Zoological Journal of the Linnean Society, 2024, **201**, zlae089
https://doi.org/10.1093/zoolinnean/zlae089
Advance access publication 25 July 2024
Original Article

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Evolution of fossoriality in microteiid lizards

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ABSTRACT

Morphology is among the most important traits influencing the interaction of individual animals with their environments. Fossoriality reflects this functional association between morphology and the use of subterranean habitats and their associated environmental characteristics. Lizards in the families Gymnophthalmidae and Alopoglossidae are model organisms to examine the interplay between morphology and fossoriality because great morphological diversity exists among species, including varying degrees of body elongation and limb reduction, and they have a wide geographical distribution in the Neotropical region. We analysed the morphology of 101 microteiid species and created an index to evaluate their degree of fossoriality. From this index, we traced the evolution of fossoriality in these lizards and assessed its primary environmental correlates. We found that fossoriality evolved independently in several lineages, mainly associated with high temperature and low precipitation, characteristic of more arid and sandy environments.

Keywords: adaptation; ecology; Gymnophthalmidae; morphology; Neotropical lizards

INTRODUCTION

Morphology impacts nearly all aspects of the biology of organisms, including physiological performance, behaviour, and ecology. For example, the evolution of lighter skulls in squamates appears linked to functional changes (Herrel *et al.* 2007). Morphology is so often associated with microhabitat use that 'ecomorphs' can often be identified (e.g. Losos *et al.* 1998). Ecomorphs are 'species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phyletically' (Williams 1972). Studies that combine the evolution of ecology and morphology have contributed significantly to understanding adaptation and diversification processes (e.g. Schulte *et al.* 2004). For instance, knowing the ecological attributes of an organism makes it possible to investigate why a particular morphological characteristic developed in an environmental context and whether morphological traits conferred a competitive advantage when similar species occur in the same habitat. Thus, an association between morphology and ecology is expected, ensuring the optimal performance in each microhabitat (Garland Jr and Losos 1994, Irschick and Losos 1999).

The association between morphology and ecology has been observed in many squamate reptiles (Warheit *et al.* 1999). For example, lizards living in open areas tend to have relatively long hindlimbs (Garland Jr and Losos 1994), whereas aquatic species tend to have a laterally compressed tail, a dual caudal crest, and a hydrodynamic body (Marques-Souza *et al.* 2018). Lizard head shape can also be associated with the environment (Barros *et al.* 2011) and the evolution of cranial morphology appears to be linked with the consumption of larger prey (Amorim *et al.* 2017). These associations presumably ensure the best performance in each niche (Irschick and Losos 1999, Irschick and Garland 2001). The relationship between morphology and habitat in squamate reptiles influences locomotor capacity, which is essential for foraging, defending territory, or escaping predators (Losos 1990, Garland Jr and Losos 1994, Herrel *et al.* 2000, Kohlsdorf *et al.* 2004).

Body elongation and limb reduction appear to be responses to fossorial habits and underground life (Garland Jr and Losos 1994, Wiens and Slingluff 2001, Barros *et al.* 2011). Fossoriality can be defined as the ability to move and perform most daily activities underground. In squamates, fossoriality and its associated morphological adaptations evolved independently in different lineages on many continents (Wiens *et al.* 2006). These similar phenotypic patterns in phylogenetically distant lineages reflect convergent evolution resulting from equivalent selective pressures (Losos 2011, Powell 2012). Specific morphological

Received 1 December 2023; revised 13 May 2024; accepted 1 July 2024

structures associated with locomotion are correlated with physical and structural features of habitats that organisms use (Arnold 1983), including fossoriality.

Although fossoriality and its morphological adaptations have been widely discussed, controversy exists about selective pressures and ecological implications of the associated morphological evolution (Wiens and Slingluff 2001, Wiens *et al.* 2006, Grizante *et al.* 2012). Some authors hypothesize that fossoriality may be favoured in open and sandy environments (Rodrigues 1996), a result of biogeographic isolation (Wiens *et al.* 2006, Lee *et al.* 2013), escape from the competition with epigean species (Wiens *et al.* 2006), or preference for thermally milder environments found underground (Camacho *et al.* 2014).

Microteiid lizards are small, ranging from 40 to 150 mm in snout–vent length, comprising two of the three families in the superfamily Gymnophthalmoidea Fitzinger, 1826—Gymnophthalmidae and Alopoglossidae. These lizards—the microteiids—exhibit great morphological diversity, with several degrees of limb reduction and body elongation. They have a wide geographical distribution, occurring from southern Mexico to southern South America, as well as on some continental islands (Presch 1980). In addition, they exhibit high ecological diversity, occupying a diversity of niches. Some are high-elevation species (e.g. *Proctoporus* spp.), others terrestrial (e.g. *Vanzosaura* spp.), semi-aquatic (e.g. *Potamites* spp.), semi-arboreal (e.g. *Placosoma* spp.), or fossorial (e.g. *Bachia* spp.) (Presch 1980, Pianka and Vitt 2003, Siedchlag *et al.* 2010, Souza *et al.* 2015), making them excellent models for studies that correlate morphological and ecological traits. One of the most spectacular examples is the diversity of fossorial species distributed in the Vale do Rio São Francisco dunes in north-eastern Brazil, which suggests speciation due to changes in the course of the river over the years (Rodrigues 1996).

