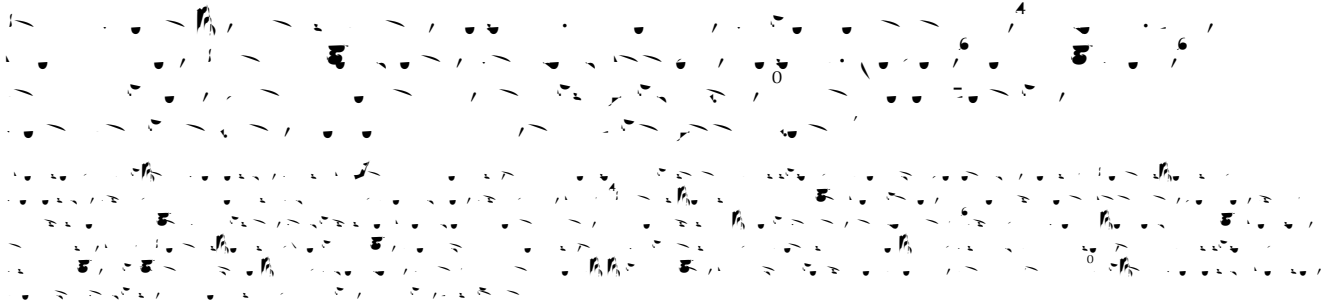


Origins and Divergence of the Roma (Gypsies)



The Roma (Gypsies) population is a highly diverse group with a complex history of migration and genetic mixing. The tree shows the genetic relationships and divergence of the Roma population, with the word *jatis* appearing in the text. The tree is highly branched and dense, indicating a complex history of migration and genetic mixing. The root of the tree is on the left, and the branches extend to the right. The tree is rendered in black lines on a white background.

Table 1**Description of the Romani Populations Included in the Study**

Population ^a	Place of Residence	Traditional Trade	Language/Dialect	History of Migrations	Religion	Sample Size
Turgovzi (Tu)	Bulgaria, Omurtag	Merchants	Romanes, Balkan dialect; Turkish	Early settlement in Bulgaria	Islam	36
Feredjelli (Fe)	Bulgaria, Omurtag	Unskilled laborers	Turkish	Early settlement in Bulgaria	Islam	21
Kalaidjii North (KN)	Bulgaria, Lom	Tinsmiths	Romanes, Balkan dialect;	Early settlement in Bulgaria	Protestant	20
Koshnichari South Central (KC)	Bulgaria, Plovdiv region	Basket makers	Romanes, Balkan dialect	Early settlement in Bulgaria	Eastern Orthodox	4
Koshnichari Southwest (KW)	Bulgaria, Gotze Delchev	Basket makers	Romanes, Balkan dialect	Early settlement in Bulgaria	Protestant	5
Kalaidjii South (KS)	Bulgaria, Gotze Delchev	Tinsmiths	Romanes, Old Vlax dialect ^b	Wallachia/Moldavia, to Bulgaria in 17th and 18th centuries	Eastern Orthodox	10
Lom (Lo)	Bulgaria, Lom	Livestock dealers	Romanes, Old Vlax dialect ^b	Wallachia/Moldavia, to Bulgaria in 17th and 18th centuries	Protestant	43
Monteni (Mo)	Bulgaria, Balkan Mountain villages	Bowl makers	Archaic Rumanian	Wallachia/Moldavia, to Bulgaria in late 19th century	Eastern Orthodox	42
Intreni (In)	Bulgaria, Letniza	Bowl makers	Archaic Rumanian	Wallachia/Moldavia, to Bulgaria in late 19th century	Eastern Orthodox	17
Lingurari North (LN)	Bulgaria, northern part	Bowl makers	Archaic Rumanian	Wallachia/Moldavia, to Bulgaria in late 19th century	Eastern Orthodox	18
Lingurari South (LS)	Bulgaria, southern part	Bowl makers	Archaic Rumanian	Wallachia/Moldavia, to Bulgaria in late 19th century	Eastern Orthodox	9
Kalderash (Ka)	Bulgaria, northern part	Coppersmiths	Romanes, New Vlax dialect ^b	Wallachia/Moldavia, to Bulgaria in late 19th century	Eastern Orthodox	23
Spanish Roma (SR)	Madrid	Merchants	Spanish	Early migration to north/Western Europe	Protestant	27
Lithuanian Roma (LR)	Vilnius, Lithuania	Merchants	Romanes	Early migration to north/Western Europe	Roman Catholic	20

^a Two-letter abbreviations of population names are used in tables throughout this article.

