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Rare males in parthenogenetic lizard Lacerta armeniaca Méhely*

By

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Abstract: It is known that karyotypes of parthenogenetic female and male Lacerta armeniaca are similar. This implies that the above males are most likely the results of hormonal inversion. A recently collected male L. armeniaca has also proved to be a diploid individual. This is supported by cytophotometrical measurement of the DNA content of somatic cells in both this male and the bisexual (control) male of L. portschinskii Kessler, as well as by haploid number of bivalents at metaphase I. The DNA content of spermatids in the two males corresponds with the haploid level, and the presence of haploid spermatids argues for normal meiosis. Histological studies supported the above conclusions. The male L. armeniaca appeared to be fertile.

Some evidence has been provided in the literature concerning the rare occurrence of fertile males in populations of some unisexual lizard species. For the Caucasian rock-lizards of the family Lacertidae, this phenomenon was originally observed by examining dead embryos obtained from eggs of unisexual species of lizards (L. armeniaca and L. dahli) that hatched in captivity (DAREVSKY 1966). These findings allowed a conclusion that in rare occurrence such males were able to complete their embryonal development to become adults. Indeed, by examining our collections and specially searching in nature we succeeded in finding some adult males for two of the four species of Lacerta known to be unisexual - L. armeniaca and L. dahli.

Our previous paper (DAREVSKY et al. 1978) reported results of morphological, cytological and chromosomal analysis of two males of L. armeniaca. The external appearance of both of the males did not differ from that of female L. armeniaca except for the size of body and head. One male had two well-developed testes, the other one appeared to be an intersex with a testis to the left and an "ovotestis" to the right. We believe that the occurrence of intersexes is not so rare a phenomenon in lacertid lizards. According to illustrations provided by LANTZ (1923) and DOBROVOLSKA (1964), males of L. saxicola and of L. dahli seemed also to be intersexes, since they had testis on their left side anatomically and on the right side the former had ovary and the latter had apparently "ovotestis".

Karyological analysis of both the male and the intersex of L. armeniaca has shown that they have the same number of chromosomes as females of L. armeniaca but the former displays in addition to the one found in females another heteromorphic pair of chromosomes, probably that

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of sex chromosomes (Plate I: Fig. : 3). Taking into consideration the nonhybrid diploid nature of the male individuals, we suggested that one of the possible causes of their origin might be a hormonal sex reversion (DAREVSKY et al. 1978).

This paper describes another male L. armeniaca captured within a mixed population of two unisexual species (L. armeniaca, L. dahli) and one bisexual species (L. portschinskii). This male was initially caged with females of L. armeniaca, and although the former was viable and active, no mating was observed. The male was maintained alive until autumn and was sacrificed and fixed in September 1979.

In this paper we report the results of karyological, cytological and cytophotometrical analyses of ordinary females of L. armeniaca and the male in question, as well as of a control male of the bisexual species L. portschinskii and a hybrid female L. dahli x L. portschinskii.

MATERIAL AND METHODS

The males of L. armeniaca, L. portschinskii and the hybrid female of L. dahli x L. portschinskii were collected from one population (in Armenia, near the town Stepanavan), the females of L. armeniaca were caught in two isolated populations near the towns Ankavan and Zurnabad.

Judging from its body size, head and body length being 48.5 mm, the L. armeniaca male was at least two years old, i.e. it was caught after its second hibernation (Plate I: Fig. 1). Its affiliation with L. armeniaca was proved, besides its characteristic colouration, by some typical features of the pholidosis, including the characteristic arrangement of some scutes of the temporal area and a discontinuous row of granules between the supraoculars and the supraciliaries. Some deviations in meristic features were observed which appeared well within the range of variation established for this particular species.

Post-mortem examination of the male L. armaniaca showed that its testes were rather well developed, likewise its hemi-penises. Of special interest is that, unlike other males of the rock-lizards mentioned above, clearly visible rudimentary oviducts were lacking in the abdomen cavity of the male in question (Plate I.: Fig. 2). In all, the picture of the inner sex organs of this male did not actually differ from that usually observed for males of bisexual species examined in the same season.

