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Patterns of morphological diversification are influenced by dietary evolution in a highly species-rich lizard radiation

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The diversification of lineages is facilitated or constrained by the simultaneous evolution of multiple components of the phenotype that interact with each other during the course of speciation. When evolutionary radiations are adaptive, lineages proliferate via the emergence of multiple phenotypic optima that underlie diversification of species across multiple ecological niches. When radiations are non-adaptive, lineage proliferation unfolds constrained by similar (or nearly identical) correlations among traits that keep phenotypic and ecological diversity across newly emerging species within a single optimum. Nature offers very few opportunities where both types of diversification occur between closely related and highly diverse lineages. The Liolaemidae family of South American lizards offers unique such opportunities given two speciose lineages that have rapidly proliferated via adaptive (*Liolaemus*) and non-adaptive (*Phymaturus*) radiations. We analyze body shape in lizards in association with type of diet (herbivory, omnivory or carnivory). In these lizards, diet types have been suggested to be linked to body size. Our results confirm this hypothesis, with three body size optima tightly linked to all three diet types when radiation is both adaptive and non-adaptive. Diet reconstruction along their evolutionary history showed that the common ancestor of Liolaemidae was likely omnivorous, which is matched by ancestral reconstruction of body size. Phylogenetic PCA revealed that herbivorous species generally have more differentiated body shape than insectivores and omnivores. Herbivorous species have evolved larger heads, shorter hindlimbs and a small difference between forelimb and hindlimb length. In contrast, omnivores and insectivores have smaller heads and longer hindlimbs. Collectively, trophic niche plays an important role in defining body shape and size across species within lineages, and the patterns of trait–ecology correlations remain consistent when lineages have diversified via adaptive and non-adaptive radiation.

KEYWORDS

Liolaemidae, evolutionary optimum, diet diversification, ancestral reconstruction, Ornstein–Uhlenbeck models

1 Introduction

The adaptive radiation of lineages is triggered when ecological opportunity – abundance in available niche space – emerges as a consequence of the formation of new environments, large-scale extinctions or the evolution of a key adaptive innovation that facilitates exploitation of niches that were previous inaccessible (Schluter, 2000). During adaptive radiation species diverge into ecologically distinct lineages that driven by natural selection, exploit their habitat in different ways (Pincheira-Donoso et al., 2018; Matsubayashi and Yamaguchi, 2020). In contrast, non-adaptive radiation is characterized by a species diversification with minimal ecological difference occupying similar niche space, and may be associated with variation in sexual selection across populations (Czekanski-Moir and Rundell, 2019). Although there are fewer studies on non-adaptive radiation, it seems to be more common than expected (Rundell and Price, 2009; Reaney et al., 2018; Czekanski-Moir and Rundell, 2019; Matsubayashi and Yamaguchi, 2020).

Adaptation to food is a major source of natural selection. Therefore, the availability and diversity of trophic resources can play a central role during adaptive divergence (Price et al., 2012; Burin et al., 2016; Ocampo et al., 2022), which is often associated with co-adaptation in morphological traits (Grant and Grant, 2003; Stokstad, 2004; Eloy de Amorim et al., 2017). Adaptive morphological changes linked to diet may have, in some cases, a greater effect than interspecific competition or predation (Jones et al., 2013). This functional association between the evolution of diet and morphological traits is expected to, therefore, influence patterns of morphological diversity within lineages, with convergent evolution in body plans (body size and shape) among species with similar diets, and divergent adaptations among species that exploit different resources. Many examples of convergence have been found across different animal groups, such as cichlid fish, anolid lizards and mammal species, mainly attributed to the link between niche availability and resource use (Muschick et al., 2012; Mahler et al., 2013; Mazel et al., 2017; Gearty et al., 2018).

The shape of the head, body, and limbs is strongly influenced by the type of diet, playing a significant role in feeding habits and food processing (Grant and Grant, 2002; Stokstad, 2004; O'Grady et al., 2005; Miles et al., 2007; Eloy de Amorim et al., 2017; Pincheira-Donoso, 2021). For example, cranial morphology and size in vertebrates mirror specific diet types given that head and skull are key for obtaining, processing and ingesting certain food items and thus, are subject to certain mechanical constraints depending on food type (Dollion et al., 2017). In the tropidurid lizard *Microlophus thoracicus*, ontogenetic changes in diet are coupled with changes in head shape. In this species adults are herbivores and exhibit proportionally wider and more robust heads, whereas insectivorous juveniles have narrower and slender heads (Toyama et al., 2018). Body size is also an important factor for diet since herbivores tend to be bigger in size than their non-herbivore sister taxa (Price et al., 2012), given that nutritional value of plant material is lower than animal-based material that high in protein. Consequently, herbivorous species compensate for a low nutritional value with greater body volume for digestion (Pough, 1973). On the other hand, insectivorous species tend to have small bodies and thin heads because they require more agility to capture insects for food (Szarski, 1962; Pough, 1973). In a similar environment, these traits tend to converge around an evolutionary optima value (O'Meara and Beaulieu, 2014).

Changes towards new evolutionary optima in functional morphology are driven by natural selection for a more efficient exploitation of new food resources, optimal foraging and efficient consumption time (Price et al., 2012). These evolutionary optima can be estimated using different Ornstein–Uhlenbeck (OU) models, which have the ability to better fit empirical data, as well as draw biological conclusions based on their parameter estimates (O'Meara and Beaulieu, 2014). The use of these models has increased the understanding of the ecological and evolutionary processes underlying species diversification as shown by various studies on different vertebrate groups (Lapiedra et al., 2013; Astudillo-Clavijo et al., 2015; Pincheira-Donoso et al., 2015; Gearty et al., 2018; Lapiedra et al., 2021). These methods are a good fit for highly diverse and broadly distributed groups. Here, we use this approach to explore how evolutionary changes in diet have driven distinct evolutionary optima of ecomorphological traits related to resource use in the lizard family Liolaemidae.

