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Ecomorphological differences among forest and rock dwelling species of *Darevskia* Arribas, 1999 (Squamata, Lacertide) in the Elburz Mountains, Iran

Seyyed Saeed Hosseinian Yousefkhani[1], Hossein Nabizadeh[2,3], L. Lee Grismer[4,5]

1 *Department of Animal Science, School of Biology, Damghan University, Damghan, Iran*
2 *Faculty of Sciences, Razi University of Kermanshah, Kermanshah, Iran*
3 *Department of Biology, Faculty of Sciences, University of Qom, Qom, Iran*
4 *Herpetology Laboratory, Department of Biology, La Sierra University, 4500 Riverwalk Road, Riverside, California 92505, USA*
5 *Department of Herpetology, San Diego Natural History Museum, PO Box 121390, San Diego, California, 92112, USA*

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Corresponding author: Seyyed Saeed Hosseinian Yousefkhani (s.hosseinian@du.ac.ir)

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Abstract

Ecological pressure is the major driver of morphological adaptation. Different habitat preferences even among closely related species, often result in the evolution of different body shapes. In the present study, we employed geometric morphometric and principal component analyses (PCA) to compare body shape and head plate morphology among seven species in the genus *Darevskia* Arribas, 1999 from the Elburz Mountains, Iran that occur in either rocky or forested habitats. The geometric morphometric analysis and the PCA of meristic characters recovered a wide degree of overlap between the rock and forest dwelling species. The PCA of the morphometric characters showed wide separation among the rock and forest dwelling species as well as among some of the rock dwelling species. These results strongly suggest that body shape is correlated with the habitat type whereas head plate morphology and scale meristics are not. Furthermore, the results suggest that the rock dwelling species may be occupying and navigating their microhabitat in different ways. Ecological observations are needed to test this hypothesis.

Key Words

Darevskia, functional morphology, habitat preference, Iran, Middle East, morphology

Introduction

Ecomorphological studies of morphological adaptations in lizards have revealed that head, body, and limb proportions bear significantly on habitat preference, regardless of phylogenetic propinquity (e.g. Arnold 1992; Losos 2011; Smith et al. 2011; Grismer and Grismer 2017; Kahrl et al. 2018; Tarkhnishvili et al. 2020; Cordero et al. 2021; Grismer 2021; Kaatz et al. 2021). Additionally, in many cases, unrelated species living in similar habitats may converge on the same morphology. Lizards are uniquely suited to disentangle the potential correlation between morphological adaptations that reflect different feeding, breeding and habitat preference strategies (Ma et al. 2019; Altunışık and Eksilmez 2020) with that of their phylogenetic relationships (Vanhooydonck and Van Damme 1999; Revell et al. 2007; Edwards et al. 2012; Kelly et al. 2014).

Body shape is one of the most important characteristics highlighting the relationship between ecology and morphology, and as such, is a significant contributor to population dynamics (Losos 2011). Separating particular morphological traits that are significantly correlated with a particular habitat preference from those that are not, can provide insight as to why, and perhaps, how such traits have

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evolved (Cordero et al. 2021). Locomotor performance is an important aspect of lizard biology as it bears heavily on the ability to escape predators and capture prey (Zheng et al. 2020; Schuck et al. 2021). Limb, body, and trunk length as well as head dimensions all have been shown to play significant roles in locomotor performance and depending on habitat preference, may evolve in different directions (e.g. Losos 2011; Grismer and Grismer 2017).

The ecomorphology of the species in the lacertid genus *Darevskia* Arribas, 1999 of the Caucasus and the Elburz Mountains, Iran has been investigated using geometric morphometric and traditional morphological characters in the context of a molecular phylogeny (Ahmadzadeh et al. 2013; Tarkhnishvili et al. 2020). The results of these studies indicated that their morphology was not necessarily influenced by their phylogenetic relationships. Tarkhnishvili et al. (2020) demonstrated that various Caucasian species grouped together based on substrate preference but showed limited correlation between phylogenetic position and head shape (body morphology was not examined in their study). A molecular analysis of the Elburz Mountain species recovered three species complexes—*D. raddei* (Boettger, 1892), *D. chlorogaster* (Boulenger, 1908) and *D. defilippii* (Camerano, 1877) (Ahmadzadeh et al. 2013). The species of these complexes were considered cryptic and showed conservative morphological evolution with respect to their phylogenetic relationships, but the potential correlation between their morphology and their habitat preference was not examined.

In the present study, we evaluated seven species of *Darevskia* in the Elburz Mountains, Iran which we classified into two groups—tree dwelling and rock dwelling (Fig. 1). The degree of morphological differentiation between these two groups and the degree to which their morphology may correlate with their habitat preference is evaluated herein.

Methods

We examined morphological characters regarding the metrics of head plates, morphometrics of head, limb, and body proportions, and meristic characters of scales counts. The analyses included 30 specimens across seven species—*Darevskia kamii* Ahmadzadeh, Flecks, Carretero, Mozaffari, Böhme, Harris, Freitas & Rödder, 2013 (N=5), *D. chlorogaster* (N=6), and *D. caspica* Ahmadzadeh, Flecks, Carretero, Mozaffari, Böhme, Harris, Freitas & Rödder, 2013 (N=2) from forested habitats and *D. schaekeli* Ahmadzadeh, Flecks, Carretero, Mozaffari, Böhme, Harris, Freitas & Rödder, 2013 (N=6), *D. defilippii* (N=5), *D. raddei* (N=3), and *D. steineri* (Eiselt, 1995) (N=3) from rocky habitats. Forest habitats include areas with an average elevation of 400 m a.s.l. and have *Quercus*, *Acer* and *Fagus* vegetation. The surfaces of the tree trunks are covered with green moss. In some areas, the tree trunks are vertical and have a relatively shallow degree of slope. In rocky habitats, the vegetation is usually shrubby and the cliffs steep. *Darevskia* lizards are usually found in the crevices between rocks where they take shelter. However, when faced with a predator, they can quickly climb the vertical cliff face. The descriptive statistics for the meristic and morphometric characters are presented in Table 1.

Table 1. Mean±SE and range for the description of 27 morphometric and meristic characters in adult male specimens of *Darevskia* species from two different habitat types. Character abbreviations occur in the Methods section.

