Zootaxa 5369 (3): 336–368
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5369.3.2
http://zoobank.org/urn:lsid:zoobank.org:pub:23071CDE-CC3A-41CB-9C5C-3562DF33833B

Taxonomic diversity of racerunners with descriptions of two new *Eremias* species (Sauria: Lacertidae) from Central Iran

VALENTINA F. ORLOVA[1], ESKANDAR RASEGAR-POUYANI[2], KHOSROW RAJABIZADEH[3], HOSSEIN NABIZADEH[4], NIKOLAY A. POYARKOV[5], DANIEL A. MELNIKOV[6] & ROMAN A. NAZAROV[1,7*]
[1]*Zoological Museum of Moscow State University, 125009, B. Nikitskaya 2, Moscow, Russia.*
val_orlova@mail.ru, r_nazarov@mail.ru
[2]*Faculty of Sciences, Hakim Sabzevari University, Sabzevar, Iran.*
rastegarpouyani45@gmail.com, https://orcid.org/ 0000-0002-9639-2058
[3]*Department of Biodiversity, Institute of Science and High Technology and Environmental Sciences, Graduate University of Advanced Technology, Kerman, Iran.*
khosro.rajabizadeh@gmail.com, https://orcid.org/0000-0002-6661-799X
[4]*Department of Biology, Faculty of sciences, University of Qom, Qom, Iran.*
Hosseinnabizadeh86@gmail.com, https://orcid.org/0000-0003-2249-2678
[5]*Faculty of Biology, Lomonosov Moscow State University, Moscow 119991, Russia.*
n.poyarkov@gmail.com
[6]*Zoological Institute of the Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034, Russia.*
melnikovda@yandex.ru, https://orcid.org/0000-0002-8011-1274
[7]*Laboratory of Comparative Ethology and Biocommunication, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences., 119071 Leninsky Prospect 33, Moscow, Russia.*
**Corresponding author: r_nazarov@mail.ru*

Abstract

We provide a diversity assessment of Iranian species of the genus *Eremias* based on the cytochrome oxidase I mtDNA gene fragment. We analyzed 93 genetic samples from the entire distribution of the *Eremias fasciata* species complex in Iran and surrounding regions, along with morphological data to support the description of two new species from Central Iran. We hypothesize that the diversification of the *Eremias fasciata* species complex was largely influenced by the fragmentation of sand massifs in the region. This same hypothesis has been used to explain the high level of endemism among the sand-dwelling species of reptiles along the Iranian Plateau in the same area. The two new species described herein can be distinguished from other congeneric species by their phylogenetic position and a combination of morphological characters. We use these data to discuss the taxonomy of *Eremias* based on morphology, habitat choice, and genetic data.

Key words: cryptic diversity, *Eremias*, Iranian Plateau, taxonomy, cytochrome oxidase I, DNA Barcoding.

Introduction

Over the past twenty years the total number of species in the Iranian herpetofauna has increased by a third and, according to recent estimates, it now includes about 260 species (Uetz *et al.* 2022). The intensive use of various diagnostic methods and molecular analyses has made it possible to discover a large number of morphologically similar new species of reptiles. About half of these newly recognized Iranian species are associated with sandy desert habitats and include sand-dwelling species in the Lacertidae (*Eremias kavirensis* Mozaffari & Parham, 2007; *Acanthodactylus khamirensis* Heidari *et al.* 2013); Scincidae (*Ophiomorus maranjabensis* Kazemi *et al.* 2011); Agamidae (*Phrynocephalus lutensis* Kamali & Anderson, 2015; *Ph. khorasanus* Solovyeva *et al.* 2018) and Gekkota (*Teratoscincus mesriensis* Nazarov *et al.*, 2017; and *Trigonodactylus persicus* Nazarov *et al.*, 2018). The uniqueness of the sand massifs of the Iranian Plateau is due to the fact that thay are isolated from each other by mountain ridges, rocky plateaus, and other barriers. These sand dunes resemble "islands" of varying formations and sizes. At the same time, the psammobiont herpetofauna of the massifs consists mainly of specialized species adapted to living on sandy substrate. This feature limits the distribution of species within sandy environment and creates conditions for speciation.

Racerunners of the genus *Eremias* represent one of the most taxonomically confusing and complicated groups of the lizard family Lacertidae. *Eremias* Fitzinger, 1834 belongs to the Tribe Eremiadini in the Subfamily Lacertinae, which is a group of sub-Saharan species with maximum diversity in Africa. Only four genera (*Acanthodactylus, Eremias*, *Mesalina* and *Ophisops*) are known from the Middle East (Arnold 1989; Harris *et al.* 1998; Fu 1998, 2000; Arnold *et al.* 2007; Mayer and Pavlicev 2007; Tamar *et al.* 2016). Among them, only the genus *Eremias* is distributed predominantly in Central Asia and taxonomic studies of this group have been ongoing since end of the nineteenth century following the exploration of Central Asian deserts (Strauch 1876; Zarudny 1896, 1897, 1898, 1902, 1903, 1904; Bedriaga 1912; Nikolsky 1915; Boulenger 1918, 1920, 1921; Lantz 1928; Szczerbak 1971, 1974; Orlova & Terbish 1997; Poyarkov *et al.*, 2014; Orlova *et al.* 2017, 2022).

Szczerbak (1974) recognized 22 nominal species grouped in five subgenera: *Aspidorhinus* Eichwald, 1841 (previously treated as a nominative subgenus, see Leviton *et al.* 1992; Zhao & Adler 1993; Eremchenko 1999; Barabanov 2009), *Eremias* sensu stricto (= *Ommateremias* Lantz, 1928 sensu Szczerbak 1974), *Pareremias* Szczerbak, 1973, *Rhabderemias* Lantz, 1928, and *Scapteira* Wiegmann, 1834. This classification was later supported by hemipenial morphology (Arnold 1986) but has been called into question by recent molecular data (Guo *et al.* 2011; Orlova *et al.* 2017; Khan *et al.* 2021).

To date, *Eremias* comprises 36–40 recognized species distributed throughout the Middle East and Asia. These species mostly inhabit arid and semiarid landscapes, e.g., steppes, sand dunes, mountainous deserts (Böhme & Szczerbak 1991, Arnold *et al.* 2007; Mozaffari & Parham 2007; Wagner *et al.*, 2016; Khan 2016; Khan *et al.* 2020; Masroor 2022; Uetz *et al.* 2022).

The highest diversity of *Eremias* is known from Iran, with 21 species, nine of them endemic to the Iranian Plateau (Anderson 1999; Rastegar-Pouyani 2001; Mozaffari & Parham 2007; Safaei-Mahroo *et al.* 2015). These species are *E. andersoni* Darevsky & Szczerbak, 1978 ; *E. lalezharica* Moravec, 1994, *E. montana* Rastegar-Pouyani, 2001, *E. nova* Rastegar-Pouyani, 2006; *E. kavirensis* Mozaffari & Parham, 2007, *E. isfahanica* Rastegar-Pouyani, 2016; *E. papenfussi* Mozaffari, 2011 and *E. fahimii* Mozaffari, 2020. *Eremias* species of Iran are grouped into several species complexes and the taxonomic structure of some the *E. fasciata* and *E. andersoni* complexes remains unresolved (Orlova & Nazarov 2017). A result the COI barcoding of Iranian species of the *Eremias fasciata* complex and a comparative analysis of the morphological characters of this group, we have recognized cryptic diversity and discovered two new sand-dwelling species. In addition, we clarified the taxonomy for the Central Asian representatives of the *Eremias scripta* complex, and for the first time all three subspecies of *E. scripta* were analysed. We also elevated *E. scripta lasdinii*, previously considered as subspecies, to a full species.

Materials and Methods

Sampling and deposition. The materials for the present study were collected during field work in central Iran between 2002 and 2022 during the Russian-Iranian joint collaboration project. The geographic position of the surveyed populations and samples included in the molecular analyses are provided in Table.1. Geographic coordinates and elevation were obtained using a Garmin *e*Trax 20 GPS receiver using the WGS84 map datum. The sampling strategy covered the entire range of the Iranian *Eremias fasciata-lineolata* species complex.

Specimens were photographed, euthanized, and tissue samples (muscle, heart, or liver) were taken prior to preservation. Tissues were stored in 96% ethanol for genetic analysis and subsequently deposited in the collections of the Zoological Museum of Moscow State University (ZMMU), in the Zoological Collection of the Department of Environments, Tehran (MMTT), and in the herpetological collection of Hakim Sabzevari University, Iran (ERP).

For morphological and molecular analysis of representatives of the genus *Eremias*, we used materials from the collections of the Zoological Institute of St. Petersburg (ZISP), ZMMU, ERP and MMTT. All studied material is mapped in Fig.1 and listed in Table 1.

TABLE 1. List of specimens used for morphological and phylogenetic analyses. The bold numbers in locality column correspond to the distribution map (Fig. 1).

No.	GenBank AN	Specimen ID	Species	Locality	°N	°E	Reference
1	OR268242	ZMMU R-12986	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
2	OR268243	ZMMU R-12986-2	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
3	OR268244	ZMMU R-15624	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
4	OR268251	ZMMU R-12986-4	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
5	OR268250	ZMMU R-15625	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
6	OR268245	ZMMU R-12986-7	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
7	OR268249	ZMMU R-12986-0	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
8	OR268246	HSUZM ERP-6127	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
9	OR268247	HSUZM ERP-1738	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
10	OR268248	HSUZM ERP-1735	*Eremias graphica* **sp. nov.**	**1 -** Iran, Khorasan prov., 150 km SW from Tabas, on the road Yazd –Tabas, 35 km NE Robat-e-Posht-e Badam	33.087	55.9121	this work
11	OR268258	ZMMU R-15513	*Eremias andersoni*	**2 -** Iran, Isfahan, near Maranjab Fort	34.283	51.817	this work
12	OR268255	HSUZM ERP-1	*Eremias andersoni*	**3 -** Iran, Semnan, Kavir N.P.	34.550	52.450	this work
13	OR268256	HSUZM ERP-2	*Eremias andersoni*	**3 -** Iran, Semnan, Kavir N.P.	34.550	52.450	this work
14	OR268252	HSUZM ERP-3	*Eremias andersoni*	**3 -** Iran, Semnan, Kavir N.P.	34.550	52.450	this work

......*continued on the next page*

TABLE 1. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	°N	°E	Reference
15	OR268257	HSUZM ERP-4	*Eremias andersoni*	**3 -** Iran, Semnan, Kavir N.P.	34.550	52.450	this work
16	OR268253	HSUZM ERP-5	*Eremias andersoni*	**3 -** Iran, Semnan, Kavir N.P.	34.550	52.450	this work
17	OR268254	HSUZM ERP-6	*Eremias andersoni*	**3 -** Iran, Semnan, Kavir N.P.	34.550	52.450	this work
18	OR268264	ZMMU R-15632	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
19	OR268259	ZMMU R-12982	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
20	OR268263	ZMMU R-15633	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
21	OR268262	ZMMU R-15634	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
22	OR268260	ZMMU R-15636	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
23	OR268261	ZMMU R-15635	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
24	OR268265	ZMMU R-15638	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
25	OR268266	ZMMU R-15639	*Eremias pseudofasciata* **sp. nov.**	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
26	MTD19341		*Eremias kakari*	**5-** Pakistan, Balochistan, Killa Saifulla district, Tanishpa village, Torghar Mountains	31.186	68.412	Khan *et al.* 2021
27	MTD19342		*Eremias kakari*	**5-** Pakistan, Balochistan, Killa Saifulla district, Tanishpa village, Torghar Mountains	31.186	68.412	Khan *et al.* 2021
28	OR268274	ZMMU R-11899-1	*Eremias fasciata*	**6 -** Iran, Sistan-Baluchistan, 40 km E from Zabol	30.900	61.550	this work
29	OR268273	ZMMU R-11899-2	*Eremias fasciata*	**6 -** Iran, Sistan-Baluchistan, 40 km E from Zabol	30.900	61.550	this work
30	OR268275	ZMMU R-11899-3	*Eremias fasciata*	**6 -** Iran, Sistan-Baluchistan, 40 km E from Zabol	30.900	61.550	this work
31	OR268277	ZMMU R-11899-4	*Eremias fasciata*	**6 -** Iran, Sistan-Baluchistan, 40 km E from Zabol	30.900	61.550	this work
32	OR268267	ZMMU R-12983-1	*Eremias fasciata*	**7** - Iran, Isfahan, 10 km S from Mesr	34.067	54.783	this work
33	OR268269	ZMMU R-13956-1	*Eremias fasciata*	**7** - Iran, Isfahan, 10 km S from Mesr	34.067	54.783	this work
34	OR268270	ZMMU R-13956-2	*Eremias fasciata*	**7** - Iran, Isfahan, 10 km S from Mesr	34.067	54.783	this work
35	OR268268	ZMMU R-12986-5	*Eremias fasciata*	**8 -** Iran, Yazd, between Yazd and Tabas	32.950	55.850	this work
36	OR268281	ZMMU R-15508	*Eremias fasciata*	**9 -** Iran, Yazd, 35 km SW Robat-e-Posht-e Badam	33.083	55.900	this work

......continued on the next page

TABLE 1. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	°N	°E	Reference
37	OR268276	ZMMU R-12229-1	*Eremias fasciata*	**10 -** Iran, Khorasan, 5 km W from Dekhselm	31.417	59.650	this work
38	OR268271	ZMMU R-12980-1	*Eremias fasciata*	**11 -** Iran, Khorasan, 60 km N from Gonabad	34.600	58.733	this work
39	OR268272	ZMMU R-12980-2	*Eremias fasciata*	**11 -** Iran, Khorasan, 60 km N from Gonabad	34.600	58.733	this work
40	OR268278	HSUZM ERP-658	*Eremias fasciata*	**12 -** Iran, Khorasan, Roshtkhar area, 40 km to Jangal	34.567	58.850	this work
41	OR268279	HSUZM ERP-659	*Eremias fasciata*	**12-** Iran, Khorasan, Roshtkhar area, 40 km to Jangal	34.567	58.850	this work
42	OR268280	HSUZM ERP-660	*Eremias fasciata*	**12 -** Iran, Khorasan, Roshtkhar area, 40 km to Jangal	34.567	58.850	this work
43	OR268282	ZMMU R-15509-1	*Eremias fasciata*	**13 -** Iran, Sistan-Baluchistan, near Zabol, Neatak sand dunes	31.067	61.633	this work
44	OR268283	ZMMU R-15509-2	*Eremias fasciata*	**13 -** Iran, Sistan-Baluchistan, near Zabol, Neatak sand dunes	31.067	61.633	this work
45	OR268285	ZMMU R-15515	*Eremias* cf. *fasciata*	**14 -** Iran, Sistan-Baluchistan, 15 km NW from Saran	27.400	61.800	this work
46	OR268284	ZMMU R-15514	*Eremias kavirensis*	**2 -** Iran, Isfahan, near Maranjab Fort	34.283	51.817	this work
47	-	ZMMU R-6861-1	*Eremias scripta scripta*	**14 -** Kazakhstan, Jambyl, Muyunqum desert, 30 km N from Uyuk	43.958	71.070	this work
48	MTD19347		*Eremias cholistanica*	**15 -** Pakistan, Pujab province, Islamia University Bahwalpur, Baghdad-i-Jadeed Campus.	29.378°	71.769°	Khan *et al.* 2021
49	MTD19350		*Eremias cholistanica*	**15 -** Pakistan, Pujab province, Islamia University Bahwalpur, Baghdad-i-Jadeed Campus.	29.378°	71.769°	Khan *et al.* 2021
50	OR268305	ZMMU R-12564-1	*Eremias lineolata*	**16 -** Kazakhstan, Kyzylorda, NW Qizilqum desert	44.950	62.950	this work
51	OR268306	ZMMU R-10970-1	*Eremias lineolata*	**17** - Kazakhstan, Kyzylorda, near Bayikonur	45.971	63.321	this work
52	OR268299	HSUZM ERP-1047	*Eremias lineolata*	**18 -** Iran, Khorasan, Sarakhs to Sangar-Dolatabad road	36.266	61.157	this work
53	OR268286	ZMMU R-12981-1	*Eremias lineolata*	**11 -** Iran, Khorasan, 60 km N from Gonabad	34.600	58.733	this work
54	OR268298	ZMMU R-12981-2	*Eremias lineolata*	**11 -** Iran, Khorasan, 60 km N from Gonabad	34.600	58.733	this work
55	OR268287	ZMMU R-12981-3	*Eremias lineolata*	**11 -** Iran, Khorasan, 60 km N from Gonabad	34.600	58.733	this work
56	OR268288	ZMMU R-12981-4	*Eremias lineolata*	**11 -** Iran, Khorasan, 60 km N from Gonabad	34.600	58.733	this work
57	OR268290	ZMMU R-12981-5	*Eremias lineolata*	**11 -** Iran, Khorasan, 60 km N from Gonabad	34.600	58.733	this work
58	OR268278	HSUZM ERP-644	*Eremias lineolata*	**19 -** Iran, Khorasan, 35 km from Gonabad to Torbat-e-Heydariyeh	34.680	58.642	this work
59	OR268304	ZMMU R-12228-1	*Eremias lineolata*	**20 -** Iran, Khorasan, 25 km N from Gonabad	34.529	58.714	this work

