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## GENETIC DIVERSITY IN TUNISIAN POPULATION: A COMPARISON STUDY BASED ON Y-CHROMOSOME STR MARKERS

*ABSTRACT: To investigate genetic structure within Tunisian populations, we analysed 546 haplotypes based on six and eleven short tandem repeat (STR) loci on the Y chromosome. Results show a high degree of heterogeneity in the Tunisian gene pool. When all populations are considered, based on six Y-STRs, results demonstrate that Jerbians of sub-Saharan origin exhibit a high level of heterogeneity. Lower haplotype diversity values were observed in samples from Zriba and Qalaat El Andalous. Drift acts strongly and particularly on the Y chromosome and this is what seemed to happen in these populations. This feature reduces intra-population diversity. Principal coordinates analysis (PCoA) of Rst values indicates a mosaic structure of Tunisian populations. These results exclude ethnic, geographic, and linguistic effects in Tunisia. Every population has its own structure.*

*KEY WORDS: Y-STRs – Tunisian populations – Genetic structure*

### INTRODUCTION

In the last few years, information on the paternally inherited NRY (non-recombining part of Y chromosome) has been extensively applied in population genetics and evolution studies to follow male-specific movements and admixture as well as mating behaviour. The NRY contains different kinds of polymorphisms with different mutation rates and consequently, scientists can select appropriate Y polymorphisms to study evolutionary events over different time scales. Short tandem repeats (STRs) on the Y chromosome can be used for analyses on a short evolutionary time scale or at the microgeographic level (Gusmao *et al.* 2003, Ploski *et al.* 2002, Weale *et al.* 2002). Y-STR haplotypes are ideal for these studies, because they behave as neutral markers, their rapid rate of evolution and smaller effective population size (due to their haploid, uniparental mode of inheritance) means that they are

more sensitive indicators of genetic differences between groups than autosomal DNA markers (Kayser *et al.* 2006). Moreover, comparing patterns of Y chromosome allows insight into the paternal history of populations, which may differ, especially in admixed populations (Kayser *et al.* 2006).

In this study, Y-STR haplotypes are used to investigate the genetic structure of Tunisian populations. Tunisia like the majority of North African countries has a complex population history (Frigi *et al.* 2010) as a result of many centuries of invasions and waves of immigration coming from different surrounding areas: Southern Iberia, Arabian Peninsula and African Sub-Sahara. These demographic movements as described by historians have influenced the cultural and ethnic structure of the population and may have also contributed to its complex genetic stratification. In order to better explore this feature, many genetic studies based on different types of polymorphic markers have

been carried out on Tunisian individuals originating from different localities (Cherni *et al.* 2009, Ennafaa *et al.* 2009, Fadhlouli *et al.* 2004, Frigi *et al.* 2010, Khodjet el khil *et al.* 2005, Yacoubi *et al.* 2006). These analyses were aimed at investigating the Tunisian population's genetic diversity and evaluating the influence of gene flow on its genetic structure at a microevolution level.

In this context, the present study is a comparative analysis of Y-chromosome STR data obtained in 13 Tunisian populations originating from different cultural, ethnic, and geographic localities: Sejnane, Takrouna (Frigi *et al.* 2006); Jerbians of sub-Saharan origin, Jerbian Arabs, Jerbian Berbers (Khodjet el khil *et al.* 2005); Testour, Al Alia, Qalaat Al Andalous, Slouguia, Zriba, Kesra, Tunis

