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Abstract

Due to its complex history of migrations and colonization of African, European and Asian people, the Tunisian territory is an ideal area to study the effects of cultural change on the genetic structure of human populations. We investigated the mtDNA genetic variation of Tunisian populations in order to detect the possible impact of recent historical events on their gene pool. Two Arab and three Berber communities were analysed using a comparison dataset of 45 other populations including African, Arabian,

Asian, European and Near Eastern groups. The results obtained were compared with those produced using a large panel of autosomal SNPs. We observed a slight but important difference between the populations that inhabit the southern and central-northern areas of the country. Furthermore, robust signatures of genetic isolation were detected in two Berber populations (Nouvelle Zraoua and Tamezret) and in the semi-nomadic Arab group of the R'Baya. Our investigation suggests that the genetic structure of investigated southern Tunisian populations retains signatures of historical events which occurred between 7th-17th century, particularly the trans-Saharan slave trade and the emigration of Berbers in remote areas of the south during the Arab conquest.

Introduction

The earliest human presence in present-day Tunisia can be traced back to the Early Stone Age (Dominguez-Rodrigo 2013), followed by several successive occupation events in the Middle and Late Stone Age (Aouadi-Abdeljaouad and Belhouchet 2012; Barton et al. 2021; di Lernia et al. 2017; Harbi-Rihai 2020). Hunter-gatherer communities, bearing the Capsian culture, persisted even after (up until 4.7 Kya; see di Lernia et al. 2017; Mulazzani 2013; Rahmani 2004) the introduction of pastoral economies which occurred through acculturation processes during the 9th/8th millennium cal BCE (Mulazzani et al. 2016). In the second millennium BCE, the Phoenicians arrived from the Levant, succeeded by Greeks, Romans, Vandals, and Byzantines. The latter resisted until the arrival of the first military Arab expeditions in the 7th century CE. While the initial phase of conquest involved only a few thousand people (McEvedy and Jones 1980), the second wave during the 11th century CE was led by larger groups of Bedouin members of the Banū Hilāl and Banū Sulaym tribes from the Arabian Peninsula, and involved up to fifty thousand warriors with their families (Abun-Nasr 1987).

The Arab invasion reshaped the cultural background of the Tunisian population, leading to the Islamization of the Berbers, the "indigenous" people of North Africa (Brett and Fentress 1997). Only several small communities avoided a rapid and general linguistic change taking refuge in southern Tunisia (Murdock

1959; Souag 2020). Between the 16th and the 17th century, the conquest by the Ottoman Empire further consolidated Muslim presence in Tunisia (Ghazali 2003; UNESCO 2009). Their tenuous control of the region ended in the 19th century with the French military occupation (Brown 2015). Today, the nearly twelve million inhabitants of Tunisia almost completely identify themselves as Arabs (about 5% of Turkish origin), with less than 1% claiming they have Berber origins and which speak traditional dialects belonging to the Zenati language branch (Kossmann 2013). These are mostly members of small communities settled in the southern and south-eastern areas of the country and the island of Jerba.

Several studies using different genetic systems (classic genetic and unilinear markers, Alu insertions, autosomal STRs, and SNPs) have detected North African, Middle Eastern, and European contributions, mirroring the complex history of the peopling of this area (Bosch et al. 1997, 2000, 2001; Cherni et al. 2005; Comas et al. 2000; Elkamel et al. 2018); a lack of significant genetic differentiation between Berbers and Arabs; and a high within-group heterogeneity (Cherny et al. 2005; Ennafaa et al. 2011). In particular, the apparent lack of correspondence between genetic and ethno-linguistic diversity has been widely emphasized (Fadhlaoui-Zid et al. 2004; Frigi et al. 2017; Kefi et al. 2015). Despite the considerable number of studies published so far, groups from southern Tunisia have yet to be thoroughly investigated, while the role of geographically and/or culturally isolated groups in determining the observed patterns of genetic variation required further investigation.

To provide further insights into the genetic structure of Tunisian populations, we analyzed mtDNA variation of two Arab (Douz and the R'Baya people) and three Berber groups (Matmata, Nouvelle Zraoua, and Tamezret) from southern Tunisia. The abundance of mtDNA data both for cosmopolitan and admixed or small and remote groups, greater than Y-chromosome or autosomal polymorphisms, offered us an important opportunity to carry out extensive

comparisons among populations. Furthermore, by studying populations not yet analyzed for mtDNA variation that have settled in areas not yet thoroughly investigated, our data can help further refine mitochondrial phylogeny (Calafell, 2021).

In order to detect the possible impact of recent historical events on the mtDNA gene pool, we investigated the genetic relations of the southern Tunisian communities with other populations from northern and sub-Saharan Africa, Eurasia, the Arabian Peninsula and the Near East. Furthermore, we detected signatures of genetic isolation by applying a re-sampling-based procedure (Anagnostou et al. 2017) which makes it possible to overcome the confounding effect of sample size variation. The inferences concerning genetic structure based on maternally inherited markers were also compared with those we previously obtained using a large panel of autosomal SNPs.

Materials and Methods

The Populations Under Study

We collected saliva samples from five southern Tunisian populations, comprising two Arab (Douz and the R'Baya people), and three Berber (Matmata, Nouvelle Zraoua, and Tamezret) communities (see Figure 1) for a total of apparently healthy and unrelated 87 donors following the "grandparent's rule" (donors selected only if they were unrelated to other donors at grandparent level and with known-family origin). A total of 38 samples of self-reported Tunisian Arabs were collected in the region of Nefzaoua, mostly in the city of Douz. Douz (33°27'0'' N, 9°1'0'' E) is a city of about 38 thousand inhabitants, in the Kebili Governorate, a settlement point for Arab newcomers in the Middle Ages (Ellefi 2016).