In the karyological analysis, the bone marrow, blood and testicular cells of the colchicined lizards were treated with hypotonic solution (0.075 M KCL), fixed in methanol acetic acid (3:1). The smears were then stained with Giemsa Solution. For preparing series of paraffine sections the right testis of males of L. armeniaca and L. portschinskii were fixed in Bouin's fluid (30 min), then placed in 70% alcohol and then stained with Heidenhain's hematoxylin. The smears of blood and testis of the males of L. armeniaca, L. portschinskii and of hybrid female L. dahli x L. portschinskii were dried and fixed in 96% methanol. The slides were treated with 1N HCL, then stained with Schiff reagent. Measurement of the DNA content in the nuclei of blood and spermatid cells of the above specimens was carried out using 2-wave cytophotometry (the long waves being equal to 500 nm and 530 nm).

Chromosomes of about 150 cells from 6 lizards were examined and DNA quantity in 271 nuclei from 3 lizards was measured.

RESULTS AND DISCUSSION

The number and morphology of the chromosomes of female L. armeniaca are the same as in the males and the intersex of L. armeniaca described earlier: 35 acrocentric macro- and 3 micro-chromosomes (Plate I.: Figs 3-4). The small size of the chromosomes of the heteromorphic (the 18th) pair makes it difficult to study and identify them. Therefore at present we cannot say exactly

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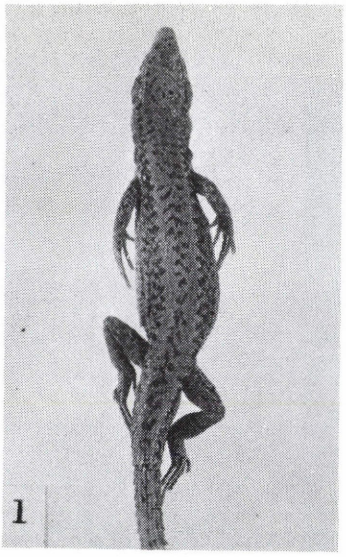
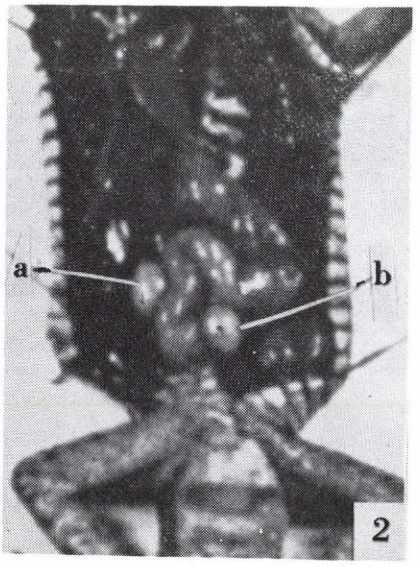
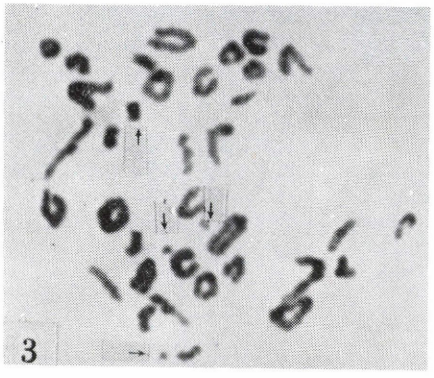
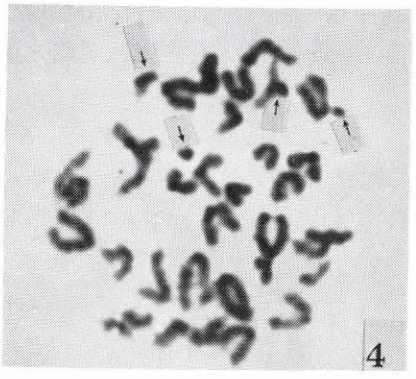
PLATE I. Figs 1-2: A male of the parthenogenetic species Lacerta armeniaca: external view (1), the same, reproductive organs a, b - testis (2). - Figs 3-6: Metaphase plates: metaphase in male L. armeniaca (3), metaphase in female L. armeniaca (4), metaphase I in male L. armeniaca (5), metaphase in male L. portschinskii (6).
Arrows mark the micro- and presumably sex (ZW) chromosomes and bivalents (x 630)

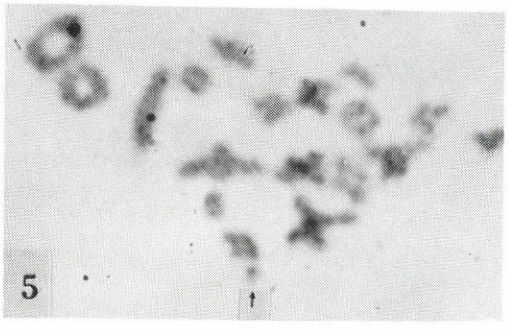
Plate I.











