The Genetic Structure of the Kuwaiti Population: mtDNA Inter- and Intra-population Variation

JASEM B. THEYAB,[1]* SUZANNE AL-BUSTAN,[2] AND MICHAEL H. CRAWFORD[1]

Abstract This study investigated: (1) the mitochondrial DNA (mtDNA) genetic variation in 116 unrelated individuals who originated from the Arabian Peninsula, Iran, or were of Bedouin ethnicity and (2) the genetic structure of Kuwaiti populations and compared it to their neighboring populations. These subpopulations were tested for genetic homogeneity and shown to be heterogeneous. Restriction fragment length polymorphism (RFLP) and mtDNA sequencing analyses of HVRI were used to reconstruct the genetic structure of Kuwait. The results indicated that the combined Kuwaiti population has a high frequency of haplogroup R0 (17%), J (12%), and U (12%) similar to other Arabian populations. In addition, contemporary African gene flow was detected through the presence of sub-haplogroup L (L1 and L2) (2%) and the absence of L3 which is reflective of an earlier migration. Furthermore, the multidimensional scaling (MDS) plot showed that the Kuwaiti population clusters with neighboring populations, including Iran and Saudi Arabia indicating gene flow into Kuwait. According to this study, the Kuwaiti population may be undergoing an expansion in a relatively short period of time, and the maternal genetic structure of Kuwait resembles both Saudi Arabia and Iran.

Kuwait is located in the Arabian Peninsula on the coast of the Arabian Gulf (Figure 1). Kuwait is bordered by Iraq on the north and Saudi Arabia on the south. Its territory is estimated at approximately 17,820 sq km (6,880 sq mi) (Casey 2007). On the early maps, Kuwait sometimes was labeled as Al-Qurayn (Grain), which means "the top of the hill," and it was also known as Kut, which means "the small castle or fort" (Alghanim 1998; Slot 2003).

To date, most of the archaeological sites in Kuwait are located on Failaka Island, located 20 km from Kuwait City and the only inhabited island off the coast of Kuwait. Recent excavation in Kuwait revealed ancient boat remains containing Ubaid pottery. These maritime excavations were found in a coastal area known as As-Sabiyah (Carter et al. 1999). According to Carter (2006) and Potter (2009), these excavations indicate maritime exchange and trade between the Arabian Neolithic communities of Eastern Arabia and the Ubaid communities

[1]Department of Anthropology, University of Kansas, Lawrence, KS 66045.
[2]Department of Biological Sciences, Faculty of Science, Kuwait University, Kuwait City, Kuwait.
*Correspondence to: Jasem B. Theyab, Department of Anthropology, University of Kansas, Lawrence, KS. E-mail: theyabj@ku.edu.

Human Biology, August 2012, v. 84, no. 4, pp. 379–403.

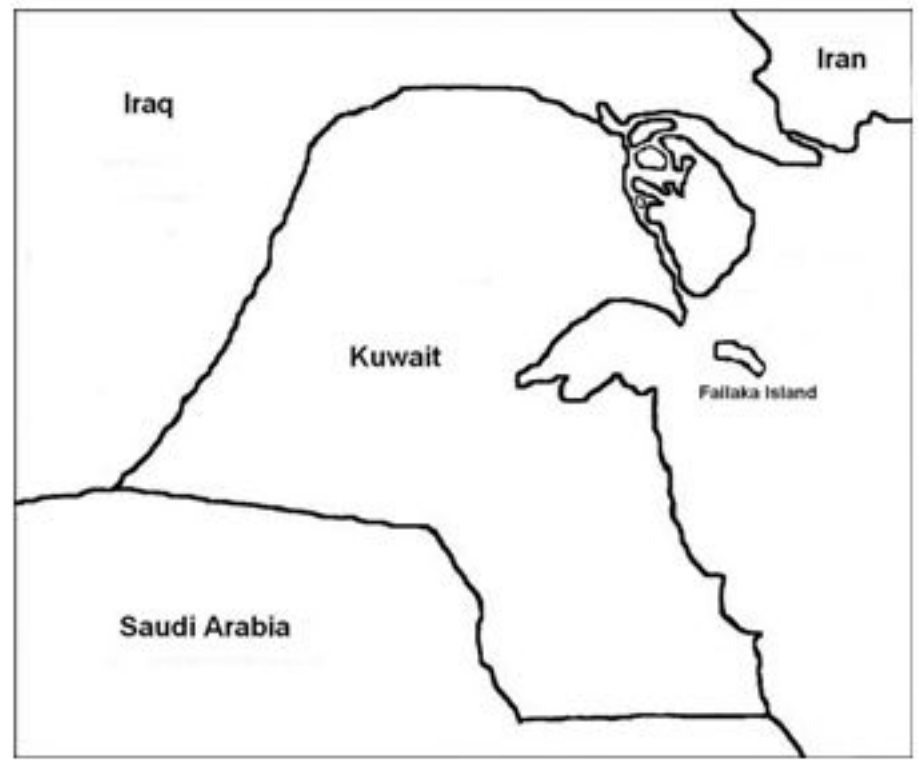

Figure 1. Map of Kuwait and Failaka Island.

of southern Mesopotamia during the sixth and fifth millennia BC (Carter 2006, 2007; Potter 2009). The artifacts excavated in Failaka date back to the beginning of the second millennium B.C.E. to the Bronze Age when the ancient Dilmun civilization established a trade and/or a military station in Failaka (Casey 2007).

Historically, Kuwait was established as a political state in the 18th century with the arrival into the region of the first settlers who belonged to the Utub families. Utub is a group of families derived from the Arab tribe Aniza, which migrated from Najd, currently located in Saudi Arabia. The Utub consisted of three principal families called Al-Sabah (the ruling family of Kuwait), Al-Khalifa (the ruling family of Bahrain), and Al-Jalahima (Anscombe 1997; Slot 2003). Prior to the first oilfield discovery, the Kuwaiti population subsisted on fishing and merchant seafaring. In 1932, oil was discovered in Kuwait, and it had a marked impact on the social and political systems of the region. The most critical impact of oil production was an exponential growth of Kuwait's population. In addition, oil-production industries offered many job opportunities that attracted approximately 100,000 skilled and unskilled workers from neighboring countries as well as other Asian and African countries (Casey 2007; Slot 2003). The immigration of these workers into Kuwait modified the gene pool, leading to the admixture of Arab with other ethnicities, thus, increasing the genetic heterogeneity of the Kuwaiti population.

The analysis of mitochondrial DNA (mtDNA) has been applied to the studies of human origins and evolution by tracking dispersal patterns and estimating times of divergence and coalescence within and between species. Mitochondrial DNA has distinct features that distinguish it from nuclear DNA (i.e., mtDNA is maternally inherited with no recombination and a high rate of mutation, making it an ideal tool for the investigation of the genetic structure of any population through maternal lines). The high substitution rates in the control region of the mtDNA allows for estimates of coalescence and phylogenetic studies of closely related populations (Bermisheva et al. 2003; Richards et al. 1996). This study investigates the genetic structure of the Kuwaiti population by

use of mtDNA analyses. The results of this study are compared to published data from comparative populations through multiple inter-population analyses such as MDS plot, analysis of molecular variance (AMOVA), and mismatch-distribution analysis.

Materials and Methods

Sampling. Blood samples were drawn into EDTA vacutainer tubes by the Ministry of Health's certified nurses from 116 unrelated Kuwaiti volunteers who participated in this study. Surnames of volunteers were screened to eliminate any potential relatives. The samples were categorized into one of three ethnicities based on their family's place of origin: Arab ($n = 48$), Bedouin ($n = 32$), or Iranian ($n = 36$). The Arab group represented individuals whose maternal and paternal ancestors originated from the Arabian Peninsula. The second group, the Bedouins, represented individuals whose maternal and paternal ancestors originated from the Arabian Peninsula and who are members of the Bedouin tribes. The Iranian group represented individuals whose families migrated from Iran to Kuwait before oil discovery and have lived in Kuwait for several generations. Permission from the Human Subject Committee of Kuwait University was acquired to conduct the research. In addition, written informed consent was obtained from each volunteer before sample collection.

