

# Distribution of Y Chromosomes Among Native North Americans: A Study of Athapaskan Population History

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**ABSTRACT** In this study, 231 Y chromosomes from 12 populations were typed for four diagnostic single nucleotide polymorphisms (SNPs) to determine haplogroup membership and 43 Y chromosomes from three of these populations were typed for eight short tandem repeats (STRs) to determine haplotypes. These data were combined with previously published data, amounting to 724 Y chromosomes from 26 populations in North America, and analyzed to investigate the geographic distribution of Y chromosomes among native North Americans and to test the Southern Athapaskan migration hypothesis. The results

suggest that European admixture has significantly altered the distribution of Y chromosomes in North America and because of this caution should be taken when inferring prehistoric population events in North America using Y chromosome data alone. However, consistent with studies of other genetic systems, we are still able to identify close relationships among Y chromosomes in Athapaskans from the Subarctic and the Southwest, suggesting that a small number of proto-Apachean migrants from the Subarctic founded the Southwest Athapaskan populations. *Am J Phys Anthropol* 137:412–424, 2008. ©2008 Wiley-Liss, Inc.

The geographic distribution of the Athapaskan language family in North America is hypothesized to result from long distance population movements (Basso, 1983). Previous studies of albumin variants (Smith et al., 2000) and mitochondrial DNA (mtDNA) (Malhi et al., 2003) have tested the migration hypothesis of Southern Athapaskan (Apachean) speakers. These studies show genetic patterns consistent with an Athapaskan migration to the Southwest from the Subarctic, followed by extensive admixture with groups in the Southwest. However, mtDNA is maternally inherited and therefore only reflects female population history. If male population history differs from female population history, it will not be reflected in patterns of mtDNA variation. For example, differences in male and female postmarital residence patterns may be investigated by comparing mtDNA and Y chromosome variation, as recently conducted by Bolnick et al. (2006) in Eastern North America. Therefore, we undertake a study of Y chromosome variation among Athapaskan speakers to gain insight into the population history of males in this group, which will broaden our understanding of the processes of population movements in prehistoric North America.

The majority of the speakers of Athapaskan languages are located in the Subarctic (Alaska and Canada), with the rest dispersed along the Pacific coastline, from

Oregon to California and into the Southwest (see Fig. 1). The Apacheans (the Navajo and Apache) are widely dispersed throughout the central region of the Southwest and speak languages that are closely related to Chipewyan, an Athapaskan language found in the Subarctic (Hoiyer, 1956). Hoiyer (1956) hypothesized that the homeland of proto-Athapaskan was in the Subarctic and that the distribution of Athapaskan languages along the Pacific coast and in the Southwest was the result of one or more migrations. Sapir (1936) demonstrated that the cultural significance of four Navajo words is indicative of a northern homeland for Southern Athapaskans and

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**Fig. 1.** Distribution of Athapaskan language family in North America. Modified from [http://en.wikipedia.org/wiki/Image:Na-Dene\\_langs.png](http://en.wikipedia.org/wiki/Image:Na-Dene_langs.png) with reference to Campbell (1997) and Goddard (1996).

hypothesized that the presence of Athapaskans in the Southwest is the result of one or more migrations from the north. Most archaeologists believe Apacheans were present in the Southwest no earlier than around 500 years ago (Cordell, 1997). In accordance with this recent arrival, glottochronological estimates place the divergence of Proto-Apachean from Northern Athapaskan languages around 1000–1300 years ago and the earliest divergence of Apachean languages around 400–600 years ago (Hoiyer, 1956; Hymes, 1957). Hence, the Southern Athapaskan migration is thought to have been a relatively recent long distance and rapid population movement from the Subarctic to the Southwest of North America.

In agreement with the archaeological and linguistic conclusions, studies of protein polymorphisms have indicated that, relative to other Native American groups, Apacheans, and Subarctic Athapaskans share recent common ancestry (Suarez et al., 1985). However, studies of mtDNA variation among Native North Americans have revealed that Apacheans are polymorphic with

regard to mtDNA haplogroups, unlike Subarctic Athapaskans, who are monomorphic for haplogroup A. Approximately half of the maternal lineages sampled in the Apache belong to haplogroup A, whereas the others are primarily from haplogroups B and C. Furthermore, many of the mtDNA haplotypes in the Apache are shared with non-Athapaskan speaking populations in the Southwest. This suggests that many of the maternal lineages in the Navajo and Apache were acquired through admixture with non-Athapaskan groups in the Southwest (Lorenz and Smith, 1996; Smith et al., 2000; Malhi et al., 2003). By contrast, mtDNA haplotypes that are common in Athapaskans from the Subarctic are not common in non-Athapaskan groups in the Southwest; thus far, haplotypes common in Subarctic Athapaskans have only been observed in the Yavapai (Monroe, 2006) and, at a low frequency, in the Zuni (Malhi et al., 2003). Further supporting this unequal pattern of gene flow, a study of albumin variants (Smith et al., 2000) demonstrated that Southern Athapaskans exhibit a relatively high frequency of Albumin\*<sup>Mexico</sup>, a variant found only

TABLE 1. Description of the Haplogroup data set

Tribe	Language Family	Latitude	Longitude	N	Q	C	R	Reference
SC Apache	Athapaskan	33.35	-110.45	23	20	2	1	This study
Pima	Uto-Aztecan	31.40	-113.40	62	58	0	4	Zegura et al., 2004, this study (38)
Papago	Uto-Aztecan	30.45	-111.00	13	8	0	5	This study
Jemez	Tanoan	35.57	-105.67	13	13	0	0	This study
Tarahumara	Uto-Aztecan	28.50	-106.25	20	19	0	1	This study
Seri	Isolate	29.98	-111.25	15	15	0	0	This study
Nahua Atocpan	Uto-Aztecan	19.03	-99.08	7	6	0	0	This study
Nahua Cuetzalan	Uto-Aztecan	19.02	-99.07	10	10	0	0	This study
Cora	Uto-Aztecan	21.73	-105.00	37	37	0	0	This study
Huichol	Uto-Aztecan	22.00	-104.33	18	18	0	0	This study
Mixtec	Otomanguen	17.15	-97.45	22	20	0	2	This study
Mixe	Mixe-Zoquean	17.01	-95.54	12	12	0	0	Zegura et al., 2004
Zapotec	Otomanguen	17.30	-96.20	16	12	0	1	Zegura et al., 2004
Chipewyan	Athapaskan	59.55	-107.30	48	15	3	30	Bortolini et al., 2003
Dogrib	Athapaskan	63.08	-117.06	15	4	5	6	This study
Tanana	Athapaskan	65.17	-152.08	11	5	5	1	Zegura et al., 2004
Apache	Athapaskan	33.35	-110.45	94	75	14	5	Zegura et al., 2004
Navajo	Athapaskan	33.83	-109.96	75	72	1	2	Zegura et al., 2004
Seminole	Muskogean	28.33	-81.23	20	9	0	10	Lell et al., 2002
TM Chippewa	Algonquian	48.84	-99.74	34	3	0	30	Bolnick et al., 2006
W Chippewa	Algonquian	45.07	-91.27	29	8	0	20	Bolnick et al., 2006
Chey/Arap	Algonquian	41.14	-104.82	50	33	8	8	Bolnick et al., 2006
SWS Sioux	Macro-Siouan	45.66	-97.05	26	14	8	4	Bolnick et al., 2006
Stillwell Cherokee	Macro-Siouan	34.26	-85.16	30	15	0	14	Bolnick et al., 2006
Choctaw	Muskogean	31.88	-88.32	12	11	0	1	Bolnick et al., 2006
Creek	Muskogean	32.46	-84.99	12	9	1	2	Bolnick et al., 2006

Language family based on Campbell (1997).

in populations of the Southwest and Mesoamerica. However, Southern Athapaskans are the only Southwest populations to exhibit Albumin\*Naskapi, an albumin variant that is also found in Subarctic populations (Smith et al., 2000).

