Chromosomal and mitochondrial DNA variation in four laboratory populations of collared lemmings (*Dicrostonyx*)

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Genetic differentiation among populations and speciation in *Dicrostonyx* is hypothesized to have resulted from either allopatric divergence in glacial refugia during the Wisconsin or sympatric processes uncorrelated with refugial isolation. We examined chromosomal and mitochondrial DNA variation in four laboratory colonies, representing three species, in a preliminary evaluation of these hypotheses. Chromosomal variation is extensive among populations, diploid numbers ranging from 38 to 50. Autosomal variation appears to be due primarily to Robertsonian rearrangements and additions of supernumerary chromosomes, and is geographically unpatterned. Sex chromosome morphology is geographically structured and correlated with proposed southern and northern refugia. Restriction fragment analysis of mitochondrial DNA revealed two ancient, divergent genotypic assemblages, corresponding to geographic distributions of sex chromosomes. Autosomal variation, and any resulting reproductive isolation, probably is recent and uncorrelated with refugial history, whereas divergence of sex chromosomes and disparate mitochondrial assemblages likely predate the Wisconsin.

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Chez *Dicrostonyx*, la différenciation génétique entre populations et la spéciation résultent d'une divergence allopatrique dans les refuges glaciaires au cours du Wisconsinien, ou alors de processus sympatriques sans corrélation avec l'isolement dans les refuges. En guise d'évaluation préliminaire de ces hypothèses, nous avons procédé à l'examen de la variation chromosomique et de la variation de l'ADN des mitochondries chez quatre colonies de laboratoire représentant trois espèces. La variation chromosomique est importante chez les populations et les nombres diploïdes varient entre 38 et 50. La variation autosomale semble due surtout à des réarrangements de type Robertson et à l'addition de chromosomes supplémentaires et elle ne semble pas suivre de pattern géographique particulier. La morphologie des chromosomes sexuels suit un schéma géographique et est en corrélation avec les présumés refuges boréal et austral. L'analyse de l'ADN des mitochondries au moyen d'enzymes de restriction a révélé l'existence de deux associations génotypiques anciennes divergentes correspondant aux répartitions géographiques des chromosomes sexuels. La variation autosomale, de même que tout isolement génétique qui peut en avoir découlé, est récente et n'est pas reliée à l'historique des refuges, alors que la divergence des chromosomes sexuels et les associations mitochondriales variées remontent probablement à une époque plus ancienne que la glaciation du Wisconsinien.

[Traduit par la rédaction]

Introduction

Collared lemmings (*Dicrostonyx*) are tundra-specific rodents renowned for their dramatic fluctuations in population size, during which inbreeding probably is periodically intense (Carothers 1980; Jarrell 1987; Stenseth 1978). *Dicrostonyx torquatus* once was considered to represent a single circumpolar species (Ognev 1948; Rausch 1963). However, karyotypic analyses revealed this widespread taxon to be unusually variable chromosomally (Rausch 1977; Rausch and Rausch 1972) and the *torquatus*-group now is considered to be a superspecies-complex, comprising at least nine allospecies (Hoffmann 1981; Honacki et al. 1982). Morhpological divergence among these taxa is slight and most are recognized primarily by pelage colour (Allen 1919; Anderson and Rand 1945), karyotype, and lack of reproductive continuity determined from laboratory breeding experiments (Rausch and

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TABLE 1. Composite mtDNA genotypes (positions 1–16) and their frequency of occurrence in four laboratory populations of collared lemmings

No.	Composite genotype[a]	Churchill (N = 8)	Arviat (N = 5)	Igloolik (N = 6)	Pearce Point (N = 9)
1	AAAAAAAAAAAAAAAA	1.0	0.0	0.0	0.0
2	AAAACAAAACAAACCC	0.0	0.600	0.0	0.0
3	AAAAAAAAACAAAACE	0.0	0.400	0.0	0.0
4	BABABBABABCABBBG	0.0	0.0	0.167	0.0
5	BABABBABABBABBBB	0.0	0.0	0.333	0.0
6	BACABBABABBABBBG	0.0	0.0	0.333	0.0
7	BACABBACABCABDBD	0.0	0.0	0.167	0.0
8	BAAABBACABCABBBF	0.0	0.0	0.0	0.444
9	BAAABBADABCABBDF	0.0	0.0	0.0	0.333
10	BAAAABACABCABBBF	0.0	0.0	0.0	0.111
11	BACABBACABCABDBF	0.0	0.0	0.0	0.111

NOTE: Lemmings from Churchill and Arviat are *D. richardsoni*, and those from Igloolik and Pearce Point are *D. groenlandicus* and *D. kilangmiutak*, respectively.