DNA Extraction and DNA Analysis. All DNA samples used in this study were extracted at Kuwait University, Faculty of Science. DNA was extracted from 5 mL of blood according to the method described by Miller et al. (1988) by use of proteinase K and salting-out procedures. Identification of the mtDNA haplogroup for each sample was determined by both the analysis of the mitochondrial DNA hypervariable region I (HVS-I) as well as the presence of common restriction sites. HVS-I was amplified by the polymerase chain reaction (PCR) based on the method described by Santos et al. (2004) and sequenced in both directions on an ABI 3730 automated capillary sequencer (Applied Biosystems, Foster City, California) by using Applied Biosystems v3.1 big dye kit and following the manufacturer's protocol at the DNA Laboratory of Arizona State University. The restriction sites at different regions of the mtDNA were initially amplified by PCR for each sample followed by restriction fragment length polymorphism (RFLP) analysis. Each amplification reaction tube contained: 2.5 μL of 10X PCR Buffer (Promega), 4.0 μL of $MgCl_2$ (25 mM), 0.5 μL of dNTP nucleotide mix, 0.2 μL of Taq polymerase (Promega), 7.8 μL of ddH_2O, 2.5 μL of forward primer (10 pmole/μL), 2.5 μL of reverse primer (10 pmole/μL), and 1 to 3 μL of sample DNA (if greater quantities of DNA was used, the ddH_2O was adjusted accordingly). The PCR reactions were run on an Applied Biosystems GeneAmp PCR System 9700. Each amplification reaction required specific annealing temperatures and primer pairs to yield a successful amplification of the designated region of the mtDNA (Table 1). Each PCR amplification product was subjected to site-specific restriction endonucleases to

Table 1. List of mtDNA Haplogroups, Primers, Annealing Temperature, PCR Product Fragment Size, and RFLP Reaction Condition for Each Polymorphic Site

mtDNA Haplogroup	*Primer*	*Annealing *T (°C)*	*PCR Product Size (bp)*	*Digestion *T (°C)*	*RFLP Product Size (bp)*
H (7025 AluI)	L6949: 5´-CCGTAGGTGGCCTGACTGGC-3´ H7052: 5´ -TGATGGCAAATACAGCTCCT-3´	56	123	37	78; 30; 15
R0 (14766 MseI)	L14603: 5´-CTAAACCCCCATAAATAGGAG-3´ H14791: 5´-AGGTCGATGAATGAGTGG-3´	50	226	65	184; 21;17; 4
HV (11719 SmaI)	L11852: 5´-GGGGGTAAGGCGAGGTTAGC-3´ H11718: 5´-CGCAGTCATTCTCATAATCGCCCCCGG-3´	58.8	180	25	155; 25
U (12308 HinfI)	L12216: 5´-CACAAGAACTGCTAACTCATGC-3´ H12338: 5´-ATTACTTTTATTTGGAGTTGCACCAAGATT-3´	53	123	37	93; 30
L (3592 HpaI)	L3388: 5´-CTAGGCTATATACAACTACGC-3´ H3717: 5´-GGCTACTGCTCGCAGTG-3´	50.9	330	37	207; 123
M (10397 AluI)	L10252: 5´-TTGATCTAGAAATTGCCCTC-3´ H10527: 5´-GTATTCCTAGAAGTGAGATG-3´	48.2	276	37	147; 129
N (10873 MnlI)	L10727: 5´-CTCAATCTCCAACACATATGGC-3´ H10920: 5´-GGTCGGAGGAAAAGGTTG-3´	51	232	37	176; 56
HVS-I targeted nucleotides	F15971: 5´-TTAACTCCACCATTAGCACC-3´ R16410: 5´-GAGGATGGTGGTCAAGGGAC-3´	56	443	Sequencing	

Table 2. Mitochondrial DNA HVSI of the Populations Included in This Study

Continent	*Population*	*Samples*	*mtDNA Sequence Source(s)*
Africa	Nigeria	63	Watson et al. 1996
	Kenya	78	Watson et al. 1996
	Somalia	5	Olivieri et al. 2006
	Ethiopia	75	Watson et al. 1996
	African San	17	Tishkoff et al. 2007
Asia	Yemen	90	Kivisild et al. 2004
	Saudi Arabia	15	Abu-Amero et al. 2007
	Kuwait	94	This study
	Iraq	116	McEvoy et al. 2004
	Syria	69	McEvoy et al. 2004
	Jordan	9	Ennafaa et al. 2009
	Kurdistan	53	McEvoy et al. 2004
	Iran	92	Nasidze et al. 2008
	India	109	Sharma et al. 2005 and Thangaraj et al. 2005
Europe	Turkey	290	McEvoy et al. 2004
	Greece	179	McEvoy et al. 2004
	England	242	McEvoy et al. 2004
	Bulgaria	141	McEvoy et al. 2004
	Romania	92	McEvoy et al. 2004
Total	19	1829	-

identify base substitutions or insertion/deletion events and to determine the relevant haplogroup (Table 1).

Comparative Population Data. The populations used for comparison with the Kuwaiti population consisted of a total of 1,735 individuals representing 18 countries from three continents: Africa, Asia, and Europe (Table 2). The mtDNA sequence of HVSI for each individual was obtained from GenBank (www.ncbi.nih.gov/Genbank/) except for the following populations: Iraq, Syria, Kurdistan, and European. The mtDNA sequences of the latter populations were obtained from (www.gen.tcd.ie/molpopgen/resources.php) (Benson et al. 2006). Table 2 represents the populations and the number of samples in each population analyzed in this study.

Statistical Analysis. Haplotype diversity and nucleotide diversity were computed by using Arlequin, version 3.11 (Excoffier et al. 2005). In addition, Arlequin version 3.11 was used to calculate Fu's Fs and Tajima's D which are measurements of selective neutrality (Fu 1997; Tajima 1993). Mismatch analysis was used to reconstruct the demographic history of the populations (Rogers and Harpending 1992). Mismatch analysis produces a distribution of pairwise differences between individuals within a population that can be used as an indication of population expansion, stability, or bottlenecks (Rogers and Harpending 1992). For instance, if the distribution has a unimodal shape, then it represents a recent population expansion while a multimodal distribution shows a population that has constant size over time (Rogers et al. 1996; Rogers and

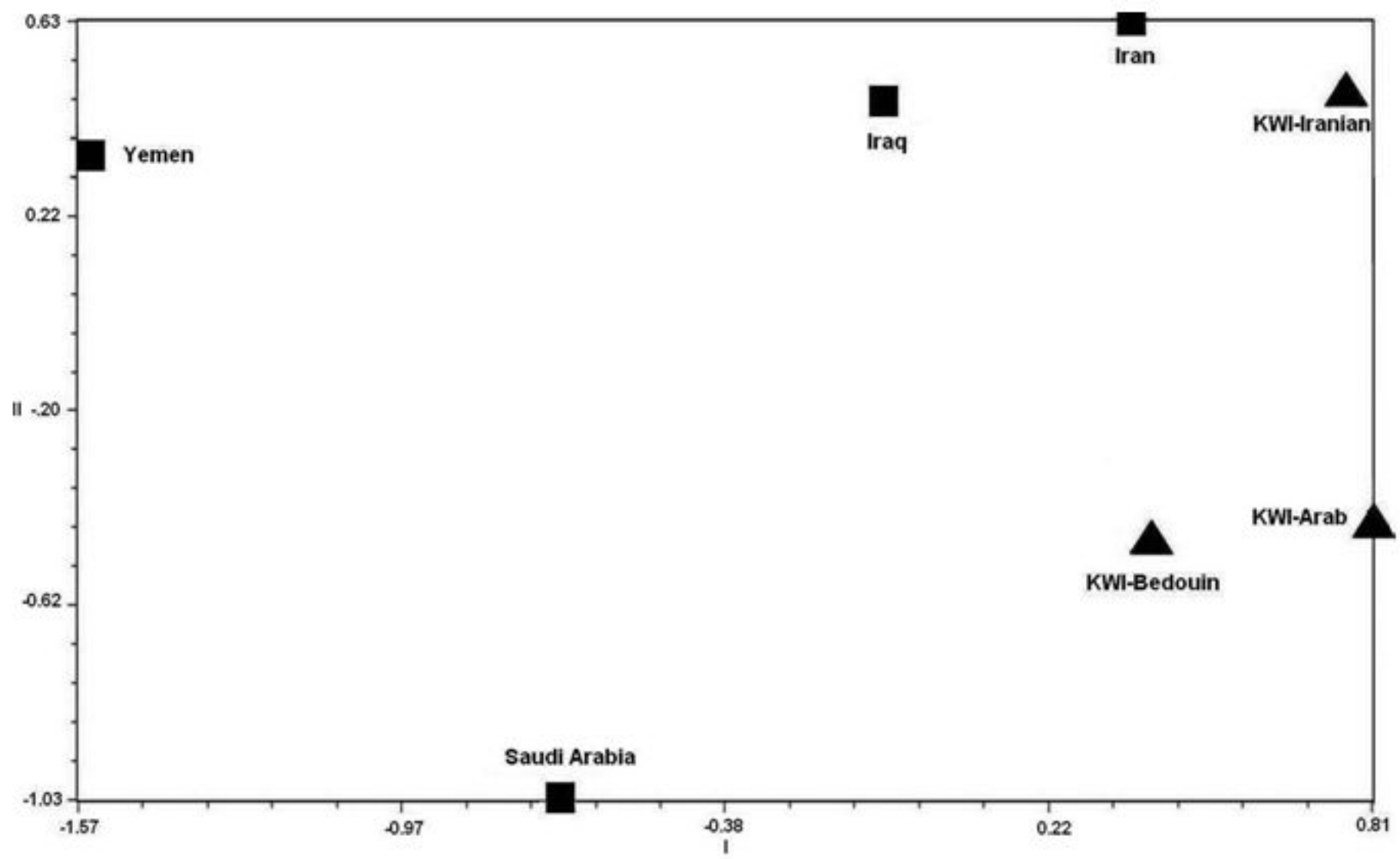

Figure 2. MDS plot of mtDNA HVS-I sequence data of the Kuwaiti subpopulations (triangle) and neighboring populations (square).

