

## Phylogeny and geographic distribution of rock lizards (Lacertidae, Reptilia) in Alborz mountain range

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### Article info

#### Original Article

<https://doi.org/10.18500/1814-6090-2023-23-3-4-93-101>  
EDN: HIAFEC

Received July 31, 2023,  
revised September 4, 2023,  
accepted September 11, 2023,  
published December 25, 2023

**Abstract.** Rock lizards of the genus *Darevskia* have long been an important model object for study of reptile evolution. To understand the overall picture, it is important to know how bisexual and parthenogenetic species are distributed within this genus. The ranges of Caucasian species of rock lizards have been studied for a long time and in detail. However, recent attention to the species inhabiting the territory of Iran has been attracted after the description of several new species in 2013. As part of the continuation of these studies, we studied the distribution and genetic diversity of five species of lizards of the *Darevskia* genus along the Alborz mountain range in Iran: *D. chlorogaster*, *D. caspica*, *D. defilippii*, *D. schaekei* and *D. raddei*. In the course of this, we discovered new localities of *D. defilippii* that are outside their known range. We assessed the phylogenetic relationships between the studied species according to the ND4 – Leu tRNA region of mitochondrial DNA and found a relatively high level of genetic variability in *D. defilippii* and *D. chlorogaster*, while *D. raddei*, despite its wide distribution, has low variability. In general, the phylogenetic position of the studied species is somewhat different from that described by Ahmadzadeh et al. (2013).

**Keywords:** *Darevskia*, rock lizards, Alborz, Iran, Caspian herpetofauna

**Acknowledgements:** The research leading to these results received funding from the Russian National Foundation under Grant Agreement № 22-14-00227 and it was also carried out within the framework of topic AAAA-A16-116021660077-3.

**For citation:** Iryshkov E. S., Solovyeva E. N., Arakelyan M. S., Rastegar-Pouyani E., Moaddab M., Milto K. D., Galoyan E. A. Phylogeny and geographic distribution of rock lizards (Lacertidae, Reptilia) in Alborz mountain range. *Current Studies in Herpetology*, 2023, vol. 23, iss. 3–4, pp. 93–101. <https://doi.org/10.18500/1814-6090-2023-23-3-4-93-101>, EDN: HIAFEC

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## INTRODUCTION

Rock lizards of *Darevskia* genus comprise about 40 species including seven parthenogenetic species. Most of them are distributed on the Armenian Highland (Darevsky, 1967), however, some species occupy rocky areas spreading to Turkmenistan in the East, and Eastern Europe, Balkans and Turkey in the West. Only a few works on rock lizards were devoted to distribution and phylogeny of rock lizards in Iran that occupied Alborz and Kopet Dagh

mountain ranges (Ahmadzadeh et al., 2013; Rastegar-Pouyani et al., 2013; Yousefi et al., 2013). Separation of two new species from *D. chlorogaster* complex (*D. caspica*, *D. kamii*) and two species from *D. defilippii* complex (*D. kopetdaghica*, *D. schaekei*) in Alborz mountains by Ahmadzadeh et al. (2013) demonstrates that taxonomy and distribution of rock lizards from this rich region were not studied well enough. Thus, we set the aim to check the relevance of distribution areas and estimate phylogenetic

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position of rock lizard species inhabiting western and central Alborz mountains after nine years have passed since discovery of the new species.

Species ranges can change quite strongly and quickly within a short time for many reasons. Ranges of reptiles and amphibians may shrink or expand due to the direct anthropogenic influence, such as habitat modification (Doherty et al., 2020), noise (Simmons, Narins, 2018) and probably light pollution (Perry et al., 2008), and indirect influence, for example climate change (Erasmus et al., 2002; Peck et al., 2009). In this case, there are difficulties associated with preventing the extinction of species and climate change observation.

Alborz mountain range is one of the main centres of origin of rock lizards (Ahmadzadeh et al., 2013; Freitas et al., 2016). Due to the diversity of the landscape and, consequently, the variety of biotopes, geographic and ecological isolation is formed between species and populations within them. In this regard, the study of the genetic diversity and distribution of rock lizards on Alborz will expand the knowledge of the evolution of the *Darevskia* genus.

## MATERIAL AND METHODS

**Sampling and Mapping.** We collected the material along the western and central parts of Alborz mountain range along the southern coast of the Caspian Sea in Iran from the spring-summer period of 2022. During the expedition we carefully searched for lizards along the roads and four times crossed the mountain ridge from North to South and vice versa in different parts; we were also guided by the distribution map in the work of Ahmadzadeh et al. (2013). Visually detected lizards were captured by noose or by hand; dorsal and ventral pictures of each lizard were taken by telephone photo camera (iPhone 12 mini). Iryshkov, Arakelyan, Moaddab, Milto and Galoyan participated in the capture of lizards.

