

A contrasted pattern of chromosome evolution in two genera of lemmings, *Lemmus* and *Dicrostonyx* (Mammalia, Rodentia)

E. A. Gileva

Institute of Plant and Animal Ecology, Urals Scientific Center, Academy of Sciences of the USSR, Sverdlovsk, 620008, USSR

Abstract

Lemmings of the genus *Lemmus* display a very moderate degree of karyotype diversity. In *L. lemmus* from the Kola Peninsula, *L. sibiricus sibiricus* from the Pechora inlet coast and the Laptev Sea coast, *L. s. portenkoi* from the Vrangell Island and *L. amurensis* from Southern Yakutia the gross chromosome morphology and C-banding pattern proved to be identical ($2n = 50$, $NF = 50$). The chromosome set of *L. s. chrysogaster* (the Chukotka Peninsula) consists of 23 pairs of acrocentrics and 2 pairs of subtelocentrics ($2n = 50$, $NF = 54$), and so it is identical to the karyotype of North American *Lemmus*. As to spatial structure of populations, population dynamics, degree of inbreeding and uniformity of habitats throughout the area, *Lemmus* is basically similar to the lemmings of another genus, *Dicrostonyx*. In the latter, however, an extensive chromosome diversity has been found. Therefore, the ecological and population characteristics mentioned above are suggested not to be essential for the rate of chromosome evolution in lemmings.

Introduction

Lemmings of two genera, *Lemmus* Link 1795 and *Dicrostonyx* Gloger 1841 represent a suitable model for examining some ideas related to factors of chromosome evolution. It has been suggested recently that a great chromosomal diversity in mammals is mainly due to a particular social structure of their populations considered to consist of relatively isolated breeding units (microdemes). Inbreeding and genetic drift resulting from the small microdeme size seem to promote the spread and fixation of newly arising chromosome rearrangements (Wilson *et al.*, 1975; White, 1978; Vorontsov & Lyapunova, 1981).

According to the more traditional point of view, karyotype diversity is the result of an adaptation to a changeable environment (Mayr, 1963; Williams, 1966), but the evidence for selective processes in chromosome evolution is purely circumstantial.

Many factors are most likely involved in regula-

tion of the rate of chromosome evolution. It is very difficult to assess the significance of every individual factor, as chromosomally diversified taxa usually differ in many respects simultaneously. *Lemmus* and *Dicrostonyx* are of interest in this connection, because these genera exhibit a noticeable resemblance in certain characteristics supposed to be essential for chromosome evolution. First, they possess nearly identical circumpolar areas. Lemmings inhabit chiefly arctic and subarctic tundra, being highly adapted to the northern environment. The distribution of lemmings in tundra is patchy, and relatively dry microhabitats of *Dicrostonyx* are usually separated from the more humid microhabitats of *Lemmus* only by several meters. Microhabitats of lemmings display a striking uniformity throughout the vast territories of the Old and New World (Marsden, 1964; Pitelka, 1973). Moreover, paleontological data show that from early Pleistocene (i.e. during the last 1–2 million of years) *Lemmus* and *Dicrostonyx* were typical members of the

same mammalian association of Eurasian and Alaskan steppe-tundra (Guthrie & Matthews, 1971; Agadzhanian, 1980; Kowalski, 1980). In other words, lemmings of both genera were affected over a long period of time by many similar ecological factors.

Secondly, *Lemmus* and *Dicrostonyx* exhibit an identical population cycle. The cycle has a rather steady period (3–4 years) and comprises a phase of low density, a phase of gradual increase and a peak of abundance (Fuller *et al.*, 1975; Chernyavsky, 1978). Strong inbreeding within microdemes seems inevitable, especially at low density and increase phases (Maynard Smith & Stenseth, 1978; Stenseth, 1978). Although the degree of inbreeding remains to be shown, the resemblance of population characteristics in *Lemmus* and *Dicrostonyx* indicates that this degree must be comparable in the genera in question.

