Convergent body shapes have evolved via deterministic and historically contingent pathways in *Lerista* lizards

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Convergent evolution can occur through similar or different evolutionary pathways, which are the sequences of trait changes that led to convergent phenotypic endpoints. These evolutionary pathways may differ, owing to historically contingent events during the evolution of each lineage, or can arise deterministically due to similar histories of selection or evolutionary constraints. Thus, the relative contribution of determinism and contingency to the evolutionary history of convergent clades affects the evolutionary pathway that each has taken. We tested for morphological convergence in body elongation and limb reduction and the evolutionary pathways that gave rise to them in two major clades of *Lerista*, a species-rich genus of semi-fossorial lizards endemic to Australia. Our analyses showed strong evidence that the two clades evolved deterministically: both clades shared multiple convergent trait optima and similar patterns of integration of the hind limbs. However, the analyses also showed evidence of historical contingency because not all trait optima were realized by both clades, front limbs were not similarly integrated, and the body parts related by linear or threshold relationships differed between clades. Our findings suggest convergence occurs through deterministic pathways that are nevertheless contingent on historical events, and may have functional and ecological implications for convergent organisms.

ADDITIONAL KEYWORDS: evolutionary morphological thresholds – morphology – phylomorphospace – trait evolution.

INTRODUCTION

Convergent evolution is the evolution of similar phenotypes between phylogenetically distant taxa, and is common at all levels of biological organization from DNA sequences to ecology (McGhee, 2011). Convergent evolution can arise through the same or different developmental genetic mechanisms (Arendt & Reznick, 2008; Wake, Wake & Specht, 2011) and evolutionary processes (Stayton, 2008, 2015), but here we use the term to refer to similar phenotypes, irrespective of mechanism or process (Stayton, 2006; Powell, 2007). Convergence can occur through deterministic means such as similar selective pressures or constraints acting on similar aspects of an organism, or through random historical events influencing possible outcomes (Gould & Lewontin, 1979; Gould, 1990; Losos, 2011; Wake *et al.*, 2011). Determinism and contingency thus offer opposing, but not mutually exclusive, explanations for how convergence occurs, and

their relative importance in guiding evolution is still debated (Gould & Lewontin, 1979; Travisano *et al.*, 1995; Taylor & McPhail, 2000; Vermeij, 2006; Kardol *et al.*, 2007; Arendt & Reznick, 2008; Losos, 2011; Wake *et al.*, 2011; Olson, 2012; Pearce, 2012).

Many classic and well-studied examples of convergent evolution show evidence of both contingency and determinism. For example, the evolution of powered flight using wings in vertebrates and invertebrates is deterministic, but the structures they arise from are different, and thus, historically contingent (Shubin, Tabin & Carroll, 1997; Losos, 2011; Wake *et al.*, 2011). Likewise, arborescence (tree-like features) in plants has independently evolved many times, but via modifications to different tissues (Niklas, 1997; Donoghue, 2005). *Anolis* lizards of the Greater Antilles also show determinism in that the same ecomorphs have evolved on different islands, but the order in which these ecomorphs have evolved on each island differs (Losos *et al.*, 1998).

These examples also demonstrate the need to study the evolutionary pathways leading to the

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convergent endpoints that we observe. Such evolutionary pathways are the characterization of the sequence of genetic, developmental or morphological changes that led to the evolution of the observed convergent phenotypic endpoints. Generally, closely related lineages that share similar endpoints are likely to share similar, underlying genetic mechanisms (Conte *et al.*, 2012). However, there are many exceptions to this (Arendt & Reznick, 2008). For example, in the Mexican cavefish (*Astyanax mexicanus*), some populations have converged upon the loss of eyes and pigmentation through different pathways because each has a mutation in a different gene of the gene network involved (Wilkens & Strecker, 2003). Other populations of Mexican cavefish show convergence in both phenotype and evolutionary pathway, as similar deletions in the *Oca2* gene have led to convergent lack of pigmentation (Protas *et al.*, 2006). Thus, even very closely related lineages can follow similar or different evolutionary pathways. When using morphometric data, evolutionary pathways can be studied by quantifying evolutionary integration among traits and by characterizing the shape of the relationships among these traits.

Evolutionary integration is the correlated change of multiple traits within an organism based on their genetic, developmental or functional interactions (Klingenberg, 2008, 2009). If the same traits are similarly integrated in different convergent clades, then this is evidence that they share similar evolutionary pathways. For example, in taxa that have evolved snake-like bodies, the relative lengths of the limbs and body are integrated, being negatively related (Wiens & Slingluff, 2001; Wiens, Brandley & Reeder, 2006; Skinner & Lee, 2009; Siler & Brown, 2011). Similarly, since the loss of the limbs in these taxa proceeds from distal to proximal to maintain limb functionality (Lande, 1978), one would expect more proximal limb elements to be more highly integrated than distal ones, which evolve more readily (Petit, Sears & Ahituv, 2017).

The shape of the relationship among traits can also be used to characterize evolutionary pathways. The shape of relationships between pairs of traits is often assumed to be gradual and linear, and although many traits are related in this way (Gould, 1966; Shingleton *et al.*, 2007; Bergmann & Berk, 2012), others are not. For example, a threshold is a sigmoidal, non-linear relationship where one trait changes only when another trait reaches a particular value (Lande, 1978; Moczek *et al.*, 2002; Moczek & Nijhout, 2003). Various lizard taxa that have evolved body elongation and limb reduction have threshold relationships between some of their body parts (Lande, 1978; Brandley, Huelsenbeck & Wiens, 2008; Siler & Brown, 2011). Convergent taxa exhibiting similar shapes of relationships between homologous pairs of traits, whether they are linear or thresholds, provides evidence of similar evolutionary pathways.

The evolution of body elongation and limb reduction has happened convergently in most major lineages of vertebrates, including fishes (Ward & Brainerd, 2007; Mehta *et al.*, 2010), amphibians (Wake, 1980; Parra-Olea & Wake, 2001), reptiles (Lande, 1978; Greer, 1991; Wiens *et al.*, 2006; Brandley *et al.*, 2008) and mammals (Buchholtz & Schur, 2004; Buchholtz, Booth & Webbink, 2007). The repeated evolution of snake-like bodies across diverse lineages argues for deterministic evolution. This is especially true in squamate reptiles (lizards and snakes), where snake-like body shapes have evolved independently at least 25 times (Wiens *et al.*, 2006; Brandley *et al.*, 2008; Sites, Reeder & Wiens, 2011). Snake-like lizards have evolved following at least two evolutionary pathways, either via the elongation of the trunk, as observed in most burrowers, or by the elongation of the trunk and tail, as seen in many surface dwellers that inhabit dense vegetation (Wiens *et al.*, 2006; Brandley *et al.*, 2008). It should be noted that while there is strong evidence for selection playing a role in the evolution and niche partitioning of convergent examples such as *Anolis* lizards (Losos *et al.*, 1998, 2003; Johnson, Revell & Losos, 2010; Ord, Stamps & Losos, 2013) or stickleback fish (McPhail, 1993; Schluter & Nagel, 1995; Schluter, 1996; Rundle *et al.*, 2000; Colosimo, 2005), the ecological implications of the evolution of snake-like body shapes have been poorly studied.

