

Morphometric variation in collared lemming (Rodentia, Arvicolinae, *Dicrostonyx*) in the Eurasian Arctic in relation to karyotype and mitochondrial DNA diversity

Nataliya I. Abramson & Elena P. Tikhonova

ABSTRACT. The degree of craniometric differences between the taxa, chromosome races and phylogeographic groups of the genus *Dicrostonyx* in the Palaearctic were assessed using discriminant function analysis. Contrary to results obtained by the previous authors it was shown that recognized taxa differ significantly in the structure of the skull and mandible. Individual characters and their combinations most suitable for the discrimination of species and subspecies have been revealed. Analysis of correlation between the chromosomal, molecular and morphological divergence in the collared lemming from the Palaearctic part of the range showed that there is consistency between morphological and molecular (mtDNA diversity) data and discrepancy between morphological and chromosomal data. Known models of chromosome speciation and phylogeographic hypotheses are discussed in the light of the data obtained.

KEY WORDS: *Dicrostonyx*, morphometric variation, chromosome races, mtDNA clades.

Nataliya I. Abramson [Nataliya@asv.mail.iephb.ru], Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia; Elena P. Tikhonova, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia.

Морфометрическая изменчивость копытного лемминга (Rodentia, Arvicolinae, *Dicrostonyx*) в Евразийской Арктике: соотношение с изменчивостью кариотипа и митохондриальной ДНК

Н.И. Абрамсон, Е.П. Тихонова

РЕЗЮМЕ. Методом канонического пошагового анализа исследована степень краниметрических различий между таксонами, хромосомными расами и филогеографическими группами рода *Dicrostonyx* в Палеарктике. В отличие от результатов исследований предыдущих авторов показано, что описанные ранее таксоны достоверно различаются по строению черепа и нижней челюсти, выделены отдельные признаки и их сочетания, наиболее пригодные для характеристики подвидов и видов. Анализ соотношения между хромосомной, молекулярной и морфологической дивергенцией у копытного лемминга в Палеарктической части ареала показал наличие соответствия между уровнем морфологической и молекулярной (изменчивостью митохондриальной ДНК) дивергенцией и отсутствием соответствия между морфологической и хромосомной дивергенцией. На основании полученных результатов обсуждаются предложенные модели хромосомного формообразования и филогеографические гипотезы.

КЛЮЧЕВЫЕ СЛОВА: *Dicrostonyx*, морфометрическая изменчивость, хромосомные расы, мтДНК клады.

Introduction

Collared lemmings (*Dicrostonyx* Gloger, 1841) and true lemmings (*Lemmus* Link, 1795) are the most mass rodents of the tundra and are almost sympatrically distributed over the major part of the Arctic. In contrast to the true lemmings, the collared lemmings display extremely high variability of karyotype (Gileva, 1983). Recent surveys revealed that there are at least five chromosome races in the Eurasian Arctic (Fredga *et al.*, 1999) and up to eighth races in North America (Raush & Raush, 1972). At the same time geographic variation of the pelage color and external characters is poorly pro-

nounced and collared lemmings from different localities of the circumpolar range appeared to be so phenotypically similar that often only one or two Holarctic species are recognized within the genus: only *D. torquatus* (Pallas, 1779) (Ognev, 1948; Corbet, 1978), or *D. torquatus* in the Palaearctic and *D. groenlandicus* Traill, 1823 in the Nearctic (Hall, 1981). Collared lemming from Labrador Peninsula is often regarded as an independent species, *D. hudsonius* (Pallas, 1778). The latter can be distinguished from all other recent forms by the primitive molar pattern similar with that in the extinct Middle Pleistocene *D. simplicior* Fejfar, 1966. After cytogenetic studies and hybridological experiments it

was suggested to consider *D. torquatus* as a Holarctic superspecies and the rank of the most cytologically studied subspecies in the Nearctic has been elevated to the species level (Corbet & Hill, 1991; Musser & Carleton, 1993). In result the taxonomy of the genus remain uncertain and the number of species ascribed to *Dicrostonyx* varies from one to eleven.