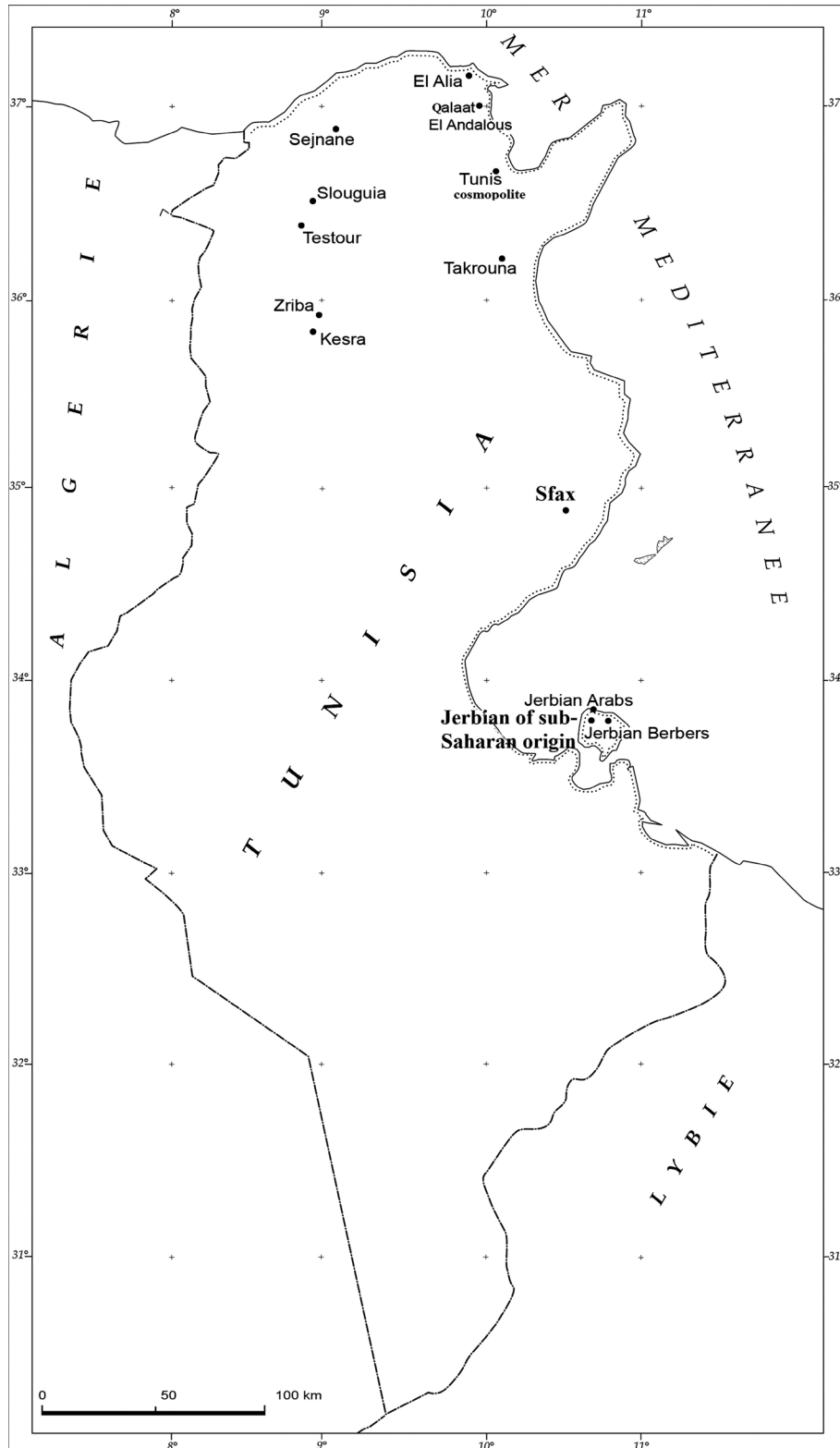


FIGURE 1. Localities of Tunisian populations.

cosmopolite (Cherni *et al.* 2005), and Sfax (Ayadi *et al.* 2006).

## MATERIALS AND METHODS

### DNA samples

This study is based on publicly available data. DNA samples were obtained from 546 male individuals from 13 different populations: 47 from Sejnane, 19 from Takrouna (Frigi *et al.* 2006); 42 from Jerbians of sub-Saharan origin, 46 from Jerbian Arabs, 47 from Jerbian Berbers (Khodjet el khil *et al.* 2005); 31 from Zriba, 23 from Kesra, 48 from Testour, 43 from Al Alia, 19 from Qalaat Al Andalous, 22 from Slouguia, 54 from Tunis cosmopolite (Cherni *et al.* 2005), and 105 from Sfax (Ayadi *et al.* 2006) (Figure 1).

### Genetic screening

All male individuals were genotyped for 11 tetra-nucleotide Y-STRs (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS385, DYS437, DYS438, and DYS439) except for the Jerbian populations where only 6 Y-STRs were available (DYS19, DYS389I, DYS390, DYS391, DYS392, and DYS393) (Ayadi *et al.* 2006, Cherni *et al.* 2005, Frigi *et al.* 2006, Khodjet el khil *et al.* 2005).

### Statistical analysis

The software package Arlequin, version 3.000 (Excoffier *et al.* 2005, Schneider *et al.* 2000) was used to calculate several population genetic parameters, including diversity of haplotype, mean number of pairwise haplotype differences (MPD); pairwise Rst values and associated *P*-values based on 10,000 permutations.

