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ORIGINAL INVESTIGATION

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Excavating Y-chromosome haplotype strata in Anatolia

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Abstract Analysis of 89 biallelic polymorphisms in 523 Turkish Y chromosomes revealed 52 distinct haplotypes with considerable haplogroup substructure, as exemplified by their respective levels of accumulated diversity at ten short tandem repeat (STR) loci. The major components (haplogroups E3b, G, J, I, L, N, K2, and R1; 94.1%) are shared with European and neighboring Near Eastern populations and contrast with only a minor share of haplogroups related to Central Asian (C, Q and O; 3.4%), Indian (H, R2; 1.5%) and African (A, E3*, E3a; 1%) affinity. The expansion times for 20 haplogroup assemblages was estimated from associated STR diversity. This comprehensive characterization of Y-chromosome heritage addresses many multifaceted aspects of Anatolian prehistory, including: (1) the most frequent haplogroup, J, splits into two sub-clades, one of which (J2) shows decreasing variances with increasing latitude, compatible with a northward expansion; (2) haplogroups G1 and L show affinities with south Caucasus populations in their geographic distribution as well as STR motifs; (3) frequency of haplogroup I, which originated in Europe, declines with increasing longitude, indicating gene flow arriving from Europe; (4) conversely, haplogroup G2 radiates towards Europe; (5) haplogroup E3b3 displays a latitudinal correlation with decreasing frequency northward; (6) haplogroup R1b3 emanates from Turkey towards Southeast Europe and Caucasia and; (7) high resolution SNP analysis provides evidence of a detectable yet weak signal (<9%) of recent paternal gene flow from Central Asia. The variety of Turkish haplotypes is witness to Turkey being both an important source and recipient of gene flow.

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Introduction

The Anatolian Peninsula (Asia Minor) provides an important geographic link between the Middle East, Asia and Europe. Accordingly, this region manifests an elaborate genetic constitution reflecting the consequences of numerous gene flow, admixture and local differentiation processes spanning from the late Pleistocene to the present day (Cavalli-Sforza et al. 1994). Both environmental and cultural influences associated with the spread of the Upper Paleolithic industries (Kuhn 2002), the Last Glacial Maximum (LGM) and Holocene warming since the Younger Dryas cold reversal, as well as the introduction of agriculture and succeeding Bronze Age, Greek, and Roman presence, may have left detectable traces in the gene pool. In addition, resettlements from Central Asia (Richards et al. 2000), as well as movements during the Ottoman Empire, including recent exchanges of numerous Greek and Turk residents based upon religious affiliation during the 1920s, would add further potential complexity to the phylogeography patterns in Anatolia. The question that we ask in this paper: is it possible to attribute any elements of the amalgamated Anatolian genetic composition to any relatively ancient and recent chronologies/populations? While most human genetic diversity is affected

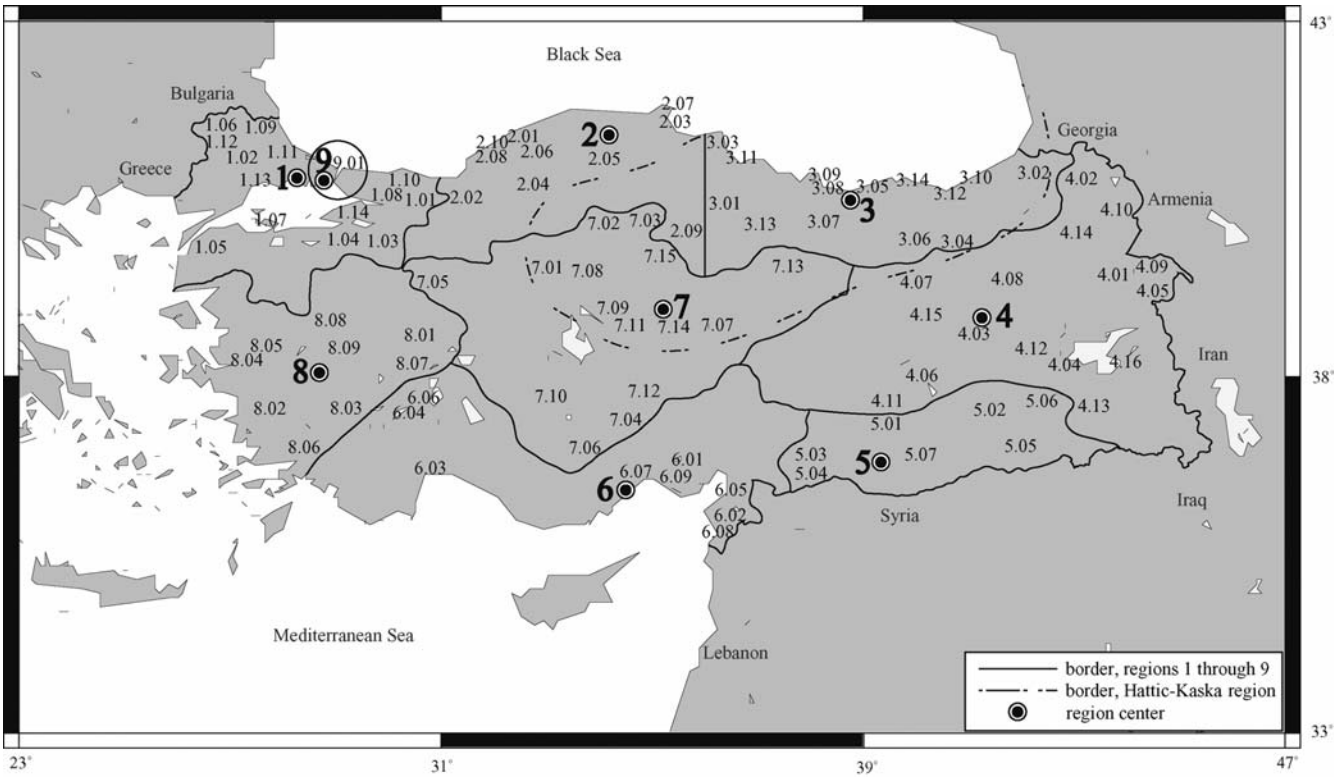

Fig. 1 Map of sample locations. City name codes by region are: *1.01* Akyazı, *1.02* Babaeski, *1.03* Bilecik, *1.04* Bursa, *1.05* Çanakkale, *1.06* Edirne, *1.07* Erdek, *1.08* Izmit, *1.09* Kırklareli, *1.10* Sakarya, *1.11* Saray, *1.12* Sumnu, *1.13* Tekirdağ, *1.14* Yalova; *2.01* Bartın, *2.02* Düzce, *2.03* Gerze, *2.04* Karabük, *2.05* Kastamonu, *2.06* Safranbolu, *2.07* Sinop, *2.08* Uzuntaş, *2.09* Zile, *2.10* Zonguldak; *3.01* Amasya, *3.02* Artvin, *3.03* Bafra, *3.04* Bayburt, *3.05* Giresun, *3.06* Gümüşhane, *3.07* Mesudiye, *3.08* Ordu, *3.09* Perşembe, *3.10* Rize, *3.11* Samsun, *3.12* Sürmene, *3.13* Tokat, *3.14* Trabzon; *4.01* Ağrı, *4.02* Ardahan, *4.03* Bingöl, *4.04* Bitlis, *4.05* Doğubeyazıt, *4.06* Elazığ, *4.07* Erzincan, *4.08* Erzurum, *4.09* Iğdır, *4.10* Kars, *4.11* Malatya, *4.12* Muş, *4.13* Pervari, *4.14* Sarıkamış, *4.15* Tunceli, *4.16* Van; *5.01* Adıyaman, *5.02* Diyarbakır, *5.03* Gaziantep, *5.04* Kilis, *5.05* Mardin, *5.06* Siirt *5.07* Urfa; *6.01* Adana, *6.02* Antakya, *6.03* Antalya, *6.04* Burdur, *6.05* Iskenderun, *6.06* Isparta, *6.07* Mersin, *6.08* Samandağ, *6.09* Tarsus; *7.01* Ankara, *7.02* Çankırı, *7.03* Çorum, *7.04* Ereğli, *7.05* Eskişehir, *7.06* Karaman, *7.07* Kayseri, *7.08* Kırıkkale, *7.09* Kırşehir, *7.10* Konya, *7.11* Nevşehir, *7.12* Niğde, *7.13* Sivas, *7.14* Ürgüp, *7.15* Yozgat; *8.01* Afyon, *8.02* Aydın, *8.03* Denizli, *8.04* Izmir, *8.05* Manisa, *8.06* Muğla, *8.07* Sandıklı, *8.08* Simav, *8.09* Uşak; *9.01* Istanbul

by recombination, the low effective population size of clonal Y-chromosome segments (Shen et al. 2000) enhances them with greater sensitivity to detect incidents in the demographic histories of the populations that may otherwise leave little imprint on the autosomal elements of the gene pool. The resulting often non-random correlations between binary marker defined haplogroups with geography (Underhill et al. 2001) and corresponding short tandem repeat (STR) variance (de Knijff 2000) provide a genetic metric with which to sieve through complex deposits of human history on both micro-geographic and temporal scales. To begin to better understand how the succession and magnitude of events spanning millennia have contributed to the current genetic composition of Turkey, we have assessed patterns of Y-chromosome diversity distributed across Turkey plus Istanbul. The data illuminate numerous long-standing themes, including the Holocene expansions, contributions of agriculturalists to the European gene pool and genetic assessment of Caucasian and Central Asian gene flows.

Materials and methods

Samples

A total of 523 samples distributed amongst 90 cities, plus Istanbul, were studied. With the exception of 79 samples from cosmopolitan Istanbul, all remaining 444 samples were assigned to regions commonly distinguished by climate and rainfall (Fig. 1), as based upon stated paternal residential heritage obtained during the informed consent process. The coordinates for each of the nine regions were determined by averaging the latitude and longitude of each regional city, weighted by the number of samples in each city. The respective latitude (N) and longitude (E) by region are: (1) 40.9, 28.1; (2) 41.5, 33.7; (3) 40.8, 38.6; (4) 39.2, 40.7; (5) 37.5, 39.1; (6) 36.7, 34.5; (7) 39.3, 34.7; (8) 38.3, 28.6; (9) 41.0, 29.1. In order to test a hypothesis of Bronze Age gene flow from the Caucasus, a different geographic definition was employed. Specifically we divided the Anatolian peninsula into two sections bounded by a curve containing cities within 50 km of the Kızılırmak River and east Pontic region 3 (Fig. 1). This region comprises the historically attested Bronze Age Hattic and Kaska cultural horizons. A χ^2 test was used to compare the frequencies of haplotypes across the two archeological regions. On the basis of the known high frequency of G-M201 in populations from the Caucasus (Semino et al. 2000a; Nasidze et al. 2003), an a priori hypothesis was tested comparing G-M201 frequencies of the Hattic-Kaska delineated zone to that outside the region. A total of 359 samples were from blood banks, 61 from paternity clinics and 103 from staff and students enrolled at Istanbul University. DNA was isolated from blood drawn leucocytes using Qiagen reagents and protocols.

