

Ancient Mitochondrial DNA Evidence for Prehistoric Population Movement: The Numic Expansion

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ABSTRACT The mitochondrial DNA of modern Native Americans has been shown to fall into one of at least five haplogroups (A, B, C, D, or X) whose frequencies differ among tribal groups. The frequencies of these five haplogroups in a collection of ancient individuals from Western Nevada dating to between approximately 350–9,200 years BP were determined. These data were used to test the hypothesis, supported by archaeological and linguistic data, that the current inhabitants of the Great Basin, the Numic speakers, are recent immigrants into the area who replaced

the previous non-Numic inhabitants. The frequency distributions of haplogroups in the ancient and modern Native Americans differed significantly, suggesting that there is a genetic discontinuity between the ancient inhabitants and the modern Numic speakers, providing further support for the Recent Numic Expansion hypothesis. The distribution of mitochondrial haplogroups of the ancient inhabitants of the Great Basin is most similar to those of some of the modern Native American inhabitants of California. *Am J Phys Anthropol* 115:1–12, 2001. © 2001 Wiley-Liss, Inc.

A long-debated question regarding Great Basin cultural history concerns the prehistoric movement of Native Americans into and within this region. Currently, Numic-speaking Native Americans inhabit most of the Great Basin (Miller, 1986).

NUMIC EXPANSION HYPOTHESIS

In 1958, Lamb used glottochronology to place the divergence of the Numic family of languages at approximately 1,000 years ago. Following Steward (1940), Lamb (1958) suggested that Numic speakers expanded into the Great Basin from a proto-Numic homeland in the southwestern Great Basin, perhaps Death Valley (as this was the area of highest linguistic diversity of Numic languages; Fig. 1). This scenario has since received support from both archaeologists and linguists. Many archaeologists see evidence, in the form of shifts in technology (e.g., point types, and basketry and pottery styles) and residence patterns, for a population replacement in the Great Basin within the last 1,000 years, accompanied by a change in subsistence strategy (Grosscup, 1960; Bettinger and Baumhoff, 1982; Sutton, 1991; Young and Bettinger, 1992; Adovasio and Pedler, 1994; Bettinger, 1994; Janetski, 1994; Delacorte, 1995). They also find evidence supporting a Numic homeland to the southwest of the Great Basin (e.g., Owens Valley). Linguists have also supported the hypothesis of an expansion of the Numic-speaking peoples northeast into the area at this time. They believe that lexicostatistics, the distribution of modern Numic languages, linguistic borrowing, and lexical analysis of floral and faunal vocab-

ulary and of place names support this hypothesis (Miller et al., 1971; Fowler, 1972; Nichols, 1981; Miller, 1986). The ethnic affiliation of the previous, presumably non-Numic, inhabitants is unknown, and all of the major Native American groups of the area have at various times been suggested as descendants of these pre-Numic inhabitants (Hopkins, 1965; D'Azevedo et al., 1966; Fowler, 1977; Jorgensen, 1980; Moratto, 1984).

However, both linguists and archaeologists have suggested alternative hypotheses. Several archaeologists have proposed that the Numic presence in the Great Basin is quite ancient. They see little evidence in the archaeological record for a discontinuity representing a population replacement at any time in the past several thousand years, or interpret such evidence as support not for a population movement but for local adaptation to increasing population density and environmental change (Swanson, 1962; Elston, 1982; Aikens and Witherspoon, 1986; Raven, 1994). Some linguists also agree that a long history in the Great Basin is compatible with the modern distribution of Numic languages (Goss, 1977; Crapo and Spykerman, 1979). It is apparent that the spread of genes, language, and material culture can