Tail tips of the lizards were fixed in 96% ethanol. Following species were included: 3 sp. belonging to *D. caspica*, 13 sp. to *D. chlorogaster*, 10 sp. to *D. defilippii*, 41 sp. to *D. raddei* and 4 sp. to *D. schaekeli*. Samples are stored in two instances: at the Hakim Sabzevari University and at the Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences.

We took GPS coordinates of each finding using GPS tracker (Garmin 64S, WGS 84) and put the point on the map. Also we added terrestrial ecoregions according to bioregions word map from onearth.org (2001). The basis of species distribution map was taken from Wikimedia Commons author NordNordWest, licensed under CC BY-SA 3.0; colours were changed, labels, points, ecoregions, scale bar and north arrow were added for the article.

When determining the distance between the capture points and the range boundary of *D. defilippii*, we calculated the distance between our point and the north-westernmost point presented in Ahmadzadeh et al. (2013) using Google maps. Then we rounded the distance up to integer values of kilometres. Using Google maps, we also obtained the approximate height of each GPS point presented in the supplementary material from Ahmadzadeh et al., 2013 and added altitudes measured by us (presented

in Table 1). We rounded the resulting height values up to tens.

### DNA Extraction, Amplification and Sequencing.

We isolated genomic DNA from the 96% ethanol-fixed tissue samples using the SDS (Sodium Dodecyl Sulfate) DNA extraction method (Kabir et al., 2006), and the quality of extracted DNA was measured using NanoDrop 1000. We chose the mitochondrial DNA fragment ND4 – Leu tRNA (907 bp) which includes fragment of the NADH dehydrogenase 4 and His, Ser and Leu tRNAs (Arevalo et al., 1994) due to its sufficient variability and the presence of a large number of reptile sequences in the GenBank.

For polymerase chain reaction (PCR) we used ND4 (forward) and Leu (reverse) primers and stuck to the amplification protocol described by Dutton et al. (1996). PCR products were sequenced by the Microsynth DNA company using the forward primer and the manufacture protocols.

**Phylogenetic Analysis.** The sequences were aligned in the program MEGA11 and adjusted manually. We used the sequences of *Podarcis muralis* [Laurenti, 1768] and *P. siculus* [Rafinesque-Schmaltz, 1810] (NC\_011607.1; NC\_011609.1) from the GenBank as an outgroup in alignment.

We used two types of datasets for phylogenetic analysis. First was a reduced dataset, including only our sequences and outgroups from GenBank, and second was a full dataset, including our sequences and sequences from the work of Ahmadzadeh et al. (2013) with outgroups from GenBank.

Phylogenetic trees were reconstructed under Bayesian criteria (BI) and using the maximum likelihood (ML) method. The optimal partitioning schemes and models for Bayesian Inference analysis were identified with PartitionFinder software (Lanfear et al., 2012) using greedy search algorithm under AIC criterion. Following schemes were identified: F81 for 1<sup>st</sup> position of ND4, GTR+G for 2<sup>d</sup> and 3<sup>d</sup> positions separately, and HKY+G for tRNAs (for reduced dataset); for the full dataset HKY+G for 1<sup>st</sup> position of ND4, GTR+G for 2<sup>d</sup>, HKY+I+G for 3<sup>d</sup> position and for tRNAs partition separately (for full dataset). BI was performed using MrBayes v3.2.6 (Ronquist, Huelsenbeck, 2003) with two simultaneous runs, each with four chains, for 5 million generations. We checked the convergence of the runs and that the effective sample sizes (ESS) were all above 200 by exploring the likelihood plots using TRACER v1.7.1 (Rambaut et al., 2018). The initial 10% of trees were discarded as burnin. Confidence in tree topology was assessed by posterior probability (PP) (Huelsenbeck, Ronquist, 2001). The ML trees were generated using IQ-tree software (Nguyen et al., 2015) with ultrafast bootstrap = 10,000 (UFBoot) (Minh et al., 2013), partitioning schemes and models were selected using ModelFinder software (Kalyanamoorthy et al., 2017). Following schemes were selected: F81+F for 1<sup>st</sup> position of ND4, TN+F for 2d, TN+F+G4 for 3d position and separately for tRNAs partition (for full dataset); F81+F for 1<sup>st</sup> position of ND4, TN+F+G4 for 2d, HKY+F+G4 for 3d position and separately for tRNAs partition (for full dataset).

