (D) *Nucras ornata*, Mozambique; (E) *Acanthodactylus cf. scutellatus*, Sudan; (F) *Eremias grammica*, Uzbekistan; (G) *Meroles cuneirostris*, Namibia; (H) *Pseudemias brenneri*, Ethiopia. Photo credits: (A) J. Ortega, (B) P. Wagner, (C, E) J M, (D, G) M.-O. Rödel, (F) N. Clemann/J. Melville, and (H) T. Mazuch.

Squamate reptiles, the clade comprising lizards and snakes, provide an ideal system for addressing these issues, as they are diverse, widespread, and exhibit extreme amounts of homoplasy associated with ecological niche (Reeder et al. 2015). Although the adaptive significance of such traits is commonly identified by correlative or functional analyses, their underlying developmental origins have received relatively little attention, despite the widely recognized role of heterochrony in squamate evolution (Bhullar 2012; Andrews et al. 2013; Werneburg and Sánchez-Villagra 2015). Previous studies on squamate ontogeny have focused on convergence among closely related species (e.g., *Anolis*; Sanger et al. 2012, 2013) or morphological specializations such as body elongation and limb loss in fossorial taxa (Sanger and Brown 2004; Werneburg and Sánchez-Villagra 2015). However, widespread convergence is also observed across more generalized forms, particularly regarding cranial morphology (Stayton 2005, 2006; Urošević et al. 2013). Given its many functional interactions with the environment (e.g., feeding, habitat use, escape behavior, sensory systems; Stayton 2005), evolution of the squamate skull is likely influenced by ecology, with selection pressures changing as individuals grow. Moreover, because squamates exhibit indeterminate growth, reproduce at small sizes, and function independently from birth, the fitness consequences of ontogenetic changes are expected to be greater than for other terrestrial endotherms (Garland 1985).

Here, we investigate the developmental dynamics of cranial convergence in a transcontinental squamate radiation, the Lacertidae. Lacertids are a large (>300 species) family of small-bodied, mainly insectivorous lizards, which despite colonizing an extraordinary array of ecosystems throughout the Old World (e.g., desert, savanna, tropical rainforest, temperate grassland) are consid-

ered highly morphologically conservative (Fig. 1; Arnold 1989; Hipsley et al. 2014). Details of their evolutionary origins are obscure, but both the fossil record and outgroup comparison support a relatively mesic, Palearctic origin extending back into the Paleocene (Estes 1983; Müller et al. 2011). Most lacertids are terrestrial generalists; however, striking degrees of convergence have been reported among desert-dwelling forms, some of which for decades were considered a single genus (*Eremias*) based on putative synapomorphies (Arnold 1989, 1991). In contrast, molecular phylogenies reveal that these taxa independently invaded Asian and African arid zones multiple times (Fig. 2A), with members of separate subclades in Saharo-Eurasia, eastern, and southern Africa displaying large numbers of shared morphological traits (Mayer and Pavlicev 2007; Hipsley et al. 2009). These homoplasies are found in not only overall body proportions, likely related to locomotion (Edwards et al. 2012; Hipsley et al. 2014), but also cranial osteology (Arnold 1989, 1991). Many of their derived cranial features appear paedomorphic (Fig. 2B; Arnold 1989), although the correlation between cranial shape and ontogeny across the family has never been tested, nor has its relationship to ecological parameters (but see Piras et al. 2011 and Urošević et al. 2013 for Palearctic species).

In this study, we use 3D landmark-based geometric morphometrics to assess cranial variation in Lacertidae in relation to ecology (here, represented by biome), and to investigate the relative roles of adaptation and constraint in generating convergent cranial shapes. In particular, we focus on patterns of cranial convergence among independent arid-dwelling species in comparison to their basal, Palearctic relatives. We use allometry, or the scaling of biological shape with size, to distinguish between sources of morphological variation associated with growth (ontogenetic

