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Review

Evolution of parthenogenetic reproduction in Caucasian rock lizards: a review

Marine Arakelyan[a,*,#], Victor Spangenberg[b,#], Varos Petrosyan[c], Alexey Ryskov[d], Oksana Kolomiets[b], and Eduard Galoyan[c,e,#]

[a]Department of Zoology, Yerevan State University, Yerevan, Armenia
[b]Vavilov Institute of General Genetics, Moscow, Russia
[c]Severtsov Institute of Ecology and Evolution RAS, Moscow, Russia
[d]Institute of Gene Biology, RAS, Moscow, Russia
[e]Zoological Museum of Moscow State University, Moscow, Russia

*Address correspondence to Marine Arakelyan. E-mail: arakelyanmarine@ysu.am
#These authors contributed equally.
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Abstract

Despite numerous works devoted to hybrid origin of parthenogenesis in reptiles, the causes of hybridization between different species, resulting in the origin of parthenogenetic forms, remain uncertain. Recent studies demonstrate that sexual species considered parental to parthenogenetic rock lizards (*Darevskia* spp.) avoid interspecific mating in the secondary overlap areas. A specific combination of environmental factors during last glaciation period was critical for ectotherms, which led to a change in their distribution and sex ratio. Biased population structure (e.g., male bias) and limited available distributional range favored the deviation of reproductive behavior when species switched to interspecific mates. To date, at least 7 diploid parthenogenetic species of rock lizards (*Darevskia*, Lacertidae) originated through interspecific hybridization in the past. The cytogenetic specifics of meiosis, in particular the weak checkpoints of prophase I, may have allowed the formation of hybrid karyotypes in rock lizards. Hybridization and polyploidization are 2 important evolutionary forces in the genus *Darevskia*. At present, throughout backcrossing between parthenogenetic and parental species, the triploid and tetraploid hybrid individuals appear annually, but no triploid species found among *Darevskia* spp. on current stage of evolution. The speciation by hybridization with the long-term stage of diploid parthenogenetic species, non-distorted meiosis, together with the high ecological plasticity of Caucasian rock lizards provide us with a new model for considering the pathways and persistence of the evolution of parthenogenesis in vertebrates.

Key words: Caucasus, glacial period, hybridization, reptiles, reticulate evolution, unisexual

Introduction

Caucasian rock lizards (*Darevskia* spp.) are the unique group of reptiles in which natural obligate parthenogenesis was first discovered among vertebrates (Darevsky 1958, 1967). Soon after, this phenomenon has been found in several different reptile families (Lowe and Wright 1966; Hall 1970; Cuellar and Kluge 1972; McDowell 1974; Nussbaum 1980; Cole et al. 1988; Moritz et al. 1992) and seems to be not as rare as it first thought (Kearney et al. 2009). As other parthenogenetic species of reptiles, the 7 parthenogenetic *Darevskia* species originated from hybridization between 2 different species of the same genus. First experiments to prove hybrid origin of unisexual rock lizards were established by I.S. Darevsky and F.D. Danielyan, who experimented on skin transplantation between different individuals of the same parthenogenetic species (Darevsky and Danielyan 1979) and then compared allozymes of parthenogenetic and sexual species (Uzzell and Darevsky 1974; MacCulloch et al. 1995). The proof became firmer with development of genetic studies and compelling evidence of the hybrid origin of parthenogenetic species in the genus *Darevskia* came with mitochondrial (Moritz et al 1992; Fu et al. 1997, 1998; Murphy et al. 2000), and nuclear DNA sequence data (Kan et al. 1998; Ryabinina et al. 1999; Tokarskaya et al. 2001; Ryskov 2008; Vergun et al. 2014; Freitas et al. 2016; Ryskov et al. 2017; Girnyk et al. 2018; Vergun et al. 2020; Yanchukov et al. 2022). These studies revealed that parthenogenetic species arose from interspecific crossing between "paternal" species *D. valentini* and *D. portschinskii* from the "rudis" phylogenetic clade, and the "maternal" species *D. raddei*, and *D. mixta* from the "caucasica" clade (Murphy et al. 1996) or "raddei" clade (Arribas 1999; Figure 1). Recently, in situ comparative genomic hybridization allowed visualizing two sets of parental chromosomes in the somatic nuclei of parthenogenetic lizards (Spangenberg et al. 2020a, 2020b, 2021).

