



Macroecological and biogeographical patterns of limb reduction in the world's skinks

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Abstract

Aim: Limb reduction is a dramatic evolutionary transition, yet whether it is achieved in similar trajectories across clades, and its environmental drivers, remain unclear. We investigate the macroevolutionary and biogeographical patterns of limb reduction in skinks, where limb reduction occurred more often than in any other tetrapod clade, and test their associations with substrate categories using a global database. We test for habitat associations of body shapes in a group of Australian skinks using quantitative habitat data.

Location: Global (Scincidae), Australia (Sphenomorphinae).

Taxon: Skinks, Australian Sphenomorphinae.

Materials and Methods: We use morphological data to explore the patterns of limb reduction in the world's skinks, investigating how body proportions differ across skink clades and subfamilies. We examine the relationships between body shape and substrate (coarsely classified). Further, we investigate the relationships between body shape and high-resolution soil and climate properties extracted from each species' distribution for Australian sphenomorphines.

Results: Relationships between limb lengths and trunk elongation show idiosyncratic patterns across skink clades. Presacral vertebrae numbers positively correlate with trunk elongation in all taxa, except *Glaphyromorphus*. Skinks from sandy habitats show greater disparity between forelimb and hindlimb lengths than all other substrate categories. In sphenomorphines, shorter limbs and elongated trunks correlate with colder, more humid microhabitats and richer soils; high limb disparity correlates with hot, arid microhabitats and sandy, poor substrates.

Main Conclusions: The evolutionary trajectories of limb reduction in skinks are clade-specific and sometimes unique. Selection for specific limb proportions and body sizes in limb-reduced forms changes across substrates. On poor, sandy substrates of arid environments, body shapes with longer hindlimbs may be more efficient for locomotion in a granular fluid (i.e. sand) and exploit the air–substrate interface than complete

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limblessness. On richer, more humid substrates, such morphology is rare, indicating that navigating cluttered substrates selects for more equal and shorter limb lengths.

KEYWORDS

Australian Sphenomorphinae, biogeography, ecomorphology, limb reduction, macroecology, morphological evolution, skinks

1 | INTRODUCTION

The acquisition of limb-reduced and elongated body shapes represents one of the most dramatic morphological transitions in the history of tetrapods (Gans, 1975). This body shape exists in amphibians and mammals, but is most widespread among squamates, where it evolved at least 60 times independently (Brandley et al., 2008; Camaiti et al., 2022; Gans, 1975; Greer, 1991), including approximately 4700 species (estimated from the Reptile Database: Uetz et al., 2021) spread across various lineages (Brandley et al., 2008). Within squamates, limb reduction indicates the miniaturisation, or loss, of limbs and digits, and tends to further involve more presacral vertebrae, narrow heads and bodies (Rieppel, 1984), and elongated trunks (Camaiti et al., 2021).

Having evolved so frequently in squamates, limb reduction represents a useful system to investigate how and why distinct lineages differ in the acquisition of similar evolutionary endpoints. Several studies (e.g. Brandley et al., 2008; Gans, 1975; Stokely, 1947) identified similarities in body shapes (e.g. limb reduction, digit loss, trunk elongation) as examples of convergent evolution. Bergmann and Morinaga (2019) examined the relationships among body parts in focal clades of skinks and gymnophthalmids. They found evidence implying that each clade evolved limb reduction following unique evolutionary pathways (i.e. the anatomical, developmental, and genetic modifications involved). The evolution of these morphologies is often discussed in systematic studies involving few selected clades (Greer, 1987, 1990; Morinaga & Bergmann, 2017; Siler & Brown, 2011), resulting in a lack of comparative data mapped over reliable phylogenies and across clades. This makes it difficult to query the adaptive correlates of limb-reduced morphologies, as significant differences in the ways limb reduction is achieved across clades can be expected.

Skinks (Scincidae) are a clade that underwent over 50 independent transitions towards limb reduction and shows the most divergent body shapes among limb-reduced morphs in squamates (Camaiti et al., 2022; Greer, 1991). Thus, they are a prime example of variation in evolutionary trajectories of limb reduction. Past studies (Brandley et al., 2008; Wiens et al., 2006; Wiens & Slingluff, 2001) identified two morphologically and functionally distinct ecomorphs of limb-reduced squamates: a short-tailed, burrowing ecomorph and a long-tailed, grass-swimming ecomorph, linked to a lifestyle below and above ground, respectively. However, both ecomorphs, but particularly the burrowing ecomorph (the most abundant among limb-reduced forms; Brandley et al., 2008), include

an array of morphotypes that go beyond the distinction between subterranean and above-ground lifestyles (e.g. sand-swimming and mulch-dwelling habits: Stepanova & Bauer, 2021). Indeed, the ecomorphological variability within fossorial/burrowing habits in limb-reduced squamates remains largely unexplored (except in amphisbaenians: Gans, 1960), as the varying adaptive outcomes to different habitats and lifestyles are collapsed into a single ecomorph category (Brandley et al., 2008), and such studies are restricted to single clades.

Differences between body shapes, and variation in locomotory strategies, may indicate adaptations to different niches even within the same broad environment (Gans & Fusari, 1994; Morinaga & Bergmann, 2020). On a large spatial scale, morphological evolution is influenced by abiotic (climate, soil, topography), and biotic (vegetation structure, predators, prey, etc.) factors (Luxbacher & Knouft, 2009; Pavón-Vázquez et al., 2022; Smith & Ballinger, 2001). Recent studies (Bergmann et al., 2020; Grizante et al., 2012) found significant effects of climate on body-shape variation and evolution in squamates, linking limb reduction and body elongation with increased aridity. Substrate properties and composition may also drive lizard morphological diversity, as fossorial species live in direct contact with—or within—soil or substrate (Stepanova & Bauer, 2021), which then affects everything from their locomotion and diet to their thermal biology. This complex three-dimensional medium can have substantial morpho-functional implications on body-shape evolution (e.g., relating to locomotion: Gans & Fusari, 1994; Morinaga & Bergmann, 2020).

