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The Origins of the Lemba “Black Jews” of Southern Africa: Evidence from p12F2 and Other Y-Chromosome Markers

Amanda B. Spurdle* and Trefor Jenkins

Department of Human Genetics, School of Pathology, The South African Institute for Medical Research and University of the Witwatersrand, Johannesburg

Summary

The Lemba are a southern African Bantu-speaking population claiming Jewish ancestry. Allele frequencies at four different Y-specific polymorphic loci, as well as extended-haplotype frequencies that included data from several loci, were analyzed in an attempt to establish the genetic affinities and origins of the Lemba. The results suggest that $\geq 50\%$ of the Lemba Y chromosomes are Semitic in origin, $\sim 40\%$ are Negroid, and the ancestry of the remainder cannot be resolved. These Y-specific genetic findings are consistent with Lemba oral tradition, and analysis of the history of Jewish people and their association with Africa indicates that the historical facts are not incompatible with theories concerning the origin of the Lemba.

Introduction

The ability of Y-chromosome polymorphisms to provide a record of male-specific gene flow and human variation has long been recognized, and numerous studies using different Y markers have indicated the value of this approach. These studies include investigations using the conventional RFLPs detected by p12F2 (Casanova et al. 1985), p49a (Ngo et al. 1986), pDP31 (Spurdle and Jenkins 1994), and the Y *Alu* polymorphism (YAP) (Hammer 1994).

The Lemba population of southern Africa constitutes a group of Bantu-speakers who claim Jewish ancestry. Historically, the Lemba were distinct from their Bantu-speaking Negroid neighbors by their means of livelihood, physical appearance, customs, and rituals (Van Warmelo 1974), and even nowadays the cultural differences between the Lemba and other Bantu-speakers are

recognized. An analysis of a collection of Y-specific RFLP data was undertaken in an attempt to establish the genetic origins of the Lemba. The data include results for the 49a, pDP31, and YAP loci, which have been presented elsewhere (Spurdle et al. 1994; Spurdle and Jenkins 1992, 1994), as well as previously unpublished findings for the p12F2 locus. Frequency data for the different Y-chromosome RFLPs were compared with data from suitable control populations (including Semitic groups), and the analysis was extended to include haplotypes incorporating data from several loci.

Subjects and Methods

The Lemba

Culture.—The Lemba population includes several clans that are widely dispersed among Bantu-speaking groups, mostly in Zimbabwe and the northern areas of South Africa. There are estimated to be $\sim 40,000$ Lemba living in South Africa and $\sim 15,000$ spread among other southern and central African countries (M. Nabarro, personal communication). Several historical facts set them apart from their Bantu-speaking Negroid neighbors (Van Warmelo 1974; Mourant et al 1978; Mathivha 1992; Parfitt 1992): they were highly regarded as master metal workers (in iron, copper, and gold) and as skilled potters; the men used to wear a long cotton garment (a khanzu) as found along the east coast of Africa; and among themselves they spoke a language not understood by their Bantu-speaking neighbors. The Lemba have also been recognized by some anthropologists as having Caucasoid physical features (Van Warmelo 1974; Mourant et al 1978). In addition, the Lemba are culturally quite distinct from other Bantu-speakers, in that they practice a religion that embraces many extraordinary rituals and laws. Although the assimilation of the Lemba into modern South African society is slowly eroding their culture, many of the rural Lemba still follow traditional ways. Marriage laws encourage strict endogamy, and acceptance of non-Lemba men into the community is especially rare (Van Warmelo and Phophi 1948). Male circumcision is practiced, and Lemba boys are initiated at about the time of puberty, in secret closed lodges. The stringent food laws (Van Warmelo 1974; Mathivha 1992) appear to be essentially Jewish.

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Address for correspondence and reprints: Dr. Trefor Jenkins, Department of Human Genetics, South African Institute for Medical Research, P.O. Box 1038, Johannesburg, 2000, South Africa.

*Present affiliation: School of Genetics and Human Variation, La Trobe University, Bundoora, Victoria, Australia.

