

ORIGINAL ARTICLE

Genetic characterization of the Berber-speaking population of Souss (Morocco) based on autosomal STRs

Noura Dahbi¹  | Khadija Cheffi¹ | Abderrazak El Khair¹ | Lamiaa Habbibeddine² | Jalal Talbi³ | Abderraouf Hilali¹ | Hicham El Ossmani^{1,4} 

¹Laboratory of Health Sciences and Technologies, Higher Institute of Health Sciences, Hassan First University of Settat, Settat, Morocco

²Faculty of Sciences, Mohammed V Agdal University, Rabat, Morocco

³General Directorate of National Security, National Laboratory of the Scientific and Technical Police, Casablanca, Morocco

⁴Royal Gendarmerie Criminalistics Institute, Rabat, Morocco

Correspondence

Noura Dahbi, Higher Institute of Health Sciences, Laboratory of Health Sciences and Technologies, Hassan First University of Settat, Settat 26000, Morocco.

Email: no.dahbi@uhp.ac.ma

Abstract

Background: The Souss, located in southern Morocco, is one of the oldest areas of human settlement in North Africa. Despite this historical relevance, the Souss has not received sufficient attention in terms of population genetic studies.

Methods: In this study, we utilized the AmpFISTR Identifier PCR amplification system to establish the allelic frequencies and statistical parameters of 15 autosomal STRs (Short Tandem Repeats) in 150 healthy unrelated Berber-speaking individuals from the Souss. We explored the genetic relationships between Souss and other reference populations based on our dataset as well as previously published population data.

Results: A total of 210 alleles were detected with corresponding allele frequencies ranging from 0.003 to 0.367. The most polymorphic locus was D18S51 with 23 alleles which was also the most discriminating locus as expected. The phylogenetic analysis clustered the Souss closer to the Azrou and southern Moroccan populations. The population comparison showed affinity between the Souss and most North African populations, as well as with Middle Easterners and Europeans.

Conclusion: Historical events and geographical proximity have contributed to the affinity between the Souss and surrounding North African, Southern European, and Middle Eastern populations. Overall, this study highlights the reliability of the 15 STRs for identifying individuals and assessing paternity in the Souss population.

KEYWORDS

autosomal STR, genetic distance, Morocco, population genetics, Souss

1 | INTRODUCTION

The Souss, which means “agricultural land,” is a northwest African region located in the southern part of Morocco, on the eastern shore of the Atlantic Ocean (Figure 1). According to archeological excavations, this region has attracted human

settlements since prehistoric times (Lafanechère, 1952). The oldest civilization in the Souss region and in Morocco as a whole was founded by the Berbers (Sadiqi, 1997). Trade, which was the main activity of the Berber population, allowed them to interact very early in history with civilizations living on the shores of the Mediterranean (Sadiqi, 1997).

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FIGURE 1 Location of the Souss region, where the samples were collected for the present study.

These included the Phoenician and Carthaginian civilizations, which traveled the coast from southern Morocco to the Sahara and founded cities to trade with the local population (Handaine, 2008). The period of the Phoenician invasion (6th century BC) also witnessed the arrival of the Jews in the southern region of Morocco where they established their kingdom at Ifrane (Souss) around 361 BC (Handaine, 2008). However, of all the civilizations that marked the Souss region, the Arab civilization had the greatest impact on the history of the local population at all levels, including religious, cultural, and linguistic (Sadiqi, 1997). The first Arab expeditions to the region date back to the early 8th century, when Moussa ben Nousair reached the Souss around 703 (Handaine, 2008). The Souss population is nowadays mainly composed of two linguistic groups: Arab speakers and a majority of Berber speakers.

Altogether, the combination of all these historical and geographical factors has allowed exchanges between migratory groups and local populations, leading to genetic flows and, subsequently, to a population-specific genetic structure (Coudray et al., 2009). However, despite its historical relevance, the genetic diversity of the Souss population has not been sufficiently studied. The only studies carried out in the region have focused on mtDNA sequences, ABO polymorphism, Alu insertion, and HLA polymorphism (Brakez et al., 2001; Chadli et al., 2007, 2009; Izaabel et al., 1998).

Therefore, in this work, we genotyped a Berber-speaking population sample ($n = 150$) from the Souss region using 15 autosomal STRs. Our aim is to provide allele frequency data of the Souss population and to study its degree of affiliation with neighboring and worldwide groups in order to understand the Souss population's genetic structure.

