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Report

Concomitant Replacement of Language and mtDNA in South Caspian Populations of Iran

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Summary

The Gilaki and Mazandarani occupy the South Caspian region of Iran and speak languages belonging to the North-Western branch of Iranian languages [1]. It has been suggested that their ancestors came from the Caucasus region, perhaps displacing an earlier group in the South Caspian [2]. Linguistic evidence supports this scenario, in that the Gilaki and Mazandarani languages (but not other Iranian languages) share certain typological features with Caucasian languages [3, 4]. We analyzed patterns of mtDNA and Y chromosome variation in the Gilaki and Mazandarani. Based on mtDNA HV1 sequences, the Gilaki and Mazandarani most closely resemble their geographic and linguistic neighbors, namely other Iranian groups. However, their Y chromosome types most closely resemble those found in groups from the South Caucasus. A scenario that explains these differences is a south Caucasian origin for the ancestors of the Gilaki and Mazandarani, followed by introgression of women (but not men) from local Iranian groups, possibly because of patrilocality. Given that both mtDNA and language are maternally transmitted, the incorporation of local Iranian women would have resulted in the concomitant replacement of the ancestral Caucasian language and mtDNA types of the Gilaki and Mazandarani with their current Iranian language and mtDNA types. Concomitant replacement of language and mtDNA may be a more general phenomenon than previously recognized.

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Results and Discussion

mtDNA Variation

We analyzed mtDNA haplogroups characteristic for southwest Asia (i.e., haplogroups *H, J, N, T,* and *U*) and sequences of the first hypervariable segment of the mtDNA control region (HV1) and found high diversity in the Gilaki and Mazandarani (Figure 1), comparable to other groups in this region (see Table S1 in the Supplemental Data available with this article online). Pairwise F_{st} comparisons, based on the HV1 sequences, showed that the Gilaki and Mazandarani groups are very similar to each other and to other Iranian and West Asian groups (Table 1). They are next most similar to Caucasus groups and then European groups, and most distant from Central Asian groups (Table 1). An MDS plot (Figure 2A) based on the pairwise F_{st} values illustrates these patterns. Specifically, the Mazandarani and Gilaki groups are located near each other, in a cluster containing other Iranian and West Asian populations. Thus, with respect to patterns of mtDNA variation, the South Caspian groups resemble their geographic and linguistic neighbors, namely other Iranian groups.

Analyses of mtDNA haplogroups further support the close relationship between South Caspian and Iranian groups. Pairwise F_{st} comparisons, based on HV1 sequences within haplogroups, indicate that the Gilaki and Mazandarani groups are closer to Iranian groups than to populations from the South Caucasus region (Figure 3). To further investigate the relationships between the Mazandarani/Gilaki and groups from Iran and the South Caucasus, we constructed networks of the HV1 sequences, grouped according to mtDNA haplogroup (Figure S1). For haplogroups *J, T,* and *U*, most of the Mazandarani/Gilaki HVI sequences cluster with Iranian sequences, whereas for haplogroups *H* and *N*, there is no clear clustering. Thus, both the F_{st} comparisons and the networks of HV1 sequences, within haplogroups, support a closer relationship of the South Caspian groups with other Iranian groups than with South Caucasian groups.

Y Chromosome Variation

Overall, seven Y-SNP haplogroups were found in the Gilaki and ten haplogroups were found in the Mazandarani (Table S2). Haplogroup J2*(M172) was found at high frequency in both groups, as was haplogroup R1*(M173); together, these two haplogroups account for more than 50% of Mazandarani and Gilaki Y chromosomes. Interestingly, the frequency of haplogroup J2*(M172) in these groups is more similar to the frequency in South Caucasus groups than in other Iranian groups [5, 6]. Moreover, haplogroup I*(M170) is found at high frequency in the Iranian groups from Tehran and Isfahan, but is absent in the Mazandarani and Gilaki and is in low frequency in the South Caucasus groups (Table S2).

