

CHROMOSOMAL DIVERSITY AND AN ABERRANT GENETIC SYSTEM OF SEX DETERMINATION IN THE ARCTIC LEMMING, *DICROSTONYX TORQUATUS* PALLAS (1779)

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Introduction

In the arctic lemming the taxonomy and genetics of sex determination are of great interest. For a long time all arctic lemmings, except *D. hudsonius*, were considered as a single polytypic species of almost circumpolar distribution, *D. torquatus* (Rausch, 1953). In recent years cytological investigations and cross-breeding experiments have shown that at least 6 American and 2 Eurasian species of the genus *Dicrostonyx* existed (Rausch & Rausch, 1972; Gileva, 1973, 1975; Kozlovski, 1974). In many of these species unusual sex chromosome systems and female biased sex ratios were discovered.

Material and methods

Karyotypes of the following three Asian forms of *Dicrostonyx* are described in this paper: *D.t. torquatus* from the Polar Urals, *D.t. chionopaes* from the Laptev Sea coast (Yakutia) and *D.t. chionopaes* from Rautan island situated close to the Arctic coast of the Chukotka peninsula. Laboratory colonies of Urals and Yakutian lemmings were established. About 1600 animals of each form were studied in breeding experiments. Among them 841 Urals lemmings, 858 Yakutian lemmings as well as 7 animals (2♂♂ and 5♀♀) from Chukotka were karyotyped.

Results and discussion

The karyotype of the Yakutian arctic lemming consists of 46 A-chromosomes and 1 to 8 small bi-armed B-chromosomes. Autosomes include 2 pairs of small

metacentrics, 2 pairs of subtelocentrics and 18 pairs of acrocentrics (Fig. 1a). As stated above, the arctic lemming was found to have an unusual sex chromosome system. 395 females from the laboratory stock had two large metacentric X chromosomes. The other 242 females and all the 221 males exhibited an identical karyotype. Besides autosome pairs they possessed only one X and a large unpaired acrocentric. The latter, as seen from its size, G-banding pattern and meiotic behaviour (Fig. 2a, 3a) proved to be homologous to the long arm of the X. Hence, all *D.t. chionopaes* possessed in fact this chromosome in double, either as two long arms of the Xs (XX females) or as the same arm coupled with the unpaired chromosome (the other females and males). Thus the odd element present in the *D.t. chionopaes* karyotype is an autosome (Nr. 5). The X chromosome of this form resulted from a Robertsonian translocation of the original X on to autosome Nr. 5, and only the short arm of the modern X of the Yakutian arctic lemming corresponds to the initial X chromosome. The Y chromosome was not revealed here. One could assume the Y to be concealed among B-chromosomes. But the mean numbers of chromosomes in males and females of both types proved to be equal. If the males had the Y, they would have on the average one chromosome more than females (Gileva, 1975). Thus males and many females of *D.t. chionopaes* should be considered as having an XO constitution.

The chromosome complement of *D.t. torquatus* is basically similar to that of the Yakutian form (Fig. 1b). Three hundred ninety eight females karyotyped had two X chromosomes identical to those of *D.t. chionopaes* from Yakutia; all the 233 males and 210 females exhibited an XO constitution. However, instead of an unpaired autosome Nr. 5 they

possessed two odd chromosomes: a large submetacentric resulting from the translocation of autosome Nr. 5 on to autosome Nr. 18, and the other member of the 18th pair (Fig. 2b). At meiosis these unpaired elements formed a trivalent with the X

(Fig. 3b). The Y chromosome was not identified either. The number of B-chromosomes varied from 0 to 7.

The karyotype of the Rautan island arctic lemming is similar to the sets of two forms described