For visualisation we used dendrograms according to the Bayesian method (BI) and also added the values obtained

## Phylogeny and geographic distribution of rock lizards

**Table 1.** Specimens used for phylogenetic analysis with localities and GenBank numbers of ND4 – Leu sequences obtained by us

Field ID	Species	Locality	Date	Latitude	Longitude	Altitude, m a.s.l.	GenBank Accession
IR41	<i>D. chlorogaster</i>	Halu Dasht, Gilan	26.06.2022	36.57161	50.03678	1800	OR340755
IR42							OR340756
IR44							OR340757
IR79							OR340788
IR45		Lashkaj, Gilan	25.06.2022	37.02103	49.55993	392	OR340758
IR46							OR340759
IR51				37.02097	49.55979	367	OR340765
IR47							OR340760
IR48							OR340761
IR49							OR340762
IR50		OR340764					
IR78		OR340787					
IR77		Titi Caravanserai, Gilan	24.06.2022	37.26928	49.45129	270	OR340786
IR7		<i>D. caspica</i>	Ab Pari waterfall, Mazandaran	28.06.2022	36.28430	51.54570	500
IR8	OR340789						
IR9	OR340790						
IR23	<i>D. schaekeli</i>	Darreh-ye Malek Dareh, Mazandaran	30.06.2022	36.51108	54.09629	2180	OR340736
IR24							OR340737
IR25							OR340738
IR62							OR340771
IR10							OR340724
IR11	OR340725						
IR71	<i>D. defilippii</i>	Halu Dasht, Gilan	26.06.2022	36.56853	50.04391	1897	OR340781
IR72							OR340782
IR73							OR340783
IR74							OR340784
IR69							OR340778
IR70							OR340780
IR37		Nilu, Gilan	26.06.2022	36.5486	50.14832	444	OR340780
IR1		Vandarbon, Mazandaran	27.06.2022	36.42739	51.03842	2238	OR340751
IR2							OR340723
IR3		<i>D. raddei</i>	Masouleh, Gilan	20.06.2023	37.09641	49.00282	819
IR13	OR340726						
IR14	OR340727						
IR16	OR340728						
IR17	OR340729						
IR18	OR340730						
IR19	OR340731						
IR20	OR340733						
IR21	OR340734						
IR22	OR340735						
IR39	OR340752						
IR40	OR340754						
IR76	OR340785						
IR35	37.12589				48.99281	1700	OR340749
IR36	37.08120				48.59701	171	OR340750
IR58							OR340766
IR61							OR340770
IR64							OR340773
IR65			OR340774				
IR66			OR340775				
IR67			OR340776				
IR68			OR340777				
IR26			OR340739				
IR27	Talesh, Gilan		23.06.2022	38.01864	48.40285	2436	OR340740
IR28							OR340741
IR29							OR340742
IR30	Keshli, Gilan		22.06.2022	38.02039	48.47516	580	OR340744
IR31							OR340745
IR32		OR340746					
IR33		OR340747					
IR34		OR340748					
IR60	Tarzuchu, Gilan	24.06.2022	37.32069	48.46161	1700	OR340769	
IR63	Subatan, Gilan	22.06.2022	38.01391	48.43095	1980	OR340772	
IR4	Shablu, Arbadil	23.06.2022	38.04001	48.33781	2260	OR340753	
IR5						OR340763	
IR6						OR340768	
IR59						OR340767	

by maximum likelihood (ML) analysis. The dendrograms were processed using FigTree v1.4.4 (tree.bio.ed.ac.uk/software/figtree/). We calculated the uncorrected inter- and intragroup pairwise distances (*p*-distances) in the MEGA11 program using 1000 bootstrap replicas.

### RESULTS AND DISCUSSION

The topologies of the phylogenetic tree of our sequences, obtained by the BI and ML methods, are consistent in all nodes, but somewhat different in the levels of support. Phylogenetic relationships between Chlorogaster (includes *D. chlorogaster* and *D. caspica*) and Defilippii (includes *D. defilippii* and *D. schaekei*) clades has temperate support – 0.94/79. *D. chlorogaster* and *D. caspica* are separated with high support, while the node between *D. defilippii* and *D. schaekei* has a high support only by BI (Fig. 1).