Cytogenetic and hybridological studies of the collared lemmings in the Palaearctic showed that lemmings from the Wrangel Island appeared to be karyologically very different from lemmings of the mainland populations and in hybridization experiments resorption of the fetus always took place (Chernyavskii & Kozlovskii, 1980). Following these results lemmings from the Wrangel Island were distinguished as an independent species *D. vinogradovi* Ognev, 1948 (Chernyavskii & Kozlovskii, 1980). It should be emphasized that unlike the case with the true lemmings from this island, the structure of the karyotype of the *D. vinogradovi* is similar to the collared lemmings from Alaska, and, possible, in hybridization with the latter they may give fertile hybrids (Jarrell & Fredga, 1993). Basing on the similarity in the karyotype structure these authors consider *D. vinogradovi* together with other Nearctic forms as subspecies of *D. groenlandicus*.

Additional cytogenetic studies involving material from the new sites in the Palaearctic part of the generic

range and the analysis of mitochondrial DNA diversity carried out recently (Fredga *et al.*, 1999) showed the existence of four chromosomal races and five phylogeographic groups. The results of these studies, however, until now had no influence on the taxonomy of the genus.

It should be noted here that wide-ranging studies of geographic variation of cranial characters in *Dicrostonyx* based on the specimens involved in the karyological and molecular-genetic studies have not been carried out yet. It contributes greatly to retaining of taxonomic uncertainty in the composition of this genus. A number of papers devoted to the variation of cranial characters in *Dicrostonyx* in the Palaearctic was published by researchers from the Institute of Animal and Plant Ecology, Russian Academy of Sciences (Ekaterinburg) in 70–80-ies of the last century (Prushinskaya, 1978; Benenson & Prushinskaya, 1979; Bol'shakov *et al.*, 1980; Gileva *et al.*, 1980; Prushinskaya *et al.*, 1984). However, material used in these works was represented by colonies of laboratory animals derived from a small number of founders sampled in only two sites within the vast range of the genus.

The objective of this study is to evaluate the differences in cranial morphology between the chromosomal races, mitochondrial DNA clades, and taxonomic units of collared lemming in the Palaearctic using multivariate analysis. We also attempt to answer the two following questions:

TABLE 1. ARRANGEMENT OF COLLARED LEMMING (*DICROSTONYX TORQUATUS*) SAMPLES USED FOR MORPHOMETRIC STUDY (SEE ALSO FIG. 1).

Taxon	n	Samples	n	Chromosomal races	n	Mitochondrial clades	n
<i>D. t. torquatus</i>	74	Malozemel'skaya Tundra, Timanskaya Tundra, Vorkuta area	18	I	83	A	23
		Polarnyi Ural	5				
		Yamal Peninsula	41			B	57
		Gydan Peninsula	16				
<i>D. t. chionopaes</i>	146	North-Western Taimyr	18			C	65
		Central Taimyr	28	II	95		
		North-Eastern Taimyr	19				
		Khatanga-Lena Interfluvial	14			D	40
		Lena delta	13				
		Yana delta	7	III	13		
		Indigirka delta	2				
		Kolyma delta, left bank	4				
		Kolyma delta, right bank	3	IV	29	E	29
		Chukotka Peninsula	26				
<i>D. t. unguatus</i>	35	Novaya Zemlya	35	no data	35	no data	35
<i>D. vinogradovi</i>	28	Wrangel Island	28	V	28	F	28

n — sample size.

TABLE 2. FIRST TWO STANDARDIZED VECTORS FROM THE DISCRIMINANT FUNCTION ANALYSIS OF FOUR MANDIBLE VARIABLES FROM *DICROSTONYX* TAXA.

Variable	Standardized canonical vectors	
	1	2
LMAND_2	-1.3111	0.848602
HSYMPH	-0.73576	-0.49332
HMAND	0.052676	-0.01701
LCONALIN	0.964192	-0.79154
Eigenvalue	0.299514	0.234511
Cumulative percent	48.03	0.856533

Results

The differences between taxonomic units

As was noted above, two species, *D. torquatus* and *D. vinogradovi* are distinguished in the Palearctic part of the *Dicrostonyx* range on the base of karyological differences and hybridization experiments. Within *D. torquatus*, in its turn, three subspecies are distinguished on the base of some differences in the pelage color. Two subspecies are inhabiting the mainland tundra: *D. t. torquatus* Pallas, 1779 (European part of Russia up to Taimyr Peninsula) and *D. t. chionopaes* Allen, 1914 (from Taimyr Peninsula up to Chukotka Peninsula). *D. t. unguulatus* (Baer, 1841) is inhabiting the archipelago Novaya Zemlya.