The Liolaemidae family is a group of South American lizards with great diversity (340 species into 3 genera) (Uetz et al., 2023), inhabiting a wide variety of environments across its range in the southern half of the continent (Pincheira-Donoso et al., 2008a; Pincheira-Donoso et al., 2008b; Pincheira-Donoso et al., 2009; Abdala and Quinteros, 2014; Roll et al., 2017; Esquerré et al., 2019). Species of the family are distributed from sea level to extreme high elevations ranging from 5000 to 5400 m (Aparicio and Ocampo, 2010; Pincheira-Donoso et al., 2013; Cerdeña et al., 2021). This family has two reproductive modes (oviparous, viviparous), and three diet types (insectivore, omnivore, herbivore) (Pincheira-Donoso et al., 2008b; Pincheira-Donoso and Tregenza, 2011; Pincheira-Donoso et al., 2013; Pincheira-Donoso et al., 2017; Zimin et al., 2022). All of these traits have been shown to contribute to the diversification of the family and promote the occupancy of novel niche space (Espinoza et al., 2004; Esquerré et al., 2019). Recent findings have unveiled the pivotal role of dietary evolution in the evolutionary radiation of the group, where evolutionary transitions from insectivory to herbivory, bridged by omnivory, have provided ecological opportunities for the rapid and successful diversification across a variety of climates (Ocampo et al., 2022). Just as in mammals (Price et al., 2012), herbivorous *Liolaemus* have evolved greater body sizes associated with other morphological changes (Pough, 1973; Cooper Jr. and Vitt, 2002). For example, O'Grady et al. (2005) compared body and gut size among 22 species of *Liolaemus* with different diets (herbivory, omnivory and insectivory) showing that herbivorous species have evolved bigger and longer digestive tract. We are yet to unravel, however, how changes in diet (source of ecological opportunity) influence changes and variation in functional ecomorphological traits and body size as a result of ecological release that triggered radiation of the group.

In Liolaemidae, the genus *Phymaturus* that is almost entirely composed of herbivorous species, it is believed to have diversified through non-adaptive radiation. Quite the reverse, the genus *Liolaemus*, which is species rich and harbors herbivorous, insectivorous and omnivorous species that commonly evolved through convergence, is believed to have diversified through adaptive radiation (Reaney et al., 2018). Therefore, in this study we hypothesize that in Liolaemidae evolutionary changes in diet type, imposed by novel selective pressures, have influenced changes in ecomorphology and body size adaptations across species in accord with the diversification of the family. We expect, traits related to the head, body, and limbs to show different evolutionary optima values across its evolutionary history under an OU process and in accordance with diet evolution. Lineages that transitioned to an herbivorous diet should have evolved a larger body, which supports longer intestines that facilitate the digestion of plant material (Clauss et al., 2013; Pincheira-Donoso, 2021). They should have also evolved optima for robust limbs as compared to omnivorous lineages. In addition, a thick skull optimum indicative of a stronger bite force should be prevalent (Herrel et al., 1999, Herrel et al., 2004). On the contrary, insectivorous lineages should have evolved towards small body and head sizes and long limb optima, to be more agile for hunting insects (Losos, 1990; Sanger et al., 2012). Lineages that share a diet type, but have evolved independently across evolutionary history, are expected to also show convergence of ecomorphological traits and body size.

2 Materials and methods

2.1 Taxon sampling and phylogenetic tree

To conduct the analyses using the phylogenetic comparative method, we employed the calibrated tree outlined in Esquerré et al. (2019). This tree is constructed based on six nuclear (B1D, EXPH5, KIF24, MXRA5, PLRL, PNN) and four mitochondrial loci (cytb, 12S, ND2, ND4) as molecular markers. The gene partitioning scheme and substitution model were determined to be GTR+G for optimal accuracy. To establish temporal parameters, a fossil representing the earliest occurrence of the Eulaemus clade in the Early Miocene was incorporated, providing a mean prior for the tree height of this subgenus. Notably, this tree encompasses approximately 66% of the presently identified species within Liolaemidae (Uetz et al., 2023), constituting 1 Ctenoblepharys, 188 Liolaemus, and 35 Phymaturus, totaling 224 species. We utilized data from 187 of these species for which we could find morphometric information.

2.2 Morphological and diet data compilation

Morphological traits used in the analyses included snout–vent length (SVL, 187 species), head length, and head width (HeLe, HeWi, respectively from 178 species), forelimbs, hindlimbs length, length difference between limbs, axilla–groin length (FoLi, HiLi, DiLi, AxGr, respectively from 141 species) (Supplementary Figure 1). Traits were analyzed independently as SVL, head and body measurements, as not all species have information for all the traits analyzed in this study. We mainly used morphological data gathered by one of us (DPD), for which we averaged trait size for males and females independently, and then averaged these two values to obtain a single value for each species. For those species that we did not have measurements, we used published data, i.e., description of the holotype, assuming that this individual is representative of the species. For some species we also used measures reported by Meiri (Meiri, 2018) (Supplementary Table 1). We used diet data reported by Ocampo et al. (2022), but updated with information for *Liolaemus polystictus* (Olivera-Jara and Aguilar, 2020). For species present in the Esquerré's et al. (2019) tree, we analyzed the diet of 187 species, which represent 55% of the Liolaemidae family. All data on diet and body measurements can be found in Supplementary Table 2.

2.3 Diet reconstruction

To infer ancestral diet states, we employed Stochastic Character Mapping (SCM) (Bollback, 2006) on the Maximum Clade Credibility (MCC) Phylogenetic Tree. This was achieved using the *make.simmap* function from the *phytools* package (Revell, 2012) within the R statistical environment (R Core Team, 2022). SCM, a Bayesian method, utilizes Markov Chain Monte Carlo (MCMC) to produce a posterior probability distribution, grounded in Maximum Likelihood (ML), of ancestral diet states and their transition times across branches on the MCC tree (Huelsenbeck et al., 2003). Before running SCM, we first extracted the 187 species from the Esquerré et al. (2019) tree. With the dietary information for each of these species, we searched for the best model among three possibilities that best fits our data. These models are: 1) an equal-rates model "ER", where a single parameter governs all transition rates, 2) a symmetric model "SYM", where forward and reverse transitions share the same parameter, and 3) an all-rates-are-different model "ARD", where each rate is a unique parameter. These models were assessed using the *fitDiscrete* function from *geiger* package, and based on the Akaike Information Criterion (AIC), we selected the best model. The parameters used to run the *make.simmap* function were: Q="mcmc"; *nsim*=500; *message*=TRUE; model="SYM"; the rest of the parameters were set to their default values. Model were constructed using 500 simulated trees. We plot the phylogenetic morphospace with the *phylomorphospace* command from the values obtained with the *make.simmap* function.