The pairwise F_{st} value (Table 1) between the Mazandarani and Gilaki groups was not significantly different

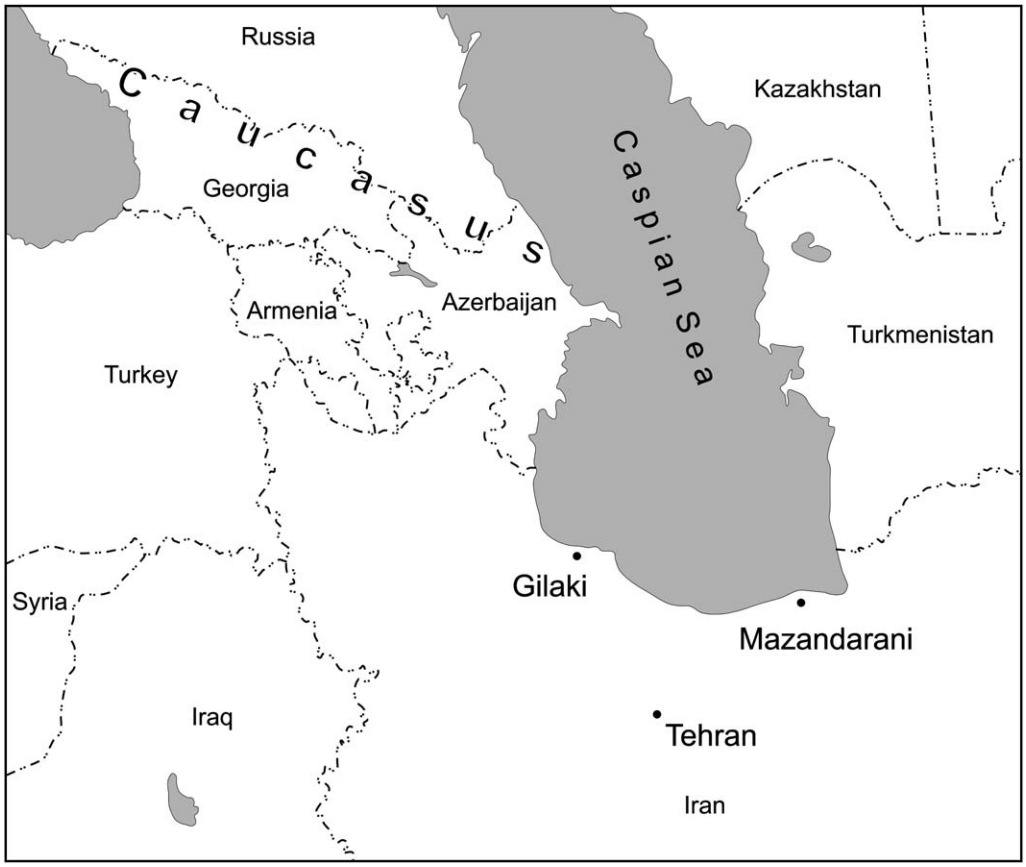

Figure 1. Location of Sampling Sites in the Mazandaran and Gilan Provinces of Iran

from zero (F_{st} = 0.003, p = 0.337). In contrast to the mtDNA results, both groups showed greater similarity with South Caucasian populations than with their geographic and linguistic neighbors, namely other Iranians (F_{st} = 0.013 and 0.084 for Mazandarani versus South Caucasian and versus Iranians, respectively; and F_{st} = 0.010 and 0.072 for Gilaki versus South Caucasian and versus Iranians, respectively).

The MDS analysis (Figure 2B) further illustrates these patterns. The Mazandarani and Gilaki groups fall inside a major cluster consisting of populations from the Caucasus and West Asia and are particularly close to the South Caucasus groups—Georgians, Armenians, and Azerbaijanians. Iranians from Tehran and Isfahan are situated more distantly from these groups.

