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Evolutionary biology

Morphological disparity opposes latitudinal diversity gradient in lacertid lizards

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While global variation in taxonomic diversity is strongly linked to latitude, the extent to which morphological disparity follows geographical gradients is less well known. We estimated patterns of lineage diversification, morphological disparity and rates of phenotypic evolution in the Old World lizard family Lacertidae, which displays a nearly inverse latitudinal diversity gradient with decreasing species richness towards the tropics. We found that lacertids exhibit relatively constant rates of lineage accumulation over time, although the majority of morphological variation appears to have originated during recent divergence events, resulting in increased partitioning of disparity within subclades. Among subclades, tropical arboreal taxa exhibited the fastest rates of shape change while temperate European taxa were the slowest, resulting in an inverse relationship between latitudinal diversity and rates of phenotypic evolution. This pattern demonstrates a compelling counterexample to the ecological opportunity theory of diversification, suggesting an uncoupling of the processes generating species diversity and morphological differentiation across spatial scales.

1. Introduction

The ecological opportunity theory predicts a link between spatial variation in taxonomic diversity and morphological disparity, as the exploitation of newly available niches is associated with phenotypic differentiation and consequently, speciation [1]. Despite widespread evidence of a latitudinal bias in diversification rates (i.e. higher rates at lower latitudes [2–4]), the extent to which morphological differentiation follows latitudinal gradients is less well known, because rates of phenotypic evolution have not been estimated for any single clade across a broad geographical range.

Here, we investigate this issue using comparative phylogenetic approaches in Lacertidae, a large family of lizards with an Old World distribution extending from the Arctic Circle to the Cape of Africa. In contrast to the global pattern of increasing diversity towards the tropics, lacertids display a nearly inverse latitudinal gradient along which species richness is lowest around the equator and highest in southern African and Mediterranean regions [5]. Previous studies indicate recent and rapid diversification of desert-dwelling lineages, accompanied by the appearance of numerous derived morphological traits [6,7]. Despite these signatures of adaptive radiation, the hypothesis that these clades exhibit elevated rates of morphological evolution has yet to be tested. Furthermore, the unusual pattern of species richness in Lacertidae presents a unique opportunity to explore morphological variation along latitudinal gradients, and to address the question of whether disparity and diversity vary in tandem.