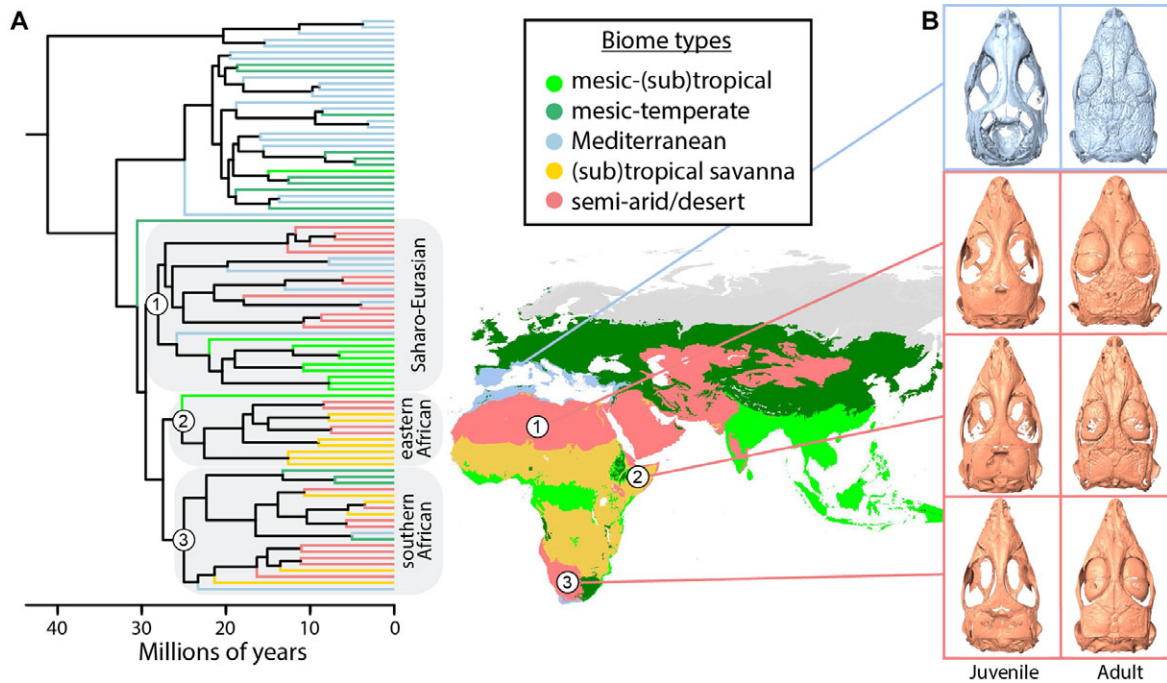


Figure 2. Lacertidae diversification patterns. (A) Evolutionary relationships of lacertid species in the present study based on the time-calibrated molecular phylogeny of Hipsley et al. (2014). Branch colors correspond to inhabited biome types (see map and inset). Numbered nodes indicate the origins of three independent subclades in Saharo-Eurasia, eastern, and southern Africa containing arid-dwelling members. The full tree with species names is given in Fig. S1. (B) Examples of juvenile and adult crania of species from each of the independent subclades (in pink) compared to their more mesic-dwelling Palearctic relative (in blue), illustrating the typical pedomorphic morphology of desert forms.

allometry), individual variability (static allometry), and phylogeny (evolutionary allometry). Given the phenotypic homogeneity observed in this clade, we expect allometries to be conserved among taxonomic levels, and that similar deviations from this relationship among convergent taxa will indicate adaptations to shared environmental factors, reflected by changes in underlying ontogenetic trajectories.

Material and Methods

MORPHOMETRIC DATA

Adult and juvenile ethanol-preserved specimens of Lacertidae were obtained from various collections (see Table S1 for details). Snout-vent length (SVL), together with the degree of cranial ossification, was used to determine the developmental stage of each individual as juvenile or adult. For CT scanning, whole preserved lizards were removed from ethanol, wrapped in bubble wrap, and transferred to a dry plastic tube. CT scans were performed at the Museum für Naturkunde Berlin in a Phoenix|x-ray Nanotom (GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany), or at the Helmholtz Centre Berlin for Materials and Energy using a microfocus X-ray tube (Hamamatsu, L8121-03) and flat panel sensor detector (Hamamatsu, C7942SK-05). X-ray parameters for each scan ranged from 60 to 110 kV, 110 to 500 μ A, 0.7 to 2s

exposure, and 500 to 1000 projections, resulting in a final voxel size of \sim 5–20 μ m.

Volumetric reconstructions were made in Datos|x-reconstruction software (GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany) or Octopus (Xraylab, Ghent, Belgium), and crania were isolated from the vertebrae and lower jaws in VGStudio Max 2.1 (Volume Graphics, Heidelberg, Germany). 3D isosurface models describing the cranium as a triangular mesh were extracted from the volume and digitally landmarked in Landmark Editor (Institute of Data Analysis and Visualization). Forty-eight homologous locations were chosen to describe cranial morphology in dorsal, lateral, and ventral views (see Fig. 3A and Table S2 for landmark details). The final dataset consisted 205 individuals (44 juveniles and 161 adults) from 92 species, representing all lacertid genera and \sim 30% of species diversity.

GEOMETRIC MORPHOMETRIC ANALYSES

Geometric information was extracted from the landmark data by a generalized Procrustes fit. The resulting Procrustes coordinates, representing the symmetric component of variation after translating, scaling, and rotating individuals to a common consensus, were used as shape variables in all analyses. Size

information, preserved in the centroid, was calculated as the square root of the sum of squared distances of landmarks to the center of their configuration. Centroid size was highly correlated with individual SVL ($R^2 = 0.92$, $F = 2218$, $P < 0.0001$). Because lizards exhibit indeterminate growth and therefore continue to grow throughout life, we considered centroid size to be a good proxy for relative age within species. We found no evidence of sexual dimorphism in cranial shape in a subset of individuals with known sexes (22 males, 23 females; ANOVA: $P = 0.13$). Therefore, for species with multiple specimens in the dataset, average adult shape and log-transformed centroid size (logCS) were used unless otherwise noted.

Due to the nonindependence of related species (Felsenstein 1985), phylogenetic comparative analyses were also performed based on the multigene supermatrix phylogeny of Hipsley et al. (2014), pruned to match our taxon sampling (Fig. S1). The original study included over 10k base pairs from 10 genes (five nuclear, five mitochondrial) for 202 lacertid species and one outgroup (Amphisbaenia). The resulting maximum clade credibility tree is in agreement with other topologies (e.g., Arnold et al. 2007; Mayer and Pavlicev 2007), recovering a basal Palearctic radiation followed by divergence of a predominantly African subfamily with its main groups corresponding to geographic distributions (Fig. 2A; Hipsley et al. 2014). Divergence dates, estimated using a Bayesian relaxed clock model and fossil-based calibrations, place their evolutionary origins in the mid-Eocene for crown clade Lacertidae and the Oligocene for African “Eremiadinae.”

Dominant features of cranial shape variation were identified by principal component analysis (PCA). To account for static allometry, that is, size-dependent shape variation, the Procrustes shape coordinates were regressed on logCS and the PCA was performed on the covariance matrix of the regression residuals. A permutation test using a multivariate generalization of the K -statistic (K_{mult} ; Adams 2014a) revealed significant phylogenetic structure in our data (see Section “Results”); we therefore tested the degree to which evolutionary allometry, or shape variation among species evolutionary associated with size, influenced cranial shape. A distance-based phylogenetic generalized least squares (D-PGLS) regression (equivalent to phylogenetically independent contrasts; Adams 2014b) of the Procrustes shape coordinates on logCS was calculated, and compared to predicted values simulated under a random model of Brownian motion to determine statistical significance. Differences between species cranial shape scores from the static and evolutionary allometry regressions were assessed by analysis of variance (ANOVA) with regression type, logCS, and their interaction as model effects.