[a]Reading from left to right, letters refer to mtDNA genotypes revealed by digestion with the following enzymes: position 1, *Bcl*I; 2, *Bgl*I; 3, *Bst*EII; 4, *Cla*I; 5, *Eco*RI; 6, *Hin*dIII; 7, *Kpn*I; 8, *Nde*I; 9, *Pst*I; 10, *Stu*I; 11, *Xba*I; 12, *Ava*I; 13, *Hin*cII; 14, *Ava*II; 15, *Nci*I; 16, *Sau*96I.

Rausch 1972). In the Palaearctic, chromosomal diversity in *Dicrostonyx* occurs through centric fusions, variation in number of supernumerary chromosomes, and, perhaps, pericentric inversions (Gileva 1983). An unusual mode of sex determination also has been reported for several taxa, with phenotypic females being either XX or XY (see Bull and Bulmer 1981; Gileva 1987; Gileva et al. 1982; Gileva and Chebotar 1979; Malcolm et al. 1986). XY females have an X-linked factor that apparently interferes with normal expression of male sex-determining genes. Males are XY with an unmodified X chromosome. The X-linked factor commonly appears as a polymorphism within populations of collared lemmings, and XY females are fully fertile with a reproductive output equal to that of XX females (Gileva 1987; Gileva et al. 1982).

Three species of the *torquatus*-group are sometimes recognized in Arctic Canada, mainly on the basis of distinct karyotypes from single localities (summarized by Gileva 1983). The extent of chromosomal polymorphism and geographic distribution of cytotypes is largely unknown, however, and the distribution of these "cytospecies" is inferred from subtle morphological differences formerly used to characterize subspecies. *Dicrostonyx kilangmiutak* ($2n$ = 47, Banks Island; Rausch 1977) purportedly occurs on Banks and Victoria islands and the adjacent mainland in the northwestern arctic; *D. richardsoni* ($2n$ = 42–44, Churchill, Manitoba; Malcolm et al. 1986; Rausch and Rausch 1972) occurs in continental Canada, west of Hudson Bay; and *D. groenlandicus* ($2n$ = 46, Devon Island; Rausch 1977) occurs in the central and eastern High Arctic, Baffin Island, and west to Southampton Island (Honacki et al. 1982; see also Hall 1981).

Rausch (1977, 1980) hypothesized that chromosomal diversity and the evolution of reproductive isolation was due to allopatric differentiation in glacial refugia during the Wisconsin (70 000 – 10 000 years ago) or earlier, in accord with the refugial model of MacPherson (1965). Given the level of polymorphism observed within some populations and the geographic pattern of interpopulation karyotypic variation, however, isolation in glacial refugia does not appear to explain all the karyotypic variation in the genus (Krohne 1982). Alternatively, Hoffmann (1981) and Modi (1987) observed that chromosomal variation in *Dicrostonyx* also was consistent with a model of sympatric chromosomal speciation (stasipatric model; White 1968), uncorrelated with isolation in refugia.

Herein, we examine variation in chromosomes and mitochondrial DNA (mtDNA) within and among laboratory colonies of *Dicrostonyx* representing the three Canadian *torquatus*-group species, in a preliminary evaluation of these alternatives. If *Dicrostonyx* was geographically fragmented during the Wisconsin, this pattern of fragmentation should be reflected in geographic partitioning of rapidly evolving, selectively neutral character sets such as mtDNA (Avise et al. 1987). If chromosomal differentiation is recent and also occurred primarily during isolation in glacial refugia, then geographic patterns of chromosomal and mitochondrial variation should be correlated. Alternatively, if chromosomal variation is due to sympatric differentiation, then geographic patterning should be spatially random and uncorrelated with phylogeographic patterns of divergence in mtDNA.

Materials and methods

Laboratory populations

Collared lemmings were taken from four captive populations established with animals from Pearce Point, N.W.T. (by R. Boonstra), and from Churchill, Manitoba, Arviat, N.W.T., and Igloolik, N.W.T. (by R. J. Brooks). Voucher specimens are deposited in the research collection of the Department of Mammalogy, Royal Ontario Museum.