2 | MATERIALS AND METHODS

2.1 | Editorial policies and ethical considerations

The Ethics Committee for Biomedical Research at the Faculty of Medicine and Pharmacy in Casablanca, Morocco, approved this study in accordance with the Helsinki Declaration (v.2008). All subjects who took part provided informed consent for their participation.

2.2 | Sample collection and DNA extraction

The present work includes 150 healthy adults (52 males and 98 females) from the Souss region. Individuals who satisfied the following requirements were considered

eligible: (i) there was no blood relationship between them; (ii) they lived at least three generations in the Souss region (both maternal and paternal grandparents were born in the Souss region). (iii) Use the Berber language as their mother tongue. A buccal swab sample was collected from each subject using a sterile cotton swab following the same procedure as Livy et al. (2012). Chelex® 100 (Bio-Rad Laboratories, CA, USA) was used to extract DNA from buccal swabs (Walsh et al., 1991). According to the manufacturer's recommendations, a NanoDrop™ 8000 spectrophotometer (Thermo Scientific) was used for measuring the concentration and quality of the DNA.

2.3 | PCR amplification, genotyping, and quality control

The AmpFISTR® Identifiler™ kit (Applied Biosystems, Foster City, CA, USA) was used to perform PCR co-amplification of 15 STR markers (D5S818, FGA, D21S11, D8S1179, D7S820, TH01, CSF1PO, D3S1358, D13S317, D19S433, D16S539, D2S1338, D18S51, VWA, and TPOX). For each sample tested, 1 ng of DNA was amplified in a final reaction volume of 25 µL using the 2720 Thermal Cycler according to the manufacturer's instructions (Applied Biosystems, USA). PCR products were analyzed by capillary electrophoresis using an ABI 3500 genetic analyzer (Applied Biosystems). Data analysis was performed using GeneMapper® ID-X Software v1.1 (Applied Biosystems) by comparing the fragment size with the allelic ladder provided with the AmpFISTR® Identifiler® kit. In each batch of PCR amplification and electrophoresis, we employed the Positive control DNA provided in the kit as positive control and deionized distilled water as negative control. All experimental procedures were performed in accordance with the laboratory's internal control standards.

2.4 | Data analysis and reference groups

The estimation of allelic frequencies and statistical parameters, including probability of match (PM), power of exclusion (PE), typical paternity index (TPI), power of discrimination (PD), and polymorphic information content (PIC), was performed using STRAF online program v1.0.5 (Gouy & Zieger, 2017). Calculation of the exact test of Hardy–Weinberg Equilibrium (HWE), expected and observed heterozygosity was performed by Arlequin v3.5. (Excoffier & Lischer, 2010). *p*-values of the exact test of HWE were adjusted and only values less than 0.0033 were considered significant ($0.05/15 = 0.0033$) after Bonferroni correction (Weir, 1996). In order to determine the genetic

relationship of our sample with other populations, we compared our allele frequency data to those published for 31 reference populations studied with the same set of markers (Alenizi et al., 2008; Amir et al., 2015; Babiker et al., 2011; Barni et al., 2007; Bernal et al., 2006; Calzada et al., 2005; Camacho et al., 2007; Coudray, Calderon, et al., 2007; Coudray, Guitard, El-Chennawi, et al., 2007; Coudray, Guitard, Keyser-Tracqui, et al., 2007; El Ossmani et al., 2010, 2007, 2009; Garcia-Bertrand et al., 2014; Gomes et al., 2009; Gurkan et al., 2015; Havaš et al., 2007; Khodjet-el-Khil et al., 2012; Kido et al., 2007; Kubat et al., 2004; Luna-Vazquez et al., 2005; Martinez et al., 2011; Omran et al., 2009; Pérez-Miranda et al., 2006; Rocabado et al., 2009; Romgaew & Aobaom, 2022; Shepard & Herrera, 2006; Shrivastava et al., 2015; Verzeletti et al., 2009; Yang et al., 2005). The information about these populations are presented in Table S1. Nei's genetic distances (Nei et al., 1983) between the studied populations were calculated using Poptree2 software (Takezaki et al., 2010). The pairwise distance matrix was used to generate a Principal Coordinates Analyses plot (PCoA) by Past v4.03 software (Hammer et al., 2001) and to construct a neighbor-joining tree using Poptree2 software (Takezaki et al., 2010). The robustness of the phylogenetic tree was evaluated using a Bootstrap analysis with 1000 replications. Locus by locus *F*_{st} and corresponding *p*-values of 15 STRs between Souss and reference populations were calculated by Arlequin v3.5 software (Excoffier & Lischer, 2010).