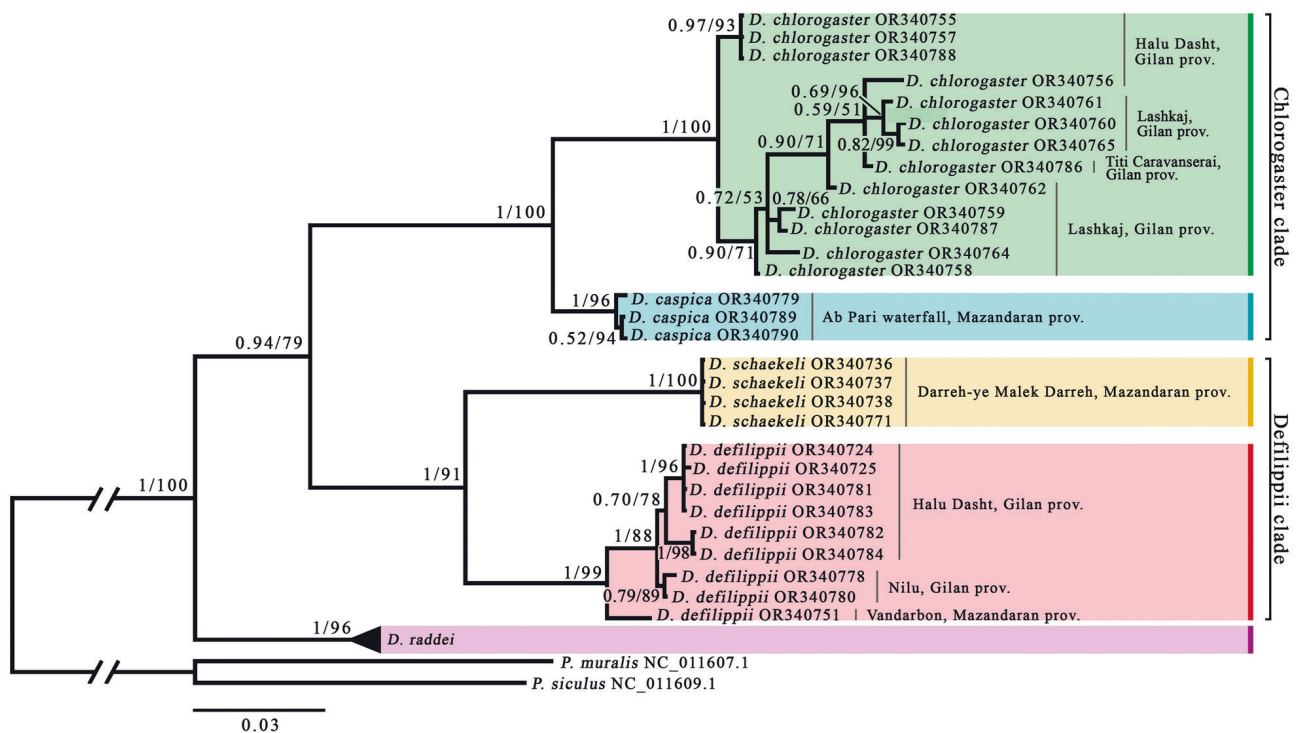
According to Figure 1 and Table 2 *D. chlorogaster* and *D. caspica* are genetically close, as they belong to the same clade and *p*-distance between them is 6.22%. *D. schaekei* and *D. defilippii* are also closely related, with *p*-distance of 9.02% since they belong to the same clade. Distances between species from different clades are much greater: 10.84% between *D. chlorogaster* and *D. defilippii*, 11.59% between *D. chlorogaster* and *D. schaekei*, 12.74% between *D. caspica* and *D. defilippii*, and 12.69% between *D. caspica* and *D. schaekei*. *D. raddei* belongs to the other clade – Raddei, it has a large distances to other species and occupies basal position on trees topology (Figs. 1, 2). Generally, *D. raddei* is a monophyletic group (1/98 support

in Fig. 1) with a low genetic variability (Table 2). It coincides with the results published in Freitas et al. (2016).

During visual sequence check we noticed a possible nuclear mitochondrial pseudogene (Bensasson et al., 2001) of ND4 – Leu tRNA fragment – the external parts of sequences were not completely read and a large number of double peaks on the electropherogram were observed (Chow et al., 2021). This was not noticed or reported in the closely related species *D. caspica* and other distant species.

Unresolved nodes (Fig. 1) in *D. caspica* and *D. schaekei* together with their low within-group *p*-distances indicate low genetic variability within these species (Table 2).

As shown in the dendrogram reconstructed from our sequences (Fig. 1), *D. defilippii* indeed has a fairly high genetic variability. This might be explained by the diverse habitats inhabited by *D. defilippii* (Ahmadzadeh et al., 2013). Phylogenetic relationships within *D. defilippii* reflect its geographical structure. Lineage consisting of specimens from Halu Dasht and Nilu villages from Gilan province diverged with the high level of support by BI, but with low support by ML – 1/88. Specimen from Vadarbon village, Mazandaran province (OR340751) separates furthest with high node support – 1/99. There is no connection between phylogenetic structure of *D. chlorogaster* and its geographic dispersal as in *D. defilippii*, although *D. chlorogaster* is also represented in several localities in Gilan province. However, genetic variability (based on uncorrected *p*-distances) within *D. chlorogaster* is two times stronger than in *D. defilippii* (2 and 1% respectively) (Table 2).



