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THE PROGRESS OF MICROEVOLUTION IN HYBRIDS OF ROCK LIZARDS OF GENUS *DAREVSKIA*

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Along with sterile triploid females, the male hybrids, intersexual individuals, female hybrids with developing follicles and eggs as well as tetraploid male hybrid are found in the mixed population of three species of rock lizards' genus *Darevskia* in mountain steppe zone of central Armenia.

Intensive microevolution takes place in this sympatric population. The evolutionary potential for hybridogenic speciation by Caucasian rock lizards is discussed.

Հայաստանի կենտրոնական մասի լեռնատափաստանային գոտում, *Darevskia* ցեղին պատկանող երկսեռ և կուսածին ժայռային մողեսների երեք տեսակների խառը պոպուլյացիաներում, ստերիլ տրիպլոիդ էգերի հետ հայտնաբերվել են տրիպլոիդ հիբրիդային էգեր՝ զարգացող օօցիտներով և ձվերեվ, հիբրիդային արու և ինտերսեքսուալ առանձնյակներ, ինչպես նաև տետրապլոիդ արու առանձնյակ:

Այդ պոպուլյացիայում ընթանում է միկրոէվոլյուցիոն գործընթաց: Քննարկվում է Կովկասյան ժայռային մողեսների հիբրիդոգեն տեսակառաջացման էվոլյուցիոն պոտենցիալը:

В горно-степной зоне центральной Армении, в смешанной популяции трех видов двуполых и партеногенетических скальных ящериц рода *Darevskia*, наряду со стерильными триплоидными гибридными самками, обнаружены триплоидные гибридные самки с развивающимися фолликулами и яйцами, гибридные самцы, интерсексуальные особи, а также тетраплоидный гибридный самец.

В данной смешанной популяции протекает интенсивный микроэволюционный процесс. Обсуждается эволюционный потенциал гибридогенного видообразования у Кавказских скальных ящериц.

A universal theory of reticulate speciation explains the hybrid origin of diploid and triploid parthenogenetic forms (Darevsky, Borkin, 1985). The appearance of diploid parthenogenetic forms as a result of natural interspecies hybridization between closely related bisexual species is the first stage of

reticulate speciation. Morphological, ecological, cytological, and genetic studies have shown that parthenogenetic species of genus *Darevskia* Arribas, 1997, are of hybrid origin (Darevsky and Danielyan, 1979; Uzell and Darevsky, 1975; Moritz et al., 1992; Grechko et al., 1993; Fu et al., 2000; Murphy et al, 2000; etc). The second stage of the scheme is the emergence of allotriploid forms as a result of hybridization of maternal diploid parthenogenetical and paternal bisexual species. On the third stage of speciation, fertile triploid females mate with males of bisexual species and give origin to a new tetraploid species (Schultz, 1969; Borkin and Darevsky, 1980).

The distributions of four parthenogeneic and four bisexual species of Caucasian rock lizard from genus *Darevskia* in Armenia often overlap and the process of natural hybridization between parthenogenetic lizards and males of the bisexual species annually occurs in the sympatric zones (Darevsky, 1967; Darevsky and Danielyan, 1968; Darevsky et al, 1985; Darevsky, 1995; Darevsky and Danielyan 2001; Danielyan, 2003 etc). Such zones of hybridization exist in mountainous regions of the central Armenia at elevations from 1800m to 2000m above sea level. Opportunities for hybridization appear in river canyons along which bisexual species penetrate the mountains and enter the ranges of parthenogenetic forms (Darevsky et al, 1985). Generally, in contact zones, the hybrids comprise 5-12% of the mixed populations (Darevsky et al, 1973; unpublished data of Danielyan).

The mixed populations of rock lizards have been a subject of multidisciplinary studies since the time of its discovery. The evolutionary potentials of the speciation by hybridization in the group of Caucasian rock lizards are summarized in this paper based on morphological, ecological, cytological, and histological studies for the last 10 years of the hybrid lizards of genus *Darevskia* in a unique hybridization zone in vicinity of Kuchak village (central Armenia) where diploid (2n), triploid (3n) and even tetraploid (4n) individuals are found.

