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Different selection regimes explain morphological evolution in fossorial lizards

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Abstract

1. Independent origins of similar phenotypes are ubiquitous to the evolutionary process and evoke strong and recurrent environmental associations. Snakelike lizards evolved multiple times and are often portrayed as limb-reduced and body-elongated outcomes from shared selection associated with fossoriality.
2. However, a refined evaluation including specific head traits and subtle differences in subterranean microhabitats unveils some degree of uniqueness even among lineages traditionally interpreted as phenotypically similar. Here, we address regimes of selection in fossorial lizards accounting for differences in the burrowing substrate and emphasizing head shape in addition to body and limbs.
3. We assembled an ecomorphological database comprising 213 species from all major lizard clades, and then characterized contemporary morphological diversity and modelled phenotypic evolution to test the hypothesis that fossoriality encompasses at least two distinct selection regimes.
4. We identified two ecomorphological groups within the fossorial lizards: moist-soil fossorial and dry-soil fossorial. Both groups evolved towards distinct adaptive optima concerning head shape and limb size. Despite some degree of uniqueness, these groups also share similar patterns in specific traits. Dry-soil fossorial lizards present less morphological variation than moist-soil fossorial, possibly due to the combination of distinct sets of selective pressures with shared ancestry.
5. Our study provides evidence that an often-interpreted general adaptive regime (e.g. fossoriality) may in fact comprise enough ecological and functional diversity to elicit several distinct ecomorphological associations despite overall convergence among phenotypic traits.

KEYWORDS
body shape, convergent patterns, ecomorphs, functional phenotype, head shape, snakelike, Squamata

1 | INTRODUCTION

Convergent evolution is the repeated origin of similar phenotypes not shared by a common ancestor (Blount et al., 2018; Hall, 2003; Losos, 2011; Moen et al., 2013; Nixon & Carpenter, 2011; Wake et al., 2011). A general interpretation is that similar phenotypes often evolve independently as outcomes of equivalent regimes of selective pressures, thus evoking the strength of natural selection

(Losos, 2011; Nixon & Carpenter, 2011; Sackton & Clark, 2019). Independent evolution of phenotypic similarities associated with specific microhabitats can be explained by the functional and ecological demands of that environmental setting. For example, fossorial lizards, which move through the soil under the surface, are often characterized by an elongated and limb-reduced or limbless body shape (also referred to as 'snakelike'), and evolved multiple times within Squamata (i.e. snakes and lizards; Bergmann & Morinaga, 2019; Brandley et al., 2008; Camaiti et al., 2021; Gans, 1975; Lee, 1998; Wiens et al., 2006). Elongated limb-reduced forms are often interpreted as advantageous for locomotion through the substrate (Camaiti et al., 2021; Gans, 1975; Herrel & Measey, 2010; Lee, 1998; Morinaga & Bergmann, 2019, 2020; Seymour et al., 1998; Sherratt et al., 2014). Fossoriality, however, has independently evolved in different habitats and substrate types (Bergmann & Berry, 2021), and therefore the 'fossorial' ecology encompasses environmental differences that may ultimately represent distinct regimes of selective pressures driving phenotypic evolution.

Evolution of snakelike morphotypes among lizards has been extensively examined with respect to limb reduction (e.g. Camaiti et al., 2021; Kohlsdorf, 2021; Kohlsdorf & Wagner, 2006; Shapiro et al., 2007; Wagner et al., 2018) and trunk elongation (e.g. Brandley et al., 2008; Grizante et al., 2012; Morinaga & Bergmann, 2019), and investigation benefits from a long history of studies on the topic (Brandley et al., 2008; Camaiti et al., 2021; Gans, 1960, 1975, 1986; Greer, 1991; Grizante et al., 2012; Kohlsdorf, 2021; Kohlsdorf et al., 2010; Lee, 1998; Morinaga & Bergmann, 2017, 2020; Skinner et al., 2008; Wiens & Slingluff, 2001; Wiens et al., 2006). However, analyses considering head shape variation remain restricted to specific fossorial lineages (e.g. Barros et al., 2011; Kearney & Stuart, 2004; Le Guilloux et al., 2020; Stepanova & Bauer, 2021; see also Bergmann & Berry, 2021 for a taxonomically comprehensive study). Head traits are particularly relevant for fossoriality because this is the region of the animal that contacts the substrate during headfirst locomotion (Barros et al., 2011, 2021; Gans, 1975; Herrel & Measey, 2010; Watanabe et al., 2019). Adaptations to fossoriality involve changes in scales and fusion of skull bones that protect the brain and sensorial organs (Gans, 1975; Lee, 1998; Roscito & Rodrigues, 2010), reduction of eyes and ear openings probably related to substrate friction during underground locomotion (Evans, 2016; Maddin & Sherratt, 2014; Yovanovich et al., 2019), and development of peculiar head shapes (Barros et al., 2011, 2021; Kearney & Stuart, 2004; Le Guilloux et al., 2020; Lowie et al., 2021; Navas et al., 2004). However, differences in substrate composition—and therefore in hardness and compression—may result in distinct head shape patterns, as outcomes of different sets of selective pressures (Barros et al., 2021; Bergmann & Berry, 2021; Herrel & Measey, 2010; Hohl et al., 2017; Kazi & Hipsley, 2018; Kubiak et al., 2018; Le Guilloux et al., 2020).

Within fossorial lineages, general associations between head shape and burrowing substrate remain vague despite the variety of microhabitats used by these species, from dry loose soils to moist compact soils such as humus and leaf-litter (Barros et al., 2021; Bergmann & Berry, 2021; Camaiti et al., 2021; Wiens et al., 2006). Previous studies evaluating the influence of particle size, moisture and compaction on headfirst burrowing in specific groups (e.g. Barros et al., 2021; Bergmann & Berry, 2021; Herrel & Measey, 2010; Stepanova & Bauer, 2021) suggested associations between head traits, such as head width and rostral pointiness, and substrate type. In fact, comparative studies focusing on specific groups, such as amphisbaenians, skinks or gymnophthalmids, indicate that species that burrow in sand and sandy soils evolved unique adaptations, such as wedge-shaped skulls and longer snouts, suggesting convergent phenotypic patterns likely associated with complex properties of these soils (Barros et al., 2021; Gans, 1968; Stepanova & Bauer, 2021). What remains compulsory is a taxonomically wide comparative evaluation that includes head shape as a key morphological structure to the evolution of snakelike fossorial lizard lineages—an approach that might unveil similar patterns and phenotype-environment associations considering the variation in burrowing substrates.

Here we evaluate if the evolution of fossoriality encompasses distinct selective regimes (at least two) due to differences in substrate types, which consequently might have resulted in different ecomorphological groups among the fossorial lizards. We assembled a large morphological database composed of all major lizard groups, focusing on snakelike lineages. We modelled phenotypic evolution by comparing different hypotheses of selection regimes to evaluate if limb reduction, body elongation and head shape evolved towards two distinct adaptive optima in fossorial lizards: dry-soil and moist-soil fossorial groups. We also characterized current morphological disparity within the fossorial lizards, as we predict that the dry-soil fossorial group encompasses less morphological diversity than moist-soil fossorial lizards, due to unique adaptations involved with headfirst burrowing in sand and dry soils. We also evaluated the profiles of morphological disparity through time, as we expect that historical processes associated with morphological diversity partitioning may reflect different combinations of shared ancestry and adaptation in distinct snakelike lineages. This combination of analytical approaches enabled a refined characterization of morphological diversity among fossorial lizards and sustained inferences on how nuances of selective regimes contribute to the evolution of phenotypic patterns.