Ecological associations

In addition to allometric variation, we tested if cranial shape varied ecologically, given its functional interactions with the envi-

ronment (Stayton 2005, 2006; Urošević et al. 2013). Previous studies have reported a climatic gradient in lacertid diversification patterns, along which basal taxa occur in relatively mesic areas, whereas advanced species are found in increasingly xeric habitats (Arnold 1981, 1991; Lamb and Bauer 2003). This transition is accompanied by the appearance of a numerous (>15) derived traits associated with survival in hot dry environments, including a complex septomaxilla, enlarged kidneys, keeled subdigital lamellae, and elongate hindlimbs (Arnold 1989; Arnold et al. 2007). To investigate whether large-scale climatic factors influence lacertid cranial morphology, we assigned species to biome types according to geographic distributions, with biome boundaries largely following a gradient of annual precipitation (Olson et al. 2001). For simplicity, some biome types were combined, for example, tropical and subtropical moist broadleaf forest, dry broadleaf forest, and coniferous forest were considered as a single mesic-(sub)tropical biome. In total, five biomes were identified to represent general climatic conditions experienced by lacertids: mesic-(sub)tropical, mesic-temperate, Mediterranean, (sub)tropical savanna, and semiarid/desert (Fig. 2A).

We first tested if cranial shape differed among ecological groups using Procrustes ANOVA, with biome as a factor. To account for allometric effects, tests were run using the size-corrected regression residuals, with and without phylogenetic correction (phylogenetic ANOVA; Adams 2014b). Next, morphological similarities within biomes were estimated using the distance-based convergence measure C_1 from Stayton (2015), which quantifies the amount of ancestral phenotypic space between putatively convergent taxa that has been “closed” by subsequent evolution. C_1 is calculated as the inverse ratio of the maximum Procrustes distance between lineages since sharing a common ancestor to the distance between their extant tips. Values range from 0 to 1, with 0 meaning that lineages are as dissimilar as they have ever been, and 1 indicating complete evolutionary convergence, that is, descendants are indistinguishable (Stayton 2015). To accommodate this test, any monophyletic clade containing members from the same biome were collapsed into a single taxon, represented by their average morphology (Fig. S2). To specifically assess whether arid-dwelling forms from the three independent subclades have evolved similar cranial shapes, C_1 was computed for the species of those groups that were closest to each other in morphospace. Scores from the first 42 size-corrected PC axes, accounting for 99% of the total morphological variation, were used as phenotypic variables.

Finally, morphological characters distinguishing biomes were identified using between-group PCA (bgPCA), involving a projection of the species residual shape data onto the eigenvectors of the group means. In contrast to other multivariate methods such as discriminant function or canonical variates analyses, bgPCA axes are orthogonal and can be computed when data are

not full rank, and when covariance matrices are nonisotropic (Mitteroecker and Bookstein 2011), making it statistically appropriate for high-dimensional landmark data.

Ontogenetic allometry

To determine the extent to which ontogenetic allometry contributes to patterns of adult cranial shape variation, we constructed growth trajectories for all species represented by juvenile and adult specimens ($N = 92$, 21 species, 2–11 specimens/species, average = 4.4; Fig. S1; Table S1). A preliminary homogeneity of slopes test supported the null hypothesis of parallel slopes, therefore ontogenetic trajectories were estimated using a pooled within-species regression of the Procrustes shape coordinates on logCS. This approach is optimal for sampled specimen series that differ in size and/or age structure, as groups with little size variation that can produce unreliable estimates of allometry are weighted less in the estimation of within-group allometry than those with large sampled ranges (Klingenberg 2016). To test if the nonallometric portion cranial ontogeny varied ecologically, indicating adaptation, residuals from the species-specific regression were used as shape variables in a Procrustes ANOVA, with logCS and species nested in biomes as model effects. Statistical results together with plots of the common and residual shape components aided in biome-level comparisons.

All analyses were made in MorphoJ v. 1.06d (Klingenberg 2011), except for K_{mult} , D-PGLS, and ANOVA, which were estimated in the geomorph v. 3.0.3 package of R (Adams et al. 2015), and C_1 calculated in the R package *convevol* v. 1.0 (Stayton 2015). Statistical significance ($\alpha = 0.05$) was determined by a random permutation procedure of 10,000 iterations, except in *convevol* which was run for 1000. Allometric patterns were visualized as shape change per unit size increase, with the cranial shape score calculated as the amount of variation predicted by the multivariate regression model, plus the residual variation in the direction of the independent vector (Drake and Klingenberg 2008). Cranial wireframes or warps were generated to illustrate the direction of landmark shifts along each vector, scaled to reflect the magnitude of estimated shape change.

Results

DIVERSIFICATION OF THE LACERTID CRANIUM

The majority of adult cranial shape variation was contained in relatively few dimensions, with the first three PCs accounting for half (49%) of the total variance. After removing the effects of static allometry ($R^2 = 0.191$, $F = 21.234$, $P < 0.0001$), the main axes of interspecific variation described changes in the size of the orbits, achieved by shortening or lengthening of the postorbital region (i.e., (post(orbito-)frontals, parietal) and lateral movement

of the jugals (PC1), relative length of the snout and depth of the cranium in lateral view (PC2), and pinching or widening of the skull laterally (PC3) (Fig. 3B).

Cranial shape exhibited significant phylogenetic structure ($K_{\text{mult}} = 0.652$, $P = 0.0001$); however, many groups overlap in morphospace and several lie more distant from the central scatter of points (Fig. 3B). Extreme morphologies are found in arid-dwelling species with exceptionally large orbits and nares (small desert-dwelling *Meroles* and *Pseuderemias* from southern and eastern Africa, respectively, but also larger-bodied *Acanthodactylus* from northern Africa), flat skulls and long snouts (equatorial arboreal *Holaspis*, crevice-dwelling *Dalmatolacerta* and *Omanosaura*), and relatively short deep skulls (*Nucras landii*). Outliers along the third PC include *Holaspis* and other crevice-dwellers with laterally expanded suborbital fenestrae (but not larger orbits), and the slender Asian grass-climbing species *Takydromus sexlineatus*.

After accounting for phylogenetic relatedness, the portion of cranial shape variation due to evolutionary allometry ($R^2 = 0.187$, $F = 20.639$, $P < 0.0001$) was nearly identical to that due to static allometry (Fig. 4; ANOVA: $F = 0.27$, $P = 0.604$).

