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A database of the morphology, ecology and literature of the world's limb-reduced skinks

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Abstract

Aim: Limb-reduced squamates are a convenient model system to investigate macroevolutionary trends in morphology. Here, we provide morphological, ecological and literature data on all known species of limb-reduced skinks (Scincidae) and their relatives, representing one of the most diverse and widely distributed groups of limb-reduced squamates.

Location: Global.

Taxon: Skinks (Reptilia, Squamata: Scincidae). Limb-reduced forms.

Methods: Morphological data were sourced from the primary literature, spanning a period of over 150 years. Linear body measurements were averaged across all values in the literature, preserving proportionality to body length. For digits and presacral vertebrae, we used maximum recorded counts. Ecological and biogeographical data were sourced from habitat assessments in the primary literature, online databases and field guides. Literature data were sorted according to type of study. To exemplify the applicability of the database, we used Markov-chain ordered models to estimate the evolutionary frequency of limb reduction and loss in skinks.

Results: We find evidence of limb reduction and loss in a total of 394 species worldwide, representing ~23% of all skink species, and ~30% of genera. The distribution of limb-reduced and limbless forms differs from that of fully limbed forms, as they are present in all biogeographic realms with the almost complete exclusion of the Americas. We estimate that limb reduction evolved more than 50 times in skinks, and that loss of at least one limb pair evolved at least 24 times.

Main conclusions: The dataset captures a broad spectrum of morphological and ecological variation in a large, globally distributed taxonomic group. It establishes a widely applicable definition of limb reduction based on limb proportions as a reference for future studies. Such an extensive collection of morphological and ecological data can pave the way for investigations of dramatic morphological transitions and their ecological drivers at a global and local scale.

KEYWORDS

ancestral reconstructions, ecology, limb loss, limb reduction, literature data, lizards, morphology, skinks

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1 | INTRODUCTION

Lizards are one of the most widespread and highly successful groups of terrestrial vertebrates (Pianka & Vitt, 2003; Rodda, 2020). A shift towards limb-reduced, snake-like body shapes is common across lizard evolutionary history, having occurred in more than 25 squamate lineages (Brandley et al., 2008; Gans, 1975; Greer, 1991). Some groups (e.g., snakes, Caldwell et al., 2015; Hsiang et al., 2015; amphisbaenians, Müller et al., 2011; and dibamids, Lee, 1998), evolved limbless, elongated forms early in their evolutionary history. Most limb-reduced squamates, however, evolved more recently, and many extant species display intermediate forms that can illuminate the evolutionary steps that make these large morphological transitions possible (Brandley et al., 2008; Skinner, 2010; Skinner et al., 2008; Skinner & Lee, 2009). Skinks (Squamata: Scincidae) are considered one of the most highly diverse groups of lizards (Pianka & Vitt, 2003), and show wide variation in body shapes (Greer, 1991). They also show high incidence of limb reduction and body elongation, including many intermediate forms. Even within genera, one can find divergent morphological patterns (e.g., the presence of fully limbed, limb-reduced and limbless species [e.g., in *Chalcides*] or the loss of hindlimbs vs. forelimbs) that hint that these evolutionary transitions are independent (Bergmann & Morinaga, 2019; Brandley et al., 2008; Camaiti et al., 2021; Gans, 1975; Greer, 1991; Miralles et al., 2015).

Studies focusing on morphological variation in limb-reduced squamates, especially skinks, have been largely based on direct measurements of museum specimens. Specimen availability can present problems for analyses of multiple taxa originating in different continents, or for rare taxa poorly represented in museum collections. Relying on published data can alleviate the problems caused by lack of accessible specimens to measure. Here, we aim to provide a tool to consistently examine morphological variation in limb-reduced skinks. To this end, we assembled a dataset of morphological traits and ecological data of the world's limb-reduced skinks, based on published sources. Our literature dataset includes more than 800 sources written over more than 250 years, giving us an in-depth perspective over the knowledge and gaps thereof on limb-reduced skink species. Making these morphological, ecological and literature datasets widely available will benefit global investigations of the biogeographical factors involved in the evolution of limb reduction, contributing newly linked integrated data to our understanding of limb reduction and its ecological associations in various clades.

2 | MATERIALS AND METHODS

2.1 | Data collection

Data are provided in a tabular form for ease of analysis. The literature survey on limb-reduced skinks was conducted using resources from the Reptile Database (Uetz et al., 2021) for all species of

limb-reduced skinks and their congeners. To assess whether a taxon fell within our definition of a limb-reduced species (see below), we surveyed the descriptions and diagnostic keys of skinks at the genus and species levels. We used the taxonomy of the Reptile Database (Uetz et al., 2021 [May]) and gathered data from the literature, field guides, and internet resources, including previously compiled datasets. We also searched Google Scholar (<http://scholar.google.com/>; Google Inc.) for the terms 'snake-like', 'limb-reduced', 'reduce-limbed', 'short-limbed', 'limbless', 'limb reduction', 'elongated' and 'elongation', in combination with skink generic names. A detailed table of contents for all is included in Appendix S1.