A study of the mtDNA haplotypes observed in the Apachean and Subarctic Athapaskans identified a pattern consistent with a founder effect for Southern Athapaskans. The Apachean exhibit a high frequency of a derived subclade of haplogroup A that likely originated in the Subarctic (defined as the A2a clade by Tamm et al., 2007); however, few individuals belong to this subclade in Subarctic populations. Based on these results, Malhi et al. (2003) suggested that the proto-Apacheans migrated to the Southwest in a single migration that included a relatively small number of females. After arriving in the Southwest, the Southern Athapaskans acquired a large number of non-Athapaskan maternal lineages through admixture with females from Southwestern tribes, but most Southwest groups did not correspondingly acquire as many maternal lineages from the Southern Athapaskans. The result of this process was a spread of Athapaskan culture in the Southwest, which has made the Navajo and Apache among the largest tribes in Native North America.

Previous studies have suggested that the distribution of Y chromosome variation among Native North Americas has been strongly influenced by (Zegura et al., 2004; Bolnick et al., 2006; Hammer et al., 2006) European admixture, in addition to other effects of European contact, such as high mortality and the relocation of indigenous individuals (Spicer, 1962). These effects may limit our ability to make inferences about prehistoric population events in North America from Y chromosome analysis alone. Hence, prior to analyzing Y chromosome variation in Athapaskans, we assess the influence of European admixture on the distribution of Y chromosome variation

among Native North Americans. We then study the male population history of Athapaskans within the context of patterns of Y chromosome variation across North America and results from corresponding mtDNA studies. Specifically, we test the hypothesis that Athapaskans in the Subarctic and Southwest share Y chromosomes, to the exclusion of non-Athapaskans in the Southwest, as a result of recent common ancestry. This result would be consistent with a migration of Athapaskans from the Subarctic to the Southwest (Hoijer, 1956; Basso, 1983; Lorenz and Smith, 1996; Smith et al., 2000; Malhi et al., 2003; Hunley and Long, 2005).

## MATERIALS AND METHODS

### Populations studied and data sets

Two separate data sets, a Haplogroup set and a Haplotype set, were analyzed in this study. The membership in Y chromosome haplogroup Q, C, or R was determined for 231 males from 12 populations in this study, including 15 Dogrib, 23 San Carlos Apache (SC Apache), 13 Jemez, 38 Akimal O'ohdam (Pima), 13 Tohono O'ohdam (Papago), 15 Seri, 20 Tarahumara, 37 Cora, 18 Huichol, 7 Nahua of San Pedro Atocpan (Nahua), 10 Nahua of Cuetzalan (Nahua Cuetzalan), and 22 Mixtec (Mixa). All samples are covered by IRB protocols at the University of California, Davis, and have been described in Smith et al. (2000) except the Seri (Infante et al., 1999), Tarahumara, Cora, Nahua Atocpan and Huichol (Kemp, 2006), and Mixe and Mixtec (Hollenbach et al., 2001). These data were combined for analysis with existing Y chromosome haplogroup data from Lell et al. (2002), Bortolini et al. (2003), Zegura et al. (2004), and Bolnick et al. (2006), resulting in a Haplogroup data set totaling 724 males from 26 Native North American populations. A description of the samples used in the Haplogroup data set is given in Table 1. Only samples that were determined to

belong to haplogroups Q (Q-M3 and Q-M242), C, or R were included in the Haplogroup data set.

The Haplotype data set is comprised of both previously published and newly presented Y chromosome haplotype data from a total of 355 males representing 16 Native North American populations (Table 2). The haplotypes were determined with the genotype data for the following eight STRs: DYS19, DYS390, DYS391, DYS392,

DYS393, DYS389I, DYS389II, and DYS439. From three populations, 43 males (22 San Carlos Apache, 9 Dogrib, and 12 Seri) were genotyped for these eight STRs in the present study. These data were combined with published haplotype data from 169 males representing three populations from Zegura et al. (2004) and 143 males from 10 populations in Kemp et al. (submitted). All individuals that did not belong to haplogroup Q and C were excluded from the Haplotype data set because these haplotypes are likely the result of non-native admixture (Tarazona-Santos and Santos, 2002; Zegura et al., 2004; Bolnick et al., 2006). Data generated in this study and that reported by Zegura et al. (2004) are given in Appendix.

TABLE 2. Sample composition and sample size of Haplotype data set

Population	N	Reference
Pima	29	Kemp et al., submitted
Cora	30	Kemp et al., submitted
Huichol	11	Kemp et al., submitted
Mixe	5	Kemp et al., submitted
Mixtec	20	Kemp et al., submitted
Nahua Atocpan	5	Kemp et al., submitted
Tarahumara	17	Kemp et al., submitted
Zapotec	6	Kemp et al., submitted
Nahua Cuetzalan	8	Kemp et al., submitted
SC Apache	22	This study
Dogrib	9	This study
Seri	12	This study
Jemez	12	Kemp et al., submitted
Navajo	71	Zegura et al., 2004
Apache	88	Zegura et al., 2004
Tanana	10	Zegura et al., 2004

DNA extraction and genotyping

DNA was extracted from 200 µl of serum or from buccal swabs using the Qiagen Blood Amp Kit. The DNA extracts were “whole genome amplified” using degenerate oligonucleotide primers (DOP) to increase the amount of DNA template (Cheung and Nelson, 1996) and analyzed for the following binary single nucleotide polymorphisms (SNP): Q-M3, Q-M242 (Seielstad et al., 2003), C-RPS4Y<sub>711</sub> (Bergen et al., 1999), and R-M173 (Underhill et al., 2000) to assign each sample to haplogroup Q, C, or R, respectively.

PCR amplifications for the SNP genotyping were carried out in 20 µl reactions containing 1.5 µl of DNA tem-

(a)