ECOLOGICAL PATTERNS OF CRANIAL SHAPE VARIATION

Cranial shape differed significantly among ecological groups, even after correcting for phylogeny (Table 1A). A *post hoc* test of pairwise distances revealed that all but two comparisons were statistically different: mesic-temperate versus Mediterranean and mesic-temperate versus mesic-subtropical (Table 1B). The strength of cranial similarities within biomes, however, varied in distance-based analyses, with only one group exhibiting significant morphological convergence (Table 2). Comparison of representatives from each of the three subclades with members in the semiarid/desert biome (*Acanthodactylus boskianus*, *Meroles cuneirostris*, and *Pseuderemias brenneri*) produced a C_1 of 0.175, indicating that nearly 18% of the phenotypic distance between these lineages has been closed by convergent evolution. In contrast, taxa in other biomes have not evolved to be closer to each other than is expected by chance, at least according to the cranial landmarks examined here. This pattern is also reflected in the PC plots in Figure 3B, showing the arid-dwelling group as having many clustered outliers from disjunct geographical regions.

Similar ecological influence was observed in the bgPCA, which showed overlap of mean values for mesic groups, whereas arid forms appear more distinct (Fig. 5). Over half of the morphological variation among biomes was captured in the first component (bgPC1), describing differences in facial angle and orbital diameter. These changes follow a gradient of environmental aridity, along which species inhabiting increasingly xeric biomes

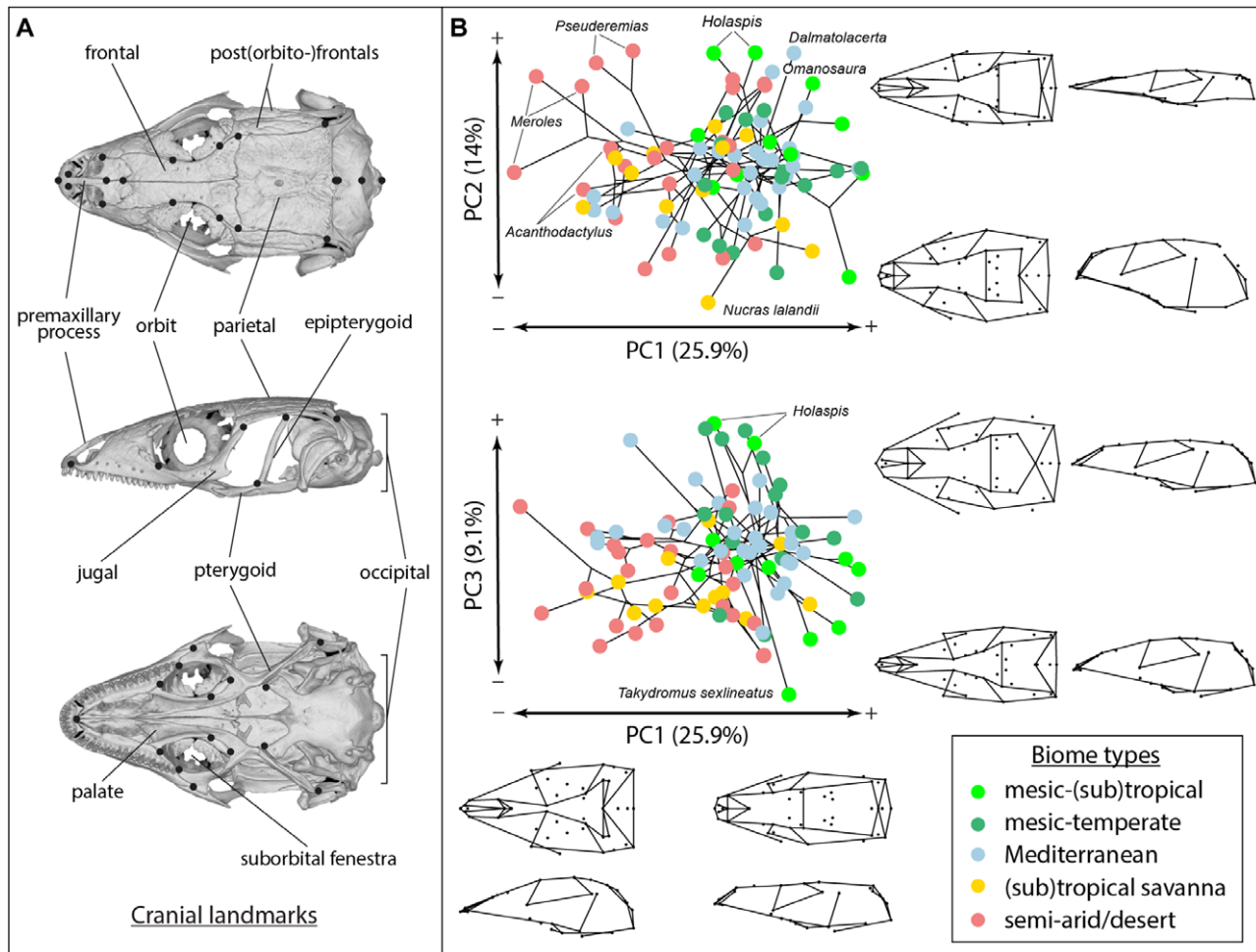


Figure 3. Lacertid adult cranial shape variation. (A) Locations of 48 cranial landmarks in dorsal, lateral, and ventral views used in morphometric analyses. Bones discussed in the text are labeled. (B) Scatter plots of species scores from the first three PC axes. The phylogeny in Figure 2A was projected into shape space using weighted square-changed parsimony (Klingenberg 2011) with species colors corresponding to inhabited biome types (see inset). Wireframes represent positive and negative shape extremes at the ends of each axis, based on the cranial landmarks.

exhibit disproportionately larger orbits and nares relative to mesic forms. In arid taxa this appears as a shovel- or wedge-shaped snout, in which the premaxillary process extends posteriorly to meet the nasals far back on the face, leaving two dorsally exposed channels for nares. Enlargement of the orbits (but not suborbital fenestrae) pushes the postorbital region back, whereas the occipital is shifted forward and down, lending a bulbous appearance to the cranium in lateral view. Large orbits also cause the frontals, which are fused in arid taxa (Arnold 1989), to become laterally pinched at their midpoint but wider where they meet the parietal, which is itself more wide than long. In most mesic and Palearctic forms, the parietal is longer than wide and the cranium tends to be long and slender, with fairly uniform depth and small eyes and nares. Biome separation is less distinct along bgPC2 (Fig. 5), reflecting gradual changes in the width of the palatal region and depth and length of the back of the skull.