2.2 | Data fields and metadata

The morphological and ecological dataset (Appendix S2) includes the following fields:

1. Species: Binomial as provided by Reptile Database (Uetz et al., 2021).
2. Higher taxon: For skinks, subfamilial classification from Pyron et al. (2013). The genus *Brachymeles* was treated as a monophyletic clade, as it is not included in the Scincinae by the more recent phylogeny of Zheng and Wiens (2016). For non-skinks included for comparative purposes, we used familial classification.
3. Snout-vent length (SVL): Mean body length measured from tip of the snout to the cloaca (this and all other measurements are in mm).
4. Forelimb length (FLL): Mean length of the forelimb stretched at a right angle to the body wall, from the back of the axilla to the longest digit.
5. Hindlimb length (HLL): Mean length of the hindlimb stretched at a right angle to the body wall, from the groin to the longest digit.
6. Tail length (TaL): Length of the tail from the vent to the tip of the tail. When tails were reported as regenerated (or when supplied measurements were clearly too short to be original) they were not considered for averaging.
7. Head length (HdL): Mean head length measured from the snout to the back of the ear. When measured from images in which the ear opening is absent (as is common in limb-reduced fossorial lizards: Greer, 2002) or not drawn, we considered tip of snout to end of the parietal scales to be a proxy for head length (as in Amey et al., 2019). When only skulls were figured we measured head length from the tip of the snout to the end of the stapedial bone (this was done only for the species *Sepsiscus pluto*: Greer & Cogger, 1985).
8. Number of fingers (digits of the manus): Maximum number of fingers recorded. Cases of single specimens with abnormal numbers of digits were excluded. When the limbs are digit-less stumps, more recent sources are given preference because older sources often confuse lack of digits with monodactyly.
9. Number of toes (digits of the pes): Same as above but with toes on the hindlimbs.



10. Number of presacral vertebrae (PSVn): The maximum number of vertebrae from the neck (included) to the sacrum (excluded) recorded in the literature.
11. Limb length disparity: An index consisting of the logarithm of the ratio between hind and forelimb lengths (adding 1 to both to include species lacking one or both pairs of limbs), formulated as $\ln\left(\frac{HLL+1}{FLL+1}\right)$. It describes how differentially developed one pair of limbs is compared to the other. A value of 0 represents limbs of equal lengths—positive values represent longer hindlimbs and negative values represent longer forelimbs.
12. Limb status: Whether a species is fully limbed, limb-reduced or limbless. We considered species with forelimbs $\leq 15\%$ of the SVL and/or hindlimbs $\leq 20\%$ of the SVL to be limb-reduced, and species with no external traces of limbs (including nubs, stumps or tubercles) to be limbless. We used these criteria rather than loss of digits because a significant proportion of taxa with four 'long' limbs are characterised by digit loss (e.g. *Carlia*, and outside of lizards, *Equus*), while some short-limbed elongated taxa (e.g., *Anepischetosia*) are characterised by no digit losses at all (Camaiti et al., 2021; Greer, 1991). We chose the arbitrary cut-offs of 15% (for forelimbs) and 20% (for hindlimbs) of SVL as we observed that virtually all species characterised by losses of digital elements and/or increased presacral vertebrae counts fall within those bounds. We did not score the genus *Tiliqua* as limb-reduced despite falling within these criteria because they do not conform to the body type of limb-reduced skinks. *Tiliqua* have laterally enlarged bodies and large heads, with four stout pentadactyl limbs that are clearly far removed from the adoption of locomotory strategies and morphologies of limb-reduced skinks in the proper sense (see Greer, 1989). By comparison, limb-reduced lizards tend to have narrow bodies and miniaturised heads (Rieppel, 1984).
13. Substrate: substrate ecology derived from the literature, including the categories 'sand', 'sandy soil', 'soil' and 'humus', on a scale that goes from the substrates that are poorest in organic matter and thus friable ('sand'), to the ones that are richest in organic matter ('humus'). Additional categories are 'terrestrial', referring to strictly non-fossorial species, and 'grass', indicating species whose substrate is thick vegetation (i.e. grass-swimmers). These were compiled based on field guides, published conservation assessments, and the primary literature for each species, following the precedent established by Stepanova and Bauer (2021). It must be noted that this classification cannot be considered as a substitute to a precise microhabitat assessment for each species. Since a vast majority of sources are vague or imprecise in their descriptions of species' habitats (and how those habitats are used), this classification is merely intended as an indicative summary of the known substrate associations of taxa.
14. Habitat notes: Notes regarding habitat and substrate composition.
15. Habitat source: Literature source for habitat and substrate data.
16. Insular endemism: Whether a species' distribution is restricted to islands or archipelagos.