Materials and Methods. The mixed population of rock lizards of the genus *Darevskia i*s located in central region of Armenia on the northeastern slope of Aragats Mountain near Kuchak village. The material used in this study, which has been conducted between 1994 and 2006, is described in Table 1. All specimens were captured within an area a few hectares and appear to belong to a single sampling site. Lizards which belong to parthenogenetic *D. unisexualis, D. armeniaca* and bisexual *D. valentini* species and their hybrids of *D. valentini* x *D. unisexualis* and *D. valentini* x *D. armeniaca* were captured with a noose and were palpated to assess their reproductive conditions. Hybrids were identified according to special features of their color pattern and certain characteristics of scutellation. The specimens that used for comparative studies were sampled simultaneously. Chloroform gas was used for euthanasia of a few lizards for cytological, histological and skeleton-chronological studies. The animals which were used for morphological and cytometrical studies, were measured, the blood was taken from clipped tail for smears and then released.

Chromosome smears were prepared from the bone marrow, spleen, intestine and testis tissues of lizards (n=11) according to the method described by Macgregor and Varley (1986). The colchicines solution (0,1%) was used intraperitoneally. The cells were treated by hypotonic KCl solution (0.56%), fixed in an ice-cold acetic acid – methanol solution (1:3). The chromosomes were stained in 5% Giemsa in the phosphate buffer at pH 6.8. The chromosome complements were detected by observation of 50 metaphase plates for each individual.

The histology of gonads of adult hybrids (n=6) and parental species (n=6) were studied on the paraffin slides following to classical microtechnical method (Romeis, 1958).

Statistical analysis of data was performed by Statistica 6.0 Software package.

Results and Discussion. Highly interesting zone of hybridization has been discovered in 1994 in the vicinity of Kuchak village (Aragatsotn Marz) on the eastern slopes of Aragats Mountain in central Armenia, where parthenogenetic species *D. armeniaca*, *D. unisexualis* and bisexual species *D. valentini* occur together (Danielyan et al., 1999). Currently, the Kuchak population is a unique hybridization zone of rock lizard species that includes diploid (2*n*), triploid (3*n*) and tetraploid (4*n*) individuals.

The studied hybridization zone is located approximately 5 km south of the Aparan town (Aragatsotn Marz) and 0.5 km north of Kuchak village (40° 31′ N, 44° 23′ E; 1920m a.s.l.), directly next to the main republic road. The habitat of hybridization site is mountains steppe with gentle slopes of volcanic origins, covered by grass and bushes. Rock lizards typically inhabit stony heaps of volcanic origin, conglomerations of rocks, and large fragments of lava which are quite common in the mountain steppe zone.

Approximately 60% of mixed population is represented by *D. unisexualis* about 10% is comprised of *D. armeniaca* and 30% - *D. valentini* (Chi-square =3.0, 2 df, P=0.22). The habitats of the sympatric species are slightly different from each other. Newly arisen hybrid lineages may have ecological requirements intermediate between those of their bisexual parents, restricting them to "hybrid" habitats (Moritz et al, 1992). Parthenogenetic lizards *D. unisexualis* prefer to live on bedrocks and large fragments of lava, whereas the bisexual *D. valentini* occupies stony heaps with shrubs and grassy vegetation. *D. armeniaca* in this zone is mainly confined to artificial constructions and wastelands along the road. The habitats of parthenogenetic *Darevskia* differ slightly from those of closely related bisexual forms. However, they tend to inhabit sites with colder, dryer, or more variable climates than their bisexual relatives (Darevsky et al, 1985).

The studied sympatric zone between parthenogenetic and bisexual species is very narrow and does not exceed 500 m^2. *D. valentini* is adapted to high mountains and can be met on the southern slopes of Mt. Aragats, in mountain steppes and alpine zone at altitudes ranging from 1900 to 2700m. *D. armeniaca* and *D. unisexualis* occur on northern slopes of Mt. Aragats at elevation 1700 – 2000m a.s.l.

The intensive process of hybridization takes place in sympatric zone of Kuchak population (Fig. 1).