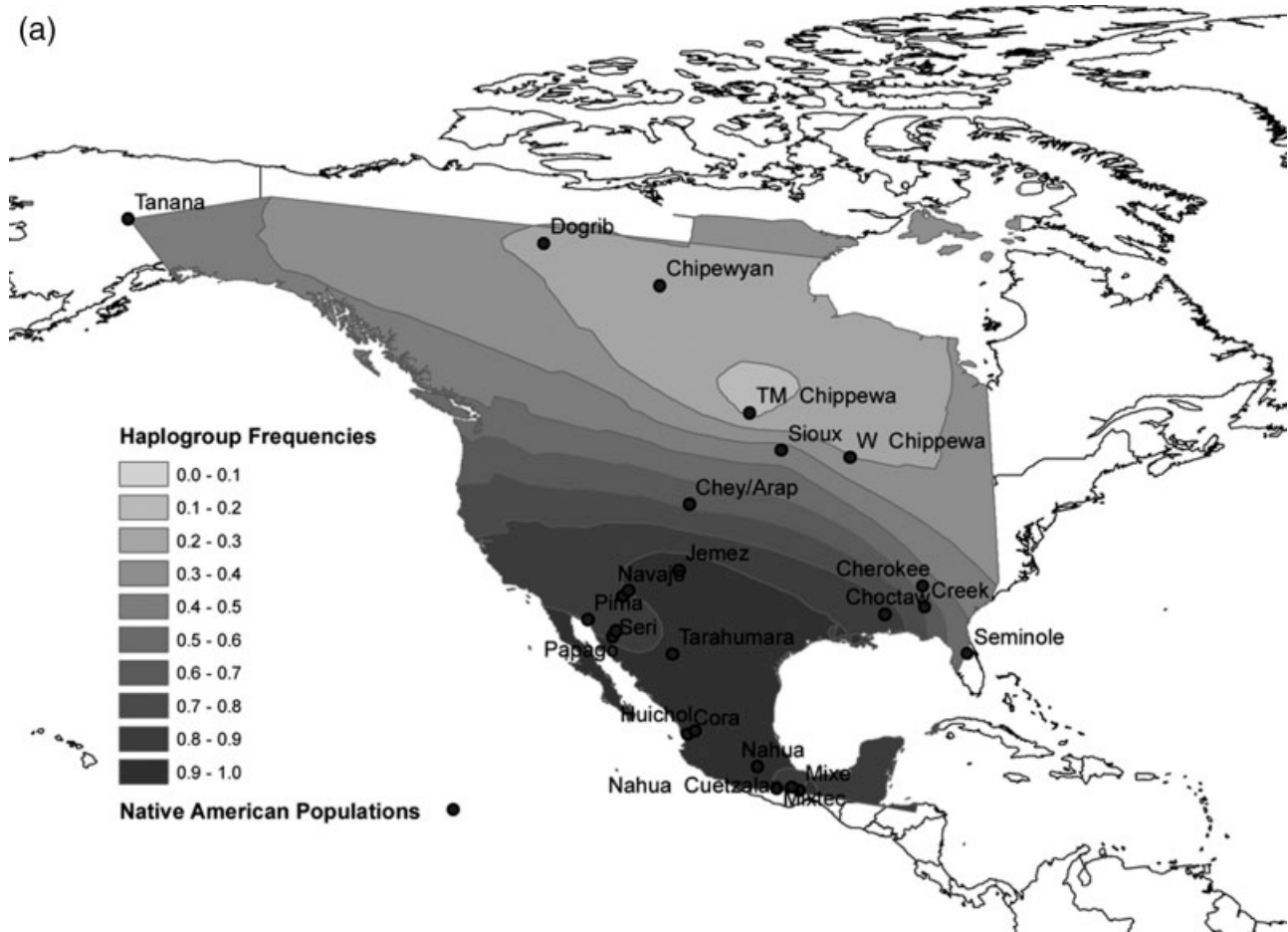
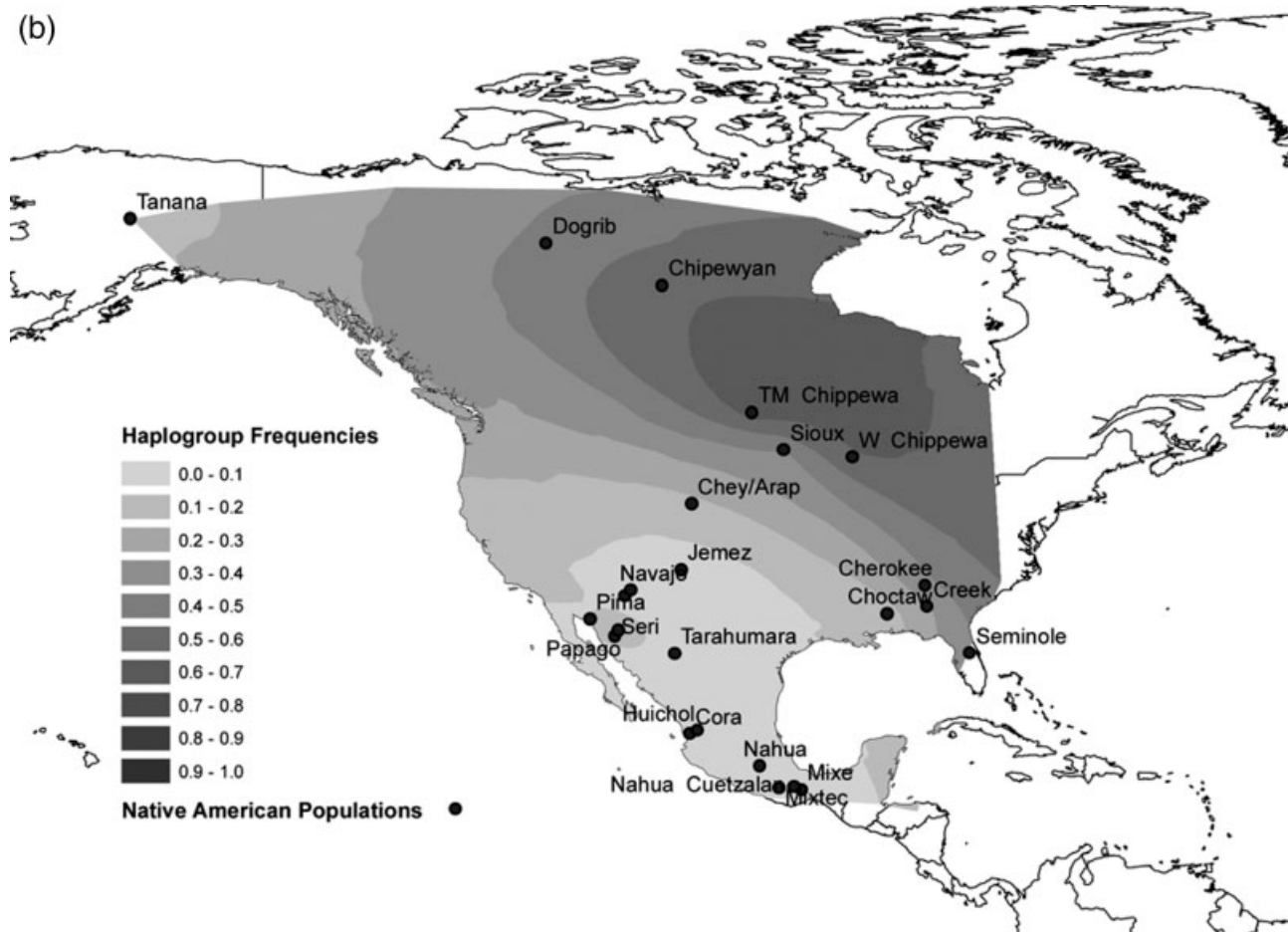


Fig. 2. (See legend page 417.)