......continued on the next page

TABLE 1. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	°N	°E	Reference
60	OR268300	HSUZM ERP-651	*Eremias lineolata*	**21 -** Iran, Khorasan, Roshtkhar area, 40 km to Jangal city	34.802	59.393	this work
61	OR268294	ZMMU R-12984-2	*Eremias lineolata*	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
62	OR268295	ZMMU R-12984-3	*Eremias lineolata*	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
63	OR268296	ZMMU R-12984-4	*Eremias lineolata*	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
64	OR268297	ZMMU R-12984-6	*Eremias lineolata*	**4 -** Iran, Khorasan, 30 km SE from Boshruiyeh	33.767	57.550	this work
65	OR268289	ZMMU R-11900-1	*Eremias lineolata*	**22 -** Iran, Khorasan, near Gonabad, environs of Kale-Shur	34.600	58.733	this work
66	OR268302	ZMMU R-12749-1	*Eremias lineolata*	**23 -** Uzbekistan, Bukhara, SW from Mubarek, Devkhana	39.183	64.633	this work
67	OR268293	ZMMU R-12082-1	*Eremias lineolata*	**24 -** Uzbekistan, Navoiy, Central Qyzilqum, near Tamdytau	41.692	64.429	this work
68	OR268291	ZMMU R-10971-1	*Eremias lineolata*	**25 -** Uzbekistan, Bukhara, 30 km E from Gazli	40.114	63.772	this work
69	OR268292	ZMMU R-10969-1	*Eremias lineolata*	**26 -** Uzbekistan, Qashqadarya, 5 km NE from Mubarek	39.302	65.200	this work
70	OR268303	ZMMU R-12693-1	*Eremias lineolata*	**27 -** Uzbekistan, N Qyzylqum desert, 10 km NW Qarantakyr	43.622	63.290	this work
71	-	ZMMU R-12274-1	*Eremias lineolata*	**28 -** Uzbekistan, Qoraqalpog'iston, 15 km SE from Bestam	42.167	60.267	this work
72	-	ZMMU R-6861-1	*Eremias scripta scripta*	**29 -** Kazakhstan, Jambyl, Muyunqum desert, 30 km N from Uyuk	43,958	71,070	this work
73	OR268314	ZMMU R-ESc-R-L-93	*Eremias scripta scripta*	**30 -** Kazakhstan, Almaty, Altyn-Emel N.P.	43.916	78.760	this work
74	OR268315	ZMMU R-EScA1-1	*Eremias scripta scripta*	**31 -** Kazakhstan, Almaty, Alakol depression, Barmakkum sands	47.083	82.481	this work
75	OR268317	ZMMU R-EScA2-1	*Eremias scripta scripta*	**32 -** Kazakhstan, Almaty, Taskarakum sands	45.887	80.558	this work
76	OR268316	ZMMU R-12448-1	*Eremias scripta scripta*	**33 -** Uzbekistan, Qoraqalpog'iston, Sarikamish depression	42.267	57.033	this work
77	OR268318	ZMMU R-12269-1	*Eremias scripta scripta*	**34 -** Uzbekistan, Qoraqalpog'iston, near Chuqurkak	42.300	62.550	this work
78	OR268301	ZMMU R-11728-1	*Eremias scripta pherganensis*	**35 -** Uzbekistan, Fergana valley, 30 km S from Dzhumandzhi	40.285	71.744	this work
79	OR268312	ZMMU R-12754-1	*Eremias scripta pherganensis*	**36 -** Uzbekistan, Fergana valley, Ak-Qum, Namangan-Chust road	40.717	71.350	this work

......*continued on the next page*

TABLE 1. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	°N	°E	Reference
80	OR268311	ZMMU R-12571-1	*Eremias scripta pherganensis*	**37 -** Uzbekistan, Fergana valley, 20 km NW from Qo'qon (Kokand)	40.676	71.232	this work
81	OR268313	ZMMU R-12747-1	*Eremias scripta pherganensis*	**38 -** Uzbekistan, Fergana valley, Quqon-Pungan road, Kamchik-Turk	40.683	70.850	this work
82	OR268310	ZMMU R-12752-1	*Eremias lasdini*	**39 -** Uzbekistan, Surhandarya, 15 km of Djaraqurgan-Termiz road	37.333	67.367	this work
83	OR268308	ZMMU R-12748-1	*Eremias lasdini*	**40 -** Uzbekistan, Saryqum, between Qumqurgan and Djaraqurgan	37.333	67.367	this work
84	OR268309	ZMMU R-12447-1	*Eremias lasdini*	**41 -** Uzbekistan,Surhandarya, Khaudag	37.561	67.376	this work
85	OR268324	NAP_t603	*Eremias pleskei*	**42 -** Armenia, Ararat dist., Gorovan sand dunes	39.897	44.735	this work
86	OR268319	NAP_t604	*Eremias pleskei*	**42 -** Armenia, Ararat dist., Gorovan sand dunes	39.897	44.735	this work
87	-	ZMMU R-3701	*Eremias pleskei*	**42 -** Armenia, Ararat dist., Gorovan sand dunes	39.897	44.735	this work
88	OR268323	ZMMU R-12475-2	*Eremias pleskei*	**43 -** Azerbaijan, Nakhchivan, NW Yayidji	38.950	45.717	this work
89	OR268320	ZMMU R-12475-3	*Eremias pleskei*	**43 -** Azerbaijan, Nakhchivan, NW Yayidji	38.950	45.717	this work
90	OR268321	ZMMU R-12475-4	*Eremias pleskei*	**43 -** Azerbaijan, Nakhchivan, NW Yayidji	38.950	45.717	this work
91	OR268322	ZMMU R-12475-5	*Eremias pleskei*	**43 -** Azerbaijan, Nakhchivan, NW Yayidji	38.950	45.717	this work
92	-	IDI-E.a. (tissue)	*Eremias acutirostris*	**44 -** Iran, Sistan-Baluchistan, Zabol	30.903	61.563	this work
93	OR268307	ZMMU R-12047-1	*Eremias vermiculata*	Mongolia, Bayan-Khongor aimag, oasis Ekhyin-Gol	50.410	101.750	this work
94	EU081524	NHMC 80.3.70.180	*Ophisops elegans*	Greece, Lesvos	—	—	Kyriazi *et al.* 2008

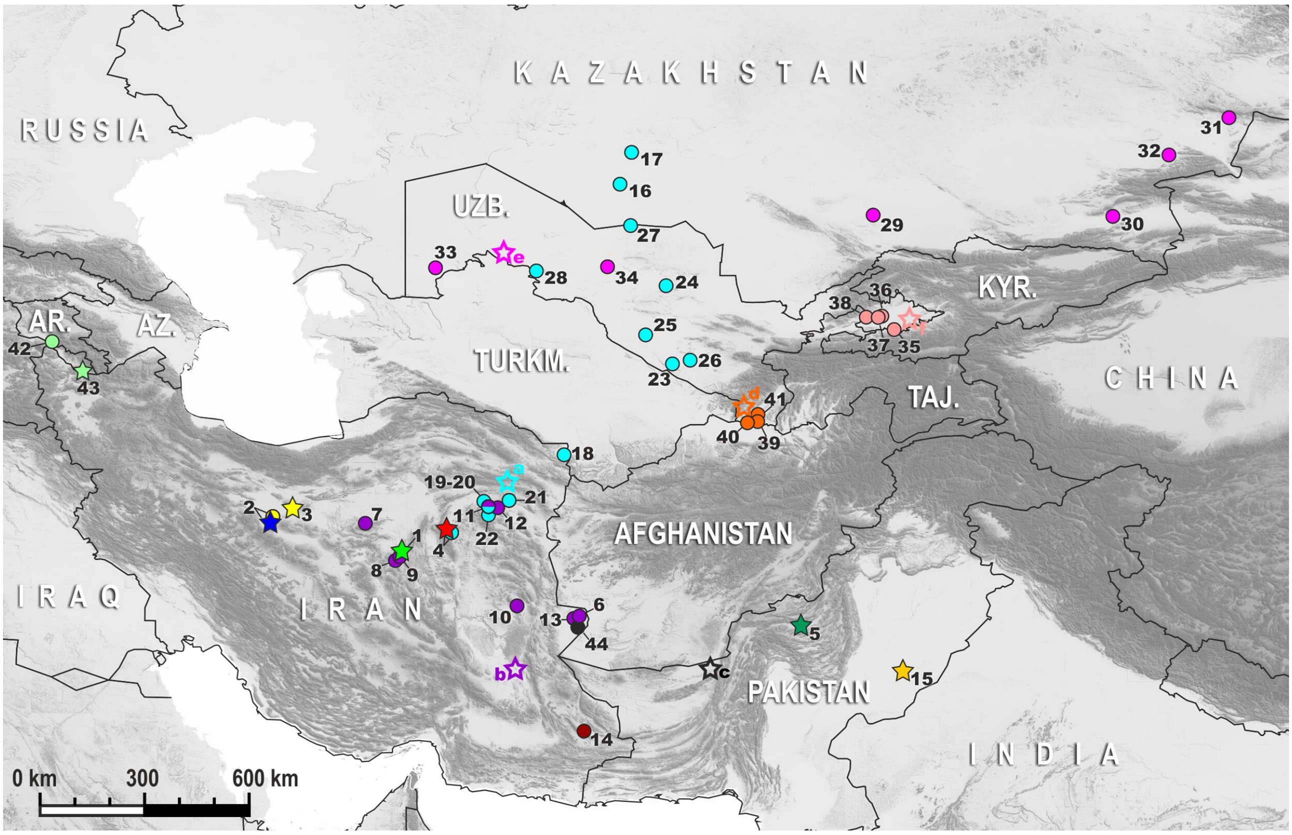

FIGURE 1. Distribution of *Eremias* species in Central Asia and sampling localities used in this study. Stars correspond to the type localities of species: a) *E. lineolata* Lectotype (designated by Szczerbak 1974) ZISP 8801.1—"Feizabad-Nusi in Persia orientali" [Feizabad, Razavi Khorasan Province, Iran, 35.02° N 58.78° E], Coll. N. A. Zarudny, IV-V.1896 (in Ananjeva *et al*. 2020); b) *E. fasciata* Lectotype (designated by Szczerbak 1974) ZMB 9329—"Karman" = Kerman, Iran (exact locality unknown); c) *E. acutirostris* Syntype BMNH 1946.8.7.46—near Nushki, N. Baluchistan, Pakistan; d) *E. scripta lasdini* Holotype ZISP 12107—Uzbekistan, Surkhandarya Region, Sands Katta-Qumy, vicinity Termez, 18.05.1915, Coll. V.J. Lazdin; e) *E. scripta scripta* Lectotype (designated by Szczerbak, 1974:213) ZISP (ZIL) 3669—Transcaspia, "Aralo-Caspian desert" (exact locality unknown); f) *E. scripta pherganensis* Holotype NMNHU (National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev) Re 6–Uzbekistan, Fergana Valley, Ak-Kum sands, 35.05.1969, Coll. E.V. Vashetko. For all other localities see Table 1.

Morphology. Morphological data include measurements, meristic characters, and coloration patterns of adult and juvenile specimens. All measurements were taken using a digital calliper under a dissecting microscope to the nearest 0.1 mm. Morphometric descriptions followed Orlova and Terbish (1997), and morphological descriptions followed Szczerbak (1974) and Rastegar-Pouyani and Rastegar-Pouyani (2001, 2006). For morphometric analysis, the following measurments were used: snout-vent length, from snout to vent (SVL); tail length, from vent to the tip of the tail (TL); pileus length from rostrum to the posterior border of parietals (Lpil); head length from rostrum to occipital sinus (HL); head width maximum width (HW); head height maximum height (HH); gleno-acetobular distance from axilla to groin, measured from the posterior edge of forelimb to the anterior edge of hind limb insertion (Ga); forelimb length, from forelimb insertion to the tip of the longest finger (Pa); hind limb length, from hind limb insertion to the tip of the longest toe (Pp).

The following meristic characters were examined: number of scales around midbody (Sq); number of gular scales along mid-line of the throat (G); number of enlarged collar scales (Coll); number of femoral pores on the left and right side (Pfm); number of transverse rows of ventral scales counted at midbody (Ventr.); the maximal number of longitudinal rows of ventral scales, counted at midbody (Ventr. long); number of scales around the 9–10th tail ring (Sq.c.cd); number of subdigital lamellae on the 4th toe of hind limb (Lam. Subdig); number of dorsal scales between parietals and the level of cloaca (Sq. dors); total number of supralabials, right/left (Lab.total); number of infralabial shields, right/left (Infralab.); number of submaxillary shields (Submax.); supraocular separated from frontal and frontoparietal by a complete row of small granular scales, yes/no (Gran.); number of supraciliars right/ left (Supracil.); number of enlarged scales in precloacal area (Precloac); number of scales between right and left rows of femoral pores (Dist. Pfm.). The pattern characters recorded are: number of dorsal longitudinal dark bands (LB) and number of roundish light spots on the femur (FSpots). All morphometric measurements were adjusted to remove the effects of body size variation (Chan & Grismer 2021). We use the allometric formula: Xadj = log(X) – b[log(BL) – log(BLmean)]. The Principal Component Analysis (PCA) and Discriminant Analysis were performed in Statistica 6.0 softwere.

Molecular analyses. Our molecular dataset consists of 93 samples of *Eremias* species including 23 samples from Iran, Pakistan, Kazakhstan, and Uzbekistan. All the locality information and collection numbers of the material used in this paper are listed in Table 1. *Ophisops elegans* and *Eremias vermiculata* were used as out-groups in all phylogenetic analyses.

DNA extraction, PCR, and sequencing. Total genomic DNA was extracted from ethanol-preserved muscle or liver tissues using a glass-fibre automatic DNA isolation protocol following Ivanova *et al.* (2006) or using standard phenol–chloroform extraction procedures (Hillis *et al.* 1996) followed by isopropanol precipitation. We amplified 655 bp of cytochrome oxidase I (COI), a mitochondrial marker proved to be useful for species identification in reptiles and widely used as a barcoding marker for vertebrates (Hebert & Gregory 2005; Smith *et al.* 2008). Primers used for both PCR and sequencing were VF1-d (5'-TTCTCAACCAACCACAARGAYATYGG-3') and VR1-d 5'-TAGACTTCTGGGTGGCCRAARAAYCA-3') (Ivanova *et al.* 2006). The obtained fragments were sequenced in both directions for each sample, and a consensus sequence was generated. PCRs were performed in 25 µl reactions using ca. 50 ng genomic DNA, 10 pmol of each primer, 15 nmol of each dNTP, 50 nmol additional $MgCl_2$, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM $MgCl_2$, and 0.01% gelatin), and 1 U of Taq DNA polymerase. The PCR conditions were: an initial denaturation step at 95 °C for 3 min, 5 cycles at 95 °C for 30 s, annealing at 45 °C for 1 min, extension at 72 °C for 2 min followed by 35 cycles at 95 °C for 30 s, annealing at 51 °C for 1 min, extension at 72 °C for 2 min, and a final extension of 5 min at 72 °C. PCR products were loaded onto 1% agarose gels, stained with GelStar gel stain (Cambrex), and visualized in a Dark Reader Transilluminator (Clare Chemical). If results were satisfying, products were purified using 2 µl, from a 1:4 dilution of ExoSapIt (Amersham), per 5 µl of PCR product prior to cycle sequencing. A 10 µl sequencing reaction included 2 µL of template, 2.5 µl of sequencing buffer, 0.8 µl of 10 pmol primer, 0.4 µl of BigDye Terminator version 3.1 Sequencing Standard (Applied Biosystems), and 4.2 µl of water. The sequence reaction was 35 cycles of 10 s at 96 °C, 10 s at 50 °C, and 4 min at 60 °C. Cycle sequencing products were purified by ethanol precipitation. Sequence data collection and visualization were performed on an ABI 3730xl automated sequencer (Applied Biosystems). Sequences are accessible on the BOLD systems website (http://www.boldsystems.org).