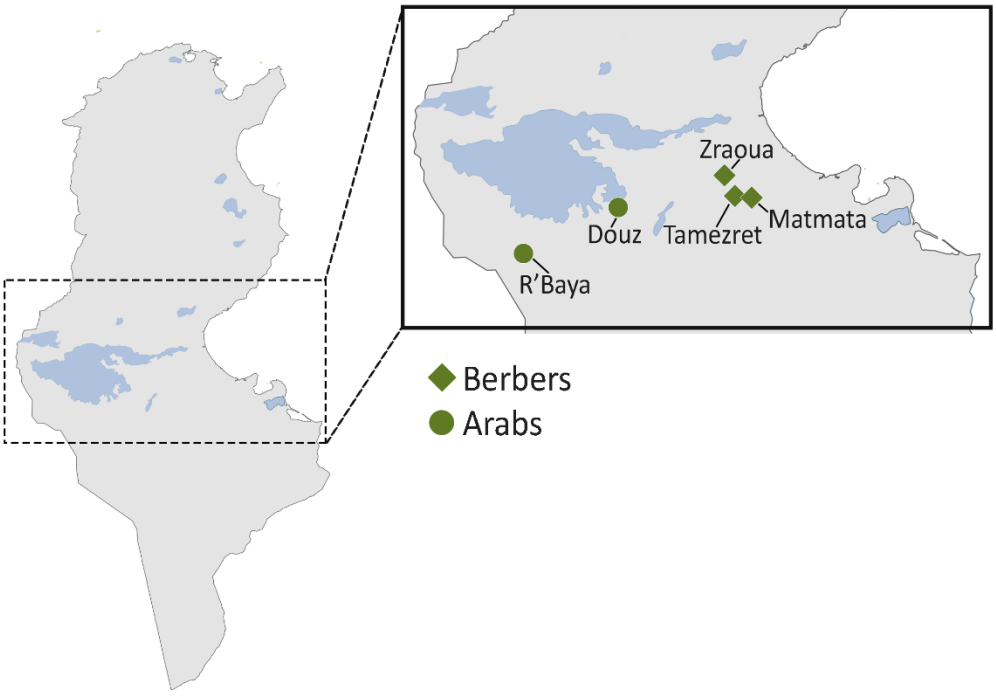

Figure 1. The geographic location of the populations analyzed in this study.

We also gathered samples from 12 individuals from the R'Baya, a small Arab-speaking group of nearly 14 thousand semi-nomadic herders settled mainly in the Grand Erg Oriental. The R'Baya are thought to have migrated as nomadic shepherds from Tripolitania, originating from the Arabs who conquered this region during the 11th century following its invasion by the Banu Hilal and Banu Sulaim tribes (Bataillon 1963; Boudebia-Baala 2012; Etherton 1971). Another 37 samples were collected in three small villages of self-reported Berbers located in the Governorate of Gabès (Boukous 2016): Matmata (n= 13; 33° 32' 33.5'' N, 9°58' 0.5'' E), Nouvelle Zraoua (n=14; 33°39'40.1''N, 9°47'34.7''E) and Tamezret (n=10; 33° 32' 00'' N, 9° 52' 00'' E).

Data obtained from the above groups were integrated with those from a total of 50 populations settled in North Africa (21), West Africa (5), East Africa

(4), the Arabian Peninsula (5), Central Asia (3), Europe (7) and the Near East (5) (see Supplementary Table S1).

Ethics Statement and Data Availability

Sampling procedures were conducted after obtaining informed consent and ethnological, linguistic, and familial information. All experimental protocols were approved by the Bioethics Committee of the Sapienza University of Rome (Rome, Italy. Prot. N. 259/19). Genetic data were uploaded as online supporting information and deposited in Zenodo (DOI 10.5281/zenodo.5810413).

Laboratory Analyses

DNA was extracted using the prepIT L2P kit (DNA Genotek) following the manufacturer's protocol. Hypervariable regions 1 (HVR-1) and 2 (HVR-2) were amplified by PCR (primers: L-15990 and H-16501 for HVR-1; L-029 and H-408 for HVR-2). The amplified DNA was purified using a High Pure PCR Product Purification Kit (Roche Diagnostics, Mannheim, Germany), sequenced, and compared with the Cambridge Reference Sequence rCRS (Andrews et al. 1999). Haplogroup classification was performed using the Haplogrep software version 2 (Weissensteiner et al. 2016) based on the HVR-1 and HVR-2 sequence and according to the updated phylogenetic tree of global human mitochondrial DNA variation (PhyloTree Build 17; van Oven and Kayser 2009).

Statistical Analyses

The intra-population genetic variation was analysed through the calculation of haplotype diversity (HD; Nei 1987) and the mean number of pairwise differences (MNPD; Tajima 1983, 1993). Pairwise differences among all the populations of

the dataset were calculated using the genetic distance measure Fst (Reynolds et al. 1983; Slatkin 1995). Analysis of molecular variance (AMOVA; Excoffier et al. 1992) was performed to examine genetic differences among populations of the same ethnic group and between ethnic groups. The same approach was carried out in the case of geographic groups. Demographic descriptive Fu's Fs test was performed to check for signs of demographic expansion (Fu 1997). All the above mentioned parameters were calculated using the Arlequin software version 3.5.2.2 (Excoffier and Lischer 2010). Multi-Dimensional Scaling (MDS) was applied to genetic distance matrices to visualize genetic differentiation among populations using R statistical software version 3.6.3 (R Core Team 2014).

We calculated the pairwise differences between mtDNA sequences using an ad hoc R script to evaluate their similarity.

Following Anagnostou et al. (2017), we performed a re-sampling based analysis to test whether the HD values observed in populations subject to geographic and/or cultural barriers fall within the range of values for broad and non-isolated groups with equal sample size. As a reference population, we used a total of 800 individuals of five Moroccan (MAB, MAR, MMX, MNC, MSW) and five Tunisian groups (TKA, TMT, TSJ, TUN, TWS; see Supplementary Table S1 for abbreviations). We extracted 10000 random sub-samples with no replacement from the reference population for each sample size of the populations showing signatures of genetic isolation. Then, we obtained a distribution of HD values for each sample size. To evaluate if our hypothesis could be accepted or not, we calculated standard scores (z-scores). We used the z-scores to compute the probability (set at a 66.7% level) that the calculated HD values fall within the range for broad and non-isolated groups with equal sample sizes.