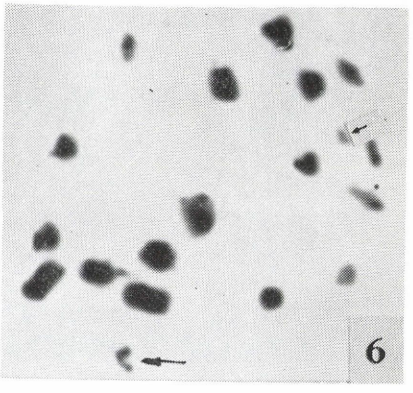
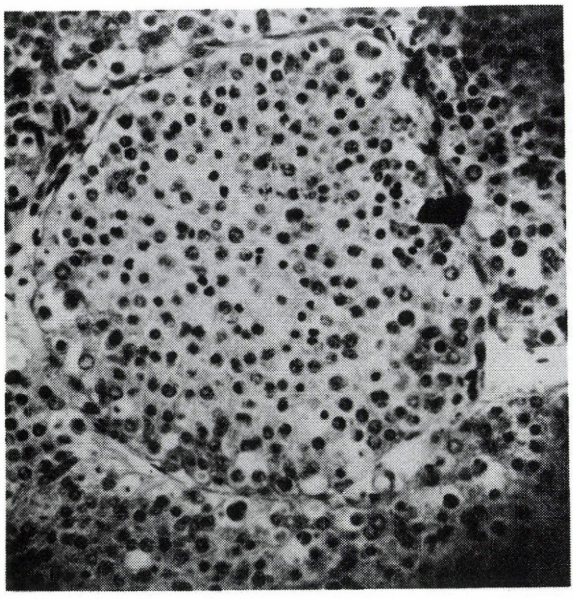


Plate II.



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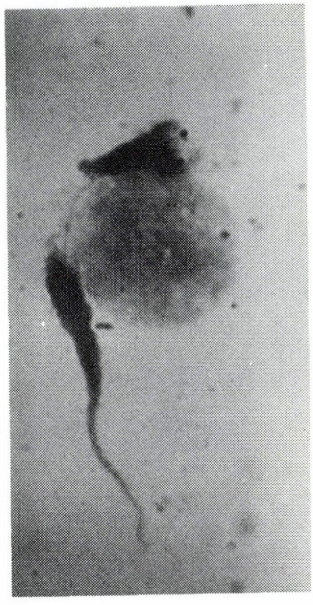

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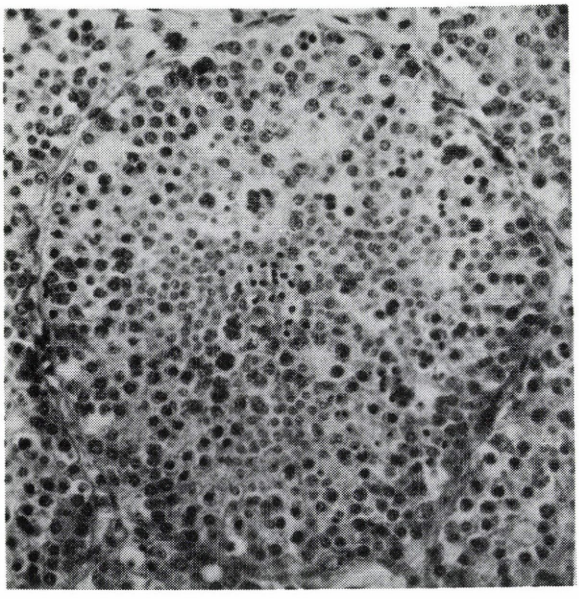