Phylogenetic analysis. Sequences were aligned by eye using BioEdit Sequence Alignment Editor 5.0.9 (Hall 1999). Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesisn Inference (BI) methods using PAUP 4.0b4a (Swofford 2002) and MrBayes 3.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) programs. Uncorrected genetic distances (*p*-distance) between sequences were calculated in MEGA5 (Tamura *et al.* 2011). JMODELTEST v.0.1.1 (Posada 2008) was used to estimate the optimal evolutionary models to be used for the data set analysis. The preferred model was (GTR + I + G), as suggested by the Akaike information criterion (AIC). We employed a heuristic search for all ML analyses with ten random-addition sequence replicates and TBR branch swapping was performed with the (GTR + I + G) model. Branches with bootstrap values 70% or greater were regarded as sufficiently resolved (Huelsenbeck & Hillis 1993). Bayesian analyses were performed with four chains for 10 million generations, with sampling every 100 generations. The first 20,000 trees were discarded as a burn-in and a majority-rule consensus tree was produced from the remaining trees. Each analysis was repeated four times with random starting trees and the results were compared to assess the convergence.

Results

Morphological analyses. Due to the wide variability of morphological characters in this group that often do not allow the identification of new species, we first discuss the main diagnostic characters that are used in this group. To facilitate the correct identification of the species of this group, we considered it expedient to present descriptions of dorsal patterns based only on the material identified by us.

A population of *Eremias fasciata* (n = 7) from the vicinity of Rafsanjan was the closest to the type locality of this species that we could examine. The number of dark longitudinal stripes in the occipital region (from the pileus) varied from 7 to 8 (7.86 ± 0.38), of which 5–6 were in contact with the pileus, and two temporal stripes on the sides of the head. In the middle of the body, the number of stripes also varied from 7 to 8 (7.28 ± 0.5), but the occipital stripe often disappears towards the middle of the body. The temporal stripes on the body sides are wide and less contrasting compared to the dorsal ones, but on the sides of the head they form a contrasting dark stripe from the eye to the tympanum with light rounded spots, sometimes with a bluish-grey tint. This stripe is especially striking in adult males, the dorsal stripes become pale, and are sometimes barely expressed. The tympanum shield in adult males and females is lemon-yellow; in juveniles, it is usually white or yellowish. There are large, rounded light or yellowish spots on the caudo-lateral surface of the femur and tibia, from 4–6 on the femur (5.14 ± 0.9) and from 4–8 on the tibia (7 ± 1.5). In males, these spots are larger than in females. The tail and thighs are yellowish at all life stages. *Eremias fasciata* is found on the desert flats with different types of soil: sandy, gravel, Hamada salt-encrusted silt, loess (drifting) silty, and alluvial. Plant associations are represented by low-growing steppe shrubs (*Artemisia*, *Alhagi*, *Tamarix*, *Acacia*). In Iran, this species inhabits a wide elevational range from 450 to 1,700 m above sea level (Fig. 1).

We were able to take data from the type series *Eremias lineolata* and additional material from around the type locality in the Khorasan Province of Iran. The number of longitudinal brown or dark brown stripes connected with the pileus; 6–2 temporal stripes are present on the sides of the head, meaning eight stripes in total (8.4 ± 0.5). The medial stripe forms near the suture between the parietal plates and stretches along the vertebrae and reaches the hind limbs. On the middle of the back, the medial stripe usually splits into two narrow stripes or forms a reticulate pattern. The occipital stripes are on both sides of the medial stripe (from the parietal shields to the base of the tail, where they fuse into one). Then narrow and most contrasting parietal stripes begin from the edge of the supraocular and parietal plates and continue to the first third of the tail, where they are gradually faint to absent. A wide and contrasting bright temporal stripe usually contains small roundish light spots. The dorsal patterns of young and adult individuals are practically the same. Small dark spots often cover the dorsal surface of the head, the limbs are brown with light rounded spots. The number of spots varies from 9–14 (11.2 ± 1.9) on the femur and 10–16 (11.8 ± 2.5) on the tibia. The underside of the tail is buff or yellow-orange (Szczerbak 1974, with our additions).

Eremias andersoni was described by Darevsky and Szczerbak (1978) from the Dasht-e Kavir Desert, 45 km east of Lake Daryache Namak. We studied all type specimens of *Eremias andersoni* and a series of specimens collected around the type locality (n = 15) (Figs. 1–2). We found that specimens collected close to the type locality did not fit the description of *E. andersoni*.

These specimens differ in having a complete row of granules separating the supraocular scutes from the frontal and frontoparietal scutes (Fig. 3), however, molecular data showed that these specimens are the same species (see below). The narrow longitudinal dorsal stripes do not differ appreciably in width. In the occipital region, the number of stripes varies from 5 to 7, along with two temporal ones, in total 7–9 (8.4 ± 0.7). In the middle of the body, there are 8–9 stripes (8.3 ± 0.5).

A median stripe stretches along the vertebrae and usually splits into two stripes with an uneven inner edge in the middle of the back. The occipital stripes run from the parietal scutes to the first third of the tail, where they merge into one. Parietal stripes run from the edge of the supraocular and parietal scutes to the middle of the tail. The temporal stripe is the same width as the parietal stripes or slightly wider, without light spots. The number of light spots varies from 6–12 (9.5 ± 1.6) on the thigh and from 10 to 14 (12.3 ± 1.6) on the lower leg. The tympanic shield in adult males is yellowish. There is a bluish tinge on the distalmost approximately two thirds of the tail.

Similar to the type description of this species, all individuals were collected in one area of semi-fixed sands, located in the rocky desert of Desht-e-Kevir. They were numerous in the lower areas between the dunes, as well as on the sands with a more developed herbage or semi-shrub vegetation. *Eremias andersoni* is good at climbing bushes and can jump from branch to branch, thus resembling typical psammobiont species, such as *E. scripta*.

In *Eremias scripta*, there are two types of dorsal patterns, striped and vermiculated. In the first case, wide temporal stripes extend onto the tail, including the occipital stripe and two parietal stripes. Each of the parietal stripes can be split into two thin winding stripes, and the inner stripe can be further divided into two more stripes. There are 5–7 stripes on the back, which can be divided into separate unequal sections that fill the middle of the back. In young, the lower surface of the tail and lower leg is lemon or greenish.

FIGURE 2. Holotype of *Eremias andersoni* MMTT 1671.

Statistical analysis of the main metric and meristic characters of five species of *Eremias* showed the following: *E. lineolata* and *E. graphica* **sp. nov**. are well distinguished from each other. These analyses further demonstrated that *E. andersoni*, *E. fasciata* and *E. pseudofasciata* **sp. nov**. form a single weakly differentiated cluster (Fig. 4).

Sexual dimorphism in these species is weakly developed and not statistically significant. However, the separate comparison of sexes shows that females exhibit greater differentiation. Differences between females of *E. fasciata* and *E. pseudofasciata* are much more significant than those between males of these species. Despite differences in some traits between males and females, the overall picture does not change when the sexes are analyzed separately (Fig. 5).

Sequence data. The resulting phylogenies from the BI and ML analyses yielded almost identical topologies. Only the Bayesian tree is presented here with postieror probabilities and bootstraps from the ML analysis at the nodes (Fig. 6). The monophyly of all three species complexes was well supported and comprises 14 clades (named A–O) (Fig. 6). Four of these clades are well structured and divided into several subclades (Figs. 1, 6).

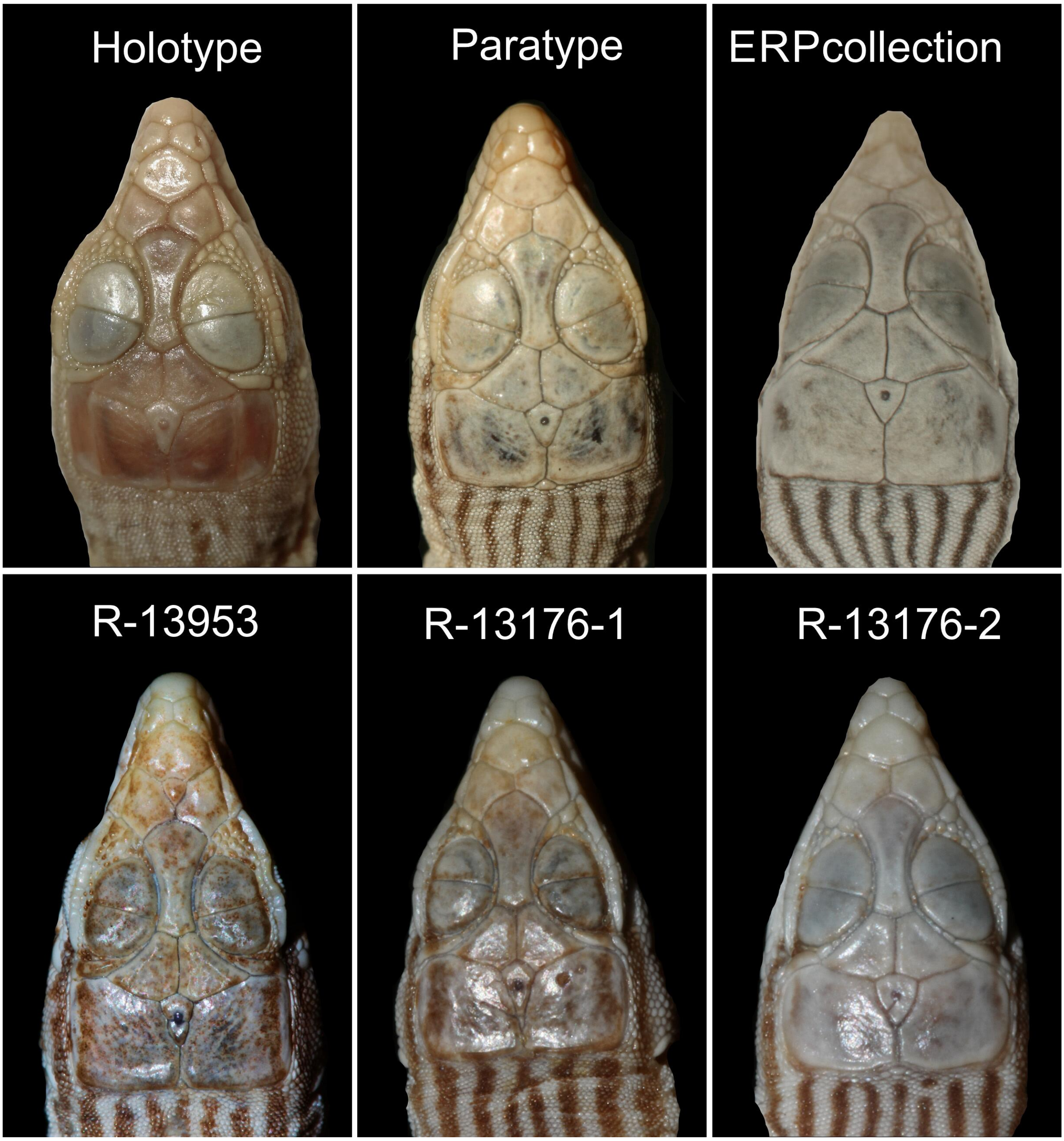

FIGURE 3. Type specimens of *Eremias andersoni* (holotype MMTT 1671; paratype ZISP 18715; topotype ERP-1) without row of granules separating the supraocular from the frontal and frontoparietal scutes and *E. andersoni* from Maranjab with partial or complete row of granules.

The *Eremias fasciata* species complex is formed by eight lineages: *E. andersoni*, *E. kakari*, *E. fasciata*, *E.* cf. *fasciata*, *E. cholistanica*, *E. kavirensis* and the two new species described in the present study. However, the phylogenetic positions of *E. kakari* and *E. cholistanica* have not been well resolved, and they clustered, albeit without statistical support, with species currently placed in the '*fasciata*' species complex (Fig. 6).

Eremias graphica **sp. nov.** (clade A) is sister to *E. andersoni* (clade B). Morphologically, both species are well distinguished. *Eremias pseudofasciata* **sp. nov**. (clade C), was recovered as a close relative to *E. graphica* and *E. andersoni*. Lastly, the *E. kavirensis* lineage (clade H) occupies a sister position to all of the above species.

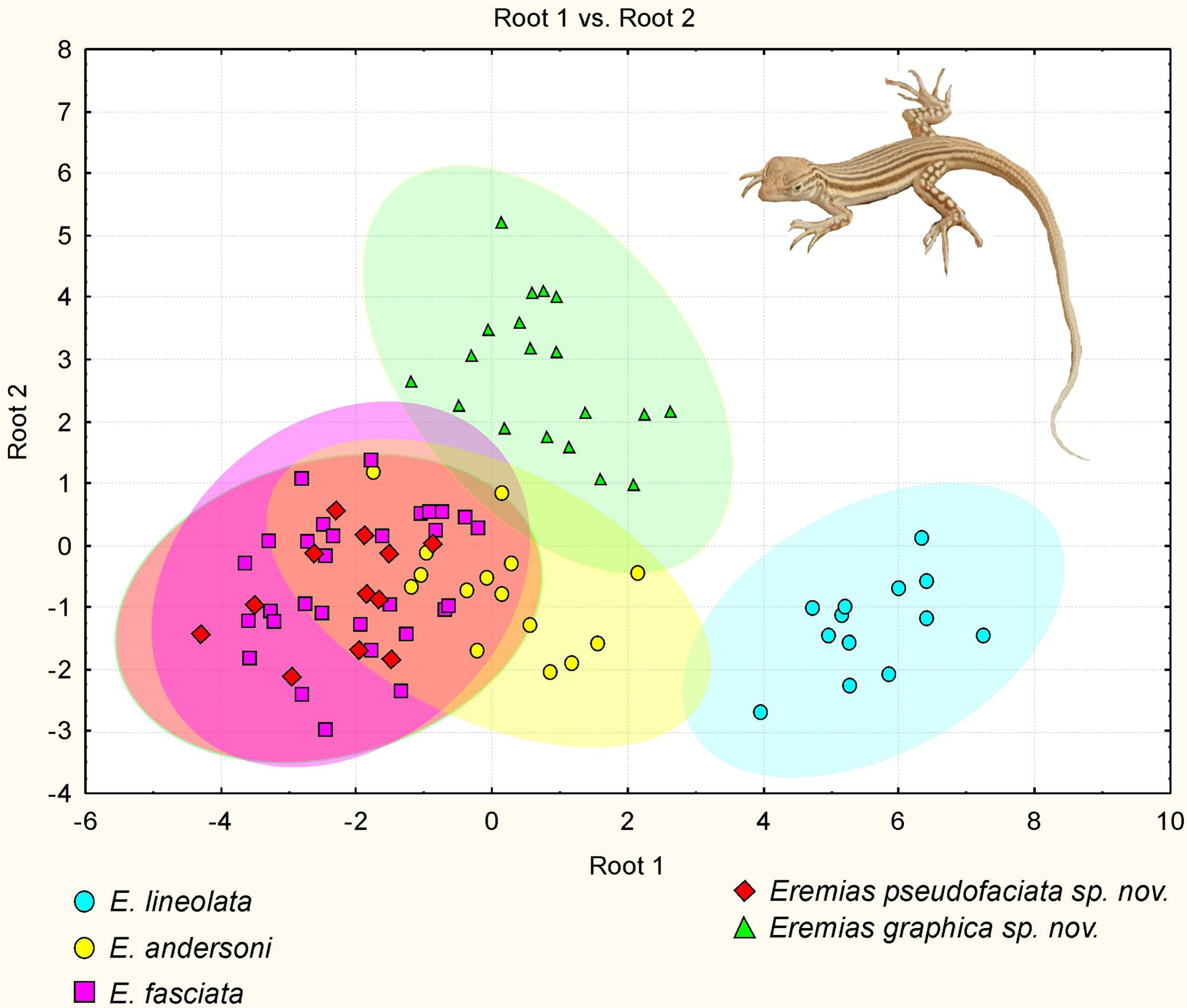

FIGURE 4. Results of discriminant analysis of 86 specimens belonging to five species of *Eremias* by 24 morphometric and meristic characters.