The results of the multiple discriminant function analysis of the subsamples of taxa listed above carried on variables of mandible are presented in Tab. 2 and Fig. 2. The graph (Fig. 2) shows the centroid of each group

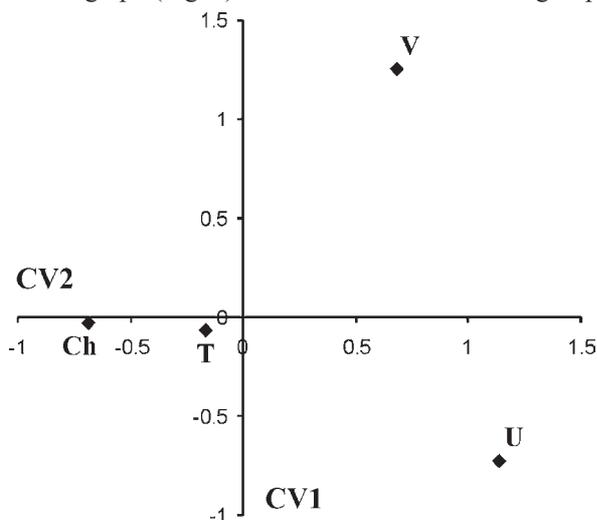


Figure 2. Projections of the centroids of the pooled samples of *Dicrostonyx* taxa onto the first two canonical axes. Analysis performed on the characters of mandible.

T — *D. t. torquatus*; Ch — *D. t. chionopaes*; U — *D. t. unguulatus*; V — *D. vinogradovi*.

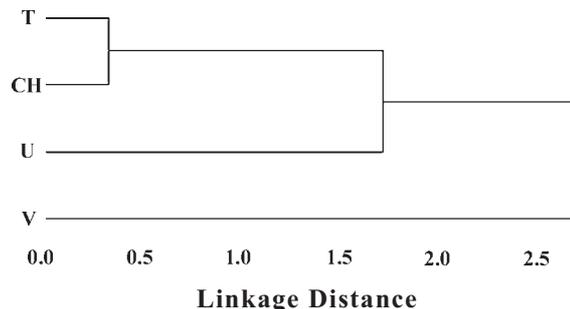


Figure 3. Distance phenogram summarizing the morphometric relationships of Palearctic taxa of *Dicrostonyx* based on the mandible characters. UPGMA cluster analysis of the matrix of generalized distances.

plotted onto the first two canonical axes. The first and the second canonical axes explain a little over 83% of the mandible variation. HSYMPH and LCONALIN contribute to a considerable extent to discrimination on the first axis. On the second axis LMAND contributes to discrimination to an important degree. The differences between centroids of the groups are highly significant ($p < 0.0001$). The results of the UPGMA cluster analysis of the matrix of Generalized Distances among the taxa considered are shown in the form of a phenogram (Fig. 3). By the structure of mandible *D. vinogradovi* differs from all other forms most considerably. Among subspecies of *D. torquatus* the differences between the island *D. t. unguulatus* and the mainland *D. t. torquatus* and *D. t. chionopaes* are much more pronounced than between the mainland subspecies (Fig. 3). *D. vinogradovi* differs by the greatest size of the mandible and height of condylar processes. *D. t. unguulatus* differs by the smallest size of the mandible.

Results of the analogous analysis performed on the cranial variables are shown in the Fig. 4A. The first two canonical axes explain a little over 97.4 % of the intergroup variance (75% and 22.4% respectively). The variables W-1, INTEROB, NASL, HSKULL contribute to discrimination of samples most significantly (Tab. 3). The differences between group centroids are highly significant both in analysis of absolute values and in analysis of indices (except difference between *D. t. torquatus* and *D. t. unguulatus*). The bivariate plot of centroids show (Fig. 4A) the clear ordination of samples studied into two groups: *D. vinogradovi* on the one hand and all the other samples (representing the subspecies of *D. torquatus*) on the other. *D. vinogradovi* differs from *D. torquatus* by wider skull in the auditory bullae region (W-1), narrower interorbital region, and narrower zygomatic arches.