Chromosomal analysis

Standard karyotypes were prepared from 29 individuals, as follows: Manitoba: Churchill (8); Northwest Territories: Arivat (6), Igloolik (4), Pearce Point (11). Standard karyotypes were prepared using the *in vivo* bone marrow technique of Patton (1967), as modified by Lee (1969). Terminology regarding relative chromosomal arm ratios follows Patton (1967). Fundamental numbers (FN) were calculated as the number of autosomal arms (excluding the presumptive sex chromosomes).

Mitochondrial DNA analysis

For each of 28 specimens (Table 1), mtDNA was isolated from livers and kidneys immediately after death or within 7 days of storage in grinding buffer with high EDTA content (Lansman et al. 1981). The isolation protocol followed is a modification of those described in Brown (1980) and Lansman et al. (1981). Approximately 2 g of tissue was chopped finely with crossed scalpels on a chilled petri

dish, and then ground with 8–10 strokes in a Dounce homogenizer. The homogenate was centrifuged to pellet the intact nuclei and later the mitochondria. The mtDNA was released from the mitochondria by lysing with SDS, and was purified with two CsCl density gradients, each run for 10 h at 436 000 × *g* in a Beckman TL-100 ultracentrifuge.

All mtDNA samples were digested with 16 restriction endonucleases: 15 six-base enzymes and 1 four-base enzyme. Fragments generated by these enzymes were end-labelled with ^{32}P, separated by electrophoresis in 1.2 or 1.8% agarose and 4% polyacrylamide gels, and visualized by autoradiography. We used a 1-kilobase (kb) ladder (BRL) as a size standard on all gels.

The net extent of nucleotide divergence between populations (d_A), corrected for within-population polymorphism, was calculated from fragment data using the method of Nei and Li (1979):

$$d_A = d_{XY} - (d_X + d_Y)/2$$

where d_X and d_Y are the nucleotide diversity values in populations *X* and *Y*, respectively, and d_{XY} is the average number of nucleotide substitutions per site between *X* and *Y*.

Results

Karyology

Dicrostonyx richardsoni

Churchill, Manitoba (2n = 43–45, FN = 48; Fig. 1A)—The diploid complement comprised 1–4 large submetacentric and (or) metacentric chromosomes, 1 or 2 large subtelocentrics, 4 small metacentric elements, and 35–39 acrocentric chromosomes in a graded series from large to small. A few of the chromosomes defined herein as acrocentric had small areas of chromatin distal to the centromere and could alternatively be termed subtelocentric. Of the eight specimens examined, one male and one female had $2n = 43$ with three large metacentric to submetacentric chromosomes, one male and four females had $2n = 44$ with two large metacentric to submetacentric chromosomes, and one female had $2n = 45$ with one large metacentric chromosome. As noted for specimens from this colony by Malcolm et al. (1986), the number of autosomal arms is invariant, regardless of diploid number. The two males had one large, obviously subtelocentric chromosome, whereas females had one or two large, obvious subtelocentrics. The length of the second arm of this chromosome appeared to vary within and between individuals. Given that XY females are hypothesized to be present in this colony (Malcolm et al. 1986), we suggest that this element likely is the X chromosome. We could not positively identify the Y chromosome, but presume it to be a medium-sized to small acrocentric chromosome.

Arviat, Northwest Territories (2n = 46, FN = 48; Fig. 1B)—The diploid complement comprised 1 or 2 large subtelocentric chromosomes, 4 small metacentric chromosomes and 40 or 41 acrocentric chromosomes in a graded series from large to small. No variation was observed among the six females examined, except that the number of large, obviously subtelocentric chromosomes varied from one to two. Based on similarity of this karyotype to that of individuals in Churchill, we presume that the large subtelocentric chromosome is the X, and that some XY females were present in this sample.

