Hereditas 130: 301–307 (1999)

The importance of ice ages in diversification of Arctic collared lemmings (*Dicrostonyx*): evidence from the mitochondrial cytochrome *b* region

VADIM B. FEDOROV and ANNA V. GOROPASHNAYA

Department of Genetics, Uppsala University, Uppsala, Sweden.

Fedorov, V. B. and Goropashnaya, A. V. 1999. The importance of ice ages in diversification of Arctic collared lemmings (*Dicrostonyx*): evidence from the mitochondrial cytochrome *b* region.—*Hereditas 130*: 301–307. Lund, Sweden. ISSN 0018-0661. Received November 26, 1998. Accepted March 14, 1999

Variation in the nucleotide sequence of the mitochondrial cytochrome *b* region (804 bp) was examined for 24 individuals of collared lemmings *Dicrostonyx* sampled over the circumpolar distribution range of this genus. The mtDNA phylogeny supports the division of *Dicrostonyx* into four species suggested on the basis of karyotypes and hybridisation experiments, the Eurasian *D. torquatus* and the North American *D. groenlandicus*, *D. hudsonius* and *D. richardsoni*. The interspecific divergence estimates (mean 4.89 %) suggest that radiation took place during the Pleistocene and gives support for the importance of vicariant events generated by the glacial–interglacial periods for speciation in the chromosomally variable *Dicrostonyx*. The monophyly of the North America species group indicates one dispersion event across the Bering Land Bridge and does not support the hypothesis that the morphologically primitive *D. hudsonius* is a relict of an earlier invasion from Eurasia while *D. groenlandicus* represents a later dispersion event. The division of the North America *D. groenlandicus* in the two phylogeographic groups with limited divergence (0.63 %) across the Mackenzie river is consistent with separation of this species in more than one refugial area located to the north west of the Laurentide ice sheet during the last glaciation. Within the Eurasian *D. torquatus*, the group of haplotypes from the area to the east of the Kolyma river has the basal position. This gives support for the importance of the Asian Beringia as a refugial area for the tundra specialist, *D. torquatus*, during one of the warm interglacials in the late Pleistocene.

Vadim B. Fedorov, Department of Genetics, Uppsala University, Box 7003, SE-750 07 Uppsala, Sweden. E-mail: vadim.fedorov@genetik.uu.se

Pleistocene glaciations were suggested as important events promoting speciation in vertebrates (MAYR 1970): glacial advances provided geographic barriers generating intraspecific divergence, and the separated gene pools were protected from mixing by hybrid zones during interglacials leading to allopatric speciation (HEWITT 1996). However, molecular systematic studies in passerine birds claimed no increase in speciation rates during the Pleistocene (ZINK and SLOWINSKI 1995), rather, mtDNA divergence estimates among North American songbirds suggest that the Pleistocene glaciations favoured diversification at the intraspecific level but did not promote speciation (KLICKA and ZINK 1997). This conclusion has recently come under challenge from reinterpretation of mtDNA phylogeographic patterns in birds suggesting that Pleistocene conditions did play an important role both in initiating intraspecific divergence, and in completing speciations that had been inaugurated earlier (AVISE and WALKER 1998). Thus, the importance of the Pleistocene glaciations in speciation of vertebrates is currently under debate.

Taxa with circumpolar distribution in the recently glaciated Arctic offer an opportunity to study the effect of the Pleistocene glaciations on speciation and intraspecific genetic divergence since, in contrast to North America Arctic, where the Pleistocene glaciations were extensive, the extent of glaciation was limited in the Eurasian Arctic (ANDERSEN and BORNS 1997). Hence, the contrasting glaciation history of North America and Eurasian parts of the Arctic makes it possible to examine the effect of the glaciation itself on levels of genetic divergence within the same genus by comparing divergence estimates across two continents.