EVOLUTIONARY SHIFTS IN CRANIAL ONTOGENY

Scaling of cranial shape with size during ontogeny was similar to that among adults ($R^2 = 0.21$, $F = 23.938$, $P < 0.0001$), with many species trajectories overlapping in allometric space (Fig. 6A). Size-related changes associated with the common allometric component (CAC, sensu Mitteroecker et al. 2004) mirror static and evolutionary allometries, by which the orbits and nares become proportionately smaller as the head grows longer and thinner. In contrast, when comparing the nonallometric component of ontogenetic variation among biomes, the y -intercepts of their regression lines differed but their slopes did not (Table 3), generating distinct parallel trajectories for each group. Examination of the first residual shape component (RSC1) against CAC revealed arid-adapted forms to be strongly downshifted along the y -axis, without accompanying changes in overall size (logCS or SVL; Table 3; Fig. 6B). Negative movement along RSC1 reflects

Table 1. Lacertid cranial shape variation among biomes.

(A)	df	SS	MS	R^2	F	Z	P
Biome	4	0.063	0.016	0.160	4.146	3.553	<0.0001
Biome (phylogenetic)	4	0.002	0.000	0.082	1.948	1.610	0.015
(B)	(sub)tropical savanna	Mediterranean	mesic-(sub)tropical	mesic-temperate	semiarid/desert		
(sub)tropical savanna	–	0.0389	0.0533	0.0460	0.0368		
Mediterranean	0.0040	–	0.0381	0.0258	0.0380		
mesic-(sub)tropical	0.0003	0.0073	–	0.0344	0.0591		
mesic-temperate	0.0017	0.1095	0.0658	–	0.0552		
semiarid/desert	0.0101	0.0002	0.0001	0.0001	–		

(A) Procrustes ANOVA results before and after phylogenetic correction. (B) Pairwise Procrustes distances of cranial shapes (above the diagonal) and P values for the null hypothesis of equal means (below the diagonal). Significant Procrustes distances and P values are in bold.

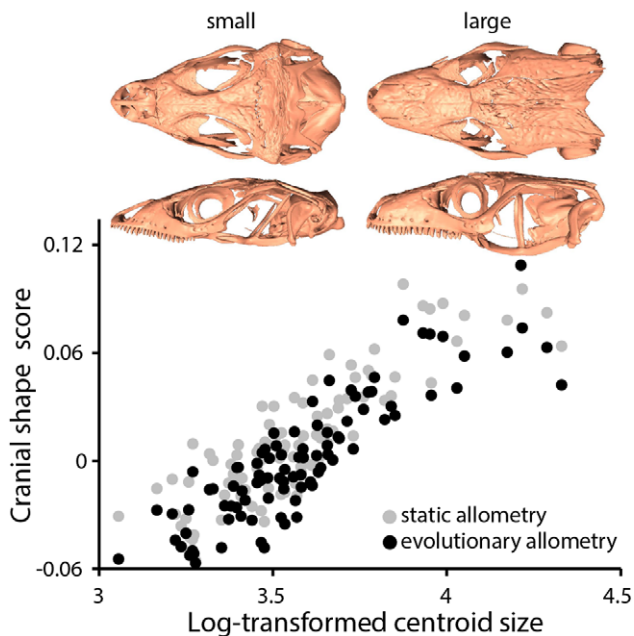


Figure 4. The relationship between static and evolutionary allometry in Lacertidae, with warped cranial surfaces illustrating small and large size extremes. Circles represent species scores from a multivariate regression of the Procrustes shape coordinates on size (gray) and after phylogenetic correction (black). Small heads tend to be wide with large orbits and large dorsally exposed nares, whereas large heads are slender with small orbits and frontally oriented nares. Size-associated changes also affect the postorbital region of the skull: in smaller species the supraoccipital is dorsally exposed and separated from the parietal by a large gap, and dorsoventral depression of the cranium causes the epipterygoids to lie diagonally toward the lateral edges of the skull. In larger species the braincase lies directly beneath the parietal table, causing a deepening of the cranium and upright position of the epipterygoids in lateral view.

Table 2. Phenotypic distance measure of lacertid species within biomes, representing the proportion of historical ancestral morphospace between lineages that has been closed by convergent evolution.

Biome	C_1	P
Mediterranean	0.013	0.878
mesic-(sub)tropical	0.087	0.087
mesic-temperate	0.034	0.139
semiarid/desert	0.175	0.003
(sub)tropical savanna	0.021	0.418

Values closer to 1 indicate greater morphological similarity. Significant P values are in bold.

a shortening of the postorbital region (post(orbito-)frontals, parietals) and lengthening of the snout, such that at any equivalent developmental stage, arid forms possess larger orbits and nares, and thus appear more juvenile-like, than lacertids from other environments. This deviation from the common allometry is manifest at the beginning of the postnatal period, indicating that differences in cranial proportions are present in early (prenatal) ontogeny, but follow a conserved allometric trajectory after birth.

