

Body-form Evolution in the Scincid Lizard Clade *Lerista* and the Mode of Macroevolutionary Transitions

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Abstract The scincid lizard clade *Lerista* provides an exceptional model for studying the mode of substantial evolutionary transformations, comprising more than 90 species displaying a remarkable variety of body forms. Patterns of character evolution in this clade, inferred from reconstructed ancestral states, are at least partly consistent with the correlated progression model of macroevolutionary change. At each stage in the transition to a highly elongate, limb-reduced body plan, alterations to the lengths of the forelimb and hind limb are accompanied by compensatory changes in snout-vent length (or vice versa), preserving locomotory ability. Nonetheless, there is evidence for moderate dissociation of hind limb evolution in some lineages, while tail length has evolved effectively independently of the substantial alterations to the lengths of the body and limbs. This indicates a significant role of evolutionary and developmental modularity in the divergence of body form within *Lerista*, and emphasises the potential variability of the strength of functional constraints within organisms and among lineages. Trends toward a highly elongate, functionally limbless body plan may be attributed primarily to a combination of the interdependence of changes in snout-vent length and limb lengths and the very low probability of re-elaborating structurally

reduced limbs. Similar asymmetries in the probabilities of interrelated phenotypic changes may be a significant cause of evolutionary trends resulting in the emergence of higher taxa.

Keywords Correlated progression · Evolutionary trend · Limb reduction · Modularity · Skink

Introduction

The mode by which phenotypically disparate clades traditionally designated as higher taxa originate has been the focus of prolonged debate in evolutionary biology (e.g., Gould 1980; Levinton 2001; Gould 2002; Budd 2006). The primary issue inciting discussion is the efficacy of the neo-Darwinian model of gradual phenotypic change mediated by natural selection in explaining the substantial differences in body plan that separate such clades from related taxa. Although large phenotypic discontinuities among contemporary species may conceivably be produced by gradual divergence in conjunction with extinction of intermediate forms, there are at least two potential difficulties for neo-Darwinian accounts of the emergence of higher taxa. Firstly, organism functionality must be preserved throughout major phenotypic transitions, however, functional intermediary stages may be difficult to envisage, raising the possibility that such transitions are at least partially saltatory (Gould 1980; Rieppel 2001). And secondly, specification of selection pressures driving phenotypic transformations may be problematic. Kemp (1999, 2007a) has argued that the origination of many higher taxa can be conceptualised as a trend, consisting of a series of directional changes in phenotype. Where such trends occur over geologically extended periods (as may be usual), the

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explanation of a consistent selection pressure may become implausible considering the temporal scale of environmental fluctuation (Gould 2002, p. 889; Kemp 2007a).

As Kemp (2007a; see also Levinton 2001) discussed, there are (at least) two general, non-saltatory modes by which substantial alterations of body form can be achieved without significant disruption of organism functionality; the first of these modes, commonly referred to as mosaic evolution, is facilitated by the modular organisation of organisms, while the second mode, termed correlated progression, emphasises the functional integration of all components of organismal phenotypes, and accords an insignificant role to modularity in macroevolutionary transitions. Adopting a process-oriented perspective (see Schlosser and Wagner 2004), modules may be characterised as internally integrated, relatively autonomous systems of interacting components that contribute to a more inclusive system or process (Schlosser 2002, 2004). This perspective implies that modules are identifiable only in relation to a specific incorporating process and, accordingly, that modules participating in one process may not necessarily qualify as modules in a second process. Recent discussion of modularity and its implications for evolutionary transformations has focused on the relationship between two distinct kinds of modules, developmental modules and evolutionary modules (see Schlosser 2002, 2004; Schlosser and Wagner 2004).

Modular organisation is a pervasive feature of organismal development, and an understanding of the consequences of developmental modularity for phenotypic evolution is considered by many authors as fundamental to a conceptual synthesis of developmental and evolutionary biology (e.g., Raff 1996; Wagner and Altenberg 1996; von Dassow and Munro 1999; Bolker 2000; Schlosser 2002; West-Eberhard 2003; Schlosser 2004; Schlosser and Wagner 2004). Modules of development are integrated, quasi-autonomous systems that contribute to ontogeny, and include transcriptional regulation mechanisms (incorporating particular *cis*-regulatory elements and transcription factors, and the basal transcriptional apparatus), signalling cascades, gene regulatory networks, specific cell types, and organ primordia (Schlosser 2004). All of these systems are able to operate or develop consistently in varying contexts (i.e., they behave in a context-insensitive, or autonomous, manner), although they may be disrupted by perturbation of any one of their components (due to the interdependence of all components). As a consequence of their relative insensitivity to external perturbation, developmental modules may preserve their functionality despite alteration of the developmental context in which they are embedded, potentially facilitating evolutionary transformations of phenotype (Schlosser 2002, 2004; Schlosser and Wagner 2004).