Despite the numerous pieces evidence indicating that most parthenogenetic vertebrates originated initially as hybrids, produced between closely related sexual species (Cuellar 1974), the causes that lead to the interspecies hybridization and overcoming the prezygotic (premating) reproductive barriers between males from one species and females from

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another remain uncertain. This is rather surprising for genus *Darevskia* spp., given the significant diversification of parental forms (Fu et al. 2000; Murtskhvaladze et al. 2020) and how genetic, morphological, and behavioral adaptations have advanced (Gabelaia et al. 2017; Tarkhnishvili et al. 2020).

Recent genetic and cytogenetic studies together with ecological niche modeling based on data of distribution of parthenogenetic and sexual rock lizards in combination with traditional ecological and ethological research provided new information to discuss the pathways of origin and evolution of parthenogenetic reptiles. Modern distribution and the evolutionary success of parthenogenetic species are different from each other. Some species, such as *D. armeniaca*, *D. dahli*, and *D. unisexualis*, have a wide distribution and abundant populations (Petrosyan et al. 2019, 2020a, 2020b). *D. rostombekowi* and *D. bendimahiensis* occupy restricted areas with low population density, while *D. sapphirina* is known in only one locality (Cuellar and Smart 1979; Schmidtler et al. 1994; Meiri et al. 2017). The challenges in studying of parthenogenetic lizards are mechanism of co-existence of these forms with sexual relative species. The parthenogenetic species in many places coexist with sexual relative species (Petrosyan et al. 2020a), where the hybridization events are ongoing, and annually, presumably sterile triploids and even tetraploid hybrids appear in mixed population of *Darevskia* spp. (Figure 1; Darevsky and Kulikova 1964; Darevsky 1966; Darrevsky and Danielyan 1968; Darevsky et al. 1973). Some authors consider parthenogenesis in rock lizards an intermediate stage of reticulate evolution directed towards the formation of new species with a higher level of ploidy (Figure 2; Borkin and Darevsky 1980; Darevsky 1992, 1995; Danielyan et al. 2008). According to scheme of hybrid speciation in *Darevskia* (Figures 1 and 2), diploid parthenogenetic species continue to evolve like a net (Figure 1), which displays a number of reticulate evolutionary events with increasing levels of ploidy. Indeed, tetraploid individuals of rock lizards have already been recorded in nature (Danielyan et al. 2008), but the process of the emergence of a new tetraploid species is proceeding. The unique model of Caucasian rock lizards can serve as evidence of reticulate evolution where only diploid forms are persists as species. Therefore, a number of questions arise: 1) what are the main causes of interspecific hybridization and switching to parthenogenetic reproduction in the evolution of reptiles and can it happen now, 2) how does polyploidization occur in parthenogenetic species of genus *Darevskia*, and 3) why, unlike other unisexual reptiles, only diploid parthenogenetic species survive through ages?

Causes of Interspecies Hybridization of Caucasian Rock Lizards

Transition from sexual reproduction to parthenogenesis in reptiles is frequently associated with a major change in geographical distribution due to glaciation, flooding, natural burning, beach dwelling, and islands (Cuellar 1977; Kearney 2005). Most studies suggest that parthenogenetic rock lizards of genus *Darevskia* appeared in the environment severely affected by the glacial cycles of the Late Pleistocene (140–22 thousand years ago) (Moritz et al. 1992; Darevsky 1966, 1995; Kupriyanova 2010; Freitas et al. 2016; Girnyk et al. 2018), associated with the major changes in the geographical distribution of the sexual species. However, recent study of sex chromosome revealed even earlier time of their origin: from 0.5 to 1 Mya (Yanchukov et al. 2022). As a result of the overlap of the distribution areas of the sexual species of *Darevskia* and unstable suboptimal environmental conditions for lizards, the interspecific hybridization between the species was probably triggered. Sexual species of rock lizards in a certain range of genetic distances, which, according to the "balance hypothesis", are acceptable for interspecific hybridization (Moritz 1989; Fu et al. 2000; Tarkhnishvili