Collared lemmings (*Dicrostonyx*) are Arctic rodents with circumpolar distribution. Although the taxonomy of *Dicrostonyx* is controversial, collared lemmings are currently regarded as three North American species: *D. groenlandicus*, *D. richardsoni*, and *D. hudsonius* and one Eurasian species, *D. torquatus* (cf. JARRELL and FREDGA 1993; ENGSTROM et al. 1993; BEREND et al. 1997). These species have been recognised on the basis of karyotypes and hybridisation experiments (SCOTT and FISHER 1983; ENGSTROM et al. 1993; cf. JARRELL and FREDGA 1993; BEREND et al. 1997). Relatively high species diversity in the extensively glaciated North American Arctic suggests the importance of the Pleistocene glaciations for the speciation in *Dicrostonyx*. Accordingly, allopatric isolation in different glacial refugia was suggested as an important

factor for diversification in this genus in North America (RAUSCH 1980; cf. EGER 1995). However, except for mtDNA study in laboratory populations of *D. groenlandicus* and *D. richardsoni* (ENGSTROM et al. 1993), the phylogenetic relationships and the timing of speciation events are unknown.

Compared to other mammals, the fossil record of *Dicrostonyx* demonstrate an extraordinary rate of increase in molar complexity during the Pleistocene (GUTHRIE and MATTHEWS 1971). In contrast, extant species of *Dicrostonyx* are morphologically similar, and only *D. hudsonius* is distinguished on the basis of molar morphology (AGADJANYAN 1976). The molar structure of *D. hudsonius* is simpler than in other extant species and similar to a relatively primitive dental pattern of extinct *D. simplicior* distributed over the Holarctic in the middle Pleistocene (ZAZHIGIN 1976; cf. EGER 1995). On the basis of this similarity, it was suggested that the North American *D. hudsonius* is a relict of earlier dispersion event from the Eurasia while other North American *Dicrostonyx* species represent a later invasion across the Bering land bridge (GUILDAY 1963; RAUSCH 1980). This hypothesis implies that the North American *D. groenlandicus*, *D. richardsoni* and the Eurasian *D. torquatus* form a monophyletic group relatively *D. hudsonius*. Alternatively, there could have been a single dispersal event from Eurasia, the separation between *D. hudsonius* and other North American *Dicrostonyx* species resulting from vicariance due to isolation by the glacial barrier in the late Pleistocene (CHALINE 1987). The phylogenetic expectation under this scenario is that all North American species, including *D. hudsonius*, represent a monophyletic group relative to the Eurasian *D. torquatus*.

Apart from speciation, the isolation by the Pleistocene glacial barriers generated genetic diversification on intraspecies level (HEWITT 1996). In North America, MACPHERSON (1965) suggested that *D. groenlandicus* survived the last glaciation in two different refugia: the Eastern Beringia refugium included large ice-free area in Alaska, on the one hand, and the non-glaciated parts of the Central Canadian Arctic Islands and coastal Greenland, on the other hand. Thus, more than one phylogeographic group could be expected within the present distribution range of *D. groenlandicus*.

In Eurasia, a shallow phylogeny in *D. torquatus* suggests contraction of the distribution range of this species to a single refugium, probably, due to warming events during one of the interglacials, followed by dispersion (FEDOROV 1999; FEDOROV et al. 1999a). The geographic position of the interglacial refugium was not identified but it may be located by using phylogenetic reconstruction rooted to an outgroup. The geographic distribution range of the basal phylogenetic group in *D. torquatus* is expected to correspond to the geographic location of the interglacial refugium.

In this study we reconstruct mtDNA phylogeny in *Dicrostonyx* over the circumpolar distribution range of this genus. The phylogenetic reconstruction is used for four purposes. First, to reveal phylogenetic relationships and divergence estimates among extant species of *Dicrostonyx* in order to examine possible effect of the Pleistocene glaciations on speciation in this genus. Second, to test biogeographical hypotheses based on morphological data: two dispersion events vs. one dispersion event from Eurasia to North America. Third, to test the hypothesis of isolation *D. groenlandicus* in more than one refugium during the last glaciation. Fourth, to locate the geographic position of the interglacial refugium for the Eurasian *D. torquatus*.