Although the modular organisation of development may enable substantial independent evolution of distinct phenotypic components (i.e., mosaic evolution), at least two conditions must be satisfied if developmental modularity is to have a primary role in evolutionary transitions (see Schlosser 2004; Schlosser and Wagner 2004). Firstly, developmental modules must affect the fitness of organisms relatively independently; if the contribution to fitness of a developmental module depends on the specific states of other modules (i.e., the developmental context), the capacity for independent evolution of modules will be limited by functional constraints. Secondly, heritable alterations of developmental modules should have few pleiotropic effects, so that distinct modules (or their phenotypic effects) may vary and be selected independently. Thus, modules of development must correspond to or produce phenotypic components that are developmentally and functionally dissociated if they are to operate as evolutionary modules (i.e., integrated, quasi-autonomous units of evolutionary change; Schlosser 2004; Schlosser and Wagner 2004). Evolutionary modules, therefore, may coincide with single developmental modules, or incorporate multiple developmental modules coupled by pleiotropy or functional dependency. As the developmental and functional connectedness of phenotypic traits varies on a continuous scale, degree of evolutionary modularity (and hence the potential for mosaic evolution) will also vary continuously; where the connectedness of traits is low, developmental modularity may promote considerable independent evolution of phenotypic components, however, as connectedness increases, this evolutionary independence will be increasingly restricted by developmental and functional constraints.

Correlated progression (Thomson 1966; Kemp 1982; Thomson 1992; Lee 1996; Kemp 1999, 2007a, b) involves the concerted evolution of multiple phenotypic components exhibiting relatively strong functional interdependence. Proponents of this model of macroevolutionary transition (most notably Kemp 2007a, b) consider that all parts of an organism are sufficiently integrated functionally that substantial modification of any part alone will severely disrupt the ability of the organism to survive and reproduce (thus, organisms are not dissoluble into functionally autonomous phenotypic components). Nonetheless, the functionality of an organism may display some resilience to minor perturbations, so that dramatic evolutionary transformations can be achieved through a series of small changes, each followed by compensatory changes to other components of the phenotype that permit further small changes. Functional integration of all phenotypic components during such evolutionary transformations would prohibit any significant role of developmental modularity; as noted above, developmental modules may operate as evolutionary modules

(enabling mosaic evolution) only when they correspond to or construct functionally independent traits. As a consequence, correlated progression and mosaic evolution (facilitated by developmental modularity) have been regarded as alternative macroevolutionary models (Kemp 2007a, b). However, as the degree of functional integration may vary continuously (see above), the two models are not sharply defined; instead, they may be considered as extremes of a continuum of models, each of which invokes a different level of functional interdependence. Moreover, the strength of functional interconnections among phenotypic components may vary substantially within an organism, so that both models may apply to different facets of the same evolutionary transformation.

Evolutionary modules may be recognised empirically by examining phylogenetic patterns of character change. As Schlosser (2004, pp. 547–549) discussed, the components of an evolutionary module should exhibit a substantial degree of dissociated coevolution; that is, evolutionary changes in different components of a module should be coordinated, while displaying no significant correlation with changes in other phenotypic components. A set of characters exhibiting this pattern of dissociated coevolution may be constructed by or correspond to a single developmental module, or two or more developmental modules connected by functional or developmental constraints (see above). Where an evolutionary module incorporates a large number of functionally interdependent characters (typically generated by numerous developmental modules), essentially the entire phenotype may evolve in a coordinated fashion, consistent with the correlated progression model. Ascertaining the extent to which components of novel body plans are assembled and modified independently is a primary empirical issue in the study of macroevolutionary transitions; evidence for dissociated evolution of phenotypic components indicates a potentially significant role of developmental modularity in evolutionary transformations, however, coordinated change in many or all components implies that functional and developmental constraints may render modular development relatively inconsequential for the emergence of higher taxa.