3 | RESULTS AND DISCUSSION

3.1 | Allele frequencies and statistical parameters of 15 autosomal STR loci

Allelic frequencies and *p*-values of HWE are summarized in Table S2. In the Berber-speaking population of Souss, a total of 210 alleles were detected for these 15 STR loci, with corresponding allelic frequencies ranging from 0.003 to 0.367. The most polymorphic locus was D18S51 with 23 alleles and the least polymorphic was D8S1179 with eight alleles. Observed heterozygosity of D5S818 and CSF1PO was found to be low, being 0.687. The other STR loci showed high values ranging from 0.707 for D16S539 to 0.887 for D8S1179, which is supportive of these data for population genetic studies. Using the Bonferroni correction, a significant deviation from the Hardy–Weinberg Equilibrium was detected for three markers: TH01, VWA, and D18S51. Several circumstances can lead to a deviation from HWE, including population size, consanguinity, population stratification, migration, mutation, and natural selection (Wigginton et al., 2005). Given the population sample size and the high consanguinity rate in Souss

(Bouadil & El Madidi, 2021), the combined effect of these two factors could be a likely explanation.

Table S2 summarizes the statistical parameters of the 15 studied markers. The highest values of PIC and PD are observed at locus D18S51 (0.883 and 0.972, respectively), while the lowest values are observed at locus CSF1PO (0.700 and 0.889, respectively). The PM ranged from 0.028 at locus D18S51 to 0.111 at locus CSF1PO. The highest values of TPI and PE are observed at locus D8S1179 were 4.412 and 0.768, respectively, while the lowest values of the two parameters were 1.596 and 0.408, respectively, at D5S818 and CSF1PO loci. The 15 STRs tested show a significant polymorphism with high powers of discrimination ($PD > 0.890$) and exclusion ($PE > 0.400$). The combined power of discrimination (CPD) and the combined power of exclusion (CPE) values were 0.99999999999999998687 and 0.99999873, respectively.

From a forensic perspective, this study reveals a high polymorphism of the selected markers ($PIC \geq 0.700$), so the combined use of the 15 STR is very efficient to discriminate between individuals ($CPD > 99\%$) and exclude false paternity ($CPE > 99\%$). These observations support the relevance of these 15 loci for forensic cases in the Souss population, that is, identification of persons and assessment of paternity.

3.2 | Analysis of genetic affinities between the Souss and the populations studied

We evaluated the genetic affinities between Berber-speaking population of Souss and reference populations using Nei's genetic distances (Table S3). Concerning our study population, the minimum genetic distance was observed between Souss and the Southern Moroccan (SM) population ($Da = 0.014$), followed by the Azrou (AZ) population ($Da = 0.025$). The Bolivians were the most distant population from the Souss ($Da = 0.100$).

Using the above pairwise genetic distances, we assessed the phylogenetic relationships between Berber-speaking population of Souss and other reference populations. Based on the phylogenetic tree (Figure 2), all populations were grouped according to their intercontinental distribution. In addition, the North African group was separated into two clusters: one of Moroccan populations, including the Souss population (SS) as well as Bejaia (DZ) from Algeria; and the other cluster of northeastern populations (Lybians, Upper Egyptians, and Siwa), which were grouped together with the sub-Saharan group. The Souss population (marked with a red square), in accordance with the genetic distances mentioned above, was closely grouped with the populations of southern Morocco (SM) and Azrou (AZ).