Principal coordinates analysis (PCoA) was performed on the Rst genetic distance matrix computed between pairs

of populations, using SAS software, version 6.2 (SAS Institute Inc.).

The genetic relationship between the different populations, based on the six locus Y-STR haplotypes, were further explored by analysis of molecular variance (AMOVA); as implemented in Arlequin. AMOVA allows a hierarchic analysis of three genetic variance components: those due to genetic differences (i) between individuals within populations, (ii) between populations within groups, and (iii) between groups (Excoffier *et al.* 1992).

## RESULTS

### Diversity parameters

All male individuals were genotyped for 11 tetra-nucleotide Y-STRs (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS385, DYS437, DYS438, and DYS439), except for the Jerbian populations where only 6 Y-STRs were available (DYS19, DYS389I, DYS390, DYS391, DYS392, and DYS393). Haplotype diversity values varied from 0.98 in Jerbians of sub-Saharan origin to 0.24 in Zriba population based on six Y-STRs. While using 11 Y-STRs, haplotype diversity varied from 0.99 in Sfax to 0.38 in Qalaat El Andalous (Table 1). Results show an increase in the diversity (haplotype diversity and MPD) for all the populations when 11 Y-STRs were used.

Using 6 Y-STRs, a comparison of haplotype diversity and mean pairwise differences (MPD) between all Tunisian populations showed great genetic diversity within the Jerbian of sub-Saharan origin (haplotype diversity=0.987±0.008; MPD=3.693±1.904). We must note that results show high diversity values for the majority of populations except for the Arabic population, Zriba, and an Andalusian one called Qalaat El Andalous.

TABLE 1. Diversity parameters in Tunisian populations.

Abbreviation	Group name	11 Y-STRs used		6 Y-STRs used	
		Haplotype diversity	MPD	Haplotype diversity	MPD
Sej	Sejnane	0.942±0.022	5.292±2.602	0.889±0.028	2.987±1.589
Tak	Takrouna	0.777±0.095	2.163±1.254	0.666±0.116	0.988±0.698
Jso	Jerbians of sub-Saharan origin	–	–	0.987±0.008	3.693±1.904
JA	Jerbian Arabs	–	–	0.957±0.016	2.996±1.593
JB	Jerbian Berbers	–	–	0.827±0.047	1.651±0.989
Zri	Zriba	0.569±0.079	1.040±0.712	0.243±0.099	0.369±0.364
Kes	Kesra	0.905±0.051	2.837±1.551	0.731±0.099	1.383±0.882
Tes	Testour	0.984±0.009	5.719±2.788	0.910±0.035	3.001±1.594
Alia	Al Alia	0.981±0.011	6.368±3.077	0.955±0.018	3.387±1.768
Tcos	Tunis cosmopolite	0.995±0.004	6.139±2.965	0.966±0.014	3.397±1.766
Qala	Qalaat Al Andalous	0.386±0.138	1.777±1.076	0.292±0.127	0.900±0.654
Slou	Slouguia	0.978±0.021	6.043±2.992	0.939±0.035	3.320±1.772
Sfa	Sfax	0.993±0.002	6.580±3.133	0.972±0.006	3.407±1.757

See Table 1 for abbreviation of group names.

TABLE 2. 6 Y-STR haplotype-sharing statistics.

	Sej	Tak	Jso	JA	JB	Zri	Kes	Tes	Alia	Tcos	Qala	Slou	Sfa
N of individuals	47	19	42	46	47	31	23	48	43	54	19	22	105
N of haplotypes	18	7	33	27	18	4	10	27	25	36	3	14	58
Discrimination (%)	38.2	36.8	78.5	58.6	38.2	12.9	43.4	56.5	58.1	66.6	15.7	63.6	55.2
Haplotype class													
Single unique													
N	5	1	25	12	6		1	10	8	11		3	30
Proportion	0.27	0.14	0.75	0.44	0.33		0.10	0.37	0.32	0.30		0.21	0.51
Multiple unique													
N	2		7	1	1			2	4	2		1	7
Proportion	0.11		0.21	0.03	0.05			0.07	0.16	0.05		0.07	0.12
Total unique													
N	7	1	32	13	7		1	12	12	13		4	37
Proportion	0.38	0.14	0.96	0.48	0.38		0.10	0.44	0.48	0.35		0.28	0.63
Non-unique													
N	11	6	1	14	11	4	9	15	13	23	3	10	21
Proportion	0.61	0.85	0.03	0.51	0.61	1.00	0.90	0.55	0.52	0.63	1.00	0.71	0.36
Ratio (unique/non-unique)	0.63	0.16	32.00	0.92	0.63		0.11	0.80	0.92	0.56		0.40	1.76
Haplotype diversity	0.889	0.666	0.987	0.957	0.827	0.243	0.731	0.911	0.955	0.966	0.292	0.939	0.972
Haplotype diversity SE	0.028	0.116	0.008	0.016	0.047	0.099	0.099	0.035	0.018	0.014	0.127	0.035	0.006

N, number; SE, standard error.

