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A Y-chromosome portrait of the population of Jerba (Tunisia) to elucidate its complex demographic history

Étude de la variabilité du chromosome Y dans la population de Jerba (Tunisie) afin d'élucider son histoire démographique

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I was driven thence by foul winds for a space of nine days upon the sea, but on the tenth day we reached the land of the Lotus-eater, who live on a food that comes from a kind of flower. Here we landed to take in fresh water, and our crews got their mid-day meal on the shore near the ships. When they had eaten and drunk I sent two of my company to see what manner of men the people of the place might be...

Homer, The Odyssey, Book IX (Translation by S. Butler)

Besides the value of a comparative approach between different markers, an additional importance of the island of Jerba is related to its location in North Africa. This article follows a previous study concerning Egypt (Manni *et al.* 2002) within the wider framework of a project on the genetic patterns of variation in North Africa. The study of the north-eastern part of Africa is likely to provide a deeper understanding of *i*) remote human history as in the farming/language dispersals hypothesis (Krings *et al.* 1999; Manni *et al.* 2002; Lucotte, Mercier 2003) as well as *ii*) more recent migrations around the Mediterranean basin. We have shown that *a*) the genetic history of Egypt is very complex with sub-Saharan, Middle Eastern and European contributions to its genetic pool and confirmed that *b*) there are no genetic signatures of admixtures between NW Africa and southern Europe (Manni *et al.* 2002). Despite the particular value of North Africa, only a few studies have defined the genetic background prevailing in modern populations from this region. We focus here on Jerba, which on a

smaller scale appears to reflect this complexity. There are four distinct human groups which have cohabited on the island for centuries, and who identify themselves as having a different ethnic origin: Arabs, Berbers, Blacks and Jews. Moreover, since Jerba is an island, possible local admixtures are likely to be traced back more successfully because of the absence of geographic continuity with surrounding populations.

- According to North African history, Berbers are believed to have their ancestors among 2 Capsians (7000-5000 B.C.) (Cavalli-Sforza et al. 1994), and several other historical records can be useful in tracing back the demographic history of this island, thus providing a strong historical background for interpretation of the genetic variation of the samples (Mourali 2000). The first Arab settlement on the island occurred in the 7th century A.D. when Islam and the Arabic language were imposed upon the Berbers. It has been proposed that the black Africans were descendants of Sudanese or Nigerians slaves who came in the 18th century A.D. (Tlatli 1967). The origin of the Jews appears to be more complex since different migrations have been proposed, one represented by Jews that migrated to the island after the destruction of the Temple in Jerusalem in the 6th century B.C., a second one during the 15th century A.D. Furthermore, additional migrations were suggested (Auctores). This picture is further complicated by the fact that between the 9th century B.C. and the 19th century A.D., Jerba was a pivotal area in the migration routes of several populations: Phoenicians, Romans, Byzantines, Bedouins, Germans, Sicilians, Turkish and French (Tlatli 1967).
- ³ Currently, Berbers, Blacks and Jews live in different areas of Jerba, whereas only Arabs are distributed over the whole island. The main language spoken by all islander groups is Arabic, even though Berbers also speak a dialect called "Chelha" that belongs to Shilha (a cover term for Berber languages in Marocco and Tunisia). Religious differences may have played a role in subdividing populations; Arabs and Blacks are orthodox Muslims, Berbers are heterodox Muslims while the Jewish group follows Judaism.
- ⁴ To portray the genetic differences and variability of the present Jerban population, we present the allelic profile of eleven specific Unique Event Polymorphisms (UEPs) meaning that each mutation defines a group of evolutionary related Y-chromosomes (haplogroups). This study is intended to provide a better understanding of the origin of the four ethnic groups living in Jerba.

Materials and methodsSample

5 Genetic analyses were performed on a sample of 127 Y-chromosomes representing 47 Jerban Arabs, 46 Jerban Berbers and 34 Jerban Jews. Since a large majority of Jerban Jews migrated to Israel in 1948 A.D., we sampled such recent immigrants from Jerba to the Israeli towns of Safed, Haifa, Ashdod, Gedera, Ashkelon, Brekhia, Eitan and Tlamim. Only Jews with a Jerban ancestry of at least four generations were included in the study. This criterium also applies the DNA donors belonging to the other ethnic groups. Overall, our sample represents almost 1‰ of the total population of 114,170 individuals. Each Y-chromosome comes from different unrelated families. Fully informed consent was obtained from all participants in this study.

Y-chromosome biallelic polymorphisms typing

6 DNA was extracted from whole blood by means of a standard phenol/chlorophorm protocol. Subsequent purified DNA was analyzed in order to identify the 11 possible Ychromosome haplogroups (Hgs) defined by 10 UEPs (Unique Event Polymorphisms) (Y-Chromosome Consortium 2002; Jobling, Tyler-Smith 2003). The markers used are the as follows: SRY-2627 (Veitia *et al.* 1997), SRY-10831a (Kwok *et al.* 1996), SRY-4064 (Whitfield *et al.* 1995), 92R7 (Mathias *et al.* 1994), Tat (Zerjal *et al.* 1997), YAP (Hammer, Horai 1995), M2 (Seielstad *et al.* 1994), LLY22g (E. Righetti, C. Tyler-Smith—unpublished), M9 (Underhill *et al.* 1997) and 12f2q (Casanova *et al.* 1985). The typing was carried out as described in Rosser *et al.* (2000). The deep-rooting markers SRY-10831a, M9, 92R7, YAP and 12f2q were typed in all samples and, in some cases, the remaining markers were typed hierarchically; *e.g.* SRY-4064 and M2 only on YAP⁺ chromosomes, LLY22g and Tat only on those chromosomes which are M9 derived and 92R7 ancestral, and SRY-2627 only on those chromosomes which are 92R7 derived.