17. Biogeographic realm: Biogeographic areas of species' distributions, based on the definition by Olson and Dinerstein (1998). Distribution data based on Reptile Database (Uetz et al., 2021).

In Appendix S3, we provide metadata for the raw morphological data for each taxon. This includes linear body measurements, and digits and presacral vertebrae numbers. These metadata include the original literature sources for each datum, with the values used for the final dataset highlighted. It also includes the reference list for the morphological and habitat data for species included for comparative purposes. An associated dataset cataloguing the literature on limb-reduced species is included in Appendix S4. It includes the following fields:

1. Species: As in Dataset A.
2. Higher taxon: As in Dataset A.
3. External descriptions: Studies based on external morphological characters.
4. Traditional internal descriptions: Studies based on methods such as osteological and myological descriptions of skeletons and stained specimens.
5. Radiographs: Studies based on X-ray projection of internal anatomical features (e.g., bones).
6. 3D-imaging: Studies based on X-ray computed tomography (CT scanning).
7. Phylogeny: Published molecular phylogenies and phylogeny-based comparative studies. Does not include squamate-wide phylogenetic assessments.

The reference list for the sources included in both datasets (including all references for morphological data in the main dataset) is provided in Appendix S5.

2.3 | Technical validation

The same types of data are often presented differently in different sources. We therefore scored traits according to the following protocol: (1) for digit and presacral vertebrae counts, we used the highest number reported. We chose maximum over average measurements to avoid having counts not expressed as integers, for the convenience of analysis; (2) for other measurements, we calculated an average of all values in the literature. When a study included averages of measurements for the highest number of specimens measured for that species, we used that value instead of calculating our own. Whenever available, we prioritised the use of measurements taken directly from museum specimens, of which we had an available sample from Australian museum collections (Museum and Art Gallery of the Northern Territory, Western Australia Museum, Museums Victoria). To preserve the average proportions of body parts relative to SVL, variables were divided by the SVL of each specimen prior to averaging, then multiplied by the weighted average SVL of all specimens. This proved necessary especially when data for variables other than SVL were available only for a few specimens or a single specimen. There are clear limitations of this method, as it may

introduce allometric biases and assumes linearity in the intraspecific variation of body proportions. However, we believe the use of this method is justified, since our dataset was constructed with the intention of data completeness, to include as many complete measurements as possible for the highest number of species, to achieve our aim of comparisons among species rather than intraspecific examination.

When measurements were only available from images, we extracted measurement data from the images that included a scale bar (or with known proportions from the text). This was common for head lengths, which are often not reported in original descriptions, but made available by the inclusion of photos and lateral and dorsal head illustrations. In the cases of species where limb lengths are not reported and limbs are described as minute but still prominent (i.e., clearly visible) (*Pygomeles braconnieri* and *Typhlacontias brevipes*) we considered them to be 2% of the average SVL, as in similar species, where such measurements are reported (18 species), they fall between 1 and 3 percent of SVL. When limb lengths were not reported because they are present as spurs, stumps, nubbins, styles, tubercles or single scales, we considered them to be of zero length, but we still scored the species as 'limb-reduced' because limbs are not fully absent.

Two hundred and twelve fully limbed species for which measurements were available were added for comparative purposes, although they are unrelated to limb-reduced or limbless taxa. We included at least one representative species for each known genus of skink (as of The Reptile Database, November 2020) when measurements were available. In the interest of practicality, given the high number of taxa involved, for these species we used mensural data

reported for a single specimen from a single study instead of averaging across multiple specimens. When available, presacral vertebrae numbers for these species were also recorded from a single source. Sources were chosen for their completeness in the presented measurements, and as such they were in most cases represented by original species descriptions (i.e., usually of the holotype).

3 | RESULTS AND EXAMPLES OF DATA USAGE

The data presented herein can be used for several types of analyses involving the morphology and ecomorphology of limb-reduced lizards. Here we present some preliminary observations based on the data.

3.1 | Taxonomic distribution of limb-reduced forms in Scincidae

The family Scincidae includes at least 1732 species (Reptile Database, Uetz et al., 2021), divided in seven subfamilies (plus *Brachymeles*; Zheng & Wiens, 2016). We find evidence of limb reduction and body elongation in 51 skink genera, representing 31.1% of the 164 extant genera (Uetz et al., 2021). Our dataset includes 606 species, of which 394 are limb-reduced or limbless skinks. These 394 species represent approximately 22.7% of all known skink species. The relative proportion and number of limb-reduced and limbless species varies across skink groups (Figure 1).