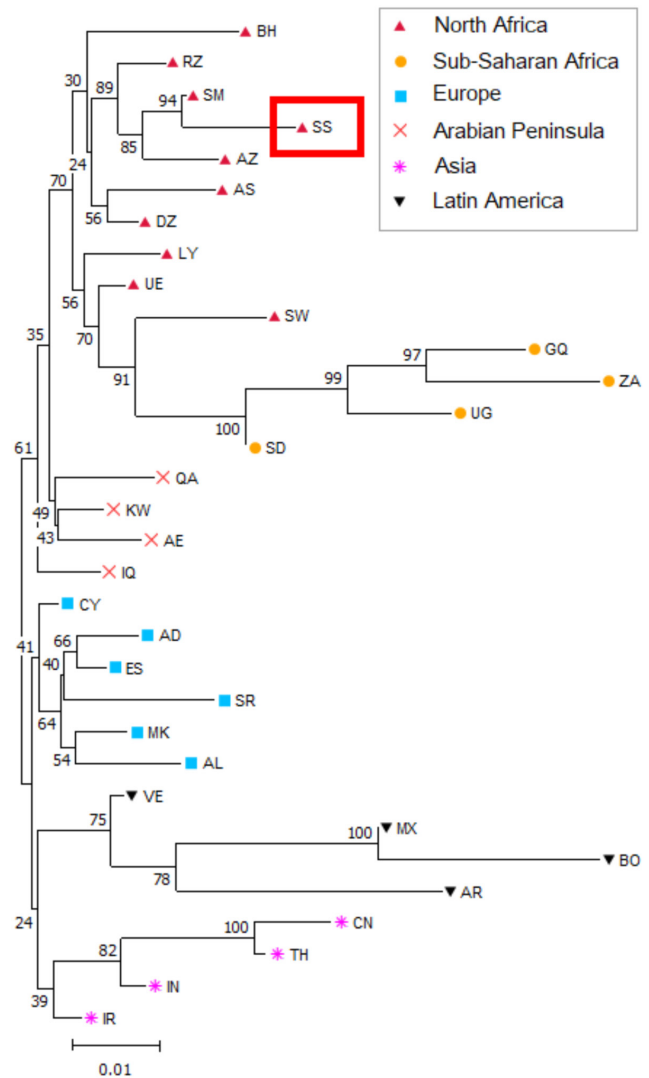


FIGURE 2 Phylogenetic tree constructed using the neighbor-joining method displaying the relationships among the Moroccan Berber-speaking population of Souss and 31 reference populations. Population codes: Souss (SS), Asni (AS), Bouhria (BH), Azrou (AZ), Rabat-Salé-Zemmour-Zaer (RZ), South Moroccan (SM), Algerian (DZ), Siwa (SW), Upper (south) Egyptian (UE), Libyan (LY), Andalusian (AD), Macedonian (MK), Spanish (ES), Albanian (AL), Sardinian (SR), Cypriot (CY), Mexican (MX), Venezuelan (VE), Argentinean (AR), Bolivian (BO), Chinese (CN), Indian (IN), Iranian (IR), Thai (TH), Equatorial Guinean (GQ), South African (ZA), Ugandan (UG), Sudanese (SD), Iraqi (IQ), Kuwaiti (KW), Qatari (QA), Emirati (AE).

For further evaluation of genetic relationships among studied populations, PCoA plots were carried out based on pairwise genetic distances (Nei et al., 1983). The first three components, as shown in Figure 3, explain 67.78% of the total variation. In the first two-dimensional scatterplot (Figure 3a) constructed based on PC1 and PC2, Sub-Saharan, European, and Latin American groups were separated from other populations. In addition, the second two-dimensional scatterplot (Figure 3b), constructed

based on PC1 and PC3, distinguished North African populations from other groups. In both plots, the North African group was closely clustered with the Arabian Peninsula group, demonstrating a genetic proximity between the Middle Easterners and the North Africans. The Sous

population was clustered closely with AZ and SM in PC1 and PC3, which was in line with the results of the NJ tree and the Da distances.

A more detailed analysis of genetic relationships between the studied populations was carried out by