The *Eremias* '*lineolata*-*scripta*' species complex consists of four clades (I–L). Clade I is relatively homogenous throughout the entire range of this species. Our dataset contains samples from northeastern Iran (type locality), Uzbekistan and Kazakhstan, but genetic distances between these populations is very low. Conversley, we observed deep divergences in *E. scripta*. *Eremias s. scripta* (Clade J) is composed of samples from Kazakhstan and Uzbekistan with low genetic distance between them. *Eremias s. lasdini* (Clade L) from south Uzbekistan demonstrates a deep divergence. There were also deep divergences found within *E. pleskei* (Clade M) from Armenia and Azerbaijan.

Lastly, *E. vermiculata* (clade O), which was previously considered as a member of *Rhabderemias*, is highly divergent from all other species and does not show close relationships to other representatives of this genus.

The *p*-distances for sequences of the mtDNA COI gene for ingroups are shown in Table 2.

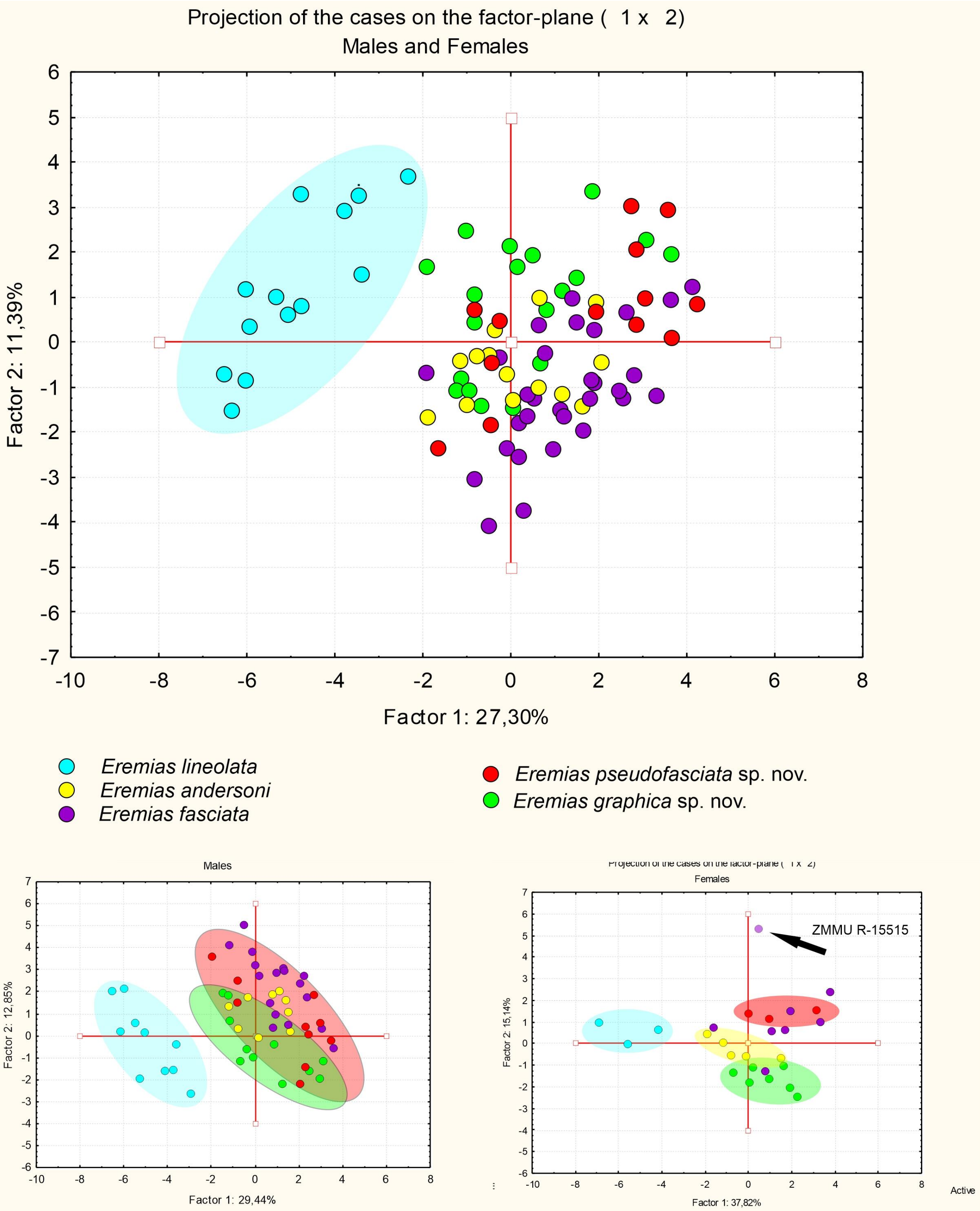

FIGURE 5. Principal Component Analysis (PCA) of the 24 metric and meristic features of five species of *Eremias*. See Material and Methods for more details.

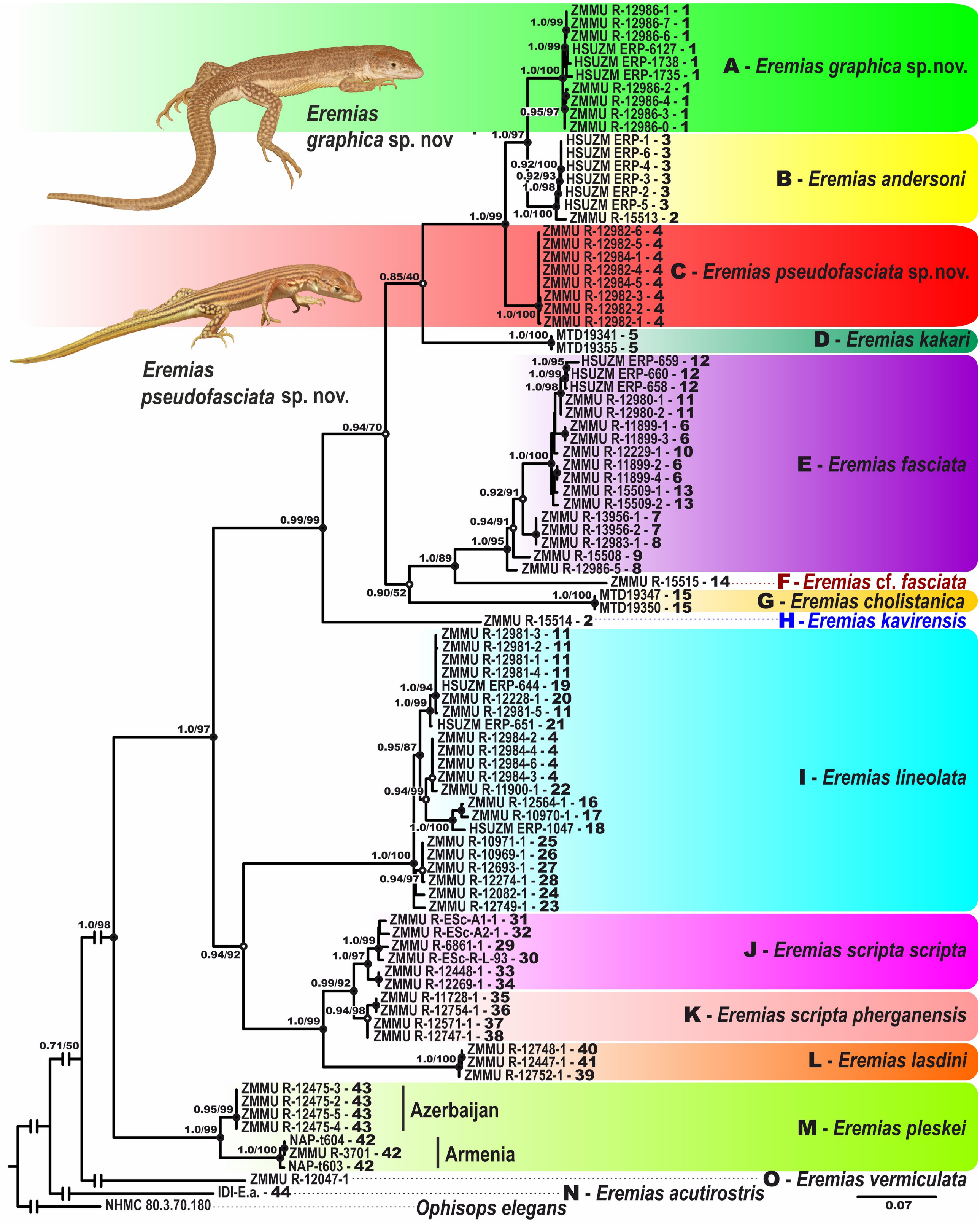

FIGURE 6. Phylogeny based on Bayesian inference analysis of *Eremias*. Values at nodes indicate posterior probabilities/ bootstrap support for BI/ML analyses, respectively. Coloration scheme representing main lineages corresponds to that in Fig. 1.

TABLE 2. Average uncorrected *p*-distances between taxa of *Eremias* (below diagonal). Values on the diagonal (shaded) correspond to intra-specific or -subspecific distances. Standard-error estimates are shown above the diagonal.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	*E. pseudofasciata* **sp. nov.**	**0.1**	1.1	1.0	1.4	1.6	1.6	1.7	1.7	1.7	1.8	1.8	1.9	1.7	1.6	1.8
2	*E. graphica* **sp. nov.**	7.8	**0.5**	0.9	1.4	1.5	1.5	1.8	1.7	1.6	1.8	1.8	1.8	1.8	1.5	1.8
3	*E. andersoni*	7.7	6.4	**0.6**	1.4	1.4	1.6	1.7	1.7	1.6	1.8	1.7	1.8	1.9	1.5	1.8
4	*E. fasciata*	14.7	15.5	15.6	**3.3**	1.4	1.6	1.8	1.7	1.7	1.8	1.7	1.6	1.7	1.6	1.7
5	*E.* cf. *fasciata*	14.7	15.1	14.4	13.1	**n/c**	1.6	2.0	1.7	1.8	1.8	1.8	1.8	1.7	1.6	1.6
6	*E. kavirensis*	17.5	17.7	16.5	16.2	16.8	**n/c**	1.7	1.7	1.7	1.9	1.8	1.5	1.7	1.5	1.7
7	*E. lineolata*	16.3	16.9	16.1	18.3	19.3	17.4	**2.7**	1.5	1.5	1.9	1.7	1.7	1.6	1.4	1.9
8	*E. s. scripta*	16.6	17.4	17.0	18.0	17.7	17.5	14.8	**2.1**	0.7	1.4	1.9	1.6	1.8	1.5	1.9
9	*E. s. pherganensis*	16.7	16.6	16.1	17.2	18.2	16.3	14.7	4.2	**0.7**	1.4	1.8	1.6	1.8	1.5	1.9
10	*E. s. lasdini*	17.3	19.0	17.5	17.9	18.6	19.5	16.0	12.2	11.5	**0.2**	1.7	1.8	1.9	1.6	1.9
11	*E. pleskei* Armenia	17.2	17.3	17.6	18.7	20.6	19.6	17.2	18.0	18.0	17.9	**0.6**	1.1	1.9	1.6	1.9
12	*E. pleskei* Azerbaijan	18.7	18.9	18.4	18.9	21.1	18.3	16.6	15.9	15.2	17.4	7.2	**0.0**	2.0	1.5	1.7
13	*E. acutirostris*	18.4	20.2	19.4	21.2	19.7	20.0	17.9	19.0	18.9	19.3	19.2	18.2	**n/c**	1.7	1.7
14	*E. grammica*	17.2	17.9	17.7	18.5	17.9	18.0	17.1	15.7	15.0	17.8	17.5	17.2	19.9	**7.8**	1.7
15	*E. vermiculata*	21.0	21.0	20.5	21.4	21.1	20.9	19.5	21.8	20.8	22.0	20.0	19.4	17.8	20.2	**n/c**

Family Lacertidae

Genus *Eremias* Fitzinger, 1834

Eremias graphica sp. nov. (Figs 7a–c, 8, 9e, g, and 13g)

Holotype. ZMMU R-13171—Iran, Khorasan Province, 150 km SW from Tabas city, on the road Yazd – Tabas, 33.087534° N; 55.912115° E; collected by R.A. Nazarov, D.A. Bondarenko & M. Rajabizadeh, 09 May 2010.

Paratypes. Five males (ZMMU R-15624–15626, R-15628, and R-15630) and four females (ZMMU R-15627, R-15629, R-15631, and R-12986) with the same data as holotype.

Diagnosis. Maximum SVL 58.3 mm, TL about two times longer than the body (max. 118 mm). Supraocular plates (preocular and postocular scales) usually separated from frontal and frontoparietal plates by small granular scales; fifth inframaxilare not in contact with infralabial plates. The collar scales are not strongly distinct from surrounding gular scales and usually only five collar scales are larger than the others. The body scales are relatively small, about 60 (54–65) scales around middle of the body (Sq); 15–18 well developed femoral pores on the left and right sides, separated from each other by 4–6 scales; series of femoral pores not reaching the knee bend by 3–4 scales.

Coloration. The main dorsal background color is beige; dorsal patterns comprise vermiculated light and dark-brown spots; no regular longitudinal dark lines on the dorsum but sometimes dark spots forming narrow longitudinal stripes are more visable on the neck. A light narrow longitudinal line begins from the upper side of tympanic region and continues to the tail, bordering the lateral body surface. Wide, dark, non-contrasting longitudinal stripes without light spots usually visible on the flanks and continue to the tail. Sometimes there is a narrow dark longitudinal line marking the lateral and ventral border of the body. No yellow spot on the tympanic plate. Dorsal surface of the limbs dark brown with round light or yellowish spots. The ventral surface of the body is whitish and the tip of the tail light greyish.

Description of the Holotype. ZMMU R-13171 (Fig.8). Adult male, SVL 56.9 mm, TL 114 mm, Pa 20.5 mm, Pp 35.7 mm, Lpil 13.5 mm. Meristic features: G 30, Coll 5, Pfm (right/left) 16/15, Dist.Pfm 6, labialia (left/right) 9/10, infralabilia (left/right) 6/7, ventralia 32. Tail scales smooth on the base, not strongly keeled; Sq.c.cd 29, subdigital lamellae subdigitalia 29. Smooth roundish and relatively small dorsal scales; Sq. 65; Sq. dorsale 153.

