

Contents lists available at ScienceDirect

Zoologischer Anzeiger



journal homepage: www.elsevier.com/locate/jcz

Head shape divergence between parthenogenetic and their paternal bisexual rock lizards in sympatry

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ARTICLE INFO

Keywords: 3D geometric morphometrics Morphology Darevskia

ABSTRACT

Head shape plays a crucial role in ecological and evolutionary processes in lizards, and scientists have studied head shape using traditional and 3D geometric morphometrics. Lizards are classic subjects for ecological studies because closely related and ecologically similar species coexist. Sympatric species tend to show higher levels of morphological divergence compared to allopatric species.

In this study, we focus on two parthenogenetic Darevskia species (Darevskia dahli and Darevskia armeniaca) that share a maternal species, Darevskia mixta, but have different paternal species (Darevskia portschinskii and Darevskia valentini). We aim to assess the relative importance of morphologically inheritable traits and environmental conditions on head shape in these parthenogenetic species. Specifically, we aim to determine whether local adaptations or intermediate phenotypes between parental species drive head shape variation in parthenogens. To accomplish this, we analyze the head shapes of samples from both parthenogens, their paternal species, and their common maternal species from 3 sites in Georgia. Our study shows that certain aspects of head shape are associated with body size and habitat climate, with high mountain species exhibiting larger and deeper heads with stronger jaws regardless of breeding mode. In addition, both parthenogens exhibit narrower and more elongated jaw areas, flatter mandibles, and thus weaker jaws compared to females of their maternal and paternal species.

1. Introduction

Head shape is an important feature in lacertid lizards. There are relationships between the morphology of lizards (head size or any other body parts) with bite force capacity, prey handling efficiency, microhabitat use (Herrel et al., 2004; Barros et al., 2011; Verwaijen et al., 2002; Oliveira et al., 2023), even with breathing and brain protection (De Meyer et al., 2019). Simultaneously, morphological variations in lizard heads are related to environmental and ecogeographic variations. For example, the altitude and/or temperature has been shown to affect the head length (Ortega et al., 2019) and shape (Alagić et al., 2021) in some Podarcis lizards; geographic gradient on Tenerife island affects the head shape of Lacertid Gallotia galloti (Thorpe and Baez, 1987). Besides these functions, one of the largest drivers of head shape variation are phylogenetic relationships of the species (Openshaw and Keogh, 2014; De Meyer et al., 2019). Closely related lizard species resemble each other more than distantly related ones (Openshaw and Keogh, 2014), the phenomenon generally referred to as phylogenetic signal in morphological traits (Blomberg et al., 2003; Tarkhnishvili et al., 2020a).

When closely related ecologically similar species coexist, their morphologies tend to diverge due to competition and/or reinforcement, and the level of divergence is commonly higher compared to areas of allopatry (Taylor, 1965; McDowall, 1998; Wijesundara and Freed, 2018), e.g. fish from the genus Paragalaxias from a lake of submontane Tasmania (McDowall, 1998), brown frogs from the Caucasus (Rana macrocnemis complex) (Tarkhnishvili et al., 2001), songbirds from the genus Zosterops in Sri Lanka (Wijesundara and Freed, 2018).

Some lizard groups include both parthenogenetic and bisexual forms (Lowe and Wright, 1966; Darevsky, 1967; Moritz, 1991; Adams et al., 2003; Tarkhnishvili et al., 2010; Petrosyan et al., 2020). Parthenogenetic species are usually of hybrid origin and share genes from both maternal and paternal ancestors. It is not clear whether the parental

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https://doi.org/10.1016/j.jcz.2024.06.002

Received 21 February 2024; Received in revised form 4 June 2024; Accepted 10 June 2024 Available online 18 June 2024

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species are able to contribute their genes to the parthenogenetic vertebrate lineages after the initial hybridization (Tarkhnishvili et al., 2020b), and whether or not the hybrid origin is reflected in the morphology of the daughter species. Parthenogenetic daughter species often do not show intermediate morphological characteristics, despite their intermediate genome (Heiser Jr et al., 1965; Bemis et al., 1970; Pembleton and Baker, 1978; Parker Jr, 1979). For example, *Aspidoscelis tesselatus* (formerly–*Cnemidophorus*) resembles more its maternal species *Aspidoscelis gularis* in size than the paternal species *Aspidoscelis tigris*, although it is more widely sympatric with the latter one.

One of the groups, combining sexually breeding and parthenogenetic species, are Caucasian rock lizards (*Darevskia*) (Arribas, 1999), found mainly in the Greater and Lesser Caucasus Mountains. Parthenogenetic species (*Darevskia dahli* and *Darevskia armeniaca*) are phenotypically similar to female individuals of their paternal species, coexist in some locations and share a similar diet in rocky habitats (Darevsky, 1967; Bakradze, 1977; Tarkhnishvili, 2012), but never overlap spatially with maternal species *Darevskia mixta* (Tarkhnishvili et al., 2010).

