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Abstract. Jordan, located in the Levant region, is a crucial area to investigate human migration between Africa and Eurasia. Even thought, the genetic history of

Jordanians is far to be clarified including the origin of the Bedouins today resident in Jordan. Here, we provide new genetic data on autosomal independent markers in two Jordanian population samples (Bedouins and general population) in order to approach the genetic diversity inside this country and to give new information about the genetic position of these populations in the frame of the Mediterranean and Middle East area. The analyzed markers are 18 Alu polymorphic insertions characterized by their identity by descent, known ancestral state (lack of insertion) and their apparent selective neutrality.

The results indicate significant genetic differences between Bedouins and General Jordanians (p= 0.038) from the 18 markers. Whereas Bedouins show a close genetic proximity to North African, General Jordanians appear genetically as more similar to other Middle East populations. In general, the data of this study are consistent with the hypothesis that Bedouins have had an important role in the peopling of Jordan and constitute the original substrate of the current population. However, migration into Jordan in recent years likely has contributed to the diversity among current Jordanian population groups.

Introduction

The Jordan state emerged in 1946 as the Hashemite Kingdom of Transjordan after World War I division of the Middle East by Britain and France. Since 1948 it has officially been known as the Hashemite Kingdom of Jordan. Jordan is a predominantly Arab nation, whose capital and largest city is Amman. It is located on the East Bank of the Jordan River and the Dead Sea, and borders Palestine and Israel states to the west, Syria to the north, Saudi Arabia to the south and east, and Iraq to the north-east.

Due to its position in the Levant region, Jordan has represented one of the major pathways for human movement. Since antiquity, traders followed this route carrying products from the lands of the Indian Ocean basin to Syria, to be distributed from there to other parts of the Mediterranean world. Jordan was a crossroads for people from all over what is known today as the Middle East. Due to its strategic position connecting Asia, Africa and Europe in the ancient world, Jordan was a major transit zone and, thus, an object of contention among the rival empires of ancient Persians, Macedonian Greeks and many others (Salibi, 1998).

Current inhabitants of Jordan are mostly Arab descendants of Trans-Jordan or Palestine, and Bedouins, a part of a predominantly desert-dwelling Arabian ethnic group traditionally divided into tribes. Historically, the inhabitants of this desert that spreads northwards into Syria, eastwards into Iraq, and southwards into Saudi Arabia, were Bedouin pastoralists (Salibi, 1998). Today around 98% of the 7.9 million Jordanians are of Arab origin, along with other small minorities such as Circassian (1%) and Armenians (1%). Culturally, the official language is Arabic and in terms of religion, over 92% of the people are Sunni Muslims, around 6% are Christians, majority Greek Orthodox, but some Greek and Roman Catholics, Syrian Orthodox, Coptic Orthodox, Armenian Orthodox, and Protestant denominations, and the remaining 2% are Shia Muslim and Druze populations (www.cia.gov/library/publications/the-world-factbook/geos/jo.html).

Historically, the term “Bedouin” has denoted both a nomadic way of life and a group identity. Bedouins were the original settlers in the Middle East. From the Arabian Peninsula, their original home, they spread out and now they live in desert regions of all the countries between the Arabian Gulf and the Atlantic. The Arab conquest of North Africa in the 7th century A.D. caused a wide dispersion, so that today the Arab culture is extended over North Africa and beyond.

The availability of historical and ethnical information about Jordanian peoples (Salibi 1998) contrasts with the lack of information about the genetic background of these groups. As far as we know, previous genetic information about Jordanian populations include two studies on uniparental markers analyzed in Bedouins and General Jordanians (Flores et al., 2005; González et al., 2008) and a survey of a reduced number of Alu insertions, fewer than those analyzed in this study, in a sample of general population (Bahri et al., 2011). The variation in the uniparental markers (Y-chromosome and mtDNA) underlines the genetic outlier position of Bedouins whereas general Jordanians are relatively close to the Middle East neighboring groups.