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Oral history.—The oral history of the Lemba forms the basis for most theories concerning their origins. Zimbabwean Lemba have a tradition that they came from the north and that their fathers did skilled metalwork for the Arabs (Hughes et al. 1976). An extensive summary of southern African Lemba oral history by Van Warmelo (1974) indicates that the Lemba ancestors are believed to have come from a huge town across the seas, where there were many craftsmen in metalwork, pottery, textiles, and shipbuilding. They came to southern Africa to trade, especially for gold. With time, they left behind men with the unsold cargo, establishing posts on the coast and further inland. One day they received the shattering news that their home town had been taken by the enemy, and they could not return. They thus began taking local wives, and the different trading posts marked the establishment of the clans known today. More detailed descriptions of Lemba oral history by Professor Mathivha of the Lemba Cultural Association (Mathivha 1992) suggest that the Jewish ancestors of the Lemba, as traders in the 7th century BC, migrated from "the north" to Yemen, where they established both a large community at Sena (Sa'na) and several trading posts along the eastern African coast. The Jewish community of Sena (Sa'na), termed "Basena," was later expanded by exiles escaping the Babylonian destruction of Jerusalem in 586 BC. At some later stage "trouble broke out between the Basena and the Arabs," resulting in the migration of some Basena to Africa. Here the group split into two, one moving westward to settle in Ethiopia (the "Falashas"), the other (the Lemba) moving southward, finally to establish communities in southern Africa. Dates for the migration from Yemen appear to be inconsistent, and those quoted for settlement en route to southern Africa range from 450 BC to 50 AD (Mathivha 1992).

Study sample.—Subjects were male volunteers who were attending the annual Lemba Cultural Association festival in the northern Transvaal region of South Africa in 1987 and 1988 and were classified, by their own assessment, as Lembas. Relatedness was determined by oral family history, and 49 unrelated individuals were included in the study.

Control Populations

Several populations were selected as control populations, to provide a basis for comparative genetic studies. These populations included South African (SA) Caucasoids (comprising the Asiatic Indian, Jewish, and European groups), Bantu-speaking Negroids, and a Khoisan sample. These populations have been described in detail elsewhere (Spurdle and Jenkins 1992). The study of all populations reported here was approved by the ethics committee of the University of the Witwatersrand.

Methods

The p12F2/*TaqI* RFLP (Casanova et al. 1985) was detected by standard Southern blotting and hybridization techniques. Details of the other Y-linked RFLPs used in this study have been summarized elsewhere (Spurdle et al. 1994). Genetic distance measurements were computed by use of the method described by Harpending and Jenkins (1973), and these distances were converted into a dendrogram by use of a simple "maximum-linkage" technique (Jenkins et al. 1971).

Results

p12F2/TaqI Allele Frequency Data

The p12F2 RFLP allele frequencies for the southern African control populations (table 1) are in agreement with data published in other sources (Casanova et al. 1985; Brega et al. 1987; Santachiara Benerecetti et al. 1993). The 8-kb allele was shown to be absent in 15 African males (Casanova et al. 1985) and 65 Senegalese (Brega et al. 1987) and was likewise absent in the 182 southern African Bantu-speaking Negroids screened. Its absence from the Khoisan sample also (table 1) suggests that it is not present in Africans per se. As seen in table 1, allele frequencies for the SA Europeans correlate well with those reported for French metropolitans (Casanova et al. 1985) and Czechoslovaks (Santachiara Benerecetti et al. 1993), as do the frequencies in the predominantly Ashkenazi SA Jewish group with those of other Semitic populations (Santachiara Benerecetti et al. 1993). The SA Asiatic Indian population, which arose from the migration of Muslims and Hindus from, largely, the Gujerat and Bengal provinces of India in the middle of the 19th century (Nurse et al. 1985), has a p12F2 8-kb allele frequency somewhat lower than that found in Semitic populations but approximately five times higher than that in Caucasoids of European origin (table 1).

The Lemba exhibit a frequency of .26 for the p12F2/*TaqI* 8-kb allele. Since this allele is absent in Africans and also was not observed in a sample of 60 Polynesians (A.B.S., unpublished data), it would appear to be specific to Caucasoids. The p12F2 data suggest, therefore, that the Lemba gene pool has received contributions from Caucasoid males.

