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New Evidence of Hybrid Males of Parthenogenetic Lizards

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Present paper reports on 29 males and 1 presumably hybrid female /found among 127 non-hybrid females/ of parthenogenetic lizards belonging to Lacerta rostombekovi population from N-Armenia. The locality is sympatrically inhabited by parthenogenetic L. armeniaca and L. dahli and non-parthenogenetic, bisexual L. raddei, parental for L. rostombekovi /cf. Uzzell et al., 1975/.

Seventeen males share some morphological features common to L. rostombekovi and L. raddei /Tab. 1/. They have both testes and oviducts whose size and morphology vary /Fig. 1/. The testes were of reduced activity like those of another triploid male from this population /Darevsky et al., 1973/. Karyological analysis of somatic cells revealed the mosaic nature of 9 males. The number of chromosomes varied from 35 to 57. In two specimens the modal class was represented by cells with 35 - 40 chromosomes, i.e. the number close to the diploid /38/ level. The other five males showed 45 - 57 chromosomes, i.e. close to the triploid /57/ level; however, cells with 36 - 40 chromosomes were also observed in these 5 males and such cells were nearly absent only in two other specimens /Figs 2, 3/. In almost all cells of males, marked submetacentric /SV/ was recorded like in L. rostombekovi /2n = 28; Kupriyanova, 1981/ /Figs 4, 5/.

Meiotic cells were found only in five males. In the first meiotic division, most chromosomes formed bivalents, but some also formed uni- or trivalents. Most bivalents had chiasmata, some terminal, and some end-to-end associations /Figs 8, 9/. Only 16 /from 109/ cells examined had 19 elements /bi-, uni- and trivalents/, 42 cells had 20 - 32 bivalents with chiasmata, the remaining 51 cells had 12 - 18 bivalents /Fig. 10/. Because of the variation in the number of bivalents and/or of the irregularities in the distribution of them in the first anaphase, different chromosome numbers /13-23, rare 28; 19 only in 4 out of 39 examined/ were found in the second metaphases /Figs 11-13/. This may suggest that the males originated via hybridization between L. rostombekovi and L. raddei, unlike the other 2 - 3 known cases of presumably autotriploid males of bisexual lizards.

The mosaic character and the behavioural specificity of chromosomes may also suggest that one or nearly one chromosome set is often lost in mitosis and before meiosis. The remaining sets do not undergo endoduplication, and meiosis proceeds more or less normally. As a result, aneuploid and rare probably haploid gametes are formed like in allotripoloid hybrids of pond frogs /Günther, 1975; Nishioka and Ohtani, 1984/.

All 9 males had a few spermatozoa. Two males, with somatic cell chromosome number close to the diploid one and with that of spermatocyte I close to haploid number, had many spermatids and spermatozoa at different stages of development like the other two males found earlier /Kupriyanova, 1981/ /Fig. 14/. Whether the process of spermiogenesis goes to the end and normal spermatozoa are formed is unclear. These two males might to be "trihybrid" diploids but their mosaic character /35-40, 42 with varying SV/ is in disagreement with this conclusion.

Table 1. Variability of some morphological characters in different populations of Lacerta rostombekovi Dar. /I: Sevkar, mixed pop.; II: Gey-Gel, pure pop./, L. r. raddei Boettger /III: Sevkar, mixed pop.; IV: Idjezevan, pure pop./, and their triploid hybrids /V: Sevkar/.

CHARACTER	FORM POP.	N	min-max	$\bar{x}$ ± SE	SD
Number of scales around the middle of the body	I	41	48-53	50.8±0.28	1.7
	II	13	49-53	50.8±0.35	1.2
	III	51	48-56	52.1±0.92	6.5
	IV	30	50-58	53.1±0.36	1.9
	V	17	49-52	50.5±0.60	2.4
Number of femoral pores	I	41	14-19	16.5±0.22	1.4
	II	13	16-21	17.4±0.29	1.0
	III	51	17-18	16.8±0.61	4.3
	IV	30	13-23	18.0±0.32	1.7
	V	17	17-19	18.0±0.70	2.8
Number of scales along the midline of throat to the collar	I	41	24-29	25.5±0.24	1.5
	II	13	21-27	24.4±0.42	1.5
	III	51	22-24	23.5±0.41	4.3
	IV	30	22-29	24.8±0.25	1.3
	V	17	22-28	25.0±0.50	2.0
Number of scales across the throat from ear to ear	I	36	29-44	38.1±0.52	3.1
	II	13	26-40	36.5±0.20	0.7
	III	51	39-44	42.0±0.60	4.2
	IV	30	40-56	48.1±0.29	1.5
	V	17	38-46	42.3±0.81	3.3
Number of enlarged preanal scales located immediately anterior to anal one	I	41	1-3	2.8±0.10	0.6
	II	13	3-3	3.0	-
	III	51	1-3	2.5±1.20	8.5
	IV	30	1-2	1.9±0.06	0.3
	V	17	1-3	2.1±0.86	4.7

The fertility of 3n hybrid males still remains obscure; therefore, their evolutionary role is uncertain. Some of their haploid gametes could perhaps contribute to the genome of females of L. raddei.

Four females of L. rostombekovi were fertilized by males of L. raddei in the laboratory. Their offspring were 14 typical L. rostombekovi and 6 hybrids; sex, habit and fertility of them are under study.