MATERIALS AND METHODS

Specimens examined

A total of 24 collared lemmings collected from 18 localities around the North Pole were used for mtDNA sequencing study (Fig. 1). One specimen of the bank vole *Clethrionomys glareolus* from central

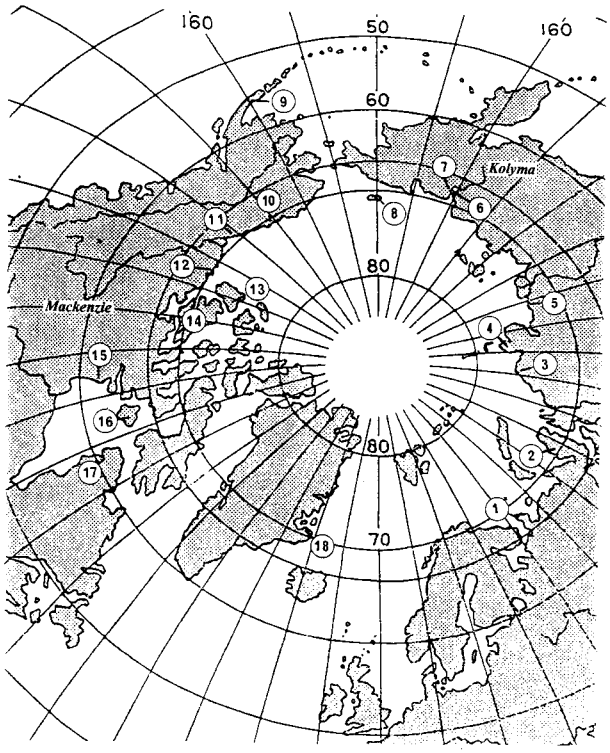

Fig. 1. Map showing the sampling localities in collared lemmings, *Dicrostonyx*.

Sweden was included as an outgroup. Lemmings were collected in the Eurasian Arctic during the summer of 1994 on the Swedish–Russian Tundra Ecology Expedition (localities 1–8). Specimens from Alaska (AF15732, AF22142, and AF22172; localities 9, 10) and Canada (localities 11–16) were obtained from the Frozen Tissue Collection, University of Alaska Museum and from the Division of Zoology, University of Oslo respectively. Three specimens from Labrador (MVZ5163, MVZ5164, and MVZ5165; locality 17) were obtained from Museum of Vertebrate Zoology, University of California. In north east Greenland (locality 18) lemmings were collected in the summer of 1995. Low mtDNA diversity has previously been found within the populations and the geographic regions in the Eurasian Arctic ($\pi = 0.00$–$0.13\,\%$, RFLP data; localities 1–6; FEDOROV et al. 1999a), north east Greenland ($\pi = 0.02\,\%$, RFLP data; locality 18; unpublished), and the Canadian Arctic (localities 12–16; EHRICH et al., in preparation). For the study on a circumpolar scale one individual from each of these localities was examined. Depending on the number of samples available, we studied from one to three specimens in localities with relatively high (7, 8, and 11) or unknown (9, 10, and 17) levels of intrapopulation mtDNA diversity. Sequences for 13 collared lemmings (2, 3, 6, 7a, 8, 10–14, and 16) are used elsewhere (FEDOROV 1999; EHRICH et al., in preparation). Sequences have been deposited with the GenBank Data Library under Accession Nos. AJ131439-AJ 131444; AJ 238421-AJ 238438.

DNA extraction, amplification, and sequencing

DNA was extracted from frozen or alcohol preserved liver samples by using proteinase K digestion, NaCl precipitation of proteins, and DNA precipitation with isopropanol following a protocol modified from MILLER et al. (1988). The mitochondrial cytochrome *b* gene was amplified by the polymerase chain reaction using the primers: L14724B and H15915 (IRWIN et al. 1991). The PCR products were gel-purified (Wizard kit, Promega Corp.) and then sequenced with the Sequenase kit (version 2.0; United States Biochemical) according to the manufacturer's specification, except that the primer annealing was done with snap-cooling technique (PALUMBI et al. 1991). We used manual sequencing with the following internal primers: universal H15149 (KOCHER et al. 1989), and specially designed: 5'GCCTCCATATTCT-T(TC)ATCTG3'; 5'TTCTTCGCATTCCA(TC)TT3'; 5'ATTTT(AG)GT(AT)TT(AG)TTTTTCCC3', which correspond to human positions L15024, L15294, and L15486, respectively. Sequences were aligned by eye with the cyt *b* of *Mus* (BIBB et al. 1981).