**Fig. 1.** Dendrogram showing phylogenetic relationships between rock lizards in different regions of Iran, based on the sequences of the ND4 – Leu tRNA fragment. Values over and under the nodes represent posterior probabilities by BI/bootstrap values by ML. The localities for each specimen are shown to the right of the vertical thin black line

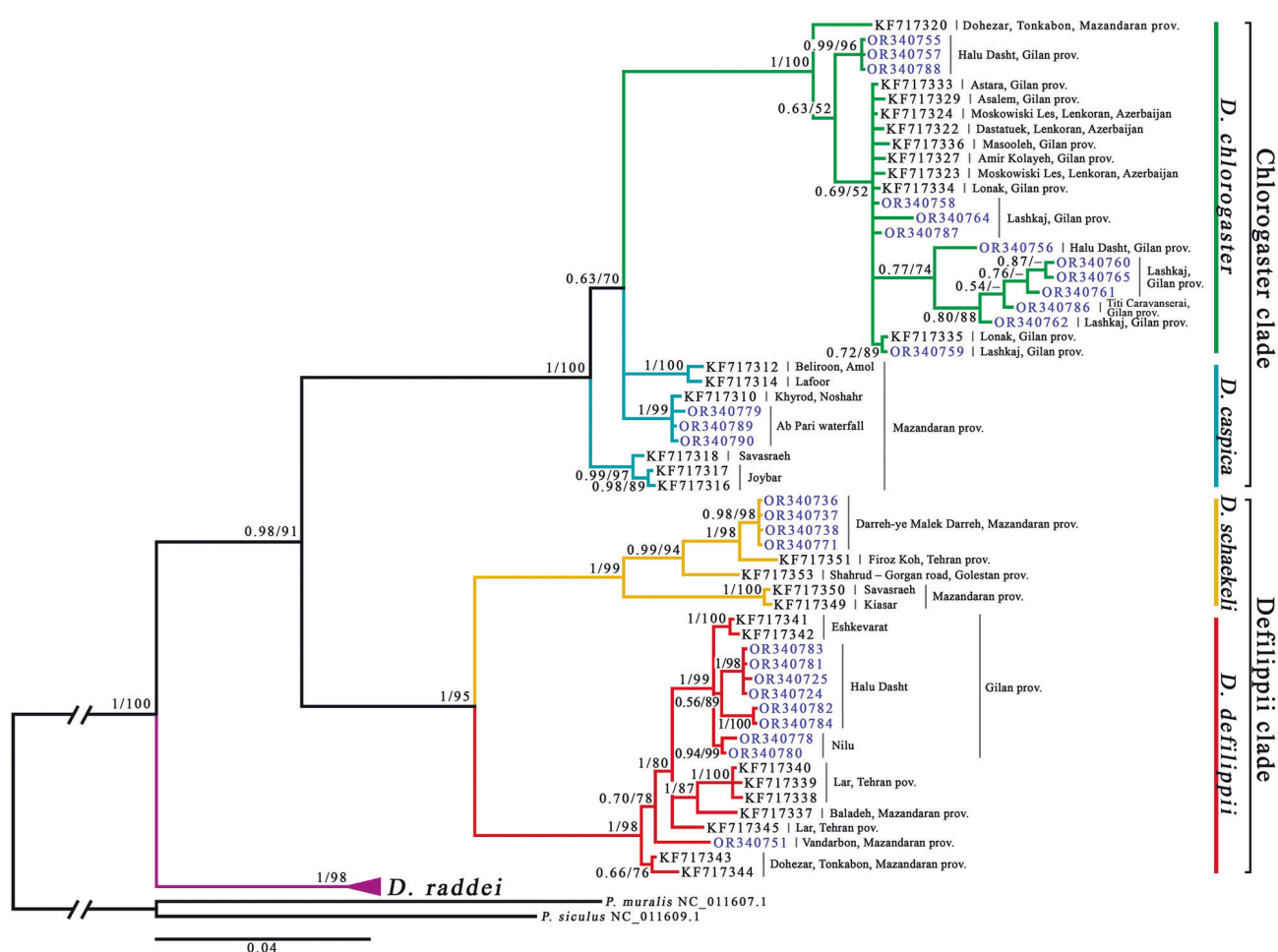
**Table 2.** Uncorrected *p*-distances (%) of reduced and full datasets of ND4 – Leu mRNA fragment: Intergroup distances are shown under the diagonal, intragroup distances – on the diagonal, standard errors – above the diagonal