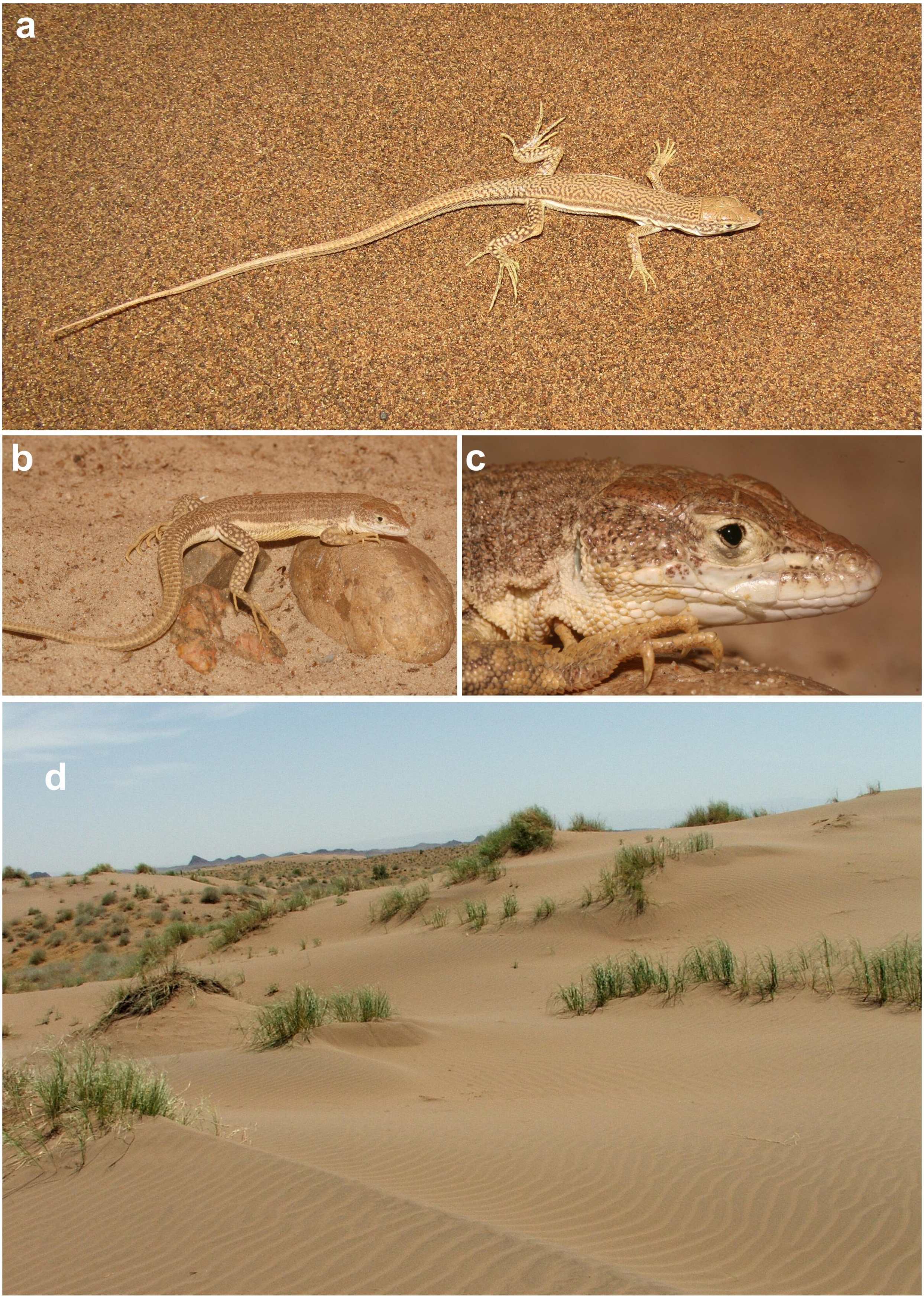

FIGURE 7. *Eremias graphica* **sp. nov.**: a–c; d: Habitat at the type locality.

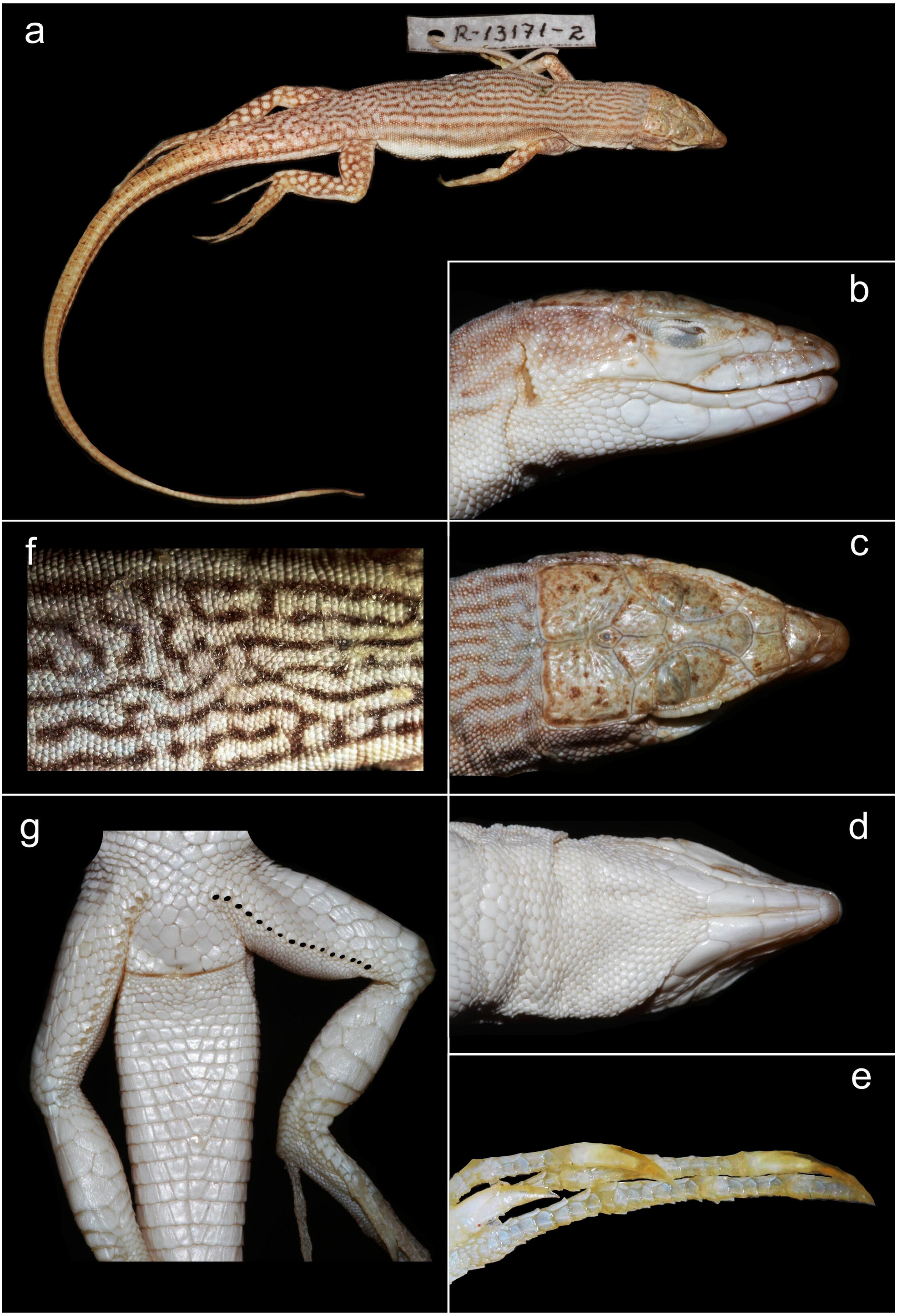

FIGURE 8. Morphological features of *Eremias graphica* **sp. nov.** a) general view of holotype ZMMU R-13171; b–d) Dorsal, lateral, and ventral views of the head; e) toes without fringes; f) dorsal patterns; g) well-developed femoral pores, marked on one side.

Head and body moderately depressed. Head length (14.5 mm) 1.74 times its width (8.3 mm) and 1.93 times its height (7.2 mm); nasals swollen; snout longer than postocular part of the head; head wider than neck. Fore and hind limbs relatively long; Pa/SVL 0.34, Pp/SVL 0.63. Hind limb reaches the axilla of forelimb and extends far beyond it. Tail about twice as long as the body, SVL/TL 0.49, cylindrical and depressed at base.

Pileus shields smooth, nasals in contact behind the rostral, the suture between them half the length of frontonasal, whose width is more than its length; length of frontonasal is half of the width; prefrontals slightly longer than broad, forming median suture, at the top of posterior edge is placed one tiny triangular plate; frontal the same size as distance from end of the snout, two-thirds times as broad as long, narrow behind; parietals as broad as long; interparietal almost equal to half of the length of frontoparietals; no occipital. Parietals, frontoparietals, and interparietal weakly rugose. Two large supraoculars (preocular and postocular), preocular slightly longer than the postocular; three larger and a few small granules in front of supraoculars; a small, band-like additional supraocular also present behind the postocular; supraoculars separated from frontal and frontoparietal by a single row of granules. Five supraciliaris. Three nasals, the lower in contact with two supralabials and not in contact with rostral; anterior loreal slightly higher than wide, shorter than the second which is wider than high; subocular smooth, bordering the mouth, wedged between sixth/seventh and seventh/eighth supralabials. Temporal scales smooth; no auricular denticulation scales; lower eyelid translucent and covered with small scales.

Five pairs of submaxillaries; anterior three pairs completely in contact on the midline, fifth not contacted with infralabials (or separate from infralabials). Thirty gular scales in a straight line between the symphysis of the submaxillary and the collar. Gular fold not distinct. Collar weakly developed, not curved, serrated, and comprising five enlarged plates. Dorsal scales granular, smooth, 65 across midbody. Ventral plates broader than long (except for the outermost series), forming oblique longitudinal rows of 14 plates, in 32 slightly angular transverse rows; first 4–5 rows of pectoral scales longer than broad, first one is twice as long as broad. Precloacal region with two enlarged median plates, just anterior to the cloaca.

Upper surface of arm with rhombic smooth scales. Scales on upper surface of hind limbs similar to dorsal scales; enlarged plates covering the lower surface of hind limbs; 16 and 15 femoral pores on right and left sides, respectively; the two series separated by six scales; length of the series of femoral pores is three and 3.5 times the distance between these two rows. Femoral pores do not reach the knee bend by three and four scales on the right and left sides, respectively. Subdigital lamellaes unicarinate, in two rows of 29 scales under fourth toe. Two enlarged precloacal plates.

Coloration. Unlike most members of *Eremias* in which the dorsal pattern is formed by dark, narrow, longitudinal stripes, the new species has a vermiculated dorsal pattern (Figs. 7a, b; 8a, f). The dorsum has a sand-colored background combined with the dark pattern forming worm-shaped vermiculations. The venter is white; ventral side of the tail is light-greyish.

Distribution. The new species is known only from the type locality—Iran, Khorasan Province, 150 km S from Tabas city, on the road from Yazd to Tabas, 33.087° N; 55.9121°E (Fig.1).

Etymology. The name of this species is derived from the Greek root graphikos, meaning “drawn” or “written,” because the dorsal pattern resembles artificial hieroglyphs.

Natural history. This species inhabits unstabilized sand dunes on gravel plains. The habitat is characterized by scattered vegetation cover consisting of sparse bushes and the desert graminoid plant genus *Stipagrostis*. *Eremias graphica* **sp. nov.** is associated with *Stipagrostis*, using this plant as cover form predators and as a source of its insect prey, and usually dig burrows under it (Fig. 7d). These lizards have a relatively short period of daily activity in the summer of approximatley 2–3 hours in the morning and the same active time in the evening. The lizards spent the rest of the day in the shadow of the bushes. In the same habitat, we recorded the following sympatric reptile species: *Bunopus tuberculatus* Blanford, 1874, *Phrynocephalus maculatus* Anderson, 1872, *Rhinogekko misonnei* De Witte, 1973, *Teratoscincus keyserlingii* Strauch, 1863, and *Eremias fasciata* Blanford, 1874.

Comparison. The new species can be distinguished from *Eremias fasciata* by the following characters: vermicular dorsal patterns *versus* striped patterns in *E. fasciata* and yellow tympanic shields (Fig. 9a, b) in *E. fasciata versus* a white tympanum in *E. graphica* (Fig.9 e, g). *Eremias graphica* has a wider interspace between the left and right rows of femoral pores (4–6 scales) than does *E. fasciata* (2–5 scales). Furthermore, *E. fasciata* has bright-yellowish coloration on the tip of the tail, whereas *E. graphica* has a light-greyish tail tip.

FIGURE 9. Sexual dimorphism in five species of Iranian *Eremias* with females in the left column and males in the right. a–b) *Eremias fasciata*; c–d) *Eremias pseudofasciata* **sp. nov.;** e–g) *Eremias graphica* **sp. nov**.; h–i) *Eremias andersoni*; j–k) *Eremias lineolata*.

Eremias graphica can be easy distinguished from *Eremias andersoni* by a greater SVL (max SVL) of 58.3 mm *versus* 40 mm, longitudinal stripes on the dorsum *versus* vermiculated pattern in *E. graphica*, and fewer ventral scales in *E. andersoni*—28–29 *versus* 32–35. In addition, *E. andersoni* has light-bluish coloration at the tip of the tail, whereas *E. graphica* has a light-greyish tail tip.

Eremias graphica differs from *E. lineolata* by the vermiculated dorsal pattern *versus* longitudinal dark strips in *E. lineolata* and the number of scales around the tail segment (Sq.c.cd) of 23–29 *versus* 12–17, in *E. lineolata*.

Eremias graphica can be clearly distinguished from *E. scripta* by a higher number of femoral pores with 8–17 *versus* 15–18 and a higher number of gular scales of 26–31 *versus* 15–23. Although the dorsal patterns in some subspecies of *E. scripta* can be vermiculated, the new species clearly differs on the basis or meresitc data.

Eremias graphica differs from *E. cholistanica* by the number of gular scales—26–31 *versus* 20–24, the number of scales around the tail segment—23–29 *versus* 27–35, and by its vermiculated *versus* striped dorsum.

TABLE 3. Morphological characters of the type series of *Eremias graphica* **sp. nov.**.

	Holotype	Paratypes								
	ZMMU R-13171	ZMMU R-15626	ZMMU R-15627	ZMMU R-15628	ZMMU R-15629	ZMMU R-15630	ZMMU R-15631	ZMMU R-12986	ZMMU R-15624	ZMMU R-15625
Sex	m	m	f	m	f	sad m	sad f	f	m	m
SVL	56.9	58.3	50.4	47.8	49.5	45	50	53.7	48.3	48.8
TL	114.6	118	101	-	-	92	98	91	114	108
Lpil	13.5	13.8	11.5	11.5	11.3	10.4	11.3	11.5	11.4	12
HL	14.5	14.8	12	11.8	12	11.2	12.2	12.2	12.7	13.1
HW	8.3	9.4	6.9	7	6.5	6.2	7	7	6.7	7.4
HH	7.2	6.5	5.3	5.1	4.8	4.5	5	4.9	5.3	6
Ga	27.8	28.4	26.3	22.9	25.6	21.6	24.5	25.8	21.7	23.7
Pa	20.5	20.5	18.5	18.3	18	16.7	17.5	16.3	18.3	18.9
Pp	35.7	35.9	31.8	31.4	30.4	29	28.6	29.3	32	33.2
Pfm (r/10)	15/16	18/15	17/16	16/16	18/17	16/17	17/16	17/16	18/18	16/16
Dist.Pfm	6	5	6	6	6	6	5	6	4	6
Sq	65	59	63	62	59	60	59	59	64	61
G	30	30	30	28	30	26	29	26	30	31
Ventr.	32	32	33	34	34	33	35	34	35	34
Ventr. long	16	16	18	16	16	15	16	14	16	16
Sq.c.cd	29	27	26	27	27	25	24	23	24	28
Lam.subdig.	29	28	26	25	26	28	22	25	24	24
Sq.dors	153	140	161	174	160	160	163	165	177	168
Lab.tot (r/l)	10/9	10/9	9/9	9/8	10/8	9/9	7/7	10/9	9/8	9/10
Inflab.(r/l)	7/6	8/8	7/6	6/6	7/6	7/6	5/6	8/7	6/7	8/8
Submax	5	5	5	5	5	5	5	5	5	5
Gran	+	+	+	-	+	+	+	+		+
Precloac	+	+	-	+	-	-	-	+	+	+
Supracil (r/l)	3/5	5/5	5/4	6/6	5/5	5/5	4/5	7/4	5/5	5/5

Eremias pseudofasciata **sp. nov. (Figures 9c–d; 10 a; 11; 12 (RAN 4201, 4203–4205, 4208); 13 c).**

Holotype. ZMMU R-12982 Iran, Khorasan Province, 20 km SE of Boshruiyeh, 33.760693° N; 57.560714° E; elevation 949 m a.s.l.; collected by R. A. Nazarov, D. A. Bondarenko & M. Rajabizadeh, 09 May 2010 (Fig. 11).