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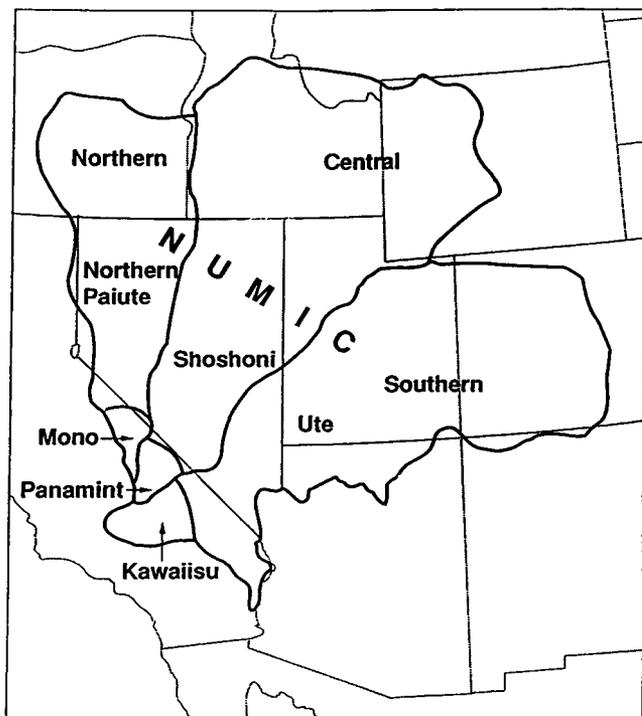


Fig. 1. Distribution of modern Numic languages at contact. After Madsen and Rhode (1994).

occur at disparate times and rates and by different routes.

NATIVE AMERICAN MITOCHONDRIAL DNA HAPLOGROUPS

Mitochondrial DNA (mtDNA) extracted from prehistoric skeletal material provides another potential source of evidence regarding prehistoric population movement in the Great Basin. Recent studies have shown that certain mtDNA mutations characterize at least five distinct founding matrilineal haplogroups A, B, C, D, and X to which most modern Native Americans belong (Schurr et al., 1990; Torroni et al., 1992; Horai et al., 1993; Scozzari et al., 1997; Brown et al., 1998; Stone and Stoneking, 1998). These haplogroups are minimally defined by four restriction fragment length polymorphisms and the presence or absence of an intergenic 9-bp deletion (Table 1), and their frequencies vary significantly among modern Native American groups (e.g., Merriwether et al., 1994, 1996; Lorenz and Smith,

1996). In fact, some tribes completely lack one or more of the lineages (Lorenz and Smith, 1996).

This variation in the frequency distribution of the five haplogroups allows us to test hypotheses of relatedness between tribes, and also ancestor-descendant relationships between ancient and modern populations. Groups that are closely genetically related should exhibit similar frequencies of the five haplogroups, while groups with very different frequencies are probably not closely related to each other. Of course, this inference is based on the assumption that the frequencies of haplogroups in modern tribal groups are similar to those of their ancestors. Major genetic bottlenecks might have accompanied population declines associated with European contact with North American tribes, and genetic drift in small populations might have resulted in significant changes in haplogroup frequencies.

However, contrary to expectations, there is limited evidence to support the assumption that the frequencies of the mitochondrial haplogroups did not change significantly due to genetic drift. First, the haplogroup frequency distribution of different tribes thought to be closely related, such as the Yuman-speaking tribes in the southwest and Baja, are often very similar (Lorenz and Smith, 1996; Smith et al., 1999). Second, comparisons of the frequencies of the four most common Native American haplogroups (A, B, C, and D) in the ancient populations of Norris Farms in Illinois (dated to AD 1300; Stone and Stoneking, 1993, 1998), the ancient Fremont from Utah (dated to 1700–750 yBP; Parr et al., 1996), and the ancient Anasazi from Utah and Arizona (dated to between 500–2000 years BP; Carlyle personal communication) to those of their probable modern descendants are consistent with ancestor/descendant relationships, and hence the absence of a large degree of genetic drift (Lorenz and Smith, 1994, 1996; Kaestle, 1995, 1998; Kaestle et al., 1999). In fact, a recent survey of mitochondrial haplogroup frequencies in modern and ancient Native North Americans found evidence that “differentiation of regional patterns of mtDNA lineage variation occurred early in North American prehistory (much more than 2,000 years B.P.), has remained relatively stable since its origin, and was little influenced by the disruptions hypothesized for other genetic systems” (O’Rourke et al., 2000, p. 15). Nonetheless, the issue of possible confounding ef-

TABLE 1. Markers identifying the five common mitochondrial haplogroups found among modern Native Americans¹

Haplogroup	HaeIII np 663	9-bp deletion	HindII np 13259	AluI np 13262	AluI np 5176	DdeI np 1715
A	+	–	+	–	+	+
B	–	+	+	–	+	+
C	–	–	–	+	+	+
D	–	–	+	–	–	+
X	–	–	+	–	+	–
Other	–	–	+	–	+	+

¹ np, nucleotide position; +, presence of a restriction site; –, absence of a restriction site.

