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The Differences Among Jewish Communities—Maternal and Paternal Contributions

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Abstract: The haplotypes of Y chromosome (paternally inherited) and mtDNA (maternally inherited) were analyzed in representatives of six Jewish communities (Ashkenazic, North African, Near Eastern, Yemenite, Minor Asian/Balkanian, and Ethiopian). For both elements, the Ethiopian community has a mixture of typically African and typically Caucasian haplotypes and is significantly different from all others. The other communities, whose haplotypes are mostly Caucasian, are more closely related; significant differences that were found among some of them possibly indicate the effects of admixture with neighboring communities of non-Jews. The different contribution of the Y chromosome and mtDNA haplotypes to the significant differences among the communities can be explained by unequal involvement of males and females in the different admixtures. In all communities, except the Ethiopians, the level of diversity ($\hat{h}$) for Y chromosome haplotypes is higher than that for mtDNA haplotypes, suggesting that in each community the people who become parents include more males than females. An opposite proportion (more females than males) is found among the Ethiopians.

Key words: Jewish communities — Y chromosome — Mitochondrial DNA — Admixture

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Introduction

The Hebrew nation that had lived in the land of Israel until about 2,000 years ago is believed to be the origin of all Jews. The genetic similarities that Jewish communities should thus show seem to contradict the large phenotypic differences that exist among them, and this problem is the basis of many arguments (Mourant et al. 1978; Bonné-Tamir et al. 1979; Kobyliansky et al. 1982; Livshits et al. 1991; Bonné-Tamir and Adam 1992).

Prominent among the mechanisms that may be responsible for the dissimilarities between members of the different communities is admixture with neighboring communities of non-Jews. The process of admixture should be analyzed with neutral genetic markers, since for markers that are affected by selection, differences could be due to the presence of each community in a different environment, and not to gene flow.

A study of the effect of admixture on Jewish communities should consider separately the contribution of each parental lineage, because there may be a difference in the tendency of the two genders to be involved in it. This can be achieved by examining female-specific and male-specific genetic markers. Such markers have recently become available: Mitochondrial DNA (mtDNA) is maternally inherited (except for mutations, the mtDNAs of all members of a population are identical to those of the mothers in the previous generation), while the Y-specific segment of the Y chromosome is paternally inherited. (It is transferred from a father to all

his sons.) Both of these markers do not undergo recombination, so differences among individuals are due exclusively to mutations, which, for these markers, are believed to be neutral (Singh and Hale 1990 and Nigro and Prout 1990 for mtDNA; Ngo et al. 1986 and Clark 1987 for the Y-specific segment of the Y chromosome).

A major difference between these two markers is the level of resolution by which they can be analyzed. In contrast to human mtDNA, for which a complete sequence has been published (Anderson et al. 1981)—and differences among individuals can occur in each of its 16,569 nucleotides—the variable segments of the human Y chromosomes are relatively limited (Malaspina et al. 1990). In the current analysis, the method of restriction fragment length polymorphism (RFLP) gave, for both markers, a similar number of fragments. Hybridization of human DNA, digested by the restriction enzyme *Taq*I, with the Y-specific probes p49f (p49a) and $p12f_2$, reveals about 20 male-specific fragments, and by digesting human mtDNA with five restriction enzymes (*Hpa*I, *Bam*HI, *Hae*II, *Msp*I, and *Ava*II), 40–45 mitochondrial DNA fragments are obtained.

The variability of mtDNA haplotypes in 270 individuals, representing seven Jewish communities, using these restriction enzymes, had been described by Ritte et al. (1993). The present paper discusses the variably of Y-chromosome haplotypes in 291 males representing 6 of these communities, and compares the results of the 2 studies.

In the human karyotype, Y is one of the smallest chromosomes (Goodfellow et al. 1985). It is composed of two distinct parts—the pseudoautosomal region, and the Y-specific region (Weissenbach et al. 1989). The pseudoautosomal region recombines with a homologous segment on the X chromosome, and its markers are not Y-specific. Most of the Y-specific region of the Y chromosome is heterochromatic (Goodfellow et al. 1985). Its DNA is composed (mostly or completely) of moderately or highly repeated sequences. The reasons for the variability among different Y's are not certain, but it is believed (Barker et al. 1984; Spurdle and Jenkins 1992) that the differences are due to CpG mutations and duplications of certain DNA segments.