^b Vlax dialects are characterized by a strong linguistic influence from Romanian.

amplification was done with fluorescently labeled primers 5'-CTGTACTCCTGGGTAGCCTGT-3' and 5'-AAGAACGATTGAACACACTAACTC-3'. The products were separated by size on a 377 DNA Analyzer (Applied Biosystems).

The 70 samples that carried the ancestral M82 allele were genotyped for specific UEPs on the basis of the identities of their Y STR haplotypes with the common haplotype(s) of the specific haplogroup in the fully char-

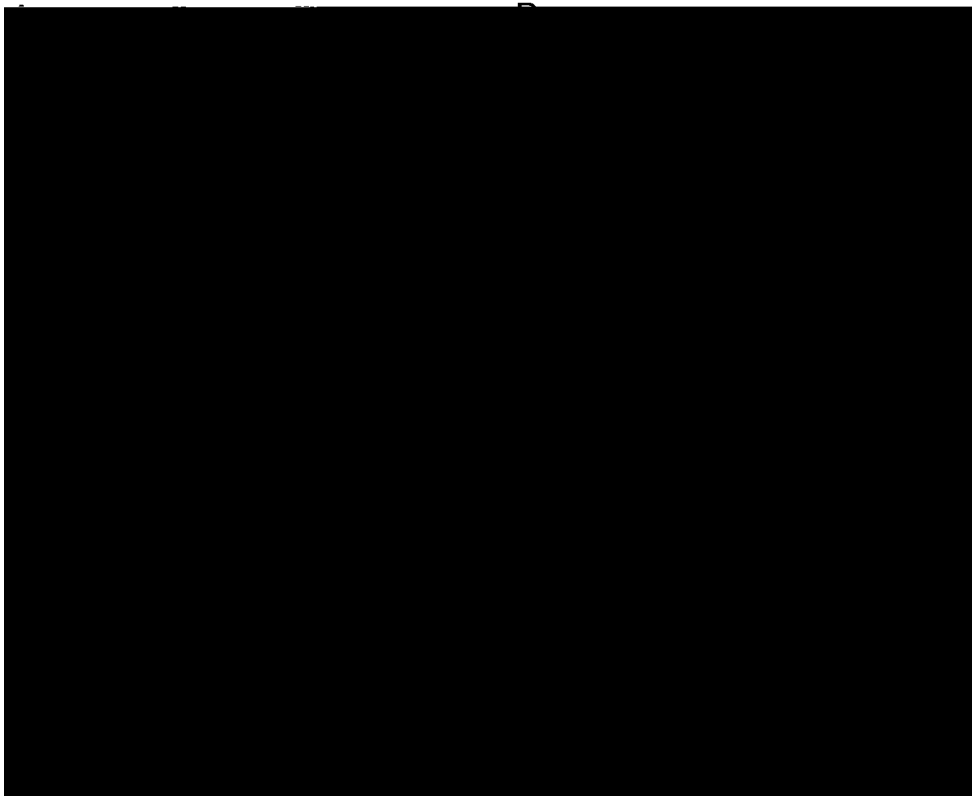


Figure 1 Median-joining networks of Y STR haplotypes within four haplogroups. A, Haplogroup VI-68 ($N = 113$; $h = 0.47$; $k = 0.56$). B, Haplogroup VI-56 ($N = 32$; $h = 0.87$; $k = 0.64$). C, Haplogroup VI-52 ($N = 57$; $h = 0.76$; $k = 3.15$). D, Haplogroup IX-104 ($N = 17$; $h = 0.94$; $k = 2.50$). The sizes of the nodes are proportional to the relative frequency of that haplotype within the haplogroup. Branch lengths within each network are proportional to the number of mutations separating haplotypes.