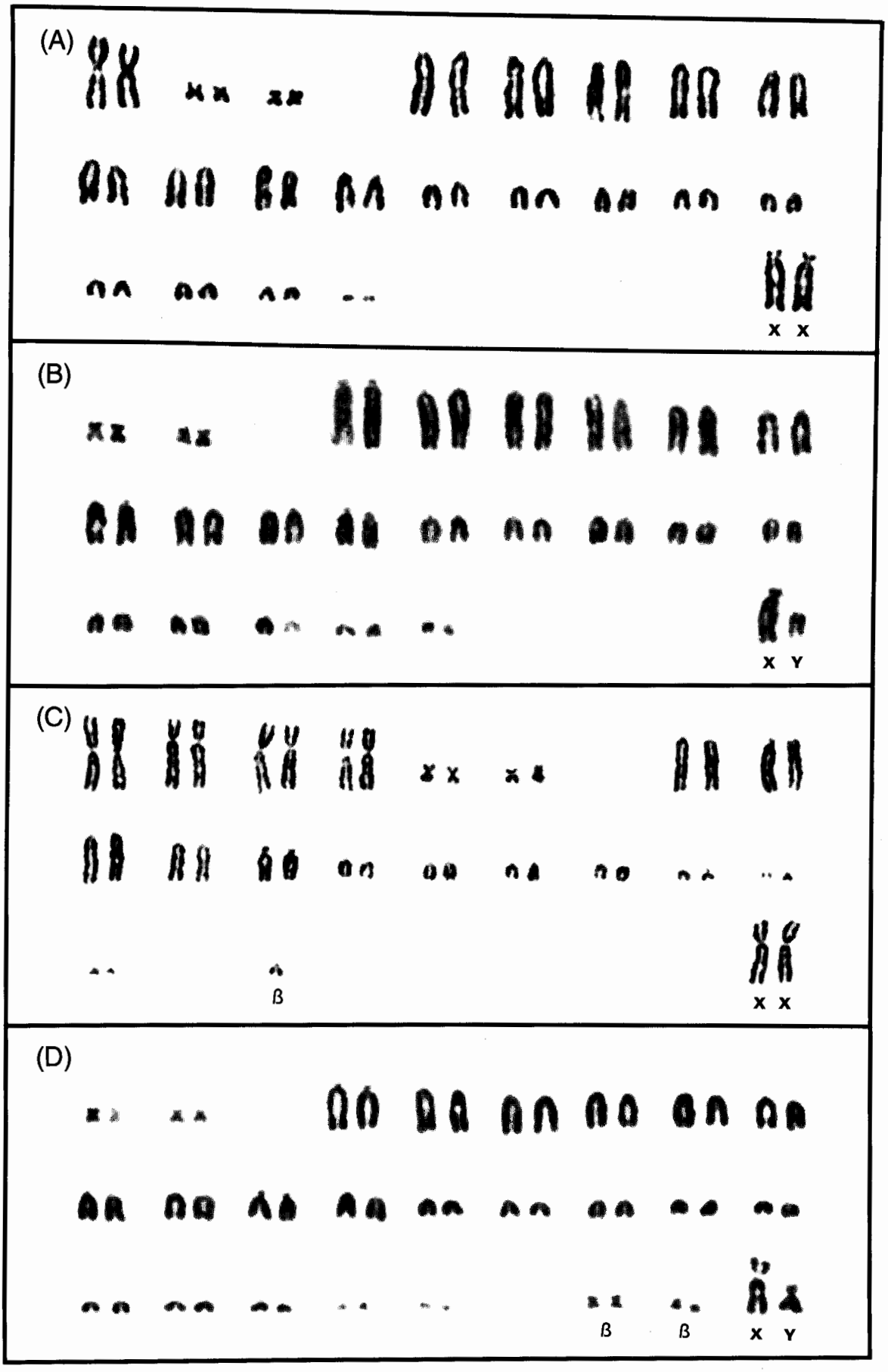
Dicrostonyx groenlandicus

Igloolik, Northwest Territories (2n = 38–44, FN = 48; Fig. 1C)—The autosomal complement comprised 8 large submetacentric to metacentric chromosomes, 4 or 5 small metacentric chromosomes, 10 medium-sized to large acrocentric chromosomes and 14–20 small acrocentric elements. Each female had an additional pair of large submetacentric chromosomes, whereas each male had one large and one medium-sized submetacentric. We presume that the large submetacentric chromosome is the X and that the medium-sized submetacentric element is the Y. No XY females were observed. Variation in diploid number among individuals was due entirely to variation in the number of small metacentric and acrocentric chromosomes present in the complement. Of the four individuals examined, one male had $2n = 38$, with 4 small metacentric and 14 small acrocentric autosomes; one female had $2n = 39$, with 4 small metacentric and 15 small acrocentric elements; one male had $2n = 41$, with 5 small metacentric and 16 small acrocentric chromosomes; and one female had $2n = 44$, with 4 small metacentric and 20 small acrocentric elements. The additional small metacentric and acrocentric elements present in some individuals are probably supernumerary ('B') chromosomes, which are common in Palaearctic members of the *torquatus*-group (Gileva 1980; Gileva and Chebotar 1979). Based on comparison with other reported karyotypes of *Dicrostonyx*, the $2n = 38$ karyotype with 4 small metacentric and 14 small acrocentric autosomes is likely to be the basic (or 'A') chromosomal complement and the autosomal FN for the population is listed tentatively as 48 (excluding B chromosomes).