2 | MATERIALS AND METHODS

2.1 | Specimens and phenotypic traits

We assembled a morphological database comprising 213 species of lizards distributed worldwide, with 1932 specimens sampled (mean of 9 individuals per species) representing all major squamate clades, except Serpentes (Zheng & Wiens, 2016). At least one representative species of each extant lizard family, except Xenosauridae, was included in our database. Amphisbaenians were also included in our sample, and we refer to amphisbaenians as lizards unless otherwise

TABLE 1 Models postulated to explain morphological evolution in lizards: five adaptive models ('M1' to 'M5') admit from one to five adaptive optima; and three non-adaptive models, two of them admitting one ('OU1') or five ('Clade') optima and the last one ('Brownian motion') corresponding to random drift.

Model	Selection regimes				
	Optimum 1	Optimum 2	Optimum 3	Optimum 4	Optimum 5
Adaptive models					
M1	Epigeal	Fossorial			
M2	Arboreal	Fossorial	Terrestrial		
M3	Arboreal	Fossorial	Grass-swimmer	Ground-dweller	
M4	Arboreal	Dry-soil fossorial	Moist-soil fossorial	Terrestrial	
M5	Arboreal	Grass-swimmer	Ground-dweller	Dry-soil fossorial	Moist-soil fossorial
Non-adaptive					
OU1	All lizards				
Clade	Gekkota	Scincoidea	Lacertoidea	Anguimorpha	Iguania
BM	Random drift (no selection regimes)				

stated. Sampling effort relied primarily on the availability of snake-like lineages in the collections accessed to maximize taxonomic coverage of snakelike lineages whenever possible. Lineages lacking extant snakelike species are coarsely represented in our database. Thus, in our database all Iguania families, most Gekkota families, and Lacertidae are represented by only a small fraction of their diversity (totalizing together 26% of all species sampled; Table S1 provides a list of all species included in our study, indicating clade and ecological classification).

Most preserved animals were measured during visits to herpetological collections or obtained by loans. Both adult males and females were included in our study. Thirteen traits were obtained from direct measurements on preserved specimens by the same researcher using a digital calliper (Mitutoyo Inc., 0–200 mm, precision 0.01 mm). In a few species, metric tape was used to measure very long tails. Damaged or regenerated structures were not considered. Our database focused on functional traits of head shape (measurements 1–9) and also four post-cranial traits related to locomotion (measurements 10–13): (1) head length (distance between the posterior extremity of the parietal scale and the tip of the snout); (2) head width (maximum distance between the temporal scales); (3) head height (maximum distance between the parietal scale and the ventral edge of the lower jaw); (4) nasal height (maximum distance between the nasal scale and the ventral edge of the lower jaw); (5) nasal distance (maximum distance between the nasal openings); (6) orbital distance (distance between the orbits, given by the distance between the lateral extremities of the frontal scale at mid-eye height); (7) rostral length (distance between the back of the jugal bone to the tip of the upper jaw); (8) lower jaw length (distance between the posterior edge of the retroarticular process and the tip of the lower jaw); and (9) quadrate-to-tip length (distance between the posterior edge of the quadrate bone [easily felt externally in the region between the skull end and the neck] to the tip of the upper jaw); (10) trunk length (distance from the posterior end of the lower jaw to the cloaca, in a ventral view); (11) tail length (distance from the cloaca to the tip of

the tail); (12) hindlimb length (maximum length of the left hindlimb); (13) forelimb length (maximum length of the left forelimb).

2.2 | Ecological classification

We tested the hypothesis that the general category of 'fossorial lizards' represents two regimes of selection that differ according to the burrowing substrate. Accordingly, we implemented different complementary approaches to classify taxa according to their ecology. First, sampled species were classified as epigeal or fossorial according to their primarily foraging habitat. All fossorial species were then classified into two groups, based on the preferred burrowing substrate, which was distinguished mainly by their moisture levels: (1) dry-soil fossorial and (2) moist-soil fossorial lizards. The dry-soil fossorial group encompasses species that forage in arid soils, such as different types of sand, with poor organic matter and vegetation, commonly associated with deserts and xeric shrublands. Moist-soil fossorial lizards, on the other hand, include species that forage through substrates with higher levels of humidity, such as leaf-litter and humus, often associated with forested regions with higher soil organic material. Complementarily, we also distinguished epigeal species in two categories: terrestrial (i.e. lizards that forage on the ground) and arboreal (i.e. species that primarily forage on trees and vegetation). Given that our study focuses on snakelike morphotypes and that epigeal lineages also include elongated limb-reduced forms, we distinguished the terrestrial species in two categories: ground-dweller (i.e. epigeal lacertiform species that forage on the ground) or grass-swimmer (i.e. epigeal snakelike lizards that forage on the ground). Different combinations of ecological categories were considered to design the hypotheses of selection regimes, as further detailed (see Table 1).

Our study uses morphological data obtained from preserved museum specimens, which often lack detailed environmental information. For this reason, species were summarized into ecological

categories based on published information available. Species interpreted in the literature as saxicolous, psammophilous and semi-aquatic were classified here as terrestrial ground-dwellers. Species referenced elsewhere as semi-fossorial were classified here as either fossorial or terrestrial according to their primary foraging habitat (following the criteria employed by Bars-Closel et al., 2017). Occasional burrowers (i.e. lizards that burrow only to avoid predators or that use galleries made by other animals) were not considered here as fossorial, but instead were classified as ground-dwellers (see Table S1 for detailed ecological classification and bibliography consulted). Our ecological classification was solely based on literature descriptions of foraging habitat and did not consider classifications based on species' overall morphology.

2.3 | Phylogeny

We implemented comparative analyses in R (R Core Team, 2022; version 4.2.2) and used RStudio (RStudio Team, 2020; version 2023.06.1) as graphical user interface. All comparative analyses considered the phylogenetic hypothesis published by Zheng and Wiens (2016). This is a time-calibrated tree for Squamata based on 52 genes that included more than 4000 species and estimated branch lengths. Sixteen out of 213 species from our database are not present in the phylogeny from Zheng and Wiens (2016), so we placed them in the topology after consulting hypotheses published for specific lineages or taxonomic descriptions (see Table S1); this procedure consisted of either replacing a given species or by dividing a branch in two. For example, we measured the gymnophthalmid species *Alexandresaurus camacan*, which was not included in the study by Zheng and Wiens (2016). Therefore, we followed the study by Goicoechea et al. (2016), which places *A. camacan* as a sister-clade of (*Iphisa elegans*, *Colobosaura modesta*), and collapsed the branch (*I. elegans*, *C. modesta*) in two equal parts to manually add *A. camacan*, which resulted in a clade (*A. camacan*, (*I. elegans*, *C. modesta*)), where the branch corresponding to *A. camacan* and that leading to (*I. elegans*, *C. modesta*) had the same length. As another example, the species *Cadea palirostrata* was positioned as a sister-lineage of *C. blanoides* because these two species are the only representatives from the genus *Cadea* and the family Cadeidae in our database. In this procedure, we divided the original branch of *C. blanoides* in two branches having same length and produced the clade (*C. palirostrata*, *C. blanoides*).

2.4 | Phylogenetic body-size correction

Our morphological dataset comprised species representing a wide range of body sizes. Because we aimed to characterize morphological patterns and model the evolution of snakelike forms associated with fossoriality focusing on head shape and other shape patterns, we implemented statistical analyses using morphological traits phylogenetically corrected for body size. Due to normality premises

and standardized practices in ecomorphological studies, we log-transformed ($\log_{10}$) the mean values of morphological measurements for each species before the body size correction. However, several snakelike lizards are limbless, which result in limb measurements corresponding to zero, thus preventing the $\log_{10}$ transformation. Therefore, we added the unit 1.0 to mean values of fore- and hindlimb lengths for all species before the $\log_{10}$ transformation (see Wiens et al., 2006). Then, we regressed all measurements against head length in a phylogenetic generalized least-squares regression (PGLS) using the function 'phyl.resid' in the R package *phytools* (version 2.0-3; Revell, 2012). We adopted head length as a proxy of body size instead of snout-vent length, a decision that follows previous studies arguing that head length is a better indicator of body size than snout-vent or total length in comparative analyses including both snakelike and non-snakelike lineages due to drastic changes in body shape derived from body elongation in snakelike phenotypes (see Wiens & Slingluff, 2001). The 12 sets of residuals from these regressions were treated as phylogenetically size-corrected traits and were employed for estimates of contemporary morphological indices and for disparity-through-time profile. For the phenotypic evolution modelling, we also implemented principal component analyses using size-corrected residuals, as described in the following subsections.