2.4 Morphological evolution

All morphological variables were standardized *via* log-transformation. To obtain the *simmap* values and calculate the evolutionary optima from them, a diet reconstruction was performed for each of the three trait trees (explained above), which are: SVL (187 species), head (HeLe, HeWi, 178 species), and body (FoLi, HiLi, DiLi, AxGr, 141 species). To assess if different morphological traits evolved toward different phenotypic optima according to the three diet types, we fitted Ornstein–Uhlenbeck models (OU) of character evolution using the R package *OUwie* (Beaulieu et al., 2012). We estimated evolutionary optima for all traits for the entire family first, and then separately for the genera *Liolaemus* and *Phymaturus*. Initially, we ran the different models with nsim=10 using the *make.simmap* function and compared their AICc values to identify the set of models with the best fit. Tested models were: a single-rate Brownian motion (BM1), a Brownian motion model with different rate parameters for each state on a tree (BMS), an Ornstein–Uhlenbeck model with a single optimum “θ” for all species (OU1), an Ornstein–Uhlenbeck model with different θ, a single strength of pull “α” and average evolutionary rate “σ^2” acting in all selective regimes (OUM), and Ornstein–Uhlenbeck models that assume different state means θ as well as either multiple σ^2 (OUMV), multiple α (OUMA), or multiple α and σ^2 per selective regime (OUMVA). Once the model with the best fit for each tree was identified, we ran it with all simulations generated by the *make.simmap* function. For each trait, we also calculated Blomberg's k phylogenetic signal to assess the independence of the data from their phylogenetic relationships (Blomberg et al., 2003).

For all traits, we performed ancestral reconstruction across lineages (Evans et al., 2009), we employed the *phenogram* function from the *phytools* package (Revell, 2012; Revell, 2013) within the statistical environment R (R Core Team, 2022). The position of nodes and branches are computed *via* ancestral character estimation using likelihood, where each trait evolves according to a Brownian motion process governed by a rate parameter β. Under this model the expected squared difference (variance) between any two species is β multiplied by the time since the species last shared a common ancestor (Schluter et al., 1997). In the case of the remaining body measurements, we corrected for size effects by using the ratio of each trait's value to snout–vent length.

2.5 Phylogenetic PCA

To compare ecomorphological changes across diets, we conducted a phylogenetic PCA for head and body data separately, considering the difference in tree size. We used logarithmically transformed standardized morphological variables, and corrected for size effects by using the ratio of each trait's value to snout–vent length, the phylogenetic PCA was performed with the *phyl.pca* function in the R *phytools* package (Revell, 2012).

3 Results

3.1 Diet reconstruction

The best evolutionary model for the distribution of characters on the tree according to the three models was “SYM” (ER=341.00, SYM=309.00, ARD=312.13). Diet reconstruction in Liolaemidae shows that the common ancestor is likely to have been omnivorous, (highest probability, p=0.37, compared to an herbivore with p=0.25, or an insectivore with p=0.34; Figure 1A). Similarly, the common ancestor between *Phymaturus* and *Liolaemus* is likely to have been omnivorous (highest probability, p=0.38, compared to an herbivore with p=0.27, insectivore p=0.35). From there, *Phymaturus* transitioned to herbivory and remained as such throughout most of its evolution, with some recent transitions to omnivory (3 species out of 28 analyzed in this study). In *Liolaemus*, ancestors were primarily insectivores, and omnivory began to reappear convergently across the five main lineages between 9 and 10 Mya. Herbivory in *Liolaemus* has evolved more recently in the last 4 Mya and has converged ten times within the genus. On mean, 205.17 transitions between diets occurred during the evolution of the family, with insectivory having a higher number of transitions towards omnivory (mean 94.63), followed by omnivory towards insectivory (mean 91.11). Transitions from omnivory to herbivory and vice versa are much lower (11.04 and 6.29 respectively) and the transitions from insectivory to herbivory and vice versa were the lowest of all (1.4 and 0.71 respectively) (Figure 1B). Proportionally, the insectivorous diet has been present for more than half of the evolutionary time (0.51), while the herbivorous diet is a more recent development (0.12). On the other hand, omnivory has been present for a considerable amount of time (0.38).

3.2 Morphological evolution

The evolutionary models that best fit the character distribution in the three analyzed trees by genus and by family are presented in Table 1. It can be observed that in the *Phymaturus* genus, traits are better fitted to a model where all rates are different, whereas in *Liolaemus*, head traits already exhibit a more symmetric model. This pattern is consistent across all traits analyzed at the family level. Phylogenetic signal and the best-fitted OU models for the traits analyzed by genus and family are presented in Table 2. The values of the OU models are the mean of the 10 runs conducted per trait, in which some instances resulted in an outlier value. This outlier was not considered in the calculation of the mean, and the model that was most frequently repeated was weighted as the best fit. In *Phymaturus*, the model that best fits all traits is OU1, which means that the different traits evolved towards a single optimum value θ, at a constant rate σ^2 and with a similar selective pull α regardless of diet type (Table 3). The phylogenetic signal was low for all traits; however, it was only significant for the SVL and HeWi traits contrary to the rest of the traits (Table 2). For *Liolaemus*, the model that best fit most traits was also an OU1. However, for HeWi and AxGr, the models that best fit were OUMV and OUMVA, respectively, which exhibited different evolutionary θ, σ^2 and α for each diet, indicating that herbivorous species evolved towards wider heads, while insectivorous species evolved towards narrower heads. The highest $\sigma^2$was for herbivores, and the lowest for omnivores. Similarly, for AxGr the best fit was an OUMVA model with different θ, σ^2, and α for each diet (Table 3). In this genus, a low phylogenetic signal was found for all traits (Table 2).