Dicrostonyx kilangmiutak

Pearce Point, Northwest Territories (2n = 47–50, FN = 48, Fig. 1D)—The autosomal complement comprised 40 acrocentric chromosomes in a graded series from large to small and 5–8 small metacentric elements. In addition, three females and all five males had one large and one medium-sized submetacentric chromosome, whereas the other three females had two large submetacentric chromosomes. The large submetacentric chromosome is identified tentatively as the X and the medium-sized metacentric element as the Y. The length of the short arm of the Y chromosome appeared to vary among individuals. Thus, three of the females examined are presumed to be XX and the other three XY. The six females examined were laboratory offspring of mothers that produced an excess of daughters, and the ratio of presumed XY to XX females in our small sample is consistent with that expected among daughters of XY females (1:1; Gileva 1987; Gileva and Chebotar 1979). Variation in diploid number among individuals was due entirely to differences in numbers of small metacentric chromosomes and there was no obvious correlation of diploid number with presumptive sex chromosome constitution. Three females (1XX, 2XY) had $2n = 47$, with five small metacentric elements; one male and two females (1XX, 1XY) had $2n = 48$, with six small metacentric chromosomes; one male and one female (XX) had $2n = 49$, with seven small metacentric elements; and three males had $2n = 50$, with eight small metacentric chromosomes. The small metacentric chromosomes

Fig. 1. Representative karyotypes of *Dicrostonyx*. (A) A female *D. richardsoni* ($2n = 44$, FN = 48) from Churchill, Manitoba. (B) A male *D. richardsoni* ($2n = 46$, FN = 48) from Arviat, N.W.T. (C) A female *D. groenlandicus* ($2n = 39$, FN = 48) from Igloolik, N.W.T., with one B chromosome. (D) A male *D. kilangmiutak* ($2n = 50$, FN = 48) from Pearce Point, N.W.T., with four B chromosomes.


(A)
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(D)
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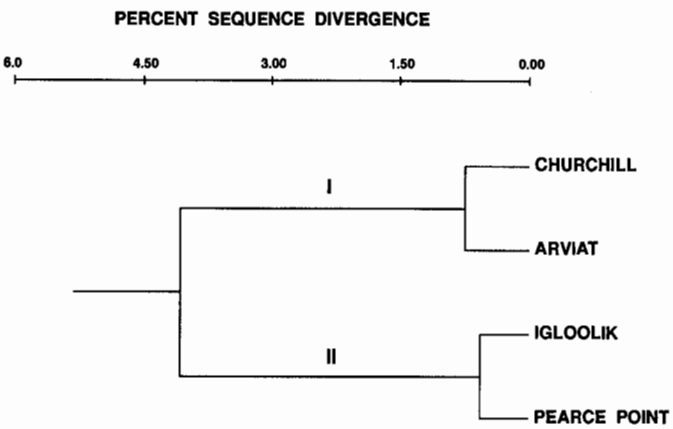

FIG. 2. Relatedness of mtDNA clones found in four laboratory populations of *Dicrostonyx*, based on UPGMA cluster analysis of percent sequence divergence among clones. Lemmings from Churchill and Arviat are *D. richardsoni* and those from Igloolik and Pearce Point are *D. groenlandicus* and *D. kilangmiutak*, respectively. I and II designate the two clonal assemblages separated by the deep branch in the gene tree.

present, in addition to the four that are ubiquitous among all *Dicrostonyx* which have been karyotyped, are most likely supernumerary chromosomes. Therefore, we tentatively list the fundamental number of the autosomal complement as 48 (excluding B chromosomes).

Mitochondrial DNA variation

Based on enzymes that produced fragments in a suitable size range for detection on our gels, we estimate the mitochondrial genome size in collared lemmings to be about 16 700 bp. This value is typical of microtine rodents (Plante et al. 1989) and of vertebrates in general (Moritz et al. 1988). The restriction enzymes we used produced an average of 87 fragments per individual, representing 425 recognized base pairs, or about 2.5% of the mitochondrial genome.