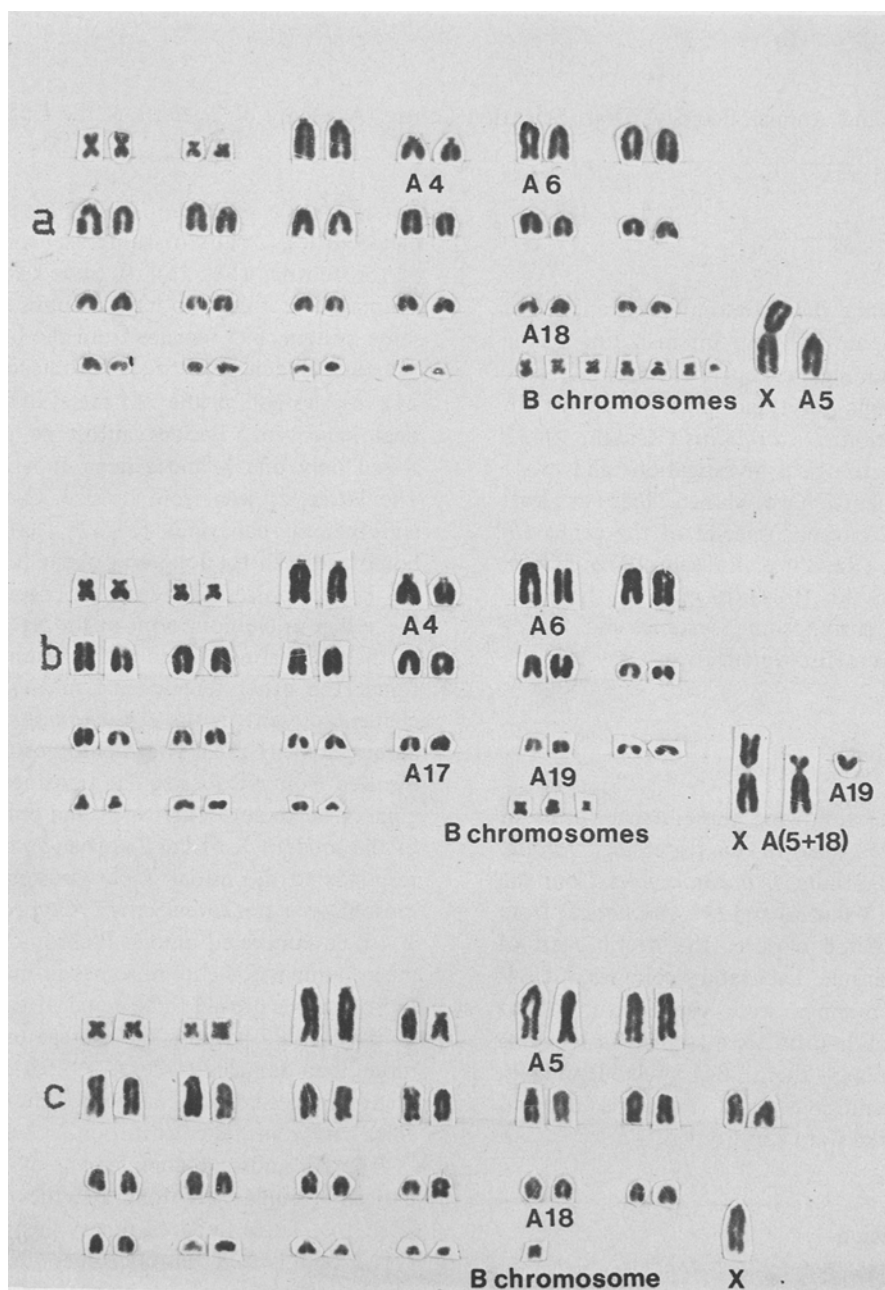


Fig. 1. Karyotypes of Palaeartic arctic lemmings: (a) Yakutian *D.t. chionopaes*; – (b) *D.t. torquatus*; – (c) Chuchotkan *D.t. chionopaes*.

above. This is in agreement with the findings of Kozlovsky (1974) in *D.t. chionopaes* of the Chaun inlet coast (Western Chukotka). All the 7 animals studied had 47 A-chromosomes (46 autosomes and one X chromosome). Three females possessed 1 B-chromosome each ($2n = 48$), the other lemmings were without them (Fig. 1c). The X is an acrocentric, having often a visible short arm. The size and G-banding pattern of the X are similar to those of the short arm of the complex X of Urals and Yakutian animals (Fig. 2c). At male diakinesis the X forms a univalent which is not associated with any other chromosome (Fig. 3c).

Thus in three remote populations of the arctic lemming numerous XO females were discovered. They were found to be quite fertile and normal phenotypically. These females occurred only in certain families and in the same families we encountered female biased sex ratio. We assume that both phenomena have a common genetic basis, i.e. that the sex of XO specimens depends after all on the X linked factor, having two alternative forms. The XO lemmings possessing the *m*-form develop as males; those bearing the *f*-form develop as females. The assumed mode of inheritance of this factor is presented in Scheme 1.

This hypothesis has been substantiated by analyzing the sex chromosome constitution and the secondary sex ratio in animals from several (11-12) captive generations of *D.t. torquatus* and Yakutian *D.t. chionopaes*. Data on *D.t. chionopaes* are more numerous; they have been reported elsewhere. Findings in *D.t. torquatus* are presented in this paper. It follows from Scheme 1 that all the males are identical in their sex chromosome genotype and that females display three types according to their sex chromosome constitution

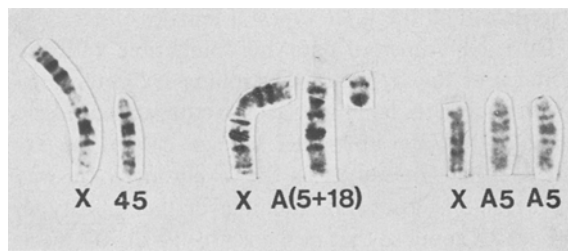


Fig. 2. G-banding pattern of the X chromosome and autosomes involved into Robertsonian translocations: (a) Yakutian *D.t. chionopaes*; – (b) *D.t. torquatus*; – (c) Chukotkan *D.t. chionopaes*.