Previous studies (Bergmann & Morinaga, 2019; Grizante et al., 2012; Wiens et al., 2006) highlight the environmental correlates of limb-reduced body shapes. Most of these studies investigated few, closely-related taxa and have a narrow comparative scope. No studies we are aware of focused on how the environment shapes morphological variation differentially across taxa. To address these gaps, we aim provide an updated ecomorphological characterisation based on a broad sample of limb-reduced taxa. We compare evolutionary patterns of body-shape change across clades and their specific habitat parameters. As skinks occur in a wide variety of environments (Chapple et al., 2021; Roll et al., 2017), and are variable in morphology and habitat use (Pianka & Vitt, 2003; Slavenko et al., 2022), they represent an optimal system to investigate the environmental correlates of limb-reduced morphologies.

We present a two-tiered approach to address our aims: (1) We update the knowledge of relationships between body proportions across limb-reduced skink clades, quantifying and comparing their

evolutionary trajectories; and (2) we address whether morphological differences across the spectrum of limb-reduced forms correlate with substrate-related habitat characteristics. We hypothesise that substrate characteristics will affect the morphological variation of limb-reduced skinks. We predict that looser, drier and poor (=low in organic carbon) substrates (such as sands) will be associated with forms adapted to substrate-swimming strategies with short limbs and small, streamlined bodies to reduce drag (Morinaga & Bergmann, 2020; Sharpe et al., 2015); conversely, we expect richer substrates that are prone to compaction and vegetational cluttering to be associated with larger species with either relatively well developed forelimbs for active digging, or completely devoid of limbs and using head-first burrowing to penetrate the substrate (Branch, 1998), or for grass-swimming.

To test our predictions, we used two approaches differing in taxonomic and geographic scope. First, to provide a clearer categorisation of burrowing ecomorphs, we examine how morphologies vary across broad substrate categories for a large sample of the world's limb-reduced skinks, as defined by Camaiti et al. (2022; also see materials and methods section of the present article). Second, to parse the specific habitat factors associated with the evolution of limb-reduced morphologies, we perform an analysis using habitat data extracted from species' distributions on a spatially-restricted sample (20.1% of the species) of limb-reduced skinks and their relatives, the Australian Sphenomorphinae. We examine relationships among body shapes, substrate properties and microclimatic conditions for this clade, expecting similar patterns as in the global analyses, with limb reduction being associated with aridity and poorer substrates. Together, both approaches can provide an in-depth ecomorphological perspective on these successful evolutionary transformations.

2 | MATERIALS AND METHODS

2.1 | Data sources

2.1.1 | Morphological data

We consider 'limb-reduced' any species with miniaturised limbs (forelimb length [FLL] <15%, hindlimb length [HLL] <20% of snout-vent length [SVL]) (following Camaiti et al., 2022), and species lacking limbs are referred to as 'limbless'. We sourced data on FLL, HLL, SVL, head length (HdL), number of fingers (Man), toes (Pes) and presacral vertebrae numbers (PSVn) for 394 species of limb-reduced and limbless skinks, and 211 of their fully limbed congeners and unrelated species for informed comparisons, from the dataset of Camaiti et al. (2022). We added measurements for 27 species of the genus *Ctenotus* (all fully limbed) to increase sampling for Sphenomorphinae. We added three species of Xantusiidae and one species of Cordylidae—the sister taxa of skinks (Zheng & Wiens, 2016), sourcing data from the literature and measurements from museum specimens (Supplementary Material S1). For phylogenetic analyses, we used the phylogeny of Zheng and Wiens (2016).

The extended dataset (636 species) was pruned of taxa missing from the phylogeny with the 'treedata' function (package GEIGER, 2.0.7: Pennell et al., 2014). Species lacking head and/or limb length measurements were excluded. This left us with 298 species, of which 208 had presacral vertebrae counts (Supplementary Material S1). Two hundred eighty-four species in this dataset are skinks, 168 of which are limb-reduced or limbless (42.64% of the limb-reduced and limbless skinks identified in Camaiti et al., 2022). Seven girdled lizards (Cordylidae), four plated lizards (Gerrhosauridae) and three night lizards (Xantusiidae) are included as the sister clade to skinks (Zheng & Wiens, 2016). These data were used both to investigate the relationships between body parts in limb-reduced forms in skinks and for ecomorphological analyses using substrate categories. For inter-group comparisons of the evolutionary trajectories of body-shape change, we considered the eight extant skink subfamilies: Acontinae, *Brachymeles* (formally a genus of Scincinae, but not included in any subfamily by Zheng & Wiens, 2016), Eugongylinae, Egerniinae, Lygosominae, Mabuyinae, Scincinae and Sphenomorphinae (Figure 2). Second, as both Scincinae and Sphenomorphinae include several distinct, independent instances of limb reduction with widely different morphologies (see Camaiti et al., 2022), we also added to the comparison six focal clades belonging to these two subfamilies. To select focal clades, we searched for genera that included at least three limb-reduced and three fully limbed representatives to maintain sufficient statistical power. If not enough limbed representatives were present, we increased our taxonomic scope to the minimum required (below the subfamily level) until this criterion was satisfied (adding a fully limbed sister genus or lumping genera with limb-reduced representatives). Whenever possible, we included more than the minimum of three limbed representatives (i.e., in numbers comparable to, but never higher than, the limb-reduced taxa) to further increase the statistical power of our analyses. This sampling approach allowed us to achieve, on the one hand, a sufficient sample size of fully limbed and limb-reduced forms, and on the other hand, general morphological consistency between members of the focal clade in other body shape parameters apart from limbs. The focal clades selected this way were: *Anomalopus* group, the genera *Chalcides*, *Glaphyromorphus*, *Hemiergis*, and *Lerista*, and the *Scelotes* group. Focal clades indicated as 'group' include more than one limb-reduced genus. For focal clade composition, see Supplementary Material S2-a.

For analyses of relationships between morphology and quantitative soil and climate data extracted from species' distributions to test our ecomorphological predictions beyond broad categories, we used a subset of our main dataset for which we had morphological, habitat, and distribution data, the Australian Sphenomorphinae. Given the limits of the sources of habitat and climate data available to us, as well as the processing time required to extract such data for a large sample of species, we focused on a narrower geographical (the Australian continent) and taxonomic scope (the Australian Sphenomorphinae). After pruning with the phylogeny of Zheng and Wiens (2016), we had data on 75 limb-reduced and limbless species (64.1% of Australian

limb-reduced and limbless sphenomorphines, estimated from Camaiti et al., (2022) belonging to eight limb-reduced genera in this clade (*Anomalopus*, *Coeranoscincus*, *Coggeria*, *Glaphyromorphus*, *Hemiergis*, *Lerista*, *Ophioscincus*, and *Saiphos*), and 46 of their fully limbed congeners and sister species.