A total of 11 composite mtDNA genotypes (clones) was detected in the 28 collared lemmings we surveyed from the four populations (Table 1). Two major clonal assemblages are apparent (Fig. 2): lemmings from the southern sampling sites at Churchill and Arviat have variations on one type of mtDNA (clonal assemblage I), whereas animals from the northern sites, Igloolik and Pearce Point, have variants of another type (clonal assemblage II). Lemmings can be assigned unequivocally to these clonal assemblages by polymorphic sites detected by three restriction enzymes (*Bcl*I, *Hinc*II, and *Hin*dIII). In addition, six enzymes (*Eco*RI, *Stu*I, *Xba*I, *Ava*II, *Nci*I, and *Sau*96I) detect clones that are restricted to populations within either the northern or the southern assemblage.

Clonal diversity varies among populations; the Churchill sample is fixed for one clone, the Arviat sample has two clones which are both well represented, and the Igloolik and Pearce Point samples each have four clones. All clones are unique to single populations.

Discussion

Chromosomal variation

Variation within laboratory stocks of collared lemmings is ascribed to additions of supernumerary (B) chromosomes, Robertsonian translocations, and, in three of four populations, the presence of XY females. Supernumerary chromosomes previously were reported in several populations of *D. torquatus* from Siberia (summarized by Gileva 1983) and apparently are present in *Dicrostonyx* from the Arctic Coastal Plain of Alaska (G. H. Jarrell, personal communication in a letter). Thus, their presence in Canadian samples was not unexpected; however, identification of specific B chromosomes in this study is tentative and needs confirmation with C-banding (Gileva 1982). Polymorphism for apparent Robertsonian translocations occurred in the colony from Churchill, as previously reported by Malcolm et al. (1986). Centric fusions are known in *D. torquatus* (Gileva 1980) and occurred in the derivation of the karyotype of Alaskan *D. rubricatus* (Modi 1987). XY females are common in the *torquatus*-group (see Gileva 1987) and, in Canada, have been hypothesized to occur in *D. richardsoni* (Malcolm et al. 1986), based on sex ratios of laboratory offspring. Our identification of XY females was based on cytological recognition of the sex chromosomes, which should be confirmed by differential banding (particularly for *D. richardsoni*, where the Y could not be positively identified).

Each laboratory sample was chromosomally distinct. Karyotypes of *D. richardsoni* from Arviat and Churchill were similar, except for polymorphism for Robertsonian rearrangements at Churchill. The 'A' autosomal complement of collared lemmings from Pearce Point was entirely acrocentric and distinct from the karyotype of *D. kilangmiutak* reported from Banks Island (Rausch 1977), wherein there are two large metacentric autosomes (M. D. Engstrom, unpublished data). The 'A' complement from Igloolik contained eight large metacentric autosomes and was distinct from the all-acrocentric karyotype previously reported for *D. groenlandicus* from Devon Island in the High Arctic (Rausch 1977). The number of autosomal arms in the karyotypes from the two samples of *D. groenlandicus* are identical and the difference in diploid number might have resulted from centric fusions or fissions.

Geographic variation in karyotypes occurs within each of the "cytospecies" recognized by previous authors, purportedly derived from single glacial refugia (as outlined by MacPherson 1965). The autosomal data, then, are not in accord with the hypothesis of chromosomal differentiation in Wisconsin refugia (Rausch 1977, 1980; Rausch and Rausch 1972), but instead are consistent with local differentiation uncorrelated with refugial isolation (Hoffmann 1981; Modi 1987). Whether individual structural rearrangements lead to speciation by disrupting meiosis in heterozygotes, as required by the stasipatric speciation model cited by the latter authors, however, has not been demonstrated. Indeed, even monobrachial fusions, hypothesized to result in speciation in other rodents (Baker and Bickham 1986; Capanna 1981), do not result in sterility in hybrid *D. torquatus* (Gileva 1980). Delineation of species boundaries solely on the basis of differences in diploid number, without concomitant breeding studies, should be viewed sceptically.

The morphology of the sex chromosomes of *D. richardsoni* is distinct from that of *D. groenlandicus* and *D. kilangmiutak*. In *D. richardsoni* the X chromosome is large and subtelocentric and the Y is presumed to be a medium-sized to small acrocentric chromosome, whereas in both *D. groenlandicus* and *D. kilangmiutak* the X is large and submetacentric and the Y is medium-sized and submetacentric. This difference is consistent with the proposed separate, southern periglacial origin for *D. richardsoni* (Van Wynsberghe and Engstrom 1993). Based on the pronounced level of mtDNA divergence among these taxa, however, this difference probably predates the Wisconsin.

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