Table 1 Description of Y-chromosome binary polymorphisms

Marker no.	Nucleotide change	Position (bp)	Forward 5′→3′	Reverse 5′→3′	Total size (bp)
M231	G to A	110	cctattatcctggaaaatgtgg	attccgattcctagtcacttgg	331
M241	G to A	54	aactcttgataaaccgtgctg	tccaatctcaattcatgcctc	366
M242	C to T	180	aactcttgataaaccgtgctg	tccaatctcaattcatgcctc	366
M253	C to T	283	gcaacaatgagggttttttg	cagctccacctctatgcagttt	400
M267	T to G	148	ttatcctgagccgttgtccctg	tgtagagacacggttgtaccct	287
M285	G to C	70	ttatcctgagccgttgtccctg	tgtagagacacggttgtaccct	287
M286	G to A	129	ttatcctgagccgttgtccctg	tgtagagacacggttgtaccct	287
M287	A to T	100	ttatcctgagccgttgtccctg	tgtagagacacggttgtaccct	287
M304	A to C	421	caaagtgctgggattacagg	cttctagcttcatctgcattgt	527
M335	T to A	162	aagaaatgttgaactgaaagttgat	aggtgtatctggcatccgtta	417
M339	T to G	285	aggcaggacaactgagagca	tgcttgatcctgggaagt	517
M340	G to C	218	ccagtcagcagtacaaaagttg	gcatttctttgattatagaagcaa	386
M342	C to T	52	agagagttttctaacagggcg	tgggaatcacttttgcaact	173
M343	C to A	402	tttaacctcctccagctctgca	acccccacatatctccagg	424
M349	G to T	209	tgggattaaaggtgctcatg	caaaattggtaagccattagct	493
M359	T to C	122	cgtctatggccttgaaga	tccgaaaatgcagacttt	447
M365	A to G	246	ccttcatttaggctgtagctgc	tgtatctttagttgagatgg	274
M367	A to G	196	ccttcatttaggctgtagctgc	tgtatctttagttgagatgg	274
M368	A to C	200	ccttcatttaggctgtagctgc	tgtatctttagttgagatgg	274
M369	G to C	45	ccttcatttaggctgtagctgc	tgtatctttagttgagatgg	274
M370	C to G	166	ccttcatttaggctgtagctgc	tgtatctttagttgagatgg	274

Polymorphisms and haplotyping

Most polymorphisms have been previously reported (Underhill et al. 2001; Y Chromosome Consortium 2002). Details for new informative markers are summarized in Table 1. Genotyping was done using DHPLC methodology (Oefner et al. 1998), following a phylogenetic hierarchical approach. Lineages are referred to in the text by haplogroup and terminal mutation according to standardized nomenclature (Jobling et al. 2003). All 523 samples were also analyzed at ten STR loci: DYS19, DYS388, DYS390, DYS391, DYS392, DYS393, DYS389I, DYS389II (Kayser et al. 1997), DYS439 (Ayub at al. 2000) and DYSA7.2 (also called DYS461) (White et al. 1999) using 5′-labeled fluorescent primers, an ABI 3100 capillary sequencer, internal size standards and GeneScan fragment analysis software. Conversion of absolute fragment size to number of allele repeats was achieved using results obtained from sequencing both strands of control samples independently amplified with unlabeled primers. Sequencing of DYS389 is complicated since the standard genotyping primers amplify two fragments (Rolf et al. 1998). Calibration of DYS389 in control DNA was achieved by using ABCDE 5′-ccatcgacctatctgtctctattata-3′ and conventional reverse primers (Kayser et al. 1997) to amplify a single approximately 518-bp fragment encompassing five tetranucleotide motifs. Subsequent sequencing using the same amplification primers allowed precise determination of the allele repeat counts for the four traditionally reported variable tetranucleotide regions (ABCD). The DYS389II (AB fragment) repeat allele number was determined by subtracting the DYS389I (CD fragment) repeat number (Cooper et al. 1996).

Haplogroup diversity

STR variance, averaged over ten loci on binary haplotype backgrounds with sample sizes ≥7, was used to assess the relative level of diversity and phylogenetic substructure with geography. The F tests, based upon the ratio of χ^2 distributions of average variances, were used to evaluate comparisons of average variances amongst geographic regions. STR data were also used to estimate haplogroup specific expansion times by two methods. Both approaches assume a stepwise mutation model, an average evolutionary STR mutation rate of 0.0007 per STR locus per generation (Zhivotovsky et al. 2003), whose value is based upon a generation time of 25 years. One method assumes a star-like genealogy characteristic of continuous population growth in which the variance is equal to the mutation rate per generation time the number of generations since expansion (Di Rienzo et al. 1994; Kittles et al. 1998). The other method employs a Bayesian algorithm. To estimate the time of Anatolian population expansions, we used the Markov chain Monte Carlo (MCMC) approach (Wilson et al. 1998) incorporated into the program BATWING to estimate posterior distributions for parameters of a given model of population history.

We considered a model of exponential growth from initial constant population size beginning at time Beta, with an effective population size prior distribution specified as a gamma (1, 0.0001) as used by Weale et al. (2001). The prior distribution for the STR mutation rate was specified as a gamma distribution with a mean of 7×10^{-4} per locus per generation and the prior distribution of the growth rate were assigned a gamma (1, 0.001). The prior distribution for Beta was assigned a broad uniform prior (0, 15). Priors were specifically chosen to be as uninformative as possible so as to minimally impact the results. We calculated the mean, median, and 2.5 and 97.5% quantiles for the posterior distributions for Beta, the estimated time of population expansion. Beta is expressed as a fraction of the initial population size multiplied here by generation time to yield values standard units of time. Calculations were based on 50,000 runs of MCMC estimator after a 20,000 run "burn in time."

Results

A total of 69 out of 89 binary polymorphisms genotyped were informative and defined 52 distinct haplotypes. Their phylogenetic relationships and frequency distribution by geographic region are shown in Fig. 2. While none of the major haplogroups (E, G, J, R) showed significant micro-geographic structure, additional binary and STR haplotype resolution analysis revealed some distinct phy-

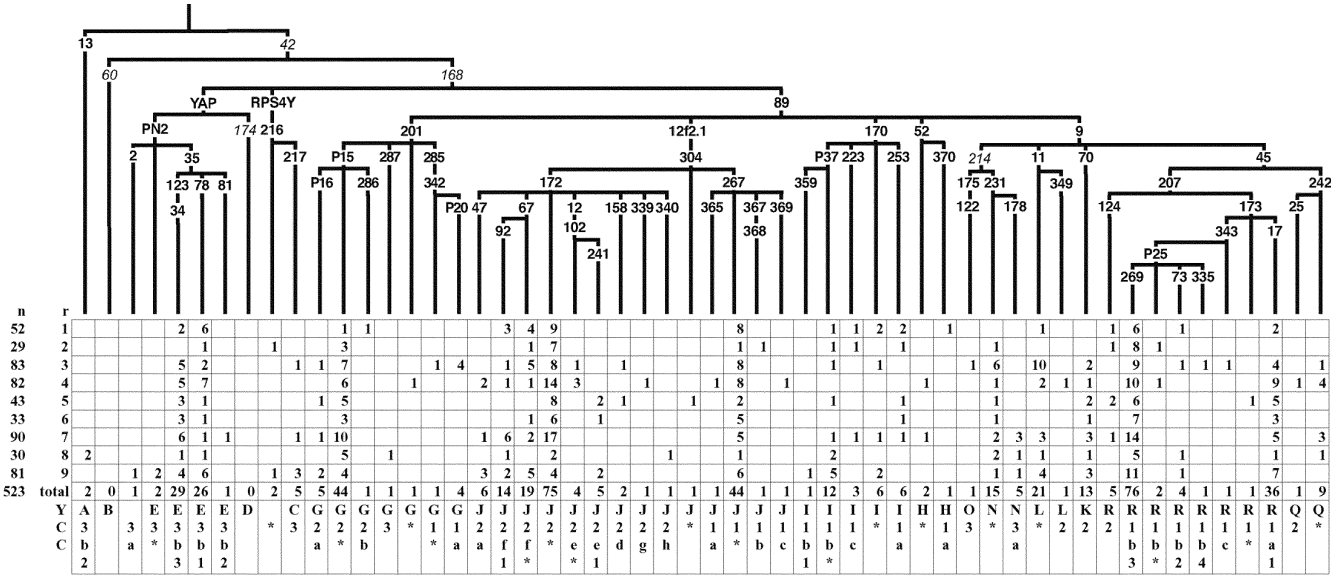

Fig. 2 Phylogenetic relationships, nomenclature and haplogroup frequencies. The 65 informative markers that were haplotyped are indicated in *dark font* and the remaining five markers shown in *italics* included to provide phylogenetic context. The following 19 polymorphisms were also genotyped but not observed: M3, M18, M26, M27, M33, M37, M38, M60, M62, M68, M75, M132, M137, M163, M166, M174, M181, M210, M222

logeographic patterns. All STR data arranged by corresponding binary composition are given in Appendix table A.

Y chromosome haplogroups and associated diversity

Haplogroup J is defined by the overarching DYS11/12f2 human endogenous retroviral polymorphism (Sun et al. 2000; Rosser et al. 2000). This polymorphism is widely distributed in Eurasia, Middle East and in North Africa (Hammer et al. 2001; Quintana-Murci et al. 2001). Although this polymorphism is recurrent (Blanco et al. 2000), occurring independently on certain D and F haplogroup lineages (Y Chromosome Consortium 2002), its association with the additional M304 transversion helps now to define the J clade with less ambiguity. The J clade was preeminent in all nine regions with an average frequency of 33%. Only one sample, with an atypical DYS388 12 repeat allele (see Appendix table A), resolved to J-M304*. All other J lineages could be assigned to two sub-clades, J1 and J2 defined by transversion mutations M267 and M172, respectively. Four new markers, M365, M367, M368 and M369 were detected on haplogroup J1-M267 samples, each associated with single representative. In contrast, haplogroup J2-M172 fractionates into nine discrete lineages, three of which – defined by M12, M47 and M67 – display informative frequency, making them useful for detecting phylogeographic patterns. Grouping all sub-lineages, the J2 frequency (24%) is evenly distributed over Turkey (χ^2=7.17, *df*=8, *P*=0.52), yet the relatively high J2 related STR variance (Table 2) shows a significant decline with increasing latitude (*r*=–0.87, *P*<0.002, Spearman).

The J2f-M67 lineages which occur at 6.3% frequency overall, show a significantly negative correlation with distance from region 1 in the northwest (Table 3). Moreover, regions 1, 7, 8, and 9 that clustered together in STR-based two-dimensional principal components analysis (not shown) displayed on average significantly higher (*P*<0.011) frequency of J2f-M67 than other regions.

Haplogroup J1-M267 occurs at 9% frequency and is also uniformly distributed across Turkey (χ^2=9.02, *df*=8, *P*=0.34), with the exception of eight samples localized to the northern geographic periphery that all have an unusual "short" 13 repeat DYS388 allele, that was confirmed by sequencing. No DYS388 intermediate size 14 tandem repeat alleles were detected in any of our J1 samples. We propose that this subset of J1 lineages have a unique heritage since, besides the suggestive micro-geography, the occurrence of a short DYS388 allele on a J background is symptomatic of a deviation of the stepwise mutational process, as already proposed for this locus in a different allelic context (Nebel et al. 2001a).

The G-M201 haplogroup occurs at (57/523) 10.9% frequency and 0.40 mean STR variance consistent with its early presence in Anatolia. One major clade, G2-P15 and two less frequent sub-clades, G1-M285 and G3-M287, account for all the variation observed except for one individual from Kars region 4 who was left unresolved to the G-M201* level. The totality of G lineages do not show micro-geographic structure on the basis of the criteria used to describe the nine geographic regions (χ^2=9.21, *df*=8, *P*=0.33), but they do significantly correlate (χ^2=4.11, *P*<0.043) when evaluated on the basis of the archeological boundaries of the Bronze Age Hattic and Kaska cultures (Fig. 1). In addition, variances of G2-P15 lineages are correlated with longitude (*r*=–0.72, *P*<0.03, *n*=9) showing higher variances towards western Anatolia. The distinctive G1-M285 lineages are restricted to region 3.