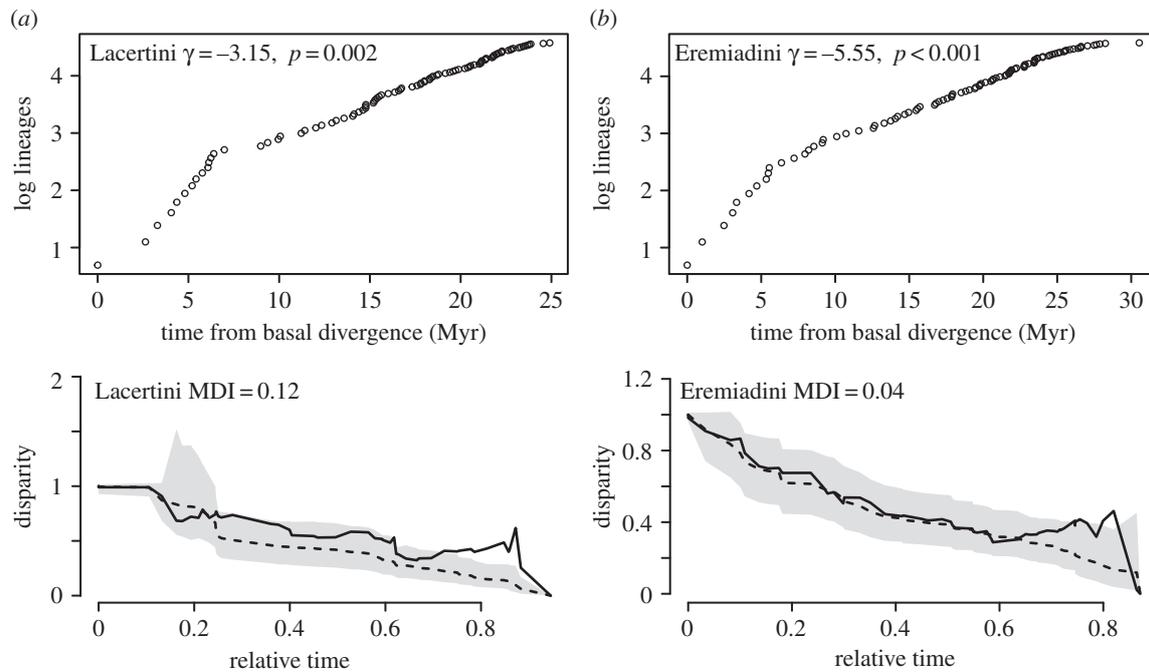


Figure 1. Lineage-through-time plots with γ and MCCR-corrected p -values, and relative disparity-through-time plots with the MDI for Lacertini (a) and Eremiadini (b). MDI was estimated as the difference between the observed (solid line) and median (dashed line) disparities simulated under BM. Grey shading indicates the 95% confidence interval of the null model.

2. Material and methods

A time-calibrated phylogeny of Lacertidae was constructed based on a 10 kb supermatrix of 10 genes (electronic supplementary material, table S1). We first tested whether lacertid subfamilies exhibit phylogenetic signatures of adaptive radiation (i.e. early bursts of cladogenesis) using the γ -statistic [8]. Significantly negative values ($\gamma \leq -1.65$) describe trees with branching events concentrated near the root, indicating deceleration of diversification rates towards the present. Because missing taxa can also give the appearance of temporal slowdowns, we corrected for undersampling using the Markov chain constant-rates (MCCR) test [8]. The critical γ -value for rejecting a constant rate was determined from the 0.05 quantile of the null γ distribution, estimated from 10 000 simulated pure-birth trees randomly pruned to match our sampling (less than 37% missing taxa).

Morphological variation was quantified from a set of linear measurements for 132 species, representing nearly two-thirds of the phylogeny (electronic supplementary material). Temporal patterns of morphological evolution were visualized in disparity-through-time plots [9], in which disparity equals the mean-squared Euclidean distance between species principal component (PC) scores (electronic supplementary material, table S2). The morphological disparity index (MDI), an indicator of among- versus within-subclade variation, was calculated as the area between the observed and expected median disparities estimated from 10 000 simulations of Brownian motion (BM) character evolution [9]. A negative MDI is characteristic of adaptive radiations, as rapidly diversifying taxa are expected to evolve distinct morphologies in response to new adaptive zones and slow once niches are filled, resulting in greater phenotypic variation among subclades [9].

To identify lineages driving observed disparity patterns, we compared rates of phenotypic evolution among subclades using the time-independent variance parameter $\hat{\sigma}^2$ [10]. Subclades were defined as non-overlapping, monophyletic groups largely corresponding to geographical distributions. For each pruned subtree, a matrix of evolutionary rates and their estimated covariances among traits was generated under BM. To obtain a single rate of shape change across all variables (PC axes 1–5), the sum of the diagonal elements in the matrix was

calculated following [11]. A higher rate of phenotypic evolution ($\hat{\sigma}^2$) for a given clade indicates greater accumulation of disparity per unit time, and thus more dissimilar taxa. All analyses were made in R packages APE v. 3.0 [12] and GEIGER v. 1.3 [13].

To determine whether morphological evolution varies along geographical gradients, we compared rates of phenotypic evolution among subclades with their latitudinal midpoints (electronic supplementary material, table S3) using phylogenetically independent contrasts calculated in Mesquite [14]. We also examined relationships between estimated rates and subclade-level attributes using linear regression, including clade size and clade age.