Results

A total of 57 different haplotypes were observed among the five southern Tunisian groups under study. They were assigned to 14 main haplogroups (H, HV, J, K, L1, L2, L3, M, N, R0, T, U, W, X) and further classified into 37 sub-haplogroups (see Supplementary Table S2). The most common were found to be L1 for Douz (23.7%), L3 for Nouvelle Zraoua, R'Baya, and Tamezret (57.1%, 41.7%, and 40%, respectively), and H, L2, M, T, and X for Matmata (15.4%). Only two haplogroups were found to be shared by all five populations under study: H (from 0.13% in Douz to 41.7% in R'Baya) and L3 (from 7.7% in Matmata to 57.1% in Nouvelle Zraoua).

Three populations (Nouvelle Zraoua, R'Baya and Tamezret) showed particularly low HD values (from 0.803 to 0.889; see Supplementary Table 1), also compared to those reported in our extended dataset (from 0.664 to 1.000; see Supplementary Table S1). However, the robustness of this evidence could be limited due to the small sample size, a problem often encountered when studying isolated communities where usually the level of consanguinity is high and the census size is small (Fareed and Afzal 2017; Peltonen et al. 2000). To overcome these limitations, we applied the re-sampling procedure described in Anagnostou et al. (2017), which provides reference values of HD to discriminate between isolation effects and random fluctuations due to sample size variation. We observed that these values are lower than expected in a large non-isolated group of the same sample size (see Supplementary Figure S1). For these populations we also observed statistically not significant values of Fu's Fs (Table 1), implying a lack in signatures of demographic expansion.

Population	Ethnicity	Abbreviation	n	k	HD	HDse	MNPD	MNPDse	HD/MNPD	Fu's Fs	p Fs
Douz	Arab	TDO	38	24	0.962	0.017	10.880	5.060	11.315	-4.791	0.069
Matmata	Berber	TMT	13	13	1.000	0.030	8.846	4.364	8.8463	-6.290	0.004
Nouvelle Zraoua	Berber	TZR	14	9	0.879	0.079	4.198	2.218	4.775	-1.959	0.126
R'Baya	Arab	TRB	12	5	0.803	0.078	8.712	4.328	10.850	4.163	0.949
Tamezret	Berber	TTM	10	6	0.889	0.075	5.644	2.958	6.350	0.676	0.602

Table 1. Genetic diversity and demographic estimates in the populations under study. Abbreviations: n, sample size; k, number of haplotypes; HD, haplotype diversity; HDse, haplotype diversity standard error; MNPD, mean number of pairwise differences; MNPDse, mean number of pairwise differences standard error.

The MNPD confirmed the low intra-population diversity of Nouvelle Zraoua and Tamezret compared to that found in the other populations analyzed, while what observed for Matmata, Douz and R'Baya is higher than the median value of the dataset. Interestingly, the ratio between the two intra-population diversity measures was found to be high in the southern Tunisia Arabs and Matmata. This could suggest that incoming gene flow introduced mtDNA lineages that were highly divergent from the pre-existing genetic pool (Battaggia et al. 2012).

We also performed a correlation analysis comparing HD and the autosomal intra-population length of shared chunks, a parameter that can be taken as a means to evaluate the degree of inbreeding (Anagnostou et al. 2020). Using a

paired dataset of mtDNA and autosomal SNP data (see Supplementary Table S3), we observed a high and statistically significant negative correlation between the two parameters (R^2=-0.92; p-value<0.001; Figure 2).

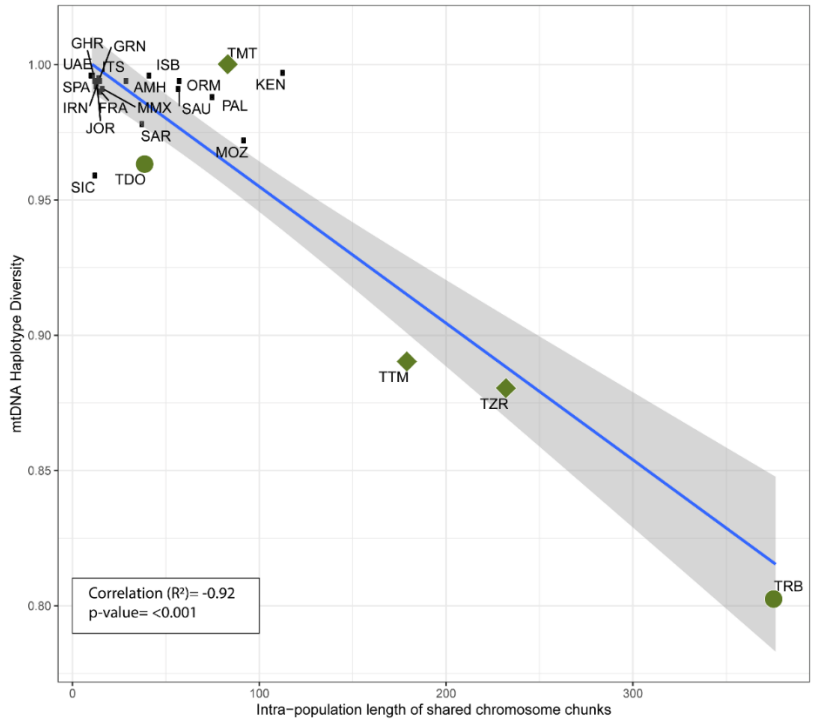

Figure 2. Linear regression between autosomal intra-population length of shared chromosome chunks and mtDNA HD. Populations under study are marked with green circles (Arab groups) and green diamonds (Berber groups). See Supplementary Table S3 for population abbreviations.