Romani VI-68A lineage. A median-joining network, constructed from all 34 haplogroup VI-68 haplotypes (12 Romani and 22 Asian non-Romani) displayed a complex topology, in which the Romani Y chromosomes represented a limited subset of closely related haplotypes within the overall diversity of haplogroup VI-68 (data not shown). The non-Romani haplotypes were widely dispersed across the network, with many inferred nodes.

A single male lineage, VI-68A, defined by the 2-bp deletion at M82 and by Y STR haplotype 15-12-16-14-22-10-11-12, was shared by 80 individuals from all Romani populations. This common lineage accounted for 71% of haplogroup VI-68 chromosomes and for 32% of all Romani Y chromosomes examined. It was separated by one mutational step (at marker DYS19) from the second most common VI-68 lineage (VI-68B). VI-68B was not as widespread as VI-68A and occurred mostly in the Lom and the Lithuanian Roma (table 2). The remaining haplogroup VI-68 lineages were rare and confined to individual Romani populations. When we considered the most frequent haplotype within haplogroup VI-68 to be the founding lineage, a coalescent

date of 992 years ago (95%CI 425–3,472 years) was estimated.

Additional Y-Chromosome Lineages

Haplogroup VI-56 accounted for 12.7% (32 chromosomes) of all Romani males (table 2). It was identified in 6 of the 14 Romani populations and occurred at high frequency in the Lithuanian (25%) and Spanish (33%) Roma. This haplogroup has been found in Pakistan, central Asia, and the Middle East (Underhill et al. 2000). Within Europe, haplogroup VI-56 has been identified in a single male individual from Sardinia (Underhill et al. 2000). In the Roma, the 32 haplogroup VI-56 chromosomes fell into nine Y STR haplotypes, VI-56A–VI-

Table 3

Y STR Haplotypes Observed in Non-Romani Y-Chromosome Haplogroups VI-68 and VI-56

Haplogroup	Frequency	DYS19	DYS388	DYS389AB	DYS389CD	DYS390	DYS391	DYS392	DYS393	
VI-68 (N = 22)	1	14	12	14	11	23	10	11	11	
	1	14	12	15	13	23	10	11	11	
	1	14	12	16	13	22	10	11	11	
	1	15	12	14	13	22	10	11	11	
	1	15	12	14	13	21	10	11	11	
	1	15	12	15	13	23	10	11	12	
	4	15	12	15	13	23	10	11	11	
	1	15	12	15	13	21	10	11	12	
	1	15	12	16	14	22	11	11	11	
	1	15	12	16	14	22	10	11	11	
	1	15	12	17	12	24	10	11	11	
	1	15	12	17	13	21	10	11	12	
	1	15	12	17	14	23	10	10	11	
	1	15	13	15	13	22	10	11	11	
	1	15	13	16	13	21	10	11	11	
	1	15	13	17	13	22	10	11	11	
	1	16	12	14	14	22	10	11	11	
	1	16	13	16	14	22	10	11	11	
	1	17	12	14	13	22	10	11	12	
	VI-56 (N = 18)	3	14	14	15	13	22	10	11	11
		1	14	14	15	14	22	10	11	11
		2	14	15	15	13	22	9	11	11
5		14	15	15	13	22	10	11	11	
1		14	15	15	13	22	9	11	11	
1		14	15	16	13	22	10	11	13	
1		14	15	17	14	23	10	11	11	
1		14	15	17	13	22	10	11	11	
1		15	15	17	14	21	10	11	11	
1		15	15	17	13	21	.	9	(5)	