Character	Rocky habitat (N=17)		Forest habitat (N=13)		P value
	Mean±SE	Range	Mean±SE	Range	
SVL	54.83±5.12	48.50–64.40	58.70±4.16	52.80–64.50	0.06
LHF	30.38±3.48	25.16–37.29	28.75±4.85	23.56–35.80	0.40
HL	12.42±1.58	10.69–15.26	14.14±0.72	13.28–14.87	**0.03**
HH	5.64±1.02	4.45–7.17	6.98±0.99	5.60–8.97	0.07
HW	8.12±1.74	5.10–11.00	9.28±0.87	8.40–10.70	0.05
LFL	17.19±2.25	12.34–20.36	20.90±1.17	19.20–22.86	**0.00**
LHL	28.85±3.92	24.91–35.68	32.86±2.52	29.22–36.28	0.09
LFO	7.99±1.51	6.33–10.87	8.60±1.17	6.42–9.98	0.29
LA	6.47±1.37	5.02–8.78	6.85±0.64	6.20–8.12	0.40
EL	2.94±0.46	2.32–3.74	3.15±0.43	2.49–3.65	0.30
RED	4.50±0.84	3.03–5.69	5.27±0.40	4.78–5.94	**0.01**
EED	4.48±0.85	3.03–5.87	4.40±0.43	3.59–5.19	0.90
NL	6.02±0.83	4.43–7.02	5.50±0.63	4.60–6.70	0.11
TD	1.86±0.55	1.00–2.60	2.46±0.20	2.20–2.90	**0.00**
IOR	5.89±0.6	5.20–7.15	6.33±0.62	5.72–7.79	0.11
LV	4.80±0.58	3.58–5.40	5.12±0.66	4.38–6.46	0.26
LBT	5.74±0.60	4.90–6.60	5.81±0.66	4.40–6.80	0.79
LWB	12.33±2.81	8.85–17.41	12.89±1.78	10.47–15.58	0.57
NSL	7.23±1.87	5.00–9.00	8.44±0.88	7.00–9.00	0.13
NIL	6.56±0.66	6.00–8.00	7.78±0.66	7.00–9.00	**0.00**
NGS	25.38±2.84	20.00–30.00	23.22±2.53	21.00–28.00	0.10
NCS	10.23±0.59	9.00–11.00	9.33±0.86	8.00–11.00	**0.01**
NVS	28.31±1.70	27.00–32.00	27.78±1.56	26.00–30.00	0.42
NDS	52.85±3.60	48.00–58.00	47.67±4.35	43.00–56.00	**0.01**
SDLT	22.08±6.73	14.00–29.00	27.00±1.73	24.00–30.00	0.22
NFP	17.31±1.03	15.00–19.00	17.44±1.33	15.00–19.00	0.67

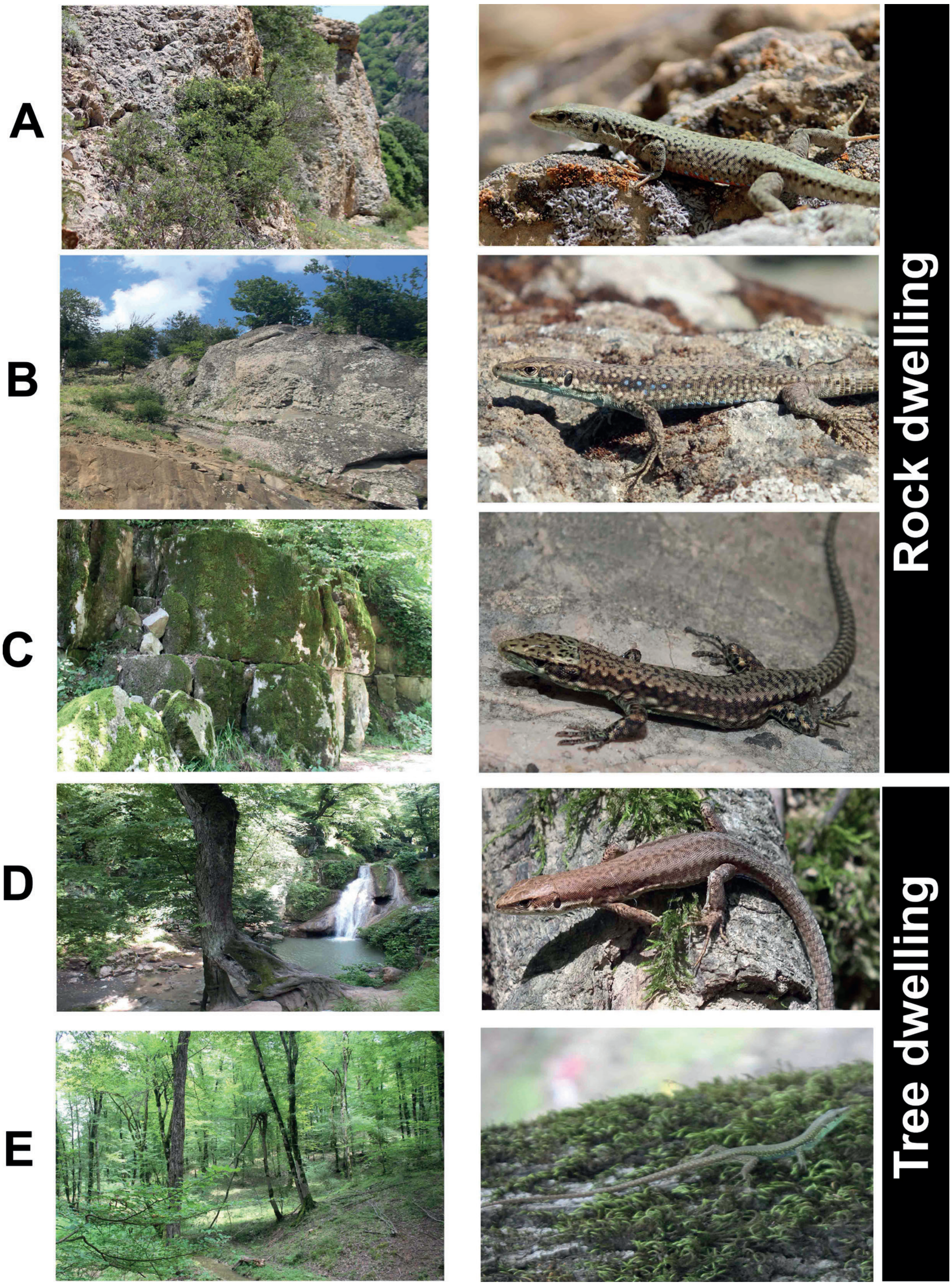

Figure 1. Habitat and target species of rock and forest species. **A.** *Darevskia schaekeli*; **B.** *Darevskia raddei*; **C.** *Darevskia steineri*; **D.** *Darevskia kamii*; **E.** *Darevskia caspica*.

Due to COVID-19 travel restrictions, we were unable to collect additional specimens from the sampled species. Therefore, the results below are presented as robust hypotheses to be tested with the additional material.