Regarding inter-population genetic variation, the MDS plot based on Fst values (Figure 3) highlighted a pronounced differentiation of Nouvelle Zraoua and R'Baya from North African, European and Asian populations with the latter exhibiting closer proximity to sub-Saharan groups. Conversely, Matmata and Tamezret fall close to the other North African groups, although for the latter a slight diversification can be appreciated. The Douz sample differentiates from the

main cluster and falls close to the Amhara and Oromo from Ethiopia.

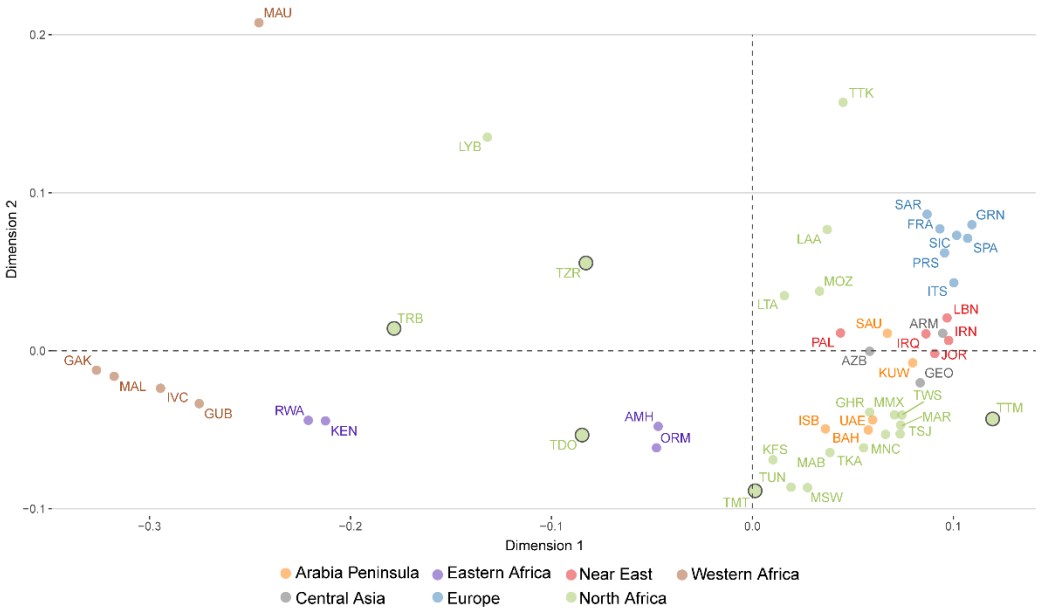

Figure 3. Multi-Dimensional Scaling plot of Fst genetic distances among populations (stress value=0.048). Population abbreviations as in Supplementary Table S1.

In order to gain further insights, we analysed the distribution of mtDNA sequence pairwise differences between each population under study and eight geographic metapopulations from Africa, Europe and Asia (see Supplementary Figure S2). Overall, our Berber populations showed more leftward distributions, toward low values of pairwise differences, than Douz and R'Baya. However, a small but noticeable proportion of zero or very few pairwise differences with eastern and western sub-Saharan Africans was observed only for our southern Tunisian Arabs.

Finally, we carried out an AMOVA (Table 2). Firstly, we grouped populations based on their ethnicity. We found no significant diversity between the Arab and Berber groups (0.005, p-value=0.126). However, we observed

statistically significant values of molecular variance among populations within-groups, both for the Berbers (0.071, p-value=0.000) and Arabs (and 0.028, p-value=0.000). Performing a jackknife procedure, a statistical non-significance was reached for both groups when removing Douz and R'Baya from the Arabs (0.010, p-value=0.017) and Takrouna and Nouvelle Zraoua from the Berbers (0.021, p-value=0.065).

Group	Populations	Among populations	p-value
Tunisian Arabs	TDO-TKA-TRB-TWS-TUN	0.028	0.000
	TKA-TWS-TUN-TDO	0.022	0.000
	TKA-TWS-TUN-TRB	0.020	0.000
	TKA-TWS-TUN	0.010	0.017
Tunisian Berbers	TMT-TSJ-TTK-TTM-TZR	0.071	0.000
	TMT-TSJ-TTM-TTK	0.058	0.000
	TMT-TSJ-TTM-TZR	0.040	0.008
	TMT-TSJ-TTM	0.021	0.065
Central-Northern Tunisia	TKA-TSJ-TTK-TUN-TWS	0.024	0.000
Southern Tunisia	TDO-TMT-TRB-TTM-TZR	0.087	0.000

Table 2. Analysis of Molecular Variance (AMOVA) in Tunisian Arab and Berber populations. Significance level at p-value<0.010. Population abbreviations and references as in Table S1.

Secondly, we grouped populations based on their geographic location. Comparing central-northern and southern populations, we found no significant between-group diversity (0.002, p-value=0.175). Instead, we obtained significant values of molecular variance among populations for both groups, nearly four times higher for the southern than the central-northern one (0.087, p-value=0.000 and 0.024, p-value=0.000, respectively).

Discussion

Tunisia represents an important area for the study of the effects of cultural change on the genetic structure of human populations. During the Arab expansion in North Africa, local Berber communities adopted the Islamic religion and for the most part also the Arabic language (Namouchi 2011). Together with the trans-Saharan slave trade routes during the Arab conquest and the isolation of certain Berber communities that were forced to emigrate to Southern Tunisia, the resulting admixture between autochthonous and newcomers played an important role in shaping the genetic diversity of Tunisian populations (Elkamel et al. 2018; Ennafaa et al. 2011; Fadhlaoui-Zid et al. 2004; Harich et al. 2010; Turchi et al. 2009).

Tunisian Arab and Berber populations were found to be more genetically heterogeneous within rather than between the respective groups. The lack of correspondence between genetic and ethnic or linguistic diversity is in line with other studies carried out in Tunisia using mtDNA (Ennafaa et al. 2011; Fadhlaoui-Zid et al. 2004; Kefi et al. 2015) and other genetic markers (Bosch et al. 1997, 2000; Comas et al. 2000). Similarly, no substantial geographical structuring was

evidenced at genetic level. However, MDS and AMOVA detected an interesting differentiation among the populations that inhabit the central-northern areas and, even more markedly, among those settled in the southern part of the country. Several historical events seem to have contributed to this picture.

