Human Diversity in Jordan: Polymorphic Alu Insertions in General Jordanian and Bedouin Groups

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ABSTRACT

Jordan, located in the Levant region, is an area crucial for the investigation of human migration between Africa and Eurasia. However, the genetic history of Jordanians has yet 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 the general population) to begin to examine the genetic diversity inside this country and to provide new information about the genetic position of these populations in the context of the Mediterranean and Middle East area. The markers analyzed were 18 Alu polymorphic insertions characterized by their identity by descent, known ancestral state (lack of insertion), and apparent selective neutrality. The results indicate significant genetic differences between Bedouins and general Jordanians ($p = 0.038$). Whereas Bedouins show a close genetic proximity to North Africans, general Jordanians appear genetically more similar to other Middle East populations. In general, these data are consistent with the hypothesis that Bedouins 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.

The State of Jordan emerged in 1946 as the Hashemite Kingdom of Transjordan when Britain and France divided the Middle East after World War II. 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 northeast.

Because of its position in the Levant region, Jordan represents one of the major pathways for human movement. Since antiquity, traders traversed this area 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. Because of 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 Transjordan or Palestine, and Bedouins, part of a predominantly desert-dwelling Arabian ethnic group traditionally divided into tribes. Historically, the inhabitants of this desert, which spreads northward into Syria, eastward into Iraq, and southward 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 Circassians (1%) and Armenians (1%). Culturally, the official language is Arabic; in terms of religion, over 92% of the people are Sunni Muslims, around 6% are Christians (mostly 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 (Central Intelligence Agency 2013–2014).

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 live in desert regions of all the countries between the Arabian Gulf and the Atlantic. The Arab conquest of North Africa in the seventh century AD caused a wide dispersion, such 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 includes 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 the general Jordanian population (Bahri et al. 2011). Variation in the uniparental markers (Y-chromosome and mitochondrial DNA) underlines the genetic outlier position of Bedouins, whereas general Jordanians are relatively close to the neighboring Middle East groups.

To provide new insight from autosomal gene variation about the distinctiveness of Bedouins suggested by uniparental markers, this study genotyped 18 autosomal Alu insertions in two different Jordanian samples: one of individuals of Bedouin origin and the other of considered as representative of the general Jordanian population. The main objective was to test whether autosomal markers confirm the previous population differentiation within Jordan revealed by uniparental markers. The secondary objectives were 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 provide 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 selective neutrality (Cordaux et al. 2006; Cordaux and Batzer 2009). The potential usefulness of specific Alu loci as ancestry-informative markers has been explored to detect differences between populations and to estimate biogeographical 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 were carried out by researchers at Yarmouk University. All participants were selected because their relatives were born in Jordan for at least three generations. 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 and the subject’s parents and grandparents were born, as well as
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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 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 DNA Midi Kit (Omega Bio-Tek, Norcross, GA) according to the manufacturer’s procedure. Eighteen human-specific Alu polymorphic elements (A25, ACE, APOA1, B65, CD4, D1, DM, FXIIIb, HS2.43, HS4.32, HS4.69, PV92, Sb19.12, Sb19.3, TPA25, Ya5NBC221, Yb6NBC120, and Yb8NBC125) located on 10 different chromosomes (Chr 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 and 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 Markov chain method (Guo and Thompson 1992) using Genepop, version 4.05 (Rousset 2008). 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 (Reynolds’s distance) and hierarchical analyses of molecular variance (AMOVA) were estimated using Phylip, version 3.69 (Tuimala 2006), and Arlequin, version 3.5 (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 Data Sets