Results from Studies Using Other Y-Linked RFLPs

The findings from the p12F2 data are in agreement with results from studies with the p49a/*TaqI* (Spurdle and Jenkins 1992), pYAP (Spurdle et al. 1994), and pDP31 (Spurdle and Jenkins 1994) RFLPs. For comparison, the frequencies of 49a/*TaqI* haplotypes occurring relatively commonly in the Lemba and other control populations are shown in table 2. Nine different haplotypes have been observed in the Lemba (Spurdle and Jenkins 1992), six of which occur at frequencies >.05

Table 1
Frequencies of the p12F2/TaqI 8-kb Allele in Various Populations

Population (n)	Frequency (Standard Error)	Reference
Lemba (46)	.26 (.06)	Present study
SA Jews (29)	.48 (.09)	
SA Europeans (43)	.07 (.04)	
SA Indians (53)	.34 (.07)	
Bantu (182)	.00 (.00)	
Khoisan (90)	.00 (.00)	Casanova et al. (1985)
French (26)	.04 (.04)	
Czechoslovaks (100)	.06 (.02)	
Sephardim Jews (80)	.40 (.06)	Santachiara Benerecetti et al. (1993)
Ashkenazi Jews (80)	.41 (.06)	
Lebanese (88)	.44 (.05)	
Ashkenazi Jews (44)	.41 (.07)	Ritte et al. (1993)
Yemenite Jews (15)	.60 (.13)	
Ethiopian Jews (17)	.06 (.09)	

NOTE.—The p12F2/TaqI RFLP is a two-allele polymorphic system, and the frequency of the 10-kb allele is therefore reciprocal to that of the 8-kb allele.

(table 2). The presence of Ht4, a typical Negroid haplotype (Torrioni et al. 1990; Spurdle and Jenkins 1992), at a frequency of .20 indicates that there has been significant Negroid male gene flow into the Lemba gene pool. Nevertheless, Caucasoid male gene flow also is indicated, by the high frequencies of Caucasoid marker haplotypes Ht7, Ht8, and Ht11, which comprise 53%

of the Lemba Y chromosomes studied (table 2). Ht7, Ht8, and Ht11 appear to be typical of Jewish populations (table 2), and, since they were shown to occur at similar frequencies in a Lebanese sample (Santachiara Benerecetti et al. 1993), they may be representative of all Semitic groups. Unfortunately, these haplotypes also occur in the Caucasoid SA Asiatic Indian population,

Table 2
Frequencies of Common 49a/TaqI Haplotypes in the Lemba and in Other, Control Populations

Haplotype	Description ^a	Lemba ^b (n = 49)	Negroid ^b (n = 325)	Indian ^b (n = 63)	European ^b (n = 53)	SA Jewish ^b (n = 36)	Ashkenazi ^c (n = 83)	Sephardic ^c (n = 83)	Yemenite Jewish ^d (n = 15)	Falashas ^d (n = 17)
Ht4	A1 B1 C0 D0 F1 I1	.20	.60	.00	.00	.00	.00	.00	.00	.00
Ht5	A2 B1 C0 D0 F1 I1	.06	.16	.00	.04	.03	.06	.14	.00	.00
Ht7	A2 B1 C0 D1 F1 I0	.12	.01	.08	.04	.22	.22	.17	.13	.00
Ht8	A2 B1 C0 D1 F1 I1	.35	.00	.17	.02	.19	.24	.23	.47	.00
Ht11	A3 B1 C0 D0 F1 I1	.06	.04	.13	.05	.17	.18	.07	.00	.00
Ht12	A3 B1 C0 D1 F1 I0	.00	.00	.03	.13	.00	.05	.05	.00	.00
Ht13	A3 B1 C0 D1 F1 I1	.00	.00	.19	.00	.00	.02	.00	.00	.00
Ht15	A3 B1 C1 D2 F1 I1	.00	.01	.00	.49	.06	.05	.01	.00	.00
Ht18	A4 B1 C0 D1 F1 I1	.12	.01	.03	.00	.00	.05	.06	.00	.00
Ht24	A2 B1 C1 D1 F1 I1	.00	.00	.09	.00	.11	.00	.02	.00	.00
Ht27	A0 B1 C0 D0 F0 I1	.00	.01	.06	.00	.00	.00	.04	.00	.00
Ht32	A3 B1 C0 D0 F0 I1	.00	.01	.00	.00	.00	.00	.00	.00	.35
Ht33	A2 B1 C0 D0 F0 I1	.00	.00	.00	.00	.00	.00	.00	.07	.59
Ht51	A2 B0 C0 D1 F1 I0	.00	.00	.00	.02	.06	.00	.00	.00	.00
Ht57	A3 B1 C1 D0 F0 I1	.00	.00	.00	.00	.06	.00	.00	.00	.00