Table 4

mtDNA Lineages Identified in Roma

HAPLOGROUP AND HVS1 VARIANT(S) ^a	NO. OF mtDNA LINEAGES IN POPULATION														Total
	LN	LS	In	Mo	Lo	KS	Ka	KN	KW	KC	Fe	Tu	LR	SR	
M: ^b															
129, 223, 291, 298	1	2	2	3	4	2		3		1	3		4	4	29
129, 223, 291			1		2		3	2			2	2			12
129, 223, 230, 233, 304			1												1
129, 223, 230, 233, 304, 344	1		3	3	2		1								10
129, 223, 230, 233, 304, 344, 355				3			1								4
129, 148, 223, 291, 298						1		1				2			4
129, 223, 291, 298, 311					1			1	1						3
129, 223, 256, 291		1				1					1				3
223, 291, 298					2										2
129, 223, 234, 291, 298	1														1
129, 223, 291, 298, 362														1	1
129, 223, 266, 291							1								1
223, 290, 318T							1								1
223, 304	1														1
H: ^c															
261, 304	3		2	8	4		1					3	2		23
186, 304	6	5	3	8											22
218, 278					3		3			1				1	8
354					6			2							8
Cambridge reference sequence				2				3			1				6
192A, 320	2			3											5
189							1	2							3
168					3										3
223					1		2								3
93	1												1		2
67								2							2
51, 145, 304												1			1
304							1								1
278, 293, 311												1			1
187, 189				1											1
189, 311									1						1
93, 291			1	1											2
174								1							1
261														1	1
242												1			1
260													1		1
362														1	1
93, 223					1										1
U3: ^d															
343				1		3			1				10	11	26
343, 260														2	2
J: ^e															
69, 126			2	3	1		4		1						11
69, 126, 145, 222, 261, 311								2			2	1			5
69, 126, 145, 222, 235, 261, 271														1	1
69, 126, 145, 222, 235, 261								1							1
69, 126, 261					1										1
69, 93, 126,							1								1
39C, 69, 126												1			1
69, 126, 193												1			1
69, 126, 278, 366														1	1
69, 126, 300														1	1
69, 126, 311												1			1

(contin ed)

Table 4 (continued)

HAPLOGROUP AND HVS1 VARIANT(S) ^a	NO. OF mtDNA LINEAGES IN POPULATION														Total
	LN	LS	In	Mo	Lo	KS	Ka	KN	KW	KC	Fe	Tu	LR	SR	
X: ^f															
126, 189A, 223, 278	1			3	2	2	1				1	2			12
93, 189, 223, 241, 278					2						1	2			5
92, 126, 189A, 223, 278											2				2
93, 96T, 189, 223, 241, 278				1											1
92, 189A, 223, 278											1				1
I: ^g															
129, 172, 223, 311					3		1					1			5
N:1b ^h															
86, 129, 145, 176G, 223		1			3					1					5
T: ⁱ															
126, 294, 296	1			1	1										3
126, 294, 324				1			1								2
126, 294, 352												1			1
U5: ^j															
28G, 192, 224, 261, 270												1			1
192, 224, 261, 270												1			1
189, 270, 311, 336							1								1
189, 270												1			1
167, 192, 270, 311, 356														1	1
256, 270												1			1
U(K): ^k															
224, 261, 311					1										1
222, 224, 261, 311											1				1
224, 311									1						1
224, 311, 344			1												1
U1: ^l															
183C, 189, 249											1				1
W: ^m															
172, 223, 231, 292											2	1			3
Total	18	9	16	42	43	10	23	20	5	3	18	25	18	25	275

^a Numbers are those given by Anderson et al. (1981), plus 16,000. All variants are transitions from the reference sequence, unless indicated with a letter.

^b Accounts for 26.5% of all mtDNA lineages in this study.

^c Accounts for 35.6% of all mtDNA lineages in this study.

^d Accounts for 10.2% of all mtDNA lineages in this study.

^e Accounts for 9.1% of all mtDNA lineages in this study.

^f Accounts for 7.6% of all mtDNA lineages in this study.

^g Accounts for 1.8% of all mtDNA lineages in this study.

^h Accounts for 1.8% of all mtDNA lineages in this study.

ⁱ Accounts for 2.2% of all mtDNA lineages in this study.

^j Accounts for 2.2% of all mtDNA lineages in this study.

^k Accounts for 1.4% of all mtDNA lineages in this study.

^l Accounts for 0.4% of all mtDNA lineages in this study.

^m Accounts for 1.1% of all mtDNA lineages in this study.

common lineages—two of haplogroup H and one each of haplogroups M and U3—accounted for 36% of all Romani individuals.

Diversity of Maternal Lineages

ages differed by a single mutation step, at position 16298 (table 4). These two lineages were present in 13 of the 14 Romani populations and accounted for 14.9% of all samples.