Highly pronounced cranial differences between two species *D. vinogradovi* and *D. torquatus* obscure the differences between subspecies within the latter. In order to evaluate the differences in the cranial morphology of subspecies of *D. torquatus* we performed a new analysis of all samples except collared lemmings from the Wrangel Island. With the new set of samples the

TABLE 3. FIRST TWO STANDARDIZED VECTORS FROM THE DISCRIMINANT FUNCTION ANALYSIS OF CRANIAL VARIABLES OF *DICROSTONYX* TAXA.

Variable	Standardized canonical vectors		
	1	2	3
W_1	-0.55921	-0.16814	0.283204
INTEROB	0.519105	0.30405	-0.10701
NASL	0.511908	-0.16685	0.362267
HSKULL	-0.36475	0.558211	-0.45705
MINMOL	-0.09489	-0.65967	-0.23455
BRAINL	-0.22206	-0.64957	-0.55503
ZYGW	0.67166	0.131619	-0.52857
LDIAST	-0.42401	0.061011	0.961306
LM1-M3	-0.07613	0.366884	-0.17952
W_2	-0.2608	0.07113	0.015957
WROSTR	0.186391	-0.03966	0.191566
Eigenvalue	0.512137	0.152338	0.017702
Cumulative percent	0.750739	0.974051	1

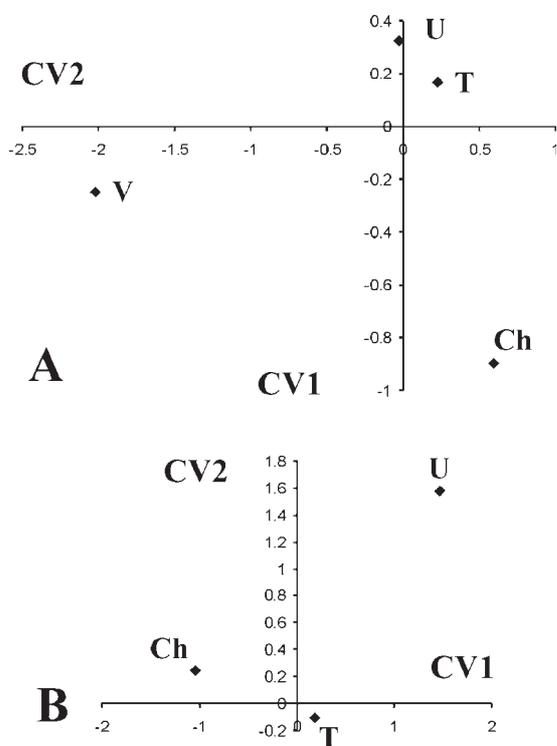


Figure 4. Projections of the centroids of the pooled samples of *Dicrostonyx* taxa onto the first two canonical axes. Designations of taxa as on Fig. 2.

A — Analysis performed on the cranial characters; B — The same analysis carried on with the subspecies of *Dicrostonyx torquatus*.

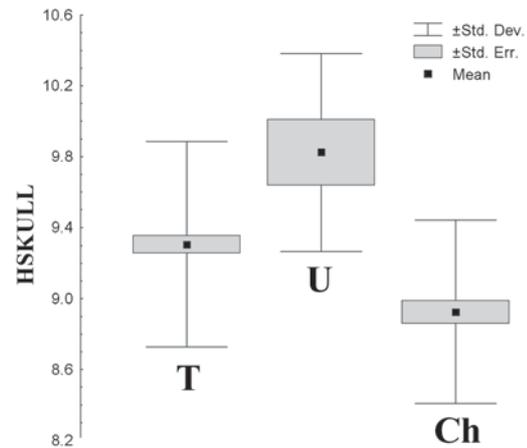


Figure 5. The differences in the height of the skull between subspecies of *Dicrostonyx torquatus*. Designations of taxa as on Fig. 2.