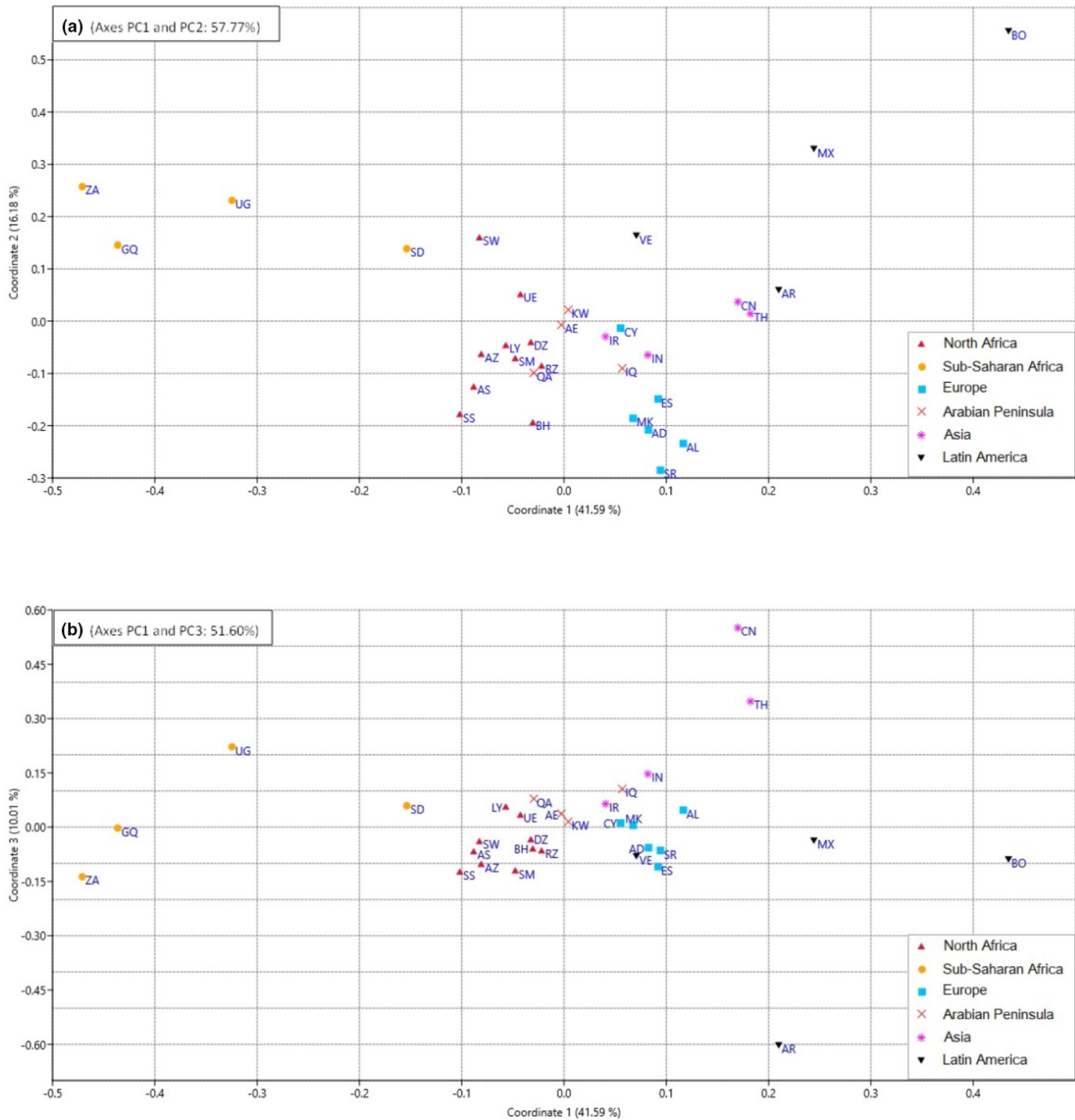


FIGURE 3 Principal Coordinates Analyses (PCoA) plots illustrating the genetic relationships between the Berber-speaking population of Sous and 31 reference populations based on pairwise distance matrix (Da) of 15 autosomal STRs. (a) PC1 and PC2; (b) PC1 and PC3. Population codes: Sous (SS), Asni (AS), Bouhria (BH), Azrou (AZ), Rabat-Salé-Zemmour-Zaer (RZ), South Moroccan (SM), Algerian (DZ), Siwa (SW), Upper (south) Egyptian (UE), Libyan (LY), Andalusian (AD), Macedonian (MK), Spanish (ES), Albanian (AL), Sardinian (SR), Cypriot (CY), Mexican (MX), Venezuelan (VE), Argentinean (AR), Bolivian (BO), Chinese (CN), Indian (IN), Iranian (IR), Thai (TH), Equatorial Guinean (GQ), South African (ZA), Ugandan (UG), Sudanese (SD), Iraqi (IQ), Kuwaiti (KW), Qatari (QA), Emirati (AE).

comparing the Berber-speaking population of Souss locus by locus with neighboring and worldwide populations. The *Fst* and corresponding *p*-values (Table S4), in accordance with the results of phylogenetic analysis and PCoA plots, confirmed the common genetic connections between Souss and North Africans, given that no significant difference was observed with populations of Azrou (AZ), Asni (AS), southern Morocco (SM), Bejaia (DZ), and Libya (LY). However, Siwa (SW) and Bouhria (BH) appeared to be the most distant North African populations from Souss, with three and two significant differences, respectively. Similarly, previous studies have highlighted a differentiation between Bouhria and other Moroccan populations from Azrou and southern Morocco (El Ossmani et al., 2009, 2010). The Siwa population was reported in other work based on mtDNA markers as an exception to the North African genetic structure due to its geographical and historical specificity (Coudray et al., 2009).

