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Morphological Variability of the *Eremias persica* Complex (Reptilia: Sauria: Lacertidae) on the Iranian plateau

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Abstract

Eremias persica is a complex and polymorphic species of lacertid lizards, distributed across Iran, Afghanistan, and Pakistan. Despite the recognition of some intraspecific variation as separate species, the morphological boundaries between the newly proposed species and other phylogenetic clades remain ambiguous. In the present study, we aim to identify the boundaries between populations and phylogenetic clades by evaluating the morphological characters of different populations within this species complex. Our morphological analyses of populations from 12 regions of the Central Iranian plateau revealed significant divergence within this lineage. While, sexual dimorphism was limited to minor variations in the ratio of tail length to snout-vent length and the number of collar scales. Our results identified six distinct morphological clusters within *E. persica*, which differed significantly from each other in characters such as head length, eye diameter, eye-to-tympanum distance, and abdominal width. Furthermore, a more limited morphological differentiation was traced among local populations in characters such as eye-to-tympanum distance, tympanum diameter, and abdominal width. In contrast to *E. nigrolateralis*, which differs from *E. persica* solely in dorsal coloration, *E. fahimii* and *E. rafiqi* were clearly distinguished from *E. persica* based on both morphology and dorsal coloration patterns. We also identified dorsal coloration patterns as a reliable diagnostic tool and a complement to morphological characters in this species complex.

Keywords: Lizard, Eremiadini, Sexual dimorphism, Biometry, Diagnostic characters, Discrimination**.**

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INTRODUCTION

The genus *Eremias* Fitzinger, 1834, comprising about 44 species and 12 subspecies, is one of the most diverse genera within the tribe Eremiadini in Eurasia, exhibiting a wide distribution range including Korea, eastern and central Asia, southeastern Europe, the Iranian plateau, Afghanistan, and Pakistan (Sindaco et al., 2008, Rastegar Pouyani et al., 2010, Uetz, 2025). The Persian racerunner, *Eremias persica* Blanford, 1875, is considered one of the most diverse species within the genus *Eremias*. Since its original description from a site near Isfahan, Iran, the species has been shown to occupy an extensive range across the Iranian plateau (Boulenger, 1921, Terentiev & Chernov, 1965, Anderson, 1999, Rastegar Pouyani et al., 2010). Recent findings indicate that prolonged isolation has led to significant morphological variation among *E. persica* populations across the Iranian plateau, giving rise to a complex of distinct species (Rastegar Pouyani & Nilson, 1997, Rastegar Pouyani & Rastegar Pouyani, 2001, Mozaffari et al., 2020). Phylogenetic studies have validated the existence of multiple geographical lineages, which have emerged as a result of the group's diversification across the Iranian plateau to Afghanistan and Pakistan (Rastegar

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Pouyani, 2007, Masroor et al., 2022). Nevertheless, to date no comprehensive studies have been carried out on the morphology of the populations within this species complex. Morphological data from certain described species in this group also remain unreliable due to number of reasons, including descriptions based on rare morphotypes (Rastegar Pouyani & Nilson, 1997), without molecular validation (Rastegar Pouyani et al., 2010), or taxonomic delineation relying on subadult specimens despite molecular evidence (Mozaffari et al., 2020).

The ambiguous morphological boundaries led to the genetic clades of *Eremias persica*, *E. rafiqi*, and *E. fahimii* being collectively considered as *E. persica* (sensu lato) in present study (Rastegar Pouyani et al., 2010, Mozaffari et al., 2020, Masroor et al., 2022). The distribution of *E. persica* (s. l.) in the Middle East is limited by the Zagros and Alborz Mountain ranges in western, southwestern and northern regions of Iran (Anderson, 1999, Szczerbak, 2003), suggesting that lineage emerged after the Alpine orogeny (about 9–11 Mya) in Iran, and has not crossed these mountain ranges since then (Rastegar Pouyani et al., 2010, Mohajjel & Fergusson, 2014). The habitat of *Eremias persica* (s. l.) typically consists of open plains and slopes, and areas with poor vegetation. However, it is absent from the central deserts Dasht-e Lut and Dasht-e Kavir, as well as the Registan Desert in southwestern Afghanistan (Rastegar Pouyani, 2007, Wagner et al., 2016). The distribution of this species across the Iranian plateau is characterized by a fragmented pattern, resulting from the presence of various elevations and desert regions in the central and eastern parts of the plateau (Rastegar Pouyani, 2007). This fragmentation has given rise to distinct geographical isolates, which have played a significant role in shaping the species' evolutionary trajectory (Rastegar Pouyani, 2007, Rastegar Pouyani et al., 2010).

The genetic variation within this complex species has been topic of considerable interest among herpetologists (Rastegar Pouyani et al., 2010, Mozaffari et al., 2011, Rastegar Pouyani et al., 2016, Ahmadzadeh et al., 2017, Mozaffari et al., 2020, Masroor et al., 2022). However, the predominant focus of studies on the molecular diversity of *E. persica* has overshadowed the contribution of morphological variations as the primary raw material shaped by natural selection (Lande, 1976, Wake, 2012).