Discussion

DEVELOPMENTAL BASIS OF ECOMORPHOLOGICAL CONVERGENCE

Under a strict constraint hypothesis, evolutionary allometry is expected to follow static allometry, and most morphological variation should be generated by differences in body size across populations or species (Voje et al. 2014). Despite significant phylogenetic signal in lacertid cranial shape, we found allometries to be remarkably conserved across taxonomic levels, accounting for approximately 20% of intraspecific variation. Similar size-dependent changes were observed among distantly

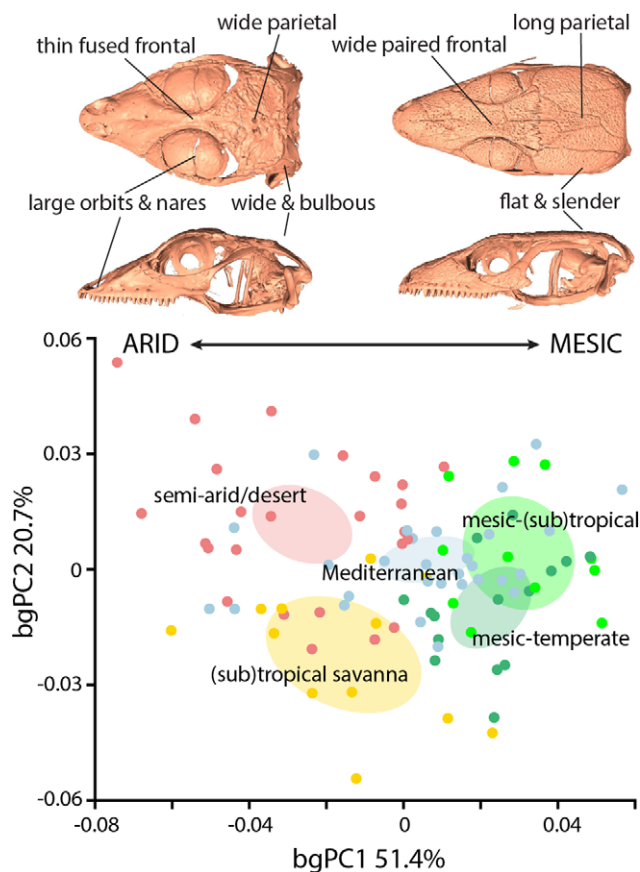


Figure 5. Ecological variation in lacertid cranial shape. Between-group PCA of size-corrected species scores, with shaded ellipses containing the 90% confidence interval of the biome means. Major shape changes (bgPC1) follow a gradient of environmental aridity from arid to mesic, as illustrated by species from arid (left, *Meroles cuneirostris*) and mesic (right, *Gastropholis vittata*) extremes.

related lineages in disjunct geographical regions, demonstrating that allometric relationships are maintained over large temporal and spatial scales. In contrast, the nonallometric component of cranial shape left after removing the effects of size showed significant differences between biomes, indicating adaptations to environmental factors. The majority of phenotypic outliers were species with specialized ecologies, most notably desert-dwelling forms and those habitually using crevices (Fig. 3B). When plotted against inhabited biome types, the major axis of phenotypic variation followed a gradient of environmental aridity with

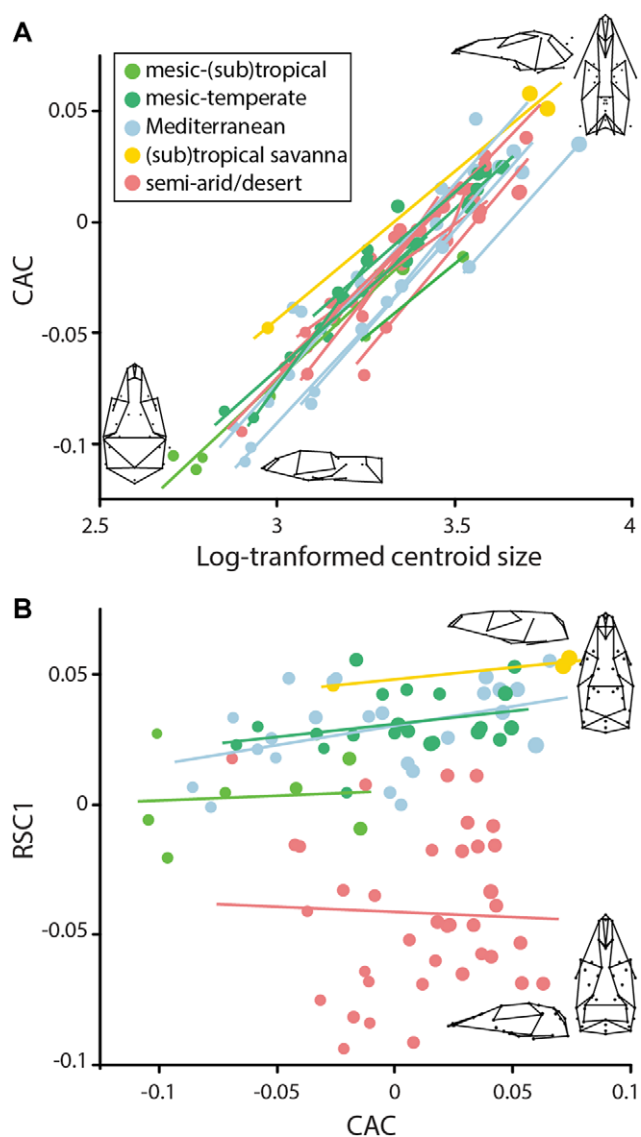


Figure 6. Lacertid ontogenetic allometry. Ontogenetic trajectories of lacertid cranial shape among (A) species and (B) biomes with spot size proportional to individual snout-vent length. Colors correspond to biome types (see inset). (A) The common allometric component (CAC) against size, representing the average allometric trend within species. (B) The first residual shape component (RSC1) against CAC, with RSC1 estimated as the first principal component of the residual shape coordinates, sensu Mitteroecker et al. (2004). Lines of best fit were added to each bivariate plot to reflect trends in multivariate space, with cranial wireframes illustrating ontogenetic changes.

Table 3. Procrustes ANOVA results of species ontogenetic trajectories among biomes.

	df	SS	MS	R^2	F	Z	P
LogCS	1	0.0103	0.0103	0.0186	4.3968	1.5011	0.0936
Species in biome (y-intercept)	16	0.1823	0.0114	0.3301	4.8729	2.9801	0.0001

Residuals from the pooled within-species regression were used as shape variables. LogCS = log-transformed centroid size. Significant P values are in bold.