In this paper, we focus on two parthenogenetic Darevskia-D. dahli (Darevsky, 1957) and D. armeniaca (Méhely, 1909), who share the maternal species D. mixta (Méhely, 1909), but have different paternal species, Darevskia portschinskii (Kessler, 1878) and Darevskia valentini (Boettger, 1892). D. dahli and its paternal species D. portschinskii, coexist in the mountain forest belt of central Georgia, 800-1200 m a.s.l. (Tarkhnishvili et al., 2010; Barateli et al., 2022) and the average length of adult individuals of both species varies between 5.4 and 5.8 cm. Relatively bigger-bodied, D. armeniaca and its paternal species D. valentini, coexist at elevations 1900-3100 m a.s.l. (Arakelyan et al., 2011; Galoyan et al., 2019; Barateli et al., 2022) with average body length-6.1-6.4 cm. D. mixta, an endemic species of Georgia (Gabelaia et al., 2017; Petrosyan et al., 2020), is distributed from 300 to 2100 m a. s.l (Ciobanu et al., 2003; Tarkhnishvili, 2012; Gabelaia et al., 2015). The average body length of D. mixta varies between 4.9 and 6.3 cm (Darevsky, 1967). The paternal species are closely related, but ecologically and morphologically distinct (Darevsky, 1967; Murphy et al., 2000) (Fig. 1). For example, according to Darevsky (1967) D. valentini has a large central temporal scale, while in D. portschinskii it is smaller or absent. Also, the postorbital or postfrontal bones are similar in length in most D. valentini and D. portschinskii, but unlike D. valentini postocular is either greater or equal to postfrontal in D. portschinskii (Arribas et al., 2022).

We tried to infer the relative importance of genetic inheritance and environmental conditions on the head shape of *D. armeniaca* and *D. dahli*. Specifically, if adaptations to local geographic conditions play an important role, one should expect a higher similarity of the parthenogens with females of the paternal species, with whom they commonly coexist, than with the females of the maternal species, which never share the habitat with the parthenogens. On the other hand, the phenotype of the parthenogens may be just intermediate between the two parental species, or show some specifics common for the parthenogenetic lineages but absent in the bisexual forms. For this purpose, we analyzed the head shapes of samples of both parthenogens (*D. dahli* and *D. armeniaca*), two paternal species from the same locations



Fig. 1. Cladogram of studied species, representing the maternal parent species (*Darevskia mixta*) of both parthenogenetic species (marked in red). Based on Murphy et al., 2000; Yanchukov et al., 2022. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(*D. portschinskii* and *D. valentini*, respectively), and their joint maternal species, *D. mixta*, from a separate location in Georgia.

2. Material and METHODS

In June–July 2018 and 2023, we collected 60 female adult individuals of five lizard species from three locations in Georgia (Table 1). Since male and female individuals of most *Darevskia* show significant sexual dimorphism in head shape, we used only female individuals from bisexual species to compare with unisexuals (Tarkhnishvili et al., 2020a). The Ilia State University Commission ethically approved all procedures with live animals for Ethical Issues and were in accordance with Article 259 of Georgian Criminal Law. General anesthesia of the lizards was used to avoid killing the animals collected in the wild. After photographing, the lizards were released to their natural habitats.

For morphological studies, we placed the individual in a plastic tube with its head pointing upwards and secured it to prevent movement. The tube was placed in the center of a cardboard circle. We then photographed 36 times from a perspective of 90° to the midline and 36 times from a perspective of 45° to the midline, moving the camera around the lizard every 10° (Fig. 2). The images were uploaded to AgiSoft Photo-Scan Pro v.2.0.2 (Agisoft, 2023), which first aligned the images in 3D space and then generated 3D models of the head surface onto which 54 homological landmarks were subsequently digitized (Fig. 3). Then we exported the 3D coordinates in a "Survey points" format and imported them in R studio (R 4.2.0, 2022) for the analysis. Missing landmarks were estimated using the function "estimate.missing" and landmarks were aligned using the "gpagen" function. We extracted symmetric components using the function "bilat.symmetry" and checked it for outliers using "plotOutliers". To illustrate the levels of differences in head shape between the individuals we conducted a principal component analysis (PCA). PCA simplifies multidimensional data by reducing dimensions to two or three, facilitating the visualization and comprehension of relationships between data points (Richardson, 2009; Paul et al., 2013). To visualize which shape patterns were reflected in these ordinations, and thus which were the most discriminating shape differences between groups, we generated landmark wireframes that reflect principal component (PC) axis variation from a PCA on the total dataset of the 54 original landmarks in R studio (R 4.2.0, 2022). The used package was "geomorph" (Adams et al., 2016; Baken et al., 2021).

In order to test for significant differences between species head shapes, we used the Procrustes aligned landmark configurations and ran Procrustes Anova with Species as terms using "lm.rrpp" in the package "RRPP" (Collyer and Adams, 2018, 2023). This function uses ordinary least squares (LS) to compute the effect coefficients by performing the randomized residual permutation (Collyer et al., 2015). Afterward, we checked if the LS means of each pair of species were significantly different using the "pairwise" function in "RRPP".

Since studied individuals substantially differ in body size, we repeated the test and included the body size in the model as a covariate to make sure the observed interspecific differences were not influenced by allometric trends. We checked in prior the model shape $\sim \log(SVL) + \text{species} + \log(SVL)$:species to make sure there is no significant difference

Table 1

Sample sizes and key characteristics of three sampling locations of 5 species of *Darevskia*.