(b)



**Fig. 2.** (See legend page 417.)

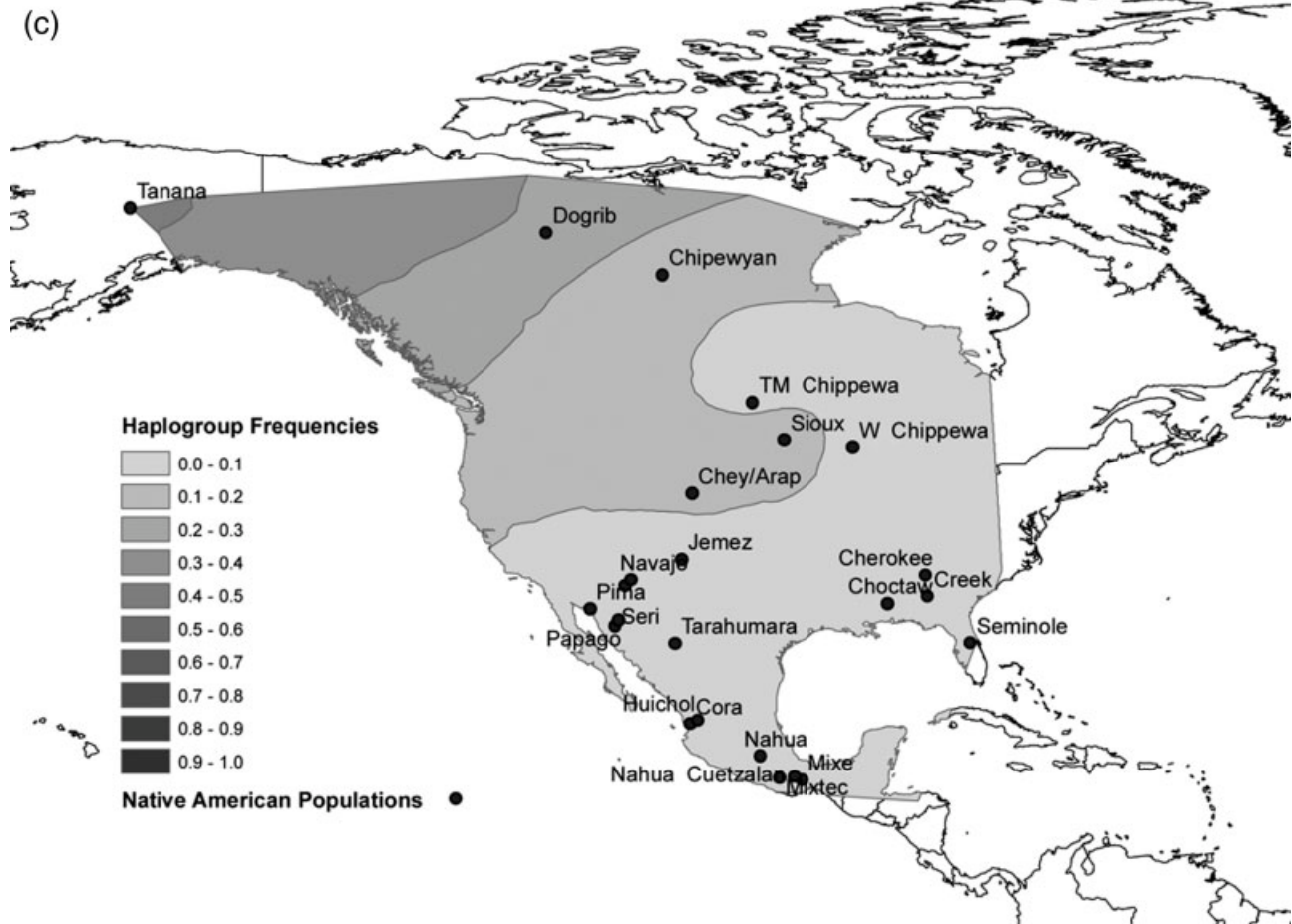
plate, 200  $\mu\text{M}$  of each dNTP, 1.2 mM  $\text{MgCl}_2$ , 0.1  $\mu\text{M}$  of each primer, 0.5 units Platinum Taq, and 2.0  $\mu\text{l}$  of the 10X buffer supplied by the manufacturer (Invitrogen). A program of 35 cycles of 1 min (min) of melting at 94°C, 1 min annealing at 61°C for Q-M3 (annealing at 56°C for Q-M242 and at 59°C for M-3), and 1 min extension at 72°C was used for PCR amplification in a Perkin-Elmer 9700 thermocycler. A program of 60 cycles of 15 seconds (sec) of melting at 94°C, 20 sec annealing at 58°C for C-RPS4Y<sub>711</sub> and at 50°C for R-M173, and 15 sec extension at 72°C was used for the remaining PCR amplifications. PCR product of 6  $\mu\text{l}$  was electrophoresed in 6% polyacrylamide gels and the size of each PCR product was determined in comparison to a known standard after staining with ethidium bromide.

PCR product of 6  $\mu\text{l}$  was tested for the presence of mutations diagnostic of lineages Q-M3, Q-M242, and C-RPS4Y<sub>711</sub>, incubated overnight at 37°C with five units of the appropriate restriction endonuclease (as described in Bolnick et al., 2006), and analyzed by electrophoresis as above. In total, 14  $\mu\text{l}$  of R-M173 PCR product were purified with *Exo I* following the supplier's recommendations. Then 8  $\mu\text{l}$  of purified product were submitted to the CA&ES sequencing facility, on the UC Davis campus, for forward and reverse sequencing on an automatic ABI 3730 genetic analyzer to identify the point mutation that defines R-M173.

Eight Y-STR loci were typed using the Reliagene Y-Plex™ Kit, which includes DYS19, DYS389I and II, DYS390, DYS391, DYS392, DYS393, DYS438, and DYS439. PCRs were carried out in 12  $\mu\text{l}$  containing 0.6  $\mu\text{M}$  of each primer, 200  $\mu\text{M}$  of each dNTP, 1.7 mM  $\text{MgCl}_2$ , 0.3 units Platinum Taq, 1.25  $\mu\text{l}$  of the 10X buffer supplied by the manufacturer (Invitrogen), and 2  $\mu\text{l}$  of DNA template. A program of 35 cycles of 1 min of melting at 94°C, 1 min annealing at 55°C, and 1 min extension at 72°C was used for PCR amplification of the STRs. About 2 or 3  $\mu\text{l}$  of Reliagene Y-Plex™ 12 kit PCR product were loaded on an ABI Prism 310 Genetic Analyzer (Perkin Elmer). The samples were injected for 22 s at 15,000 V for 25 min with a run temperature of 60°C using a 310 Genetic Analyzer POP™4. The allele sizes were determined with GeneScan version 3.1 software.

### Statistical analysis

Two previous studies (Zegura et al., 2004; Bolnick et al., 2006) have demonstrated that frequencies of Native North American Y chromosome haplogroups exhibit a significant correlation with geography. To visualize patterns of Y chromosome haplogroup structure across North America, we interpolated haplogroup frequency using kriging, a commonly used geostatistical interpolation technique



**Fig. 2.** (a) Frequency of haplogroup Q in North America. (b) Frequency of haplogroup R in North America. (c) Frequency of haplogroup C in North America.

based on the weighted linear combination of point data. This same methodology was used to visualize patterns of mtDNA haplogroup structure in North America (Malhi et al., 2002). Kriging uses fitted variogram models to characterize spatial structure in the data (Jensen, 2007). The most parsimonious variogram model was chosen based on least squares fitting. Because of areas of North America that lack adequate data, only results that were supported by additional evidence are discussed here.

Genetic distance ( $F_{ST}$  and  $R_{ST}$ ) were estimated using ARLEQUIN 2.0 (Schneider et al., 2000). The congruence between the two genetic distance matrices was measured using Kendall's W with the program CADM (Legendre, 2004). Principal coordinates were calculated from estimates of  $F_{ST}$  using the program SPSS. Because of the small sample sizes of some of the groups used in this analysis,  $F_{ST}$  was used instead of  $R_{ST}$  to be more conservative in our analysis (Caglia et al., 2003).