Although direct evidence for phylogenetic patterns of character change is typically available only from the fossil record, ancestral character state reconstruction may be employed to infer such patterns indirectly (see Schluter et al. 1997; Pagel 1999). The latter approach is applicable not only to taxa that are poorly represented in the fossil record, but also characters that are rarely (if ever) preserved (e.g., soft anatomy, behaviour) or liable to taphonomic distortion (e.g., morphometric variables). In this study, we apply this approach to investigate the evolution of body form in *Lerista*, a morphologically diverse clade of Australian scincid lizards including species that possess

pentadactyl limbs and resemble typical non-fossorial scincids in body proportions, as well as species exhibiting varying degrees of limb reduction and body elongation, including two species that are highly elongate and entirely limbless (Greer 1989; Cogger 2000; see Fig. 1). As Wiens (2009, p. 19.1) noted, the transition from ‘a four-limbed lizard-like body plan to an elongate, limbless snake-like one’ is ‘one of the most dramatic changes in body form in animals’; the repeated evolution of a highly elongate, limb-reduced body form within *Lerista*, and the existence of extant species displaying a range of intermediate phenotypes, affords an exceptional opportunity to study the mode and causes of this significant macroevolutionary transformation (see Skinner et al. 2008). Our principal goal here is to evaluate the contribution of evolutionary modularity to



Fig. 1 Selected species of *Lerista* illustrating the considerable divergence of body form within this clade; from top to bottom, *L. microtis*, *L. punctatovittata*, and *L. ameles*. Photographs by Mark Hutchinson (*L. microtis* and *L. punctatovittata*) and Marco Sacchi (*L. ameles*)

the considerable divergence of body form evident within *Lerista* and, accordingly, the relative significance of developmental modularity and functional and developmental constraints in macroevolutionary change. Additionally, we consider the selection pressures that may have driven this divergence and propose a general explanation for observed evolutionary trends.

Materials and Methods

Aside from the evident reduction and loss of limbs, a suite of phenotypic alterations may accompany the evolution of an elongate, limbless body form (inferred to be apomorphic; see below), including an increase in the length of the body (achieved, for example, by augmenting the number of presacral vertebrae), a decrease in the diameter of the body, an increase in the length of the tail, lengthening of the viscera, and unilateral reduction of paired organs (Gans 1975). We examined five morphometric variables, recorded from series of 1–5 specimens for 69 species of *Lerista* and one outgroup taxon (*Ctenotus robustus*): snout-vent length, forelimb and hind limb lengths (measured from the axilla and groin, respectively, to the tip of the longest digit), head width (an index of body diameter, measured at the widest point of the head), and tail length. Although a complete description of the evolution of body form in *Lerista* would incorporate information from numerous additional characters (see Berger-Dell'mour's 1983 comprehensive study of body elongation and limb reduction in the cordylid clade *Tetradactylus*), these variables capture the most prominent external variation in body form among species. Specimen registration and collection locality data are provided in Table S1. All measurements were divided by head length (measured from the tip of the snout to the anterior margin of the auricular opening) to negate the effect of varying absolute body size (see Lande 1978; Greer and Wadsworth 2003). As a means of reducing any influence of allometric growth, only the largest available specimens were measured. Mean values calculated for each species were employed in reconstructing ancestral states.

Ancestral states for each variable were reconstructed via maximum likelihood, assuming a Brownian motion model of phenotypic evolution (see Schluter et al. 1997) and a phylogeny for *Lerista* inferred from nucleotide sequences for six mitochondrial genes and a nuclear intron (see Figs. S1, S2; Skinner et al. 2008, their Fig. 1). The inferred ancestral values were then used to calculate the amount of change occurring along each branch of the phylogeny (see Tables S2, S3; Huey and Bennett 1987; Losos 1990). Partial correlation coefficients (r ; see Sokal and Rohlf 1995, pp. 649–654) were calculated for each pair of variables, considering inferred amounts of change for

individual branches as variates. Prior to computation, we added an arbitrary value of 10 to all variates (so that all values were positive) and logarithmically transformed the resulting sum. As tail lengths were unavailable for a number of species (regenerated tails were not measured; see Fig. S2 and Table S3), we performed two sets of calculations; the first set of calculations excluded tail length and included all species, whereas the second set of calculations included all variables and excluded those species for which tail lengths were unavailable. Partial correlation coefficients computed in the first set of calculations measure the association of each pair of variables when the remaining two variables are held constant; these second-order partial correlations were calculated using equation 16.21 of Sokal and Rohlf (1995, p. 650). The third-order partial correlation coefficients computed in the second set of calculations measure the association of each pair of variables when three remaining variables are held constant, and were computed using a straightforward extension of Sokal and Rohlf's (1995) equation for second-order partial correlations. All calculations were performed using R (R Development Core Team 2008).