^a Nomenclature is that of Spurdle and Jenkins (1992). Only haplotypes occurring at a frequency >.05 in at least one population (with n > 20) were selected for comparison.

^b Values are from Spurdle (1992) and Spurdle and Jenkins (1992).

^c Values are from Santachiara Benerecetti et al. (1993).

^d Values are from Ritte et al. (1993).

Table 3
Population Allele Frequencies: pDP31 and Y *Alu* Polymorphisms

POPULATION	YAP LOCUS ^a		pDP31 LOCUS ^b			
	<i>Alu</i> ⁺	(<i>n</i>)	N	D	T	(<i>n</i>)
Lemba	.30	(47)	.84	.13	.03	(38)
SA Jewish	.14	(36)	.72	.28	.00	(29)
SA European	.04	(51)	.29	.71	.00	(31)
SA Indian	.00	(36)	.47	.50	.03	(44)
Negroid	.78	(426)	.88	.05	.07	(93)
Khoisan	.46	(68)	.92	.06	.02	(54)

NOTE.—Data are from Spurdle and Jenkins (1994) and Spurdle et al. (1994).

^a The *Alu*⁺ allele represents the *Alu* insertion.

^b The N allele represents the ancestral DNA configuration.

and it is thus impossible to distinguish between Caucasoid gene flow from Semitic and Asiatic Indian sources, by use of frequencies of these three haplotypes alone. However, the Indian-specific Ht13, which occurs at a frequency of .13 in SA Asiatic Indians, is absent from the Lemba, suggesting that the Caucasoid male genes present in the Lemba are of Semitic rather than of Indian origin. This argument is further supported by the observation that Lembas lack the Y-linked XY275 *low* allele, which occurs at notable frequency in SA Asiatic Indians (Spurdle et al. 1992). Likewise, gene flow from European Caucasoids is excluded by the absence of their characteristic marker Ht15 (Torroni et al. 1990; Spurdle and Jenkins 1992). The remaining two haplotypes, Ht5 and Ht18, are not as easily explained. Ht18 occurs at much higher frequency in the Lemba than in any of the control populations (table 2), and it can only be presumed that this frequency has been skewed by genetic drift. The frequency data in table 2 imply that Ht18 and Ht5 may be Jewish (or perhaps Semitic) in source, but a Negroid source is equally possible for Ht5.

Allele frequencies for both the Y *Alu* polymorphism (Spurdle et al. 1994) and the pDP31 polymorphism (Spurdle and Jenkins 1994) have been summarized, for convenience, in table 3. These data are also indicative of Caucasoid gene flow into the Lemba population. The Y *Alu* polymorphism results from the insertion of an *Alu* element at Yq11 (Hammer 1994). The insertion occurs at high frequencies in Negroid populations and thus acts as a marker for Negroid male gene flow (Hammer 1994; Spurdle et al. 1994). It is interesting to note that the allele frequencies of the Lemba are significantly different from those of both the Bantu-speaking Negroid population ($P \ll .005$) and the SA European population ($P < .005$) but not from those of the SA Jewish group ($.05 < P < .10$). The pDP31 rearrangement polymorphism is more complex, and origin of the duplication

(D) and triplication (T) alleles appears to have occurred more than once during human evolution (Spurdle et al. 1994). However, the D allele occurs commonly only in Caucasoids and can be used to follow Caucasoid gene flow (Spurdle and Jenkins 1994). This allele was found at significant frequencies in the Lemba group and only in association with 49a/*TaqI* haplotypes Ht8 or Ht11 (Spurdle and Jenkins 1994).