Prior to analyses, we log-transformed mensural variables. For limb lengths, we added 1 before log-transformation to include species lacking limbs. We log-transformed PSVn to normalise them for regressions. We refrained from size-correcting by dividing by a size variable, to avoid confounding effects of having a variable as the combination of two variables (Nakagawa et al., 2017). Instead, we included HdL as a covariate in our models (except when regressing variables against HdL).

To account for variation in limb proportions, we used a limb disparity index (modified from Camaiti et al., 2022), a new metric consisting of one minus the ratio between the length of the shortest limb and that of the longest limb (after 0.001 is added to both to include species lacking limbs), formulated as $1 - (\text{Shortest limb length} + 0.001) / (\text{Longest limb length} + 0.001)$. To distinguish species with longer forelimbs, their disparity is considered to be negative (the index is multiplied by -1). The ratio is subtracted from one to make the scale symmetrical between -1 and 1 , depending, respectively, on whether forelimbs or hindlimbs are the longer limb pair, and with species with equal forelimb and HLLs (including limbless species) having a disparity of 0. It describes the extent of differential development between hindlimbs and forelimbs (Figure 1), similar to the intermembral index used to describe mammalian limb proportions $[(\text{humerus} + \text{radius}) / (\text{femur} + \text{tibia}) \times 100]$;

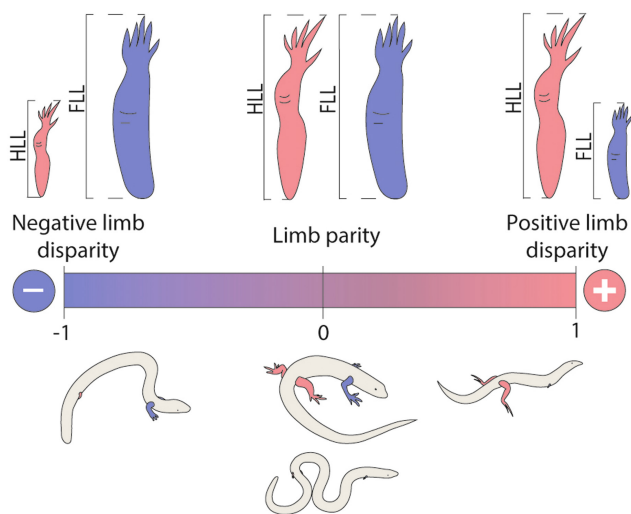


FIGURE 1 Schematic representation of limb disparity. To the left, species with negative disparity (e.g., *Anomalopus verreauxii*) have longer forelimbs than hindlimbs. In the centre, species with limb parity have forelimbs and hindlimbs of similar lengths (this applies to limbless species as well, as both limb pairs have length zero). To the right, species with positive disparity (e.g., *Lerista miopus*) have longer hindlimbs than forelimbs. The scale is bounded between -1 (species with only forelimbs tend to this value) and 1 (species with only hindlimbs tend to this value). FLL, forelimb length; HLL, hindlimb length.

Granatosky, 2018], with the differences that it includes the lengths of manus and pes, and it can be calculated if either pair of limbs is absent.

2.1.2 | Substrate categories, climate and soil data

Substrate categories for the species in our dataset were sourced from Camaiti et al. (2022). Following Stepanova and Bauer (2021), the classification was compiled based on field guides and the primary literature for each species. Species were classified into four categories, from the poorest to the richest substrates in terms of organic content: 'sand', 'sandy soil', 'soil', and 'humus'. Non-fossorial species (such as surface-dwelling, arboreal, or semi-aquatic) are included in the 'terrestrial' category, and 'grass' indicates species that locomote through low, dense vegetation (i.e. grass-swimmers).

For Australian sphenomorphines, we extracted data for soil properties (percentage of granulometric components of sand, silt, clay; richness in organic carbon; water capacity; density) using QGIS (3.14) by overlaying raster map files for six soil descriptor variables (Table 1) measured at 0–5 cm in the soil column, with the shapefiles of species' distribution obtained from the IUCN's latest assessments of Australian squamates (Chapple et al., 2019; Cox et al., 2022; IUCN, 2022; Tingley et al., 2019). Maps for soil descriptors were obtained from the Soil and Landscape Grid of Australia (Grundy et al., 2015; downloaded: 20/10/2020), generated by combining digital soil mapping products from 2000 to 2013. For each shapefile, we used the 'zonal statistics' function in QGIS to extract average, minimum and maximum values for each soil descriptor. Overlaying large distribution shapefiles on small grids could lead to biases due to commission errors (Di Marco et al., 2017), which can limit the effectiveness of our approach. However, as the use of coarser resolution maps would have also greatly decreased the accuracy of our data,

TABLE 1 Range descriptors of soil and microclimate at soil level, with abbreviations and units of measurement

Variable	Description	Unit
AWC	Available water capacity	%
BDW	Bulk density of the whole soil	g/cm^3
CLY	Clay: $<2 \mu\text{m}$ mass fraction of the soil	%
SLT	Silt: $2\text{--}20 \mu\text{m}$ mass fraction of the soil	%
SND	Sand: $20 \mu\text{m}\text{--}2 \text{mm}$ mass fraction of the soil	%
SOC	Soil organic carbon	%
T	Temperature (2.5 cm in soil column)	$^{\circ}\text{C}$
TS	Air temperature (1 cm above soil)	$^{\circ}\text{C}$
HUM	Humidity (5 cm in soil column)	g/m^3
RH	Soil relative humidity	%
WET	Wetness index (2.5 cm in soil column)	%
Rain	Rainfall	mm
MOI	Moisture (2.5 cm in soil column)	g/m^3
POT	Soil water potential (2.5 cm in soil column)	kPa

we considered data extracted through our approach as a reasonable representative of soil characteristics within each species' potential distribution.

For variables expressed as percentages, we rounded to 100 all values that exceeded 100 due to the estimation methods used to construct maps. To normalise data for regressions, we applied arc-sine transformations to variables expressed as percentages, and log-transformed the rest.