The phenotypic and morphological variation of *Eremias persica* populations on the Iranian plateau, similar to that of other *Eremias* species (Hosseinian Yousefkhani et al., 2016, Chirikova et al., 2019), is strongly influenced by habitat type (Rastegar Pouyani & Nilson, 1997, Riki et al., 2015). Hence, habitat diversity and the resulting wide morphological variation within *E. persica* (s. l.) can be one of the reasons for preferring molecular studies over morphology (Rastegar Pouyani, 2007). While the status of phylogenetic clades of this lacertid lizard lineage has been substantially clarified after many studies on the Iranian plateau (Rastegar Pouyani et al., 2010, Khan et al., 2021), persistent discrepancies in morphological characterizations continue to impede the operational delimitation of putative cryptic species (Rastegar Pouyani & Nilson, 1997, Rastegar Pouyani & Rastegar Pouyani, 2001, 2005). The present study seeks to resolve the existing ambiguities in this lineage by addressing the morphological variations among populations and phylogenetic clades of *Eremis persica* (s. l.).

MATERIAL AND METHODS

Sampling and study system

Following the recommendations of Soulsbury et al. (2020), we prioritized the use of museum specimens to minimize anthropogenic impacts on populations of this species. The specimens utilized in this study, acquired on loan from the Zoology Laboratory of Hakim Sabzevari University, had been collected between 2002 and 2023 during both government-funded research projects (Iranian Ministry of Environment) and independent field campaigns. However, sampling of the gaps was unavoidable. Therefore, sampling was conducted to fill the existing gaps during June to July 2024. A total of 78 adult specimens (48 males and 30 females) of the target species were collected, covering almost the entire distribution range of the species in Iran (Figure 1, Appendix table 1). Here, samples from 12 sites in the central plateau of Iran were collected. Among these specimens, according to Rastegar Pouyani et al. (2010), six phylogenetic clades with significant genetic distance from the type locality near Isfahan province are present among the samples (Figure 1).

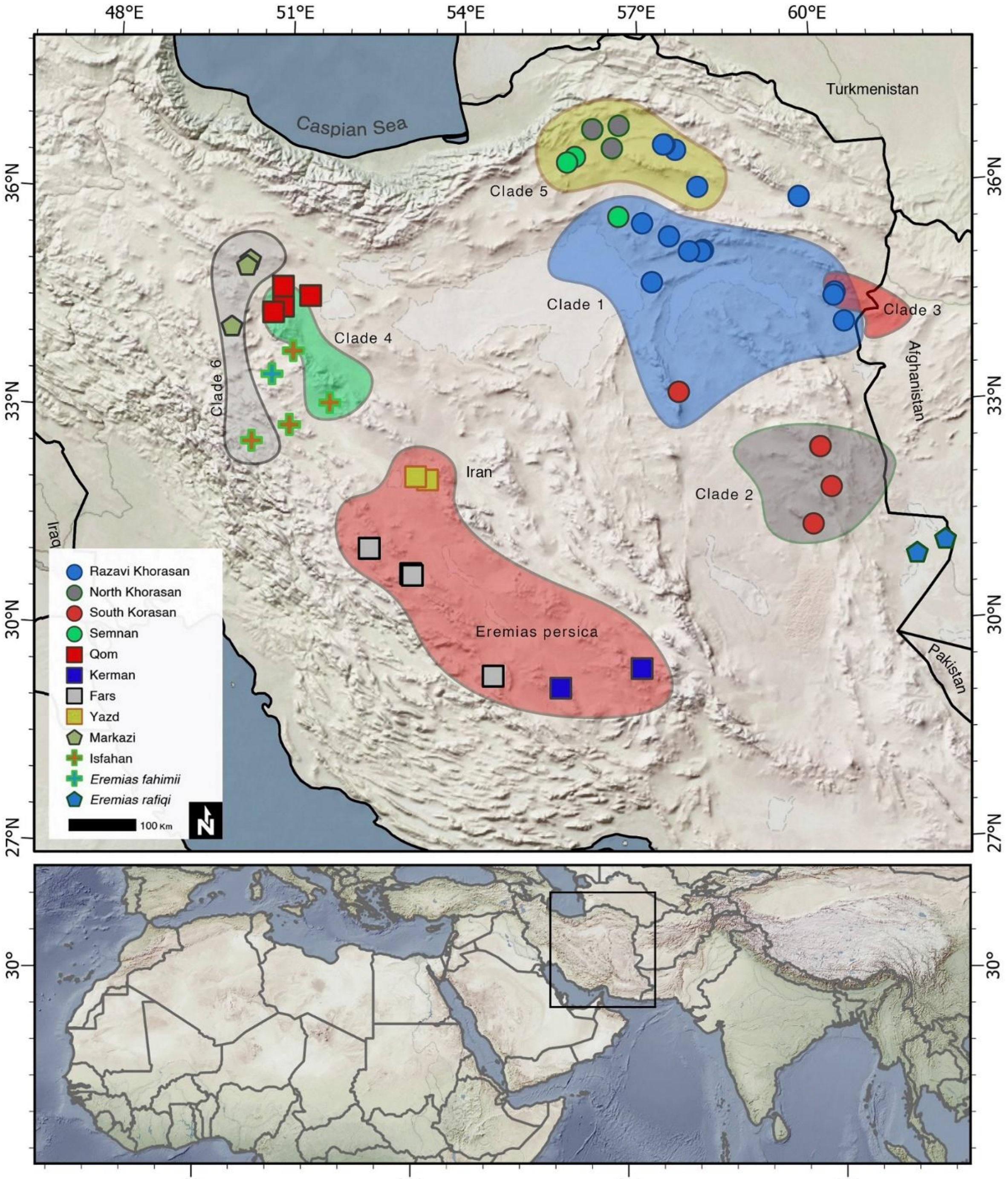

FIGURE 1. Sampling locations of the *Eremias persica* complex used in the present study, divided by phylogenetic clades and geographic location.