The analysis of Y-specific DNA is done by digesting total genomic DNA with a restriction enzyme and hybridizing it with Y-specific probes. Most available Y-specific probes do not reveal differences between individuals (Jakubiczka et al. 1989; Malaspina et al. 1990). The probes that do show differences are $p12f_2$ (Casanova et al. 1985; Leroy et al. 1985), p49a, and p49f (Lucotte and Ngo 1985; Ngo et al. 1986). These probes were used in the present study.

Table 1. The fragment patterns of probe $p12f_2$ (numbers of individuals and in parentheses percent of total)

Community	Fragment pattern 8	Fragment pattern 10	Total # analyzed
Ashkenazic	18 (41)	26 (59)	44
North Africans	32 (30)	75 (70)	107
Near Easterns	27 (31)	59 (69)	86
Minor Asians & Balkanians	10 (45)	12 (55)	22
Yemenites	9 (60)	6 (40)	15
Ethiopians	1 (6)	16 (94)	17
Total	97 (33)	194 (67)	291

Materials and Methods

The Sample. DNAs of 291 unrelated males who live in Israel were analyzed by the Y-specific probes of $p12f_2$, p49a, and p49f. After the country of origin of the paternal line of each one was determined, they were divided into the following 6 communities: (1) Ashkenazic (Jews from Central and Eastern Europe)—44; (2) North African—107 (72 from Morocco; the others from Tunisia, Algeria, Egypt, and Libya); (3) Near Eastern—86 (51 from Iraq, 22 from Iran, 8 from Kurdistan, and 5 from Syria); (4) Minor Asians and Balkanians—22 (12 from Turkey and 10 from Bulgaria); (5) Yemenites—15; and (6) Ethiopians—17.

DNA Purification. Placentas of male babies (obtained at the delivery rooms of Hadassah University Hospital, Mount Scopus, and Misgav Ladach Hospital, both in Jerusalem) and blood clots from male donors (obtained from the Blood Bank, Hadassah medical Center, Ein Kerem, Jerusalem) served as sources of genomic DNA.

Small samples of placenta tissue were minced and washed with Hank's solution, and the blood clots were washed with 0.016 M Tris, 0.14 M NH_4Cl, pH 7.2, to remove red blood cells. After incubation with 0.25% SDS and 0.2 mg/ml proteinase K, the solution underwent phenol extraction. The precipitated DNA was dissolved in TE (10 mM Tris pH 7.5; 1 mM EDTA pH 8.0).

DNA Analysis. About 10 μg from each DNA was digested with restriction enzyme *Taq*I (4 units of enzyme per 1 μg DNA). The DNA fragments were separated in 0.8% agarose horizontal gels in TEA buffer (40 mM Tris; 10 mM EDTA pH 8.0; 20 mM acetic acid) and transferred to a nylon membrane (Hybond N, Amersham).

On the membrane, the DNA fragments were hybridized separately with the three Y-specific probes. These probes, originally obtained from Dr. P.N. Goodfellow in Britain and Dr. M. Fellous in France, were radioactively labeled by the random-primer-extension method.

Probe $p12f_2$, which is a 2.2-kb-long fragment that is mapped to the interval Yq11.1-Yq11.22 (Casanova et al. 1985), identifies many Y-specific fragments. Two of them—8 kb and 10 kb long—are clear-cut. The 10-kb-long fragment is polymorphic—some DNAs show both bands, while in the others only the 8-kb-long fragment is present.

Probe p49f, which is a 2.8-kb-long fragment that is mapped to the Yq11.2 region (Quack et al. 1988), identifies about 16 Y-specific fragments (named alphabetically, according to size, A–R). We refer to six of them (A, B, C, D, F, and I). Each of these fragments could be present or absent, and fragments A and D also showed variation in size.

Probe p49a, which is a 0.9 kb-long fragment that is separated

Table 2. The haplotypes of probes p49f and p49a found in our sample, the number of each haplotype (according to Spurdle and Jenkins 1992; numbers 63–77 are new haplotypes), and their distribution among the different Jewish communities