D. unisexualis (2n)	×	*D. valentini* (2n)	×	*D. armeniaca* (2n)
parthenogenetic species ↓		bisexual species ↓		parthenogenetic species
female		male		female
? (2n) × *armeniaca* (3n)		*D. valentini*× *D. unisexualis* (3n)		*D.valentini*×*D.*
	↓	hybrid		hybrid
		female, male		female, male

Fig. 1. Scheme of hybridization of bisexual *D. valentini* and parthenogenetic *D. unisexualis, D. armeniaca* species of rock lizards.

The number of hybrids that appear annually in this sympatric zone is extremely high and exceeds 35% of the mixed population. However, the percent of hybrid individuals in other mixed populations is about 7-12% (Darevsky and Danielyan, 2001). Furthermore, there is an evidence that the percent of hybrids in "Kuchak" population is increasing over time. The ratio of hybrids to lizards of parental species was 33% in 1994, 35% in 1997, 41% in 1999, 47% in 2003, and 52% in 2004 (Fig. 2).

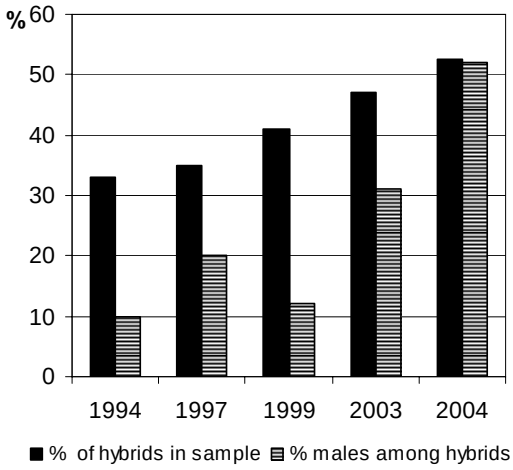

Fig. 2. The proportion of hybrids in samples and occurrence of males among hybrids during 1994 – 2004 years.

Nineteen fertilized parthenogenetic females with male's jaw marks on their abdomens were collected in 1997 and their eggs were incubated in the laboratory (unpublished data of Danielyan). Out of 22 new hatchlings 8 were triploid hybrids that constitute 36.3% of total progeny. The success of hybridization in this population should be attributed to the optimal time of maturation of gonads in both parental species.

The ratio of hybrid individuals *D. valentini x D.unisexualis* to *D. valentini x D. armeniaca* in the studied mixed population is approximately 4:1 (Chi-square=2.0, 1 df, P=0.16). In an experiment conducted by Darevsky and Danielyan (1968) many hybrids were obtained from an artificial hybrid zone created by introducing males of *D. valentini* into isolated population of *D. unisexualis* and *D. armeniaca.* Judging from the size of the marks left by jaws of males on the bellies of females during copulation, the larger males *D. valentini* mated more frequently with females of *D. unisexualis,* which are relatively larger and have brightly colored bell similar to that of *D. valentini* females.

Usually *D. valentini* shares common range more often with *D. armeniaca* (6 known sites) than with *D. unisexualis* (two sites, including Kuchak population). The higher success of hybrids forming in "Kuchak" population may also explain the high percentage of *D. unisexualis* which is more frequently mating with *D. valentini*, than *D. armeniaca.*

Hybrids resulting from mating of parthenogenetic females *D. armeniaca*, *D. unisexualis* with males *D. valentini* of bisexual species of rock lizards are often sterile triploid females. Their sterility is caused by gross anomalies in structure and development of gonad (Fig. 4-1). The ovary of hybrids differs from cluster ovary of parental species. They are usually smaller in size and lack oocytes. On our histological samples of triploid hybrid females the main part of stroma of the ovary is weakly delineated and the cortex is poorly developed. Some of them have one or two empty false follicles up to 1 mm in diameter (Fig 5-8). The size of hybrid follicles is not increasing during breeding season, because vitellogenesis is not activated. The oviducts have rudimentary structure and are represented by two straight tubs with germinal funnel.