To investigate the relationship between haplotypes sampled from Southwest Athapaskans and those sampled from Subarctic Athapaskans, a median joining network of haplogroup C haplotypes, defined by eight STRs (those used in the Haplotype data set) was constructed using the program NETWORK (Bandelt et al., 1999). The contributions of STRs to the network were inversely weighted with allele frequency variances as in Bolnick et al. (2006).

## RESULTS

### Haplogroup frequency distribution in North America

Gene map interpolations (Fig. 2A–C) indicate that the frequency of haplogroup Q is highest in Southwestern North America/Mesoamerica. The frequency of haplogroup C is highest in Northwestern North America and the frequency of haplogroup R, the presence of which is attributed to European admixture, reaches its maximum in Northeastern North America. In total, 73% percent of the populations analyzed exhibited haplogroup R, which ranges in frequency from 4 to 88% (Table 1).

### Haplotype analysis among Athapaskans

Matrices of  $F_{ST}$  and  $R_{ST}$  show a high congruence (Kendall's  $W = 0.829$ ). In the Southwest, only the Athapaskans exhibit haplotypes that belong to haplogroup C. (Table 1, Fig. 3). The Apachean groups cluster more closely with Southwestern and Mesoamerican groups than with other Athapaskan populations in the principal coordinates analysis (see Fig. 4).

The median joining network for haplogroup C haplotypes (see Fig. 5) reveals that a majority of the haplotypes found in the Apachean populations belong to a derived subclade, as also reported by Zegura et al.

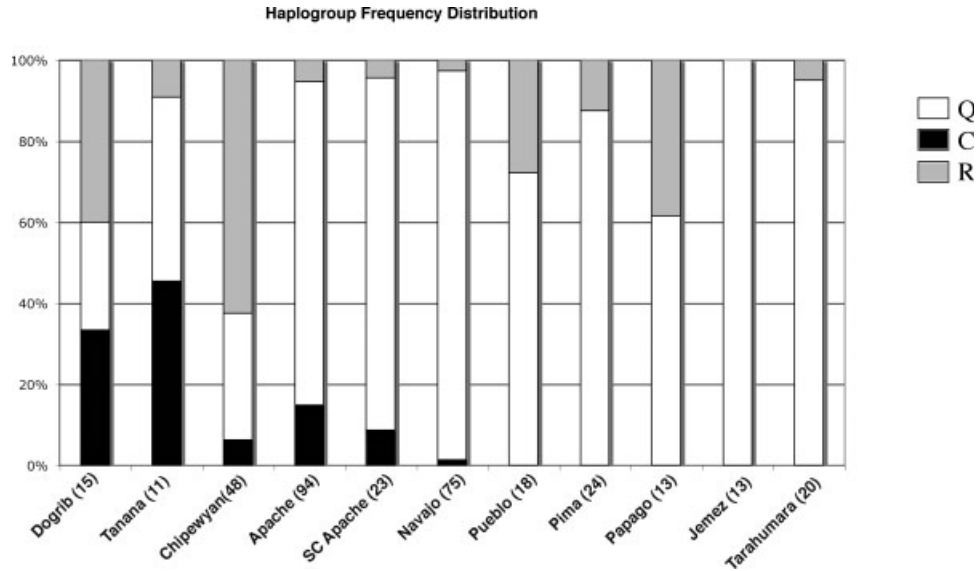


Fig. 3. Y-chromosome haplogroup frequency distribution for Athapaskan and Southwest populations.

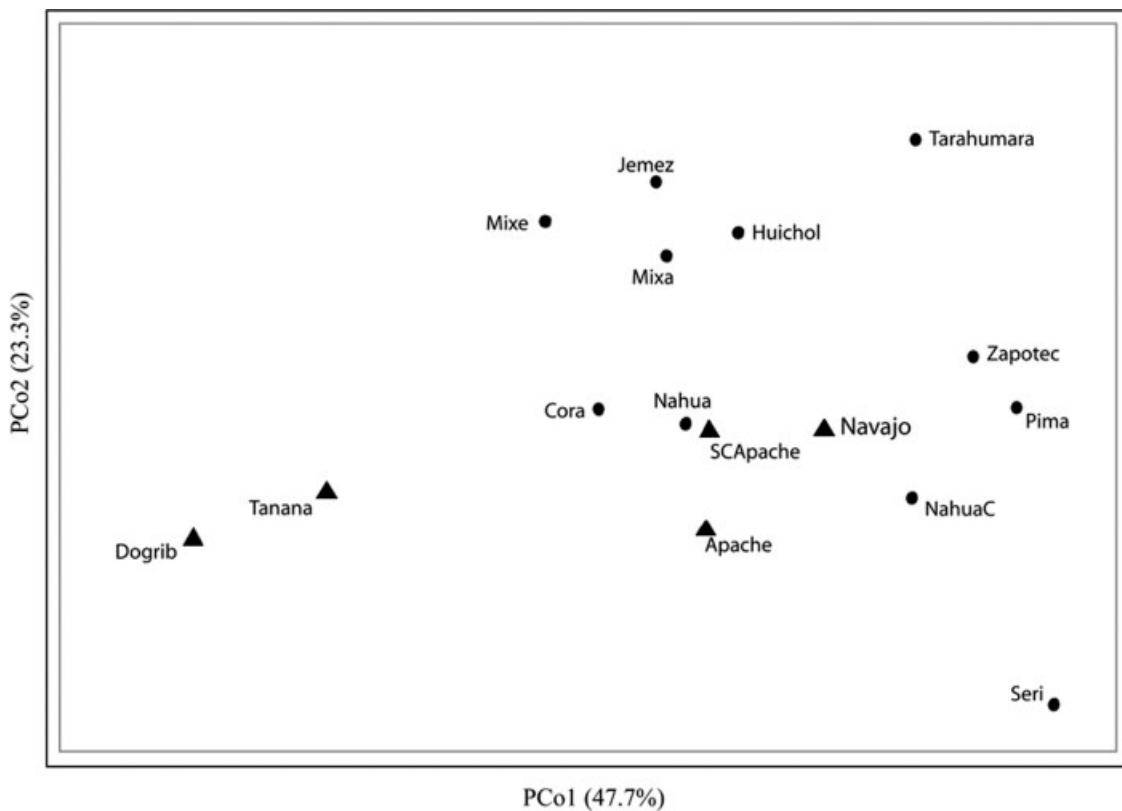


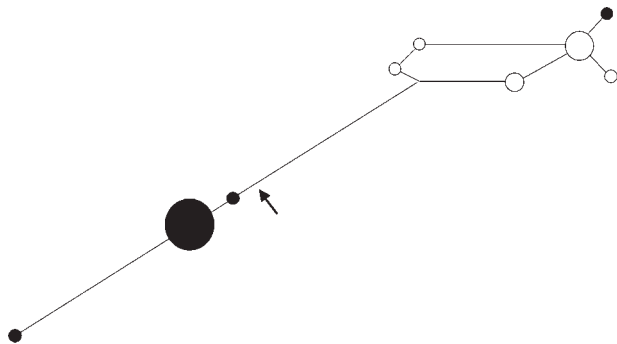
Fig. 4. Principal coordinates analysis of the Haplotype data set based on 8 STRs. Athapaskans are represented by ▲.

(2004). Subarctic Athapaskans are not found in the derived clade in this study or in Zegura et al. (2004).