Haplotype							Jewish communities						
A	B	C	D	F	I	Haplotype number	Ashkenazic	North African	Near Eastern	Minor Asians & Balkanians	Yemenites	Ethiopians	Total
0	1	0	0	0	0	39			1				1
0	1	0	0	0	1	27	1						1
0	1	0	0	1	1	1		1	2				3
0	1	0	1	0	1	63			1	1			2
1	1	0	0	0	1	34		1					1
1	1	0	1	0	1	65		1	1				2
1	1	0	1	1	1	42[SB]			12		1		13
2	0	0	1	1	0	45[SB]	1	2	2	1			6
2	0	0	1	1	1	66		2					2
2	1	0	0	0	0	55	1						1
2	1	0	0	0	1	33		3	3		1	10	17
2	1	0	0	1	0	56	1	1					2
2	1	0	0	1	1	5		5	3				8
2	1	0	1	0	0	44[SB]		4	7				11
2	1	0	1	0	1	6		11	6	4		1	22
2	1	0	1	1	0	7	12	10	4	1	2		29
2	1	0	1	1	1	8	8	18	14	2	7		49
2	1	0	2	0	1	67			1				1
2	1	0	2	1	1	68					1		1
2	1	1	1	0	1	69		1					1
2	1	1	1	1	1	24		1					1
2	1	1	1	1	0	22		1					1
3	1	0	0	0	0	29			1				1
3	1	0	0	0	1	32		1		1		6	8
3	1	0	0	1	1	11	4	1	2		1		8
3	1	0	1	0	1	70		4	3	1			8
3	1	0	1	1	0	12	1	2	1				4
3	1	0	1	1	1	13	1	4	6				11
3	1	0	½	1	1	71		1					1
3	1	1	0	0	1	57	2				1		3
3	1	1	0	1	1	28[T]	1	1	4	1	1		8
3	1	1	1	0	1	72				1			1
3	1	1	2	0	1	31[T]		1					1
3	1	1	1	1	1	14			2				2
3	1	1	2	1	1	15		1		1			2
4	1	0	0	1	1	36		1					1
4	1	0	1	0	1	73		3	1	1			5
4	1	0	1	1	1	18	1	2					3
5	1	0	1	0	1	74		1					1
5	1	0	1	1	1	42			1				1
⅔	1	0	1	1	1	64		1					1
¾	1	0	1	0	1	75		1					1
¾	1	0	0	0	1	44		1					1
¾	1	0	0	1	1	40	1						1
¾	1	1	0	1	1	48[SB]		3					3
¾	1	1	0	0	1	76		1					1
¾	1	1	1	1	1	77		1					1
¾	1	1	2	1	1	60		1		1			2
Number of individuals							35	94	78	16	15	17	255

[SB] This haplotype was first described, and given that number, by Santachiara Benerecetti et al. (1992)
[T] This haplotype was first described, and given that number, by Torroni et al. (1990)

from p49f by 6 kb (Ngo et al. 1986), identifies the same fragments as p49f. The resolution of the fragments was improved when the DNAs were hybridized with both probes.

Each different fragment pattern of p49f (p49a) is called a haplotype. Because of the inconsistencies that arose in the numbering of the different haplotypes, this paper follows the arabic numeral system of Spurdle and Jenkins (1992). New haplotypes were given successive numbers, starting at 63.

Statistical Analysis. The Y chromosome haplotype distribution of each community was compared to that of each of the

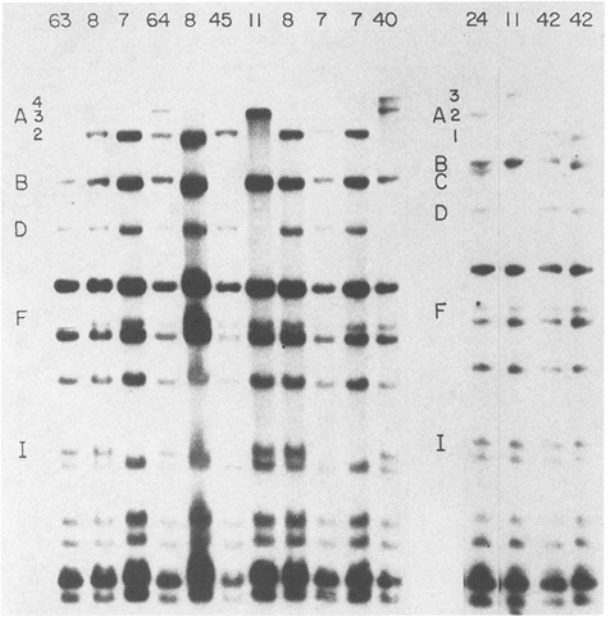

Fig. 1. A demonstration of some of the haplotypes. The haplotype number is written above each lane. The *letters* refer to the six polymorphic fragments.

other five communities by a chi-square method. Altogether, 15 pairwise comparisons were carried out. In order to achieve an overall significance level α, it is advisable to test each comparison at a lower significance level α', where $\alpha' = 1 - (1 - \alpha)^{1/m}$ (m is the number of comparisons). Thus, for an overall significance level $\alpha = 0.05$, each comparison should be tested at $\alpha' = 0.0034$. The results are presented in Table 3.