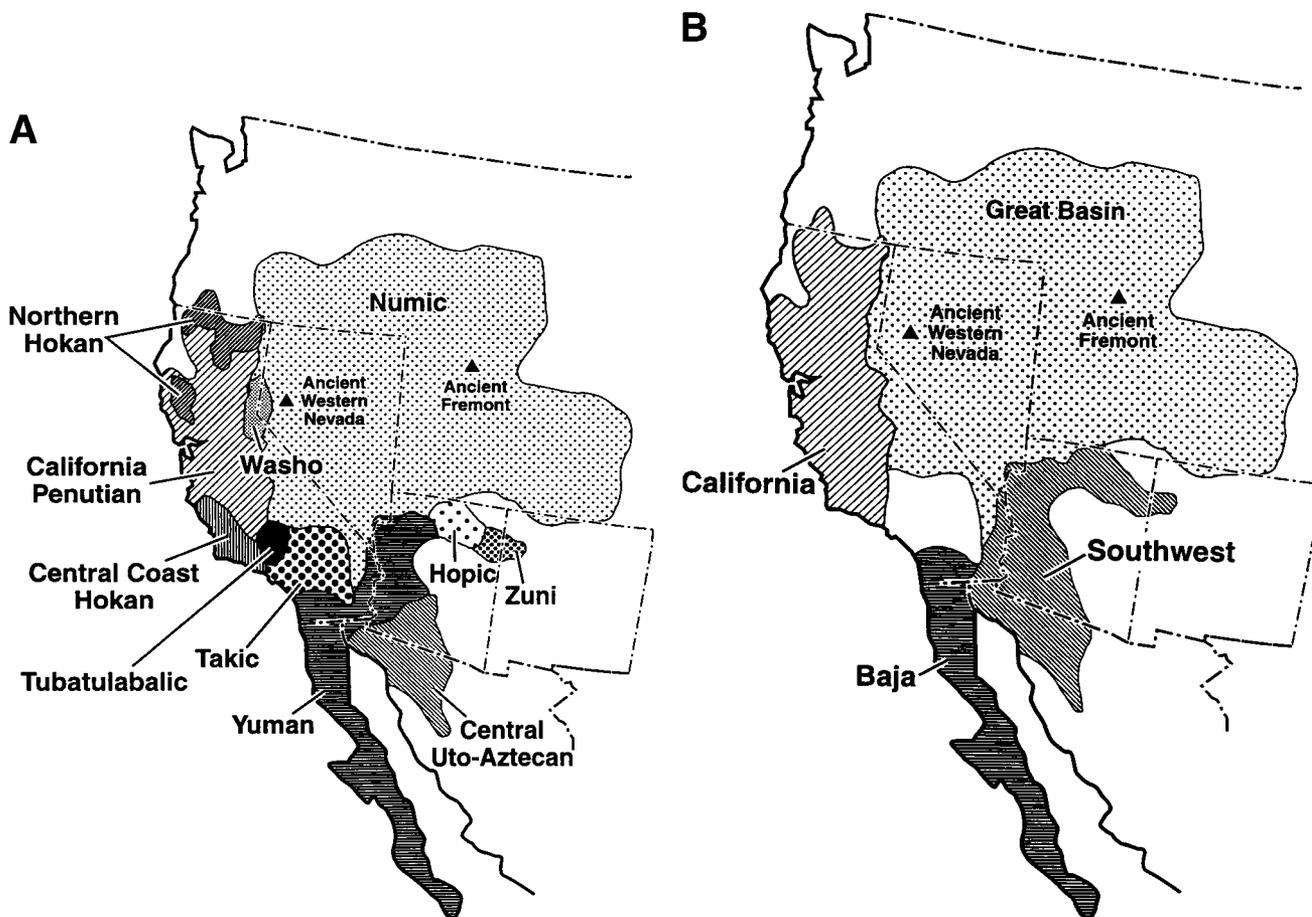


Fig. 2. Distribution of modern groups as defined for this study. A: Language groups. B: Geographic groups.

facts of genetic drift on our comparisons will be revisited below.

