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SHORT COMMUNICATIONS

Genetic Variability of Tree Junipers of Section Sabina: Data from Dagestan, Armenia, and Crimea

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Abstract—An analysis was performed of the variability of intergenic spacers *pet*N–*psb*M, *trn*D–*trn*T, *trn*L–*trn*F, and trnS–*trn*G chloroplast DNA in the endangered closely related species of junipers *Juniperus excelsa*, *J. polycarpos*, and *J. foetidissima* in the Caucasus and Crimea—the northern limits of their distribution. Analysis of molecular variance (AMOVA) showed a high degree of differentiation of the three taxa ($G_{CT} = 0.9905$, $P < 0.0001$). Seven haplotypes have been identified in total. The population of *J. foetidissima* from Armenia is characterized by high genetic diversity ($H = 0.442$); the genetic diversity was smaller in *J. excelsa* ($H = 0.200$); the *J. polycarpos* populations were found to be monomorphic. The studied samples, together with those included in the analysis from GenBank from the main part of the range, formed three clades corresponding to three taxa, with high statistical support.

Keywords: *pet*N–*psb*M, *trn*D–*trn*T, *trn*L–*trn*F, *trn*S–*trn*G, population structure, genetic variability

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Taxonomic identification of a species is reduced to its comprehensive assessment of morphology, anatomy, developmental biology, geography, ecology, and other traits on which phenotypic systematics is based. In turn, in addition to classical phenosystematics, data from genosystematics serve to clarify and streamline the taxonomic structure of closely related species.

The objects of research are *Juniperus polycarpos* C. Koch, *J. excelsa* Bieb., and *J. foetidissima* Willd, species with similar morphology, representatives of the Sabina section. These are rare and protected species, relics listed in the Red Data Book of Russia [1] or regional Red Data Books [2–4]. The area of their distribution is the Black Sea coast of the Caucasus (from Anapa to Gelendzhik), Crimea, and Dagestan; outside Russia, they are found in the Balkans and in Southwest Asia (Iran, Afghanistan, Turkey, Syria, Lebanon, Iraq).

The investigated species are treelike junipers forming sparse forests and open woodlands. Juniper woodlands of the Caucasus and Crimea are subdivided into two geographical variants. The first is the Eastern Mediterranean; it is widespread on the Black Sea coast of the Caucasus (in the region of Novorossiysk) and in South Crimea and is formed by mesoxerophytes *J. excelsa* and *J. foetidissima*. The second is Western Iranian; it is widespread in Eastern and Southern Transcaucasia (Armenia, Azerbaijan) and in Dagestan and is formed by xerophyte *J. polycarpos* [5]. Both types of woodlands are unique plant communities of juniper forests, including many rare and protected species, and thus fulfill an important ecological function [6, 7].

In the broad sense, *J. excelsa* s.l. includes *J. polycarpos* and *J. excelsa*, as well as *J. seravschanica* Kom and *J. turcomanica* B. Fedtsch. common in Central Asia, forming a complex of morphologically similar taxa. The taxonomic status of these species has changed several times [8], but even today the systematic position of *J. polycarpos* and *J. excels* growing in the Caucasus remains controversial. So, for example, in the *Conspectus of the Flora of the Caucasus* [9], *J. polycarpos* is given in the rank of subspecies (*J. excelsa* subsp. *polycarpos*), but is considered by many authors as an independent species [10–13]. The species status *J. foetidissima* is not considered controversial; however, a similar ecological confinement and co-growth with *J. polycarpos* or *J. excelsa* (for example, in Krasnodar krai and Armenia) often complicates its species identification by morphological characters.