Since these tests involved a substantial number of expected frequencies which are rather small, the chi-square distribution cannot be a reliable approximation. The P values (i.e., the probabilities of rejecting the null hypothesis that the two compared distributions are the same) were thus estimated by computer simulations. For each comparison, 1,000 simulated samples were drawn under the assumption that the distribution of Y chromosome haplotypes is independent of the community. The proportion of samples which had a chi-square statistic larger than the observed chi-square was taken as an estimate of the real P value.

Pairwise genetic distances between the different communities were calculated using the approach suggested by Nei (1975, p. 177). The genetic distance between two communities is calculated as

$$1 - \frac{\Sigma x_i y_i}{\sqrt{\Sigma x_i^2}\sqrt{\Sigma y_i^2}}$$

where x_i and y_i are the frequencies of haplotype i in each community. The more frequently used D statistic cannot be used in cases like ours, in which several I values (normalized identities between two communities) equaled zero. This leads to an inability to draw a phylogenetic tree. Table 4 includes the different values of genetic distance.

The diversity value of the different haplotypes in each community, $\hat{h}$, has been calculated according to the equation

$$\hat{h} = \left(1 - \sum_{i=1}^{m} x_i^2\right) n/(n-1)$$

in which x_i = frequency of haplotype i, m = number of different haplotypes, and n = sample size (Nei and Tajima 1981). The $\hat{h}$ values of the Y chromosome haplotypes of each community, together with the corresponding $\hat{h}$ value of mtDNA haplotypes (Ritte et al. 1993), are presented in Table 5.

Results

The 2 fragments of probe $p12f_2$ by which the Y-specific DNAs are compared are 8 and 10 kb long. The fragment pattern that has both fragments is called 10, and the pattern that shows only the 8-kb-long fragment is called 8. The distribution of these two patterns, separately in each community and in the total sample of 291 individuals, is given in Table 1.

Six fragments—A, B, C, D, F and I—were polymorphic with probes p49f and p49a. All six could be present (A1, B1, C1 . . .) or absent (A0, B0, C0 . . .), and A and D showed additional variation in the length of the fragments (A1, A2, A3 . . .). Some patterns had two A or two D fragments.

The 255 individuals for whom we could identify all 6 polymorphic fragments of probes p49a and p49f had 48 different haplotypes, of which 15 were new. A list of these haplotypes, together with the number given to each, and its relative frequency in each community and in the entire sample, is presented in Table 2.

Following the numbering system of Spurdle and Jenkins (1992), the new haplotypes are numbered 63–77. Several of the haplotypes are shown in Fig. 1.

When the fragment patterns for probes $p12f_2$ and p49a/p49f were combined, 58 different haplotypes were found (in 234 individuals).

Among the haplotypes of Table 2, the most common (haplotype 2-1-0-1-1-1) was found in almost 20% of the total sample, except for Ethiopians, who did not have it. Twenty-two haplotypes were each found in a single individual.

Considering the variability of individual fragments, it should be pointed out that pattern 8 of probe $p12f_2$ (Table 1) was extremely rare among the Ethiopians. For the fragments of probes p49a and p49f, A2 was the most common among the A fragments. A1, which was previously found mostly among Africans (Torroni et al. 1990), in our study was found in 13 Near Eastern Jews (8 of whom from Iran) but not among Ethiopians. Patterns that had two A fragments were found mostly (9/11) among the North Africans; Santachiara Benerecelli et al. (1992) also found such a combination in Sephardic Jews.

Discussion

Table 3 presents the chi-square statistics of the pairwise comparisons of Y chromosome haplotype dis-

Table 3. The chi-square values of pairwise comparisons between Y-chromosome haplotype distributions of six Jewish communities[a]

Community	North Africans	Near Easterns	Minor Asians & Balkanians	Yemenites	Ethiopians
Ashkenazic	58.39 (42) $P = 0.019$*	53.36 (31) $P = 0.001$**	31.84 (20) $P = 0.002$**	13.96 (13) $P = 0.402$	46.00 (13) $P = 0.000$**
North Africans		62.24 (47) $P = 0.002$**	48.52 (41) $P = 0.201$	52.27 (39) $P = 0.078$	77.20 (36) $P = 0.000$**
Near Easterns			45.45 (31) $P = 0.036$*	29.44 (27) $P = 0.363$	69.72 (26) $P = 0.000$**
Minor Asians & Balkanians				19.52 (18) $P = 0.334$	29.99 (14) $P = 0.000$**
Yemenites					30.00 (10) $P = 0.000$**