Specimens were euthanized using a conventional and approved method by inducing cooling followed by freezing (Shine et al., 2015), after recording the coordinates of the location and taking photographs. After humane killing, specimens were deposited in the Sabzevar University Herpetological Collection (SUHC). The entire research process was conducted in accordance with the approval of the Ethics Committee of Razi University of Kermanshah (Approval ID: IR.RAZI.AEC.1403.056).

The measurement of metric characters carried out using a digital caliper with 0.01 mm accuracy, enabling for precise quantification of metric traits. Additionally, meristic characters were examined and counted under a stereo microscope, and sex was determined by cloacal probing using a smooth, blunt instrument. The color patterns and other descriptive characters were also recorded and documented. Finally, a schematic of the dorsal color patterns was created based on the current dataset and observations extracted from iNaturalist.org (Van Horn et al., 2018), providing a visual summary of the observed patterns.

Overall, a total of 19 metric and 9 meristic characters were chosen from previous studies (Anderson, 1999, Rastegar Pouyani et al., 2016, Orlova et al., 2023), of which, six ratio characters were derived and used in the morphological analyses (Table 1).

Statistical analysis

Considering the sample size of the present study (<100), it is necessary to check the normality of the data (Mishra et al., 2019). Consequently, the data distribution was examined using SPSS Statistics V. 29.0.2.0 software (SPSS, 2023), using a combination of graphical and numerical methods, and the Kolmogorov-Smirnov test (Mishra et al., 2019). Outliers were identified using Mahalanobis distance test and box plots, and re-measured to verify the accuracy of the outlier identification (Kannan & Manoj, 2015). The presence of Sexual dimorphism was tested using Independent Sample t-test (2-tailed) (Kim, 2015), and Mann-Whitney U test (Mann & Whitney, 1947, Wilcoxon, 1992), for parametric and non-parametric data, respectively. Characters with significant sex-based differences (P-Value ≤ 0.05) were excluded from Operational Taxonomic Units (OTUs) variance analysis. In addition, Principal Component Analysis (PCA) was performed separately for all characters on gender. Following the exclusion of sex-dependent characters, the metric characters were adjusted using the *GroupStruct* R package, to remove the effect of body size variations (Thorpe, 1983, Chan & Grismer, 2021, 2022).

A pairwise comparison of characters between populations and phylogenetic clades were performed using parametric One-way ANOVA and non-parametric Kruskal-Wallis tests (Armstrong & Hilton, 2010). Multivariate analyses for all traits were performed using Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA) based on the two considered OTUs. PCA reduces morphometric data redundancy, extracting independent variables for population differentiation. The DFA adopts a similar methodology as to the PCA, but its objective is to determine a linear function that accentuates the differences between groups, rather than simply reducing dimensionality (Davis, 1986).

RESULTS

Sexual dimorphism

We identified a weak sexual dimorphism in two characters of NCS (P-Value = 0.04) and the ratio of TL to SVL (P-Value = 0.03) (Figure 2, Table 2). Among these, TL/SVL can be a better indicator of sexual size dimorphism (SSD) (Braña, 1996, Liang et al., 2022, Candan et al., 2024), which is commonly observed in lacertids. However, the results of the PCA test show a high overlap of traits based on sex (Figure 2). We did not include these two characters in the analysis between OTUs in order to prevent the generation of error signals in our calculations.

Intergroup variation

Analysis of variance between OTUs revealed significant differences (P-Value ≤ 0.05) in the characters LWB, ETD and TD among populations, and HL, ED, ETD, LWB and IOD among phylogenetic clades (Table 2). Descriptive statistics for OTUs are provided separately for populations and phylogenetic clades in supplementary Tables S2 and S3, respectively.

TABLE 1. List of morphometric and meristic characters examined in the present study along with their abbreviations.