Thus, comparisons of distributions of haplogroups in modern and prehistoric populations in at least some regions can be used to test hypotheses about ancestor/descendant relationships (e.g., Hagelberg and Clegg, 1993; Kaestle, 1995, 1997; O'Rourke et al., 1996; Parr et al., 1996). For the reasons stated above, it seems unlikely that the ancient population in Western Nevada is ancestral to any modern group from which its frequencies of the five mtDNA haplogroups differ significantly. Therefore, if the recent Numic expansion hypothesis is correct, a genetic discontinuity between the ancient Native Americans in the Great Basin, who predate the time of Numic expansion, and the modern local inhabitants, who are descendants of the Numic immigrants, should be apparent in the frequencies of these five haplogroups. If, on the other hand, the modern Numic groups of the Great Basin have inhabited the region for millennia, the frequencies of the five haplogroups in the ancient Great Basin groups should be similar to those seen in the modern inhabitants.

POPULATIONS SAMPLED

Data for the modern Native American groups studied were taken from the literature (Schurr et

al., 1990; Torroni et al., 1992; Merriwether et al., 1995; Lorenz and Smith, 1996; Kaestle, 1997; Smith et al., 1999). Because the relationship among genes, language, and geography is often complicated (Campbell, 1986; Weiss and Woolford, 1986; Ruvolo, 1987; Lorenz and Smith, 1994), the modern samples were sorted into both language groups and geographic regions for estimating and comparing frequencies of the four most common mtDNA haplogroups. The language groups compared (Jorgensen, 1980; Greenberg, 1987; Campbell, 1997) consist of eight subsets of three larger groups: Penutian (California Penutian and Zuni), Hokan (Northern Hokan, Yuman, Washo, and Central Coast Hokan), and Uto-Aztecan (Northern Uto-Aztecan, which includes the Numic, Tubatulabalic, Takic, and Hopic speakers, and Central Uto-Aztecan, all Piman; Fig. 2A), although the validity of the first two of these large groups is very controversial. The geographic regions (Fig. 2B) include four of those defined by Driver (1961): California, Baja, the Great Basin, and the Southwest (Driver's "Oasis"). The languages and geographic affiliations, and mtDNA haplogroup frequencies of the tribal groups sampled for this study, are given in Table 2.

TABLE 2. Frequencies of five common Native American haplogroups in modern language and geographic groups and in ancient groups¹

Group	Subgroup	Sample size ²	% A	% B	% C	% D	% X
Penutian	California Penutian	16	12	44	0	44	0
	Zuni	20	20	70	10	0	0
Hokan	Northern Hokan	6	0	33	17	33	17
	Yuman	80	4	62	34	0	0
	Washo	28	0	53	36	11	0
	Central Coast Hokan	11	46	18	9	27	0
Uto-Aztecan	Northern Uto-Aztecan	116	0	42	15	43	0
	Central Uto-Aztecan	37	5	57	38	0	0
Great Basin		127	0	44	17	39	0
California		37	19	35	8	35	3
Southwest		98	8	61	31	0	0
Baja		43	0	44	17	39	0
Ancient	Fremont	30	0	83	10	7	0
	Stillwater Marsh	21	5	38	0	57	0
	Pyramid Lake	18	11	33	0	56	0
	West. Nev. Combined	39	8	36	0	56	0

¹ Data on frequency of haplogroup X are from Smith et al. (1999).