Among lizard lineages that have evolved snake-like taxa, several are particularly well suited for studying evolutionary pathways because they have evolved phenotypes ranging from a typical pentadactyl lizard-like form to a limbless snake-like form, with many intermediate phenotypes (Lande, 1978; Wiens & Slingluff, 2001; Whiting, Bauer & Sites, 2003; Kohlsdorf & Wagner, 2006; Skinner & Lee, 2009; Siler & Brown, 2011). Among these lineages, *Lerista* is particularly diverse encompassing 94 putative species (Uetz, 2010), 72 of which are represented on recent phylogenies (Skinner, 2010; Pyron & Burbrink, 2013; Pyron, Burbrink & Wiens, 2013). *Lerista* exhibit at least 12 different digit morphs, which differ in the numbers of digits and limb elements on the front and hind limbs, from a complete absence of limbs to the pentadactyl condition (i.e. five digits on both front and hind limbs) (Greer, 1987, 1990; Kendrick, 1991; Wilson & Swan, 2008; Skinner & Lee, 2009). *Lerista* can be divided into two major clades that have comparable species richness (Pyron *et al.*, 2013) with a similar range of digit morphs (Skinner, Lee & Hutchinson, 2008; Skinner, 2010). The coastal clade is found primarily along the coastal regions of Western and Southern Australia, while the interior clade occurs in some coastal areas and has radiated across much of the interior of

Australia (Supporting Information, Fig. S1). Most species in both clades inhabit arid areas (Wilson & Swan, 2008) and are semi-fossorial (Kendrick, 1991; Benesch & Withers, 2002), found largely at the interface between leaf litter and sand.

In the present study, we use morphological data to test two hypotheses about the evolution of convergent phenotypes and the pathways that led to their evolution in the coastal and interior clades of *Lerista*. First, we test whether the coastal and interior clades converged upon similar body shapes. It is clear that both clades have superficially convergent digit morphs (Skinner, 2010), but whether these digit morphs exhibit convergent body shapes is unknown. We expect that many of the morphs will exhibit convergent morphologies between the two clades. Second, we test whether the coastal and interior clades evolved following similar evolutionary pathways. Even if both clades have evolved convergent morphologies, species from each clade could have achieved these morphologies through different pathways. We expect that most digit morphs will have been realized through similar changes in the body and limbs, indicative of deterministic processes playing a dominant role. If we see major discrepancies in how the clades evolved their morphs, this would be indicative of a greater role of historical contingency in their evolution.

METHODS

MORPHOMETRIC DATA AND PHYLOGENY

We measured 398 alcohol-preserved specimens belonging to 62 species of *Lerista* from the Western Australian Museum (Supporting Information, Table S1). We sampled 1–8 specimens per species (median = 7), and sampled adult specimens with original tails when possible. We measured snout-vent length, head length, body width, tail length, and the lengths of the upper front limb, lower front limb, palm of the manus and longest digit of the front limb, and the thigh, crus, sole of the pes and longest digit of the hind limb (Supporting Information, Methods S1). We summed elements of each limb to get front limb length and hind limb length. We also counted the number of digits on the front and hind limbs. P.J.B. took all measurements thrice using a Mitutoyo digital caliper (Kanagawa, Japan) to the nearest 0.01 mm. We averaged all measurements and natural log-transformed (ln) the averages prior to analysis, except where noted. We added one to all measurements prior to transformation because limb measurements in limbless taxa were zero, which becomes undefined when ln-transformed. We then calculated relative trait values, correcting them for size by dividing by ln(head length). We used head length as a proxy for size because it is standard for elongate taxa (Stokely, 1947; Wiens & Slingluff, 2001; Wiens *et al.*, 2006; Siler

& Brown, 2011). We used ratios rather than residuals since the latter approach can bias results and inflate Type I error (Berthou, 2001; Freckleton, 2009), however, we note that there are also drawbacks to using ratios (Albrecht, Gelvin & Hartman, 1993; Jasieński & Bazzaz, 1999; Franks & Cabo, 2014). For all of our analyses, we took the effect of phylogeny into account (Felsenstein, 1985) using the published phylogeny of squamates (Pyron *et al.*, 2013), which included 4161 species and branch lengths proportional to substitutions per site. We pruned the tree to only include the species in our data set, ultrametricized and scaled it such that the distance from root to tips was one using penalized likelihood (Sanderson, 2002), as implemented in ape (Paradis, Claude & Strimmer, 2004) for R ver. 3.1.3 (R Core Team, 2015). Of the phylogenies available (Skinner *et al.*, 2008; Skinner, 2010; Pyron *et al.*, 2013; Pyron & Burbrink, 2013), that of Pyron *et al.* (2013) had the highest support for the coastal and interior clades (SHL = 85, 98, respectively), which appear in all of them. Phylogeny choice did not affect our overall results. We also added a sister branch at the midpoint of the terminal branch to *L. lineopunctulata*, because we distinguished between the northern (absent front limb/1 toe, denoted A/1) and the southern (stump for front limb/2 toes, denoted S/2) morphs. Thus, most of our analyses included 62 taxa, although a few analyses excluded some species. Specifically, we omitted six species (*L. wilkinsi*, *L. robusta*, *L. walker*, *L. edwardsae*, *L. tridactyla*, *L. yuna*) from analyses that used tail lengths because no individuals with complete tails could be sampled. We also omitted nine other species (*L. kalumburu*, *L. neander*, *L. puncticauda*, *L. macropisthopus*, *L. axillaris*, *L. gerrardii*, *L. punctatovittata*, *L. planiventralis*, *L. strictopleura*) from analyses that used limb element lengths because their limbs were too small to distinguish between different elements. Our morphometric data set is available online, as part of the Supporting Information (Table S1).

TESTING FOR CONVERGENCE IN BODY SHAPE

We performed all statistical analyses using R ver. 3.1.3 (R Core Team, 2015). We first characterized body shape in *Lerista* with a phylogenetic principal component analysis (pPCA) that accounted for phylogenetic signal using Pagel's λ (Pagel, 1999), and a covariance matrix, as implemented in phytools (Revell, 2011). We ran three pPCAs: one including relative tail length ($n = 56$), one excluding it ($n = 62$) and one including head length ($n = 62$). The results from these analyses were qualitatively similar and did not affect our conclusions, so we present the pPCA excluding tail and head length here (see Supporting Information, Table S2 for the pPCA loadings, including relative tail length and head length). We determined the number of pPCs to

interpret using a scree plot (Jackson, 1993), looking for a sharp decrease in variance explained. Recent work has shown that interpretation of pPCA can be biased when a Brownian motion (BM) model is used but does not fit the underlying evolution of the traits being analysed, and when only a subset of pPCs is interpreted (Uyeda, Caetano & Pennell, 2015). The latter concern is ameliorated when the first pPC explains the majority of variance in the data (Uyeda *et al.*, 2015). To address these concerns, we used a pPCA that accounts for phylogenetic signal by estimating λ, which allows for flexible modelling of trait evolution (Revell, 2010). Furthermore, in our analysis, the first pPC explained 74% of the variance and the first three pPCs explained 95% of the variance in the data (Table 1).

We then iteratively fit Ornstein–Uhlenbeck (OU) models (Hansen, 1997; Butler & King, 2004) to the first three pPCs, using the package SURFACE (Ingram & Mahler, 2013) in R to test for convergence. SURFACE uses a forward phase to identify shifts in trait optima on the branches of a phylogeny, and a backward phase in which optima identified in the forward phase are collapsed together such that they evolve convergently on multiple lineages (Ingram & Mahler, 2013). Both addition and collapsing of optima are only accepted when associated with an improvement in the model Akaike Information Criterion (AIC; Burnham & Anderson, 2002). Thus, a SURFACE analysis identifies the number of shifts in trait optima on the phylogeny (k) and the number of optima in the final model (k'). This results in two metrics of convergence: $\Delta k = k - k'$, which is the reduction in model complexity due to convergence, and c, which is the number of shifts to convergent trait optima (Ingram & Mahler, 2013).

To test whether our data set contained more instances of convergence than expected by chance, we simulated 1000 data sets evolving under a BM model and 1000 evolving under an OU model generated at the end of the forward phase of SURFACE. We ran the SURFACE analysis on each of them to create a null distribution of Δk and c, and assessed the significance of the real data using a one-tailed test. We visualized the results of the pPCA and SURFACE analyses by creating a phylomorphospace (Sidlauskas, 2008) of the first two pPCs using phytools in R, painting its branches corresponding to SURFACE trait optima, and plotting the trait optima values on the graph.