The significance of observed partial correlations was assessed by comparing coefficients of partial determination (i.e., r^2) for the empirical data with values derived from data simulated under the assumption of independent evolution. A modified version of the R function 'evolve.phylo' (included in Paradis et al.'s 2008 'ape' package) was employed to simulate 1000 data sets for each variable (each data set consisting of a set of values for terminal nodes), assuming the same phylogeny used in inferring ancestral states and a rate parameter value estimated from the empirical data ('evolve.phylo' implements a simple Brownian motion model of character evolution). Ancestral states reconstructed for each data set were used to calculate the amount of change occurring along each branch of the phylogeny, as described above. Coefficients of partial determination for all pairs of variables were then calculated for each simulation replicate, considering amounts of change for individual branches as variates (a value of 10 was added to all variates and the resulting sum was logarithmically transformed prior to computation, as for the empirical data; see above). As data were simulated for each variable independently (i.e., within each simulation replicate), frequency distributions for the resulting 1000 coefficients approximate probability distributions under a model of independent phenotypic evolution (assuming characters evolve according to a Brownian motion model); observed r^2 values in the upper tails of these distributions (we accepted a probability of type I error of 0.05) were regarded as evidence for coordinated change and, accordingly, the contribution of two characters to a single evolutionary module.

Results and Discussion

Modularity, Correlated Progression, and Functional Continuity

Significant negative correlations exist between changes in snout-vent length (i.e., measured relative to head length) and forelimb length, and snout-vent length and hind limb length (Table 1), indicating that the lengths of the body and limbs have evolved in a coordinated manner. An association of limb reduction and body elongation in squamates has been noted by many authors (e.g., Gans 1975; Lande 1978; Greer 1987; Greer et al. 1998; Wiens and Slingluff 2001; Brandley et al. 2008), and may be ascribed to the complementary relationship of limb-mediated locomotion and locomotion by lateral undulation; as lateral undulation, facilitated by body elongation, increases in significance, reliance on limb-mediated locomotion decreases, resulting in reduction of the limbs (Greer and Wadsworth 2003). This interpretation indicates a simple evolutionary scenario in which an elongate, limbless body form is attained through a series of coordinated changes in snout-vent length and limb lengths. An initial increase in the length of the body enables more efficient movement by lateral undulation, prompting (or permitting) greater reliance on this locomotory mode (see Berger-Dell'mour 1983). This increased reliance on undulatory locomotion is followed by reduction in the lengths of the forelimb and hind limb; this reduction could be passive, resulting from an absence of selection against deterioration of disused structures, or actively selected for (as a means of reducing frictional resistance during undulatory locomotion, for example). Reduction of the limbs, in turn, places increased emphasis on undulatory locomotion, leading to selection for further body elongation.

The evolutionary scenario presented above assumes a significant functional relationship between the lengths of the body and limbs, implying that body elongation and limb reduction are functionally constrained. As Greer and Wadsworth (2003) have discussed, a stout body supporting diminutive limbs would be unable to perform either limb-mediated or undulatory locomotion, imposing an evident constraint on limb reduction in the absence of body elongation. A highly elongate body bearing unreduced limbs similarly may be poorly suited for efficient locomotion, constraining body elongation in the absence of limb reduction (see Greer and Wadsworth 2003). As the body is elongated (and hence attenuated), it may become insufficiently strong to provide support as a lever base or muscular anchor point for limbs large enough to generate effective propulsive forces. Moreover, the delivery of these forces (primarily by the hind limbs) increasingly far from the centre of mass would reduce locomotory control. At the same time, the presence of unreduced limbs could impede subsurface undulatory locomotion by increasing the effective diameter of the body, and hence frictional resistance (Gans 1975). Nonetheless, there is evidently some capacity for at least minor limb reduction in the absence of body elongation, and vice versa, considering the imperfect relationships between snout-vent length and forelimb and hind limb lengths among extant species of *Lerista* (see Fig. S3). Thus, although substantial, independent alteration of body and limb lengths may be prohibited by functional constraints, there is evidence for the potential independence of at least small changes, enabling evolutionary transformation by correlated progression (see also Berger-Dell'mour 1985).