In order to get a new insight from autosomal gene variation about the distinctiveness of Bedouins suggested by uniparental markers, this study analyzes two different Jordanian samples, one made up of individuals of Bedouin origin and the other of a sample that could be considered as representative of the general Jordanian population. The main objective is to test if autosomal markers confirm the previous population differentiation within Jordan revealed by uniparental markers. This was approached by genotyping 18 autosomal Alu insertions in these two Jordanian groups. The partial objectives of the survey are to determine the degree of genetic heterogeneity in Jordan, the genetic position of Bedouins and general Jordanians in the general context of the Mediterranean and the Middle East areas, and to get new data about the potential influence of Bedouins, as representatives of Arab origins, in North Africa.

In this study 18 *Alu* insertion markers were selected because they are a useful tool for population studies on the basis of their identity by descent, known ancestral state and their selective neutrality (Cordaux et al., 2006; Cordaux & Batzer, 2009). The potential usefulness of specific *Alu* loci as ancestry informative markers has been explored to detect differences between populations and to estimate bio geographical ancestry (Luizon et al., 2007). Polymorphic *Alu* insertions have also been used in several studies tackling many historical and demographical questions (González-Pérez et al., 2010; Terreros et al., 2009).

Materials and methods

Samples and markers. A total of 96 blood samples from healthy unrelated individuals of both sexes, collected from different regions of the North, Center and South of Jordan, were classified into two groups: Bedouins (N=43) and General Jordanians (N=53). Collection, classification, and DNA isolation of all samples was carried out by researchers at Yarmouk University. All participants were selected due to their relatives for at least three generations being born in Jordan. The general Jordanian group was mostly sampled in Jordanian cities such as Amman and Irbid. The Bedouin samples were collected from the Badia desert in collaboration with the “Jordan Badia Research and Development Center”. These samples were classified according to the towns or village in which the subject, his/her parents and grandparents were born, as well as the last names of the families and the tribes they belong to. All subjects signed an informed consent and the study was approved by the Ethical Committees of the University of Barcelona and the Yarmouk University. The protocols and procedures used in this research were in compliance with the Declaration of Helsinki.

Genomic DNA was extracted from blood cells using a Blood Midi kit (Omega Biotek, USA) according to manufacturer procedure. Eighteen human-specific *Alu* polymorphic elements (A25, ACE, APO-A1, B65, CD4, D1, DM, FXIIIB, HS2.43, HS4.32, HS4.69, PV92, Sb19.12, Sb19.3, TPA25, Ya5NBC221, Yb8NBC120 and Yb8NBC125) located on ten different chromosomes (Nº 1, 3, 8, 11, 12, 16, 17, 19, 21 and 22) were typed by PCR amplification and electrophoretic analysis. Primers and amplification conditions have been previously described (Batzer & Deininger, 1991; González-Pérez et al., 2010; Stoneking et al., 1997). Positive and negative controls for the polymorphisms examined were included in all PCR runs.

Statistical analyses. Standard human population genetic parameters were obtained. Allele frequencies were estimated by direct counting. Hardy–Weinberg equilibrium was assessed by an exact test based on the Markow chain method (Guo & Thompson, 1992) using the Genepop program version 4.2 (Rousset, 2008). Heterozygosity values by locus and population according to Nei's formula (Saitou & Nei, 1987) were calculated using Genetix 4.05 software. Differences in allele frequency distribution between the two Jordanian samples and, in general, between all pairs of populations, were assessed by an exact test based on Fisher's exact probability test using the Genepop software.

Genetic distances (Reynold's distance) and hierarchical analyses of molecular variance (AMOVA) were estimated using Phylip version 3.69 (Tuimala, 2006) and Arlequin v 3.5 packages (Excoffier et al., 2005). Genetic relationships among populations were assessed by a principal component (PC) plot using the FactoMineR package of R (Josse, 2008).

Comparisons with published datasets. In order to evaluate the genetic position of Bedouins and General Jordanians in the Mediterranean and the Middle East areas, two comparative analyses were carried out, based on the population data available in the literature.

The main analysis focused on the whole Mediterranean area using 18 polymorphic *Alu* insertions in 16 populations as indicated in Figure 1. These populations included three Spanish regions (Southern Spain: Andalusia; Northern Spain: Asturias; Central Spain: Sierra de Gredos), Southern France (Toulouse), Turkey (Anatolia Peninsula), Greece (Attica region), five Mediterranean islands (Sardinia, Corsica, Sicily, Crete and Menorca) and five Berber groups from Morocco, Algeria, and Egypt. The Moroccan samples came from High Atlas (Amizmiz Berbers), Middle Atlas (Berbers from the Khenifra region), and North East Moroccan Berbers (Bouhria area). Other Berber samples were Mzab from Algeria and Siwi from the Siwa Oasis in Egypt (Gonzalez-Perez et al., 2007; González-Pérez et al., 2010).