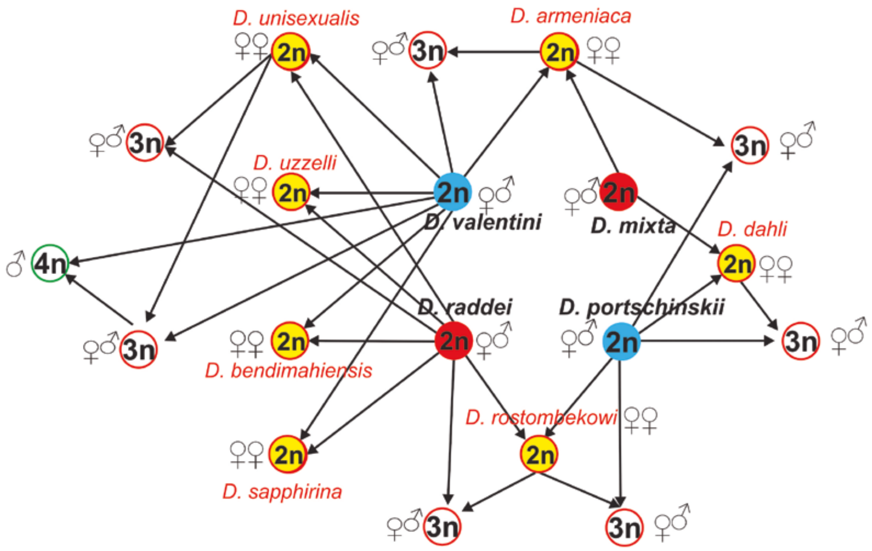

Figure 1. The web of hybridization events among lizards in the genus *Darevskia*. The filled cycles represent species, the empty cycles—individuals, the numbers within the cycles are the level of ploidy of lizards, and the arrows show the parents of interspecies hybridization. Females of the sexual species (marked by black bold font) of the *Darevskia* clade "caucasica" (red cycles) and males of the sexual species of the clade "rudis" (blue cycles) participated in hybridization and gave rise to seven parthenogenetic species (yellow cycles, red font of species names) in past. The triploid hybrids (white cycles circled in red) arise annually from backcrossing between parthenogenetic and sexual species, and tetraploid individuals (male only) arise from backcrossing between triploid hybrids and sexual species (white cycle circled in green). For color, please refer to the online images.

