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EXPERIMENTAL WORKS

Molecular Genetic Characteristics of the Allelic Variants of Microsatellite Loci Du281, Du215, and Du323 in Parthenogenetic Lizards *Darevskia rostombekovi* (Fam. Lacertidae)

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Abstract—Assessment of genetic diversity of unisexual (parthenogenetic) species of vertebrates is among the major objectives of research in these species. Various nuclear or mitochondrial genome markers can be used for such an assessment. Microsatellite DNAs are among the most efficient genetic markers, since the mutation rate in these fragments is high. Identification and characterization of such markers are the basic stages of genetic research in parthenogenetic species. Allelic polymorphism of three microsatellite loci in populations of the parthenogenetic species *Darevskia rostombekovi* ($n = 42$) and bisexual parent species *D. raddei* ($n = 6$) and *D. portschinskii* ($n = 6$) has been assessed by locus-specific PCR for the first time. All representatives of the parthenogenetic species *D. rostombekovi* used in the present study turned out to be heterozygous. The number of alleles of the different loci ranged from two to five in the populations investigated. The nucleotide sequence of the allelic variants of the loci investigated has been determined. The differences between the alleles were apparently related to variation in the structure of microsatellite clusters and single-nucleotide substitutions in DNA fragments located in the vicinity of the clusters at fixed distances from the latter. Structural variants of the alleles formed allele-specific haplotype markers that were inherited from the bisexual parent species. The origin (inheritance from the maternal or paternal species) has been determined for each allele of the parthenogenetic species. The distribution, frequency of occurrence, and pattern of combination of the alleles of microsatellite loci in *D. rostombekovi* populations have been characterized; these features determined the identity of each population. The data obtained can be used for assessment of the clonal diversity of the parthenogenetic species *D. rostombekovi* and the identification of a possible scenario of the emergence of the diversity in the populations.

Keywords: parthenogenesis, unisexual and bisexual lizards of the genus *Darevskia*, microsatellite loci, allelic polymorphism, haplotype markers

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INTRODUCTION

The discovery of unisexual (parthenogenetic) lizard species by I.S. Darevskii in 1958 raised a range of general biological questions related to clonal reproduction, the emergence of genetic and clonal diversity, and the origin and evolution of these vertebrate forms. The origin of parthenogenetic species of the genus *Darevskia* from interspecies hybridization of representatives of bisexual species had been established previously using the analysis of allozymes and mitochondrial DNA (mtDNA); the same process accounts for the origin of the absolute majority of unisexual vertebrates [1, 2].

The genus *Darevskia* includes seven parthenogenetic species, one of which is named *D. rostombekovi*. The origin of *D. rostombekovi* upon the hybridization of male *D. portschinskii* individuals and female *D. raddei* individuals has been proven [3–5]. Importantly, the bisexual parent species belong to different phylogenetic clades of the genus *Darevskia* [3, 5]: the maternal species belongs to the caucasica clade, whereas the paternal species belongs to the rudis clade. Notably, the phylogenetic factors that restrict the formation of parthenogenetic species have been identified in other lizards as well [6, 7].

Biogeographic studies showed that the living range of *D. rostombekovi* lizards is relatively small and includes isolated populations from North Armenia and the adjacent territories of Azerbaijan, as well as an isolated high-mountain population on the southwest shores of Lake Sevan (near the Zagalu settlement). Allozyme analysis of various *D. rostombekovi* populations (with the exception of the Zagalu population) did not reveal any allozyme variability, and this led to the idea that the monoclonal genetic structure of the spe-

cies [8] is different from that of the parthenogenetic species *D. dahli*, *D. armeniaca*, and *D. unisexualis* composed of two to five allozyme clones [9]. Genetic homogeneity of *D. rostombekovi* populations revealed by allozyme analysis contradicted the results of morphological studies that revealed considerable differences between the populations [3]. The model of genetic and morphological diversity of hybrid parthenogenetic species implies that there are genetic differences between morphologically dissimilar clones [10].