In the analysis of the Liolaemidae family, most of the traits exhibit a θ for each diet type, except FoLi that showed a single θ for all diet types (Table 3). The SVL has a well-defined θ for each diet type, the herbivorous species reached an evolutionary optimum at 87 mm of

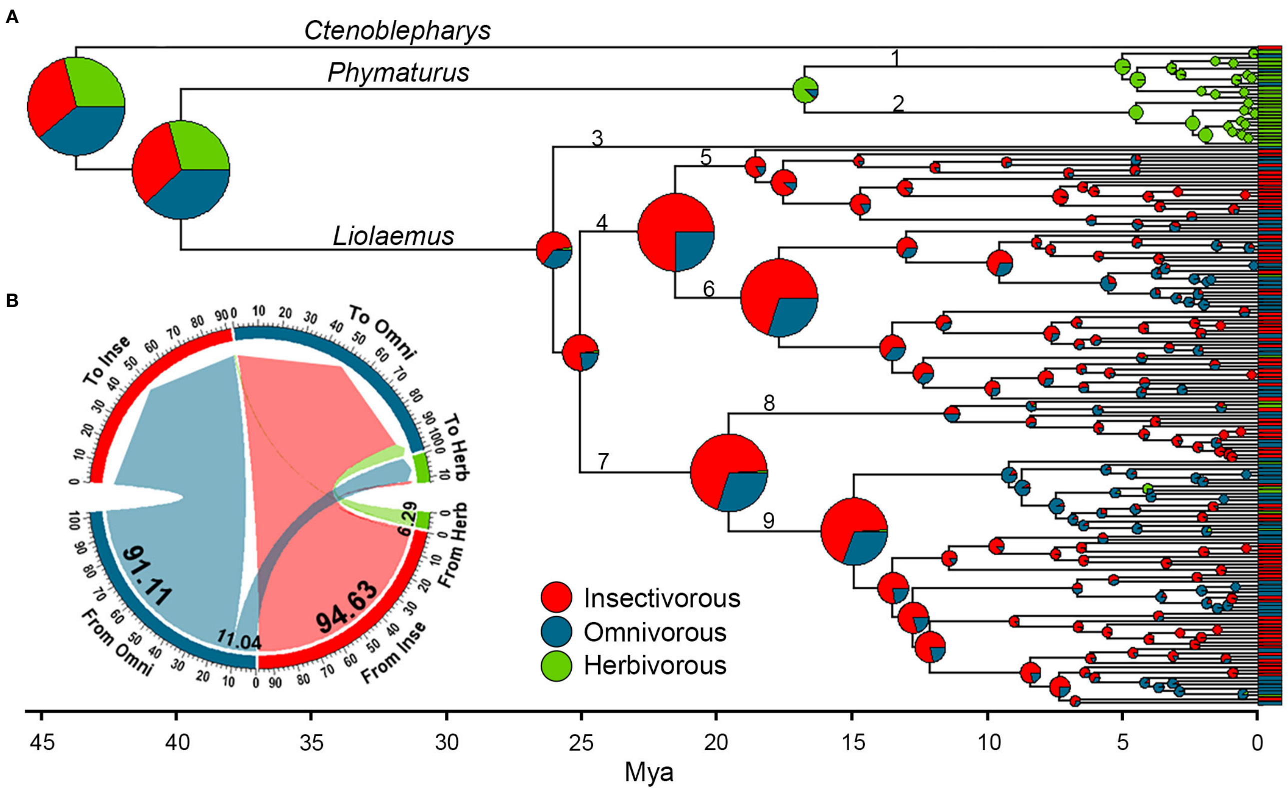

FIGURE 1
Ancestral reconstruction of dietary diversification throughout the evolutionary history of Liolaemidae (pie charts at nodes represent posterior probabilities of each diet class), averaged across 500 trees. **(A)** (1) *Phymaturus palluma* group; (2) *Phymaturus patagonicus* group; (3) *Liolaemus walkeri* group; (4) *Liolaemus* subgenus; (5) *Liolaemus nigromaculatus* section; (6) *Liolaemus chiliensis* section; (7) *Eulaemus* subgenus; (8) *Liolaemus lineomaculatus* series; (9) *Liolaemus montanus* series. The probability of the common ancestor being omnivorous is slightly higher than the probabilities of the other two diets. While ancestors of the *Liolaemus* genus were primarily insectivorous or omnivorous, herbivorous species have independently evolved in different groups within this genus. **(B)** Mean transitions from one diet type to another, where insectivory had more transitions towards omnivory, followed by a reversal between these two diets. The transitions to and from herbivory are very unlikely, especially the one from herbivory to insectivory, which is represented by only one line with a value of 0.71.

TABLE 1 Results of the model comparison, indicating the best fit based on the obtained AIC values, were conducted for the SVL, head (HeLe, HeWi), and body (FoLi, HiLi, DiLi, AxGr) trees, both for the *Phymaturus* and *Liolaemus* genera, as well as an analysis of the entire Liolaemidae family.

Group	Traits	ER	SYM	ARD
Phymaturus	SVL	26.75	26.75	**23.55**
Phymaturus	Head	26.75	26.75	**23.55**
Phymaturus	Body	14.96	14.96	**12.46**
Liolaemus	SVL	289.09	253.55	**251.94**
Liolaemus	Head	281.11	**245.49**	245.67
Liolaemus	Body	233.22	208.95	**205.12**
Family	SVL	341.19	**309**	312.28
Family	Head	315.24	**278.43**	279.77
Family	Body	254.61	**227.64**	230.61

The values of the best-fitting models are shown in bold.

SVL, while the omnivores reach their evolutionary optimum at 70 mm, and the insectivores at 57 mm (Figure 2). A trait that showed different θ´s and σ^2s for each diet was HeLe, where herbivores have longer head and insectivores have shorter head, while σ^2 was highest for herbivores, and the lowest for omnivores (Figure 3A). Only HeWi exhibited significantly different θs and αs, where herbivores have wider heads and insectivores have narrower ones; the highest α was for herbivores, and the lowest for omnivores (Figure 3B), DiLi where omnivores and insectivores have the greatest θ´s difference between their fore and hind limbs, while herbivores have the smallest difference. The highest σ^2 was for herbivores, and the lowest for insectivores (Figure 3C), AxGr where herbivores have the greatest axial growth, and insectivores have the lowest. The highest σ^2 was for omnivores, and the lowest for insectivores (Figure 3D). HiLi only exhibits differences in θ´s where insectivores have longer Hind limbs and herbivores have shorter Hind limbs (Figure 3E), In most traits, the phylogenetic signal was significantly low ($p < 0.001$), indicating a general tendency for less phylogenetic signal than expected under Brownian motion. Only in the genus *Phymaturus*, the traits HeLe, FoLi, HiLi, DiLi, AxGr were not significant (Table 2).