YAP/p12F2 Haplotypes

The Y *Alu* polymorphism is an extremely useful Y-chromosome marker, since sequence data suggest that the mutation event is unique in human evolution (Hammer 1994). Y-chromosome haplotype construction incorporating the YAP locus has been used to validate the reliability of a number of different Y polymorphisms (Spurdle et al. 1994), and this approach was applied to the p12F2 polymorphism. The YAP/p12F2 haplotypes observed in southern African populations are shown in table 4. Only three of the possible four haplotypes were detected in a total of 436 individuals representing the Caucasoid, Negroid, and Khoisan groups, providing assurance that the p12F2 2-kb insertion/deletion polymorphism (Casanova et al. 1985) is a unique mutation event. The data indicate, furthermore, that the p12F2 polymorphism arose as a deletion on an *Alu*⁻ background.

Unfortunately the YAP/p12F2 haplotype data (table 4) do not provide more information about the origins of the Lemba than does either of the polymorphic systems considered alone. Consequently, the YAP/p12F2 haplotype was extended to include data from the 49a/*TaqI* polymorphism.

49a/YAP/p12F2 Haplotypes

Construction of extended haplotypes incorporating information from the 49a locus with the stable markers YAP and p12F2 (table 5) considerably facilitates analysis. First, it is clear that the 49a haplotypes Ht7 and

Table 4**YAP/p12F2 Haplotypes Occurring in Southern African Populations**

YAP/p12F2 Allele	Lemba	Jewish	European	Indian	Negroid	Khoisan
<i>Alu</i> ⁻ /8 kb	12	14	3	13	0	0
<i>Alu</i> ⁻ /10 kb	18	11	39	35	38	29
<i>Alu</i> ⁺ /10 kb	<u>14</u>	<u>4</u>	<u>1</u>	<u>0</u>	<u>144</u>	<u>61</u>
Total (<i>n</i> = 436)	44	29	43	48	182	90

NOTE.—Data are number of individuals.

Ht8 present in the Lemba population are of Caucasoid origin, since they occur in extended haplotypes (7/-/8, 8/-/8, and 8/-/10) that are present only in Caucasoids. In contrast, the Lemba 49a Ht11 frequency probably results from Negroid gene flow—and not from Caucasoid—as might be expected from 49a haplotype population-frequency data (Spurdle and Jenkins 1992; present study, table 2). It is also now possible to propose a Negroid origin for 49a Ht5 and to confirm one for Ht4.

The origin of Ht18 remains unclear on the basis of data in table 5. Association of pDP31 alleles with Ht18 was analyzed in an attempt to clear up the confusion (data not shown). All six Lemba individuals with Ht18 possessed the pDP31 N allele, whereas in the

Negroid and both Indian individuals Ht18 was associated with the pDP31 D allele. This would suggest that the Ht18 found in the Lemba has originated from another source. Ht18 has been observed in the Richtersveld population of mixed ancestry (Spurdle and Jenkins 1992), in Italian Caucasoids (Torroni et al. 1990), and in Amerindians (Torroni et al. 1994), but the corresponding pDP31 data unfortunately are not available for these groups.

In summary, 50% of the Lemba Y chromosomes analyzed appear to be of Caucasoid origin, and 36% appear to be of Negroid origin, and the ancestry of the remainder cannot be resolved at this stage. Cluster analysis of the extended-haplotype data indicates that the overall

Table 5**49a/YAP/p12F2 Extended Haplotypes in Southern African Populations**

49aHt/YAP/p12F2 ^a	Lemba	Jewish	European	Indian	Negroid
7/-/8	5	7	1	4	0
8/-/8	6	2	0	3	0
11/-/8	0	1	0	0	0
12/-/8	0	0	0	1	0
15/-/8	0	0	1	0	0
24/-/8	0	2	0	4	0
51/-/8	0	0	1	0	0
57/-/8	0	2	0	0	0
4/-/10	0	0	0	0	3
5/-/10	3	0	0	0	19
7/-/10	0	0	0	0	1
8/-/10	10	2	1	7	0
11/-/10	0	4	2	7	3
12/-/10	0	0	6	0	1
13/-/10	0	0	0	10	0
15/-/10	0	2	20	0	2
18/-/10	6	0	0	2	1
57/-/10	0	2	0	0	0
4/+ /10	10	0	0	0	99
5/+ /10	0	1	1	0	1
11/+ /10	<u>2</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>5</u>
Total	42	25	33	38	135

NOTE.—Data are number of individuals.

