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# Detection of Genotypic Changes in Parthenogenetic Lizards (*Darevskia armeniaca* (Mehely)) Introduced from Armenia to Ukraine

**A. V. Omelchenko[a, *], A. E. Girnyk[b], F. A. Osipov[b, c], V. G. Petrosyan[a], A. A. Vergun[b, c, **], and A. P. Ryskov[b, ***]**

[a] *Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia*
[b] *Institute of Gene Biology, Russian Academy of Sciences, Moscow, 119334 Russia*
[c] *Moscow State Pedagogical University, Moscow, 119991 Russia*
**e-mail: omi@bk.ru*
***e-mail: vermand@mail.ru*
****e-mail: ryskov@mail.ru*
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**Abstract**—The article provides data on allelic and genotypic diversity of Ukrainian and Armenian populations of a parthenogenetic lizard of Darevskia armeniaca. The individual genotypes of studied specimens were established due to combination of alleles of three microsatellite loci. It is supposed that in the introduced Ukrainian population after the invasion two new genotypes appeared. Molecular mechanisms of the emergence of these new genotypes are suggested. Values of observed heterozygosity and genetic Fst-distances for the introduced Ukrainian population, native Armenian population and group of other Armenian populations are provided.

*Keywords:* invasion, introduction, Ukraine, Armenia, populations, lizards, parthenogenesis, *Darevskia*, microsatellites, genetic diversity, heterozygosity, genetic distances, Wright's *F*-statistics

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## INTRODUCTION

Variations in biological and genotypic characteristics of animals under new habitat conditions are of great scientific interest, in particular, for the understanding of the initial stages of species divergence and formation. The investigation of amphibians and reptilians is especially promising, because they are sensitive to many environmental factors, are not very mobile, and do not change their habitats. A tentative introduction of animals with a fixed start of the experiment enables the time correlation of all the changes in the population. Parthenogenetic animal species with clonal inheritance are of special interest in such experiments.

In 1963, an experiment on introduction of a parthenogenetic lizard species *Darevskia armeniaca* from Transcaucasia to Ukraine was started (Darevsky and Shcherbak, 1967). The initial population of *D. armeniaca* was represented by 126 reproductive females caught at the Semenovskii Pass in the Stepanovan okrug of northern Armenia (49°56′10″ N, 28°53′10″ E, 1450 m above sea level). These lizards were released in a canyon of the Teterev River 22 km upstream of the city of Zhitomir (41°01′15″ N, 44°22′54″ E, 243 m above sea level). The region was chosen because of the similarity of the rock biotopes: an area in the Teterev River basin was analogous to a ravine in the Caucasus. The introduction was successful, and the range of the Ukrainian population increased about tenfold by 1998 despite the death of a considerable part of the resettled animals in the first severe winter of 1963–1964 (Dotsenko, 2007).

The comparison of 12 phenotypic parameters of the initial and introduced populations over the 35-year period showed that they remained unchanged except for one: the size of animals of the Ukrainian population became greater because of the colder climate (Dotsenko et al., 2008–2009). The molecular-genetic methods (RAPD and DNA fingerprinting) did not show any considerable differences between the populations (Darevsky et al., 1998). Genotyping data on *D. armeniaca* of the initial population (Semenovskii Pass, Armenia) and of the population introduced to Ukraine and on the distribution pattern of the revealed genotypes in these populations are given in this work. For the genotyping, three microsatellite loci (Du215, Du281, and Du323) were used. The genotypic differences between the initial and introduced populations of *D. armeniaca* were revealed.


**Fig. 1.** Location of *D. armeniaca* populations in Ukraine and Armenia: (1) Ukrainian (introduced) population, (2) Semyonov pass population (initial) (shown by black square), (3) Papanino population, (4) Lchashen population, (5) Tezh population, (6) Kuchak population, (7) Alaverdi population, (8) Stepanavan population, (9) Pushkin Pass population, (10) Medved-gora population, (11) Artik population, (12) Lchap population, (13) Takyarlu population, (14) Meghradzor population, (15) Sotk population.