Table 2 Y-chromosome haplogroup variance and expansion times based on ten STR loci

Haplogroup	*n*	Variance	T (kyr)[a]	Beta and percent quantiles (kyr)[b]				Initial effective population size per 1,000 individuals
				Mean	Median	2.5%	97.5%	
E3b1-M78	26	0.18	6.4	8.0	4.8	0.8	50.7	0.161 (0.045–0.630)
E3b3-M123	29	0.51	18.2	44.6	3.7	0.1	991.5	1.489 (0.140–0.569)
G-M201	57	0.40	14.3	44.6	20.3	0.3	489.6	0.161 (0.032–1.353)
G2-P15	50	0.35	12.5	31.0	15.5	0.4	372.6	0.780 (0.035–1.112)
G-M201(xP15)	7	0.42	15.0	36.0	10.4	0.1	891.4	0.570 (0.061–3.317)
I-M170	28	0.50	17.9	13.4	8.0	0.1	79.0	1.340 (0.543–6.669)
I-M170(xP37)	15	0.40	14.3	19.6	5.8	0.1	126.4	1.366 (0.198–3.764)
I1b-P37	13	0.23	8.2	19.1	9.1	0.9	101.2	0.183 (0.015–0.286)
J-M304	175	0.56	20.0	36.1	13.9	0.2	473.2	0.184 (0.036–1.306)
J1-M267	47	0.51	18.2	39.6	15.4	0.4	604.8	0.366 (0.061–1.895)
J1-M267, long DYS388 alleles	39	0.39	13.9	31.9	18.9	0.5	273.9	0.113 (0.030–0.751)
J1-M267, short DYS388 allele	8	0.25	8.9	14.3	1.4	0.0	512.4	0.385 (0.045–2.041)
J2-M172	127	0.52	18.6	17.9	14.5	2.0	78.5	0.821 (0.281–2.575)
J2-M172*	75	0.47	16.8	36.1	16.9	0.6	471.8	0.349 (0.051–1.514)
J2f-M67	33	0.33	11.8	16.4	12.5	1.7	92.0	0.285 (0.850–1.076)
J2e-M12	9	0.24	8.6	12.5	4.0	0.0	306.6	0.334 (0.052–1.833)
K2-M70	13	0.36	12.9	39.4	9.0	0.0	1,093.4	0.647 (0.063–3.889)
L-M11	22	0.41	14.6	26.3	2.4	0.0	1,044.8	1.386 (0.150–5.181)
N-M231	20	0.28	10.0	20.6	6.9	0.2	326.0	0.176 (0.023–1.062)
Q-M242	10	0.46	16.4	23.3	10.7	0.1	289.4	0.600 (0.120–3.550)
R-M207	126	0.65	23.2	15.3	13.1	2.7	63.4	0.889 (0.369–2.452)
R1b3-M269	76	0.33	11.8	23.4	17.5	1.9	127.7	0.085 (0.029–0.349)
R1a1-M17	36	0.25	8.9	4.9	4.1	0.8	23.2	0.896 (0.342–2.947)

[a]Continuous growth
[b]Bayesian exponential growth, posterior probabilities are shown

Table 3 Correlations of Y-chromosome haplogroup frequencies with geography

Haplogroup	*n*	Spearman's correlation coefficient		
		Latitude	Longitude	Distance from region 1
E3b1-M78	26	0.430	–0.430	–0.420
E3b3-M123	29	–0.717**	0.633	0.633
G-M201	57	–0.367	0.250	0.333
G-P15	50	–0.333	0.100	0.150
I-M170	28	0.550	–0.817	–0.850*
J1-M267	47	0.133	–0.067	–0.050
J2-M172	128	0.267	–0.033	–0.133
J2f-M67	33	0.667**	–0.600	–0.733**
L-M11	22	0.289	0.119	0.017
N-M231	20	–0.418	0.042	0.092
R1a1-M17	36	–0.600	0.680**	0.650
R1b3-M269	76	–0.183	–0.183	–0.100

*P<0.01 Spearman, n=9, two tailed; **P<0.05 Spearman, n=9, two tailed

Haplogroup I-M170 is a major lineage cluster largely restricted to populations of Europe (Semino et al. 2000a). Despite its relatively low average frequency (5.3%) in Turkey five major sub-clades were detected. The I-M170 chromosomes are more localized towards the west and show a significant correlation (r=–0.82) with longitude and geographic distance from region 1 (r=–0.85), the European pole of Turkey (Table 3). While haplogroup I-M170 displays overall with high STR variance (Table 2) the I1-P37 sub-clade accounts for almost one half of the lineages overall, but it shows significantly lower variance relative to other I lineages (Table 2).

Haplogroup E3b-M35 occurs at an overall 10. 7% frequency with E3b1-M78 and E3b3-M123 accounting for all E representatives except a single E3b2-M81 chromosome. Although E3b1-M78 and E3b3-M123 occur at similar frequencies (5.0% and 5.5%, respectively) their associated mean STR variances (Table 2) are significantly different [F (280,250) = 2.83, P<0.01]. The more diverse Turkish E3b3-M123 lineages are correlated with latitude (Table 3).

Haplogroup R-M207 lineages occur at 24.1 frequency on the whole with the majority belonging to the R1-M173 sub-clade (Fig. 2). Only one R1-M173* lineage was observed in eastern region 5. All but one (R1c-M343) of the remaining R1-M173 associated lineages allocate to R1a1-M17 and R1b-P25 sub-clades with R1b3-M269 being preponderate at 14.5% overall in Turkey. Although R1b3-M269 lineages are found throughout Europe at considerable frequency (Cruciani et al. 2002), no additional PCR compatible binary markers are currently known that show additional informative subdivision within this clade. However, two *Taq*I haplotypes ht15 and ht35 associated with the complex RFLP 49a,f locus, are associated with R1b3-

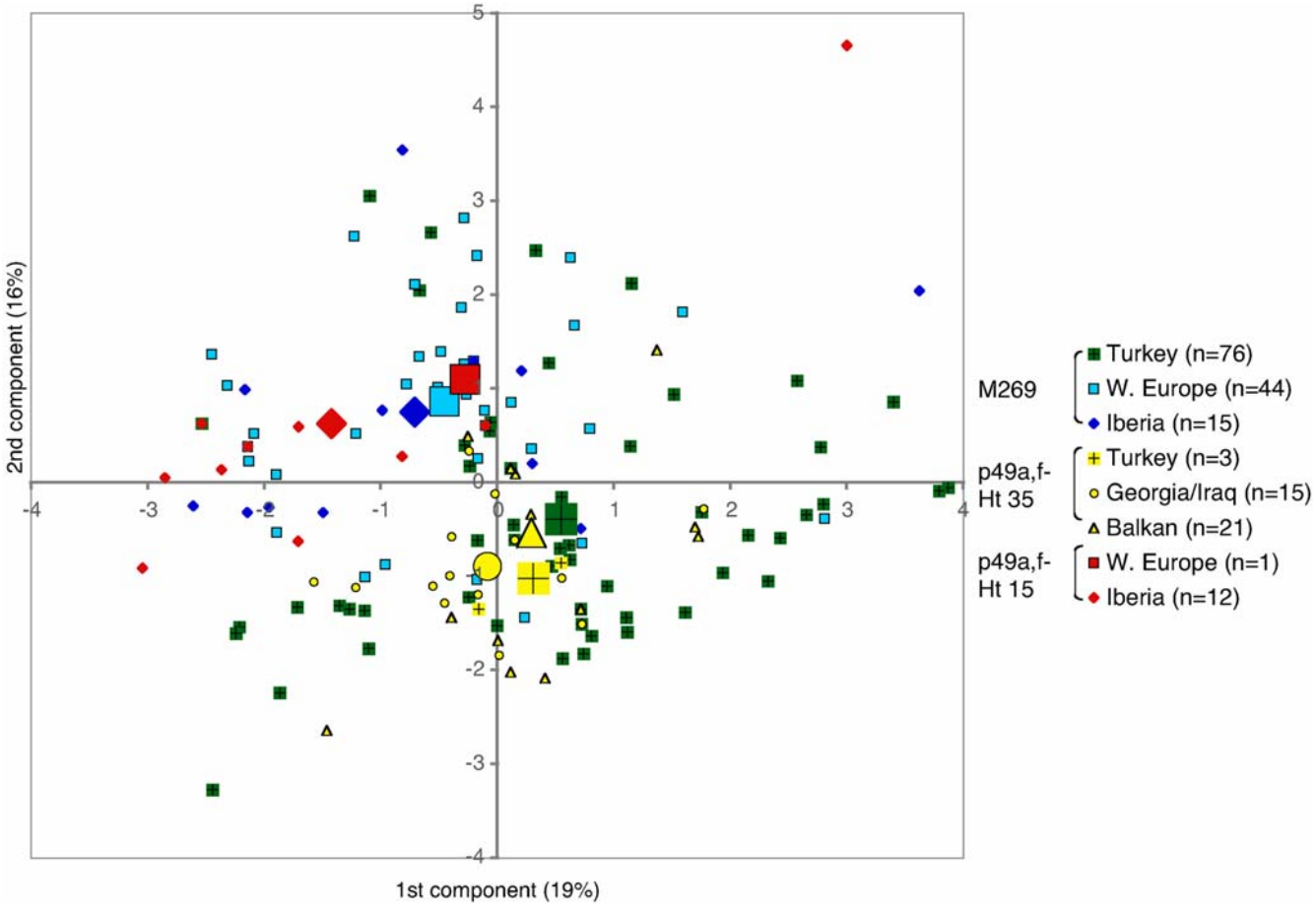

Fig. 3 Plot of 187 R1b3-M269 derived lineages against values for the initial two principal components for ten microsatellite loci variables. The first component accounts for 19% of the total variance, whereas the second component accounts for 16%. Samples whose p49a,f ht15 (*n*=13) or ht35 (*n*=39) status is known are indicated in r*ed* and *yellow*, respectively. Geographic areas include: *Iberia* (*n*=27), *W. Europe* (*n*=45), *Turkey* (*n*=79), *Balkans* (*n*=21), *Georgia/Iraq* (*n*=15). *W. Europe* includes France, Italy, Germany, Norway; *Balkans* includes Albania and Greece. *Large symbols* represent the means for the eight groups. The one Iberian ht15 outlier reflects the influence of an unusual DYS388 allele. Both M269 and DYS388 results for this sample were confirmed by sequencing

Table 4 Variance of R1b3-M269 and *Taq*I p49a,f Ht15, Ht35 STR haplotypes

Population[a]	*n*	Variance
Turkey	79	0.31
Iberia	27	0.24
W. Europe	45	0.22
Georgia	15	0.22
Balkan	21	0.18
p49a,f-Ht35	39	0.19
p49a,f-Ht15	13	0.18

[a]Populations grouped as given in Fig. 3

M269 lineages. The 49a,f ht15 form is rare in Turkey but common in Iberia (Semino et al. 1996), while 49a,f ht35 representatives are distributed across Europe (Torroni et al. 1990; Santachiara-Benerecetti et al. 1993; Semino et al. 2000b) and occurs at ~10% in the Balkan region (Santachiara-Benerecetti, personal communication). In an attempt to better understand the affinity of the frequent Turkish R1b3-M269 lineages relative to other regions, we have analyzed the same battery of STR loci in 52 additional R1b3-M269 defined samples from Iberia, the Balkans, Iraq, Georgia, and Turkey that were previously determined to be 49a,f ht15 or ht35, as well as an additional 59 European R1b3-M269 derived samples. STR haplotype data for these 111 samples are given in Appendix table B. Principal component analysis of all 187 R1b3-M269 samples at ten STR loci variables reveals distributions coinciding with samples of known 49a,f ht15 and ht35 constitution (Fig. 3). Most of the Turkish samples group with the Balkan and the Caucasian 49a,f ht35 samples, while the West European samples associate with the 49a,f ht15 samples. The variance of 49a,f ht35 related chromosomes are lower in the Balkan, Caucasian and Iraqi representatives than those in Turkey (Table 4). Similarly, the variance is higher in Iberia than in Western Europe. The decreasing diversity radiating from Turkey towards Southeast Europe, Caucasus and Mesopotamia approximates similar results from Iberia tracing the re-colonization of Northwest Europe by hunter-gatherers during the Holocene as suggested by others (Torroni et al. 1998; Semino et al. 2000a; Wilson et al. 2001).

In Turks R1b3-M269 and R1a1-M17 occur at 14.7% and 6.9%, respectively. In addition R1b3-M269 related YSTR variance is significantly higher than that of R1a1-M17 [F (750,350) = 1.32, P<0.01). While no micro-geographic substructure is detected in Turkey for R1b3-M269, the frequency of R1a1-M17 is higher in Eastern Turkey and its distribution significantly correlates with longitude across the nine regions (Table 3). The majority of L-M11 chromosomes occur in the most eastern regions 3 and 4 (χ^2=17.99, df=8, P<0.021) and also have high levels of variance (Table 2).