Geometric morphometric analysis

High resolution photographs were taken using an Andonstar digital microscope AD207 of all lizard specimens. The digital microscopy allowed us to ensure all photographs were taken in the same position and parallel to the camera. Graph paper divided into 1 mm cells was placed beneath the lizards' heads to standardize the scale of each photograph. All photographs were transformed and grouped using TPSUtil (Rohlf 2005). The geometric morphometric (GM) analysis employed 16 specific landmarks using TPSDig (Fig. 2) (Rohlf 2005). To compare the shapes of all specimens, we employed a Procrustes superimposition method using MorphoJ 1.02 (Klingenberg 2011) in order to standardize the size and configure the rotation and form

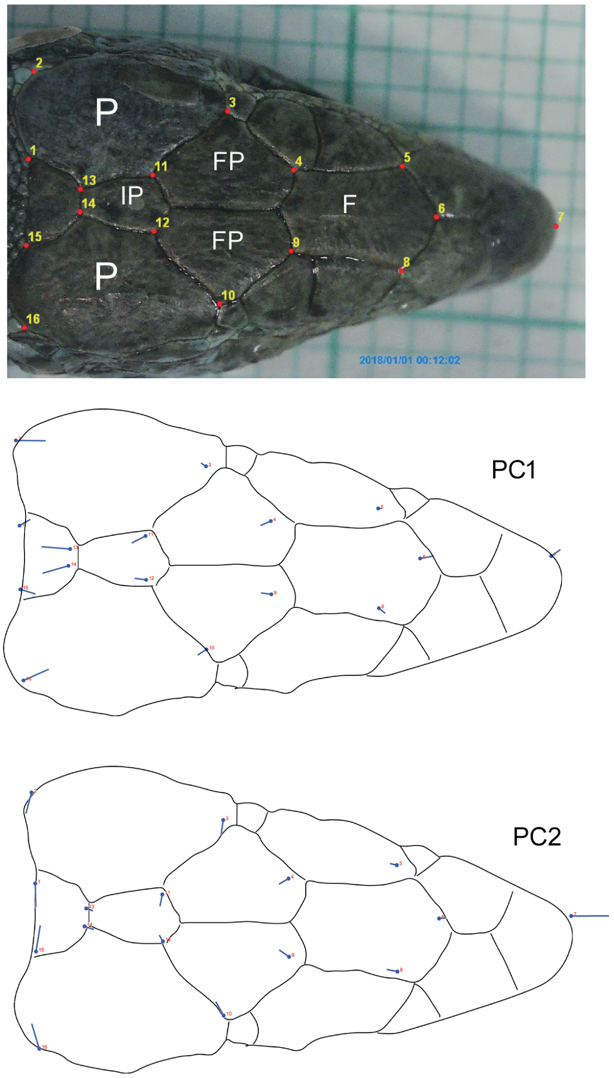

Figure 2. Upper head of *Darevskia raddei* and the 16 landmark position on the angle of scales.

of each photograph (Adams et al. 2004). A covariance distance matrix was generated and subject to a PCA to visualize and assess the degree of difference in morphospatial clustering between each species and the two habitat groups.

Morphometric analysis

The morphometric analysis included the following 19 characters measured using digital caliper (±0.01 mm): snout-vent length (SVL; from tip of snout to anterior edge of cloaca), tail length (TL; from posterior edge of cloaca to tip of tail), trunk length (LHF; distance between hindlimb and forelimb), head length (HL; from tip of snout to the posterior edge of tympanum), head height (HH; maximum distance between upper head and lower jaw), head width (HW; distance between posterior eye corners), length of forelimb (LFL; from top of shoulder joint to tip of fourth toe), length of hind limb (LHL; from hip joint to tip of fourth toe), length of femur (LFO; from hip joint to top of knee), length of tibia (LA; from top of knee to beneath wrist), length of eye (EL; distance from anterior corner to posterior corner to its posterior), snout length (RED; from tip of nostril to anterior corner of eye), distance between posterior edge of eye and tympanum (EED), length of neck (NL; distance between posterior edge of tympanum and shoulder joint), tympanum diameter (TD; largest size), interorbital distance (IOR; largest size), length of cloaca crevice (LV; largest size), length of widest part of tail base (LBT), and length of widest part of belly (LWB). In order to minimize the effects of allometry (sec. Chan and Grismer 2022), size was normalized using the following equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVL_{mean} = overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000), accessible in the R package GroupStruct (available at https://github.com/chankinonn/GroupStruct). The morphometrics of each species were normalized separately and then concatenated so as not to conflate potential intra- with interspecific variation (Reist 1986; McCoy et al. 2006). All data were scaled to their standard deviation to ensure they were analyzed on the basis of correlation and not covariance. These data were then subjected to a PCA. A subsequent discriminant analysis of principal components (DAPC) from the ADEGENET package in R (Jombart and Collins 2015) was employed. Unlike an unsupervised PCA, a DAPC groups individuals *a priori* according to species and relies on data calculated from its own PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Dimension reduction of the DAPC prior to plotting is accomplished by retaining the first set of principal components that account for 90–95% of the variation as determined from a scree plot generated as part of the analysis.

A non-parametric permutation multivariate analysis of variance (PERMANOVA) from the *vegan* package 2.5–3 in R (Oksanen et al. 2020) was used to determine if the centroid locations and group clustering of each species in the PCA were statistically different from one another (Skalski et al. 2018). The analysis was based on the calculation of a Gower (dis)similarity matrix using 50,000 permutations based on the loadings of the first four dimensions of the PCA. A pairwise *post hoc* test calculates the differences between all combinations of species pairs, generating a *p*-value, a Bonferroni-adjusted *p*-value, and a pseudo-*F* ratio (*F* statistic). A $p < 0.05$ is considered significant and larger *F*-statistics indicate more pronounced group separation. A rejection of the null hypothesis (i.e. centroid positions and/or the spread of the data points [i.e. clusters] are no different from random) signifies a statistically significant difference between the species.

A Levene tests for the normalized morphometric and meristic characters were conducted to test for equal variances across all groups. Characters with equal variances were analyzed with an analysis of variance (ANOVA) and TukeyHSD *post hoc* to test for mean comparisons involving more than three groups. Those with unequal variances were subjected to Welch's *F*-test and a Games-Howell *post hoc* test.

Meristic analysis

The meristic analysis included the following eight characters counted using Andonstar digital microscope AD207: number of labial scales anterior to the center of eye on the right side of head (NSL), number of scales on the right lower labial region (NIL), number of gular scales in a straight median series (NGS), number of collar scales (NCS), number of transverse series of ventral scales counted in straight median series between the collar and the row of scales separating the series of femoral pores (NVS), number of dorsal scales across midbody (NDS), number of subdigital lamellae along underside of 4th toe (defined by their width, the one touching the claw included), counted bilaterally (SDLT), and the number of femoral pores (NFP). These data were subjected to a PCA.

All statistical analyses were conducted using R Core Team (2018). All specimens were in good condition and deposited at Damghan University Zoological lab, Iran and preserved in 96% ethanol.

Results

Geometric morphometrics analysis

The PCA of shape of the head plates among all species recovered a wide range of overlap, including overlap between the forest and rock dwelling species (Fig. 3). Principal component (PC) 1 accounted for 39.4% of the variation in the data set and loaded most heavily for coordinates 2, 4, 6, 8, 10, 22, 26, 28 and 31 (Fig. 3; Table 2). PC2 accounted for an additional 33.9% of the data set and loaded most heavily for coordinates 5, 7, 9, 11, 15, 17, 19, 21, 23, 25, and 27.

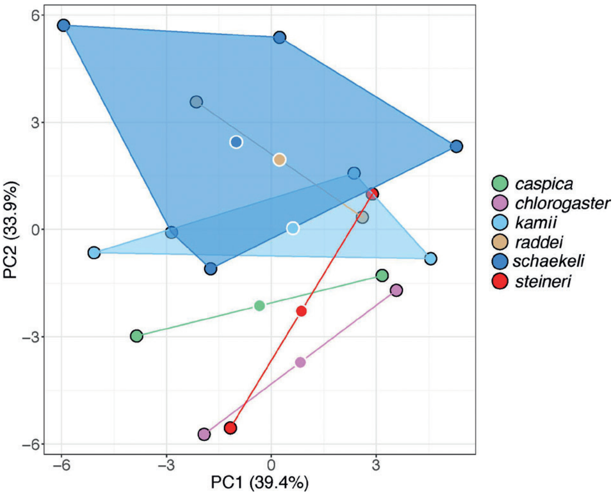

Figure 3. Principal component analysis of the geometric morphometric data.