3. Results

Both Lacertini and Eremiadini display moderate temporal slowdowns in lineage accumulation, with observed negative γ -values significantly different from the simulated null distribution (figure 1). By contrast, the subfamily Gallotiinae maintains a nearly constant rate over time ($\gamma = -0.5$, $p = 0.21$; electronic supplementary material, figure S1a). Within-subclade disparity is greater than expected for the majority of lacertid evolution, as indicated by low but positive MDIs for each group (figure 1; Gallotiinae MDI = 0.147; electronic supplementary material, figure S1a). However, temporal patterns of disparity accumulation vary, with Eremiadini closely matching the null (BM) model over most of its history. Lacertines experience a slight drop in relative disparity concurrent with an increase in diversification at approximately 16–19 Ma, implying that the initial burst of cladogenesis was accompanied by increased phenotypic variation among subclades. Both clades exhibit recent (less than 7 Ma) disparity peaks, most likely not as a result of missing taxa (see Discussion). A subset of morphological data including tail length reflects similar patterns (electronic supplementary material, figure S1b).

Estimated rates of phenotypic evolution vary among subclades (figure 2a) and for datasets with and without tail

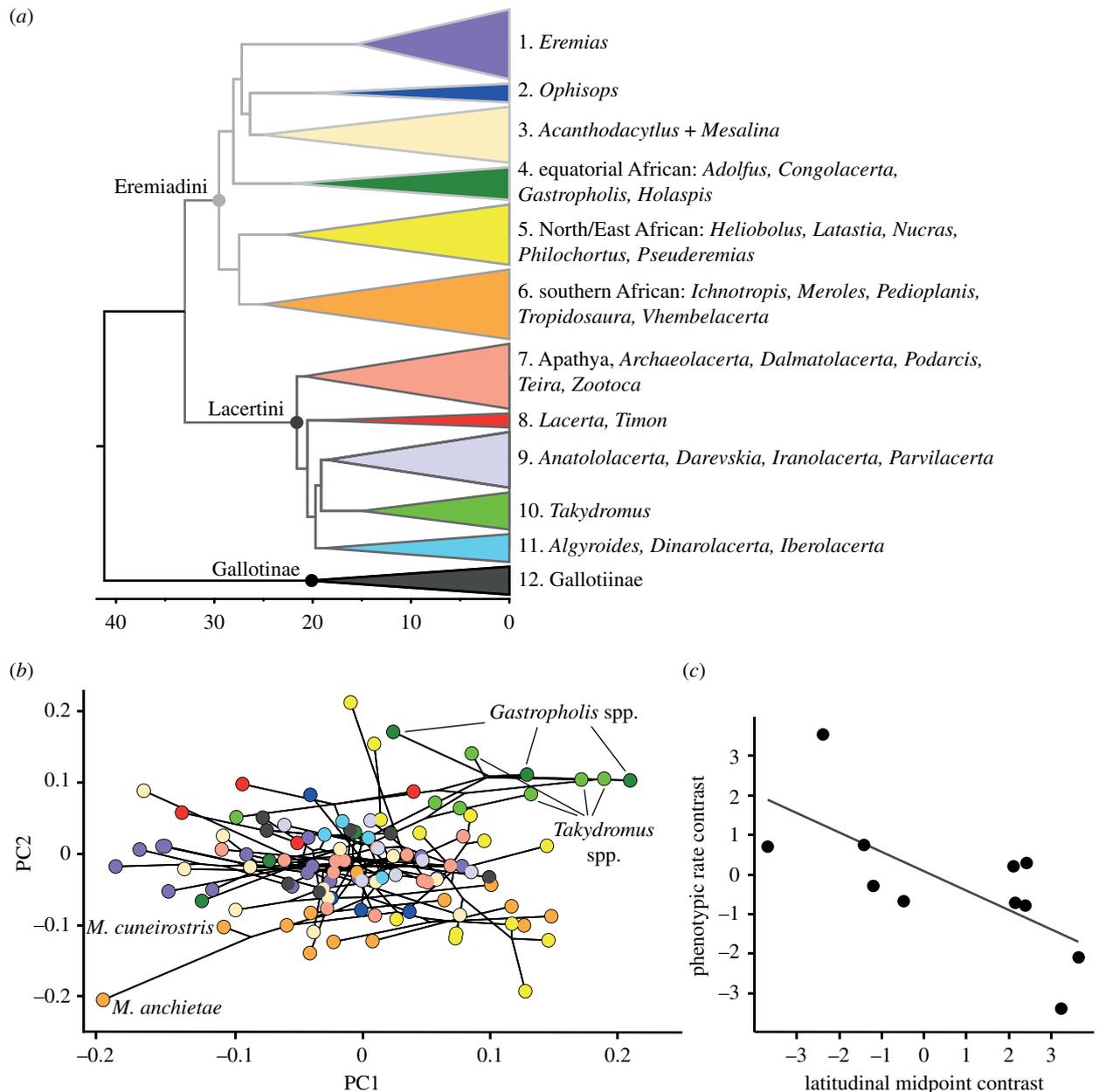


Figure 2. (a) Simplified lacertid phylogeny of 12 subclades used to estimate rates of phenotypic evolution. (b) Phylomorphospace plot, based on the subset of morphological data including tail length. Black lines connect related taxa through hypothetical ancestors, as reconstructed using maximum likelihood in Mesquite [14]. Species colours match subclade assignments in (a). (c) Phylogenetically independent contrasts between subclade phenotypic rate and latitudinal midpoint, showing that as latitude increases, phenotypic rate decreases.

length (table 1). Two groups show consistently high rates: *Acanthodactylus* + *Mesalina*, consisting of 54 species distributed across the subtropical arid belt of Africa and the Middle East, and the equatorial African clade, which, although nearly equal in age, contains only 11 species (the primarily arboreal *Adolfus*, *Congolacerta*, *Gastropholis* and *Holaspis*). Inclusion of tail length increases rates of phenotypic evolution for nearly every group, most notably equatorial African taxa and east Asian grass lizards, *Takydromus*, both of which are characterized by elongated forelimbs and tails. These taxa overlap morphologically far from their closest relatives (figure 2b), suggesting evolutionary convergence in response to vertical climbing. In the opposite region of phylomorphospace, Namib dune-dwelling species *Meroles anchietae* and *Meroles cuneirostris* are also separated by long branches, reflecting relatively long hindlimbs and short tails advantageous for running on loose sand [15].