Std. Dev. — Standard deviation; Std. Err. — Standard error.

cranial differences between subspecies appeared to be significantly higher, the distances between centroids of all samples are highly significant. Therewith, *D. t. unguulatus* not only significantly differs from *D. t. torquatus* and *D. t. chionopaes*, but the difference between the collared lemmings from the archipelago Novaya Zemlya and each of the mainland subspecies significantly exceeds the difference between mainland subspecies (Fig. 4B). The greatest contribution into discrimination of samples in this case belongs to the HSKULL, NASL, BRAINL. *D. t. unguulatus* differs from other forms by the largest height of the skull (Fig. 5) and smallest length of the nasals.

Analysis of morphometric differences between the chromosomal races

Within the Palearctic range of the collared lemmings five chromosomal races (Tab. 1, Fig. 1) were distinguished based on the structure and chromosome sets (Fredga *et al.*, 1999). If distribution of these races is compared with the distribution of the taxa considered above, it becomes clear that *D. t. torquatus* is represented only by the race I, and *D. t. chionopaes* by races I–IV. *D. vinogradovi* differs considerably in the structure of karyotype from all other Palearctic races and designated here as the race V. The karyotype of *D. t. unguulatus* is unknown. Analysis of morphometric differences between the chromosomal races both by cranial and mandible characters confirmed the data obtained earlier in the analysis of taxonomic groups in the case when the borders of taxon and chromosomal race coincide. Thus, the chromosome race V considerably differs from all other races, and significant differences are marked between the races I and II. Just the border between these races almost coincides with the border of two mainland subspecies. No difference was found between the races II and III and races I and IV. The projection of the centroids of the

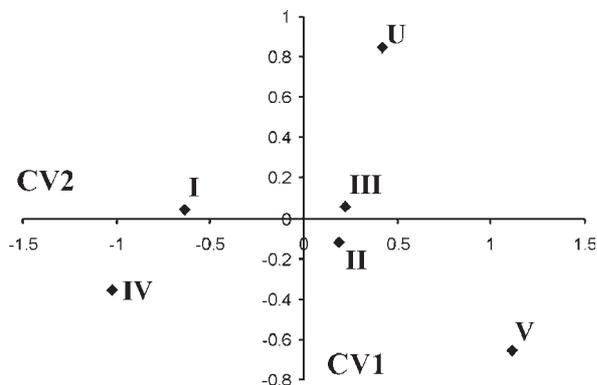


Figure 6. Projections of the centroids of chromosome races samples onto two first canonical axes. Designations of races as on the Fig. 1 and taxa as on Fig. 2.

samples considered onto the first two canonical axes is shown in the Fig. 6. Lemmings from the archipelago Novaya Zemlya that are not studied karyologically morphometrically differ from all known chromosomal races, but appeared to be most close to races II and III.

Morphometric differences between phylogeographic groups

Five phylogeographic groups distinguished on the base of the mtDNA diversity correspond to the taxonomic structure of the genus and chromosome races in the following way: *D. t. torquatus* is represented by two phylogeographic clades (A and B) and chromosome race I; *D. t. chionopaes* is represented by three phylogeographic clades (C, D, and E) and by three chromosome races (see above). However, there is no correspondence between chromosome races and phylogeographic clades. The clade C is partly overlapping the chromosome races I and II, the clade D overlaps the chromosome races II and III, and only the clade E corresponds to the chromosome race IV. Like in the case with karyotype, the difference in mtDNA diversity between *D. vinogradovi* and all other forms is so significant that Fredga *et al.* (1999) refused to consider it together with other Palaearctic forms. Here we designated this clade as F (chromosome race V).

Unlike the chromosomal races, discriminant function analysis performed on cranial and mandibular characters showed that the differences between the centroids of samples from all phylogeographic clades are significant ($p < 0.0001$; Fig. 7).