## MATERIALS AND METHODS

We used the following collection samples of DNA of lizards *D. armeniaca*: (i) one population (16 animals) of Ukraine (50°11′33.7″ N, 28°19′04.3″ E); (ii) one parent population (for the first Ukrainian population) (eight animals) of the Semyonov pass, Armenia (40°39′52.6″ N, 44°53′24.4″ E); and (iii) 13 populations from Armenia: Papanino (40°42′27.7″ N, 44°45′43.9″ E), four animals; Lchashen (40°30′45.9″ N, 44°54′3.2″ E), one animal; Tezh (40°42′8.1″ N, 44°36′30.8″ E), eight animals; Kuchak (40°31′49.8″ N, 44°17′3.4″ E), seven animals; Alaverdi (41°04′50.8″ N, 44°39′27.1″ E), three animals; Stepanavan (41°03′21.8″ N, 44°21′33.5″ E), nine animals; Pushkin Pass (40°54′42.1″ N, 44°25′55.6″ E), seven animals; Medved-gora (40°58′45.8″ N, 44°24′32.7″ E), 12 animals; Artik (40°38′25.9″ N, 43°54′14.4″ E), 18 animals; Lchap (40°28′02.4″ N, 45°03′43.5″ E), one animal; Takyarlu (40°37′20.2″ N, 44°34′51.4″ E), 21 animals; Meghradzor (40°36′45.1″ N, 44°36′23.5″ E), nine animals; and Sotk (40°12′43.8″ N, 45°52′42.6″ E), three animals. The location of the populations is shown in Fig. 1. The molecular-genetic methods of investigation (DNA separation and selection of primers and PCR conditions) correspond to those used by us earlier (Malysheva et al., 2008). The genotyping was performed with the use of alleles of microsatellite loci Du215 (three alleles), Du281 (four alleles), and Du323 (three alleles). All the revealed alleles were sequenced in an ABI PRISM 3100-Avant automatic sequencer and deposited in GenBank (Malysheva et al., 2008). The allele structure of the genotype of each animal was determined by these approaches. The data on the variability of the allele variants are given in Table 1. The genetic characteristics of the populations (heterozy-

**Table 1.** Allelic variants of Du215, Du281, and Du323 microsatellite loci of *D. armeniaca* parthenogenetic species

| Allele | Length (bp) | Sequence of microsatellite cluster | Fixed nucleotide replacements in flanks* | Gene Bank ac. no. |
|---|---|---|---|---|
| Du215(arm)1 | 236 | 5'(GAT)(GACA)$(GATA)_8(GACA)_5$(GATA)(GCAA)3' | T (–58), G (–38), C (–19) | GU972533 |
| Du215(arm)2 | 232 | 5'(GAT)(GACA)$(GATA)_7(GACA)_5$(GATA)(GCAA)3' | T (–58), G (–38), C (–19) | GU972534 |
| Du215(arm)3 | 192 | 5'(GAT)$(GATA)_5$3' | A (–58), C (–38), C (–19) | GU972535 |
| Du281(arm)1 | 229 | 5'$(CA)_2$...(GGTA)$(GATA)_{10}$(GAT)(GATA)$(GGTA)_2$(GAT)$(GATA)_4$3' | T (+15) | HM070259 |
| Du281(arm)2 | 225 | 5'$(CA)_2$...(GGTA)$(GATA)_9$(GAT)(GATA)$(GGTA)_2$(GAT)$(GATA)_4$3' | T (+15) | HM070260 |
| Du281(arm)3 | 187 | 5'$(CA)_2$...$(GATA)_9$3' | C (+15) | HM070261 |
| Du281(arm)4 | 183 | 5'$(CA)_2$...$(GATA)_8$3' | C (+15) | HM070262 |
| Du323(arm)1 | 215 | 5'$(AC)_6$...$(GATA)_{11}$(GAT)$(GATA)_2(GA)_4$3' | C (–23), T (+39) | HM013992 |
| Du323(arm)2 | 211 | 5'$(AC)_6$...$(GATA)_{10}$(GAT)$(GATA)_2(GA)_4$3' | C (–23), T (+39) | HM013993 |
| Du323(arm)3 | 184 | 5'$(AC)_5$...(GATA)(GGT)$(GATA)_3$(GAT)(GATA)$(GA)_4$3' | A (–23), C (+39) | HM013994 |

* Distances (bp) are given prior to (–) and after (+) microsatellite cluster according to (Malysheva et al., 2008).

gosity and $F_{st}$) were determined with the use of the Web version of the POPTREEW software program (http://www.med.kagawa-u.ac.jp/~genomelb/takezaki/poptreew/index.html). Statistical parameters (average values, variance, range, standard deviation, and errors) and data of the analysis of variance (ANOVA) were calculated by the STATISTICA 7 software program.