To further quantify the degree of convergence in our data set, we measured Stayton's C_1 from the first three pPCs using the convevol package (Stayton, 2014). C_1 is the ratio of the Euclidean distance between two taxa and the maximum Euclidean distance between any two taxa in the two lineages (Stayton, 2015). We calculated C_1 for all pairwise species comparisons that belonged to the same morph but different clades (i.e. coastal and interior), and assessed the significance of each using 1000 simulated data sets that followed a BM model of evolution. We performed these analyses for morphs that had species represented in both clades (i.e. 4/4, 2/3, 1/2, A/2 and A/S morphs). We corrected *P*-values for multiple comparisons using the Benjamini–Hochberg method (Benjamini & Hochberg, 1995).

TESTING FOR CONVERGENCE OF EVOLUTIONARY PATHWAYS IN BODY SHAPE

We quantified patterns of integration among size-corrected traits using evolutionary correlation analyses (Olson & Miller, 1999; Klingenberg, 2008, 2009). We calculated evolutionary correlations among relative snout-vent length, relative front limb length and relative hind limb length, as well as among the elements of the front and hind limbs. We did these analyses for all taxa as well as separately for the coastal and interior clades, allowing us to compare patterns of integration between these clades. We calculated evolutionary correlations and *P*-values using R code we wrote (Supporting Information, Methods S2). The code calculates an evolutionary variance–covariance (eVCV) matrix under a multivariate BM model, using trait data and a phylogeny, and then converts that to an evolutionary correlation matrix. It then simulates s replicate data sets of the same size as the original, where traits evolve by uncorrelated BM with equal rates as the original data. Next, it calculates evolutionary correlation matrices for each replicate to create a null distribution of Pearson's correlation coefficients (R). The *P*-values are calculated as the quotient of R equal to or more extreme than each empirical R and the number of simulated replicates, s. Using this code, we simulated 10^5 null data sets for these analyses. We also compared evolutionary correlation matrices of front and hind limb elements between the coastal and interior clades using a permuted Mantel

Table 1. Size-corrected phylogenetic principal component analysis (pPCA) loadings, eigenvalues and per cent variance explained for the first three pPCs of the morphometric variables of *Lerista*, n = 62

Variable	pPC-1	pPC-2	pPC-3
Snout-vent length	−0.504	−0.165	−0.737
Body width	0.157	0.169	−0.421
Front limb length	0.938	−0.308	−0.097
Hind limb length	0.750	0.651	−0.065
Front digit number	0.921	−0.308	0.114
Hind digit number	0.888	0.347	0.054
Eigenvalues	0.267	0.062	0.013
% Variance	74.2%	17.6%	3.5%

test (Mantel, 1967) as implemented in vegan (Oksanen *et al.*, 2016). Because a 4 × 4 matrix can only be permuted 24 times, the lowest possible *P* was $24^{-1} = 0.0416$ (Knijnenburg *et al.*, 2009). We did not perform Mantel tests on correlation matrices between relative snout-vent, relative front limb and relative hind limb lengths, because these 3 × 3 matrices could not be randomized a sufficient number of ways to provide an informative test. We corrected *P*-values for multiple comparisons using the Benjamini–Hochberg method.

We also tested for convergent evolutionary pathways by determining whether the coastal and interior clades had gradual or threshold relationships between the same pairs of traits. Previous studies visually inspected bivariate plots for morphological thresholds, looking for either a sudden change in one variable relative to another (Lande, 1978; Brandley *et al.*, 2008) or for gaps representing unrealized morphologies (Siler & Brown, 2011). Here, we developed a phylogenetically informed, model-based approach to test for and identify thresholds. We did this by fitting logistic, linear and null models to our data using generalized non-linear least squares (gnls) as implemented in the nlme package (Pinheiro *et al.*, 2015). We accounted for phylogeny by simultaneously optimizing phylogenetic signal (λ) in the model residuals (Revell, 2010). We did this by estimating the phylogenetic correlation structure of the gnls model residuals along with model parameters, similar to those done for phylogenetic generalized least squares methods implemented in R packages like caper (Orme *et al.*, 2013).

We chose a logistic function to represent a threshold because of its sigmoidal shape, a linear function to represent a gradual, linear trend and a null model that only estimated an intercept (i.e. $y = a$). The logistic and linear models can be described using the following equations:

$$\text{Logistic model}: y = A - \frac{A}{1 + \left(\dfrac{x}{K}\right)^{S}}$$

$$\text{Linear model}: y = a + bx$$

In the logistic model, *A* defines the horizontal asymptote of the curve, representing the maximum possible value of the *y*-variable. *K* defines the location of the inflection point along *x*, and *S* is the slope of the curve at the inflection, representing the abruptness of the threshold. We set $A = 5$ when fitting the function to digit counts because no *Lerista* species has more than five digits. For the linear model, *a* is the *y*-intercept and *b* is the slope. To compare models, we calculated the log-likelihood for each from its sum of squared residuals and used this to calculate AIC_c and Δ values

(Burnham & Anderson, 2002). To ensure robust support for a more complex model (threshold over linear or linear over null), the delta value for the worse model had to be greater than two for us to choose the more complex model. We fit these three models to untransformed variables that we size-corrected by dividing each by untransformed HL (Lande, 1978; Brandley *et al.*, 2008; Siler & Brown, 2011). We chose to use untransformed variables to maintain comparability with past studies (Lande, 1978; Brandley *et al.*, 2008; Siler & Brown, 2011). We tested for thresholds of digit counts against relative snout-vent length, relative front and hind limb length, as well as thresholds of relative front and hind limb lengths against relative snout-vent length.

Since this method of testing for thresholds is novel, we performed a power analysis to quantify its performance for detecting thresholds over the linear and null models. We did this by simulating phylogenies with 100 species and evolving pairs of traits on them that were related by a threshold. We then applied the method described above and calculated power as the proportion of data sets for which the threshold model was the best by at least two AIC values (i.e. $\Delta_{AIC} \geq 2$). We then successively randomly pruned 10% of species and redid the power analysis to quantify the effect of incomplete taxon sampling on power. A complete description of our approach is included in Supporting Information, Methods S3. The results of the power analysis are also shown in Figure S2, showing that our approach maintains a power for detecting thresholds above 0.8 even when taxon sampling drops below 30% and 30 species, which is fewer than what we had in our data set.

RESULTS

BODY SHAPE VARIATION IN *LERISTA*

We characterized variation in *Lerista* body shape using pPCA, interpreting the first three pPCs, which explained 94.8% of the variance in our data set (Table 1). We interpreted pPC-1 as an index of how snake-like or lizard-like a species is because all limb variables loaded strongly positively, while relative snout-vent length loaded negatively (Table 1). Species with high pPC-1 scores had robust limbs and relatively short bodies while species with low scores had reduced limbs and relatively elongate bodies.

pPC-2 was characterized by weak and opposite-signed loadings of relative snout-vent length and relative body width, and strong and opposite-signed loadings of the limb lengths and digit numbers (Table 1), reflecting differences in the size of front and hind limbs; front limbs tend to be more reduced than hind limbs in *Lerista*. Species with low pPC-2 scores had lost or almost lost both front and hind limbs (the A/A, A/S morphs).

Species that scored high on pPC-2 had different morphologies of their front and hind limbs (A/2 and S/2 morphs), while species with middling pPC-2 scores had four robust limbs (5/5, 4/4 and 3/3), but with front limbs smaller than hind limbs. pPC-3 was primarily an index of relative body robustness, where species with long, thick bodies (e.g. *L. lineopunctulata*, *L. macropisthopus*, *L. picturata*, *L. neander*) had high pPC-3 scores and species with diminutive bodies (e.g. *L allochira*, *L. vermicularis*, *L. aericeps*, *L. apoda*) had low pPC-3 scores (Table 1), indicating that there were both large and small bodied species that were limb reduced. Our interpretations of the first two pPCs did not change with the inclusion of head length as a proxy for size, but pPC-3 changed slightly. When head length was included, species with higher pPC-3 scores were absolutely larger with relatively shorter bodies than those with lower scores (Table S2).