Species	<i>D. chlorogaster</i>	<i>D. caspica</i>	<i>D. schaeckeli</i>	<i>D. defilippii</i>	<i>D. raddei</i>
<i>D. chlorogaster</i>	<b>2</b>	0.88	1.16	1.06	0.91
<i>D. caspica</i>	6.22	<b>0</b>	1.23	1.1	1.1
<i>D. schaeckeli</i>	11.59	12.69	<b>0</b>	0.98	1.16
<i>D. defilippii</i>	10.84	12.74	9.02	<b>1</b>	0.97
<i>D. raddei</i>	11.59	12.69	13.13	10.66	<b>0</b>

It contradicts the results obtained in Ahmadzadeh et al. (2013), where analysis of cytochrome b and ND4 genes concluded that the variability of this species is low. In this regard, it can be assumed that the genetic variability of *D. defilippii* is primarily exists due to geographic isolation in populations, while the causes of genetic diversity in *D. chlorogaster* are obscure.

With the addition of sequences from Ahmadzadeh et al. (2013) the topology of the tree changed (Fig. 2). Relationships between main clades and between *D. defilippii* and *D. schaeckeli* are resolved with a high support unlike the first tree, that contains only our sequences

(Fig. 1). *D. caspica* is not monophyletic, it splits into three separate clusters. One cluster has high support, while two others form a trichotomy with *D. chlorogaster* within a low-supported group (0.63/70). *D. schaeckeli* specimens with high levels of support are divided according to localities from different provinces. Localities from Mazandaran province are divided separately – with individuals caught by us in Darreh-ye Malek Darreh and individuals from GenBank from Savasraeh (KF717317) and Kiasar (KF717316) which are the most distant from the others. *D. defilippii* specimens form a clade with trichotomy divided by localities Eshkevarat, Halu Dasht, and Nilu villages



**Fig. 2.** Dendrogram showing phylogenetic relationships between rock lizards in different regions of Iran and some localities from Azerbaijan based on sequences of the ND4 – Leu tRNA fragment obtained by us and sequences of ND4 gene by Ahmadzadeh et al. (2013) from GenBank. Values over and under the nodes represent posterior probabilities by BI/bootstrapped values by ML. Branches coloured by species according to Figure 1. Blue coloured sequence numbers – received by us, black – by Ahmadzadeh et al. (2013). The localities for each specimen are shown to the right of the vertical thin black line

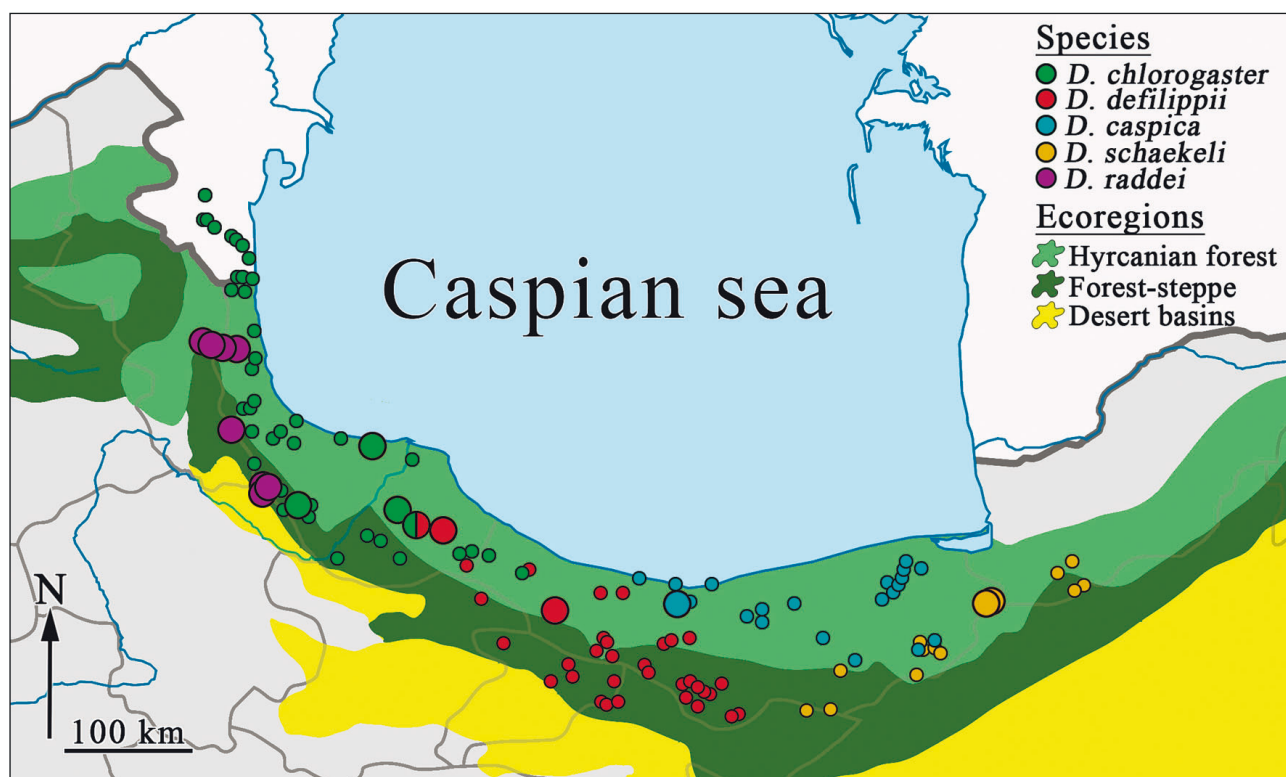
from Gilan province. Phylogenetic distribution of *D. defilippii* by localities has not been confirmed: nodes do not form distinct clusters and nodes supports are low. Phylogenetic relationships within *D. chlorogaster* still remain unclear: individual clusters by locality have not been formed, almost all nodes have low support, and many of them are unresolved. However, the most distant specimen within *D. chlorogaster* clade is from Dohezar, Mazandaran province (KF717320), and it is significantly divided from others.