See Table 1 for abbreviation of group names.

TABLE 3. Number of shared haplotypes based on 6 Y-STRs.

	Sej	Tak	Jso	JA	JB	Zri	Kes	Tes	Alia	Tcos	Qala	Slou	Sfa
Sej	0												
Tak	3	0											
Jso	0	0	0										
JA	3	1	1	0									
JB	3	1	1	10	0								
Zri	2	1	0	3	3	0							
Kes	4	4	0	4	3	3	0						
Tes	4	4	0	3	3	3	5	0					
Alia	4	3	0	4	4	3	4	6	0				
Tcos	9	4	0	4	3	2	6	8	7	0			
Qala	2	1	0	1	1	1	1	1	1	2	0		
Slou	4	2	0	2	1	1	3	5	4	7	2	0	
Sfa	8	4	0	5	4	3	5	10	7	15	2	5	0

See Table 1 for abbreviation of group names.

TABLE 4. Number of shared haplotypes based on 11 Y-STRs.

	Sej	Tak	Zri	Kes	Tes	Alia	Tcos	Qala	Slou	Sfa
Sej	0									
Tak	2	0								
Zri	3	2	0							
Kes	3	2	4	0						
Tes	3	3	2	2	0					
Alia	3	2	2	2	3	0				
Tcos	7	2	4	5	5	2	0			
Qala	1	0	1	0	0	0	1	0		
Slou	1	2	1	2	2	1	1	1	0	
Sfa	6	2	7	6	5	2	12	1	1	0

See Table 1 for abbreviation of group names.

TABLE 5. Results of AMOVA: Northern populations versus Southern populations.

Source of molecular variation	Variance (%)
Among groups	0.08 ( $P=0.356$ )
Among populations within groups	-1.27 ( $P=0.891$ )
Within populations	101.19

Northern populations: Sejnane, Takrouna, Zriba, Kesra, Testour, Qalaat Al Andalous, Al Alia, Slouguia.  
 Southern populations: Jerbian Arabs, Jerbian Berbers, Jerbians of sub-Saharan origin, Sfax.

TABLE 6. Results of AMOVA: Berbers versus Arabs versus Andalusians.

Source of Molecular Variation	Variance (%)
Among groups	0.23 ( $P=0.353$ )
Among populations within groups	-1.52 ( $P=0.763$ )
Within populations	101.29

Berbers: Sejnane, Takrouna, Jerbian Berbers, Kesra.  
 Arabs: Zriba, Jerbian Arabs.  
 Andalusians: Testour, Al Alia, Qalaat El Andalous, Slouguia.

### Haplotype distribution

A total of 280 different compound Y-STR haplotypes were observed among 546 individuals. A total of 112 haplotypes (40.0%) were observed in just a single male in a single population (these haplotypes were designated "single unique"). 27 (9.6%) haplotypes were shared only by male individuals within a single population (these haplotypes are designated "multiple unique"). Single and multiple unique haplotypes combined (total unique) are the number of haplotypes that are specific to a single population (Table 2).

The remaining haplotypes (n=141, 50.4%) were observed in multiple male individuals in multiple populations (non-unique haplotypes) and thus are shared by populations. We must note that the number of single unique haplotypes was not distributed evenly across the populations. Jerbian of sub-Saharan origin population displayed a large number (75%) of single unique Y haplotypes whereas Zriba and Qalaat El Andalous populations displayed the lowest level (0%) of single unique haplotypes. Jerbians of sub-Saharan origin displayed also the highest rates of multiple-unique haplotypes (21%). High (greater than 50%) frequencies of population-specific haplotypes were observed among Jerbians of sub-Saharan origin and Sfax populations. Low (<50%) frequencies were noted in the remaining populations except for Zriba and Qalaat El Andalous where the frequency of population specific haplotypes were still 0%. For these two latter populations, the proportion of non unique haplotypes was the highest (100%). For Sejnane, Takrouna, Jerbian Arabs, Jerbian Berbers, Kesra, Testour, El Alia, Tunis cosmopolite, and Slouguia the proportion of non-unique was either higher than or nearly equal to 50%. Jerbian of sub-Saharan origin and Sfax populations

TABLE 7. Rst distance matrix based on 6 Y-STRs.