2.5 | Phylogenetic principal components analysis

We implemented a phylogenetic principal component analysis (pPCA) to characterize the morphological variation in our database using the function 'phyl.pca' in the *phytools* package (Revell, 2012). This approach was chosen instead of a conventional PCA because it recognizes that taxa are not phylogenetically independent. We used a correlation matrix and assumed the Brownian motion model (Revell, 2009, 2012). To interpret the results from the pPCA and the subsequent analyses, we considered only the principal components (PC) with eigenvalues higher than 1.0 (PC1 to PC4 in our results), focusing on those that represent together at least 50% of all variation (PC1 and PC2). We evaluated loading magnitudes and direction within each PC and among the PCs considered to identify the contribution of morphological traits to the variation observed along each PC axis. We considered absolute values of loadings equal or higher than 0.5 as indicative of the contribution of a trait in the axis of variation. We also plotted the PC scores in a phylomorphospace to visualize how species and ecomorphological groups are distributed in the morphospace while accounting for phylogenetic relationships.

2.6 | Contemporary morphological disparity

We estimated contemporary morphological disparity to test the hypothesis that moist-soil and dry-soil fossorial lizards differ in distribution patterns in the morphospace, which might reflect the morphological diversity within each group. We expect that dry-soil

fossorial lizards encompass less morphological disparity than the moist-soil fossorial lineages, as several studies describe similar skull adaptations associated with dry-soils across different lizard families (see Barros et al., 2021; Gans, 1968; Stepanova & Bauer, 2021). Morphological disparity indices enable comparisons of morphological variation among ecological groups, clades or localities, and combination of two or more metrics can be potentially more informative (Guillerme et al., 2020). Here, we calculated two morphological disparity metrics using the residuals of the phylogenetically size-corrected morphological traits. We considered five ecological groups: arboreal, grass-swimmer, ground-dweller, dry-soil fossorial and moist-soil fossorial. The first metric calculated was the 'sum of variances', which represents the size of the distribution of each group in the morphospace, where higher values indicate a larger area occupied in the morphospace as well as the presence of more extreme phenotypes. The second metric, 'functional divergence', accounts for the abundance of species deviating from the centroid of an ecological group, in which higher values denote prevalence of extreme phenotypes within the group (following Villéger et al., 2008). All contemporary disparity analyses were performed using the package *dispRity* (version 1.7.0; Guillerme, 2018). The morphological disparity indices were estimated using the function 'dispRity.per.group'. To test for statistically significant differences among groups in their calculated morphological disparity, we estimated the Bhattacharyya distance, a coefficient that accounts for the probability of similarity in disparity indices between two groups. The Bhattacharyya coefficient evaluates the degree of overlap between the groups, with higher values indicating higher probability of the metrics calculated for each group to be statistically similar. This test is also available in *dispRity* package (Guillerme, 2018). Additional information regarding the metrics and tests used here are available in Guillerme et al., 2020.

2.7 | Modelling of microhabitat use transitions and ancestral character states reconstructions

We modelled the rates of evolutionary transitions between different ecological categories in our sample and then estimated ancestral character states. We aimed to map the occupation of distinct microhabitats along the phylogeny and the multiple origins of fossoriality in the context of the multiple origins of snakelike lizard forms. We simulated the evolution of microhabitat use on the phylogeny using the Mk model (i.e. discrete k-state Markov process; see Revell & Harmon, 2022). Evolution occurring by Mk process assumes that (1) changes can occur between discrete states at any time, and (2) the rate depends only of the current state with no influence of previous changes. Thus, when transition rate is high, the rate of change between two states is fast (Revell & Harmon, 2022). We modelled the rates of change among five ecological groups: arboreal, grass-swimmer, ground-dweller, dry-soil fossorial and moist-soil fossorial. We fitted three models using the function 'fitMk' in R package *phytools* (Revell, 2012): (1) ER (equal-rates) model, which adopts

transition rates between all pairs of states as being the same; (2) SYM (symmetric) model, assuming that transition rates are the same in a pair of states but can vary between different pairs; and (3) ARD (all-rates-different) model, which allows every transition to have a different rate. Akaike information criterion (AIC) values were considered to determine the best-fit model.

We assumed the best-fit model of rates of ecological transitions to reconstruct ancestral character states and to estimate node probabilities. We simulated 1000 stochastic character maps on the phylogenetic tree and used the function 'make.simmap' in *phytools* (Revell, 2012) to implement maximum likelihood reconstructions. The same parameters were considered to estimate the node probabilities, using the function 'ace' in the *ape* package (Paradis & Schliep, 2019).

2.8 | Phenotypic evolution modelling

We modelled phenotypic evolution using an Ornstein-Uhlenbeck (OU) process model with discrete switches of the adaptive regime applied along the phylogeny. This approach evaluates alternative evolutionary hypotheses based on a Hansen model by comparing distinct hypotheses of selective regimes as well as non-adaptive hypotheses (Butler & King, 2004; Hansen & Martins, 1996). Here, we applied OU models of evolution to test the hypothesis that fossorial lizards evolved towards two distinct adaptive optima, as morphological traits reflect different regimes of selective pressures associated with burrowing substrate. All OU-model analyses were performed using the package *ouch* (version 2.19; King & Butler, 2022). Results from this approach provide at least three parameters: optimal trait value (θ), strength of selection towards optima (α) and variance of stochastic evolution ($\hat{\sigma}^2$) (Butler & King, 2004; Scales et al., 2009). We calculated phylogenetic half-life ($t_{1/2}$) using α values as an estimation of the time required by a given species entering a new ecological regime to evolve halfway towards its new expected adaptive optimum (Cooper et al., 2016; Grabowski et al., 2023; Hansen, 1997). We tested OU models separately for each principal component (PC1 and PC2), as we consider that each PC represents a specific trait or set of traits. Models were compared based on Akaike's information criterion with correction for small sample sizes (AICc values). Lowest AICc values were interpreted as indicative of the best-fit model explaining evolution of phenotypic traits across the phylogeny. We also considered Akaike's weight values to compare two or more models that differed less than 2.0 in the AICc values (Burnham & Anderson, 2004; Butler & King, 2004; Scales et al., 2009; Wagenmakers & Farrell, 2004).

We postulated eight evolutionary models to explain morphological evolution in lizards (Table 1). The first three models represent non-adaptive (null) hypotheses for the evolution of morphological traits. The first model assumes that morphological evolution is explained by random drift, following Brownian motion ('BM'). The second model ('OU1') considers stabilizing selection directing morphological change towards a single optimum for all lizards, regardless

of ecological differences. The third model ('Clade'), assumes multiple optima but refers to a scenario in which different lizard clades exhibit distinct optima, reflecting the phylogeny rather than the ecology. We considered five major Squamata groups in this model: Iguania, Anguimorpha, Lacertoidae, Scincoidae and Gekkota (which here also includes Dibamidae). In addition to these three null models, five remaining models ('M1' to 'M5'; Table 1) assume multiple optima based on different hypotheses of regimes of selection. These models were designed to test the hypothesis that at least two distinct regimes of selection, reflecting differences in the burrowing substrate, explain phenotypic diversity among fossorial lizards, so that 'fossoriality' does not represent a single selective regime. For these five adaptive models, we implemented different combinations of ecological categorizations. More specifically, models 'M1', 'M2' and 'M3' assume one single selection regime for all fossorial lizards, while models 'M4' and 'M5' assign two optima for fossorial species, one for those that burrow in dry soils and another for those that live in moist soils. If either 'M4' or 'M5' were selected as best-fit models, we corroborated the hypothesis that morphological evolution reflects at least two regimes of selection within fossorial lizards (dry-soil fossorial and moist-soil fossorial).