In order to have a geographically more comprehensive dataset in the Middle East, a second comparative analysis adding samples from Iran, Cyprus, United Arab Emirates, Syria, and Bahrain was performed. This analysis was based on only 8 *Alu* marker data available in the literature (Bahri et al., 2013; González-Pérez et al., 2010; Romualdi et al., 2002; Stoneking et al., 1997).

Results

Alu insertion frequencies and gene diversities in Bedouins and General Jordanians are shown in Table1. The highest insertion frequencies correspond to the Ya5NBC221 locus in Bedouins (0.941) and to the APOA1 locus in General Jordanians (0.950), whereas the lowest frequency values are found in the Hs2.43 locus (0 in Bedouins and 0.08 in General Jordanians).

As expected, the lowest gene diversity values correspond to loci showing extreme allele frequencies [Ya5NBC221 (H= 0.112) in Bedouins and APOA1 (H= 0.096) in General Jordanians, and Hs2.43 in both Bedouins (H=0) and (H= 0.149) General Jordanians]. The highest diversity values corresponding to loci with frequencies close to 0.5 were B65 and TPA25 (H= 0.506) in Bedouins and TPA25 (H= 0.500) in General Jordanians.

The test for Hardy-Weinberg equilibrium indicates significant deviations only for D1 (p=0.0000) and FXIII (p=0.0000) in General Jordanians after Bonferroni correction. Chance is the most likely explanation for this departure because there is no particular reason to expect an H-W deviation for these markers and the deviations are not shared by the two population samples.

The comparison between the two Jordanian samples shows that the average gene diversity in General Jordanians (0.366±0.142) is only slightly higher than in Bedouins (0.349±0.146). In general, the Jordanian frequencies and gene diversities found show intermediate values within the variation range of other

Mediterranean populations. Extreme values are only found for Hs2.43 and ACE in Bedouins corresponding to the lowest frequencies in the literature revised; and for Hs4.69 and CD4 (in Bedouins) and Hs4.32 and YbNBC125 (in General Jordanians), which are the highest values in the literature revised.

Allele frequency comparisons show significant differences across all 18 loci ($p= 0.038$; 36 d.f.) between Bedouins and General Jordanians. Locus by locus comparisons indicate significant differences for DM ($p= 0.015$), Hs2.43 ($p=0.01$), and ACE ($p=0.005$) markers.

Concerning population relationships, the PC analysis based on the whole set of *Alu* insertion polymorphisms in 16 populations indicates that the two first axes account for 49.31% of the total genetic variance (Figure 2).The first axis (33.76% of the total variance) clusters Bedouins along with North African samples with a certain separation from the rest. Within this group, the Siwa Oasis sample appears in the most distant position. The second component underlines the separation of the Western Mediterranean samples (Centre of Spain, France, North of Spain, Corsica and Sicily) from East Mediterranean groups (Greece, Turkey, Crete) and General Jordan. When the analysis is repeated in order to remove the effect of the Siwa Oasis sample (not shown), the observed pattern was substantially the same. Population relationships within Jordan indicate that the Bedouins, closer to North Africans, show an intermediate position between these populations and Eastern Mediterraneans, while General Jordanians cluster with

Eastern Mediterranean populations. Both genetic distance and AMOVA analyses support the distribution revealed by the PC analysis. So, the average Reynolds genetic distance (Table 2) of Bedouins to the remaining populations ($31x10^{-3}$) is of the same order of magnitude as the average distance among all the populations ($32x10^{-3}$) whereas the distance of General Jordanians to Middle Eastern populations ($23x10^{-3}$) is lower than that corresponding to Bedouins ($28x10^{-3}$) (Table 2).