Discussion

Under an assumption of a negligible role of natural selection on Y-chromosome haplogroup distribution, the assessment of background STR variance can provide insights into haplogroup subdivision, size fluctuation, directionality of distribution and relative chronology amongst haplogroups. The haplogroup-specific variances may reflect potential associations with Upper Paleolithic, Holocene and agriculturalist processes. Although the occurrence of early agriculture in the Near East is almost contemporaneous with the onset Holocene climatic warming, the consequences of growth and migration specifically due to agriculture are likely to be more recent.

Haplogroup J and the transition to agriculture

Although the entire J-M304 clade demonstrates a large microsatellite variance that under a continuous growth model dates to around 20 kyr, consistent with the LGM, the BATWING exponential growth model reveals a more recent post-LGM expansion (13.9 kyr). This secondary expansion originates from a low effective population size (n=184) and may indicate that the J clade in Turkey began to participate in demographic expansions during the onset of sedentism in Anatolia and the Levant; e.g., the Natufians (Bar-Yosef 1998). Previously, J clade representatives would have been accumulating STR diversity via genetic drift within various small groups of mobile hunter-gathers during the LGM. We detected a significant reduction of variance of J2-M172 northwards in Turkey This latitudinal trend could be a consequence of an Upper Paleolithic presence of J2-M172 in southern Anatolia and its subsequent spread north and west during the Holocene likely catalyzed by the transition to agriculture (Ammerman and Cavalli-Sforza 1984; Underhill 2002). The northward gradient in J2-M172 variance is consistent with the archeological evidence that agro-pastoral economies of Northwest Anatolia were derived from the Çatal Höyük area in region 7 (Thissen 1999). The presence of J2-M172 related lineages successfully predicted the distribution of both Neolithic figurines and painted pottery attributed to agriculturalists (King and Underhill 2002). The Upper Paleolithic sites in Turkey (Öküzini cave, region 6) have been dated to 17,800 BC and suggest a continuous occupation into the subsequent Neolithic period (Kuhn 2002) while Neolithic sites are considerably fewer in Central and Northern Turkey (Roberts 2002). The J1-M267 and J2-M172 distributions in the Near East and Europe can be inferred from previously reported DYS388 data associated with Eu10 and Eu9, respectively (Semino et al. 2000a; Nebel et al. 2001b; Malaspina et al. 2001; Al-Zahery et al. 2003). While both J1 and J2 are found in the Near East, haplogroup J1-M267 typifies East Africans and Arabian populations, with a decreasing frequency northwards. Alternatively the majority of J lineages in Europe are J2-M172 that radiated from the Levant, coherent with the distributions of mitochondrial J, K, T1 and pre-HV clades (Richards et al. 2002).

Although we currently lack additional binary polymorphisms capable of defining further informative subdivision within haplogroup J1-M267, the unusual short DYS388 13 repeat allele lineage provides a proxy. These peculiar chromosomes distribute along the northern tier of Turkey. While this lineage has not been observed in Greece, it has been detected in Georgia (Semino, unpublished results), suggesting Black Sea coastal gene flow. A few lineages with potentially similar affinity have been observed scattered throughout the Middle East (Nebel et al. 2001b), although it is not possible to distinguish their affinity to haplogroup J-M304* or J1 since M267 data are unavailable. When the DYS388 "short" allele representatives are excluded on the assumption that they have a common origin, the residual assemblage of J1-M267 DYS388 "long" allele lineages contain numerous haplotypes including both the purported "Cohen" and "Arab" modal haplotypes (Thomas et al. 2000; Nebel et al. 2002). The similarity of variances associated with the two counterbalancing J1 and J2 sub-clades suggests an enduring common demography. At this level of molecular resolution, the data do not distinguish between agricultural and pastoral domestic livelihoods despite the observation that lifestyle differences exist (Khazanov 1984). Notably, nomads are often more endogamous and participate in transhumant seasonal migrations (Cavalli-Sforza et al. 1994).

The J2f-M67 clade is localized to Northwest Turkey. It is well known that during this period, Northwest Anatolia developed a complex society that engaged in widespread Aegean trade referred to as "Maritime Troia culture," involving both the western Anatolian mainland and several of the large islands in the eastern Aegean, Chios, Lemnos and Lesbos (Korfmann 1996). Another J2 component is intriguing. Although J2e-M12 lineages occur at low frequencies, they are widely distributed in the Middle East (Scozzari et al. 2001) and India (Kivisild et al. 2003), as well as in Saami from Kola, Russia (Raitio et al. 2001). By comparing data sets (Malaspina et al. 2001; Scozzari et al. 2001) we deduced that J2e-M12 lineages are distinctive from all other J2-M172 lineages on the basis of complex DYS413 and YCAII dinucleotide STRs. In corroboration we confirmed by sequencing the simple repeat locus DYSA7.2 that J2e-M12 is exclusively associated with shorter seven- or eight-tetranucleotide repeat alleles in Turkey. The considerable diversification observed in

the J clade as exemplified by high variance of J2-M172 and a J-M304* lineage in southeastern Anatolia, is consistent with the early onset of post glacial sedentism found in the archeological record of Anatolia and the Levant (Bar-Yosef 1998).

G-M201 and post ice-age expansions in Europe

Although recurrent mutation can occur in the complex 49a,f RFLP polymorphic system the *Taq*I ht8 restriction profile occurs only within haplogroup J and G lineages (Semino et al. 2000a) suggesting common ancestry. The overlap of J and G lineages with geography bolsters this putative affinity. The apparent scarcity of Upper Paleolithic sites in Anatolia (Kuhn 2002) and the considerable diversification of haplogroup G and J ancestors is consistent with a Upper Paleolithic/Mesolithic Middle East/Mesopotamian origin and the subsequent gradual proliferation of agriculturalists, including their presence (e.g., Çatal Höyük, region 7) during the early Pre-Pottery Neolithic B period (~9,500 BP). Haplogroup G-M201 lineages occur at ~30% in Georgia (Semino et al. 2000a) and the north Caucasus (Nasidze et al. 2003). Haplogroup G-M201 also occurs in Southeast Europe and the Mediterranean (Semino et al. 2000a) and in Iraq (Al-Zahery et al. 2003). In a material context, the Bronze Age Hattic and Kaska cultural region in Anatolia (Fig. 1) has affinity to the Maikop culture of the Caucasus and linguistic affinities to the northwest Caucasian languages (Renfrew 1998). Populations that speak such languages show a high frequency of G-M201 (Nasidze et al. 2003). Haplogroup G2-P15 is the most frequent (9%) G sub-clade in Turkey. G2-P15 lineages have been observed throughout the Middle East with a maximum of 19% in the Druze (Hammer et al. 2000) and an average of 5% in Italy and Greece (Di Giacomo et al. 2003). The expansion time estimates for G2-P15 closely approximate those predicted for R1b3-M269.

Role of R1b3-M269 in the Aurignacian and Neolithic eras

Haplogroup R1b3-M269 is one of the most common binary lineages observed in Turkey. The phylogenetic and spatial distribution of its equivalent in Europe (Cruciani et al. 2002), the R1-M173 (xM17) lineage for which considerable data exist (Semino et al. 2000a; Wells et al. 2001; Kivisild et al. 2003) implies that R1b3-M269 was well established throughout Paleolithic Europe, probably arriving from West Asia contemporaneous with Aurignacian culture. Although the phylogeographic pattern of R1b3-M269 lineages in Europe suggest that R1-M173* ancestors first arrived from West Asia during the Upper Paleolithic, we cannot deduce if R1b3-M269 first entered Anatolia via the Bosporus isthmus or from an opposite eastward direction. However, archeological evidence supports the view of the arrival of Aurignacian culture to Anatolia from Europe during the Upper Paleolithic rather than from the Iranian plateau (Kuhn 2002).

Haplogroup R1b3-M269 occurs at 40–80% frequency in Europe and the associated STR variance suggests that the last ice age modulated R1b3-M269 distribution to refugia in Iberia and Asia Minor from where it subsequently radiated during the Late Upper Paleolithic and Holocene. The R1b3-M269 related, but opposite *Taq*I p49a, f ht 15 and ht35 distributions reflect the re-peopling of Europe from Iberia and Asia Minor during that period. The R1b3-M269 variances and expansion time estimates of Iberian and Turkish lineages are similar to each other (Table 2) but higher than observed elsewhere (Table 4). Low variances for R1b3-M269 lineages have also been reported for Czech and Estonian populations (Kivisild et al. 2003).

In contrast, the R1-M173 related but offsetting clade R1a1-M17, is frequent (30–60%) in East Europe, Central Asia, and Northwest India (Semino et al. 2000a; Wells et al. 2001; Passarino et al. 2001; Kivisild et al. 2003). This pronounced R1-M173 related Y-chromosome substructure contrasts to the observed uniform frequency spectrum of the major mitochondrial DNA haplogroups in Europe. The higher frequency of R1a1-M17 lineages in eastern Turkey is consistent with an entry into Anatolia via the Iranian plateau where the associated variance is appreciably higher (Quintana-Murci et al. 2001). The most common R1a1-M17 haplotype in Armenia (Weale et al. 2001) matches the most common in Turkey.

Haplogroup I-M170 indicates gene flows from Croatia

The phylogeography and high associated variance of I-M170 is consistent with an in situ European origin of M170 in the Balkans (Semino et al. 2000a), possibly near the Dinaric Mountain chain in Croatia where it has been observed at the highest frequency known so far (Barac et al. 2003). I-M170 lineages radiated both towards north central Europe and into western Turkey. Comparison of STR haplotypes indicates that the Dinaric modal haplotype is associated with the I-P37 lineages observed in Turkey. Molecular analyses of I-M170 group lineages at equivalent resolution in modern day Bulgaria, Croatia and Greece will be required to better understand the phylogeography of I-M170 sub-clades.

Haplogroup E3b and Neolithic expansions

While both E3b1-M78 and E3b3-M123 occur at similar frequency in Turkey, the variance of the former is considerably lower than the latter suggesting either temporal or effective population size differences. The prevalence of haplogroup E (xM2) chromosomes in northern Egypt may reflect the source of non-African E3b lineages (Manni et al. 2002). Haplogroup E3b1-M78 haplotypes typify European lineages (Semino, unpublished) and have expansion dates consistent with expansion of agriculturalists (Table 2). Haplogroup J2-M172 lineages likely reflect the introduc-

tion of agriculture to India from the Middle East (Kivisild et al. 2003). However, the absence of E3b lineages in India supports the inference that the higher variance and older expansion dates for E3b3-M123 in Turkey do not reflect an earlier dispersal, but rather multiple founders with more associated diversity.

The spread of haplogroup L-M11 lineages is largely restricted to populations of the south Caucasus (Weale et al. 2001), Middle East (Nebel et al. 2001b), Pakistan (Qamar et al. 2002) and India (Kivisild et al. 2003). Interestingly Turkish L lineages lack the M27 mutation that characterizes Indian and Pakistani L lineages. Although no M27 data exist for Armenians, the haplogroup L modal haplotype of the six STR loci in Armenians haplotype (Weale et al. 2001) matches the most common Turkish counterpart. An attempt to interpret other informative lineages in Turkey such as I1a-M253, J2a-M47, J2f-M67, K2-M70, N-M231 is premature until they are adequately surveyed elsewhere.