Although a positive relationship between changes in forelimb and hind limb lengths is apparent when these variables are considered alone (Fig. 2), an insignificant

Table 1 Partial correlation coefficients (r) calculated for all variables (*upper panel*) and all variables except tail length (*lower panel*)

	Snout-vent length	Forelimb length	Hind limb length	Head width
Forelimb length	−0.6543*			
Hind limb length	−0.5225*	0.0260		
Head width	−0.2129	−0.1666	0.1841	
Tail length	0.2918	0.2318	−0.0017	0.1309
	Snout-vent length	Forelimb length	Hind limb length	
Forelimb length	−0.6089*			
Hind limb length	−0.4660*	0.0914		
Head width	−0.1267	0.0072	0.1713	

Two sets of calculations were performed as tail lengths were unavailable for a number of species (regenerated tails were not measured; see Fig. S2 and Table S3); the first set of calculations (excluding tail length) included all species, while the second set of calculations (incorporating all variables) included only those species for which tail lengths were available. Significant values (see text) indicated by an asterisk, provide evidence for the concerted evolution of two traits

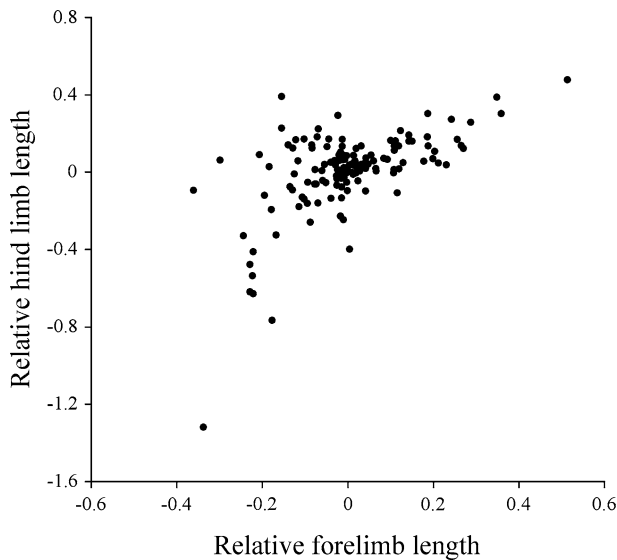


Fig. 2 Relationship between changes in relative forelimb length (i.e., forelimb length divided by head length) and relative hind limb length. Points represent inferred amounts of change occurring along individual branches

partial correlation coefficient (see Table 1) indicates that this relationship reflects the correlation of changes in both variables with changes in the remaining variables (primarily snout-vent length), as opposed to a direct association. Nonetheless, the pattern of relationship may provide insight into the mode of limb reduction in *Lerista*. While decreases (i.e., negative changes) in forelimb length are associated with both increases and decreases in hind limb length, decreases in hind limb length are nearly invariably accompanied by decreases in forelimb length (Fig. 2). Thus, forelimb reduction may proceed without hind limb reduction, however, hind limb reduction generally occurs in conjunction with forelimb reduction. This is consistent with a more significant role of the hind limb in limb-mediated locomotion and selection in several lineages for preserving some ability to employ limb-mediated locomotion as body elongation and limb reduction progress, a conclusion also indicated by patterns of digit loss (see Skinner et al. 2008).

There are no significant correlations between changes in either head width or tail length and changes in the remaining variables (Table 1). Accordingly, the diameter of the body and length of the tail may be considered to have evolved independently of the extensive alterations to the lengths of the body and limbs. Although the tail contributes to the long axis of the body and, consequently, may have a significant role in undulatory locomotion (see Gans 1975), the predominantly fossorial habits of limb-reduced species of *Lerista* may have emphasised elongation through an increase in snout-vent length, moderating functional constraints on alterations to tail length. A consistent

association of fossoriality and relatively short tails in highly elongate, functionally limbless squamates has been noted by several authors (e.g., Camp 1923; Gans 1960; Wiens and Slingluff 2001; Wiens et al. 2006; Brandley et al. 2008), and suggests that elongation of the trunk (as opposed to the tail) confers a general, presumably locomotory advantage in fossorial species (see Berger-Dellmour 1985). The capacity for caudal autotomy in *Lerista* may also have contributed to the dissociation of changes in tail length, as the potential for partial or entire tail loss presumably would inhibit reliance on the tail in undulatory locomotion, accentuating elongation of the presacral portion of the axial skeleton.