**DISCUSSION**  
**European admixture**

The influence of European admixture is evidenced by the strong gradient of haplogroup R from Northeastern

to Southwestern North America. This gradient corroborates findings from previous studies of Y chromosome variation in Native Northeastern America (Bolnick et al., 2006; Hammer et al., 2006). The gradient might result from the earlier occurrence of European contact in Northeastern North America, which has provided a longer period of time for admixture to occur. Unlike mtDNA analysis (Smith et al., 1999), Y chromosome analysis shows that Native Americans harbor a high frequency of



**Fig. 5.** Haplogroup C network of Athapaskan speakers based on 8 STRs. Arrow indicates the branch leading to the Apachean subclade. The size of each circle corresponds to the number of individuals belonging to that haplotype. Black circles represent haplotypes identified in Apachean individuals. White circles represent haplotypes identified in Subarctic Athapaskan individuals. The lengths of the lines correspond to the number of mutational differences between haplotypes.

alleles of European ancestry, likely a result of European male introgression following the time of European contact. In addition, it is hypothesized that European contact altered the population structure of indigenous males in other ways as well, since historical records document a high mortality and forced relocations of males beginning shortly after initial European contact (Spicer, 1962). This study provides evidence of the former, and places future studies of Y chromosomes from prehistoric native American populations in a key position to test these hypotheses.

### Southern Athapaskan male population history

Previous mtDNA studies of Athapaskan groups have demonstrated that a high frequency of Apacheans belonged to a specific subclade of haplogroup A (defined as the A2a clade by Tamm et al., 2007), which exhibits transitions at nucleotide positions (nps) 16,192, 16,233, and 16,331 (Malhi et al., 2003). This pattern is consistent with a founder effect and suggests that Apachean maternal lineages may be traced to a small number of females. Similarly, the Y chromosome data analyzed in this study reflect a pattern consistent with a founder effect, suggesting that Apachean paternal lineages also may be traced to a small number of males. Y chromosome haplogroup C is observed at a moderate frequency in the Subarctic Athapaskan groups and at a low frequency in the Navajo and Apache, but is otherwise absent from the Southwest. Nearly all Navajo and Apache Y chromosomes within haplogroup C belong to a specific, well-defined subclade (Zegura et al., 2004). Hence, it is likely that ancestral Subarctic Athapaskan speakers provided the source for Y chromosome haplogroup C as well as the mtDNA A2a subclade in Apachean groups.

However, Apachean groups cluster with other Southwest and Mesoamerican groups in the principal coordinates analysis, rather than with Athapaskans from the Subarctic. This suggests that the majority of non-C Y chromosomes in the Navajo and Apache were contributed by non-Athapaskan populations in the Southwest, which mirrors the presence in the Apachean of mtDNA lineages belonging to haplogroups B and C. It is also possible that the effects of European contact may have

significantly skewed the frequency of haplotypes in the Southwest.

The founder effect exhibited by the Apachean Y chromosome data is compatible with several different scenarios. It is possible that a large group of emigrants began the journey from the Subarctic but only a small proportion of this group was successful in reaching the Southwest. Alternatively, a large group of closely related migrants could have migrated to the Southwest. However, there is no archaeological evidence of a large migration of Athapaskans to the Southwest (Basso, 1983; Cordell, 1997), despite the relatively recent occurrence of the migration and extensive archaeological investigations in the Southwest over the past century. Nor is the scenario of a large number of migrants reaching the Southwest compelling given the mtDNA evidence that Apacheans spread their language and culture predominantly by assimilating native Southwestern individuals. Rather, if a large group of migrants reached the Southwest with a successful culture, one might expect to find evidence of population growth in the data. In light of the mtDNA, archaeological, and linguistic evidence, the scenario of a small number of male and female migrants traveling from the Subarctic to the Southwest and subsequently spreading their language and culture by assimilation of Southwest individuals is the most likely explanation for the patterns observed in the Y chromosome data in this study.

The idea that a very small population of Apachean speakers was responsible for the geographically extensive spread of Apachean languages is in some ways counter-intuitive because it implies a level of language/cultural assimilation often thought to correspond to a situation in which the donor group is viewed as being culturally dominant or superior to the indigenous groups (Spicer, 1962). It is scarcely conceivable that the occupants of the large Puebloan agricultural centers regarded the comparatively meager material and social culture of Apachean hunter-gatherers sufficiently superior to abandon their own ways of life. Nor can the capture of individuals from these well-defended centers have been a major source of Apachean recruitment. The more likely source was very small social units living on the Puebloan fringe, partly supporting themselves by trade with major population centers (Cordell, 1997). These socially and economically marginalized peoples may have assimilated with less difficulty into Apachean society. Disruption within the Pueblo world caused by environmental deterioration and social conflict during the 13th and 14th centuries would have added to this fringe Puebloan population, the likely source of the Southwestern genetic markers that came to dominate Apachean populations. Archaeological investigation of fringe groups and material culture surrounding major Puebloan centers could provide a test of this proposed fringe Puebloan absorption scenario.

### CONCLUSION

The results of this study suggest that the Y chromosome population structure of Native North America was significantly altered by European admixture. European admixture has resulted in a decreasing gradient of haplogroup R from Northeastern to Southwestern North America. The large effect of European admixture suggests that caution should be used when inferring prehistoric



population events in Native North Americans from Y chromosome data alone.

In addition, we identified closely related Y chromosomes among Athapaskans in the Subarctic and the Southwest to the exclusion of non-Athapaskans in the Southwest. Consistent with mtDNA studies of Athapaskan speakers, the Y chromosome analysis identifies a pattern concordant with a founder effect in Apachean groups. Together with archaeological and linguistic evidence, the genetic (Y chromosome and mtDNA) data suggests a scenario of a small number of male and female migrants traveling from the Subarctic to the Southwest and subsequently spreading their language and culture by assimilating members of native Southwestern tribes.

This study provides a clear example of how linguistic and genetic variation were de-coupled and evolved independently in a population as predicted by Boas (1911). It is through the interdisciplinary comparison of linguistic, archaeological, and genetic information that we were

able to infer the processes (e.g. long-distance migration, gene flow, cultural diffusion) that likely resulted in the current distribution of Southern Athapaskan languages. As with this study, additional interdisciplinary efforts will likely provide insight into the biological and cultural evolution of human populations.

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## APPENDIX

TABLE A1. Haplogroup and Haplotype data for individual subjects

Sample ID	Population	Haplogroup	DYS19	DYS390	DYS391	DYS392	DYS393	DYS389-I	DYS389-II	DYS439	Reference
IM022	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM025	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM046	Apache	C	15	23	10	11	13	13	28	11	Zegura et al., 2004
IM049	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM053	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM057	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM079	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM092	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM093	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM095	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM103	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM112	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM116	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
IM123	Apache	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
32	SC Apache	C	15	22	9	11	12	13	30	11	This study
396	SC Apache	C	16	23	10	11	13	13	28	11	This study
AR01	Navajo	C	16	23	10	11	13	13	28	11	Zegura et al., 2004
AK02	Tanana	C	15	23	9	11	12	13	30	11	Zegura et al., 2004
AK14	Tanana	C	15	23	9	11	12	13	na	11	Zegura et al., 2004
AK20	Tanana	C	15	23	9	11	12	13	29	11	Zegura et al., 2004
AK24	Tanana	C	15	23	9	11	12	13	31	11	Zegura et al., 2004
AK28	Tanana	C	15	23	9	11	12	13	29	11	Zegura et al., 2004
11	Dogrib	C	15	23	9	11	12	13	30	11	This study
31	Dogrib	C	15	23	9	11	12	13	30	11	This study
52	Dogrib	C	15	23	9	11	12	13	29	11	This study
59	Dogrib	C	15	23	9	11	12	13	30	11	This study
60	Dogrib	C	15	23	9	11	12	13	30	11	This study
IM026	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM027	Apache	Q	13	23	10	15	13	14	32	10	Zegura et al., 2004
IM028	Apache	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
IM029	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM031	Apache	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
IM032	Apache	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
IM033	Apache	Q	13	24	10	14	14	13	30	11	Zegura et al., 2004
IM035	Apache	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
IM037	Apache	Q	13	22	11	14	13	13	30	12	Zegura et al., 2004
IM038	Apache	Q	13	23	10	14	13	13	30	11	Zegura et al., 2004
IM039	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM040	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM042	Apache	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
IM044	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM045	Apache	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
IM047	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM050	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004