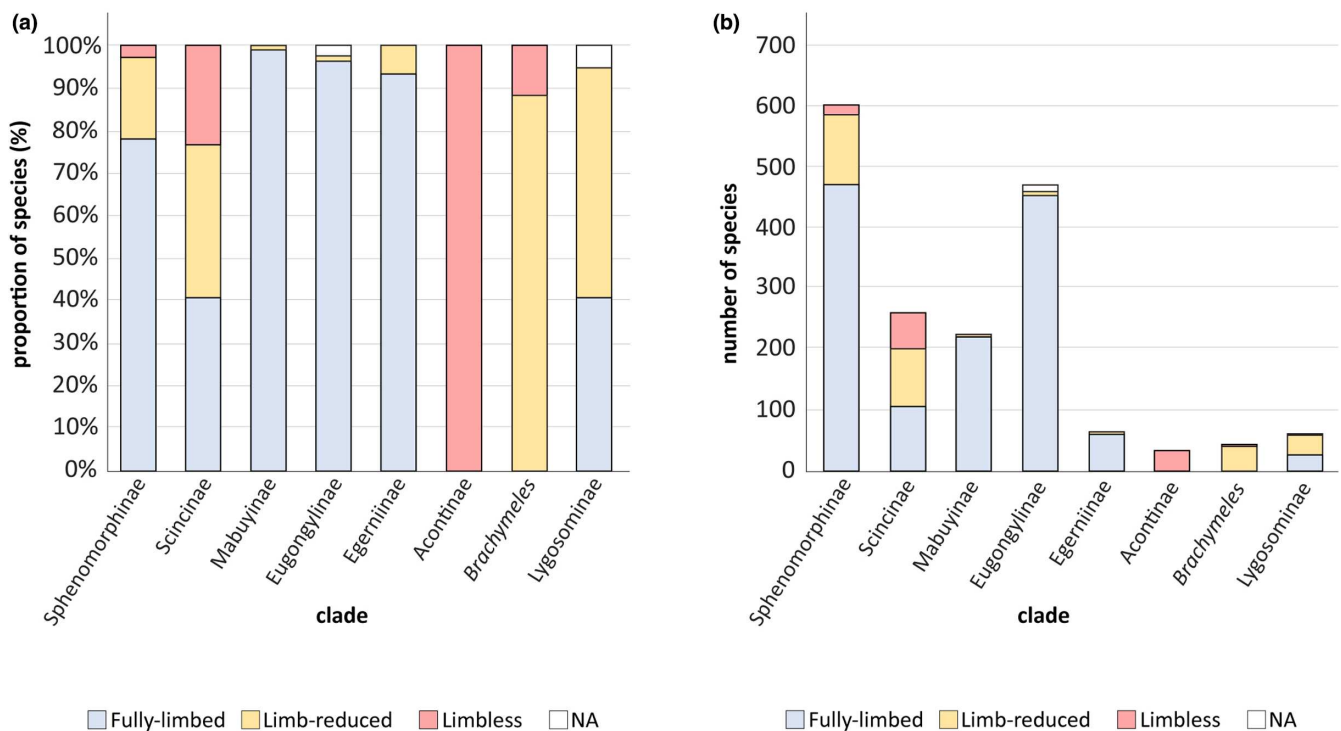


FIGURE 1 (a) Stacked bar chart showing the percentages of fully limbed, limb-reduced and limbless species across the eight main clades of skinks; (b) stacked bar chart showing the number of fully limbed, limbless and limb-reduced species across the eight main clades of skinks. Species indicated with NA lack data to determine their limb reduction status.



The Scincinae and Sphenomorphae have the highest number of limb-reduced and limbless species, followed by the Philippine genus *Brachymeles*, the Acontinae (a clade including only limbless taxa) and the Lygosominae. The remaining subfamilies (Eugongylinae, Mabuyinae, Egerniinae) have very few limb-reduced species, and no limbless species (Figure 1).

3.2 | Biogeography of limb-reduced skinks

Skinks are present on every continent except Antarctica, in habitats ranging from deserts to tropical rainforests (Chapple et al., 2021). The distribution of limbless and limb-reduced forms differs from that of fully limbed skinks (Figure 2). The Afrotropical (particularly South Africa and Madagascar) and the Australasian (only Australia) biogeographic realms are especially species-rich (respectively, 40.6% and 31.2% of limb-reduced species inhabit these realms), followed by the Indomalayan (27.7% of limb-reduced species, with scattered areas of richness in India, Indonesia, Southeast Asia and Philippines) and Palearctic (5.8% of limb-reduced species) (Figure 2). No limb-reduced skinks inhabit South America, and a single species (*Plestiodon reynoldsi*) inhabits North America. The evolution of limb-reduced forms in these continents might have been hindered by the presence of established limb-reduced competitors such as gymnophthalmids, amphisbaenids and anguimorphs in South America, and amphisbaenids, anguimorphs and dibamids in North and Central America (Pianka & Vitt, 2003).