Identifying environmental variables that drive the evolution of species is essential to understanding the origins and diversification of life on the planet (Roxo *et al.* 2017). Therefore, our objective was to identify environmental pressures involved in the evolution of fossoriality in these lizards. First, we analysed morphometric variables associated with fossoriality and produced a fossoriality index ranking the species' degree of fossoriality. Next, we investigated the evolutionary patterns of fossoriality based on reconstructions of ancestral characters. Finally, we evaluated the selective and environmental pressures involved in the evolution of fossoriality, testing the hypothesis discussed by Rodrigues (1996), that fossoriality in these lizards was favoured by dry and sandy environments from open vegetation.

MATERIALS AND METHODS

Data collection

We compiled morphometric data on 3130 individual lizards, including 94 species of the family Gymnophthalmidae and seven species of the family Alopoglossidae. We obtained data from fieldwork conducted by the authors over the last decades and specimens housed in the Museu de Zoologia da Universidade de São Paulo (MZUSP). In the latter case, we assigned the maximum value of 30 adult individuals of each species to obtain morphometric data.

For each lizard, we recorded the following morphometric variables: snout–vent length (from the tip of the snout to the opening of the cloaca), body width (from the middle of body), forelimb and hindlimb lengths (from the longest finger to the root of forelimb/thigh).

We calculated weighted averages for each variable for species represented by more than one population, using the sample size from populations as weights. We created an index to rank the degree of fossoriality of the species in a sample. Although there is no numerical value to assess the fossoriality of the species, there is a consensus that fossoriality results in body elongation followed by limb reduction (e.g. Gans 1975, Wiens *et al.* 2006, Barros *et al.* 2011, Grizante *et al.* 2012, Camacho *et al.* 2014). Thus, we propose a fossoriality index (f) considering these features.

First, we estimated body elongation (e) and limb reduction (r) using the following formula:

$$e = \frac{SVL}{BW}; r = \frac{SVL}{(FLL + HLL + 1)}$$

where SVL is snout–vent length, BW is the body width, and FLL and HLL are forelimb and hindlimb lengths, respectively. We added +1 to the sum of the limbs' length to avoid dividing by zero in limbless species.

Subsequently, the values obtained from e and r were adjusted and standardized to values between 0 and 1 to ensure the same weight for each variable, using the following equation:

$$x_{adj.} = \frac{x - x_{min.}}{x_{max.} - x_{min.}}$$

where x corresponds to the variable's value (e or r) to be adjusted. It is important to emphasize that high values of 'e' correspond to a greater elongation of the body and high values of 'r' correspond to a greater reduction of the limbs, i.e. species with smaller or absent limbs.

Finally, we obtained the fossoriality index (f) as the average between adjusted values of body elongation (e) and limb reduction (r). Thus, higher values are associated with the most elongated lizards with smaller limbs (the most fossorial). The lowest values correspond to less elongated lizards with larger limbs (less fossorial). We validated our fossoriality index by comparing our results with data described (fossorial or non-fossorial) for these species in the literature.

We also obtained climate, land cover, and soil property data for localities of each sampled lizard population. Climate variables included (i) annual mean temperature, (ii) temperature seasonality, (iii) annual precipitation, (iv) precipitation seasonality, and (v) aridity index. We retrieved the first four climate variables from the WorldClim project database (Hijmans *et al.* 2005) with a spatial resolution of 2.5 min. We estimated the aridity index using the following formula (Tieleman *et al.* 2003):

$$Q = \frac{P}{(Tmax + Tmin) \times (Tmax - Tmin)} \times 1000,$$

where P is annual precipitation, $Tmax$ is the highest monthly mean temperature, and $Tmin$ is the lowest monthly mean temperature. For interpretation, lower Q values correspond to more arid environments.

We obtained land cover data from the Global Land Cover Share database (GLS-SHARE) (Latham *et al.* 2014). GLS-SHARE is a land cover database composed of 11 layers, which represent the percentage of soil density coverage, defined as (i) artificial surface; (ii) cropland; (iii) grassland; (iv) tree-covered area; (v) shrub-covered area; (vi) herbaceous vegetation; (vii) mangroves; (viii) sparse vegetation; (ix) bare soil; (x) snow and glaciers and (xi) waterbodies.

We obtained soil property variables from SoilGrids 2.0 database (available at https://soilgrids.org/): (i) sand content, (ii) clay content, and (iii) silt content, both in soil extract 0–5 cm, 5–15 cm, and 15–30 cm.

Phylogeny

We used the time-calibrated tree proposed by Tonini *et al.* (2016) and pruned the phylogeny to include only those taxa represented in our dataset. From the tree, we deleted all unsampled and randomly assigned species by authors and all polytomic taxa. Then, we used the Taxonomic Addition for Complete Trees (TACT) (Chang *et al.* 2020). TACT uses taxonomic information from clades combined with a time-calibrated phylogeny to position unsampled lineages in a compatible way using a birth–death estimator (Chang *et al.* 2020).

In Tonini *et al.* (2016), the family Gymnophthalmidae is paraphyletic due to the position of *Riolama*, and the family Alopoglossidae is within Gymnophthalmidae as a subfamily. As the focus of our study is not phylogenetic and since we analysed both families here, we chose to use this tree, due to (i) its better species sampling, (ii) that these two families are closed related, and (iii) that we do not use *Riolama* data in our analysis.

Evolution of fossoriality and its relationship with the environment

To analyse the evolution of habitat use and fossoriality in these lizards, we used our fossoriality index and the crucial variables indicated in MuMIn results (described below), considering a given trait evolution model. We performed a stochastic mapping for continuous characters to estimate ancestral states on multiple tree nodes. We used the *ContMap* function from PHYTOOLS R's package (Revell 2012) for ancestral state reconstruction.