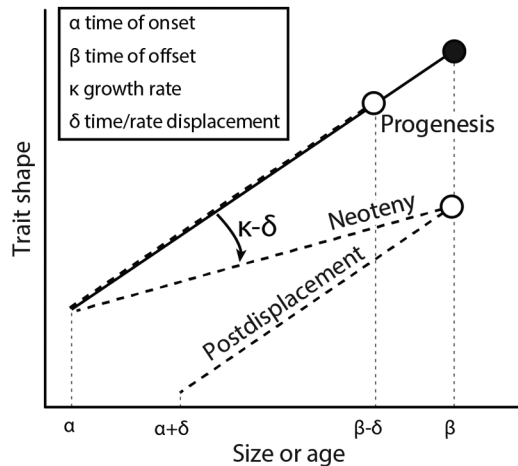


Figure 7. Heterochronic perturbations of growth parameters generating paedomorphosis through delayed onset of growth (postdisplacement), early termination (progenesis), and decreased developmental rate (neoteny). The ancestral growth trajectory is indicated by a solid line with a black circle at its termination. Figure modeled after Alberch et al. (1979) and Klingenberg (1998).

arid-adapted species possessing disproportionately larger orbits and nares than their mesic-dwelling relatives (Fig. 5).

Within Lacertidae, independent origins of arid-dwelling lineages in Sahara-Eurasia, eastern and southern Africa are currently recognized, composed of up to seven distinct genera (Mayer and Pavlicev 2007; Hipsley et al. 2009). Many of these species cluster in morphospace at the ends of long phylogenetic branches (Fig. 3B), converging on a novel cranial shape after nearly 30 million years of independent evolution. The degree of phenotypic similarity among arid-dwelling lineages, as indicated by the distance-based measure C_1 , was significantly greater than would be expected by chance, further supporting an adaptive process. Many of their shared derived features are found in juveniles (but not adults) of basal Palearctic taxa, including large narial openings, narrow frontals, a short broad parietal, and an overall decrease in cranial ossification (Arnold 1989). When comparing the nonallometric component of cranial growth among biomes (a significant predictor of adult cranial shape), we observed differences in elevation of the ontogenetic slope associated with the above traits, with arid-adapted forms shifted to the negative side of RSC1 (Fig. 6B). This divergence from the common allometry is independent of variation in head size or SVL in adults, thus rejecting the hypothesis that cranial shape differences are driven by scaling with body size alone.

Parallel shifts of the ontogenetic trajectory, known as lateral transposition, involve a dissociation of size and shape among traits prior to the analyzed period, meaning that alterations in growth dynamics occurred in an earlier developmental stage (Klingenberg 1998). Decrease in y-intercept of a constant ontogenetic slope, as

observed in the residual shape component of arid-dwelling lacertids, is consistent with the definition of allometric postdisplacement, one of three heterochronic processes leading to paedomorphosis (Alberch et al. 1979; Fig. 7). According to this definition, when a trait begins to grow later in the descendent without accompanying changes in rate (i.e., slope), for any given body size that trait will appear smaller than in the ancestor, leading to a lower y-intercept (Klingenberg 1998). Our results indicate that the convergent paedomorphic appearance of arid-dwelling lacertids is achieved through delayed onset of growth for certain cranial elements (e.g., post(orbito-)frontals, frontals, parietal) relative to the ancestral state, leading to the retention of juvenile characteristics throughout the postnatal period.

Allometric postdisplacement has been observed in diverse groups, including fish (Frédérich and Sheets 2010), insects (Klingenberg and Spence 1993), amphibians (Larson 2005), rodents (Verzi et al. 2010), and even early hominins (e.g., Neanderthal and *Homo sapiens*; Bastir et al. 2007). These shifts tend to be more pronounced than changes in allometric slope, leading some to argue for greater evolutionary flexibility during early (prenatal) ontogeny than for rate changes later in life (Klingenberg 1998; Voje et al. 2014).

In contrast to the previous prediction that the more the distantly related species are, the more likely one is to observe changes in ontogenetic slope (Weston 2003; Wilson and Sánchez-Villagra 2010), our results imply that directional changes during postnatal ontogeny are selected against, as novel allometries generate new phenotypic proportions that can break down functional relationships between traits. This would be particularly relevant for squamate reptiles, which lack parental care after birth and emerge as fully functional young (Garland 1985). As such, the consequences of changes in allometry may be too great on morphological integration to modify postnatal growth rate without a cost to individual fitness.

POTENTIAL TARGETS OF SELECTION

Habitat use has been shown to be a strong selective force on patterns of diversification, with documented effects on rates of size and shape change in various lizard groups (e.g., varanids, Collar et al. 2010, Openshaw and Keogh 2014; iguanians, Blankers et al. 2013). Whereas most studies of lacertid morphology have tested for correlations between external body measurements and aspects of microhabitat use such as rock versus ground (Orriols et al. 2011) or open versus closed (Edwards et al. 2012), our results show that large-scale climatic factors, such as availability of water, may also be important determinants of adult phenotype in this clade. This is especially apparent among arid-adapted forms, because species in the semi-arid/desert biome use a variety of structural niches including sandy and stony soils with grasses and bushes (*Ichnotropis*, *Philochothus*), rocky or compact

substrate with sparse vegetation (*Mesalina*, *Pedioplanis*, *Pseud-eremias*), loose aeolian sand and dunes (*Meroles*), or a mixture of the above (*Acanthodactylus*, *Eremias*) (Arnold 1989). Although saxicolous habits have been shown to directly influence squamate head morphology (Revell et al. 2007; Openshaw and Keogh 2014), the lack of a consistent relationship between head shape and microhabitat use in lacertids (e.g., Vanhooydonck and Van Damme 1999; McBrayer 2004; Verwajen and Van Damme 2007; Edwards et al. 2012) further supports the hypothesis that forces other than habitat structure are driving cranial similarities in arid regions.