[a] For each pair of communities, the chi-square statistic is presented together with the number of degrees of freedom (in parentheses). The P values are estimated by computer simulations. A single asterisk indicates values which are significant at a level between 0.0034 and 0.050. A double asterisk indicates values which are significant at a level smaller than 0.0034 (see text)

Table 4. Pairwise genetic distances for Y-chromosome haplotypes among six Jewish communities

Community	North Africans	Near Easterns	Minor Asians & Balkanians	Yemenites	Ethiopians
Ashkenazic	0.4234	0.5677	0.6571	0.3262	1.0000
North Africans		0.4447	0.5570	0.6503	0.8547
Neat Easterns			0.6417	0.4632	0.8488
Minor Asians & Balkanians				0.5347	0.9804
Yemenites					1.0000

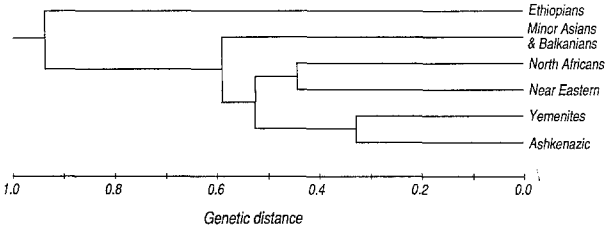

Fig. 2. A population tree, based on the genetic distances for Y-chromosome haplotypes, of six Jewish communities.

tributions in the different communities, together with their levels of significance. The Ethiopian community is significantly different from all others. Among the 10 other comparisons, each community shows at least one nonsignificant difference with the others. The significant differences may indicate admixture, but this cannot be verified because no information is available about Y chromosome haplotypes in the corresponding communities of non-Jews. The inclusion of the Yemenites in many of the nonsignificant differences indicates that their admixture did not involve many males. In a similar table of differences for mtDNA haplotypes (Ritte et al. 1993), the community that participated in most nonsignificant pairwise comparisons was from North Africa (Morocco). The discrepancy in the results of the two sets of comparisons may indicate

Table 5. The diversity values ($\hat{h}$; Nei and Tajima 1981), their standard errors, and sample sizes (in parentheses), of the different Jewish communities, for both Y-chromosome and mtDNA haplotypes

	$\hat{h}$ value ± SE for	
Community	Y chromosome	mtDNA[a]
Ashkenazic	0.830 ± 0.045 (35)	0.681 ± 0.043 (75)
North Africans	0.933 ± 0.014 (94)	0.528 ± 0.122 (22)
Near Easterns	0.922 ± 0.014 (78)	0.671 ± 0.106 (26)
Minor Asians & Balkanians	0.942 ± 0.042 (16)	0.786 ± 0.152 (8)
Yemenites	0.790 ± 0.106 (15)	0.510 ± 0.073 (65)
Ethiopians	0.559 ± 0.078 (17)	0.724 ± 0.050 (57)

[a] From Ritte et al. (1993)

differences in the contribution of the two sexes to the processes of admixture.

Table 4 shows the pairwise genetic distances for the Y-chromosome haplotypes. Most closely related are the Ashkenazic and Yemenite communities. Other pairs of communities that are closely related are North African–Ashkenazic, North African–Near Eastern, and Yemenite–Near Eastern.

A population tree, based on a cluster analysis of these genetic distances, is presented in Fig. 2.

The Ethiopian community is most distantly re-

lated, supporting the view of many historians (Ullendorf 1968) that these people are descended from inhabitants of Ethiopia who were converted to Judaism. For both mtDNA and Y chromosome, they show a combination of typically African and typically Caucasian haplotypes.

Table 5 lists the $\hat{h}$ values for the Y-chromosome haplotypes and compares them with the $\hat{h}$ values for mtDNA haplotypes (Ritte et al. 1993), separately for each community. A comparison of the $\hat{h}$ values of each community shows that in all communities, except the Ethiopians, the $\hat{h}$ value of the Y chromosome is higher than the corresponding value of mtDNA. (All these differences are significant at the 0.05 level, except for the Minor Asian/Balkanian community, where the difference is not significant, apparently because of small sample size.) This difference may suggest that in these communities there are more males than females in the effective population size. On the other hand, more females than males characterize the effective population size of the Ethiopians (as was found for other Africans by Torroni et al. 1990).

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