	Character	Definition
Metric	SVL	Snout-vent length (from tip of snout to anterior edge of cloaca)
	TL	Tail length (from posterior edge of cloaca to tip of tail)
	LHF	Trunk length (gleno-acetabular distance from axilla to groin, measured from the posterior edge of forelimb to the anterior edge of hind limb insertion)
	HL	Head length (from tip of snout to the posterior edge of tympanum)
	HH	Head height (maximum distance between upper head and lower jaw)
	HW	Head width (distance between posterior eye corners)
	LFL	Length of forelimb (from top of shoulder joint to tip of 4th finger)
	LHL	Length of hindlimb (from hip joint to tip of 4th toe)
	LFO	Length of femur (from hip joint to top of knee)
	LT	Length of tibia (from top of knee to beneath wrist)
	ED	Eye diameter (distance from anterior corner to posterior corner to its posterior)
	RED	Rostral length (from tip of nostril to anterior corner of eye)
	ETD	Distance between posterior edge of eye and tympanum
	NL	Length of neck (distance between posterior edge of tympanum and shoulder joint)
	TD	Tympanum diameter (largest size)
	IOD	Interorbital distance (largest size)
	LV	Length of cloaca crevice (largest size)
	LBT	Length of widest part of tail base
	LWB	Length of widest part of belly
Meristic	MNSLS	Mean Number of supralabial scales (Right/Left)
	MNILS	Mean Number of infralabial scales (Right/Left)
	NCS	Number of gular scales along mid-line of the throat
	NGS	Number of collar scales
	NLVS	Number of longitudinal rows of ventral scales, (Maximum count in the middle of the body)
	NTVS	Number of transverse series of ventral scales (counted in straight median series between collar and the row of scales separating the series of femoral pores)
	NDS	Number of dorsal scales across midbody
	MNSDLT	Mean Number of subdigital lamellae along underside of 4th toe (defined by their width, the one touching the claw included), counted bilaterally
	MNFP	Mean Number of femoral pores (Right/Left)
Ratio	TL/SVL	Tail length / snout-to-ventral length
	HL/HW	Head length / head width
	HW/HH	Head width / head height
	LHL/LFL	Hind limb length / forelimb length
	RED/HL	Rostral length / head length
	LHF/LWB	Trunk length / abdominal width

TABLE 2. Probability values of statistical tests based on three groups of sex, populations, and phylogenetic clades among measured characters for *Eremias persica* (sensu lato) on the Iranian plateau.

		Probability Value						
		Sexual dimorphism			Population		Phylogenetic clades	
	Character	Levene's Test	T test	U test	ANOVA	Kruskal-Wallis	ANOVA	Kruskal-Wallis
Metric characters	SVL	0.61	0.92		0.06	-	0.31	-
	TL	0.27	0.08		0.50	-	0.26	-
	LHF	-	-	0.55	0.39	-	-	0.87
	HL	0.93	0.87		0.38	-	**0.01**	-
	HH	0.96	0.65		0.28	-	0.14	-
	HW	0.75	0.74		-	0.86	-	0.61
	LFL	0.54	0.69		0.08	-	-	-
	LHL	0.24	0.18		0.80	-	-	-
	LFO	0.58	0.94		0.91	-	0.15	-
	LT	0.09	0.52		0.11	-	0.34	-
	ED	0.82	0.50		0.65	-	**0.03**	-
	RED	0.88	0.95		-	0.48	-	1.00
	ETD	0.93	0.45		**0.01**	-	**0.01**	-
	NL	0.43	0.75		0.45	-	0.30	-
	TD	0.25	0.31		**0.04**	-	0.58	-
	IOD	0.27	0.82		0.26	-	**0.01**	-
	LV	0.45	0.54		-	0.68	0.63	-
	LBT	0.55	0.22		0.09	-	0.21	-
	LWB	0.26	0.17		**0.05**	-	**0.03**	-
Ratio characters	TL/SVL*	0.34	**0.03**		*	-	*	-
	HL/HW	0.79	0.59		-	-	-	0.40
	HW/HH	0.51	0.59		0.58	-	0.96	-
	LHL/LFL	0.12	0.13		0.98	-	0.85	-
	RED/HL	-	-	0.63	-	-	-	0.61
	LHF/LWB	0.26	0.52		0.05	-	0.36	-
Meristic characters	MNSLS	-	-	0.22	-	0.06	-	-
	MNILS	-	-	0.99	-	0.17	-	0.51
	NCS*	-	-	**0.04**	-	*	-	*
	NGS	-	-	0.21	-	0.91	-	-
	NLVS	-	-	0.97	-	0.70	-	0.59
	NTVS	-	-	0.47	-	0.46	-	0.44
	NDS	-	-	0.27	-	0.17	-	0.22
	MNSDLT	-	-	0.92	-	0.15	-	0.43
	MNFP	-	-	0.25	-	0.29	-	0.14
	NFPR	-	-	0.27	-	0.54	-	0.26

* Sex- dependent character

Table 3. Pairwise differentiation matrix of *Eremias persica* complex phylogenetic clades, *E. fahimii*, and *E. rafiqi* based on significant morphological characters (*P*-value≤0.05).

	Clade 1	Clade 2 (Type)	Clade 3	Clade 4	Clade 5	Clade 6	*E. fahimii*	*E. rafiqi*
Clade 1		HH-HW-RED-ETD-NL	HL	HL-HH-LFL-LHL-LFO-ED-ETD-MNSLS	HL-HH-HW-LFL-ED-IOD-LBT-MNSDLT	LT-ED-MNSDLT	NTVS-NDS	MNSLS
Clade 2 (Type)	HH-HW-RED-ETD-NL		ETD	LFL-LHL-ED		IOD-LWB-MNILS	LWB-MNILS-NTVS-NDS-MNFP-NFPR	
Clade 3	HL	ETD		TL-LFL-ETD-MNSLS	MNSDLT	IOD-LWB-MNSDLT	LWB-NTVS-NDS	SVL-MNFP
Clade 4	HL-HH-LFL-LHL-LFO-ED-ETD-MNSLS	LFL-LHL-ED	TL-LFL-ETD-MNSLS		LHF-ETD	LHF-HL-LFL-LHL-ETD-IOD-LWB-MNSLS	TL-LHF-HL-LHL-LFO-ETD-LWB-MNSLS	LFO-ETD
Clade 5	HL-HH-HW-LFL-ED-IOD-LBT-MNSDLT		MNSDLT	LHF-ETD		NTVS	LWB-NTVS-NDS	
Clade 6	LT-ED-MNSDLT	IOD-LWB-MNILS	IOD-LWB-MNSDLT	LHF-HL-LFL-LHL-ETD-IOD-LWB-MNSLS	NTVS		IOD-NDS	IOD
E. fahimii	NTVS-NDS	LWB-MNILS-NTVS-NDS-MNFP-NFPR	LWB-NTVS-NDS	TL-LHF-HL-LHL-LFO-ETD-LWB-MNSLS	LWB-NTVS-NDS	IOD-NDS		MNSLS-NTVS-MNFP
E. rafiqi	MNSLS		SVL-MNFP	LFO-ETD		IOD	MNSLS-NTVS-MNFP	