Minor genetic influence of Turkic speakers

Various estimates exist of the proportion of gene flow associated with the arrival of Central Asian Turkic speaking people to Anatolia. One study based on analyses of six STR loci in 88 Y-chromosomes from Turkey suggested only a 10% contribution (Rolf et al. 1999). Another study suggests roughly 30% based upon mtDNA control region sequences and one binary and six STR Y-chromosome loci analyzed in 118 Turkish samples (Di Benedetto et al. 2001). While it is likely that gene flow between Central Asia and Anatolia has occurred repeatedly throughout prehistory, uncertainties regarding source populations and the number of such episodes between Central Asia and Europe confound any assessment of the contribution of the 11th century AD Oghuz nomads responsible for the Turkic language replacement. These new Y-chromosome data provide candidate haplogroups to differentiate lineages specific to the postulated source populations, thus overcoming potential artifacts caused by indistinguishable overlapping gene flows. The best candidates for estimations are Asian-specific haplogroups C-RPS4Y (Wells et al. 2001; Karafet et al. 2001; Zerjal et al. 2003) and O3-M122 (Su et al. 2000). These lineages occur at 1.5% in Turkey (8/523). Using Central Asian Y-chromosome data from either 13 populations and 149 samples (Underhill et al. 2000) or 49 populations and 1,935 samples (Wells et al. 2001) where these diagnostic lineages occur at 33% and 18%, respectively, their estimated contributions range from 0.0153/0.329×100=4.6% to 0.0153/0.180×100=8.5%. During the Bronze Age the population of Anatolia expanded, reaching an estimated level of 12 million during the late Roman Period (Russell 1958). Such a large pre-existing Anatolian population would have reduced the impact by the subsequent arrival of Turkic speaking Seljuk and Osmanlı groups from Central Asia. Although the genetic legacy of Anatolia remains somewhat inchoate, our excavations of these new levels of shared Y-chromosome heritage and subsequent diversification provide new clues to Anatolian prehistory, as well as a substantial foundation for comparisons with other populations. Our results demonstrate Anatolia's role as a buffer between culturally and genetically distinct populations, being both an important source and recipient of gene flow.

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Electronic-database information

BATWING. Bayesian analysis of trees with internal node generation, http://www.maths.abdn.ac.uk/~ijw (Aberdeen, UK: Department of Mathematical Sciences, University of Aberdeen).

Appendix

Table A

The distribution of Y-chromosome haplotypes in nine regions of Turkey (the populations are grouped as given in Fig. 3):

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
1	A3b2-M13	8	15	11	21	10	11	13	13	17	12	11	1
2	A3b2-M13	8	16	11	21	10	11	12	13	18	14	10	1
3	C*-M216	2	14	13	25	9	11	11	13	19	11	10	1
4	C*-M216	9	15	13	25	11	11	13	14	16	11	11	1
5	C3-M217	3	15	13	24	10	11	13	13	16	12	9	1
6	C3-M217	9	15	13	23	9	11	13	15	16	11	10	1
7	C3-M217	9	15	13	24	10	11	13	13	16	12	11	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
8	C3-M217	7	16	13	25	9	13	13	14	16	11	10	1
9	C3-M217	9	17	15	25	10	11	13	13	17	10	10	1
10	E3*-PN2	9	13	12	20	10	11	13	14	17	12	10	1
11	E3*-PN2	9	14	12	21	10	11	13	13	18	13	10	1
12	E3a-M2	9	14	12	21	10	11	13	13	16	11	10	1
13	E3b1-M78	1, 2, 4, 6	13	12	24	10	11	13	13	17	12	10	7
14	E3b1-M78	1, 3, 5	13	12	24	10	11	13	14	17	12	10	3
15	E3b1-M78	1, 3, 4	13	12	24	10	11	13	13	18	12	10	3
16	E3b1-M78	1	13	12	24	11	11	13	14	19	12	10	1
17	E3b1-M78	1	13	12	26	10	11	13	14	17	13	10	1
18	E3b1-M78	1	13	12	24	10	11	13	15	17	13	10	1
19	E3b1-M78	4	13	12	24	10	11	13	12	17	10	10	1
20	E3b1-M78	4	13	12	25	10	11	13	13	17	12	11	1
21	E3b1-M78	4	13	12	25	11	11	13	13	17	13	10	1
22	E3b1-M78	6	13	12	24	10	11	13	13	17	12	10	1
23	E3b1-M78	7	13	12	24	10	11	13	14	17	11	10	1
24	E3b1-M78	8	13	12	25	10	11	13	13	17	13	9	1
25	E3b1-M78	9	13	12	23	10	11	13	13	17	12	9	1
26	E3b1-M78	9	13	12	24	10	11	13	13	18	12	11	1
27	E3b1-M78	9	13	12	26	10	11	13	13	18	11	10	1
28	E3b1-M78	9	13	12	23	10	11	13	14	17	12	10	1
29	E3b2-M81	7	13	12	24	9	11	13	14	16	11	11	1
30	E3b3-M123	4, 5, 9	13	12	22	10	11	13	12	18	12	10	4
31	E3b3-M123	3, 9	13	12	23	9	11	14	14	18	13	9	3
32	E3b3-M123	1	13	12	24	10	11	13	13	20	13	10	1
33	E3b3-M123	3	13	12	24	9	11	14	14	17	11	9	1
34	E3b3-M123	3	13	12	24	10	11	13	13	19	11	10	1
35	E3b3-M123	3	13	12	26	9	11	13	13	18	11	10	1
36	E3b3-M123	4	13	11	24	10	11	13	13	15	13	10	1
37	E3b3-M123	4	13	12	23	10	12	13	13	19	11	10	1
38	E3b3-M123	4	13	12	24	10	11	13	13	18	13	10	1
39	E3b3-M123	4	13	12	24	10	11	13	13	18	13	10	1
40	E3b3-M123	5	13	12	22	10	11	14	12	18	12	10	1
41	E3b3-M123	6	13	12	23	10	12	13	12	17	12	11	1
42	E3b3-M123	6	13	12	24	10	11	13	13	18	12	8	1
43	E3b3-M123	7	13	12	21	10	11	13	12	18	12	10	1
44	E3b3-M123	7	13	12	23	8	11	13	12	19	10	11	1
45	E3b3-M123	7	13	12	25	10	11	13	12	16	13	11	1
46	E3b3-M123	7	13	12	25	9	11	13	13	18	12	9	1
47	E3b3-M123	8	13	12	21	9	11	14	14	17	12	9	1
48	E3b3-M123	9	13	12	22	10	11	13	12	18	11	10	1
49	E3b3-M123	9	13	12	24	10	11	13	12	18	12	11	1
50	E3b3-M123	7	14	12	24	10	11	13	13	17	11	10	1
51	E3b3-M123	7	14	12	24	9	11	14	14	17	11	9	1
52	E3b3-M123	1	15	12	23	10	11	13	13	17	11	9	1
53	E3b3-M123	6	15	12	23	9	11	14	14	19	12	9	1
54	G*-M201	4	16	12	23	10	11	13	13	16	11	10	1
55	G1a-P20	3	15	12	24	12	12	13	13	17	13	11	1
56	G1a–P20	3	15	12	23	10	12	13	13	17	13	11	1
57	G1a–P20	3	16	12	23	10	12	13	13	17	12	10	1
58	G1a–P20	3	16	12	23	10	12	13	13	17	13	11	1
59	G1*-M342	3	15	12	23	11	12	15	12	16	11	10	1
60	G2*-P15	4, 5, 9	15	13	22	10	11	13	13	17	11	10	5