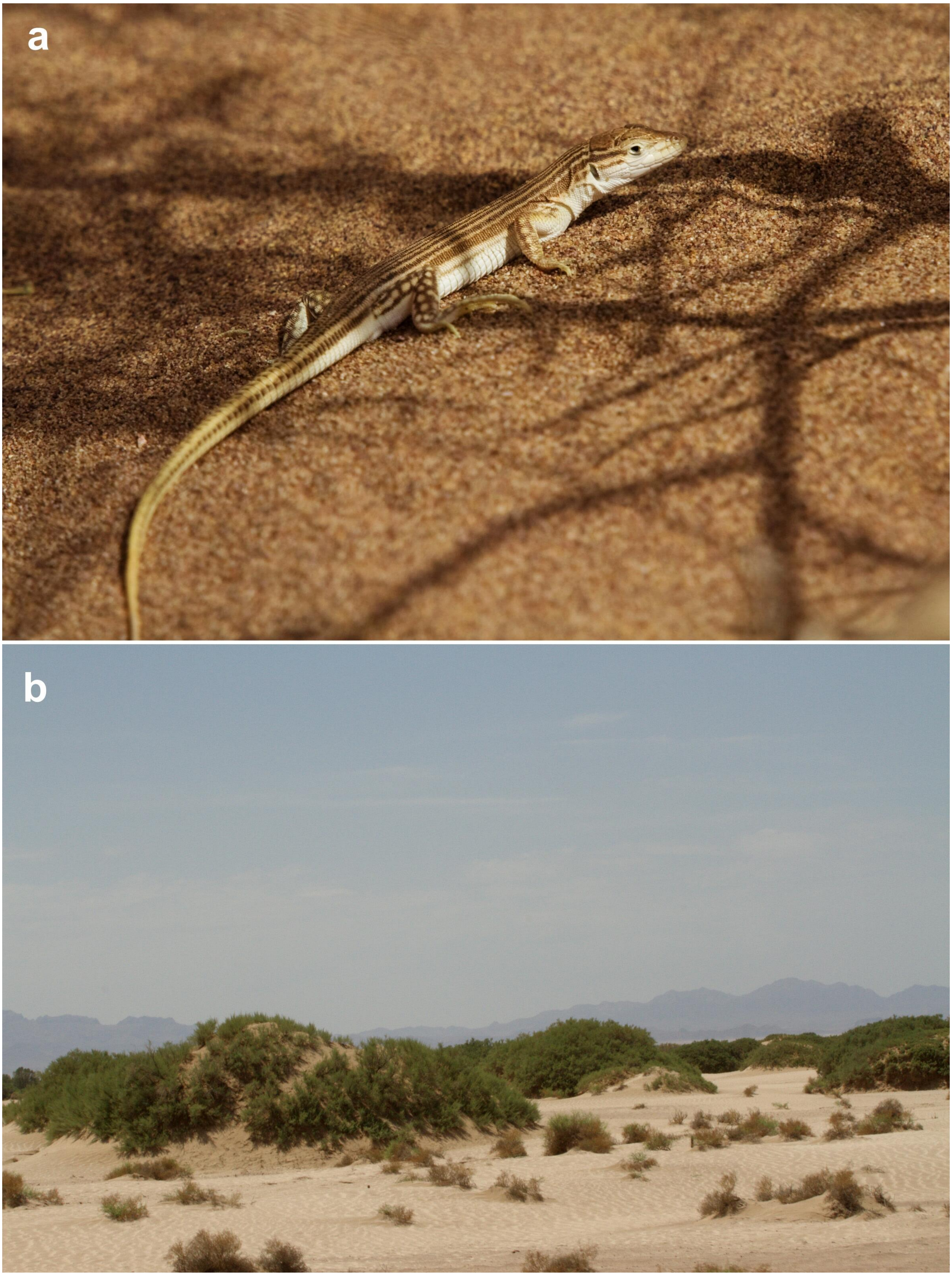

FIGURE 10. *Eremias pseudofasciata* **sp. nov.** a) *in situ* at the type locality; b) habitat of the new species near Boshehr city (type locality).

Paratypes. Eleven specimens including five males (ZMMU R-15632–15633, R-15635, and R-15638–15639) and one female (ZMMU R-15634) with the same locality data as the holotype and four males (ZMMU RAN 4201, 4203, 4204, 4208) and one female (ZMMU RAN 4205) from Iran, Khorasan Province, 15 km NE of Boshruiyeh, 33.972851° N; 57.517912° E; elevation 980 m a.s.l. collected 13 May 2021 by R. A. Nazarov, H. Nabizadeh.

Diagnosis. A medium sized *Eremias*, maximum SVL 57 mm, TL more than two times longer than the body (max. 122 mm). Supraocular plates usually in contact with frontal and frontoparietal plates, no full row of small granular and roundish scales in between, but sometimes tiny elongate scales between the supraocular and frontal plates are visible; fifth submaxillary small, 5–6 times smaller than fourth submaxillary, usually in contact with infralabials or separated by one row of granular scales; collar scales not strongly distinct from surrounding gular scales, usually only a few larger than the others. Scales at midbody 44–51; 14–19 well developed femoral pores in row, left and right rows separated by 4–7 scales; series of femoral pores not reaching the knee bend by 2–3 scales.

Coloration. Dorsal pattern comprising alternating dark and light longitudinal, regular, contrasting stripes, usually seven dark stripes in total. Two stripes on the sides of the body are darker, wider, and not as contrasting as the stripes on the dorsum. Wide, dark, longitudonal stripes without light spots begin behind the eye and pass along the sides of the body, continuing along the tail. Narrow, dark, longitudinal line between fore and hind limbs marking the ventrolateral border of the body. Juveniles have vermiculated patterns on the middle of the dorsum, formed by dark and light stripes. Sometimes adult specimens have a narrow vermiculate pattern along the vertebral line. No yellow spot on the tympanic plate. Dorsal limb surface dark brown with round light or yellowish spots. The belly is whitish and the tip of the tail light yellowish.

Description of Holotype (Fig. 11)**.** ZMMU R-12982. Adult male, SVL 56.7 mm, TL 112.3 mm, Pa 21.5 mm, Pp 36.7 mm, L.pil. 12.5 mm. Meristic features: G 26, Pfm (right/left) 18/18, Dist.Pfm 4, labialia (left/right) 9/9, infralabilia (left/right) 7/7, ventralia 31. Tail scales smooth on the base, not strongly keeled; Sq.c.cd 23, subdigital lamellae 26. Smooth, roundish dorsal scales; Sq 51, Sq. dorsal 151

Head and body moderately elongated and slightly depressed. Head length (14.5 mm) 1.88 times its width (7.7 mm) and 2.3 times as its height (6.3 mm); nasals smooth or slightly swollen; rostrum approximately the same size as postocular part of the head; head wider than neck.

Fore and hind limbs relatively long; Pa/SVL 0.37, Pp/SVL 0.64. Hind limb reaches the axilla of forelimb and extends far beyond it. Tail about twice the length of the body, TL/SVL 0.5, cylindrical and slightly depressed at the base.

Pileus (Lpil 12.5mm) plates slightly swollen. Nasals in broad contact behind the rostral, the suture between them approximately 2/5 the length of frontonasal. Frontonasal width 1/3 more than its length. Prefrontal slightly longer than broad, forming median suture. Length of frontal same as the distance between rostral to frontal, two times wider in front than behind and narrow in the middle. Frontoparietals somewhat longer than broad, weakly rugose. Interparietal teardrop-shaped, wider in front, with parietal window. Parietals somewhat longer than broad, weakly rugose, surrounded by a row of small elongate scales, different from other dorsal scales, and the next row on the middle of neck formed by triangular scales. No occipital.

Two large roundish, approximately equal sized and one small elongate posterior supraoculars. The space in front of the supraoculars occupied by one large plate, another half that size, and several granules. Supraoculars in contact with frontoparietals, but anterior supraocular plates separated from frontal by very tiny and elongate scales (not granular). Five supraciliars, anterior and posterior enlarged, separated by a single series of granules from supraoculars. Three nasals, the lower in contact with first and second supralabials and not touching the rostral. Large loreal slightly higher than broad, with two additional plates 2.5–3 times smaller anteriorly and posteriorly. Subocular smooth with broad contact with mouth, wedged between sixth and seventh supralabials. Six supralabials before subocular and three more posteriorly, the seventh infralabial on each side. Temporal scales smooth; no auricular denticulation scales; lower eyelid translucent and covered with small scales.

Five pairs of submaxillaries, three anterior pairs in full contact with each other on the midline, 4th and 5th pairs in contact with 5th, 6th, and 7th infralabials. Between 6th and 7th infralabials and 4th and 5th submaxillaries, there is one small additional scale.

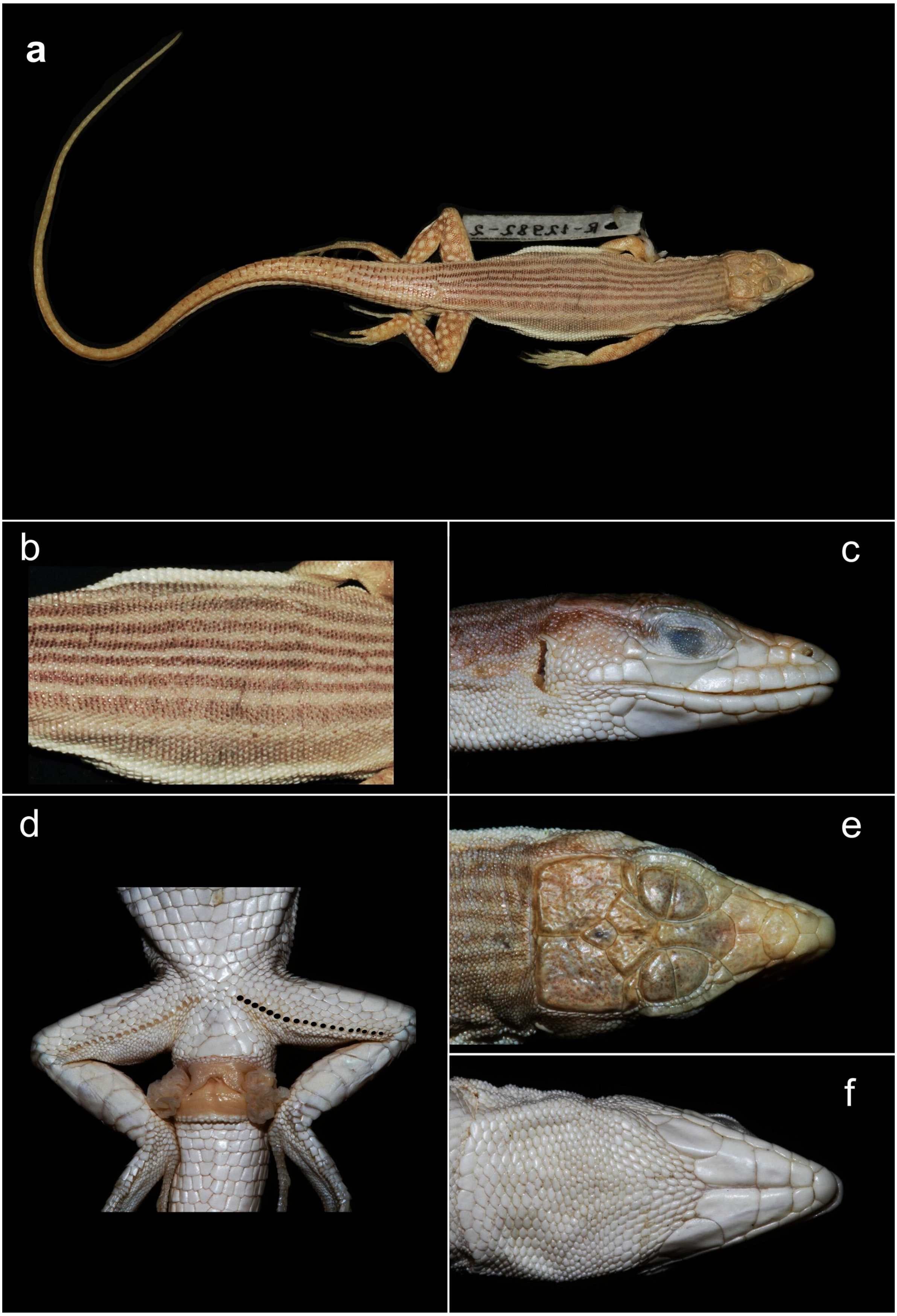

FIGURE 11. Morphological features of *Eremias pseudofasciata* **sp. nov.** a) general view of holotype ZMMU R-12982; b) dorsal patterns; c, e, f) three views of the head; d) precloacal region with well developed pores, marked on one side.

FIGURE 12. Dorsal patterns of syntopic *Eremias pseudofasciata* **sp.nov.** (RAN 4201; 4203–4205; 4208) and *E. fasciata* (RAN 4202, 4206) from type locality of the new species. Rounded light spots on the femur and tibia are noticeably smaller in *E. pseudofasciata*.

Twenty six gular scales in a straight line between the symphysis of the submaxillary and the collar. Collar weakly developed and formed by seven slightly enlarged scales. Dorsal scales granular, smooth, 51 across middle of the body and 151 along middle of dorsum. Ventral plates, broader than long, forming oblique longitudinal rows of 16 plates, in 31 slightly angular transverse rows. Precloacal region with one enlarged median plate, just above the cloaca; 18 femoral pores on each side, separated by four scales; length of the series of femoral pores is four times the distance between these two rows. Femoral pores do not reach the knees bend by two ventral femoral scales on the right and left sides.

Upper surface of arm with rhombic, smooth scales. Scales on upper surface of hind limbs similar in size to the dorsal scales, enlarged plates covering the lower surface of hind limbs. Subdigital lamellae weakly carinate, 29 scales under fourth toe. Three scales around the toes.

Tail expanded at the base, covered by weakly keeled elongate scales, around 9–10 tail segments with 23 scales.

Coloration and patterns. The dorsal pattern of *Eremias pseudofasciata* comprises alternating dark and light longitudinal contrasting stripes, with eight dark strips on the dorsum. On the body sides, the dark stripes are wider and not as contrasting as those on the dorsum. A wide, dark, longitudinal stripe begins behind the eye, passes along the sides of the body, and continues along the entire tail. A narrow dark longitudinal line is present between the fore and hind limbs, marking the ventrolateral border of the body. A white tympanic plate is present. The dorsal surface of the limbs is dark brown with round light or yellowish spots. The tip of the tail slightly yellowish. The ventral surface of the body is white.

Distribution. *Eremias pseudofasciata* is only known from the type locality and a nearby location (see Paratypes).

Etymology. Since this new population more closely resembles *Eremias fasciata* on the basis of morphology and molecular analysis (Fig. 5–6), we named this new species "*pseudofasciata*," i.e., false *fasciata*.

FIGURE 13. The main species of *Eremias* discussed in the present work: a) *E. andersoni*, b) *E. acutirostris*, c) *E. pseudofasciata* **sp. nov.**, d) *E. fasciata*, e) *E. lineolata*, g) *E. graphica* **sp. nov.**, h) *E. kavirensis*, i) *E. s. scripta*, j) *E. scripta pherganensis*, k) *E. lasdinii*.

TABLE 4. Morphological characters of the type series *of Eremias pseudofasciata* **sp. nov.**.