Thus, *Lemmus* and *Dicrostonyx* are alike in being exposed to many similar ecological factors at present and in the past, and in population structure and dynamics as well. If the relevant characteristics are really essential for chromosomal evolution, the pattern of chromosome divergence within these genera is expected to be similar. The karyotype variability in *Dicrostonyx* was investigated by many authors (Rausch & Rausch, 1972; Gileva, 1973, 1980; Gileva *et al.*, 1981; Kozlovsky, 1974; Krohne, 1982). Cytogenetic studies in *Lemmus* are less numerous. In 1957 Matthey has found 50 acrocentric chromosomes in the diploid complement of *L. lemmus* ($2n = 50$, $NF = 50$). Rausch and Rausch (1975) described the gross morphology and G-banding pattern of the chromosomes of *L. lemmus* from Fennoscandia ($2n = 50$, $NF = 50$), *L. trimucronatus* from 3 Alaskan localities and *L. nigripes* from St. George Island (near Alaska). All North American forms possess 23 pairs of acrocentrics and 2 pairs of biarmed chromosomes ($2n = 50$, $NF = 54$ or 52 , due to the small size of short arms). Taking into consideration the chromosome difference between *L. lemmus* and *L. trimucronatus* and the resemblance of pelage color in *L. trimucronatus* and *L. sibiricus chrysogaster* (Krivosheev & Rossolimo, 1966), Rausch and Rausch suggested that all North American lemmings belonged to *L. sibiricus*. They considered this suggestion as provisional until Siberian lemmings would be studied cytogenetically. Later chromosomes of *L.s. chrysogaster* from 4

Chukotkan regions were reported to be identical to those of Alaskan lemmings (Kozlovsky & Khvorostyanskaya, 1978), but the karyotype of *L.s. sibiricus* from the Polar Urals proved to be similar to the *L. lemmus* diploid complement ($2n = 50$, $NF = 50$) (Bykova, 1977). It was clear that further cytogenetic investigation of *L. sibiricus* would be desirable. In the Amur lemming, *L. amurensis* (South Yakutia) the diploid set consists of 50 acrocentric chromosomes (Chernyavsky *et al.*, 1980).

It follows from this brief survey that the genus *Lemmus* is rather homogeneous as far as the gross chromosome morphology is concerned. In *L. lemmus* and *L. trimucronatus* the G-banding pattern is practically identical except that of the Y chromosome (Rausch & Rausch, 1975). It was of particular interest to investigate C-banded chromosomes in *Lemmus*, since variability of C-heterochromatin is often observed on the intra- and interspecific level even if other differential staining techniques do not reveal a karyotypic diversity in the same taxa (Arnaason, 1980; Sen & Sharma, 1979; etc.). In the present paper I describe routinely stained and C-banded chromosomes of *Lemmus* from 6 palaeartic localities and estimate their diversity in comparison with that of *Dicrostonyx*.

Material and methods

Nomenclature of lemmings is given according to Gromov and Poljakov (1977). Animals of the following species and subspecies were investigated: 1 female and 2 males of *L. lemmus* L. 1758 from the Kola Peninsula (Laplandian Reserve); 2 females and 6 males of *L.s. sibiricus* Kerr 1792 from the coast of the Pechora inlet; 4 females and 3 males of *L.s. sibiricus* from the Laptev Sea coast (Buor-Khaya inlet); 1 female and 3 males of *L.s. chrysogaster* Allen 1903 from Western Chukotka (the coast of the Chaun inlet); 2 males of *L.s. portenkoi* Tschernyavsky 1967 from the Vrangell Island; 1 female and 2 males of *L. amurensis* Vinogradov 1924 from Southern Yakutia. Localities from which the animals were taken are shown in Figure 1. Chromosome preparations of bone marrow were made in the standard way. C-bands were induced according to Sumner (1972). The length of the C-banded sex chromosomes was measured on photographs of 42 cells.