² Tribal groups and number of individuals from each tribe included in each language group, with geographic assignments of each tribal group in parentheses (NI, not included), are as follows: California Penutian includes 5 Costanoan/Ohlone (CA), 1 Miwok (CA), 1 Maidu (CA), and 9 Yokuts (CA) individuals; Zuni includes 20 Zuni (SW) individuals; Northern Hokan includes 1 Karok (CA), 1 Achumawi (CA), and 4 Pomo (CA) individuals; Yuman includes 5 Walapai (SW), 5 Havasupai (SW), 5 Yavapai (SW), 8 Paipai (BJ), 19 Quechan (SW), 3 Mojave (SW), 16 Kumiai (BJ), 3 Cocopa (BJ), 3 Kiliwa (BJ), and 13 Cochimi (BJ) individuals; Washo includes 28 Washo (GB) individuals; Central Coast Hokan includes 2 Salinan (CA) and 9 Chumash (CA) individuals; Northern Uto-Aztecan includes 98 Northern Paiute/Shoshone (BG), 1 Kawaiisu (GB), 4 Tubatulabal (CA), 4 Kitanemuk (NI), 1 Gabrieleno (NI), 1 Luiseno (NI), 1 Juaneno (NI), 1 Fernandeno (NI), 1 Cahuilla (NI), and 4 Hopi (SW) individuals; Central Uto-Aztecan includes 37 Pima (SW) individuals. CA, California; SW, Southwest; BJ, Baja; GB, Great Britain.

Bone samples from 21 prehistoric individuals from the Pyramid Lake region and 27 prehistoric individuals from the Stillwater Marsh region of Western Nevada were obtained from the Nevada State Museum. All of the samples from Pyramid Lake have been ¹⁴C dated to between 860 ± 75 and 9200 ± 60 yBP (Dansie, 1997, and personal communication); some of those from Stillwater Marsh, and organic remains associated with them, have been ¹⁴C dated to between 290 ± 80 and 3290 ± 90 yBP (Raven and Elston, 1988; Kelly, 1995; Larsen, 1995). Projectile points recovered at Stillwater Marsh also indicate a date between 3250–650 yBP (Kelly, 1995; Larsen, 1995). Therefore, the individuals sampled for this study date to a time period that almost completely precedes the hypothesized date of the Numic expansion. The osteological homogeneity of the Stillwater Marsh skeletal series (Brooks et al., 1988; see also Kelly, 1995) and the geographical proximity of the Stillwater Marsh and Pyramid Lake sites (within 40 miles of each other) suggest that these two ancient samples can be regarded as members of a single population for the purposes of a genetic analysis. A prehistoric Fremont sample of 30 individuals from the Great Salt Lake wetlands, dating to between 700–1750 yBP (Parr et al., 1996), was also included in the analysis for comparison. Since the haplogroup frequency distribution of this sample was found not to differ from that of the prehistoric Anasazi populations of Grand Gulch and Canyon del Muerto in southeastern Utah and northeastern Arizona, respectively (Carlyle, personal communication), only the Fremont sample was included in our comparisons.

METHODS

DNA extraction and amplification

Extraction and amplification setup were performed in a laboratory physically separate from that in which amplification took place, using an ultraviolet (UV)-irradiated, bleach-sterilized glovebox with dedicated equipment, and DNA-free disposables. Precautions cited by Kelman and Kelman (1999) designed to prevent contamination of the ancient samples were followed as closely as possible. Bone samples from the Stillwater Marsh individuals had been previously processed (ground to a powder and deproteinized in a buffered saline solution) for a study of albumin polymorphism (Smith et al., 1995). Bone samples from the Pyramid Lake individuals were intact fragments. To eliminate any minor surface contamination, the bone fragments from the Pyramid Lake individuals were cross-linked for 10 min on each side with UV light (254 nm), and in some cases soaked for approximately 5 min in a 5% bleach solution. These samples were then ground to a powder in bleach-sterilized, UV-irradiated electric coffee grinders. Approximately 0.25 g of powdered bone from the Pyramid Lake individuals or 0.25 g of deproteinized bone residue from the Stillwater Marsh individuals were incubated with slight agitation for 72–96 h at 4°C in 0.5 M EDTA, pH 8.0, changing the EDTA solution every 24 h. The decalcified bone powder was then incubated overnight at 55°C in a proteinase K buffer (50 mM Tris, pH 8.0, 1 mM CaCl₂, 1 mM DTT, 5% Tween-20, and 1 mg/ml proteinase K). Samples were then successively extracted with phenol, phenol-chloroform (1:1), and

chisam (chloroform:isoamyl alcohol, 24:1), concentrated to approximately 50 μ l with Centricon[®] 100 microconcentrators (Amicon), washed twice with Tris-EDTA, pH 8.0 (TE) or ddH₂O, and then re-concentrated to 50–100 μ l. Negative controls were also processed at each step of the extraction protocol, and multiple independent extracts were performed for each sample.