The hierarchical analysis of the allele frequency variance, classifying the populations into two groups (North Africa plus Bedouins and the rest) indicates a significant variation between the two groups, as already plotted along the first PC axes (F_{ST} = 3.4%, $p<0.001$; F_{CT}=1.6%, p=<0.001, and F_{SC}=1.8%, $p<0.001$). Likewise, the population distribution associated with the second PC component is also supported by the AMOVA analysis. In this case, the genetic variance between the three population groups formed by North Africa plus Bedouins, Middle East plus General Jordanians, and Western Mediterranean, also indicates statistically significant variation (F_{ST} =3%, $p<0.001$; F_{CT}=1,2%, p=<0.001, and F_{SC}=1,8%, $p<0.001$).

A second comparison, partial because it is based only on the variation of 8 *Alu* markers but including a wider number of populations (21) (PCA population plot not shown), also separates Bedouins from General Jordanians. However, in this case, the relative position of the two Jordanian samples versus other populations shows some differences in comparison with the results of the previous analysis. For instance, the General Jordanian group tends to be closer to Western Mediterranean than to Middle East.

Discussion

This study provides the first comparative genetic analysis between two Jordanian ethnic groups selected according to strict and reliable criteria: Bedouins and General Jordanians. This has been done through the analysis of 18 autosomal *Alu* insertion polymorphisms.

In general, Jordanian allele frequencies and gene diversity estimates show intermediate values within the variation range of other Mediterranean populations. In comparison with previous data, *Alu* frequencies in general Jordanians are substantially similar to those previously reported for a partial sub-set of *Alu* markers (10 out the 18) in a Jordanian sample (Bahri et al., 2011), except for 2 *Alu* (D1: p=0.02 and HS4.32: p=0.006). These few differences could be related to the potentially diverse origin of the individuals sampled in each case.

Concerning differentiation within Jordan, this study indicates a significant difference between Bedouins and urban inhabitants of Jordan (p=0.038). Out of the 18 autosomal insertion markers, three of them are statistically different (DM: p= 0.015, Hs2.43: p=0.01, and ACE: p=0.005). Considering the relatively small sample size, the genetic differences found point to a clear separation between these two groups. This could be related to the fact that in recent times urban areas have been subject to several external influences but Bedouins have conserved their own genetic background due to their nomadic and isolated lifestyle. In fact, among all the considered populations in the comparative analyses, Bedouins appear to be the most diverse group in contrast to general Jordanians who cluster with other Middle Eastern groups. However, we should not ignore the fact that the markers analyzed (number and/or low mutation rate) may be not powerful enough to uncover relatively recent demographic events. In this way, the small inconsistencies in the relative genetic position of the two Jordanian samples with respect to other populations found in the two analyses using a different number of *Alu* loci (18 vs 8), are most likely a reflection of the role of chance when few markers are used to characterize human populations. In any case, the genetic differentiation observed between Bedouin and General Jordanians using 18 *Alu* insertions polymorphisms is consistent with the differentiation reported from the mtDNA and Y-chromosome uniparental loci in two recent studies (Flores et al., 2005; González et al., 2008).

Assuming that Bedouins represent the original substrate of current-day Jordanians, the differentiation found between them and the general Jordanian group could be explained by a higher Mediterranean influence in the general population due to Jordan’s position as a crossroads since ancient times and/or the recent contribution of immigrants in the last half of the 20th century.

In a Mediterranean context, Bedouins seem to be closer to North African groups while general Jordanians tend to group with North Mediterraneans, especially with the easternmost populations. Greater genetic proximity of Bedouins and North Africans could be explained by the impact of Arabic expansion into North Africa in the VIIth century. However, the outlier position of the Egyptian sample from Siwa, also acknowledged in other studies (Athanasiadis et al., 2007), together with the significant lack of *Alu* data in most points of North Africa, does not allow definite conclusions.

To sum up, this *Alu* population analysis reinforces the genetic distinctiveness of Bedouins suggesting that they have had an important role in the peopling of Jordan and probably constitute the original substrate of this population. Their relative genetic proximity to North African groups supports the idea that they share the genetic background of the populations that spread the Arab culture into North Africa. The genetic differentiation found between the two groups of current Jordanian population could be attributed to some extent to a relatively recent contribution of immigrants coming from neighboring areas. However, this conclusion needs to be confirmed with additional markers to avoid random effects associated with the use of a low number of markers.