Morphometric analysis

The PCA recovered reasonable overlap among the forest dwelling species *D. caspica*, *D. chlorogaster*, and *D. kamii* along PC1 and PC2 and complete separation of these species from the remaining rock dwelling species *D. defilippii*, *D. raddei*, *D. schaekeli*, and *D. steineri*. The PCA also recovered wide separation of the rock dwelling species *D. schaekeli* and *D. defilippii* from each other and all other species and wide overlap among the rock dwelling species *D. raddei* and *D. steineri*. Principal component (PC) 1 accounted for 53.9% of the variation in the data set and loaded most heavily for the metrics of the head and limbs: HL, HW, LFL, LHL, LFO, LA, and IOR (Fig. 4; Table 3).

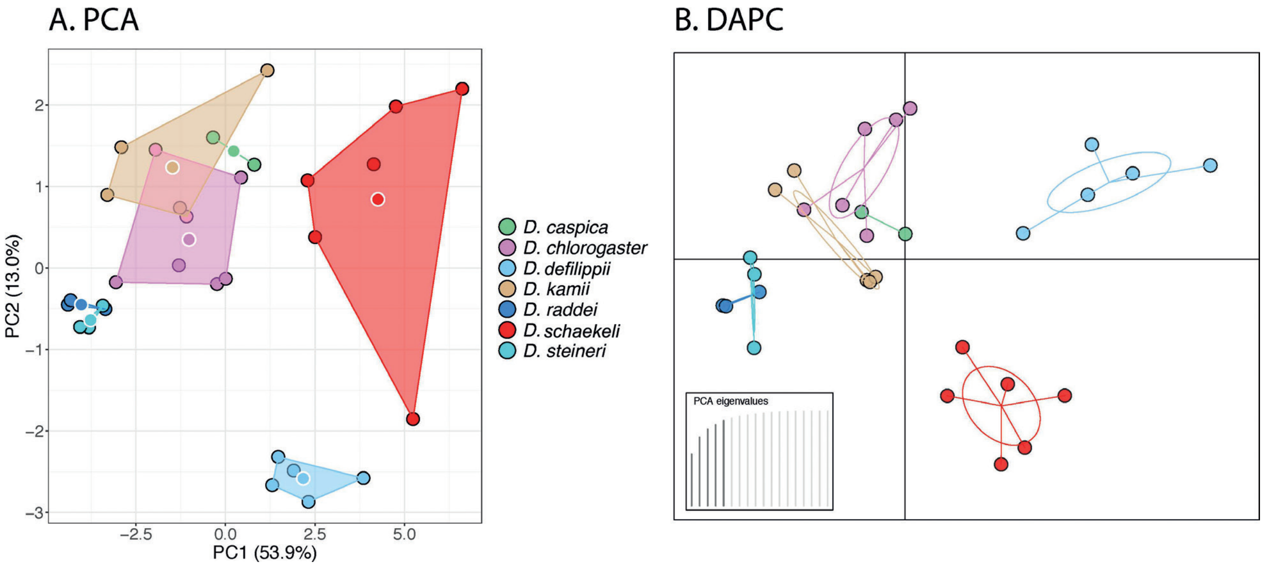

Figure 4. A. Principal component analysis of the morphometric data; **B.** Discriminant analysis of principal components based on the retention of the first five PCs accounting for 94.7% of the variation.