Harpending 1992). A raggedness index (r), used to assess the significance of mismatch plots, was calculated in Arlequin version 3.11 (Excoffier et al. 1992; Harpending et al. 1993). In addition, AMOVA was conducted by using Arlequin 3.11 (Excoffier et al. 1992).

The biological relationships among different populations were represented in a multi-dimensional scaling plot (MDS). The MDS plot was constructed by using NTSYS 2.1 computer program (Rohlf 2008). The MDS plot is based on F_{ST} pairwise differences between population samples.

Results

In this study, 116 individuals were successfully analyzed for the mtDNA RFLPs. Out of these 116, only 94 individuals were successfully sequenced for the hypervariable region I (HVS-I) of the mitochondrial DNA—A list of the HVS-I mutations is included as supplementary material in the Appendix. The failure in sequencing the mtDNA of 22 individuals was caused by the low concentration of the DNA. To examine the contribution of the Kuwaiti ethnic groups to the total Kuwaiti gene pool, the Kuwaiti samples were subdivided into three subpopulations according to their origins: 48 Arabian Peninsula, 36 Iranian, and 32 Bedouins, who represented more than one tribal group. A chi-square test was used to determine if the three subpopulations were statistically homogenous. Heterogeneity among the three subpopulations ($X^2 = 17.35$; $P < 0.005$, df = 12) was observed. An MDS method was applied to assess the relationship of the three groups to geographically neighboring populations (Figure 2). The stress value for

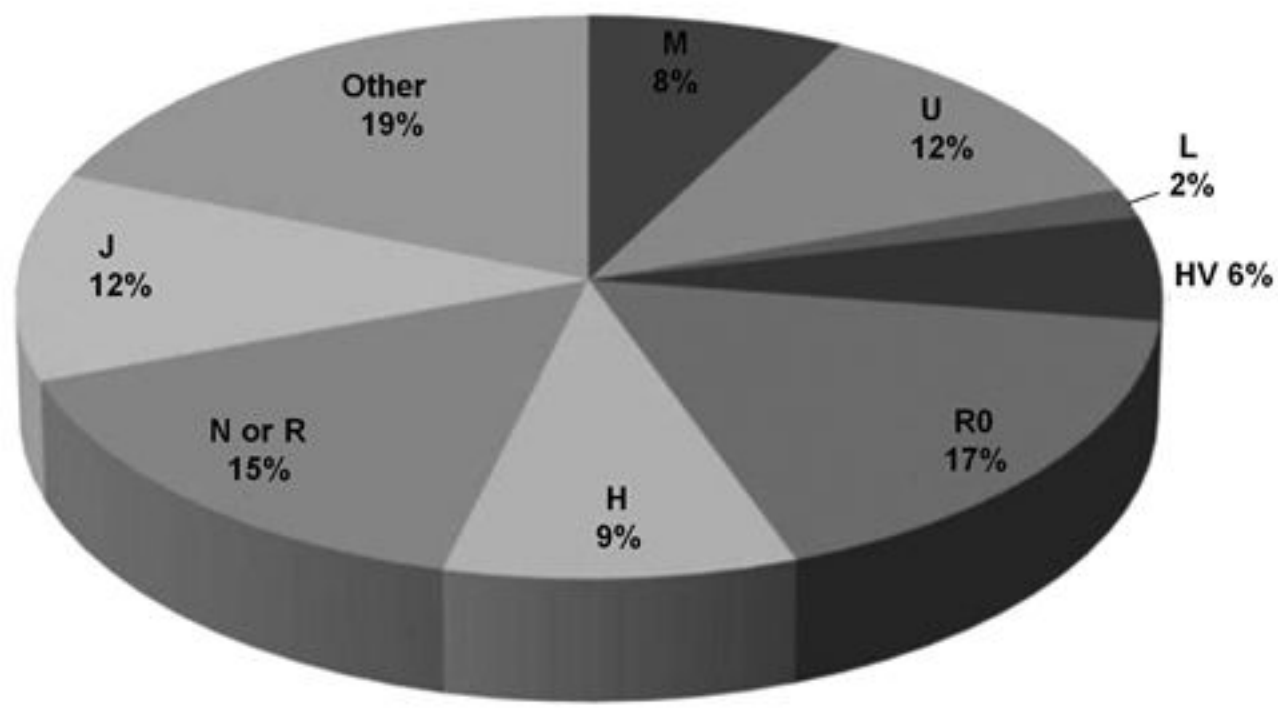

Figure 3. Mitochondrial haplogroup frequencies of the Kuwaiti Population.

the MDS plot was 0.948 (Groenen and Velden, 2004), indicating a good representation of the genetic relationship among the populations.

Based on the RFLP analysis, the Kuwaiti population was found to be a mix of many haplogroups that originated in Africa, Asia, and Eurasia. The most common haplogroup among Kuwaiti individuals is R0 (17%), followed by U and J haplogroups (12%). Haplogroup L is the least common in Kuwaiti population. However, 19% of the total Kuwaiti sample could not be assigned to a specific haplogroup. Figure 3 summarizes the haplogroup frequencies in the Kuwaiti population.

Table 3 compares mtDNA haplogroup frequencies in the Kuwaiti population to other populations of the Middle East. The haplogroup frequencies of the Kuwaiti population are similar to those observed in Iranian and Arabian populations. However, the Kuwaiti haplogroup frequencies differ from those observed in either Syria or Palestine. Haplogroups R0, HV, H, M, N or R, L, J, and U encompass about 81% of the Kuwaiti subjects. Compared to other haplogroups, R0 is the most common one observed in Kuwait and Arabia, 17% and 15.2%, respectively. Furthermore, the influence of African L haplogroup is low in Kuwait (2%) and Iran (2.2%), but much higher in Arabia (10.5%). According to RFLP analysis, Kuwait served as a gene recipient from both the Asian and African continents. The presence of particular haplogroups is an indication of gene flow to Kuwait and a possible founder effect of the founding families. The presence of haplogroup L (L1 and L2) in Kuwait (2%) reveals the African gene flow into Kuwait. In addition, haplogroup M and N or R are an indication of Asian gene flow.

The results of the mtDNA diversity and neutrality measures for Kuwaiti and comparative populations are presented in Table 4. The genetic diversity of Kuwait (0.9799) is similar to neighboring populations: Iran (0.9895), Iraq (0.9918), and Saudi (0.9905). The remaining populations all have gene diversities that fall between 0.9960 and 0.7941. Tajima's D (−1.87839) and Fu's Fs

Table 3. Estimated mtDNA Haplogroups Frequencies in Kuwait and Comparative Populations

	Estimated mtDNA Haplogroups Frequency (%) in Populations						
Haplogroup	*Iraqi*[a]	*Arabia*[b]	**Kuwait**	*Palestinian*[c]	*Syrian*[c]	*Iranian*[b]	*Anatolia*[b,d]
Sample size	216	389	**116**	117	69	451	388
R0	4.2	15.2	**17.0**	2.6	5.8	2.4	2.8
HV	10.6	3.6	**6.0**	1.7	4.3	5.5	3.6
H	19.9	12.9	**9.0**	30.8	24.6	17.1	25.0
V	0.5	0	**nr**	0	2.9	0	0
J	9.3	20.8	**12.0**	9.4	10.1	13.5	10.9
T	8.8	4.6	**nr**	12.8	10.1	8.4	11.9
K	3.2	3.6	**nr**	6.8	4.3	7.5	5.9
U	19.0	10.5	**12.0**	7.6	15.9	21.5	19.3
I	1.9	0.8	**nr**	0	0	2.0	2.3
X	2.8	1.8	**nr**	3.4	0	2.9	4.4
W	1.9	1.8	**nr**	2.6	2.9	2.0	3.9
B	0.9	nr	**nr**	0	0	nr	0
M	1.4	nr	**8.0**	1.7	1.4	nr	4.4
N or R	nr	12.6	**15.0**	nr	nr	6.1	1.8
L1-L3#	4.2	10.5	**2.0**	5.2	5.8	2.2	0.3
Other	11.5	6.2	**19.0**	15.4	11.6	8.6	4.5

nr: Not reported.
[a]Al-Zahery et al. (2003).
[b]Kivisild et al. (2003).
[c]Richards et al. (2000).
[d]Tambets et al. (2000).