CONVERGENCE OF BODY SHAPES BETWEEN CLADES

We found strong evidence that the coastal and interior clades of *Lerista* evolved very similar limb morphs and body shapes. From the digit morphs alone, we found that both clades have evolved five of 12 digit morphs (Fig. 2). The digit morphs that evolved in both clades were also largely convergent in their body shape, where species of the A/S, A/2, 2/3 and 4/4 morphs occurred in the same restricted areas of morphospace for the coastal and interior clades (Fig. 3; Supporting Information, Fig. S3). Several digit morphs were only found in one clade, but were represented by relatively few species (Fig. 2). For example, the completely limbless *L. apoda* is part of the interior clade, while the more robustly limbed 3/3 and 5/5 digit morphs only occur in the coastal clade.

The SURFACE analysis identified 19 shifts (k) to 13 different optima (k'), and 12 of the shifts were to six convergent optima ($c = 12$, $\Delta k = 6$), leaving seven non-convergent optima. All six of the convergent optima were bouts of convergence between the coastal and interior clades, rather than convergence within clades (Fig. 1). We found that the incidence for convergence, measured by Δk and c, was significantly higher in *Lerista* than expected under both BM and non-convergent OU models ($P = 0.001$ for both Δk and c under both null models). To further understand how digit morphs mapped to the trait optima identified by the SURFACE analysis, we created a classification matrix of digit morphs to optima, which showed that many of the optima mapped closely to one or a few similar digit morphs (Supporting Information, Table S3), further supporting the convergent evolution of similarly shaped morphs. The ancestral optimum (black branches; Figs 1, 4) only included robustly limbed digit morphs (5/5, 4/4, 3/3) from both clades.

All four species of the A/S morph and 18 of 20 species of the A/2 morph were assigned to their own optima (yellow and red branches, respectively; Figs 1, 3). In contrast, the nine 2/3 morph species were split between four different optima, two of them convergently containing species from both clades. The very similar 1/2 and 1/3 morphs mapped to the same optimum (blue branches; Figs 1, 3). Other digit morphs were either only represented by a single species (i.e. A/A, A/1), or were on non-convergent optima (i.e. S/2).

Analysis of Stayton's (2015) C_1 complemented our SURFACE results. Of the 153 comparisons of species belonging to the same morph but different clades, 108 were significant (Supporting Information, Tables S4–S7). We found that all comparisons within the 4/4 and A/S digit morphs were convergent, as well as 73% of those in the A/2 morph and one of the two comparisons in the 1/2 morph (Table 2). Almost all of the comparisons that showed non-significant C_1 for the A/2 morph belonged to two different SURFACE regimes (Supporting Information, Tables S3, S6). Evidence was weak for convergence in the 2/3 digit morph, with only one of 18 (6%) of comparisons being significantly convergent (Table 2). Species belonging to this morph mapped onto four different regimes in the SURFACE analysis (Supporting Information, Table S3).

CONVERGENCE OF EVOLUTIONARY PATHWAYS BETWEEN CLADES

Our study of integration among body parts and the shapes of the relationships between body parts in *Lerista* largely supported the hypothesis that the coastal and interior clades evolved their digit morphs following convergent evolutionary pathways. Qualitatively, the phylomorphospace also supported this hypothesis because branches for the two clades follow similar courses for the two clades (Fig. 3; Supporting Information, Fig. S2).

The patterns of integration among body parts were congruent between the coastal and interior clades. We found that relative snout-vent length was significantly negatively correlated with both relative front and hind limb lengths (Table 3), and that relative front and hind limb lengths were significantly positively correlated in all *Lerista* species (Table 3). We found qualitatively identical patterns for the coastal and interior clades, although some of these correlations were not significant due to smaller sample sizes (Table 3).

The relative lengths of limb elements were also highly integrated with one another (all $P < 0.0001$), and the patterns of integration were again congruent between coastal and interior clades (Table 4). For both front and hind limbs, all relative lengths of limb elements were significantly positively correlated (Table 4). In the coastal clade and for all *Lerista*, more distal
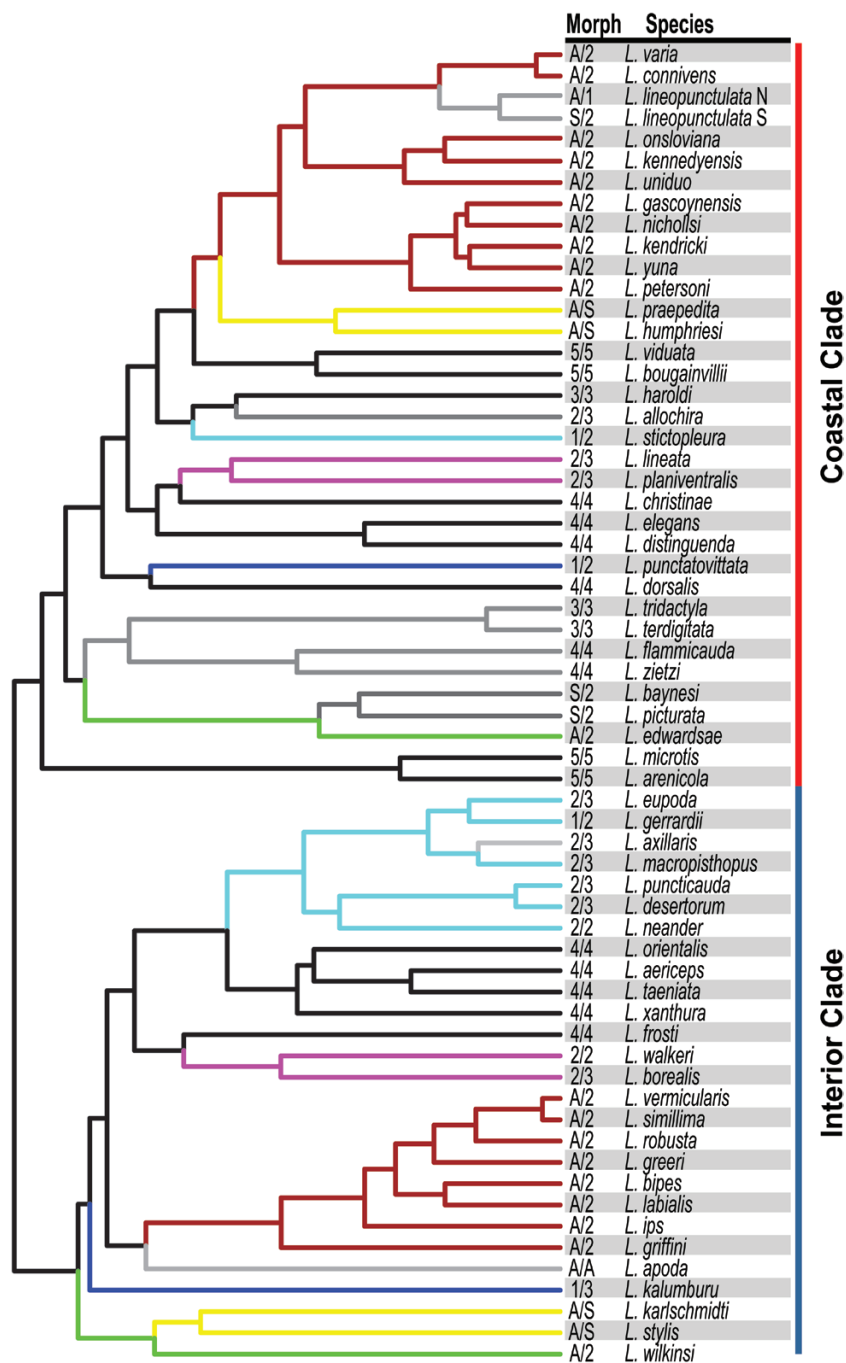
Figure 1. Phylogeny of *Lerista* from Pyron *et al.* (2013) including the 62 species studied, with coastal and interior clades identified. Colours of the branches represent different trait optima identified by the SURFACE analysis, where same coloured branches in different locations on the tree represent convergent optima, black branches represent the ancestral optimum and gray branches are non-convergent optima. The digit morph of each species is given to the left of the species name, with the number of digits for the front and hind limb separated by a slash (A, absent limb; S, stump limb). For *L. lineopunctulata*, 'N' and 'S' stand for 'North' and 'South', respectively.