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
61	G2*-P15	3, 7	15	12	20	10	11	14	12	16	13	9	3
62	G2*-P15	5, 7	15	12	23	10	11	14	12	17	11	9	2
63	G2*-P15	8	14	12	21	10	11	14	12	18	11	10	1
64	G2*-P15	4	14	12	22	10	11	14	12	17	11	10	1
65	G2*-P15	3	15	11	21	10	11	14	12	18	12	10	1
66	G2*-P15	6	15	12	21	10	11	15	12	16	11	9	1
67	G2*-P15	6	15	12	21	10	11	15	12	17	14	9	1
68	G2*-P15	7	15	12	21	10	11	14	13	16	11	9	1
69	G2*-P15	3	15	12	21	10	11	14	12	16	11	9	1
70	G2*-P15	7	15	12	21	10	11	13	12	16	11	9	1
71	G2*-P15	7	15	12	21	10	11	15	12	16	11	9	1
72	G2*-P15	4	15	12	21	10	11	14	12	17	11	9	1
73	G2*-P15	3	15	12	21	10	11	15	12	16	11	9	1
74	G2*-P15	3	15	12	21	10	11	14	12	16	12	9	1
75	G2*-P15	8	15	12	21	8	11	15	12	17	13	9	1
76	G2*-P15	8	15	12	21	8	11	15	12	16	13	9	1
77	G2*-P15	5	15	12	21	10	11	14	12	18	11	9	1
78	G2*-P15	3	15	12	21	10	11	15	12	18	11	9	1
79	G2*-P15	9	15	12	21	11	11	14	12	16	12	9	1
80	G2*-P15	2	15	12	21	10	11	14	12	16	11	9	1
81	G2*-P15	4	15	12	22	10	11	14	12	18	11	10	1
82	G2*-P15	4	15	12	22	10	10	14	12	18	11	11	1
83	G2*-P15	8	15	12	22	10	10	14	13	17	12	11	1
84	G2*-P15	6	15	12	22	10	11	14	12	16	12	9	1
85	G2*-P15	9	15	12	22	10	10	14	11	17	12	10	1
86	G2*-P15	7	15	12	23	10	11	14	12	16	12	10	1
87	G2*-P15	2	15	12	23	10	11	14	12	18	11	9	1
88	G2*-P15	7	15	12	23	10	12	14	13	18	11	10	1
89	G2*-P15	8	15	13	21	11	11	14	12	18	12	9	1
90	G2*-P15	7	15	13	21	10	11	15	12	17	11	9	1
91	G2*-P15	7	16	12	22	10	10	13	12	17	11	10	1
92	G2*-P15	2	16	12	22	10	10	14	12	17	13	10	1
93	G2*-P15	5	16	12	22	11	10	14	12	17	12	9	1
94	G2*-P15	9	16	13	21	10	11	14	12	16	12	9	1
95	G2*-P15	7	17	12	21	10	11	15	12	16	11	9	1
96	G2*-P15	1	17	12	22	10	11	14	12	17	11	10	1
97	G2a-P16	5, 9	15	12	22	10	10	14	11	16	12	10	2
98	G2a-P16	3	15	12	22	10	11	14	12	17	11	10	1
99	G2a-P16	9	15	12	22	10	10	15	12	17	12	10	1
100	G2a-P16	7	16	12	22	10	10	14	13	17	12	10	1
101	G2b-M286	1	15	12	22	10	11	15	13	17	12	11	1
102	G3-M287	8	15	12	22	10	10	13	12	17	11	10	1
103	H*-M52	7	15	12	22	10	11	12	13	16	11	10	1
104	H*-M52	4	15	13	22	10	12	12	14	17	11	10	1
105	H1a-M370	1	15	12	22	10	11	12	14	16	11	10	1
106	I*-M170	1	14	14	22	10	11	13	12	16	10	10	1
107	I*-M170	9	14	13	21	10	11	13	13	17	10	11	1
108	I*-M170	9	15	13	24	10	11	14	13	17	12	10	1
109	I*-M170	1	15	13	24	10	11	15	14	17	12	10	1
110	I*-M170	3	15	13	24	10	11	13	13	17	11	10	1
111	I*-M170	7	15	13	24	10	11	14	14	17	13	10	1
112	I1a-M253	2, 5, 7	14	14	23	10	11	13	12	16	12	10	3
113	I1a-M253	1	14	14	23	10	12	13	12	16	11	10	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
114	I1a-M253	1	14	14	23	10	11	14	12	16	10	10	1
115	I1a-M253	6	15	14	23	10	11	13	12	17	11	10	1
116	I1b*-P37	5, 9	16	13	24	11	11	13	13	18	12	10	2
117	I1b*-P37	8	15	13	24	11	11	13	13	19	12	10	1
118	I1b*-P37	9	15	13	24	11	11	13	13	18	13	10	1
119	I1b*-P37	1	16	13	24	11	11	13	14	18	12	9	1
120	I1b*-P37	3	16	13	24	11	11	13	13	18	12	11	1
121	I1b*-P37	7	16	13	24	10	11	13	12	18	11	9	1
122	I1b*-P37	9	16	13	24	10	11	13	13	17	12	10	1
123	I1b*-P37	9	16	13	24	12	11	13	13	18	12	10	1
124	I1b*-P37	9	16	13	24	11	11	13	13	19	12	10	1
125	I1b*-P37	2	17	13	24	10	11	13	13	19	11	11	1
126	I1b*-P37	8	17	13	24	10	11	13	13	19	13	10	1
127	I1b1-M359	9	16	13	24	11	11	13	12	18	14	10	1
128	I1c-M223	1	15	13	23	10	12	14	13	16	12	10	1
129	I1c-M223	2	15	13	23	10	12	13	14	16	12	12	1
130	I1c-M223	7	15	13	23	10	11	14	14	17	11	9	1
131	J*-M304	5	15	12	23	10	11	14	13	18	11	9	1
132	J1*-M267	4	13	15	25	10	11	12	12	17	12	9	2
133	J1*-M267	3, 4	14	13	23	10	11	12	14	18	11	9	2
134	J1*-M267	3, 7	14	13	23	10	11	12	13	16	12	10	2
135	J1*-M267	2, 7	14	15	25	9	11	12	13	17	12	9	2
136	J1*-M267	6	14	16	23	10	11	12	13	18	11	9	2
137	J1*-M267	3, 9	14	17	23	11	11	12	13	17	11	9	2
138	J1*-M267	4 ,9	14	17	24	10	11	12	13	17	11	9	2
139	J1*-M267	1	15	16	23	10	11	12	13	16	11	9	2
140	J1*-M267	3	14	13	23	10	11	12	14	18	11	9	1
141	J1*-M267	3	14	13	23	10	11	12	14	19	11	11	1
142	J1*-M267	1	14	13	23	10	11	12	14	16	11	10	1
143	J1*-M267	8	14	15	24	10	13	12	13	16	12	9	1
144	J1*-M267	9	14	15	25	11	11	12	13	16	12	9	1
145	J1*-M267	3	14	15	25	10	11	12	13	17	12	10	1
146	J1*-M267	7	14	16	21	10	11	12	13	18	13	9	1
147	J1*-M267	1	14	16	21	10	11	12	13	17	11	9	1
148	J1*-M267	5	14	16	22	10	11	12	13	17	12	9	1
149	J1*-M267	6	14	16	23	10	11	12	13	16	11	9	1
150	J1*-M267	6	14	16	23	10	11	12	13	15	11	9	1
151	J1*-M267	5	14	16	23	10	11	12	13	18	12	9	1
152	J1*-M267	7	14	16	23	10	11	12	13	16	12	9	1
153	J1*-M267	3	14	16	23	10	11	12	13	17	12	9	1
154	J1*-M267	4	14	16	24	10	13	13	13	16	12	9	1
155	J1*-M267	3	14	16	24	9	11	12	13	18	12	9	1
156	J1*-M267	4	14	17	23	11	11	12	14	17	12	9	1
157	J1*-M267	1	14	17	23	11	11	12	13	17	10	9	1
158	J1*-M267	4	14	17	23	9	11	12	13	18	12	9	1
159	J1*-M267	9	14	17	23	10	11	12	13	17	11	9	1
160	J1*-M267	9	14	17	23	11	11	12	12	16	12	9	1
161	J1*-M267	9	14	17	23	10	11	12	13	17	11	10	1
162	J1*-M267	7	14	17	24	10	11	12	13	18	12	9	1
163	J1*-M267	4	15	13	23	9	11	12	14	17	11	10	1
164	J1*-M267	1	15	15	23	11	13	12	13	16	11	9	1
165	J1*-M267	6	15	15	23	11	11	12	13	17	12	9	1
166	J1*-M267	1	15	16	23	10	11	12	13	16	11	9	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
167	J1*-M267	1	15	16	24	10	11	12	13	17	11	11	1
168	J1a-M365	4	15	16	22	10	11	14	13	15	12	8	1
169	J1b-M368	2	14	15	22	10	11	12	13	17	12	11	1
170	J1c-M369	4	14	16	23	10	11	12	13	17	11	9	1
171	J2*-M172	4	16	15	23	10	11	12	13	16	11	12	5
172	J2*-M172	4, 7	14	15	23	10	11	12	14	16	11	10	3
173	J2*-M172	7	15	16	23	9	11	12	13	16	11	12	2
174	J2*-M172	5, 6	15	15	23	11	11	12	13	16	11	12	2
175	J2*-M172	1	13	15	22	10	11	12	14	18	11	11	1
176	J2*-M172	7	13	15	23	10	11	12	13	16	11	10	1
177	J2*-M172	4	13	15	24	10	11	12	13	16	11	11	1
178	J2*-M172	7	13	17	23	11	11	12	12	14	11	11	1
179	J2*-M172	3	14	15	23	10	10	12	14	16	11	11	1
180	J2*-M172	3	14	15	24	10	10	12	13	16	11	11	1
181	J2*-M172	7	14	14	21	10	11	12	13	17	12	11	1
182	J2*-M172	2	14	14	23	10	11	12	13	16	12	11	1
183	J2*-M172	2	14	14	23	10	11	12	14	16	11	10	1
184	J2*-M172	1	14	14	24	10	11	12	13	16	11	11	1
185	J2*-M172	1	14	14	24	10	11	12	13	16	12	11	1
186	J2*-M172	8	14	14	24	10	11	12	13	16	13	11	1
187	J2*-M172	7	14	14	24	10	11	12	14	17	11	11	1
188	J2*-M172	9	14	15	22	9	11	12	14	15	11	10	1
189	J2*-M172	1	14	15	23	9	11	12	13	16	11	10	1
190	J2*-M172	8	14	16	22	9	11	12	14	16	10	9	1
191	J2*-M172	1	14	15	23	10	11	12	13	15	13	11	1
192	J2*-M172	4	14	15	23	10	11	12	14	16	11	11	1
193	J2*-M172	2	14	15	25	10	11	12	12	17	11	10	1
194	J2*-M172	7	14	16	23	10	11	12	12	16	13	9	1
195	J2*-M172	9	14	16	23	10	11	12	12	17	12	9	1
196	J2*-M172	3	14	16	25	10	11	12	13	16	13	10	1
197	J2*-M172	5	14	17	23	10	11	12	13	16	12	10	1
198	J2*-M172	3	14	17	23	10	11	12	12	16	14	11	1
199	J2*-M172	4	14	17	23	10	11	12	12	16	12	8	1
200	J2*-M172	5	14	17	23	10	11	12	12	16	12	10	1
201	J2*-M172	7	14	17	23	10	11	12	12	16	11	11	1
202	J2*-M172	1	14	14	24	10	11	13	13	16	11	11	1
203	J2*-M172	7	14	15	22	11	11	12	13	17	12	10	1
204	J2*-M172	1	14	15	23	11	11	12	13	17	11	11	1
205	J2*-M172	1	14	15	25	11	11	12	13	17	12	11	1
206	J2*-M172	7	14	15	25	11	11	12	14	17	12	10	1
207	J2*-M172	5	14	17	23	11	11	12	12	16	13	11	1
208	J2*-M172	7	14	17	23	11	11	12	12	17	12	10	1
209	J2*-M172	5	14	17	23	11	11	13	12	17	12	10	1
210	J2*-M172	2	15	16	23	9	11	12	14	16	11	11	1
211	J2*-M172	7	15	16	24	9	11	12	13	16	12	11	1
212	J2*-M172	6	15	15	24	9	11	15	13	16	12	10	1
213	J2*-M172	6	15	16	23	9	11	15	13	16	12	10	1
214	J2*-M172	2	15	14	24	10	11	12	13	18	13	11	1
215	J2*-M172	4	15	14	25	10	11	12	13	18	12	11	1
216	J2*-M172	3	15	15	22	10	11	12	13	17	11	10	1
217	J2*-M172	7	15	15	23	10	11	12	13	16	11	11	1
218	J2*-M172	4	15	15	23	10	11	12	13	16	11	12	1
219	J2*-M172	5	15	15	23	10	11	12	13	16	11	10	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
220	J2*-M172	9	15	15	23	10	11	12	13	17	12	10	1
221	J2*-M172	1	15	15	23	10	11	12	13	17	13	11	1
222	J2*-M172	6	15	15	23	10	11	12	13	18	12	11	1
223	J2*-M172	7	15	15	23	10	11	12	14	18	11	12	1
224	J2*-M172	7	15	15	23	10	11	12	13	18	11	11	1
225	J2*-M172	3	15	15	24	10	11	12	12	16	13	10	1
226	J2*-M172	3	15	15	24	10	11	12	12	16	12	10	1
227	J2*-M172	3	15	15	24	10	11	12	12	16	12	10	1
228	J2*-M172	6	15	15	24	10	11	12	13	17	11	11	1
229	J2*-M172	7	15	15	24	10	11	12	13	19	12	10	1
230	J2*-M172	4	15	15	25	10	11	12	13	17	11	10	1
231	J2*-M172	2	15	16	23	10	11	12	13	16	12	11	1
232	J2*-M172	9	15	16	23	10	11	12	13	17	11	11	1
233	J2*-M172	5	15	17	23	10	11	12	12	16	11	12	1
234	J2*-M172	2	15	15	24	11	11	12	13	16	13	11	1
235	J2*-M172	6	15	15	24	11	11	12	13	17	11	11	1
236	J2*-M172	5	16	15	23	10	11	12	13	17	12	12	1
237	J2*-M172	4	16	15	24	10	11	12	13	16	11	12	1
238	J2a-M47	9	14	15	23	10	11	12	13	16	11	9	2
239	J2a-M47	4	14	15	23	10	11	12	13	16	11	8	1
240	J2a-M47	7	14	15	21	10	11	12	13	16	11	9	1
241	J2a-M47	4	14	15	23	10	11	12	13	17	11	8	1
242	J2a-M47	9	14	15	23	10	11	12	14	17	11	10	1
243	J2d-M158	3	15	15	25	10	11	12	14	16	12	11	1
244	J2d-M158	5	15	17	23	10	11	12	12	16	11	11	1
245	J2e*-M12	4	15	15	24	11	11	12	12	15	12	8	2
246	J2e*-M12	3	15	15	23	10	11	12	12	16	11	8	1
247	J2e*-M12	4	15	15	24	11	11	12	12	15	13	8	1
248	J2e1-M241	9	15	14	24	10	11	12	12	16	11	8	1
249	J2e1-M241	9	15	15	24	10	11	12	12	16	12	8	1
250	J2e1-M241	6	15	16	24	10	11	12	12	15	11	8	1
251	J2e1-M241	5	16	15	24	10	11	13	12	16	11	7	1
252	J2e1-M241	5	17	15	25	10	11	13	12	16	11	7	1
253	J2f1-M92	1	14	15	22	10	11	12	13	15	12	10	1
254	J2f1-M92	7	14	15	22	10	11	12	13	16	11	11	1
255	J2f1-M92	1	14	15	22	10	11	12	13	16	11	10	1
256	J2f1-M92	7	14	15	22	10	11	12	13	17	12	11	1
257	J2f1-M92	7	14	15	22	10	11	12	13	17	11	10	1
258	J2f1-M92	8	14	15	22	10	11	12	12	17	11	11	1
259	J2f1-M92	7	14	16	23	10	11	12	13	17	11	11	1
260	J2f1-M92	4	14	15	22	11	11	12	13	16	11	11	1
261	J2f1-M92	3	14	15	23	11	11	12	14	17	12	10	1
262	J2f1-M92	7	14	15	22	11	12	12	13	17	11	11	1
263	J2f1-M92	9	15	15	22	9	11	12	13	15	11	11	1
264	J2f1-M92	9	15	15	22	9	11	12	13	NAb	12	11	1
265	J2f1-M92	1	15	15	22	10	12	13	13	18	11	11	1
266	J2f1-M92	7	17	15	22	10	11	12	13	15	11	11	1
267	J2f*-M67	1	14	15	22	9	11	12	13	16	11	11	1
268	J2f*-M67	2	14	15	23	10	11	12	14	16	11	11	1
269	J2f*-M67	9	14	15	23	10	11	12	13	16	11	10	1
270	J2f*-M67	3	14	15	23	10	11	12	14	16	10	9	1
271	J2f*-M67	1	14	15	23	10	11	12	14	17	11	11	1
272	J2f*-M67	9	14	15	23	10	11	12	14	17	12	12	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
273	J2f*-M67	3	14	15	23	10	11	12	13	17	11	12	1
274	J2f*-M67	9	14	15	23	10	11	13	15	18	12	11	1
275	J2f*-M67	3	14	15	23	11	11	12	13	17	11	11	1
276	J2f*-M67	9	14	15	23	11	11	12	14	17	11	11	1
277	J2f*-M67	7	14	15	23	11	11	12	13	17	12	11	1
278	J2f*-M67	1	14	15	24	10	11	12	13	16	11	11	1
279	J2f*-M67	1	14	16	23	10	11	12	13	17	11	10	1
280	J2f*-M67	7	14	16	23	10	11	12	14	17	11	10	1
281	J2f*-M67	3	14	16	23	10	11	12	14	17	13	12	1
282	J2f*-M67	6	14	16	23	10	11	12	13	18	11	9	1
283	J2f*-M67	4	14	16	23	10	11	12	13	18	11	11	1
284	J2f*-M67	9	15	14	23	11	11	12	13	16	10	10	1
285	J2f*-M67	3	15	15	23	11	13	12	13	18	11	11	1
286	J2g-M339	4	14	17	23	10	11	12	12	16	12	12	1
287	J2h-M340	8	14	14	24	10	11	12	14	16	14	10	1
288	K2-M70	7	14	12	24	10	13	13	13	16	11	9	2
289	K2-M70	3	13	12	23	10	13	13	14	16	12	9	1
290	K2-M70	9	13	12	24	10	13	13	14	16	11	9	1
291	K2-M70	3	13	13	23	10	13	13	14	16	12	9	1
292	K2-M70	5	14	12	22	10	13	13	14	16	11	9	1
293	K2-M70	4	14	12	23	10	13	14	14	16	12	9	1
294	K2-M70	5	14	12	24	10	13	13	14	16	11	9	1
295	K2-M70	7	14	12	24	11	13	14	13	17	12	10	1
296	K2-M70	6	14	13	22	9	11	13	13	17	12	9	1
297	K2-M70	9	14	14	23	11	13	13	13	17	12	9	1
298	K2-M70	9	15	12	23	11	14	12	13	17	12	9	1
299	K2-M70	8	16	13	24	11	13	13	14	16	13	9	1
300	L*-M11	1, 3	15	12	23	10	13	11	13	17	12	10	2
301	L*-M11	3	15	12	23	10	13	11	13	17	12	10	2
302	L*-M11	4, 9	16	12	24	10	15	11	13	16	11	10	2
303	L*-M11	7	12	12	22	10	14	11	12	16	12	9	1
304	L*-M11	7	12	12	22	10	14	11	12	16	13	9	1
305	L*-M11	8	14	13	23	9	14	11	13	17	11	12	1
306	L*-M11	4	15	12	23	11	15	11	13	17	12	10	1
307	L*-M11	3	15	12	23	10	13	11	13	17	13	10	1
308	L*-M11	3	15	12	23	10	15	11	13	17	13	9	1
309	L*-M11	3	15	12	23	11	13	11	13	17	13	10	1
310	L*-M11	3	15	12	23	10	13	11	13	17	13	10	1
311	L*-M11	9	15	12	23	10	13	11	13	17	12	10	1
312	L*-M11	3	15	12	23	10	13	12	13	17	12	10	1
313	L*-M11	3	15	12	23	10	13	11	13	18	13	10	1
314	L*-M11	7	15	12	23	10	14	11	14	17	12	10	1
315	L*-M11	9	16	12	23	10	16	11	14	17	12	10	1
316	L*-M11	3	16	12	23	11	13	13	13	17	12	10	1
317	L*-M11	9	16	12	23	10	14	11	13	17	14	10	1
318	L2-M349	4	14	12	23	10	14	12	14	16	13	9	1
319	N*-M231	3, 4	14	12	23	10	14	13	13	16	10	11	4
320	N*-M231	3	14	12	23	10	14	13	13	16	11	11	1
321	N*-M231	3	14	12	23	10	14	13	13	16	10	10	1
322	N*-M231	9	14	12	23	10	14	13	13	17	10	11	1
323	N*-M231	3	14	12	23	10	13	13	13	16	10	11	1
324	N*-M231	7	14	12	23	10	14	13	13	17	10	11	1
325	N*-M231	8	14	12	23	10	14	13	13	15	10	11	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
326	N*-M231	8	14	12	23	10	14	13	11	16	10	11	1
327	N*-M231	3	14	13	24	10	14	13	14	17	11	9	1
328	N*-M231	5	15	12	23	11	14	13	13	16	10	11	1
329	N*-M231	6	15	12	23	10	14	13	13	16	10	11	1
330	N*-M231	7	15	12	24	10	14	13	15	16	10	11	1
331	N3a-M178	7	14	12	23	10	14	14	14	16	10	10	1
332	N3a-M178	8	14	12	23	10	14	14	13	17	10	10	1
333	N3a-M178	9	14	12	23	11	17	15	14	16	10	10	1
334	N3a-M178	7	14	12	23	11	15	15	14	16	10	10	1
335	N3a-M178	7	15	12	23	11	14	14	14	16	11	10	1
336	O3-M122	3	15	10	23	10	14	12	12	15	12	11	1
337	Q*-M242	7	13	12	22	10	15	13	14	16	11	11	1
338	Q*-M242	4	13	12	22	10	15	13	13	16	12	11	1
339	Q*-M242	7	13	12	22	10	15	13	13	16	11	11	1
340	Q*-M242	8	13	12	22	10	15	13	13	17	12	11	1
341	Q*-M242	4	13	12	22	10	14	14	13	17	12	10	1
342	Q*-M242	7	13	12	22	9	15	13	13	16	12	11	1
343	Q*-M242	3	13	12	25	10	13	13	13	18	13	11	1
344	Q*-M242	4	14	12	22	11	15	13	13	16	11	12	1
345	Q*-M242	4	15	12	24	10	14	14	12	17	13	10	1
346	Q2-M25	4	13	12	23	10	16	13	13	15	13	10	1
347	R1*-M173	5	15	12	23	11	13	13	13	17	13	9	1
348	R1a1-M17	4, 5, 8	16	12	25	11	11	13	13	17	10	9	5
349	R1a1-M17	4	15	12	25	11	11	13	14	16	10	9	2
350	R1a1-M17	1, 9	17	12	25	11	11	13	13	17	11	10	2
351	R1a1-M17	7	14	13	25	11	11	13	13	17	11	9	1
352	R1a1-M17	3	15	12	24	10	11	13	12	17	10	9	1
353	R1a1-M17	5	15	12	24	12	11	13	13	17	10	9	1
354	R1a1-M17	4	15	12	25	11	11	13	13	18	10	9	1
355	R1a1-M17	5	15	12	25	11	11	13	13	17	10	9	1
356	R1a1-M17	7	15	12	25	11	11	13	14	16	11	10	1
357	R1a1-M17	3	15	12	25	11	11	14	14	16	10	9	1
358	R1a1-M17	4	15	12	25	11	11	13	14	18	10	9	1
359	R1a1-M17	9	15	12	25	10	11	13	13	17	10	9	1
360	R1a1-M17	4	15	12	25	11	11	13	12	17	10	9	1
361	R1a1-M17	7	15	12	25	11	11	13	13	19	10	9	1
362	R1a1-M17	5	16	11	25	10	11	13	13	15	11	9	1
363	R1a1-M17	7	16	12	23	11	11	13	13	17	11	9	1
364	R1a1-M17	9	16	12	24	11	11	13	13	17	10	9	1
365	R1a1-M17	3	16	12	24	10	11	13	13	18	11	9	1
366	R1a1-M17	6	16	12	24	11	11	13	13	17	10	9	1
367	R1a1-M17	3	16	12	24	11	11	13	13	16	10	9	1
368	R1a1-M17	7	16	12	25	10	11	13	13	16	11	9	1
369	R1a1-M17	9	16	12	25	10	11	13	14	17	10	9	1
370	R1a1-M17	1	16	12	25	11	11	14	13	19	10	9	1
371	R1a1-M17	9	16	12	25	11	11	13	12	18	11	9	1
372	R1a1-M17	9	16	12	25	10	11	13	13	17	10	10	1
373	R1a1-M17	4	16	12	25	11	11	13	12	18	11	9	1
374	R1a1-M17	5	16	12	25	10	11	13	13	17	10	9	1
375	R1a1-M17	6	16	12	26	10	11	13	13	18	10	10	1
376	R1a1-M17	9	16	12	26	10	11	13	13	16	11	9	1
377	R1a1-M17	6	17	12	25	11	11	13	13	18	10	10	1
378	R1b*-P25	2	15	12	24	10	14	13	13	16	12	10	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
379	R1b*-P25	4	15	13	23	10	13	13	13	16	13	9	1
380	R1b3-M269	1, 4, 6, 7	14	12	24	11	13	12	13	16	12	9	7
381	R1b3-M269	5, 6	14	12	25	11	13	12	13	16	11	9	3
382	R1b3-M269	7, 9	14	12	23	10	13	12	13	16	12	9	2
383	R1b3-M269	3, 5	14	12	24	10	13	12	13	16	12	11	2
384	R1b3-M269	4	14	12	24	11	13	12	13	16	13	9	2
385	R1b3-M269	3	14	12	24	11	13	13	12	16	14	9	2
386	R1b3-M269	1, 9	14	12	24	11	14	12	13	15	12	9	2
387	R1b3-M269	7, 8	15	12	24	11	13	12	13	16	12	9	2
388	R1b3-M269	3	13	12	24	11	13	12	13	17	14	9	1
389	R1b3-M269	4	13	12	25	11	13	12	13	16	12	9	1
390	R1b3-M269	9	13	12	25	11	13	12	13	18	11	9	1
391	R1b3-M269	8	13	12	25	11	13	12	13	17	12	9	1
392	R1b3-M269	2	14	12	23	11	13	13	13	15	12	10	1
393	R1b3-M269	9	14	12	23	10	14	12	13	15	12	9	1
394	R1b3-M269	4	14	12	23	11	11	12	13	15	12	9	1
395	R1b3-M269	3	14	12	23	11	13	12	13	16	11	10	1
396	R1b3-M269	2	14	12	23	10	13	12	14	17	12	10	1
397	R1b3-M269	7	14	12	24	10	12	12	13	16	12	10	1
398	R1b3-M269	9	14	12	24	10	13	12	13	18	11	9	1
399	R1b3-M269	2	14	12	24	10	13	12	14	16	13	10	1
400	R1b3-M269	5	14	12	24	10	14	12	12	15	12	10	1
401	R1b3-M269	5	14	12	24	10	14	12	12	15	12	9	1
402	R1b3-M269	2	14	12	24	10	14	12	13	15	13	9	1
403	R1b3-M269	3	14	12	24	10	14	12	12	15	12	10	1
404	R1b3-M269	7	14	12	24	10	14	12	13	16	13	9	1
405	R1b3-M269	7	14	12	24	10	14	12	13	15	11	10	1
406	R1b3-M269	3	14	12	24	10	15	12	13	15	12	9	1
407	R1b3-M269	7	14	12	24	11	12	12	14	16	11	9	1
408	R1b3-M269	4	14	12	24	11	13	12	13	16	13	9	1
409	R1b3-M269	4	14	12	24	11	13	12	13	16	11	9	1
410	R1b3-M269	1	14	12	24	11	13	12	13	16	13	10	1
411	R1b3-M269	7	14	12	24	11	13	12	14	16	11	9	1
412	R1b3-M269	2	14	12	24	11	13	12	13	16	13	9	1
413	R1b3-M269	6	14	12	24	11	13	13	14	16	11	10	1
414	R1b3-M269	6	14	12	24	11	13	13	14	16	11	10	1
415	R1b3-M269	6	14	12	24	11	13	13	13	16	12	10	1
416	R1b3-M269	8	14	12	24	11	13	13	13	16	12	11	1
417	R1b3-M269	9	14	12	24	11	13	13	13	16	11	9	1
418	R1b3-M269	9	14	12	24	11	13	13	13	16	12	9	1
419	R1b3-M269	3	14	12	24	11	13	13	13	16	12	11	1
420	R1b3-M269	9	14	12	24	11	13	14	12	16	11	9	1
421	R1b3-M269	7	14	12	24	11	13	14	13	16	12	11	1
422	R1b3-M269	9	14	12	24	11	14	12	13	15	13	9	1
423	R1b3-M269	7	14	12	24	11	14	12	13	15	13	9	1
424	R1b3-M269	8	14	12	24	11	15	12	13	15	13	9	1
425	R1b3-M269	9	14	12	24	11	15	13	13	16	12	11	1
426	R1b3-M269	1	14	12	24	12	13	13	13	16	12	9	1
427	R1b3-M269	3	14	12	25	10	13	12	13	16	13	9	1
428	R1b3-M269	7	14	12	25	10	13	12	13	17	12	9	1
429	R1b3-M269	2	14	12	25	10	13	12	14	17	12	9	1
430	R1b3-M269	1	14	13	23	10	13	12	14	16	11	9	1
431	R1b3-M269	9	14	12	25	11	13	12	13	16	12	9	1