While heterochronic processes are often interpreted as outcomes of selection on the morphological structures they affect (McNamara 1990), we propose that other factors such as life-history strategy may be the primary targets of selection, generating phenotypic changes as a by-product of allometric scaling with other traits (e.g., age at sexual maturity, longevity). Variation in reproductive investment has been shown to be a critical component of fitness in arid-dwelling taxa (e.g., plants; Venable 2007, rodents; Bronson 2009, invertebrates; Punzo 2000), favoring sets of coadapted traits to cope with environmental stress such as limited water, extreme heat, and solar radiation. Particularly among lizards, climatic variables such as temperature and precipitation can have a greater influence on development than differences in microhabitat (Adolph and Porter 1993), leading to the evolution of convergent reproductive strategies in distantly related species (Sun et al. 2013). Similar developmental plasticity has been demonstrated in lacertids, which in areas of low productivity (via low rainfall) lay smaller clutches of larger, more rapidly growing offspring than conspecifics from higher elevations (Iraeta et al. 2012). Both in these and other groups, such populational differences in life history may become genetically fixed over time, giving rise to highly adapted local forms (Du et al. 2010; Iraeta et al. 2012).

Although detailed life-history data are lacking for most arid-dwelling lacertids, current evidence suggests that at least among Namib Desert forms (*Meroles*), individuals are short-lived, mature quickly, and produce multiple clutches of few, relatively large young (Robinson and Barrows 2013). This observation is congruent with heterochronic patterns in other taxa, most notably various clades of salamanders that exhibit a close relationship between specific reproductive traits (i.e., early maturation, increased survival to first reproduction, shortened generation times) and paedomorphosis (Ryan and Semlitsch 1998; Denoël and July 2000; Bonett et al. 2014). Future studies incorporating information on age-specific fecundity and survival in lacertids would make it possible to compare the reproductive success of alternative developmental pathways, thereby linking them to selective pressures in different environments. Because early reproduction also contributes to a high intrinsic rate of natural increase (Denoël and

July 2000), we expect that selection for paedomorphosis in lacertids would have been particularly strong following colonization of desert regions, which are characterized by harsh climatic conditions and increased competition for limited resources. Under such a scenario, adaptive allometries may not only give rise to convergent morphologies, as shown in distantly related lacertids, but may also be implicit in the evolutionary success of arid-dwelling groups, generating a positive feedback loop of selection, heterochrony, adaptation, and diversification.

IMPLICATIONS FOR SQUAMATE PHYLOGENETICS

Heterochrony is a common phenomenon in squamate evolution, responsible for diverse morphological transformations including cranial kinesis (Tarazona et al. 2008), miniaturization (Bhullar 2012), limb reduction (Werneburg and Sánchez-Villagra 2015), and body elongation (Sanger and Gibson-Brown 2004). Our study demonstrates that at least during lacertid ontogeny, both ecology (e.g., crevice-dwelling) and environment have a strong influence on cranial shape, potentially via selection on adaptive life-history strategies. Given that convergent morphologies in response to selection tend to obscure evolutionary relationships, allometric information could play an important role in choice of characters for phylogenetic reconstruction (Weston 2003). In this study, we identified size-dependent changes in the position of the braincase, the anteroposterior extent of postorbital and postfrontals, depth of the cranium, and angle of the epipterygoids within the cranial cavity. In contrast, ecological variation was mainly reflected in the shape of the snout and inter- and postorbital regions, size of the suborbital fenestra, and overall facial angle. When this variation is partitioned into discrete morphological characters traditionally used in squamate systematics, we found that at least 12 characters from the most recent analysis (Gauthier et al. 2012: #29, #48, #49, #67#, #76, #77, #96, #99, #118, #160, #271, #291) may not only be inappropriate for deciphering lacertid relationships, but are also likely to be positively misleading.

For several decades, desert lacertids were falsely thought to be monophyletic (Arnold 1989), and many others were placed in groups that are now considered artificial based largely on the above mentioned traits. Given the influence of ontogenetic variation on many aspects of squamate morphology, we predict that similar effects will be present in other clades of lizards and snakes, posing substantial problems for the use of morphological characters in squamate phylogenetics. This represents a serious challenge for multiple biological disciplines, as many squamate groups serve as model systems for studies of morphology (Stayton 2005; Gauthier et al. 2012), behavior (Garland 1985), ecology (Losos 2009), and reproduction (Adolph and Porter 1993; Du et al. 2010; Iraeta et al. 2012; Sun et al. 2013). As such, the accuracy of squamate phylogenetic relationships is critical to our generalizations of diverse evolutionary phenomena.

Conclusions

Whether convergent evolution is driven by adaptation or constraint is the subject of long-standing biological debate in which allometry—the covariation between size and shape—plays a central role (Klingenberg 1998; Gould 2002; Klingenberg 2010; Pélabon et al. 2014; Voje et al. 2014). Although allometry has long been considered a phenotypic constraint (Klingenberg 2010), our results show that evolutionary flexibility during early ontogeny can produce convergent morphological adaptations over deep phylogenetic time scales, without the need of de novo developmental systems. In contrast to a strict dichotomy (i.e., adaptation vs constraint), we suggest that allometric relationships represent a continuum of developmental flexibility allowing species to respond to environmental change via the rapid evolution of adaptive life-history traits, thus shaping macroevolutionary patterns of diversification. Finally, our study emphasizes the power of allometry as a quantitative framework for the investigation of convergence in complex morphological features, even in the absence of known genetic or developmental mechanisms.

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DATA ARCHIVING

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Supporting Information

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

- Figure S1.** The complete species tree of Lacertidae used in the present study, based on the time-calibrated molecular phylogeny of Hipsley et al. (2014). Species included in ontogenetic analyses are indicated with an asterisk (*).
- Figure S2.** The simplified lacertid phylogeny used in distance-based convergence tests.
- Table S1.** Lacertid specimens examined in the current study, with snout-vent length, developmental stage (juvenile or adult), and assigned biome.
- Table S2.** Locations of 48 landmarks placed on dorsal, posterior, and ventral sides of the cranium.