Analysis of paternal genetic relationship of ancient Hungarian, modern Hungarian and modern Szekler populations

Summary of Ph. D. thesis

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INTRODUCTION

The main biological importance of Y chromosome is its role in sex determination and male fertility. The singular characteristics of the Y chromosome, which include haploid state, male specificity, paternal inheritance and absence of recombination through most of its length (95%), make this chromosome a powerful tool for tracing and comparing paternal lineages and studying genetic diversity of human populations.

Y chromosome variation consists of large amount of different types of polymorphisms, they may roughly be divided into two large groups: bi-allelic markers and polymorphisms of tandem repeats or multi-allelic markers. Biallelic markers include point mutations (**S**ingle **N**ucleotide **P**olymorphisms - SNP markers), insertions and deletions. These binary polymorphisms define the Y-chromosomal haplogroups, which show geographical clustering (Jobling & Tyler-Smith 2003). Haplogroup assignment of a sample is based on derived states of biallelic markers.

One specific Y-chromosomal base substitution, the T→C point mutation in the RBF5 locus, called the Tat C allele, is of interest in the Finno-Ugric context (Zerjal et al. 1997). It defines the Y chromosome haplogroup N3, which is present in northern and eastern Europe, but is virtually absent in the west and south. It is also frequent in northern Asia (Zerjal et al. 1997, Rootsi et al. 2000, Semino et al. 2000a, Tambets et al. 2004). The C allele of the Tat polymorphism is widespread in all Uralic-speaking populations studied so far, including Voguls and Ostyaks who are the two closest linguistic cognates of Hungarians; but it is hardly found in modern Hungarian populations (e.g. Rootsi et al. 2000, Tambets et al. 2004), even ethnic groups of Hungarians such as Csángós (Lahermo et al. 1999) or Palóc (Semino et al. 2000b).

Several explanations have been suggested for the striking absence of Tat C in the linguistically Uralic modern Hungarian population (Rootsi et al. 2000, Semino et al. 2000b). One is that Voguls and Ostyaks, and many other Siberian populations obtained this Y-chromosomal lineage only relatively recently, after the ancestors of the Magyars had left the Siberian forests for the great Eurasian steppe. Another is that Hungarians and Siberian Ugric-speaking populations have always been genetically unrelated despite their linguistic affinities. A third possibility is that the ancestral Magyars did have the Tat C allele, but lost it through genetic drift during their migration to Hungary, or after their settlement there.

These data raise the question of whether the ancient Hungarians who settled in the Carpathian Basin at the end of the 9th century and spoke a Uralic language, possessed this polymorphism or not.

To answer this question we attempted to screen for the Tat polymorphism in ancient DNA from skeletal remains from the (IX)-Xth century. The problems in ancient DNA research arise from the fact that very little, usually heavily damaged and highly fragmented DNA survives in ancient tissues (Lindahl 1993). Nuclear genes are typically 5 000-10 000 times less abundant per cell than those of mitochondrial origin, which is probably the reason for ancient nuclear DNA being much more difficult to amplify than mitochondrial DNA from the same ancient DNA extracts. Nuclear DNA appears to be more limited by amplification length than mitochondrial DNA (Binladen et al. 2006).

In order to enhance the efficiency of our analyses random primers and the modified improved PEP (**P**rimer **E**xtension **P**reamplification) method (Hanson & Ballantyne 2005) were used. In this way we tried to increase the effective number of starting templates. This whole genome amplification method utilizes a mixture of two polymerases among which one possesses a 3'-5' exonuclease or "proofreading" activity, allowing for a more accurate amplification of the genomic sequence.

To prevent any possible risk of contamination during the handling and analysis of the ancient remains strict precautions were taken.

In addition, to gain further insight into the paternal genetic diversity of the modern Hungarian-speaking populations, we have typed additional markers from the non-recombining region of the human Y chromosome; we present the analysis of 22 biallelic polymorphisms in Hungarian samples, predominantly from the Great Hungarian Plain, and Szeklers from Transylvania. The results are compared with data from other European populations studied by Semino et al. (2000a), and the phylogeographic context of the Y chromosome pool of the populations studied has been analysed.