Data analyses

Sequence variation and substitution pattern were examined using the program MEGA version 1.01 (KUMAR et al. 1993). Kimura 2-parameter distances, Jukes-Cantor distances, and uncorrected p-distances were calculated among haplotypes and a neighbor-joining (NJ) phylogenetic tree was constructed from distance estimates with the MEGA program. Distances were calculated including both transversions and transitions and missing sites were completely excluded. Significance of the branch lengths of the NJ tree was tested by the standart error test (RZHETSKY and NEI 1992). Maximum-likelihood phylogenetic reconstructions were carried out with the Phylip 3.5 DNAML program (FELSENSTEIN 1993), using empirical base composition and transition/transversion (6:1) biases. Estimates of nucleotide diversity (π) within groups, nucleotide divergence (dxy, daxy) among species and groups of haplotypes and their variances were calculated according to NEI (1987).

RESULTS

Compositional biases and sequence variation

Excluding missing sites, a total of 804 bp of the cytochrome *b* gene were scored for the 24 *Dicrostonyx* specimens. Nucleotide composition and the substitution patterns are typical for mammalian cytochrome *b* gene (IRWIN et al. 1991). There is a low level of guanines in the overall composition of the light strand (13.5 %), especially in third positions (3.4 %), but least so in first positions (23.7 %). Observed substitutions are not evenly distributed, but are most abundant at third positions and least abundant at second positions. Among the 24 *Dicrostonyx* sequences, 85 variable sites of 97 (88 %) are at the third position of the codon, while 10 (10 %) sites are at the first, and only 2 (2 %) are at the second.

Phylogenetic relationships among species

The proportion of site differences (p), Jukes-Cantor and Kimura 2-parameter distances gave similar values for divergence estimates among the 24 *Dicrostonyx* haplotypes (data not shown). The highest p-distance value is 7 %, and this value gives no indication for multiple substitutions (NEI 1987). The NJ tree (Fig. 2) rooted to the distant outgroup is based on Kimura 2-parameter distances. Divergence estimates among species and groups of haplotypes within *Dicrostonyx* as well as nucleotide diversity estimates were calculated with the Jukes-Cantor correction because it has a smaller variance (KUMAR et al. 1993).

The NJ tree (Fig. 2) shows that except for *D. richardsoni*, for which we analysed only single speci-

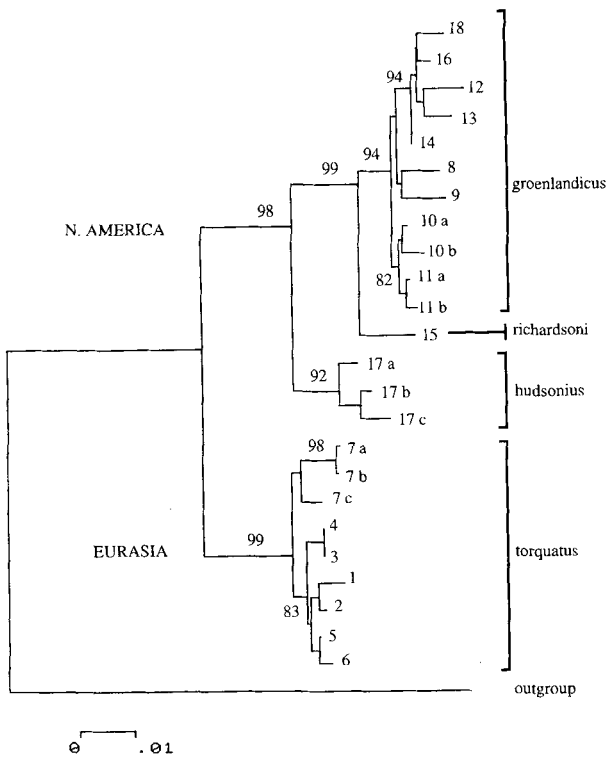

Fig. 2. Neighbour-joining tree illustrating phylogenetic relationships among 24 mtDNA haplotypes observed in collared lemmings, *Dicrostonyx*. The tree is based on the cytochrome *b* sequence data. Haplotypes are numbered according to the sampling localities as in Fig. 1. Numbers to the left of the nodes are percentages of the confidence probability obtained from the standard error test.