	Location	Easting	Northing	Altitude a.s.l.	Female
D. dahli	Kojori	44.683337°	41.648891°	1120	13
D. portschinskii	Kojori	44.683337°	41.648891°	1120	11
D. armeniaca	Sagamo Lake	43.730600°	41.293600°	2015	16
D. valentini	Sagamo Lake	43.730600°	41.293600°	2015	15
D. mixta	Rveli	43.416361°	41.871489°	824	5



Fig. 2. Set–up for photographing the head of an immobilized lizard at different degrees and angles.

between the allometric trends of each species. After running ANCOVA, we predicted the head shape means based on the fitted values of the model and by keeping the body size associated head shape component constant. For that, we used the "predict" function in "RRPP". All calculations were done in the R studio (R 4.2.0, 2022).

3. Results

3.1. ANOVA test on head shape

The Procrustes ANOVA and pairwise tests based on the head symmetric landmarks significantly separated all studied species pairs. According to the effect sizes (Z), females of *D. valentini* are better separated from both parthenogenetic species, *D. dahli* and *D. armeniaca* than *D. portschinskii*. *D. mixta* is in general more similar to the parthenogenes than both paternal species (Table 2).

Species exhibited an allometric effect on head shape, but it was not significantly different between the studied species (p = 0.09), so we excluded the interaction effect (logSVL:species) from the model and reran the model as shape $\sim \log(SVL) + \text{species}$. After correcting for body size, *D. mixta* and *D. armeniaca* were not significantly differentiated (Table 3). The rest of the species had a similar pattern to the previous test, e.g. *D. valentini* was most strongly separated from both parthenogenetic species, then *D. portschinskii* and *D. mixta* (Table 3).

3.2. Principle component analysis of head shape

Principal Component Analysis (PCA) resulted in five meaningful components comprising 73 % of the total variation.

Shape variation in PC1 (29 % of the total variation) was mainly concentrated in the jaw area. It varied from a narrow and elongated head shape with a flattened mandible in the jaw area (lower PC1 scores) to a wide and shortened head with a deepened mandible in the jaw area (higher PC1 scores). The PC1 axis separated *D. valentini* (higher PC scores) from *D. dahli* and *D. armeniaca* (lower PC scores), while *D. mixta* and *D. portschinskii* had intermediate scores on this axis (Fig. 4). In short,



Fig. 3. Digitized three-dimensional landmarks. Landmarks are shown with black numbers. A-dorsal view of the head; B-ventral view of the head; C-view of the right profile of the head; D-view of the left profile of the head. The specimen in the photograph is Darevskia armeniaca.

Table 2

Results for Procrustes ANOVA for the model shape ~ species, and pairwise distances between the Least Square means on only female individuals. The statistics are performed based on randomized residual permutations. The abbreviations in the Anova table: Df-degrees of freedom, SS–Sum of Squares, MS–Mean Squares, Rsq–R–squared, F–effect size, Z–effect size which is a standard deviation of observed statistics from distributions of random outcomes, Pr (>F)–P value of the F statistics. Abbreviations in the pairwise test table: d–the difference between Species Least Square means, UCL–upper confidence limits, Pr > d–P value of the difference between Species Least Square means.

ANOVA table	Df	SS	MS	Rsq	F	Z	Pr(>F)
species	4	0.085	0.021	0.482	12.8	9.4	0.0001
Total	55 59	0.091	0.002	0.518			
Pairwise tests		d	UCL (95 %)		Z-effect Size		$\Pr > d$
armeniaca:dahli		0.048	0.028		3.7		0.0001
armeniaca:mixta		0.054	0.039		3		0.0011
armeniaca:portschinskii		0.061	0.03		4.5		0.0001
armeniaca:valentini		0.067	0.028	8	5.1		0.0001
dahli:mixta		0.051	0.04		2.7		0.0029
dahli:portschinskii		0.052	0.031		3.6		0.0001
dahli:valentini		0.07	0.029		5		0.0001
mixta:portschinskii		0.059	0.04	1	3.1		0.0007
mixta:valentini		0.066	0.039	9	3.9		0.0001
portschinskii:valentini		0.062	0.03		4.4		0.0001

Table 3

Results for the linear model shape $\sim \log(SVL) + \text{species}$, and pairwise distances between the means on only female individuals with its statistics. The abbreviations in the linear model table: Df-degrees of freedom, SS–Sum of Squares, MS–Mean Squares, Rsq–R–squared, F–effect size F, Z–effect size, Pr(>F)–P value of the F statistics. Abbreviations in the pairwise test table: d–the difference between Species Least Square means, UCL–upper confidence limits, Pr > d–P value of the difference between Species Least Square means.