## RESULTS AND DISCUSSION

Individual genotypes of all the studied lizards were determined by the combination of allelic variants of three microsatellite loci (Table 1). The alleles differed in the structure of microsatellite clusters and single nucleotide variations in the parts of DNA adjacent to the microsatellite.

We suppose that these differences in alleles point to the fact that the parthenogenetic species of *D. armeniaca* originated as a result of interspecies hybridization of bisexual parent species *D. valentini* (father species) and *D. mixta* (mother species) (Moritz et al., 1992) and possible mutations (first of all, of the microsatellite DNA) in the course of the evolution of this parthenospecies.

Data on the structure of genotypes of *D. armeniaca* and their distribution in the studied populations are given in Table 2. We specified seven genotypes of *D. armeniaca*.

With respect to the variability, each of the allele variants has several microsatellite clusters with different amount of repeats, their mutations, and stable nucleotide replacements in the genome areas at the flanks of the microsatellite clusters. Genotype 1 predominates the total sampling of *D. armeniaca*, while genotype 2 is the most abundant in the Semyonov Pass and Ukrainian populations (Table 2). The predomination of genotype 2 in Ukraine is obviously inherited from the initial Semyonov Pass population. It should be mentioned that the combination of genotypes in it strongly differs from that of other populations in Armenia in the presence of genotype 2, which is unique in this region, and the absence of genotypes 5 and 6. Genotype 3 was not sampled in the Semyonov Pass population, but it is obviously present here. This is proved by the fact that the Ukrainian population has this genotype and its independent formation here is hardly probable, taking into consideration a complicated combination of different microsatellite repeats and nucleotide replacements in the flank areas of loci of this genotype. The processes of genetic differentiation are typical of the Ukrainian population (Table 2), which is proved by variations in the ratio between the genotypes inherited from the initial Armenian popula-

**Table 2.** Allelic structure and distribution pattern of genotypes in the initial (Semyonov Pass, Armenia) and introduced (Ukrainian) populations and in the group of other Armenian populations of lizards (*D. armeniaca*)

| No. | Allelic structure of genotype | Amount of animals | | |
|---|---|---|---|---|
| | | population introduced in Ukraine (%) | initial population of Semyonov Pass (%) | total sampling of the group of other populations in Armenia (%) |
| 1 | Du215(arm)2+Du215(arm)3+Du281(arm)2+Du281(arm)4+ Du323(arm)2+Du323(arm)3 | 3 (18.75%) | 1 (12.5%) | 93 (90.29%) |
| 2 | Du215(arm)2+Du215(arm)3+Du281(arm)2+Du281(arm)3+ Du323(arm)2+Du323(arm)3 | 8 (50%) | 7 (87.5%) | 0 |
| 3 | Du215(arm)2+Du215(arm)3+Du281(arm)2+Du281(arm)4+ Du323(arm)1+Du323(arm)3 | 1 (6.25%) | 0 | 7 (6.8%) |
| 4 | Du215(arm)1+Du215(arm)3+Du281(arm)2+Du281(arm)3+ Du323(arm)2+Du323(arm)3 | 3 (18.75%) | 0 | 0 |
| 5 | Du215(arm)2+Du215(arm)3+Du281(arm)1+Du281(arm)4+ Du323(arm)2+Du323(arm)3 | 0 | 0 | 2 (1.94%) |
| 6 | Du215(arm)1+Du215(arm)3+Du281(arm)2+Du281(arm)4+ Du323(arm)2+Du323(arm)3 | 0 | 0 | 1 (0.97%) |
| 7 | Du215(arm)2+Du215(arm)3+Du281(arm)2+Du281(arm)3+ Du323(arm)1+Du323(arm)3 | 1 (6.25%) | 0 | 0 |

