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Genetic Variation and Phylogeography of *Lacerta strigata* Eichwald, 1831 (Lacertidae, Sauria)

I. V. Doronin[a, *], **M. A. Doronina**[a], **K. Yu. Lotiev**[b, c], **S. A. Lukonina**[d], **L. F. Mazanaeva**[e], **and K. D. Milto**[a]

[a] *Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia*
[b] *Sochi National Park, Sochi, 354000 Russia*
[c] *Kislovodskii National Park, Kislovodsk, 357700 Russia*
[d] *Penza State University, Penza, 440026 Russia*
[e] *Dagestan State University, Makhachkala, 367025 Russia*
**e-mail: igor.doronin@zin.ru*

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Abstract—76 sequences of the *cytb* gene region of mitochondrial DNA (1143 bp) and 27 sequences of i7 β-*fib* nuclear DNA (483 bp) of *Lacerta strigata* from 57 localities in Abkhazia, Azerbaijan, Armenia, Georgia, Iran, and Russia were analyzed. A large number of new samples were included in analysis with special focus to the species' range at the Caucasus Isthmus. An identical topology and four supported clades (lineages) resulted for both mtDNA and sequences combined with nucleDNA (Bayesian and Maximum Likelihood). Four haplogroups (clusters) have been identified in the median *cytb* haplotype network. The lizards of clade A (haplogroup I) are widespread throughout the species range, while lizards of clade D (haplogroup IV) show the most limited distrubytion. No genetically unique populations of *L. strigata* were detected in the Caucasian xerophilous refugia. Also, no genetically distinct populations of the species were recorded in the Hyrcanian refugium (Southern Caspian region). An exception is the East Hyrcanian refugium, that is characterized by the most distant clade D (IV). The territory of Ciscaucasia and the Transcaucasian depression are occupied by a single clade each: A (I) and B (II), respectively. We detected several clades distributed in the four geographic areas (contact zones): in the Greater Caucasus, Alborz, Armenian Highland, and West Turkmenian Lowland. We associate the divergence of the *L. strigata* phylogenetic lineage with the Turkmen-Khorasan and, in particular, the Kopet Dag orogeny, as well as with the Late Miocene fluctuations in the level of the Eastern Paratethys, while the leading factor of intraspecific differentiation is the Pleistocene regressions and transgressions of the Caspian Sea. According to the current distribution pattern and species evolutionary history, *L. strigata* should be assigned to the Hyrcano-Caucasian zoogeographic group.

Keywords: green lizards, Caspian Sea, Caucasus, Kopet Dagh

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INTRODUCTION

The Caspian green lizard, *Lacerta strigata* Eichwald, 1831, is the only species of the genus *Lacerta* Linnaeus, 1758, which lives throughout the southern and western Caspian region and practically does not occur beyond the Caucasus ecoregion and Alborz (Darevskij, 1984; Tuniyev et al., 2009). It is confinred to areas with grassy, steppe, mountain-steppe, and semi-desert vegetation and settles in thickets along the banks of watercourses, near swamps and unflooded meadows, and on the edges of steppe forests, penetrating along river valleys into the mid-mountain areas up to an altitude of 2500 m above sea level (Bannikov et al., 1977). Starting from the first half of the 20th century, its phylogenetic position has repeatedly become a subject of discussion. For example, Cyrén (1924) placed "*Lacerta viridis* var. *strigata*" among the most basal taxa in the "*Lacerta agilis-viridis-ocellata-Gruppe*". The study of the chromosome sets of lacertid lizards showed that *L. strigata* has interpopulation chromosomal differences and, in addition, a pair of small submetacentric chromosomes, which distinguishes its karyotype from the karyotype typical of green lizards (Orlova and Orlov, 1969; Darevskij, 1984). Comparison of external morphological traits of green lizards made it possible to identify a number of plesiomorphic features in *L. strigata* (Schmidtler, 1986). Hybridization experiments demonstrated the greatest reproductive isolation of *L. strigata* from other species of the genus (Rykena, 1996). Roytberg (1994) believed that the absence of intraspecific morphological differentiation in *L. strigata* may indicate its later divergence (or, at least, dispersal) compared to the extremely variable sand lizard (*L. agilis* Linnaeus 1758), which forms many subspecies and morphotypes. According to another version of this author, the lower degree of phenetic differentiation of *L. strigata*, which is manifested both at the micro- and macrogeographic levels, may indicate the influence on its evolution of not only historical processes, but also factors associated with the canalization of morphogenesis (according to Schmalhausen, 1968).

Original hypotheses about the phylogeny of *L. strigata* and the formation of its range in terms of the genesis of the herpetofauna of the Caspian region were proposed. Cyrén (1924) believed that the center of its speciation was on the Iranian Plateau, from where it penetrated into the central part of the Alborz foothills and then distributed along this mountain range to the east and west; in his opinion, the prochoresis in the Caucasus proceeded from the western Caspian region. Leister (1930) believed that "*L. viridis strigata*", on the contrary, arose in Europe, and the territory of Iran was colonized by this species at the final stages of the formation of its range. Darevsky (1959) outlined a possible route of penetration of this species into the Sevan Basin in Armenia from the south from Araks, and Muskhelishvili (1966) assumed that it penetrated into Georgia from the south and southeast from the territory of Armenia, excluding its penetration from the southwest. Later, Darevsky (1977) suggested that the records of *L. strigata* in the south of Turkmenistan could be explained by recent colonization, probably from the Caucasus, where, in his opinion, the evolutionary radiation of green lizards occurred (Darevsky, 1990). Shcherbak (1994) was of the same opinion. Tertyshnikov and Vysotin (1986) believed that the colonization of the sandy massifs of the Terek-Kuma Lowland in the Ciscaucasia by the sand lizard and *L. strigata* occurred in the periods of climate humidification in the Holocene during the transformation of the desert into steppe, along the valleys of the Kuma (from the Stavropol Upland), Terek, and the North Caucasian Kura (from the foothills of the Greater Caucasus). Lotiev and Tuniyev (2017) suggested the formation of the modern range of the species in the Holocene and the dispersal of *L. strigata* to Eastern Transcaucasia through the Kura Depression.

The use of genetic methods made it possible to clarify the phylogenetic position of the species. On the basis of analysis of a mitochondrial *cytb* gene fragment of green lizards, Kalyabina-Hauf and Ananjeva (2004) concluded that *L. strigata* was the first to diverge from a common ancestor. Godinho et al. (2005), based on the analysis of a fragment of the 12*S* and 16*S* rRNA genes, suggested that *L. strigata* is a sister species to *L. agilis*, and based on the analysis of the *cytb* gene, it is sister to all studied species of the genus. Ahmadzadeh et al. (2013a), using a set of markers similar to the set used in the previous work, showed that this species is sister to *L. viridis* and *L. bilineata*. According to the data of Kornilios et al. (2019) on *cytb*, *L. strigata* diverged at the first stage of species radiation of the genus of green lizards approximately 11.1 (9.1–13.7) million years ago.

Saberi-Pirooz et al. (2021) published a special work on the phylogeny of *L. strigata* (*cytb*, 12*S*, *C*-mos, and β-*fib*) and on the effect of climatic fluctuations in Pleistocene on the genetic diversity of this species. According to their data, samples from the eastern part of the range formed a separate regional "eastern" clade, and other individuals from the central and western parts of the range formed the "western" clade, which divided into two poorly isolated subclades (a and b). According to their calculations, *L. strigata* was the first to diverge from the common ancestor of green lizards 10.6 (8.20–12.93) million years ago. The age of intraspecific divergence is estimated at 1.1 (0.57–1.58) million years. It should be noted that verification of the hypotheses and constructions proposed above is complicated by the complete absence of finds of the species in the paleontological record.

In the cited publications of the last two decades, the main material for research was collected in the territory of Iran, whereas the phylogeography and phylogenetic relationships of the populations of the Caucasian Isthmus remain poorly studied. It should be noted that the Caucasus ecoregion (including parts of northern Iran and northeastern Turkey) contains the major part of the distribution area and record points of *L. strigata*: according to our cadastre, more than 95% of the species records were made here. The presence of herpetofauna refugia in this area (*L. strigata* occurs in five of them) (Tuniyev, 1995; Tuniyev et al., 2019) may indicate the possibility of discovering genetically unique populations. Of particular interest in this regard are the isolated enclave on the Black Sea coast in Abkhazia (the distance between it and the nearest known record points of *L. strigata* in Transcaucasia is approximately 200 km) (Rudik, 1986; Doronin et al., 2018) and the populations of the Terek-Kuma Lowland. In the Caucasus, finding a refugium indicating ancient colonization of the region or confirming a relatively recent dispersal of this species can be expected.