(−25.40242) for the Kuwaiti population are significant at $P < 0.05$ and $P < 0.005$, respectively. These results suggest that the Kuwaiti population may be undergoing an expansion and gene flow in relatively a short period of time. Populations with negative Fs values are indicative of a population expansion.

Mismatch distributions of Kuwaiti and comparative populations are provided in Figure 4. The distributions of Kuwait, Iran, Iraq, and Yemen show unimodal distributions. These populations reach a peak in the number of pairwise differences between six and eight with frequency ranging between 15 and 20%. The Harpending's raggedness index was calculated for each population, and it was below 0.03 which is insignificant ($P = 0.05$). The smooth bell-shaped distributions accompanied by low raggedness index (below 0.03) suggest that these populations are expanding demographically. However, the multimodal (including bimodal) mismatch distribution of Somalia and Bushmen is suggestive of a constant population size over time.

An MDS method represents the relationship of the Kuwaiti population to comparative populations. Figure 5 presents a multidimensional scaling plot which is based on F_{ST} pairwise differences between population samples. The plot indicates that there are three distinct clusters of populations: (1) Represented by black circles are African populations except for African Bushmen. The African Bushmen group, located in the upper-left corner of the graph, reflects high

Table 4. Summary Statistics for Kuwaiti and Comparative Populations Based on mtDNA HVS-I Sequence Data (np 16080−16380), Including the Number of Samples (N), Gene Diversity (H), Nucleotide Diversity, the Number of Pairwise Differences between Haplotypes (π)

Population	*N*	*H*	*Nucleotide Diversity*	π	*Tajima's D*	*Fu's FS*
Nigeria	63	0.9949 (0.0039)	0.024693 (0.013067)	6.815 (3.60656)	−1.40382	−25.12808*
Kenya	78	0.9960 (0.0029)	0.034584 (0.017767)	9.545 (4.90382)	−1.34071	−24.63881*
Somalia	5	0.9000 (0.1610)	0.023980 (0.015946)	6.618 (4.40119)	0.18621	−0.96395
Ethiopia	75	0.9910 (0.0044)	0.034005 (0.017499)	9.385 (4.82985)	−1.19564	−24.68836*
African San	17	0.7941 (0.0783)	0.027642 (0.015181)	7.629 (4.18986)	−0.05484	−11.62028*
Yemen	90	0.9793 (0.007)	0.028242 (0.014703)	7.795 (4.05790)	−1.42630*	−24.87694*
Saudi Arabia	15	0.9905 (0.0281)	0.023429 (0.013172)	6.466 (3.63536)	−1.36306	−10.25005*
Kuwait	**94**	**0.9799 (0.0074)**	**0.019810 (0.010660)**	**5.448 (2.93155)**	**−1.87839***	**−25.40242***
Iraq	116	0.9918 (0.0036)	0.020573 (0.011)	5.678 (3.03595)	−2.10200*	−25.27107*
Syria	69	0.9881 (0.007)	0.019950 (0.010766)	5.506 (2.97134)	−2.14505*	−25.44552*
Kurdistan	53	0.9833 (0.0095)	0.019922 (0.010801)	5.498 (2.98117)	−1.99134*	−25.45367*
Iran	92	0.9895 (0.0049)	0.021020 (0.011240)	5.802 (3.10213)	−2.10033*	−25.30259*
India	109	0.9674 (0.0088)	0.019047 (0.010274)	5.257 (2.83567)	−1.95946*	−25.39018*
Turkey	290	0.9858 (0.0037)	0.017938 (0.009686)	4.951 (2.67337)	−2.22379*	−25.06563*
Greece	179	0.9760 (0.0055)	0.014409 (0.008016)	3.977 (2.21243)	−2.17981*	−25.74642*
England	242	0.9667 (0.0076)	0.014809 (0.008196)	4.087 (2.26215)	−2.24347*	−25.49169*
Bulgaria	141	0.9762 (0.0065)	0.015306 (0.008459)	4.224 (2.33476)	−2.12006*	−25.72313*
Romania	92	0.9811 (0.0051)	0.015691 (0.008678)	4.331 (2.39506)	−1.97053*	−25.81281*
			0.022064	6.0885 (3.33172)	−1.59729	−21.38537

*Tajima's D are significant at $P < 0.05$ and Fu's Fs are significant at $P < 0.005$.

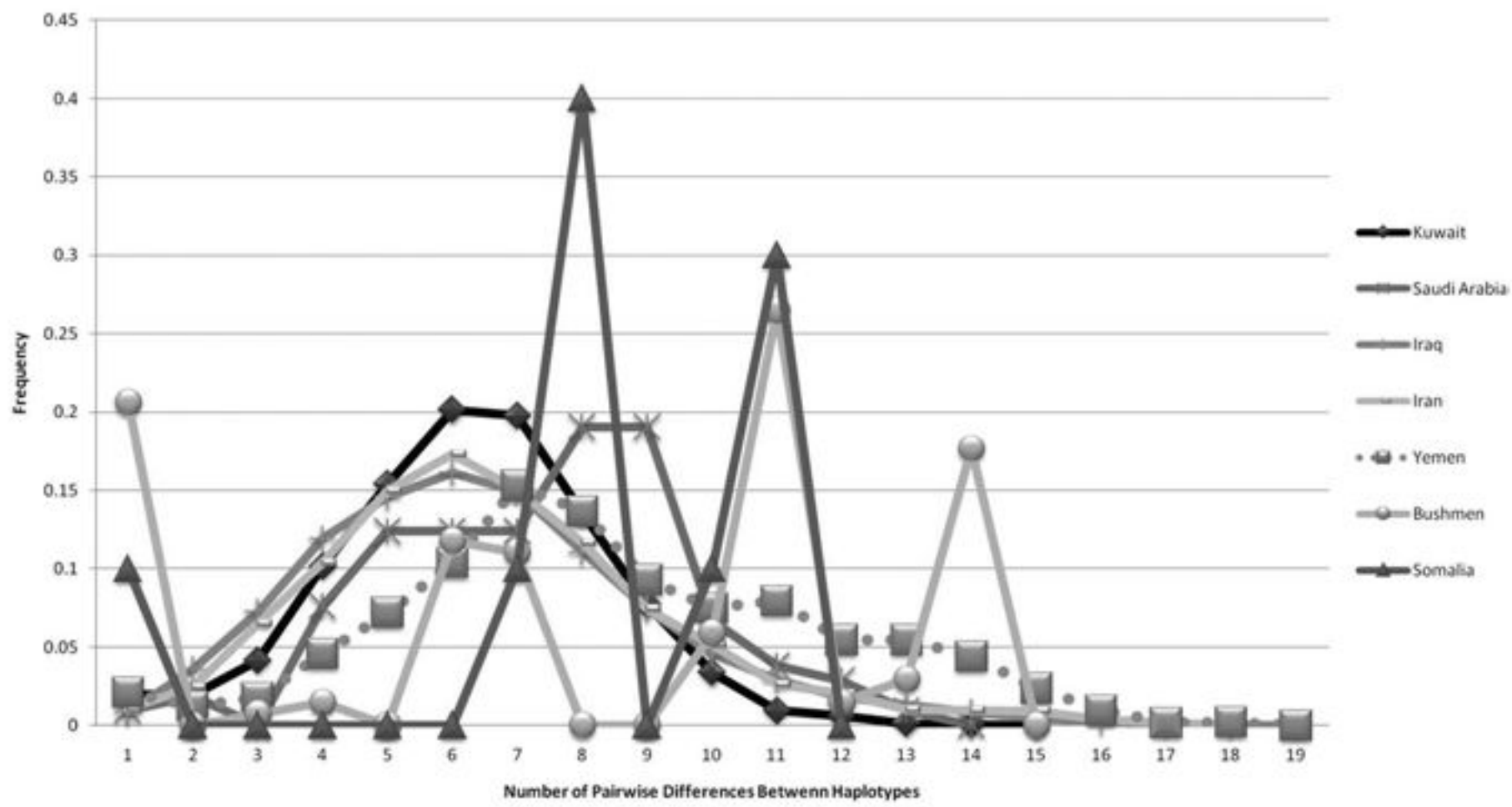

Figure 4. Mismatch distributions of the Kuwaiti and geographically neighboring populations.