To extract microclimatic data, we gridded the shapefiles of each species using the 'st_make_grid' and 'st_centroid' functions in R (package *sf* 1.7: Pebesma, 2018); to account for differences in species' range sizes, we used a 100×100 km² grid for species with range size >20,000 km², a 20×20 km grid with range sizes between 1000 and 20,000 km², and a 10×10 km² grid with range sizes <1000 km². For coordinates of each intersection point in the grids, climate data were extracted using the 'micro_global' function from the *NICHEMAPR* package in R (3.2.1: Kearney & Porter, 2020), using a microclimatic model to downscale gridded climate data from the long-term (1960–1990) climatological average of New et al. (2002) to microclimatic conditions. We obtained maximum, minimum and average data for soil temperature (at 2.5 cm in the soil), humidity (at 5 cm), soil wetness, rainfall, soil moisture (at 2.5 cm), soil water potential (at 2.5 cm), surface air temperature (at 1 cm above soil) and relative soil humidity (Table 1), which we then averaged across each point of the grid. Microclimate and soil data were standardised using the 'scale' function in R (4.0.2: R Core Team, 2020; see Supplementary Material S3).

2.2 | Data analysis

2.2.1 | Phylomorphospace and relationships among body parts

To visualise the relationships between morphological variables across our dataset, we performed a principal component analysis (PCA) on log-transformed morphological data (limb lengths, SVL and HdL) using the 'prcomp' function, in the R base package *stats* (R Core Team, 2020). We did not include digit numbers, which, having a small number of character states, cause artefacts in morphospace occupation. We plotted the first two axes of the PCA in a phylomorphospace using the 'phylomorphospace' function in the R package *phytools* (0.7.70: Revell, 2012). To visualise the effect of PSVn, we also performed a PCA including log-transformed PSVn.

To assess how relationships among body parts change as limb reduction and body elongation evolve, we compared the effects of absence/presence of limbs against SVL, HdL and PSVn using phylogenetic logistic regressions ('*phylglm*' function, package *PHYLOLM* 2.6.2: Tung Ho & Ané, 2014). We then performed phylogenetic generalised least-squares regressions of morphological variables (including digits and PSVn) against each other in all possible permutations ('*lm.rpp*' function, package *RRPP* 0.6.1: Collyer & Adams, 2018). Regression models were fitted both to our phylogenetically pruned

global dataset of skinks and outgroups (298 species), and then individually for each of the subfamilies and focal clades to identify and compare evolutionary trajectories of body-shape change across clades.

2.2.2 | Ecomorphological analyses

To investigate the associations of limb-reduced body shapes and substrate type in the species in our global skink dataset, we performed phylogenetic analysis of variance (ANOVA) tests with body measurements across substrate categories. For limb disparity, we conducted an additional test excluding limbless species, which, having both limb lengths of 0, inflate the representation of limb parity (Figure 1). To examine associations of morphology and microhabitat based on quantitative data, we conducted analyses on the dataset of Australian sphenomorphines. For these, we regressed the PC scores from the PCA, as well as body measurements (the same used in the global analyses) and limb disparity, against range descriptors of microclimate and soil. Analyses were performed using the '*lm.rpp*' function, applying a phylogenetic variance–covariance matrix created using the '*vcv.phylo*' function (package *GEIGER*, 2.0.7: Pennell et al., 2014). The '*anova*' and '*pairwise*' functions were applied when performing ANOVA, using *RRPP* (0.6.1: Collyer & Adams, 2018). All analyses were performed in R environment (4.0.2: R Core Team, 2020).

3 | RESULTS

3.1 | Body shape

3.1.1 | PCA and phylomorphospace

Principal component (PC) axes loadings for the PCA are summarised in Supplementary Material S2-a. PC1 is highly correlated with absolute limb lengths, describing a spectrum from fully limbed (negative PC1) to limbless species (positive PC1) (Figure 2). PC2 correlates with SVL. Head length loads negatively on PC1 and positively on PC2. Limbless species are clustered at the positive end of PC1, represented by members of four of the seven main scincid clades: Scincinae (sensu stricto), Sphenomorphinae, Acontinae, and *Brachymeles*. The negative end of PC1 is mainly represented by forms with large heads, belonging to Scincinae, Mabuyinae and Sphenomorphinae, brought to an extreme in Egerniinae such as *Corucia zebrata* and *Tiliqua scincoides* (Figure 2a,b). Most skinks have small (i.e. *Pygmaeascincus timlowi*, ~22 mm: Figure 2i) to medium (i.e. *Anomalopus verreauxii*, ~150 mm: Figure 2d) SVL. At both ends of PC1, medium to large SVLs are common, with the highest values held by the Egerniinae and the limbless Acontinae (e.g. *Acontias plumbeus*, ~334 mm: Figure 2e).

When included into the PCA, PSVn load positively on both axes (Supplementary Material S2-a). Limbless forms have the most