Alterations to the diameter of the body may be more severely constrained, permitting negligible directional change. As the body becomes increasingly slender, the effectiveness of locomotory forces produced by lateral undulation will eventually decrease (due to the increasing ratio of the surface and cross-sectional areas of the body), establishing a lower limit on body diameter (see Greer and Wadsworth 2003). An upper limit on body diameter could result from the decreasing efficiency of movement through substrates such as loose soil or sand as the cross-sectional area of the body increases (Gans 1975). Among extant species of *Lerista*, relative head width varies considerably less than the other variables, deviating from the mean by no more than 16% (the corresponding values for snout-vent length, forelimb and hind limb lengths, and tail length are 85%, 162%, 100%, and 42%, respectively). Thus, the insignificant correlations between changes in head width and body and limb lengths are perhaps attributable to minimal modification of the diameter of the body (i.e., there is no substantial phenotypic divergence to be explained).

The inferred patterns of character change discussed above indicate that a significant component of body form in *Lerista*, specifically, the lengths of the trunk and limbs, has evolved as an integrated unit; thus, the presacral portion of the axial skeleton and the limbs may be considered to contribute to a single evolutionary module. As Schlosser (2004, p. 538) noted, ‘The vertebrate limb bud is probably the most prominent example of a complexly integrated organ primordium that nonetheless develops relatively autonomously and, thus, constitutes a [developmental] module’. Axis elongation and somitogenesis (which are highly coordinated and, in conjunction, determine the number of vertebrae composing the axial skeleton) may also be regarded as a developmental module, involving a complex ‘clock-and-wavefront’ mechanism that incorporates multiple signalling pathways (Dequéant and Pourquié 2008; Gomez et al. 2008). Perturbation of specific components of this mechanism can severely disrupt the regular formation of somites during embryogenesis (see Dequéant

and Pourquié 2008), indicating substantial internal integration. At the same time, somitogenesis is largely dissociable from axial patterning and associated developmental events (see Richardson et al. 1998) and, accordingly, exhibits some degree of context insensitivity. The relatively autonomous development of the length of the axial skeleton and the limbs could be expected to promote their independent evolutionary modification. Nonetheless, as these phenotypic components each affect locomotory performance, their evolutionary fate is effectively linked by functional constraints. Organism functionality requires that at each step in the attainment of an elongate, limb-reduced body plan, alterations to the lengths of the forelimb and hind limb are accompanied by compensatory changes in snout-vent length (or vice versa), preserving locomotory ability. This mode of evolutionary transformation conforms well with that envisaged by proponents of correlated progression.

Despite a general association of changes in snout-vent length and limb lengths, there is evidence for at least partial dissociation of hind limb evolution in some lineages. As Fig. 2 reveals (see above), substantial forelimb reduction (and associated body elongation) may proceed in the absence of hind limb reduction, so that several elongate species of *Lerista* with dramatically reduced forelimbs possess comparatively well-developed hind limbs (e.g., the highly elongate *L. vermicularis* has no external forelimbs, however, the relative length of the didactyl hind limb exceeds that for 61 of the 70 species of *Lerista* examined, including a number of pentadactyl and tetradactyl species). This suggests that functional (and possibly developmental) interconnections between the hind limb and the axial skeleton and forelimb may be reduced to a sufficient extent that relatively independent modification of these phenotypic components is permitted. An ability to fold the hind limbs against the tail and the loss of peripheral digits from the pes would serve to minimise frictional resistance during subsurface undulatory locomotion, and may contribute significantly to this reduction in functional interdependence. Inasmuch as the dissociated evolution of the hind limb depends on the construction of the axial skeleton and fore- and hind limbs by relatively autonomous developmental systems, the patterns of change inferred for the lengths of the body and limbs indicate at least a partial contribution of developmental modularity to the assembly of distinct body plans within *Lerista*.