Table 2. PCA summary statistics of the coordinate data from the geomorphometric analysis.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**	**PC16**
Standard deviation	3.55	3.29	2.43	1.17	0.68	0.52	0.40	0.30	0.27	0.26	0.22	0.19	0.15	0.11	0.09	0.00
Proportion of Variance	0.39	0.34	0.19	0.04	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cumulative Proportion	0.39	0.73	0.92	0.96	0.98	0.98	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00
eigenvalues	12.61	10.83	5.92	1.37	0.47	0.27	0.16	0.09	0.07	0.07	0.05	0.04	0.02	0.01	0.01	0.00
RawCoord1	0.03	-0.15	-0.34	0.05	-0.17	0.06	0.12	-0.06	-0.28	-0.14	0.08	-0.19	-0.01	0.24	-0.06	0.10
RawCoord2	0.24	0.08	0.02	-0.26	-0.40	-0.21	-0.03	-0.15	0.05	0.15	0.23	0.06	0.18	-0.12	-0.35	-0.02
RawCoord3	0.04	-0.12	-0.36	0.02	-0.35	0.11	-0.09	0.17	0.20	-0.24	-0.15	0.01	-0.01	-0.01	0.23	-0.04
RawCoord4	0.25	0.01	0.17	-0.12	-0.14	-0.15	0.11	0.03	-0.17	-0.50	-0.21	0.30	0.02	-0.05	0.17	0.11
RawCoord5	0.12	-0.27	0.00	-0.02	0.01	0.05	0.14	-0.16	0.05	0.03	0.16	-0.02	0.28	0.00	-0.21	-0.22
RawCoord6	0.25	0.03	0.16	0.06	-0.15	-0.15	0.06	0.23	0.03	0.05	0.12	0.34	-0.27	-0.05	0.02	0.09
RawCoord7	0.12	-0.26	0.11	-0.02	0.00	-0.02	0.13	0.03	0.07	-0.09	0.18	-0.24	-0.02	0.01	0.00	0.06
RawCoord8	0.26	0.05	0.10	0.05	-0.10	-0.08	-0.22	-0.03	-0.30	0.19	-0.09	-0.38	-0.26	-0.09	0.06	-0.04
RawCoord9	0.11	-0.24	0.17	-0.03	-0.11	0.19	-0.04	0.14	-0.05	0.02	0.14	-0.24	0.03	-0.02	0.26	-0.32
RawCoord10	0.25	0.06	0.11	0.26	0.02	0.05	-0.26	-0.11	0.14	-0.09	0.02	-0.02	0.01	-0.13	0.18	0.02
RawCoord11	0.10	-0.23	0.19	0.01	-0.05	0.38	-0.08	0.03	0.31	-0.01	-0.56	0.03	0.09	0.05	-0.24	-0.03
RawCoord12	0.23	0.11	-0.01	0.38	0.03	-0.02	0.04	-0.10	-0.04	0.14	-0.22	-0.18	0.45	-0.34	0.01	0.05
RawCoord13	0.09	-0.23	0.21	0.02	0.09	0.39	-0.18	-0.12	-0.38	0.12	0.13	0.42	-0.01	-0.04	0.12	-0.10
RawCoord14	0.19	0.08	0.01	0.58	-0.02	-0.01	-0.23	-0.01	0.13	-0.26	0.27	0.13	0.02	0.26	-0.31	0.03
RawCoord15	0.11	-0.24	0.18	0.01	-0.14	0.19	-0.01	0.10	0.04	0.12	0.10	-0.07	-0.28	0.02	0.02	0.20
RawCoord16	0.22	0.15	-0.10	0.24	0.20	-0.07	0.19	0.22	-0.04	0.07	0.13	-0.02	-0.06	0.14	0.15	-0.08
RawCoord17	0.11	-0.27	0.11	-0.01	0.03	-0.04	0.18	0.02	0.06	-0.08	0.16	-0.20	0.01	0.21	-0.18	-0.08
RawCoord18	0.22	0.17	-0.11	0.06	0.18	0.12	0.26	0.07	0.20	0.19	-0.08	0.04	-0.01	0.22	0.23	-0.26
RawCoord19	0.13	-0.26	0.01	0.07	0.09	-0.04	0.30	-0.15	0.05	0.20	-0.02	-0.03	0.00	0.00	0.13	0.65
RawCoord20	0.20	0.16	-0.17	-0.08	0.13	0.14	-0.10	-0.27	-0.10	0.28	-0.18	0.05	-0.34	0.09	-0.30	0.01
RawCoord21	0.11	-0.25	-0.12	-0.05	0.19	-0.27	-0.07	-0.35	0.07	-0.15	-0.16	0.13	-0.04	-0.03	0.00	0.04
RawCoord22	0.26	0.08	0.09	-0.09	-0.16	-0.25	-0.09	0.19	-0.15	0.19	-0.24	-0.04	0.17	0.28	0.12	0.06
RawCoord23	0.11	-0.26	-0.13	0.00	0.16	-0.25	0.03	-0.25	-0.01	0.06	-0.09	0.16	-0.01	0.33	0.20	-0.27
RawCoord24	0.23	0.13	-0.09	-0.15	0.09	0.16	0.23	-0.25	0.10	-0.10	0.25	0.05	0.02	-0.41	0.20	-0.08
RawCoord25	0.11	-0.23	-0.18	-0.12	0.25	-0.20	-0.36	0.31	0.16	0.10	0.06	-0.07	0.08	-0.21	0.05	0.08
RawCoord26	0.25	0.10	-0.01	-0.22	-0.11	0.06	0.26	0.23	0.09	0.13	-0.04	0.16	0.13	0.07	-0.17	-0.09
RawCoord27	0.09	-0.24	-0.19	-0.08	0.24	-0.16	-0.21	0.29	0.00	0.09	0.06	0.18	-0.03	-0.18	-0.16	-0.09
RawCoord28	0.26	0.09	-0.01	-0.21	-0.01	-0.05	-0.15	-0.22	0.07	-0.29	-0.05	-0.29	-0.22	0.02	0.00	-0.15
RawCoord29	0.02	-0.15	-0.34	0.13	-0.17	0.08	0.03	0.06	-0.47	0.00	-0.08	0.06	0.18	-0.09	-0.04	-0.07
RawCoord30	0.22	0.12	-0.10	-0.17	0.42	0.27	0.09	0.26	-0.22	-0.34	-0.04	-0.13	0.00	-0.02	-0.25	0.16
RawCoord31	0.03	-0.11	-0.36	0.21	-0.24	0.07	0.19	0.03	0.16	0.09	-0.08	0.06	-0.38	-0.25	-0.07	-0.07
RawCoord32	0.13	0.13	-0.28	-0.23	-0.08	0.31	-0.32	-0.09	0.16	0.09	0.23	0.05	0.23	0.28	0.22	0.29

PC2 accounted for an additional 13.0% of the data set and loaded most heavily for NL and TD. The PERMANOVA recovered significant differences in the morphospatial relationships among various pairs of species (Table 4). The ANOVA of the characters that loaded most heavily along the PC1 and PC2 recovered significant differences among various pairs of species across all characters (Table 5). The species complex containing *D. chlorogaster*, *D. kamii*, and *D. caspica* bear morphological similarities in nine characters (Fig. 5).

Meristic analysis

The PCA of the meristic characters recovered wide overlap among nearly all species in morphospace regardless of habitat preference (Fig. 6). PC 1 accounted for 40.0% of the variation in the data set and loaded most heavily for NSL, NIL, and SDLT (Fig. 6; Table 6). PC2 accounted for an additional 21.2% of the data set and loaded most heavily for NGS.

Discussion

The results of the above analyses indicate that head plate morphology and meristic characters do not correlate with habitat preference, although morphometrics do. It is well established that habitat preference can be a significant driver of body morphology (e.g. Melville and Swain 2000; Iglesias et al. 2012; Grismer and Grismer 2017; Grismer et al. 2017) as a means to increase the overall efficiency of a species' occupation in a particular microhabitat or ecological niche (Herczeg et al. 2003; Kneitel 2019). The PCA analysis of the morphometric data indicate that the overall morphological similarity among the forest species departs widely from that of the rock dwelling species (Fig. 4). However, some of the rock dwelling species differ significantly from one another as well (Tables 4, 5). This would indicate that, although these species occupy rocky habitats, they may be doing so differently as has been seen in other closely rock-dwelling species (e.g., Grismer and Grismer 2017; Grismer 2021). Within other studies, a correlation between habitat type and

