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Comparison of Maternal Lineage and Biogeographic Analyses of Ancient and Modern Hungarian Populations

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ABSTRACT The Hungarian language belongs to the Finno-Ugric branch of the Uralic family, but Hungarian speakers have been living in Central Europe for more than 1000 years, surrounded by speakers of unrelated Indo-European languages. In order to study the continuity in maternal lineage between ancient and modern Hungarian populations, polymorphisms in the HVSI and protein coding regions of mitochondrial DNA sequences of 27 ancient samples (10th–11th centuries), 101 modern Hungarian, and 76 modern Hungarian-speaking Sekler samples from Transylvania were analyzed. The data were compared with sequences derived from 57 European and Asian populations, including Finno-Ugric populations, and statistical analyses were performed to investigate their genetic relationships. Only 2 of 27 ancient Hungarian samples are unambiguously Asian: the rest belong to one of the western Eurasian haplogroups, but some Asian affinities, and the genetic effect of populations who came into contact with ancient Hungarians during their migrations are seen. Strong differences appear when the ancient Hungarian samples are analyzed according to apparent social status, as judged by grave goods. Commoners show a predominance of mtDNA haplotypes and haplogroups (H, R, T), common in west Eurasia, while high-status individuals, presumably conquering Hungarians, show a more heterogeneous haplogroup distribution, with haplogroups (N1a, X) which are present at very low frequencies in modern worldwide populations and are absent in recent Hungarian and Sekler populations. Modern Hungarian-speaking populations seem to be specifically European. Our findings demonstrate that significant genetic differences exist between the ancient and recent Hungarian-speaking populations, and no genetic continuity is seen. Am J Phys Anthropol 134:354–368, 2007.

Hungarian is one of the few non-Indo-European languages in Europe, and the only one in Central Europe (Rédei, 1998). It belongs to the Finno-Ugric branch of the Uralic linguistic family, a diverse group of people related by an ancient common linguistic heritage (Hajdú, 1976; Napolskikh, 1995). Of the approximately 25 million Finno-Ugrian speakers, three form separate nations: the Estonians and Finns on the Eastern Baltic Littoral, and the Hungarians (Magyars) in the Danubian plain. Hungarian is also widely spoken by Magyars in western Romania, by Seklers (Székelys) in Transylvania, and by Csángós east of the Carpathians. Other Finno-Ugric speakers include the Saamis (Lapps) in northern Finno-Scandian and Kola Peninsulas, the Erzas, Moksas, Maris, Udmurts, and Komis in the northern woodland zone of European Russia and the Voguls and Ostyaks around the river Ob in western Siberia (Vékony, 2002). Distantly related to the Finno-Ugrians are the various Samoyed peoples of Siberia, the Nenets, Enets, Nganassans, and Selkups (Chen et al., 1995).

Hungarians entered central European history as seven major Magyar tribes that invaded the Danubian Basin from across the Carpathians in 895 AD (Regino, 1890). This was the last in a series of migrations (see Figure 1). At an earlier stage of their history they must have been far further east, for their closest linguistic affinities are with the Voguls and Ostyaks of the forest steppes of western Siberia (Fodor, 1982). The Hungarians left the forests and split off from them sometime in the Late Bronze Age or Early Iron Age (around 500 BC); this separation marks the time from when we can speak of independent proto-Hungarian people, the only Finno-Ugric people to have become horse-riding steppe pastoralists and nomads (Róna-Tas, 1999). Migrating westwards, they settled between the Urals and the Middle Volga region (Fodor, 1976) in a region lying at the Kama-Volga confluence, still known to Europeans in the 13th century as *Magna Hungaria*, "Old Hungary" (Fodor, 1982). Around 700–750 AD the ancient Hungarians left Magna Hungaria and drifted southwards, settling in the steppe and forested steppe zone around the river Don, in a region they called Levedia. Here they were neighbors and allies of the Khazars, a Turkic-speaking people of

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Fig. 1. The migrations route of the ancient Hungarians.

nominally Jewish religion, whose steppe subjects and allies included the Turkic-speaking Onogur-Bulgars, Savirs and Kabars (Kristó, 1980), and Iranian-speaking Alans from whom the Caucasian Ossetes are descended (Berta Róna-Tas, 2002). The contact between these people and the ancient Hungarians is reflected in both Hungarian language and culture.

In the early 850s the Hungarians, under pressure from the Petchenegs, another Turkish tribe, moved westward from Levedia to Etelköz, the Dnieper-Dnester-Prut region, accompanied by the Kabars who had rebelled against the Khazars (Bálint, 1989). Around 830 they moved into the eastern Carpathian Mountains. 895 is the traditional date when seven major Magyar and Kabar hordes under King Arpad forced the Verecke, Uzsok, and Dukla passes across the mountains (Regino-Pertz, 1890). This migration took the Magyars into the great plain drained by the Danube and Tisza rivers, a region that corresponds roughly to present-day Hungary (Fodor, 1996), and into the more fertile parts of Transylvania among the mountains.

These regions had been settled for thousands of years before the Magyars' arrival, by Dacians, Romans, Sarmatians, Goths, Huns, Avars, Slavs, and others: it is probable on the eve of the Hungarian conquest the overwhelming majority of the indigenous population was Slavic. The arrival and settlement of the Slavs has already begun under the Avars, earlier migrants from the Eurasian steppes, some of whom perhaps lived to see the Hungarian conquest (Bóna, 1990, 2000). Estimates of the fraction of the total population of the Carpathian Basin consisting of newly arrived Hungarians range from 10% to 50% (Cavalli-Sforza, 1994).

The origin of the Hungarian-speaking Seklers, currently an isolated minority in Romanian Transylvania, which was formerly an autonomous principality under the Hungarian kingdom, is still debated. Some suggest that the Seklers were one of the tribes of the original Hungarian conquest, who settled at the eastern border; others, that they migrated from Hungary later, during the Middle Ages (Bóna, 1990).

The genetic relationships of speakers of the Uralic languages to the neighboring Indo-European-speaking populations are complex, and not entirely understood (Lahermo et al., 1996; Kittles et al., 1998; Lahermo et al., 1999; Laitinen et al., 2002; Kasperaviciute et al., 2004). Previous analysis of modern Hungarian mitochondrial sequences indicated an essentially European maternal lineage (Lahermo et al., 2000). The aim of the present study was to analyze the mitochondrial lineages of human bone samples originating from archaeologically Hungarian graves, from the 10th–11th century, in the Carpathian Basin, and compare them to samples from modern Hungarians and Seklers. In particular, we have tested the hypothesis that no genetic continuity exists between ancient and modern Hungarian-speaking populations.

MATERIALS AND METHODS

Sampling

Seventy-nine bone samples from ancient remains from the age of the Hungarian conquest were included in the analysis. Samples were excavated in cemeteries from the 10th–11th centuries from different regions of Hungary (Table 1, Fig. 2) and were provided by the Archaeological Institute of the Hungarian Academy of Sciences. Burial sites and bones were archeologically and anthropomorphologically well defined before the analysis. In 42 cases, we have got PCR results with at least one of the primer pairs. Fifteen of the 42 samples did not correspond to the criteria for authentication described below, and were discarded at this stage. The remaining 27 bone samples were submitted to genetic analysis.

Hair samples were collected from 101 maternally unrelated modern Hungarian individuals from all regions of Hungary, and from 76 maternally unrelated Sekler individuals living in Romanian Transylvania.

DNA isolation

Ancient DNA (aDNA) was isolated from femoral bones. Standard isolation methods were used as described by Kalmar et al. (2000) and alternatively when needed, a modified method incorporating the DNeasy Tissue Kit (Qiagen) was used. In this modified method, DNA was precipitated from 350-μl extract from bone powder and extraction buffer, incubated overnight at 37°C (Kalmar et al., 2000), by treatment with 350 μl 4M NH_4-acetate and 700 μl 96% EtOH at −70°C for 10 min. The mixture was transferred into DNeasy Mini spin column and centrifuged at 6000*g* for 1 min. The column was washed twice and DNA was eluted in a final volume of 40 μl.