Molecular genetic studies of all three species and ones closely related to them are presented in numerous works [13–18] and analyzed in the most detail in the monographic summary on the genus *Juniperus* [19]. The analysis of the distribution of the species was carried out for the territory of Turkey, Lebanon, Greece,

Table 1. Geographic coordinates of collection sites and indicators of cpDNA genetic diversity in the studied samples of juniper

Populations	Coordinates, N/E	*N*	N_h	*H*
1. *J. excelsa*—Crimea, Sudak	44°52′/34°55′	7	h6:7	0
2. *J. excelsa*—Krasnodar krai, Gelendzhik	44°39′/37°56′	10	h6:(9); h7:(1)	0.200
3. *J. polycarpos*—Dagestan, Talga Gorge	42°52′/47°24′	5	h5:(5)	0
4. *J. polycarpos*—Dagestan, Antsukh	42°20′/46°27′	5	h5:(5)	0
5. *J. polycarpos*—Armenia, Vayk	39°41′27″/45°32′31″	5	h5:5	0
6. *J. foetidissim*—Armenia, Hovk	40°47′/45°03′	16	h1:(12); h2:(1); h3:(1); h4:(2)	0.442

N—sample size, N_h—the number of haplotypes, *H*—indicator of haplotype diversity.

Bulgaria, Azerbaijan, Armenia, and Iran, as well as the territories of the Western and Eastern Caucasus (Krasnodar krai, Dagestan), Crimea, and Transcaucasia [12].

In this work, the parameters of genetic diversity and the structure of natural populations of *J. excelsa*, *J. polycarpos*, and *J. foetidissima* in the northern territories (limits) of distribution were assessed, and genetic links with representatives from the main part of the range were revealed using intergenic spacers of chloroplast DNA (**cpDNA**). Data on genetic variability and refinement of the taxonomy of these species will supplement the information on speciation in the Sabina section and will also be relevant in the development of conservation measures.

A total of 48 samples of juniper from six natural populations were analyzed: *J. excelsa*—17 specimens, *J. polycarpos*—15 specimens, *J. foetidissima*—16 specimens (Table 1). Total DNA was isolated by the CTAB method [20] from leaves dried in silica gel. Amplification of noncoding regions *pet*N–*psb*M, *trn*D–*trn*T, *trn*L–*trn*F, and *trn*S–*trn*G was performed using universal primers, temperature regimes, and protocols recommended for these regions by F. Hojjati et al. [13]. Nucleotide sequences of cpDNA regions were determined using an ABI 3130 genetic analyzer (Applied Biosystems, USA); alignment and integration into a single matrix was performed using the Bio Edit program [21]. Calculation of the number of haplotypes (N_h), the indicator of haplotype diversity (*H*), the levels of differentiation, and the distribution of genetic variability within and between populations (analysis of molecular dispersion, AMOVA) was performed using the Arlequin v. 3.5.1.2 program [22]. The relationship tree of cpDNA haplotypes was constructed in the Network v. 4.6.1.2 program [23]. The phylogenetic tree for all samples was constructed using Bayesian analysis in MrBayes v. 3.1.2 [24] on the basis of the GTR + G + I nucleotide substitution model. Each mutation (mononucleotide substitution or indel, regardless of size) was coded as a single mutational event. To construct trees, we included data from GenBank for samples from the main part of the range. These additional samples are from F. Hojjati et al. [13]. For *J. polycarpos*, the samples are numbered 8761, 14162, 14164, 14166, 14167, 141171; for *J. excelsa*, 8785, 8786, 9433, 13720, 13721, 14155, 14742; for *J. foetidissima*, 73845, 5645, 5646, 17035, 20431. The haplotypes of the samples were compiled according to the sequences of the corresponding fragments taken from the GenBank (according to the numbers indicated in [13]). As the outgroup, *Juniperus sabina* sample 14316 from Azerbaijan [13] was selected, belonging to the same section Sabina (Mill.) Spach.

The length of the combined sequence for four fragments was 2916 bp (*trn*D-*trn*T: 679 Mon, *trn*S-*trn*G: 690 Mon, *trn*L-*trn*F: 712 Mon, *pet*N-*psb*M: 835 mon). There were 45 variable sites identified (Table 2), of which in the fragment *trn*D-*trn*T were seven mononucleotide substitutions and two indels; in the fragment *trn*S-*trn*G were six monocucleotide substitutions, one dinucleotide substitution, and five indels; in the fragment *trn*L-*trn*F were four mononucleotide substitutions and three indels; in the fragment *pet*N-*psb*M were nine mononucleotide substitutions, one trinucleotide substitution, and seven indels. The variability was grouped into seven haplotypes (h1–h7). The sequences of the set of fragments for each haplotype were placed in GenBank under accession numbers MW186935–MW186951.