Considering locations as OTUs, multivariate principal component analysis identified HL, LHF/LWB, and LHL as the most weighted and the main effective characters for PC 1, and HL/HW, HW, and TL for PC 2, in separating populations. Meanwhile, discriminant function analysis identified LWB, LFL, and HH most informative characters for the first function, and IOD, LT, and ETD for the second function, for the separation of populations. The informative characters between phylogenetic clades, in the principal component analysis, were HL, HW, TD, and ETD for PC1, and MNFP, LHF/LWB, NFPR, and MNSDLT for PC2. Furthermore, the discriminant function analysis scores identified NL, HL, NDS,

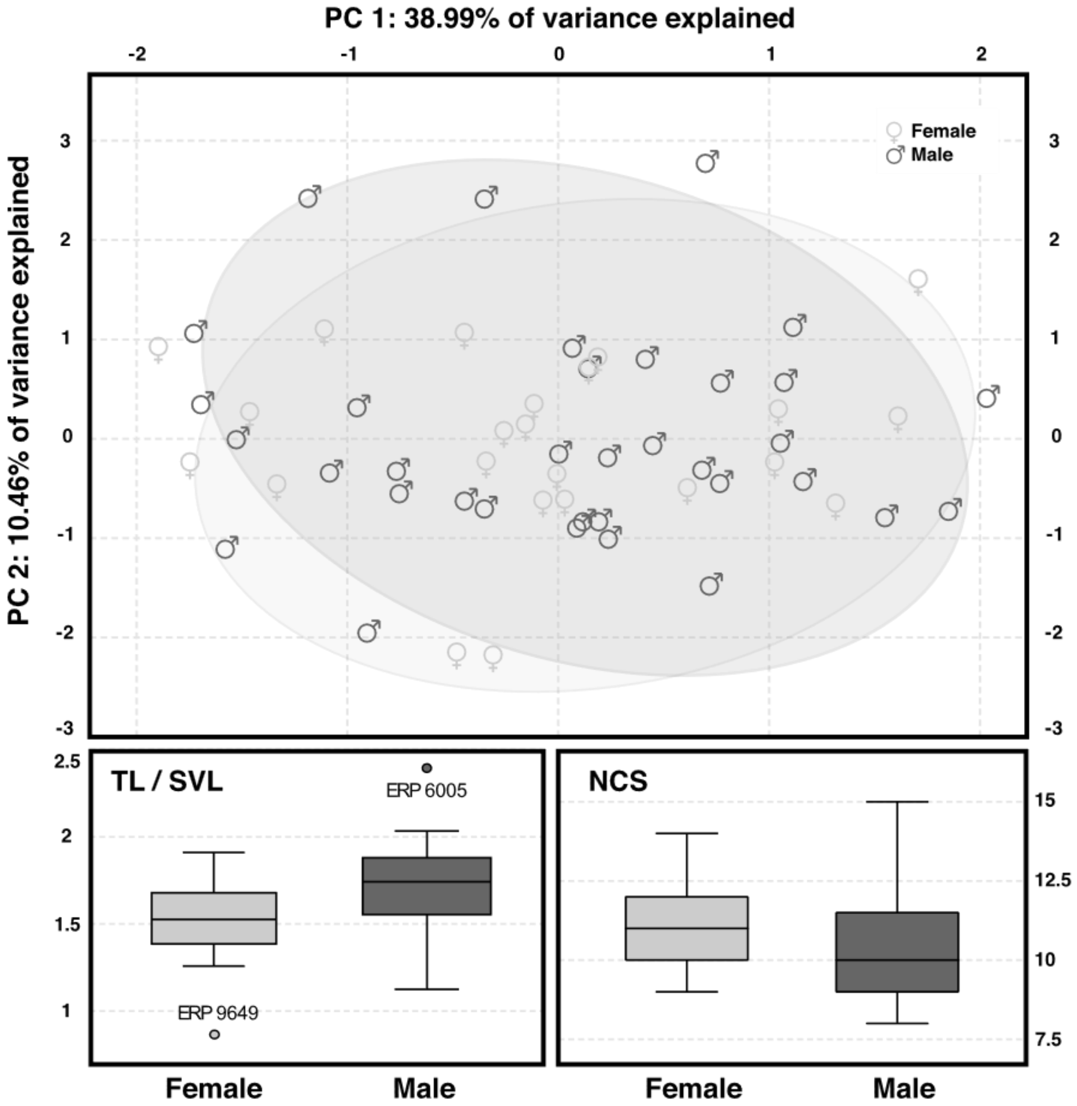

FIGURE 2. Scatter plot of the first and second principal component scores based on sex among the studied specimens, Upper; Box plot of NCS and TL/SVL characters based on sex, Bottom.

and RED for the first function, and ETD, NL, MNILS, and MNSLS for the second function, as the most weighted characters, in separating the clades. The scores of principal component analysis and discriminant function analysis for the first three components or functions are presented in supplementary Tables 4 and 5, respectively, based on locations and phylogenetic clades.