(continued)

TABLE A1. (Continued)

Sample ID	Population	Haplogroup	DYS19	DYS390	DYS391	DYS392	DYS393	DYS389-I	DYS389-II	DYS439	Reference
IM051	Apache	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
IM054	Apache	Q	13	22	10	14	13	13	30	12	Zegura et al., 2004
IM056	Apache	Q	13	24	10	14	13	13	30	12	Zegura et al., 2004
IM058	Apache	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
IM060	Apache	Q	13	23	10	14	13	13	30	11	Zegura et al., 2004
IM064	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM066	Apache	Q	13	24	10	14	12	13	30	12	Zegura et al., 2004
IM067	Apache	Q	13	24	10	16	13	12	28	12	Zegura et al., 2004
IM068	Apache	Q	14	24	10	16	13	12	28	14	Zegura et al., 2004
IM069	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM073	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM077	Apache	Q	13	24	10	14	13	13	30	12	Zegura et al., 2004
IM080	Apache	Q	14	24	9	14	14	13	30	12	Zegura et al., 2004
IM081	Apache	Q	13	23	10	14	14	13	31	11	Zegura et al., 2004
IM089	Apache	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
IM091	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM098	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM101	Apache	Q	13	23	10	15	13	14	32	10	Zegura et al., 2004
IM102	Apache	Q	13	24	10	15	14	13	29	13	Zegura et al., 2004
IM104	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM106	Apache	Q	13	23	10	12	13	12	31	13	Zegura et al., 2004
IM107	Apache	Q	13	23	10	15	13	12	29	12	Zegura et al., 2004
IM109	Apache	Q	13	24	10	14	12	13	30	14	Zegura et al., 2004
IM110	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM118	Apache	Q	13	24	10	15	14	13	30	12	Zegura et al., 2004
IM120	Apache	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
IM122	Apache	Q	13	23	10	14	13	13	30	12	Zegura et al., 2004
IM124	Apache	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
NC001	Apache	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
IM041	Apache	Q	14	25	10	14	13	13	30	11	Zegura et al., 2004
IM043	Apache	Q	13	24	10	14	13	13	30	11	Zegura et al., 2004
IM048	Apache	Q	13	24	10	14	14	13	29	13	Zegura et al., 2004
IM055	Apache	Q	13	24	10	14	14	13	29	13	Zegura et al., 2004
IM083	Apache	Q	13	24	10	14	14	13	29	13	Zegura et al., 2004
IM097	Apache	Q	14	24	10	16	13	13	30	11	Zegura et al., 2004
IM105	Apache	Q	13	23	10	14	13	13	29	12	Zegura et al., 2004
IM113	Apache	Q	13	24	10	14	14	13	29	13	Zegura et al., 2004
IM021	Apache	Q	14	23	10	14	13	13	32	11	Zegura et al., 2004
IM024	Apache	Q	15	23	10	14	13	13	29	11	Zegura et al., 2004
IM036	Apache	Q	13	24	10	16	13	14	30	13	Zegura et al., 2004
IM059	Apache	Q	13	24	10	14	14	13	29	13	Zegura et al., 2004
IM061	Apache	Q	13	24	10	14	14	13	29	13	Zegura et al., 2004
IM065	Apache	Q	13	23	11	16	13	13	29	13	Zegura et al., 2004
IM070	Apache	Q	13	25	10	14	14	13	29	13	Zegura et al., 2004
IM082	Apache	Q	14	23	10	14	13	13	32	11	Zegura et al., 2004
IM084	Apache	Q	13	24	11	15	14	13	30	11	Zegura et al., 2004
IM085	Apache	Q	13	24	10	14	13	12	29	11	Zegura et al., 2004
IM086	Apache	Q	14	25	10	16	13	13	30	11	Zegura et al., 2004
IM087	Apache	Q	14	25	10	16	13	13	30	11	Zegura et al., 2004
IM088	Apache	Q	14	25	10	16	13	13	30	11	Zegura et al., 2004
IM090	Apache	Q	14	25	10	16	13	13	30	11	Zegura et al., 2004
IM094	Apache	Q	14	25	10	16	13	13	30	11	Zegura et al., 2004
IM096	Apache	Q	13	24	10	14	14	13	29	13	Zegura et al., 2004
IM099	Apache	Q	14	23	10	14	13	13	32	11	Zegura et al., 2004
IM108	Apache	Q	14	24	10	16	13	13	30	11	Zegura et al., 2004
IM114	Apache	Q	14	23	10	14	13	13	32	11	Zegura et al., 2004
IM115	Apache	Q	14	24	10	15	13	14	30	13	Zegura et al., 2004
23	SC Apache	Q	13	24	11	14	14	13	31	11	This study
26	SC Apache	Q	13	24	10	15	14	13	29	11	This study
77	SC Apache	Q	13	23	10	14	14	13	30	11	This study
124	SC Apache	Q	13	24	11	16	13	13	30	12	This study
166	SC Apache	Q	14	23	10	14	13	13	30	13	This study
220	SC Apache	Q	13	24	11	16	13	13	30	12	This study
228	SC Apache	Q	13	23	10	14	13	13	31	11	This study
239	SC Apache	Q	13	23	10	14	13	13	30	11	This study
243	SC Apache	Q	13	24	11	14	14	13	31	11	This study
248	SC Apache	Q	13	24	11	14	14	13	30	11	This study
258	SC Apache	Q	13	24	10	14	13	13	30	12	This study
263	SC Apache	Q	13	23	11	16	13	13	29	13	This study
318	SC Apache	Q	13	24	10	14	14	13	29	13	This study

(continued)

TABLE A1. (Continued)