genetic diversity. Furthermore, Ethiopia was found to be the closest African population to the Asian populations. (2) The black squares represent the Asian populations that are intermediate between African and European populations. However, India is located in the lower-right side of the graph, separate from other Asian (Middle Eastern) population. As expected, Iraq, Kurdistan, and Syria were found to be close to Turkey. (3) Next are the European populations, and they are represented by diamond-shape symbols. Kuwait was located on the upper-right side of the graph and near both Iranian and Saudi populations, reflecting the geographical location of Kuwait and the contribution of gene flow from these

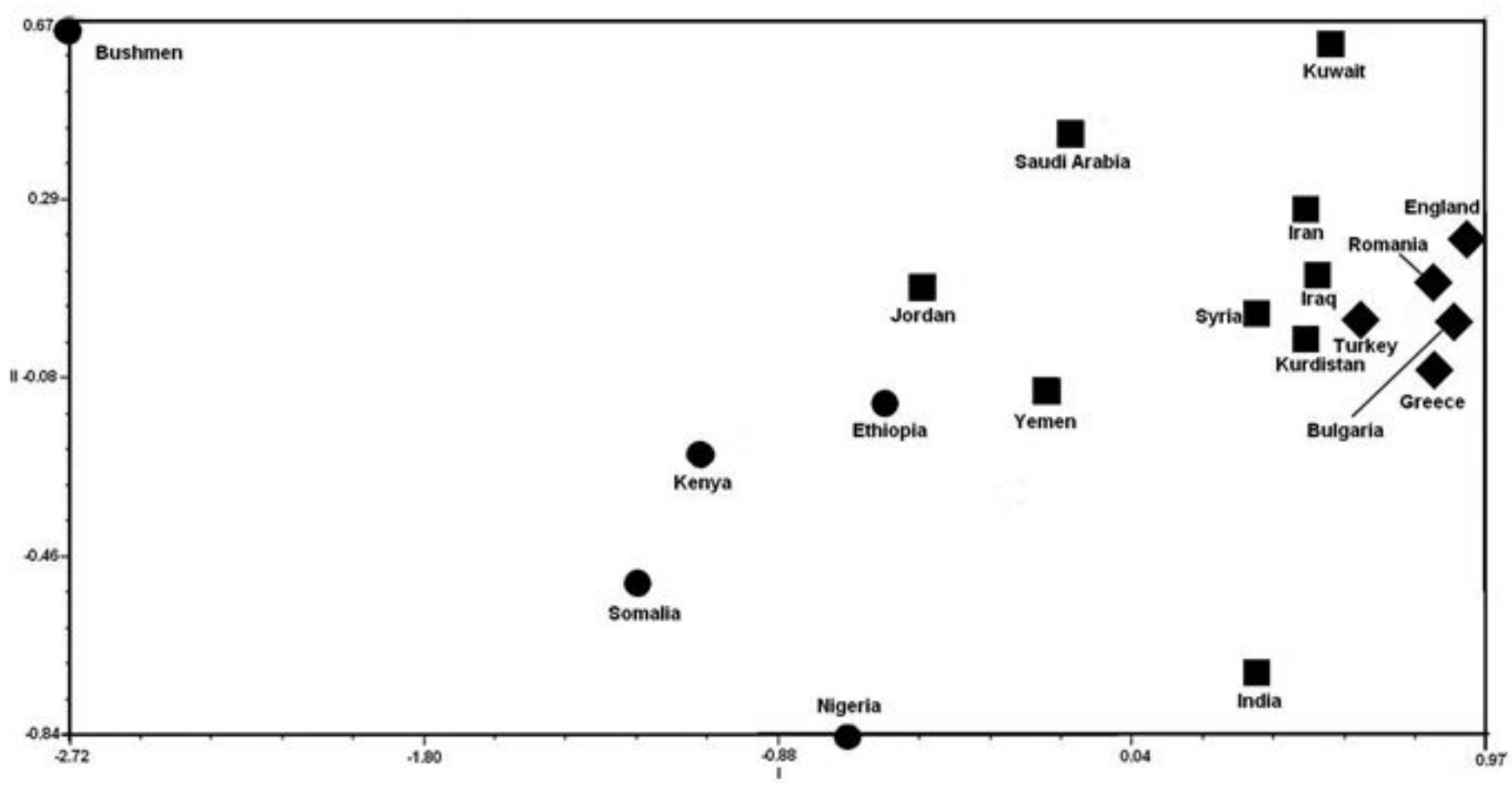

Figure 5. MDS plot of mtDNA HVS-I sequence data with 19 populations. African populations represented by circles; Asian populations represented by squares; European populations represented by diamond shape symbols.

Table 5. AMOVA Results for Comparison of Three Groups (Africa, Asia, and Europe)

Source of Variation	*d.f.*	*Sum of Squares*	*Variance Components*	*Percentage of Variation*	*F-Statistics*
Among groups	2	240.779	0.19637	6.68	$\phi_{CT} = 0.06676$*
Within groups	16	194.017	0.10423	3.54	$\phi_{SC} = 0.03797$*
Within populations	1810	4779.490	2.64060	89.78	$\phi_{ST} = 0.10220$*
Total	1828	5214.286	2.94120		

**P*-value = 0.00000.

countries into the Kuwaiti gene pool. The stress value of the MDS plot is good (0.09584). The original distance matrix was compared to an MDS matrix by using a two-way Mantel test. The correlation was highly significant (0.98228), indicating that the MDS plot provides a good fit to the data.

To determine the genetic structure of 19 populations based on the mtDNA HVS-I sequence data, an AMOVA was conducted. All populations were classified according to their geographical locations. The first group contains the African populations: Nigeria, Somalia, Kenya, Ethiopia, and African Bushmen. The second group is composed of Asian populations: India, Yemen, Jordan, Saudi Arabia, Iran, Iraq, Kurdistan, Syria, and Kuwait. The last group contains European populations: Turkey, England, Romania, Bulgaria, and Greece. The result of AMOVA analysis is shown in Table 5. The greatest amount of variation was observed within populations and accounted for 89.78% of the total variation, followed by among-groups variation (6.68%) and finally within-groups variation (3.54%). All variance components are significant.

Discussion

Studies of mtDNA variation have proven to be useful for examining evolutionary processes in humans and reconstructing population histories (Horai et al. 1995; Torroni et al. 1994; Vigilant et al. 1991). This research investigated the genetic structure of the Kuwaiti population through mtDNA analyses to elucidate the phylogenetic relationship of the Kuwaiti population to other Middle-Eastern groups. The genetic structure of the Kuwaiti population was previously investigated by using classical genetic markers such as blood groups (Al-Bustan et al. 2002; Al-Nassar et al. 1981a, 1981b; El-Zawahri and Luqmani 2008; Sawhney et al. 1984). These studies indicated that the Kuwaiti population differs significantly from the genetic structure of Iraq, Iran, and Saudi Arabia (Al-Bustan et al. 2002; El-Zawahri and Luqmani 2008). However, Al-Bustan et al. (2002), El-Zawahri and Luqmani (2008), and Sawheny et al. (1984) demonstrated that the Kuwait genetic structure is similar to geographically neighboring populations. Our study indicated that the maternal genetic structure of the Kuwaiti population resembles the maternal genetic structure of both Iran and Saudi Arabia and that is expected since the Kuwaiti population experienced

gene flow mostly from Iran and Saudi Arabia. Because Iraq is geographically close to Kuwait, as is Saudi Arabia and Iran, it was expected that the Kuwaiti gene pool would be influenced by Iraqi gene flow. However, this study did not detect an Iraqi gene-flow influence on the Kuwaiti gene pool, possibly because of the small sample size. In addition, the MDS plot in Figure 2 indicates that the Kuwaiti subpopulation that claims Iranian origin is genetically closer to Iran than to the other two Kuwaiti subpopulations.