Previously, based on the results of studies of external morphology, it was proposed to consider the groups of populations of *L. strigata* of the Caucasian Isthmus and Alborz as independent subspecies (Cyrén, 1924, 1933; Darevskij, 1984; Schmidtler, 1986), which also requires verification.

In a significant part of its range, *L. strigata* is one of the most common reptile species, with a population density of tens and even hundreds of individuals per hectare (Bannikov et al., 1977; our data). However, on the periphery of its distribution area, its population size significantly decreases. For this reason, in a number of regions, the species received a protected status or its inclusion in the list of protected taxa was proposed. This applies to the territory of Kalmykia (Zhdokova, 2013), Krasnodar Krai (Ostrovskikh, 2017), and Turkmenistan (Shestopal and Rustamov, 2018). Isolated Abkhazian populations also should be added to this list. The obtained data on genetic diver-

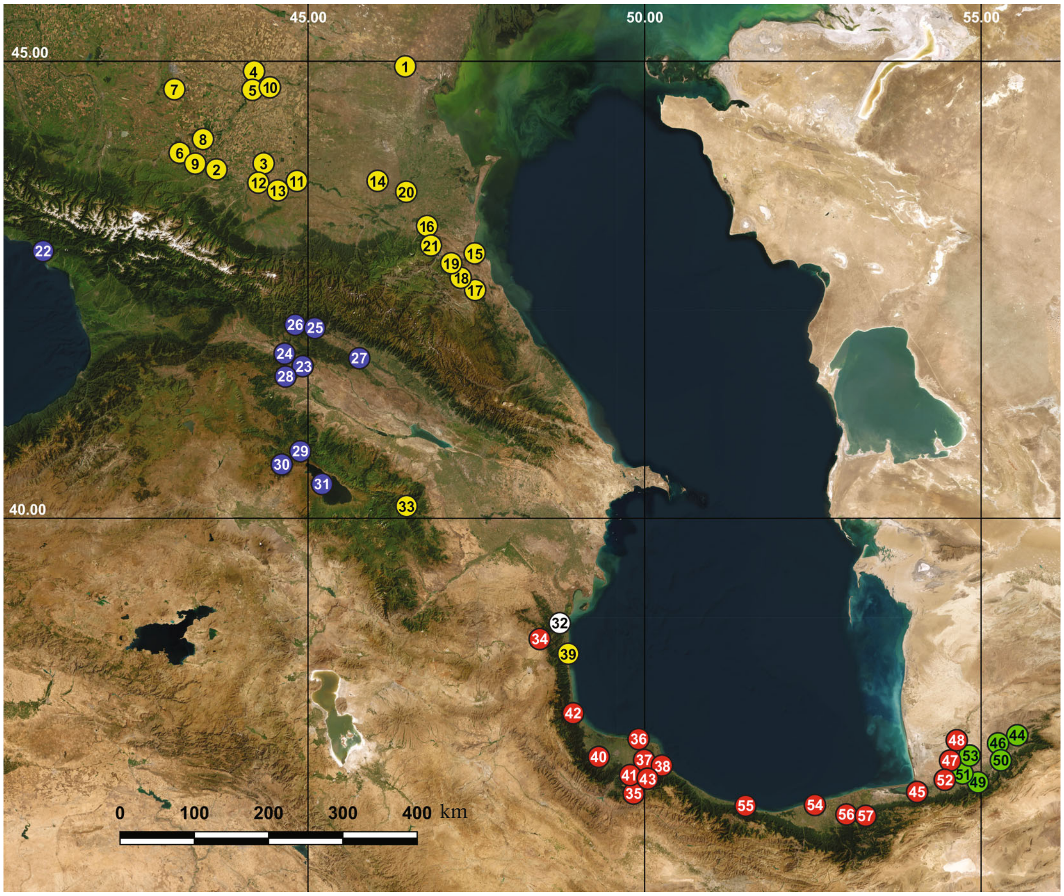

Fig. 1. Collection points of *Lacerta strigata* specimens used for molecular genetic analysis. Mitochondrial clades: A—yellow, B—blue, C—red, D—green. The locality (no. 32) from which only the β-*fib* sequence is available is shown in white. The numbering and letter designations correspond to those in Table 1.

sity will make it possible to assess their uniqueness and will help to develop conservation measures.

The aim of this work was to perform a genetic analysis of *L. strigata* specimens from the areas that were not previously covered by sampling points and to compare new data with the results of previous studies and the hypotheses on the history of the species' range formation. Since some of the *L. strigata* samples originate from the zone of sympatry with *L. agilis*, the possibility of hybridization of these species in natural conditions was also studied.

MATERIALS AND METHODS

Genomic DNA was isolated from parts of regenerated tails or phalanges of the forelimb digits of lizards, whcih were fixed in 96% ethanol. Thirty-nine voucher specimens and tissue fragments are stored in the collection of the Herpetology Laboratory of the Zoological Institute of the Russian Academy of Sciences (ZISP and ZISP TS). A total of 76 sequences of the mitochondrial cytochrome *b* gene (*cytb*, 1143 bp) and 27 sequences of the nuclear gene region of intron 7 of beta-fibrinogen (β-*fib*, 483 bp) from 57 localities (Table 1, Fig. 1) were included in the phylogenetic analysis. Of these, 48 sequences were obtained during the studies, and 55 seqeuces were taken from GenBank (http://www.ncbi.nlm.nih.gov/gene/). As noted above, these genetic markers have previously been used in studies of the phylogeny and phylogeography of the species.

Total DNA was isolated using the standard salt method with proteinase K lysis (Aljanabi and Martinez, 1997). The *cytb* gene was amplified using the primer pair GluDG 5'-GCC CCA AAA TAA GGA GAT GG-3' and ThR 5-TAG TGA TGG GGG ATT AAA GC-3' was used (Marzahn et al., 2016; Kukushkin et al., 2020) under the following conditions: initial denaturation at 95°C for 3 min, then 32 cycles (at 95°C for 30 s, at 56°C for 30 s, and at 72°C for 90 s), and final elongation at 72°C for 5 min.

The β-*fib* region was amplified using the primer pair FIB-BI7U 5'-GGA GAA AAC AGG ACA ATG ACA ATT CAC-3' and FIB-BI7L 5'-TCC CCA GTA GTA TCT GCC ATT AGG GTT-3' (Prychitko and Moore, 1997) under the following conditions: initial

Table 1. Collection specimens and tissue samples of *Lacerta strigata* used in molecular genetic analysis

Locality numberin Fig. 1	Localities	Collection numbers	Numbers in GenBank		*cytb* clades	*cytb* haplotype numbers	Collection dates	Collectors	Sources of information	Geographic coordinates	Elevation ASL, m
			cytb	β-*fib*							
1	2	3	4	5	6	7	8	9	10	11	12
1	Russia, Kalmykia, Chernozemelsky district, Okhotnich’e natural landmark	ZISP TS 3028	OQ914981	–	A	Hap 1	22.05.2021	R.A. Gorelov	This publication	46.4442, 44.9392	–20
2	Russia, Stavropol Krai, Kirovsky district, Staropavlovskaya Village	ZISP 29867	OQ914982	–	A	Hap 1	14.05.2018	I.V. Doronin, M.A. Doronina	″	43.6398, 43.8458	330
		ZISP 29868	OQ914983	–		Hap 1					
		ZISP 29869	OQ914984	OQ915466		Hap 1					
		ZISP TS 2980	OQ914985	–		Hap 17	27.06.2020	M.A. Doronina			
		ZISP TS 2932	OQ914986	–		Hap 1	24.06.2020				
		ZISP TS 2933	OQ914987	–		Hap 1					
3	Russia, Stavropol Krai, Kursky district, Baltiisky Village vicinities, near the pond	ZISP 30275	OQ914988	–	A	Hap 7	13.08.2018	I.V. Doronin	″	44.3407, 43.8862	190
		ZISP 30276	OQ914989	–		Hap 1					
4	Russia, Stavropol Krai, Budennovsky district, shore of Buivola Lake	ZISP TS 2912	OQ914990	OQ915467	A	Hap 1	30.05.2017	″	″	44.1986, 44.7935	90
5	Russia, Stavropol Krai, Budyonnovsky district, Orlovka Village	–	MW592674	–	A	Hap 1	–	–	Saberi-Pirooz et al., 2021	44.1746, 44.6915	110

Table 1. (Contd.)