We have also discovered two new locality records of *D. defilippii* beyond the distribution range (Ahmadzadeh et al., 2013). Records were taken 23 (OR340778 and OR340780 sequences) and 30 km (OR340724 and OR340725 sequences) northwest of previously documented locations. On the first point we caught individuals on a dry sandstone slope along an unpaved road surrounded by steppe and on the second point on a rocky slope with cracks along an asphalt road surrounded by mixed forest. In this regard, it can be concluded that either the range is initially wider, or it could expand towards the northwest during the last nine years.

The presented species also have different altitude distributions. *D. caspica* occupies Hyrcanian mixed forest (Fig. 3) at an altitude mainly between 130 and 580 metres a.s.l., but also there was a population from the altitude of about 1590 m in Savasraeh (KF717318 sequence). Although it separated from the specimens (KF717316, KF717317 sequences) from Joybar (altitude is about 400 m a.s.l.), it forms with these specimens one group with 0.99/97 support

(Fig. 2) which indicates the lack of strong isolation. *D. chlorogaster* has a range with a large elevation difference: from 10 to 1250 m a.s.l., and confined to Hyrcanian forest and forest-steppe ecozones. *D. raddei* also occupies a wide elevation range of 840–2040 m a.s.l. within forest and forest-steppe zones. *D. defilippii* lives in the high altitudes of 1290–2500 m a.s.l. in the forest-steppe. Moreover, an altitudinal distribution of this species is wider – some populations are known from the forested areas at 440 and 640 m a.s.l. *D. schaeckeli* is also a high altitudinal species and, according to our and already published data, distributed only at 1560–2300 m a.s.l. in forest-steppe ecozones.

The Hyrcanian forest consists of a large variety of woody plant species with high densities. The humidity level is high due to the large number of mountain streams flowing down the mountain slopes (Naqinezhad et al., 2008; Jafari et al., 2013), high precipitation (Heshmati, 2007) and mild climate due to low altitude (Beck et al., 2018). The forest-steppes are characterised by their mosaic vegetation: in some areas there are quite dense wet forest fragments and arid steppe spaces between them. Precipitation is generally low (Heshmati, 2007). Due to the high altitude, there is a high annual temperature range (Beck et al., 2018). Desert basins are characterised by sparse vegetation and low precipitation. Daily and annual temperature differences there are quite high (Breckle, 2002). In this regard, it can be concluded that the existing distribution of species can be explained not only by altitude, but also by preferred humidity level



**Fig. 3.** Distribution of studied species of rock lizards within Alborz mountain ridge in Iran. Small circles indicate localities of the species according to Ahmadzadeh et al. (2013). Big circles indicate the localities we discovered during the expedition. Each colour corresponds to the species of lizards and coincides with the colour from Figs. 1, 2. Coloured areas – terrestrial ecoregions according to Safaei-Mahroo et al. (2015) that showed only for Iran

and vegetation. Available data of distribution suggest that *D. chlorogaster* and *D. caspica* prefer wet habitats with dense vegetation, while *D. defilippii* and *D. schaeckeli* prefer dry, sparsely vegetated but more rocky biotopes. *D. raddei*, apparently, can occupy an intermediate position between the presented species, but at the moment there is not enough data for accurate conclusions.