It is known that, as a rule, frequent 3n mosaic hybrids between parthenogenetic and bisexual lacertid species are females /Darevsky and Kulikova, 1964; Kupriyanova, 1973/. Therefore, male hybrids are of special interest. Considering the heterozygosity /ZW/ of sex chromosomes of most lacertid females we have suggested /Darevsky and Kupriyanova, 1982/ that the W chromosome plays a dominant role in sex determination. Thus, one possible explanation of the presence of hybrid males in question is that the W chromosome, at least in L. rostombekovi, is not dominant. However, we have revealed typical sterile 3n females resulting from the hybridization of L. rostombekovi and bisexual L. portschinskii /another parent for L. rostombekovi; Fig. 7/ in another mixed population /L. raddei - L. portschinskii - L. rostombekovi/. Some typical 3n sterile hybrid females of L. raddei and parthenogenetic L. unisexualis or L. dahli were also observed.

All this suggests that the hybrid males examined involved either a suppressor in L. raddei, which directs the development of embryos towards maleness, or an interaction between 3 genomes /2 raddei and 1 portschinskii/. This interaction may indirectly be supported by the fact that females of L. raddei have sex heterochromosomes /ZW/ but females of L. rostombekovi and L. portschinskii do not have them /Figs 4-6/. Therefore, one may suppose that L. rostombekovi involves the female genome of L. portschinskii and the male genome of L. raddei. As a result, the 3n hybrid males examined may have one female portschinskii genome and two male raddei genomes. The development then goes toward maleness. An individual analysis of chromosomes may clarify this question.

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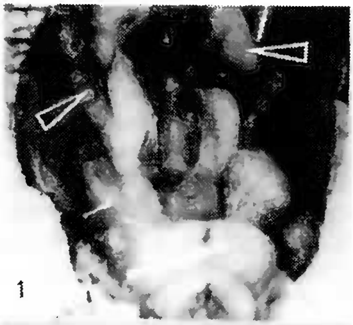

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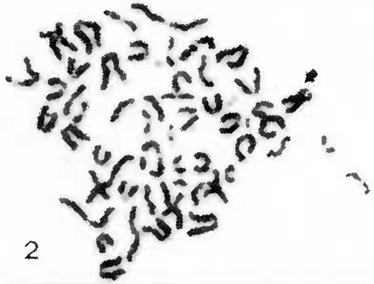

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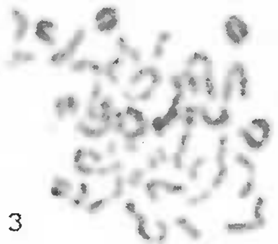

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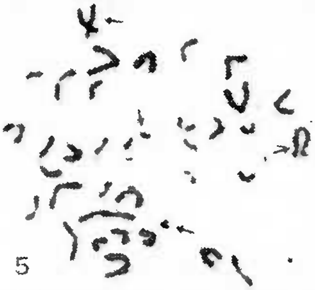

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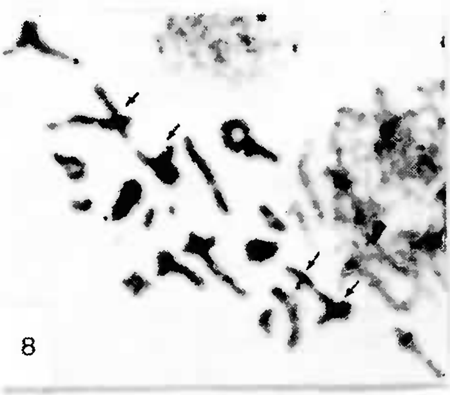
Fig. 1: Reproductive system of hybrid male Lacerta rostombekovi x L. raddei. Arrows point to both testes and oviducts. Figs 2, 3: Somatic cell metaphases of hybrid males with 59 - 60 and 44 - 45 chromosomes. Arrow points to submetacentric /SV/. Figs 4, 5 Somatic cell metaphases of females L. rostombekovi with 2n = 38. Arrows point to SV, secondary constriction and the 18th pair of presumable sex chromosomes. Fig. 6: Somatic cell metaphase of female L. raddei. Arrows point to the 19th and 18th /sex, ZW/ pairs of chromosomes. Fig. 7: Somatic cell metaphase of hybrid female L. rostombekovi and L. portschinskii with 3n = 57. Arrow points to SV.



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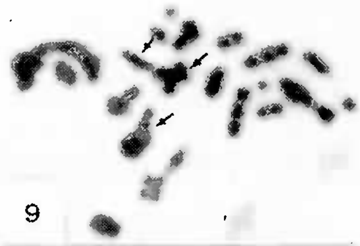

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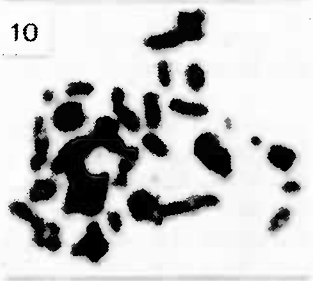

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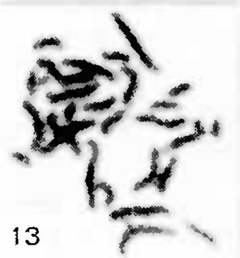

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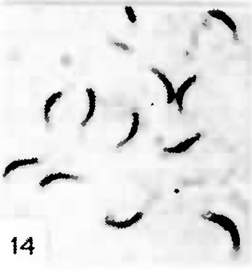

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Figs 8-10: Meiotic metaphases I of hybrid males with n = 20 - 21; 27 - 28. Arrows point to uni-, trivalents, and bivalents with chiasmata. Figs 11-13: meiotic metaphase II plates of hybrid males with n = 19; 27 - 28. Arrows point to SV and centrometric association. x 700. Fig. 14: Spermatozoa of male hybrids described.