Anova table	Df	SS	MS	Rsq	F	Z	Pr(>F)
logsvl	1	0.022	0.022	0.126	13.4	5.2	0.0001
species	4	0.065	0.016	0.369	9.9	7.4	0.0001
Residuals	54	0.089	0.002	0.505			
Total	59	0.176					
Pairwise tests		d	UCL	(95 %)	Z-effect	t Size	$\Pr > d$
armeniaca:dahli		0.044	0.032		2.9		0.001
armeniaca:mixta		0.043	0.045		1.4		0.0758
armeniaca:portschinskii		0.058	0.042		2.9		0.0011
armeniaca:valentini		0.07	0.029		4.7		0.0001
dahli:mixta		0.049	0.039		2.6		0.0035
dahli:portschinskii		0.053	0.032		3.4		0.0001
dahli:valentini		0.072	0.04		3.8		0.0001
mixta:portschinskii		0.06	0.03	9	3.2		0.0001
mixta:valentini		0.064	0.05	4	2.3		0.0091

both parthenogens had narrower and more elongated jaws and flatter mandibles than the females of any of their ancestral species.

PC2 (16 % of the total variation) varied from a long dorsal head with a shorter and flatter mandible and in general flat head (low PC2 scores) to a short dorsal head with a longer and deeper mandible and overall deeper head shape (high PC2 scores). It separated *D. portschinskii* and partially *D. dahli* (lower PC2 scores) from *D. armeniaca* and *D. valentini* (higher PC2 scores). *D. mixta* was grouped with *D. valentini* and *D. armeniaca*, but leaned toward intermediate scores on the PC2 axis (Fig. 4). PC2 positively correlated with the log-transformed snout-vent-length (Pearson's R = 0.62) (Fig. 5).

PC3 (15 % of the total variation) varied from the deep head with rounded dorsal and deep mandible (low PC3 scores) to the flatter head and wide and flatter mandible (high PC3 scores). PC4 (8 % of the total variation) varied from a shorter and laterally more curved (outwards) mandible and narrow dorsal head (low PC4 scores) to a longer and inward–curved mandible and wider dorsal head (high PC4 scores).



Fig. 4. Principal component analysis (PCA) score plot. Black lines represent maximum PC values and gray-minimum PC values. PC1-shows that *D. valentini* has a wider head, while according to PC2–*D. dahli* and *D. portschinskii* have longer and flatter heads, with slightly wider jaw areas. The numbers in the parentheses represent the percentage from the total variation for each axis.



Fig. 5. Principal component analysis (PCA) score plot. PC3 overlaps in all species. PC4 shows that *D. dahli* has a longer and flatter mandible and a larger/ broader interparietal scale compared to the other four species. The numbers in the parentheses represent the percentage from the total variation for each axis.

Combined, PC3 and PC4 axes separated *D. mixta* from both parthenogens and *D. valentini*, with *D. portschinskii* keeping the intermediate position (Fig. 5).

To visualize the morphospace after excluding the effect of body length on head shape, we used the fitted values from the model shape $\sim \log(\text{SVL}) + \text{species}$ and predicted the 95 % confidence intervals for the mean shape of each species, by keeping the body length effect on the head shape constant (Fig. 6). The 73 % of the total allometry–free shape variation showed that maternal *D. mixta* is much closer based on the head shape to the parthenogenetic species, than paternal *D. valentini* and *D. portschinskii*. Also, *D. valentini* and *D. armeniaca* are less similar to each other than *D. portschinskii* and *D. dahli* (Fig. 6).

4. Discussion

To summarize our results, there is no clear reflection of mixed genetic ancestry in the head shape of the parthenogens, although they have more affinity to females of the maternal, than of the paternal species. Simultaneously, there are certain specifics of head shape associated with



Fig. 6. 95 % confidence ellipses of the predicted values for species means generated by bootstrapped residuals. Residuals are derived from the model fit with the formula: shape $\sim \log(SVL) + \text{species}$.

body size and/or climate of the habitat (high mountain species are bigger irrespective of the breeding mode and have deeper heads with stronger jaws). Besides, both parthenogens have narrower and more elongated jaw areas with flatter mandibles, hence weaker jaws than females of their respective paternal and maternal species. For example, *D. armeniaca* from Sagamo Lake have stronger jaws and deeper heads than low elevation inhabiting species, but weaker (narrower) jaws compared to females of paternal *D. valentini*, which also live at Sagamo Lake.

The morphological variation of lizard species is influenced by genetic (e.g. gene drift, mutations) as well as environmental factors (e.g. temperature, humidity, food availability, etc.) (Runemark et al., 2010; Oliveira et al., 2023). According to Adams (2011), despite shared selection pressures, different genetic patterns could drive unique head--shape evolution in Plethodon salamanders. If the environment has a substantial impact on head shape in Darevskia, we should expect higher similarity of the parthenogens with females of the paternal species, with whom they commonly coexist, than with the females of the maternal species, with whom they never share the habitat. Simultaneously, the previous morphological studies on parthenogenetic hybrids show that unisexual species tend to exhibit an intermediate morphological resemblance to either both parental species or a closer resemblance to one of them (Espeche et al., 2023). According to studies on parthenogenetic Teius suquiensis, it demonstrated intermediate morphological traits compared to bisexual T. teyou and T. oculatus (Espeche et al., 2023), whereas parthenogenetic A. tesselatus is morphologically more similar to its maternal than to the paternal species (Parker Jr, 1979).