Locality numberin Fig. 1	Localities	Collection numbers	Numbers in GenBank		*cytb* clades	*cytb* haplotype numbers	Collection dates	Collectors	Sources of information	Geographic coordinates	Elevation ASL, m
			cytb	β-*fib*							
1	2	3	4	5	6	7	8	9	10	11	12
6	Russia, Stavropol Krai, Pyatigorsk, Goryachevodsky urban settlement	–	MW592673	MW591732	A	Hap 1	–	–	″	43.0921, 44.0235	500
7	Russia, Stavropol Krai, Aleksandrovsky district, Aleksandrovskoe Village	ZISP 31115	OQ914991	–	A	Hap 1	11.08.2020	I.V. Doronin	This publication	43.0149, 44.6985	350
8	Russia, Stavropol Krai, Georgievsk district, Georgievsk	ZISP TS 2910	OQ914992	OQ915468	A	Hap 9	29.05.2019	″	″	43.4401, 44.1701	330
9	Russia, Stavropol Krai, Kirovsky district, north-east of Zolskaya Village, Zolka riverbed	ZISP 31093	OQ914993	–	A	Hap 8	31.07.2020	I.V. Doronin, M.A. Doronina	″	43.3246, 43.9080	505
10	Russia, Stavropol Krai, Budyonnovsky district, Praskoveya Village	ZISP TS 2929	OQ914994	–	A	Hap 1	14.07.2020	K.Yu. Lotiev, K.D. Milto	″	44.2004, 44.7184	160
11	Russia, Stavropol Krai, Kursky district, Stoderevskaya Village	ZISP TS 2921	OQ914995	–	A	Hap 10	02.07.2020	″	″	44.8356, 43.7215	120
		ZISP TS 2922	OQ914996	–		Hap 1					
12	Russia, North Ossetia–Alania, Mozdok district, Novoossetinskaya Village	ZISP TS 2923	OQ914997	–	A	Hap 11	03.07.2020	″	″	44.3951, 43.7034	150

Table 1. (Contd.)

Locality numberin Fig. 1	Localities	Collection numbers	Numbers in GenBank		*cytb* clades	*cytb* haplotype numbers	Collection dates	Collectors	Sources of information	Geographic coordinates	Elevation ASL, m
			cytb	β-*fib*							
1	2	3	4	5	6	7	8	9	10	11	12
13	Russia, North Ossetia–Alania, Mozdok district, Malgobek Village vicinities	ZISP TS 2924	OQ914998	–	A	Hap 12	04.07.2020	″	″	44.4510, 43.6198	210
14	Russia, Chechnya, Shelkovskoy district, Kissyk natural landmark	ZISP 24667	OQ914999	OQ915469	A	Hap 3	29.06–01.07.2008	K.Yu. Lotiev	″	46.0339, 43.7224	40
15	Russia, Dagestan, Makhachkala, Tarki Village vicinities, slope of Tarki-Tau Mount	ZISP 30280	OQ915000	–	A	Hap 1	10.09.2018	L.F. Mazanaeva	″	47.4769, 42.9396	400
		ZISP 30283	OQ915001	–		Hap 18					
16	Russia, Dagestan, Kizilyurtovsky district, Novoye Gadari Village vicinities	ZISP 22036	OQ915002	OQ915470	A	Hap 1	22.04.2001	Z.S. Ismailova	″	46.7688, 43.1880	130
17	Russia, Dagestan, Karabudakhkent district, Chonkatau Ridge	ZISP TS 2981	OQ915003	–	A	Hap 1	17.07.2020	L.F. Mazanaeva	″	47.4498, 42.5393	910
18	Russia, Dagestan, Buinaksky district, Bouglen Settlement	ZISP TS 2988	OQ915005	–	A	Hap 13	14.07.2020	″	″	47.2025, 42.7468	530
19	Russia, Dagestan, Buinaksky district, Bouglen Settlement vicinities	ZISP TS 2984	OQ915004	–	A	Hap 13	14.07.2020	″	″	47.1946, 42.7587	580

Table 1. (Contd.)

Locality numberin Fig. 1	Localities	Collection numbers	Numbers in GenBank		*cytb* clades	*cytb* haplotype numbers	Collection dates	Collectors	Sources of information	Geographic coordinates	Elevation ASL, m
			cytb	β-*fib*							
1	2	3	4	5	6	7	8	9	10	11	12
20	Russia, Dagestan, Babayurt district, kutan Urgul (= Urgulay, Urgalai) Tsumadinsky district	ZISP TS 2985	OQ915006	–	A	Hap 16	19–22.06.2020	″	″	46.4590, 43.6058	0
		ZISP TS 2986	OQ915007	–		Hap 14					
		ZISP TS 2987	OQ915008	–		Hap 1					
21	Russia, Dagestan, Kazbekovsky district, Dubki Settlement	ZISP TS 2990	OQ915009	–	A	Hap 1	14.07.2020	″	″	46.8265, 43.0249	860
22	Abkhazia, Sukhum (= Sukhumi), Kelasuri River mouth	ZISP 23570	OQ915010	–	B	Hap 2	19.04.2006	K.D. Milto, M.V. Pestov	″	41.0644, 42.9718	0
23	Georgia, Tbilisi	–	LN835024	–	B	Hap 4		C. Kehlmaier	Marzahn et al., 2016	44.7867, 41.7087	720
24	Georgia, Mtskheta-Mtianeti, Mtskheta	ZISP 28770	OQ915011	OQ915471	B	Hap 4	06.05.2014	I.V. Doronin	This publication	44.7187, 41.8468	480
25	Georgia, Mtskheta-Mtianeti, Tianeti Urban Settlement	ZISP 29872	OQ915012	OQ915472	B	Hap 5	18–19.05.2018	I.V. Doronin, M.A. Doronina	″	44.9756, 42.1165	1110
		ZISP 29873	OQ915013	OQ915473							
		ZISP 29874	–	OQ915474	–	–					
		ZISP 29875	–	OQ915475	–	–					
26	Georgia, Mtskheta–Mtianeti, Tianeti urban settlement vicinities	ZISP 29876	OQ915014	–	B	Hap 6				44.9683, 42.1298	1190
		ZISP 29877	OQ915015	–		Hap 15					
27	Georgia, Kakheti, Akhasheni Settlement vicinities	–	MH974536	–	B	Hap 30	–	–	Saberi-Pirooz et al., 2021	45.7616, 41.7972	370

Table 1. (Contd.)

Locality numberin Fig. 1	Localities	Collection numbers	Numbers in GenBank		*cytb* clades	*cytb* haplotype numbers	Collection dates	Collectors	Sources of information	Geographic coordinates	Elevation ASL, m
			cytb	β-*fib*							
1	2	3	4	5	6	7	8	9	10	11	12
28	Georgia, Kvemo Kartli, Asureti Settlement	–	MH974535	MW591723	B	Hap 29	–	–	″	44.6654, 41.5940	760
29	Armenia, Tavush region, Dilijan	–	MH974527	–	B	Hap 24	–	–	″	44.8863, 40.7587	1200
30	Armenia, Kotayk region, Gorgoch Village vicinities	–	MH974530	–	B	Hap 36	–	–	″	44.6089, 40.6094	1870
31	Armenia, Gegharkunik region, Noratus (= Noratus, Noratuz) Village vicinities	–	MW592672	–	B	Hap 4	–	–	″	45.2092, 40.3881	1920
32	Azerbaijan, Lenkoran district, Istisu (= Isti-su, Kirovsk) urban-type settlement	ZISP 22085	–	OQ915476	–	–	2001	S.N. Litvinchuk	This publication	48.7406, 38.7961	0
33	Azerbaijan, Kelbajar region, Getavan Village		MH974520	MW591731	A	Hap 21	–	–	Saberi-Pirooz et al., 2021	46.4645, 40.1309	810
34	Iran, Ardabil, Talysh Range, Fethmeksud Village vicinities	–	MH974524	MW591724	C	Hap 23	–	–	″	48.4428, 38.6124	2330
		–	MH974525								
35	Iran, Gilan, Diarjan Village vicinities	ZISP TS 3036	OQ915016	OQ915477	C	Hap 20	25.06.2022	K.D. Milto	This publication	50.0120, 36.8799	1388
36	Iran, Gilan, Bujag National Park	–	MH974521	MW591727	C	Hap 22	–	–	Saberi-Pirooz et al., 2021	49.9115, 37.4421	–20
37	Iran, Gilan, Shirin Nisa (= Shir Nesa, Shirnesa) Village vicinities	–	MH974522	–	C	Hap 20	–	–	″	50.0607, 37.1422	90

Table 1. (Contd.)