2.9 | Disparity through time

We modelled patterns of phenotypic evolution through time to evaluate the contribution of origins of snakelike forms and the occupation of distinct fossorial contexts (i.e. burrowing substrate) to overall morphological disparity. We calculated the profile of morphological disparity through time (DTT; Harmon et al., 2003) considering all species sampled in our study and all morphological traits. The DTT profiles were generated using the residuals of phylogenetically body-size corrected traits and the function 'dtt' in the package *geiger* (version 2.0.11; Pennell et al., 2014).

Traditionally, DTT profiles are estimated for clades in the context of adaptive radiation hypotheses (Casadei-Ferreira et al., 2022; Harmon et al., 2003, 2010; Slater et al., 2010). We ran 1000 simulations to calculate the expected DTT, considering a confidence level of 95%. To generate DTT profiles, we calculated the disparity based on average squared Euclidian distance among all pairs of points, the most common distance metric for this analysis in macroevolutionary studies (Casadei-Ferreira et al., 2022; Harmon et al., 2003, 2010; Slater et al., 2010). We then calculated the morphological disparity index (MDI), a statistic that accounts for the overall difference between observed DTT and the DTT expected under the simulations. When the MDI value is positive, observed morphological variation is greater than expected from simulations, indicating that disparity tends to be distributed among subclades; when the MDI value is negative, variation is lower than expected under Brownian motion, suggesting that variation is distributed within subclades. Similarly, when DTT profiles show higher levels of subclade disparity than expected under a Brownian motion of evolution, we interpret the result as evidence for a higher-than-expected disparity within

subclades, suggesting more overlap in morphospace occupation. When we observe lower subclade disparity than expected, most of the variation is observed among subclades, indicating a greater partitioning of morphological diversity (see Harmon et al., 2003; Slater et al., 2010, for details on this method).

3 | RESULTS

3.1 | Phylogenetic principal component analysis

We implemented a phylogenetic principal component analysis (pPCA) that included 12 morphological traits corrected by body size (here head length was used as a proxy for body size), four of them concerning the post-cranium (trunk, tail, fore- and hindlimb relative lengths) and the remaining variables related to head shape. We interpreted two principal components with eigenvalues larger than 1.0 (PC1 to PC2), which together explained 52.66% of total morphological variation (Figure 1; Table 2). Two other principal components, PC3 and PC4, had eigenvalues larger than 1.0, but only represented 13.7% and 9.2%, respectively of the overall variance (Table S2), so these will not be further discussed. The first principal component (PC1: 30.1% of cumulative variation, eigenvalue = 3.61) expressed negative loadings equal or larger than 0.5 for head width, head height, snout length, lower jaw length and quadrate-to-tip length. The second principal component (PC2: 22.6% of cumulative variation, eigenvalue = 2.72), exhibited higher negative loadings for orbital distance and trunk length. Nostril distance and height, as well as fore- and hindlimb lengths, also scored high loading values in both PCs (Table 2). Evaluation of the direction of trait vectors within each PC suggested that limb lengths contribute more to the variation along PC1, while nostril dimensions equally contribute for both PCs (Figure 1). Altogether, these results suggest that PC1 is mostly related to head shape, while PC2 is best represented by orbital distance and trunk length, with limb size contributing to both axes of variation. Accordingly, larger PC1 scores correspond to species with less robust heads and smaller limbs, while lower PC2 scores correspond to species with larger orbital distances, elongated trunks and shorter limbs.

Distribution of groups in the morphospace suggested considerable overlap of snakelike lizards (i.e. dry-soil fossorial, moist-soil fossorial and epigeal grass-swimmers) in the region of positive values for PC1 and negative values for PC2 (Figure 1). The PC1 scores for most dry-soil fossorial species ranged between −40 and 22 (Table S1; Figure 1), In this group, while species like *Calyptommatus nicterus* (Lacertoidea: Gymnophthalmidae; PC1 score = 3.34) and *Lerista muelleri* (Scincoidea: Scincidae; PC1 score = 3.42) fall in a central position of the variation axis, *Bipes biporus* (Lacertoidea: Amphisbaenia) and *Aprasia repens* (Gekkota), represent more extreme phenotypes, with PC1 scores of −38.39 and −22.03, respectively. These two species deserve attention: *Bipes* is the only amphisbaenian with short forelimbs (all other living amphisbaenians are limbless), while *A. repens* represents the only transition
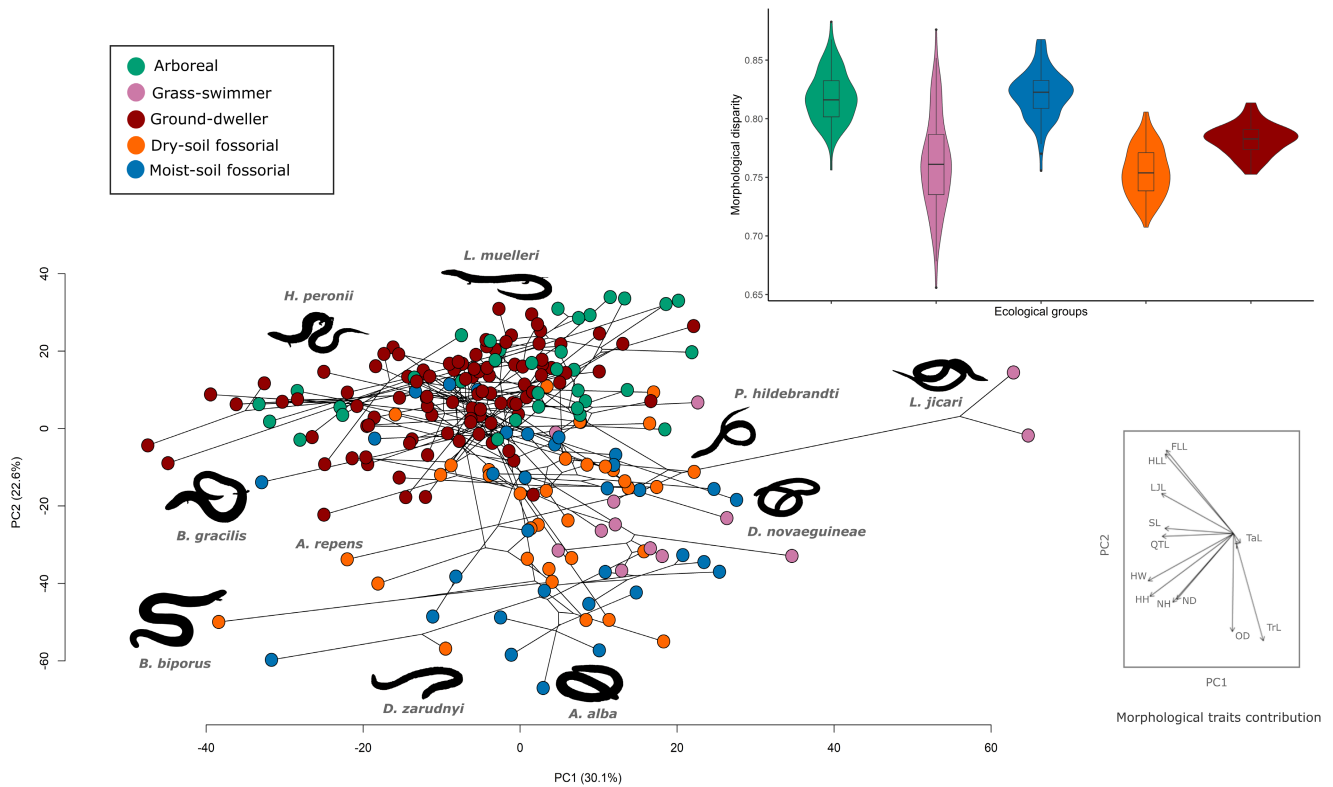
FIGURE 1 Phylomorphospace illustrating the morphological diversity of ecomorphological groups: the patterns of morphological diversity within the category of 'fossorial lizards' reflect two distinct substrate-dependent regimes of selection. Dry-soil fossorial and moist-soil fossorial lineages tend to occupy a different region in morphospace than the ground-dwellers and arboreal lizards, especially along the PC2 axis. Snakelike lizards (dry-soil fossorial, moist-soil fossorial and epigeal grass-swimmers) tend to have positive PC1 scores and negative PC2 scores. The variation axes correspond to loadings and indicate morphological traits that contribute more in each PC. Violin plot shows differences in morphological disparity indices (functional divergence) between dry-soil and moist-soil fossorial lizards (orange and blue respectively). Moist-soil fossorial lineages encompass more morphological diversity than dry-soil fossorial ones. Silhouettes indicate some species located in extremes of the axes (clockwise): *Lerista muelleri* (dry-soil fossorial), *Lialis jicari* (grass-swimmer), *Paracontias hildebrandti* (dry-soil fossorial), *Dibamus novaeguineae* (moist-soil fossorial), *Amphisbaena alba* (moist-soil fossorial), *Diplometopon zarudnyi* (dry-soil fossorial), *Bipes biporus* (dry-soil fossorial), *Brachymeles gracilis* (moist-soil fossorial) and *Hemiergis peronii* (moist-soil fossorial). The silhouette for *B. biporus* was obtained from phylopic.org under a free Creative Commons licence.

