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Mitochondrial DNA Sequence Analysis in the Lithuanian Population

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Analysis of mitochondrial DNA (mtDNA) diversity has proved to be a useful tool in our understanding of the origin and history of human populations and also provided insights into the pathophysiology of mitochondrial disease. In order to investigate the genetic composition of the Lithuanian population, we have analysed mtDNA variation in 180 individuals from six Lithuanian ethnolinguistic subgroups. The sequencing of the first hypervariable segment (HV1) in the control region of the mtDNA and restriction fragment length polymorphism typing allowed us to classify mtDNA molecules to previously described haplogroups. This analysis revealed the presence of all major European mtDNA haplogroups (H, V, U, K, J, T, I, W, X) in the Lithuanian sample. Haplogroup H was the most common in Lithuanians, comprising 46% of all sequences. The frequencies of the rest haplogroups ranged from 1% to 20%. No significant differences, which could indicate influence of different Baltic tribes, were detected among ethnolinguistic subgroups of Lithuanians. The analysis of molecular variance (AMOVA) further confirmed the absence of internal genetic structuring in the Lithuanian population. Comparisons with other European populations demonstrated that the Lithuanian mtDNA gene pool is more closely related to the mtDNA gene pool of Northern European populations, while molecular diversity indices (gene diversity 0.971 ± 0.008, nucleotide diversity 0.012 ± ± 0.007 and the mean number of pairwise differences between sequences 4.41 ± 2.19) indicate that the Lithuanians are among the more diverse populations in Europe.

Key words: mitochondrial DNA, Lithuania, population, polymorphism, hypervariable region 1

INTRODUCTION

The territory that Lithuania encompasses today was settled relatively late. The land became inhabitable only about 12,000 BP, after the last glaciation. The first people to settle were hunter-gatherers belonging to late Palaeolithic cultures. Anthropological findings regarding Mesolithic and Neolithic inhabitants of the present-day Lithuanian territory are very limited, and there is a degree of uncertainty concerning the processes of neolithization, Indo-European dispersal and formation of the Baltic tribes. During the period 2000 and 1000 BP the Baltic tribes are believed to have inhabited the forested expanses between the Wisla and the Volga and the Oka riverhead, the Daugava and the central section of the Dnieper. This large Baltic territory was at that time covered by virtually impenetrable forests and for a long time remained isolated from major migration and trade routes (1). Since the Neolithic period the native inhabitants of the Lithuanian territory have not been replaced by any other ethnic group, so there is a high probability that the inhabitants of present day Lithuania have preserved the genetic composition of their forebears relatively undisturbed by the major demographic movements (2).

The human mitochondrial DNA (mtDNA) is a small, 16569 nucleotide pair long genome located

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within the mitochondria in the cytoplasm of the cell. Each human cell contains hundreds of mitochondria and thousands of mtDNA molecules. The mtDNA is strictly maternally inherited and its mutation rate is in the order of 10 times higher than of nuclear DNA. This has resulted in the accumulation of a broad spectrum of mtDNA sequence polymorphisms in human populations, and also may be a common source of mutations causing mitochondrial disease. Analysis of population mtDNA polymorphisms has been used to infer multiple aspects of human history, including human origins, migrations, population origins and relationships (3–7).

In the present study we report the results of analysis of mtDNA diversity in the Lithuanian population.

MATERIALS AND METHODS

Population samples

Peripheral blood samples were collected from unrelated individuals from six ethno-linguistic subgroups of Lithuanians (East, South and West Aukštaièiai, and North, South and West Þemaièiai). Informed consent and information about birthplace, parents and grandparents were obtained from all donors. Genomic DNA was extracted using the standard salting out procedure (8).

Mitochondrial DNA sequencing

Mitochondrial DNA variation was analysed in 180 samples (30 from each ethno-linguistic subgroup). Primers L15996 and 16401 (9) were used for amplifying the first hypervariable segment (HV1) of the mtDNA control region using recombinant Taq DNA polymerase (Fermentas, Vilnius, Lithuania). The same primers were used for direct sequencing of HV1, using a DNA sequencing kit on an ABI 310 automated DNA sequencer (Applied Biosystems, Foster City, CA, USA) following the protocol recommended by the supplier. The statuses of positions 00073, 7028 and 14766 were determined by restriction enzyme digestion with *Alw*44I, *Alu*I and *Mse*I respectively in all samples. On the basis of specific nucleotide substitutions in HV1 and positions 00073, 7028 and 14766, the obtained sequences were classified to specific European haplogroups and their statuses were confirmed by additional restriction fragment length polymorphism typing according to Macaulay et al., 1999 (10).