Three haplogroups were found at high frequencies in the Mazandarani and Gilaki groups (R1*(M173), G*(M201), and J2*(M172)); to further investigate the relationships of these groups based on these three Y-SNP haplogroups, we typed nine Y-STR loci in individuals with these Y-SNP haplogroups and compared the results with the same set of Y-STR loci on the same Y-SNP background that were typed previously in the groups from the South Caucasus and Iran [7]. Reduced median networks of the Y-STR haplotypes (Figure S2) further indicate a closer relationship of the Mazandarani/Gilaki

Table 1. Mean Pairwise F_{st} Values between Mazandarani and Gilaki Groups and between South Caucausian, European, and West and Central Asian Groups

	Mazandarani	Gilani	S. Caucasus	E. Europe	W. Europe	Centr. Asia	Iran	West Asia w/o Iran
Mazandarani		0.007	0.030	0.039	0.036	0.048	0.004	0.022
Gilaki	0.003		0.016	0.021	0.020	0.036	0.011	0.015
S. Caucasus	0.013	0.010		0.028	0.019	0.071	0.018	0.035
East Europe	0.206	0.158	0.197		0.013	0.078	0.021	0.035
West Europe	0.233	0.176	0.238	0.326		0.092	0.021	0.041
Centr. Asia	0.136	0.106	0.128	0.306	0.339		0.061	0.048
Iran	0.084	0.072	0.061	0.123	0.235	0.106		0.019
West Asia w/o Iran	0.060	0.037	0.064	0.185	0.241	0.124	0.061	

Below diagonal empty cells are shown pairwise F_{st} values based on Y-SNP haplogroups; above diagonal empty cells are shown pairwise F_{st} values based on mtDNA HVI sequences.