tion and by the appearance of new ones. For example, genotypes 4 and 7, which are absent in Armenia, appeared in Ukraine, which is probably related to the process resulting in de novo formation of mutant alleles. The part of the major genotype in the Ukrainian population strongly dropped owing to the rise in the part of genotypes 1 and 3 and of the new genotypes 4 and 7. We suppose that such a quick change in the ratio between the existing genotypes is explained by the fact that the Ukrainian population underwent the effect of "bottleneck" after the introduction. It is known that most of the 129 introduced lizards died in the first winter (1963–1964), because they did not have sufficient time to find wintering places (Dotsenko, 2007). In 1964, only six relocated lizards were revealed in the area of release, while in 1965, there were six adult and two young (born in that year) animals. Only in the fourth year did the introduced population account for 33 lizards (including six young ones). Further observations performed by the collaborators of the Zoological Museum, National Academy of Sciences of Ukraine, showed that the introduced animals settled all over the rocky plot on the bank of the Teterev River and the adjacent areas (Dotsenko, 2007; Dotsenko et al., 2008–2009). The area of their distribution increased to 3000–4000 $m^2$ and was very unevenly populated with respect to the insolation rate. In general, the population density here was higher than in the Caucasus. Today, the total number of *D. armeniaca* in Ukraine is several tens of thousands of animals. Therefore, the revealed variations in the genotypic (clonal) structure of the introduced animals are obviously related to the specific conditions of development of their population, in particular, to weather factors, wintering specificity, and different kinds of anthropogenic impact.

The mutations exerting an effect on the number of microsatellite repeats of the alleles of the studied loci, the nucleotide composition of the repeat, and nucleotide replacements in the flank areas of microsatellite clustersare obviously characterized by different rates, generation time, and molecular mechanisms. Our previous investigation of another parthenogenetic species *Darevskia dahli* (Vergun et al., 2014) showed that stable combinations of single nucleotide replacements in the flank areas of microsatellite clusters were generated in the time of hybridization of phylogenetically initial bisexual parent species and were reliably inherited by the populations of filial species with formation of haplotypes in the amount equal to the number of hybridization acts of the parent species. The study of the three marked loci show that all representatives of *D. armeniaca* in Armenia and Ukraine belong to one haplotype and the mutations of nucleotide composition of microsatellite repeats do not differ from the inherited maternal and paternal alleles (Table 1). All the genotype variations are seen only in the number (GATA) of repeats in the same clusters for the maternal and paternal branches. This makes the applied combination of loci informative for the reconstruction of the processes of origination of genotypes in the studied populations. We constructed the phylogenetic networks of the ori-