It is important to note that the map presented in Safaei-Mahroo et al. (2015) was built using data of Olson et al. obtained in 2001. Therefore, the distribution of ecoregions at the moment of our data collection (2022) can be significantly different due to the desertification (Cherlet et al., 2018). In particular, the localities we found (Fig. 3) are located in the forest zone, but this zone, according to our observations, is a forest-steppe. For this reason, the range of *D. defilippii* could be shifted to the northwest.

Although studied species have some differences in their preferred biotopes, the borders between them are very fuzzy. Thus, further research should be aimed at clarifying the boundaries of the ranges of species and studying the reasons for such distribution.

## CONCLUSIONS

1. We confirmed that the species *D. defilippii* has a high genetic variability mediated by geographic isolation.
2. *D. chlorogaster* is one of the most genetically variable among studied species. This may be explained by the possible presence of a nuclear mitochondrial ND4 – Leu tRNA fragment pseudogene.
3. Despite the wide distribution range and diverse habitat preferences *D. raddei* has a low variability of the ND4 – Leu tRNA fragment of mDNA.
4. The range of the species *D. defilippii* is broader than previously suggested.
5. The distribution limits for considered species require clarification and presence of the secondary contact zones is very likely.

## Acknowledgments

We thank Andrey Stukalov and Irena Martirosyan for help in interpreting results of this work, Ali Moaddab for assistance in organising transportation to and within the study areas and Victor Spangenberg for participation in the collection and transportation of the material.

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## Филогенетика и географическое распространение скальных ящериц (*Lacertidae*, *Reptilia*) на горной системе Эльбурс

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### Информация о статье

Оригинальная статья

УДК 598.132.4:339.5

[https://doi.org/10.18500/1814-6090-2023-23-](https://doi.org/10.18500/1814-6090-2023-23-3-4-93-101)

3-4-93-101

EDN: HIAFEC

Поступила в редакцию 31.07.2023,  
после доработки 04.09.2023,  
принята 11.09.2023  
опубликована 25.12.2023

**Аннотация.** Скальные ящерицы из рода *Darevskia* давно стали модельным объектом для изучения эволюции рептилий. Для понимания направлений и механизмов эволюции в этой группе важно знать, каким образом распространены обоеполые и партеногенетические виды в рамках данного рода. Ареалы кавказских видов скальных ящериц изучены давно и подробно, однако внимание к видам, обитающим на территории Ирана, было привлечено относительно недавно после описания нескольких новых в 2013 г. В рамках продолжения этих исследований была проведена работа по изучению распространения и генетического разнообразия пяти видов ящериц рода *Darevskia* вдоль горного хребта Эльбурс в Иране: *D. chlogogaster*, *D. caspica*, *D. defilippii*, *D. schaekeli* и *D. raddei*. В ходе этой работы были обнаружены новые места обитания *D. defilippii*, находящиеся за пределами известного для них ареала. Были оценены филогенетические отношения между изучаемыми видами по участку ND4 – тРНК Leu митохондриальной ДНК и обнаружен сравнительно высокий уровень генетической изменчивости у видов *D. defilippii* и *D. chlogogaster*, в то время как *D. raddei*, несмотря на широкое распространение, обладает низкой изменчивостью. В целом филогенетическое положение изученных видов несколько отличается от того, что было описано в работе Ahmadzadeh et al. (2013).

**Ключевые слова:** *Darevskia*, скальные ящерицы, Эльбурс, Иран, Каспийская герпетофауна

**Финансирование:** Исследование выполнено при финансовой поддержке Российского научного фонда (проект № 22-14-00227) и Государственного задания Института проблем экологии и эволюции им. А. Н. Северцова РАН (№ АААА-А16-116021660077-3).

**Образец для цитирования:** Iryshkov E. S., Solovyeva E. N., Arakelyan M. S., Rastegar-Pouyani E., Moaddab M., Milto K. D., Galoyan E. A. Phylogeny and geographic distribution of rock lizards (*Lacertidae*, *Reptilia*) in Alborz mountain range. *Current Studies in Herpetology*, 2023, vol. 23, iss. 3–4, pp. 93–101. <https://doi.org/10.18500/1814-6090-2023-23-3-4-93-101>, EDN: HIAFEC [Ирышков Е. С., Соловьёва Е. Н., Аракелян М. С., Растегар-Пуяни Е., Моаддаб М., Мильто К. Д., Галоян Э. А. 2023. Филогенетика и географическое распространение скальных ящериц (*Lacertidae*, *Reptilia*) на горной системе Эльбурс]. Современная герпетология. Т. 23, вып. 3/4. С. 93 – 101. <https://doi.org/10.18500/1814-6090-2023-23-3-4-93-101>, EDN: HIAFEC

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