A master PCR mix containing all reagents (0.6 mM primers, 1 \times manufacturer's buffer, ddH₂O, 1 mg/ml BSA, 200 nM dNTPs) except the Taq polymerase and the ancient DNA template was UV cross-linked for 10 min to eliminate any exogenous DNA contamination. Coordinates for primers used to amplify the fragment containing the restriction site (or 9-bp deletion) characteristic of each haplogroup indicated are as follows: A, 591–611 and 765–743 (Stone and Stoneking, 1993) or 610–635 and 698–677 (Handt et al., 1996); B, 8249–8267 and 8352–8332 (Parr et al., 1996) or 8195–8215 and 8316–8297 (Wrischnik et al., 1987); C, 13237–13256 and 13419–13397 (Parr et al., 1996) or 13236–13257 and 13310–13290 (Handt et al., 1996); D, 5099–5120 and 5246–5229 (Parr et al., 1996) or 5106–5127 and 5211–5190 (Handt et al., 1996); X, 1651–1670 and 1793–1776 (designed by F.A.K. using Amplify 1.2; Engels, 1992); and I, 9911–9932 and 10107–10088 (Torroni et al., 1996). The equivalents of "hot start" amplifications were performed in 25- μ l volumes using 3–5 μ l ancient DNA extract and 1.5 units of Amplitaq Gold DNA polymerase (Perkin Elmer) or Platinum Taq DNA polymerase (Gibco BRL). The amplifications were subjected to an initial 4–11-min denaturation step at 95°C, then 35–45 cycles in which reactions were denatured at 95°C for 15 s, annealed at 49–59°C for 15 s, and extended at 72°C for 25 s, followed by a final extension step of 3 min at 72°C. The negative controls cited above were included in each amplification, and multiple extractions were analyzed for each sample.

Haplogroup assignment

Five to ten microliters of amplification product containing the restriction site gain that characterizes haplogroup A and the restriction site losses that characterize haplogroups C, D, and X were digested overnight at 37°C with 5 units *Hae*III, *Hind*II/*Alu*I, and *Alu*I and *Dde*I, respectively, according to manufacturers' recommendations. Restriction fragments and the presence/absence of the 9-bp deletion were resolved on 6% polyacrylamide gels, stained with ethidium bromide, visualized, and then photographed, on a UV transilluminator using an IS2000 imaging system (Alpha Innotech).

Statistical analysis

The frequencies of the five haplogroups in the modern and ancient groups were compared, using a chi-square test for homogeneity, to test the null hypothesis that the two samples were drawn from the

same population (Thomas, 1976). The modern Northern Hokan language group was excluded from this comparison due to its small sample size ($N = 6$). Due to sampling error, it is possible that a sample size as small as 39 individuals provides an inaccurate estimate of the frequencies of the five haplogroups in the ancient inhabitants of Western Nevada, even if those inhabitants were both ancestral and genetically identical to the modern inhabitants. To test this hypothesis, simulations were run to produce 10,000 replicate samples of 39 individuals, each drawn randomly from the pool of modern individuals in the Northern Uto-Aztecan and Numic language groups and the Great Basin geographic group, each with its empirically observed frequency distribution of mtDNA haplogroups. The haplogroup frequency distribution of each of these 10,000 samples was compared to that of the original modern sample, and the (10,000) values of chi-square (for homogeneity) were calculated (program written by P.A. Vick, 1998, personal communication). The actual observed chi-square values for comparisons between the ancient and the modern samples were then compared to the distribution of simulated chi-square values to assess the probability of drawing such an atypical sample of 39 individuals from the (modern) population under consideration.