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 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 comprised 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 Minorca), and five Berber groups from Morocco, Algeria, and Egypt. The Moroccan samples came
Table 1. Alu Insertion Frequencies, Gene Diversities, and p-Values of Hardy-Weinberg (H-W) Equilibrium in Bedouins and General Jordanians

| Locus      | Bedouin N | Insertion | Heterozygosity | H-W    | General_Jordan N | Insertion | Heterozygosity | H-W    | Frequency Range            |
|------------|-----------|-----------|----------------|--------|------------------|-----------|----------------|--------|---------------------------|
| DM         | 25        | 0.640     | 0.470          | 0.187  | 37               | 0.405     | 0.489          | 0.048  | Siwa (0.356) Sicily (0.674) |
| HS4.69     | 42        | 0.452     | 0.501          | 0.530  | 50                | 0.440     | 0.498          | 0.011  | Mzab (0.287) Bedouin (0.452) |
| HS4.32     | 38        | 0.776     | 0.352          | 0.059  | 51                | 0.824     | 0.294          | 0.638  | Central Spain (0.493) General_Jordan (0.824) |
| Ya5NBC221  | 34        | 0.941     | 0.112          | 0.000  | 41                | 0.939     | 0.116          | 0.121  | Southern Spain (0.725) Northern Spain (0.978) |
| Sb19.3     | 42        | 0.750     | 0.380          | 1.000  | 53                | 0.755     | 0.374          | 0.259  | AMBE (0.613) Sardinia (0.945) |
| HS2.43     | 38        | 0.000     | <0.001         |        | 50                | 0.080     | 0.149          | 0.261  | Bedouin (0) Sardinia (0.171) |
| Sb19.12    | 43        | 0.267     | 0.396          | 0.133  | 53                | 0.274     | 0.401          | 1.000  | Mzab (0.135) Central Spain (0.4) |
| B65        | 40        | 0.500     | 0.506          | 0.536  | 48                | 0.563     | 0.497          | 0.140  | Siwa (0.150) Crete (0.647) |
| Yb8NBC120  | 33        | 0.394     | 0.485          | 0.270  | 43                | 0.430     | 0.496          | 1.000  | Siwa (0.023) AMBE (0.569) |
| YbNBC125   | 41        | 0.134     | 0.235          | 1.000  | 53                | 0.226     | 0.354          | 0.048  | Siwa (0.045) General_Jordan (0.226) |
| PV92       | 27        | 0.261     | 0.373          | 0.613  | 35                | 0.143     | 0.248          | 0.526  | Siwa (0.079) MABE (0.368) |
| D1         | 39        | 0.385     | 0.479          | 0.005  | 51                | 0.412     | 0.489          | <0.001 | United Arab Emirates (0.08) Sicily (0.474) |
| FXIIIB     | 43        | 0.302     | 0.427          | 1.000  | 52                | 0.298     | 0.423          | 1.000  | Iran (0.214) Turkey (0.584) |
| A25        | 43        | 0.105     | 0.190          | 0.372  | 53                | 0.132     | 0.231          | 0.575  | Syria (0) Central Spain (0.175) |
| CD4        | 37        | 0.797     | 0.328          | 0.616  | 43                | 0.663     | 0.452          | 0.041  | Crete (0.593) Bedouin (0.797) |
| TPA25      | 38        | 0.487     | 0.506          | 0.204  | 49                | 0.551     | 0.500          | 0.251  | Siwa (0.317) NEBE (0.661) |
| APOA1      | 38        | 0.868     | 0.232          | 0.098  | 50                | 0.950     | 0.096          | 0.100  | Siwa (0.84) France (0.981) |
| ACE        | 42        | 0.202     | 0.327          | 0.657  | 53                | 0.387     | 0.479          | 0.772  | Bedouin (0.202) Central Spain (0.467) |

Average heterozygosity: 0.349±0.146 0.366±0.142

Abbreviations: N: number of chromosomes; AMBE: Amizmiz Berbers, MABE: Middle Atlas Berbers, NEBE: Northeast Moroccan Berbers, MZAB: Mzab Berbers. Variation ranges are given according to data from reviewed literature for populations represented in Figure 1.