The distribution of haplotypes in populations and their frequencies are shown in Fig. 1a. For related reconstructions, the studied juniper samples were grouped with those from GenBank. The median network of genealogical connections between haplotypes revealed three haplogroups corresponding to three species (Fig. 1b). On the phylogenetic tree (Fig. 1c), samples from different populations are grouped according to taxonomic affiliation with high statistical support (*P-value* = 0.96–1.00). According to AMOVA results, the genetic differentiation between the three groups is quite high: $F_{CT} = 0.8287$ ($P < 0.0001$), even higher taking into account the relationship of haplotypes: $G_{CT} = 0.9905$ ($P < 0.0001$).

The population of *J. foetidissima* from Armenia turned out to be the most polymorphic, four haplo-

Table 2. Segregating sites for seven cpDNA haplotypes. Reference haplotype h1

Haplotype	Position of nucleotide																				
	*trn*D-*trn*T									*trn*S-*trn*G											
	12	56	90	118	339	464	498	557	589	16	42	52	95	116	193	202	203	235	295	360	603
h1	T	C	A	A	**a**	T	G	C	–	AC	A	–	T	T	C	–	G	–	G	–	**e**
h2	T	C	A	A	–	T	G	C	–	AC	A	–	T	T	C	–	G	–	G	–	**e**
h3	T	C	A	A	**a**	T	G	C	–	AC	A	–	T	T	C	–	G	–	G	–	**e**
h4	T	C	A	A	–	T	G	C	–	AC	A	–	T	T	C	–	G	–	G	–	**e**
h5	T	A	–	A	–	T	T	T	b	CT	G	**c**	C	C	C	T	T	**d**	A	T	–
h6	A	A	–	C	–	C	T	T	b	CT	A	–	C	C	A	T	T	**d**	A	T	–
h7	A	A	–	C	–	C	G	T	b	CT	A	–	C	C	A	T	T	**d**	A	T	–

Haplotype	Position of nucleotide																							
	*trn*L-*trn*F							*pet*N-*psb*M																
	146	278	390	483	508	523	543	49	129	238	301	363	414	431	448	479	568	581	639	642	643	661	671	673
h1	T	A	C	C	TA	–	C	A	C	TAT	G	C	C	C	**f**	–	–	A	AAA	A	A	A	C	C
h2	T	A	C	C	TA	–	C	A	C	TAT	G	C	C	C	**f**	–	–	A	AAA	A	T	A	C	C
h3	T	–	C	C	TA	A	C	G	C	TAT	G	C	C	C	**f**	–	–	A	AAA	A	A	A	C	C
h4	T	A	C	C	TA	–	C	A	C	TAT	G	C	C	C	**f**	–	–	A	AAA	A	A	A	C	C
h5	C	A	G	C	–	–	G	A	A	ATA	T	T	G	A	–	–	**g**	A	AAA	T	A	A	A	A
h6	C	A	G	A	–	–	G	A	A	CTA	T	T	G	A	**f**	T	–	C	–	–	–	–	C	A
h7	C	A	G	A	–	–	G	A	A	CTA	T	T	G	A	**f**	T	–	C	–	–	–	–	C	A

a—TTATAGTACCTAATTAGGTACTATAATGACTTTCCTAGCCTACCTAG; **b**—GTTCTA; **c**—AATTAT; **d**—CAGATTAGAATCT-GGAT; **e**—TTCTTA; **f**—AAAAA; **g**—ATCCAAAA.

types h1–h4 ($H = 0.422$, Table 1). These samples showed a large insert (45 bp) in the fragment *trn*D-*trn*T in the case of haplotypes h1 and h3, also typical of specimens of this species from Iran, taken from GenBank (haplotypes f1 and f3, Fig. 1b; Table 2). The h2 haplotype is characterized by the replacement of nucleotide A with T in the fragment *pet*N-*psb*M. This mutation does not occur in samples from the GenBank and is apparently characteristic only of this population. Haplotype h4 corresponds to the haplotype also found in this species in Greece and Iran (f2, Fig. 1b; Table 2).