Fig. 3. Diakinesis in males of the arctic lemming: (a) Yakutian *D.t. chionopaes*. Solid arrow shows bivalent composed of the X chromosome and autosome No. 5; dotted arrow indicates univalent formed by the B; – (b) *D.t. torquatus*. Arrow indicates trivalent formed by the X chromosome and autosomes No. 5 and No. 18; – (c) Chukotkan *D.t. chionopaes*. Arrow indicates univalent formed by the X chromosome.

Scheme I

Inheritance of X linked *mf*-factor controlling sex determination in arctic lemming

		Female type				
		1 X^mX^m	2 X^mX^f		3 X^fO	
Gametes		X^m	X^m	X^f	X^f	O
Male X^mO	X^m	X^mX^m	X^mX^m	X^mX^f	X^mX^f	X^mO
		♀	♀	♀	♀	♂
	O	X^mO	X^mO	X^fO	X^fO	OO
		♂	♂	♀	♀	inviable
Sex ratio, ♀ : ♂		0.50	0.75		0.67	

Table 1

Progeny of diverse types of females of *D.t. torquatus*

Progeny		Type and number of females mated		
		1(X^mX^m)*	2(X^mX^f)	3(X^fO)
		5	20	19
Mean sex ratio in litters (% ♀)	Expected	0,50	0,75	0,67
	Observed	0,48	0,80	0,70
Number of daughters	1 type	2**	3	—
	2 type	—	6	2
	3 type	—	47	47
	Unknown type (XX)	44	55	39

* 62 female progenies of the 2-6th generations descending from these dams were also karyotyped. All these progenies have an XX constitution.

** These females were classified as the 1st type at a 9% level of significance because they produced 6-7 XX daughters and no XO ones.

and that of their female progeny. The X^fO type is cytologically readily revealed. X^mX^m and X^mX^f females can be distinguished only by their progeny: X^mX^m dams are unable to produce XO daughters. Scheme 1 shows that an XX female can be classified as an X^mX^m at a 5% level of significance if she gives birth to not less than 8 XX daughters and to none of the XO type. The XX dam can be considered as an X^mX^f type if she has at least one XO daughter. The following predictions could be done on the ground of scheme 1: all female progenies of the 1st type dams of any generation should have an X^mX^m constitution. All the three types of daughters should be observed in the progeny of the 2nd type of females; the 3rd type dams could produce daughters of the 2nd and 3rd

types only. As seen from Table 1, breeding data are fully consistent with these predictions. The observed secondary sex ratio agrees with values expected for offsprings of all the three types of females either.

Thus, experimental data are compatible with the existence of the *mf*-factor controlling sex determination in the arctic lemming. This factor is most likely X-linked, but its autosomal linkage cannot be excluded either. Inasmuch as the Y chromosome was not revealed as a separate member of the karyotype, we have to suppose that in the genotype of XO specimens there is a certain male determinant, either a microtranslocation of the Y, or a mutant autosomal gene. From breeding data the most probable location of the male determinant is the unpaired autosome

(Nr. 5 of Yakutian *D.t. chionopaes* and Nr. 5 + 18 of *D.t. torquatus*). The nature and mode of action of the *mf*-factor are not clear yet. We may assume that this factor corresponds to the structural locus for H-Y antigen and that the male determinant located on the autosome possesses a regulatory function. The *m*-form can be a normal allele producing H-Y antigen in the presence of the male determinant and the *f*-form is the mutant allele which has lost this ability. This genetic mechanism seems to be evolutionary stable because a rather similar sex determining system was discovered in a related species, in the wood lemming, *Myopus schisticolor* (Fredga et al., 1977).

Both wood lemmings and arctic lemmings attain at regular intervals high numerical densities followed by decline phases. Changes of frequencies of the two *mf*-factor forms can be considered as one of the genetic mechanisms responsible for peaks of abundance in lemmings. Males of these species are polygamous, so an excess of females can cause a rapid increase of density. This is confirmed by Chernyavsky (1978): in the arctic lemming on Wrangel island a female biased sex ratio was observed just before the peak of density while at other stages of the population cycle the sex ratio was close to 1:1.

Some taxonomic implications of our findings should be discussed. As shown above, the three examined forms of arctic lemming exhibited similar karyotypes; they differed only in 1-2 Robertsonian translocations. Such differences usually do not lead to reproductive isolation. Indeed, progeny of crosses between *D.t. torquatus* and Yakutian *D.t. chionopaes* was indefinitely fertile (Pokrovsky, Gileva, 1976). Thus, arctic lemmings of the Asian continent and Rowtan island may be provisionally recognized as conspecific. The morphological uniformity of Palaearctic arctic lemmings (Chernyavsky, 1972) supports this conclusion. However, the arctic lemming on Wrangel island appears to represent another distinct species of genus *Dicrostonyx* in Palaearctic (Kozlovsky, 1974).

The occurrence of similar aberrant systems of sex determination in two genera of lemmings, *Myopus* and *Dicrostonyx*, and the apparent absence of such a system in the third genus, *Lemmus* (Rausch, Rausch, 1975) seem essential in studying taxonomic relationships between diverse genera of lemmings.

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