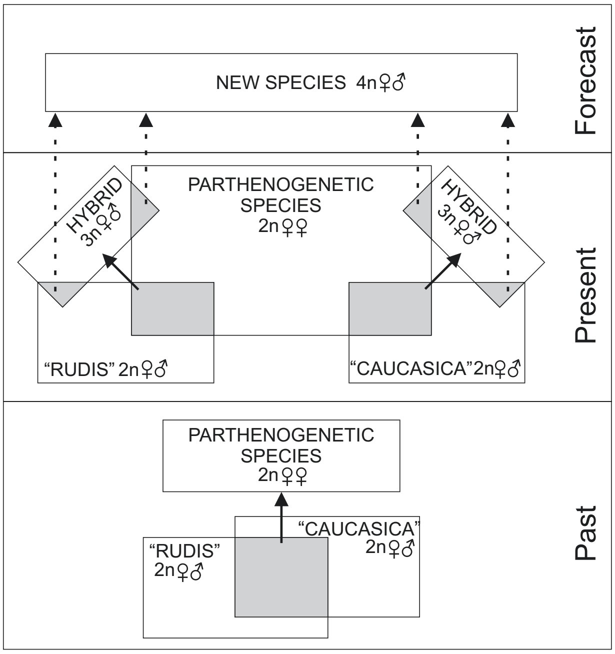

Figure 2. Consequences of stepwise hybridization with increasing the ploidy level of lizards in process of reticulate evolution in the genus *Darevskia*. The grey areas correspond to known hybrid zones between species, the arrows show on the result of interspecies hybridization and punctuate arrows show on the possible result of hybridization during 3 stages of reticulate evolution in rock lizards. In "rudis" phylogenetic clade of lizards are *D. valentini* and *D. portschinskii* "paternal" sexual species, in "caucasica" clade of lizards—*D. raddei* and *D. mixta* "maternal" sexual species, parthenogenetic species are *D. armeniaca*, *D. dahi*, *D. unisexualis*, *D. rostombekowi*, *D. uzzelli*, *D. bendimahiensis*, and *D. sapphirina*.

et al. 2013; Freitas et al. 2019), occurred in the same territory and could potentially interbreed with each other.

The existing populations of sexual species of *Darevskia* seem to demonstrate a pre-mating reproductive isolation in sympatric zones of 2 species. Several secondary overlap areas of parental sexual species are present in the Caucasus (Darevsky 1967; Darevsky and Danielyan 1979; Tarkhnishvili et al. 2010; Petrosyan et al. 2019, 2020a). Recent studies of sympatric populations of *D. portschinskii* and *D. raddei*, which are parental for parthenogen *D. rostombekowi* (Murphy et al. 2000; Freitas et al. 2016) in the Karvachar area (Petrosyan et al. 2020a) showed that both species exploit the same habitats and overlap in periods of gameto- and oogenesis. They are also similar in their daily and seasonal activities and occupy close ecological niches (Galoyan et al. 2019). Cytogenetic studies revealed that the mechanisms of post-zygotic isolation are not strict among them and both species possess similar sets of chromosomes with the same morphology (Spangenberg et al. 2017). However, a microsatellite study of individuals within this population revealed an absence of hybrids (Galoyan et al. 2020). Behavioral observations proved presence of reproductive pre-mating isolation between *D. r. raddei* and *D. portschinskii*: individuals of both species do not mate with heterospecifics and distinguish between conspecifics and heterospecifics of both sexes (Galoyan et al. 2019).

However, it is obvious that since the parthenogenetic lineages are of hybrid origin, the sexual species successfully overcame the reproductive barrier in the past. Here we assume that harsh climate and reducing the suitable habitats for rock lizards collapsed reproductive barrier in glacial period but it restored again after stabilization of environment conditions. Behavioral adjustment is the common response in animal adaptation to environmental change (Wong et al. 2015). Due to an imbalance of sex ratio in population of lizards under suboptimal conditions, which is often male-biased (Veen et al. 2001; Donald 2007; Kurek et al. 2019), interspecific mating among sexual species of *Darevskia* became frequent, which provided opportunities for the origin of parthenogenetic lizards. A growing number of examples in the literature have documented cases where environment changes (e.g., human activities, climate change) have altered long-established species interactions, including hybridization (Grabenstein and Taylor 2018). The importance of the environment as a factor affecting hybridization probability is the best demonstrated by the wall lizards *Podarcis*, where different species of this genus hybridize in the cities after multiple introductions of non-native lineages (Beninde et al. 2018).

Thus, the hybridization between the sexual species of *Darevskia* is not observed nowadays because of the pre-mating reproductive barrier, but it likely happened due to behavioral changes in response to increased environmental stress factors in period of the glacial cycles of the Late Pleistocene, which caused the appearance of parthenogenetic individuals in the newly created hybrid zones. The lack of evidence for the *de novo* appearance of parthenogenetic species after a period of glaciation may also indicate the role of stress factors during the glacial cycles for overcoming the prezygotic (or premating) reproductive barrier for interspecific hybridization (Figure 1).