^a Alleles for YAP are presented as “-” or “+,” and those for the p12F2 polymorphism are represented as “8” or “10.”

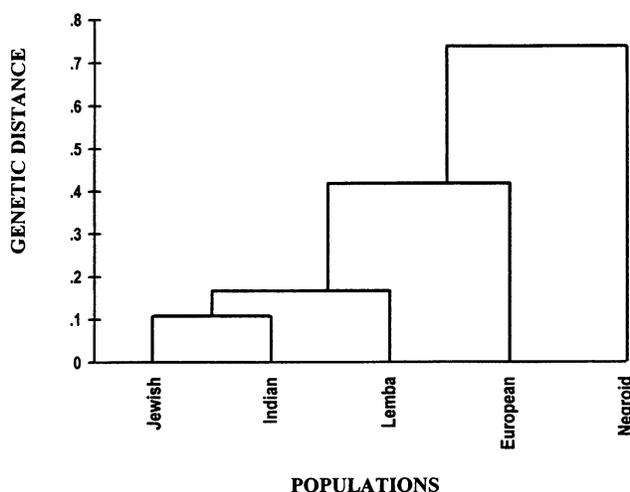


Figure 1 Population clustering implied by 49a/YAP/p12F2 extended-haplotype frequency data. Genetic distances were calculated using a complete data set incorporating figures from table 5, as well as data for extended haplotypes which include rarer 49a haplotypes (data not shown).

genetic affinity of the Lemba is with Caucasoid groups rather than with Negroids (fig. 1).

Data from table 5 are also in agreement with that reported by Santachiara Benerecetti et al. (1993), in that they present evidence for strong disequilibrium between the 49a and p12F2 polymorphisms. All Ht24 chromosomes and all Caucasoid Ht7 chromosomes are associated with the p12F2 8-kb allele. In addition, all chromosomes with Ht4, Ht5, and Ht13 possess the p12F2 10-kb allele, as do 24/25 (96%) of Ht15 chromosomes.

Discussion

The Genetic Origins of the Lemba

It is apparent that the Lemba gene pool has received substantial contributions from Semitic males and smaller contributions from Negroid males. In contrast, data from serogenetic (Mourant et al. 1978), red-cell enzyme and serum-protein (T.J., unpublished data), and mitochondrial (Soodyall 1993; Soodyall et al. 1996) studies reveal a Negroid genetic profile for the Lemba. These data combined are consistent with oral history—namely, that Lemba men married “foreign” (i.e., local) women after migration to Africa (Mathivha 1992). However, it is apparent from the Y-specific findings that male Negroids were also incorporated into the Lemba community, albeit to a lesser extent than were Negroid females. There is no clear evidence for Indian ancestry, a possibility discussed by Parfitt (1992) in view of the fact that, at the appropriate historical times, Indians were active traders in eastern African ports and may have been involved in gold mining and trading on the Zimbabwe plateau.

It is not possible, on the basis of the Y-specific genetic data, to distinguish between Jewish and Arabic Semitic ancestry of the Lemba. This is not surprising, since a common ancient history of Jews and Arabs is reflected both in their languages and as similarities in the stories of Judaism and Islam recorded in the Jewish Bible and the Koran, respectively. However, certain features of Lemba culture would seem to suggest that Jewish ancestry is more likely than an Arabic one. These include the practice of separating milk and meat, a dietary law observed in Judaism but not in Islam, and many other food laws that are essentially Jewish. In addition, certain Lemba sacrifices call for the use of liquor (Mathivha 1992), and Muslim law forbids the consumption of alcohol.

Although less obvious, Lemba customs associated with male circumcision also favor Jewish origins. The method used differs markedly from that of Muslims (M. Nabarro, personal communication), in that the incision is small and possibly similar to the mode of circumcision practiced in biblical times, before the introduction of more extensive circumcision during the Talmudic period (Gutmann 1987).