First of all, the trans-Saharan slave trade (7^{th}–17^{th} century), operated by the Arab invaders during the conquest of North Africa, was a significant event (Lovejoy 1983). At genetic level, evidence of this huge population movement, involving nearly five million people (Lovejoy 1983), has been associated with the presence of L sub-haplogroups, especially those characterizing sub-Saharan populations such as L1 (Harich et al. 2010). We found that this event also had an impact on the genetic diversity of all our southern Tunisian populations, except Matmata, which is similar to other groups living all over the country (Harich et al. 2010; Turchi et al. 2009). However, the intensity of this phenomenon could have been greater in the southern Tunisian Arabs than anywhere else. We were able to find evidence of a closer mtDNA genetic affinity between the latter and Sub-Saharan Africans. More specifically, L1 is the most represented haplogroup in Douz, reaching the highest frequencies among every other Tunisian population studied so far (Elkamel et al. 2018; Frigi et al. 2017). Moreover, genetic distances differentiate Douz from the other Tunisian Arabs, which are more closely related to North Africans, Europeans, and Middle Easterns, placing it close to eastern sub-Saharan groups. Interestingly, this pattern was also observed in the distributions of the individual estimates of local ancestry proportions based on autosomal SNPs (Anagnostou et al. 2020).

Combining mtDNA with genomic data, we could get further insights into the historical and demographic events that contributed to the current population structure of Douz. Our previous genomic analyses suggest that the first settlement of Arab people to the oasis of Douz dates back to the mid 13th century, as inferred by the most ancient admixture event involving Douz people and western sub-

Saharan Africans (Anagnostou et al. 2020). This is consistent with current historical knowledge that indicates the core of the Douz people as represented by the Marazig people, semi-nomadic Bedouins related to the Banu Sulaim tribe who settled in the area probably at the same time period (Marzougi 1979; Wright 2007). The haplotype-based analyses revealed a sub-Saharan component in Douz resulting from the stratification of multiple migratory waves of already mixed Arab newcomers and the acquisition of additional slaves (Anagnostou et al. 2020). The mitochondrial data add another piece to the reconstruction of the genetic history of the current population of Douz. The large representation of sub-Saharan female lineages in Douz's current gene pool matches historical and demographic evidence that female slaves were preferred to men, even twice as much, due to their importance to Muslim merchants as maids and concubines (Gakunzi 2018; Segal 2002).

A second important historical event involved in shaping the Tunisian genetic makeup regards the emigration of Berbers to remote areas of the south as a consequence of the Arab conquest. As pointed out in previous studies, this could have played an important role in determining the genetic isolation of these communities (Ennafaa et al. 2011; Fadhlaoui-Zid et al. 2004, 2011; Kefi et al. 2015). The Berber communities of Nouvelle Zraoua and Tamezret who have retained their original "Tamazight" language (Achab 2012) are settled in a rural and semi-desertic context, at a considerable distance from communities of Arab origin. We observed that they are characterized by a haplotype diversity reduction, an outlying position in the MDS plot and a state of demographic stationarity, showing that genetic isolation left an important signature not only on their autosomal SNPs (Anagnostou et al. 2020) but also on mtDNA variation. This suggests that the high female mobility associated with a patrilocal social structure, as in the case of Berbers (Bobrovnikov 2000), may not have been sufficient to prevent a strong action of genetic drift on maternally transmitted

lineages.

Finally, we discuss the genetic variation of the semi-nomadic group of the R'Baya, whose origins are linked with the Arab invasion. Interestingly, Africa offers a unique opportunity to study the genetic structure of populations subject to isolation factors, but so far studies have mainly focused on sub-Saharan populations (e.g. Destro Bisol et al. 2000). According to Boudebia-Baala (2012), after the 11th century North African conquest, the initial nucleus of this group settled in Tripolitania and moved as nomadic shepherds to the Tunisian region of Ben Gardane. Around the 17th-18th century, they migrated westwards to the Souf region in Algeria due to disputes with the local authorities (Bataillon 1963; Etherton 1971). The present-day R'Baya people live mainly in the Algerian province of El Oued during the winter, and in the Tunisian Grand Erg Oriental in summer, where they move to graze their herds (Zecchini and Zecchini 2000). Genomic evidence showed that their gene pool was already enriched with sub-Saharan African lineages at the time of their arrival (Anagnostou et al. 2020). Our results suggest that the combined effect of their relatively small population size, the desert environment and the maintenance of Bedouin traditions limited the genetic mixing of maternally transmitted characters with Berber and Arab communities, leaving detectable signatures of isolation in their genetic structure.

In conclusion, this study made it possible to highlight how historical and demographic events and cultural factors have contributed in relatively recent times to modelling the genetic structure of maternally transmitted traits of Tunisian populations. These findings will help design further investigations into genomic and Y chromosome diversity aimed at understanding in more detail the relationships between genes, history and culture in this important region of North Africa.

Declaration of Interest

The authors report no conflict of interest.

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Supplementary Materials

Supplementary Table S1. Intrapopulation diversity measures and demographic parameters in the 50 populations analysed in the present study. Abbreviations: n: sample size, k: number of unique haplotypes, HD: haplotype diversity; MNPD: mean number of pairwise differences.