Insular endemics represent approximately 30.3% of the limb-reduced and limbless skink species. Madagascar is home to seven distinct genera of Scincinae that have independently evolved limb reduction (Andreone & Greer, 2002; Miralles et al., 2015). Sri Lanka and the Philippines each have a single lineage of skink (*Nessia* and *Brachymeles*, respectively) that radiated into several forms with varying degrees of limb reduction (Siler et al., 2011; Smith, 1935).

3.3 | Using the dataset to determine the evolutionary frequency of skink limb reduction

Historically, reconstructions of the number of independent instances of limb reduction and loss in skinks has been complicated, as different methods and alternative definitions of what constitutes limb reduction have been used. Greer (1991) used a broad definition of limb reduction—that is, loss of limb bones, including phalanges—to identify a total of 25 instances of limb reduction in skinks, but without a phylogenetic framework to support this estimation. Subsequent studies have used phylogenetic comparative methods to obtain more accurate reconstructions based on phylogenies. Wiens et al. (2006) identified 14 independent instances of the evolution of limb reduction in skinks (not stated explicitly, but mapped on a phylogeny in a figure), defining species as limb-reduced based on a combination of limb and tail proportions and numbers of digits. Skinner (2010), and Skinner et al. (2008), found 27 instances of limb reduction in the genus *Lerista* alone, defining limb reduction based on the loss of digits only, but did not extend their analysis to other scincid clades. Finally, Bergmann and Morinaga (2019) reconstructed a total of 31 independent instances of limb reduction in skinks based on digit loss (not stated explicitly, but mapped on one of their main figures; however, several taxa are excluded from their analysis).

We used ancestral reconstructions of discrete character histories to determine how many times the limb-reduced and limbless body shapes have evolved in our dataset, and how often limbs have been lost in skinks. Our definition of limb reduction is based on the relative length of limbs to SVL (see above). To estimate how many times limb-reduced and limbless body shapes have evolved in skinks, we employed a variation of the methods for ancestral character estimation from Brandley et al. (2008) and Bergmann and Morinaga (2019). These methods use Markov-chain models that estimate transitions between discrete character states using maximum likelihood (Pagel, 1999). We coded species as limbless and as limb-reduced according to the

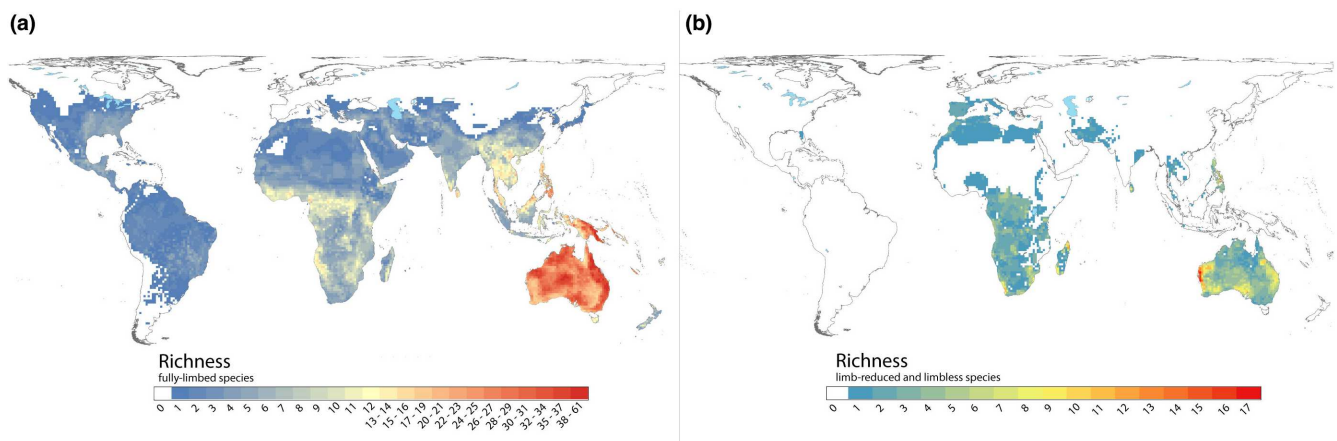


FIGURE 2 World maps showing the distribution and richness of (a) fully limbed skink species and (b) limb-reduced and limbless skink species. Richness and distribution data modelled after de Oliveira Caetano et al. (2022).

definition used for our dataset. We coded as fully limbed all remaining skink species included in the phylogeny by Zheng and Wiens (2016). Limbless species were coded as character state 1, limb-reduced ones as 2, and fully limbed species as 3. All models considered treated limb status as an ordered character, as to become limbless a species must necessarily first become limb-reduced (Bergmann & Morinaga, 2019; Brandley et al., 2008; Camaiti et al., 2021).