For phylogenetic analysis, published data on 2164 HV1 sequences from European, Near East and Caucasus populations was retrieved from HvrBase database (11), also HV1 sequences from 436 Poles and 200 Russians (12) were included.

Data analysis

HV1 sequences were manually aligned with the published reference sequence (13). The Arlequin 2.0 software package (14) was used to calculate the haplotype and nucleotide diversity and their standard deviations (SD), mismatch distributions, mean pairwise differences and their SD, and F_{ST} distances between pairs of populations/groups and associated *P*-values based on 10,000 permutations. Analysis of molecular variance (15) (AMOVA) was performed to evaluate the genetic structure of the population, with the significance of variance components tested with 10,000 permutations.

Genetic distances between European populations, based on mtDNAs haplogroup frequencies, were computed as Cavalli-Sforza chord distances (16) using the GENDIST program implemented in PHYLIP3.5c software package (17). Based on obtained distances the multidimensional scaling (MDS) was performed by means of STATISTICA.

RESULTS

Sequences of the mtDNA HV1 region comprising nucleotide positions 16024–16400 (13) were determined for 180 Lithuanian individuals (30 from each ethnolinguistic group). To compare the sequences reported here with published data, analyses were restricted to 356 bp (nucleotide positions 16028–16383) of HV1. We detected 76 polymorphic sites, which defined 95 distinct HV1 haplotypes. The proportion of transitions was 92.4%. Some individuals exhibited length variation between nucleotide positions 16181 and 16183; these positions were removed from the subsequent analyses.

Table 1 reports the mtDNA sequence diversity indices for all Lithuanian ethnolinguistic groups and European reference populations. On average, the nucleotide and gene diversities and the mean number of pairwise nucleotide differences between pairs of sequences are within the range found in European populations. Nearly in all cases, potential estimation errors due to sample variance are too great to allow any confidence in apparent differences among populations/groups. However, if the observed values are taken at face value, the Lithuanians are among the more diverse populations of Europe. The distribution of the observed number of differences between pairs of sequences (mismatch distributions) in the Lithuanian population sample was computed (Fig. 1). It was unimodal, approximately bell-shaped, with the raggedness index $r = 0.009$. Similar unimodal mismatch distributions are found in most European populations, except Saami. They are interpreted as indicative of a prehistoric population demographic expansion, while *r*

Table 1. **mtDNA HV1 sequence diversity parameters in Lithuanians and some European populations**

Population	Sample size (n)	Number of haplotypes	Gene diversity ± SD	Mean number of pairwise nucleotide differences ± SD	Nucleotide diversity ± SD
Aukštaièiai:					
East Aukštaièiai	30	23	0.982 ± 0.013	3.79 ± 1.96	0.011 ± 0.006
South Aukštaièiai	30	23	0.949 ± 0.033	4.12 ± 2.11	0.012 ± 0.007
West Aukštaièiai	30	24	0.984 ± 0.013	4.98 ± 2.49	0.014 ± 0.008
Aukštaièiai total	90	56	0.972 ± 0.010	4.29 ± 2.14	0.012 ± 0.007
Þemaièiai:					
North Þemaièiai	30	24	0.979 ± 0.016	4.85 ± 2.43	0.014 ± 0.008
South Þemaièiai	30	22	0.947 ± 0.033	3.61 ± 1.89	0.010 ± 0.006
West Þemaièiai	30	24	0.984 ± 0.013	4.77 ± 2.40	0.013 ± 0.008
Þemaièiai total	90	58	0.970 ± 0.011	4.51 ± 2.24	0.013 ± 0.007
Lithuanians total	180	95	0.971 ± 0.008	4.41 ± 2.19	0.012 ± 0.007
Polish[a]	436	219	0.967 ± 0.006	4.47 ± 2.21	0.013 ± 0.007
Russians[a]	200	110	0.977 ± 0.006	4.48 ± 2.22	0.013 ± 0.007
Estonians[b]	28	23	0.979 ± 0.018	4.36 ± 2.22	0.012 ± 0.007
Finns[b]	147	75	0.967 ± 0.009	3.96 ± 1.99	0.011 ± 0.006
Norway[b]	216	126	0.954 ± 0.011	3.90 ± 1.96	0.011 ± 0.006
British[b]	100	67	0.975 ± 0.009	4.45 ± 2.21	0.013 ± 0.007
Icelanders[b]	433	119	0.975 ± 0.003	4.60 ± 2.26	0.013 ± 0.007
Germans[b]	267	162	0.948 ± 0.011	3.72 ± 1.89	0.010 ± 0.006
Bulgarians[b]	30	22	0.977 ± 0.014	4.55 ± 2.30	0.013 ± 0.007
Austrians[b]	117	71	0.957 ± 0.014	4.45 ± 2.21	0.014 ± 0.007
French[b]	50	42	0.988 ± 0.009	4.28 ± 2.16	0.012 ± 0.007
Swiss[b]	76	43	0.967 ± 0.010	3.54 ± 1.82	0.010 ± 0.006
Saami[b]	176	33	0.813 ± 0.020	3.63 ± 1.85	0.011 ± 0.006