Locality numberin Fig. 1	Localities	Collection numbers	Numbers in GenBank		*cytb* clades	*cytb* haplotype numbers	Collection dates	Collectors	Sources of information	Geographic coordinates	Elevation ASL, m
			cytb	β-*fib*							
1	2	3	4	5	6	7	8	9	10	11	12
38	Iran, Gilan, Khalifeh Mahalla Village vicinities	–	MH974523	–	C	Hap 20	–	–	″	50.2256, 37.1294	–10
39	Iran, Gilan, Astara	–	MH974533	MW591725	A	Hap 28	–	–	″	48.8666, 38.4333	–20
		–	MW592675	–		Hap 21					
40	Iran, Gilan, Fumen (= Fuman, Fauman)	–	MH974537	–	C	Hap 20	–	–	″	49.3183, 37.2313	30
41	Iran, Gilan, Lonek Waterfall vicinities	–	MH974539	–	C	Hap 19	–	–	″	49.8513, 37.0160	970
42	Iran, Gilan, Balade (= Bala Dekh) Village vicinities	–	MW592676	–	C	Hap 33	–	–	″	48.9396, 37.7459	20
		–	MW592677	–		Hap 34	–	–			
43	Iran, Gilan, 5 km N from Omam Village	–	MW592678	–	C	Hap 20	–	–	″	50.0749, 36.9375	1860
		–	MW592679	–			–	–			
44	Iran, Golestan, env. Tamer-e Kara Kuzi (= Tamer, Temir) Village	–	MH974531	MW591736	D	Hap 27	–	–	″	55.5043, 37.4868	110
		–	MW592690	MW591737		Hap 32	–	–			
45	Iran, Golestan, Karasu Village vicinities	–	MH974532	MW591729	C	Hap 22	–	–	″	54.0498, 36.8162	–30
46	Iran, Golestan, Atalar Village vicinities, reservoir on the Gorgan River	–	MH974538	MW591735	D	Hap 31	–	–	″	55.3195, 37.3652	60
47	Iran, Golestan, Anbar Olum (= Anbarol, Embarol) vicinities	–	MW592686	MW591726	C	Hap 22	–	–	″	54.6066, 37.1350	0
48	Iran, Golestan, Ullugol (= Almagol) Lake shore	–	MW592680	–	C	Hap 25	–	–	″	54.6387, 37.4281	10

Table 1. (Contd.)

Locality numberin Fig. 1	Localities	Collection numbers	Numbers in GenBank		*cytb* clades	*cytb* haplotype numbers	Collection dates	Collectors	Sources of information	Geographic coordinates	Elevation ASL, m
			cytb	β-*fib*							
1	2	3	4	5	6	7	8	9	10	11	12
49	Iran, Golestan, Kushkorpi Village vicinities	–	MW592681	–	D	Hap 31	–	–	″	54.8547, 36.9839	60
		–	MW592683	–			–	–			
50	Iran, Golestan, Pashmak Panade Village vicinities	–	MW592682	–	D	Hap 31	–	–	″	55.2612, 37.2177	60
51	Iran, Golestan, road between Uchtepe (= Ush-Tepe) Village and Khivali (= Kheyvali) Village	–	MW592684	MW591733	D	Hap 31	–	–	″	54.6909, 37.0620	10
		–	MW592685	–							
52	Iran, Golestan, Sakar Yelki Village vicinities	–	MW592687	–	C	Hap 26	–	–	″	54.5277, 37.0136	–10
53	Iran, Golestan, Yolme Salian Village vicinities, Voshemger reservoir	–	MW592688	MW591734	D	Hap 35	–	–	″	54.7287, 37.1949	10
		–	MW592689	–		Hap 31	–	–			
54	Iran, Mazandaran, Feridunkenaar vicinities	–	MH974526	–	C	Hap 22	–	–	″	52.5314, 36.6612	–20
55	Iran, Mazandaran, Noushehr	–	MH974528	MW591730	C	Hap 26	–	–	″	51.5009, 36.6516	20
56	Iran, Mazandaran, Semeskande Reserve vicinities	–	MH974529	MW591728	C	Hap 22	–	–	″	53.1322, 36.5477	60
57	Iran, Mazandaran, Zarrinabade Sofla Village	–	MH974534	–	C	Hap 22	–	–	″	53.1864, 36.5314	160

Table 2. Genetic diversity indices in the studied sample of *Lacerta strigata* according to the analysis of gene fragment sequences *cytb* (1143 bp)

Clades	n	S/η	h	π	K	Tajima's D	Fu's Fs
A	34	16/16	0.62 ± 0.10	0.002 ± 0.0004	1.32	−2.20 ($p < 0.01$)	−3.11 ($p < 0.05$)
B	12	8/8	0.77 ± 0.13	0.002 ± 0.0005	1.61	−1.57 ($p > 0.1$)	−1.49 ($p > 0.1$)
C	20	11/11	0.83 ± 0.06	0.002 ± 0.0005	2.13	−1.11 ($p > 0.1$)	−1.20 ($p > 0.1$)
D	10	3/3	0.38 ± 0.18	0.001 ± 0.0004	0.6	−1.56 ($0.1 > p > 0.05$)	−1.78 ($p > 0.1$)
Total	76	49/49	0.90 ± 0.02	0.01 ± 0.001	7.83	−0.71 ($p > 0.1$)	−2.04 ($0.1 > p > 0.05$)

n—Sample size, S—total number of polymorphic positions, η—total number of substitutions, h—haplotype diversity, π—nucleotide diversity per site, K—mean number of nucleotide substitutions, Tajima's D—Tajima's test value, Fu's Fs—Fu's neutrality test value.

denaturation at 95°C for 3 min, then 30 cycles (at 95°C for 30 s, at 60°C for 30 s, and at 72°C for 50 s), and final elongation at 72°C for 5 min.

The PCR reaction mixture (25 μL) contained 50–100 ng of DNA, 0.5 μM of each primer, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 2.5 μL of 10× PCR buffer (10 mM Tris-HCl (pH 8.3) and 50 mM KCl), and 2 units of Taq polymerase (Thermo Scientific). Sequencing was performed in an ABI PRIZM 3500xL genetic analyzer (Applied Biosystems).

Sequence alignment was performed using Geneious Prime 2021.0.1 (https://www.geneious.com) and AliView 1.6 software (Larsson, 2014). Phylogenetic relationships were reconstructed using the Bayesian analysis (BA) in Mr. Bayes 3.1.2 software (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003; Altekar et al., 2004) and the maximum likelihood (ML) method in the MEGA X software package (Kumar et al., 2018). For the combined mtDNA and nDNA sequence dataset, the ML method was used in RAxML software (Stamatakis 2016) via CIPRES Science Gateway V. 3.3 (http://www.phylo.org/sub_sections/portal/) (Miller et al., 2010). We used the RAxML-HPC BlackBox tool with 10000 bootstrap iterations followed by ML search using the General-Time-Reversible (GTR) algorithm and gamma-distributed substitution rates (GTR+G) for each section independently. For BA, 5 million generations were used; the statistical significance of ML tree nodes was assessed by bootstrap analysis (1500 pseudo-replicates). The robustness of dendogram nodes in case of Bayesian analysis was assessed by calculating posterior probabilities. The node support level of 0.95 is high, 0.90–0.95 is average, and less than 0.90 is unsupported. Bootstrap support values in ML analysis are as follows: more than 75% is significant, 50–75% is a trend, and less than 50% is unsupported (Felsenstein, 2004).