We also set out to estimate the number of independent losses of limbs. Loss of both limb pairs was coded as character state 0,

loss of only one pair of limbs as 1, and retention of both limbs as 2. The extended dataset used for these analyses is included in Appendix S6.

The phylogeny by Zheng and Wiens (2016) was used to prune the dataset and to map ancestral reconstructions. A strict, directional Dollo model (Bergmann & Morinaga, 2019; Dollo, 1893) was used for both estimations, allowing no reversions from a limb-reduced or limbless state for the first analysis, and no reversion from loss of one or both limb pairs in the second analysis. This was justified

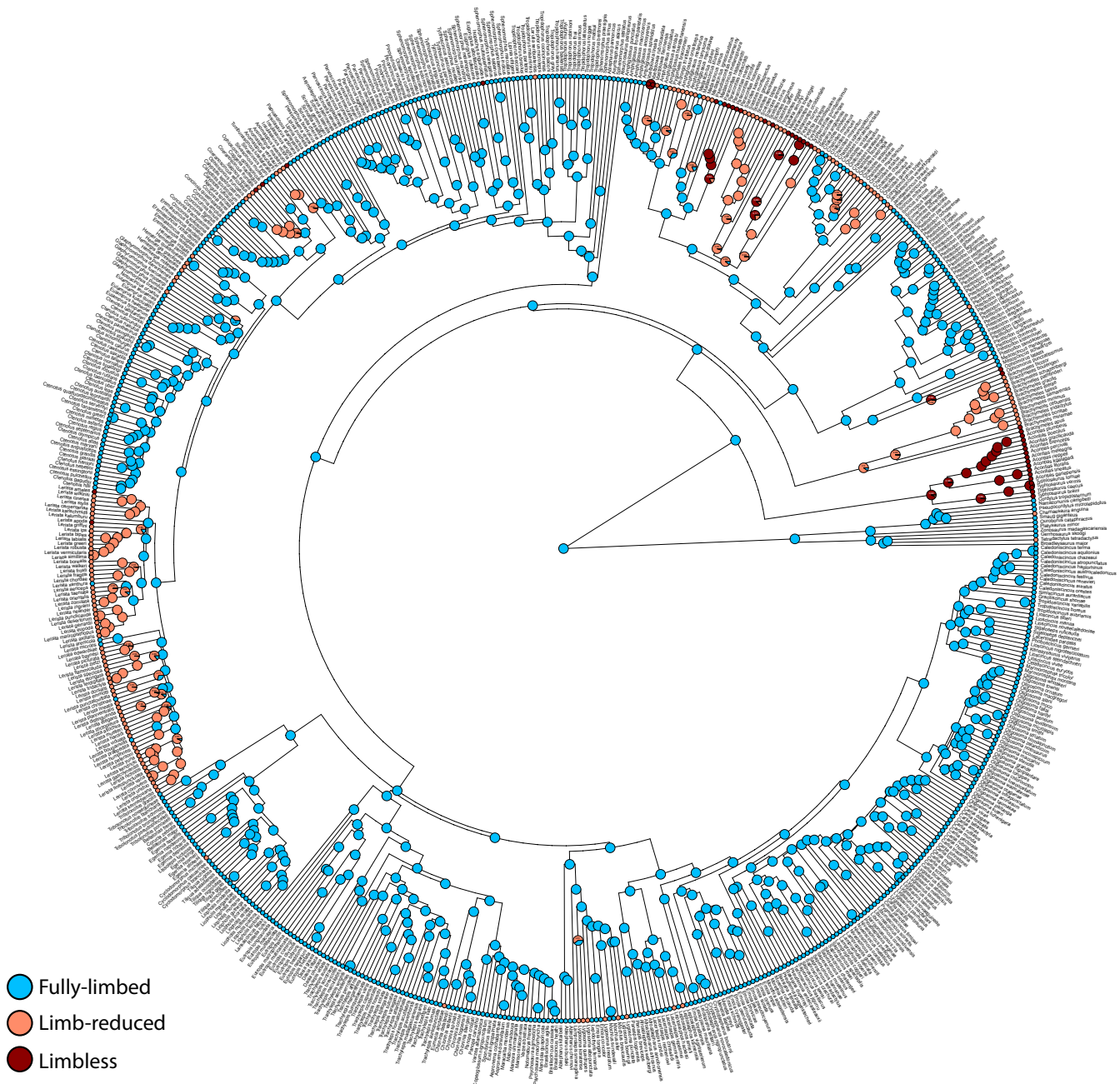


FIGURE 3 Phylogenetic tree (from Zheng & Wiens, 2016) mapped with transitions to limb reduction and limblessness, reconstructed using a maximum likelihood approach (simmap) and implementing a strict Dollo model allowing no reversions from a limbless or limb-reduced state. Node support is indicated within the percentage pies of posterior probabilities mapped at each node (only when there is character state uncertainty).