element pairs in both front and hind limbs were more strongly correlated than more proximal ones, contrary to our expectations (Table 4; Supporting Information, Table S8). We also documented this pattern in the hind limb elements of the interior clade, but not front limb elements (Table 4). Our Mantel test results supported

these observations in that the patterns of integration of hind limb elements ($R = 0.994$, $P = 0.0416$), but not front limb elements ($R = -0.413$, $P = 0.7917$), were significantly related between coastal and interior clades.
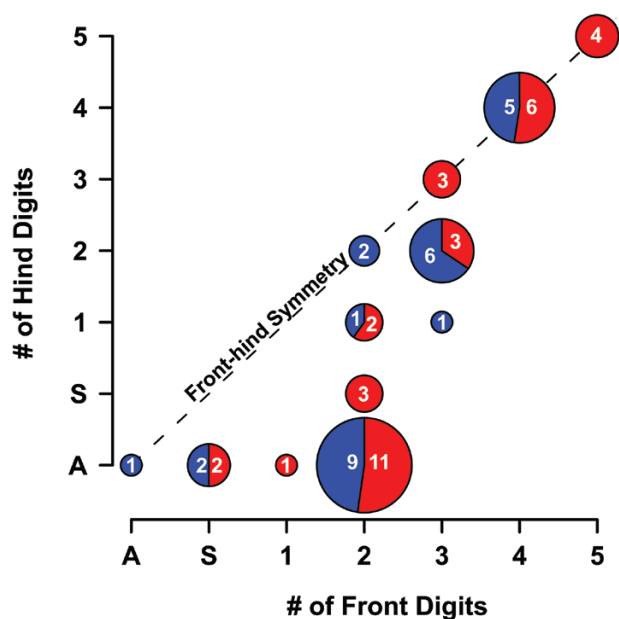

Figure 2. Limb morphologies of *Lerista* and the proportions of species from each clade. Size of the pie represents the total number of species of each limb morph with numbers written in for clarity ($n = 62$). A stands for 'absent limb' and S stands for 'stump limb'. Colours correspond to the different clades (blue: interior clade, red: coastal clade).

When we characterized the relationship between pairs of untransformed, size-corrected variables, we found differences between the coastal and interior clades for four out of the six pairs of traits (Tables 5, 6; Fig. 4; Supporting Information, Table S9). For relative snout-vent length and number of front digits, the coastal clade exhibited a negative threshold while the interior clade exhibited a negative linear relationship (Fig. 4A). For relative snout-vent length and number of hind digits, both clades exhibited a negative linear relationship (Fig. 4B). For relative snout-vent length and relative front limb length, the coastal clade exhibited a negative threshold while the interior clade exhibited no relationship (Fig. 4C). For relative snout-vent length and relative hind limb length, both clades exhibited a negative threshold (Fig. 4D). For relative front limb length and number of front digits, the coastal clade exhibited a positive threshold while interior showed a positive linear relationship (Fig. 4E). Lastly, for relative hind limb length and number of hind digits, the coastal clade showed a positive linear relationship while the interior clade showed a very gradual positive threshold (Fig. 4F).

DISCUSSION

DETERMINISTIC EVOLUTIONARY PATHWAYS AND CONVERGENT ENDPOINTS

Here we tested for convergence in snake-like body shapes and the pathways taken to evolve those body shapes in two clades of *Lerista* skinks to help elucidate the relative
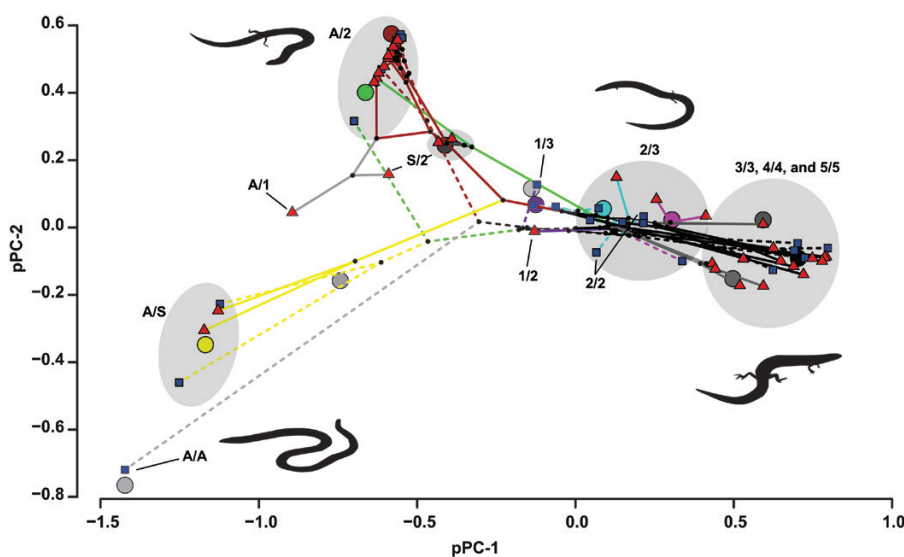
Figure 3. Phylomorphospace of *Lerista*, defined by the first two phylogenetic principal components (pPCs). Colours of the branches and large circles correspond to trait optima from Figure 1. The interior clade is represented by dashed lines for branches and blue squares for species; the coastal clade is represented by solid lines for branches and red triangles for species. Silhouettes show representative body shapes of *Lerista*.
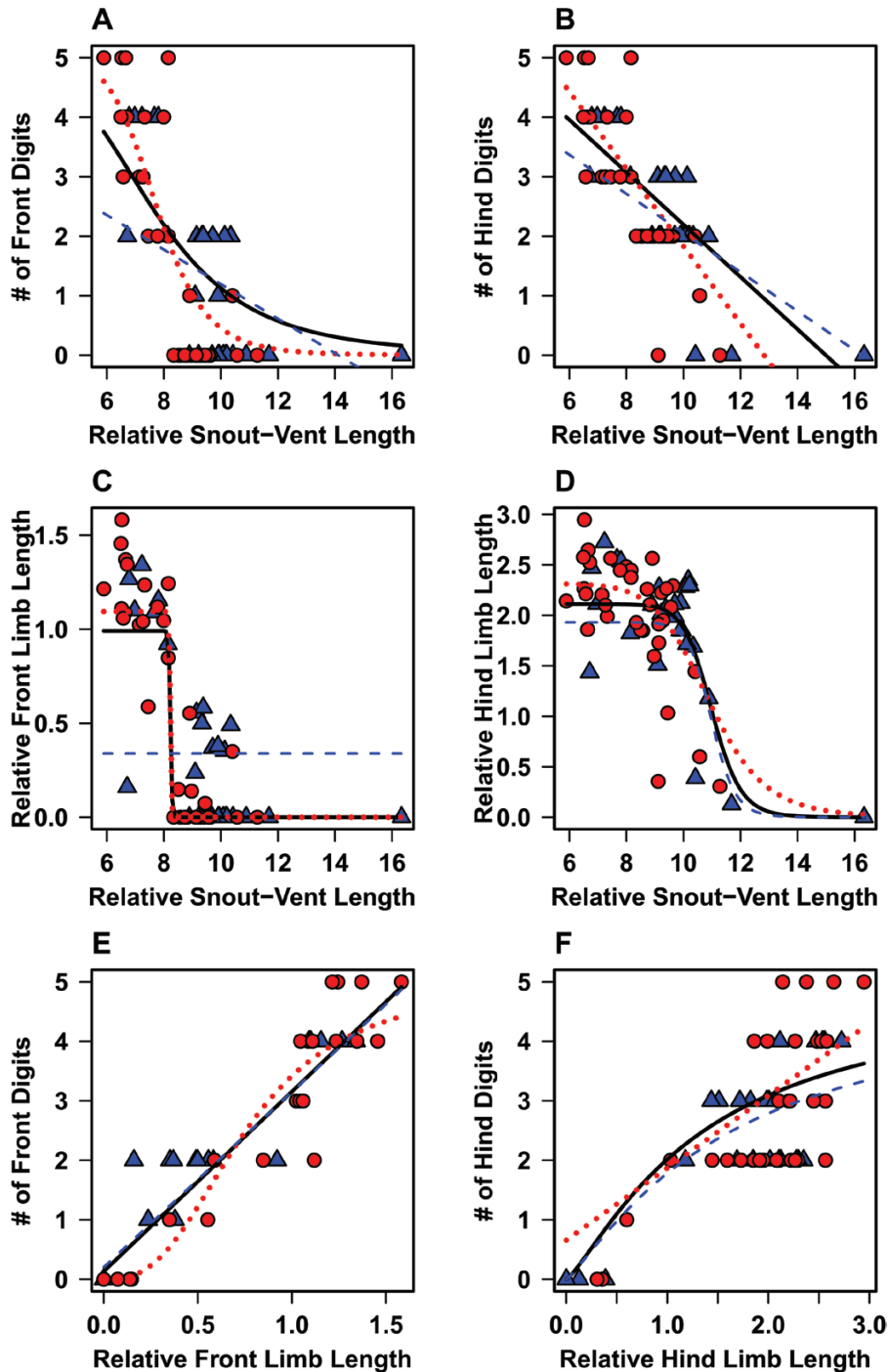
Figure 4. Bivariate plots for pairs of morphological traits for both clades of *Lerista*. Plots include front (A) and hind (B) digit numbers, and relative front (C) and hind (D) limb lengths plotted against relative snout-vent length, as well as front (E) and hind (F) digit numbers against respective relative limb lengths. The solid black lines represent the best model for all *Lerista*, red dotted lines and red circles represent the coastal clade model and species, and blue dashed lines and blue triangles represent the interior clade model and species; n = 62, 27, 35, respectively.