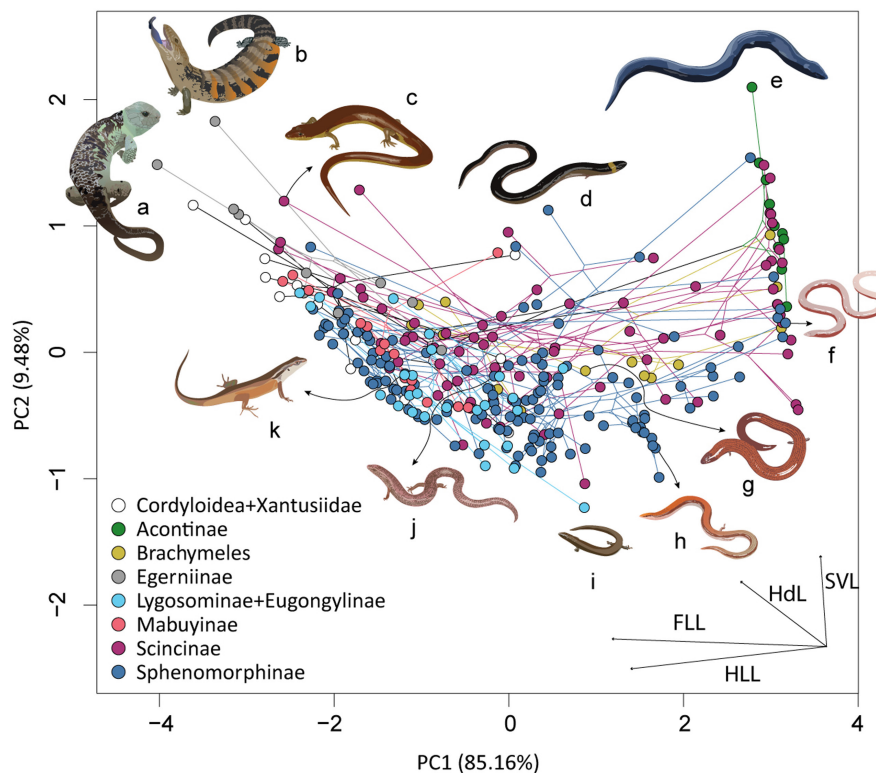


FIGURE 2 Phylomorphospace of the skinks in our dataset. The main clades of skinks plus the outgroup are indicated as distinct colours (see legend). PC1 correlates with the absolute length of the limbs, increasing from right to left, whereas PC2 correlates most with absolute SVL. The vectors of the principal component analysis of morphological variables are illustrated on the bottom right. For the purpose of visualisation, the following species illustrations (not drawn to scale) are included in the proximity of their location in phylomorphospace (or positions indicated with arrows): (a) *Corucia zebrata*; (b) *Tiliqua scincoides*; (c) *Amphiglossus astrolabi*; (d) *Anomalopus verreauxii*; (e) *Acontias plumbeus*; (f) *Lerista apoda*; (g) *Brachymeles elerae*; (h) *Lerista bipes*; (i) *Pygmaeascincus timlowi*; (j) *Glaphyromorphus punctulatus*; (k) *Carlia tetradactyla*. FLL, forelimb length; HdL, head length; HLL, hindlimb length; SVL, snout-vent length.

presacral vertebrae, which increase with a decrease in limb lengths and an increase in SVL. PSVn does not increase with SVL in fully limbed forms and increases more slowly in limb-reduced ones compared with limbless ones.

3.1.2 | Evolutionary correlations among body parts

Skinks lacking at least one pair of limbs have significantly shorter heads, more elongated bodies (SVL, with HdL as a covariate), and significantly more presacral vertebrae compared with fully limbed skinks (Supplementary Material S2-b). Applying these same analyses to skink subfamilies (restricted to clades including both limbed forms and forms lacking forelimbs and/or hindlimbs), we find significant associations in both the Scincinae (presence of either limb pair to HdL, trunk elongation and presacral vertebrae number) and Sphenomorphinae (same as Scincinae, but no relationship between forelimb presence and HdL). When zooming into focal clades, the *Scelotes* group has the same relationships as the Scincinae, *Lerista* the same as Sphenomorphinae (except with hindlimb presence), and the *Anomalopus* group displays no significant relationships at all.

We find a positive relationship between fore and HLLs, and a positive relationship between limb lengths and their respective digit count (however, this relationship is not significant for half of the subfamilies and focal clades considered in isolation, likely due to a lack of statistical power: see Supplementary Material S2-b-e), between limb lengths and HdL, and between SVL and HdL (Supplementary Material S2-b-e). A negative relationship exists between limb lengths and trunk elongation. When comparing this relationship across clades, there is substantial variation in its polarity (i.e. whether it is positive or negative). We find negative associations between limb lengths and trunk elongation in all subfamilies except *Brachymeles* and Scincinae (forelimbs only, hindlimbs always have a negative association with trunk elongation). Smaller clades have all negative associations with trunk elongation for both pairs of limbs except *Glaphyromorphus* and *Hemiergis* (which have positive associations), and *Chalcides* (no significant associations with HLL).

Forelimb lengths scale negatively with PSVn, with the notable exceptions of Mabuyinae, *Hemiergis* (both showing positive associations), and Egerniinae (no significant association). Hindlimbs also scale negatively with PSVn, with no significant associations found in the Egerniinae, Eugongylinae, the *Anomalopus* group, and the *Scelotes* group. Lastly, trunk elongation positively correlates with

PSVn in all clades except *Glaphyromorphus*, where the association is negative, and Egeriinae and Eugongylineae, where there is no significant relationship.

3.2 | Ecomorphological correlations

3.2.1 | Global analyses across substrate categories

Comparing categories of substrate ecology, terrestrial species have lower values of PC1 than all other categories, associated with longer absolute limb lengths (Figure 3a). Grass-swimmers have significantly higher PC1 values than species inhabiting sandy soils, while humus-dwellers have significantly higher PC1 values (associated with shorter limbs) than all categories except grass. In terms of PC2 (correlating most with SVL, secondarily with HdL), sand, sandy soil and humus species have significantly lower values than all other categories (Figure 3b). When examined in isolation, we find SVL to

be significantly higher in grass dwellers than humus and sandy soil dwellers, and significantly lower in humus dwellers compared with soil and grass dwellers and terrestrial species (Figure 3c).

Heads are significantly shorter in humus-dwellers compared to all other categories except grass-swimmers; sand and sandy soil species have significantly shorter heads than terrestrial species (Figure 3d). Relative limb lengths (i.e., with HdL as a covariate) do not differ across categories (Figure 3e,f). Humus-dwellers differ from sandy soil species by exhibiting higher trunk elongation (Figure 3g).

Sand-dwellers have significantly higher limb disparity compared to all other substrates, often missing forelimbs altogether, while sandy soil species have higher disparity than the remaining categories; additionally, the disparity of soil species is lower than of terrestrial species (Figure 3h). When excluding limbless species, soil and terrestrial categories do not significantly differ, and sandy soil species are not significantly different from grass-swimmers (Figure 3i). The full output of the ANOVA tests is included in Supplementary Material S4-a.