DNA isolation from the hair samples was performed by using Chelex, according to the published protocol (Walsh et al., 1991).

mtDNA analysis: HSVI region

Mitochondrial DNA (mtDNA) analysis was performed on the hypervariable region I (HVSI) of the mtDNA control region, between nucleotide positions 16024–16383. In cases of ancient samples, two partially overlapping subregions were amplified with the primer pairs L16040 (5′-TCTGTTCTTTCATGGGGAAG-3′)/H16239 (5′-GTG GCTTTGGAGTT-GCAGTT-3′) (240bp; 16020–16259) and L16201 (5′-AACCCCCTCCCCATGCTTA-3′)/H16400 (5′-TGATTTCACGGAGGATGGTG-3′ (239bp; 16182–16420), respectively. DNA derived from modern samples was amplified with the primer pair L16040/H16400.

TABLE 1. The origin, age and sex of investigated bone samples

Sample	Origin		Estimated age (century)	Sex
anc1	Izsák-Balázspuszta (1)	Hungarian Lowland	Middle 10th	Male
anc2	Magyarhomoróg 120.tomb (2)	Hungarian Lowland	Middle 11th	Male
anc3	Orosháza-Görbics tanya 2.tomb (3)	Hungarian Lowland	10th	Female
anc4	Szabadkígyós-Pálliget 7.tomb (4)	Hungarian Lowland	Middle10th	Male
anc5	Szegvár-Oromdűlő 412. tomb (5)	Hungarian Lowland	Early 11th	Female
anc6	Szegvár-Oromdűlő 593. tomb	Hungarian Lowland	Late 11th	Female
anc7	Aldebrő-Mocsáros 25. tomb (6)	North-eastern Hungary	Late 10th	Female
anc8	Besenyőtelek-Szőrhát 1. tomb (7)	North-eastern Hungary	10th	Male
anc9	Eger-Szépasszonyvölgy 4. tomb (8)	North-eastern Hungary	10th	Nd
anc10	Sárrétudvar-Hízóföld 5. tomb (9)	Hungarian Lowland	Late10th	Male
anc11	Sárrétudvar-Hízóföld 9. tomb	Hungarian Lowland	Late10th	Male
anc12	Sárrétudvar-Hízóföld 118. tomb	Hungarian Lowland	Middle 10th	Female
anc13	Sárrétudvar-Hízóföld 213. tomb	Hungarian Lowland	Early 10th	Male
anc14	Fadd-Jegeshegy 62.tomb (10)	South-western Hungary	Late 10th	Female
anc15	Fadd-Jegeshegy 63.tomb	South-western Hungary	Late 10th–early 11th	Female
anc16	Fadd-Jegeshegy 74.tomb	South-western Hungary	Late 10th–early 11th	Male
anc27	Fadd-Jegeshegy 78.tomb	South-western Hungary	Late 10th–early 11th	Male
anc17	Fadd-Jegeshegy 88.tomb	South-western Hungary	10–11th	Male
anc18	Mözs-Szárazdomb 2.tomb (11)	South-western Hungary	Middle 10th	Female
anc19	Mözs-Szárazdomb 41.tomb	South-western Hungary	Middle 10th	Male
anc20	Mözs-Szárazdomb 60.tomb	South-western Hungary	Middle 10th	Female
anc21	Őrménykút 3/c tomb (12)	Hungarian Lowland	Late 10th	Male
anc22	Őrménykút 8. tomb	Hungarian Lowland	Late 10th	Male
anc23	Őrménykút 12. tomb	Hungarian Lowland	Late 10th	Female
anc24	Zalavár-Kápolna 270.tomb (13)	South-western Hungary	11th-12th	Male
anc25	Harta-Freifelt 10.tomb (14)	Hungarian Lowland	Early 10th	Female
anc26	Lébény-Kaszás 80.tomb (15)	North-western Hungary	11th	Male

ND: not determined.
Numbers in brackets refer to cemeteries on the map in Fig. 2.

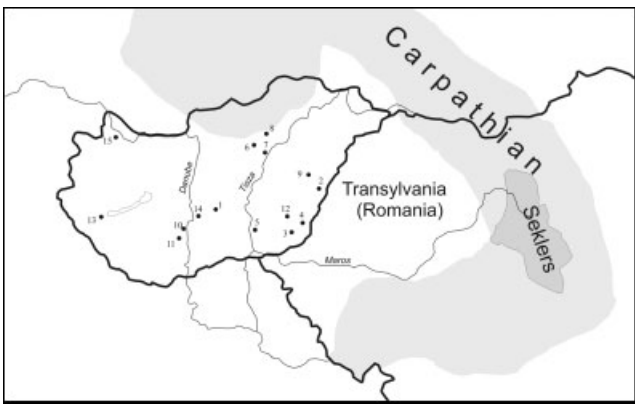

Fig. 2. Location of cemeteries where bone samples were excavated and the homeland of the Seklers (Seklerland).

The standard amplification reaction contained 4 μl of bone extract, 1.5 U AmpliTaq Gold DNA polymerase (Applied Biosystem), 200 μM each of dNTP (Fermentas), 25 pmol each of primers, 1× PCR buffer and 3 mM $MgCl_2$ in 40 μl total volume of reaction mixture. Amplification conditions were: denaturation at 94°C for 6 min, 38 cycles of denaturation at 93°C for 30 s, annealing at 56°C for 1 min, extension at 72°C for 40 s, and final extension at 72°C for 5 min. Amplification reaction was checked on 8% native polyacrylamide gel and visualized after ethidium bromide staining with UV transilluminator (UVP).

Sequencing

Products of successful and contamination-free amplifications were purified and concentrated with a Montage PCR Centrifuge Filter Device (Millipore) in a final volume of 10 μl in cases of ancient DNA, and 30 μl of modern DNA respectively, according to the manufacturer's recommendation.

Sequencing reactions were performed using the ABI Prism BigDye™ Terminator v3.0 Cycle Sequencing Ready Reaction Kit. Ten microliters of purified PCR product, 12.5 pmol of the same primer which had been used for the amplification, and 8 μl Terminator Ready Reaction Mix were mixed in a final volume of 20 μl sequencing reaction. The sequences were determined on an ABI Prism 310 sequencer (PE Applied Biosystem).

Cloning of ancient samples

The InsT/Aclone PCR Product Cloning Kit (Fermentas) was used for cloning of ancient DNA fragments. DNA from six selected clones was sequenced in each cases with the universal M13 forward primer (5′-CGCCAG GGTTTTCCCAGTCACGAC-3′).

mtDNA classification

mtDNA haplogroups were assigned to each sample by the use of published criteria (Torroni et al., 1993, 1996, 1998, 2001; Richards et al., 1998; Macaulay et al., 1999; Quintana-Murci et al., 1999; Richards et al., 2000; Finnila et al., 2001; Herrnstadt et al., 2002; Kivisild et al., 2004), relative to the revised Cambridge Reference Sequence (rCRS) (Andrews et al., 1999).

mtDNA analysis: HVSII and coding regions

In cases when haplogroup categorization was not possible on the basis of HVSI motifs alone, analysis of the diagnostic polymorphic sites in the HVSII region and mtDNA coding region was also performed. Polymorphic

TABLE 2. The haplogroup-associated polymorphic sites in the HVSII and coding regions, the primers used for amplification and the type of detection