roles of determinism and historical contingency. Our findings showed that the body shape/digit morphs that have evolved in the two clades are indeed convergent (Fig. 3), but that the evolutionary pathways taken to arrive at these morphs were very similar, but differed in important ways. Our findings suggested that the coastal

and interior clades had deterministic evolutionary pathways in terms of having similar patterns of integration between the body and hind limb elements (Tables 3, 4). However, these clades also had different patterns of integration of front limb elements (Table 4), and different structural relationships (linear vs. threshold) between most of the pairs of traits we tested (Table 5; Fig. 4), which is suggestive of a role of historical contingency.

Our findings are relevant to the debate about the relative roles of historical contingency and determinism on the evolution of life (Gould & Lewontin, 1979; Travisano *et al.*, 1995; Taylor & McPhail, 2000; Vermeij, 2006; Kardol *et al.*, 2007; Arendt & Reznick, 2008; Losos, 2011; Wake *et al.*, 2011; Olson, 2012; Pearce, 2012). We hypothesized that *Lerista* digit morphs have evolved largely deterministically along similar evolutionary pathways. Previous studies in other systems have shown evidence of both determinism and contingency playing a role, but the relative importance of these phenomena differs in each case. The repeated evolution of similar *Anolis* lizard ecomorphs on the Greater Antilles (Losos *et al.*, 1998, 2003; Johnson et al., 2010; Ord *et al.*, 2013) and the parallel evolution of benthic and limnetic ecomorphs of threespine stickleback in various Holarctic lakes (McPhail, 1993; Schluter & Nagel, 1995; Schluter, 1996; Rundle *et al.*, 2000; Colosimo, 2005) are examples of a high degree of determinism in evolution. However, in both of these examples there is also evidence of historical contingency. In *Anolis*, the order in which the

ecomorphs evolved on each island is contingent on past evolutionary events (Losos *et al.*, 1998), male territorial behaviour is contingent upon whether a species belongs to the Eastern or Western radiation of *Anolis* (Ord, 2012), and there are island-specific morphological differences in some *Anolis* ecomorphs (Langerhans, Knouft & Losos, 2006). In threespine stickleback, whether both ecomorphs evolve in the same lake is contingent upon the double invasion of the lake by marine stickleback (McPhail, 1993; McKinnon & Rundle, 2002), and ecomorphs other than the benthic and limnetic ones have evolved in different types of freshwater habitats (McKinnon & Rundle, 2002).

Stronger effects of historical contingency with less determinism are seen in the evolution of durophagy in moray eels (Collar *et al.*, 2014), herbivory in lizards (Stayton, 2006) and suction feeding among benthic populations of stickleback (McGee & Schluter, 2013). Several lineages of moray eels have converged in feeding on hard-shelled prey, but have not converged morphologically, instead evolving durophagy through modification of different sets of feeding structures in each lineage (Collar *et al.*, 2014). Likewise, herbivorous lizards have functionally converged in diet, but it is believed that they have done so via different evolutionary pathways towards increased mechanical advantage of the skull because the morphology of the ancestors differs in each lineage (Stayton, 2006). Lastly, different populations of benthic stickleback converged in increased suction performance but not in trophic morphology (McGee & Schluter, 2013). These three examples exhibit functional convergence, but incomplete, or imperfect convergence in morphology (Stayton, 2006; Collar *et al.*, 2014), with various lineages achieving similar function through different evolutionary pathways due to many-to-one mapping of phenotype to function (Wainwright *et al.*, 2005) and leading to the evolution of disparate phenotypes.

Our findings for *Lerista* suggest strong roles of both determinism and historical contingency in body shape evolution. Similar to *Anolis* (Losos, 1992; Losos *et al.*, 1998) and threespine stickleback (Schluter & Nagel, 1995; Schluter, 1996; Rundle *et al.*, 2000; Colosimo, 2005), we found that the coastal and interior clades of *Lerista*

Table 2. Mean ± SD of the convergence statistic (C_1) for all species comparisons within each digit morph but belonging to different clades of *Lerista*

Morph	n	Mean C_1 ± SD	P/X	% Significant
4/4	5/6	0.872 ± 0.069	30/30	100
2/3	6/3	0.522 ± 0.267	1/18	6
1/2	1/2	0.649 ± 0.112	1/2	50
A/2	9/11	0.693 ± 0.383	72/99	73
A/S	2/2	0.885 ± 0.074	4/4	100

n represents the number of species in the interior/coastal clades in each morph, and P/X is the number of significant comparisons after Benjamini–Hochberg correction out of total comparisons.

Table 3. Evolutionary correlations between size-corrected (relative) body and limb lengths

Variables		All species (n = 62)		Interior clade (n = 27)		Coastal clade (n = 35)	
X	Y	R	P	R	P	R	P
Snout-vent length	Front limb length	−0.363	**0.0041**	−0.256	0.1980	−0.399	**0.0169**
Snout-vent length	Hind limb length	−0.405	**0.0012**	−0.417	**0.0294**	−0.302	0.0795
Front limb length	Hind limb length	0.518	**<0.0001**	0.545	**0.0028**	0.468	**0.0046**

Significant *P*-values after Benjamini–Hochberg correction are in bold.

have evolved many of the same digit morphs (Figs 1–3), whose species are assigned to the same trait optima in our OU models (Supporting Information, Table S3), and are significantly convergent (Table 2). Furthermore, they exhibit similar patterns of integration, particularly in the hind limb (Tables 3, 4). This may suggest similar or the same adaptations in both clades to fossorial life histories, as most *Lerista* are found in arid, sandy regions of Australia at the interface between sand and leaf litter (Kendrick, 1991; Wilson & Swan, 2008; Lanier, Edwards & Knowles, 2013). Alternatively, *Lerista* may be functionally constrained in body shape due to low levels of many-to-one mapping in the traits that we studied (Alfaro, Bolnick & Wainwright, 2004; Wainwright *et al.*, 2005; Bergmann & McElroy, 2014). Redundancies that arise in complex functional systems, such as the four-bar linkage in fish jaws, can alleviate the effects of trade-offs (Alfaro *et al.*, 2004; Wainwright *et al.*, 2005; Holzman *et al.*, 2011). However, it is unknown whether the serial

arrangement of limb elements limits the number of combinations of element lengths that are functional. These constraints may be further strengthened by how the limbs get reduced (Lande, 1978). Thus, the high degree of integration and the patterns of integration may be an indicator of these functional constraints (Gould & Lewontin, 1979; Losos, 2011; Collar *et al.*, 2014). Furthermore, functional integration between body and limb lengths likely arises from *Lerista* species increasingly relying on bending of the body axis during locomotion as their limbs get reduced (Bergmann & Irschick, 2010). Such constraints may place both clades of *Lerista* on a common evolutionary path towards a snake-like body shape, with only minor differences between clades.