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whether L. armeniaca shows any interpopular variation in these chromosomes, although such facts have been known for sex chromosomes of other species of lizards (WRIGHT 1973). An analogical heteromorphic (the 18th) pair of chromosomes was also observed in the karyotypes of females of several species of the family Lacertidae: L. triliniata, Eremias olivieri, E. arguta, E. velox, L. strigata, Ophisops elegans and was absent in male karyotypes of the 4 latter species studied (GORMAN 1969, IVANOV & FEDOROVA 1970, IVANOV 1973, BHATNAGAR & YONISS 1976). The authors assumed that these chromosomes were sex chromosomes, and that sex determination in these species was of the ZW(♀)/ZZ(♂) type. We suppose that the heteromorphic pair of chromosomes in females of L. armeniaca are also sex chromosomes inherited from the ancestral species. The W-chromosome seems to contain the genes determining female sex and is involved in actively determining femaleness. This fact almost certainly implies that mating of diploid parthenogenetic females of L. armeniaca with bisexual species of the genus Lacerta always produces only triploid females. The only exception is the triploid hybrid male L. rostombekovi x L. raddei, though it should be noticed that the animal had oviducts in addition to well-developed testes.

The karyotypical identity of diploid females, the male and the intersex of L. armeniaca indicates the nonhybrid nature of the two latter individuals which was supported by our earlier assumption that a cause of the appearance of diploid male individuals in L. armeniaca, presumably with ZW chromosomes, lies probably in their hormonal sex reversion. Karyological study of the somatic cells of the newly captured male L. armeniaca confirmed its diploid nature, too (2n = 38). Unfortunately, only a few dividing cells at metaphase with well-spread chromosomes were at our disposal, which may perhaps be explained by the time of fixation, late in autumn. This prevented us from studying the morphology of the chromosomes in greater detail to identify the heteromorphic pair in the karyotype. The diploid nature of the male is supported by cytophotometric investigations of the DNA contents in their blood cell nuclei. The DNA quantity in somatic cells of this male and in the control diploid male of L. portschinskii (2 n = 38) is practically the same, while this value in the hybrid female L. dahli x L. portschinskii is almost 1.5 times higher, which corresponds to the triploid level (Table 1).

Special attention was paid to the study of spermatogenesis in the male of L. armeniaca. Meiosis is well known to be a critical moment for an animal as its normal course provides the production of normal gametes. As it was expected for the autumn fixation, we have not observed many dividing cells at metaphase I and II in both of the males examined, but both of them displayed a haploid set of bivalents (n = 19, Plate I.: Figs 5-6). The bivalents were cross- and ring-shaped and had only terminal associations. The two smallest bivalents showed no features characteristic of sex bivalents (heterocyclicity, "end-to-end" conjugation) and did not differ from each other; they formed a symmetrical ring-shaped figure and were not associated with other bivalents.

The success of unisexual species depends in many respects on the capability of females to reproduce mature eggs with a somatic chromosome complement. One of the mechanisms contributing to this end is the blocking of cytokinesis in one of the mitoses prior to meiosis, which leads to doubling the chromosome number. This has been demonstrated for gynogenetic fishes, amphibians and unisexual lizards of the genus Cnemidophorus (MACGREGOR & UZZELL 1964, CUELLAR 1971, CIMINO 1972). The same mechanism is presumably operating in parthenogenetic lizards of the genus Lacerta (UZZELL 1970). At the same time, the haploid number of bivalents at metaphase I of the diploid male of L. armeniaca shows that the blocking of cytokinesis is lacking in it. Whether this mechanism is operating during meiosis of some tri- and tetraploid hybrid males and females of the genus Cnemidophorus that have been studied remains unknown (LOWE et al. 1970, NEAVES 1971, CUELLAR & McKINNEY 1976, COLE 1979).

Whether the gametes will have balanced chromosome sets depends on the regularity of chromosome disjunction in meiosis. Therefore of special interest was the measurement on mean DNA content of the spermatids on smear preparations of both the study and the control males. This value was found to be almost half as much as that in the nuclei of the blood cells of the same specimens, that is, conforming to their haploid level (Table 1). The great number of haploid spermatids in both of the males shows that in the course of meiosis the bivalents undergo the first and then the second division of maturation and then normally disjunct to the poles, forming haploid gametes.