Nucleotid position	Location	Substitution	Primers	Detection of mutation[a]
72	HVSII	T→C	L28 5′-CAGGTCTATCACCCTATTAACCA-3′ H132 5′-GGATGAGGCAGGAATCAAAG-3′	Sequencing
73	HVSII	A→G	L28 5′-CAGGTCTATCACCCTATTAACCA-3′ H132 5′-GGATGAGGCAGGAATCAAAG-3′	+73*ApaLI*
4580	Coding reg.	G→A	L4521 5′-TACCATCTTTGCAGGCACAC-3′ H4660 5′-AAGGATTATGGATGCGGTTG-3′	−4580*Nhe*I
7028	Coding reg.	C→T	L6962 5′-TTTTCACCGTAGGTGGCCTG-3′ H7126 5′-TGAAATGGATTTTGGCGTAGG-3′	+7025*AluI*
10238	Coding reg.	T→C	L10146 5′-TGACTACCACAACTCAACGGCT-3′ H10288 5′-AGGTTAGTTGTTTGTAGGGCTC-3′	+10237*HphI*
10310	Coding reg.	G→A	H10220 5′-GCGTCCCTTTCTCCATAAAA-3′ L10348 5′-GGCCAGACTTAGGGCTAGGA-3′	Sequencing
10400	Coding reg.	C→T	L10292 5′-CCTTTTACCCCTACCATGAGCC-3′ H10466 5′-TTTATGTAAATGAGGGGCATTTGG-3′	Sequencing
10873	Coding reg.	T→C	L10767 5′-AACCTAAACCTACTCCAATGCTAAA-3′ H10965 5′-GTGAGGGGTAGGAGTCAGGTAG-3′	−10871*MnlI*
11719	Coding reg.	G→A	L11674 5′-CAGCCATTCTCATCCAAACC-3′ H11852 5′-GGGGTAAGGCGAGGTTAGC-3′	Sequencing
12308	Coding reg.	A→G	L12214 5′-CCCCTTATTTACCGAGAAAGC-3′ H12398 5′-TTGTTAGGGTTAACGAGGGTGG-3′	Sequencing
12705	Coding reg.	C→T	L12622 5′-CATCCCTGTAGCATTGTTCG-3′ H12764 5′-AATTCCTACGCCCTCTCAGC-3′	Sequencing
14410	Coding reg.	T→C	H14396 5′-CTCCATCGCTAACCCCACTA-3′ L14527 5′-TTCTGAATTTTGGGGGAGGT-3′	Sequencing
14766	Coding reg.	C→T	L14638 5′-ACCCCACAAACCCCATTACT-3′ H14837 5′-AGGAGTGAGCCGAAGTTTCA-3′	+14766*MseI*

[a] Sites are numbered from the first nucleotid of the recognition sequence. A plus (+) sign indicates the presence while minus (−) sign the absence of recognition site.

sites in the HVSII and mtDNA protein coding regions were amplified with specific primers and analyzed either by restriction enzyme cleavage or by sequencing. The haplogroup-associated polymorphic sites, the primers used for amplification and the restriction endonucleases used for detection of polymorphisms are reported in Table 2. The amplification reaction and conditions were the same as described previously for the HVSI sequences.

The restriction enzyme cleavage reaction mix contained 25 μl PCR product from ancient DNA or 10 μl from modern DNA, 1× buffer and 3 U enzyme in 50 μl final volume. Reaction was performed for 2 h at 37°C. The sizes of the resulted fragments were checked on 8% native polyacrylamide gel and visualized with an UV transilluminator after ethidium bromide staining.

Database comparison and statistical analysis

The sequences obtained were compared with previously published sequences of 7752 Eurasian individuals, sampled from 57 Eurasian populations. The published sources of these data are presented in Table 3.

A 276 bp (np 16090–16365) long control-region of HVSI sequences from 204 Hungarian-speaking individuals together with the sequences of 7752 individuals was grouped into populations. Genetic distances were estimated between all populations as linearized Fst statistics by the use of ARLEQUIN version 2.000 (Schneider et al., 2000). The Fst values were calculated by pairwise comparison using the Tamura–Nei model (Tamura and Nei, 1993). Gamma distribution was $\alpha = 0.26$ (Meyer et al., 1999). The resulting matrix of interpopulation Fst values was summarized in two-dimensional scaling (MDS) performed by SPSS package version 5.0. Analysis of molecular variance (AMOVA) of the Hungarian-speaking populations was performed by the ARLEQUIN package. Reduced median network from the sequences of Hungarian-speaking populations was also constructed with the Network 4.1 program. Sites with lower mutation rates were given greater weight.

The distribution of mtDNAs present in the ancient Hungarian population was assessed by searching for their associated control region motifs in the world-wide mtDNA database (NCBI, Table 3). Comparisons were performed by the Blastn program (NCBI).

Contamination precautions and authentication

During each step of sample preparation, appropriate precautions were taken in order to prevent possible contamination with modern DNA. All steps of sample preparation (excavation and laboratory work) were carried out wearing the appropriate protective clothing (gloves, face mask and laboratory coats). All workspaces (laminar flow surfaces, PCR boxes) and appliances (pipettes, drills, pincers, tubes, cell culture dishes, containers) were cleaned with bleach and subsequently irradiated with 1.0 J/cm^2 UV-C light for 60 min before use. All solutions used were filtered with 0.22 μm (Millipore) filter and subsequently (except for proteinase K) irradiated with UV-C light for 30 min. Throughout all manipulations Universal Fit Filter Tips (Corning Incorporated) were used for pipetting. PCR and Eppendorf tubes were sterilized before use by autoclaving.

TABLE 3. Populations, number of samples of which mtDNA HVSI sequence was used for statistical analysis

Populations	Number of samples	References
Adygei	84	Lebedeva et al. (NCBI Database)
Albanian[a]	42	Belledi et al. (2000)
Armenian[a]	191	Richards et al. (2000)
Austrian[a]	99	Parson et al. (1998)
Azerbaijani[a]	48	Richards et al. (2000)
Basque[a]	156	Bertranpetit et al. (1995), Corte-Real et al. (1996), Richards et al. (2000)
Belarus	51	Belyaeva et al. (NCBI Database)
BoscoGurin	13	Pult et al. (1994)
Bosnian	163	Harvey et al. (NCBI Database)
Bulgarian[a]	141	Calafell et al. (1996), Richards et al. (2000)
Buryat	180	Tajima et al. (2004); Shimada et al. (NCBI Database)
Croatian	60	Harvey et al. (NCBI Database)
Cumanian	11	Bogácsi-Szabó et al. (2005)
Czech[a]	83	Richards et al. (2000)
Danish[a]	38	Richards et al. (1996), Richards et al. (2000)
English[a]	242	Helgason et al. (2001), Piercy et al. (1993)
Estonian[a]	149	Sajantila et al. (1995), Sajantila et al. (1996), Richards et al. (2000)
European-Caucasian	236	Coble et al. (2004)
Evenki	37	Kaessmann et al. (2002)
Finnish	230	Kaessmann et al. (2001), Sajantila et al. (1995)
French[a]	379	Richards et al. (1996), Rousselet and Mangin (1998), Cali et al. (2001), Dubut et al. (2004), CEPH Database
Galician[a]	135	Salas et al. (1998), Gonzalez et al. (2003)
Georgian	168	Reidla et al. (NCBI Database)
German[a]	582	Richards et al. (1996), Hofmann et al. (1997), Baasner et al. (1998), Lutz et al. (1998), Pfeiffer et al. (1999)
Greek	43	Vernesi et al. (2001)
Greek-Cretean	185	Villems et al. (NCBI Database)
Iraqi[a]	116	Richards et al. (2000)
Irish[a]	300	Richards et al. (1996), McEvoy et al. (2004)
Italian[a]	248	Francalacci et al. (1996), Richards et al. (2000), Mogentale-Profizi et al. (2001), Tagliabracci et al. (2001)
Karelian[a]	83	Sajantila et al. (1995)
Kazakh	82	Yao et al. (2000), Comas et al. (1998)
Kirghiz-Highland	43	Comas et al. (1998)
Kirghiz-Lowland	49	Comas et al. (1998)
Komi	15	Voevoda et al. (NCBI Database)
Kurdistanian[a]	53	Richards et al. (2000)
Mari	14	Sajantila et al. (1995)
Moksha	20	Sajantila et al. (1995)
Mongolian	101	Kolman et al. (1996)
North-Ossetian[a]	106	Richards et al. (2000)
Norwegian[a]	629	Opdal et al. (1998), Richards et al. (2000), Helgason et al. (2001), Passarino et al. (2002)
Oberwallis	20	Pult et al. (1994)
Ossetian	197	Kaldma et al. (NCBI Database)
Palestinian[a]	117	Di Rienzo and Wilson (1991), Richards et al. (2000)
Polish[a]	473	Richards et al. (2000), Malyarchuk et al. (2002)
Retoroman	15	Pult et al. (1994)
Romanian[a]	92	Richards et al. (2000)
Russian[a]	379	Orekhov et al. (1999), Richards et al. (2000), Malyarchuk and Derenko (2001), Malyarchuk et al. (2002)
Saami	114	Sajantila et al. (1995)
Serbian	56	Harvey et al. (NCBI Database)
Slavonic-Russian	88	Markina et al. (NCBI Database), Bermisheva et al. (NCBI Database)
Slovakian	128	Metspalu et al. (NCBI Database)
Swedish[a]	32	Sajantila et al. (1996)
Swiss[a]	224	Pult et al. (1994), Dimo-Simonin et al. (2000)
Syrian[a]	69	Richards et al. (2000)
Turkish	28	Calafell et al. (1996)
Uighur	98	Yao et al. (2000), Comas et al. (1998)
Ukrainan	17	Malyarchuk and Derenko (2001)
Total	7752	

[a] HVSI sequence data were retrieved from the web site www.gen.tcd.ie/molpopgen/data.htm (McEvoy et al., 2004).