Haplotype number	Haplogroup	Region	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I(CD)	DYS389II(AB)	DYS439	DYSA7.2	
432	R1b3-M269	2	14	12	25	11	13	12	12	16	13	9	1
433	R1b3-M269	1	14	12	25	11	14	13	13	16	11	11	1
434	R1b3-M269	2	14	12	24	10	13	12	13	16	13	9	1
435	R1b3-M269	4	14	12	24	10	13	12	13	16	12	9	1
436	R1b3-M269	8	14	12	21	10	13	12	13	16	12	9	1
437	R1b3-M269	6	15	12	25	10	12	12	14	15	11	9	1
438	R1b3-M269	5	15	12	24	10	13	12	12	15	11	10	1
439	R1b3-M269	6	15	12	24	10	13	13	12	17	13	10	1
440	R1b3-M269	7	15	12	23	10	14	12	12	15	12	9	1
441	R1b3-M269	7	15	12	21	10	13	12	13	16	12	9	1
442	R1b2-M73	1	14	12	19	11	13	13	13	17	12	9	1
443	R1b2-M73	3	14	12	19	11	13	13	14	16	12	9	1
444	R1b2-M73	8	14	12	25	10	13	12	13	15	11	9	1
445	R1b2-M73	9	15	13	24	11	11	14	13	16	12	10	1
446	R1b4-M335	3	15	12	25	10	13	13	14	17	12	11	1
447	R1c-M343	3	15	12	24	10	13	13	14	17	11	10	1
448	R2-M124	1	14	11	21	10	10	14	14	16	11	11	1
449	R2-M124	7	14	13	23	10	10	14	14	17	10	10	1
450	R2-M124	5	15	12	23	10	10	14	14	16	11	10	1
451	R2-M124	2	15	12	23	10	10	14	12	16	10	9	1
452	R2-M124	5	15	12	23	10	10	14	14	16	11	10	1