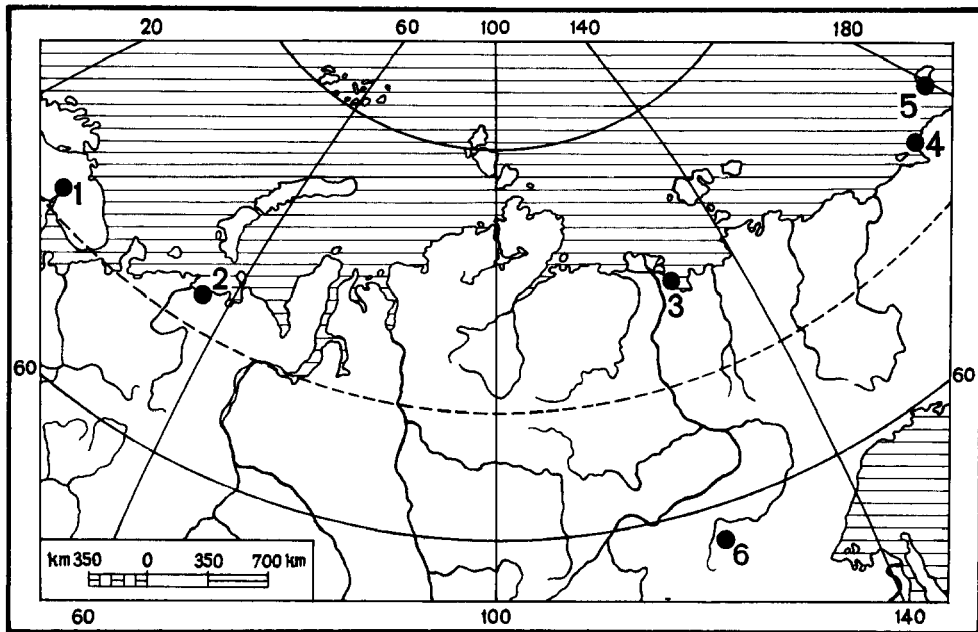


Fig. 1. Localities from which lemmings were taken: (1) Laplandian Reserve (*L. lemmus*); (2) the Pechora inlet coast (*L.s. sibiricus*); (3) the Buor-Khaya inlet coast (*L.s. sibiricus*); (4) the Chaun inlet coast (*L.s. chrysogaster*); (5) the Vrangell Island (*L.s. portenkoi*); (6) Southern Yakutia (*L. amurensis*).

Results

Chromosome complements of *L. lemmus*, *L.s. sibiricus* from two populations, *L.s. portenkoi* and *L. amurensis* proved to be identical in chromosome number and gross morphology as well as C-banding pattern. As an example, the karyotype of *L. amurensis* is shown in Figure 2. The chromosome sets consist of 50 acrocentrics ($2n = 50$, $NF = 50$). Centromeric regions of most autosomes are C-positive. There are 4–5 pairs among the large autosomes that show no demonstrable pericentromeric C-bands. The X chromosome can easily be identified by the interstitial C-band near the centromere. The Y chromosome is about half the length of the X (from 49.5% to 56.1% in the taxa in question) and consists entirely of C-heterochromatin.

The karyotype of *L.s. chrysogaster* from Chukotka (Fig. 3), differs from that of the other taxa examined in several respects. The diploid number is 50 but besides 46 acrocentrics the complement comprises 2 pairs of subtelocentric autosomes, Nos. 2–3. In both subtelocentrics short arms are seen even in the most contracted metaphases. Hence, in

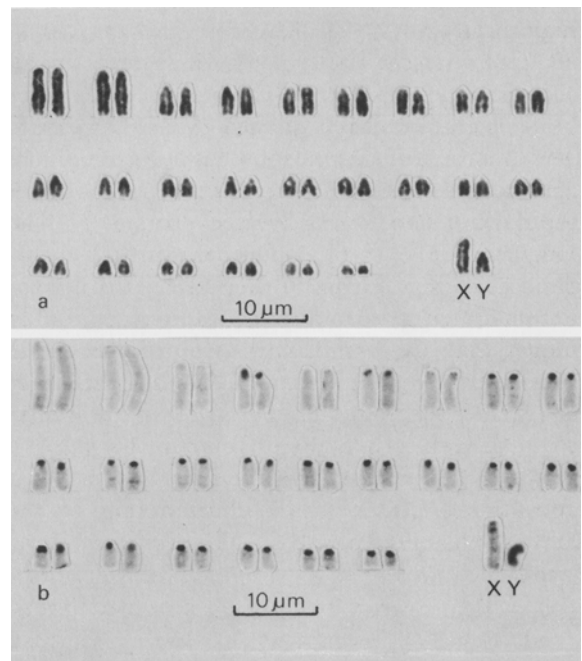


Fig. 2. Karyotype of a male *L. amurensis*: (a) standard staining; (b) C-banding.