In high dimensionality datasets, especially for environmental data, it is important to select the most relevant characteristics to avoid overfitting and to improve the model's interpretability and robustness. Therefore, to identify the critical environmental variables for fossoriality, we used an algorithm implemented in the function *Boruta* from BORUTA R's package (Kursa and Rudnicki 2010). This algorithm compares the importance of variables with shadow attributes. Shadow attributes are fictitious variables created by the BORUTA algorithm to represent noise in the data, generated through random permutations of the original variables. Variables with larger values than their corresponding shadow attributes are considered significant and maintained in the set of selected variables, while those variables with smaller values than shadow attributes are deemed irrelevant or redundant to the model and discarded (Kursa and Rudnicki 2010). Then, based on the importance values of each variable, we eliminated the collinear variables using the function *vifstep* from USDM R's package (Naimi *et al.* 2014). We performed phylogenetic regression models with the remaining variables using phylogenetic generalized least squares' models (PGLS) with CAPER R's package (Grafen and Hamilton 1989). Finally, we performed model selection using the function *pdredge* from MuMIn R's package (Bartoń 2023) to select the significantly important environmental variables for fossoriality.

RESULTS

Our fossoriality index ranked *Bachia*, *Scriptosaura*, *Calyptommatus*, and *Notobachia* with the highest values, indicating a higher degree of fossoriality. Three species of *Bachia* [*B. micromela* ($f = 0.96$), *B. scaea* ($f = 0.93$), and *B. dorbignyi* ($f = 0.89$)] had the highest scores, indicating a greater degree of fossoriality (Fig. 1). The least fossorial species were *Arthrosaura kockii* ($f = 0.01$), *Alopoglossus angulatus* ($f = 0.01$), and *Cercosaura schreibersii* ($f = 0.03$) (Fig. 1; Supporting Information, Table S1).

Our results indicate that fossoriality evolved at least twice: once in Bachiinae, an exclusively fossorial subfamily, and once within Gymnophthalminae [in the ancestor of *Notobachia*, *Calyptommatus*, and *Scriptosaura* (Fig. 2)], both within Gymnophthalmidae.

Rhachisaurus brachylepis, the only species of the subfamily Rhachisaurinae, retained values of fossoriality constant throughout the tree, assimilating to ancestral values (Fig. 2). The most recent common ancestor of Gymnophthalmidae had a higher degree of fossoriality than most living species, being similar to the current *Rhachisaurus*. The evolution of fossoriality continued in Gymnophthalmidae within Bachiinae and Gymnophthalminae, regressing in other subfamilies, and also regressed in Alopoglossidae (Fig. 2). A tendency toward fossoriality is occurring in other gymnophthalmids genera, like *Anotosaura* and *Heterodactylus* and in *Gymnophthalmus speciosus*, when compared with their close ancestors (Fig. 2).

Our Boruta analysis selected 15 environmental variables as the most important predictors of fossoriality: all climatic variables, nine soil properties, and shrub-covered area (Fig. 3). Of these, eight variables had collinearity issues and were removed from subsequent analyses. After exclusion of collinear variables, mean temperature and temperature seasonality, annual precipitation and precipitation seasonality, shrub-covered areas, clay content (between 15 and 30 cm), and silt content (between 0 and 5 cm) were the most relevant variables for fossorial habits among species (Fig. 4). Based on the phylogenetic regression and model selection results, annual precipitation was the environmental variable significantly related to fossoriality (Table 1).

DISCUSSION

Our index proved effective in ranking the degree of fossoriality when we compared our results with ecological data available in the literature. Fossorial species such as *Bachia* spp. and *Calyptommatus* spp. had the highest values of fossoriality. Also, non-fossorial species like *Alopoglossus* spp., or aquatic species such as *Potamites* spp., had very low values.

Although our index is based only on body elongation and limb reduction, other morphological traits such as head size