The Liolaemidae family currently encompasses a wide range of body sizes across lineages, from the large (112.1 mm) to the small (44.7

TABLE 2 Mean of the AIC values obtained for each OU models for the traits analyzed by genus (PHYMA, *Phymaturus*; LIOLA, *Liolaemus*) and by family.

Group	Trait	BM1	BMS	OU1	OUM	OUMV	OUMA	OUMVA	K	*p*
Phyma	SVL	−113.86	−111.35	**−121.18**	−119.79	−119.07	−117.72	−117.38	0.2	< 0.05
Phyma	HeLe	−118.49	−117.88	**−139.84**	−137.79	−138.03	−133.93	−134.12	0.12	0.08
Phyma	HeWi	−141.51	−140.73	**−147.11**	−145.05	−143.73	−143.38	−142.63	0.34	< 0.001
Phyma	FoLi	−87.2	−85.14	**−94.49**	−91.51	−92.4	−90.16	−86.35	0.14	0.24
Phyma	HiLi	−87.05	−84.97	**−95.96**	−93.64	−94.74	−94.16	−88.71	0.08	0.72
Phyma	DiLi	−47.94	−45.83	**−53.79**	−51.15	−51.03	−53.04	−44.11	0.16	0.11
Phyma	AxGr	−83.27	−81.77	**−99.36**	−97.01	−99.02	−97	−94.4	0.13	0.36
Liola	SVL	−346.4	−344.1	**−359.44**	−358.44	−356.85	−356.75	−354.58	0.41	< 0.001
Liola	HeLe	−691.58	−697.57	**−723.97**	−721.07	−723.34	−721.39	723.84	0.39	< 0.001
Liola	HeWi	−681.88	−685.24	−691.11	−690.74	**−692.4**	−691.89	−690.48	0.42	< 0.001
Liola	FoLi	−611.82	−611.81	**−633.84**	−631.89	−631.08	−630.88	−631.46	0.49	< 0.001
Liola	HiLi	−687.65	−688.2	**−704.41**	−702.99	−702.29	−702.52	−702.87	0.52	< 0.001
Liola	DiLi	−556.4	−555.94	**−562.35**	−560.87	−559.46	−560.15	−558.91	0.52	< 0.001
Liola	AxGr	−626.18	−630.79	−638.25	−636.71	−646.75	−645.39	**−651.75**	0.44	< 0.001
Family	SVL	−464.35	−460.93	−476.4	**−481.12**	−478.37	−477.06	−476.55	0.32	< 0.001
Family	HeLe	−786.33	−831.86	−853.82	−851.25	**−865.23**	−858.7	−860.64	0.23	< 0.001
Family	HeWi	−824.83	−829.47	−839.4	−842.67	−841.79	**−844.1**	−842.34	0.36	< 0.001
Family	FoLi	−703.01	−703.08	**−731.83**	−731.65	−729.89	−727.07	−725.42	0.31	< 0.001
Family	HiLi	−769.37	−780.03	−792.36	**−794.14**	−793.18	−791.26	−792.88	0.31	< 0.001
Family	DiLi	−546.89	−605.01	−576.83	−584.6	**−611.74**	−593.17	611.46	0.23	< 0.001
Family	AxGr	−709.55	−715.14	−723.95	−731.03	**−737.07**	−726.7	−736.75	0.38	< 0.001

The traits are: SVL Snout-vent length, HeLe Head length, HeWi Head width, FoLi Front limbs, HiLi Hind limbs, DiLi Differences in limbs, AxGr Axial growth. AIC values in bold are the best-fitting values. Phylogenetic signal (k) and its probability (p).

TABLE 3 Optimal values, sigma, and alpha obtained in the OUwie analysis by genus (PHYMA, *Phymaturus*; LIOLA, *Liolaemus*) and by family. *Phymaturus* exhibits a single optimum for all its traits, while *Liolaemus* begins to show some traits that have more than one evolutionary optimum. However, at the family level, almost all traits present optima for each type of diet.

Group	Trait	Model	optimum (θ)			Sigma (σ^2)			Alfa (α)		
			Herb	Inse	Omni	Herb	Inse	Omni	Herb	Inse	Omni
Phyma	SVL	OU1	1.96			7.0e-4			0.42		
Phyma	HeLe	OU1	0.63			3.7e-3			6.01		
Phyma	HeWi	OU1	0.63			2.5e-4			0.34		
Phyma	FoLi	OU1	0.78			2.8e-4			0.91		
Phyma	HiLi	OU1	0.85			3.3e-4			1.19		
Phyma	DiLi	OU1	0.57			2.7e-3			0.78		
Phyma	AxGr	OU1	0.86			4.4e-3			20.69		
Liola	SVL	OU1	1.80			1.5e-3			8.7e-2		
Liola	HeLe	OU1	0.63			1.7e-4			0.14		
Liola	HeWi	OUMV	0.68	0.58	0.59	4.2e-4	1.7e-4	9.3e-5	8.0e-2		
Liola	FoLi	OU1	0.76			1.1e-4			0.12		

(Continued)