	Holotype	Paratypes										
	ZMMU R-12982	ZMMU R-15632	ZMMU R-15633	ZMMU R-15634	ZMMU R-15635	ZMMU R-15638	ZMMU R-15639	ZMMU R-16919	ZMMU R-16920	ZMMU R-16921	ZMMU R-16922	ZMMU R-12923
Sex	m	m	m	f	m	m	M	m	m	m	f	m
SVL	56.7	54.3	55	47.2	33	46.6	39.5	48.2	52.3	57	49.1	55.1
TL	112.3	117.2	122	78	69.1		72.4	107	105.5	107.6	102.2	112.7
Lpil	12.5	13.3	12.5	10.7	8.4	10.6	9.7	11.7	11.9	13.1	11.1	13.2
HL	14.5	14	14	11.3	9.5	11.3	10.9	13.05	13.3	14.7	12.4	14.6
HW	7.7	7.3	7.7	7	4.5	6	5.7	7.21	7.7	8.38	7.3	8.01
HH	6.3	6.5	6.3	3.7	3.1	4.2	4.2	5.44	5.9	6.2	5.7	6.18
Ga	24.5	25.7	27.3	23.1	15.8	22.8	19.6	23.3	23.7	26.1	25.2	26.4
Pa	21.5	19	20.8	16.5	12.7	18.6	15	19.94	19.4	20.5	18.9	21.0
Pp	36.7	34.2	37.7	30.2	23.8	30.8	27.2	33.95	34.9	35.3	32.9	33.7
Pfm (r/10)	18/18	15/16	17/15	16/14	17/18	15/14	16/16	17/17	19/19	15/15	16/16	18/18
Dist.Pfm.	4	3	4	4	4	4	4	4	4	5	7	4
Sq.	51	50	51	49	50	47	49	44	44	48	45	49
G	26	26	28	29	26	28	26	28	33	30	29	32
Ventr	31	31	32	32	33	31	32	34	32	34	34	34
Ventr. long	16	14	15	14	16	16	14	14	13	15	14	14
Sq.c.cd.	23	22	24	21	25	22	26	22	24	21	24	23
Lam. subdig	26	26	30	26	-	24	25	28	31	30	28	31
Sq.dors.	151	150	157	150	146	142	146	162	142	134	144	138
Lab.tot (r/l)	9/9	8/8	9/9	9/9	8/9	9/9	7/7	9/9	10/9	9/7	10/10	8/8
Inflab.(r/l)	7/7	6/6	7/7	8/8	6/6	6/6	6/6	6/7	6/6	8/8	6/6	7/7
Submax	5	5	5	5	5	5	5	5	5	5	5	5
Gran	-	-	-		-	-	-	-	-	-	-	-
Precloac.	+	+	+	-	+	-	+	+	+		-	+
Supracil (r/l)	5/5	4/5	7/7	5/5	5/6	6/6	5/5	5/5	5/6	5/6	4/6	5/6

Natural history. *Eremias pseudofasciata* inhabits weakly stabilized, isolated sand dunes on a gravel plain. The vegetation in this habitat is represented by the genera *Salsola* and *Astragalus*, and the families Brassicaceae and Poaceae (Fig. 10 b). In the same habitat, we recorded the following sympatric reptile species: *Eremias fasciata* Blanford, 1874, *E. lineolata* (Nikolsky, 1897), *Phrynocephalus mystaceus* (Pallas, 1776), *Crossobamon eversmanni* (Wiegmann, 1834), *Teratoscincus keyserlingii* Strauch, 1863 and *Bunopus tuberculatus* Blanford, 1874.

Comparison. *Eremias pseudofasciata* **sp. nov.** is most closely related to *E. fasciata* (Fig. 12) and can be distinguished by the following characters: lower number of femoral pores, with 14–19 *versus* 15–22 in *E. fasciata*, supraocular plates in a contact with frontal and frontoparietals *versus* separate supraocular from frontal, and full row of small granular and roundish scales in *E. fasciata*, colour of the tympanic plate yellow in *E. fasciata versus* white in *E. pseudofasciata*, contrasting longitudinal dark stripes in *E. pseudofasciata versus* no contrasting stripes in *E. fasciata*. Additionally, *E fasciata* has a dark, wide contrasting stripe on the upper part of the temporal region beginning at the posterior margin of the eye and ending above the ear opening, with 2–3 bluish-grey light roundish spots on it, while *E. pseudofasciata* has two dark stripes on the temporal region without light spots. One of these stripes is wider and begins at the posterior side of the eye and continues along the body to the tail, the second stripe starts at the posterior margin of the suboculars and runs to the middle of the ear opening. Rounded light spots on the femur and tibia are noticeably smaller in *E. pseudofasciata* in contrast to *E. fasciata* (Fig. 12).

Eremias pseudofasciata **sp.nov.** clearly differs from *E. graphica* **sp. nov.** by lower number of Sq—44–51 *versus* 54–65, by its striped dorsal pattern *versus* vermiculate, and by its number of femoral pores—14–19 *versus* 8–17 in *E. graphica*.

Eremias pseudofasciata differs from *E. lineolata* by the mean number of femoral pores 16.07 (14–19) *versus* 13.6 (9–17), the distance between the series of femoral pores being four times the distance in *E. pseudofasciata versus* two times the distance between right and left rows in *E. lineolata*, the number of scales around the 9th–10th tail segment—21–26 *versus* 12–17, supraocular plates separated from frontals and frontoparietals by full row of small granular and roundish scales in *E. lineolata versus* contact between supraocular and frontal in *E. pseudofasciata*, the number of subdigital lamellae on the fourth toe—24–30 *versus* 19–24, color of the tail venter slightly yellow *versus* orange-reddish in *E. lineolata*, and two dark stripes on the temporal region without any light spots in *E. pseudofasciata versus* two dark contrasting stripes in the temporal region with the upper being wider and containing light spots in *E. lineolata.*

E. pseudofasciata can be distinguished from *E. andersoni* by its larger SVL (max SVL) of 57 mm *versus* 40 mm, smaller number of ventral scales—28–29 *versus* 31–33 in *E. andersoni*, and length of the series of femoral pores four times the distance between these two rows in *E. pseudofasciata versus* three times in *E. andersoni*. In addition, *E. andersoni* has light-bluish coloration on the tip of tail *versus* a light-yellowish tail tip in *E. pseudofasciata*.

Eremias pseudofasciata can be clearly distinguished from *E. scripta* by the greater number of femoral pores—8–17 *versus* 14–18, the row of femoral pores almost reaching the knee in *E. pseudofasciata* but noticeably shorter in *E. scripta*, and gular scales 26–29 *versus* 15–23. In addition, the new species is characterised by smooth caudal scales, whereas for *E. scripta* has clearly visible keels on subcaudal scales.

Eremias pseudofasciata differs from *E. cholistanica* by its larger number of gular scales—26–29 *versus* 20–24 and the number of scales around the tail segment 21–26 *versus* 27–35.

From all other *Eremias* species inhabiting the region, the new species can be distinguished by a combination of the above-described characters.

Discussion

The revealed cryptic diversity among sand-dwellig species of *Eremias* confirms the uniqueness of the isolated sand massifs of the Iranian Plateau, and the process of adaptation to psammobiotic lifestile is the main driver in the diversification within the *Eremias fasciata* complex. The deep genetic diversity of *Eremias fasciata* complex originated in the sand deserts of the Iranian Plateau and is correlated with disjunct distribution of the sandy massifs. We suggest that *E. fasciata* is the most basal and widespread eurytopic species in the region. It was the first to exploit new ecological niches in sandy areas, which allowed them to adapt quickly to extreme conditions. The high divergence in *Eremias fasciata* (Fig. 6. clade E), can be explained by the high level of diversification of landscapes in Central Iran. Therefore, we can observe several haplotypes at one locality (point 8 on the map and Fig. 6). *Eremias* cf. *fasciata* (ZMMU 15515) is placed in a separate clade due to the significant number of differences in morphological characteristics (Fig. 5), as well as its greater genetic distances from *E. fasciata* (Fig.6. clade F).

A different situation is observed in the deserts of Uzbekistan and Kazakhstan, where there are large areas that comprise more-or-less continuous and homogenous habitats. As a result, there is practically no genetic divergence between the populations of *E. lineolata* (Fig. 6). Thus, *E. lineolata* is a relatively more plastic species and not strictly related to the sandy environment and can be found both on semi-stable and stable sands, whereas *E. scripta* complex taxa are obligate psammobionts and linked to sand dunes habitat. *Eremias scripta* shows a well-developed geographical structure of populations with deep genetic divergence (Fig. 6). We hypothesize that this is simillar to the *E. faciata* complex, with different levels of adaptation to the sandy environment driving divesification.

One of the key factors in the origin of the current diversity of reptiles on sand massifs is the history of origin these habitats. According to the literature, huge plains of central Iran, in the territory of Dasht-e Kavir and Dasht-e Lut, were filled with water before the beginning of the Quaternary Period (Berberian *et al.*, 1981; Popov *et al.*, 2010; Mattei *et al.* 2015). The sand massifs of the Iranian Plateau are unique in their mosaic distribution and composition and were formed in the Pliocene by wind action on the remaining soil after the draining of water bodies (Berberian *et al.*, 1981). The disjunct distribution of the sand massifs is the key cause of the high level of local endemism among psammobiont reptiles in central Iran. We hypothesize that the unique conditions on each sand massif result in allopatric speciation, driving the evolution of endemic species of sand-dwelling reptiles on the Iraininan Plateau. The sand dune environment itself is a very dynamic system where isolation and fragmentation can occur rapidly. The nature of sand dunes eventually led to diversification of sand-dwelling species and can be identified as a main factor influencing evolutionary processes.

For the two last centuries, most herpetologists have recognized the complicated taxonomic issues surrounding species complexes in *Eremias*. Using molecular data allows researchers to solve some problems in taxonomically complicated groups such as *Eremias*. However, recent molecular studies have not supported the monophyly of the currently recognized subgenera of *Eremias* (Khan *et al.* 2021). The subgenera *Aspidorhinus*, *Pareremias*, and

Rhabderemias were found to be paraphyletic (Khan *et al.* 2021) and our study is in full agreement with that. We can draw the following major taxonomic conclusions about the *Eremias* studied here. The deep divergence within each species complex (Fig. 6) allows us to hypothesize that there is a significant understimation of species diversity. The phylogenetic position of *E. kavirensis* has long been problematic and we recover it in an isolated position closer to the *E. fasciata* complex than to the *E. scripta* complex, which is inconsistent with the morphological data. The phylogenetic position of this species should be checked using a multi-locus analysis or additional nuclear markers. Lastly, the deep genetic distance of the southern subspecies *E. scripta lasdini*, indicates that the status of this form needs to change as a full species—*Eremias lasdini* **comb. nov.**

Diagnosis of *Eremias lasdini* (Tzarevskyi, 1918) **comb. nov.** (based on Szczerbak 1974):

The dorsal pattern is striated. Occipital stripe in the middle of the back pronounced to the base of the tail, number of scales around the 9–10 rings of the tail 17–21, on average 19. Between the bend of the knee and the row of femoral pores 2–3 scales; the fifth submaxillary usually in contact to the infralabial. Distributoin: SE Uzbekistan and SW Tajikistan, possibly present in the bordering regions of Afghanistan and Turkmenistan.

Acknowledgments

This study was conducted within the framework of a long-term Russian-Iranian cooperation for the study of the herpetofauna of Iran. We would like to thank the Department of Environment (DOE) in Tehran for issuing the permit for the field work in Iran. We are very grateful to Natalia Ananjeva and Konstantin Milto (ZISP) for the opportunity to study the collection materials under their care. RN would like to thank Evgenia Lazareva for her constant help with the design and preparation of this manuscript. (VO and RN) This research was fulfilled within the framework of the State Themes of ZMMU 121032300105-0. (NAP and RAN) The molecular study was supported of Russian Science Foundation grant (RSF) no. 22-14-00037 to NAP. (DM) The present study was carried out within the framework by the State Theme of Zoological Institute of Russian Academy of Sciences No. 122031100282-2. (ER, NP, DM and RN) This study was financially supported by the Iran National Science Foundation (INSF) and Russian Foundation of Basic Research (RFBR) under an international (Iran- Russian) project with proposal number of INEF 99003440 and RFFS 20-54-56033, respectively. The authors are grateful to Aaron Bauer, Jesse Grismer and another anonymous reviewer for valuable comments and suggestions for the improvement of this work.

References

Anderson, J. (1872) On some Persian, Himalayan, and other Reptiles. *Proceedings of the Zoological Society of London*, 1872, 371–404.

Anderson, S.C. (1999) *The Lizards of Iran*. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 442 pp.

Arnold, E.N. (1986) The hemipenis of lacertid lizards (Reptilia: Lacertidae): structure, variation and systematic implications. *Journal of Natural History*, 20, 1221–1257.
https://doi.org/10.1080/00222938600770811

Arnold, E.N. (1989) Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bulletin of the British Museum Natural History*, *Zoology*, 55 (2), 209–257.

Arnold, E.N., Arribas, O. & Carranza, S. (2007) Systematics of the Palearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*, 1430 (1), 3–86.
https://doi.org/10.11646/zootaxa.1430.1.1

Baig, K.J. & Masroor, R. (2006) A new species of *Eremias* (Sauria: Lacertidae) from Cholistan Desert, Pakistan. *Russian Journal of Herpetology*, 13 (3), 167–174.

Barabanov, A.V. (2009) *Aspidorhinus* Eichwald, 1841 as a valid subgeneric name for *Eremias velox* species group (Sauria, Lacertidae). *Current Studies in Herpetology*, 9 (1–2), 59–61. [in Russian with English abstract]

Bedriaga, J.V. (1912) Amphibians and Reptiles. Part 4 (Zoological Section III (1)). *In*: *Nauchnye rezultaty puteshestviy N. M. Przewalskogo po Tsentralnoy Azii [Scientific results of N.M. Przewalskii's Travels in Central Asia].* Imperial Academy, St. Petersburg, pp. 503–769, pls. VIII–X. [in Russian and German]

Berberian, M. & King, G.C.P. (1981) Towards a paleogeography and tectonic evolution of Iran. *Canadian Journal of Earth Sciences*, 18 (2), 210–265.
https://doi.org/10.1139/e81-019

Böhme, W. & Szczerbak, N. (1991) Ein neuer Wüstenrenner aus dem Hochland Afghanistans, *Eremias* (*Eremias*) *afghanistanica* sp. n. (Reptilia: Sauria: Lacertidae). *Bonner zoologische Beiträge*, 42, 137–141.

Boulenger, G.A. (1918) A synopsis of the lizards of the genus *Eremias*. *Journal of Zoological Research*, 3, 1–12.
Boulenger, G.A. (1920) *Monograph of the Lacertidae. Vol. 1*. Trustees of the British Museum of Natural History, London, 352 pp.
https://doi.org/10.5962/bhl.title.8312
Boulenger, G.A. (1921) *Monograph of the Lacertidae. Vol. 2*. Trustees of the British Museum of Natural History, London, 352 pp.
https://doi.org/10.5962/bhl.title.8312
Blanford, W.T. (1874) Descriptions of new lizards from Persia and Baluchistàn. *Annals and Magazine of Natural History*, Series 4, 13 (4), 453–455.
https://doi.org/10.1080/00222937408680903
Blanford, W.T. (1875) List of Reptilia and Amphibia collected by the late Dr. Stoliczka in Kashmir, Ladak, eastern Turkestan, and Wakhan, with descriptions of new species. *Journal of the Asiatic Society of Bengal*, 44 (2), 191–196 + 201, 2 pls.
Blanford, W.T. (1876) Eastern Persia. *In*: *An Account of the Journeys of the Persian Boundary Commission, 1870-1872. Vol. 2. Zoology and Geology*. Macmillan and Co., London, 516 pp.
Brushko, Z.K. (1995) *Lizards of Desert Regions of Kazakhstan*. Almaty, Konzhik, 231 pp. [in Russian]
Darevsky, I.S. & Shcherbak, N.N. (1978) *Eremias andersoni*, a new lizard (Reptilia, Lacertilia, Lacertidae) from Iran. *Journal of Herpetology*, 12 (1), 13–15.
https://doi.org/10.2307/1563496.
Eichwald, E. (1841) *Fauna Caspio-Caucasia Nonnulis Observationibus Novis*. Litteris Typographiae Diarii Gall. Politic. Petropol., Petropoli, 233 pp., 40 col. Pls.
https://doi.org/10.5962/bhl.title.126375
Eremchenko, V.K. (1999) Nomenclature of Asian racerunners *Eremias* Wiegmann, 1884 in relation with following designation of monotypy (Sauria: Lacertidae). *Izvestiya Natsionalnoy Akademii Nauk Kyrgyzstana*, 1, 72–73. [in Russian]
Guo, X., Chen, D.X., Papenfuss, T., Ananjeva, N.B., Melnikov, D.A. & Wang, Y. (2011) Phylogeny and divergence times of some racerunner lizards (Lacertidae: *Eremias*) inferred from mitochondrial 16S rRNA gene segments. *Molecular Phylogenetics and Evolution*, 61 (2), 400–412.
https://doi.org/10.1016/j.ympev.2011.06.022
Fu, J.Z. (1998) Towards the phylogeny of the family Lacertidae: implications from mitochondrial DNA 12S and 16S gene sequences (Reptilia: Squamata). *Molecular Phylogenetics and Evolution*, 9 (1), 118–130.
https://doi.org/10.1006/mpev.1997.0456
Fu, J.Z. (2000) Towards the phylogeny of the family Lacertidae—why 4708 base pairs of mtDNA cannot draw the picture. *Biological Journal of the Linnaean Society*, 71, 203–217.
https://doi.org/10.1111/j.1095-8312.2000.tb01254.x
Ivanova, N.V., Dewaard, J.R. & Hebert, P.D.N. (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes*, 6 (4), 998–1002.
https://doi.org/10.1111/j.1471-8286.2006.01428.x
Hall, T. (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
Harris, D.J., Arnold, E.N. & Thomas, R.N. (1998) Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proceedings of the Royal Society of London B*, 265, 1939–1948.
https://doi.org/10.1098/rspb.1998.0524
Hillis, D.M., Moritz, C. & Mable, B.K. (1996) *Molecular Systematics. 2nd Edition*. Sinauer Associates, Inc, Sunderland, Massachusetts, xvi + 655 pp.
https://doi.org/10.2307/1447682
Heidari, N., Rastegar Pouyani, N., Rastegar Pouyani, E. & Radjabizadeh, M. (2013) A new species of *Acanthodactylus* Fitzinger 1834 (Sauria: Lacertidae) from southern Iran. *Zootaxa*, 3722 (3), 333–346.
https://doi.org/10.11646/zootaxa.3722.3.3
Hebert, P.D.N. & Gregory, T.R. (2005) The promise of DNA barcoding for taxonomy. *Systematic Biology*, 54, 852–859.
https://doi.org/10.1080/10635150500354886
Huelsenbeck, J.P. & Hillis, D.M. (1993) Success of phylogenetic methods in the four-taxon case. *Systematic Biology*, 42, 247–264.
https://doi.org/10.1093/sysbio/42.3.247
Huelsenbeck, J.P., Ronquist, F. (2001) MrBayes: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
https://doi.org/10.1093/bioinformatics/17.8.754
Kamali, K. & Anderson, S. (2015) A New Iranian *Phrynocephalus* (Reptilia: Squamata: Agamidae) from the hottest place on earth and a key to the genus *Phrynocephalus* in southwestern Asia and Arabia. *Zootaxa*, 3904 (2), 249–260.
https://doi.org/10.11646/zootaxa.3904.2.4
Kazemi, S.M., Qomi, M.F., Kami, H.G. & Anderson, S.C. (2011) A new species of *Ophiomorus* (Squamata: Scincidae) from Maranjab Desert, Isfahan Province, Iran, with a revised key to the genus. *Amphibian & Reptile Conservation*, 5 (1), 23–33.
Khan, M.A., Jablonski, D., Nadeem, M.S., Masroor, R., Kehlmaier, C., Spitzweg, C. & Fritz, U. (2021) Molecular phylogeny