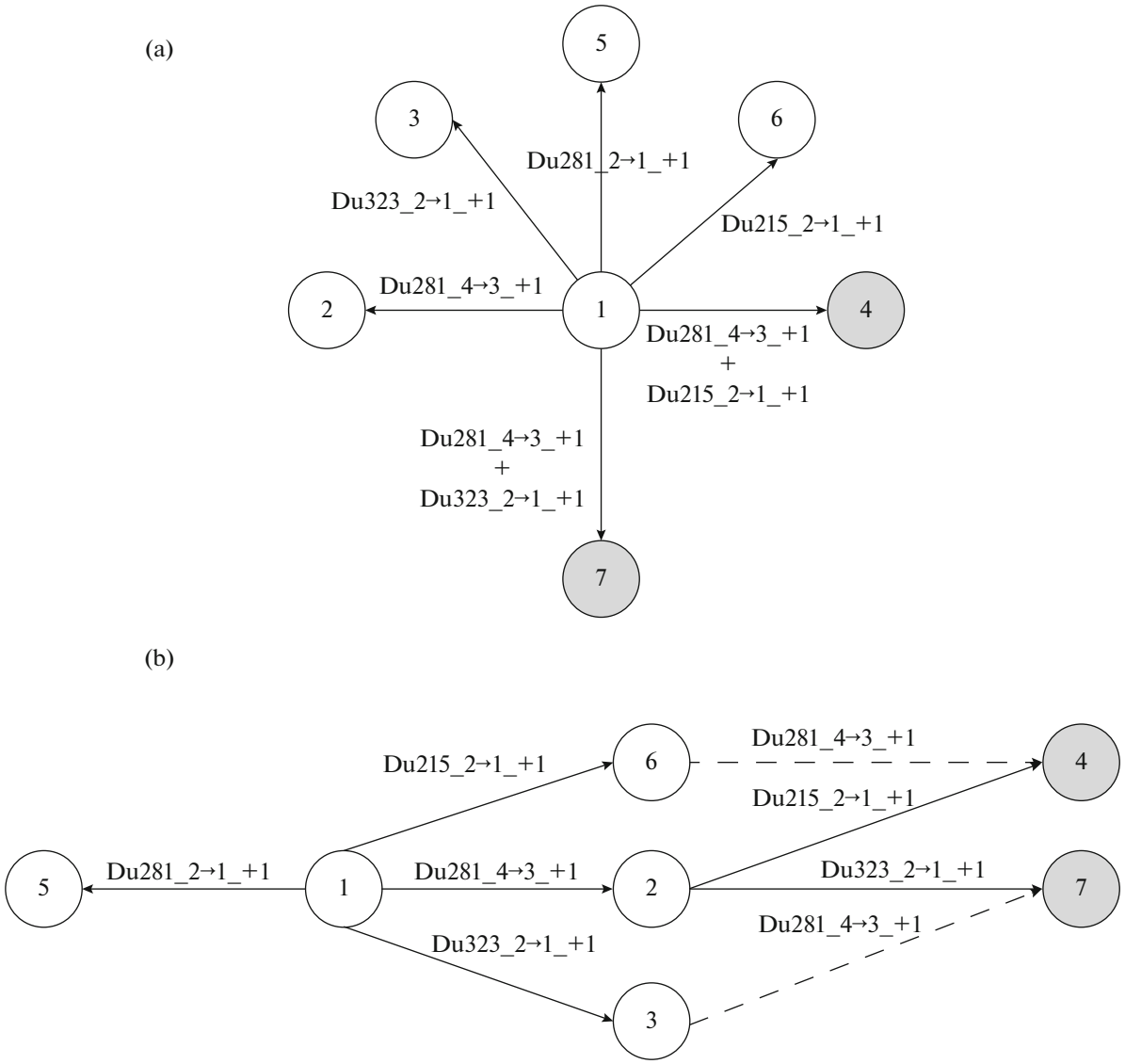


**Fig. 2.** Phylogenetic networks of origin of genotypes according to hypotheses of (a) simultaneous and (b) successive fixation of mutations. Genotypes formed in the population introduced to Ukraine are colored gray. The least probable mutations (explanations are in the text) are shown by dashed line. Designations above arrows should be read as follows: Locus_no. of initial allele→no. of mutation allele (+)increase/(–)decrease of GATA cluster by *n* repeats.

gin of genotypes on the basis of the hypothesis of simultaneous (Fig. 2a) and successive (Fig. 2b) fixation of new mutations in the populations. Genotype 1 was chosen as the initial one for the following reasons: (i) this is the major and most widespread genotype in the gene pool of the *D. armeniaca* species; (ii) in the case of its choice as the initial genotype, the directions of all the mutations result in the increase by only one GATA repeat for each microsatellite cluster in all the genotypes. This corresponds to the principle of minimal evolution and the thermodynamic criteria of the molecular evolution of microsatellites discussed by us (Omelchenko and Korchagin, 2009). We have come to a conclusion that the microsatellite clusters with similar structure are characterized by the same mutation tendencies, which result in an increase or decrease in the number of microsatellite repeats with respect to the local minimum of the Gibbs energy of allele.

The analysis of Fig. 2 also shows that there are different possible trends of evolution of the given genotypes. If we accept the hypothesis that the mutations in different loci are simultaneous and are fixed in populations at the same time (Fig. 2a), it may be concluded that each genotype was formed from genotype 1 via an increase in the microsatellite cluster by one GATA repeat. The exception is represented by genotypes 4 and 7, which were formed by two simultaneous one-step mutations. According to this model, the mutation

rates in the loci of the Ukrainian population are considerably higher than those in the same loci of the Armenian populations. With respect to the second hypothesis, the mutation rates in the same loci and microsatellites are identical independently of the population, and the mutations are successively fixed (Fig. 2b). This hypothesis corresponds to the Stepwise mutation (SM) model of microsatellite variability. According to it, the mutations of microsatellite cause its successive changes by its decrease or increase by only one repeat per each mutation act (Oliveira et al., 2006; Badaeva et al., 2008). This explains the origin of genotypes 4 and 7 of the Ukrainian population from genotype 2. Paths of formation of genotype 4 from genotype 6 and genotype 7 from genotype 3 are hardly probable, because genotypes 3 and 4 were not revealed in the population of Semyonov Pass. Contrary to them, genotype 2 most often occurs in the populations of Ukraine and Semyonov Pass. It may be concluded that, knowing the time of the appearance of genotype 2 in Ukraine (the introduction of 1963) and of the revelation of genotypes 4 and 7 in the Ukrainian population (the catch of lizards in 2001), we may determine that the upper time limit of the latest one-step microsatellite mutation and its fixation in the population was 38 years. As a result of the studied mutation processes, the diversity of genotypes in the introduced Ukrainian population became higher than that in the initial population of Semyonov Pass (five compared to two genotypes) and even exceeded the genotypic diversity of the species in Armenia (four genotypes). At the level of allelic diversity, this phenomenon is confirmed by the observed heterozygosity ($H_{obs.}$) of the populations: $H_{obs} = 0.575$ (SE = 0.011) for the Ukrainian population, $H_{obs} = 0.518$ (SE = 0.018) for the Semyonov Pass population, and $H_{obs} = 0.515$ (SE = 0.010) for the total sampling of the other populations in Armenia. Taking into consideration the standard errors, one may state that the intrapopulation parameter of genetic diversity (heterozygosity) of the initial population of Semyonov Pass is equal to that of all the remaining populations in Armenia. This enables the assumption that, if any other Armenian population were used as the initial one for the introduction, the intrapopulation genetic diversity of the Ukrainian population would also increase at the levels of alleles and genotypes. So it may be supposed that the high allelic and genotypic diversity of *D. armeniaca* in Ukraine is not related to the greater genetic diversity of the initial population, but is explained by other reasons.