PLATE II. Figs 7-9: Histological section of testes: Lacerta portschinskii, general view, x 400 (7), L. armeniaca, general view, x 400 (8), L. armeniaca, presence of spermatozoa, x 630 (9)

Table 1. Contents of DNA-fuxin in the nuclei of cells of males L. armeniaca, L. portschinskii and a female L. dahli x L. portschinskii

Species	Tissues	Number of nuclei	Average value of DNA-fuxin (in nominal units) X ± S	Coefficient of variation (%) V	Ploidy level
L. armeniaca	blood	100	106.3 ± 6.9	6.3	2n
L. portschinskii	"	30	108.2 ± 6.8	6.3	2n
L. dahli x L. portschinskii	"	50	140.0 ± 5.5	3.9	3n
L. armeniaca	testis (spermatids)	50	59.7 ± 7.3	12.2	n
L. portschinskii	"	41	51.0 ± 4.0	7.6	n

The pictures of spermatogenesis on paraffine sections of the gonads of both of the males practically did not differ. A usual picture was observed: spermatogonial cells were placed at the base of the basal membrane, then followed several rows of dividing spermatocytes I and II and spermatids at different stages of development, and rather scarce spermatozoids (Plate II.: Figs 7-9).

The pictures described above do not differ essentially from those which are observed in males of other lizards at this period of the year (CHRISTIAN 1971). It should be noted that unlike the male and the intersex of L. armeniaca studied earlier, in the newly discovered male the typical order of cell row disposition was observed.

Thus, females of L. armeniaca (from 2 populations) have a diploid set of acrocentric chromosomes with probably sex (ZW) chromosomes: 2 n = 38:354A+3m. Complex studies of the male of L. armeniaca show this male to be diploid, and by its nature, to be analogous to the other two diploid nonhybrid male individuals of L. armeniaca and is different from the triploid hybrid male L. rostombekovi x L. raddei (DAREVSKY et al. 1973) and from tetraploid and also hybrid females (DAREVSKY & KULIKOVA 1964, KUPRIYANOVA 1973). The pictures of spermatogenesis do not differ from those in the control male. Mitotic and meiotic activities are observed in the testes which end in forming numerous spermatids and a small number of spermatozoids. Mean DNA content in the spermatids approximately fits the haploid level. It remains unknown, whether spermatogenesis is completed by the process of spermatid maturation and by the formation of fertile spermatozoids. In any case, proceeding from all what has been said above, it is only possible to assume that the diploid male of the parthenogenetic species L. armeniaca is fertile and has originated as a result of sex reversion.

Returning to the reasons of appearance of such males in natural populations, we think it is reasonable to consider some problems revelant to sex determination.

Sex differentiation is known to be genetically and hormonally regulated. Classical, morphological and experimental data disclose the sexual bipotentuality of the gonads. WONDER (1980) writes "in mammals, in the absence of a testes, the female sex differentiation of the reproductive system occurs". As the male in mammals is heterogametic, the author comes to the conclusion that the determining factor of sex differences of the reproductive system is the gonad of the heterogametic sex.

This assumption is supported by the fact that in birds, where the female, unlike in mammals, is the heterogametic sex, the determining factor of the differentiation is not the testes but the ovary. The gonad of the heterogametic sex, as a rule, grows quicker than and therefore suppresses the growth of the gonad of the alternative sex. In mammals the testes suppress the growth of the potential ovary tissue of the testes (the cortex), in birds on the contrary the quickly growing ovary suppresses the testicular tissue of the ovary (the medula) (WOLF 1980).

More and more information is now available concerning the genetic control of sexual determination.

According to MITTWOCH (1975, 1979), segments of sex chromosomes regulating the rate of growth of the bipotential gonad, induce its development into the testes or the ovary.

In humans mutations (i.e. tfm, the testicular feminization), structural abberations (the deficiency of Y chromosome) inducing the abnormal development of male genotype are known to occur (SIMPSON 1979, ROSENFELD et al. 1979). In wood lemming of the genus Myopus the deficiency of X^+ chromosome has been also demonstrated: the short arm of the X^+ chromosome of X^+Y females appeared to be considerably shorter than that of the X chromosome of normal XX females (HERBST et al. 1978). Analogical abberation has also been discovered in the sex chromosome of rare males of the parthenogenetic stick insect Carausius morosus Br. (PIJNACKER & FERWERDA 1980).