Measures of genetic diversity and differentiation

7 Two genetic diversity estimators were computed by means of the Arlequin version 2.1 software (Schneider et al. 2000). Intra-population diversity was measured through the gene diversity index (Nei 1987) as shown in table I. Inter-population diversity was calculated through conventional F-statistics (Wright 1965). Two measures of differentiation are provided: F_{ar} accounts for genetic divergence between samples (*table*)

II); F_{cr} accounts for genetic divergence between different groups of samples (*table III*). A

group of reference samples (*table III, IV*) was designated according to geographic criteria as follows: NW-Africa (North African composite sample [includes different Berber and Wahabi populations], Morrocan Arabs and Berbers, Algerians); Middle East (Egyptians, Druses, Palestinians, Lebanese, Saudi Arabians and Syrians); SE-Europe (Turks, Greeks, Georgians); western Europe (Spanish, French, Italian). A matrix of F_{cr}

values concerning the four Jerban samples and these groups was computed to identify the putative mother population of each Jerban sample (*table III*).

Multivariate analysis

- ⁸ Principal component analysis (PCA) was applied to the data to graphically identify possible patterns of genetic similarity between the four Jerban ethnic groups and a reference sample of 19 populations around the Mediterranean basin (*table IV*). The PCA method involves a mathematical procedure that transforms a number of (possibly) correlated variables into a (smaller) number of uncorrelated variables called principal components. The first principal component accounts for as much of the variability in the data as possible, and each succeeding component accounts for as much of the remaining variability as possible.
- 9 Multidimensional relationships between items can be seen in a bivariate plot (if two or three axes are plotted one against each other). The analysis was performed with the Excel applet GenAlEx by Peakall and Smouse (2001) freely available at the following Internet address: http://www.anu.edu.au/BoZo/genAlEx ResultsY-chromosome biallelic profiles

Allelic profiles of the 11 Y-chromosome lineages in the total sample of 165 Jerban Ychromosomes are shown in table I. The first result concerns the total homogeneity of the Jewish group where all the 34 typed individuals share the same haplogroup Hg J

the Jewish group where all the 34 typed individuals share the same haplogroup Hg J that is also present, at a very low frequency (4.3%), in the Arab group. This haplogroup presents its highest frequencies in the Fertile Crescent and has been suggested to be a genetic signature of migrations from the Middle East in Neolithic and post-Neolithic times (Semino *et al.* 1996, 2004; Rosser *et al.* 2000; Quintana-Murci *et al.* 2001; Arredi *et al.* 2004; Di Giacomo *et al.* 2004).

The only haplogroup spread between the remaining two ethnic groups is the 21. High 11 frequencies of this lineage are recorded in the Jerban Berbers (80.4%) and Arabs (93.6%). This haplogroup shows its highest frequencies in North Africa. Hg P(xR1a, R1b3f) lineage has been found predominantly in Europe, showing increasing frequencies from the Middle East to north-western Europe (Semino et al. 1996; Rosser et al. 2000) and was found at a very low frequency in Berbers (2.2%). Hgs B, C and F (xK, J) is found at significant frequency in Berbers (13.2%) but are absent in Arabs. However, little information can be deduced from this latter lineage since it is present in both Europe and Asia and does not show any informative geographic variation in the Eurasian landscape. We recorded the presence of Hg K (xN, P) in a single individual in the Arab sample. Given the little information conveyed by a single Y-chromosome we will not discuss it further in this context. Hg A and Hg E3a are found at high frequency in sub-Saharan African lineages and they have been suggested to be genetic signatures of Khoisan and Bantu language families, respectively. They have never been recorded outside Africa (Hammer et al. 1998; Rosser et al. 2000; Jobling, Tyler-Smith 2003) and their presence is unusual in North Africa (Bosch et al. 1999); they were found to be absent in all three groups.

Measures of genetic diversity

¹² Nei's measures of genetic diversity (*table I*) mirror the homogeneity of Jewish population and the very low variability of the Arab sample. Berbers show an intermediate level of genetic diversity with a fairly low level of variability. F_{st} distance

measures (*table II*) give an overall view of the genetic difference existing among the four Jerban samples. The Jewish group is the most divergent from all the others (Jewish-Berbers $F_{sr} = 0.827$; Jewish-Arabs $F_{sr} = 0.898$) while Arabs and Berbers are found very similar ($F_{sr} = 0.099$).

	Jewish	Berber	Arab
N	34	46	47
Nei's diversity	0.000	0.341	0.124
Std. dev. of Nei div.	+/- 0.000	+/- 0.083	+/- 0.064
Hg 1 Hg P (xR1a, R1b3f)*	0	2.2	0
Hg 2 Hgs B, C, F (xK, Y)*	0	13.0	0
Hg 3 Hg Rla*	0	4.4	0
Hg 7 Hg A*	0	0	0
Hg 8 Hg E3a*	0	0	0
Hg 9 Hg J*	100	0	4.3
Hg 21 Hg XE3a*	0	80.4	93.6
Hg 26 Hg K (xN, P)*	0	0	2.1

Bulletins et mémoires de la Société d'Anthropologie de Paris, 17 (1-2) | 2005

Table I–DNA profile of the four ethnic minorities living on the island of Jerba (Tunisia), 10 different UEPs, SRY-2627; SRY-10831a; SRY-4064; 92R7; Tat; YAP; M2; LLY22g; M9; 12f2q; were typed in order to identify the 11 possible Y-chromosome haplogroups (Hgs) that can be defined according to them (only recorded Hgs are listed). In the first column the old and new (Y-Chromosome Consortium 2002; Jobling, Tyler-Smith 2003) nomenclature are provided. Sample size (N) and Nei's standard diversity index (with its standard deviation) are provided as computed by the Arlequin package (Schneider *et al.* 2000).