Results

Alu insertion frequencies and gene diversities in Bedouins and general Jordanians are shown in Table 1. The highest insertion frequencies correspond to the Ya5NBC221 locus in Bedouins (0.941) and to the APOA1 locus in general Jordanians (0.950); 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, APOA1 (H = 0.096) in general Jordanians, and HS2.43 in both Bedouins (H = 0) and general Jordanians (H = 0.149). 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, after Bonferroni correction, indicates significant deviations only for D1 (p = 0.0000) and FXIIIB (p = 0.0000) in general Jordanians. Chance is the most likely explanation for this departure because there is no particular reason to expect a Hardy-Weinberg deviation for these markers, and the deviations are not shared by the two population samples.

Comparison of 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 show values within the variation range of other Mediterranean populations. Extreme values were found only 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 Yb8NBC125 in general Jordanians, which are the highest values in the literature revised. Allele frequency comparisons show significant differences across all 18 loci ($p = 0.038; 36 \text{ df}$) 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 (central Spain, France, north of Spain, Corsica, and Sicily) from Eastern Mediterranean groups (Greece, Turkey, Crete) and general Jordan. When the analysis was repeated to remove the effect of the Siwa Oasis sample (data 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, whereas general Jordanians cluster with Eastern Mediterranean populations. Results from both genetic distance analysis and AMOVA support the distribution revealed by the PC analysis. Thus, the average Reynolds genetic distance of Bedouins to the remaining populations ($31 \times 10^{-3}$) is of the same order of magnitude as the average distance among all the populations ($32 \times 10^{-3}$), whereas the distance of general Jordanians to Middle Eastern populations ($23 \times 10^{-3}$) is lower than that corresponding to Bedouins ($28 \times 10^{-3}$; Table 2).

The hierarchical analysis of the allele frequency variance, classifying the populations into two groups (North Africa plus Bedouins, and all others) indicates a significant variation between the two groups, as plotted along the first PC axes ($F_{\text{ST}} = 3.4\%; p < 0.001; F_{\text{CT}} = 1.6\%; p \leq 0.001; F_{\text{SC}} = 1.8\%; p < 0.001$). Likewise, the population distribution associated with the second PC component is also supported by the AMOVA results. 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 \( (F_{ST} = 3\%, p < 0.001; F_{CT} = 1.2\%, p \leq 0.001; F_{SC} = 1.8\%, p < 0.001) \).

A second comparison, partial because it is based on the variation of only eight Alu markers but including a wider number of populations (21; PC analysis 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 compared with results of the previous analysis. For instance, the general Jordanian group tends to be closer to Western Mediterranean than to Middle East populations.

**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, by analyzing 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. Compared with previous data, Alu frequencies in general Jordanians are substantially similar to those previously reported for a partial subset of Alu markers (10 of the 18) in a Jordanian sample (Bahri et al. 2011), except for two Alu markers: 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 \( (p = 0.038) \). Of the 18 autosomal insertion markers, three 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 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 because of 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

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### Table 2. Reynolds’s Genetic Distances Estimated among All 18 Populations using 18 Alu Insertion Markers

|            | Bedouin | GJ  | Greece | Crete | Turkey | Asturias | C_Spain | Andalusia | Balearic_I | France | Corsica | Sardinia | Sicily | AMBE | MABE | NEBE | MZAB | Siwa |
|------------|---------|-----|--------|-------|--------|----------|---------|-----------|------------|--------|---------|----------|--------|------|------|------|------|------|
| Bedouin    | —       |     |        |       |        |          |         |           |            |        |         |          |        |      |      |      |      |      |
| GJ         | 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     | 0.094  | 0.075   | 0.100   | 0.102  | 0.065 | 0.083 | 0.057 | —    |

Abbreviations: AMBE: Amizmiz Berbers, GJ, general Jordanians, MABE: Middle Atlas Berbers, NEBE: Northeast Moroccan Berbers, MZAB: Mzab Berbers.
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 different numbers of Alu loci (18 vs. 8) most likely reflect 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 mitochondrial DNA 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 twentieth century.

In a Mediterranean context, Bedouins seem to be closer to North African groups, whereas 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 seventh 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.

In summary, this Alu population analysis reinforces the genetic distinctiveness of Bedouins, suggesting that they 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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