A transition at position 16129, which defines subhaplogroup M5 (Bamshad et al. 2001), was present in 11 of the 14 HVS1 sequences of Romani haplogroup M. One of the three lineages that do not bear the 16129 variant—namely, the lineage defined by variants at positions 16223, 16291, and 16298—are closely related to haplogroup M5 lineages and may represent a back mutation at position 16129, a known mutational hotspot (Stoneking 2000). Subhaplogroup M5 was thus found to account for 97.3% of haplogroup M. A modified median-joining network (fig. 2) was used to compare haplogroup M lineages in the Roma to those observed in India (Kivisild et al. 1999; Quintana-Murci et al.

1999). All but two Romani lineages clustered together as a small subset of the overall diversity present within the Indian haplogroup M. The coalescence of haplogroup M lineages in the Roma was estimated to be 4,625 years ago (95%CI 2,000–7,250 years). This date was obtained by considering that an average of 0.6896 mutations have accumulated from the putative ancestral haplotype—that is, the haplotype with variants at positions 16129, 16223, 16291, and 16298.

Haplogroup H was the most frequent mtDNA haplogroup among the Roma (table 4). It was detected in 13 of 14 Romani populations and represented 35.6% (98 individuals) of the total sample. Haplogroup H is most common in Europe (Simoni et al. 2000) and the Near East (Richards et al. 2000) but is also found in India (Kivisild et al. 1999). HVS1 analysis of haplogroup H identified 23 sequences, 2 of which (defined by var-