[a] Sequence data from Malyarchuk & Derenko (12).
[b] Sequence data retrieved from HvrBase database (11).

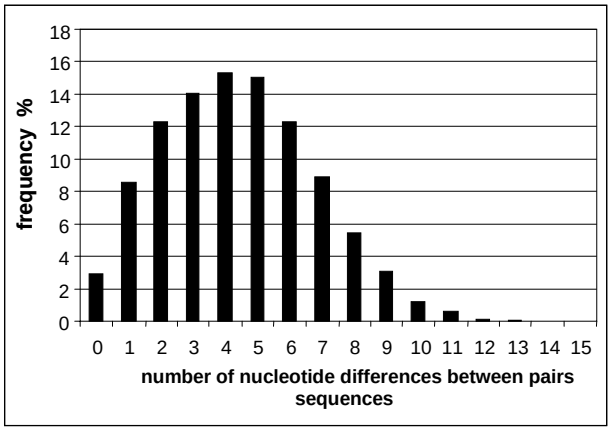

Fig. 1. Mismatch distribution of mtDNA HV1 sequences in Lithuanian population

values less than 0.05 also suggest prehistoric population expansions (18).

The population structure of Lithuanians was estimated by calculating F_{ST} distances based on HV1 sequences between ethnolinguistic subgroups and by the analysis of molecular variance (AMOVA) (15). F_{ST} distances among the subgroups ranged from 0 to 0.028 and were statistically not significant ($p > 0.01$) based on 10,000 permutations, indicating population homogeneity. The absence of the phylogeographic structure of mtDNA HV1 sequence variation in our data set was further confirmed by AMOVA analysis. When six Lithuanian ethnolinguistic subgroups were treated as a single group, 99.58% of the total variations was within subgroups and 0.42% among subgroups (which was not significant ($p > 0.05$) different from zero based on 10,000 permutations). When the subgroups were grouped into two groups, Aukštaièiai and Þemaièiai, (which is consistent with both the geographic and linguistic grouping), 99.45% of the total variation was due to differences among sequences within the subgroups, while 0.23% of the variation was due to differences among subgroups within the groups, and 0.32% of the variation was due to differences between groups (Aukštaièiai and Þemaièiai). The slightly higher percentage of variation due to differences between groups might indicate some differentiation between Aukštaièiai and Þemaièiai, however, the values of differences among subgroups within the groups and differences among groups are not significantly ($p >$

> 0.05) different from zero based on 10,000 permutations.

Classification of mtDNA sequences revealed the presence of all nine major European haplogroups (H, V, U, K, J, T, I, W, X) in our sample, and they accounted for 97% of all sequences. Table 2 reports the frequencies of mtDNA haplogroups in Lithuanians. The most frequent haplogroup, comprising almost half of the sequences, is H, which is also the most frequent haplogroup in Europe and the Near East. Using the haplogroup frequencies in Lithuanians and other European populations (adapted from analysis of Helgason et al. 2001 (6)), the genetic distances between pairs of populations were computed using the Cavalli-Sforza method (16). They are shown in the form of multidimensional scaling plot in Fig. 2. Even though no obvious pattern is seen across Europe, the Lithuanians seem to be closer to other populations of Northern Europe (European Russians, Estonians and Finns).