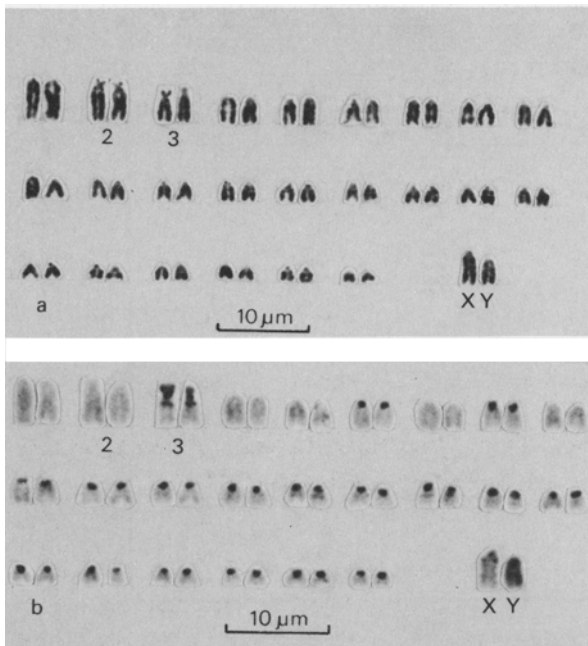


Fig. 3. Karyotype of a male *L.s. chrysogaster*: (a) standard staining; (b) C-banding.

L.s. chrysogaster the NF is 54, and its karyotype is similar to that of lemmings from other Chukotkan regions (Kozlovsky & Khvorostyanskaya, 1978) and from Alaska. The centromeric segments in all chromosomes of *L.s. chrysogaster* except 6 autosomal pairs are darkly stained by the C-method. The short arm of chromosome 2 is euchromatic. In chromosome 3 the short arm is entirely C-positive, the darkest band being located proximally. The long arm of this chromosome has a prominent C-band near the centromere. Because of the heterochromatic arm chromosome 3 is recognizably longer than the homoeologous autosome of the other lemmings. The size and C-banding pattern of the X chromosome of *L.s. chrysogaster* are similar to those of the other taxa of *Lemmus*, but the Y is distinctly longer than half the length of the X; it constitutes 76.0% of the X chromosome, on the average.

Discussion

Some taxonomic implications of our findings can be considered. As was shown above, *L.s. sibiricus* from various populations and *L.s. portenkoi*

have identical karyotypes. The differences between them and *L.s. chrysogaster* in gross morphology and C-banding pattern of chromosomes are clear-cut but not sufficiently large to recognize the latter as a separate species if chromosome characteristics were the only criterion. There is, however, some other evidence for the autonomy of *chrysogaster*. First, the Chukotkan lemmings can be distinguished from the other subspecies of *L. sibiricus* by the pelage color (Krivosheev & Rossolimo, 1966). Secondly, the crossing of *L.s. sibiricus* from the Pechora inlet coast with *L.s. chrysogaster* from the coast of the Chaun inlet resulted in fertile female and sterile male F_1 hybrids (Pokrovsky & Makaranets, 1981). Hence, it is reasonable to consider *L. chrysogaster* as a single species separated from *L. sibiricus*. This inference is consistent with the earlier opinions of G. M. Allen (1914) and Bobrinsky *et al.* (1944). Most likely the species includes North American lemmings as well, as Rausch and Rausch (1975) suggested.

So in the Holarctic there are only two chromosomal types of *Lemmus*, and these types exhibit a very moderate degree of divergence. As for the Eurasian chromosomal type ($2n = 50$, NF = 50), occurring from the Kola Peninsula up to Chukotka, not even the C-banding technique was able to reveal any differences between *L. lemmus*, *L.s. sibiricus*, *L.s. portenkoi* and *L. amurensis* from populations separated by vast distances (several thousands of kilometers). Among lemmings of the second type ($2n = 50$, NF = 54) which can be designated as the Beringian type, C-banding was performed only for animals from one region (the present paper), but the gross morphology of chromosomes turned out to be identical in rodents from 5 distantly located Chukotkan regions, 3 Alaskan localities and St. George Island.

Hence, lemmings of the genus *Lemmus* do not exhibit a considerable diversification of karyotypes, even being isolated on islands. Taking into consideration the extensive distribution of these lemmings, their chromosome complement should be considered as rather stable. This stability could be allocated to the unchangeability of their habitats at present and in the past, as Rausch & Rausch (1975) supposed when considering North American lemmings. Another possible cause of the karyotype stability could be the peaks of abundance, occurring every third or fourth year in lemmings that are

Table 1. Karyotypes of *Dicrostonyx* from 18 natural populations.