The model of evolution for nucleotide sequences was selected in the MrModeltest 2.4 software (Nylander, 2004) using the Akaike information criterion (AIC): GTR + G for *cytb* and GTR+G for β-*fib*.

Graphic images of trees were obtained using the FigTree 1.4.4 software (http://tree.bio.ed.ac.uk/software/figtree). The haplotype network was constructed using the TCS method in the PopART software (Leigh and Bryant, 2015). When analyzing genetic variability using the DnaSP v.5.10.01 software (Librado and Rozas, 2009), the following parameters were calculated: the total number of polymorphic positions (S), the total number of substitutions (η), the number of haplotypes (H), the diversity of haplotypes (h), the diversity of nucleotides per site (π), the average number of nucleotide substitutions (K), the Tajima test value (Tajima's D), and the Fu neutrality test (Fu's Fs). Genetic distances (p-distances) were calculated in the MEGA X software.

To identify taxonomic boundaries by molecular genetic features, the ASAP (Automated simultaneous analysis phylogenetics) (Sarkar et al., 2008) and ABGD (Automatic barcode gap discovery) (Puillandre et al., 2012) algorithms were used. They allow designating conditional molecular operational taxonomic units (MOTUs), which are monophyletic clades of uncertain rank. The analysis was performed using the following parameters: Pmin (minimum a priori distance) = 0.01, Pmax (maximum a priori distance) = 0.1, and X (relative interval width) = 0.5; a matrix of pairwise K80 distances was used.

RESULTS

All new sequences were deposited in GenBank (NCBI) under accession numbers OQ914981–OQ915016 and OQ915467–OQ915477.

The 76 *cytb* gene sequences form 36 haplotypes. A total of 49 (4.3% of the total fragment length) variable positions were identified, 29 (2.5%) of which are wereparsimony-informative. The ratio of transitions to transversions was 6.96. The indices of genetic diversity in the sample are given in Table 2.

The 27 β-*fib* gene sequences of *L. strigata* form seven haplotypes. Seven (1% of the total fragment length) variable positions were revealed, 5 (0.71%) of which were parsimony-informative. The ratio of transitions to transversions was 1.37. The indices of genetic diversity in the sample were as follows: $S = 7$, $\eta = 9$, $h = 0.42$ (± 0.08), $\pi = 0.002$ (± 0.001), $K = 0.917$, Tajima's $D = -1.48$ ($p > 0.1$), Fu's $Fs = -1.33$ ($p > 0.1$).

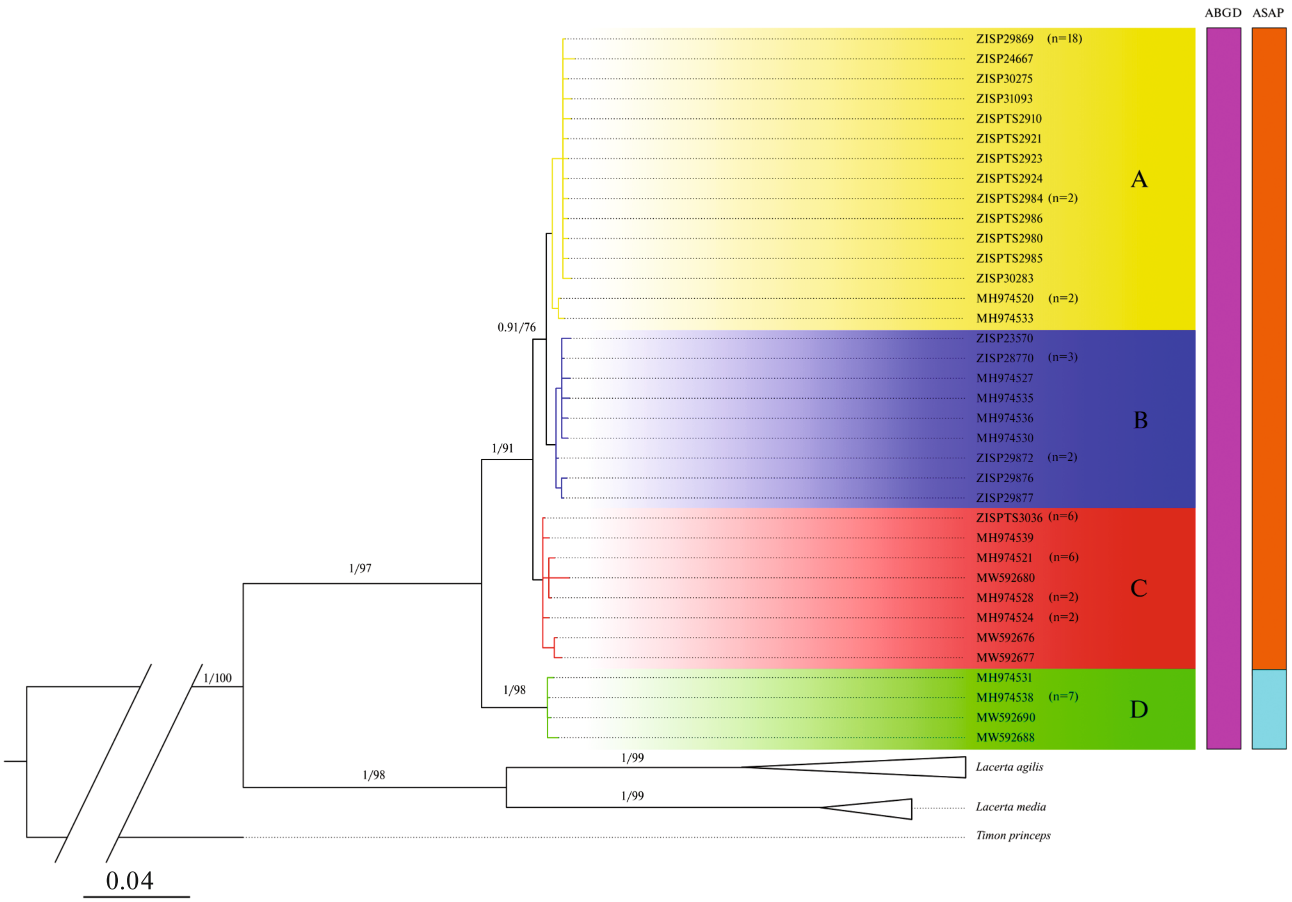

Fig. 2. Dendrogram of phylogenetic relationships of *Lacerta strigata* representatives based on the analysis of the *cytb* gene (1143 bp). Bayesian posterior probabilities and bootstrap supports (BA/BS) are indicated at the nodes. Letter designations of clades correspond to those in Tables 1 and 2. The selected molecular operational taxonomic units (MOTUs) are indicated in different colors in two columns.

The results of the reconstruction of the phylogenetic relationships of representatives of this species (*cytb* and *cytb* + β-*fib*) were used to construct dendrograms with identical topology, on which four supported clades can be distinguished (Figs. 2, 3). The minimum value of uncorrected genetic distances (*p*-distance) was found between clades A and B (0.53%); the maximum value, between clades A and D (2.95%) (Table 3). As mentioned above, two clades with two subclades were previously known for *L. strigata* (Saberi-Pirooz et al., 2021). If we apply the hierarchical approach used by these authors[1], then in our case we will also obtain a division into two clades, one of which is formed by three subclades.

Table 3. Mean genetic *p*-distances (%) (below the diagonal) and their standard deviations (above the diagonal) between clades of *Lacerta strigata* based on *cytb* (1143 bp) gene fragment sequence analysis

Clades	A	B	C	D
A		0.22	0.30	0.60
B	0.53		0.26	0.58
C	0.84	0.72		0.53
D	2.95	2.80	2.33	

Four haplogroups (clusters) can be identified on the obtained median network of *cytb* haplotypes (Fig. 4). Haplogroup IV is the most distant from all the others: it is located 23 nucleotide substitutions away from I, 24 from haplotype II, and 16 from haplotype III. Unlike the network for *cytb*, the differences between β-*fib* haplotypes are represented mainly by single-mutation transitions, and the predicted haplotypes are practically absent (Fig. 5). The network showed the conserved nature of this marker due to its relatively low variability.