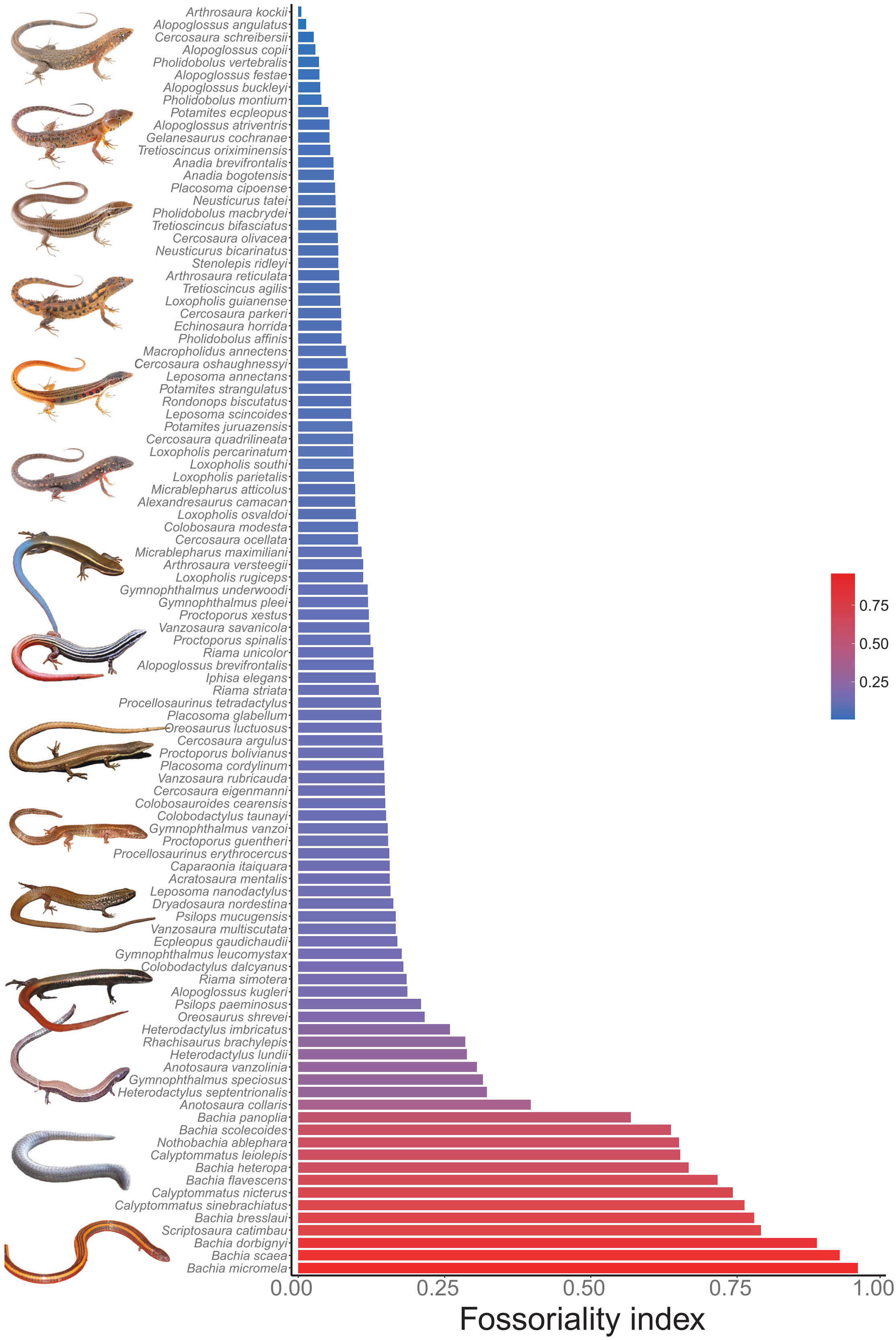

Figure 1. Fossoriality index obtained from lizard species sampled in this study. Photo credits (from least to the most fossorial): *Alopoglossus copii* (Alejandro Arteaga); *Gelanesaurus cochranae, Pholidobolus macbrydei, Echinosaura horrida* (Jose Vieira); *Cercosaura oshaughnessyi* (Alejandro Arteaga); *Leposoma parietalis* (Jose Vieira); *Micrablepharus maximiliani* (Willianilson Pessoa); *Vanzosaura savanicola* (Laurie Vitt); *Placosoma glabellum* (Willianilson Pessoa); *Colobosauroides cearensis* (Adrian Garda); *Acratosaura mentalis, Psilops paeminosus* (Willianilson Pessoa); *Anotosaura vanzolinia* (Bruno Halluan); *Calyptommatus sinebrachiatus* (Daniel Mesquita); *Bachia scaea* (Wirven Fonseca).