All steps of work (bone powdering, DNA extraction, amplification, post-PCR analysis) were carried out in separate rooms.

Bone surfaces, before extraction, were washed with bleach and distilled water. The surface of a 2 × 5 cm part of the bone diaphysis was removed with a sand disk

TABLE 4. Polymorphisms in ancient Hungarian samples

Sample	HVSI haplotypes (−16000)[a]	HVSII and coding region haplotypes[a]	Haplogroup
anc1*	140C 182C 183C 189C 217C 274A	9bp del	B
anc25*	294T 304C	−73*ApaLI* −7025*AluI* −14766*MseI* 10310G	H
anc2	CRS	−73*ApaLI* −7025*AluI* −14766*MseI*	H
anc5	CRS	−73*ApaLI* −7025*AluI* +14766*MseI*	H
anc17	304C	−73*ApaLI* −7025*AluI* −14766*MseI*	H
anc19	093C 366T	−73*ApaLI* −7025*AluI* −14766*MseI*	H
anc21*	CRS	−73*ApaLI* −7025*AluI* −14766*MseI*	H
anc26	311C 362C	−73*ApaLI* −7025*AluI* −14766*MseI*	H
anc27	311C	−73*ApaLI* −14766*MseI* +7025*AluI*	HV
anc10	129A 148T 223T	+10237*HphI* 12705T	I
anc20	223T 311C	10400T	M
anc3*	147A 172C 183C 189C 223T 320T 355T	+10237*HphI* 10400C	N1a
anc8*	147A 172C 183C 189C 223T 248T 320T 355T	+10237*HphI* +10871*MnlI*	N1a
anc14	CRS	+73*ApaLI* −7025*AluI* 11719A 12308A +14766*MseI*	R
anc13*	311C	+73*ApaLI* 11719A 12308A 12705C +14766*MseI*	R
anc12*	126C 182C 183C 189C 294T 296T 298C		T
anc16	051G 126C 147T 294T 296T	10400C +10871*MnlI*	T
anc18	126C 148T 218T 294T 304C		T2
anc11	126C 294T 304C		T2
anc9*	259A 311C	−73*ApaLI* +7025*AluI* 12308G +14766*MseI*	U
anc24	311C 343G	12308G	U3
anc7*	356C	12308G	U4
anc4*	223T 356C	10400C 12308G 12705C +73*ApaLI*	U4
anc6	114A 192T 256T 270T 294T	12308G	U5a1
anc15	153A 298C	72C −73*ApaLI* +4580*NheI* +7025*AluI* −14766*MseI*	V
anc22*	183C 189C 223T 278T	+10871*MnlI* 14470C	X
anc23*	183C 189C 223T 278T	+10871*MnlI* 14470C	X

[a] Sites are numbered according to revised CRS (Andrews et al., 1999).
* Sequences belonging to the classical conquerors.

to 3–4-mm depth in order to eliminate possible surface contamination. The cleaned surface was irradiated with UV light at 1.0 J/cm^2 for 30 min. Bone powder was produced by boring, and collected into a sterile tube. Each bone sample was powdered by at least two scientists, at least two times each. In each case, two independent DNA extractions were carried out, and at least two PCR amplifications were performed from each extract, to assess the reproducibility and authenticity of results.

Both subregions of the analyzed mtDNA HVSI sequences were sequenced from both directions. The whole 360 bp sequence was assembled from the four independently produced part of the sequence. Sequences were considered authentic only if partial sequences were assembled unambiguously, and if both collaborators reproduced at least one partial sequence.

In order to detect possible contamination by exogenous DNA, extraction and amplification blanks (with no bone powder) were used as negative controls. Haplotypes of all persons involved in processing the samples were determined and compared with the results obtained from the ancient bone samples. To prove the authenticity of ancient human DNA further, aDNA from a fractional horse burial (only the horse skull and the first two legs are buried with the human remains), excavated from the burial site at Harta-Freifelt, buried with human sample *anc25*, was isolated with the same procedure as the human aDNA. Horse aDNA was amplified with both horse- (L15561 5′-CACCATACCCACCTGACATGCA-3′ and H15741 5′-GCTGATTTCCCGCGGCTTGGTG-3′; 225 bp (15539–15763)) and human-specific primers (L16040/H16239). Only the horse-specific primers resulted in amplification product, which was homologous with the previously published horse sequences. This proves that it is possible to isolate aDNA with this method, free of exogenous contamination.

RESULTS

Haplogroup identification of ancient Hungarian samples

Twenty-seven sequences derived from ancient Hungarian bones were analyzed for mtDNA polymorphisms. All sequences could be assigned to definitive haplogroups. Twenty-five different haplotypes were distinguished, which could be assigned to 15 different haplogroups. These polymorphisms in ancient sequences are shown in Table 4.

Two sequences (*anc1*, *anc20*) belong to typical Asian haplogroups B (3.9%) and M (3.9%), respectively (Table 5). The others were assigned to European-specific haplogroups. The most frequent (26.9%) was haplogroup H, the commonest European haplogroup. However, the ancient Hungarian frequency is lower than in modern Europe (40–60%, in average 46%; Richards, 1998). Haplogroups U and T were represented with 19.4% and 15.2% frequencies, respectively. Two samples were assigned to each of the N1a and R haplogroups (7.9% each) and one each to HV, I, and preV haplogroups (3.9% each). Two samples (*anc22*, *anc23*), belonging to haplogroup X, posses the same haplotype and were derived from the same burial site; those two individuals could be maternally related. Only one of them was included in the subsequent statistical analysis to avoid the bias of inbred samples.

Cloning

Some of the ancient sequences (*anc4*, *anc6*, *anc8*, *anc12*, *anc15*, *anc22*, *anc23*, *anc25*) were cloned, in order to prove that the results of the direct sequencing are correct and the ancient samples are free of contamination,

TABLE 5. Haplogroup frequencies in Hungarian-speaking populations in percentages

Haplogroups	Recent Hungarian	Sekler	Ancient Hungarian	Classical conquerors	Commoners
B			3.9	9.1	
C		2.7			
H	39.6	36.9	26.9	18.2	33.2
HV	3.0	2.7	3.9		6.7
I	2.0	1.4	3.9		6.7
J	5.9	5.3			
J1	1.0				
J1a	1.0				
J2		1.4			
JT	1.0	2.7			
K	7.9	10.6			
M			3.9		6.7
N1a			7.6	18.2	
R			7.6	9.1	6.7
T	2.0	2.7	7.6	9.1	6.7
T1	2.0	7.9			
T2	4.0	2.7	7.6		13.3
T3	1.0	1.4			
T4		1.4			
U	4.0	2.7	3.9	9.1	
U3		2.7	3.9		6.7
U4	4.0	1.4	7.6	18.2	
U5	1.0				
U5a	2.0				
U5a1	2.0	9.3	3.9		6.7
U5a1a	2.0	1.4			
U5b1	1.0				
preV	1.0		3.9		6.7
V	4.8				
W	7.9	2.7			
X			3.9	9.1	
Total	100	100	100	100	100

and to eliminate ambiguities obtained by direct sequencing. As the result of cloning, the sequence of the 240 bp and the 239 bp long portion of the HVSI region was established in five (*anc6*, *anc12*, *anc15*, *anc23*, *anc25*) and four cases (*anc4*, *anc8*, *anc12*, *anc22*) respectively. In addition in case of *anc4* the sequence containing the 12705 position was determined after cloning.