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[1] At present, there is no single approach to describing phylogenetic trees. For example, the terms “clade” and “subclade” (the term “lineage” should be added to this list) denote a monophyletic group of organisms containing a common ancestor and all its direct descendants, i.e., the same entire “clade” (Cracraft and Donoghue, 2004).

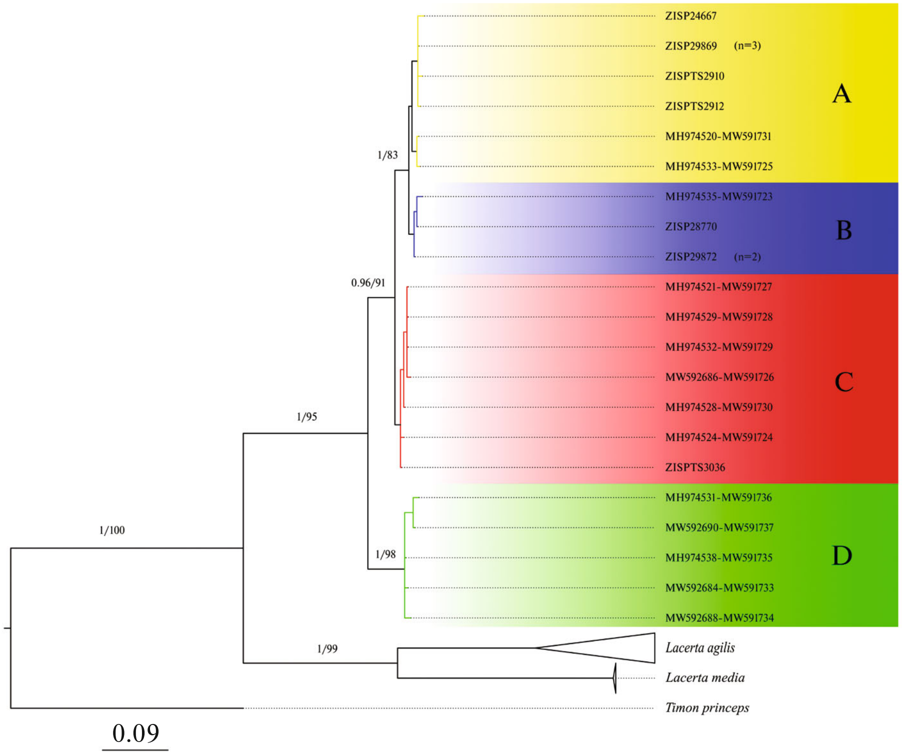

Fig. 3. Dendrogram of phylogenetic relationships of *Lacerta strigata* representatives based on *cytb* + β-*fib* analysis (1626 bp). Bayesian posterior probabilities and bootstrap supports (BA/BS) are indicated at nodes. Letter designations of clades correspond to those in Tables 1 and 2.

Relatively high *h* values and low π values in *L. strigata* are characteristic of populations with rapid population growth from an initially small number of founders in case when the elapsed time is sufficient for the restoration of haplotypic variability through the mutation process but insufficient for accumlation of significant differences between nucleotide sequences (Abramson, 2007). Low values of other indices of genetic diversity (S, η, and K) may also indicate a possible recent dispersal of *L. strigata*. The minimum indices of haplotypic and nucleotide diversity were found in clade D. Negative values of Tajima's D and Fu's Fs neutrality tests (although they are not statistically significant) may also indicate expansive population growth in the past and/or positive selection (Fu, 1997; Grant, 2015).

In our study of the variability of the mitochondrial gene fragment of the first subunit of cytochrome oxidase (COI) for *L. strigata*, the lowest genetic diversity indices among green lizards of the Caucasus and adjacent territories were also obtained (Doronina et al., 2023).

The ASAP/ABGD analysis showed a clear gap between the values of population variability (treshold distance = 1.40%, barcoding gap = 3.40%). The use of these algorithms allowed us to identify two and one monophyletic MOTU, respectively, in *L. strigata* volume (Fig. 2). In the first case, clade D was delimited.

In seven studied syntopic and sympatric populations of *L. agilis* and *L. strigata* (Abkhazia: Sukhum; Russia: Aleksandrovskoe, Zolskaya, Makhachkala, Pyatigorsk, Staropavlovskaya; Georgia: Tianeti), genetic characters of interspecific hybridization (borrowing mtDNA and heterozygosity for nDNA) were not detected. This confirms the conclusions of Roytberg (1982), made on the basis of studying external morphology, about the absence of crossing of this pair of species in nature.

DISCUSSION

On the basis of the analysis of phylogenetic dendrograms and the median network of *cytb* haplotypes, in which clade D or group IV of haplotypes occupies a basal position, it can be assumed that the isolation of the species is associated with the area in the southeastern Caspian region adjacent to Kopet Dag or with the Turkmen-Khorasan Mountains in a broader sense. The beginning of the formation of these mountains is attributed to the Late Miocene (9.75–7.65 million years ago), to the era of the Alpine orogeny (Sborshchikov et al., 1981). At this time, the divergence of the *L. strigata* phylogenetic lineage also occurred (Kornilios et al., 2019; Saberi-Pirooz et al., 2021). This dating is also consistent with the early divergence of a number of other reptile groups in West and Central Asia and

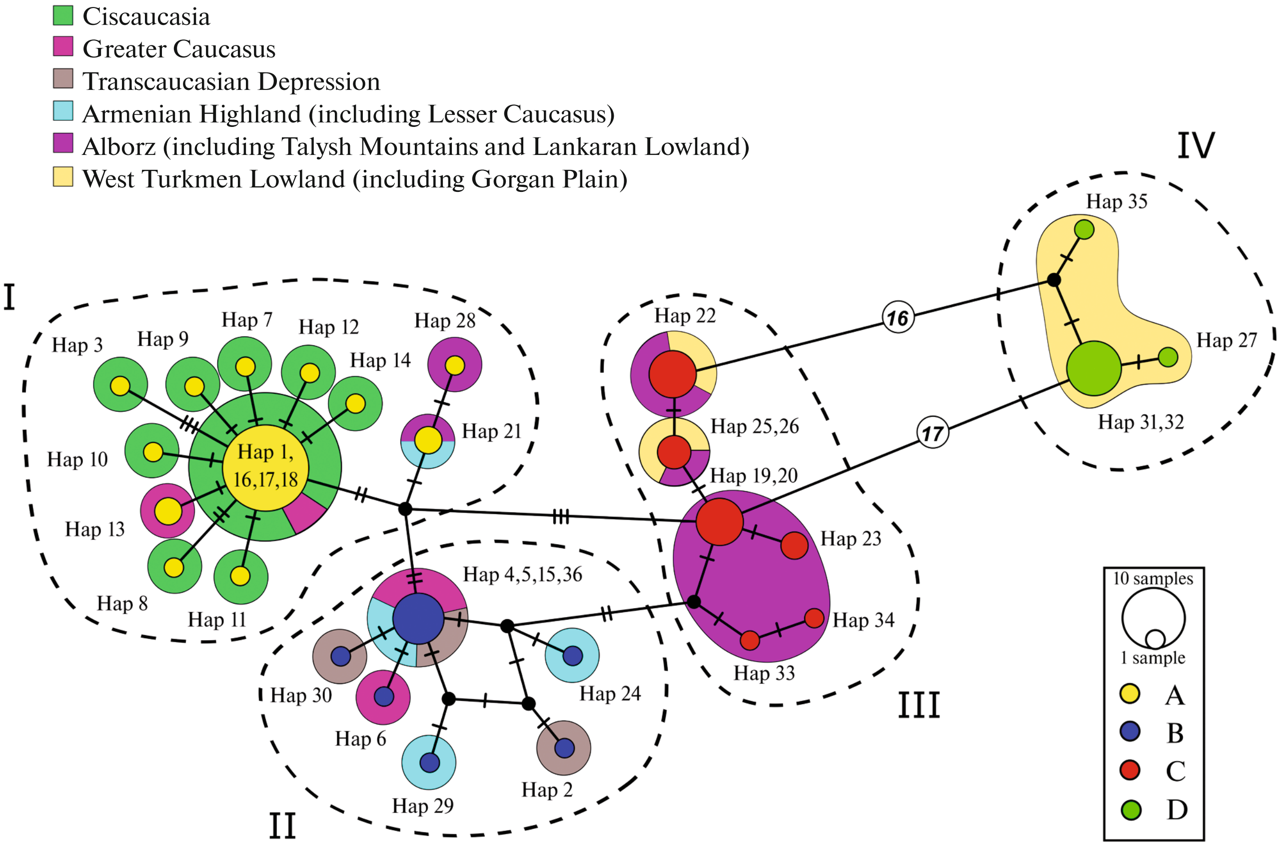

Fig. 4. Median network of *cytb* haplotypes of *Lacerta strigata* representatives (1143 bp). Each colored circle is a unique haplotype; the size of the icon is proportional to its occurrence in the sample, its color corresponds to the color of the clade in Figs. 1 and 2. Connecting lines are probable evolutionary relationships, notches are nucleotide substitutions, black circles at the nodes of the lines are predicted haplotypes. Geographic regions are indicated by colored fill. Haplotype groups are delimited by a dotted line. Roman numerals are numbers of haplotype groups.

suggests parallelism in the evolution of regional biota determined by environmental changes (Guo et al., 2004; Jablonski et al., 2023).