Cytogenetic Mechanism of Parthenogenesis

Understanding the cytogenetic mechanism through which parthenogenesis can evolve after hybridization events between sexual species remains a key issue for explanation of speciation by hybridization in vertebrates. In general, parthenogenetic reproduction may allow lizards to overcome the barrier of hybrid sterility of interspecific offspring derived from divergent parent species. (Figure 2). Notably, the cytogenetic specifics of meiosis of *Darevskia* spp., in particular the weak checkpoints of prophase I, may have allowed the formation of hybrid karyotypes in rock lizards (Spangenberg et al. 2017). Therefore, after the primary act of interspecific hybridization between different sexual species of rock lizards, the germ cells of the hybrid individuals were able to overcome the problems of chromosomal synapsis in meiosis (Spangenberg et al. 2020a). In the following generations, the processes associated with overcoming the so-called genomic shock may have followed, which "forced the genome to restructure itself in order to overcome a threat to its survival" (McClintock 1984).

Gametes of vertebrates are produced by several different cytogenetic mechanisms (Dedukh et al. 2020). A common way of restoration of set of chromosomes in parthenogenetic reptiles (*Aspidoscelis*) includes premeiotic DNA endoreplication during the proliferation of germ cells, which allows synapsis of identical chromosome copies (pseudobivalents) in meiosis I and leads to the production of unreduced gametes (Lutes et al. 2010; Newton et al. 2016; Dedukh et al. 2020). Detailed study of meiosis in the parthenogenetic *Darevskia* species suggests diploidy restoration through automixis, which proceeds according to the "central fusion" mechanism (Darevsky et al. 1973; Spangenberg et al. 2020a). Parthenogenetic species of

Darevskia lizards undergo meiosis, which includes synapsis of homeologous chromosomes (inherited from different species) in the normal ploidy oocytes I (Spangenberg et al. 2020a, 2021). This conclusion arose from the detection of the numerous nuclei with non-distorted late (pachytene and diplotene) stages of meiotic prophase I in parthenogenetic *Darevskia*. As well as from the study of meiosis in $2n = 37$ *D. unisexualis* population, where formation of the autosomal trivalent reliably confirmed true synapsis of homeologues but not formation of "pseudobivalents" (Spangenberg et al. 2021). On the other hand, the possibility of detection premeiotic endoreplication as the most obvious way to freeze recombination cannot be ruled out in the future (Newton et al. 2016).

Ecological Plasticity of Parthenogenetic Rock Lizards

Parthenogenetic reproduction of vertebrates is theoretically associated with 2-fold demographic advantage of producing all-female offspring (Maynard-Smith 1978; Otto 2009) and high acquired heterozygosity in the hybrid genome, which fit well into different ecological niches. Lowe and Wright (1966) suggested the "weed hypothesis" to explain why rapid distribution of parthenogenetic lizards of *Aspidoscelis* genus occurred during the Pleistocene climate fluctuations. According to them, parthenogenetic species occupy unstable areas due to double reproduction ability and they often inhabit the historically unstable areas (Wright and Lowe, 1968). In a similar way, several parthenogenetic lineages of gecko species, *Lepidodactylus lugubris* widely distribute through the Pacific islands but the parental sexual species occurred only in a limited range (Ineich 1999; Karin et al. 2021). The geographical parthenogenesis hypothesis suggests that parthenogenetic forms have broader distribution areas than their sexual relatives, especially in previously glaciated areas, since they occupy the 'marginal' suboptimal habitats (Kearney 2005; Vrijenhoek and Parker 2009).