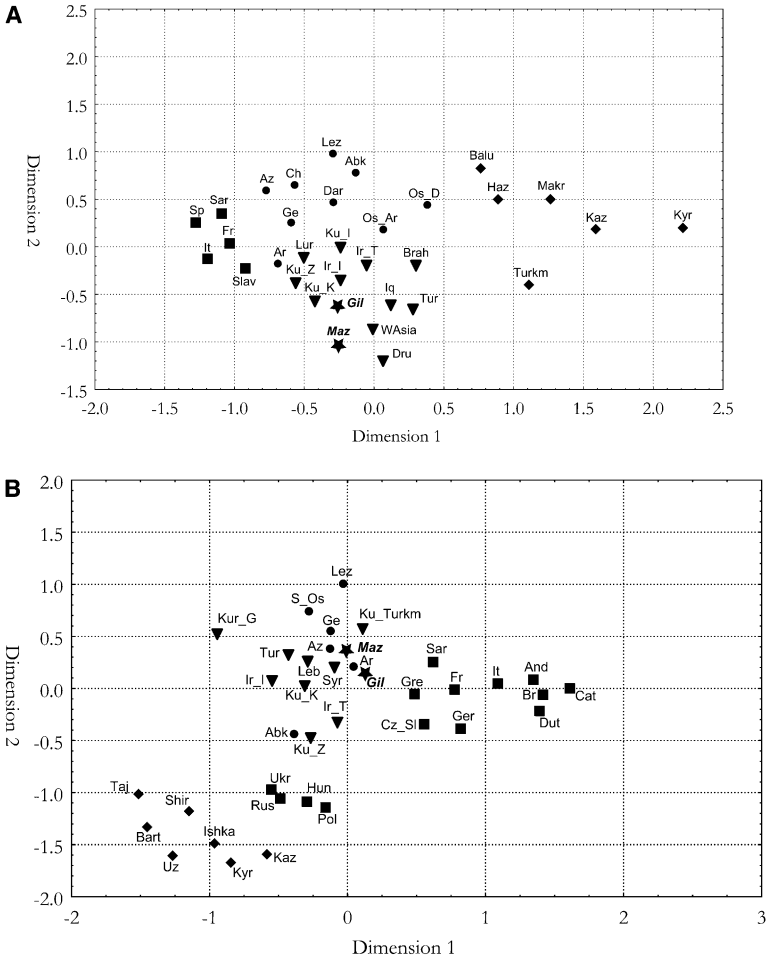

Figure 2. Multidimentional Scaling Plots

Multidimensional scaling (MDS) plots (STATISTICA package [StatSoft Inc.]) based on pairwise F_{st} values, showing relationships among the Mazandarani and Gilaki groups, and Caucasian, European, and Central and West Asian groups. Mazandarani and Gilaki groups are represented by stars; Caucasus groups by circles; European groups by squares; Central Asian groups by diamonds; and West Asian groups by triangles.

(A) Based on mtDNA HVI sequence data. The stress value for the MDS plot is 0.125.

(B) Based on Y chromosome SNP data. The stress value for the MDS plot is 0.142. Names of the groups are abbreviated as follows: Abk, Abkhazians; And, Andalusians; Ar, Armenians; Az, Azerbaijanians; Balu, Baluch; Bart, Bartangi; Br, British; Brah, Brahui; Cat, Catalans; Ch, Cherkessians; Cz-Sl, Czech & Slovaks; Dar, Darginians; Dru, Drusi; Dut, Dutch; Fr, French; Ge, Georgians; Ger, Germans; Gil, Gilaki; Gre, Greeks; Haz, Hazar; Hung, Hungarians; Iq, Iraqi; Ir_Isf, Persians from Isfahan; Ir_Teh, Persians from Tehran; It, Italians; Ishka, Ishkinasi; Kaz, Kazakh; Ku_G, Kurds from Georgia; Ku_I, Kurds from Iran; Ku_K, Kurmanji speaker Kurds; Ku_Turkm, Kurds from Turkmenistan; Ku_Z, Zazaki speaker Kurds; Kyr, Kyrgiz; Leb, Lebanese; Lez, Lezginians; Makr, Makrani; Maz, Mazandarani; Os_A, Ossetians from Ardon; Os_D, Ossetians from Digora; Pol, Polish; Rus, Russians; S_Os, South Ossetians; Sar, Sardinians; Shir, Shiraz; Slav, Slavs; Sp, Spanish; Syr, Syrians; Taj, Tajik; Tur, Turks; Turkm, Turkmens; Ukr, Ukrainians; Uz, Uzbeks; WAsia, West Asians.

Y-STR haplotypes with South Caucasian Y-STR haplotypes than with Iranian Y-STR haplotypes. This is most evident in the network for Y-STR haplotypes on the background of haplogroup R1*(M173), in which 9 of 11 Mazandarani/Gilaki Y-STR haplotypes fall into a single cluster that connects with South Caucasian Y-STR haplotypes, and for haplogroup G*M201, in which 9 of 12 Mazandarani/Gilaki Y-STR haplotypes group with South Caucasian Y-STR haplotypes while the other three could be of either Iranian or South Caucasian origin (Figure S2). For haplogroup J2*(M172), the pattern is less clear: six Mazandarani/Gilaki Y-STR haplotypes group with South Caucasian haplotypes and three group with Iranian haplotypes, while the remaining six