Table 3. Summary statistics of the morphometric PCA. Bold values refer to the significant characters and most effective characters of the variation.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18
Standard deviation	3.117414	1.531629	1.281116	1.118149	0.921263	0.790621	0.658954	0.581851	0.475208	0.422375	0.364450	0.342473	0.228142	0.190096	0.154509	0.134161	0.103017	0.052403
Proportion of variance	0.5399	0.13033	0.09118	0.06946	0.04715	0.03473	0.02412	0.01881	0.01255	0.00991	0.00738	0.00652	0.00289	0.00201	0.00133	0.001	0.00059	0.00015
Cumulative proportion	0.5399	0.67023	0.76141	0.83087	0.87802	0.91275	0.93687	0.95568	0.96823	0.97814	0.98552	0.99203	0.99492	0.99693	0.99826	0.99926	0.99985	1.00000
Eigen	9.71827	2.34589	1.64126	1.25026	0.84873	0.62508	0.43422	0.33855	0.22582	0.17840	0.13282	0.11729	0.05205	0.03614	0.02387	0.01800	0.01061	0.00275
SVL	-0.20787	0.12118	0.21729	-0.16765	0.19358	-0.57771	0.56495	-0.38438	-0.00731	0.09538	0.13054	-0.00692	0.01942	-0.02541	0.01499	-0.03280	0.00568	-0.00770
LHF	0.13770	-0.22680	0.42566	0.38191	0.38491	0.02878	0.18744	0.40529	0.03224	0.27499	-0.02029	0.00214	-0.21271	0.18497	-0.10481	-0.13112	0.09180	-0.24706
HL	**-0.29973**	0.06702	-0.19429	0.10728	0.05996	-0.03254	-0.04068	0.00614	0.04910	0.09711	-0.34306	-0.23962	-0.01317	0.06440	0.48027	-0.42703	-0.42088	-0.26199
HH	-0.23748	0.34232	0.01638	0.24191	-0.28384	0.15541	0.12870	-0.03334	-0.05668	-0.02374	-0.09957	-0.06755	-0.06048	-0.18159	-0.16918	-0.47446	0.58017	0.00346
HW	**-0.30396**	-0.02345	0.00198	0.12703	0.07675	-0.07641	-0.01296	0.33415	0.04825	-0.09879	0.26936	-0.04412	-0.08476	-0.74383	-0.16560	0.03772	-0.30102	0.02921
LFL	**-0.26605**	0.06117	-0.23763	0.26529	0.22725	0.01107	-0.00837	0.05438	0.40995	-0.02049	0.26949	-0.43530	0.22170	0.34526	-0.13139	0.09672	0.06903	0.33689
LHL	**-0.30736**	-0.02254	-0.15241	-0.04976	0.03098	0.00504	0.06761	0.19605	0.07451	-0.15283	0.06912	0.21552	0.39611	0.04316	0.11873	0.29531	0.29534	-0.63866
LFO	**-0.26600**	-0.23699	0.03761	-0.12529	-0.13166	-0.06296	-0.18847	-0.06943	0.60002	0.15779	0.04204	0.54994	-0.17664	0.08172	-0.05379	-0.23712	0.00574	0.09037
LA	**-0.27770**	-0.17119	0.04497	0.05597	-0.00269	-0.31679	-0.09734	0.36174	-0.43275	-0.01502	-0.22226	0.25158	0.32694	0.13952	0.06260	-0.07853	0.06597	0.45469
EL	-0.19034	0.21328	0.40907	-0.18453	-0.34144	0.28752	0.16079	0.17944	0.13854	0.46950	-0.10653	-0.12989	0.15459	-0.03239	0.18303	0.32399	-0.08500	0.14531
RED	-0.22453	0.13488	0.01778	-0.07506	0.57160	0.23510	-0.39312	-0.34151	-0.21031	0.39811	-0.04427	0.09968	0.08678	-0.16170	-0.08530	0.05112	0.11867	0.00262
EED	-0.23311	-0.41158	-0.02891	-0.03872	-0.05964	-0.18268	-0.14392	-0.06712	-0.01103	0.00240	-0.21282	-0.34357	-0.47678	-0.10502	0.22049	0.33204	0.38781	0.02667
NL	-0.17857	**-0.43979**	0.19554	-0.15902	-0.15250	0.26713	-0.01961	-0.13263	-0.28865	-0.01050	0.58922	-0.17278	0.09981	0.10646	0.14796	-0.30300	-0.01046	-0.05493
TD	-0.20433	**0.45594**	-0.11883	-0.07945	0.05289	0.03334	-0.01437	0.23175	-0.23320	-0.04711	0.34583	0.21104	-0.55179	0.30646	0.19244	0.11667	-0.03379	0.03453
IOR	**-0.28473**	0.03624	0.16078	0.10791	-0.30251	-0.17055	-0.24910	-0.13237	-0.17578	0.01560	-0.10274	-0.12854	-0.07501	0.27529	-0.59947	0.12041	-0.28753	-0.28944
LV	-0.17467	-0.21442	-0.18040	0.52506	-0.07542	0.33571	0.39706	-0.32540	-0.13890	-0.01050	-0.08336	0.30421	-0.07187	0.00213	0.04322	0.25317	-0.17318	0.11543
LBT	-0.16732	-0.17528	-0.26054	-0.53586	0.18781	0.31284	0.38834	0.19396	-0.04455	-0.05909	-0.27033	-0.07618	-0.12288	0.07579	-0.37944	-0.10568	-0.04964	0.04340
LWB	-0.17856	0.09775	0.55074	-0.03040	0.22132	0.21555	-0.07392	-0.11158	0.12889	-0.67936	-0.19457	0.01567	-0.01208	0.05008	0.10192	0.02936	-0.05229	0.08985

Table 4. Significant differences between species based on the PERMANOVA analysis.

Species pairs	F.Model	R2	p.value	p.adjusted
D. kamii vs *D. chlorogaster*	0.68773197	0.07098999	0.54814904	1
D. kamii vs *D. caspica*	2.21230125	0.30673999	0.14285714	1
D. kamii vs *D. schaekeli*	14.3172884	0.6140203	0.00221996	0.04661907
D. kamii vs *D. defilippii*	21.0386808	0.72450539	0.00867983	0.18227635
D. kamii vs *D. raddei*	5.3554893	0.47162118	0.03571429	0.75
D. kamii vs *D. steineri*	5.1829789	0.46347033	0.03571429	0.75
D. chlorogaster vs *D. caspica*	2.46469555	0.29117356	0.10714286	1
D. chlorogaster vs *D. schaekeli*	15.8785066	0.61357894	0.00213996	0.0449391
D. chlorogaster vs *D. defilippii*	18.8850495	0.6772464	0.00201996	0.04241915
D. chlorogaster vs *D. raddei*	8.30439592	0.54261507	0.01183976	0.24863503
D. chlorogaster vs *D. steineri*	7.69991429	0.52380675	0.01233975	0.25913482
D. caspica vs *D. schaekeli*	5.74124917	0.48898112	0.03571429	0.75
D. caspica vs *D. defilippii*	22.9080785	0.82084041	0.04761905	1
D. caspica vs *D. raddei*	59.0794926	0.95167486	0.1	1
D. caspica vs *D. steineri*	62.5067198	0.95420317	0.1	1
D. schaekeli vs *D. defilippii*	10.2489853	0.53244289	0.00215996	0.04535909
D. schaekeli vs *D. raddei*	26.2929358	0.78974519	0.01099978	0.23099538
D. schaekeli vs *D. steineri*	25.0286747	0.78144584	0.01195976	0.25115498
D. defilippii vs *D. raddei*	78.155169	0.92870313	0.01785714	0.375
D. defilippii vs *D. steineri*	73.5754238	0.92459984	0.01785714	0.375
D. raddei vs *D. steineri*	0.48872024	0.10887741	0.6	1

Table 5. Significant differences (p adjusted < 0.05) based on ANOVAs between species for characters that loaded most heavily in the PCA analysis along PC1 and PC2.