Only sporadic and inconsequential differences were found between cloned and direct sequences of ancient samples (Table 6). In case of fragments *anc6*, *anc12*, and *anc25* (240 bp fragments) all the six cloned sequences were identical to that obtained by direct sequencing (not shown). In case of fragments *anc12* (239 bp) and *anc23* (240 bp) obscurities in the directly sequenced samples (at nps 16294, 16296; and nps 16183, 16189, 16192, respectively) could be defined unambiguously from the sequences of the clones. According to the direct sequencing sample *anc4* displays 16223T, and it also bears 12705C. These two mutations contradict to each other, since 12705T also splits off the 16223C cluster (Macaulay et al., 1999). The cloned sequences confirmed the coexistence of these mutations in the same sample. However, one of the six clones shows C in the np16223, which raises the possibility of heteroplasmy at this position.

Status comparison of the two groups of ancient samples

The ancient samples originated from burial sites of the 10th–11th centuries. The bone findings archaeologically could be divided into two major groups. Twelve of them were excavated from cemeteries with rich grave goods, unambiguously typical of classical Hungarian conquerors—horse's skull, horse harness, and decorations, arrow-or spear-heads, mounted belts, braid ornaments, earrings (Mesterházy, 1997; Szőke, 1962). These samples came mostly from the cemeteries of nuclear families (Révész, 1991). The other 15 bone samples originated from commoners' cemeteries, with poor archaeological remains (no horse harness; fewer, simpler, and poorer grave goods) (Szőke, 1962; Bálint, 1991). These are burial sites with many tombs, typically those of plebeians: who could be either Hungarian invaders or members of other populations who had been in the Carpathian Basin before the Hungarian conquest (Mesterházy, 1996). Comparing these two groups on the basis of haplogroup frequencies and haplotype identities significant genetic differences were found (Table 4). However, this statement because of the small sample size must be considered with utmost cautions.

Among the classical Hungarian conquerors one sequence belongs to the typical Asian-specific haplogroup B (9.1%). Two sequences each are members of haplogroups H, N1a, and U4 (18.2% each) and one of haplogroups R, T, U, and X, respectively (9.1% each). The frequency of haplogroup H is rather low compared with the average in Europe. The N haplogroup is of Near Eastern origin (Richards et al., 2000). The frequency of N1a mtDNA lineage today is very low anywhere in the world, at about 0.2% (Haak et al., 2005). This haplogroup is present in the Carpathian Basin from the Neolithic. However, *anc3* and *anc8* show 16189C which is characteristic of the Central Asian

TABLE 6. Sequences of cloned PCR fragments compared to the Cambridge Reference Sequence and the results of direct sequencing[a]

	16035	16039	16048	16049	16054	16074	16153	16183	16189	16192	16210	16223	16248	16259	16260	16267	16278	16294	16296	16298	16319	16320	16344	16355	16356	16358	16365	16371	16376	16378
CRS	G	G	G	G	A	A	G	A	T	C	A	C	C	C	C	C	C	C	C	T	G	C	C	C	T	C	C	A	C	C
anc4-direct								.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.
anc4-clone1								.	.	.	.	T	.	.	.	T	.	.	.	.	.	.	T	.	C	.	.	.	.	.
anc4-clone2								.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.
anc4-clone3								.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	C	T	.	.	.	.
anc4-clone4								.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.
anc4-clone5								.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.
anc4-clone6								.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.
anc8-direct								.	.	.	.	T	T	.	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.
anc8-clone1								.	.	.	.	T	T	T	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.
anc8-clone2								.	.	.	.	T	T	.	.	.	.	.	.	.	.	T	.	T	.	.	.	T	.	.
anc8-clone3								.	.	.	.	T	T	.	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	T
anc8-clone4								.	.	.	.	T	T	.	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.
anc8-clone5								.	.	.	.	T	T	.	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.
anc8-clone6								.	.	.	.	T	T	.	.	.	.	.	.	.	.	T	.	T	.	.	.	.	.	.
anc12-direct								.	.	.	.	.	.	.	.	.	.	Y	Y	T	.	.	.	.	.	.	.	.	.	.
anc12-clone1								.	.	.	.	.	.	.	.	.	.	T	T	C	.	.	.	.	.	.	.	.	.	.
anc12-clone2								.	.	.	.	.	.	.	.	.	.	T	T	C	.	.	.	.	.	.	.	.	.	.
anc12-clone3								.	.	.	.	.	.	.	.	.	.	T	T	C	.	.	.	.	.	.	.	.	.	.
anc12-clone4								.	.	.	.	.	.	.	.	.	.	T	T	C	.	.	.	.	.	.	.	.	.	.
anc12-clone5								.	.	.	.	.	.	.	.	.	.	T	T	C	.	.	.	.	.	.	.	.	.	.
anc12-clone6								.	.	.	.	.	.	.	.	.	.	T	T	C	.	.	.	.	.	.	.	.	.	.
anc15-direct	.	.	.	.	R	.	A	.	.	.	.	.																		
anc15-clone1	A	.	A	.	A	.	A	.	.	.	.	.																		
anc15-clone2	.	A	.	A	A	.	A	.	.	.	.	.																		
anc15-clone3	.	.	.	.	A	.	A	.	.	.	.	.																		
anc15-clone4	.	.	.	.	A	.	A	.	.	.	.	.																		
anc15-clone5	.	.	.	.	A	.	A	.	.	.	.	.																		
anc15-clone6	.	.	.	.	A	.	A	.	.	.	.	.																		
anc22-direct								.	.	.	.	T	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
anc22-clone1								.	.	.	G	T	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
anc22-clone2								.	.	.	.	T	.	.	T	.	T	.	.	.	.	.	.	.	.	.	.	.	.	T
anc22-clone3								.	.	.	.	T	.	.	.	.	T	.	.	.	C	.	.	.	.	.	.	G	.	.
anc22-clone4								.	.	.	.	T	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
anc22-clone5								.	.	.	.	T	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
anc22-clone6								.	.	.	.	T	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
anc23-direct	.	.	.	.	.	.	.	M	Y	Y	.	.																		
anc23-clone1	.	.	.	.	.	.	.	C	C	C	.	.																		
anc23-clone2	.	.	.	.	.	G	.	C	C	C	.	.																		
anc23-clone3	.	.	.	.	.	.	.	C	C	C	.	.																		
anc23-clone4	.	.	.	.	.	.	.	C	C	C	.	.																		
anc23-clone5	.	.	.	.	.	.	.	C	C	C	.	.																		
anc23-clone6	.	.	.	.	.	.	.	C	C	C	.	.																		

[a] Only variable sites are shown. Dots mean the identical nucleotid with the CRS.

branch. *Anc8* is identical with only one sequence originated from a Buryat tribe and is a one step neighbor (at np16183) of other Central Asian type sequences. *Anc3* is at np16248 one step neighbor of Central Asian sequences. So these haplotypes might have come through Asia to the Carpathian Basin. Among the classical Hungarian conquerors the frequency of haplogroup U* was high (27.3%), compared to the other populations. This haplogroup occurs mainly in the southern but also in the eastern region of Europe (Richards, 1998). Two sequences were assigned to the U4 haplogroup, which appears with high frequency in populations of the Volga, Ural region, and West Siberia (Malyarchuk, 2004). The *Anc4* sample belonging to the U4 haplogroup has equivalent sequences in the Siberian Nenets, Finnish, and Estonian populations.

Among those samples who originated from commoners' cemeteries, one (*anc20*) was assigned to the Asian-specific haplogroup M (Macaulay et al., 1999; Richards et al., 2000). The frequency of haplogroup H is 33.3%, which approaches that in modern European populations. The T2 haplogroup is represented by two samples (13.3%), while haplogroups HV, I, R, T, U3, U5a1, and preV are represented by one sequence only (6.75%). *Anc10,* a member of haplogroup I, shares haplotypes found in Korean, Bosnian, and Ossetian populations. The *Anc6* sequence belongs to the U5a1 haplogroup, which is characteristic of northeastern Europe (Pericic et al., 2005). This haplotype is shared between Finnish, Norwegian, Estonian, Slovakian, Serbian, and Georgian sequences. Seven of the 15 sequences belong to the haplogroups H, HV, and R, which are most common in Europe. Three of the four sequences belonging to the European-specific T* haplogroups (Macaulay et al., 1999) originate from commoners' cemeteries.