Tabl. I - Profils génétiques des quatre minorités ethniques vivant sur l'île de Jerba (Tunisie). 10 différents UEP's SRY-2627 ; SRY-10831a ; SRY-4064 ; 92R7 ; Tat ; YAP ; M2 ; LLY22g ; M9 ; 12f2q ; ont été typés de façon à identifier les 11 haplogroupes (Hgs) du chromosome Y, comme l'indique le tableau. Dans la première colonne sont présentées l'ancienne et la nouvelle nomenclature de ces haplogroupes (Y-Chromosome consortium 2002 ; Jobling, Tyler-Smith 2003). Les colonnes successives indiquent la taille de l'échantillon (N) et l'index standard de Nei calculé par le logiciel Arlequin (Schneider *et al.* 2000).

	Y-chromosom	e UEPs, classic Present study	al F _{st} distances	
Jewish	0			
Blacks	1.50	0		
Berbers	0.827	3 • 7	0	
Arabs	0.898		0.099	0
	Y-chromosome n Khod	nicrosatellites, G ljet el Khil <i>et al.</i>		s
Jewish	-			
Blacks	848	0		
Berbers		1.325	0	
Arabs	1.0	0.791	0.076	0
Jewish	Yacou	bi Loveslati <i>et a</i>	4. 2001	
Jewish Blacks	840	0		
Blacks Berbers	1. 1. . .	0.100	0	
Arabs		0.100		0
Arabs	- CM alla		n.s.	0
		types, Prevosti o bi Loveslati et a		
Jewish	-			
Blacks	14	0		
Berbers	1970	0.505	0	
Arabs	849	0.513	0.108	0
	ABO syst	em, classical F _{st} Mourali 2000	distances	
Jewish	242			
Blacks	1.00	0		
Berbers	141	0.013	0	
Arabs		0.014	0.012	0

Table II—Genetic distances computed between the different ethnic groups of the island of Jerba are summarized. Unlike the present study the Jewish sample was always missing in previous studies. Each matrix is based on a different marker. Further details about the sampling strategy adopted can be found in the original publications.

Tabl. II - Distances génétiques entre les différentes ethnies de l'île de Jerba. Un échantillon juif, absent dans les études précédentes, a été inclus dans la présente étude. Chaque matrice est basée sur un marqueur différent. Les détails sur la stratégie d'échantillonnage peuvent être retrouvés dans les publications originales.

13 Based on a list of reference populations (*table IV*), we computed F_{T} distances (*table III*)

between our four samples and four groups of populations designated according to their geographic location, that is N Africa, Middle East, SE Europe and western Europe (see *table IV*). Results suggest a north African origin for the Arab and Berber samples. Concerning the Jewish sample, the Middle Eastern origins can be inferred and are much more obvious when Egypt is withdrawn from the north African group of samples (F_{cr} =

2.7). Nevertheless, since we had no intermediate populations between Egypt and Algeria, we decided to include Egypt with the Middle Eastern group since the sample comes from the Cairo area.

5	N Africa(N-A)	Middle East (ME)	SE Europe (SE-E)	W Europe (WE)
Jews (Jerba)	61,81	17,64	30,73	51,48
Berbers (Jerba)	2,48	33,64	30,36	41,96
Arabs (Jerba)	5,15	39,21	39,13	49,84

Table III—FCT measures accounts for genetic divergence between different groups of samples. Groups of reference samples (table IV) were designed according to geographic criteria as follows: North Africa NA (North African composite sample [Saharawis and Berbers], Moroccan Arabs and Berbers, Algeria); Middle East ME (Egypt, Druses, Palestine, Lebanon, Saudi Arabia and Syria); SE Europe SE-E (Turkey, Greece, Georgia); W Europe W-E (Spain, France, Italy). A matrix of FCT values concerning the four Jerban samples and these groups was computed to identify the putative ancestral population of each Jerban sample.

Tabl. III - Mesures de distances génétiques de FCT entre les différents groupes ethniques vivant sur l'île de Jerba. Les groupes de référence (tabl. IV) ont été définis sur la base de la localisation géographique des populations qui les composent : Afrique du Nord (NA) (échantillon composite d'Afrique du Nord [Saharawis et Berbères], Arabes du Maroc, Berbères du Maroc, Algérie) ; Moyen Orient (ME) (Egypte, Druzes, Palestine, Liban, Arabie Saoudite, Syrie) ; Sud-est de l'Europe (SE-E) (Turquie, Grèce, Géorgie) ; Europe de l'ouest (W-E) (Espagne, France, Italie). Afin d'identifier l'éventuelle population-mère des échantillons de Jerba nous avons calculé une matrice de FCT entre les 4 populations de Jerba et les groupes de populations définis plus haut (NA ; ME ; SE-E ; WE).

14 Voir document Annexe n°1

Table IV—Reference populations used to estimate a possible ancestral population of the Jerban samples (see *table III*). These populations also appear in the PCA plot of figure 1. Sample size (N) and Nei's diversity measures (Nei's diversity) are provided, they were computed on the same markers reported in *table I*.

Tabl. IV - Populations de référence servant à retracer les éventuelles populations-mères pour chacun des 4 échantillons de Jerba (voir *tabl. III*). Ces populations apparaissent également dans l'Analyse en Composantes Principales (ACP-PCA) visualisée en figure 1. La taille des échantillons (N) ainsi que l'indice de diversité de Nei ont été obtenus à partir des mêmes marqueurs, décrits dans le *tableau 1*.