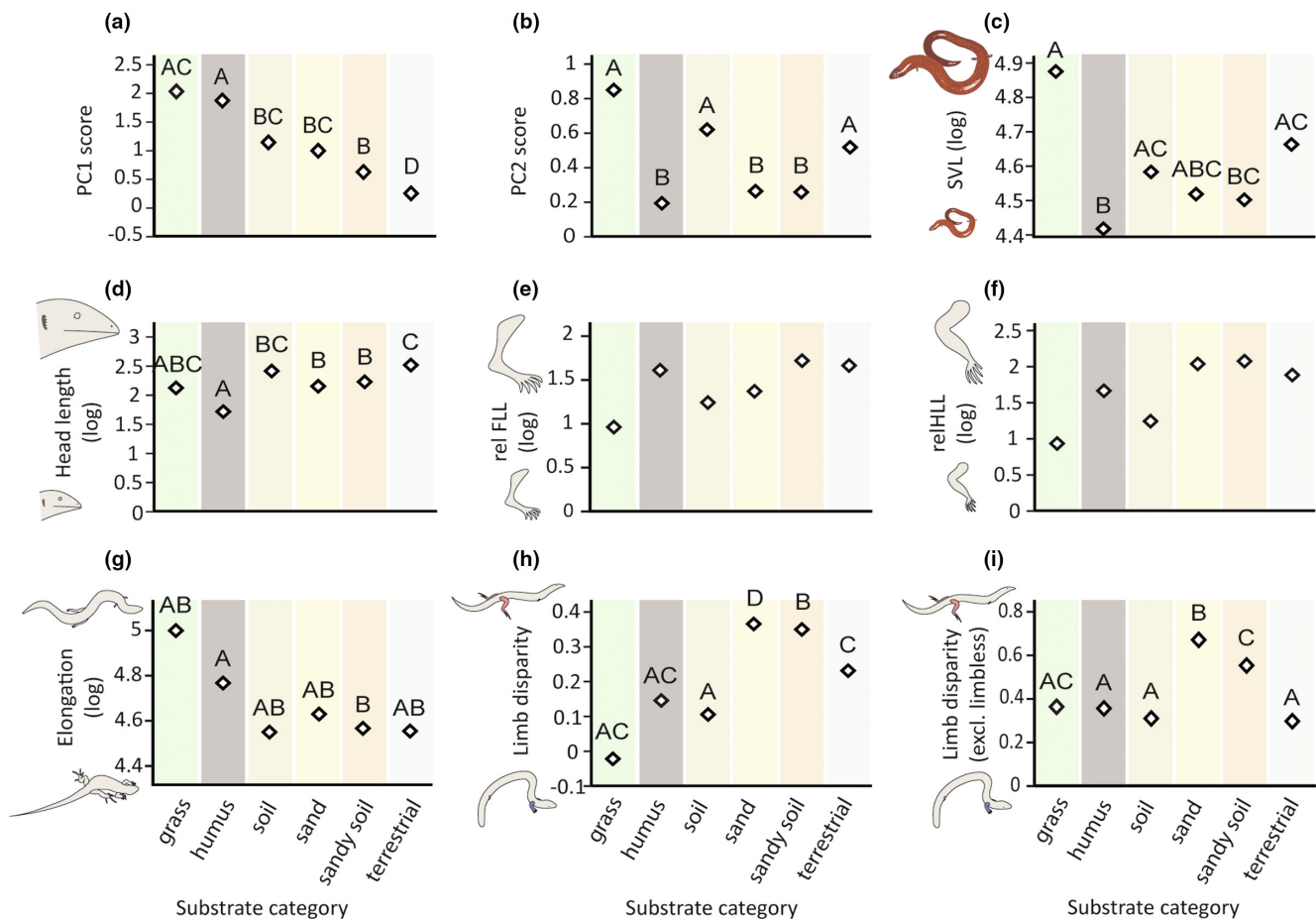


FIGURE 3 Plots showing significant differences across substrate categories among phylogenetic least-square means of morphological variables, as follows: (a) Principal component 1 [PC1] score; (b) Principal component 2 [PC2] score; (c) Snout-vent length [SVL]; (d) Head length; (e) Relative forelimb length [relFLL]; (f) Relative hindlimb length [relHLL]; (g) Elongation; (h) Limb disparity; (i) Limb disparity (excluding limbless species). Groups that do not share a capital letter are considered statistically significantly different from one another. Error bars are not displayed (there is no implementation for residual-randomised and phylogenetically corrected ANOVA RRPP analyses). Full ANOVA output is found in Supplementary Material S4-a. Substrate categories are colour-coded for visualisation purposes: Green—grass; dark brown—humus; light brown—soil; yellow—sand; orange—sandy soil; grey—terrestrial. ANOVA, analysis of variance.

3.2.2 | Environmental associations of the Australian Sphenomorphinae

Results for the ecomorphological analyses of the Australian sphenomorphines are summarised in Supplementary Material S4-b. The strongest correlations between morphology and substrate (in terms of R^2) involve limb lengths adjusted by HdL (relative HLL and relative FLL), showing a highly consistent pattern of correlation with soil descriptors (Supplementary Material S4-b,c). Relative limb lengths increase with sand percentage and bulk density, and decrease with soil organic carbon, silt and clay percentage; they decrease with measures of humidity (moisture, soil water potential, wetness, and relative and absolute humidity), and generally increase with temperature (in the soil and at surface level), decreasing only with minimum temperature within the soil. Relative limb lengths increase towards western parts of Australia. All these correlations are stronger (in terms of R^2) for hindlimb than FLL. In some cases, hind and forelimbs show opposite correlations (mean available water capacity and longitude). Overall, trunk elongation shows the opposite polarity of correlation compared to limb lengths (Supplementary Material S4-b,c). PC axes, SVL and limb disparity show weaker relationships with soil and microclimate descriptors but follow the same patterns of correlation as the other variables (PC axes and SVL follow trunk elongation; disparity follows HLL; none of these correlate with latitude). PSVn positively correlate with indicators of humidity, but otherwise PSVn and HdL seldom correlate with climatic and geographic variables, showing only weak relationships when significant.

4 | DISCUSSION

We aimed to quantify morphological variation in skinks, and to test the possible explanations for this variation from a macroecological perspective. Our key findings are that: (1) there is significant variation in evolutionary trajectories of limb reduction across skink subfamilies and smaller clades, as quantified by the varying relationships among body parts, consistent with previous studies but with some previously unidentified patterns; and (2) environmental adaptation, in particular to substrate, is a major driver of body-shape evolution in skinks. This emerges from our analyses on how the body shapes of skinks vary depending on broad substrate categories, as well as in the Australian sphenomorphines using quantitative habitat data.