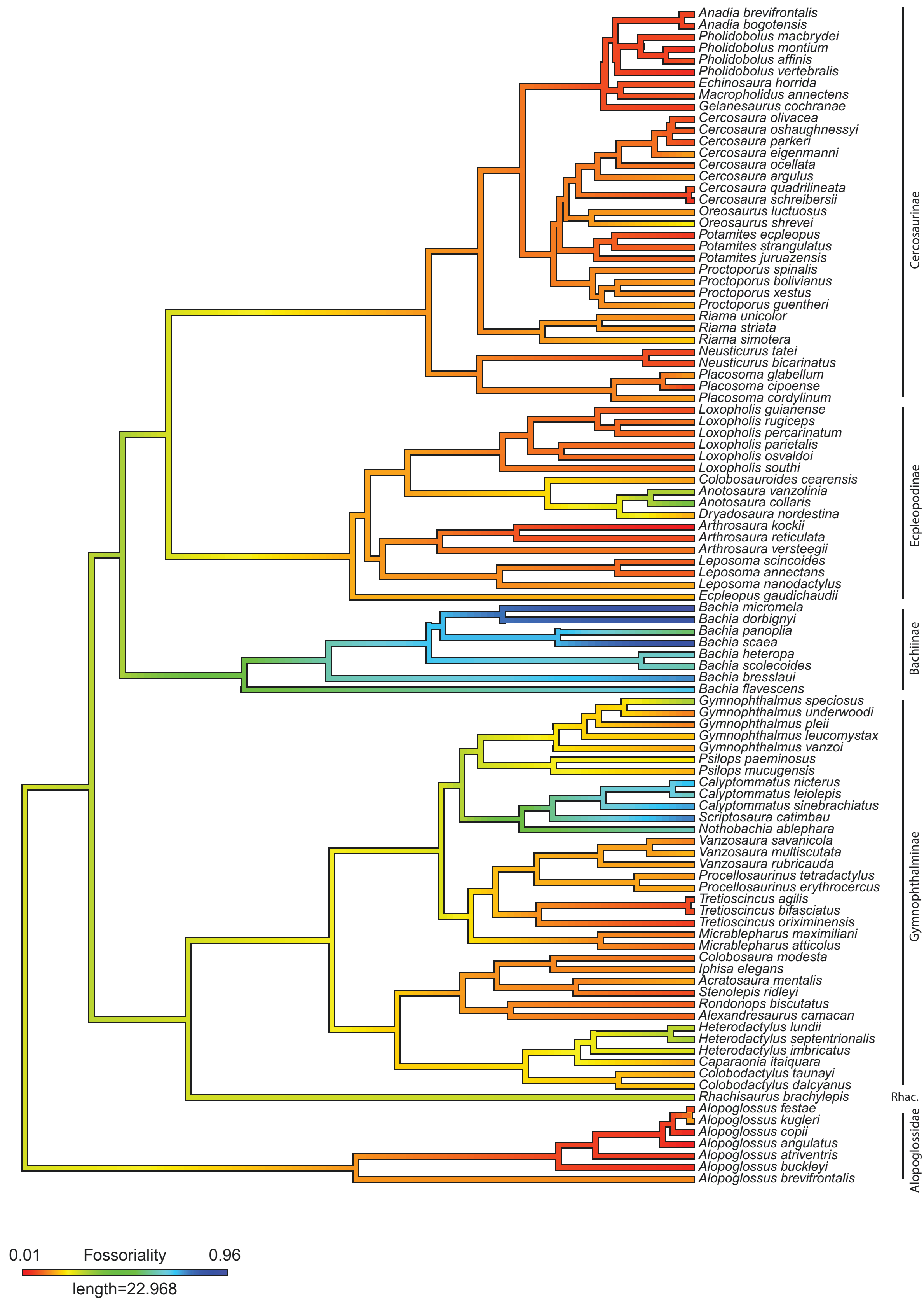

Figure 2. Ancestral reconstruction of the degree of fossoriality among the lizard species sampled in this study.

and shape or tail length have been associated with fossoriality in several squamate reptiles (Wiens *et al.* 2006, Barros *et al.* 2011, Anelli *et al.* 2024). However, the selective pressures that act during the evolution of these morphological traits can be diverse, even within the same ecological category. For example, Wiens *et al.* (2006) demonstrated that species with long tails and

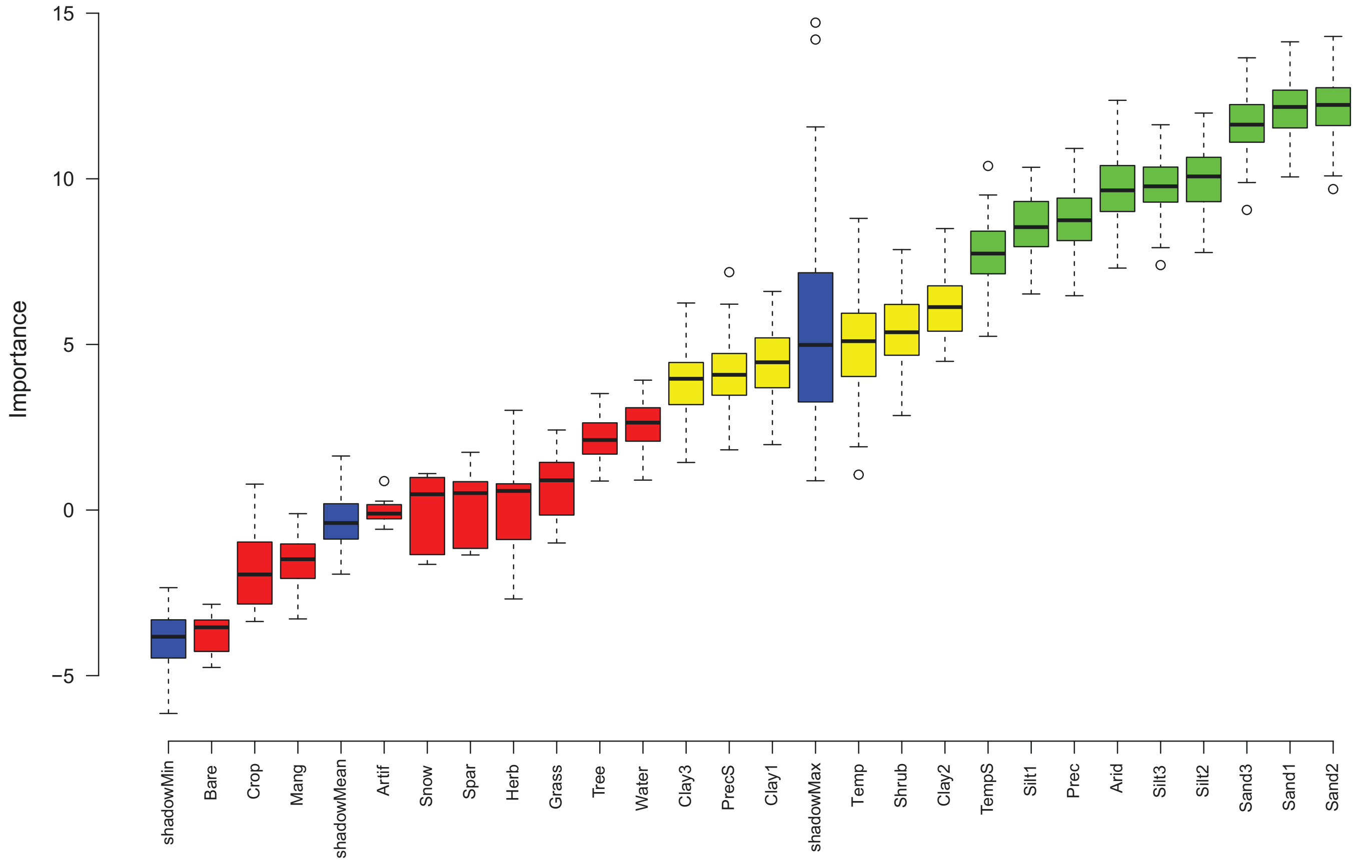

Figure 3. Important environment variables for fossoriality selected from BORUTA analysis. Tentative variables are classified as relevant or non-relevant comparing its median *Z*-score with the median *Z*-score of the best shadow attribute. Bare: bare soil; Crop: cropland; Mang: mangroves; Artif: artificial surface; Snow: snow and glaciers; Spar: sparse vegetation; Herb: herbaceous vegetation; Grass: grassland; Tree: tree-covered; Water: waterbodies; Clay3: clay content (15–30cm); PrecS: precipitation seasonality; Clay1: clay content (0–5cm); Temp: mean temperature; Shrub: shrub-covered; Clay2: clay content (5–15cm); TempS: temperature seasonality; Silt1: silt content (0–5cm); Prec: annual precipitation; Arid: aridity index; Silt3: silt content (15–30cm); Silt2: silt content (5–15cm); Sand3: sand content (15–30cm); Sand 1: sand content (0–5cm); Sand2: sand content (5–15cm).