Principal component analysis

- ¹⁵ In the Principal Component Analysis (PCA) plot of figure 1 the Jerban Berbers overlap the north African composite sample [that includes Berber and Wahabi populations] and the Moroccan Berber samples, leading to the conclusion that these three groups could be considered as part of the same population. Similarly, the Jerban Arabs fall close to Berber populations and to the Moroccan Arab sample. This close correspondence between some of the reference populations and our samples is lost for the Jerban Jewish samples. The Jerban Jews appear to cluster together with other Middle Eastern populations (Palestine, Lebanon, Syria), nevertheless they are plotted far apart from them. This feature could be explained by the fact that Jerban Jews encountered a significant bottleneck that is mirrored by allelic profiles and diversity values.
- 16 Voir document Annexe n°2

Fig. 1–Principal Component Analysis (PCA) plot that enables the visualization of the FST inferred genetic similarities/differences of the four ethnic groups of the island of Jerba together with 19 reference populations according to *table IV*. $F_{\rm ST}$ accounts for genetic distance between samples. For a better display both axes are rotated upside-down (visible in the direction of the arrows). Percentage of variation explained by the first 3 axes: (1st) 50.82; (2nd) 28.71; (3rd not shown) 10.42. A simplified representation of data, showing the 1st principal component axis only, is provided at the bottom of the page to remove the possible 'horseshoe effect' (see discussion).

Fig. 1 - Analyse en Composantes Principales (ACP-PCA) représentant les distances génétiques ($F_{\rm ST}$) entre les échantillons de Jerba et les 19 populations de référence indiquées dans le *tableau IV*. Pour une meilleure lisibilité de l'image, les axes ont été inversés comme l'indique le sens des flèches. La variance décrite par chaque axe (en pourcentage) est de 50,82, 28,71 et 10,42 pour le 1er, 2e et 3e axe respectivement (le 3e axe n'étant pas représenté). Afin de minimiser le « horseshoe effect » (voir discussion) nous proposons, au bas de la figure, une représentation simplifiée des distances entre populations sur le seul premier axe.

17 The topology of samples in the PCA plot suggests a Gutman (horseshoe) effect, meaning that the second axis is curved and twisted relative to the first, and is likely not to represent a true secondary gradient. It can be noted that, if we only sampled a small enough section of the gradient, the data might be linear enough to allow the use of PCA. The horseshoe effect happens because genetic variables, like most environmental variables, can be monotonically related to underlying factors and to each other as is expected in close populations exchanging migrants. To provide an alternative representation, we visualize only the first principal component at the bottom of figure 1. The third axis still describes 11% of the total genetic variance, but we were unable to depict any pattern in it. A large proportion of studied populations cluster together with two major exceptions represented by Basques and Jerban Jews, who occupy a very lateral position on the axis. This axis just confirms the deviant allele profile of the latter sample; therefore, to provide a more readable plot, we decided to not display the third PCA axis.

DiscussionDiversity and differentiation of Jerban samples

- The present-day Jerban population is composed of four different ethnic groups that have been cohabiting on the island for centuries. Ethnological and anthropological studies suggest that each group maintained and developed a specific identity (Benoît, Kossovitch 1930). Furthermore, a number of historical records, as well as local traditions, provide information on the different geographic origin for these communities (Stablo 1941; Tlatli 1962, 1967). Our results clearly point to the very low level of diversity of both the Jewish and the Arab population (*table 1*) and reflects a severe bottleneck together with the effects of drift. This conclusions can apply also to the Berber sample, which exhibits a low diversity index which may be explained by a more rapid genetic drift due to longer isolation on the island and/or by any patrilinear social structure as recently shown by Chaix *et al.* (2005). Since our results contradict those of Yacoubi Loveslati *et al.* (2001) based on restriction polymorphisms of IGHG genes that are known to be under selective pressure, future research will probably give more definite answers concerning this point.
- These findings are confirmed by results from a genealogical study on marriages that provides clear evidence of high levels of endogamy in the island in recent times (Mourali 2000). According to such genealogical results, the Jewish group was found to be 100% endogamous (in the island) and mixed Black-Berber marriages were not recorded. Other possible mixed marriages were recorded at very low frequencies. Such a picture suggests that gene flow from the Berber to the Black group (and vice-versa) is

possible only through preliminary mixed unions with Arabs. The genetic profiles of the Jewish group from Jerba is very different from the ones of Berbers and Arabs. Further, migration levels are very low. Overall, the results suggest that each community may have been founded by a different migration event to the island.

Genetic profiles of the Jerban samples and their geographic origin

²⁰ The genetic profiles of the four ethnic groups provide further evidence of their separate origin; in fact some haplogroups are specific of each sample: (*i*) Hg P (xR1a, R1b3f) was found at a very low frequency only in the Berber group, (*ii*) Hg J is specific to Jews while (*iii*) Hg R1a is recorded only among Berbers. The most widespread Y-chromosome lineage is Hg E (xE3a), absent only in the Jewish sample. These specificities highlight the genetic differences found in the Jerban samples and point to different ancestral populations as is also shown by F_{cr} distances (*table III*). These

differences are presented in details in the next subsections. We would like to note that we also sampled and typed the Black minority for the purposes of an early version of this article but, according to a new nomenclature (Cruciani *et al.* 2002), it was shown that the two different haplogroups "R1-M173*" and "R1-M269" (usually considered as a single one Hg P [xR1a, R1b3f]) are respectively distributed in Europe and sub-Saharan Africa. When our samples were typed, only the previous nomenclature and typing method were available; therefore we decided to widhraw this sample from analyses. The Jewish population