The scatter plots of DFA and PCA clearly show the differentiation of traits between populations and phylogenetic clades (Figures 3, 4). However, the distribution pattern of the distinct functions reveals that the differentiation of phylogenetic clades is more pronounced and evident than among geographic localities, indicating a clearer distinction between the clades. Based on DFA and PCA results and Table 3, the phylogenetic clades, exhibit significant levels of morphological divergence and *E. fahimii* and *E. rafiqi* are distinguished from the rest. Fars population as type locality of *E. nigrolateralis*, exhibits a lesser degree of separation compared to the other two species, *E. fahimii* and *E. rafiqi* (Figure 3). Finally, pairwise comparisons based on significant morphological characters between populations and between phylogenetic clades, as presented in Tables S6 and 3, respectively, provide a clearer delineation of divergence boundaries among these groups.

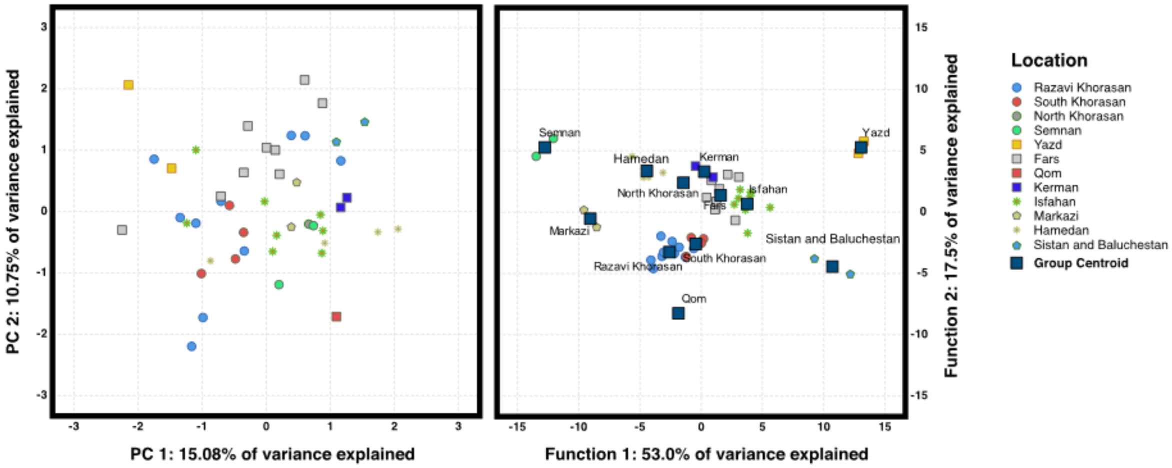

FIGURE 3. Scatter plots of the first and second principal components (PCA), left; First and second discriminant functions, right; Based on ten sampling sites of *Eremias persica* complex and *E. fahimii* from Hamedan Province, and *E. rafiqi* from Sistan and Baluchestan Province on the Iranian plateau.

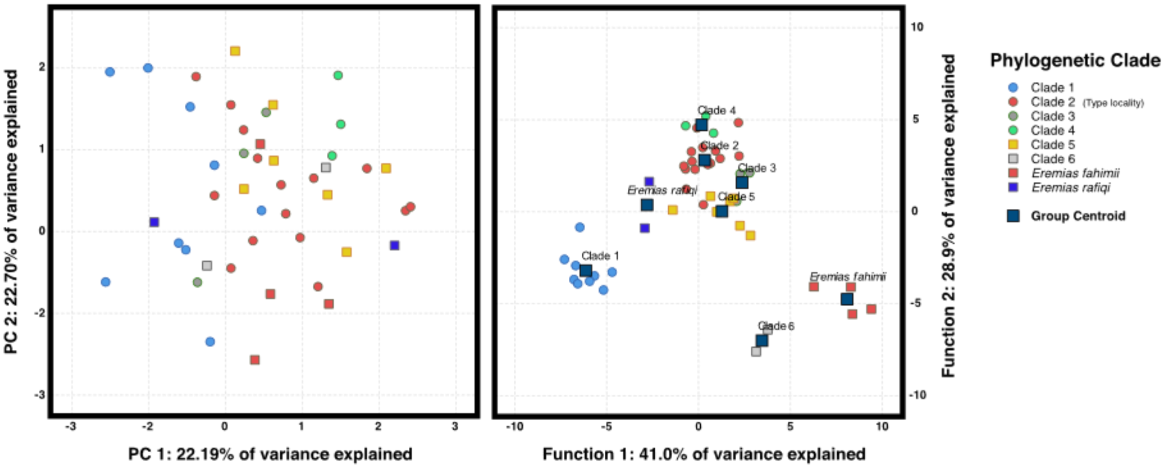

FIGURE 4. Scatter plots of the first and second principal component analysis, left; first and second discriminant functions, right; based on six phylogentic clades of the *Eremias persica* complex and *E. fahimii*, and *E. rafiqi* on the Iranian plateau.