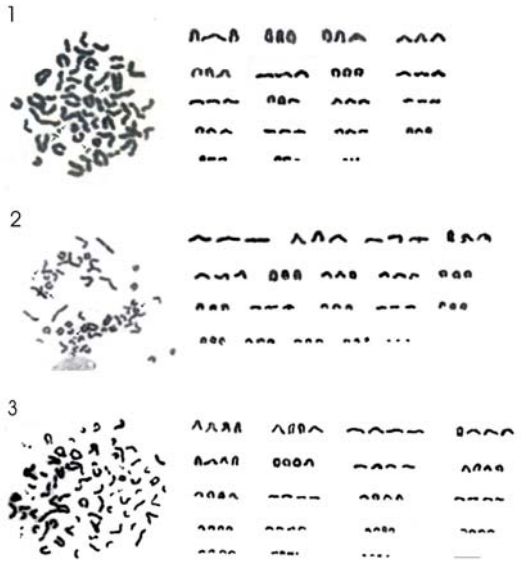

Fig. 3. Somatic metaphase and karyotypes (bar equals 10mkm) of hybrids *D.valentini x D.unisexualis*: 1 - triploid female; 2 - triploid male; 3 - tetraploid male

The study of karyology of hybrids has shown that the majority of mitotic metaphase plates of triploid female hybrids consist of 57 chromosomes (Fig 3-1) when diploid set of chromosomes of parental species is made of 38 chromosomes (*NF*=38). The karyotype of hybrid sterile females include 53 acrocentric macrochromosomes and 4 microchromosomes (*3n*=57, *NF*=57). According to data in literature, they have sex chromosomes of *wZZ* type (Kupriyanova, 1999).

In spite of the hypothesis that in the group of rock lizards hybrid females are usually sterile (Darevsky et al, 1985; Kupriyanova, 1999), we have collected the evidence of rare occurrence of presumable fertile females among *D. valentini x D. armeniaca* and *D. valentini x D. unisexualis* hybrids in the mixed population near the village Kuchak. The first hybrid female with two eggs in oviducts was discovered in 1999. Then, rare hybrid females with developing oocytes (Fig. 4-2), eggs and corpora lutea were collected in 2000, 2001 and 2006.

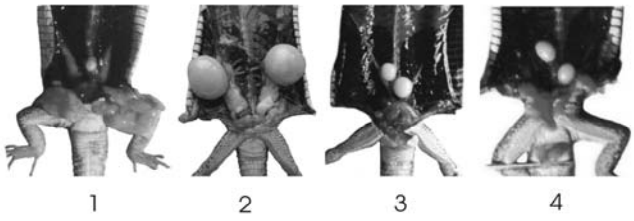

Fig. 4. Reproductive system of hybrids *D.valentini x D.unisexualis*:
1 - triploid sterile female; 2 - triploid probably fertile female;
3 - triploid probably fertile male; 4 - tetraploid probably fertile male

The comparative histological analysis of developing oocytes of "fertile" hybrids and their parents have shown their resemblance. The nuclei of hybrids and parental females are similar in size and structure (Fig. 5-3 and 5-4). The ovarian follicle cell layer of hybrid female was complete and well structured (Fig. 5-2). However, the surface area of tunica granulose of hybrid was comparatively thinner than that of parthenogenetic females on the similar stage of ovary development (young oocytes were 1.5 mm in diameter). As a result, the number of pyriform cells in tunica granulose of presumably fertile hybrids was less than of parthenogenetic rock lizards. The larger oocytes (4–6 mm) of presumable fertile hybrids were vitellogenenic where the yolk deposition was in progress like in normal oocytes (Arakelyan, 2001, Arakelyan, Danielyan, 2003). The oviducts were well-developed and structured.

So, the hypothesis of complete sterility of hybrid females becomes questionable. However, only progeny obtained from female hybrids of Caucasian rock lizards will provide solid evidence for the statement that hybrid females can produce viable and fertile eggs.

The natural hybridization between parthenogenetic and bisexual species can also produce triploid male hybrids (Darevsky et al., 1973, 1978, 1986. In Kuchak population the occurrence of male hybrids is quite high. Moreover, the proportion of males was increasing during period of study (Fig. 2).

Our examination has shown that the majority of hybrid individuals appeared to be typical bisexual males in all details. Most of them had two fully-developed testes (Fig 4-3). Their hemipenes were more or less of the same shape and size as those of bisexual males. Some lizards had two testes: one is well-developed, whereas the other is abnormal.

Different degrees of fertility were observed on histological preparations of male hybrids. All stages of spermatogenesis and mature spermatozoa of hybrid males with well-developed testes were detected. Thus, some of triploid males were probably reproductive and capable of producing sperm that looked normal.