Along with orogeny, large-scale and frequent fluctuations in the level of the Eastern Paratethys in the Late Miocene, which also covered the territories of the modern southeastern Caspian region (Palcu et al., 2021), could also cause the isolation of the species. This territory of the species formation did not experience complete flooding by the waters of the Akchagyl and Apsheron transgressive basins (Popov et al., 2004, 2006; Svitoch, 2015, 2016), and mountain glaciation in the Pleistocene in the Kopet Dag Mountains, according to available data, did not develop (Dumitraşko, 1982) and was small-scale in the subsequent period (Selivanov, 1984). Probably, this allowed the most genetically isolated clade of the species to survive. It is known that Kopet Dag is characterized by pronounced endemism of reptiles (Darevsky, 1981; Shcherbak, 1994). Using the phylogeny and phylogeography of rock lizards of the genus *Darevskia* Arribas, 1999 (Ahmadzadeh et al., 2013) and the Caucasian pit viper, *Gloydius caucasicus* (Nikolsky, 1916) (Asadi et al., 2019) as an example, the importance of the eastern part of Alborz and Kopet Dag as a center of speciation and refugium was shown. Apparently, from this territory, *L. strigata* penetrated into the Caucasus along the Alborz mountain range (clade C/haplogroup III) in the Pleistocene, which was shown earlier (Saberi-Pirooz et al., 2021). This contradicts the hypothesis of the Caucasian origin of the species, i.e., its distribution from west to east.

In our opinion, one of the key factors of intraspecific differentiation of *L. strigata*, along with climatic fluctuations (Saberi-Pirooz et al., 2021), was the changes in the Caspian basin (i.e. the presence/absence of geographic barriers), in particular, the Turkic regression. Its onset (0.78 million years ago, Early Neopleistocene) (Yanina, 2012) chronologically coincides with the divergence of clades according to molecular clock data (Saberi-Pirooz et al., 2021). Before this, during the existence of the Akchagyl basin, the dispersal of the species could have been hindered by the flooding of the modern territory of the Southern and Western Caspian region (Popov et al., 2006; Van Baak et al., 2019).

Clades A and B, judging by the haplotype network, originated from clade C. Most likely, their divergence began on the southwestern coast of the Caspian Sea. Two of the haplotypes found in this region (Hap 19 and 20) are likely ancestors for them. This assumption is supported both by modeling of the species distribution area during the Last Glacial Maximum (approximately 21 thousand years ago) (Saberi-Pirooz et al., 2021) and by its altitudinal preferences (Doronina et al., 2022a).

It can be assumed that, simultanelusly with the colonization of the Armenian Highlands, the Transcaucasian Depression, and the southern macroslope of the Greater Caucasus (B/II), the species penetrated into the Ciscaucasia and the northern slope of the Greater Caucasus (A/I) through the Eastern Caucasus. The last migration route has been repeatedly shown for a number of taxa and individual evolutionary lineages of reptiles (Mazanaeva and Orlova, 2009; Mazanaeva and Tuniyev, 2011; Jablonski et al., 2023). The expansion of *L. strigata*'s range in the North Caucasus could have been facilitated by the aridization of the early Holocene climate (about 11.7–7.8 thousand years ago), when an extensive invasion of xerophytes from the North-Eastern Caucasus took place (Taisumov et al., 2018). The fast pace of this process is indicated by the presence of a distinct star-shaped cluster of the haplotype network consisting of samples from the Ciscaucasia and the northern macroslope of the Greater Caucasus. Probably, the source of colonization in this case were the xerophilic refugia of Dagestan (the first has been preserved on the Caspian coast of the foothills of Dagestan, and the second includes semiarid mid-mountain basins between the Bokovoi and Skalistyi Ranges, some of which are located in Dagestan (Gunib and Botlikh). At present, *L. strigata* inhabits both refugia, and the haplotypes distributed in the North-Eastern Caucasus (Hap 1, 16-18) form the core of the star-shaped cluster of the haplotype network.

We associate the appearance of *L. strigata* on the Black Sea coast (B/II) with the xerothermic period of the Holocene (about 4.5–2.5 thousand years ago), when, according to Tuniyev et al. (2019), in dry and warm climate conditions, the ranges of Mediterranean species of flora and fauna within the Black Sea refugium expanded. During this period, *L. strigata* could have colonized the spurs of the southern macroslope of the Greater Caucasus up to the area of modern Sukhum, from where it reached Cape Pitsunda along the coast. Further cooling and increased precipitation (Vekua et al., 1991) should have led to the extinction of populations of this xerophilic and thermophilic species in Western Transcaucasia, with the exception of the Abkhazian enclave.

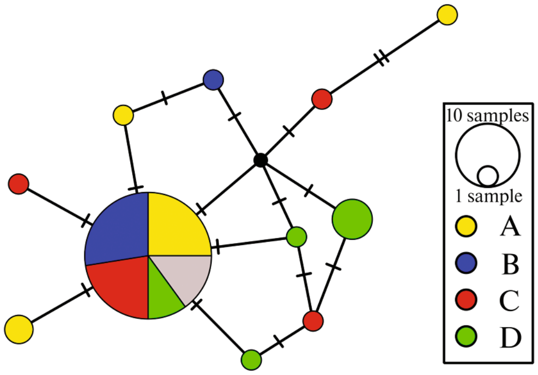

Fig. 5. Median network of β-*fib* haplotypes of *Lacerta strigata* representatives (483 bp). Each colored circle is a unique haplotype; the size of the symbol is proportional to its occurrence in the sample, its color corresponds to the color of the clade in Figs. 1 and 2. Connecting lines are probable evolutionary relationships, notches are nucleotide substitutions, black circles at the nodes of the lines are predicted haplotypes.

The representatives of clade A (haplogroup I) found in the Ciscaucasia, in the northeast of the Greater Caucasus, in the east of the Armenian Highlands, and the northwestern tip of Alborz were most widespread in the range (Figs. 1, 4). This clade is characterized by minimal values of the Tajima test and the Fu neutrality test (Table 2). A separate subgroup on the network within haplogroup I was formed by Hap 21 and 28 (Astara, Iran). In general, we observe a poorly expressed internal structuring of Caucasian populations, where almost all groups, one way or another, are related by hypothetical haplotypes. The smallest area is occupied by clade D (IV), localized within one physical-geographical section.

Comparison of the geographic and haplotype distribution (Figs. 1, 4) revealed the following zones of cohabitation of representatives of different clades/haplogroups (contact zones): the Greater Caucasus (A/I on its northern macroslope and B/II on the southern macroslope), the northeastern part of the Armenian Highland (A/I and B/II), the northwestern part of Alborz (A/I and C/III), and the West Turkmen Lowland (C/III and D/IV). The presence of one clade/haplogroup has been currently found only within the Ciscaucasia and the Transcaucasian Depression (A/I and B/II, respectively). It is noteworthy that earlier we discovered the presence of two clades/haplogroups for another species of green lizards, *Lacerta media* Lantz et Cyrén, 1920, in the Armenian Highland (Doronina et al., 2022).