Our study suggested a complex interaction of inheritance and environment in the determining head shape of the parthenogens. The general shape, relative size and depth of the head, and size of jaws are correlated with the body size of the individuals, which in turn is under the strong influence of climate and elevation (Darevsky, 1967). Indeed, body size growth with the elevation and related temperature and precipitation is shown for many *Darevskia* species, including the studied *D. valentini*, and other *Darevskia*, such as *Darevskia caucasica*, *Darevskia*

parvula (Darevsky, 1967; Volynchik, 2014; Bülbül et al., 2016) and some other lizard species, such as *Podarcis liolepis* (Ortega et al., 2019), *Liolaemus* spp. (Pincheira–Donoso et al., 2008). This is most likely a simple pattern following Bergmann's rule (1847), suggesting that a decrease in surface/volume ratio makes body temperature better controlled because heat loss is slower. However, this is not the sole trend in lizards (Ashton and Feldman, 2003), e.g. lacertid *Eremias argus* shows the reverse of Bergmann's rule (Deme et al., 2023). Many squamates at higher altitudes have larger individuals of the same species than at lower altitudes. Obviously, head shape is linked with body size with allometric dependencies, which causes the inevitable shape change following the size change.

4.1. Differences between bisexuals and parthenogens

Even though there were slight differences in the sizes of D. dahli (SD-0.35) with D. portschinskii (SD-0.40) and D. armeniaca (SD-0.32) with D. valentini (SD-0.36), in addition to the latter two being much larger than the former two, the differences between the parthenogens and paternal species' females were clearly expressed in the degree of head and mandible width. The parthenogens have much narrower and elongated heads with flatter mandibles, whereas the paternal species have a stronger head shape, especially D. valentini. Moreover, these differences account for nearly one-third of the total variation in head shape, whereas body size-associated changes explain only 16 % of the variation. One potential reason for that could be behavioral differences between the parthenogens and their bisexual ancestors. Specifically, it was repeatedly shown that both males and females of bisexual rock lizards perform territorial behavior, forcing conspecific females to avoid occupied individual plots (Galoyan, 2011; Galoyan, 2013; Tsellarius et al., 2016; Barateli et al., 2021) and, wider jaws lead to stronger bites (Kohlsdorf et al., 2008; De Meyer et al., 2019), which is obviously important for successful defense of the territory. In contrast, parthenogens do not display territorial behavior, and having broad and strong jaws is way less important. Although the strength of the jaws may also be related to the size and morphology of most commonly consumed food organisms (Verwaijen et al., 2002), this is an unlikely explanation of the differences between coexisting parthenogenetic and paternal lizards, since the lizards are not specialized feeders and just consume invertebrates that are present in a specific habitat (Darevsky, 1967).

The impact of shared ancestry on the morphology of the parthenogens is way less clear. The body size of D. armeniaca and D. dahli is closer to their respective parental species than to the body size of the parental species of the other parthenogen; however, this can equally be a result of the concurrent adaptation of a parthenogen and its parental species to a similar environment. Procrustes ANOVA analysis showed a higher similarity of size-removed head shape of the parthenogens, especially that of D. armeniaca, to their maternal D. mixta than to the females of the patrilineal ancestors. A stronger maternal effect on the head shape is recorded for some other squamates, including parthenogenetic lizard A. tesselatus (Parker Jr, 1979) or meadow viper (Vipera ursini rakosiensis) (Oliveira et al., 2023). Noble et al. (2014) had shown experimentally that maternal effect rather than simple Mendelian inheritance determines body size and some behavioral characteristics in skinks. Maternal effect can explain the higher similarity of the parthenogens to their matrilineal than to the patrilineal ancestors. On the other hand, females of some of the parental species may be less territorial than the others, dependent on their habitat type (e.g. D. mixta is more broadly using various microhabitat types than D. valentini and especially D. portschinskii, which are strict rock dwellers (Darevsky, 1967; Tarkhnishvili, 2012)), and parallel behavioral adaptations could explain different degree of similarity between the parthenogens and their ancestors rather than direct ancestral influence. Detailed behavioral observations on these species may shed light on this question in the future.

In summary, some characteristics differentiate the parthenogens from their bisexual ancestral species, and others are associated with body size and elevation of typical habitats. Although the effect of maternal species is also likely present, the impact of intermediate genetics or habitat type on head shape is shaded by the differences between the reproductive biology, which is not associated with aggressive territorial behavior in parthenogens, in contrast with their bisexual ancestors.

CRediT authorship contribution statement

Natia Barateli: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Mariam Gabelaia: Writing – review & editing, Visualization, Supervision, Software, Methodology, Formal analysis, Conceptualization. Giorgi Iankoshvili: Writing – review & editing, Investigation, Data curation. David Tarkhnishvili: Writing – review & editing, Methodology, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Natia Barateli reports administrative support and equipment, drugs, or supplies were provided by Ilia State University. Natia Barateli reports a relationship with Ilia State University that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgment

We would like to express our gratitude to Prof. Mzia (Ia) Zhvania and Dr. Nino Pochkhidze for giving us access to their research facilities. We would also like to thank Mr. Vasil Metreveli for generously allowing us to use personal computer for the development of the 3D models. We thank two anonymous reviewers for their valuable comments on the article. The study was funded by the Shota Rustaveli National Science Foundation of Georgia (award no. FR-23-17324).