Altogether, these observations suggest that some abberation and in heterogametic sex often the deficiency of sex chromosomes may lead to alternative gonad differentiation, that is, sex reversion. Cases of sex reversion in both directions induced by hormon (steroid) on the fish Oryzias latipes shows that in this organism the sex chromosomes do not differ fundamentally from the autosomes and the chromosome mechanism of sex determination is in an early stage of evolution (MITTWOCH 1975). The same reasoning may also be applied to explain the influence of temperature of the gonad differentiation of both the male and the female sexes in amphibian larvae and embryos of turtles (PIO 1973, PIEAU 1975). The fact that in lizards sex chromosomes are found only in comparatively few species, also testifies to their recent origin. However, some facts give opportunity to suppose that, at any rate, the Y-chromosome of male Cnemidophorus tigris (COLE 1979) and W-chromosome of female L. armeniaca are already sufficiently stabilized and play the determining role in their sex differentiation.

At present many works have been devoted to the investigation of the role of H-Y antigen in gonad differentiation. But we know no works of this kind done on lizards. It has been established that H-Y antigen is detected in the gonads of individuals of the heterogametic sex. In the uncaudata amphibia with homomorphic sex chromosomes heterogamety was revealed by the presence of H-Y antigen (ZABORSKI 1979). However, recently it has been shown that H-Y antigen is also expressed in the gonads of sex-reversed male chicken embryos with homomorphic sex chromosomes, in intersex saansky goats and some human families (in man with XX chromosomes) (ENGEL & WENIGER 1979, WACHTEL 1979). The authors made an assumption that genes for H-Y antigens exist in the genome of both sexes. According to MITTWOCH's (1979) opinion, H-Y antigen is detected in individuals of that sex whose gonads grow quicker (i.e. in the testes in mammals and in the ovary in birds). FREDGA and his coauthors (FREDGA et al. 1980) believe that the abberation of the X^+-chromosome of the wood lemming of the genus Myopus interferes with the development of H-Y antigen in XY embryos and therefore these embryos become females. Considering the observation described above, we suggest that the rare males of parthenogenetic lacertid lizards with ZW sex chromosomes, whose gonadal sex does not correspond with their chromosomal sex, could be used as a model for the investigation of H-Y antigen and of its role in the process of development and disturbance of sexual differentiation of these lizards.

Rare males, as it was mentioned, occur in parthenogenetic teiid lizards of the genus Cnemidophorus. Karyological study has shown that the males appeared to be tri- (3n C. neomexicanus x C. inornatus) and tetraploid (4n C. sonorae x C. tigris) individuals which originated from matings of di- and triploid unisexual females with males of bisexual species (LOWE et al. 1970, CUELLAR & McKINNEY 1976). The mitotic and meiotic activity as well as a few spermatids of unknown ploidy and no mature spermatozoa were observed in the testes of the above and other hybrid teiid males. It was just the infrequency of spermatids which prevented the authors from stating with certainty anything about their fertility.

No males were discovered among teiid parthenogenetic lizards which were diploid and indistinguishable from the females, like the males of L. armeniaca. This phenomenon could possibly be explained by the fact that lacertid females are of the heterogametic (ZW) sex. It is known that the actively induced process of the development of the heterogametic sex is more complex than that of the homogametic one and it presents more opportunities for different kinds of abnormalities. Teiid males of C. tigris, unlike lacertid males, are of the heterogametic (XY) sex (COLE et al. 1969, BULL 1978, COLE 1979) and parthenogenetic teiid females are probably of the homogametic sex. The same explanation could be given to the fact that unlike lacertid lizards, where hybridization results in the appearance of hybrid but sterile females, in teiid lizards this leads to both hybrid tri- and tetraploid males (C. sonorae x C. tigris with XXXY sex chromosomes; LOWE et al. 1970) and females (C. sonorae x C. tigris with XXXX sex chromosomes; COLE 1979).

The extremely rare occurrence of males in populations of unisexual lizards of the genus

Lacerta, as well as the absence of definite information on the degree of their fertility make it difficult to clarify the role of these occasional males in the evolution of parthenogenetic species. With the full fertility of such males, it would be reasonable to expect the appearance of fertile triploid hybrids resulting from their mating with females of their own species. However, no such triploids have been found so far. It is worth mentioning, however, that in the collection of the Zoological Institute of the USSR Academy of Sciences, among the rock lizards there are two apparently hybrid females (L. armeniaca x L. dahli) whose mechanism of appearance still remains obscure and urgently needs further examination.

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