The geographic origins of some mtDNA haplogroups have been documented; thus, these haplogroups can be used to reconstruct the genetic history of populations (Abu-Amero et al. 2007; Abu-Amero et al. 2008; Ennafaa et al. 2009; Kivisild et al. 2003a; Santos et al. 2004; Torroni et al. 1996, 1994; Underhill and Kivisild 2007). According to the RFLP analysis, Kuwaiti maternal genetic structure is similar to other populations of Arabia—they share a high frequency of haplogroup R0 (17%) and a low frequency of the African haplogroup L (2%). These two haplogroups are unique to the maternal gene pool of Arabia (Abu-Amero et al. 2007; Al-Zahery et al. 2003). The European and Caucasian populations exhibit a high frequency of haplogroup H (45%) and low frequencies of haplogroups HV or R0 (when present) (Abu-Amero et al. 2007). However, the haplogroup frequency of R0 and HV occurs at 18.8% in the Arabians (Kivisild et al. 2003b), 20.6% among the Arabian Bedouins (Di Rienzo and Wilson 1991), 14.8% in Iraq (Al-Zahery et al. 2003), and in this study of a Kuwaiti sample, the rate was found to be 23%, which is high compared to other haplogroup frequencies in the Arabian populations (Abu-Amero et al. 2007). Recent phylogeographic analyses of R0 haplogroup detected several radiations of this clade and several of its subclades in areas centered in the Middle East and Arabia and dated from the Neolithic period and beyond. According to Richards et al. (2000, 2003) the haplogroup R0 has a Middle-Eastern origin that eventually evolved into haplogroup H—the most abundant haplogroup in Europe (45%) and the Near East (25%).

This study documents the presence of the African haplogroup L (2%) in the Kuwaiti gene pool similar to the patterns observed in Saudi Arabian and Yemeni gene pools (Abu-Amero et al. 2007; Cerny et al. 2008). Approximately 2,500 years ago, the slave trade from Africa to the Arabian Peninsula introduced maternal haplotypes to the Kuwaiti gene pool. The presence of African mtDNA haplotypes (L1 and L2) in the Kuwaiti gene pool can be explained by the practice of assimilating the offspring of slaves into the community (Abu-Amero et al. 2007; Lewis 1990).

According to the mtDNA HVS-I MDS plot in Figure 5, the Kuwaiti population clusters with Iranian and Saudi Arabian populations. This finding indicates that the maternal genetic structure of the Kuwaiti population resembles both the Iranian and Saudi Arabian maternal genetic structure. Furthermore, gene flow from Saudi Arabia and Iran to Kuwait has been documented. These results are consistent with the findings of Alenizi et al. (2008) and Mohammad et al. (2009), who indicated that the paternal genetic structure of the Kuwaiti population is similar to the paternal genetic structure of Saudi Arabia, Iraq, and Iran. However, this study failed to support the

presence of maternal gene flow from Iraq which can be explained by the limited genetic contribution of Iraq into the Kuwaiti gene pool compared to Iran and Saudi Arabia. Another explanation is the relatively small sample size used in this study that may not have included any individuals with Iraqi origin. The mismatch analysis indicates that the Kuwaiti population is a rapidly expanding population—in part because of the gene flow. This conclusion is supported by the demographic data (Figure 4) and the smooth bell-shape distribution with raggedness-index value below 0.03. In contrast to Kuwait, the mismatch analyses of Saudi Arabia, Somalia, and African Bushmen show ragged-shaped distributions that suggest that these populations were of constant size over a long period of time.

Conclusion

Kuwait is one of seven countries located in the Arabian Peninsula. The critical location of the Arabian Peninsula is believed to have played a major role in the expansion of early *Homo* out-of-Africa (Cabrera et al. 2009; Jeffrey and Michael 2009; Petraglia et al. 2011). To understand its role in the early expansion, recent studies investigated the genetic structure and the archaeology of the Arabian Peninsula (Alshamali et al. 2009; Beyin 2006; Crassard 2009; Derricourt 2005; Gonzalez et al. 2008). However, to date, not all of the regions of the Arabian Peninsula have been investigated, and this study attempted to fill a gap in the understanding of the genetic structure of the Arabian Peninsula.

The Kuwaiti subpopulations are genetically homogenous, and they shared the same haplogroup frequencies as the other populations in Arabia. In addition, Kuwait is influenced by gene flow from neighboring populations and especially from both Saudi Arabia and Iran as indicated in the MDS plots. The mismatch-distribution plot indicates that the Kuwaiti population has a recent demographic expansion. These results reflect the recent history of population formation in Kuwait. Further studies are needed to investigate the other haplogroup frequencies in Kuwait. In addition, the genetic study of Y-chromosome markers is needed to better understand the genetic structure and past history of Kuwait.

Acknowledgments We would like to thanks all the DNA donors and the laboratory technician at Kuwait University, Babitha Annice, for her assistance and guidance of the lab work.

Received 6 May 2012; revision accepted for publication 26 July 2012.

Literature Cited

Abu-Amero, K. K., A. M. Gonzalez, J. M. Larruga et al. 2007. Eurasian and African mitochondrial DNA influences in the Saudi Arabian population. *BMC Evol Biol.* 7:32.

Abu-Amero, K. K., J. M. Larruga, V. M. Cabrera et al. 2008. Mitochondrial DNA structure in the Arabian Peninsula. *BMC Evol. Biol.* 8.

Al-Bustan, S., M. El-Zawahri, D. Al-Azmi et al. 2002. Allele frequencies and molecular genotyping of the ABO blood group system in a Kuwaiti population. *International Journal of Hematology* 75(2):147–153.

Alenizi, M., W. Goodwin, S. Ismael et al. 2008. STR data for the AmpFlSTR Identifiler loci in Kuwaiti population. *Leg. Med. (Tokyo)* 10(6):321–325.

Alghanim, S. 1998. *The Reign of Mubarak al-Sabah, Shaikh of Kuwait, 1896–1915.* New York: St. Martin's Press.

Al-Nassar, K. E., P. M. Conneally, C. G. Palmer et al. 1981a. The genetic structure of the Kuwaiti population. I. Distribution of 17 markers with genetic distance analysis. *Hum Genet.* 57(2):192–198.

Al-Nassar, K. E., C. G. Palmer, P. M. Conneally et al. 1981b. The genetic structure of the Kuwaiti population II: The distribution of Q-band chromosomal heteromorphisms. *Hum Genet.* 57(4):423–427.

Alshamali, F., L. Pereira, B. Budowle et al. 2009. Local population structure in Arabian Peninsula revealed by Y-STR diversity. *Human Heredity* 68(1):45–54.

Al-Zahery, N., O. Semino, G. Benuzzi et al. 2003. Y-chromosome and mtDNA polymorphisms in Iraq, a crossroad of the early human dispersal and of post-Neolithic migrations. DOI: 10.1016/S1055-7903(03)00039-3. *Mol. Phylogenet. Evol.* 28(3):458–472.

Anscombe, F. F. 1997. *The Ottoman Gulf : The Creation of Kuwait, Saudi Arabia, and Qatar.* New York: Columbia University Press.

Benson, D. A., I. Karsch-Mizrachi, D. J. Lipman et al. 2006. GenBank. *Nucleic Acids Res.* 34(Database issue): D16–20.

Bermisheva, M. A., T. V. Viktorova, and E. K. Khusnutdinova. 2003. Polymorphism of human mitochondrial DNA. *Russian J. Genet.* 39(8):849–859.

Beyin, A. 2006. The Bab al Mandab vs. the Nile-Levant: An appraisal of the two dispersal routes for early modern humans out of Africa. *African Archaeological Review* 23(1):5–30.

Cabrera, V., K. Abu-Amero, J. Larruga et al. 2009. The Arabian Peninsula: Gate for human migrations out of Africa or cul-de-sac? A mitochondrial DNA phylogeographic perspective. In *The Evolution of Human Populations in Arabia: Paleoenvironments, Prehistory and Genetics.* The Netherlands: Springer, 79–87.

Carter, R. 2006. Boat remains and maritime trade in the Persian Gulf during the sixth and fifth millennia BC. *ANTIQUITY-OXFORD*-80(307):52.

Carter, R., H. Crawford, S. Mellalieu et al. 1999. The Kuwait-British Archaeological Expedition to As-Sabiyah: Report on the first season's work. *Iraq* 61:43–58.

Carter, R. W. 2007. Mitochondrial diversity within modern human populations. *Nucleic Acids Res.* 35(9):3039–3045.

Casey, M. S. 2007. *The History of Kuwait.* Westport, Connecticut: Greenwood Press.

Cerny, V., C. J. Mulligan, J. Ridl et al. 2008. Regional differences in the distribution of the sub-Saharan, West Eurasian, and South Asian mtDNA lineages in Yemen. *Am. J. Phys. Anthropol.* 136(2):128–137.

Crassard, R. 2009. The Middle Paleolithic of Arabia: The view from the Hadramawt region, Yemen. In *The Evolution of Human Populations in Arabia: Paleoenvironments, Prehistory and Genetics.* M. D. Petraglia and J. I. Rose, eds. The Netherlands: Springer, 151–168.