MATERIALS AND METHODS

Samples

In this study 100 Hungarian, 97 Szekler and 7 ancient samples were analysed. All the Hungarian paternally unrelated, healthy males selected for the analysis had a birthplace in different parts of Hungary, but the most represented area (90 samples) was the Great Hungarian Plain. The Szekler sample consists of 97 unrelated, healthy Szekler volunteer donors born and living in Corund, Transylvania, Romania. Most of the DNA samples (94 Hungarian and 97 Szekler samples), extracted from blood, were anonymously obtained from the DNA collection of the Department of Forensic Medicine (University of Szeged, Hungary). Six additional Hungarian DNA samples, isolated from hairbulbs, were from our DNA depository.

The 7 ancient samples were derived from 6 different well-documented archaeological excavations from the Carpathian Basin, dating from the (IX)-Xth century.

Methods

1, DNA extraction from the archaeological remains (femoral bones) (Kalmár et al. 2000., Qiagen, DNeasy Tissue Kit) and modern blood (salting-out procedure -Miller et al. 1988. or Chelex-based method -Walsh et al. 1991) or hair samples (Chelex method-Walsh et al. 1991)

2, PCR amplification

- Mitochondrial DNA amplification
- Whole genome amplification (modified improved Primer Extension Preamplification method - Hanson & Ballantyne 2005 -High Fidelity PCR Enzyme Mix: Taq DNA Polimerase + Pfu DNA Polimerase with proofreading activity)
- Multiplex PCR (Markers M96, M89, M9, M45)
- PCR amplification of Y-chromosomal DNA fragments containing biallelic markers M35, M78, M170, M253, P37, M26, M201, P15, M304, M267, M172, M102, M67, M92, Tat, M173, M17, M269
- dCAPS (**d**erived **C**leaved **A**mplified **P**olymorphic **S**equence)-PCR method (Neff et al. 2002)

3, Polyacrylamide gel electrophoresis
4, Restriction analyses of PCR products
5, PCR-RFLP analysis of Tat polymorphism on ancient DNA with ALF (**A**utomated **L**aser **F**luorescent DNA Sequencer) system
6, Contamination prevention and authentication
7, SNaPshot technique (ABI PRISM SNaPshot ddNTP Primer Extension Kit)
8, Capillary electrophoresis (ABI PRISM 310 Genetic Analyzer rendszeren) (fragment analysis)
9, DNA sequencing, sequence analysis
10, Statistical analyses (Arlequin package, version 2.000. -Schneider et al. 2000., population genetic diversity (H), pairwise Fst genetic distances, MDS analysis)

RESULTS AND DISCUSSION

Out of the 7 successfully typed 9-10th century skeletal remains two possess (samples 13/1, B1/3c) the mutation, while the others carry the ancestral T allele. The samples 13/1 and B1/3c were from two burial sites (13/1-Szabadkígyós-Pálliget, B1/3c-Örménykút) in the same county (Békés), they were excavated with rich grave goods, unambiguously typical of burial practices of Hungarian conquerors. In case of the sample T2/41 the presence of the ancestral Tat T allele was confirmed by typing the ancestral state (C allele) of the marker M9 (C→G).

The fact that two of seven ancient samples possessed the Tat C allele, is more than intriguing, considering that from the 197 modern Hungarian-speaking males only one had this polymorphism. This latter finding is consistent with previous studies and gives further evidence for the fact that this polymorphism is practically absent in modern Hungarian-speaking populations. The single observation of this particular lineage in the Szekler group may reflect some past contribution.

On the other hand, the low number of ancient samples has to be taken into consideration. However the occurrence of this genetic variation in ancient Magyars could be the result of admixture or sharing a common male ancestor with other Uralic-speaking populations.

Our data suggest that the Tat C allele, which is widespread in Uralic-speaking populations, was present in the ancient Magyar population when they crossed the Carpathians and settled in the Carpathian Basin and the Tat polymorphism is an appropriate marker to investigate the ancient Hungarian gene pool.
No one from the Archaeological Institute (excavator, anthropologist) who has handled the bones and nobody from our group has the Tat C mutation, which strongly supports the authenticity of the ancient DNA.