men, each species represents monophyletic group with good support from the standart error test. The North American *D. groenlandicus*, *D. richardsoni* and *D. hudsonius* form a well supported monophyletic group relative to the Eurasian *D. torquatus*. The same tree topology was obtained with maximum likelihood searches (not shown).

Interspecies divergence and timing of speciation

The divergence estimates calculated as the average pairwise Jukes-Cantor distances among all haplotypes across each pair of species (dxy; Table 1) may be used to obtain estimates of the timing of speciation. It has been recently shown that the divergence rate of the rodent cytochrome *b* for third-position transversions is 1.87–2.55 % per myr (SMITH 1998; LESSA and COOK 1998). The average divergency estimate for third-position transversions between *D. torquatus* and *D. groenlandicus* is 2.4 % (95 % CI: 2.3–2.5 %). This gives time estimate of about 1 myr for the division across the Bering Strait and suggests that the divergence rate for all nucleotide substitutions in the cytochrome *b* region is about 7 % per myr (Table 1). This time estimate does not contradict the timing obtained from the fossil record and the same divergence rate was used for the restriction fragment data from a complete mtDNA genome in *Dicrostonyx* (FEDOROV et al. 1999a). The average divergence estimate for the three North American species is 3.6 % (0.65 %, SE) which, applying the rate of 7 % myr, suggests an average divergence time of about 500 kyr.

Intraspecific phylogeography

There are only two clades of haplotypes well supported by the standard error test within *D. groenlandicus* (Fig. 2). One clade includes haplotypes from North West Alaska (localities 10, 11); haplotypes from the Central Canadian Arctic (localities 12–14, and 16) and North East Greenland (locality 18) form another clade. None of the well supported clades includes the two haplotypes from Wrangel Island (8) and east Alaska (9). The phylogenetic division between the two phylogeographic groups is at the Mackenzie river (Fig. 1). The average divergence between the groups (daxy) is 0.63 % (0.43 %, SE) which gives the time of separation at around 100 kyr. Despite the imprecision of this estimate, it suggests that the two phylogeographic groups in *D. groenlandicus* were separated during the late Pleistocene.

Within the Eurasian *D. torquatus* clade, the group of haplotypes from the Asian part of Beringia (locality 7, Fig. 1) has a basal position (Fig. 2). The average divergence (π) among all haplotypes in *D. torquatus* is 1.04 % (0.13 %, SE) and this estimate is not significantly different ($t = 0.96$, $P > 0.10$, Student *t*-test) from 1.23 % (0.15 %, SE), the average divergence among all haplotypes in *D. groenlandicus*. The similarity in the average divergence estimates indicates the similar time of subdivision within the Eurasian *D. torquatus* and the North America *D. groenlandicus*.

Table 1. *Estimates of the cytochrome b sequence divergence (dxy) among species of collared lemmings, Dicrostonyx, and their standard errors (SE)*

Species	dxy (%)	SE (%)
D. *torquatus* vs. D. groenlandicus	6.78	0.92
D. torquatus vs. *D. richardsoni*	6.90	2.17
D. torquatus vs. *D. hudsonius*	4.86	1.19
D. groenlandicus vs. *D. richardsoni*	2.33	0.68
D. groenlandicus vs. *D. hudsonius*	3.98	0.90
D. richardsoni vs. *D. hudsonius*	4.47	2.21
Mean	4.89	0.71