References

- Adams, M., Foster, R., Hutchinson, M.N., Hutchinson, R.G., Donnellan, S.C., 2003. The Australian scincid lizard *Menetia greyii*: a new instance of widespread vertebrate parthenogenesis. Evolution 57 (11), 2619–2627.
- Adams, D.C., 2011. Quantitative genetics and evolution of head shape in *Plethodon* salamanders. Evol. Biol. 38 (3), 278–286.
- Adams, D.C., Collyer, M., Kaliontzopoulou, A., Sherratt, E., 2016. Geomorph: Software for Geometric Morphometric Analyses.
- Alagić, A., Krofel, M., Lazić, M., Žagar, A., 2021. Effects of biotic and abiotic stressors on asymmetries and head size in two sympatric lizard species. Anim. Biol. Leiden 71 (3), 329–347.
- Ashton, K.G., Feldman, C.R., 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57 (5), 1151–1163.
- Arakelyan, M.S., Danielyan, F.D., Corti, C., Sindaco, R., Leviton, A.E., 2011. Salt Lake City. Herpetofauna of Armenia and Nagorno–Karabakh. Society for the Study of Amphibians and Reptiles.
- Arribas, O.J., 1999. Phylogeny and relationships of the mountain lizards of Europe and Near East (Archaeolacerta Mertens, 1921, sensu lato) and their relationships among the Eurasian lacertid radiation. Russ. J. Herpetol. 6, 1–22.
- Arribas, O., Candan, K., Kornilios, P., Ayaz, D., Kumlutaş, Y., Gül, S., Yilmaz, C., Caynak, E.Y., Ilgaz, C., 2022. Revising the taxonomy of *Darevskia valentini* (Boettger, 1892) and *Darevskia rudis* (bedriaga, 1886) (squamata, lacertidae): a morpho-phylogenetic integrated study in a complex anatolian scenario. Zootaxa 5224 (1), 1–68.
- Baken, E.K., Collyer, M.L., Kaliontzopoulou, A., Adams, D.C., 2021. Geomorph v4. 0 and gmShiny: enhanced analytics and a new graphical interface for a comprehensive morphometric experience. Methods Ecol. Evol. 12 (12), 2355–2363.

- Bakradze, M.A., 1977. Sympatric Populations of Parthenogenetic and Bisexual Species of Rock Lizards of the Genus *Lacerta* in Georgia. PhD Dissertation. IV. Javakhishvili Tbilisi State University [In Russian].
- Barateli, N., Tarkhnishvili, D., Iankoshvili, G., Kokiashvili, L., Dvali, N., Janiashvili, Z., 2021. Fine-scale analysis of habitat occupancy by Kura lizard (*Darevskia portschinskii*) and its daughter parthenogenetic form (*Darevskia dahli*). HERPETOZOA 34, 71–81.

Barateli, N., Tarkhnishvili, D., Iankoshvili, G., Kokiashvili, L., 2022. Reproductive effort of unisexual and bisexual rock lizards (genus *Darevskia*). Zool. Anz. 301, 196–204.