by our focus on estimating only an indicative number of independent transitions, without going into the merit of whether such transitions are reversible or not, as this was beyond the scope of our study. The question of reversibility of limb reduction is still far from settled (Bergmann & Morinaga, 2019; Galis et al., 2010; Kohlsdorf et al., 2010; Skinner, 2010), also due to issues in the methodology used. Ancestral character estimations based exclusively on the distributions of character states at the tips of tree branches have been found to be biased by the lack of consideration of heterogeneity in the rate of character evolution across clades (King & Lee, 2015), a method whose implementation is not yet fully possible with the instruments we had available. From a developmental standpoint it can

also be argued that transitions towards a more reduced state will be more likely than the reverse due to the accumulation of correlated sets of changes that would need to be reversed as well (Dollo, 1893; Galis et al., 2010). For these reasons, a restricted model not allowing reversions was used in both analyses.

The extended dataset (Appendix S6) was pruned of taxa absent from the phylogeny with the 'treedata' function, and models were fitted using the 'fitDiscrete' function. All of the above was performed in the R package 'geiger' (2.0.7: Pennell et al., 2014). The 'make.simmap' function (package 'phytools', 0.7.70: Revell, 2012) was used to fit the models to the phylogeny, simulating character histories based on the models and the tip states of the tree.