Indeed, some parthenogenetic species of *Darevskia* genus have an apparent success under natural conditions, attain high population densities, wide distribution, and even exclude their sexual relative species (Arakelyan et al. 2011, 2019; Freitas et al. 2016; Tarkhnishvili et al. 2017). Among 7 parthenogenetic species of *Darevskia*, several (*D. saphpirina*, *D. bendimahiensis*, *D. uzzeli*, and *D. rostombekowi*) occupy restricted areas (Cuellar and Smart 1979; Schmidtler et al. 1994; Meiri et al. 2017), while *D. unisexualis*, *D. dahli*, and *D. armeniaca* have a relatively wide distribution (Arakelyan et al. 2011; Petrosyan et al. 2020a).

In order to understand the consequences of parthenogenetic reproduction of *Darevskia* species, it is required to define the niche differences between parthenogenetic and sexual species in accordance with frozen niche variation (FNV) model. This model suggests that sexual species are not able to co-exist with a large number of parthenogenetic lineages that can suppress them. According to Darevsky (1966) the parthenogenetic populations of rock lizards survived extreme environmental conditions, whereas the sexual populations either died out or were pushed to the south under the influence of glacier (Cuellar 1977). Modeling ecological niches for parthenogenetic *D. dahli* and its parental species *D. mixta* and *D. portschinskii* demonstrated the differentiation between lizard ecological niches and species-specific requirements for environmental variables and support the geographical parthenogenesis hypothesis in a group of rock lizards (Petrosyan et al. 2019). The indicators of the overlap of ecological niche indices are low between parthenogenetic *D. dahli* and maternal *D. mixta*, but are high between *D. dahli* and paternal *D. portschinskii*. Thus, the ecological niches breadth of parthenogenetic forms D. *dahli* is significantly larger than this in "maternal" species *D. mixta* (Petrosyan et al. 2020b). Therefore, in case of *Darevskia* species, the FNV model is supported by the fact that range modeling of *D. armeniaca* and *D. dahli* has shown that they continue to spread and even suppress the parental species (Petrosyan et al. 2019, 2020b). Parthenogenetic rock lizards usually have intermediate requirements for habitat variables relative to those of their parental species, but some variables strongly differ from their parental species (Petrosyan et al. 2019, 2020b). Moreover, the competition between the maternal sexual species *D. mixta* with daughter parthenogenetic *D. dahli* and *D. armeniaca* caused a shift in the range boundary of *D. mixta* to the west of its native range due to displacement by both parthenogenetic forms (Tarkhnishvili et al. 2010; Petrosyan et al. 2020a). The wide distribution of parthenogenetic *D. armeniaca* may also be explained by its complex origin, since it has been previously suggested that this parthenogenetic species appeared after two hybridization events (Tarkhnishvili et al. 2010).

The next popular mechanisms of co-existence of sexual and parthenogenetic forms is described in the frameworks of the "General Purpose Genotype" hypothesis (GPG), which assumes the existence of a multiclonality of parthenogenetic forms because natural selection can act more efficiently towards polyphyletic clones (Vrijenhoek & Parker, 2009). The study of genetic variability of *Darevskia* parthenogenetic species evidences that the ecological adaptations of species correlated with high clonal diversity and GPG model showed a reliable prediction in case of *Darevskia* species. There are at least 11 lineages (microsatellite genotypes) known for *D. dahli* (Vergun et al. 2014), five for *D. rostombekowi* (Ryskov et al. 2017), 13 for *D. armeniaca* (Girnyk et al. 2018), and 12 for *D. unisexualis* (Vergun et al. 2020). A comparative study of microsatellite mutations at highly unstable loci of parthenogenetic lizards and their offspring revealed *de novo* mutations that significantly contributed to the population variability of parthenogenetic species (Badaeva et al. 2008). The ecological and genetic plasticity of parthenogenetic *D. armeniaca* and *D. dahli* has been proved experimentally. In 1963, I.S. Darevsky and N.N. Shcherbak initiated an experiment on the introduction of *D. armeniaca* from Armenia to Ukraine. More than half a century later, successfully introduced lizards have increased their range, population density and genetic diversity (Darevsky and Shcherbak 1967; Nekrasova and Kostiushyn 2016; Omelchenko et al. 2016). Similar to sexual reproduction, which increases genetic and phenotypic variability through recombination, parthenogenetic forms have their own evolutionary pathways that remain to be explored, at least in terms of a large range of geographical distribution (Arakelyan et al. 2011; Petrosyan et al. 2020a) and low rate of infestation by blood parasites of parthenogenetic lizards in mixed populations of rock lizards, (Arakelyan et al. 2019). In accordance with the parasitological version of the 'Red Queen' hypothesis (Moritz et al. 1991), obligate parthenogens have become less responsive in the arms race between hosts and parasites due to their low genetic variability (Moritz et al. 1991; Darevsky 1995). Moreover, parthenogenetic *Darevskia* lizards were not overloaded with blood parasites and helminths when compared to their sexual relatives in areas where they share the same habitat (Arakelyan et al. 2019), supporting their adaptive success to parasite infection and deviates from the predictions of the 'Red Queen' dynamics for rock lizards. Thus, different hypotheses on the persistence of parthenogenetic reproduction in the group of rock lizards suggest that, in accordance with the genetic combination of parental species in parthenogenetic lineages, some of them have promising prospects in withstand long-term competition with their sexual relatives.