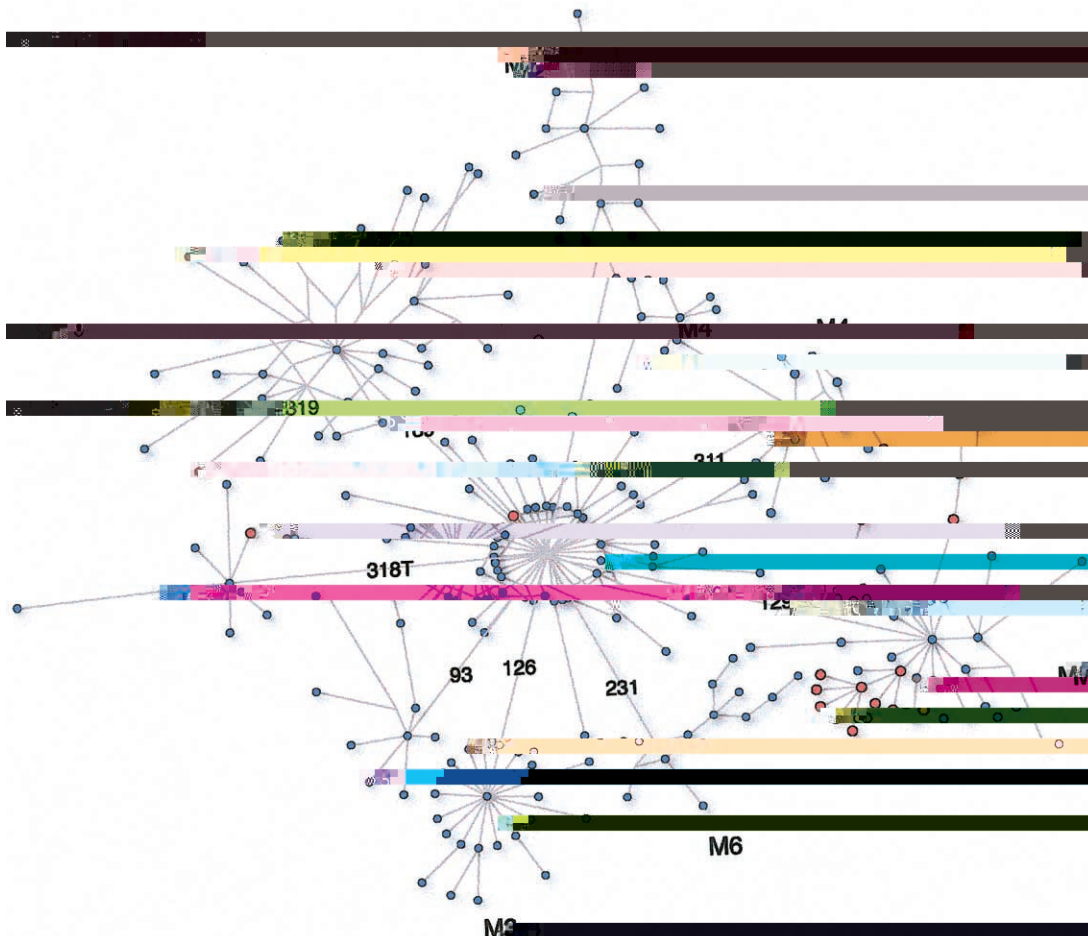


Figure 2 Modified median-joining network of mtDNA haplogroup M, constructed from data presented in studies by Quintana-Murci et al. (1999) and Kivisild et al. (1999) and in the present study. All numbers are those given by Anderson et al. (1981), plus 16,000. Sequences identified in the Roma are shown in red; sequences reported for Indian samples are shown in blue. Subhaplogroup designations are as proposed by Bamshad et al. (2001), plus additional subclades defined by frequent variants at positions 16189, 16318, and 16093. Branches are proportional to the number of mutations separating sequence types, except those that connect subhaplogroups.

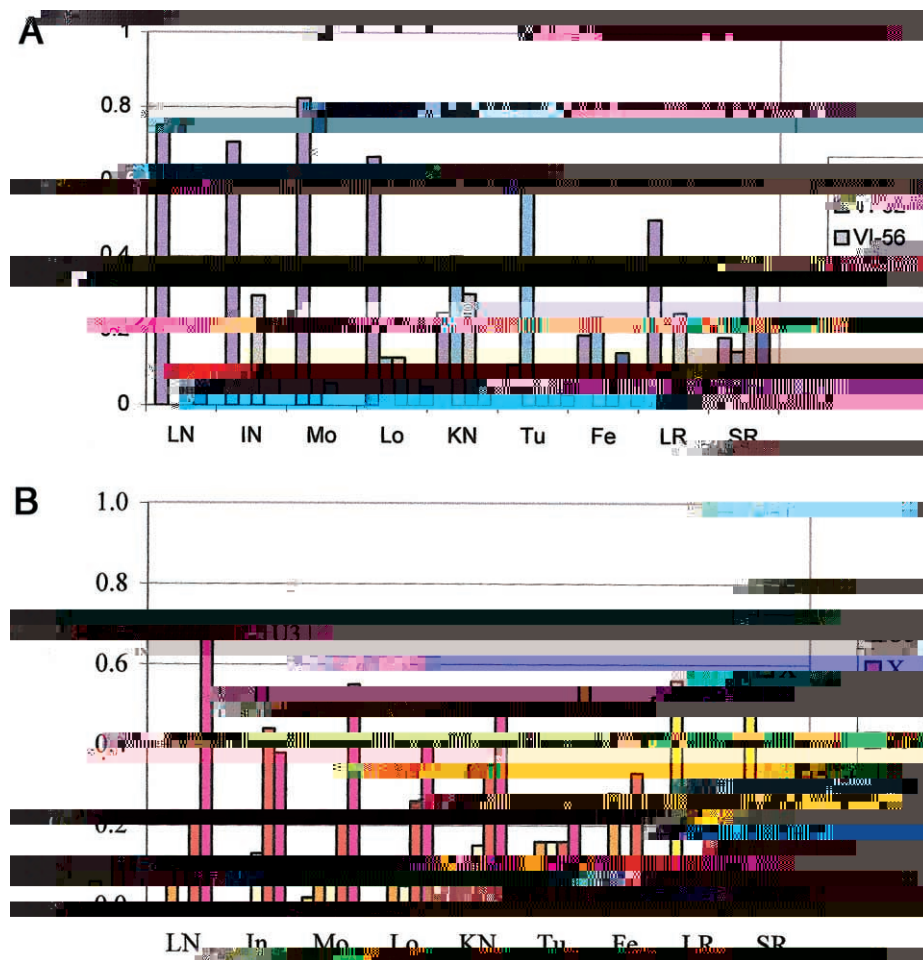


Figure 3 Frequency distributions of the common (overall frequency 15%) male (A) and female (B) haplogroups in Romani populations. Populations in which sample size was ≤ 15 for either Y-chromosome or mtDNA haplogroup data were excluded from the analysis.

variants at positions 16261 and 16304 and at positions 16218 and 16278, respectively) each accounted for ~22% of haplogroup H and together comprised 20%

PC analysis was based on Y-chromosome and mtDNA haplogroup frequencies in Romani populations. The resultant PC plots provided better resolution of the genetic structure than was provided by a neighbor-joining tree (Nei 1987) using Y STR haplotypes (not shown). The PC plots are presented in figure 4.