to fossoriality in our dataset that evolved from a snakelike lineage previously epigeal (Gekkota: Pygopodidae) and exhibits a more robust head in comparison to most dry-soil fossorial species. An average moist-soil fossorial head shape is seen in the amphisbaenians *Amphisbaena alba* (PC1 score = 2.94) and *Monopeltis guentheri* (PC1 score = 3.09), while extreme head shapes are exemplified by *Brachymeles gracilis* (Scincidae) and *Trogonophis wiegmanni* (Lacertoidea: Amphisbaenia), two species associated with low PC1 scores (−32.95 and −31.66, respectively). Differences between moist-soil and dry-soil fossorial lineages were less clear along the PC2 axis, both regarding morphospace distribution (Figure 1) and the associated scores (Table S1). A considerable degree of overlap between all ecological groups is observed in morphospace. Along the PC2 axis of variation, the snakelike (fossorial and epigeal) and lacertiform groups diverge more conspicuously, as elongated forms with reduced limbs tend to show negative values. Interestingly, the relative proportion of head traits (i.e. PC1 axis of variation) exhibits a remarkable degree of overlap on a broad

taxonomic scale (Figure 1). Although grass-swimmers tend to overlap with other snakelike groups, *Lialis burtonis* (PC1 score = 64.72) and *Lialis jicari* (PC1 score = 62.85) occupy a distant region in the morphospace, representing extreme phenotypes regarding head shape and limb size, possibly due to their highly specialized skulls (Patchell & Shine, 1986; Wall et al., 2013).

3.2 | Contemporary morphological disparity

Morphological disparity was higher in the moist-soil fossorial group in comparison to dry-soil fossorial lizards when the metric 'functional divergence' is considered (Figure 1; Table 3). Among all pairwise comparisons for 'functional divergence', the Bhattacharyya coefficient of similarity was smallest when contrasting moist-soil and dry-soil fossorial lizards, suggesting a statistically significant difference between group disparities (Table S3). However, results of the 'sum of variances' metric indicate high similarity in the comparison between

dry-soil fossorial and moist-soil fossorial lizards. 'Functional divergence' and 'sum of variances' represent different aspects of morphological disparity: while the last represents the size of the distribution of the group in morphospace, the first accounts for the density of species that deviate more from a group centroid (Guillerme et al., 2020). Altogether, these results suggest that moist-soil and dry-soil fossorial groups occupy morphospace areas that are similar in size (as denoted by similar sum of variances), although the moist-soil fossorial group encompasses more species diverging from the group centroid than the sand-soil fossorial lizards, which denotes more species with extreme phenotypes (as indicated by significantly higher functional divergence metric in moist-soil fossorial). These results corroborate our prediction that the dry-soil fossorial group encompasses species that tend to be more similar among each other than the moist-soil fossorial category.

TABLE 2 Results of phylogenetic principal component analysis (PCA) shown for the first two principal components retained (PC1 and PC2).

	PC1	PC2
Morphological traits		
Head width	**−0.75**	−0.34
Head height	**−0.74**	−0.46
Nostril distance	**−0.50**	−0.48
Nostril height	**−0.54**	**−0.50**
Orbital distance	−0.01	**−0.71**
Snout length	**−0.61**	0.04
Lower-jaw length	**−0.64**	0.29
Quadrate-to-tip length	**−0.63**	−0.02
Trunk length	0.26	**−0.78**
Tail length	0.06	−0.07
Forelimb length	**−0.59**	**0.61**
Hindlimb length	**−0.60**	**0.58**
% variance	30.06	22.60
Eigenvalue	3.61	2.72

Note: Contributions for morphological traits for each PC are shown as loading values, and traits interpreted as contributing more to each PC are highlighted. Proportion of explained variation and eigenvalues are also shown for each PC. All traits are relative to 'head length'.

3.3 | Modelling of microhabitat transitions and ancestral character states reconstructions

Among the 213 species of lizards included in our ecomorphological database, we identified 80 as representatives of the snakelike morphotype (i.e. elongated limb-reduced forms): 66 of them were classified as fossorial and the remaining 14 corresponded to epigeal grass-swimmers (Table 3; Table S1). Evolutionary transitions to the snakelike morphotype involved single origins in the lineage of amphisbaenians (families Rhineuridae, Bipedidae, Blanidae, Cadeidae, Trogonophidae and Amphisbaenidae) and the families Pygopodidae, Anniellidae and Dibamidae, two independent origins in Gymnophthalmidae, and at least six origins in Scincidae (Figure 2). We modelled the evolution of microhabitat use along the phylogeny considering the symmetrical SYM model, which had a better fit than ARD (delta AIC = 5.11) and ER (delta AIC = 17.23) models. This result suggests that transitions within pairs of microhabitats had similar rates (Figure 2). The fastest transition rates were observed between dry-soil and moist-soil fossorial lineages (rate = 0.007). Transitions between ground-dweller and dry-soil fossorial were estimated to be two times faster than those to moist soils. These results suggest that less time was required for ground-dwellers to evolve into snakelike dry-soil specialists than into snakelike moist-soil burrowers. Interestingly, only a single event of a fossorial species evolving from an already snakelike ancestor (in a grass-swimmer lineage) is observed, in Australian pygopodids (*Aprasia repens*). Results from these analyses suggest that fossoriality evolved more often and faster from non-snakelike epigeal lineages than from snakelike epigeal ancestors.

3.4 | Phenotypic evolution modelling

Model comparisons were performed separately for PC1 and PC2. The first PC was mostly related to head shape and limb length, for which the adaptive model 'M5' was strongly supported (Table 4). According to this model, the evolution of head shape involved five distinct adaptive optima in lizards: arboreal, grass-swimmer, ground-dweller, dry-soil fossorial and moist-soil fossorial (Table 5). Concerning the parameters provided by best-fit models, species occupying a new niche would require 55.6 million of years to arrive halfway to their new

TABLE 3 Morphological disparity indices in ecological lizard groups.