Derricourt, R. 2005. Getting "Out of Africa": Sea crossings, land crossings and culture in the Hominin migrations. *Journal of World Prehistory* 19(2):119–132.

Di Rienzo, A., and A. C. Wilson. 1991. Branching pattern in the evolutionary tree for human mitochondrial DNA. *Proc. Natl. Acad. Sci. USA* 88(5):1597–1601.

El-Zawahri, M. M., and Y. A. Luqmani. 2008. Molecular genotyping and frequencies of A(1), A(2), B, O-1 and O-2 alleles of the ABO blood group system in a Kuwaiti population. *International Journal of Hematology* 87(3):303–309.

Ennafaa, H., V. M. Cabrera, K. K. Abu-Amero et al. 2009. Mitochondrial DNA haplogroup H structure in North Africa. *BMC Genet.* 10:8.

Excoffier, L., G. Laval, and S. Schneider. 2005. Arlequin (version 3.0): An integrated software package for population genetics data analysis. *Evol. Bioinform. Online* 1:47–50.

Excoffier, L., P. Smouse, and J. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. *Genetics* 131(2):479.

Fu, Y. X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics* 147(2):915–925.

Gonzalez, A. M., N. Karadsheh, N. Maca-Meyer et al. 2008. Mitochondrial DNA variation in Jordanians and their genetic relationship to other Middle East populations. *Annals of Hum. Biol.* 35(2):212–231.

Groenen, P. J. F. and Velden, M. van de. 2005. Multidimensional scaling. In *Encyclopedia of Statistics in Behavioral Sciences Vol. 2,* B.S. Everitt and D. C. Howell, eds. Chichester, Wiley, 1280–1289.

Harpending, H., S. T. Sherry, A. R. Rogers et al. 1993. The genetic structure of ancient human populations. *Current Anthropology* 34 (4):483–496.

Horai, S., K. Hayasaka, R. Kondo et al. 1995. Recent African origin of modern humans revealed by complete sequences of hominoid mitochondrial DNAs. *Proc. Natl. Acad. Sci. USA* 92(2):532–536.

Kivisild, T., M. Reidla, E. Metspalu et al. 2004. Ethiopian mitochondrial DNA heritage: Tracking gene flow across and around the gate of tears. *Am. J. Hum. Genet.* 75(5):752–770.

Kivisild, T., S. Rootsi, M. Metspalu et al. 2003a. The genetic heritage of the earliest settlers persists both in Indian tribal and caste populations. *American Journal of Human Genetics* 72(2):313–332.

Kivisild, T., S. Rootsi, M. Metspalu et al. 2003b. The genetics of language and farming spread in India. In *Examining the Farming/Language Dispersal Hypothesis,* P. Bellwood and C. Renfrew, eds. Cambridge, UK: McDonald Institute for Archaeological Research, 215–222.

Lewis, B. 1990. *Race and Slavery in the Middle East.* New York: Oxford University Press.

McEvoy, B., M. Richards, P. Forster et al. 2004. The Longue Duree of genetic ancestry: Multiple genetic marker systems and Celtic origins on the Atlantic facade of Europe. *Am. J. Hum. Genet.* 75(4):693–702.

Miller, S. A., D. D. Dykes, and H. F. Polesky. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Res.* 16(3):1215.

Mohammad, T., Y. Xue, M. Evison et al. 2009. Genetic structure of nomadic Bedouin from Kuwait. *Heredity* 103(5):425–433.

Nasidze, I., D. Quinque, M. Rahmani et al. 2008. Close genetic relationship between Semitic-speaking and Indo-European-speaking groups in Iran. *Ann. Hum. Genet.* 72(Pt. 2):241–252.

Olivieri, A., A. Achilli, M. Pala et al. 2006. The mtDNA legacy of the Levantine early Upper Palaeolithic in Africa. *Science* 314(5806):1767–1770.

Petraglia, M. D. 2011. Archaeology: Trailblazers across Arabia. *Nature* 470(7332):50–51.

Potter, L. G. 2009. The archaeology and early history of the Persian Gulf. In *The Persian Gulf in History,* L. G. Potter, ed. New York: Palgrave Macmillan, 27−56.

Quintana-Murci, L., R. Chaix, R. S. Wells et al. 2004. Where west meets east: The complex mtDNA landscape of the southwest and Central Asian corridor. *American Journal of Human Genetics* 74(5):827–845.

Richards, M., H. CorteReal, P. Forster et al. 1996. Paleolithic and neolithic lineages in the European mitochondrial gene pool. *American Journal of Human Genetics* 59(1):185–203.

Richards, M., V. Macaulay, E. Hickey et al. 2000. Tracing European founder lineages in the near eastern mtDNA pool. *American Journal of Human Genetics* 67(5):1251–1276.

Richards, M., C. Rengo, F. Cruciani et al. 2003. Extensive female-mediated gene flow from sub-Saharan Africa into near eastern Arab populations. *American Journal of Human Genetics* 72(4):1058–1064.

Rogers, A. R., A. E. Fraley, M. J. Bamshad et al. 1996. Mitochondrial mismatch analysis is insensitive to the mutational process. *Mol Biol Evol.* 13(7):895–902.

Rogers, A. R., and H. Harpending. 1992. Population growth makes waves in the distribution of pairwise genetic differences. *Mol. Biol. Evol.* 9(3):552–569.

Rohlf, F. 2008. *NTSYS-pc: Numerical Taxonomy System, Version 2.1.* Setauket, New York: Exeter Publishing Limited.

Rose, J. I., and M. D. Petraglia. 2009. Tracking the origin and evolution of human populations in Arabia. In *The Evolution of Human Populations in Arabia: Paleoenvironments, Prehistory and Genetics,* P. MD and R. JI, eds. The Netherlands: Springer, 1–12.

Santos, C., R. Montiel, N. Angles et al. 2004. Determination of human Caucasian mitochondrial DNA haplogroups by means of a hierarchical approach. *Hum. Biol.* 76(3):431–453.

Sawhney, K. S., E. Sunderland, and V. Woolley. 1984. Genetic Polymorphisms in the Kuwaiti Arabs. *Human Heredity* 34(5):303–307.

Sharma, S., A. Saha, E. Rai et al. 2005. Human mtDNA hypervariable regions, HVR I and II, hint at deep common maternal founder and subsequent maternal gene flow in Indian population groups. *J. Hum. Genet.* 50(10):497–506.

Slot, B. 2003. Kuwait: *The Growth of a Historic Identity*. London: Arabian.

Tajima, F. 1993. Simple methods for testing the molecular evolutionary clock hypothesis. *Genetics* 135(2):599–607.

Tambets, K., T. Kivisild, E. Metspalu et al. 2000. The topology of the maternal lineages of the Anatolian and Trans-Caucasus populations and the peopling of Europe: Some preliminary considerations. In *Archaeogenetics: DNA and the Population Prehistory of Europe,* C. Renfrew, and K. Boyle, eds. Cambridge 219–235.mcThangaraj, K., V. Sridhar, T. Kivisild et al. 2005. Different population histories of the Mundari- and Mon-Khmer-speaking Austro-Asiatic tribes inferred from the mtDNA 9-bp deletion/insertion polymorphism in Indian populations. *Hum. Genet.* 116(6):507–517.

Tishkoff, S. A., M. K. Gonder, B. M. Henn et al. 2007. History of click-speaking populations of Africa inferred from mtDNA and Y chromosome genetic variation. *Mol. Biol. Evol.* 24(10):2180–2195.

Torroni, A., K. Huoponen, P. Francalacci et al. 1996. Classification of European mtDNAs from an analysis three European populations. *Genetics* 144(4):1835–1850.

Torroni, A., M. T. Lott, M. F. Cabell et al. 1994. mtDNA and the origin of Caucasians: Identification of ancient Caucasian-specific haplogroups, one of which is prone to a recurrent somatic duplication in the D-loop region. *American Journal of Human Genetics* 55(4):760–776.

Underhill, P. A., and T. Kivisild. 2007. Use of Y chromosome and mitochondrial DNA population structure in tracing human migrations. *Annual Review of Genetics* 41:539–564.

Vigilant, L., M. Stoneking, H. Harpending et al. 1991. African populations and the evolution of human mitochondrial DNA. *Science* 253(5027):1503–1507.

Watson, E., K. Bauer, R. Aman et al. 1996. mtDNA sequence diversity in Africa. *American Journal of Human Genetics* 59(2):437–444.

Wilson, A. C., and R. L. Cann. 1992. The recent African genesis of humans. *Scientific American* 266(4):68–73.