Analysis of mtDNA revealed that the maternal ancestors of all northern *D. rostombekovi* populations (from the vicinity of the towns of Spitak, Gosh, and Papanino) belonged to a single Southern Armenian population of *D. raddei* (the Egegnadzor population) [11]. Analysis of mtDNA of the Sevan (Zagalu) population of *D. rostombekovi* showed that this population originated from the Egegnadzor population of *D. raddei* as well [12, 13]. However, a single nucleotide substitution (C → T transition at 535 bp) was detected in the cytochrome *b* gene of all representatives of this population, this being indicative of the second *D. rostombekovi* mitotype specific for the Zagalu population. Moreover, analysis of fingerprint and RAPD markers resulted in the subdivision of all *D. rostombekovi* individuals investigated into two groups: the first group included representatives of the Zagalu population, whereas the second group included individuals from all North Armenian populations (from Spitak, Gosh, and Papanino) [12, 13]. These findings may be due to early-stage intraspecies differentiation of *D. rostombekovi* or to hybrid origin of the parthenogenetic species. The use of more efficient markers, such as microsatellite DNA, is required for finding a solution to this problem and for the identification and molecular genetic characterization of allelic variants of loci that contain microsatellite DNA in the parthenogenetic species *D. rostombekovi*.

Cloning, sequencing, and genetic characterization of alleles of microsatellite loci Du215, Du281, and Du323 in the parthenogenetic species *D. rostombekovi* is reported in the present work.

MATERIALS AND METHODS

Previously collected DNA samples from lizards of the species *D. rostombekovi* (42 individuals), *D. raddei* (6 individuals), and *D. portschinskii* (6 individuals) were used in the study. DNA samples of the parthenogenetic species *D. rostombekovi* were derived from three North Armenian populations (Papanino, $n = 21$; Spitak, $n = 9$; and Gosh, $n = 4$) and from the Sevan population (Zagalu, $n = 8$). Primers selected previously for the loci Du215, Du281, and Du323 of the parthenogenetic species *D. unisexualis* [14] were used for monolocus analysis by polymerase chain reaction (PCR). The total volume of the PCR mixture was 20 μL, and the amount of DNA template used in the reaction was 50 ng. The experiments were performed using the GenePak® PCR Core reagent kit (IsogeneLab Ltd, Russia). Amplification was performed in a Tertsik TP4-PCR-01 four-channel DNA-amplifier (DNK-tekhnologiya, Russia) according to the thermal cycling protocols described in [14]. Amplification products were fractionated in 8% neutral polyacrylamide gel (PAAG), isolated from the gel, and cloned into a pGEM®-T Easy Vector System I plasmid vector (Promega, United States) as recommended by the manufacturer. Sanger sequencing of the DNA was performed using an ABI PRISM® BigDye™ Terminator V.3.1 reagent kit (GE Healthcare, United States) on a DNA Applied Biosystems 3730 DNA Analyzer (automatic sequencer) from Applied Biosystems (United States). DNA sequences were aligned using the Clustal W algorithm implemented in the MEGA 6.0.6 software [15].

RESULTS AND DISCUSSION

The Molecular Nature of Allelic Polymorphism of Microsatellite Loci in the Parthenogenetic Species D. rostombekovi

Locus-specific PCR analysis revealed heterozygosity in the microsatellite loci Du215, Du281, and Du323 of all *D. rostombekovi* individuals investigated. The number of alleles from the different loci varied from two to five in the parthenogenetic species populations analyzed. The distinct structural features of these alleles are listed in Table 1. The differences are apparently due to the structure of the microsatellite cluster and single-nucleotide variations in the adjacent DNA fragments (the latter were not observed in case of the allele Du215). Interallelic variations of a similar type were previously detected upon the analysis of polymorphism of a number of microsatellite loci in parthenogenetic species *D. dahli* and *D. unisexualis* [16, 17]. Notably, these allelic variations in the DNA structure are evidence of the emergence of parthenogenetic species in a hybridization event and characterize the level of heterozygosity of the genome of a certain species. The level of heterozygosity of the genome of a hybrid individual acting as the founder of a parthenogenetic species is apparently correlated to the degree of divergence of the genomes of individuals that participated in interspecies hybridization. The level of heterozygosity may influence the number of single-nucleotide allelic variations and the structural variability of microsatellite DNA associated with the alleles.