Comparison of ancient samples with two current Hungarian-speaking populations

The sequences of ancient samples were compared with recent samples from 101 Hungarian and 76 Sekler individuals.

All of the recent Hungarian sequences are members of European type haplogroups. Among the recent Sekler sequences two are members of the Asian-specific haplogroup C, the others belong to western Eurasian haplogroups. Haplogroup H is the most frequent in all populations, but while the percentage in modern Hungarian-speaking populations (39.65% and 36.9%) are similar to that in Europe among ancient samples and in particular among samples from the classical conquerors this value is rather low (26.95% and 18.2%, respectively). The ancient sequences lack the J, K, and W haplogroups while the N1a and X haplogroups are missing among modern individuals analyzed in this study.

Haplotype variations among Hungarian-speaking populations under consideration were summarized by a reduced median network. (Bandelt, 1999; see Fig. 3). The ancient Hungarian samples are not separated from the other sequences derived from modern Hungarians and Seklers, they appear in all branches together with the other sequences but mostly show individual haplotypes.

As far as the comparison with ancient samples is concerned, the CRS which is common in Europe (Richards et al., 2000) was found in two ancient, eight modern Hungarian and six Sekler samples. It seems that in case of the Hungarians, apart from CRS sequences, only five of the modern haplotypes can be traced back to one of the older (*anc11*, *anc17*, *anc25*, *anc27*) haplotypes. Among the recent Sekler sequences, apart from CRS sequences only one has an older equivalent in *anc10* haplotype, while one share the same HVSI but not RFLP haplotype with *anc13* and *anc27* sequences, respectively. On the whole 13% of recent Hungarian and 9% of the Sekler haplotypes can be traced back to ancient haplotypes, while 23% of ancient haplotypes occur in recent Hungarian and 12% in Sekler populations.

Statistical analysis

AMOVA was performed with different grouping of the studied Hungarian-speaking populations (Table 7). Considering the modern populations the percentage of variance between populations is very low (0.26%) while comparing the two groups of ancient samples 12.38% of variance was observed. When the two modern and the two ancient populations were grouped and related 1.62% variance was among the two groups and 2.31% within the groups. The two ancient populations were independently compared with the modern Hungarian-speaking populations (taking as one group) at variance level. While there was a variance of 12.65% between the classical conquerors and modern Hungarians, the variance between the commoners and modern Hungarians is negligible.

Our data were compared with 7752 sequences from 57 populations from Europe, the Middle East, and Central Asia. On the basis of Fst values (Table 8) the ancient samples show the lowest genetic distance from some populations from the Levant (Syrian, Palestinian), Central Asia (Turkish, Azerbaijani, Moksha), and Europe (Oberwallis, Ukrainian). The modern Hungarian population shows very low genetic distances ($Fst < 0.005$) to populations from Central, Eastern, and Western Europe (Czech, Ukrainian, Croatian, Swedish, French, Spanish, Slovakian, Austrian, Serbian, Swiss), while Seklers have very low distances ($Fst < 0.005$) to 25 populations, mostly from Eastern Europe and the Balkans, but with some from Central and Western Europe, and also the Finno-Ugrian Komi, Moksha, and Mari. When the samples of classical Hungarian conquerors and commoners were analyzed, the former group have a relatively low distance ($Fst < 0.05$) from Central Asian (Kazakh, Kirghiz, Mongolian), Turk, Syrian, and Oberwallis populations, while samples from commoners' cemeteries show very low distances ($Fst < 0.001$) from populations from Asia (Turkish, Azerbaijani, Adygei, Georgian, Moksha) and also from Europe (Italian, Swedish, Austrian, Slovakian, Polish, Russian, Estonian, French, Croatian, Swiss, Czech, English, Bosnian, Ukrainian, Greek).

All ancient samples show significant distances ($P < 0.05$) from the recent Hungarian-speaking populations, as do classical Hungarian conquerors from the commoners and recent Hungarian-speaking populations. The distance between the commoners and recent Hungarian and Sekler samples is insignificant.

Fst values were visualized by the use of multidimensional scaling (MDS) (Fig. 4a,b). Most of the populations studied are concentrated in a group composed of mainly European populations, including recent Hungarians and Seklers. A group of Central Asian populations split off

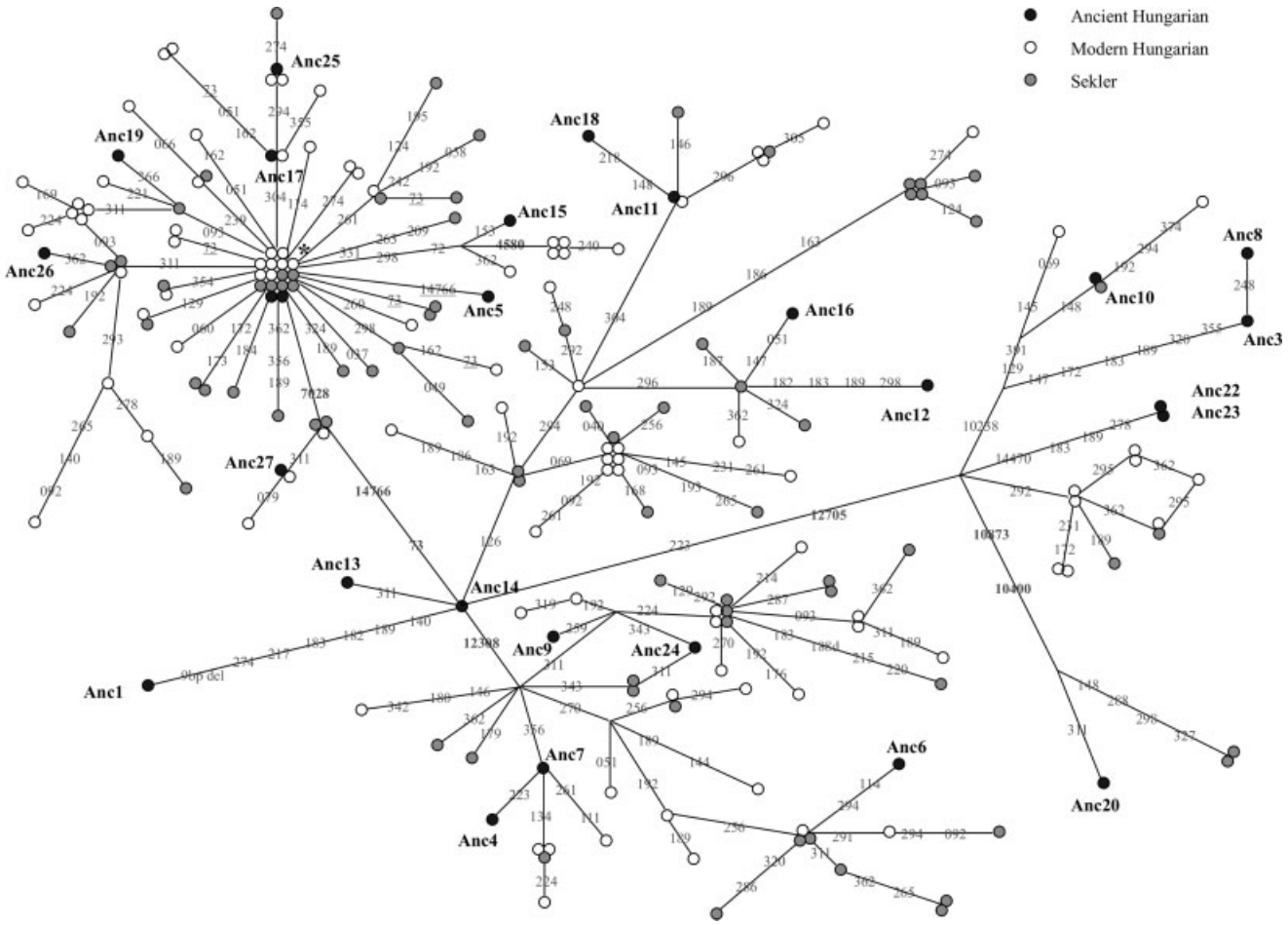

Fig. 3. Reduced median network of the haplotypes identified among ancient Hungarian and modern Hungarian-speaking populations. * Indicates the Cambridge Reference Sequence. The amount of circles indicates the number of samples with the given haplotypes. Coding region and HVSII sites which define main branches of haplogroups are bold.