DISCUSSION

Pattern and timing of speciation

This study shows that the main phylogenetic split in *Dicrostonyx* is at the Bering Strait as was previously revealed by the mtDNA restriction fragment analysis on a smaller data set (FEDOROV et al. 1999a). The divergence estimate suggests that, despite the Bering Land Bridge, the Eurasian and North American phylogenetic groups were separated at least since the mid Pleistocene. The well supported monophyly of the North American species group indicates one dispersion event across the Bering Land Bridge, and so does not support the hypothesis that the morphologically primitive *D. hudsonius* is a relict of an earlier invasion from Eurasia while *D. groenlandicus* represents a later dispersion event (GUILDAY 1963; RAUSCH 1980). Thus, the mtDNA phylogeny does not support the phylogenetic relationships based on molar morphology (ZAZHIGIN 1976). This lack of concordance indicates that the morphological similarity between the Eurasian *D. torquatus* and the North American *D. groenlandicus* resulted from convergent morphological evolution on both sides of the Bering Strait.

The mtDNA phylogeny supports the division of *Dicrostonyx* into the four species suggested on the basis of karyotypes and hybridisation experiments (cf. JARRELL and FREDGA 1993; SCOTT and FISHER 1983; ENGSTROM et al. 1993; BEREND et al. 1997), the Eurasian *D. torquatus* and the North American *D. groenlandicus*, *D. hudsonius* and *D. richardsoni*. The divergence estimates indicate that radiation took place during the Pleistocene and support the importance of the glacial–interglacial periods for speciation in this genus. The main phylogenetic division between the Eurasian *D. torquatus* and the North American group of species had resulted from isolation by intermittent inundation of the Bering Strait during the interglacial periods (FEDOROV et al. 1999a). In North America the following glacial vicariant separation in three refugial areas probably generated the extant species diversity. *D. groenlandicus* evolved in ice-free areas to the north west of the Laurentide ice sheet, whereas *D. hudsonius* and *D. richardsoni* likely derived from the southeastern and southwestern periglacial areas, respectively (MACPHERSON 1965; CHALINE 1987; ENGSTROM et al. 1993; EGER 1995). However, the estimate of divergence among the three North America species suggests that the vicariant events predated the last glaciation (Wisconsin; 10–115 kyr; ANDERSEN and BORNS 1997).

The average divergence estimate among *Dicrostonyx* species is within the range of mtDNA divergence on intraspecies level in other rodents (cf. HEWITT 1996; FEDOROV et al. 1999b; DA SILVA and PATTON 1998). The fixation of chromosome rearrangements in separated gene pools of collared lemmings could have resulted in reproductive isolation and, thus, led to an increase of the rate of allopatric speciation in this genus (cf. JARRELL and FREDGA 1993). The mtDNA phylogeny indicates that vicariant events generated by the glacial–interglacial periods were likely important for speciation in the chromosomally variable *Dicrostonyx*. However, this conclusion should not be extended to other mammals without further molecular systematic studies.

Intraspecific phylogeography

The division of *D. groenlandicus* in the two clearly defined phylogeographic groups with limited divergence across the Mackenzie river is consistent with separation of this species in more than one refugial area during the last glaciation (MACPHERSON 1965). The phylogenetic split in *D. groenlandicus* across the Mackenzie river was previously revealed by the analysis of the cyt *b* variation on a smaller data set (EHRICH et al., in preparation). The group of haplotypes from north west Alaska probably represents populations that survived the glaciation in the Neoarctic part of Beringia, the ice-free mainland to the north west of the Mackenzie river. The group of haplotypes from the formerly glaciated Canadian mainland to the east of the Mackenzie river, the Arctic Islands and north east Greenland colonized deglaciated areas from the ice-free area on the Canadian Arctic Islands or the coastal part of north Greenland (MACPHERSON 1965; cf. EGER 1995). None of the two phylogenetic groups includes the two haplotypes from Wrangel Island (8) and east Alaska (9). This may indicate that *D. groenlandicus* from Alaska was subdivided within the Beringian refugium. Additional sampling in the Neoarctic is needed to reveal a complete refugial history of this species.