In the studied samples four hybrid individuals of *D. valentini x D. unisexualis* with intersexual characteristics were detected. They had "female" oviducts, "male" hemipenes and "ovotestis" gonads. Our histological study of gonads shows that intersexual type of hybrids has ovotestis, because they include both "female" and "male" parts of gonads.

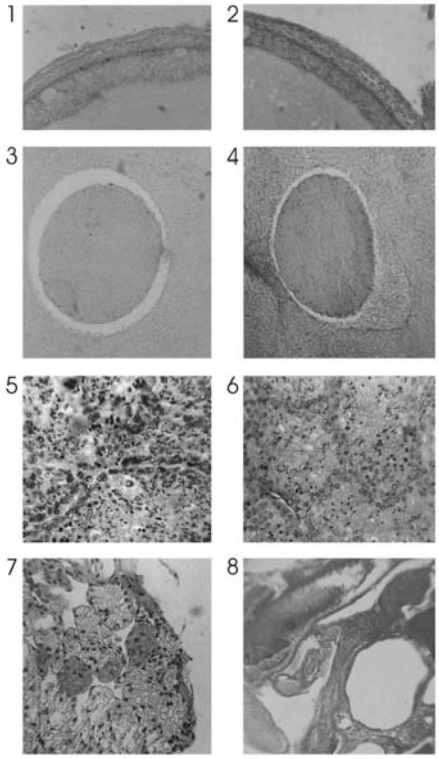

Fig. 5. Histological picture of gonads; 1 - ovarian layers of follicle cell of *D. unisexualis*, 2 – same for presumably fertile hybrid *D.valentini x D. unisexualis,* 3 – nucleus of oocyte of *D. unisexualis*. 4 – same for presumably fertile hybrid *D.valentini x D. unisexualis*, 5 - testis of *D. valentini*, 6 – same for hybrid *D.valentini x D.unisexualis*, 7 – ovotestis of intersexual hybrid *D.valentini x D.unisexualis*, 8 – ovary of sterile hybrid *D.valentini x D.unisexualis.*

The main part of the cortical tissue is thinner tunica albuginea, similar to that of male of bisexual lizards, but 1/5 of the cortical layer looked like a thick tunica vasculosa which is similar to females (Fig. 5-7). The medullar tissue is more developed in male gonads, but again 1/5 fraction of ovotestis includes segments of ovary, which is wedged into the testis tissue. In the tissue of testis poorly developed seminiferous tubules were visible. Only few spermatogonia were present in seminiferous tubules.

Table 1. Material: number of hybrids and specimens of parental species of rock lizards of genus *Darevskia* in samples.

Collecting date	*D.valentini x D.unisexualis*	*D.valentini x D.armeniaca*	*D.valentini* ♂♀	*D.unisexualis* ♀♀	*D.armeniaca* ♀♀
06.07.1994	8	2	9	11	0
21.05.1997	14	5	6	25	4
21.04.1999	12	6	8	15	2
18.07.1999	12	4	2	12	10
08.06.2003	14	2	4	8	6
28.04.2004	17	4	8	6	5
28.05.2006	7	2	3	5	2
TOTAL	84	25	40	82	29

Mitotic metaphases and meiotic metaphases I and II of one male (Fig.4-2) and two "intersex" hybrids were studied (Table 1). This hybrid had karyotypes (3*n*=57, *NF*=57) with 53 acrocentric chromosomes and 4 microchromosomes. The intersex individuals included sex chromosomes like hybrid females (18th triplet has sex chromosomes of *wZZ* type). The number of cells in diakinetic stages and metaphase I meiosis of studied triploids was low. Numbers of diakinetic bivalents vary from 19 to 33. In the testis preparations of triploid male and intersexes single spermatides (1-2%) were observed. The formation of mature spermatozoids was not detected.

A unique finding was made in spring of 2004 in Kuchak population when a tetraploid hybrid male was caught and examined for the first time in the group of rock lizards. This lizard was similar to triploid males in coloration, pattern of dorsal picture and pholidosis. However, karyological analysis has shown tetraploid set of chromosomes of this lizard. The karyotype of this hybrid was represented by 71 acrocentric chromosomes and 5 microchromosomes (4*n*=76, *NF*=76). So, this was a tetraploid male with *wZZZ* type sex chromosomes (Fig. 3-3).