Phylogenetic analysis

Excluding haplogroup X, which was absent in all the modern samples except one Northern Hokan individual and unconfirmed in the ancient samples, the frequencies of the Native American haplogroups can be treated as four alleles at a single (the mtDNA) locus. Genetic distances between the populations studied were calculated from the frequencies of these haplogroups in each population (Cavalli-Sforza and Edwards, 1967; Nei, 1972). These genetic distances, unlike the chi-square test for homogeneity, are independent of sample size (although the small sample sizes for some modern groups in this study might have resulted in biased haplogroup frequency distributions in some cases). The GENDIST program from the PHYLIP 3.572c software package (Felsenstein, 1998) was used to estimate chord distances (Cavalli-Sforza and Edwards, 1967) between the ancient and modern groups. Phylogenetic trees were produced from these data using the unweighted pair group method of analysis (UPGMA), Neighbor-Joining, and Fitch-Margoliash methods (with randomized input order) of the FITCH and NEIGHBOR programs, and were drawn using the DRAWTREE program from the PHYLIP 3.572c software package (Felsenstein, 1998).

RESULTS

Nineteen of the 21 ancient Pyramid Lake samples could be assigned to one of the five modern Native American haplogroups (Table 3). One sample (NSM25) does not belong to any of these haplo-

TABLE 3. Mitochondrial haplogroup assignments of ancient individuals from Pyramid Lake sites (NSM) and Stillwater Marsh sites (SW)¹

Laboratory ID	Museum ID	A (<i>Hae</i> III)	B (9-bp del)	C (<i>Hinc</i> II)	C (<i>Alu</i> I)	C (com- bined)	D (<i>Alu</i> I)	X (<i>Dde</i> I)	I (<i>Alu</i> I)	Haplo- group	Date (yBP)
NSM1	Ahur 2016	-(2), +(2)	-(2)	+(1)	-(3)	(4)	+(2), -(2)			A/D	3725 ± 105
NSM2	Ahur 2017	-(2)	+(2)	+(1)	-(1)	(2)	+(2)			B	860 ± 75
NSM6	Ahur 830	-(2)	-(2)	+(1)	-(1)	(2)	-(2)			D	2935 ± 140
NSM7	Ahur 869	-(3)	-(2)	+(2)	-(1)	(3)	-(3)			D	4745 ± 115
NSM8	Ahur 870	-(2)	-(2)	+(2)		(2)	-(2)			D	2735 ± 100
NSM9	Ahur 871	-(2)	-(2)	+(2)		(2)	-(2)			D	2434 ± 85
NSM10	26DO524 b1	-(2)	-(2)	+(1)	-(1)	(2)	-(2)			D	1620 ± 50
NSM11	26DO524 b2	-(2)	-(2)	+(2)		(2)	-(2)			D	1490 ± 50
NSM12	Ahur 862	-(3)	+(2)	+(3)	-(2)	(3)	+(3)			B	1820 ± 180
NSM13	Ahur 2007	-(2)	+(2)	+(2)		(2)	+(2)			B	1360 ± 80
NSM14	Ahur 2011	+(2)	-(2)	+(2)		(2)	+(3)			A	1520 ± 90
NSM15	Ahur 2022	-(2)	+(2)	+(2)		(2)	+(2)			B	5905 ± 125
NSM16	Ahur 2023	-(2)	-(2)	-(1)	+(1)	(2)	+(2)			C	9200 ± 60
NSM17	Ahur 840	-(3)	-(3)		-(3)	(3)	-(3)			D	3630 ± 60
NSM18	Ahur 846	-(2)	-(2)		-(2)	(2)	-(2)			D	2430 ± 100
NSM19	Ahur 853	-(3)	-(2)	+(1)	-(3)	(4)	-(3)			D	3165 ± 370
NSM20	Ahur 778	-(2)	-(2)		-(2)	(2)	-(2)			D	1620 ± 90
NSM21	Ahur 779	-(3)	+(3)		-(3)	(3)	+(3)			B	1950 ± 100
NSM22	Ahur 844	-(2)	+(2)	+(1)	-(1)	(2)	+(2)			B	3540 ± 95
NSM23	Ahur 845	+(2)	-(2)	+(1)	-(1)	(2)	+(2)			A	4504 ± 105