We previously suggested on the basis of the mtDNA phylogeography that the distribution range of *D. torquatus* in Eurasia was contracted to a single refugia by northward forest expansions in combination with sea transgressions during the warming events in one of the interglacials (FEDOROV 1999; FEDOROV et al. 1999a). Within the *D. torquatus* clade, the basal position of the group of haplotypes from the Asian part of Beringia, the area to the east of the Kolyma River, indicates that this area might have provided a refugium for tundra specialist *D. torquatus*. This suggestion is supported by some paleoecological evidence. The Asian part of the Beringian mainland was less affected by forest expansions and sea transgressions during the warm interglacials than

other parts of the Siberian Arctic (cf. SHER 1991), and this area has been previously suggested as the interglacial refugium for the Eurasian *Dicrostonyx* (AGADJANYAN 1976). The average divergence estimate of 1.04% (CI 95%: 0.78–1.30) within *D. torquatus* gives the average time estimate of 140 kyr. This time estimate implies that the distribution range of *D. torquatus* might have been contracted during warming events of the last interglacial (Eemian; 130–115 kyr; ANDERSEN and BORNS 1997) and dispersal took place with onset of the last glaciation.

The similarity in the average divergence estimates within the Eurasian *D. torquatus* and the North American *D. groenlandicus* suggests similar timing of dispersal events and the subsequent vicariant separation within each species. However, the range contractions and following dispersal events within each species on different continents might result from different historical events. There is insufficient information to characterize the last interglacial environment in the Neoarctic and additional phylogeograhic data in *D. groenlandicus* are needed to reveal historical factors contracting the distribution range of this species.

ACKNOWLEDGEMENTS

We thank J. A. Cook, D. Ehrich, G. H. Jarrell, A. Kenney, C. J. Krebs, and J. L. Patton for providing specimens from the North American Arctic, M. Lascoux for comments on the manuscript, and K. Fredga for support. This study was supported by grants from Sven and Lilly Lawski Foundation to V. F., and to Karl Fredga from the Swedish Natural Science Research Council.

REFERENCES

Agadjanyan AK, (1976). The history of collared lemmings in the Pleistocene. In: Beringia in the Cenozoic Era (ed. VI Kontrimavichus), Academy of Sciences of USSR, Vladivostok, (in English: 1984 New Delhi: Amerind Publishing), p. 379–388.

Andersen BG and Borns JrHW, (1997). The Ice Age World. An Introduction to Quaternary History and Research with Emphasis on North America and Europe During the Last 2.5 Million Years. Scandinavian University Press, Oslo.

Avise JC and Walker D, (1998). Pleistocene phylogeographic effects on avian populations and the speciation process. Proc. R. Soc. Lond. B 265: 457–463.

Berend SA, Hale DW, Engstrom MD and Greenbaum IF, (1997). Cytogenetics of collared lemmings (Dicrostonyx groenlandicus). Cytogenet. Cell Genet. 79: 288–292.

Bibb MJ, Van Etten RA, Wright CT, Walberg MW and Clayton DA, (1981). Sequence and gene organization of mouse mitochondrial DNA. Cell 26: 167–180.

Chaline J, (1987). Arvicolid data (Arvicolidae, Rodentia) and evolutionary concepts. Evol. Biol. 21: 237–310.

Da Silva MNF and Patton JL, (1998). Molecular phylogeography and the evolution and conservation of Amazonian mammals. Mol. Ecol. 7: 475–486.

Eger JL, (1995). Morphometric variation in the Nearctic collared lemming (Dicrostonyx). J. Zool., Lond. 235: 143–161.

Engstrom MD, Baker AJ, Eger JL, Boonstra R and Brooks RJ, (1993). Chromosomal and mitochondrial DNA variation in four laboratory populations of collared lemmings (Dicrostonyx). Can. J. Zool. 71: 42–48.

Fedorov VB, (1999). Contrasting mitochondrial DNA diversity estimates in two sympatric genera of Arctic lemmings (Dicrostonyx, Lemmus) indicate different responses to Quaternary environmental fluctuations. Proc. R. Soc. Lond. B 266: 621–626.

Fedorov VB, Fredga K and Jarrell GH, (1999a). Mitochondrial DNA variation and the evolutionary history of chromosome races of collared lemmings (Dicrostonyx) in the Eurasian Arctic. J. Evol. Biol. 12: 134–145.