- Barros, F.C., Herrel, A., Kohlsdorf, T., 2011. Head shape evolution in *Gymnophthalmidae*: does habitat use constrain the evolution of cranial design in fossorial lizards? J. Evol. Biol. 24 (11), 2423–2433.
- Bemis, W.P., Rhodes, A.M., Whitaker, T.W., Carmer, S.G., 1970. Numerical taxonomy applied to Cucurbita relationships. Am. J. Bot. 57 (4), 404–412.
- Blomberg, S.P., Garland Jr, T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57 (4), 717–745.
- Boettger, O., 1892. Kriechthiere der Kaukasusländer, gesammelt durch die Radde–Valentin'sche Expedition nach dem Karabagh und durch die Herren Dr. J. Valentin un P. Reibisch. Ber. Senck. Ges, pp. 131–150.
- Bülbül, U., Kurnaz, M., Eroğlu, A.İ., Koç, H., Kurrup, B., 2016. Age and growth of the red-belied lizard, Darevskia parvula. Anim. Biol. Leiden 66, 81–95.
- Ciobanu, D.G., Grechko, V.V., Darevsky, I.S., 2003. Molecular evolution of satellite DNA CLsat in lizards from the genus *Darevskia* (Sauria: lacertidae): correlation with species diversity. Russ. J. Genet. 39, 1292–1305.
- Collyer, M.L., Sekora, D.J., Adams, D.C., 2015. A method for analysis of phenotypic change for phenotypes described by high-dimensional data. Heredity 115, 357–365.
- Collyer, M.L., Adams, D.C., 2018. RRPP: an R package for fitting linear models to "highdimensional data using residual randomization. Methods Ecol. Evol. 9, 1772–1779. https://doi.org/10.1111/2041–210X.13029.
- Collyer, M.L., Adams, D.C., 2023. RRPP: Linear Model Evaluation with Randomized Residuals in a Permutation Procedure. R Package Version 1.4.0. https://CRAN.R-pr oject.org/package=RRPP.
- Darevsky, I.S., 1957. Systematics and ecology of rock lizards (Lacerta saxicola Eversmann) in Armenia. Zool. sb. AN Armenia SSR 10, 27–57 [in Russian].
- Darevsky, I.S., 1967. Rock Lizards of the Caucasus: Systematics, Ecology, and Phylogenesis of the Polymorphic Groups of Caucasian Rock Lizards of the Subgenus *Archaeolacerta*. Nauka, Leningrad [in Russian].
- Deme, G.G., Liang, X., Okoro, J.O., Bhattarai, P., Sun, B., Malann, Y.D., Martin, R.A., 2023. Female lizards (*Eremias argus*) reverse Bergmann's rule across altitude. Ecol. Evol. 13 (8), e10393.
- De Meyer, J., Irschick, D.J., Vanhooydonck, B., Losos, J.B., Adriaens, D., Herrel, A., 2019. The role of bite force in the evolution of head shape and head shape dimorphism in *Anolis* lizards. Funct. Ecol. 33 (11), 2191–2202.
- Espeche, B.A., Brigada, A.M., Rivera, P.C., 2023. Morphometric variability in lizards of the genus *Teius*: a comparative study of species with different reproductive modes. J. Herpetol. 57 (2), 238–245.
- Gabelaia, M., Tarkhnishvili, D., Murtskhvaladze, M., 2015. Phylogeography and morphological variation in a narrowly distributed Caucasian rock lizard, *Darevskia mixta*. Amphibia-Reptilia 36 (1), 45–54.
- Gabelaia, M., Adriaens, D., Tarkhnishvili, D., 2017. Phylogenetic signals in scale shape in Caucasian rock lizards (*Darevskia* species). Zool. Anz. 268, 32–40.
- Galoyan, E.A., 2011. The Role of Social Interactions in the Density Regulation in Populations of Parthenogenetic and Bisexual Species of Rock Lizards. PhD Dissertation. M. Lomonosov Moscow State University [In Russian].
- Galoyan, E.A., 2013. Joint space use in a parthenogenetic Armenian rock lizard (*Darevskia armeniaca*) suggests weak competition among monoclonal females. J. Herpetol. 47, 97–104. https://doi.org/10.1670/11-242.
- Galoyan, E., Bolshakova, A., Abrahamyan, M., Petrosyan, R., Komarova, V., Spangenberg, V., Arakelyan, M., 2019. Natural history of Valentin's rock lizard (*Darevskia valentini*) in Armenia. Zool. Res. 40, 277–292. https://doi.org/10.2427 2/j.issn.2095-8137.2019.036.
- Heiser Jr, C.B., Soria, J., Burton, D.L., 1965. A numerical taxonomic study of Solanum species and hybrids. Am. Nat. 99 (909), 471–488.
- Herrel, A., Vanhooydonck, B., Van Damme, R., 2004. Omnivory in lacertid lizards: adaptive evolution or constraint? J. Evol. Biol. 17 (5), 974–984.
- Kessler, K.F., 1878. Description of *Darevskia portschinskii*. In: Kessler, K.F. (Ed.), Transcaucasian Voyage. Travaux de la Société des Naturalistes de St. Petersbourg., St. Petersbourg, pp. 160–163 [in Russian].
- Kohlsdorf, T., Grizante, M.B., Navas, C.A., Herrel, A., 2008. Head shape evolution in *Tropidurinae* lizards: does locomotion constrain diet? J. Evol. Biol. 21 (3), 781–790.
- Lowe, C.H., Wright, J.W., 1966. Evolution of parthenogenetic species of *Cnemidophorus* (whiptail lizards) in western North America. J. Ariz. Acad. Sci. 4 (2), 81–87.
- Méhely, L.V., 1909. Materialien zu einer Systematik und Phylogenie der muralis--ähnlichen Lacerten. Annales Musei Nationalis Hungarici, vol. 7, pp. 409–621.
- Moritz, C., 1991. The origin and evolution of parthenogenesis in *Heteronotia binoei* (*Gekkonidae*): evidence for recent and localized origins of widespread clones. Genetics 129 (1), 211–219.
- Murphy, R.W., Fu, J., Macculloch, R.D., Darevsky, I.S., Kupriyanova, L.A., 2000. A fine line between sex and unisexuality: the phylogenetic constraints on parthenogenesis in lacertid lizards. Zool. J. Linn. Soc. 130 (4), 527–549.
- McDowall, R.M., 1998. Phylogenetic relationships and ecomorphological divergence in sympatric and allopatric species of *Paragalaxias* (Teleostei: *galaxiidae*) in high elevation Tasmanian lakes. Environ. Biol. Fish. 53, 235–257.

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Noble, D.W., McFarlane, S.E., Keogh, J.S., Whiting, M.J., 2014. Maternal and additive genetic effects contribute to variation in offspring traits in a lizard. Behav. Ecol. 25 (3), 633–640.