In the studied populations of *J. excelsa*, haplotype h6 predominates (Fig. 1a), also widespread in the main part of the range (haplotype e3, Fig. 1b). In the population from Krasnodar krai, haplotype h7 was encountered, which differs from h6 in a point substitution in the fragment *trn*D-*trn*T (replacing T with G, Table 2). The studied West Caucasian and Crimean samples form a joint clade with samples from GenBank from the territory of Greece, Turkey, Bulgaria, and Lebanon, in which, in addition to the main one, there are closely related haplotypes (haplotypes e1 and e2, Fig. 1b).

The studied populations of *J. polycarpos* from Armenia and Dagestan are monomorphic; they are dominated by the h5 haplotype, which is widespread (according to GenBank data) in Azerbaijan (p2 haplotype in Fig. 1b) and differing by one mutation from the haplotype of two more samples from GenBank from the territory of Azerbaijan and Armenia (Fig. 1c).

Thus, the geographical distribution of haplotypes and differentiation according to the data of cpDNA variability correspond to the three described taxa.

Between the populations of the species of Crimea and Krasnodar krai (*J. exelsa*), as well as Dagestan and Armenia (*J. polycarpos*), for which the main task was set to determine the taxonomic status, a number of mutations were identified that support the independence of each of the taxa, despite the similar morphology. The morphological differences between species *J. polycarpos* and *J. excelsa* boil down to the following: *J. polycarpos* has thicker shoots with tightly pressed, slightly keeled, blunt leaves, with an oval swollen gland; shoots of *J. excelsa* are thinner and the leaves are strongly bluish, with a long pointed tip at the top, concave from the back (below the middle), with an oval or almost round gland. *J. polycarpos* are dioecious trees; *J. excelsa* are monoecious trees [10, 25–28]. The general design of the anatomical structure is similar in one-, two-, and three-year shoots of *J. polycarpos* and *J. excelsa* to genus- and species-specific traits. Genus-specific traits: one- and two-year-old shoots in cross section are bilobate and three-lobed, and three-year shoots are three-lobed. Species-specific traits for *J. excelsa* are the absence of stony cells and poorly expressed oily cells in the parenchyma of leaf cushions. In *J. polycarpos*, stony cells are located in groups or one at a time; oily cells are collected in groups. The diameter of the shoots in the cross section of annual shoots in *J. excelsa* is 1.5 times less than that in *J. polycarpos*; however, with age, the differences in the diameter of the cross section are leveled [29].

Juniperus foetidissima has more noticeable morphological differences from *J. excelsa*. End branches of *J. foetidissima* are thicker (1.1mm) than *J. excelsa* (0.75 mm). The shoots of the plant are thick, quadrangular; the leaves are scaly, slightly keeled; in contrast to *J. excelsa*, the leaves are not very close to the shoot, and their tips are usually pointed [33, 34]. However, owing to the variation in traits depending on the age of individuals, these species are often difficult to distinguish from each other, especially when they grow together. It should be noted that, according to recent studies, for *J. seravschanica* (one of the species of the complex *J. excelsa* s.l.), the origin is assumed to be the result of ancient introgressive hybridization between *J. foetidissima* and *J. polycarpos* [20], which indicates their close relationship and lack of reproductive isolation in the past. However, there are no data on modern hybridization between these species.

Thus, our data on the variability of cpDNA samples from Crimea and the Caucasus support the thesis of the independence of two taxa *J. excelsa* and *J. polycarpos.* The observed differentiation reflects the existence of two genetic lines—western and eastern—which arose in a once ancestral form during the his-