reduced legs are surface species, such as *Ophiodes*, while species with short tails and reduced legs are fossorial. However, the same author states that there are exceptions, and not all short-tailed lizards are fossorial. This suggests that there are two ecomorphs of fossorial lizards: short-tailed burrowers and long-tailed grass-swimmers (Wiens and Slingluff 2001). Head shape is also highly variable, with differences between clades and substrate composition (Bergmann *et al.* 2020, Bergmann and Berry 2021). Many dry-ground fossorial species have sharp and angled heads, while fossorial lizards on moist substrates have compact and cylindrical heads (Anelli *et al.* 2024).

On the other hand, body elongation and limb reduction are associated with fossoriality in several lineages of squamate reptiles in different contexts and under different environmental patterns (Withers 1981, Benesch and Withers 2002, Wu *et al.* 2015, Morinaga and Bergmann 2020, Barros *et al.* 2021). Therefore, although our index was based on morphological traits of microteiid lizards, it can be effective with other lizard groups. However, as discussed previously, additional morphological traits may be necessary to evaluate better the degree of fossoriality of other reptiles, on a case-by-case basis.

Our index is standardized to vary from 0 to 1 within a given sample, with 1 being the most fossorial species and 0 being the least fossorial species. Species like *Riama simotera*, *Pholidobolus montium*, or *Dryadosaura nordestina* have been considered as fossorial or semi-fossorial in several ecological studies (Sánchez-Pacheco 2010, Torres-Carvajal and Mafla-Endara 2013, Garda *et al.* 2014, Torres-Carvajal *et al.* 2016, Venegas *et al.* 2016), but in our study they reached fossoriality values of $f = 0.18$, $f = 0.16$, and $f = 0.04$, respectively. This does not mean that these species do not have fossorial habits, but that, when compared to other fossorial species, such as *Bachia* or *Calyptommatus*, they have lower degrees of fossoriality, which is consistent. If these same species are used in other samples with other lizards, they may reach higher or lower fossoriality values. Therefore, our index is not intended to categorize species as fossorial or non-fossorial, but rather to evaluate, within a sample group, the degree of fossoriality of the species sampled.

Fossoriality and the associated morphological specializations in the microteiid lizards are primarily present in the subfamilies Bachiinae and Gymnophthalminae from Gymnophthalmidae. Our results highlight a convergent evolution of fossoriality, with at least two independent origins within the group. The evolution of fossoriality in Bachiinae seems to be more basal, emerging at the origin of the clade. In contrast, fossoriality in Gymnophthalminae is more recent, evolving mainly in a lineage