Population	Geographic Area	Nation	Abbreviation	n	k	HD	HDse	MNPD	MNPDse	Fu's Fs	p Fs
Mozabites (Berbers)	North_Africa	Algeria	MOZ	26	19	0,972	0,018	6,329	3,101	-7,858	0,006
Armenians	Central_Asia	Armenia	ARM	30	30	1,000	0,009	7,621	3,656	-24,402	0,000
Azerbaijani	Central_Asia	Azerbaijan	AZB	30	30	1,000	0,009	8,037	3,840	-21,041	0,000
Bahraini	Arabia_Peninsula	Bahrain	BAH	213	163	0,997	0,001	10,242	4,694	-24,143	0,001
Gharbia	North_Africa	Egypt	GHR	56	51	0,996	0,005	9,736	4,527	-24,641	0,000
Kafrelsheikh	North_Africa	Egypt	KFS	45	39	0,993	0,007	10,127	4,714	-24,542	0,000
Amhara	Eastern_Africa	Ethiopia	AMH	90	74	0,994	0,003	10,877	4,993	-24,411	0,000
Oromo	Eastern_Africa	Ethiopia	ORM	83	66	0,994	0,003	11,226	5,148	-24,404	0,000
French	Europe	France	FRA	50	44	0,990	0,008	5,869	2,851	-25,308	0,000
Georgians	Central_Asia	Georgia	GEO	28	28	1,000	0,010	7,635	3,670	-24,727	0,000
Ashanti-Akan	Western_Africa	Ghana	GAK	192	110	0,989	0,002	11,613	5,284	-24,065	0,000
Greeks	Europe	Greece	GRN	319	229	0,995	0,001	6,838	3,228	-24,486	0,000
Guinea Bissau	Western_Africa	Guinea Bissau	GUB	79	65	0,993	0,004	12,691	5,783	-24,310	0,000
Iranians	Near_East	Iran	IRN	30	28	0,993	0,012	6,961	3,366	-23,148	0,000
Iraqis	Near_East	Iraq	IRQ	203	107	0,988	0,002	7,785	3,640	-24,488	0,001
Bedouins	Arabia_Peninsula	Israel	ISB	44	40	0,996	0,006	11,555	5,338	-24,478	0,000
Italians	Europe	Italy	ITS	103	88	0,994	0,003	7,170	3,389	-24,887	0,000
Ivorians	Western_Africa	Ivory Coast	IVC	100	80	0,990	0,005	10,244	4,716	-24,446	0,000
Jordanians	Near_East	Jordan	JOR	202	169	0,992	0,003	8,071	3,763	-24,448	0,000
Kenyans	Eastern_Africa	Kenya	KEN	103	93	0,997	0,002	14,055	6,356	-24,143	0,001

Kuwaitians	Arabia_Peninsula	Kuwait	KUW	381	281	0,997	0,001	9,391	4,322	-24,013	0,001	
Lebanese	Near_East	Lebanon	LBN	195	159	0,995	0,002	7,714	3,610	-24,530	0,000	
Lybians	North_Africa	Lybia	LYB	269	183	0,992	0,002	9,058	4,183	-24,187	0,000	
Al Awaynat (Berber Tuaregs)	North_Africa	Lybia	LAA	111	17	0,664	0,049	6,306	3,014	1,097	0,680	
Tahala (Berber Tuaregs)	North_Africa	Lybia	LTA	18	6	0,732	0,096	6,843	3,379	3,647	0,938	
Malians	Western_Africa	Mali	MAL	124	99	0,993	0,003	10,219	4,697	-24,364	0,000	
Maure	Western_Africa	Mauritania	MAU	64	40	0,968	0,012	7,565	3,577	-22,807	0,000	
Moroccan (Arabs)	North_Africa	Morocco	MAR	42	39	0,993	0,009	8,760	4,124	-24,477	0,000	
Moroccan (Berbers)	North_Africa	Morocco	MAB	69	55	0,992	0,004	8,672	4,053	-24,737	0,000	
Moroccans	North_Africa	Morocco	MMX	345	244	0,991	0,002	8,555	3,964	-24,155	0,002	
Moroccans (Northern-Central)	North_Africa	Morocco	MNC	56	46	0,984	0,010	8,266	3,888	-24,835	0,000	
Sahrawi	North_Africa	Morocco	MSW	53	46	0,993	0,006	9,343	4,360	-24,694	0,000	
Palestinians	Near_East	Palestine	PAL	43	34	0,988	0,008	7,890	3,743	-22,110	0,000	
Portuguese	Europe	Portugal	PRS	59	47	0,967	0,018	6,288	3,026	-25,201	0,000	
Rwandans	Eastern_Africa	Rwanda	RWA	153	98	0,991	0,002	14,799	6,658	-23,957	0,001	
Sardinians	Europe	Italy	SAR	70	53	0,978	0,011	6,054	2,918	-25,237	0,000	
Saudi Arabs	Arabia_Peninsula	Saudi Arabia	SAU	513	288	0,991	0,001	9,368	4,309	-23,908	0,003	
Sicilians	Europe	Italy	SIC	118	86	0,959	0,015	6,507	3,099	-24,982	0,000	
Spanish	Europe	Spain	SPA	312	217	0,994	0,001	6,755	3,192	-24,476	0,000	
Douz (Arabs)	North_Africa	Tunisia	TDO	38	24	0,962	0,017	10,881	5,060	-4,791	0,069	
Kairouan (Arabs)	North_Africa	Tunisia	TKA	50	43	0,994	0,006	8,853	4,151	-24,764	0,000	
Matmata (Berbers)	North_Africa	Tunisia	TMT	13	13	1,000	0,030	8,846	4,364	-6,290	0,004	
Tunisians (North)	North_Africa	Tunisia	TUN	64	52	0,992	0,005	10,388	4,800	-24,551	0,000	
Nouvelle Zraoua (Berbers)	North_Africa	Tunisia	TZR	14	9	0,879	0,079	4,198	2,218	-1,959	0,126	
R'Baya (Arabs)	North_Africa	Tunisia	TRB	12	5	0,803	0,078	8,712	4,328	4,163	0,949	
Sejnane (Berbers)	North_Africa	Tunisia	TSJ	47	36	0,987	0,008	8,920	4,184	-21,017	0,000	
Takrouna (Berbers)	North_Africa	Tunisia	TTK	33	11	0,903	0,023	4,155	2,120	-0,689	0,410	
Tamezret (Berbers)	North_Africa	Tunisia	TTM	10	6	0,889	0,075	5,644	2,958	0,676	0,602	
Wesletia (Arabs)	North_Africa	Tunisia	TWS	61	52	0,993	0,005	8,024	3,779	-24,858	0,000	
Dubai	Arabia_Peninsula	United Arab Emirates	UAE	249	175	0,996	0,001	10,367	4,745	-24,075	0,000	

Supplementary Table S2. Inferred haplogroups and quality of classification in the five southern Tunisia populations. Abbreviations: TDO: Douz; TMT: Matmata; TZR: Nouvelle Zraoua; TRB: R'Baya; TTM: Tamezret.