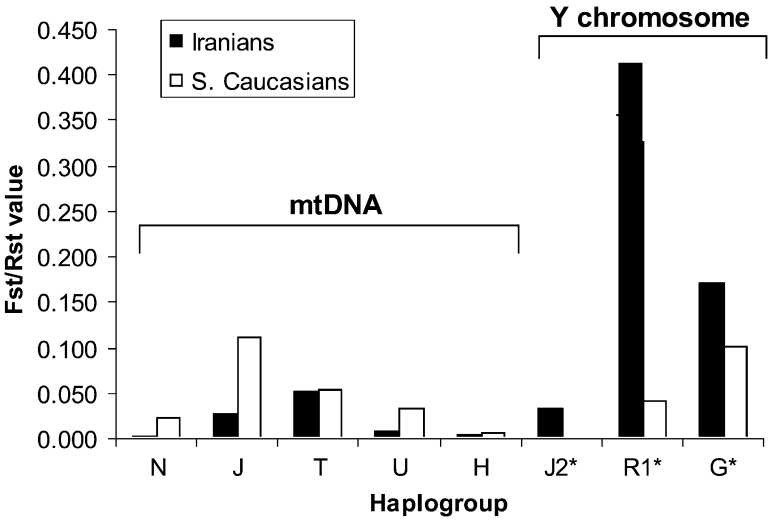

Figure 3. Pairwise F_{st} and R_{st} Values for Mazandarani/Gilaki versus South Caucasian Groups and for Mazandarani/Gilaki versus Iranian Groups

Pairwise F_{st} values based on HVI sequences within mtDNA haplogroups, and R_{st} values based on Y-STR haplotypes on the background of some Y-SNP haplogroups, for Mazandarani/Gilaki versus South Caucasian groups and for Mazandarani/Gilaki versus Iranian groups.

haplotypes could be of either Iranian or South Caucasian origin (Figure S2).

The patterns observed in the median networks are further supported by pairwise R_{st} comparisons for Y-STR haplotypes within each Y haplogroup (Figure 3); the Mazandarani/Gilaki are more similar to South Caucasian groups than to Iranian groups for Y-STR haplotypes within all three Y-SNP haplogroups. Nevertheless, the sample sizes in these analyses are small and thus the results could change with further sampling. However, while some contribution of Y chromosomes of Iranian origin to the Mazandarani/Gilaki cannot be excluded, overall the Y chromosome data do indicate a closer relationship of the Mazandarani and Gilaki with South Caucasian groups than with Iranian groups.

Origins of the South Caspian Groups

The mtDNA and Y chromosome data give conflicting views on the relationships of the South Caspian groups: the mtDNA data suggest that they are most closely related to their geographic and linguistic neighbors, namely other Iranian groups, whereas the Y chromosome data suggest that they are most closely related to South Caucasian groups. How can these be reconciled?

One possible scenario would be an origin for the Gilaki and Mazandarani in the South Caucasus and migration to the South Caspian region, followed by the incorporation of females (but not males) from the local Iranian groups. Such preferential incorporation of females would be expected if the ancestors of the Gilaki and Mazandarani groups were patrilocal, which is the case today, and would lead to the introgression of mtDNA types (but not Y chromosomes) from the local Iranian groups. Over time, the mtDNA gene pool of the South Caspian groups would come to resemble that of their geographic neighbors, while the Y chromosome gene pool would still reflect their South Caucasian origin.

Presumably the ancestors of the Gilaki and Mazandarani spoke a Caucasian language; therefore, their original Caucasian language must have been replaced by the local Iranian language under the above scenario. Indeed, typological analysis of the Gilaki and Mazandarani languages does indicate some sharing of features with south Caucasian languages [3, 4]. While the process of language replacement may have been completely independent of the introgression of mtDNA types, it is tempting to speculate that they were in fact related: the influx of local women, speaking the local Iranian language, may have caused (or accelerated) the replacement of the original Caucasian language of the ancestors of the Gilaki and Mazandarani. Thus, the concomitant replacement of both the language and the mtDNA types of the ancestors of the South Caspian groups may have been the result of the incorporation of local females, under the influence of patrilocality.

How widespread is this phenomenon? Other cases of discrepancies between the mtDNA and Y chromosome relationships of populations are rare, but where they do occur, the linguistic relationships do tend to reflect the mtDNA relationships, rather than the Y chromosome relationships. For example, Polynesians have high frequencies of mtDNA types of Asian origin and high frequencies of Y chromosomes of Melanesian origin [8, 9], and they speak Austronesian languages of Asian origin, matching their mtDNA relationships. Also, Jewish populations in different geographic regions are generally characterized by similar Y chromosomes that are distinct from the Y chromosomes of their geographic neighbors, indicating a common paternal origin, but different mtDNA types that are related to the mtDNA types of their geographic neighbors [10]. Moreover, they speak the language of their geographic region, which also is the origin of their mtDNA types—exactly as in the case of the South Caspian populations. The concomitant replacement of mtDNA and language after the migration of a group to a new region may thus be a more general phenomenon than previously recognized, and furthermore emphasizes the role of maternal transmission of language as a means of language replacement.