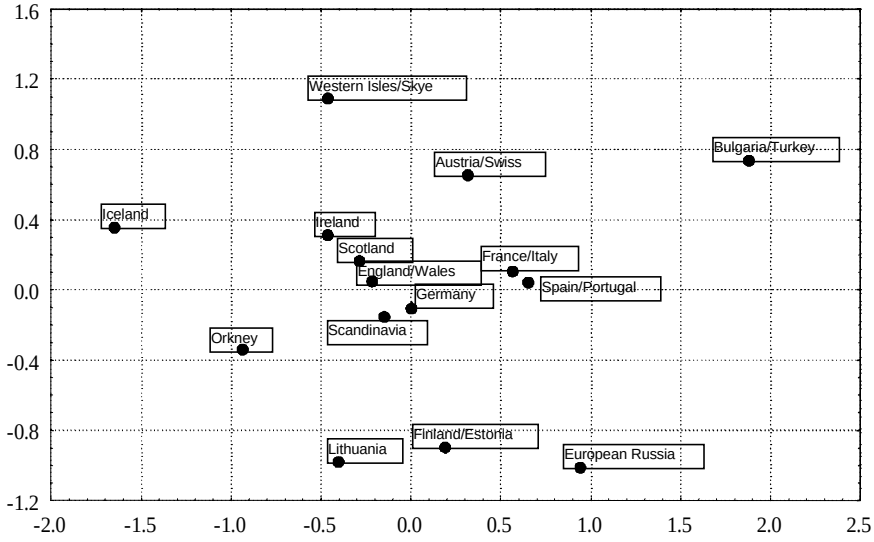

Fig. 2. Multidimensional scaling plot of genetic distances among populations on the basis of haplogroup frequencies

Table 2. **MtDNA haplogroup frequencies in the Lithuanian population**

Haplogroup, subhaplogroup	Total Lithuanian sample (N = 180)	
	n	%
H	60	33.3
H1	3	1.7
H3	8	4.4
H4	7	3.9
H5	2	1.1
H8	3	1.7
V	8	4.4
HV	4	2.2
preHV	1	0.6
U	5	2.8
K	4	2.2
U3	3	1.7
U4	9	5.0
U5a	5	2.8
U5a1	2	1.1
U5b	6	3.3
U5b1	2	1.1
U5	1	0.6
J	9	5.0
J1	1	0.6
J1b1	4	2.2
T	13	7.2
T1	5	2.8
I	7	3.9
W	2	1.1
X	1	0.6
Others	5	2.8

In the analyses of shared sequences among populations, 32.2% of Lithuanian sequences were found to be private (not detected previously in other populations). However, no specific combinations of haplotypes or their subclusters clearly distinguishing the Lithuanians from the neighbouring European populations were found.

DISCUSSION

The mtDNA variation studies have proven to be a useful tool for studying evolutionary processes in humans and population histories both on a global level and regionally. The current study reports the mtDNA diversity analysis results in the Lithuanian population, which can be compared directly with data published on other European populations (4–7, 12, 19).

Historically, two main groups of Lithuanians, Aukštaièiai and Þemaièiai, developed over a long time period as two independent Baltic tribes. Previous studies showed minor differences between these groups in blood group and serum markers, which might reflect the differences of their original gene pools (20). However, our results of mitochondrial DNA HV1 sequence and RFLP polymorphisms in Lithuanian population did not reveal significant differences among the ethno-linguistic subgroups of Lithuanians. Genetic distances among the subgroups were not significantly different from zero, and the

analysis of molecular variance showed that more than 99% of mtDNA HV1 sequence variations fall within the groups. These findings demonstrate that the Lithuanian population is not internally structured at the mtDNA sequence level. Thus it is likely that even if genetic differences between the Baltic tribes did exist, they are not preserved in the present day population, at least in its female part. These results are consistent with anthropological data, according to which anthropometric differences among the regions of Lithuania disappear already in material of the Middle Ages and Lithuanian population is very homogeneous in the context of Eastern or whole Europe (2).

The mtDNA HV1 sequences diversity level was similar to that in other European populations. The gene diversity, nucleotide diversity and mean number of pairwise differences between sequences were within the range usually found in Europe. MtDNA haplogroup distribution analysis demonstrated that Lithuanians are characterized by the same West Eurasian mtDNA haplogroups which describe 95% of mtDNA variation in Europe and the Near East (21–23). It has been shown by previous studies that no obvious differentiation between European populations can be found in terms of haplogroup distribution pattern (24); however, analysis of lineages within the haplogroups and shared sequences among the populations can reveal a relationship even between closely related populations (5, 6). Based on haplogroup and subhaplogroup frequencies, the Lithuanians are close to other populations of Northern Europe (European Russians, Estonians and Finns). These populations are also geographically closest in the analysed data set.