- Oliveira, D., Halpern, B., Martínez–Freiría, F., Kaliontzopoulou, A., 2023. Head shape heritability in the Hungarian meadow viper *Vipera ursinii rakosiensis*. Animals 13 (2), 322.
- Ortega, J., Martin, J., Crochet, P.A., López, P., Clobert, J., 2019. Seasonal and interpopulational phenotypic variation in morphology and sexual signals of *Podarcis liolepis* lizards. PLoS One 14 (3), e0211686.
- Openshaw, G.H., Keogh, J.S., 2014. Head shape evolution in monitor lizards (*Varanus*): interactions between extreme size disparity, phylogeny and ecology. J. Evol. Biol. 27 (2), 363–373.
- Paul, L.C., Suman, A.A., Sultan, N., 2013. Methodological analysis of principal component analysis (PCA) method. International Journal of Computational Engineering & Management 16 (2), 32–38.
- Parker Jr, E.D., 1979. Phenotypic consequences of parthenogenesis in *Cnemidophorus* lizards. II. Similarity of *C. tesselatus* to its sexual parental species. Evolution 1167–1179.
- Pembleton, E.F., Baker, R.J., 1978. Studies of a contact zone between chromosomally characterized populations of *Geomys bursarius*. J. Mammal. 59 (2), 233–242.
- Petrosyan, V., Osipov, F., Bobrov, V., Dergunova, N., Omelchenko, A., Varshavskiy, A., Danielyam, F., Arakelyan, M., 2020. Species distribution models and niche partitioning among unisexual *Darevskia dahli* and its parental bisexual (*D. portschinskii*, *D. mixta*) rock lizards in the Caucasus. Mathematics 8 (8), 1329.
- Dicketara-Donoso, D., Hodgson, D.J., Tregenza, T., 2008. The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? BMC Evol. Biol. 8, e68.
- Richardson, M., 2009. Principal Component Analysis. https://people.duke.edu/~hp gavin/SystemID/References/Richardson-PCA-2009.pdf, 30.5. 2024.
- Runemark, A., Hansson, B., Pafilis, P., Valakos, E.D., Svensson, E.I., 2010. Island biology and morphological divergence of the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? BMC Evol. Biol. 10, 1–15.
- Tarkhnishvili, D., Hille, A., Böhme, W., 2001. Humid forest refugia, speciation and secondary introgression between evolutionary lineages: differentiation in a Near Eastern brown frog, *Rana macrocnemis*. Biol. J. Linn. Soc. 74 (2), 141–156.

- Tarkhnishvili, D., Gavashelishvili, A., Avaliani, A., Murtskhvaladze, M., Mumladze, L., 2010. Unisexual rock lizard might be outcompeting its bisexual progenitors in the Caucasus. Biol. J. Linn. Soc. 101 (2), 447–460.
- Tarkhnishvili, D., 2012. Evolutionary history, habitats, diversification, and speciation in Caucasian rock lizards. Advances in Zoology Research 2, 79–120.
- Tarkhnishvili, D., Gabelaia, M., Adriaens, D., 2020a. Phenotypic divergence, convergence and evolution of Caucasian rock lizards (*Darevskia*). Biol. J. Linn. Soc. 130 (1), 142–155.
- Tarkhnishvili, D., Yanchukov, A., Şahin, M.K., Gabelaia, M., Murtskhvaladze, M., Candan, K., Galoyan, E., Arakelyan, M., Iankoshvili, G., Kumlutas, Y., Ilgaz, Ç., Matur, F., Çolak, F., Erdolu, M., Kurdadze, S., Barateli, N., Anderson, C.L., 2020b. Genotypic similarities among the parthenogenetic *Darevskia* rock lizards with different hybrid origins. BMC Evol. Biol. 20 (1), 1–25.
- Taylor, H.L., 1965. Morphological Variation in Selected Populations of the *Teiid* Lizards: *Cnemidophorus Velox* and *Cnemidophorus Inornatus*. University of Colorado Press.
- Thorpe, R.S., Baez, M., 1987. Geographic variation within an island: univariate and multivariate contouring of scalation, size, and shape of the lizard *Gallotia galloti*. Evolution 41 (2), 256–268.
- Tsellarius, A.Y., Tsellarius, E.Y., Galoyan, E.A., 2016. Social relationships between males and females in the rock lizard (*Darevskia brauneri, Lacertidae*): 1. Friendly monogyny in males and polyandry in females. Biol. Bull. 43, 1077–1086.
- Verwaijen, D., Van Damme, R., Herrel, A., 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. Funct. Ecol. 16 (6), 842–850.
- Volynchik, S., 2014. Climate-related variation in body dimensions within four lacertid species. Int. J. Zool. 2014 (1), 795387.
- Wijesundara, C.S., Freed, L.A., 2018. Divergence of morphological characters in two white-eye species (Passeriformes: Zosteropidae) in sympatry. Ecosphere 9 (6), e02317.
- Yanchukov, A., Tarkhnishvili, D., Erdolu, M., Şahin, M.K., Candan, K., Murtskhvaladze, M., Gabelaia, M., Iankoshvili, G., Barateli, B., Ilgaz, Ç., Kumlutas, Y., Matur, F., Çolak, F., Arakelyan, M., Galoyan, E., 2022. Precese paternal ancestry of hybrid unisexual ZW lizards (genus *Darevskia*: lacertidae: Squamata) revealed by Z–linked genomic markers. Biol. J. Linn. Soc. 136 (2), 293–305.