21 The genetic profile of the Jewish sample is related to populations in the Middle East where Hg E3a has its highest frequencies. Moreover, the Middle Eastern origin of the Jewish group is confirmed by preliminary results on Y-chromosome microsatellites of 15 individuals sampled in Tlamim; 13 of them carried for the Cohen Modal Haplotype (CMH). This haplotype is frequent in the Jewish diaspora and it has been suggested that it might be particularly frequent in families which trace patrilineal ancestry to the Jewish priesthood (Thomas *et al.* 2000). While the CMH is not specific of Jews, being widespread in several Middle Eastern populations (Brinkmann *et al.* 1999, Zoosman-Diskin 2000), such a datum seems to support two different scenarios for the Jewish colonization of Jerba: *a*) a founding group that migrated to Jerba in an early dispersal of Jewish population from the Middle East or *b*) a recent migration of families of ancient Jewish ancestry. The first scenario seems unrealistic because microsatellite markers are rapidly evolving, therefore we would expect more variable microsatellite haplotypes in the case of an ancient founding event, unless some bottlenecks occurred in the male lineage of Jerban Jews.

Arab and Berber populations

²² The Arab and Berber samples are almost totally characterized by Hg E (xE3a), which is present at its highest frequencies in North Africa, frequencies that decrease in a gradient shape towards the south. Hg E (xE3a) is also observed at moderate frequencies in the northern Mediterranean basin, thus relating Jerban Arabs and Berbers to North African populations as confirmed by F_{cr} values (*table III*).

Distances between Jerban populations

²³ The population of the island of Jerba has attracted the interest of several scholars, therefore it is possible to compare our results on Y-chromosome UEP with a wide range of studies based on different markers. To this end, we have compared our F_{sr} distance matrix (*table II*) with other distance matrices accounting for the variability of Y-

chromosome microsatellites (Khodjet El Khil *et al.* 2001), GM hallotypes (Yacoubi Loveslati *et al.* 2001), and ABO blood groups (Mourali 2000). Our Jewish sample could not be compared because it is absent in all previous published studies. According to $F_{\rm sc}$

distances based on UEPs Y-chromosome profiles, we show that there is almost no differentiation between the Berber and Arab samples. This data is strongly confirmed by all the systems with the exception of ABO, a result that is not surprising since this system is unlikely to portray genetic differences at fine geographic scale. Moreover, in a previous study based on mitochondrial DNA (Fadhlaoui-Zid *et al.* 2004), no significant differences between Arabs and Berbers were found, thus suggesting that maternal and paternal lineages in Jerba may lead to a similar demographic scenario.

²⁴ This paper shows that an accurate portrayal of the inter-group Y-chromosome variability of three ethnic groups living in Jerba was possible through accurate sampling of the population of the island. When an ethnological and historical approach in the definition of populations is lacking, there is a risk of unrepresentative results, as shown by the position of a grouped sample of Jerban inhabitants on the Principal Component Analysis (PCA) of figure 1. Such a sample falls very close to Algeria and Egypt, thus mirroring the geographic position of the island. Actually this topology just reflects a "centre of gravity" of the genetic variability of the four ethnic groups, which are shown to have very different geographic origins.

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BIBLIOGRAPHY

ARREDI (B.), POLONI (E.S.), PARACCHINI (S.), ZERJAL (T.), FATHALLAH (D.M.), MAKRELOUF (M.), PASCALI (V.L.), NOVELLETTO (A.), TYLER-SMITH (C.) 2004, A Predominantly Neolithic Origin for Y Chromosomal DNA Variation in North Africa, *American Journal of Human Genetics* 75: 338-345.

BENOÎT (F.), KOSSOVITCH (N.) 1930, Recherches sur les berbérophones, Djerba, Hoggar, Maroc, Institut International d'Anthropologie, Paris.

BOSCH (E.), CALAFELL (F.), SANTOS (F.R.), PEREZ-LEZAUN (A.), COMAS (D.), BENCHEMSI (N.), TYLER-SMITH (C.), BERTRANPETIT (J.) 1999, Variation in short tandem repeats is deeply structured by genetic background on the human Y-chromosome, *American Journal of Human Genetics* 65: 1623-1638.

BRINKMANN (C.), FORSTER (P.), SCHURENKAMP (M.), HORST (J.), ROLF (B.), BRINKMANN (B.) 1999, Human Y chromosomal STR haplotypes in a Kurdish population sample, *International Journal of Legal Medicine* 112: 181-183. CASANOVA (M.), LEROY (P.), BOUCEKKINE (C.), WEISSENBACH (J.), BISHOP (C.), FELLOUS (M.), PURRELLO (M.), FIORI (G.), SINISCALCO (M.) 1985, A human Y-linked DNA polymorphism and its potential for estimating genetic and evolutionary distance, *Science* 230: 1403-1406.

CAVALLI-SFORZA (L.L.), MENOZZI (P.), PIAZZA (A.) 1994, The history and geography of human genes, Princeton University Press, Princeton, New Jersey.

CHAIX (R.), AUSTERLITZ (F.), KHEGAY (T.), JACQUESSON (S.), HAMMER (M.F.), HEYER (E.), QUINTANA-MURCI (L.) 2005, The genetic or mythical ancestry of descent groups: lessons from the Y-chromosome, *American Journal of Human Genetics* 75: 1113-1116.