4.1 | Patterns and evolutionary trajectories of limb reduction in skinks

For most subfamilies and focal clades, the relationship between limb lengths and trunk elongation was negative; in others it was positive, consistently so in *Brachymeles*, *Hemiergis*, and *Glaphyromorphus*. Our results casts doubt on the notion that limb reduction and trunk elongation go hand-in-hand in squamates, being considered a general 'rule' on how limb reduction is achieved (Gans, 1975). Moreover,

PSVn are not tightly correlated with limb lengths, despite increasing the number of presacral vertebrae being considered the main mechanism by which trunk elongation is achieved (but see below for a more thorough exploration of the concept). Below, we illustrate two non-mutually exclusive explanations for these results.

First, the observed differences in relationships between body parts could arise through different evolutionary trajectories in the acquisition of limb reduction and trunk elongation across skink clades. Gans (1975) and Brandley et al. (2008) noted differences in the way limb reduction is achieved that could reflect adaptations to differential lifestyles and locomotory habits. Both limb reduction and trunk elongation have been repeatedly linked to the adoption of undulating locomotion, in which the appendicular system is substituted in its ambulatory role by the axial system, which becomes elongated and streamlined to increase the efficiency of lateral movement (Gans, 1975; Gans & Fusari, 1994; Leonard, 1979). Different environments and life strategies might affect locomotory performance in alternative ways, providing distinct selective pressures towards independent instances of reduction in limbs and/or trunk elongation across taxa. Moreover, different taxa might follow clade-specific genetic and developmental pathways to achieve these body transformations, making them phylogenetically constrained (Bergmann & Morinaga, 2019; Camaiti et al., 2021). Our findings agree with Bergmann and Morinaga (2019), showing probable evidence of historical contingency in the evolution of limb-reduced body shapes. This may indicate that phylogenetic history influences the observed variation in the patterns of limb reduction across clades.

Second, despite multiple attempts of developmental studies to establish a genetic and developmental link between limb reduction and trunk elongation (Gasc & Renous, 1989; Hugi et al., 2012; Leal & Cohn, 2016, 2018; Sanger & Gibson-Brown, 2004), evidence remains unconvincing as to whether the two processes are ontogenetically associated, or independent. Our findings lend support to the view that these processes may become disentangled as limb reduction evolves. Leonard (1979) and Berger-Dell'mour (1985) suggested that the relationships between limb reduction and trunk elongation may be lost in limb-reduced clades, as these are prone to high intraspecific variability in body proportions compared to fully limbed taxa. Tied to this, the high level of variation in the patterns found in our analyses might indicate that the relationship between limb proportions and trunk elongation, and between limb proportions and PSVn, tends to become less strict in limb-reduced taxa, as the locomotory mode comes to rely less on the limbs and more on axial undulation. This would provide relaxed selection towards specific arrangements of body proportions, in contrast with fully limbed taxa in which high specificity would be retained depending on clade and environment (e.g., Losos, 1990; Losos & Sinervo, 1989). Thus, limb reduction and trunk elongation may be associated by a functional link that becomes weaker as both processes become more pronounced.

Bergmann and Morinaga (2019) found the only common pattern across limb-reduced clades of skinks and gymnophthalmids to be the contribution of PSVn to trunk elongation. This supports the hypothesis that in squamates, trunk elongation is mainly

determined by the addition of presacral vertebrae (Greer, 1987; Presch, 1975; Stokely, 1947). We found this to be the case in most subfamilies and focal clades of skinks, with the notable exception of *Glaphyromorphus* (Figure 2j), in which the acquisition of a longer trunk is seemingly achieved through lengthening, instead of addition of vertebral elements. *Glaphyromorphus* could be interpreted as another example of how different clades follow distinct evolutionary trajectories in their acquisition of superficially similar morphologies. While these results should be interpreted with caution, given that taxon sampling for *Glaphyromorphus* is poor (5 of the 12 species were included after phylogenetic pruning) and the deviation from ancestral PSVn is moderate (up to 36 presacral vertebrae vs. the ancestral 26; Greer, 1991), they still point towards a distinct way in which elongation is achieved. This mechanism finds parallels in some vertebrate taxa like plethodontid salamanders (Parra-Olea & Wake, 2001; Wake, 1991) in which trunk elongation is achieved through the lengthening, instead of the addition, of presacral vertebrae. Hence, the developmental processes involved in determining elongation might also vary across squamates.

4.2 | Untangling the ecomorphology of skink limb reduction

We found a significant difference in PC2 axis scores (which correlate most with SVL, secondarily with HdL) between sand-, sandy soil- and humus-dwelling species as opposed to other substrate categories (Figure 3b). This can be linked to locomotory specialisation of distinct ecomorphs due to functional interactions with the environment. The challenges to navigating three-dimensional settings with different properties may be active agents of selection, especially given the physical properties of different substrate matrices. Sand (and by extension, sandy soil) is known to behave like a frictional granular fluid (Attum et al., 2007; Crofts & Summers, 2011), which would select for smaller body sizes due to the low relative force needed to penetrate it (Arnold, 1995; Pough et al., 1997). Substrates rich in organic matter ('humus') would select for smaller body sizes as they tend to be relatively soft, not requiring much applied force to penetrate—and thus, not a large mass or size (Stepanova & Bauer, 2021). Indeed, when considering SVL in isolation, we find that species living in humus are significantly shorter than all categories except sand and sandy soil (Figure 3c). Conversely, more compacted substrates (the 'soil' category) would require larger bodies to push through more resistant material, associated with head-first burrowing strategies (Bergmann & Berry, 2021; Kazi & Hipsley, 2018; Müller et al., 2011; Stepanova & Bauer, 2021). An example of such a functional niche-driven size differentiation is the sub-Saharan skink subfamily Acontinae, whose larger forms are associated with more compact soils, whereas smaller ones are sand-swimmers (Branch, 1998; Lamb et al., 2010; Stepanova & Bauer, 2021).