Independent modification of the length of the tail similarly may indicate a significant role of developmental modularity in the evolution of body form in *Lerista*. Although the tail develops as part of the axial skeleton, determination of the numbers of caudal and presacral vertebrae may be dissociable, as the reduced number of caudal vertebrae in mice with the *vestigial tail* mutation

demonstrates (vestigial-tailed mutants usually exhibit the normal complement of presacral vertebrae; see Heston 1951; Greco et al. 1996). Thus, the independence of evolutionary changes in tail length may be facilitated by at least partially autonomous development of the caudal portion of the axial skeleton.

Patterns of phenotypic evolution within *Lerista* are at least partly consistent with the correlated progression model of macroevolutionary change. At each stage in the transition to a highly elongate, limb-reduced body plan, modifications to the lengths of the trunk and limbs are coordinated, permitting the maintenance of locomotory ability. Nonetheless, there is evidence for moderate dissociation of hind limb evolution in some lineages, while tail length has evolved effectively independently of the substantial alterations to the lengths of the body and limbs. This indicates a significant role of evolutionary and developmental modularity in the divergence of body form, and emphasises the potential variability of the strength of functional constraints within an organism and among lineages. An inclusive account of the evolution of body form in *Lerista* would therefore incorporate elements of both correlated progression and mosaic evolution, validating the proposal that these models should perhaps be considered as extremes of a continuum of models, each invoking a different level of functional interdependence among phenotypic components, and not as discrete categories of macroevolutionary change (cf. Kemp 2007a, b).

Evolutionary Trends

All highly elongate species of *Lerista* have evolved from a comparatively non-elongate ancestor via a series of directional changes in snout-vent length; successive changes along direct paths from the root node to these species are nearly all positive, with negative changes occurring along single branches and representing no more than a 9% decrease in relative snout-vent length (for comparison, positive changes occurring along all of the 10 consecutive branches separating *L. apoda* from the ancestor of *Lerista* produce a total increase in relative snout-vent length of 102%). Moreover, there is minimal evidence for the reverse trend of non-elongate species evolving from elongate species; the greatest inferred negative change occurs along four consecutive branches and represents a decrease in relative snout-vent length of 24%. Almost certainly, the recurring evolution of a limb-reduced, elongate body form in *Lerista* is a consequence of adaptation to increasingly fossorial habits (Gans 1975; Greer 1989). Absolute age estimates obtained using relaxed molecular clock methods indicate that *Lerista* originated in the late mid-Miocene (see Skinner et al. 2008), so that the expansion of seasonally dry and arid habitats (associated with loosely

consolidated, sandy substrates) in Australia from the late Miocene (Archer et al. 2000; Martin 2006) provides a suitable environmental context for the repeated evolution of fossoriality; however, this alone does not explain the overwhelming predominance of limb reduction and body elongation within the clade. Arid and semi-arid habitats sustain diverse assemblages of both fossorial and surface-active species of *Lerista* and, accordingly, it is not evident that aridification should bias the direction of evolutionary change so significantly.

The deficiency of trends toward a non-elongate body form in *Lerista* may be explained by a combination of the interdependence of evolutionary changes in snout-vent length and limb lengths, and the improbability of re-elaborating reduced limbs. Skinner et al. (2008) found no compelling evidence for the acquisition of digits in *Lerista*, consistent with the prevalent, although often implicit assumption that limb reduction is rarely (perhaps never) reversed (e.g., Presch 1975; Greer 1987, 1990, 1991). Although increases in the lengths of the forelimb and hind limb may be possible (indeed, these are inferred; see Fig. 2), the re-evolution of functional limbs could be inhibited by effective irreversibility of structural reduction (i.e., the loss of distinctive skeletal elements). It should be noted, however, that this proposed cause of directional evolution does not require that reversals of limb reduction are impossible, and is entirely compatible with recent studies indicating the reacquisition of digits in some squamate clades (Kohlsdorf and Wagner 2006; Brandley et al. 2008); even if re-elaboration of reduced limbs is possible, it is generally accepted that this phenomenon is exceptional. Thus, the transition from an elongate to a non-elongate body form, while unproblematic in principle, may be prevented by the absence of necessary modifications to the limbs. Although there may be no intrinsic bias toward body elongation, directionality is imposed by the requirement of organism functionality and the very low probability of limb re-elaboration. Similar asymmetries in the probabilities of interrelated phenotypic changes may be a significant cause of evolutionary trends resulting in the emergence of higher taxa.

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