Sample	Haplogroup	Overall Rank (Haplogrep2; Phylotree Build 17)
TDO_1	L2a	90%

TDO_2	W6	87%
TDO_3	J2a	92%
TDO_4	W6	87%
TDO_5	J2a	95%
TDO_6	H4a	100%
TDO_7	U6a	100%
TDO_8	L1b	97%
TDO_9	U6a	100%
TDO_10	U6a	100%
TDO_11	L3d	92%
TDO_12	R0a	80%
TDO_13	L1b	97%
TDO_14	U1a	89%
TDO_15	L1b	97%
TDO_16	U3	84%
TDO_17	L3b	97%
TDO_18	H11a	100%
TDO_19	L1b	92%
TDO_20	M1a	100%
TDO_22	L3h	87%
TDO_23	U3	84%
TDO_24	L2a	96%
TDO_25	L1b	97%
TDO_26	U3	84%
TDO_27	L1b	97%
TDO_28	W6	76%
TDO_30	L1b	97%
TDO_31	N1b	89%
TDO_32	R0a	80%
TDO_33	L1b	97%
TDO_34	L1b	97%
TDO_35	H57	73%
TDO_36	K1a	100%
TDO_37	U5b	86%
TDO_38	H57	73%
TDO_39	L3e	100%
TDO_40	H4a	100%

TMT_2	T1a	94%
TMT_3	U9a	100%
TMT_4	M1a	93%
TMT_5	X2e	98%
TMT_6	H1a	85%
TMT_8	X3a	98%
TMT_9	L3f	100%
TMT_10	T1a	92%
TMT_11	M1b	100%
TMT_12	J2b	100%
TMT_13	L2a	95%
TMT_14	H101	73%
TMT_15	L2e2	91%
TZR_1	L3e5	88%
TZR_2	H2a	100%
TZR_3	L3e	91%
TZR_4	H5b	86%
TZR_5	L3e	88%
TZR_6	L3e	84%
TZR_7	H24	100%
TZR_8	M1a	100%
TZR_9	L3e	88%
TZR_10	K	98%
TZR_12	L3e	100%
TZR_13	HV0	100%
TZR_14	L3e	88%
TZR_15	L3e	84%
TRB_15_1	L1b	95%
TRB_15_2	L3b	86.35%
TRB_15_3	L3b	93%
TRB_1	L3b	93%
TRB_2	H57	89%
TRB_3	H57	89%
TRB_5	L3b	93%
TRB_6	H2a	100%
TRB_7	L1b	95%
TRB_8	H57	89%
TRB_9	L3b	93%

TRB_10	H57	89%
TTM_1	L3d	100%
TTM_2	HV0	100%
TTM_4	H2a	100%
TTM_5	L3h	88%
TTM_6	UV0	90%
TTM_7	H1k	94%
TTM_8	L3d	100%
TTM_9	L3b	97%
TTM_10	H2a	100%
TTM_11	HV0	100%

Supplementary Table S3. Autosomal SNPs data references of the 23 populations used for the correlation analysis reported in Figure 2. Data resolution: 258,609 SNPs.

Population	Reference
Bedouins	Li et al., 2008
Egyptians	Behar et al., 2010
Amhara	Behar et al., 2010
Oromo	Behar et al., 2010
French	Li et al., 2008
Greeks	Hellenthal et al., 2014
Iranians	Li et al., 2008; Behar et al., 2010
Italians	Hellenthal et al., 2014
Jordanians	Li et al., 2008
Kenyans	Li et al., 2008
Matmata (Berbers)	Anagnostou et al., 2020
Moroccans	Behar et al., 2010; Hellenthal et al., 2014
Mozabites	Li et al., 2008
Palestinians	Li et al., 2008
Sardinians	Li et al., 2008
Saudi Arabs	Behar et al., 2010
Sicilians	Hellenthal et al., 2014
Spanish	Behar et al., 2010; Hellenthal et al., 2014
Douz (Arabs)	Anagnostou et al., 2020

Nouvelle Zraoua (Berbers)	Anagnostou et al., 2020
R'Baya (Arabs)	Anagnostou et al., 2020
Tamezret (Berbers)	Anagnostou et al., 2020
United Arab Emirates	Behar et al., 2010