Discussion

Analysis of morphometric differences between the forms distinguished within the genus *Dicrostonyx* in the Palaearctic showed a good consistency between the level of divergence both in the structure of the skull and mandible and recognized taxonomic structure. Therefore, the level of morphological divergence of the sub-

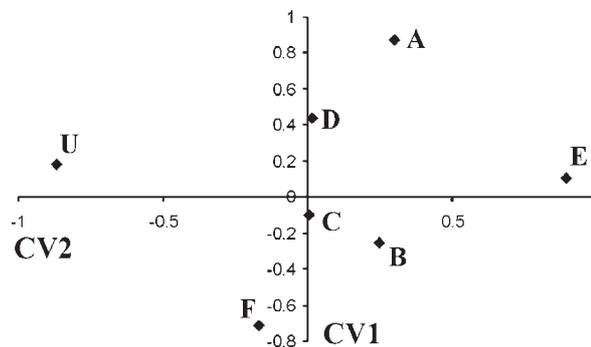


Figure 7. Projections of the centroids of mitochondrial DNA clades samples onto two first canonical axes. Designations of races as on the Fig. 1 and taxa as on Fig. 2.

species from the archipelago Novaya Zemlya (*D. t. unguulatus*) considerably exceeds the level observed between two mainland subspecies. In previous studies (Chernyavskii, 1972; Prushinskaya *et al.*, 1984) stability of cranial characters in *Dicrostonyx* within the whole Palaearctic range was emphasized. The diagnostics of subspecies was based exclusively on the details of the pelage color (Gromov & Erbaeva, 1995). However, multivariate analysis of cranial characters revealed both individual characters and their combinations which discriminate the taxa rather reliably.

Analysis of morphological differences between five phylogeographic groups, distinguished on the base of mtDNA diversity, showed significant differences between all groups. It is interesting to note that the differences between chromosomal races which occur at the same territory are poorly pronounced or have a random character. Discrepancy in morphological and chromosomal variation has been observed earlier for other species that display chromosome polymorphism (Wojcik *et al.*, 2000).

How the morphometric data presented here correspond to known models of chromosome speciation and phylogeographic hypothesis? Up to now there are two hypothesis most popular for explaining the chromosome variation and the pattern of speciation in collared lemming. According to the first one (hypothesis of refugia by Macpherson, 1965) differentiation onto the chromosome races occurred in the Late Pleistocene during the fragmentation of the range by ice sheets and following isolation of populations in individual refugia. If this hypothesis to be true then the geographic patterns of chromosome and mtDNA variation should coincide. According to the second hypothesis (sympatric chromosome speciation – stasipatric model of White 1968, 1978) the pattern of geographic distribution of chromosomal races and mtDNA clades may be different. Two independent studies carried on *Dicrostonyx* (Engstrom *et al.*, 1993; Fedorov *et al.*, 1999) showed that there are no any substantial correspondence between chromosome races and mtDNA clades, and the second model of chromosome race origin is more appropriate.

Our data on cranial and mandibular morphology also favor the second hypothesis. Similar results and conclusions have been obtained in the study of morphological and chromosomal variation in *Sorex araneus* (Wojcik *et al.*, 2000). Differentiation on the phylogeographic clades inferred from mtDNA diversity by general opinion is determined by past events such as ice ages, which cause populations, genomes and species to contract and expand their ranges enormously (Hewitt, 1989, 1996; Avise, 1994). It becomes well established that Pleistocene glacial cycles had a great influence on the population genetic differentiation and speciation. Consistency between morphological and mtDNA variation then seems to be logical.

Conclusions

The previous studies of craniometric variation in *Dicrostonyx* (e.g., Chernyavskii, 1972; Prushinskaya *et al.*, 1984) considered variation of individual characters and did not take in account their interrelation. It led to underestimation of craniometric differences in characterization of taxa. The multivariate approach allowed us to reveal significant differences in the structure of the skull and mandible, to underline individual characters and their combination that are most suitable for the characteristics of species and subspecies. Analysis of correlation between the chromosomal, molecular and morphological variation in collared lemming in the Palaearctic part of the range showed a rather good consistency between morphological and mtDNA variation and the lack of consistency between the morphological and chromosomal variation.

What influence may have the data obtained on the generally recognized taxonomic structure of the genus in the Palaearctic? The results of the study show that morphological differentiation of collared lemmings has it adequate reflection in the taxonomic scheme adopted today.

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