It should be mentioned that the introduction of a species may be accompanied by both a rise and a drop in genetic diversity, and the heterozygosity of the introduced population may remain similar to that of the initial population. A decrease in heterozygosity may be seen by the example of the populations of house sparrow *Passer domesticus*, where $H_{obs}$ varies from 0.77 to 0.89 for the initial populations and from 0.59 to 0.81 for the invasive ones (Schrey et al., 2011). A considerable drop in the heterozygosity is seen for the introduced populations of the four fish species of the *Neogobius* genus living in the Ponto-Caspian water basin (Ondrackova et al., 2012). The values of $F_{st}$ between the initial and invasive populations vary widely from 0.053 to 0.591. Successful invasion of parthenogenetic species of an initial population with low genotypic diversity and preservation of its level in the introduced population may take place. This is shown by the example of the populations of mud snail *Potamopyrgus antipodarum* in the United States of America (Dybdahl and Drown, 2011). The tendency for preservation of heterozygosity in the initial and introduced populations is also seen for lizard *Podarcis muralis* at its invasion from Eastern France to Germany (Schulte et al., 2012). Similar heterozygosity is also seen in the initial (in the United States, $H_{obs} = 0.656$ on average) and introduced (in Sweden, Denmark, Germany, Great Britain, and France, $H_{obs} = 0.644$ on average) populations of sea mollusks *Crepidula fornicata* (Riquet et al., 2013). Parallel to the given examples, there are introduced populations with high heterozygosity: the population of two crab species—*Hemigrapsus sanguineus* and *Hemigrapsus takanoi*—with heterozygosity up to 0.935 and 0.781, respectively (Poux et al., 2015). The authors of the given works point out that heterozygosity rises when the introduced populations hybridize with the existing ones of this species. For lizard *Podarcis muralis*, this was experimentally proved (Schulte et al., 2012).

Though the population of Semyonov Pass is similar to the other populations of Armenia with respect to intrapopulation genetic characteristics (heterozygosity), it strongly differs from them in the interpopulation parameter $F_{st}$. The values of $F_{st}$ for the studied populations are shown in Fig. 3, in which the genetic differences between them and the group of Armenian populations are seen. The parameter $F_{st}$ for the group of the Armenian populations in Fig. 3 shows interpopulation genetic distances in the group. The population of Semyonov Pass is characterized by the greatest $F_{st}$ ($F_{st} = 0.109$, SE = 0.009). It should be mentioned that the three population groups reliably differ in this parameter: $F(2, 207) = 33.218$ ($p = 0.00000$). The analysis of these variations by the Tukey's post-hoc test shows that they are mainly related to the interpopulation differences of the group of Armenian populations from the population of Semyonov Pass ($p = 0.000022$) and the Ukrainian population ($p = 0.000026$). The difference in the $F_{st}$ criterion of the Ukrainian and Semyonov Pass populations is not statistically significant ($p = 0.252953$). It corresponds to $F_{st} = 0.01$, which is significantly lower than the mean $F_{st}$ between the initial and introduced populations of lizard *Podarcis muralis* (0.275) (Schulte et al., 2012). These differences may be explained by the fact that this lizard is an bisexual reptilian, and its invasion started prior to its dispersal in