CRUCIANI (F.), SANTOLAMAZZA (P.), SHEN (P.), MACAULAY (V.), MORAL (P.), OLCKERS (A.), MODIANO (D.), HOLMES (S.), DESTRO-BISOL (G.), COIA (V.), WALLACE (D.C.), OEFNER (P.J.), TORRONI (A.), CAVALLI-SFORZA (L.L.), SCOZZARI (R.), UNDERHILL (P.A.) 2002, A back migration from Asia to sub-Saharan Africa is supported by high-resolution analysis of human Y-chromosome haplotypes, *American Journal of Human Genetics* 70: 1197-1214.

DI GIACOMO (F.), LUCA (F.), POPA (L.O.) 2004, Y chromosomal haplogroup J as a signature of the post-Neolithic colonization of Europe, *Human Genetics* 115: 357-371.

FADHLAOUI-ZID (K.), PLAZA (S.), CALAFELL (F.), BEN AMOR (M.), COMAS (D.), BENNAMAR EL GAAIED (A.) 2004, Mitochondrial DNA heterogeneity in Tunisian Berbers, *Annals of Human Genetics* 68: 222-233.

GHERIB (B.) 1962, Recherches séro-anthropologiques sur les populations tunisiennes, Thèse de Doctorat, Université de Marseille.

HAMMER (M.F.), HORAI (S.) 1995, Y chromosomal DNA variation and the peopling of Japan, American Journal of Human Genetics 56: 951-962.

HAMMER (M.F.), KARAFET (T.), RASANAYAGAM (A.), WOOD (E.T.), ALTHEIDE (T.K.), JENKINS (T.), GRIFFITHS (R.C.), TEMPLETON (A.R.), ZEGURA (S.L.) 1998, Out of Africa and back again: nested cladistic analysis of human Y-chromosome variation, *Molecular Biology and Evolution* 15: 427-441.

HAMMER (M.F.), KARAFET (T.M.), REDD (A.J.), JARJANAZI (H.), SANTACHIARA-BENERECETTI (S.), SOODYALL (H.), ZEGURA (S.L.) 2001, Hierarchical patterns of global human Y-chromosome diversity, *Molecular Biology and Evolution* 18: 1189-1203.

JOBLING (M.A.), TYLER-SMITH (C.) 2003, The human Y-chromosome: an evolutionary marker comes of age, *Nature Reviews Genetics* 4: 598-612.

KAYSER (M.), BRAUER (S.), WEISS (G.), SCHIEFENHÖVEL (W.), UNDERHILL (P.), SHEN (P.), OEFNER (P.), TOMMASEO- PONZETTA (M.), STONEKING (M.) 2003, Reduced Y-chromosome, but not mitochondrial DNA, diversity in human populations from West New Guinea, *American Journal of Human Genetics* 72: 281-302.

KHODJET EL KHIL (H.), TRIKI MARRAKCHI (T.R.), YACOUBI LOVESLATI (B.), LANGANEY (A.), FELLOUS (M.), BENAMMAR ELGAAIED (A.) 2001, Y-chromosome microsatellite variation in three populations of Djerba Island (Tunisia), *Annals of Human Genetics* 65: 263-270.

KHODJET EL KHIL (H.), TRIKI MARRAKCHI (T.R.), YACOUBI LOVESLATI (B.), LANGANEY (A.), FELLOUS (M.), BENAMMAR ELGAAIED (A.) in press, Distribution of Y-chromosome lineage in Jerba island population, *Forensic Science International.*

KRINGS (M.), SALEM (A.E.), BAUER (K.), GEISERT (H.), MALEK (A.K.), CHAIX (L.), SIMON (C.), WELSBY (D.), DI RIENZO (A.), UTERMANN (G.), SAJANTILA (A.), PAABO (S.), STONEKING (M.) 1999, mtDNA analysis of Nile

River Valley populations: A genetic corridor or a barrier to migration? *American Journal of Human Genetics* 64: 1166-1176.

KWOK (C.), TYLER-SMITH (C.), MENDONCA (B.B.), HUGHES (I.), BERKOVITZ (G.D.), GOODFELLOW (P.N.), HAWKINS (J.R.) 1996, Mutation analysis of the 2 kb 5' to SRY in XY females and XY intersex subjects, *Journal of Medical Genetics* 33: 465-468.

LUCOTTE (G.), MERCIER (G.) 2003, Y-chromosome haplotypes in Egypt, American Journal of Physical Anthropology 121: 63-66.

MANNI (F.), LEONARDI (P.), BARAKAT (A.), ROUBA (H.), HEYER (E.), KLINTSCHAR (M.), MCELREAVEY (K.), QUINTANA-MURCI (L.) 2002, Y-chromosome analysis in Egypt suggests a genetic regional continuity in Northeastern Africa, *Human Biology* 74: 645-658.

MATHIAS (N.), BAYES (M.), TYLER-SMITH (C.) 1994, Highly informative compound haplotypes for the human Y-chromosome, *Human Molecular Genetics* 3: 115-123.

MOURALI (S.), 2000, Consanguinité et distances génétiques: mesure du déficit en hétérozygotes dans deux contextes différents, Thèse de Doctorat, Muséum National d'Histoire Naturelle, Paris.

NEI (M.) 1987, Molecular evolutionary genetics, Columbia University Press, New York.

OOTA (H.), KITANO (T.), JIN (F.) YUASA (I.), WANG (L.), UEDA (S.), SAITOU (N.), STONEKING (M.) 2002, Extreme mtDNA homogeneity in continental Asian populations, *American Journal of Physical Anthropology* 118: 146-153.

PEAKALL (R.), SMOUSE (P.E.) 2001, GenAlEx vs. 5: Genetic analysis in Excel, Population genetics software for teaching and research, Australian National University, Canberra.