Latitudinally, we find a significant inverse relationship between rates of phenotypic evolution and clade ranges ($r = -0.705$, $p < 0.01$; figure 2c), meaning that taxa closer to the equator tend to have faster rates of shape change than those further away. Estimated rates were independent of clade size (actual and sampled) and age ($p > 0.17$ for all comparisons), suggesting that phylogenetic structure does not determine latitudinal disparity gradients in Lacertidae.

4. Discussion

We found no evidence of adaptive radiation in Lacertidae, although African lineages tended to have higher rates of phenotypic evolution than their palaeartic sister taxa, particularly when tail length was included. The majority of morphological variation appears to have originated during

Table 1. Estimated rates of phenotypic evolution ($\hat{\sigma}^2$) for lacertid subclades in figure 2a based on datasets with and without tail length, with sample sizes and ages in millions of years.

clade	N (actual/sampled/ sampled _(tail))	age (Myr)	$\hat{\sigma}^2$	$\hat{\sigma}^2$ _(tail)
Eremiadini				
(1) <i>Eremias</i>	33/16/15	15.6	0.00007	0.00012
(2) <i>Ophisops</i>	8/5/5	19.8	0.00006	0.00014
(3) <i>Acanthodactylus</i> , <i>Mesalina</i>	54/13/13	25.1	0.00015	0.00019
(4) equatorial African: <i>Adolfus</i> , <i>Congolacerta</i> , <i>Gastropholis</i> , <i>Holaspis</i>	11/8/6	22.0	0.00017	0.00028
(5) North/East African: <i>Heliobolus</i> , <i>Latastia</i> , <i>Nucras</i> , <i>Philochortus</i>	37/14/13	22.6	0.00013	0.00016
(6) southern African: <i>Australolacerta</i> , <i>Ichnotropis</i> , <i>Meroles</i> , <i>Pedioplanis</i> , <i>Tropidosaura</i> , <i>Vhembelacerta</i>	32/16/13	25.0	0.00010	0.00018
Lacertini				
(7) <i>Apathya</i> , <i>Archaeolacerta</i> , <i>Dalmatolacerta</i> , <i>Podarcis</i> , <i>Teira</i> , <i>Zootoca</i>	28/15/13	20.9	0.00008	0.00011
(8) <i>Lacerta</i> , <i>Timon</i>	14/4/4	18.8	0.00010	0.00016
(9) <i>Anatololacerta</i> , <i>Darevskia</i> , <i>Iranolacerta</i> , <i>Parvilacerta</i>	34/13/7	18.5	0.00015	0.00011
(10) <i>Takydromus</i>	21/9/7	15.0	0.00006	0.00032
(11) <i>Algyroides</i> , <i>Dinarolacerta</i> , <i>Iberolacerta</i>	14/7/4	18.8	0.00014	0.00002
Gallotinae				
(12) Gallotiinae	14/7/7	20.3	0.00005	0.00011