Taxon	Locality	2n	A chromosomes		Number of B chromosomes	Reference
			Number	NF		
<i>Eurasia</i>						
<i>D.t. torquatus</i>	Pechora inlet coast	53-60	45-46	51-52	7-15	Gileva <i>et al.</i> , 1981
	Middle Yamal	48-54	45-46	51-52	3-8	Gileva <i>et al.</i> , 1981
	Polar Urals	46-49	45-46	51-52	1-3	Gileva, 1973
<i>D.t. chionopaes</i>	Buor-Khaya inlet coast	48-53	46	51-52	2-7	Gileva <i>et al.</i> , 1981
	Big Rautan Island	47-48	47-48	51-52	0-1	Gileva, 1980
	Chauin inlet coast	57-60	47-48?	51-52?	10-13?	Kozlovsky, 1974
	Lawrence Lagoon	84-85	47-48?	51-52?	37-38?	Chernyavsky & Kozlovsky, 1980
<i>D.t. vinogradovi</i>	Vrangell Island	28	28	54	absent	Chernyavsky & Kozlovsky, 1980
<i>North America</i>						
<i>D.t. exsul</i>	St. Lawrence Island	34	34	54	absent	Rausch & Rausch, 1972
<i>D.t. nelsoni</i>	Seward Peninsula	30	30	54	absent	Rausch & Rausch, 1972
<i>D.t. richardsoni</i>	Churchill, Canada	42-44	42-44	50	absent	Rausch & Rausch, 1972
<i>D.t. rubricatus</i>	Anaktuvuk Pass	34-35	34-35	54	absent	Rausch & Rausch, 1972
	Beaufort Lagoon	32-33	32-33	55	absent	Rausch & Rausch, 1972
	Point Barrow	33	33	54	absent	Rausch & Rausch, 1972
	Umnak Island	34	34	54	absent	Rausch & Rausch, 1972
<i>D.t. groenlandicus</i>	Devon Island	46	46	52	absent	Rausch, 1977
<i>D.t. kilangmiutak</i>	Banks Island	47	47	56	absent	Rausch, 1977
<i>D. hudsonius</i>	Hudson Bay coast	48	48	54	absent	Krohne, 1982

The intrapopulation variability of A chromosomes results mainly from unusual sex chromosome systems (Gileva & Chebotar', 1979)

accompanied by an intense gene and chromosome flow even between remote microdemes. As a result, the interdemic chromosome differentiation which may begin during the low density phase, could be destroyed. Both explanations seem to be unfit as in the arctic lemming, *Dicrostonyx* that displays similar uniformity of habitats and population dynamics, an extensive chromosome diversity occurs.

G- and C-banding patterns were investigated in few populations of the arctic lemmings only (Gileva & Chebotar', 1979; Gileva, 1982), but the diploid number and the morphology of their chromosomes are known to be extremely variable. Table 1 gives chromosome complements of *Dicrostonyx* from 18 natural populations. It is to be stressed that in many cases karyotypes of *Lemmus* from the same localities were studied and, as pointed out earlier, they displayed a very low variability. For *Dicrostonyx*, on the contrary, a specific karyotype was found in each region investigated (*D.t. exsul* from St. Lawrence Island and *D.t. stevensoni* from Umnak Island, with identical diploid and fundamental numbers, differ in chromosome morphology). The chromosome diversity originates mainly from the variability of the B-chromosome number, numerous chromosome fusions and, probably, pericentric

inversions. It is of interest that in *Dicrostonyx* Eurasian and Beringian types can also be distinguished; however, their distribution differs from that of *Lemmus*. The arctic lemmings of the first type inhabit the whole Eurasian continent and the second type is observed in Alaska and on the Vrangell Island, but the karyotype of *D. hudsonius* proved to be basically similar to that of *D. torquatus* from Yakutia.

Hence, it can be concluded that at least in the genera *Lemmus* and *Dicrostonyx*, such characteristics as spatial population structure, population dynamics, degree of inbreeding and uniformity of habitats on vast territories are not decisive for the rate of chromosome evolution. The causes of the difference in chromosome diversity within these genera are not clear. In this connection it must be noted that the reconstruction of the Pleistocene history of lemmings is not complete. It is possible that *Lemmus* and *Dicrostonyx* in certain periods could have been exposed to different constellations of environmental factors, e.g. during glacial advances and recessions (Rausch, 1980). A possible indirect evidence for this might be the not fully coinciding distribution of Eurasian and Beringian types of *Lemmus* and *Dicrostonyx*.

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