Character	Group	diff	lwr	upr	p adj
HL	*D. schaekeli-D. caspica*	-0.0902136	-0.1413955	-0.0390316	0.00015667
	D. defilippii-D. chlorogaster	-0.0469112	-0.0848688	-0.0089537	0.00905456
	D. schaekeli-D. chlorogaster	-0.0867031	-0.1228942	-0.050512	1.49E-06
	D. kamii-D. defilippii	0.05386749	0.01422213	0.09351285	0.00355339
	D. raddei-D. defilippii	0.07172598	0.02594747	0.1175045	0.00071061
	D. schaekeli-D. defilippii	-0.0397919	-0.0777494	-0.0018343	0.03571683
	D. steineri-D. defilippii	0.04930259	0.00352407	0.0950811	0.02914281
	D. schaekeli-D. kamii	-0.0936594	-0.1316169	-0.0557018	9.05E-07
	D. schaekeli-D. raddei	-0.1115179	-0.1558427	-0.067193	6.49E-07
	D. steineri-D. schaekeli	0.08909447	0.04476961	0.13341933	2.41E-05
HW	*D. raddei-D. caspica*	0.09979694	0.01960027	0.1799936	0.00849183
	D. schaekeli-D. caspica	-0.0770482	-0.1487783	-0.0053181	0.02973992
	D. steineri-D. caspica	0.09787592	0.01767926	0.17807259	0.01016826
	D. defilippii-D. chlorogaster	-0.073984	-0.1271805	-0.0207876	0.00277692
	D. schaekeli-D. chlorogaster	-0.134557	-0.1852779	-0.0838362	2.58E-07
	D. kamii-D. defilippii	0.06617993	0.01061805	0.12174181	0.0126613
	D. raddei-D. defilippii	0.1162721	0.05211477	0.18042943	0.00010711
	D. schaekeli-D. defilippii	-0.060573	-0.1137695	-0.0073766	0.01864865
	D. steineri-D. defilippii	0.11435109	0.05019376	0.17850842	0.00013467
	D. raddei-D. kamii	0.05009217	-0.0140652	0.11424951	0.199327
	D. schaekeli-D. kamii	-0.126753	-0.1799494	-0.0735565	1.63E-06
	D. schaekeli-D. raddei	-0.1768451	-0.2389652	-0.1147251	7.31E-08
	D. steineri-D. schaekeli	0.17492412	0.11280405	0.23704419	8.91E-08
LA	*D. raddei-D. caspica*	0.13245427	0.04819711	0.21671142	0.00068242
	D. steineri-D. caspica	0.10994247	0.02568531	0.19419962	0.00536844
	D. raddei-D. chlorogaster	0.0976496	0.03238429	0.16291491	0.00122865
	D. schaekeli-D. chlorogaster	-0.1088724	-0.1621613	-0.0555835	1.88E-05
	D. steineri-D. chlorogaster	0.0751378	0.00987249	0.14040311	0.01700173
	D. raddei-D. defilippii	0.11269337	0.04528764	0.18009909	0.00031507
	D. schaekeli-D. defilippii	-0.0938286	-0.1497185	-0.0379388	0.00029861
	D. steineri-D. defilippii	0.09018157	0.02277584	0.15758729	0.00416969
	D. raddei-D. kamii	0.10370428	0.03629855	0.17111	0.00088497
	D. schaekeli-D. kamii	-0.1028177	-0.1587076	-0.0469278	8.69E-05
	D. steineri-D. kamii	0.08119247	0.01378675	0.1485982	0.01145471
	D. schaekeli-D. raddei	-0.206522	-0.2717873	-0.1412567	1.03E-08
	D. steineri-D. schaekeli	0.18401019	0.11874488	0.24927551	8.71E-08

Character	Group	diff	lwr	upr	p adj
LFO	*D. steineri-D. caspica*	0.14914533	0.02151579	0.27677488	0.01496402
	D. schaekeli-D. chlorogaster	-0.091309	-0.172029	-0.0105889	0.01969792
	D. steineri-D. chlorogaster	0.11421692	0.0153555	0.21307834	0.01650175
	D. schaekeli-D. defilippii	-0.0956247	-0.1802846	-0.0109648	0.01993878
	D. steineri-D. defilippii	0.10990117	0.00779753	0.21200481	0.02927053
	D. schaekeli-D. kamii	-0.112517	-0.1971769	-0.0278572	0.00446193
	D. schaekeli-D. raddei	-0.1831513	-0.2820128	-0.0842899	7.88E-05
	D. steineri-D. schaekeli	0.20552588	0.10666445	0.3043873	1.45E-05
NL	*D. raddei-D. caspica*	0.13426954	0.01773927	0.25079982	0.01688189
	D. steineri-D. caspica	0.12746376	0.01093348	0.24399404	0.02582643
	D. raddei-D. kamii	0.09608013	0.0028559	0.18930435	0.04043886
	D. schaekeli-D. raddei	-0.0995003	-0.1897643	-0.0092364	0.02429089
	D. steineri-D. schaekeli	0.09269456	0.0024306	0.18295852	0.04149884
TD	*D. defilippii-D. caspica*	-0.2426602	-0.3880856	-0.0972349	0.00032306
	D. defilippii-D. chlorogaster	-0.2189552	-0.3242064	-0.1137041	1.43E-05
	D. kamii-D. defilippii	0.23067763	0.1207464	0.34060886	1.25E-05
	D. raddei-D. defilippii	0.2497717	0.12283405	0.37670935	3.31E-05
	D. schaekeli-D. defilippii	0.12432083	0.01906969	0.22957197	0.01363015
	D. steineri-D. defilippii	0.21685613	0.08991848	0.34379378	0.00023774
	D. schaekeli-D. kamii	-0.1063568	-0.2116079	-0.0011057	0.04650968
	D. schaekeli-D. raddei	-0.1254509	-0.2483577	-0.002544	0.04333775
LFL	*D. defilippii-D. caspica*	-0.0706117	-0.1227745	-0.0184488	0.00369411
	D. schaekeli-D. caspica	-0.1293966	-0.1803023	-0.0784909	5.44E-07
	D. defilippii-D. chlorogaster	-0.073244	-0.1109967	-0.0354913	4.07E-05
	D. schaekeli-D. chlorogaster	-0.1320289	-0.1680247	-0.0960332	5.87E-10
	D. kamii-D. defilippii	0.06396186	0.02453046	0.10339325	0.00046294
	D. raddei-D. defilippii	0.04968497	0.00415352	0.09521643	0.02631444
	D. schaekeli-D. defilippii	-0.058785	-0.0965376	-0.0210323	0.00076611
	D. steineri-D. defilippii	0.05187387	0.00634242	0.09740533	0.01856271
	D. schaekeli-D. kamii	-0.1227468	-0.1604995	-0.0849941	6.13E-09
	D. schaekeli-D. raddei	-0.1084699	-0.1525556	-0.0643843	9.50E-07
	D. steineri-D. schaekeli	0.11065883	0.06657319	0.15474447	6.75E-07
IOR	*D. raddei-D. defilippii*	0.07345436	0.00614812	0.14076059	0.02629129
	D. steineri-D. defilippii	0.07245092	0.00514469	0.13975715	0.02925627
	D. schaekeli-D. kamii	-0.0624579	-0.1182652	-0.0066505	0.02149984
	D. schaekeli-D. raddei	-0.0952181	-0.1603871	-0.0300491	0.00161264
	D. steineri-D. schaekeli	0.09421464	0.02904566	0.15938362	0.00181677