Morphological disparity			
	N	Functional divergence	Sum of variances
Arboreal	35	0.82	10.04
Grass-swimmer	14	0.75	11.15
Ground-dweller	98	0.78	6.69
Dry-soil fossorial	34	0.74	10.12
Moist-soil fossorial	32	0.82	11.97

Note: Two metrics were considered for the disparity index: functional divergence and sum of variances; '*N*' corresponds to the number of observations (i.e. sampled species) in each group.
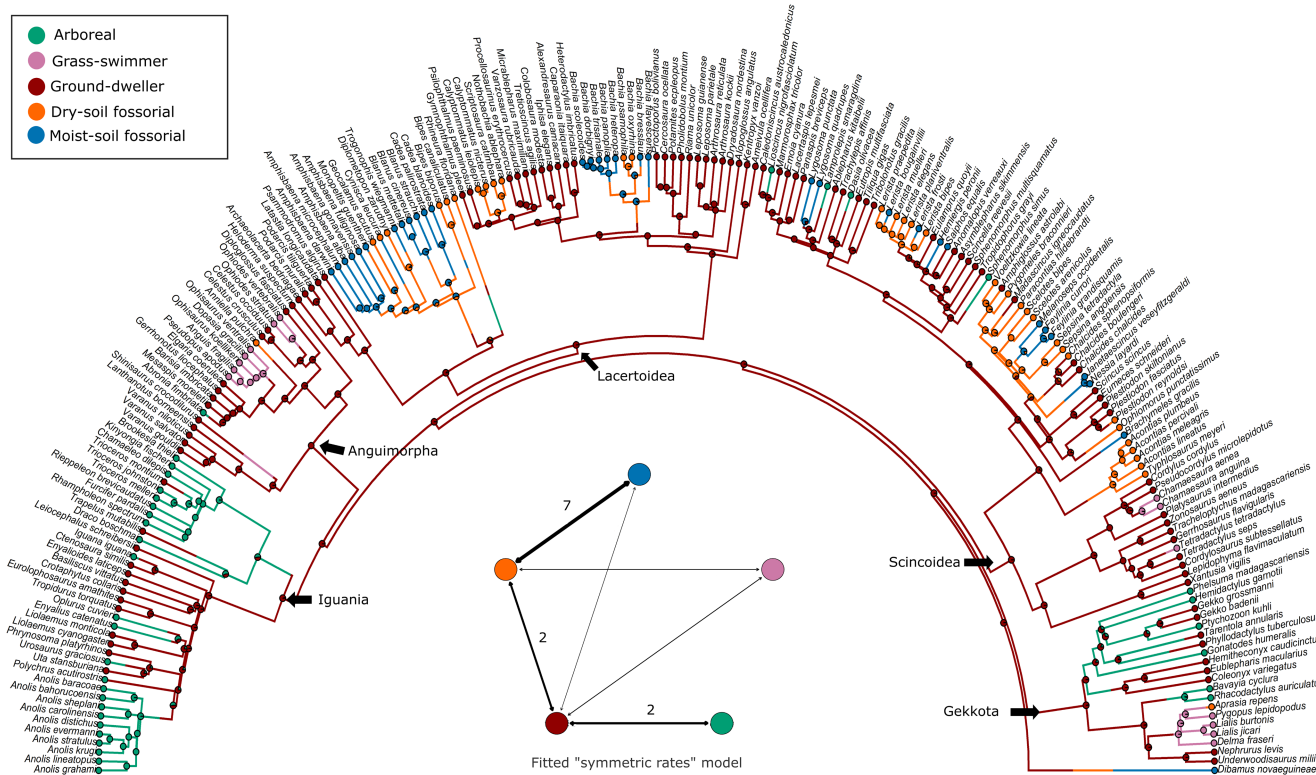
FIGURE 2 Multiple origins of snakelike phenotypes in lizard clades associated with fossoriality. Maximum likelihood reconstruction of ancestral character states regarding microhabitat use across the phylogeny of lizards, showing node character state probabilities using a fitted 'symmetric rates' model. Transition rates between ecological groups show higher rates between dry-soil and moist-soil fossorial lineages. Transition rates are depicted as coefficients of scientific notation (coefficient $\times 10^{-3}$); only rate values higher than 1×10^{-3} are indicated. Arrows along the phylogeny indicate nodes for major lizard clades.

TABLE 4 Comparisons of phenotypic evolution models for PC1 and PC2.

Model	PC1		PC2	
	ΔAICc	Weight	ΔAICc	Weight
M1	26.12	0.00	18.54	0.00
M2	26.53	0.00	17.86	0.00
M3	18.55	0.00	**0.00**	**0.70**
M4	28.71	0.00	19.84	0.00
M5	**0.00**	**0.99**	**1.71**	0.30
OU1	30.60	0.00	78.09	0.00
Clade	46.40	0.00	83.19	0.00
BM	48.93	0.00	73.81	0.00

Note: The ΔAICc (i.e. difference between model AICc and the lowest AICc in the comparisons set) and Akaike weight are provided, and values associated with the best-fit model for each principal component are highlighted.

adaptive optimum—a remarkable time when estimated age of most extant snakelike lineages is considered (Figure 3). Optimal trait values (θ) suggest that dry-soil fossorial species evolved towards adaptive optima represented by higher PC1 values than the moist-soil fossorial ones. Accordingly, dry-soil fossorial lizards usually exhibit less robust heads characterized by relatively smaller head width, head height,

snout length, quadrate-to-tip length and lower jaw length than species classified as moist-soil fossorial. Nostril height is also smaller in dry-soil fossorial lizards, reflecting a more angulated rostral region. The limbs also tend to be shorter in relation to total body size in dry-soil fossorial lizards. Interestingly, snakelike epigeal grass-swimmers evolved towards the highest optimal trait values for PC1, a result suggesting smaller values of head traits when compared to snakelike fossorial groups. In summary, these results corroborate the prediction that head shape and limb size evolved in association with burrowing substrate in fossorial lizards, given the best-fit of a model assuming distinct adaptive optima for moist-soil and dry-soil fossorial lineages ('M5') for a PC strongly associated with head traits and limb lengths (PC1, see Tables 4 and 5).

The traits orbital distance and trunk length were mostly associated with PC2, for which the model 'M3' had a slightly better fit than 'M5' in AICc, but twice the value of Akaike weight (Table 4). Model 'M3' assumes one single adaptive optimum for all fossorial species, but retains two optima for terrestrial species (i.e. ground-dwellers and grass-swimmers). Both fossorial and grass-swimmers exhibit high negative optima compared to lacertiform arboreal and ground-dwellers (Table 5), reflecting a distinction between snakelike and lizard-like species. Accordingly, morphological evolution of robust frontal skulls and elongated trunks might reflect selective demands shared by all fossorial species, regardless of the burrowing substrate. However, the

	$t_{1/2}$	σ^2	Selective regimes	Adaptive optima
PC1—M5	55.6	1117.58	Arboreal	2.11
			Grass-swimmer	57.92
			Ground-dweller	−8.66
			Dry-soil fossorial	12.85
			Moist-soil fossorial	7.18
PC2—M3	78.01	632.96	Arboreal	15.80
			Fossorial	−50.33
			Grass-swimmer	−48.41
			Ground-dweller	9.23

TABLE 5 Parameters of best-fit models selected for PC1 (head shape and limbs length) and PC2 (orbital distance, trunk and limb lengths).

Note: The $t_{1/2}$ value refers to the phylogenetic half-life of the trait (in millions of years) and the σ^2 value refers to the strength of drift.

difference between AICc values smaller than 2.0 provides poor statistical support to differentiate model M3 as a best fit over model M5.