Despite deterministic evolutionary pathways in *Lerista* leading to similar body shapes, our findings also suggest a role of historical contingency. Considering that *Lerista* is a recent radiation (13.4 Myr; Skinner *et al.*, 2008), the differences in evolutionary pathways towards convergent endpoints are somewhat unexpected (Conte *et al.*, 2012). First, each clade evolved a number of unique morphs (Fig. 2), and thus had some non-convergent trait optima, which would suggest different evolutionary pathways. Second, even within morphs, a subset of species were not significantly convergent (Fig. 1; Table 2), and thus may be indicative of differences in evolutionary paths taken in the evolution of digit morphs. Third, the shape of the relationship between traits (Fig. 4; Tables 5, 6) and the pattern of integration among front limb elements (Table 4) differed between clades. These differences may be the result of many-to-one mapping (Alfaro *et al.*, 2004; Wainwright *et al.*, 2005), with different aspects of body shape differently affecting locomotion, but resulting in similar performance.

Our findings of strong negative evolutionary correlations between the body and relative limb lengths coincide well with those of Skinner and Lee (2009) in *Lerista*, but also differ in that we documented a positive correlation between relative front and hind limb

Table 4. Matrices of evolutionary correlations between limb elements

	Upper front limb	Lower front limb	Manus	Front digit
Upper front limb		0.984	0.986	0.972
Lower front limb	0.820		0.959	0.949
Manus	0.828	0.984		0.993
Front digit	0.825	0.989	0.996	

	Thigh	Crus	Pes	Hind digit
Thigh		0.796	0.794	0.788
Crus	0.760		0.911	0.911
Pes	0.735	0.867		0.996
Hind digit	0.732	0.873	0.989	

Shaded cells show Pearson's correlation coefficients for the interior clade ($n = 21$), and unshaded cells show these values for the coastal clade ($n = 31$). All correlations are significant ($P < 0.01$) after Benjamini–Hochberg correction.

Table 5. Δ_{AIC} values for the threshold, linear and null models for each pair of traits for the interior and coastal clades

X	Y	Interior ($n = 27$)			Coastal ($n = 35$)		
		Threshold	Linear	Null	Threshold	Linear	Null
Snout-vent length	Number of front digits	0.04	**0.00**	7.06	**0.00**	7.87	25.27
Snout-vent length	Front limb length	0.13	0.00	**1.93**	**0.00**	25.98	43.37
Front limb length	Number of front digits	3.47	**0.00**	33.72	**0.00**	3.21	71.31
Snout-vent length	Number of hind digits	2.79	**0.00**	13.08	0.11	**0.00**	24.56
Snout-vent length	Hind limb length	**0.00**	10.15	13.48	**0.00**	2.26	10.51
Hind limb length	Number of hind digits	**0.00**	2.85	19.01	0.00	**1.85**	21.21

The Δ_{AIC} value for the best model (plotted in Fig. 5) is in bold. Snout-vent and limb lengths are untransformed and relative, being divided by head length to correct for size. A more complicated model had to beat a simpler model by at least two Δ_{AIC} units to be counted as better.

Table 6. Parameter estimates of the best models (identified in Table 4, plotted in Fig. 5) for each pair of traits for interior and coastal clades

X	Y	Interior (n = 27)			Coastal (n = 35)		
		Model	Parameter	Estimate ± SE	Model	Parameter	Estimate ± SE
Snout-vent length	Number of front digits	Linear	a	4.096 ± 0.943	Threshold	K	6.421 ± 0.914
			b	−0.290 ± 0.088		S	−2.786 ± 0.915
			λ	1.000		λ	1.000
Snout-vent length	Front limb length	Null	a	0.339 ± 0.129	Threshold	A	0.560 ± 0.147
						K	10.272 ± 0.411
			λ	1.000		S	−19.145 ± 15.250
						λ	1.000
Front limb length	Number of front digits	Linear	a	0.202 ± 0.159	Threshold	K	0.602 ± 0.048
			b	2.947 ± 0.234		S	1.364 ± 0.206
			λ	0.444		λ	<0.001
Snout-vent length	Number of hind digits	Linear	a	5.338 ± 0.792	Linear	a	5.338 ± 0.792
			b	−0.328 ± 0.073		b	−0.328 ± 0.073
			λ	1.000		λ	1.000
Snout-vent length	Hind limb length	Threshold	A	1.931 ± 0.202	Threshold	A	1.931 ± 0.202
			K	10.985 ± 0.328		K	10.985 ± 0.328
			S	−26.748 ± 12.549		S	−26.748 ± 12.549
			λ	1.000		λ	1.000
Hind limb length	Number of hind digits	Threshold	K	1.646 ± 0.317	Linear	a	0.387 ± 0.421
			S	1.186 ± 0.420		b	1.126 ± 0.223
			λ	1.000		λ	1.000

Snout-vent and limb lengths are untransformed and relative, being divided by head length to correct for size, n is the number of species.

lengths, which the other authors did not. Skinner and Lee (2009) suggested that the hind limbs could get relatively longer or shorter, depending on the species, as the front limbs were reduced. Our pPCA results may support this effect to some degree because our pPC-2 seems to reflect differential bias in how the front and hind limbs are reduced (Table 1).

A snake-like body shape in *Lerista* may have evolved for functional reasons associated with locomotion. It is thought that an initial increase in body elongation allowed for greater reliance on undulatory locomotion, which was then followed by decreasing limb lengths as a result of relaxed selective pressure for maintaining a disused structure, or due to interference of the limbs with undulation (Gans, 1975; Greer, 1987, 1990; Skinner et al., 2008; Skinner & Lee, 2009; Bergmann & Irschick, 2010). However, complete digit loss in *Lerista* may have occurred very rapidly (3.6 Myr for *Lerista*) and intermediate forms also arose rapidly, but have persisted (Skinner et al., 2008). This casts doubt on the relaxed selection hypothesis for limb loss, as this suggests that the intermediate forms are not taxa on their way to complete limb reduction, but rather, maintained by selection (Brandley et al., 2008). One possible adaptive scenario could be that even reduced limbs can aid in locomotion through leaf litter and other structural components

of the habitat (Brandley et al., 2008 Pers. Obs. for *Brachymeles* in the Philippines). While Kendrick (1991) found some evidence that *Lerista* partition microhabitat by substrate type and their relation to *Acacia*, it remains unknown how differential limb reduction and the persistence of partial limbs might be adaptive.

In studying the evolutionary pathways of various other snake-like squamates, threshold patterns between various combinations of relative elongation, limb lengths and digits numbers have also been documented in *Brachymeles* (Siler & Brown, 2011), *Chalcides* (Greer et al., 1998) and other snake-like lizards in general (Brandley et al., 2008). In *Brachymeles*, relationships between relative snout-vent length and relative limb lengths for the number of front and hind digits appear to follow a pattern resembling a logistic curve (Siler & Brown, 2011). In *Chalcides*, a similar pattern can be seen in the number of phalanges, relative to snout-vent length and limb lengths (Greer et al., 1998). When snake-like lizards are more broadly considered, a pattern resembling a logistic curve can be seen between relative limb lengths and number of front and hind digits, but thresholds between relative snout-vent length and digit numbers show patterns that resemble exponential decay curves (Brandley et al., 2008). Although the correlation between limb reduction

and body elongation is well documented in salamanders (Jockusch, 1997; Parra-Olea & Wake, 2001; Wiens & Hoverman, 2008) and fishes (Ward & Brainerd, 2007; Suzuki, Brandley & Tokita, 2010; Mehta *et al.*, 2010; Ward & Mehta, 2010), none of these studies have considered the shape of the relationship. From previous studies and our work on *Lerista*, threshold relationships between various body and limb traits appear to be common in the transition from lizard-like to snake-like body shapes in squamates, but whether this is also the case for other clades of vertebrates that have evolved snake-like body shapes remains unknown. Determining if this is indeed the case will help to elucidate whether the mechanisms behind this transition are conserved among all vertebrates, or just squamates.