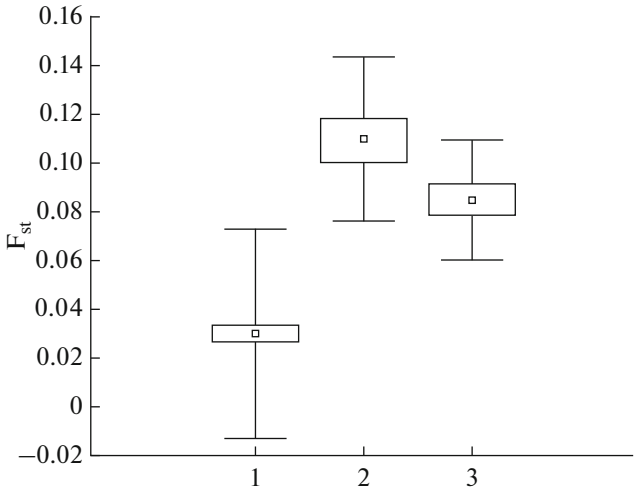


**Fig. 3.** $F_{st}$ of the studied populations in comparison with Armenian populations. Squares are mean $F_{st}$, rectangles are the range of standard errors, and straight lines are the range of standard deviations. (1) Total sampling of Armenian populations, (2) sampling of the initial population of Semyonov Pass, (3) sampling of the introduced Ukrainian population.

Ukraine. It may be concluded that the initial $F_{st}$ of the Semyonov Pass population strongly differed from $F_{st}$ of the Armenian populations ($F_{st}$ = 0.029, SE = 0.010), while their interpopulation variabilities were similar. After the introduction to Ukraine, the mutations in the studied loci became more intense and were fixed, which made its interpopulation genetic differences smaller in comparison with the Armenian populations ($F_{st}$ = 0.084, SE = 0.006); i.e., the mutations in the two populations were similar. This assumption corresponds to the hypothesis of *k* alleles of microsatellite variability. According to it, the alleles with a particularly favorable number of microsatellite blocks begin to predominate in the population as a result of the rate and direction of mutations in microsatellite clusters (Oliveira et al., 2006).

The introduced populations of mammals (for example, the population of black rat *Rattus rattus*) are characterized by similar $F_{st}$ distances in the range from 0.132 to 0.228 with respect to the geographical distances between the invading populations (Konecny et al., 2013).

## CONCLUSIONS

Within the 38-year period after the introduction of *D. armeniaca* lizards to Ukraine, the mutations in the microsatellite loci of their genomes were seen only in one repeat of microsatellite clusters and were absent in the flanks on genomes. The allelic structure of the initial Armenian population exerted a strong effect on the composition of alleles of the introduced population. Within the period of development under new conditions, the allelic and genotypic diversity of the introduced population increased. The general directions of fixed mutations in the Ukrainian and initial Armenian populations of *D. armeniaca* are similar, which may point to the predominating role of molecular intergenomic processes in microsatellite loci under the effect of ecological factors of the environment (at least, in the studied period).

Though the experiment of the introduction of parthenogenetic lizards *D. armeniaca* to Ukraine may have dangerous ecological consequences, it formed the basis for important population and genetic investigations and for studying the regularities of formation of genetic and clonal diversity of animals under the effect of new habitat conditions.

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## REFERENCES

Badaeva, T.N., Malysheva, D.N., Korchagin, V.I., and Ryskov, A.P., Genetic variation and de novo mutations in the parthenogenetic Caucasian rock lizard *Darevskia unisexualis, PLoS One*, 2008, vol. 3, no. 7, p. e2730. doi 10.1371/ journal.pone.0002730

Darevsky, I.S. and Shcherbak, N.N., Acclimatization of parthenogenetic lizards in Ukraine, *Priroda* (Moscow, Russ. Fed.), 1967, no. 3, pp. 93–94.

Darevsky, I.S., Kan, N.G., Ryabinina, N.L., Martirosyan, I.A., Tokarskaya, O.N., Grechko, V.V., Shcherbak, N.N., Danielyan, F.D., and Ryskov, A.P., Biochemical, molecular, and genetic characteristics of parthenogenetic lizards *Lacerta armeniaca* (Mehely), introduced from Armenia to Ukraine, Dokl. Akad. *Nauk*, 1998, vol. 363, no. 6, pp. 846–848.

Dotsenko, I.B., The Condition of experimental population of Caucasian rock lisards of genus Darevskia in Zitomir province of Ukraine, *Nauk. Visn. Uzhgorod. Univ., Ser. Biol.,* 2007, no. 21, pp. 14–19.