TABLE 7. AMOVA in samples of Hungarian-speaking populations

Groups[a]	Among groups[b]	Among populations within groups	Within populations
Modern (Hun vs. Sek)		0.26 (0.234)	99.74 (0.234)
Ancient (Class vs. Comm)		12.38 (0.0048)	87.62 (0.0048)
Hun+Sek vs. Ancient	2.62 (0.326)	0.21 (0.229)	97.17 (0.0137)
Hun+Sek vs. Class+Comm	1.62 (0.332)	2.31 (0.007)	96.06 (0.000)
Hun+Sek vs. Class	12.65 (0.338)	0.26 (0.165)	87.10 (0.000)
Hun+Sek vs. Comm	−1.26 (0.655)	0.34 (0.172)	100.91 (0.416)

[a] Hun: Modern Hungarian, Sek: Sekler, Class: Classical conquerors, Comm: Commoners.
[b] *P* values are given in parentheses.

unambiguously from them. Saamis, Evenkis, and European Caucasians are well separated from all studied populations.

The group of the ancient Hungarian samples is mapped within a group that includes Palestinian, Syrian, Ukrainian, Turkish, Kurdish, and the Finno-Ugric Komi populations; and it is close to the Azerbaijani, North-Ossetian, Oberwallis populations, and to the mediaeval Cumanian population that migrated into Hungary in the 13th century. This group further was mapped between a group of Central Asian (Mongolian, Kazakh, Uighur, Kirghiz) and western Eurasian populations, including the modern Hungarians and Seklers. Analyzing the samples of classical conquerors and commoners separately, the commoners' samples are mapped with Adygei, Serbian, and Ossetian populations close to Western Eurasian populations. The classical conquerors are well separated from all the populations under consideration, but they are closest to populations from Central Asia.

DISCUSSION

According to our results, the ancient Hungarian population from the 10th–11th centuries was heterogeneous at the levels of mitochondrial haplogroup and haplotype.

TABLE 8. Fst values calculated from mtDNA HVSI sequence data

Populations	Modern Hungarian	Sekler	Ancient Hungarian	Classical conquerors	Commoners
Iraqi	0.01675	0.00942	0.00724	0.06241	−0.00202
Syrian	0.02186	0.01542	0.00414	0.04670	0.00771
Palestinian	0.01449	0.01038	0.00344	0.05399	−0.00444
Armenian	0.01146	0.00785	0.00940	0.06400	0.00251
Azerbaijani	0.00332	−0.00520	0.00378	0.06651	−0.01475
North-Ossetian	0.01951	0.01290	0.01420	0.06779	0.00704
Bulgarian	0.00757	−0.00070	0.01698	0.10213	0.00576
Romanian	0.01276	−0.00013	0.01184	0.09060	0.00352
Albanian	0.07064	0.04771	0.05762	0.10941	0.05535
Italian	0.00974	0.00177	0.01138	0.08971	−0.00339
Glacial	0.00486	0.01374	0.02771	0.13045	0.01142
Basque	0.01164	0.01872	0.05304	0.18765	0.03327
Swiss	0.00422	0.00330	0.01993	0.12231	−0.00236
Austrian	0.00295	−0.00321	0.01856	0.11010	−0.00124
Polish	0.00566	0.00641	0.01129	0.09689	−0.00126
Russian	0.00644	0.00262	0.01513	0.10703	−0.00347
Czech	−0.00361	−0.00515	0.01492	0.11565	−0.01335
Danish	0.00668	0.00146	0.01631	0.11320	0.00301
Sweden	−0.00194	−0.00129	0.01840	0.11208	−0.01270
Norwegian	0.00502	0.00392	0.02587	0.13064	0.00322
Estonian	0.00348	0.00339	0.01556	0.10251	0.00063
Karelian	0.02076	0.01162	0.02540	0.10656	0.02561
English	0.00340	0.00275	0.01690	0.11356	−0.00152
German	0.00612	0.00452	0.02032	0.11701	0.00801
Irish	0.00185	0.00463	0.03060	0.14113	0.00676
Kurdistanian	0.01191	0.00753	0.01136	0.06311	0.00698
French	−0.00022	0.00346	0.01842	0.12108	−0.00315
Adygei	0.01266	0.01081	0.01407	0.08331	−0.00794
Belarus	0.01535	0.00460	0.01116	0.07145	0.00684
BoscoGurin	0.01798	0.02680	0.05174	0.18442	0.06995
Bosnian	0.00542	0.01096	0.01587	0.11704	−0.00629
Buryat	0.13606	0.14129	0.09912	0.11421	0.11083
Croatian	−0.00611	−0.00112	0.01858	0.12111	−0.00462
European-Caucasian	0.02851	0.02424	0.06349	0.22219	0.02521
Evenki	0.25371	0.24119	0.18491	0.17773	0.20320
Finn	0.02469	0.03138	0.02132	0.07472	0.02876
Georgian	0.00833	0.00198	0.00813	0.07671	−0.00192
Greek	0.00651	−0.00060	0.01831	0.10602	0.00390
Greek-Cretan	0.01102	0.00728	0.01476	0.10747	−0.00419
Kazakh	0.06618	0.07059	0.02401	0.04136	0.03228
Kirghiz-High	0.07964	0.07693	0.02858	0.04438	0.04968
Kirghiz-Low	0.13972	0.13345	0.08103	0.08389	0.10080
Komi	0.01996	−0.00257	0.00876	0.09576	0.00932
Mari	0.00462	−0.00967	0.03129	0.11508	0.01377
Moksha	0.00462	−0.00511	−0.00107	0.07410	−0.00630
Mongolian	0.06776	0.07162	0.03695	0.04144	0.02898
Oberwallis	0.01481	0.01533	−0.00002	0.04311	0.02410
Ossetian	0.03570	0.03066	0.03038	0.07655	0.02338
Retoroman	0.02460	0.01860	0.03161	0.09332	0.03682
Saami	0.16259	0.14186	0.13755	0.16310	0.16809
Serbian	0.00376	0.00638	0.02943	0.12206	0.00274
Slavonic-Russian	0.01323	0.00834	0.00850	0.06363	0.01211
Slovakian	0.00034	−0.00032	0.01573	0.11408	−0.01070
Turkish	0.02124	0.01210	−0.01115	0.02065	−0.00488
Uighur	0.07063	0.07801	0.03660	0.05911	0.04939
Ukrainian	−0.00414	−0.01558	−0.00919	0.06093	−0.02135
Cumanian	−0.00607	−0.00382	0.01358	0.10033	0.01578
Modern Hungarian	0.00000	0.00254	0.02273	0.13190	−0.00662
Sekler		0.00000	0.01767	0.10787	−0.01050
Classicals					0.10033

Fifteen haplogroups and 25 haplotypes were distinguished among the 27 samples studied. However, all but two (*anc1*, *anc20*) ancient samples belong to potentially European haplogroups. Analyzing the haplotypes, we detect some Asian affinities, and the genetic effect of populations who came into contact with ancient Hungarians during their movement. The difference is more conspicuous when analyzed according to the burial status: Commoners show a clear dominance of haplotypes and haplogroups (H, R, T) common in west Eurasia, while classical conquerors show a more heterogeneous haplogroup representation. Some could be classified to haplogroups (N1a, X) which frequencies are very low in recent worldwide populations, and are absent in recent Hungarian