Relating Oral History and Genetic Data to Historical Facts

Historical data concur with many of the suggestions based on Lemba oral history. Jews are believed to have entered Yemen before the destruction of Jerusalem in the 6th century (Nyrop 1985), may well have been involved in trade at this stage (Wenner 1991), and certainly played a role in the crossroad of caravan routes during the 2d and 3d centuries A.D. Jewish settlements were common up to the 6th century A.D. (Baron 1952), although it is likely that some of these Jewish tribes were Arab proselytes (Baron 1952)—a fact reflected in the present-day genetic profile of Yemenite Jews, which shows them to be similar to their Arabic neighbors (Mourant et al. 1978; Livshits et al. 1991). Furthermore, Sa'na was a powerful city controlling trade routes of the Sabeen empire (Lewcock 1986), and Jews of Sa'na worked mostly as artisans and craftsmen, specializing in pottery and metalwork (Goitein 1971). Thus it is entirely possible that the ancestors of the Lemba were Jewish craftsmen and traders from Sa'na in Yemen. However, the migration of Semitic women with the Lemba men is doubtful, since mtDNA variation in the Lemba provides no evidence of Semitic admixture (Soodyall 1993).

The proposed genetic relationship between the Ethiopian Jews and the Lemba, as suggested by Mathivha (1992) is highly questionable. Data from various classical, nuclear-DNA, and mtDNA genetic studies (Mourant et al. 1978; Zoosmann-Diskin et al. 1991) indicate that the Ethiopian Jews are similar to other Ethiopian

populations, exhibiting a genetic profile that represents admixture between African and Caucasoid (probably Mediterranean) groups. The genetic evidence also suggests that the African contribution was introduced more by females and that the Caucasoid contribution was introduced more by males (Zoosmann-Diskin et al. 1991). However, results from Y-chromosome studies on a small ($n = 17$) sample of Ethiopian Jews (Ritte et al. 1993) are not entirely consistent with this hypothesis: 16 (94%) of the male individuals were shown to possess 49a/*TaqI* haplotypes Ht32 or Ht33, which are rare or absent in both Negroids and Caucasoids (Torrioni et al. 1990; Spurdle and Jenkins 1992), and Ht33 is found at notable frequencies only in Khoisan populations (Spurdle and Jenkins 1992). These findings would seem to suggest either that the study on Ethiopian Jews was subject to sampling error due to the small sample size or that tremendous genetic drift has taken place in this largely endogamous group. The currently available Y-chromosome genetic data do not support a close genetic relationship between the Ethiopian Jews and the Lemba. In conclusion, the historical facts are not incompatible with theories concerning the origin of the Lemba, and the Y-specific genetic findings presented here are consistent with Lemba oral history.