Dotsenko, I.B., Peskov, V.N., and Miropolskaya, M.V., Comparative analysis of genus Darevskia rock lizards external morphology from the territory of Ukraine, and the species belonging of them, *Zb. Zool. Muz.*, 2008–2009, no. 40, pp. 129–140.

Dybdahl, M.F. and Drown, D.M., The absence of genotypic diversity in a successful parthenogenetic invader, *Biol. Invasions*, 2011, vol. 13, pp. 1663–1672.

Konecny, A., Estoup, A., Duplantier, J.M., Bryja, J., Ba, K., Galan, M., Tatard, C., and Cosson, J.F., Invasion genetics of the introduced black rat (*Rattus rattus*) in Senegal, West Africa, *Mol. Ecol.*, 2013, vol. 22, no. (2), pp. 286–300.

Malysheva, D.N., Vergun, A.A., Martirosyan, I.A., Tokarskaya, O.N., and Ryskov, A.P., Molecular and genetic characterization of allelic variants of microsatellite loci in parthenogenetic caucasian rock lizards *Darevskia armeniaca* (Lacertidae), *Mol. Genet. Mikrobiol. Virusol.*, 2008, vol. 23, no. 4, pp. 195–201.

Moritz, C., Uzzel, T., Spolsky, C., Hotz, H., Darevsky, I.S., Kupriyanova, L., and Danielyan, F., The maternal ancestry and approximate age of parthenogenetic species of Caucasian rock lizards (Lacerta: Lacertidae), *Genetics*, 1992, vol. 87, no. 1, pp. 53–62.

Oliveira, E.J., Padua, J.G., Zucchi, M.I., Vencovsky, R., and Vieira, M.L.C., Origin, evolution and genome distribution of microsatellites, *Genet. Mol. Biol.*, 2006, vol. 29, no. 2, pp. 294–307.

Omelchenko, A.V. and Korchagin, V.I. Thermodynamic characteristization of di-, tri-, and tetranucleotide microsatellite loci in parthenogenetic lizards *Darevskia unisexualis, Russ. J. Genet.*, 2009, vol. 45, no. 8, pp. 1004–1008.

Ondrackova, M., Simkova, A., Vyskocilova, M., and Jurajda, P., Parasite diversity and microsatellite variability in native and introduced populations of four *Neogobius* species (Gobiidae), *Parasitology*, 2012, vol. 139, no. 11, pp. 1493–1505.

Poux, C., Gothland, M., Holl, A.C., Spilmont, N., and Arnaud, J.F., Highly polymorphic microsatellite markers in two species, the invasive shore crabs *Hemigrapsus sanguineus* and *Hemigrapsus takanoi* (Decapoda, Varunidae), *Conserv. Genet. Resour.*, 2015, vol. 7, no. 2, pp. 569–572.

Riquet, F., Daguin-Thiebaut, C., Ballenghien, M., Bierne, N., and Viard, F., Contrasting patterns of genome-wide polymorphism in the native and invasive range of the marine mollusc *Crepidula fornicata, Mol. Ecol.*, 2013, vol. 22, no. 4, pp. 1003–1018.

Schrey, A.W., Grispo, M., Awad, M., Cook, M.B., McCoy, E.D., Mushinsky, H.R., Albayrak, T., Bensch, S., Burke, T., Butler, L.K., Dor, R., Fokidis, H.B., Jensen, H., Imboma, T., Kessler-Rios, M.M., et al., Broad-scale latitudinal patterns of genetic diversity among native European and introduced house sparrow (*Passer domesticus*) populations, *Mol. Ecol.*, 2011, vol. 20, no. 6, pp. 1133–1143.

Schulte, U., Veith, M., and Hochkirch, A., Rapid genetic assimilation of native wall lizard populations (*Podarcis muralis*) through extensive hybridization with introduced lineages, *Mol. Ecol.*, 2012, vol. 21, pp. 4313–4326.

Vergun, A.A., Martirosyan, I.A., Semyenova, S.K., Omelchenko, A.V., Petrosyan, V.G., Lazebny, O.E., Tokarskaya, O.N., Korchagin, V.I., Ryskov, A.P., Clonal diversity and clone formation in the parthenogenetic Caucasian rock lizard *Darevskia dahli, PLoS One*, 2014, vol. 9, no. 3, p. e91674. doi 10.1371/journal.pone.0091674

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