Table S1. List of Mitochondrial HVS-1 Mutations

	16017T	16018T	16051A	16069C	16071C	16086T	16092T	16093T	16114C	16115C	16124T	16145G	16146T	16172A	16178C	16189G	16196T	16209G	16223T	16224G	16227C	16228C	16233G	16238A	16239A	16268C	16269C	16292T	16296C	16304C	16311C	16319C	16320C	16325C	16327T	16362C	16363C	16368C	16390C	16399C	16400T	16401G	16402A	16404C	16405C	16406C	16411T	16423C	16424A	16429C	16430C	16431C	16434T	16445A	16452C	16455C	16456C	16519C	16523A	16527C	16529A	16530C	16531C
KWI-8	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.
KWI-16	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.
KWI-15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.
KWI-18	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.
KWI-20	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-21	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-22	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-32	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	?	?	?	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.
KWI-33	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-40	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-50	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-51	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.
KWI-52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-53	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-58	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.
KWI-59	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.

Table S1. (*continued*)

	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	1	1	5	6	7	8	9	9	1	1	2	2	2	2	2	2	3	4	4	4	5	5	6	6	6	7	7	8	8	8	8	8	9	9	0	0	1	2	2	2	2	2	3	4	5	5	6	6	7	7	7	8
	7	8	1	9	1	6	2	3	4	5	4	5	6	7	8	9	6	5	7	8	3	8	3	8	9	2	6	4	5	6	8	9	2	3	1	9	3	0	1	2	3	4	5	2	6	9	1	5	0	5	8	7
	T	T	A	C	C	T	T	T	C	C	T	G	T	A	C	G	T	G	C	C	G	A	A	C	C	T	C	C	C	C	C	T	C	C	C	T	G	A	C	C	C	T	A	C	C	C	C	A	C	A	C	C
KWI-67	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-68	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.
KWI-78	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-81	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-82	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-85	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-87	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.
KWI-88	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	T	.	.	.	.	.	.	.	.	G	.	.	.
KWI-89	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-90	.	.	G	T	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-92	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T
KWI-97	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-98	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.
KWI-99	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-102	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	C	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-104	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.
KWI-108	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	T	.
KWI-111	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table S1. (*continued*)

	16017T	16018T	16015A	16069C	16071C	16086T	16089T	16093T	16114C	16115C	16124T	16125G	16126T	16167A	16228C	16229G	16236T	16245G	16247C	16248C	16253G	16258A	16263A	16268C	16269C	16272T	16276C	16284C	16285C	16286C	16288C	16289T	16292C	16293C	16301C	16319T	16320G	16321A	16322C	16322C	16322C	16323T	16324A	16325C	16355C	16356C	16359C	16361A	16365C	16370A	16375A	16378C
KWI-116	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-117	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.	.
KWI-120	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-121	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-124	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.
KWI-125	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	T	.	.	.	.	.	.	.	.	.	T	.
KWI-127	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.
KWI-132	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-137	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-138	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	T	.	.	.	.	.	.	.
KWI-143	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.
KWI-145	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.
KWI-146	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	T	.	.	.	.	.	.	.
KWI-147	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-148	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	.	.	.	.	.	.	.	.	.	.
KWI-154	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.	.
KWI-155	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.
KWI-156	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table S1. (*continued*)

	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	1	1	5	6	7	8	9	9	1	1	2	2	2	2	2	2	3	4	4	4	5	5	6	6	6	7	7	8	8	8	8	8	9	9	0	0	1	2	2	2	2	2	3	4	5	5	6	6	7	7	7	8
	7	8	1	9	1	6	2	3	4	5	4	5	6	7	8	9	6	5	7	8	3	8	3	8	9	2	6	4	5	6	8	9	2	3	1	9	3	0	1	2	3	4	5	2	6	9	1	5	0	5	8	7
	T	T	A	C	C	T	T	T	C	C	T	G	T	A	C	G	T	G	C	C	G	A	A	C	C	T	C	C	C	C	C	T	C	C	C	T	G	A	C	C	C	T	A	C	C	C	C	A	C	A	C	C
KWI-157	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	T	.
KWI-159	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-161	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-168	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	C	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.
KWI-170	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.
KWI-171	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-173	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-174	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-175	.	.	.	.	.	.	.	.	.	.	.	.	?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.
KWI-195	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-196	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-198	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	T	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-201	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-203	A	?	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-204	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-206	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	G	.	.	.	.	T	.	.	.	.	.
KWI-207	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-209	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table S1. (*continued*)

	16017	16018	16015	16019	16017	16016	16029	16023	16014	16015	16024	16025	16026	16027	16028	16029	16036	16045	16047	16048	16053	16058	16063	16068	16069	16072	16076	16084	16085	16086	16089	16092	16093	16095	16096	16101	16102	16103	16104	16105	16106	16109	16120	16122	16123	16124	16125	16126	16129	16161	16165	16170	16175	16178
	T	T	A	C	C	T	T	T	C	C	T	G	T	A	C	G	T	G	C	C	G	A	A	C	C	T	C	C	C	C	C	T	C	C	C	T	G	A	C	C	C	T	A	C	C	C	C	A	C	A	C	C
KWI-210	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	T	.	.	.	.	.
KWI-212	A	A	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-213	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-214	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-216	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-217	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	T	.	.
KWI-218	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	T	.
KWI-235	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-238	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-249	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-263	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-452	.	.	.	T	.	.	.	.	.	.	.	.	C	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-467	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-471	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-473	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.
KWI-478	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.
KWI-480	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-482	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-487	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-494	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-497	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.
KWI-504	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.

Table S1. (*continued*)

	162923C	162923A	162924C	162925C	162926C	162928T	163030A	163030T	163039A	163111T	163118A	163120C	163124T	163125T	163127C	163143A	163152T	163154C	163155C	163156T	163159T	163162T	163168T	163190G
KWI-8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-15	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.
KWI-21	.	.	.	.	.	.	G	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-22	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-32	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-33	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-40	.	.	.	.	.	.	G	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-51	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-52	.	.	.	.	.	.	.	.	G	.	T	.	.	.	.	G	.	.	.	.	.	C	.	.
KWI-53	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-58	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-59	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-67	.	.	.	.	.	.	.	.	G	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-68	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-78	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-81	.	.	.	.	.	.	.	.	G	.	T	.	.	.	.	G	.	.	.	.	.	C	.	.
KWI-82	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-85	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table S1. (*continued*)

	162920C	162923A	162924C	162925C	162926C	162928T	163000A	163004T	163009A	163311T	163318A	163320C	163324T	163325T	163327C	163430A	163452T	163554C	163555C	163556T	163559T	163562T	163568T	163690G
KWI-87	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-88	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-89	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-90	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-92	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.
KWI-97	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.
KWI-98	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A
KWI-99	T	.	T	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-102	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-104	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A
KWI-108	.	.	.	.	.	C	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-111	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-116	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-117	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-120	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-121	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-124	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-125	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	A
KWI-127	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-132	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-137	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-138	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	C	.	.	.	.
KWI-143	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.

Table S1. (*continued*)

	162920C	163A	162934C	162945C	162956C	162968T	303080A	303084T	303099A	311391T	311818A	322080C	322044T	322055T	322077C	334343A	355332T	355424C	355535C	355556T	355659T	356262T	366268T	393960G
KWI-145	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.
KWI-146	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.
KWI-147	.	.	T	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-148	.	.	.	.	.	.	.	.	G	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-154	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-155	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A
KWI-156	.	.	T	.	T	.	.	C	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.
KWI-157	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-159	.	.	T	.	T	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-161	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	?	.	.	.	.	.	.
KWI-168	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.
KWI-170	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-171	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-173	.	.	T	.	T	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-174	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
KWI-175	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-195	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.
KWI-196	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.
KWI-198	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A
KWI-201	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.
KWI-203	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-204	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.
KWI-206	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-207	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table S1. (*continued*)

	162923C	162923A	162924C	162925C	162926C	162928T	163300A	163304T	163309A	163311T	163318A	163320C	163324T	163325T	163327C	163443A	163452T	163454C	163455C	163556T	163559T	163662T	163668T	163690G
KWI-209	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-210	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-212	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.
KWI-213	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.
KWI-214	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-216	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	T	C	.	C	.	.
KWI-217	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-218	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-235	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-238	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-249	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.
KWI-263	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
KWI-452	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-467	.	.	.	.	.	.	.	.	G	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-471	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	T	C	.	C	.	.
KWI-473	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-478	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-480	.	T	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	T	.	.	C	.	.
KWI-482	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-487	.	.	T	.	T	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.
KWI-494	.	.	.	.	.	.	.	.	G	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-497	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
KWI-504	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.