The "balance" hypothesis [18, 19] implies a decisive role or a level of total heterozygosity for the emergence of oocytes with nonreduced chromosome numbers in individuals that serve as founders of the parthenogenetic species; the transition to clonal reproduction can occur if the overall degree of heterozygosity is below a certain level. Five alleles of the locus Du215, four alleles of the locus Du281, and two alleles of the locus

Table 1. Structural differences between the alleles of microsatellite loci Du215, Du281, and Du323 in the parthenogenetic species *D. rostombekovi*

Allele	Size, bp	Sequence of the microsatellite cluster	Conserved nucleotide substitutions in the flanking sequences*	Gene Bank ac. no.
Du215(rost)1	256	5' $(GATA)_{10}(GCAA)_{11}$ 3'	–	GU972528
Du215(rost)2	252	5' $(GATA)_{9}(GCAA)_{11}$ 3'	–	GU972529
Du215(rost)3	250	5' $(GATA)_{9}(GCAA)_{10}$ 3'	TT (–98/99)	GU972530
Du215(rost)4	248	5' $(GATA)_{8}(GCAA)_{11}$ 3'	–	GU972531
Du215(rost)5	227	5' $(GATA)_{4}(GAT)(GATA)_{7}(GCAA)_{12}$ 3'	–	GU972532
Du281(rost)1	265	5' $(GATA)_{2}(GAGAT)(GATA)_{11}$ $(GAT)(GATA)_{12}$ 3'	T (–84), A (–19), T (+15), A (+25)	HM114225
Du281(rost)2	261	5' $(GATA)_{2}(GAGAT)(GATA)_{10}(GAT)(GATA)_{12}$ 3'	T (–84), A (–19), T (+15), A (+25)	HM070256
Du281(rost)3	253	5' $(GATA)_{2}(GAGAT)(GATA)_{11}(GAT)(GATA)_{9}$ 3'	T (–84), A (–19), T (+15), A (+25)	HM070257
Du281(rost)4	191	5' $(GATA)_{10}$ 3'	C (–84), G (–19), C (+15), G (+25)	HM070258
Du323(rost)1	195	5' $(AC)_{6}$...$(GATA)_{6}(GAT)(GATA)_{2}$ 3'	C (–23), T (+39)	HM013995
Du323(rost)2	184	5' $(AC)_{4}$...(GATA) $(GGT)(GATA)_{3}(GAT)(GATA)$ 3'	A (–23), C (+39)	HM013996

Here and in Table 2: * distance upstream (–) or downstream (+) of the microsatellite cluster, base pairs (bp).

Du323 were detected in *D. rostombekovi* individuals investigated. Similarly to the other cases [20], alleles of microsatellite loci of *D. rostombekovi* could be subdivided into two groups according to the specific structural features of the DNA related to the origin of individual DNA fragments from a certain parent species.

All five alleles of the locus Du215 included microsatellites of a complex structure that contained GATA, GCAA, and GAT repeats (Table 1). None of the alleles exhibited single-nucleotide variations outside the microsatellite; however, a dinucleotide insert (TT) was detected in vicinity of the microsatellite in allele 3. Alleles of the locus Du215 could be formally subdivided into two groups using the presence of this insert as the criterion.

Alleles of the locus Du281 differed both with regard to the structure of the microsatellite cluster and with regard to single-nucleotide variations at fixed positions outside the cluster; these structural features could be used to divide all the alleles into two groups. Three alleles with the same set of single-nucleotide variations that form the T-A-T-A haplotype together were assigned to the same group. These alleles differed with regard to the structure of the associated $(GATA)_n$-microsatellites of a complex structure. The fourth allele of the Du281 locus belonged to the second group, since the set of single-nucleotide variations characteristic of this allele was different (haplotype C-G-C-G) and the associated $(GATA)_n$-microsatellite had a simple structure.

Alleles of the locus Du323 differed with regard to the structure of two independent microsatellite clusters $(AC)_n$ and $(GATA)_n$, as well as with regard to the combination of single-nucleotide polymorphisms at fixed positions outside the microsatellites; these variants formed two haplotype groups (C-T and A-C).

In general, the combination of certain microsatellites and single-nucleotide variations at fixed distances in the adjacent DNA can probably be considered a generalized haplotype specific for each allele and dependent on its origin from the maternal or paternal bisexual species.