Color and pattern variation

On the Central Iranian Plateau, thirteen dominant dorsal pattern morphs were recognised in in the adult form of *Eremias persica* (s. l.) (Figure 5). In some areas, such as the southern part of Kavir National Park, the western area of the Kalmand protected area, southern Yazd, and Ahmadabad village in Semnan Province, pattern of 14 has been observed, which is related to the sub-adult form. In the populations of Razavi Khorasan, patterns 8, 7, and 10 can be observed, while in the northeast and North Khorasan, dorsal pattern 4 is dominant, and in Semnan, pattern 3 is prevalent. Patterns 1 and 9 are seen in South Khorasan and Fars, but pattern 13 exclusively belongs to *E. nigrolateralis* from Fars and western Yazd Provinces, and in Qom, two distinct patterns, 6 and 2, can be observed. Additionally, from north of Qom to south of Tehran, the pattern 5 is seen in the populations. The patterns 11 and 12 are unique to *E. fahimii* and *E. rafiqi*, respectively, making them readily distinguishable from other species.

Adaptation to various environments has given rise to a diverse range of patterns on *E. persica* s. l., which is also evident in their coloration. In the north-east and south, the dorsal region is beige to ochraceous, while the front limbs are cream-colored, and the hind limbs and tail are cream to earthy in the

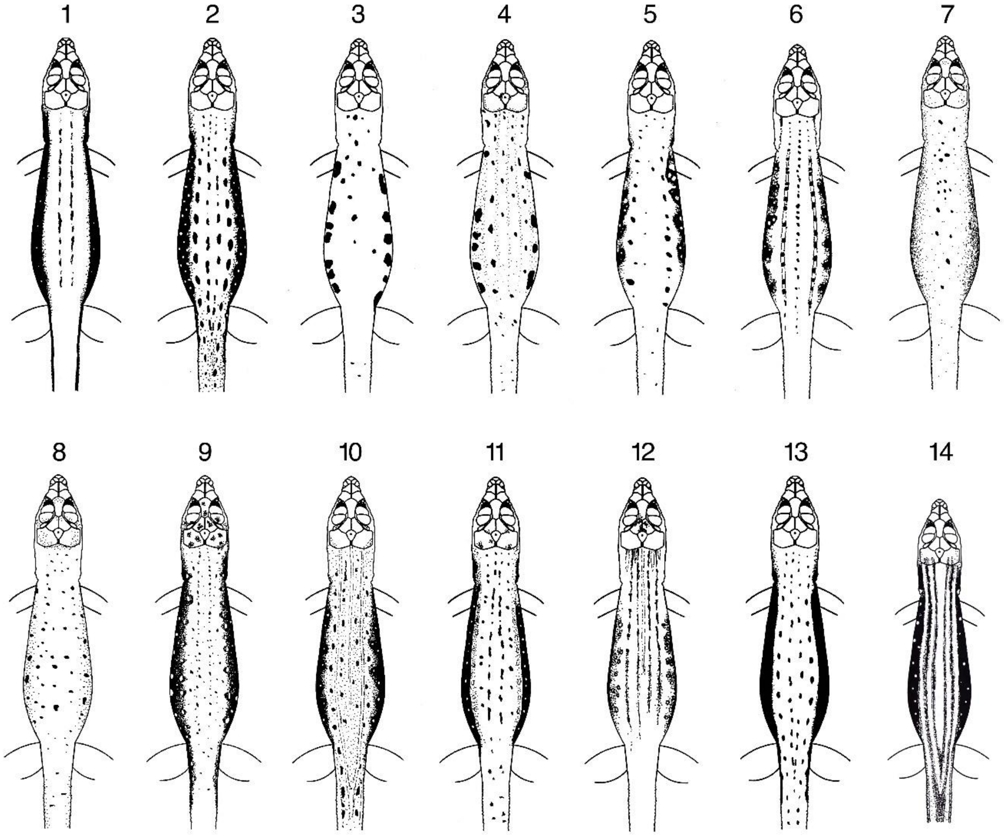

FIGURE 1. Variations in dorsal color patterns among populations of *Eremias persica* (1-10), *E. fahimii* (11), *E. rafiqi* (12), and *E. nigrolateralis* (13); Sub-adult form of *E. persica* (14); on the Iranian plateau.

southern population and grullo in the north-eastern population. In the central plateau region, the coloration is darker, with silver to fuscous colors. *Eremias rafiqi* has a lighter coloration, with a pastel gray head and viridian dorsal region, accompanied by olivaceous stripes. *Eremias fahimii* has a dominant viridescence to emerald green coloration on its head and dorsal region, with thick fuscous stripes.

DISCUSSION

Distinct lineages within *Eremias persicus* (s. l.) are suggested by the observed morphological diversity, mirroring the genetic variation previously reported in this complex species by Rastegar Pouyani et al. (2010). The morphological diversifications in *E. persicus* (s. l.), supported by molecular data, have been shaped through a divergence event dated to approximately 7–10 Mya (Rastegar Pouyani, 2007) , which has been coincident with a geological event responsible for the current configuration of the Zagros and Alborz Mountain ranges (Allen et al., 2004, Khadivi, 2010).