3.5 | Disparity through time

The profile of morphological disparity through time suggested a considerable contribution of snakelike lineages to overall disparity (Figure 3). Throughout most of the evolutionary time (approximately 200 million of years), profiles of observed disparity were generally under the disparity values expected by Brownian motion (Figure 3). Although overall the observed and the expected disparity did not seem to differ through time under Brownian motion (*p*-value=0.93; MDI value=0.10), two peaks of disparity higher than expected under Brownian motion deserve attention: one between 190 and 175 million of years before present and another starting approximately 20 million of years ago until present (Figure 3). The first peak matches the estimated origin of almost all major lizard clades except Gekkota. The second peak, however, is associated with the independent evolution of several snakelike lineages, including fossorial lineages in Scincidae, epigeal and fossorial snakelike anguimorphs, and also sand-swimming and leaf-litter dweller gymnophthalmids. This observation suggests that the repeated evolution of snakelike lineages associated with fossorial microhabitats drove a higher-than-expected disparity within subclades starting approximately 25 million of years ago, which results in more overlap in the morphospace by species occupying similar habitats. Furthermore, grass-swimmers have more recent origins in comparison with fossorial lineages such as amphisbaenians and skinks. Overall, these results corroborate that the repeated evolution of snakelike bodies associated with distinct microhabitats contributed for increasing morphological disparity within lizard subclades in recent time.

4 | DISCUSSION

Snakelike morphotypes independently evolved more than 20 times in fossorial squamate lineages, and encompass phenotypic similarities mostly described in terms of body elongation and limb reduction (see Bergmann & Morinaga, 2019; Camaiti et al., 2021; Wiens et al., 2006). In this study, we suggest that fossoriality comprises at least two different selection regimes related to the type of burrowing substrate, which involved differences not only in limb size but also in head shape among ecological groups. Therefore, we refine the ecological classification of fossorial lizards and expand a discussion previously concentrated on postcranial traits, highlighting the functional relevance of the head as a complex anatomical structure directly involved in burrowing (e.g. Barros et al., 2011, 2021; Bergmann & Berry, 2021; Herrel et al., 2011; Herrel & Measey, 2010; Le Guilloux et al., 2020; Navas et al., 2004; Sherratt et al., 2014; Stepanova & Bauer, 2021; Watanabe et al., 2019). We provide evidence for distinct ecomorphological groups within the broad 'fossorial' category which differ in the patterns of morphological variation and adaptive trajectories. Such morphological differences, especially in head shape, likely enhance burrowing performance in specific soil types: while many dry-soil fossorial lizards have angulated sharp heads, wedge-shaped snouts and counter-sunk lower jaws (see also Barros et al., 2021; Edwards et al., 2016; Stepanova & Bauer, 2021), compact cylindrical heads may benefit headfirst burrowing in moister substrates, such as humus and leaf-litter (see Bergmann & Berry, 2021). In fact, soil characteristics, including moisture, granulation and compaction, seem to affect burrowing behaviour in different tetrapod lineages: while some species move through the substrate by displacing granular media, others compact and perforate through the soil (Bergmann & Berry, 2021; Herrel & Measey, 2010; Sharpe et al., 2015). Some associations between morphology and locomotor performance may be detectable only in specific substrates (Barros et al., 2021), which stresses the importance of large-scale comparative studies assuming refined ecological classifications. Moist soils are more resistant to perforation and locomotion by head-first burrowing in comparison to dry soils (Sharpe et al., 2015). While locomotion strategies and burrowing kinematics might change depending on burrowing substrate (Sharpe et al., 2013, 2015), particular head shapes may facilitate perforation of specific granular media (Bergmann & Berry, 2021). Although associations between head shape and burrowing substrate have been suggested for specific
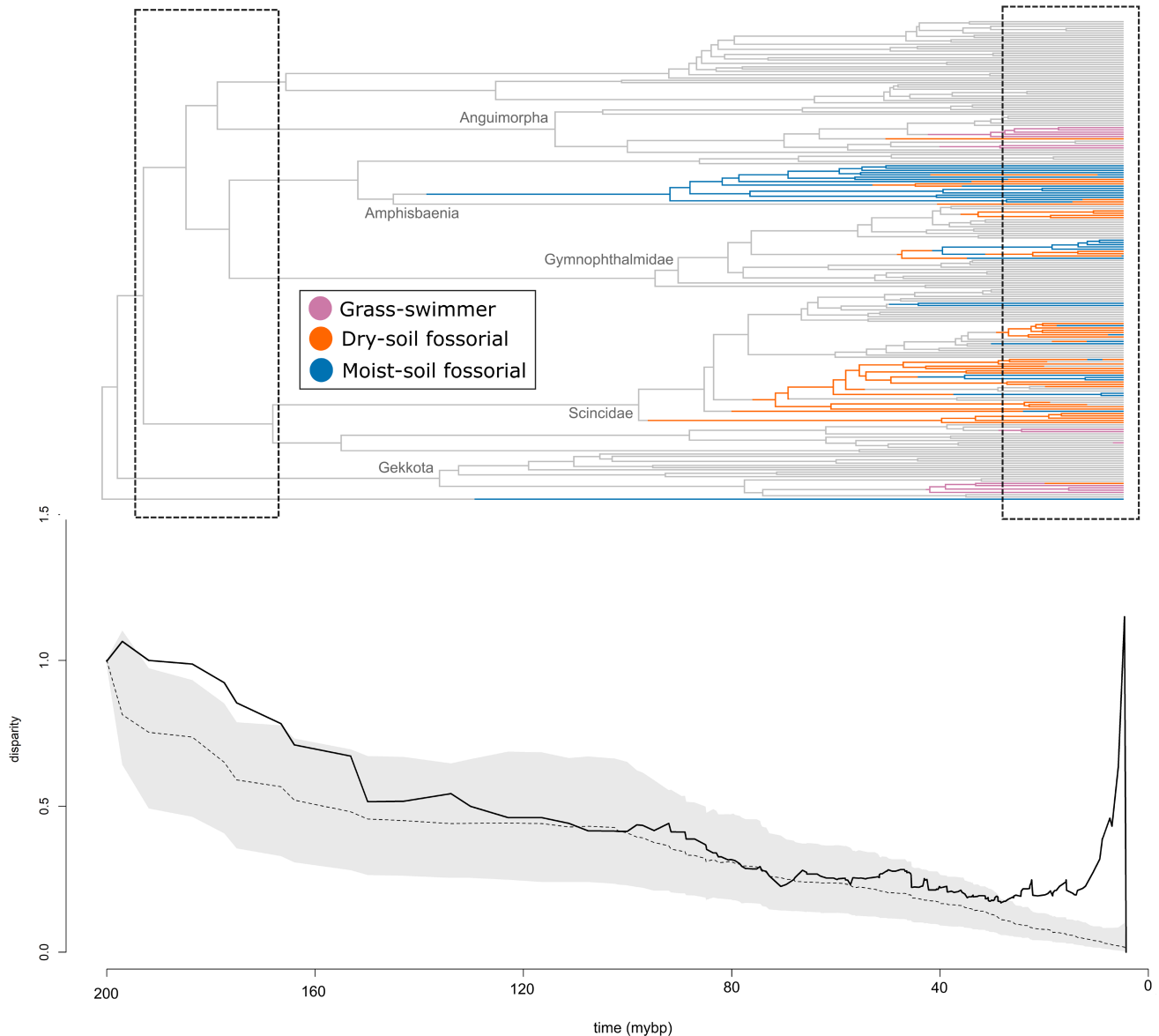
FIGURE 3 Profile of morphological disparity through time (bottom graph) considering all lizards sampled in our study. The solid black line represents the observed disparity, and the dashed grey line corresponds to the expected disparity median under Brownian motion. The grey shade indicates the 95% confidence interval of 1000 simulations under the Brownian motion null-hypothesis. On top, we present a stochastic map for the phylogeny of all species included in our study, to indicate lineages and time (millions of years before present) corresponding to the two peaks of higher-than-expected disparity within subclades. Phylogeny branches are coloured according to ecology, indicating estimated transitions from epigeal (grey) to grass-swimmer (pink), dry-soil fossorial (orange) or moist-soil fossorial (blue).

lizard lineages (amphisbaenians: Gans, 1978; Hohl et al., 2017, 2018; Kazi & Hipsley, 2018; Kearney, 2003; gymnophthalmids: Barros et al., 2011, 2021; and skinks: Le Guilloux et al., 2020; Vanhooydonck et al., 2011), this is the first time that different patterns of head shape evolution are discriminated among fossorial lineages considering all major lizard clades.