Further Step of Reticulate Evolution in Rock Lizards

Polyploidy is considered to be an important driving force in evolution as it increases the genetic material on which mutation and selection can act in fishes, amphibians and reptiles (Pandian 1998; Stenberg and Saura 2013). Unlike most parthenogenetic reptiles (*Aspidoscelis* spp., *Heteronotoa binoei*, and *Indotyphlops braminus*), where triploidy is common (Penncock 1965; Simon 1996; Grismer et al. 2014; Wynn et al. 1987; Lutes et al. 2010), a unique feature of all *Darevskia* parthenogenetic lizards are diploid (Kupriyanova 2010; Spangenberg et al. 2020a, 2021). According to recent studies in genus *Aspidoscelis*, diploid unisexual animals of this genus are considered mostly as a temporary stage before the formation of parthenogenetic triploid forms (Barley et al. 2021). Thus, the question of selective advantages of seven diploid unisexual lineages of rock lizards and the absence of the populations of unisexual tripoid forms is of great interest.

In theory, in syntopic populations of *Darevskia* lizards, a new sexual species with a higher level of ploidy may arise as the next stage of reticulate evolution (Figure 1) due to low pre- and post-zygotic barriers between parthenogenetic and sexual species. Most biological features of parthenogenetic and sexual species of rock lizards are similar (Galoyan 2010; Tarkhnishvili et al. 2010). Females of the lizards of both reproduction modes have a similar home range size and structure, although home ranges in parthenogens overlap among many individuals (Galoyan 2013). Significant overlap in seasonal and daily activities, as well as periods of their reproduction, has been described (Abrahamyan et al. 2014). Comparisons of longevity, growth rate, reproductive age, and number of eggs in a clutch in parthenogenetic and sexual lizards have shown that these parameters depend more on the size of the lizards than on the reproduction mode (Arakelyan 2002; Arakelyan et al. 2013). Moreover, it has been experimentally recorded that parthenogenetic rock lizards are more resistant to deficits of humidity at the first stages of embryonic development (Danielyan 1971), which increases their survival in harsh environmental conditions. Similarly, embryonal viability in parthenogenetic forms was higher in the parthenogenetic gecko *Heteronotia binoei* with less sensitivity to incubation temperature (Kearney and Shine 2004) than their sexual relatives.