QUINTANA-MURCI (L.), KRAUSZ (C.), ZERJAL (T.), SAYAR (S.H.), HAMMER (M.F.), MEHDI (S.Q.), AYUB (Q.), QAMAR (R.), MOHYUDDIN (A.), RADHAKRISHNA (U.), JOBLING (M.A.), TYLER-SMITH (C.), MCELREAVEY (K.) 2001, Y-chromosome lineages trace diffusion of people and languages in Southwest Asia, *American Journal of Human Genetics* 68: 537-542.

RANQUE (J.), NICOLI (R.M.), GHERIB (B.), BATTAGLINI (P.F.) 1964, Étude séro-anthropologique des Juifs de l'île de Djerba (Tunisie), Proceedings of the IX congress of the International Society of Blood Transfusion (Mexico), *Bibliotheca Hæmatologica* 19: 210-212.

ROSSER (Z.H.), ZERJAL (T.), HURLES (M.E.), ADOJAAN (M.), (57 names follow), JOBLING (M.A.) 2000, Y chromosomal diversity in Europe is clinal and influenced primarily by geography (rather than by language), *American Journal of Human Genetics* 67: 1526-1543.

schneider (S.), ROESSLI (D.), EXCOFFIER (L.) 2000, Arlequin ver 2.0: A software for population genetics data analysis, Laboratoire de Génétique et de Biométrie, Université de Genève.

SEIELSTAD (M.T.), HEBERT (J.M.), LIN (A.A.), UNDERHILL (P.A.), IBRAHIM (M.), VOLLRATH (D.), CAVALLI-SFORZA (L.L.) 1994, Construction of human Y chromosomal haplotypes using a new polymorphic A to G transition, *Molecular Genetics* 3: 2159-2161.

SEIELSTAD (M.T.), MINCH (E.), CAVALLI-SFORZA (L.L.) 1998, Genetic evidence for a higher female migration rate in humans, *Nature Genetics* 20: 278-280.

SEMINO (O.), MAGRI (C.), BENUZZI (G.), LIN (A.A.), AL-ZAHERY (N.), BATTAGLIA (V.), MACCIONI (L.), TRIANTAPHYLLIDIS (C.), SHEN (P.), OEFNER (P.J.), ZHIVOTOVSKY (L.A.), KING (R.), TORRONI (A.), CAVALLI-SFORZA (L.L.), UNDERHILL (P.A.), SANTACHIARA-BENERECETTI (A.S.) 2004, Origin, diffusion and differentiation of Y-chromosome haplogroups E and J: inferences on the neolithization of Europe and later migratory events in the Mediterranean area, *American Journal of Human Genetics* 74: 1023-1034.

SEMINO (O.), PASSARINO (G.), BREGA (A.), FELLOUS (M.), SANTACHIARA-BENERECETTI (A.S.) 1996, A view of the neolithic demic diffusion in Europe through two Y-chromosome-specific markers, *American Journal of Human Genetics* 59: 964-968.

STABLO (R.) 1941, Les Djerbiens, Une communauté arabo-berbère dans une île de l'Afrique française, SAPI, Tunis.

THOMAS (M.G.), PARFITT (T.), WEISS (D.A.) SKORECKI (K.), WILSON (J.F.), LE ROUX (M.), BRADMAN (N.), GOLDSTEIN (D.B.) 2000, Y-chromosomes travelling south: the Cohen modal haplotype and the origins of the Lemba-the "Black Jews of Southern Africa", *American Journal of Human Genetics* 66: 674-686.

TLATLI (S.E.) 1962, Djerba et les Djerbiens, Aloccio, Tunis.

TLATLI (S.E.) 1967, Djerba l'île des lothophages, Cerès Production, Tunis.

UNDERHILL (P.A.), JIN (L.), LIN (A.A.), MEHDI (S.Q.), JENKINS (T.), VOLLRATH (D.), DAVIS (R.W.), CAVALLI-SFORZA (L.L.), OEFNER (P.J.) 1997, Detection of numerous Y-chromosome biallelic polymorphisms by denaturing high-performance liquid chromatography, *Genome Research* 7: 996-1005.

VEITIA (R.), ION (A.), BARBAUX (S.), JOBLING (M.A.), SOULEYREAU (N.), ENNIS (K.), OSTRER (H.), TOSI (M.), MEO (T.), CHIBANI (J.), FELLOUS (M.), MCELREAVEY (K.) 1997, Mutations and sequence variants in the testisdetermining region of the Y-chromosome in individuals with a 46,XY female phenotype, *Human Genetics* 99: 648-652.

wHITFIELD (L.S.), SULSTON (J.E.), GOODFELLOW (P.N.) 1995, Sequence variation of the human Ychromosome, *Nature* 378: 379-380.

WRIGHT (S.) 1965, The interpretation of population structure by F-statistics with special regard to systems of mating, *Evolution* 19: 395-420.

YACOUBI LOVESLATI (B.Y.) 1999, Étude du polymorphisme des immunoglobulines et de l'ADN mitochondrial dans la population de l'île de Jerba, Thèse, Faculté des Sciences Mathématiques, Physiques et Naturelles de l'Université de Tunis.

YACOUBI LOVESLATI (B.Y.), SANCHEZ-MAZAS (A.), ENNAFAA (H.), MARRAKCHI (R.), DUGOUJON (J.M.), LEFRANC (J.M.), ELGAAIED (A.B.) 2001, A study of Gm allotypes and immunoglobulin heavy gamma IGHG genes in Berbers, Arabs and sub-Saharan Africans from Djerba Island, Tunisia, *European Journal of Immunogenetics* 28: 531-538.

Y-Chromosome Consortium 2002, A nomenclature system for the tree of human Y chromosomal binary haplogroups, *Genome Research* 12: 339-348.