Table S3 References

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Supplementary Figures

Figure S1

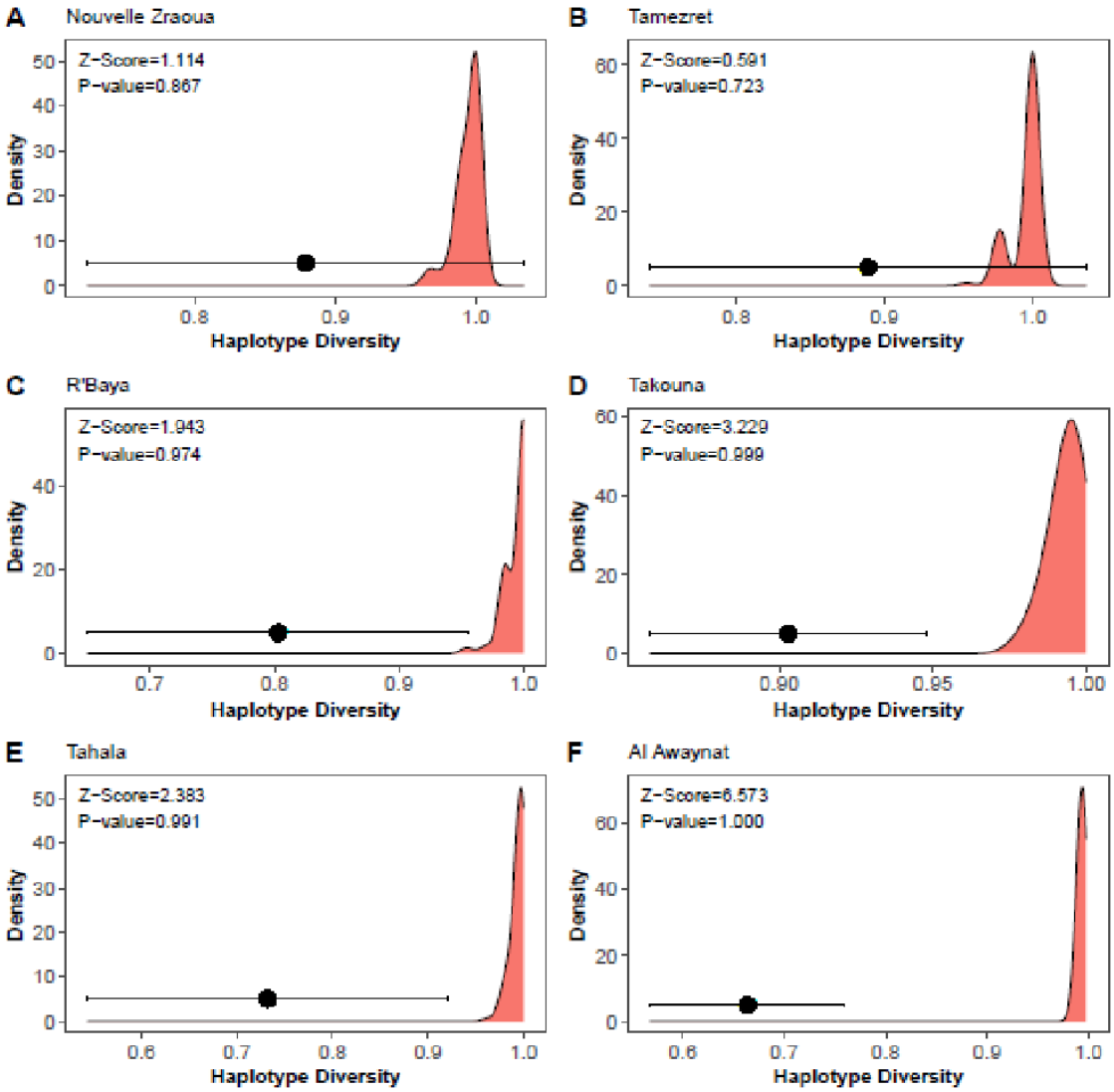

Figure S1. Comparison between the observed HD value and the distribution obtained through resamplings, at an equal sample size, from the reference North-African metapopulation in (A) Nouvelle Zraoua, (B) Tamezret, (C) R'Baya, (D) Takrouna, (E) Tahala and (F) Al Awaynat. Horizontal bars indicate 95% confidence intervals.

Figure S2

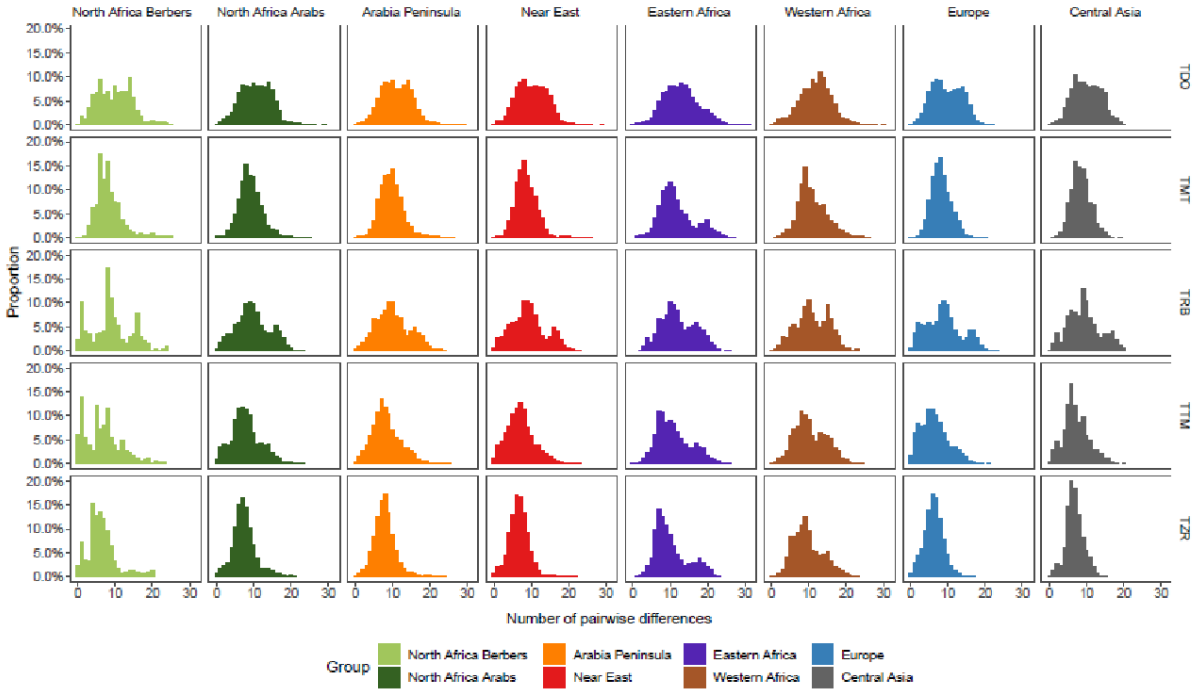

Figure S2. Distributions of the pairwise differences among the five populations under study and eight geographic groups.