Contrary to opinion that parthenogenetic forms suggesting competitive exclusion of their sexual relatives (Cuellar 1977), the mixed populations of rock lizards where co-existing the lizards with two mode of reproduction are quite common (Petrosyan et al. 2020b). They often coexist as one metapopulation in the areas of the secondary overlap areas (Darevsky 1966; Wright and Lowe 1968; Cuellar and Smart 1979) and breed with the parental species (Figure 1; Darevsky and Kulikova 1964' Darevsky et al. 1973; Darevsky and Danielyan 1979; Paulissen et al. 1992; Spangenberg et al. 2017). Recent studies suggested that mate choice in sexual females might be affected by UV-blue spots on the females` body; however, there were no significant differences in the number of these spots between parthenogenetic females and females of parental species (Abramjan et al. 2020). Visual observations of interspecific mating between parthenogenetic *D. unisexualis* and *D. armeniaca* and males of paternal *D. valentini* (Galoyan 2013) and abundant mating marks on the bodies of parthenogenetic females (Carretero et al. 2018) support the idea of parthenogenetic female attractiveness for males of sexual species. As a result of interspecies backcrossing, the triploid male and females with different levels of fertilities as well the tetraploid male with fully developed reproductive system were recorded in mixed population of 2 parthengenetic (*D. unisexualis* and *D. armeniaca*) and sexual *D. valentini* species (Danielyan et al. 2008). However, tetraploid species (not individuals) with sexual reproduction are not documented in reptiles, however, are known among fish and amphibians (Stenberg and Saura 2013; Yang et al. 2022). On current stage of evolution, the interspecific hybridization between diploid parthenogenetic rock lizards and males of parental species in sympatry gives rise to triploid and tetraploid hybrid individuals (Danielyan et al. 2008; Freitas et al. 2019), which is a main prediction of continuous reticulate evolution with potential formation of new sexual species on a higher level of ploidy (Figures 1 and 2). Usually, triploid females and intersexes of rock lizards are considered sterile individuals with deep disturbances in their reproductive systems (Danielyan et al. 2008). Nevertheless, the cytogenetic studies evidence that triploid males can produce abnormal and aneuploid spermatozoa due to an absence of strict checkpoints in meiosis I (Spangenberg et al. 2017). The possible role of polyploid hybrid males and females of *Darevskia* in the scheme of reticulate evolution is a subject of future studies.

Conclusion

Environmental extremes can act as evolutionary forces for the ectothermic animals to overcome prezygotic barriers in areas of secondary overlap between related species, thus facilitating interspecies matings and switching to parthenogenetic breeding mode in the case of reptiles. Accordingly, the hybridization between closely related *Darevskia* spp. in the past was possible due to the action of environmental stress factors during the last glaciation period, which shifted habitats of the lizards to refugia and decreased the population density of species. The low number of individuals and sex ratio imbalance in suboptimal conditions influenced the behavior of lizards and may stimulated mating between different species. A high population density, low intraspecific competition, and a high level of acquired heterozygosity allowed parthenogenetic hybrids to colonize marginal habitats to survive under harsh environmental conditions. Currently, seven diploid hybrid parthenogenetic species of the genus *Darevskia* have favorable long-term, albeit different, prospects of survival. Some *Darevskia* parthenogenetic species have a wide distribution and even displace the related sexual species. The prosperity of parthenogenetic rock lizards of the genus *Darevskia* is likely due to meiotic plasticity, successfully passing through key stages of the first division of meiosis and automixis via a "central fusion" mechanism. Backcrossing with the sexual species in hybrid zones is also considered a possible way to maintain the stability of parthenogenetic forms. Nevertheless, triploid and tetraploid hybrids appear regularly in the sympatric zones of parthenogenetic and parental species, due to both low pre- and post-mating barriers between parthenogenetic and sexual species. However, at present, we have recorded the block of premating barriers between two sexual syntopic species. Also of great interest is the fact that, unlike other parthenogenetic lizards, including triploid clones, the genus *Darevskia* includes only diploid parthenogenetic lizards. The impact of climate change on the fitness of parthenogenetic species and the study of exact genetic and cytogenetic mechanisms behind in context of the evolution of these species should be the subject of future research, especially in view of the role of parthenogenetic reproduction under changing environmental conditions.

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Conflict of Interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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