	Sej	Tak	Jso	JA	JB	Zri	Kes	Tes	Alia	Tcos	Qala	Slou	Sfa
Sej	0												
Tak	0.28147	0											
Jso	0.42822	0.60317	0										
JA	0.02917	0.33956	0.33156	0									
JB	0.11600	0.46648	0.54508	0.08857	0								
Zri	0.32792	-0.02052	0.65261	0.39215	0.53479	0							
Kes	0.16499	0.02982	0.54501	0.25643	0.34511	0.06109	0						
Tes	0.01419	0.15954	0.45480	0.08380	0.14483	0.20300	0.06831	0					
Alia	0.00228	-0.02114	-0.00252	0.00159	0.00279	-0.00709	-0.01541	0.00268	0				
Tcos	-0.00713	0.26378	0.38030	0.01822	0.13013	0.30760	0.16897	0.02180	0.00543	0			
Qala	0.32732	0.79159	0.52990	0.28286	0.63708	0.88022	0.59538	0.33184	-0.02118	0.23194	0		
Slou	0.01344	0.19714	0.36050	0.03423	0.12016	0.27350	0.10654	-0.01122	-0.01728	0.00550	0.36794	0	
Sfa	-0.00856	-0.02612	-0.01096	-0.00891	-0.00853	-0.01494	-0.02121	-0.00839	-0.00903	-0.00684	-0.02559	-0.02239	0

See Table 1 for abbreviation of group names.

displayed the lowest number of non unique haplotypes which was 0.3% and 36%, respectively.

Based on six Y-STRs, we note that of the 78 pairwise population comparisons, 10 (12.8%) had no shared haplotype, 14 (17.9%) had one, 8 (10.2%) had two, 15 (19.2%) had three, 15 (19.2%) had four and 16 (20.5%) had five or more (Table 3).

Based on 11 Y-STRs, results show that of the 45 pairwise population comparisons, 4 (8.8%) had no shared haplotype; 10 (22.2%) had one; 15 (33.3%) had two; 6 (13.3%) had three; 2 (4.4%) had four and 8 (17.7%) had five and more (Table 4). These results show the high capacity of discrimination of the 11 Y-STRs compared with the 6 Y-STRs.

**AMOVA and genetic distances**

Using AMOVA, we estimated the relative contribution to the total observed genetic variance of: (i) the genetic variance between individuals within populations, (ii) the genetic variance between populations within groups, and (iii) the genetic variance between groups (Tables 5, 6). In order to evaluate geographic and ethnic effects in Tunisia population groups, molecular variances have been computed considering:

- Firstly, 2 groups: Northern populations versus Southern populations.

- Secondly, 3 ethnic groups: Berbers versus Arabs versus Andalusians.

Results show that Tunisian populations present neither geographic nor ethnic effects. Estimations of molecular variance show that in the two considered cases the contribution of genetic variance among groups was very low (0.08% and 0.23%, *P*-value not significant). However, most of the genetic variance present among our samples could be explained by intrapopulation differences.

Rst genetic distances based on STR haplotype frequencies were computed for our samples using the six Y chromosome microsatellite loci (Table 7). A significant genetic differentiation between the majorities of pairs considered.

**Principal coordinates analysis (PCoA)**

Principal coordinates analysis (PCoA) was performed on the base of Rst distance matrix (using only the 6 STRs dataset). The two-dimensional plot of the first two PC axes, which account for 79% of the variance showed that Tunisian populations are dispersed (Figure 2):

- Slouguia, Jerbian Arabs, Tunis cosmopolite, Sejnane, Alia, and Sfax are grouped together.
- Takrouna is located close to Zriba.
- Qalaat El Andalous form a distinct cluster with the Jerbians of sub-Saharan origin.



FIGURE 2. Principal coordinates analysis (PCoA) of 13 Tunisian populations. The first axis accounts for 55.7% of the total variance. The second axis accounts for 23.3% of the total variance.

- Kesra and Jerbian Berbers are distant from the other groups and every population is isolated.

These results show neither a geographic effect nor an ethnic or linguistic effect. This reflects the mosaic structure of Tunisian populations.