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References

- Baron SW (1952) A social and religious history of the Jews, 2d ed. Vol 3: Heirs of Rome and Persia. Columbia University Press, New York
- Brega A, Torrioni A, Semino O, Maccione L, Casanova M, Scozzari R, Fellous M, et al (1987) The p12f2/*TaqI* Y-specific polymorphism in three groups of Italians and in a sample of Senegalese. *Gene Geogr* 1:201–206
- Casanova M, Leroy P, Boucekkine C, Weissenbach J, Bishop C, Fellous M, Purrelo M, et al (1985) A human Y-linked DNA polymorphism and its potential for estimating genetic and evolutionary distance. *Science* 230:1403–1406
- Goitein SD (1971) Jewish society and institutions under Islam. In: Ben-Sasson HH, Ettinger S (eds) Jewish society through the ages. Schocken, New York, pp 170–184
- Gutmann J (1987) The Jewish life cycle: iconography of religions. Sec 23: Judaism. EJ Brill, Leiden
- Hammer MF (1994) A recent insertion of an Alu family member on the Y chromosome is a useful marker for human population studies. *Mol Biol Evol* 11:749–761
- Harpending HC, Jenkins T (1973) Genetic distance among southern African populations. In: Crawford MH, Workman PL (eds) Methods and theories of anthropological genetics. University of New Mexico Press, Albuquerque
- Jenkins T, Harpending HC, Gordon H, Keraan MM, Johnston S (1971) Red-cell-enzyme polymorphisms in the Khoisan peoples of southern Africa. *Am J Hum Genet* 23:513–532
- Lewcock R (1986) The old walled city of Sa'na. Unesco, Paris
- Livshits G, Sokal RR, Kobylansky E (1991) Genetic affinities of Jewish populations. *Am J Hum Genet* 49:131–146
- Mathivha MER (1992) The Basena/Vamwenya/Balemba. Moreseter, Toyandu, South Africa
- Mourant AE, Kopec AC, Domaniewska-Sobczak K (1978) The genetics of the Jews. Clarendon, Oxford
- Ngo KY, Vergnaud G, Johnsson C, Lucotte G, Weissenbach J (1986) A DNA probe detecting multiple haplotypes of the human Y chromosome. *Am J Hum Genet* 38:407–418
- Nurse GT, Weiner JS, Jenkins T (1985) The peoples of southern Africa and their affinities. Clarendon, Oxford
- Nyrop RF (1985) The Yemens—country studies. American University Foreign Area Studies. US Government Printing Office, Washington DC
- Parfitt T (1992) Journey to the vanished city—the search for a lost tribe of Israel. Hodder & Stoughton, London
- Ritte U, Neufeld E, Broit M, Shavit D, Motro U (1993) The differences among Jewish communities—maternal and paternal contributions. *J Mol Evol* 37:435–440
- Santachiara Benerecetti AS, Semino O, Passarino G, Torrioni A, Brdicka R, Fellous M, Modiano G (1993) The common, Near-Eastern origin of Ashkenazi and Sephardi Jews supported by Y-chromosome similarity. *Ann Hum Genet* 57:55–64
- Soodyall H (1993) Mitochondrial DNA variation in southern African populations. PhD thesis, University of the Witwatersrand, Johannesburg
- Soodyall H, Vigilant L, Hill AV, Stoneking M, Jenkins T (1996) mtDNA control-region sequence variation suggests multiple independent origins of an “Asian-specific” 9-bp deletion in sub-Saharan Africans. *Am J Hum Genet* 58:595–608
- Spurdle AB (1992) Y-specific restriction fragment length polymorphisms in southern African populations. PhD thesis, University of the Witwatersrand, Johannesburg
- Spurdle AB, Hammer MF, Jenkins T (1994) The Y *Alu* polymorphism in southern African populations and its relationship to other Y-specific polymorphisms. *Am J Hum Genet* 54:319–330 (Erratum: *Am J Hum Genet* 54:929)
- Spurdle A, Jenkins T (1992) Y chromosome probe p49a detects complex *PvuII* haplotypes and many new *TaqI* haplotypes in southern African populations. *Am J Hum Genet* 50:107–125
- (1994) The Y-specific pDP31 rearrangement polymorphism in southern African populations. *Hum Hered* 44:261–265
- Spurdle A, Ramsay M, Jenkins T (1992) The Y-associated XY275 *low* allele is not restricted to indigenous African peoples. *Am J Hum Genet* 50:1301–1307

- Torroni A, Chen Y-S, Semino O, Santachiara-Benerecetti AS, Scott CR, Lott MT, Winter M, et al (1994) mtDNA and Y-chromosome polymorphisms in four Native American populations from southern Mexico. *Am J Hum Genet* 54:303–318
- Torroni A, Semino O, Scozzari R, Sirugo G, Spedini G, Abbas N, Fellous M, et al (1990) Y chromosome DNA polymorphisms in human populations: differences between Caucasoids and Africans detected by 49a and 49f probes. *Ann Hum Genet* 54:287–296
- Van Warmelo NJ (1974) The classification of cultural groups. In: Hammond-Tooke WD (ed) *The Bantu-speaking peoples of southern Africa*. Routledge & Kegan Paul, London, pp 56–84
- Van Warmelo NJ, Phophi WMD (1948) Venda law. Part 1: Betrothal, thakha, wedding. *Ethnological publications* 23. Department of Native Affairs, Pretoria, South Africa.
- Wenner MW (1991) *The Yemen Arab Republic—development and change in an ancient land*. Westview profiles—nations of the contemporary Middle East. Westview, Boulder, CO
- Zoossmann-Diskin A, Ticher A, Hakim I, Goldwitsch Z, Rubinstein A, Bonne-Tamir B (1991) Genetic affinities of Ethiopian Jews. *Isr J Med Sci* 27:245–251