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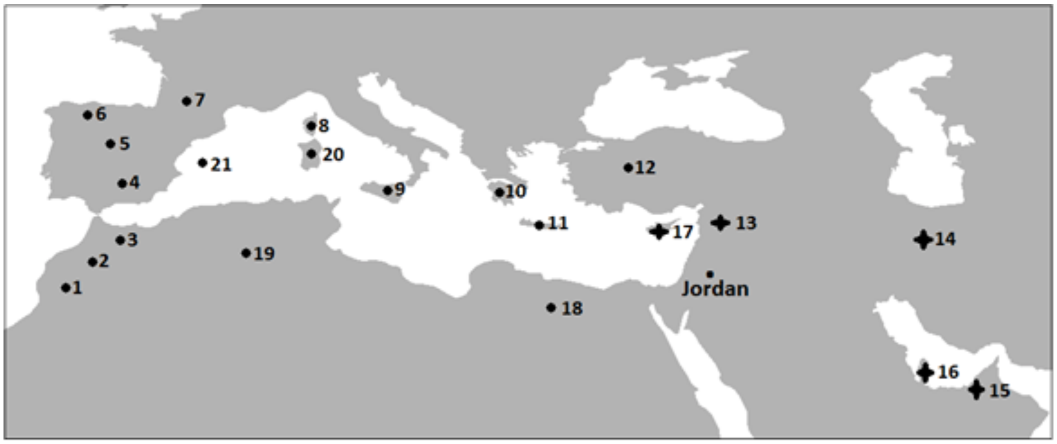


1. Amizmiz Berbers (Ambe)
2. Middle Altas Berbers (Mabe)
3. North East Maroccan Berbers (Nebe)
4.S_Spain
5. C_Spain
6. N_Spain
7. France
8. Corsica
9. Sicily
10. Greece
11. Crete
12. Turkey
13. Syria
14. Iran
15. UAE
16. Baharain
17.Cyprus
18. Siwa Berbers (Siwa)
19. Mzab Berbers (Mzab)
20. Sardinia
21. Menorca

Figure 1. Geographic location of the populations analyzed in the study.

Populations analyzed using 18 Alu (.) and populations analyzed using the only 8 Alu insertion polymorphisms available in the literature (+).