Two clusters, consistently present in both Y-chromosome and mtDNA analysis, were formed by the Monteni, Intreni, Lingurari, Kalderash, and Lom on one hand and by the Feredjelli and Turgovtzi on the other. The Spanish and Lithuanian Roma clustered together in the mtDNA analysis, and the Kalaidjii North and South clustered together in the Y-chromosome comparisons.

To examine the relevance of different cultural, historical, and geographic classification criteria to the genetic structure of the Roma, we used AMOVA based on

Y STR data and mtDNA HVS1 sequences (table 5). The country-of-residence, in which all Roma from Bulgaria were compared versus those from Lithuania versus those from Spain, showed no significant intergroup differences. The same result was obtained with comparisons based on place of residence, in which three pairs of Romani populations living in close proximity in three small towns in Bulgaria were examined. In the analysis based on ethnonym reflecting traditional trade, the comparison of bowl makers, tinsmiths, traders, and livestock dealers showed no significant intergroup differences.

Intergroup differences accounted for a significant proportion of the variance only when language and the history of migrations were used for classification of Romani populations. In the language-based classification, the comparisons included speakers of (a) Balkan dialects of



Figure 4 Two-dimensional PC plots based on Y STR haplotype frequencies (A) and mtDNA haplogroup frequencies (B). The population affinities shown are based on 51% and 42.6%, respectively, of the variation that, on the basis of Y-chromosome and mtDNA data, is present within the entire sample.

Table 5

AMOVA Using Y STR and mtDNA Data for Romani Populations

GROUPING CRITERION	VARIATION (P^a)					
	Among Groups		Among Populations within Groups		Within Populations	
	Y STR	mtDNA	Y STR	mtDNA	Y STR	mtDNA
Total sample			13.0% (!.00001)	6.2% (!.00001)	87.0% (!.00001)	93.8% (!.00001)
Country of residence ^b	5.1% (.79277)	4.0% (.01760)	15.2% (!.00001)	4.8% (!.00001)	89.9% (!.00001)	91.2% (!.00001)
Town of residence ^c	6.7% (.21408)	.5% (.32551)	7.5% (.00391)	.8% (.26686)	85.8% (!.00001)	98.7% (.16618)
Trade/group (ethnonym) ^d	7.9% (.08113)	4.7% (.01622)	8.5% (!.00001)	2.1% (.05083)	83.6% (!.00001)	93.2% (!.00001)
Religion ^e	6.2% (.03617)	4.3% (.00196)	8.0% (!.00001)	2.9% (!.00001)	85.8% (!.00001)	92.8% (!.00001)
Language ^f	6.5% (.07234)	6.3% (!.00001)	7.2% (!.00001)	0.7% (!.00001)	86.3% (!.00001)	92.9% (!.00001)
Historical migration ^g	10.5% (!.00001)	5.0% (!.00001)	5.3% (!.00001)	3.0% (!.00001)A	84.2% (!.00001)	92.0% (!.00001)

^a With Bonferroni correction, $P \neq .0083$.

^b For Group 1 populations Tu, Fe, KN, KC, KW, Mo, In, Lo, Ka, LN, LS, and KS; Group 2 population SR; and Group 3 population LR.

^c For Group 1 populations Lo and KN; Group 2 populations Tu and Fe; and Group 3 populations KS and KW.

^d For Group 1 populations Mo, In, LN, and LS; Group 2 populations Tu and SR; Group 3 populations KN and KS; and Group 4 population Lo.

^e For Group 1 populations Tu, Fe, KS, and KC; Group 2 populations Mo, In, Ka, LN, and LS; Group 3 populations Lo, SR, KN, and KW; and Group 4 population LR.

^f For Group 1 populations Tu, KN, KC, and KW; Group 2 population Fe; Group 3 populations KS, Lo, and Ka; Group 4 populations Mo, In, LN, and LS; Group 5 population LR; and Group 6 population SR.

^g

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