The origins of some mtDNA haplogroups are established, and therefore these haplogroups can be used to reconstruct the genetic history and composition of extant carrier populations. The most frequent haplogroup among Lithuanians is H, comprising almost half (46%) of all sequences. This is also the most frequent haplogroup in Europe and Near East, with highest frequencies (40–60%) in Western and Northern Europe. Torroni et al. (25) calculated the age of haplogroup H and dated its expansion in Europe to 20,000–25,000 BP, *i.e.* the time intermediate between the appearance of modern *Homo sapiens* in Europe (>40,000 BP) and the Neolithic expansion (starting ~10,000 BP) (26), and suggested that haplogroup H could represent a second Paleolithic wave of expansion in Europe. Some of the lineages in this haplogroups are shown to mark distinct historical processes. For example, Malyarchuk and Derenko (7) have shown that a specific lineage characterized by 16304C–16311C mutations marks the Slavonic migrations from Central to East Europe. Interestingly, this lineage was not detected among Lithuanians, which could indicate a low level of admixture between Baltic and Slavic populations.

The sequences of haplogroup U represent a more ancient demographic expansion (21). It probably originated in Africa ~50,000 BP and subsequently expanded into the Middle East and Europe (23). Our previous study suggested a slightly higher frequency of haplogroup U sequences in Lithuanians than in other Europeans (27). However, a study on a larger population sample did not support these results.

The haplogroups J and T originated in the Near East and have been brought into Europe within the last 10,000 years (21). They represent the Neolithic component of the early farmers in the modern European population. The frequencies of haplogroups J and T imply that the Neolithic component comprises about 18% of the total Lithuanian mtDNA gene pool. It is interesting to note the relatively high frequency of haplogroup J (8%). It has already been noted by Passarino et al. (19) that its frequency in Northern Europe is even higher than in those areas from where it probably arrived. This could indicate that this haplogroup might be influenced by positive selection in Northern Europe (19).

In conclusion, the mtDNA variation analyses demonstrated the absence of internal genetic structuring of the Lithuanians and a similarity between the Lithuanians and North European populations. However, more data on the populations of Northern Europe are needed for a comprehensive evaluation of the geographic patterns and relationships among population groups within this region.

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MITOCHONDRINËS DNR SEKØ ANALIZË LIETUVOS POPULIACIJOJE

S a n t r a u k a

Mitochondrinës DNR (mtDNR) ávairovës tyrimai padeda atkurti þmogaus populiacijø istorijà, jø tarpusavio ryðius, migracijø kryptis bei kilmës laikà, taip pat suprasti mitochondriniø ligø molekulinius mechanizmus. Norëdami ávertinti lietuviø populiacijos genetinæ struktûrà, iðtyrëme 180 asmenø ið ðeðiø lietuviø etnolingvistiniø grupiø mtDNR sekø ávairovæ. Nustaèius kontrolinës mtDNR srities pirmo hipervariabilaus segmento nukleotidø sekas bei atlikus restrikciniø fragmentø ilgio polimorfizmø tyrimus, mtDNR sekos buvo priskirtos pagrindinëms Europos populiacijoms bûdingoms mtDNR sekø haplogrupëms. Lietuvoje nustatytos visø Europai bûdingø mtDNR haplogrupiø (H, V, U, K, J, T, I, W, X) sekos. Daþniausios yra H haplogrupës sekos, sudaranèios 46% visø sekø. Kitø haplogrupiø daþniai yra tarp 1% ir 20%. Statistiðkai patikimø skirtumø tarp lietuviø etnolingvistiniø grupiø, kurie galëtø atspindëti skirtingø baltø genèiø átakà, nenustatyta. Molekulinës dispersijos analizë (AMOVA) taip pat patvirtino, jog lietuviø populiacija viduje nestruktûrizuota. Palyginus lietuviø mtDNR sekas su kitomis Europos populiacijomis nustatyta, kad lietuviø mtDNR genofondas artimesnis kitø Ðiaurës Europos populiacijø mtDNR genofondui. Tuo tarpu molekulinës ávairovës indeksai (genø ávairovë 0,971 ± 0,008, nukleotidø ávairovë 0,012 ± 0,007 ir vidutinis skirtingø nukleotidø skaièius tarp sekø porø 4,41 ± 2,19) rodo, kad lietuviai yra tarp tø Europos populiacijø, kuriø mtDNR ávairovë didesnë.