In the future, individuals from the territories not covered by the sampling points (including those from the "transit zones" between the areas of distribution of evolutionary lineages) should be included in the analysis. This will allow us to detail the history of the range formation. The northern boundary of distribution C/III and the eastern boundary B/II cannot currently be established due to the poor study of the territory of

Azerbaijan, where, presumably, representatives of A/I were most widespread.

Apparently, the question of the origin of the *L. strigata* population that presumably inhabited the vicinities of Krasnovodsk (the shores of the Krasnovodsk or Balkhan Bay in Turkmenistan), from where the species was described by Eichwald, remains open. The only record was made in 1823, after which *L. strigata* has never been found here again (Doronin et al., 2017). It can be assumed that the colonization of the eastern coast of the Caspian Sea proceeded either along the foothills of the Kopet Dag and Greater Balkhan or along the sea coast. Archaeological evidence of greater moisture on the eastern coast of the Caspian Sea testifies to possible habitation of *L. strigata* in this part of Turkmenistan in the historical past (Lisitsyna, 1973; Kes et al., 1980). Taking into account the fact that *L. strigata* is often found in anthropogenic landscapes (in particular, along drainage canals, on the banks of reservoirs, in gardens, etc.), the existence here of a branched network of canals in the Middle Ages could have contributed to the dispersal of this species in the south of Turkmenistan in the conditions of a subtropical arid climate. It should be noted that the second record of the species in Turkmenistan after Eichwald was made in a cultivated area, in a pomegranate grove in the Akyayla Village in the Atrek River valley on the border with Iran (Bogdanov, 1956). The time of the appearance of *L. strigata* on the Absheron Peninsula in Azerbaijan is also debatable. According to Alekperov (1971, 1973), this happened only after the territory was flooded in the 1960s; however, the existence of a relict population here cannot be ruled out.

Another scenario of chorogenesis is also possible. In the period of numerous regressions of the Caspian Sea (see Svitoch, 2016) and the formation of a land bridge in the Apshero-Balkhan uplift zone, which directly connected the Krasnovodsk Gulf region and the Apsheron Peninsula (Apsheron threshold) (Klenova, 1954), this territory could have been colonized by *L. strigata* from the west, provided that a population existed on Apsheron in this period. This corridor has been repeatedly mentioned as one of the possible routes of penetration of Central Asian (Turanian) reptile species into the Caucasus (Darevsky, 1957; Akhmedov, 1977; Tertyshnikov, 1992). The possibility of an accidental introduction of lizards to the Krasnovodsk region also remains. The loss of the holotype and the absence of other specimens from the eastern coast of the Caspian Sea do not allow us to answer these questions.

Currently, *L. strigata* continues to spread across the Caucasus and adjacent territories. Ostrovskikh (1998) pointed out the probable modern expansion of the species' range in the Kuban River valley (Krasnodar Krai, most likely, A/I). Its penetration into the forest belt of the Talysh Mountains in Azerbaijan as a result of logging began to be recorded in the 1980s (Berezhnoi, 1984); this process is still actively ongoing (Kidov and Matushkina, 2016). We have noted range shifts in Eastern Georgia. Muskhelishvili (1966, 1970) established that the species was distributed in the upper reaches of the Iori River to the Bochorma Village (h ≈ 950 m ASL). However, *L. strigata* was not recorded upstream, in the urban-type settlement Tianeti (h ≈ 1140 m ASL), which is located between the Kakheti and Kartli Ridges on the southern slope of the Greater Caucasus (for this locality, the author reported only *L. agilis*). In May 2018, in Tianeti and its vicinities, *L. strigata* (B/II) was the most numerous reptile species (Doronin et al., 2019). The dispersal of the species probably took place along the Iori River valley and/or along the roadsides of the roads built along the bed of this river. In the North Caucasus, in 1982–2018, *L. strigata* (A/I) has become widespread within the Terek sand massif due to sand overgrowth (Lotieva and Batkhiev, 2019). Previously, only isolated populations of the species were known for this territory (Tertyshnikov et al., 1984). Notably, the specimen from the Kissyk tract in Chechnya (ZISP 24667, Hap 3) showed the greatest distance (three nucleotide substitutions from the central pool) in the star-shaped cluster of haplogroup I on the haplotype network, which indicates the isolation of the population in the past.

It can be assumed that *L. strigata* appeared in the northernmost record point within the Astrakhan oblast (the environs of the urban-type settlement Liman) (Doronin et al., 2018) (probably A/I) also in the last decades. This process may be part of the modern pan-European trend of the northward expansion of the ranges of thermophilic lacertid species (Maier et al., 2022). A similar process was recorded in the North Caucasus for meadow lizards of the *Darevskia* (*praticola*) complex (Doronin, 2015; Doronin and Smirnova, 2022), sympatric and syntopic with *L. strigata* over a significant part of the range. Further dispersal of the species in the west of the Caspian Lowland within the administrative boundaries of the Astrakhan oblast and in the Kuban-Azov Lowland in the Krasnodar krai can be expected.

For the xerophilic herpetofauna refugia distinguished in the Caucasus (Tuniyev, 1995; Tuniyev et al., 2019), we found no genetically unique (significantly diverged within their clade/haplogroup) populations of *L. strigata*: the Daghestan Hills refugium, similarly to the entire North Caucasus, is colonized by representatives of A/I (most likely, this also applies to the refugia of the North-Eastern Caucasus); the Black Sea Coast, by B/II, widespread in Transcaucasia; and the Kuro-Araksian, by A/I and B/II. A similar picture can be seen when the geographical distribution of clades/haplogroups is compared with the scheme of the Hyrcania refugia (Kidov, 2022): the West Hyrcanian (Talysh Mountains and adjacent western sections of Alborz, as well as the Lankaran Lowland within southeastern Azerbaijan and the Iranian provinces of

Ardabil and Gilan) and Central Hyrcanian (eastern Gilan and Mazandaran in Iran) are inhabited by representatives of C/III, with an insignificant presence of A/I in the west. An exception is the East Hyrcanian refugium (Golestan, Kopet Dag in Turkmenistan and Northern Khorasan), whcih is inhabited by representatives of the most distant clade/haplogroup D/IV.

On the basis of all data obtained, it can be concluded that the level of genetic diversity of *L. strigata* is low and that there are no populations that could be considered as subspecies. For comparison, the *p*-distance for *cytb* between the recognized subspecies of the *L. viridis* (Laurenti, 1768), is 5.3–6.9% (Marzahn et al., 2016). This index, as well as the divergence time of clades, coincide maximally in *L. strigata* with *L. m. media*: 1.39–2.07% and approximately 1 million years ago (Ahmadzadeh et al., 2013a; Doronina et al., 2022). Here, we do not consider the subspecies of *L. agilis*, since its intraspecific taxonomy needs revision (Doronina et al., 2023).

Regarding the zoogeographic status of *L. strigata*, it should be noted that, in previous papers, it was classified as belonging to the West Asian (Sobolevsky, 1929), Asia Minor (Darevsky, 1957; Muskhelishvili, 1966; Alekperov, 1978), Mediterranean (Anderson, 1968; Tuck, 1971; Berezhnoi, 1984), Caucasian-Asia Minor (Rustamov and Shammakov, 1982; Shammakov, 2008), East Mediterranean (Dzhafarov, 1949; Tertyshnikov, 1977; Tuniyev, 1990), and Near Asian (Lotiev and Tuniyev, 2017) zoogeographic group. Engelmann et al. (1985) implicitly associated *L. strigata* with the East Caucasian refugium and noted a wide distribution of this species within the Near East. Kireev (1984, 1987) considered it as an East Mediterranean element and included it in the group of species of the Caucasian origin. Sindaco and Jeremčenko (2008) associated this species with the European-Mediterranean-Iranian (Iranian-Caucasian) transition zone (chorotype). If we adhere to the approach according to which the zoogeographic identity of a taxon should be assessed by the type of its range, origin, and phylogenetic position (Hoffmann, 2001; Borkin and Litvinchuk, 2013), then *L. strigata* should be assigned to the Hyrcanian-Caucasian zoogeographic group.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The experimental protocols were approved by the Bioethics Commission of the Zoological Institute of the Russian Academy of Sciences (conclusion no. 1-3/15-06-2021).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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