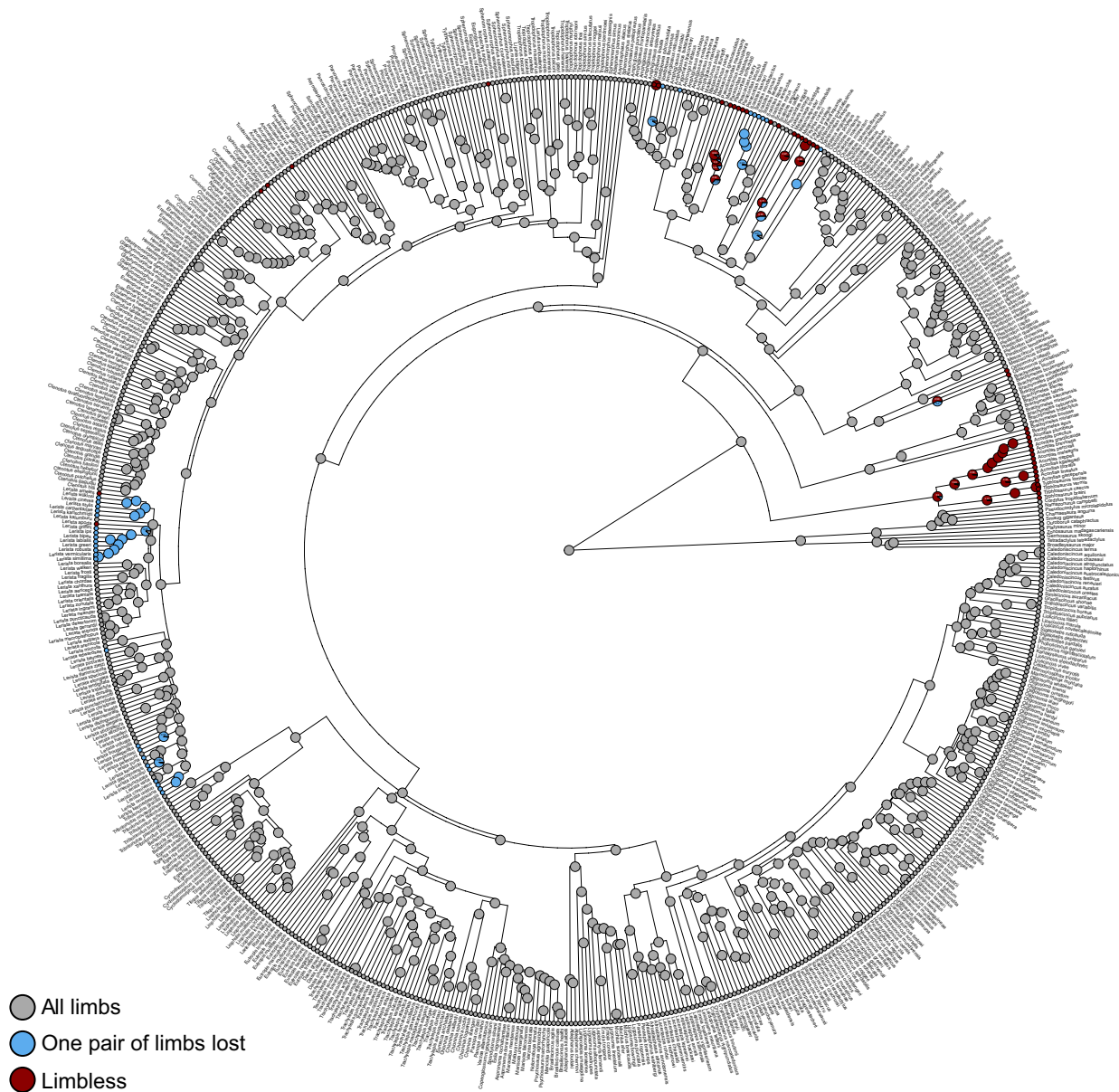


FIGURE 4 Phylogenetic tree (from Zheng & Wiens, 2016) mapped with transitions to limb loss, reconstructed using a maximum likelihood approach (simmap) and implementing a strict Dollo model allowing no reversions from a loss of one or both pairs of limbs. Node support is indicated within the percentage pies of posterior probabilities mapped at each node (only when there is character state uncertainty).

To account for uncertainty in the posterior probabilities reconstructed at the nodes of the tree, when counting the number of independent transitions between states, only character states with a posterior probability higher than 75% were considered to be highly supported for that node. Nodes with lower probability were considered to be indicative of one or the other possible character states in our low and high estimates.

To extend our estimation beyond the taxa present in the phylogeny, we also considered limb-reduced and limbless taxa in our main dataset, as several genera and single species lack associated phylogenetic information. Each genus was taken to represent an independent instance of limb reduction/loss. In some cases, phylogenetic information from other sources (not Zheng & Wiens, 2016) was associated with taxa, which helped inform our estimation. This information and the sources used are included in Appendix S7.

Accounting for uncertainties in character probabilities in the reconstructed nodes, we find 53–57 independent evolutionary instances of limb reduction and loss in skinks (Figure 3). When counting limb-reduced or limbless clades from our dataset that were not included in the phylogeny of Zheng and Wiens (2016), under the assumption that each non-sampled clade represents a single event of loss, we estimate limb reduction and loss to have evolved 67–71 times (Appendix S7a).

Loss of at least one limb pair in skinks occurred at least 24 times independently (Figure 4), rising to a range of 36–41 when counting clades absent from the phylogeny (Appendix S7b). With the sole exceptions of the genera *Voeltzkowia* (s.s., two out of three species) and *Jarujinia*, which have completely lost their hindlimbs but maintained some of their forelimbs, all remaining instances are of loss of forelimbs only. Skinks in lineages represented in the phylogeny completely lost both pairs of limbs 17–22 times (Figure 4), rising to 25–32 times when also counting clades not included in the phylogeny (Appendix S7b).

4 | SUGGESTIONS FOR FUTURE STUDIES

Future studies are likely to benefit from this dataset, given its focus on providing as much morphological data as possible on limb-reduced and limbless skinks, and on their environmental and biogeographical context. As this dataset constitutes the first global data collection focused on limb-reduced skinks, studies could benefit from such a convenient model system by linking morphological variation and species' distributions. Moreover, the specific relationships between habitat and morphology in limb-reduced taxa have only seldom been explored (Brandley et al., 2008; Wiens & Slingluff, 2001), and rarely beyond the distinction between surface-dwelling and underground lifestyles (e.g., Grizante et al., 2012, for gymnophthalmids). The habitat and morphological data provided herein could represent an important basis to investigate these associations in an ecomorphological, as well as biogeographical, framework. At the same time, our tabulation reveals the incomplete and often vague nature of the data

that are available for (micro)habitat and ecologies of many species, indicating topics requiring better descriptions in the future.

The literature dataset associated with the main dataset could instead prove useful to identify the gaps in knowledge regarding limb-reduced skinks and their closest relatives, given it identifies the areas of study, as well as the taxa, that have received little to no attention during the history of herpetological studies.

To conclude, we recommend that this dataset be used to explore and further our understanding of the evolution of limb reduction in skinks, which by extension will inform us about the rules and trends of morphological evolution across terrestrial vertebrates, and how these are associated with the surrounding environment.

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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 materials.

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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



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SUPPORTING INFORMATION

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