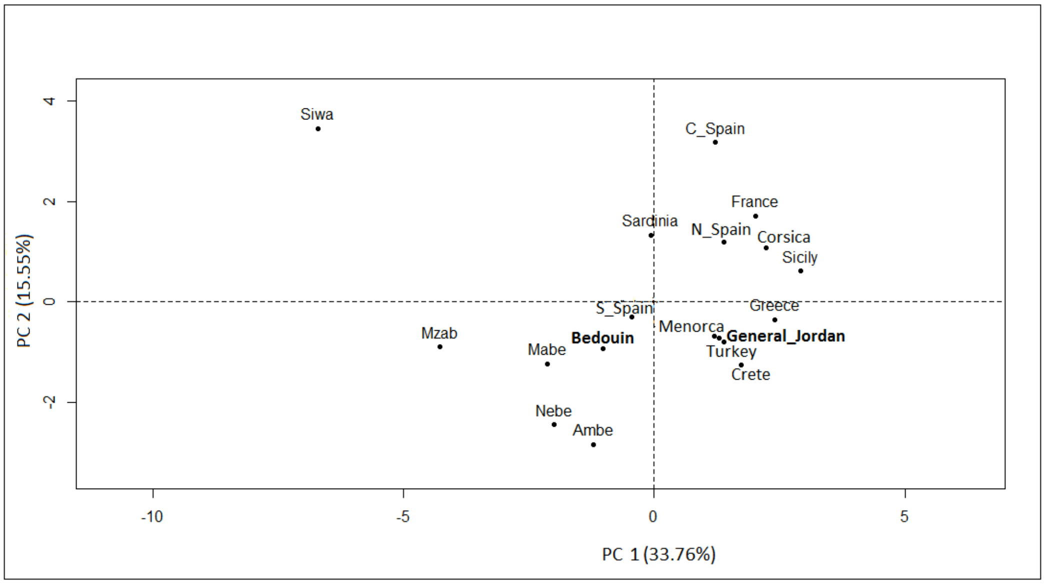
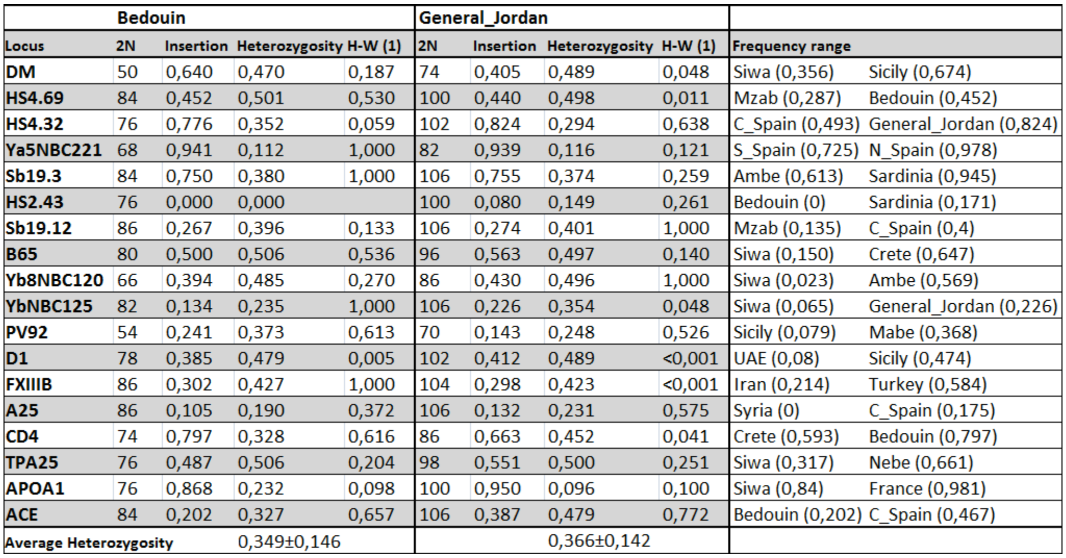
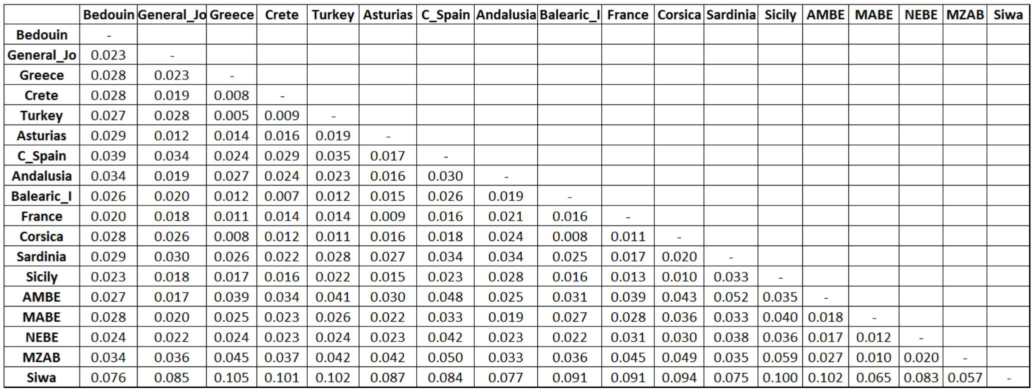


Figure 2. PC plot of sixteen populations from the Mediterranean area based on the variation of eighteen *Alu* insertion polymorphisms.