We recovered associations between fossoriality and post-cranial traits (trunk and tail lengths and limb proportions) concerning the independent origins of snakelike phenotypes already described for Squamata (e.g. Bergmann et al., 2020; Bergmann & Morinaga, 2019; Brandley et al., 2008; Camaiti et al., 2021; Kohlsdorf, 2021; Kohlsdorf & Wagner, 2006; Morinaga & Bergmann, 2020; Wagner et al., 2018;

Wiens et al., 2006), so we could retrieve recent literature to interpret the patterns of limb reduction (e.g. Bergmann & Morinaga, 2019) and body elongation (e.g. Brandley et al., 2008; Grizante et al., 2012; Morinaga & Bergmann, 2019, 2020) identified from our dataset. Our study, however, reorients the focus of this topic from body elongation and limb reduction towards including a more prominent role of head shape patterns associated with the evolution of fossoriality in different burrowing substrates. The head is a complex structure composed of several elements involved in distinct functions, including locomotion, sexual display, prey capture and food processing, defensive behaviours and communication (Barros et al., 2011; Bergmann & Berry, 2021; De Schepper et al., 2005;

Herrel et al., 2001; Kohlsdorf et al., 2008; Le Guilloux et al., 2020; Sherratt et al., 2014; Vanhooydonck et al., 2011). In our study, this is observed when distinct head traits are considered separately. We identified that, despite a general association between head shape and burrowing substrate, specific head traits, such as orbital distance, might have evolved towards a single adaptive optimum shared by all fossorial lizards regardless of their burrowing substrate. Fossorial lizards often exhibit robust skulls and reduced eyes, two patterns interpreted as adaptive because bone fusion may protect the brain and major sensory organs in headfirst burrowers (Gans, 1975; Lee, 1998; Rieppel, 1984; Roscito & Rodrigues, 2010; Stepanova & Bauer, 2021) and the lower dependence of visual stimuli in subterraneous environments acquiesces eye reduction in these animals (Yovanovich et al., 2019). When trunk length is also considered, we retrieve a clear distinction between snakelike lizards associated with different habitats: fossorial (less elongated animals with more robust frontal skull) and epigeal (more elongated grass-swimmers; see Wiens et al., 2006). Grass-swimmers actually represent a remarkable aspect of the repeated evolution of snakelike bodies among lizards: they are more elongated than fossorial lizards and exhibit head traits considerably smaller in relation to body size, comprising species characterized by striking modifications in head shape such as the pygopodid *Lialis* (Wall et al., 2013), which in our study occupies particular regions of the morphospace.

Evolution of fossoriality in Squamata is frequently discussed regarding morphological specialization (e.g. Brandley et al., 2008; Gans, 1975; Lee, 1998; Rieppel, 1984; Wiens et al., 2006) and reduced diversification rates in specific lineages (Bars-Closel et al., 2017). The refined classification for fossorial species used here enabled identification of differences between moist-soil and dry-soil fossorial lizards in the morphospace distribution. Specific properties of sand and arenaceous soils may represent selective regimes for phenotypic evolution (see Barros et al., 2021; Robinson & Barrows, 2013; Stepanova & Bauer, 2021) and require specific adaptations to headfirst burrowing (Edwards et al., 2016). This eventually restrictive selective regime might result in greater morphological specialization when compared to the condition of fossoriality associated with moist soils, which could explain why distribution of the dry-soil fossorial category is more restricted than that of moist-soil fossorial lizards in the morphospace. The 'moist-soil fossorial lizards' may represent a more generalist group and encompass considerable ecological variation, as moist-soil fossorial lizards can be found foraging through the leaf-litter (e.g. *Nessia layardi*), under rocks and logs (e.g. *Dibamus novaguineae*), or through compact humus (e.g. *Hemiergis peronii*). Thus, we admit that this category may comprise more than one selective regime, an explanation that can be tested by future studies that refine even substrate types within the moist-soil fossorial group of lizards, relying on additional ecological information becoming available for specific lineages in the next years. Alternatively, it is possible that moist-soil fossorial lizards represent a conspicuous ecological group, but that moist burrowing substrates are less constraining than dry microhabitats. Finally, multiple phenotypic patterns might

be functionally equivalent, in a 'many-to-one' mapping of form to function (see Losos, 2011; Wainwright et al., 2005), so that moist-soil fossorial lineages evolved several functionally equivalent forms because foraging in these substrates allows higher morphological variation.

Patterns of morphological change through time also seem to reflect differences in tempo and mode of evolution among snake-like lizards (Edwards et al., 2015; Harmon et al., 2003; Machado et al., 2018; Reaney et al., 2018; Slater et al., 2010). Observed disparity through time suggests that evolution of snakelike lineages contributed to more recent increments of morphological disparity within lizard subclades. Occupation of dry and moist soils by fossorial lineages, as well as the evolution of grass-swimmers, seems to drive more disparity within subclades than expected—an outcome of similar phenotypes evolving independently in distant lineages. Nevertheless, a combination of shared ancestry and functional demands associated with burrowing in different microhabitats (e.g. dry soil or moist soil) seem to influence general patterns observed in the occupation of morphospace and the partitioning of phenotypic disparity among extant lizards.

Here we demonstrate that fossoriality encompasses at least two different selective regimes related to the type of burrowing substrate, a hypothesis corroborated by the identification of two ecomorphological groups related to head shape and limb size, one associated with moist-soils and the other with dry environments. These two ecomorphological groups differ in several traits related to head shape, which can be interpreted according to functional demands imposed by each burrowing substrate. Our results reorient the focus of the discussion regarding the multiple origins of snakelike phenotypes in Squamata from body elongation and limb reduction towards a preeminent role of the evolution of specific head shape patterns associated with being fossorial in different soil types. By integrating patterns of morphological diversity with phenotypic evolution modelling, we provide compelling evidence suggesting that 'fossoriality'—often evoked as a selective regime driving phenotypic evolution towards a broad single optimum (i.e. snakelike forms; Gans, 1975; Lee, 1998; Wiens et al., 2006)—encompasses at least two distinct ecomorphological groups that reflect distinct trajectories concerning head shape. Nonetheless, the repeated occupation of distinct burrowing substrates by several lineages contributed to more recent increments of morphological disparity within lizards. Fossorial lizards are often claimed as a striking example of convergent evolution leading to multiple origins of snakelike forms, but this group in fact reflects a complex interplay of manifold associations between distinct environmental settings, integrated multi-trait phenotypes and a degree of phylogenetic legacy.

AUTHOR CONTRIBUTIONS

VA, TK and AH conceived the study. VA, TK, MB-C and AH delimited the experimental design. VA collected the data and performed the analyses. VA and TK wrote the manuscript, which was revised by MB-C and AH.

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CONFLICT OF INTEREST STATEMENT

The authors have no competing interests.

DATA AVAILABILITY STATEMENT

Data are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.x95x69psc (Anelli et al., 2024).

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SUPPORTING INFORMATION

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

Table S1: Species included in the analyses (in alphabetical order), family, sample size (*n*), mean morphological measurements, PC1 and PC2 scores, clade, ecological category within models, herpetological collection accessed and consulted sources for ecological classification.

Table S2: Detailed phylogenetic principal component analysis results.

Table S3: Detailed contemporary morphological disparity results.