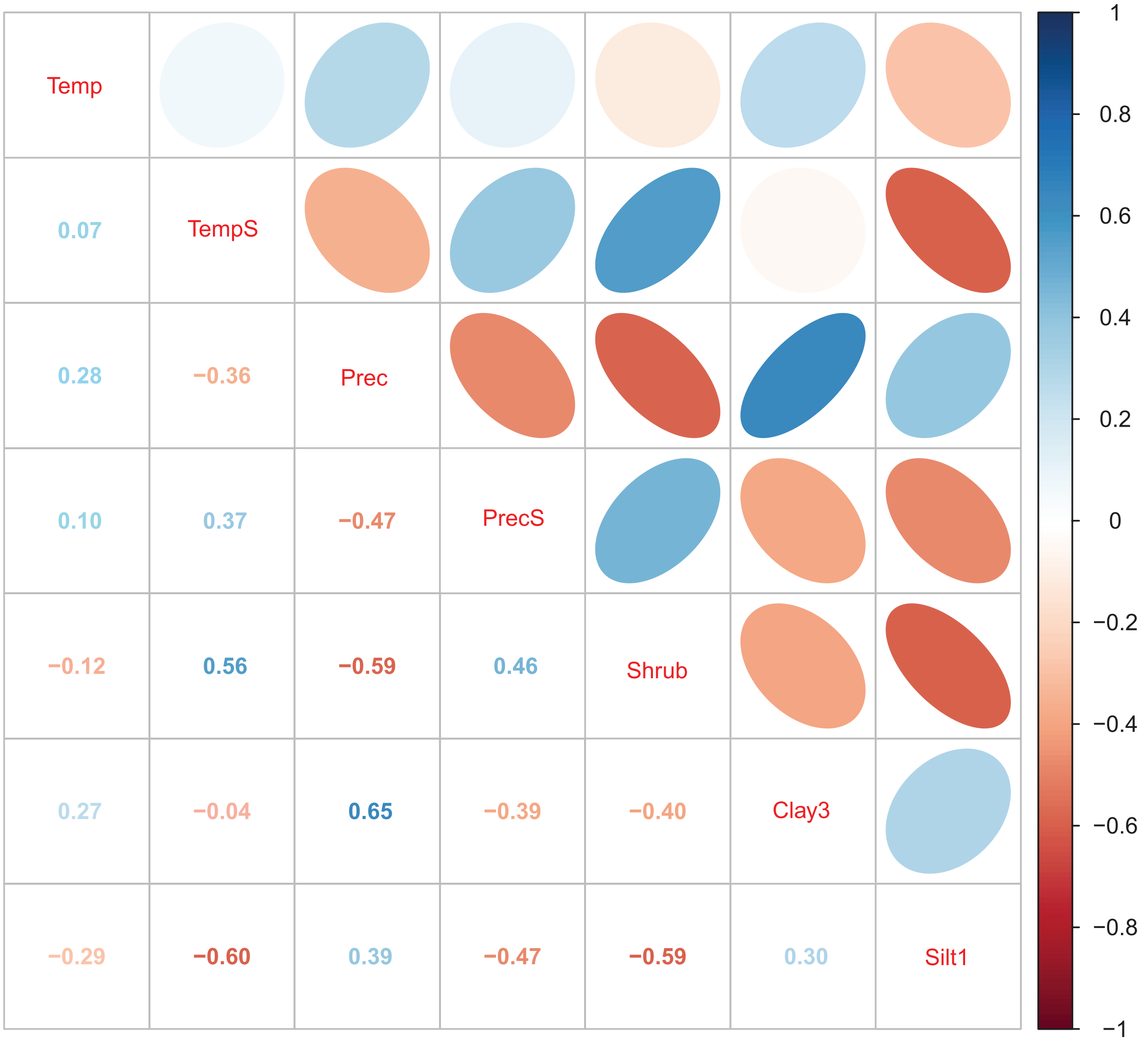

Figure 4. Pairwise correlation between the most relevant variables for the fossoriality after excluding the collinear variables. Numbers represent correlation coefficients and ellipses represent the strength and direction of the correlation. Strong correlations are indicated by flat ellipses, whereas weak correlations are indicated by rounded ellipses, as shown in the scale bar. Temp: mean temperature; TempS: temperature seasonality; Prec: annual precipitation; PrecS: precipitation seasonality; Shrub: shrub-covered; Clay3: clay content (15–30cm); Silt1: silt content (0–5cm).

Table 1. Results of phylogenetic generalized least squares' models (PGLS) between critical environmental variables, obtained from Boruta analysis, with fossoriality of microteiid lizards. Values in italic bold were statistically significant (< 0.05).

	Estimate	SE	*Z*-value	*P*
Annual precipitation	-0.041	0.013	3.052	***0.002***
Precipitation seasonality	-0.019	0.010	1.854	0.067
Mean temperature	0.020	0.014	1.411	0.158
Silt content (0–5 cm)	-0.012	0.014	0.866	0.386
Clay content (15–30 cm)	0.011	0.012	0.908	0.364
Shrubs covered	0.003	0.012	0.275	0.783
Temperature seasonality	-0.001	0.015	0.093	0.926

of eyelid-less gymnophthalmids that comprises the genera *Calyptommatus*, *Notobachia*, and *Scriptosaura*. In addition, some minor changes in fossoriality evolution can be observed in some other clades from Gymnophthalmidae, like *Anotosaura* (Ecpleopodinae) and *Heterodactylus* (Gymnophthalminae, Heterodactylini).

The degree of fossoriality of the monotypic *Rhachisaurus brachylepis* remained constant and did not vary, from its ancestral origin to the living species. *Rhachisaurus brachylepis* is known from Serra do Cipó, in south-eastern Brazil, and is the only species in the subfamily Rhachisaurinae, created by Pellegrino *et al.* (2001) to house the species, since this species differs from all subfamilies of Gymnophthalmidae, but still has morphological and molecular characters sufficient to place it within Gymnophthalmidae (Rodrigues *et al.* 2009, Goicoechea *et al.* 2016, Gomides *et al.* 2020). According to the phylogeny adopted here, *Rhachisaurus brachylepis* diverged earlier from other gymnophthalmids, and perhaps for this reason it has more primitive characteristics and remains similar to the ancestral state, with little variation over time, and can be used as a model of the ancestral state of fossoriality for the microteiid lizards.

The evolution of fossoriality and the adaptations resulting from it, not only in microteiids but also in other squamate clades, has been the subject of studies by many researchers (e.g. Roscito and Rodrigues 2010, 2013, Camacho *et al.* 2014, Cyriac and Kodandaramaiah 2018, Yovanovich *et al.* 2019). From these studies, fossoriality in Squamata evolved independently in almost all major continental regions. In addition, there were few dispersions from one continental area to another. Only amphisbaenians, anguids, dibamids, and snakes dispersed to more than one region (Wiens *et al.* 2006). Biogeographic isolation can increase the number of times a trait evolves, and competition can restrict the number of origins (Wiens *et al.* 2006). Thus, the limited geographical distribution of the fossorial Gymnophthalminae was probably a critical factor for the emergence of fossoriality in this group since they are isolated on the sandy fields of north-eastern Brazil, in Caatinga (Rodrigues 1984, 1991, Rodrigues and Santos 2008).

Nevertheless, considering the ancestral reconstruction of fossoriality in Gymnophthalminae, the primary changes in fossorial morphology coincided with divergences of the lineages for more shrubbery, sandy, and arid environments, indicating that these isolated environments may have favoured the fossorial evolution in the clade (see Supporting Information, Figs. S1, S2). This relationship of fossoriality versus geographic isolation is also observed in skinks of the genus *Lerista* (Lee *et al.* 2013, Morinaga and Bergmann 2020). Species of these Australian skinks exhibit a variety of body shapes, from less elongated species to intermediate and elongated fossorial forms. Comparative studies have shown that fossorial lizards with long bodies and reduced limbs have significantly smaller geographical ranges, while less elongated and surface species have more extensive geographical ranges (Lee *et al.* 2013, Morinaga and Bergmann 2020).