	Bedouin				General_Jordan					
Locus	**2N**	**Insertion**	**Heterozygosity**	**H-W (1)**	**2N**	**Insertion**	**Heterozygosity**	**H-W (1)**	**Frequency range**	
DM	50	0,640	0,470	0,187	74	0,405	0,489	0,048	Siwa (0,356)	Sicily (0,674)
HS4.69	84	0,452	0,501	0,530	100	0,440	0,498	0,011	Mzab (0,287)	Bedouin (0,452)
HS4.32	76	0,776	0,352	0,059	102	0,824	0,294	0,638	C_Spain (0,493)	General_Jordan (0,824)
Ya5NBC221	68	0,941	0,112	1,000	82	0,939	0,116	0,121	S_Spain (0,725)	N_Spain (0,978)
Sb19.3	84	0,750	0,380	1,000	106	0,755	0,374	0,259	Ambe (0,613)	Sardinia (0,945)
HS2.43	76	0,000	0,000		100	0,080	0,149	0,261	Bedouin (0)	Sardinia (0,171)
Sb19.12	86	0,267	0,396	0,133	106	0,274	0,401	1,000	Mzab (0,135)	C_Spain (0,4)
B65	80	0,500	0,506	0,536	96	0,563	0,497	0,140	Siwa (0,150)	Crete (0,647)
Yb8NBC120	66	0,394	0,485	0,270	86	0,430	0,496	1,000	Siwa (0,023)	Ambe (0,569)
YbNBC125	82	0,134	0,235	1,000	106	0,226	0,354	0,048	Siwa (0,065)	General_Jordan (0,226)
PV92	54	0,241	0,373	0,613	70	0,143	0,248	0,526	Sicily (0,079)	Mabe (0,368)
D1	78	0,385	0,479	0,005	102	0,412	0,489	<0,001	UAE (0,08)	Sicily (0,474)
FXIIIB	86	0,302	0,427	1,000	104	0,298	0,423	<0,001	Iran (0,214)	Turkey (0,584)
A25	86	0,105	0,190	0,372	106	0,132	0,231	0,575	Syria (0)	C_Spain (0,175)
CD4	74	0,797	0,328	0,616	86	0,663	0,452	0,041	Crete (0,593)	Bedouin (0,797)
TPA25	76	0,487	0,506	0,204	98	0,551	0,500	0,251	Siwa (0,317)	Nebe (0,661)
APOA1	76	0,868	0,232	0,098	100	0,950	0,096	0,100	Siwa (0,84)	France (0,981)
ACE	84	0,202	0,327	0,657	106	0,387	0,479	0,772	Bedouin (0,202)	C_Spain (0,467)
Average Heterozygosity			0,349±0,146				0,366±0,142			

Table 1. Alu insertion frequencies, gene diversities and p-value of Hardy-Weinberg equilibrium (1) in Bedouins and General Jordanians. 2N: Number of chromosomes. Variation ranges are given according to data from reviewed literature for populations represented in Figure 1.



	Bedouin	General_Jo	Greece	Crete	Turkey	Asturias	C_Spain	Andalusia	Balearic_I	France	Corsica	Sardinia	Sicily	AMBE	MABE	NEBE	MZAB	Siwa
Bedouin	-																	
General_Jo	0.023	-																
Greece	0.028	0.023	-															
Crete	0.028	0.019	0.008	-														
Turkey	0.027	0.028	0.005	0.009	-													
Asturias	0.029	0.012	0.014	0.016	0.019	-												
C_Spain	0.039	0.034	0.024	0.029	0.035	0.017	-											
Andalusia	0.034	0.019	0.027	0.024	0.023	0.016	0.030	-										
Balearic_I	0.026	0.020	0.012	0.007	0.012	0.015	0.026	0.019	-									
France	0.020	0.018	0.011	0.014	0.014	0.009	0.016	0.021	0.016	-								
Corsica	0.028	0.026	0.008	0.012	0.011	0.016	0.018	0.024	0.008	0.011	-							
Sardinia	0.029	0.030	0.026	0.022	0.028	0.027	0.034	0.034	0.025	0.017	0.020	-						
Sicily	0.023	0.018	0.017	0.016	0.022	0.015	0.023	0.028	0.016	0.013	0.010	0.033	-					
AMBE	0.027	0.017	0.039	0.034	0.041	0.030	0.048	0.025	0.031	0.039	0.043	0.052	0.035	-				
MABE	0.028	0.020	0.025	0.023	0.026	0.022	0.033	0.019	0.027	0.028	0.036	0.033	0.040	0.018	-			
NEBE	0.024	0.022	0.024	0.023	0.024	0.023	0.042	0.023	0.022	0.031	0.030	0.038	0.036	0.017	0.012	-		
MZAB	0.034	0.036	0.045	0.037	0.042	0.042	0.050	0.033	0.036	0.045	0.049	0.035	0.059	0.027	0.010	0.020	-	
Siwa	0.076	0.085	0.105	0.101	0.102	0.087	0.084	0.077	0.091	0.091	0.094	0.075	0.100	0.102	0.065	0.083	0.057	-

Table 2. Reynolds genetic distances estimated among all 18 populations using 18 Alu insertion markers.