ZERJAL (T.), DASHNYAM (B.), PANDYA (A.), KAYSER (M.), ROEWER (L.), SANTOS (F.R.), SCHIEFENHOVEL (W.), FRETWELL (N.), JOBLING (M.A.), HARIHARA (S.), SHIMIZU (K.), SEMJIDMAA (D.), SAJANTILA (A.), SALO (P.), CRAWFORD (M.H.), GINTER (E.K.), EVGRAFOV (O.V.), TYLER-SMITH (C.) 1997, Genetic relationships of Asians and Northern Europeans (revealed by Y chromosomal DNA analysis, *American Journal of Human Genetics* 60: 1174-1183.

ZOOSSMANN-DISKIN (A.) 2000, Are today's Jewish priests descended from the old ones? *Homo, Journal of Comparative Human Biology* 51: 156-162.

ABSTRACTS

The Island of Jerba has a long demographic history that is related to its central position in the Mediterranean Sea. The island was in contact with different civilizations and its population is heterogeneous (Arabs, Berbers, black Africans and Jews).

We sampled 127 males (Jewish sample N = 32; Berber sample N = 46; Arab sample N = 47) in order to identify the Y-chromosome variability of the population according to 10 Unique Event Polymorphisms (UEPs): SRY-2627; SRY-10831a; SRY-4064; 92R7; Tat; YAP; M2; LLY22g; M9; 12f2q. We also sampled the Black group living in Jerba but typing ambiguities forced us to exclude it from further analyses.

The results suggest a very low degree of genetic differentiation between Jerban Arabs and Berbers, who can be considered genetically, as belonging to the same group. In contrast, pairwise $F_{_{ST}}$ measures show that the genetic distances between the Jewish sample and the other ethnic

groups are the highest in the island. This datum implies a low level of gene flow between the different communities that reside in Jerba, with the exception of Arabs and Berbers. Since geographic isolation plays no role, the different allelic profiles of the three ethnic groups are related to their different geographic origins, which are likely to have been maintained by the cultural differences existing between Arabs, Berbers and Jews.

By comparing the observed haplogroup profiles with 19 reference populations located around the Mediterranean basin, we confirm a North African origin for the Berber and Arab sample and a Middle Eastern ancestral population for Jerban Jews.

L'histoire démographique de l'île de Jerba est très ancienne en raison de sa position centrale dans le bassin de la mer Méditerranée, c'est la raison pour laquelle plusieurs populations se sont succédées sur l'île dont la population est, de nos jours, hétérogène (Arabes, Berbères, Noirs, Juifs).

Afin d'étudier la variabilité du chromosome Y de la population de Jerba nous avons analysé 10 polymorphismes, SRY-2627 ; SRY-10831a ; SRY-4064 ; 92R7 ; Tat ; YAP ; M2 ; LLY22g ; M9 ; 12f2q sur un échantillon de 127 individus (Juifs N = 32 ; Berbères N = 46 ; Arabes N = 47). Nous avions aussi échantillonné la population noire de Jerba mais des ambiguïtés, lors du génotypage, nous ont forcé à exclure l'échantillon de l'article.

Les résultats indiquent une très faible différenciation génétique entre les échantillons arabe et berbère qui peuvent être considérés, d'un point de vue génétique, comme une seule population. Inversement, les mesures de F_{ex} montrent que les distances entre l'échantillon juif et les autres

groupes ethniques de l'île sont considérables. Ce résultat implique un faible niveau d'échange génétique entre les communautés qui habitent l'île, à la seule exception des Arabes et des Berbères.

Comme l'isolement géographique est inexistant à Jerba, les différences des profils alléliques entre les trois groupes s'expliquent par une provenance géographique différente et une barrière culturelle relative concernant Arabes, Berbères et Juifs.

La comparaison entre la composition haplotypique de Jerba et celle de 19 populations de référence, localisées autour du bassin de la mer Méditerranée, montre la provenance nordafricaine des Berbères et des Arabes de Jerba. De la même façon, l'échantillon juif vient d'une population mère localisée au Moyen-Orient.

INDEX

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AUTHORS

FRANZ MANNI

Équipe de Génétique des Populations, Département Hommes, Natures, Sociétes, Musée de l'Homme, MNHN, 17 place du Trocadéro et du 11 novembre, 75016 Paris, France, e-mail: manni@mnhn.fr

PASCAL LEONARDI

Équipe de Génétique des Populations, Département Hommes, Natures, Sociétes, Musée de l'Homme, MNHN, 17 place du Trocadéro et du 11 novembre, 75016 Paris, France

ÉTIENNE PATIN

Équipe de Génétique des Populations, Département Hommes, Natures, Sociétes, Musée de l'Homme, MNHN, 17 place du Trocadéro et du 11 novembre, 75016 Paris, France

ALAIN BERREBI

Hematology Institute, Kaplan Medical Center, Rehovot, Israel

HOUSSEIN KHODJET EL KHIL

Laboratoire de Génétique Moléculaire, Immunologie et Biotechnologie, Faculté des Sciences, Tunis, Tunisia

KARL SKORECKI

Technion, Israel Institute of Technology, Haifa, Israel

DROR ROSENGARTEN

Technion, Israel Institute of Technology, Haifa, Israel

HASSAN ROUBA

Institut Pasteur, Casablanca, Morocco

EVELYNE HEYER

Équipe de Génétique des Populations, Département Hommes, Natures, Sociétes, Musée de l'Homme, MNHN, 17 place du Trocadéro et du 11 novembre, 75016 Paris, France

MARC FELLOUS

Inserm E0021, Hôpital Cochin, 75014 Paris, France.