## DISCUSSION AND CONCLUSION

In general, reconstructions of the recent history of human populations based on genetic data, whether classic markers, nuclear DNA polymorphisms, or mitochondrial DNA, reveal heterogeneity in North African populations, perhaps greater than in other continents (Varela *et al.* 2008). With the aim of adding information to the proposed existence of heterogeneity amongst North African populations, we analyzed the genetic variance of six and eleven Y-STR loci among 546 male individuals from 13 Tunisian populations. All loci used in this study are located in the non recombining part of the human Y chromosome and thus are completely linked, lacking any recombination. In addition we must notice that Y chromosome has a strictly paternal mode of inheritance. These characteristics render the Y chromosome extremely sensitive to genetic drift, so potentially very informative for the study of human evolution (Kayser *et al.* 2002, 2006).

The marked genetic variation of Y-STR haplotypes across 13 Tunisian populations is reflected in the haplotype diversity values, which are greater than 0.9 in 7 out of 13 populations (*Table 1*) based on 6 Y-STRs. While using 11 Y-STRs, haplotype diversity increases in all populations and it becomes higher than 0.9 in 7 out of 10 populations. MPD shows also high values. These results indicate a heterogeneous Tunisian gene pool. The Jerbians of sub-Saharan origin have the highest values for MPD and haplotype diversity. This group settled in the island within the last three centuries, its diversity level was most probably present before it came to the island (Khodjet el khil *et al.* 2005).

Lower haplotype diversity values were observed in samples from Zriba and Qalaat El Andalous. Reduced haplotype diversity for Takrouna (compared with other Tunisian populations) was also observed. In general, these low values were observed in small and isolated populations and might be due to the small population size and inbreeding. Moreover drift acts strongly and particularly on the Y chromosome and this is what seemed to happen in these populations. Such feature reduces intra-population diversity.

Our results show a high level of diversity in the majority of populations studied. These results are in agreement with studies using different types of markers that reported the highest genetic diversity in African populations. This has also been reported for Y chromosome (Jorde *et al.* 2000, Seielstad *et al.* 1999). Investigation of haplotype sharing within populations (multiple unique haplotypes) and of population specific haplotypes (single and multiple unique

haplotypes) allows some insight into population structure (*Table 3*). High amounts of haplotype sharing within populations and/or of population-specific haplotypes, were observed in Jerbians of sub-Saharan origin and Sfax. These populations are isolated from the other samples used in the study. In fact, the Jerbian of sub-Saharan origin population could represent an interesting example of population inhabiting relatively small area shared with other groups (Arabs and Berbers), but still retaining its original gene pool and genetic diversity. In the context of the evolution of human genetic variation, the high haplotype diversity in this population seems to reflect its sub-Saharan origin, where the highest diversity and the most ancient lineages were reported up to date by many studies. Regarding Sfax population, it originates from rather large area of the coastal part of Tunisia (Ayadi *et al.* 2006) and most probably represents heterogenous, not well defined population sample.

On the other hand high numbers of non unique haplotypes and haplotype sharing between populations indicate a close relationship between populations. This was observed in the vast majority of the Tunisian populations. Besides "Jso" sample (3%), all others contain 36% to 100% of the shared (non-unique) haplotypes.

Considering all Tunisian populations, the emerging picture from the non-recombining part of Y chromosome analysis is complex. In fact, the PC plot shows a dispersion of Tunisian populations. AMOVA analysis indicates insignificant intergroup variance between Berbers, Arabs, and Andalusians which is in accordance with the lack of ethnic and geographic effect in Tunisia. This situation for Tunisian population reflects the complex settlement history. Admixture of autochthonous North African people with sub-Saharan people in prehistorical times, and the contribution of different waves of migration in historical times from Europe (Romains, Vandals, Andalusians, Italians, Spanish, French, etc.), from the Middle East (Arabs, Bedouin), have led to the settlement of some communities with a founder effect (Zriba and Qalaat El Andalous) related to the settlement of new populations (Zriba, 400 years). For Jerbian of sub-Saharan origin sample the high endogamy rates have as consequence weak gene flows between this population and others settled in the same region.

In conclusion, the present study demonstrates that Y-STRs are powerful tool for the study of Tunisian population structure. Using Y-STRs, we confirm the different genetic structures of Tunisian populations. This result is reflected by the complex population history as a result of many centuries of invasions and waves of immigration coming from different surrounding areas.

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