Table 6. Summary statistics of the meristic PCA.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Standard deviation	1.76529004	1.30143875	1.1373617	1.01014864	0.68960351	0.49787583	0.30248416	0.24715652
Proportion of Variance	0.38953	0.21172	0.1617	0.12755	0.05944	0.03099	0.01144	0.00764
Cumulative Proportion	0.38953	0.60125	0.76295	0.8905	0.94994	0.98093	0.99236	1
eigenvalue	3.11624891	1.69374282	1.29359165	1.02040028	0.475553	0.24788034	0.09149667	0.06108635
NSL	-0.5144197	-0.0704081	0.23061154	-0.221254	0.07961578	-0.1553723	-0.2976844	-0.7135719
NIL	-0.4944198	0.1276862	-0.2932786	-0.1132037	0.26785698	0.0281929	0.75354751	-0.0064627
NGS	0.12461508	0.64759436	0.04178163	0.22727992	0.55251287	0.38331307	-0.1896187	-0.1534149
NCS	0.23453268	-0.2979153	0.68351693	-0.0893866	0.08336852	0.42964031	0.40999382	-0.146354
NVS	-0.2022453	0.1703482	0.42635416	0.72372573	-0.1180587	-0.422797	0.17130757	0.04980024
NDS	0.20337835	0.42684335	0.34430295	-0.5702381	0.11088133	-0.5260119	0.0913298	0.18815317
SDLT	-0.4769167	-0.238019	0.25705883	-0.0684681	0.38097065	0.11263355	-0.3171246	0.62188209
NFP	0.33267317	-0.4502667	-0.159572	0.15794655	0.66205892	-0.418823	0.03527835	-0.145598

morphology indicate that head and limbs may show clear correlation with habitat use (Herrel et al. 2001). A flat head and long body can be found in rock-dwelling lizards, but a narrow body shape is prevalent in tree-dwelling lizards (Herrel et al. 2001). *Darevskia schaekeli* and *D. raddei* are the most distinctive species of the rock dwellers yet they are generally the most divergent in most characteristics (Fig. 5). A detailed study of their natural history may reveal the underlying nature of their morphological differences. Investigating the correlative intersection among habitat preference, phylogeny, and morphology could demonstrate the efficacy of morphology to life history (Ahmadzadeh et al. 2013). Here, we demonstrate that habitat preference and morphology are not always sufficient to explain the morphological variation among species occupying the same habitat and that studies on the natural

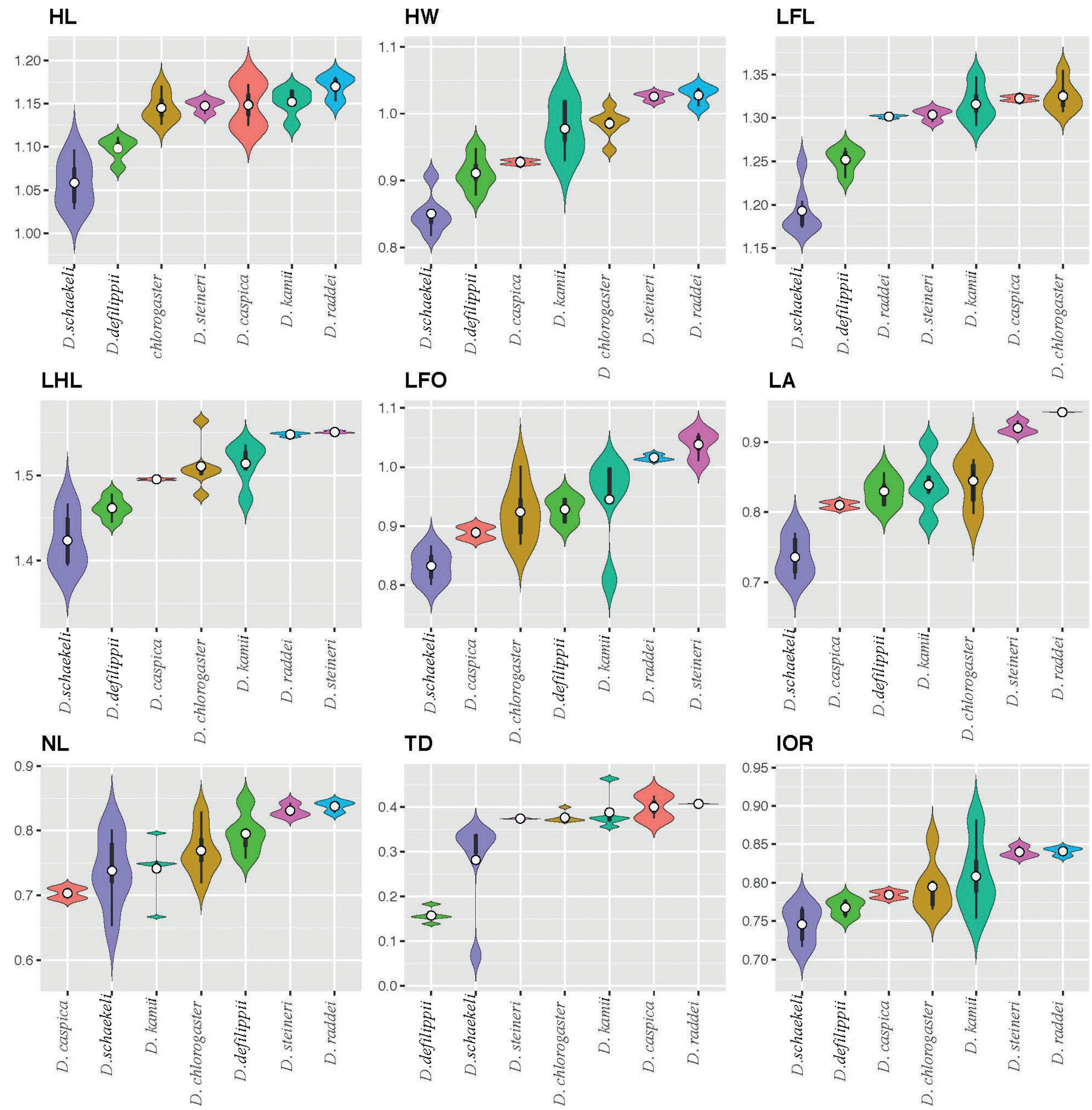

Figure 5. Violin plots showing the range, frequency, mean (white dot), and 50% quartile (black rectangle) of the size-adjusted morphometric characters that loaded most heavily in the PCA.

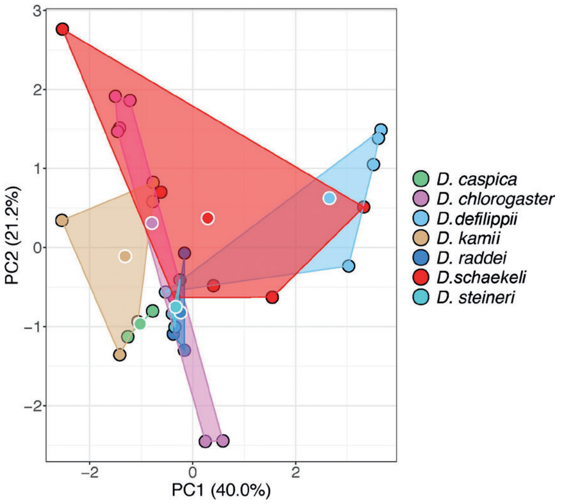

Figure 6. Principal component analysis of the meristic data.

history of all these species will potentially illuminate the reasons why some rock dwelling species are so divergent from other rock dwelling species. In a broader sense, such studies apply to a multitude of ecological principles where phenotypic differences within and among species can influence the rate and direction of evolution, population dynamics, and the outcome of several other community interactions (Bolker et al. 2003; Werner and Peacor 2003; Krohne 2018; Gomes et al. 2020; Naretto et al. 2022).

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