EVOLUTIONARY DEVELOPMENT OF LIMBS AND DIGITS IN *LERISTA*

Evolutionary development in *Lerista* remains unstudied. However, when phalangeal formulae are considered, the pentadactyl species, *L. microtis*, exhibits phalangeal formulae that are the same as the ancestral formulae for squamates (Romer, 1956), and the pentadactyl *L. bougainvillii* has lost a single phalanx on hind digit V (Greer, 1987, 1990, 1991). This is in stark contrast with other clades that exhibit uniform, or largely uniform phalangeal formulae (Zangerl, 1945; Kohlsdorf & Wagner, 2006; Brandley *et al.*, 2008; Siler & Brown, 2011). However, it is thought that these clades have re-evolved their digits, something that is not supported in *Lerista* (Skinner *et al.*, 2008; Skinner & Lee, 2010). The loss of digit identity suggested by these phalangeal formulae in these other clades are similar to *Gli3* knockout mice, which also show similar patterns of digit identity loss (Litingtung *et al.*, 2002; Welscher et al., 2002). The uniformity of these phalangeal formulae may point to novel evolutionary developmental pathways for distal limb patterning (Kohlsdorf & Wagner, 2006), but pentadactyl *Lerista* are more likely to exhibit the ancestral developmental programme for squamates.

When the phalangeal formulae of limb-reduced *Lerista* are considered, they do not correspond to any known intermediate developmental states (Greer, 1991), and thus limb reduction is unlikely to be a mere truncation of the pentadactyl limb development programme. This observation matches developmental findings for *Hemiergis* skinks (Shapiro, 2002). Limb-reduced *Hemiergis* exhibit a shorter duration of *Sonic hedgehog (Shh)* gene expression relative to fully limbed species (Shapiro, Hanken & Rosenthal, 2003) and so it is possible that the same mechanism is behind limb reduction in *Lerista*. Because *Shh* mediates proliferation of limb mesenchyme through fibroblast growth

factors, it may ultimately lead to the failure of anterior and posterior digit formation, while retaining the identities of digits that do form (Shapiro *et al.*, 2003). However, that digit identity can undergo homeotic frameshifts, a phenomenon that has been documented in birds (Wagner & Gauthier, 1999; Larsson & Wagner, 2002) and in other limb-reduced skinks (*Chalcides chalcides* - Young *et al.*, 2009). Thus, a necessary first step in characterizing limb development and reduction in *Lerista* will be to observe ossification sequences and the timing and duration of expression of the genes implicated in limb development, particularly *Shh*.

Recent phylogenetic studies in limb-reduced lizard taxa have found evidence suggesting that some of these lineages may have re-evolved limbs or digits. Indeed, robustly limb species appear to be nested within clades of limb-reduced species in *Bachia* (Kohlsdorf & Wagner, 2006; Kohlsdorf *et al.*, 2010), *Brachymeles* (Siler & Brown, 2011), *Bipes* and *Scelotes* (Brandley *et al.*, 2008). In *Lerista*, ancestral state reconstructions did not find evidence for digit re-evolution (Skinner *et al.*, 2008; Skinner & Lee, 2010). Our SURFACE analysis also showed no instances where a highly limb reduced optimum gave rise to a more robustly limb optimum (Fig. 1).

USING MODEL SELECTION TO IDENTIFY MORPHOLOGICAL THRESHOLDS

Morphological thresholds have been studied in the evolution of limb morphology in snake-like lizards (Lande, 1978; Brandley *et al.*, 2008; Siler & Brown, 2011), the evolution of various dimorphic traits in a variety of animals (Roff, 1994, 1996) and the evolution of horn length in beetles (Moczek *et al.*, 2002; Moczek & Nijhout, 2003). These examples suggest that threshold-type relationships between traits may be a widespread phenomenon that is understudied. Furthermore, while statistical methods for analysing non-linear data abound, these methods have been confined to intraspecific data (Moczek *et al.*, 2002; Moczek & Nijhout, 2003), or comparative data with binary response variables (Felsenstein, 2005; Ives & Garland, 2010). Using a model-based, phylogenetically informed approach allowed us to rigorously differentiate between linear and threshold relationships for continuous traits (Tables 5, 6; Fig. 4). Model selection using AIC and Δ_{AIC} values is an appropriate framework for comparing the fit of the logistic threshold and linear models because these two models differ structurally, so are not nested (Burnham & Anderson, 2002). A critical component of modern comparative methods is that they take phylogeny into account (Garamszegi & Mundry, 2014). Thus, another important advantage of our approach over previous considerations of

thresholds is that we were able to take phylogenetic relatedness among species into account (Felsenstein, 1985; Garamszegi & Mundry, 2014) in the curve-fitting procedures. This is of paramount importance because as the phylogenetic signal in the residuals increases (Revell, 2010), a fitted curve may increasingly deviate from that expected from visual inspection (e.g. Fig. 4F coastal clade). Indeed, we found that in some cases, the best-fitting model differed if phylogeny was taken into account *versus* not – something that requires further investigation.

CONVERGENCE OF PHENOTYPE, FUNCTION AND ECOLOGY

We have shown that two clades of *Lerista* have converged in digit morphs and body shapes by following similar evolutionary pathways to arrive at their extant phenotypes, but that there are also important differences in how they have reached those phenotypes. This work builds on a growing body of literature, finding that convergent phenotypes can evolve through subtly different pathways (Stayton, 2006; McGee & Wainwright, 2013; Collar *et al.*, 2014). The implications of this may be far-reaching in how they affect the biology of convergent organisms. If clades have differently evolved equivalent phenotypes, it is possible that different selective pressures or sets of constraints have shaped the evolution of each clade (Losos, 2011; Wake *et al.*, 2011). Different selective pressures open the possibility that phenotypically convergent clades are not convergent functionally or ecologically – phenotypically similar species may be playing different roles in their ecosystems. Indeed, a growing body of work has shown decoupling between convergence of genes and phenotypes (Wilkens & Strecker, 2003; Hoekstra *et al.*, 2006), phenotypes and function (Stayton, 2006; McGee & Schluter, 2013; Collar *et al.*, 2014) and hypothesized the decoupling of convergence between phenotype and ecology (Gans, 1975; Wiens & Slingluff, 2001; Wiens *et al.*, 2006). The next step is to integrate these different avenues of studying convergence and assess their collective effect on macroevolutionary patterns.

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SUPPORTING INFORMATION

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

Methods S1. Description of morphometric variables.
Methods S2. Code for calculating evolutionary correlations.
Methods S3. Threshold detection approach power analysis.
Figure S1. Map of Australia with *Lerista* clade ranges.
Figure S2. Power analysis results.
Figure S3. Phylomorphospace of *Lerista* using pPC-1 and pPC-3.
Table S1. Table of specimens used for this study and their voucher numbers.
Table S2. Phylogenetic PCA loadings with relative tail length included.
Table S3. Classification matrix of trait optima to digit morphs.
Table S4. Stayton's C1 for all unique combination of pairs between clades for the 4/4 morph.
Table S5. Stayton's C1 for all unique combination of pairs between clades for the A/S and 1/2 morphs.
Table S6. Stayton's C1 for all unique combination of pairs between clades for the A/2 morph.
Table S7. Stayton's C1 for all unique combination of pairs between clades for the 2/3 morph.
Table S8. Evolutionary correlations of limb elements for all *Lerista*.
Table S9. Model selection and parameter estimates for threshold analyses for all *Lerista*.