In order to additional Y-chromosomal markers will be examined on ancient remains in future studies the primer pairs for all studied markers in case of recent samples were redesigned or chosen from literature, resulting in shorter PCR products (below 170 bp), to serve the special needs of amplification of ancient DNA. We optimized and checked the PCR conditions of these primer pairs, so they are ready to use on ancient DNA.

In case of the modern Hungarian and Szekler populations (in 197 individuals) twenty-two biallelic markers (M96, M89, M9, M45, M35, M78, M170, M253, P37, M26, M201, P15, M304, M267, M172, M102, M67, M92, Tat, M173, M17, M269) were examined in hierarchical order in agreement with the Y-chromosome phylogeny (Y Chromosome Consortium 2002, Jobling & Tyler-Smith 2003).

All samples were surveyed for the M96, M89, M9 and M45 markers. These markers were typed by multiplex PCR followed by SNaPshot technique. Additional genotyping of samples was restricted to markers on the appropriate branch of the YCC haplogroup tree (Jobling & Tyler-Smith 2003). Markers M35, M78, M170, M253, P37, M26, M201, P15, M304, M267, M172, M102, M67, M92, Tat, M173, M17 and M269 were analysed by the PCR-RFLP assay.

In case of the ancient sample T2/41 out of four Y-chromosomal DNA fragments, containing the four basal markers (M96, M89, M9 and M45), the two shorter fragments (106 bp (marker M45) and 121 bp (marker M9) long specific PCR products) were successfully amplified. In case of these markers the ancestral C allele was typed. The ancestral state at marker M9 indicates that this sample could not carry the derived Tat C allele in accordance with Y-chromosome phylogeny (YCC 2002, Jobling & Tyler-Smith 2003). This finding confirms the result of the PCR-RFLP analysis of this sample.

The markers used allowed the classification of the modern samples into the E, F*, G, I, J, K*, N3, P* and R1 haplogroups.

The modern Hungarian and Szekler populations share similar components described for other Europeans, except for P-M45*(xM173) in Szekler samples. The presence of central-Asian haplogroup P-M45*(xM173) in Szeklers is unusual for a European population, since it is almost absent in continental Europe and presumably reflects some Asian contribution.

In the present study, haplogroup J was unexpectedly common in the Hungarian-speaking populations (Hungarians: 16%, Szeklers: 21.6%).

The elevated frequency of haplogroup J may reflect Anatolian and southern Balkan contributions to the gene pools of Hungarians and Szeklers, however in the Szekler samples it might be partially attributed to genetic drift, since they lived in relative isolation for a long time. On the other hand, the elevated frequency of J in both groups could also be due to a range of historical events.

One is the expansion of the Ottoman Empire from the 16th century AD; refugees from the Balkan area fled to Hungarian territory. Historical data and the comparative analyses of maternal lineages of ancient Hungarian population suggest that the earlier migrations of the Magyars may also have contributed to the presence of this lineage in the Carpathian Basin.

Statistical analyses of Y chromosome data of two modern Hungarian-speaking populations were also performed. Based on haplogroup frequencies population genetic diversity and pairwise Fst genetic distances (between the examined Hungarian and Szekler groups and other European populations studied by Semino et al. (2000a)) were calculated by using the Arlequin package, version 2.000. Pairwise values of Fst were visualized in two dimensions by the use of multidimensional scaling (MDS) analysis.

According to statistical analyses the Hungarian and Szekler populations are genetically heterogeneous, closely related, and close also to other populations from Central Europe and the Balkans. However, the second dimension clearly separates our samples from those Hungarians studied by Semino et al. (2000a). The latter group has closer genetic relationships with Polish and Ukrainian populations. A possible explanation might be that Hungarian samples analyzed by Semino et al. (2000a) primarily originated from subjects (mainly Palócs) from northern regions in Hungary, where in the 19th century extensive admixture occurred with inhabitants of neighbouring northern regions.

According to our results the Y chromosome data of Semino et al. (2000a) are not representing the modern Hungarian population.

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