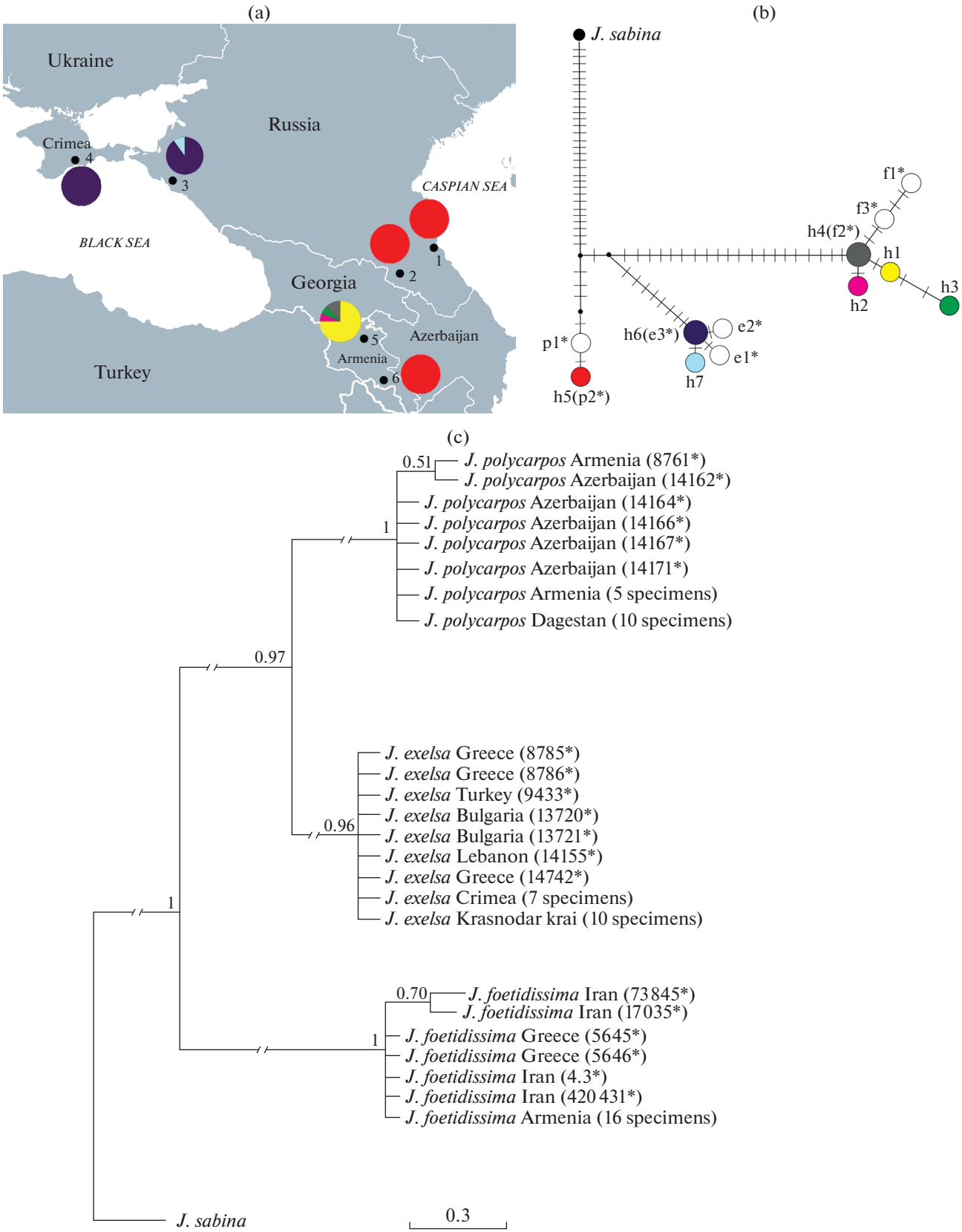

Fig. 1. (a) Location of the studied samples, distribution of detected cpDNA haplotypes. (b) cpDNA haplotype tree (h1–h7). The transverse thin strokes on the branches of the tree are mutational events. Additional haplotypes f1–f3, e1–e3, and p1 – p2 were drawn from the sequences of the corresponding intergenic spacers taken from the GenBank. (c) Phylogenetic tree of the studied samples of *J. excelsa*, *J. polycarpos*, and *J. foetidissima*. (*) Marked samples sequences for which were taken from GenBank.

tory of the formation of its range. This pattern of genetic structure is consistent with belonging to different types of vegetation with a certain ecological confinement. In the populations studied by us, a decrease in genetic variability is observed (in comparison with the main range of species), which is characteristic of marginal populations and is explained by their location in the northern limits of their distribution.

The obtained molecular genetic data can be used to develop programs for monitoring and preserving these rare species, as well as to develop measures for the rational use of natural resources. A set of four marker fragments is suitable for species identification, if this is difficult to do on the basis of morphological characters.

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COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain any research using animals or people as objects of research.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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