Fedorov VB, Goropashnaya AV, Jarrell GH and Fredga K, (1999b). Phylogeographic structure and mitochondrial DNA variation in true lemmings (Lemmus) from the Eurasian Arctic. Biol. J. Lin. Soc. 66: 357–371.

Felsenstein J, (1993). PHYLIP: Phylogeny Inference Package version 3.5c. The University of Washington, Seatle, Washington 98195.

Guilday JE, (1963). Pleistocene zoogeography of the lemming, (Dicrostonyx). Evolution 17: 194–197.

Guthrie RD and Matthews JrVJ, (1971). The Cape Deceit fauna—early Pleistocene mammalian assemblage from the Alaskan Arctic. Quaternary Research 1: 474–510.

Hewitt GM, (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. Biol. J. Linn. Soc. 58: 247–276.

Irwin DM, Kocher TD, Wilson AC, (1991). Evolution of the cytochrome b gene of mammals. J. Mol. Evol. 32: 128–144.

Jarrell GH and Fredga K, (1993). How many kinds of lemmings? A taxonomic overview. In: The Biology of Lemmings (eds. NC Stenseth and RA Ims), Academic Press, London, p. 45–57.

Klicka J and Zink RM, (1997). The importance of recent ice age in speciation: a failed paradigm. Science 277: 1666–1669.

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanka FX and Wilson AC, (1989). Dynamics of mitochondrial DNA evolution in mammals: amplification and sequencing with concerved primers. Proc. Natl. Acad. Sci. USA 86: 6196–6200.

Kumar S, Tamura K and Nei M, (1993). MEGA: Molecular evolutionary genetics analysis, version 1.01. Pennsylvania State University.

Lessa EP and Cook JA, (1998). The molecular phylogenetics of tuco-tucos (genus Ctenomys, Rodentia: Octodontidae) suggests an early burst of speciation. Mol. Phyl. Evol. 9: 88–99.

Macpherson AH, (1965). The origin of diversity in mammals of the Canadian Arctic tundra. Syst. Zool. 14: 153–173.

Mayr E, (1970). Populations, Species, and Evolution. Belknap Press/Harvard Univ. Press, Cambridge, MA.

Miller SA, Dykes DD and Polesky HF, (1988). A simple salting procedure for extracting DNA from human nucleated cells. Nucleic Acids Res. 16: 215.

Nei M, (1987). Molecular evolutionary genetics. Columbia Univ. Press, New York.

Palumbi S, Martin A, Romano S, McMillan WO, Stice L and Grabowski G, (1991). The simple fool's guide to PCR version 2.0. University of Hawaii, Honolulu.

Rausch RL, (1980). The systematic position of the genus Dicrostonyx Gloger, 1841. Can. J. Anthropol. 1: 53.

Rzhetsky A and Nei M, (1992). A simple method for estimating and testing minimum-evolution trees. Mol. Biol. Evol. 9: 945–967.

Scott GW and Fisher KC, (1983). Sterility of hybrids of two subspecies of the varying lemming Dicrostonyx groenlandicus bred in captivity. Can. J. Zool. 61: 1182–1183.

Sher AV, (1991). Problems of the last interglacial in Arctic Siberia. Quat. Intern. 10–12: 215–222.

Smith MF, (1998). Phylogenetic relationships and geographic structure in pocket gophers in the genus Thomomys. Mol. Phyl. Evol. 9: 1–14.

Zazhigin VS, (1976). Early evolutionary stages of collared lemmings (Dicrostonychini, Microtinae, Rodentia) as characteristic representatives of Beringian Subarctic fauna. In: Beringia in the Cenozoic Era (ed. VL Kontrimavichus), Academy of Sciences of USSR, Vladivostok, (in English: 1984 New Delhi: Amerind Publishing), p. 280–288.

Zink RM and Slowinski JB, (1995). Evidence from molecular systematics for decreased avian diversification in the Pleistocene epoch. Proc. Natl. Acad. Sci. USA 92: 5832–5835.