recent divergence events, resulting in increased partitioning of disparity within subclades. Although incomplete sampling can bias observed evolutionary patterns (by increasing the perceived distance between younger nodes [8]), recent disparity peaks for the main clades are likely robust given that: (i) MCCR simulations showed no effect of missing taxa on estimated branching patterns, (ii) the disparity method used is thought to be insensitive to sample size [9] and (iii) taxon sampling among clades was relatively even, i.e. all genera were represented with similar proportions of measured species.

Overall, phenotypic evolution in Lacertidae is remarkably slow compared with other lizard groups like agamids [16] and *Anolis* [17], which display rates up to six orders of magnitude higher. The highest rates in our study were found in tropical arboreal taxa, suggesting that locomotion in vertical habitats (e.g. rainforest canopy and tropical grasslands) may favour the rapid evolution of traits associated with climbing, particularly regarding limb and tail proportions [15]. Likewise, sand-dwelling lacertids in northern and southern Africa (e.g. *Acanthodactylus*, *Meroles*) also showed elevated phenotypic rates, possibly related to movement on shifting substrates. Although locomotion is generally associated with body shape (e.g. [16]), the relationship between habitat use and rates of morphological evolution in lizards is still unclear. For example, Greater Antillean anoles rapidly evolve suites of arboreal ecomorphs following island colonization [17], while arboreal agamids experience lower rates of shape change than terrestrial ones [16]. Unfortunately, we are unable to distinguish the effects of arboreality from other selection pressures in tropical lacertids (e.g. competition, predation), because no similar ecomorphs exist outside the tropical range. However, the fact that many lineages displaying elevated rates also possess locomotory specializations like prehensile tails (*Gastropholis*), fringed toes (*Acanthodactylus*, *Meroles*) and rib-spreading (*Holaspis*) suggests that substrate is an important selective agent.

Among reported rates of phenotypic evolution, lacertids are most comparable to plethodontid salamanders, a species-rich clade with substantial morphological overlap [11]. Like plethodontids, phenotypic divergence in lacertids appears to be independent of the evolutionary processes underlying lineage diversification, even when species richness patterns are in direct opposition (tropical plethodontids being most speciose [11]). Of course, observed morphological patterns are largely dependent on the traits under consideration, which here are restricted to body and limb proportions. Previous studies, however, indicate a large degree of interspecific variation in lacertid cranial osteology, as well as in other features like osteodermal covering, scalation and dorsal pattern [18]. Future quantification (and qualification) of such traits may therefore reveal hidden morphological variation not captured in this study.

Much of our understanding of diversity dynamics is based on studies of rapidly diversifying clades (i.e. adaptive radiations), often conducted on limited geographical scales like lakes or islands [1]. Lacertids offer a compelling counterexample in that they constitute a large continental radiation with relatively steady rates of diversification and low morphological disparity. We showed that rates of phenotypic evolution, however, vary substantially among subclades, forming a latitudinal disparity gradient in direct opposition to species richness. This evidence runs counter to the ecological opportunity theory, which predicts a link between the processes generating species diversity and morphological differentiation. By contrast, our results demonstrate that variation in morphology is independent of spatial dynamics of diversification, implying that processes other than speciation promote or constrain body shape evolution in lacertids.

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