TABLE 3 Continued

Group	Trait	Model	optimum (θ)			Sigma (σ^2)			Alfa (α)		
			Herb	Inse	Omni	Herb	Inse	Omni	Herb	Inse	Omni
Liola	HiLi	OU1	0.87			5.5e-5			0.10		
Liola	DiLi	OU1	0.62			1.3e-4			5.9e-2		
Liola	AxGr	OUMVA	0.80	0.81	0.81	7.7e-7	1.4e-4	6.6e-5	1.8e-1	0.10	9.5e-2
Family	SVL	OUM	1.95	1.79	1.84	1.3e-3			8.7e-2		
Family	HeLe	OUMV	0.64	0.63	0.63	4.1e-4	1.8e-4	1.3e-4	0.15		
Family	HeWi	OUMA	0.63	0.56	0.57	1.8e-4			7.0e-2	5.7e-2	5.3e-2
Family	FoLi	OU1	0.76			1.1e-4			0.13		
Family	HiLi	OUM	0.85	0.87	0.87	7.27e-5			1.39e-1		
Family	DiLi	OUMV	0.54	0.63	0.64	8.4e-4	1.1e-4	1.7e-4	6.5e-2		
Family	AxGr	OUMV	0.85	0.80	0.82	1.0e-4	6.0e-5	2.1e-4	0.14		

mm) species, representing a 2.7-fold increase in size. The SVL reconstruction shows that the ancestor of the family may have had around 71 mm of SVL (Figure 2), very close to the optimal size for omnivores. This result supports the likelihood that the common ancestor could have been omnivorous. Additionally, the rest of the traits tend to show the same outcome, except for hind limb length (Supplementary Figure 2). *Phymaturus* evolved to the largest sizes, *Ctenoblepharys* to a lower medium size, and *Liolaemus* evolved a wide range of sizes showing the greatest variation in SVL of the three genera.

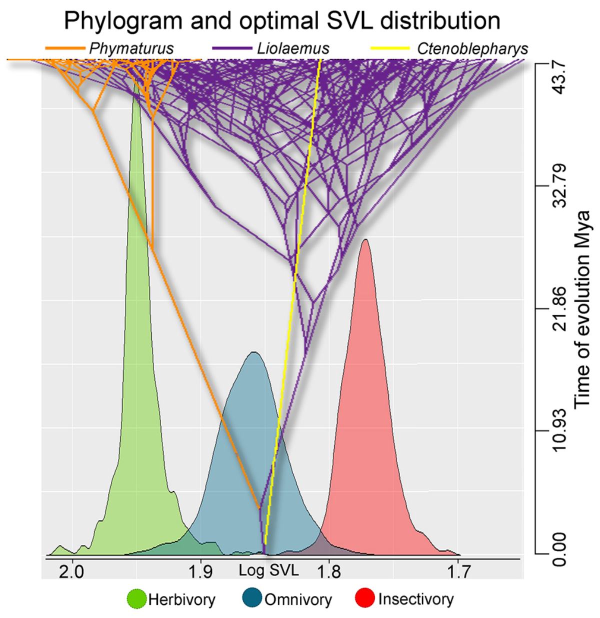

FIGURE 2
Snout–vent length (SVL) evolution in Liolaemidae, phenogram of the ancestral reconstruction of SVL where the values on the x-axis are in logarithm, and the y-axis shows the evolution time of the trait. Histograms are the values of the optimal sizes θ for each diet estimated with Ornstein–Uhlenbeck models. The ancestral reconstruction of the (SVL) of the common ancestor of the family, suggests that it may have had a size very close to the optimal value for omnivorous species. There is a significant variation in size ranges between the genera *Phymaturus* and *Liolaemus*, indicating that the latter has acquired a wide variety of sizes beyond the optimal ranges.

3.3 Phylogenetic PCA

Phylogenetic PCA shows that herbivory has a particular body and head shape that differentiates it from omnivory and insectivory (Figure 4). In the head analysis, the principal component 1 explains 87% of the variation, and both head width and length are good traits to separate groups. In the results of the body the principal component 1 explains 58% of the variation, and difference between limbs is a good trait to separate groups (Table 4).

4 Discussion

Our findings elucidate that the evolution of distinct dietary regimes steered the Liolaemidae family towards optimal head and body morphologies, underscoring the presence of both adaptive and non-adaptive evolutionary processes in size and body form within its two most abundant genera. These evolutionary optima manifest with greater clarity when considering the entire family. Herbivorous species emerge as the lizard subgroup exhibiting the most pronounced morphological variations attributable to dietary adaptation. Head width emerges as a pivotal trait, notably distinguished by its differential response to interacting selective forces.

Our results support the hypothesis that diet evolution has driven the evolution of three optimal body sizes in the family. Pincheira-Donoso et al. (2015) previously examined body size in the genus *Liolaemus* in search of an adaptive radiation pattern. They found that this trait was best explained by an OU stabilizing selection model with three distinct evolutionary optima (e.g., OUM). These three optimal body sizes closely align with our results, differing only in the central