In general, the existing affinity between North African populations could be explained by geographical proximity that has contributed to a common historical background. Indeed, between the 12th and 13th centuries, North Africa witnessed the expansion of the Almohad Berber Empire, which started in the Anti-Atlas (Souss) and extended from Morocco to western Libya (Lazhar, 2015). This territorial union has allowed for population movements in North Africa (Lefèvre-Witier, 2012).

As far as Arab populations are concerned, the Souss population showed a significant difference at two loci with Iraqis (IQ) and Emiratis (AE). These results are supported by the above-mentioned observations (PCoA plots). Indeed, the genetic proximity between the Souss population and the Arabs from the Middle East could be related to ancient waves of migration that started with the arrival of the Maakil Arabs in 1218 in the Bani valley (Souss) (Handaine, 2008).

As for the European populations, Macedonians (MK) and Andalusians (AD) show more affinity with the Souss population with only one significant difference. A previous work based on HLA class II polymorphism (Izaabel et al., 1998), revealed the same close relationship between Souss and southwestern Europe, emphasizing that the Italian and Sardinian (eastern Mediterranean) populations are more distant. Conversely, other study conducted on the Northwest African population (Bosch et al., 2000) has reported a genetic discontinuity between the Northwest African and the Iberian populations, with the exception of the Andalusians, who seem to be influenced by a northwest African gene flow. In fact, human migrations associated with historical events have been encouraged across the Strait of Gibraltar, which connects Europe and North Africa at its narrowest point (Bosch et al., 2001). Indeed, in 711 AD, Berbers from Morocco and Algeria, led by the

Arabs, occupied the Iberian Peninsula where they settled for over seven centuries (Comas et al., 2000; Hitti, 1990). The expulsion of the Andalusians in 1492, and particularly the Sephardic Jews, forced many of them to migrate and settle in northwest Africa (including Morocco) and in Eastern Europe, in the cities of Macedonia (Benbassa & Rodrigue, 2000).

The Cypriot (CY) and Iranian (IR) populations show one and two significant differences with the Souss population, respectively. In fact, these two populations are an exception because, besides their continental affiliation (to Europe or Asia), they are part of the Middle East region, which could explain their genetic affinities with Arabs and North Africans.

In several of the analyses presented, we found clear genetic differentiation between Souss and sub-Saharan populations. However, a previous study based on mtDNA markers revealed that the Souss population has incorporated sequences from sub-Saharan via a recent trans-Saharan gene flow (Brakez et al., 2001). These observations may suggest that sub-Saharan populations, for historical or geographical reasons, have not participated equally in the recent gene flow across Africa (from south to north).

As for Morocco, the above analyses revealed a variable degree of affinity between Berber speakers and Arab speakers, bringing populations of different linguistic affiliations closer together, as between Souss (Berber-speaking) and southern Morocco (Arab-speaking), or further apart, as between Souss and Rabat-Salé-Zemmour-Zaer (Arab-speaking). This suggests that linguistic affiliation may not be the only factor determining genetic distance between populations. Actually, a previous study conducted by Amir et al., 2015 on North African populations revealed that the language currently spoken was not a reflection of the population's history due to the Arabization phenomenon that started in the 7th century after the Arab conquest of North Africa (Bosch et al., 2001). Genetic drift, gene flow between Berber speakers and Arabic speakers and many other factors have obscured the impact of linguistic differences on genetic distances (Amir et al., 2015).

4 | CONCLUSION

Overall, the genetic landscape of a given population is a combination of many factors, such as historical events, geographical distance, cultural and religious backgrounds, that participate in increasing or minimizing genetic distances between populations. Our results revealed a close phylogenetic relationship between the Berber-speaking population of Souss and most North African populations, particularly with the Arab speakers from southern Morocco and the Berber speakers from Azrou. In addition,

we observed that the Souss population had a close genetic affinity with south Europeans and Arabs, confirming the historical connections between these populations. Our dataset could provide useful reference data for forensic, anthropological, and genetic studies. However, for a deeper understanding of the Souss genetic landscape, a large population-based sample, and additional genetic markers could be added in the future.

AUTHOR CONTRIBUTIONS

H.A. was involved in the study design. D.N. was involved in sample collection, writing of the initial manuscript, and data analysis. E.H. was involved in experimental work. T.J. was involved in revision. H.L, C.K., and E.A. were involved in data analysis. All authors reviewed the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that might appear to influence the work disclosed in this study.

ORCID

Noura Dahbi  <https://orcid.org/0000-0002-3254-1130>

Hicham El Ossmani  <https://orcid.org/0000-0002-1592-6733>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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