Table B

The distribution of Y-chromosome haplotypes affiliated with haplogroup R1b3-M269 in five regions of Europe (the populations are grouped as given in Fig. 3):

Haplotype Number	Haplogroup	Population	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I	DYS389II	DYS439	DYSA7.2	
1	R1b3-M269	W. Europe, Iberia	14	12	24	11	13	13	16	13	12	10	6
2	R1b3-M269	W. Europe	14	12	25	11	13	13	16	13	12	10	4
3	R1b3-M269	W. Europe	13	12	23	10	13	13	16	13	12	10	2
4	R1b3-M269	W. Europe	14	12	24	11	13	14	16	13	12	10	2
5	R1b3-M269	W. Europe, Iberia	15	12	24	11	13	13	16	13	12	10	2
6	R1b3-M269	W. Europe	14	12	24	11	13	13	16	13	11	10	1
7	R1b3-M269	W. Europe	14	12	24	10	14	13	16	13	13	10	1
8	R1b3-M269	W. Europe	14	12	25	11	14	13	16	13	12	11	1
9	R1b3-M269	W. Europe	14	13	24	11	13	13	17	13	12	10	1
10	R1b3-M269	Iberia	14	12	24	11	13	13	16	14	11	9	1
11	R1b3-M269	Iberia	14	12	23	10	13	13	16	14	12	10	1
12	R1b3-M269	Iberia	14	12	23	11	13	14	16	14	13	10	1
13	R1b3-M269	Iberia	14	12	25	10	13	12	16	13	13	10	1
14	R1b3-M269	Iberia	14	12	23	11	13	15	15	13	11	10	1
15	R1b3-M269	Iberia	14	12	24	11	13	13	16	14	11	10	1

Haplotype Number	Haplogroup	Population	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I	DYS389II	DYS439	DYSA7.2	
16	R1b3-M269	Iberia	14	12	24	10	13	13	16	11	12	10	1
17	R1b3-M269	Iberia	14	12	23	10	13	13	16	13	13	10	1
18	R1b3-M269	Iberia	14	12	24	10	13	13	15	13	11	10	1
19	R1b3-M269	W. Europe	14	12	24	11	13	12	17	13	13	9	1
20	R1b3-M269	W. Europe	14	12	23	12	13	13	16	13	11	11	1
21	R1b3-M269	W. Europe	14	12	24	11	13	13	16	14	12	10	1
22	R1b3-M269	W. Europe	14	12	24	11	13	13	16	12	12	10	1
23	R1b3-M269	W. Europe	14	12	24	10	13	12	16	13	13	10	1
24	R1b3-M269	W. Europe	14	12	25	12	13	13	16	14	12	10	1
25	R1b3-M269	W. Europe	14	12	23	11	13	13	16	14	12	10	1
26	R1b3-M269	Iberia	14	12	24	11	13	13	17	13	12	10	1
27	R1b3-M269	W. Europe	14	12	25	10	13	13	16	13	12	10	1
28	R1b3-M269	W. Europe	14	12	24	11	13	14	16	13	13	10	1
29	R1b3-M269	W. Europe	14	12	24	11	13	12	16	12	13	9	1
30	R1b3-M269	W. Europe	14	12	25	11	13	12	17	13	12	9	1
31	R1b3-M269	W. Europe	14	12	24	10	13	13	17	13	11	10	1
32	R1b3-M269	W. Europe	14	12	24	10	13	13	16	13	13	10	1
33	R1b3-M269	W. Europe	14	12	25	11	12	13	16	13	12	10	1
34	R1b3-M269	W. Europe	14	12	23	10	13	13	16	13	12	11	1
35	R1b3-M269	W. Europe	14	12	24	11	13	13	16	13	13	10	1
36	R1b3-M269	W. Europe	14	11	24	11	13	13	16	13	12	10	1
37	R1b3-M269	W. Europe	14	12	24	10	13	13	18	13	12	9	1
38	R1b3-M269	W. Europe	14	12	24	10	13	13	16	13	11	10	1
39	R1b3-M269	W. Europe	14	12	25	10	13	13	16	13	11	10	1
40	R1b3-M269	W. Europe	14	12	23	11	13	13	18	13	11	10	1
41	R1b3-M269	W. Europe	14	12	23	11	13	13	16	13	12	10	1
42	R1b3-M269	W. Europe	14	12	24	12	13	13	15	13	13	10	1
43	R1b3-M269	Iberia	15	12	23	10	13	13	16	14	13	10	1
44	R1b3-M269	Iberia	15	12	24	10	13	13	17	14	12	10	1
45	R1b3-M269	W. Europe	15	12	23	11	13	13	16	14	12	11	1
46	R1b3-M269	W. Europe	15	12	23	10	14	12	16	14	12	10	1
47	R1b3-M269	W. Europe	15	12	24	10	13	13	16	14	12	10	1
48	R1b3-M269	W. Europe	15	12	24	11	13	13	15	13	11	11	1
49	p49a,f-Ht35	Balkan	14	12	24	11	13	13	16	13	12	9	7
50	p49a,f-Ht35	Balkan	14	12	24	10	13	13	16	13	12	9	2
51	p49a,f-Ht35	Balkan	14	12	24	10	13	12	16	13	12	9	2
52	p49a,f-Ht35	Turkey	14	12	24	11	13	12	16	13	12	9	2
53	p49a,f-Ht35	Balkan	14	12	24	10	11	12	16	13	13	9	1
54	p49a,f-Ht35	Balkan	14	12	24	11	13	12	16	13	12	10	1
55	p49a,f-Ht35	Balkan	14	12	24	11	13	12	17	12	12	9	1
56	p49a,f-Ht35	Balkan	14	12	25	11	13	12	16	13	11	10	1
57	p49a,f-Ht35	Balkan	14	12	24	10	13	12	17	13	12	9	1
58	p49a,f-Ht35	Balkan	14	12	24	10	13	12	17	13	11	9	1
59	p49a,f-Ht35	Balkan	14	12	23	10	13	13	16	12	11	10	1
60	p49a,f-Ht35	Balkan	14	12	24	10	13	12	17	14	13	9	1
61	p49a,f-Ht35	Balkan	14	12	23	10	13	12	17	13	13	9	1
62	p49a,f-Ht35	Balkan	15	12	24	11	13	12	15	13	13	9	1
63	p49a,f-Ht35	Georgia	14	12	23	11	13	12	16	13	12	9	1
64	p49a,f-Ht35	Georgia	15	12	24	11	13	12	17	12	12	9	1
65	p49a,f-Ht35	Georgia	14	12	23	10	13	12	16	13	12	9	1
66	p49a,f-Ht35	Georgia	14	12	22	10	13	13	17	13	12	9	1
67	p49a,f-Ht35	Georgia	14	12	24	11	13	12	16	13	11	9	1
68	p49a,f-Ht35	Georgia	14	12	23	10	13	12	17	13	12	9	1
69	p49a,f-Ht35	Georgia	14	12	24	11	14	12	16	14	11	9	1
70	p49a,f-Ht35	Georgia	14	12	24	10	13	13	16	14	12	9	1

Haplotype Number	Haplogroup	Population	Allele status at										Total
			DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	DYS389I	DYS389II	DYS439	DYSA7.2	
71	p49a,f-Ht35	Georgia	14	12	23	11	13	12	17	13	11	9	1
72	p49a,f-Ht35	Georgia	14	12	24	11	13	12	17	13	12	9	1
73	p49a,f-Ht35	Georgia	14	12	24	11	13	12	16	13	11	10	1
74	p49a,f-Ht35	Georgia	14	12	23	11	13	12	16	13	12	9	1
75	p49a,f-Ht35	Georgia	14	12	25	10	13	12	17	13	12	10	1
76	p49a,f-Ht35	Georgia	14	12	24	12	13	12	16	13	11	9	1
77	p49a,f-Ht35	Georgia	14	12	24	11	11	12	16	13	12	9	1
78	p49a,f-Ht35	Turkey	14	12	23	11	13	12	17	13	12	9	1
79	p49a,f-Ht15	Iberia	14	12	24	11	13	13	16	14	11	10	2
80	p49a,f-Ht15	W. Europe, Iberia	14	12	24	11	13	13	16	13	12	10	2
81	p49a,f-Ht15	Iberia	14	10	24	11	13	13	16	12	11	10	1
82	p49a,f-Ht15	Iberia	14	12	24	11	13	13	17	14	12	10	1
83	p49a,f-Ht15	Iberia	14	12	24	11	13	12	16	14	12	10	1
84	p49a,f-Ht15	Iberia	14	12	24	10	13	13	16	14	11	10	1
85	p49a,f-Ht15	Iberia	14	12	24	11	13	13	16	14	12	10	1
86	p49a,f-Ht15	W. Europe	14	12	24	10	13	13	17	13	12	10	1
87	p49a,f-Ht15	W. Europe	14	12	25	11	13	13	18	13	12	10	1
88	p49a,f-Ht15	W. Europe	14	12	24	10	13	13	16	13	12	10	1
89	p49a,f-Ht15	Iberia	14	13	24	11	13	13	16	14	12	10	1
Total													111

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