Unlike Gymnophthalminae, species of Bachiinae are found in various regions of Central and South America, ranging from Cerrado savannas to Amazonian forests (Colli *et al.* 1998, Teixeira Jr *et al.* 2013a, b, Ribeiro-Júnior *et al.* 2016, Ribeiro-Júnior and Amaral 2017, Murphy *et al.* 2019). Fossoriality in Bachiinae emerged at the origin of the clade, about 50 million years ago, even before the origin of fossorial forms in Gymnophthalminae. In Bachiinae, we observed no changes or divergences in habitat use, which remained constant over time, occurring with only minor modifications in some extant species. Thus, we conclude that convergent patterns in the evolution of these species reflect different processes and contexts of phenotypic evolution. In fossorial Gymnophthalminae, the morphology pattern is characterized by forelimb reduction. Conversely, in Bachiinae, the reduction is more pronounced on hindlimbs, evidencing distinct processes of morphological evolution (Roscito *et al.* 2014).

To explain the different origins of fossoriality, some authors suggest the evolutionary changes associated with ecological factors, such as environmental patterns or ecological relationships between species (Gans 1975, Wiens and Slingluff 2001, Brandley *et al.* 2008). Here, for Gymnophthalminae, we found an association of fossoriality with dry environments in shrubby open areas. Similarly, Grizante *et al.* (2012) found a positive relationship between body elongation in gymnophthalmid lizards and aridity.

Arid regions have high temperatures and low precipitation. These environments impose a series of evolutionary adaptations necessary to increase performance in these extreme habitats. This is especially applicable to ectothermic animals like lizards. Fossorial lizards, although having high thermal tolerance, similar to epigean lizards, have a lower thermal preference when compared to other sympatric epigean lizards (Camacho *et al.* 2014). Several other authors have already reported that fossorial species tend to prefer lower temperatures, whether lizards (Withers 1981), snakes (Clark 1967), or amphisbaenians (López *et al.* 1998). Thus, fossoriality in some microteiids may have evolved as an escape from hot environments. This is true when we observe fossorial gymnophthalmines, which have small ranges in warm and arid regions of north-eastern Brazil (Rodrigues 1984, 1991). In addition, other fossorial gymnophthalmids, such as *Anotosaura*, are associated with habitats with milder temperatures (Rodrigues *et al.* 2013, Oliveira *et al.* 2018).

Although fossorial species of *Bachia* are widely distributed across different environments, in our database, species with higher degrees of fossoriality (*Bachia micromela* and *Bachia dorbignyi*) are often found in open areas, like Cerrado. In contrast, those with lower fossoriality values (*Bachia panoplia* and *Bachia scolecoides*) are more associated with forested Amazonian regions, reinforcing our idea that open and shrubby areas favour the evolution of fossoriality.

Although fossoriality evolved several times in many vertebrate clades, it seems to have a close relationship with physiological parameters and optimal activity temperatures (Withers 1981, López *et al.* 1998, 2002, Civantos *et al.* 2003). Thus, in ectothermic animals, a burrowing lifestyle could have evolved as a thermal refuge for milder microenvironments, such as leaf litter or even underground, against environmental stresses like long dry periods and high temperatures or climate changes (Kearney *et al.* 2009, Closel and Kohlsdorf 2012), probably because thermal patterns underground are more stable than on the surface, which are highly variable throughout the day (Huey *et al.* 1989, López *et al.* 1998). Many fossorial lizards, for example, increase their burrowing performance or burrow deeper as environmental temperatures increase (Camacho *et al.* 2014, Wu *et al.* 2015).

Other factors associated with the evolution of fossoriality are less forested and sandier environments. As mentioned above, many fossorial lizards studied here are typically found in open areas with sandy soil. The low vegetation cover should favour locomotion in the sand, while the absence of plant roots should facilitate burrowing (Greenville and Dickman 2009). In addition, homogeneous and sandy soils are known to increase locomotor performance, as has been reported for several species of fossorial reptiles (López *et al.* 1998, Greenville and Dickman 2009, Barros *et al.* 2011, 2021).

CONCLUSION

Our results show convergent evolution of fossoriality in some lineages of these lizards, especially in the family Gymnophthalmidae, and that the primary selective pressures involved are arid and shrubby open areas, supporting our initial hypothesis. Furthermore, the relationship between aridity and fossoriality found here, associated with the biogeographic isolation of these species, can serve as a basis for future studies about the effects of recent climate changes and global warming on the dispersion and evolution of fossorial and non-fossorial lizard species.

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We thank Hussam Zaher and Aline Benetti at the Museu de Zoologia da Universidade de São Paulo (MZUSP) for allowing us to analyze the specimens from the MZUSP. We also would like to thank to Willianilson Pessoa, Adrian Garda, Wirven Fonseca, Paulo Bernarde, Alejandro Arteaga, and Jose Vieira for giving us the photos of the species of lizards in life illustrated in this study. BHSO thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a research fellowship. DOM and GRC thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a research fellowship. DOM thanks Fundação de Apoio à Pesquisa do Estado da Paraíba (Fapesq) and CNPq for the Programa de Apoio aos Núcleos de Excelência (PRONEX) fellowship.

CONFLICTS OF INTEREST

None declared.

DATA AVAILABILITY

We include all used data as an Appendix, which could be available in the *Zoological Journal of Linnean Society* website.

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