of *Eremias* spp. from Pakistan contributes to a better understanding of the diversity of racerunners. *Journal of Zoological Systematics and Evolutionary Research*, 59, 466–483.
https://doi.org/10.1111/jzs.12426

Lantz, L.A. (1928) Les *Eremias* de l'Asie occidentale. *Bulletin du Musée de Géorgie*, 4–5, 1–136 + (1), pls. I–III.

Leviton, A.E., Anderson, S.C., Adler, K. & Minton, S.A. (1992) *Handbook to Middle East Amphibians and Reptiles.* Society for the Study of Amphibians and Reptiles, Oxford, Ohio, 252 pp.

Masroor, R., Khisroon, M., Khan, M.A. & Jablonski, D. (2020) A new species of *Eremias* (Squamata: Lacertidae) from the arid mountains of Pakistan. *Zootaxa*, 4786 (1), 101–121.
https://doi.org/10.11646/zootaxa.4786.1.8

Masroor, R., Khan, M.A., Nadeem, M.S., Amir, S.A., Khisroon, M. & Jablonski, D. (2022) Appearances often deceive in racerunners: integrative approach reveals two new species of *Eremias* (Squamata: Lacertidae) from Pakistan. *Zootaxa*, 5175 (1), 55–87.
https://doi.org/10.11646/zootaxa.5175.1.3

Mayer, W. & Pavlicev, M. (2007) The phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: convergent adaptations to arid habitats within the subfamily Eremiainae. *Molecular Phylogenetics and Evolution*, 44, 1155–1163.
https://doi.org/10.1016/j.ympev.2007.05.015

Mattei, M., Cifelli, F., Muttoni, G. & Rashid, H. (2015) Post-Cimmerian (Jurassic–Cenozoic) paleogeography and vertical axis tectonic rotations of Central Iran and the Alborz Mountains. *Journal of Asian Earth Sciences*, 102, 92–101.
https://doi.org/10.1016/j.jseaes.2014.09.038

Moravec, J. (1994) A new lizard from Iran, *Eremias* (*Eremias*) *lalezharica* sp. n. (Reptilia: Lacertilia: Lacertidae). *Bonner zoologische Beiträge*, 45 (1), 61–66.

Mozaffari, O. & Parham, J.F. (2007) A new species of racerunner lizard (Lacertidae: *Eremias*) from Iran. *Proceedings of the California Academy of Sciences*, 58 (28), 569–574.

Mozaffari, O., Ahmazadeh, F. & Parham, J.F. (2011) *Eremias papenfussi* sp. nov., a new lacertid lizard (Sauria: Lacertidae) from Tehran Province, Iran. *Zootaxa*, 3114 (1), 57–62.
https://doi.org/10.11646/zootaxa.3114.1.6

Mozaffari, O., Ahmazadeh, F. & Saberi-Pirooz, R. (2020) Fahimi's racerunner, a new species of the genus *Eremias* Fitzinger, 1834 (Sauria: Lacertidae) from Iran. *Zootaxa*, 4768 (4), 565–578.
https://doi.org/10.11646/zootaxa.4768.4.7

Nazarov, R.A., Radjabizadeh, M., Poyarkov, N.A., Ananjeva, N.B., Melnikov, D.A. & Rastegar-Pouyani, E. (2017) A New Species of Frog-Eyed Gecko, genus *Teratoscincus* Strauch, 1863 (Squamata: Sauria: Sphaerodactylidae), from Central Iran. *Russian Journal of Herpetology*, 24 (4), 291–310.
https://doi.org/10.30906/1026-2296-2019-24-4-291-310

Nazarov, R.A., Melnikov, D.A., Radjabizadeh, M. & Poyarkov, N.A. (2018) A new species of short-fingered geckos *Stenodactylus* (Squamata, Geckonidae) from South Iran with taxonomic notes on validity of the genus *Trigonodactylus* Hass, 1957. *Zootaxa*, 4457 (1), 93–113.
https://doi.org/10.11646/zootaxa.4457.1.4

Nikolsky, A.M. (1897) Les reptiles, amphibiens et poissons recueillis (part.) Mr. N. Zaroudny dans la Perse orientale. *Annuaire Musée Zoologique de l'Académie Impériale des Sciences de St.-Pétersbourg*, 2, 306–348. [in Russian with French title]

Nikolsky, A.M. ("1899" 1900) Reptiles, amphibiens et poissons, recueillis pendant le voyage de Mr. N. A. Zaroudny en 1898dans la Perse. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St. Pétersbourg*, 4 (4), 375–417. [in Russian with French title]

Nikolsky, A.M. (1905) Herpetologia Rossica. *Mémoires de l'Académie Imperiale des Sciences, Phys.-Math. Classe, St.-Pétersbourg*, XVII (1), 1–518

Nikolsky, A.M. (1915) *The Fauna of Russia and Adjacent Countries. Reptiles (Reptilia). Vol 1. Chelonia and Sauria*. Academy of Science, Petrograd, 534 pp. [in Russian]

Orlova, V.F. & Terbish, Kh. (1997) Family Lacertidae Cope, 1864. *In*: Ananjeva, N.B., Munkhbayar, Kh., Orlov, N.L., Orlova, V.F., Semenov, D.V. & Terbish, Kh. *Amphibians and Reptiles of Mongolia. Reptiles*. KMK Ltd., Moscow, pp. 133–266. [in Russian]

Orlova, V.F. & Nazarov, R.A. (2017) Diversity of racerunners (Sauria: Lacertidae, *Eremias*) of Iran: Review of species and taxonomy issues. *In*: *Spatial-temporal Dynamics of Biota and Ecosystems in the Aral-Caspian Basin. Materials of the II International Conference, Dedicated to the Memory of the Outstanding Naturalist and Traveler Nikolai Alekseevich Zarudny*. IPK "University", Orenburg, pp. 298–302. [in Russian]

Orlova, V.F., Poyarkov, N.A., Chirikova, M.A., Nazarov, R.A., Munkhbaatar, M., Munkhbayar, K. & Terbish, K. (2017) MtDNA Differentiation and Taxonomy of Central Asian Racerunners of *Eremias multiocellata–E. przewalskii* species complex (Squamata, Lacertidae). *Zootaxa*, 4282 (1), 1–42.
https://doi.org/10.11646/zootaxa.4282.1.1

Orlova, V.F., Solovyeva, E.N., Dunayev, E.A. & Ananjeva, N.B. (2022) Integrative taxonomy within *Eremias multiocellata* complex (Sauria, Lacertidae) from the western part of range: evidence from historical DNA. *Genes*, 13, 941.
https://doi.org/10.3390/genes13060941

Popov, S.V., Antipov, M.P., Zastrozhnov, A.S., Kurina, E.E. & Pinchuk, T.N. (2010) Sea-level fluctuations on the northern shelf of the Eastern Paratethys in the Oligocene-Neogene. *Stratigraphy and Geological Correlation*, 18 (2), 200–224. https://doi.org/10.1134/s0869593810020073

Posada, D. & Crandall, K.A. (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818. https://doi.org/10.1093/bioinformatics/14.9.817

Poyarkov, N.A., Jr., Orlova, V.F. & Chirikova, M.A. (2014) The mitochondrial phylogeography and intraspecific taxonomy of the Steppe Racerunner, *Eremias arguta* (Pallas) (Lacertidae: Sauria, Reptilia), reflects biogeographic patterns in MiddleAsia. *Zootaxa*, 3895 (2), 208–224. https://doi.org/10.11646/zootaxa.3895.2.4

Rastegar-Pouyani, N. & Rastegar-Pouyani, E. (2001) A new species of *Eremias* (Sauria: Lacertidae) from Highlands of Kermanshah Province, Western Iran. *Asiatic Herpetological Research*, 9, 107–112. https://doi.org/10.5962/bhl.part.15563

Rastegar-Pouyani, N. & Rastegar-Pouyani, E. (2006) A new form of *Eremias* (Sauria: Lacertidae) from the Alvand Mountains, Hamedan Province, Western Iran. *Iranian Journal of Animal Biosystematics (UAB)*, 1 (1), 14–20.

Rastegar-Pouyani, E., Hosseinian, S., Rafiee, S., Kami, H.G., Rajabizadeh, M. & Wink, M. (2016) A new species of the genus *Eremias* Fitzinger, 1834 (Squamata: Lacertidae) from Central Iran, supported by mtDNA sequences and morphology. *Zootaxa*, 4132 (2), 207–220. https://doi.org/10.11646/zootaxa.4132.2.2

Ronquist, F.& Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Safaei-Mahroo, B., Ghaffari, H., Fahami, H., Broomad, S., Yazdanian, M., Najafi Majd, E., Hosseinian Yousefkhani, S., Rezzadeh, E., Hosseinzadeh, M., Nasrabadi, R., Rajabizadeh, M., Mashayekhi, M., Motesharei, A., Naderi, A. & Kazemi, S. (2015) The herpetofauna of Iran: Checklist of taxonomy, distribution and conservation Status. *Asian Herpetological Research*, 6 (4), 257–290. https://doi.org/10.16373/j.cnki.ahr.140062

Szczerbak, N.N. (1971) Taxonomy of the genus *Eremias* (Sauria, Reptilia) in connection with the focuses of the desert-steppe fauna development in Paleoarctic. *Vestnik Zoologii*, 2, 47–55. [in Russian]

Szczerbak, N.N. (1974) *Racerunners of the Palaearctic*. Naukova Dumka, Kiev, 293 pp. [in Russian]

Smith, A.M., Poyarkov, N.A. & Hebert, P.D.N. (2008) CO1 DNA barcoding amphibians: take the chance, meet the challenge. *Molecular Ecology Notes*, 8 (2), 235–246. https://doi.org/10.1111/j.1471-8286.2007.01964.x

Solovyeva, E.N., Dunayev, E.N., Nazarov, R.A., Radjabizadeh, M. & Poyarkov, Jr. N.A. (2018) Molecular and morphological differentiation of Secret Toad-headed agama, *Phrynocephalus mystaceus*, with the description of a new subspecies from Iran (Reptilia, Agamidae). *ZooKeys*, 748, 97–129. https://doi.org/10.3897/zookeys.748.20507

Strauch, A. (1863) Characteristik zweier neuen Eidechsen aus Persien. *Bulletin de l'Académie Impériale des Sciences de St. Pétersbourg*, 6, 477–480.

Strauch, A.A. (1876) Reptiles and amphibians. *In*: Przewalski, N.M. (Ed.), *Mongolia, the Tangut Country, and the Solitudes of Northern Tibet: Being a Narrative of Three-Years in Journey in Eastern High Asia. Vol. 2*. Russian Geographical Society, St. Petersburg, pp. 1–55. [in Russian]

Swofford, D. (2002) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods).* Sinauer Associates, Sunderland, Massachusetts. [program]

Tamar, K., Carranza, S., Sindaco, R., Moravec, J., Trape, J.F. & Meiri, S. (2016) Out of Africa: Phylogeny and biogeography of the widespread genus *Acanthodactylus* (Reptilia: Lacertidae). *Molecular Phylogenetics and Evolution*, 103, 6–18. https://doi.org/10.1016/j.ympev.2016.07.003

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739. https://doi.org/10.1093/molbev/msr121

Uetz, P., Freed, P., Aguilar, R. & Hošek, J. (Eds.) (2022) The Reptile Database, http://www.reptile-database.org (accessed 28 July 2022)

Wiegmann, A.F.A. (1834) *Herpetologia Mexicana, seu Descriptio Amphibiorum Novae Hispaniae. Saurorum Species [Pars Prima Ed.]*. Sumptibus C. G. Luderitz, Berlin, 54 pp., 10 pls. [reprint (1969) Society for the Study of Amphibian and Reptiles, Athens, Ohio, USA]

Witte, G.-F. de (1973) Description d'un Gekkonidae nouveau de l'Iran (Reptilia, Sauria). *Bulletin de l'Institut royal des sciences naturelles de Belgique*, 49 (1), 1–6

Zarudny, N.A. (1896) Itinéraire de l'expédition dans la Perse orientale en 1896. *Annuaire du Musée Zooloogique de l'Academie Impériale des Sciences de St. Petersburg*, I, XVIII–XXI. [in Russian]

Zarudny, N.A. (1897) Une note sur les reptiles écailleux et nus du nord-est de la Perse. *Annuaire du Musée Zoologique del'Academie Impériale des Sciences de St. Petersburg*, II, 349–361. [in Russian]

Zarudny, N.A. (1898) Itinéraire de l'expédition dans la Perse orientale en 1898. *Annuaire du Musée Zoologique de l'Academie*

Impériale des Sciences de St. Petersburg, III, V–XII. [in Russian]
Zarudny, N.A. (1902) Itinéraire de l'expédition de la Société Impériale Russe de Géographie dans la Perse orientale en 1900–1901. *Annuaire du Musée Zoologique de l'Academie Impériale des Sciences de St. Petersburg*, VII, I–IX. [in Russian]
Zarudny, N.A. (1903) About reptiles and fishes of East Persia. Herpetological and ichthyological results of the excursion in Eastern Persia in 1898. *Bulletin of the Imperial Russian Geographical Society, St. Petersburg*, 36 (3), 1–42. [in Russian]
Zarudny, N.A. (1904) Itinéraire de l'expédition dans la Perse occidentale en 1903–1904. *Annuaire du Musée Zoologique del'Academie Impériale des Sciences de St. Petersburg*, IX, I–VII. [in Russian]
Zhao, E. & Adler, K. (1993) *Herpetology of China*. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, 522 pp., 42 figs., 48 pls.