Experimental Procedures

Samples and DNA Extraction

A total of 100 cheek cell samples from unrelated males, representing two populations from Iran (Figure 1)—Mazandarani (50 samples) and Gilaki (50 samples)—were collected. Genomic DNA from cheek cell swabs was extracted by a standard salting-out procedure [11]. Informed consent and information about birthplace, parents, and grandparents was obtained from all donors.

mtDNA Analysis

The first hypervariable segment (HV1) of the mtDNA control region was amplified via primers L15996 and H16410 [12], as described previously [8], and sequences for both strands of the PCR products were determined with the DNA Sequencing Kit (Perkin-Elmer), following the protocol recommended by supplier, and by an ABI 3700 automated DNA sequencer. Individuals with the "C-stretch" between positions 16184 and 16193 were sequenced again in each direction, so that each base was determined twice. The mtDNA HVRI sequences will be published online on the authors' web page at the time of publication (http://www.eva.mpg.de/genetics/files/pubs_stoneking.html).

Published mtDNA HV1 sequences were included from Caucasus, West and Central Asian, and West and East European groups [6, 13–24].

mtDNA haplogroups that are most informative in southwest Asia, i.e., haplogroups H, J, N, T, and U, defined by SNPs at nucleotide positions 7025, 13704, 10671, 13366, and 12308, respectively [23], were determined by PCR-RFLP assays of the relevant SNP, as described elsewhere [23, 24].

Y Chromosome Analysis

All 100 samples were typed for the X- and Y-linked zinc finger protein genes in order to confirm the gender of the sample [25]. Genotyping was carried out for ten Y chromosomal SNP markers (*RPS4Y (M130), M9, M89, M124, M45, M173, M17, M201, M170,* and *M172* [26]) and *YAP Alu* insertion polymorphism [27] as described elsewhere [6, 9, 27–29]. The samples were genotyped according to the hierarchical order of the markers as described in [26]. Published Y-SNP data for Caucasian, European, West Asian, and Central Asian groups [6, 22, 30–32] were also included in some analyses.

Eleven samples belonging to Y-SNP haplogroup *R1**(M173), 12 samples belonging to haplogroup *G**(M201), and 17 samples belonging to haplogroup *J2**(M172) were genotyped for nine Y chromosome short tandem repeat (Y-STR) markers: *DYS19 (DYS394), DYS385a, DYS385b, DYS389I, DYS389II, DYS390, DYS391, DYS392,* and *DYS393* as described elsewhere [33, 34]. The resulting Y-STR haplotypes were compared to published Y-STR haplotypes from these same haplogroups from Iran and the south Caucasus [7].

Statistical Analysis

Basic parameters of molecular diversity and population genetic structure were calculated with the software package Arlequin

2.000 [35]. F_{st} values for mtDNA HVI sequences were calculated with the Kimura 2 parameter model, and for Y-SNP data with no molecular distance; for the Y-STR data, R_{st} values [36] were calculated. The statistical significance of F_{st} and R_{st} values was estimated by permutation analysis, with 10,000 permutations. The STATISTICA package (StatSoft Inc.) was used for multidimensional scaling (MDS) analysis based on pairwise F_{st} values for mtDNA HVI and Y-SNP data sets; the default starting configuration (i.e., principle components analysis) was used, and the number of dimensions was set to two. Network analysis for Y-STR and mtDNA HV1 sequence data was carried out with the software package NETWORK version 3.1 [37].

Supplemental Data

Supplemental Data include two figures and two tables and can be found with this article online at http://www.current-biology.com/cgi/content/full/16/7/668/DC1/.

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