Sample ID	Population	Haplogroup	DYS19	DYS390	DYS391	DYS392	DYS393	DYS389-I	DYS389-II	DYS439	Reference
400	SC Apache	Q	13	24	10	14	14	13	29	13	This study
406	SC Apache	Q	13	23	10	14	13	13	30	11	This study
416	SC Apache	Q	14	25	10	14	14	14	31	11	This study
459	SC Apache	Q	13	24	11	13	14	14	30	11	This study
495	SC Apache	Q	14	23	10	14	13	13	30	13	This study
510	SC Apache	Q	13	23	10	14	13	13	31	11	This study
524	SC Apache	Q	na	23	10	na	13	13	31	11	Zegura et al., 2004
NC2	Navajo	Q	13	23	10	15	13	12	29	13	Zegura et al., 2004
NC5	Navajo	Q	13	23	10	14	13	15	31	13	Zegura et al., 2004
NC6	Navajo	Q	13	25	10	14	12	14	31	13	Zegura et al., 2004
NC13	Navajo	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
NC24	Navajo	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
NC29	Navajo	Q	13	23	10	15	13	14	32	10	Zegura et al., 2004
NC30	Navajo	Q	13	23	10	15	13	14	32	10	Zegura et al., 2004
NC43	Navajo	Q	13	23	10	14	13	15	31	14	Zegura et al., 2004
NC045	Navajo	Q	13	23	10	15	13	14	32	14	Zegura et al., 2004
NC100	Navajo	Q	13	23	10	15	13	14	32	10	Zegura et al., 2004
NC101	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
NC104	Navajo	Q	13	23	10	15	13	12	30	13	Zegura et al., 2004
NC107	Navajo	Q	13	23	10	15	13	12	29	12	Zegura et al., 2004
NC109	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
NC113	Navajo	Q	13	23	10	15	13	12	29	14	Zegura et al., 2004
NC118	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
NC119	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
Nj371	Navajo	Q	13	24	10	16	13	12	28	12	Zegura et al., 2004
Nj373	Navajo	Q	13	23	10	15	13	12	30	12	Zegura et al., 2004
Nj391	Navajo	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
Nj395	Navajo	Q	13	26	10	14	13	13	30	12	Zegura et al., 2004
Nj402	Navajo	Q	13	23	10	14	14	14	30	14	Zegura et al., 2004
Nj414	Navajo	Q	15	23	10	14	14	14	31	11	Zegura et al., 2004
Nj416	Navajo	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
Nj422	Navajo	Q	13	23	10	15	13	12	29	12	Zegura et al., 2004
Nj445	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
Nj473	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
NM09	Navajo	Q	13	23	10	15	13	12	29	12	Zegura et al., 2004
NM11	Navajo	Q	13	23	10	14	13	14	30	11	Zegura et al., 2004
NM13	Navajo	Q	13	24	10	16	13	12	29	12	Zegura et al., 2004
NM14	Navajo	Q	13	23	10	15	13	14	32	10	Zegura et al., 2004
NM15	Navajo	Q	13	23	10	15	13	12	29	12	Zegura et al., 2004
NM16	Navajo	Q	13	24	10	16	13	12	28	12	Zegura et al., 2004
NM18	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
NM19	Navajo	Q	13	24	10	16	13	12	28	12	Zegura et al., 2004
NM20	Navajo	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
NM22	Navajo	Q	13	23	10	15	13	14	31	10	Zegura et al., 2004
NM24	Navajo	Q	13	24	10	16	13	12	29	12	Zegura et al., 2004
NM25	Navajo	Q	13	23	10	14	13	14	30	14	Zegura et al., 2004
NC105	Navajo	Q	15	23	10	14	13	14	32	11	Zegura et al., 2004
NC124	Navajo	Q	14	25	10	14	13	13	29	11	Zegura et al., 2004
NM04	Navajo	Q	14	25	10	16	13	13	30	11	Zegura et al., 2004
NM05	Navajo	Q	14	24	10	15	13	13	29	12	Zegura et al., 2004
NM06	Navajo	Q	13	24	10	14	13	13	28	11	Zegura et al., 2004
NAV01	Navajo	Q	13	24	10	14	13	13	30	11	Zegura et al., 2004
NAV10	Navajo	Q	14	25	10	14	13	13	29	11	Zegura et al., 2004
NC011	Navajo	Q	13	23	12	16	13	13	29	13	Zegura et al., 2004
NC041	Navajo	Q	14	23	10	14	13	13	31	11	Zegura et al., 2004
NC042	Navajo	Q	14	25	10	14	13	13	29	11	Zegura et al., 2004
NC044	Navajo	Q	13	24	10	14	13	13	30	11	Zegura et al., 2004
NC102	Navajo	Q	14	25	10	14	13	13	29	12	Zegura et al., 2004
NC103	Navajo	Q	13	24	10	14	13	13	30	11	Zegura et al., 2004
NC106	Navajo	Q	14	23	10	14	13	14	32	11	Zegura et al., 2004
NC110	Navajo	Q	13	24	10	14	13	13	28	11	Zegura et al., 2004
NC111	Navajo	Q	13	24	10	14	13	13	30	11	Zegura et al., 2004
NC112	Navajo	Q	14	25	10	14	13	13	29	11	Zegura et al., 2004
NC114	Navajo	Q	14	23	10	14	13	13	31	11	Zegura et al., 2004
NC115	Navajo	Q	14	25	10	14	13	13	30	11	Zegura et al., 2004
NC120B	Navajo	Q	13	24	10	14	13	13	28	11	Zegura et al., 2004
NC123	Navajo	Q	13	23	10	14	13	13	31	10	Zegura et al., 2004
Nj439	Navajo	Q	13	24	10	14	13	13	30	11	Zegura et al., 2004
Nj446	Navajo	Q	13	24	11	16	13	12	29	12	Zegura et al., 2004
Nj481	Navajo	Q	14	25	10	14	13	13	30	12	Zegura et al., 2004

(continued)

TABLE A1. (Continued)

Sample ID	Population	Haplogroup	DYS19	DYS390	DYS391	DYS392	DYS393	DYS389-I	DYS389-II	DYS439	Reference
Nj495	Navajo	Q	13	23	10	14	13	13	30	11	Zegura et al., 2004
NM01	Navajo	Q	15	23	10	14	13	13	30	11	Zegura et al., 2004
NM03	Navajo	Q	13	24	10	14	13	13	30	11	Zegura et al., 2004
NM08	Navajo	Q	14	23	10	14	13	14	32	11	Zegura et al., 2004
NM10	Navajo	Q	13	22	11	14	13	14	30	12	Zegura et al., 2004
NM12	Navajo	Q	14	23	10	14	13	14	33	11	Zegura et al., 2004
NM23	Navajo	Q	13	23	11	16	13	13	29	12	Zegura et al., 2004
AK18	Tanana	Q	13	24	10	14	12	13	30	14	Zegura et al., 2004
AK31	Tanana	Q	13	24	10	14	14	14	31	12	Zegura et al., 2004
AK32	Tanana	Q	13	23	10	14	13	13	31	11	Zegura et al., 2004
AK33	Tanana	Q	13	23	10	14	13	13	32	11	Zegura et al., 2004
AK36	Tanana	Q	13	22	10	14	13	13	30	12	Zegura et al., 2004
1	Dogrib	Q	13	23	10	14	13	13	30	11	This study
8	Dogrib	Q	13	23	10	14	13	13	31	11	This study
54	Dogrib	Q	13	23	10	14	13	13	31	11	This study
57	Dogrib	Q	13	23	10	14	13	14	32	11	This study
Seri 59	Seri	Q	13	24	9	15	13	12	31	10	This study
Seri 58	Seri	Q	13	24	9	15	13	13	31	10	This study
Seri 9	Seri	Q	13	24	9	15	13	13	31	10	This study
Seri 102	Seri	Q	13	24	9	15	13	13	31	10	This study
Seri 57	Seri	Q	13	24	10	15	13	12	28	12	This study
Seri 23	Seri	Q	13	24	10	16	13	12	28	12	This study
Seri 29	Seri	Q	13	24	10	16	13	12	28	12	This study
Seri 40	Seri	Q	13	24	10	16	13	12	28	12	This study
Seri 79	Seri	Q	13	24	10	16	13	12	28	12	This study
Seri 86	Seri	Q	13	24	10	16	13	12	28	12	This study
Seri 36	Seri	Q	13	24	10	16	13	13	30	12	This study
Seri41	Seri	Q	13	24	10	14	13	13	30	12	This study

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