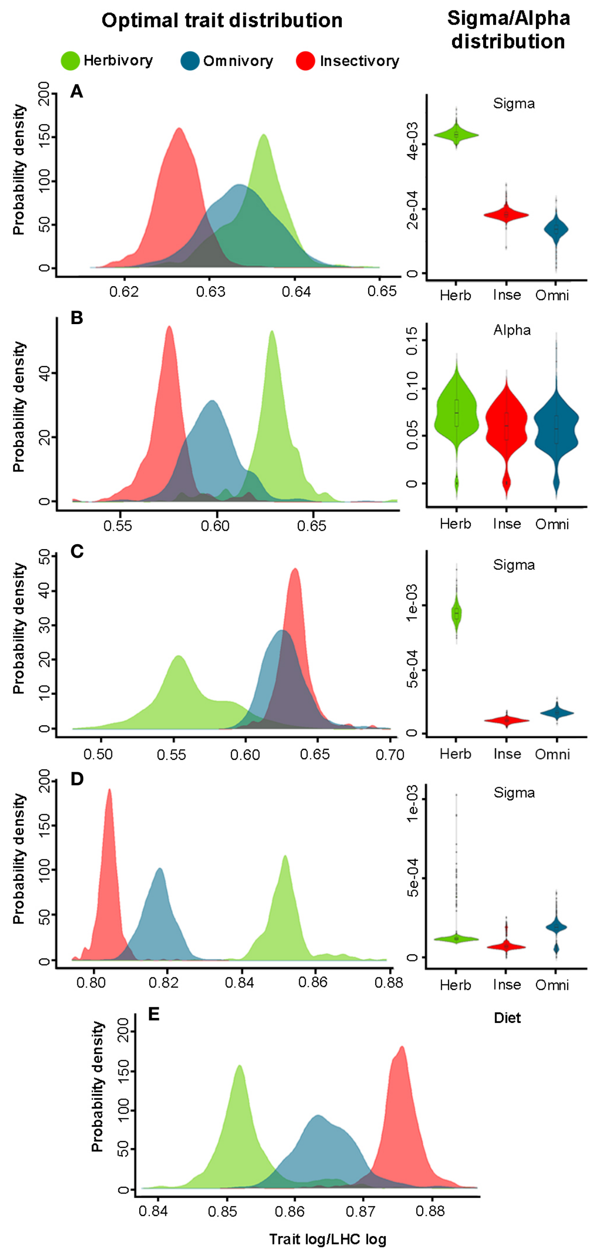

FIGURE 3
Differences in θ, σ^2, and α among three types of diets in Liolaemidae, where **(A)** is head length, **(B)** Head width, **(C)** differences in limbs, **(D)** axial growth length, **(E)** hindlimbs length. Herbivorous species exhibit larger heads and bodies, while their limbs are smaller. Her σ^2 rate was higher in head and limb traits, as well as the selective force α on head width.

value. In our analysis, it corresponds to the size of omnivorous diets (70 mm in this study compared to 80 mm in Pincheira-Donoso et al., 2015). It's worth noting that their study focused solely on the *Liolaemus* genus (109 species), yet our analysis encompasses all three genera and a larger portion of the family (187 species). Therefore, the difference in SVL optima for omnivores could potentially be attributed to sample size bias. In this context Cooper and Vitt (2002) examined herbivory and body size across 450 species from 23 lizard families, although their primary goal was not to identify evolutionary optima, their results indicated that the majority of herbivorous species closely approached the optimum size value we report here (Cooper Jr. and Vitt, 2002). Similarly, Van Damme (1999) analyzed 97 populations representing 52 species within the Lacertidae family and found body size averages very much in line with our findings for herbivorous and insectivorous diets (Van Damme, 1999). These results suggest that the Liolaemidae family can serve as a representative model for lizards in general.

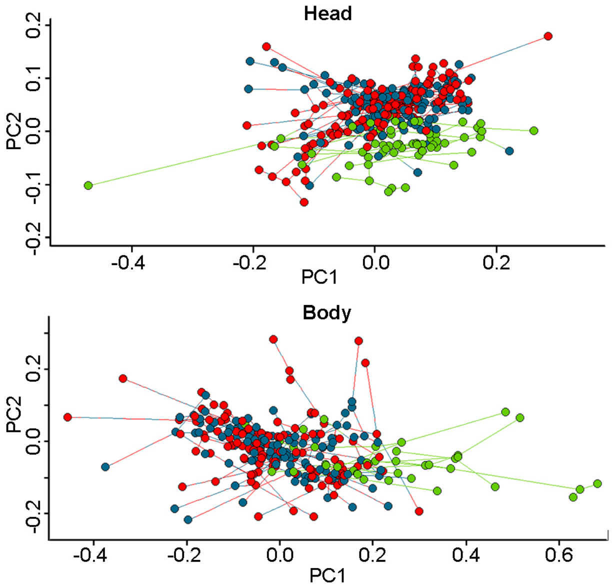

FIGURE 4
Phylogenetic morphospace of the traits measured in the head and body of the different species of the Liolaemidae family. Green points represent herbivorous species, blue points omnivorous, and red points insectivorous. In both graphs, herbivorous species tend to diverge from the other diets, while insectivores and omnivores do not show significant morphological differences.

Reconstruction of the evolution of diet in Liolaemidae showed that the common ancestor of the family is likely to have been omnivorous, challenging what was found previously by other authors (Espinoza et al., 2004; Ocampo et al., 2022). This result might be far from conclusive, because probabilities of the three diet types at the ancestral node are very similar in value. In addition, the combination of diet and genetic data of almost half of the Liolaemidae family has yet to be completed for definitive analysis and conclusion. However, our reconstruction of the SVL size of the common ancestor (55% representativeness) support our result that the ancestor could have been omnivorous, increasing this probability, and this makes a lot of sense, since there is more likely to be a transition from omnivore to herbivore or insectivore, allowing the divergence of the family in three genera with different diets (Ocampo et al., 2022).

The analyses of evolutionary optima in SVL related to diet in *Liolaemus* and *Phymaturus* (analyzed separately) reveal distinct patterns of radiation within each genus. *Phymaturus* showed evidence of widespread evolution toward a single optimum in morphology and body size in relation to diet, exhibiting lack of clade variation in resource usage. This finding aligns with previous studies that indicate minimal ecological differentiation in reproduction coupled with limited dispersal ability (Scolaro et al., 2013; Pincheira-

TABLE 4 Summary statistics and phylogenetic PCA factor loadings for morphological traits.

Head analysis	PC1	PC2
Eigenvalues	2.09E-4	3.07E-5
Variation explained (%)	0.87	0.13
Standard deviation	0.01	0.01
HeLe	−0.95	0.31
HeWi	−0.91	−0.41

Body analysis	PC1	PC2	PC3	PC4
Eigenvalues	2.08E-4	8.54E-5	6.21E-5	2.84E-6
Variation explained (%)	0.58	0.24	0.17	0.01
Standard deviation	0.01	0.01	0.01	0.00
FoLi	−0.02	0.99	0.08	0.11
HiLi	−0.65	0.72	−0.12	−0.22
DiLi	−0.99	−0.10	0.03	0.03
AxGr	0.03	−0.02	0.99	−0.03

Abbreviations are listed in methodology. The length and width of the head, the length of the hind limbs, and the difference in length between limbs are the traits that best explain the separation between the groups.