This hybrid has two fully developed testes (2.4 x 3.2 mm), well organized hemipeneses and marked femoral pores (Fig. 4-4). The Giemsa-stained smears of testes have shown diakinetic stages of meiosis and middle, late spermatides (60%). Compared with triploid hybrids, tetraploid male had numerous spermatids and spermatozoa.

The origin of this tetraploid male is unclear. The most possible pattern is a crossing between hybrid triploid female with a male of *D. valentini.* In this case the tetraploid hybrid with *wZZZ* sex chromosomes can arise from mating of triploid females with *wZZ* sex chromosomes with a male of *D. valentini* with *Z* sex chromosome. Other possible scenario is mating of a hybrid triploid male with a female of *D. valentini.* The female of *D. valentini* has *WZ* sex chromosomes. In this case, the egg with *Z* chromosomes fuses with spermatozoa of triploid hybrid male with *wZZ* sex chromosomes. In any case, appearance of a tetraploid individual is a conclusive evidence of the fertility of either females or males of triploid hybrids.

Sex chromosomes may play a key role in the formation of unisexual species. *Darevskia* have chromosomal mechanism of sex determination and female is the heterogametic sex (Murphy et al, 2000). The karyological study of teiid lizards of genus *Cnemidophorus* has shown that unlike rock lizards of genus *Darevskia*, their females, are homogametic, whereas the diploid males of *C. tigris* are heterogametic (*XY*). Probably, the appearance of triploid and tetraploid males of hybrid *C. sonorae x C. tigris* (with *XXXY* sex chromosomes) and females (with *XXXX* sex chromosomes) takes place easier because the actively induced process of the development of heterogametic sex is more complicated than that of homogametic one (Darevsky and Kupriyanova, 1982). According to histological study of Taylor et al (2001) there is no evidence that female hybrids of *Cnemidophorus tesselatus* × *C. tigris marmoratus* can produce viable and fertile eggs and hybrid males of teiid lizards are capable of producing sperm that looked normal. Although, for genus *Cnemidophorus*, Lowe et al. (1970) discovered a tetraploid male in a mixed population of triploid parthenogenetic *C. sonorae* and diploid *C. tigris.*

Fertility of triploid hybrids is a significant prerequisite in reticulate evolution. The universal theory of reticulate speciation (Borkin and Darevsky, 1985) is based upon the following premises: hybridization, unisexuality and polyploidy. When fertile triploid females can mate with males of bisexual species and give origin to new tetraploid species, the hybrids of rock lizards can move away from evolutionally dead end and give them a chance to reproduce parthenogenetically. As a result of changes in environmental conditions, some generations of hybrid females can give rise to triploid species as was shown for lizards of genus *Cnemidophorus* (Cole, 1975).

As a rule, polyploid individuals with unpaired set of chromosomes often become sterile. According to Kupriyanova (1999) the bisexual reproduction of triploids males *D. valentini x D. unisexualis* from Kuchak has been considered to be impossible because of the problem of equal distribution of three chromosome sets in meiosis. On the other hand, appearance of triploid individuals with successful combination of genes is theoretically possible, which can increase their number due to parthenogenetic reproduction. The formation of haploid, diploid and triploid gametes allows speculating future evolutional pathway of such hybrids. Especially interesting is the case, when triploid nucleus of hybrid fuses with haploid nucleus of female of paternal species, and gives rise to tetraploid form. The result can be second generations of ploid hybrids of both sexes and return to bisexuality on a polyploidy level. Probably this scenario led to the origin of tetraploid lizards of genus *Cnemidophorus* (Moritz et al, 1989).

Based on the above noted evidences of increasing of proportion of hybrids as well as abundance of hybrid males and females with fully developed reproductive system among them, it can be inferred that there is an intensive process of hybridization in Kuchak population. So, in this population suitable conditions can be established for the next stage of the progressive process of speciation by hybridization. Thus, the occurrence of tetraploid male hybrid with fully developed reproductive system is significant precondition for the opportunity of advancing to the following stages of reticulate evolution in *Darevskia* rock lizards.

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