We did not find a differentiation in relative limb lengths, and only slight differences in trunk elongation and HdL across substrate categories (Figure 3d–g). In contrast, we found that species inhabiting

sand and sandy soils display significantly higher limb disparity than other substrate categories, with sand species having significantly higher disparity than sandy soil species (Figure 3h,i). This suggests that the evolution of limb reduction is driven by the need to navigate a complex, three-dimensional environment—regardless of substrate type (Camaiti et al., 2019, 2021; Gans, 1975)—but different types of limb reduction (e.g., differences in limb disparity) are tied to different substrates. Our findings show that body shapes with high limb disparity, often characterised by a marked reduction or loss of the forelimbs and retention of proportionally long hindlimbs (e.g., *Lerista*, *Scelotes*, *Pygomeles*; Camaiti et al., 2022), correlate with sandy soils and likely with sand-swimming locomotion. As previously suggested (Gans & Fusari, 1994; Morinaga & Bergmann, 2020; Mosauer, 1932), these forms might arise from the necessity to balance sand-swimming and superficial habits, facilitating exploitation of resources in both contexts without sacrificing surface mobility. This supports the hypothesis that the evolution of 'intermediate' body shapes with specific proportions—here, large differences in the lengths of fore- and hindlimbs—is adaptive rather than transitional. This confirms the findings of studies highlighting the long evolutionary persistence of limb-reduced forms (Brandley et al., 2008; Skinner et al., 2008), as well as functional tests of body-shape evolution and patterns of locomotion (Benesch & Withers, 2002; Bergmann & Irschick, 2010; Gans & Fusari, 1994; Morinaga & Bergmann, 2020).

While sand-adapted forms represent morphological extremes in terms of limb disparity, we also found that species with equal-sized limbs or longer forelimbs are associated with humus and soil, whether limbless species are considered or not. Most limbed squamates have longer hindlimbs than forelimbs, but some clades evolved limbs of comparable length, and some reduced their hindlimbs more than their forelimbs (e.g. *Anomalopus*; Greer & Cogger, 1985). Equal or forward-driven propulsion compared to rear propulsion may represent an adaptation to more cluttered environments compared to sand. The necessity to displace obstacles to locomotion could explain why retaining forelimbs to power through less giving terrain rather than push themselves on the surface would prove advantageous to these species.

4.3 | Ecomorphology at a finer scale: Drivers of body shape in the Australian Sphenomorphinae

As in our global analyses, in Australian Sphenomorphinae we detected correlations between environmental variables and body shapes: limb-reduced and elongated body shapes, and larger body sizes, correlate with higher humidity and rainfall, and lower temperatures, following a longitudinal gradient. In terms of species numbers, several limb-reduced sphenomorphines inhabit arid regions of the Australian continent (e.g. *Lerista*; Pianka, 1972), but most limb-reduced sphenomorphine genera (e.g. *Anomalopus*, *Coeranoscincus*, *Ophioscincus*, *Saiphos*; Greer & Cogger, 1985) are not arid-adapted but depend on, and are geographically restricted to, cool and humid environments associated with the great dividing

range (GDR; Pepper & Keogh, 2021). This is highlighted by the correlation with longitude, showing that species tend to become larger, more limb-reduced and trunk-elongated, going eastward (towards the GDR).

Our results show that more limb-reduced and elongated bodies correlate with increased percentages of fine soil granulometries (silt and clay, as opposed to sand), a decrease in soil density (bulk density of the whole soil, higher in soils poor in organic matter, like desert sands: Soane, 1990), and higher percentages of organic carbon. These findings contrast with our expectations, i.e., that limb reduction and trunk elongation would increase with aridity, as observed by Grizante et al. (2012) on gymnophthalmids. Differences in arid zones between South America and Australia could explain this contrast; fossorial gymnophthalmids inhabit arid zones with compact substrates that are more resistant to locomotion, requiring the evolution of more limb-reduced, elongated forms to facilitate forced, head-first burrowing strategies (Grizante et al., 2012). Conversely, fossorial skinks from Australia's arid zones associate with friable and easily penetrable substrates (Gans & Fusari, 1994) providing relaxed selection towards limb reduction and trunk elongation; traits that are instead favoured in humid areas to locomote through less giving substrates due to higher humidity and organic carbon decreasing soil penetrability (Angers & Chenu, 2018).

Additionally, the finding that limb disparity positively correlates with arid, hot, and poor soils, as well as with sandy substrates with low proportions of finer granulometries (silt and clay) further supports our hypothesis that the evolution of 'intermediate', limb-reduced morphologies (i.e., with different-sized fore- and hindlimbs) as opposed to limbless forms is indeed driven by functional adaptations to specific conditions, limited to arid, sand-dominant substrates. These results align with and bring better resolution to the findings of the global analyses, showing that the hot and dry microclimatic conditions, associated soil poorness and increased sand percentage of arid environments such as deserts might select for 'intermediate' body shapes. These properties might determine a lower degree of soil resistance to locomotion due to dryness and lack of organic, soil-aggregating components (Angers & Chenu, 2018), and due to the behaviour of sand as a granular fluid (Crofts & Summers, 2011). This is compatible with sand-swimming strategies, also given that burrowing behaviours might have arisen to enable reptiles to avoid heat stress and desiccation in these arid conditions (Benesch & Withers, 2002).

5 | CONCLUSIONS

Across skinks, distinct instances of limb reduction and body elongation represent independent evolutionary transformations. Divergence in patterns of morphological correlation between body-shape traits supports the hypothesis that each transition towards limb reduction is an independent evolutionary event with a clade-specific component, as well as a shared adaptive response resulting in superficial morphological similarity. Ecomorphological analyses

show that there are evolutionary patterns linked to specific environmental adaptations, which may contribute to determining body shape and size in limb-reduced skinks. These adaptations likely evolved to increase the efficiency of movement through the substrate. While other processes can impact the evolution of limb morphology (e.g., predation pressure: Zamora-Camacho et al., 2014), we found a strong link between substrate types and morphology, highlighting a stark evolutionary differentiation between dwelling in soft, arid and carbon-poor, and cool, humid, carbon-rich substrates.

Future studies should apply similar approaches to incorporate ecological explanations into the evolution of morphological variation in limb-reduced squamates, using larger samples of taxa and high-resolution predictors. Directly-sourced and precise ecological data from each species' immediate environmental context may provide a greater resolution regarding drivers of body-shape and size differentiation. Functional studies should be conducted to test adaptive hypotheses.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its Supplementary Material.

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BIOSKETCH

Marco Camaiti is a herpetologist interested in the evolution of vertebrate diversity, with a focus on repeated and dramatic transitions in the morphology of squamates. His current research topics include investigating several aspects of the evolution of limb reduction in skinks, and how it relates to functional adaptations to different environments. He also makes use of computerised-tomography (CT) scanning techniques to visualise and compare the internal anatomies of lizards.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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