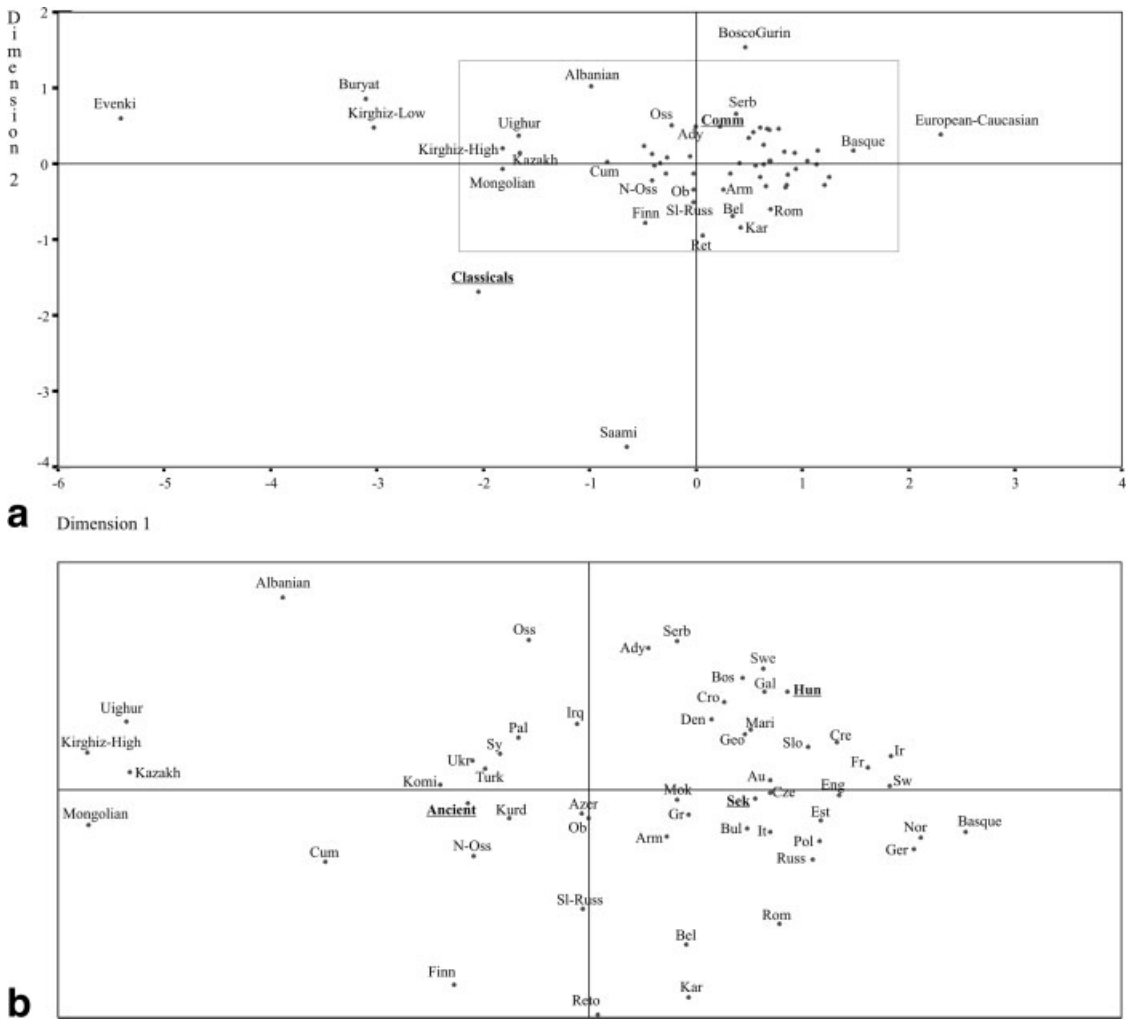

Fig. 4. MDS plot of interpopulation Fst values. a: the localization of commoners and classical conquerors b: the localization of ancient Hungarian and modern Hungarian speaking populations. Population labels are as follows: Irq = Iraqi, Sy = Syrian, Pal = Palestinian, Arm = Armenian, Azer = Azerbaijani, N-Oss = North-Ossetian, Bul = Bulgarian, Rom = Romanian, It = Italian, Gal = Galician, Sw = Swiss, Au = Austrian, Pol = Polish, Russ = Russian, Cze = Czech, Dan = Danish, Swe = Swedish, Nor = Norwagian, Est = Estonian, Kar = Karelian, Bel = Belgian, Eng = English, Ger = German, Ir = Irish, Kurd = Kurdistanian, Fr = French, Ady = Adygei, Bel = Belarus, Bos = Bosnian, Cro = Croatian, Finn = Finnish, Geo = Georgian, Gr = Greek, Cre = Cretean, Kaz = Kazakh, Mok = Moksha, Ob = Oberwallis, Oss = Ossetian, Reto = Retoroman, Serb = Serbian, Sl-Russ = Slavonic-Russian, Slo = Slovakian, Turk = Turkish, Ukr = Ukrainan, Cum = ancient Cumanian, Hun = recent Hungarian, Sek = Sekler, Classicals = classical Conqueror, Comm = Commoners, Ancient = ancient Hungarians.

and Sekler populations. Statistical analysis clearly reveals this difference. The explanation could be that the commoners' cemeteries might contain the remains of pre-Hungarian populations.

This level of analysis may very probably underestimate the proportion of Hungarian invaders whose maternal ancestry, over the last few centuries, was in the steppes. Not only were they in contact there with Indo-European speakers such as the Alans, but recent analysis has shown that the mitochondrial characteristics of the Finno-Ugric populations of the Volga and Ural regions have significant west Eurasian elements (Bermisheva et al., 2002; Malyarchuk, 2004), as do even the Turkish-speaking populations of the Altai (Derenko et al., 2003). The Magyar invasion of Europe was only one in a most complex series of population movement across the Eurasian steppe, over many millennia, in all directions.

Statistical analysis shows the Asian genetic influence in the Hungarian conqueror population unambiguously. Genetic distances suggest a clear relationship with populations from Central Asia. On a distance matrix tree they can be placed between Asian and European populations closest to Turks, Ukrainians, and the Finno-Ugric Komis. By contrast, recent Hungarian-speaking populations seem to be specifically European populations, in accordance with the data of Lahermo et al. (2000).

The genetic effect of populations who lived in close contact with the Hungarians during their migration from the Ural region to the Carpathian Basin—Khazars, Petchenegs, Onogur-Bulgars, Savirs, and Iranian-speaking Alans—seems to have left imprints in the ancient Hungarian gene pool, as well as in Hungarian language and culture.

However, the linguistic and cultural inheritance of modern Hungary, which can be traced back for over

1000 years, does not correspond to much genetic continuity. There is little direct genetic relationship between the Hungarian conquerors and the recent Hungarian-speaking populations. On the basis of the results of samples of commoners' cemeteries and the recent Hungarian-speaking populations, it is probable that a relatively small number of Hungarian conquerors arrived in the Carpathian Basin, who mixed with other populations had been living here earlier (Slavs, Avars, Germans, Romans, Dacians, ...); this mixture may have been less in the case of the Seklers, who show the lowest genetic distance to populations of Finno-Ugric origin (Moksha, Mari, Komi).

The classical Hungarian conquerors and the modern populations differ at the levels both of haplogroups and haplotypes. This is not surprising, since during the centuries after the Hungarian conquest, further large population movements have taken place in this area, further diluting the original Magyar contribution to the gene pool; again, this may have been less in the Seklers, who have however acquired more affinities with southern European populations. A similar result was obtained when nuclear genetic markers were also studied. According to Cavalli-Sforza, modern Hungarians have 90% European and 10% Uralic genes. This also is consistent with the Hungarian invaders being only a small fraction of the total population of the Carphatian Basin after the conquest (Cavalli-Sforza et al., 1994).

This study shows that the linguistic isolation of Hungarian-speaking populations in the Carpathian Basin has not lead to significant genetic isolation. Gene flow from neighbors and migrations has affected the Hungarian gene pool: maternal lineages in the modern Hungarian gene pool bear the imprints of populations who have been living in the region for centuries. In the recent Hungarians, there is a dominating effect of Slav populations (Slovakian, Czech, Ukrainian, Croatian), with influence from the Balkans and West Eurasia, while in the Seklers the genetic effect of Eastern and Southern Europeans is more visible.

ELECTRONIC-DATABASE INFORMATION

Accession numbers for data presented here are as follows: GenBank, http://www.ncbi.nlm.nih.gov/Genbank/index.html (for Hungarian sequences [accession numbers AF487583, AF487586, AF487590, AF487494, AF487596, AF487598–AF487600, AF487602, AF487604, AF487612–AF487614, and DQ246265–DQ246352], for Sekler sequences [accession numbers AF487556–AF487559, AF487561–AF487570, AF487574–AF487576, AF487580, and DQ246353–DQ246411] and for ancient sequences [accession numbers DQ246412–DQ246437, EF646857]).

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