Imperfect insertions, such as GAT, GGT, GAGAT, and TA, were detected in the majority of microsatellite DNA fragments. These insertions could have emerged due to nontriplet frameshifts, recombination events, or transition- and transversion-type mutations [21–23]. Allelic differences manifested as variation in the number of repeats in the microsatellite cluster can emerge upon the slipping of DNA polymerase during DNA replication [24–28]. The majority of such changes in *D. rostombekovi* are in agreement with the single-step model of mutational variability of microsatellite DNA [29] or with a modified version of this model [26]. For example, the changes in the GATA cluster in the alleles Du215 1–4 consisted in single-nucleotide shifts. The putative mutations that occur during clonal reproduction should apparently be taken into account upon the analysis of interallelic differences of microsatellite DNA in parthenogenetic species, along with inheritance from two different bisexual species. Our previous studies resulted in the detection of microsatellite mutations in parthenogenetic first-generation progeny of *D. unisexualis* lizards [30]. These mutations occurred at an early stage of embryogenesis and consisted in deletions or insertions of microsatellite repeats detected in a single allele or in both alleles of a locus. Importantly, single-nucleotide mutations outside the microsatellite were not detected.

Table 2. Structural differences between the alleles of microsatellite loci Du215, Du281, and Du323 in bisexual species *D. raddei* and *D. portschinskii*

Allele	Size, bp	Sequence of the microsatellite cluster	Conserved nucleotide substitutions in the flanking sequences*
Du215(rad)1	231	5' $(GATA)_4GAT(GATA)_8(GCAA)_2$ 3'	–
Du215(rad)2	223	5' $(GATA)_4GAT(GATA)_6(GCAA)_2$ 3'	–
Du215(rad)3	219	5' $(GATA)_4GAT(GATA)_5(GCAA)_2$ 3'	–
Du215(rad)4	215	5' $(GATA)_4GAT(GATA)_4(GCAA)_2$ 3'	–
Du215(port)1	268	5' $(GATA)_{12}(GCAA)_{12}$ 3'	–
Du215(port)2	264	5' $(GATA)_{11}(GCAA)_{12}$ 3'	–
Du215(port)3	256	5' $(GATA)_9(GCAA)_{12}$ 3'	–
Du215(port)4	256	5' $(GATA)_{11}(GCAA)_{10}$ 3'	–
Du281(rad)1	220	5' $(GATA)_7(GAT)(GATA)_8$ 3'	T (–84), A (–19), T (+15), A (+25)
Du281(rad)2	214	5' $(GATA)_2(GAGAT)(GATA)_4(GACA)_3(GATA)_4$ 3'	T (–84), A (–19), T (+15), A (+25)
Du281(rad)3	208	5' $(GATA)_{11}(GAT)(GATA)$ 3'	T (–84), A (–19), T (+15), A (+25)
Du281(rad)4	196	5' $(GATA)_8(GAT)(GATA)$ 3'	T (–84), A (–19), T (+15), A (+25)
Du281(port)1	195	5' $(GATA)_{11}$ 3'	C (–84), G (–19), C (+15), G (+25)
Du281(port)2	191	5' $(GATA)_{10}$ 3'	C (–84), G (–19), C (+15), G (+25)
Du281(port)3	187	5' $(GATA)_9$ 3'	C (–84), G (–19), C (+15), G (+25)
Du281(port)4	183	5' $(GATA)_8$ 3'	C (–84), G (–19), C (+15), G (+25)
Du323(rad)1	184	5' $(AC)_4GC...(GATA)(GGT)(GATA)_3(GAT)(GATA)$ 3'	A (–23), C (+39)
Du323(rad)2	180	5' $(AC)_4GC...(GATA)(GGT)(GATA)_2(GAT)(GATA)$ 3'	A (–23), T (+39)
Du323(port)1	215	5' $(AC)_6...(GATA)_{11}GAT(GATA)_2$ 3'	C (–23), T (+39)
Du323(port)2	211	5' $(AC)_6...(GATA)_{10}GAT(GATA)_2$ 3'	C (–23), T (+39)
Du323(port)3	203	5' $(AC)_6...(GATA)_8GAT(GATA)_2$ 3'	C (–23), T (+39)

Identification of Paternal and Maternal alleles in Microsatellite Loci of D. rostombekovi Genome

As mentioned above, the parthenogenetic species *D. rostombekovi* was formed due to interspecies hybridizations of representatives of bisexual species *D. raddei* (maternal species) and *D. portschinskii* (paternal species) [4]. Therefore, the allelic variants of the loci analyzed were inherited from the parent species of *D. rostombekovi*. We isolated and sequenced alleles of homologous loci from several representatives of the parent species in order to discriminate between alleles of paternal and maternal origin.