Donoso et al., 2015; Scolaro et al., 2016; Reaney et al., 2018). Altogether, these patterns support the evidence of non-adaptive radiation observed in their range distribution and habitat use (Scolaro and Pincheira-Donoso, 2010). This genus is nearly invariably viviparous, herbivorous, and saxicolous, with species often isolated due to their dependence on these rocky outcrops as their habitat (Ibargüengoytía et al., 2008; Díaz, 2009). Conversely, *Liolaemus* shows multiple optimal sizes associated to head width in relation to each diet type which accounts for the great variation in resource use within the genus. The head represents a remarkably complex part of the body due to its multifunctionality, encompassing feeding, breathing, vision, chemoreception, defense, combat, sexual attraction, brain protection, and communication (Herrel et al., 2001; Lappin and Husak, 2005; Kohlsdorf et al., 2008). For all these functions, the head is subject to diverse and intricate selective forces that may sometimes be in conflict (Kohlsdorf et al., 2008). The optimal head shape observed in herbivores in this study aligns with the morphological requirements for acquiring and consuming plant material, which is characterized by large heads (Herrel, 2007). The pterygoid, the largest jaw muscle in lizards (Gröning et al., 2013), provides substantial bite force and is highly developed in herbivorous species, enabling efficient reaping of tough, fibrous items such as leaves (Herrel, 2007). In contrast, insectivorous species exhibit smaller heads, offering less bite force but potentially enhancing agility for capturing mobile prey (Herrel, 2007). On the other hand, the distinct optima found in axial development for each dietary type in *Liolaemus* are accompanied by a clear separation of herbivorous species from the other diets. This trait developed at a slower rate but with higher selective pressure. Selective pressures interacting with body size can be of various types and may be in opposition, but they can also be related to the type of food consumed (Tennis et al., 1979; Winne et al., 2010). *Liolaemus* exhibits greater ecological differentiation in its reproduction, diet, habitat use, dispersal among others (Pincheira-Donoso, 2011; Pincheira-Donoso et al., 2015; Edwards et al., 2022). Therefore, it is undoubtedly a completely different type of radiation than *Phymaturus*. The great ecological differences related to resource use as basis for divergent selection, couple with the frequent convergence in morphology and body size associated with diet evolution, further supports an adaptive radiation-based diversification of the genus. This opens up a huge possibility for further evolutionary studies using this family as an example group given the contrasting evolutionary patterns found across clades.

In the family, most traits exhibited a higher rate of change (σ^2) in herbivores, possibly due to increased selective pressure, as indicated by our results on head width. This finding is of particular interest as it supports the hypothesis that head morphology evolves more rapidly than overall body shape, a pattern observed in the evolutionary history of various species, including tyrannosaurids, geckos, and finches (Grant and Grant, 2002; Stokstad, 2004; Eloy de Amorim et al., 2017). Another example of this pattern can be found in human evolution, where changes in brain size and reductions in bite force due to dietary shifts have significantly influenced body shape and size (Aiello and Wheeler, 1995; Lieberman, 2011). Changes in evolutionary rate (i.e., σ^2) with a change in diet can trigger a series of morphological and physiological adaptations, including an extended intestinal length (Pincheira-Donoso, 2021); including the presence of colonic valves in the intestines, which slow down food passage to facilitate digestion by the necessary intestinal flora for cellulose degradation (Iverson, 1982), and symbiotic associations with other organisms (bacteria and protozoa) aiding in the digestion of plant material (Cooper Jr. and Vitt, 2002; Espinoza et al., 2004).

The relatively high variation observed between front and hind limbs is indicative of the need to change body morphology to adopt a novel foraging strategies and habitat utilization with a change in diet (Miles et al., 2007). Our findings indicate that herbivorous species tend to adapt towards shorter limbs with minimal variation between them. An herbivorous diet often involves less active food searching (Cooper Jr., 1995). Conversely, omnivorous and insectivorous species exhibit longer hind limbs, which enable them to run faster and capture mobile prey, sometimes even resorting to bipedal locomotion (Losos, 1990; Irischick and Jayne, 1999; Aerts et al., 2003; Miles et al., 2007). Notably, omnivores display longer forelimbs, which could represent an intermediate stage between insectivores and herbivores. According to our results, they seem to be in the process of reducing the variation between forelimbs and hind limbs to achieve the body proportions of herbivores. The transition from insectivory to herbivory through omnivory was also reported by Ocampo et al. (2022). Losos et al. (2000) have proposed that limb length can be influenced by various factors, including differences in microhabitat utilization, given its considerable phenotypic plasticity (Losos et al., 2000). It is important to note, however, that intrapopulation variation of a trait typically does not surpass the species baseline morphology. Furthermore, this trait in limb length may be subject to strong exaptation, representing a product of an original and suitable function (Revell et al., 2007) such as dietary adaptation.

The phylogenetic PCA highlights significant differences in head and body morphology from herbivorous species compared to the other two diets, underscoring the implications of physical and physiological adaptations associated with this dietary type (Iverson, 1982; Espinoza et al., 2004; Ocampo et al., 2022). The shift to herbivory represented a pivotal innovation within the family, enabling them to exploit new ecological niches in their environment (Miller et al., 2022). Notably, aside from SVL, traits of omnivorous species closely resemble those of insectivores. This observation may be linked to the rapid and drastic morphological changes in the head that accompany the transition to herbivory, while changes in size occur more gradually.

5 Conclusion

Our findings underscore the significant role of diet in shaping the evolution of body form within the Liolaemidae lizard family, giving rise to distinct optimal body shapes corresponding to each dietary preference. While factors such as sexual selection, predation, competition, and others also exert considerable influence on this process, diet emerges as a consistent and prevalent driver in this group. The influence of diet evolution and the evolution of Liolaemidae can be observed when we compare diet evolution at the clade level (i.e., genus level). When diet change very little though evolution, such as in *Phymaturus*, the is low morphological variation and the high diversification does not reflect adaptive radiation. *Phymaturus* has been previously described as a genus that evolved through non-adaptive radiation (Reaney et al., 2018). On the contrary, when diet evolution shows great diversity (e.g., the evolution of three diet types), it is repeatably convergent and has generated great morphological and size variation across species, high diversification is linked to adaptive radiation *vis a vis* the use of food resources.

The rapid evolution of head relative to body length in herbivores presents a compelling avenue for future research. Furthermore, the remarkable diversity within the Liolaemidae family, coupled with its broad spectrum of habitat utilization, positions it as a valuable representation of the entire lizard group.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

MO: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. DP: Conceptualization, Supervision, Writing – review & editing. RR: Conceptualization, Methodology, Supervision, Writing – review & editing, Formal Analysis.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1361799/full#supplementary-material

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