Sexual dimorphism in this group, similar to other *Eremias* species, is hardly recognizable (Orlova et al., 2017, Chirikova et al., 2019). Although males have a higher TL/SVL and females have more NCS, but sexual dimorphism is absent in other characters. The populations of *E. persica* (s. l.) overlap in meristic characters, making them less distinguishable from one another. In contrast, mensural traits exhibit the highest degree of differentiation among populations and phylogenetic clades. Morphological clustering is relatively apparent in *E. persica* (sensu stricto) populations on the Iranian plateau, particularly in characters related to escape strategy, especially those associated with the head region. Specifically, characters related to the head region (such as head length and snout length) and abdominal muscles reflect a unique evolutionary adaptation in the Eremiadini tribe of lizards, which is noteworthy in itself (Edwards et al., 2016, Hosseinian Yousefkhani et al., 2022). Habitat diversity on the Iranian plateau

(Dehshiri, 2018), habitat preferences, and resulting ecological limitations are the second factor that, in turn, create functional and morphological differences (Vanhooydonck & Van Damme, 1999). The adaptation of characters related to limbs and body shape (e.g., LHL, LFL, TL, LWB, and LHF/LWB in our study) is shaped by specific conditions and environmental pressures (Herrel et al., 2002). This adaptation has been observed in numerous groups of reptiles under environmental conditions (Hosseinian Yousefkhani et al., 2014, Kamali et al., 2024). In desert lacertid lizards, such as *E. persica*, which occupy relatively simple and open environments compared to their montane counterpart *E. montana*, longer hind limbs are observed (Losos, 1990, Herrel et al., 2002). This adaptation leads to increased speed and sprinting ability, rather than maneuverability. Changes in head shape are another outcome of habitat preferences (Vicent-Castelló et al., 2025). Our findings showed that HL, ED, ETD, IOD, and LWB were significantly different among phylogenetic clades, while LWB, ETD and TD were also distinct at the population level.

The presence of morphological variations in this lineage of Lacertidae, as first interpreted by Arnold (1989) for other genera of Eremiadini, can be considered as synapomorphies that arose under the influence of an adaptive radiation process (Mayer & Pavlicev, 2007). This cladogenesis may have been influenced by the formation of fragmented arid habitats resulting from the gradual cooling and desiccation of the Iranian plateau (Kargaranbafghi & Neubauer, 2018, Sun et al., 2021). Considering that lacertid lizards typically exhibit a highly conserved morphology (Arnold, 1987, Arnold, 1989), Consistent with the findings of Hosseinian Yousefkhani et al. (2013) and Boroumand et al. (2024), the morphological variations present in the *E. persica* complex may also indicate the existence of distinct lineages or species.

Considering the pattern of distribution of morphological clusters in the present study (Figure 1)and phylogenetic clades in Rastegar Pouyani et al. (2010), it can be inferred that, it is likely that geographical separations (e.g., physical barriers, isolation) contributed to the formation of the lineage. In contrast to the sister lineage, *E. montana*, where orogenesis has primarily acted as a corridor (Rastegar Pouyani & Rastegar Pouyani, 2005, Rastegar Pouyani, 2007), the speciation of the *E. persica* lineage was likely driven by the orogenic events of the Iranian plateau, which served as a barrier to population separation, and habitat loss and desertification may have intensified this process (Rodwell & Hoskins, 1996).

Concurrent with the Zagros Mountains reaching their mid-elevation in the Oligocene, the Alborz orogeny in the north began in the early-middle Miocene and continued until the late Miocene (Hatzfeld & Molnar, 2010, Pirouz et al., 2017). The initial populations of the *E. persica* lineage, after gaining access to a new and vast niche on the Iranian plateau, dispersed throughout the region, entering the area while the Kopet Dagh and Khorasan mountains were forming in the northeast and east of the country (Robert et al., 2014).

Accordingly, the similarity between all measured mensural traits between the populations of Fars and Kerman provinces in southern Iran can be attributed to the integrity and similarity of their habitats (Table S6), something that is not observed in the isolated population of western Yazd province, despite genetic similarity (Rastegar Pouyani et al., 2010). As previously suggested by Rastegar Pouyani et al. (2010), *E. nigrolateralis* can be considered conspecific with the type population in southern Isfahan in most morphological characters. It is emphasized that the most significant morphological characteristic of *E. nigrolateralis* is its color pattern, which has also been observed in certain subadult forms of eastern populations and adult forms from western population of Yazd Province. In conclusion, despite *E. nigrolateralis* being rejected as one of the Phenotypes within *E. persica*, it is proposed that the morphological clusters previously separated by molecular data (Rastegar Pouyani et al., 2010), should be classified as subspecies or distinct species. Future comprehensive studies on the phylogeny of this lineage, addressing the gaps in previous research, can help clarify the remaining ambiguities regarding the taxonomy of the clades within this species complex. Additionally, examining the changes in head shape as a strong taxonomic signal in this group of lacertid lizards can be helpful. (see Edwards et al. 2016). Also, identifying the suitable niches and the degree of habitat overlap between the morphological and genetic clusters of *E. persica* can provide valuable insights.

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SUPPLEMENTARY MATERIAL

Supplementary material is available at Iranian Journal of Animal Biosystematics online.

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