Nucleotide sequences of the nonidentical fragments of alleles of three microsatellite loci of representatives of the parent species are listed in Table 2. Microsatellite structure of the alleles of bisexual species was apparently quite diverse, and the loci Du281 and Du323 included single-nucleotide variations outside the microsatellites as well. The combination of these variations and the specific structure of the microsatellite allows identification of the parent species from which a specific allele of each locus of the parthenogenetic species was inherited. Thus, alleles with a C-T haplotype in the Du323 locus of the parthenogenetic species were inherited from the paternal species *D. portschinskii*, whereas the alleles with an A-C haplotype were inherited from the maternal species *D. raddei*. The alleles with a C-G-C-G haplotype in the Du281 locus were inherited from the paternal species, and those with a T-A-T-A haplotype were inherited from the maternal species. Parent alleles with TT duplication outside the microsatellite were not detected in case of the locus Du215. Tracing of allele inheritance was difficult, since no single-nucleotide markers were available for the locus in question. The specific structure of the microsatellite clusters allowed for the conclusion that Du215 alleles 1–4 of the parthenogenetic species were inherited from *D. portschinskii* (the microsatellites of these alleles had a simple structure), whereas the allele Du215/5 characterized by higher structural complexity of the microsatellite cluster was inherited from *D. raddei*. Thus, the majority of alleles of the parthenogenetic species (except for Du215/3) have been traced to the parent species, and the origin of the alleles was thus determined.

Table 3. Frequency of occurrence of allelic variants of the loci Du215, Du281, and Du323 in populations of the parthenogenetic species *D. rostombekovi*

Allele	Population			
	Gosh, $n = 4$	Zagalu, $n = 8$	Papanino, $n = 21$	Spitak, $n = 9$
Du215(rost)1	1	–	–	–
Du215(rost)2	2	–	21	9
Du215(rost)3	1	–	–	–
Du215(rost)4	–	8	–	–
Du215(rost)5	4	8	21	9
Du281(rost)1	3	–	14	8
Du281(rost)2	1	–	7	1
Du281(rost)3	–	8	–	–
Du281(rost)4	4	8	21	9
Du323(rost)1	4	8	21	9
Du323(rost)2	4	8	21	9
Number of allelic variants	9	6	7	7

Character of the Distribution of Allelic Variants of Microsatellite Loci Du215, Du281, and Du323 in the Populations of the Parthenogenetic Species D. rostombekovi

The distribution of alleles of microsatellite loci in *D. rostombekovi* populations is illustrated by Table 3. The populations apparently differ with regard to the frequency of occurrence of certain alleles and combinations thereof. The allele Du215/5 was distributed uniformly in all four populations and detected in all individuals. The allele Du215/2 was detected in three populations; notably, only half of the individuals of one of these populations (Gosh) carried the allele. All other alleles (Du215/1, 3, and 4) turned out to be rare: they were detected in two populations only (in half of the individuals of the most polymorphic Gosh population and in all individuals of the least polymorphic Zagalu population).

Three alleles of the locus Du281 (Du281/1, 2, and 4) were found in all or part of the individuals in all or most populations. One of the alleles (Du281/3) was shown to be rare; it was detected in all individuals of the Zagalu population.

The monomorphic locus Du323 was represented by two alleles in all individuals. The number of alleles and combinations thereof was the highest in individuals from the Gosh population, notwithstanding the small size of the sample. However, the most unusual distribution and the unique combinations of alleles (such as Du281/3 + Du281/4 and Du215/4 + Du215/5) were detected in the high-mountain Zagalu population. These features of the Zagalu population may be due to its isolated character (absence of contact with other populations).

Thus, allelic variants of three microsatellite loci of the genome of the parthenogenetic species *D. rostombekovi* were identified, cloned, and sequenced for the first time; the molecular nature of allelic polymorphism of the loci investigated has been characterized; inheritance of specific alleles of the parthenogenetic species from the maternal or paternal bisexual species has been demonstrated; and the distribution of the alleles in *D. rostombekovi* population has been assessed in the present study.

The data obtained can be used for the elucidation of clonal structure of *D. rostombekovi*, investigation of the phylogenetic relationships between the parthenogenetic species and other representatives of the genus *Darevskia*, and the assessment of the degree of divergence of these species.

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Conflicts of interest. We declare that there is no conflict of interest.

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