NSM25	Ahur 866	-(3)	-(3)	+(1)	-(1)	(2)	+(3)	+(2)		other	4435 ± 110
SW1	(26CH1043) 5-2-4(a)	-(2)	-(3)	+(1)	-(2)	(3)	-(2)			D	
SW2	(1043) 37-3-30(a)	-(2)	-(3)		-(2)	(2)	-(2)			D	
SW3	(1043) 61-1-18	-(2)	-(2)	+(1)	-(1)	(2)	-(4)			D	
SW4	(1044) 1-2-32(a)	-(3)	+(3)	+(1)	-(1)	(2)	+(3)			B	
SW5	(1044) 2-3-30(b)	-(2)	-(2)	+(1)	-(2)	(2)	-(4)			D	1140 ± 80
SW6	(1045) 1-2-15(a)	-(2)	-(3)	+(1)	-(1)	(2)	-(4)			D	
SW7	(1046) 2A-3-29(a)	-(2)	-(2)		-(2)	(2)	-(2)			D	
SW8	(1046) 2B-3-27(a)										
SW9	(1046) 9-11-31(b)	-(2)	-(3)	+(1)	-(2)	(2)	+(2), -(1)	-(3)	-(3)	D/X	
SW10	(1047) 1-1-13	-(2)	+(2)		-(2)	(2)	+(3)			B	
SW11	(1050) 3-5-31(b)	-(2)	+(2)	+(1)	-(1)	(2)	+(2)			B	290 ± 80
SW12	(1054) 1-3-26(b)	-(2)	-(4)	+(1)	-(1)	(2)	-(3)	+(6)	-(3)	D	
SW13	(1055) 1-4-9(b)	-(2)	-(3)		-(2)	(2)	-(3)			D	1860 ± 70
SW14	(1058) 12-10-(a)	-(2)	-(2)	+(1)	-(1)	(2)	-(3)	+(1)		D	
SW15	(1062) 1-2-30(a)	-(2)	+(2)	+(1)	-(1)	(2)	+(2)			B	1100 ± 120
SW16	(1063) 20-2-16	-(2)	+(2)	+(1)	-(1)	(2)	+(2)			B	
SW17	(1064) 1-2-19	+(2)	-(3)		-(3)	(3)	+(3)			A	
SW18	(1070) 3-3-31	-(2)	-(2)		-(3)	(3)	-(3)			D	
SW19	(1070) 4-3-42	-(2)	+(3)		-(2)	(2)	+(3)			B	660 ± 30
SW20	(1158) 1-1-13	-(3)	-(2)		-(2)	(2)	+(3)	-(2), +(1)	-(2)	X/other	
SW21	(1159) 4-1-32(b)	-(2)	-(3), +(1)		-(2)	(2)	+(3)	+(3)		B/other	1080 ± 50
SW22	(1159) 6-1-29	-(3)	+(2)		-(3)	(3)	+(2)			B	
SW23	(1159) 7-1-31(c)	-(2)	-(2)		-(3)	(3)	-(3)			D	
SW24	(1159) 200	-(2)					+(1)				2265 ± 70
SW25	L53										
SW26	(1160) 2-10-1	-(2)	+(2)		-(2)	(2)	+(3)	+(1)		B	
SW27	L72-200	-(2)	-(1)		-(2)	(2)	-(2)			D	820 ± 70

¹ Numbers in parentheses indicate number of ancient DNA extracts from an individual giving those results.

groups, and could represent either a sixth Native American haplogroup, a recent mutation causing the loss of the restriction site used to identify its true haplogroup, or contamination of the bone sample. The remaining sample (NSM1) did not amplify well and could not be placed unambiguously into one haplogroup; both samples were excluded from the analysis. The only sample possessing the C haplogroup markers was also excluded from the analysis because it is more than 3,000 years older than any of the other samples studied. Of the 18 remaining samples from Pyramid Lake whose haplogroups were identified, 2 (11.1%) were A, 6 (33.3%) were B, and

10 (55.6%) were D (see Table 2). These haplogroup assignments were confirmed in preliminary analyses of sequencing data from the first hypervariable segment of the mitochondrial control region (Kaestle and Smith, unpublished data). The dates for the oldest representative of each of these three haplogroups fell between 4500–6000 yBP, and the haplogroup membership (with the exception of the single sample assigned to haplogroup C, dated at 9200 yBP, that was eliminated from statistical comparisons) appears to be uncorrelated with date of samples.

Twenty-one of the 27 ancient Stillwater Marsh samples could be assigned to one of the modern

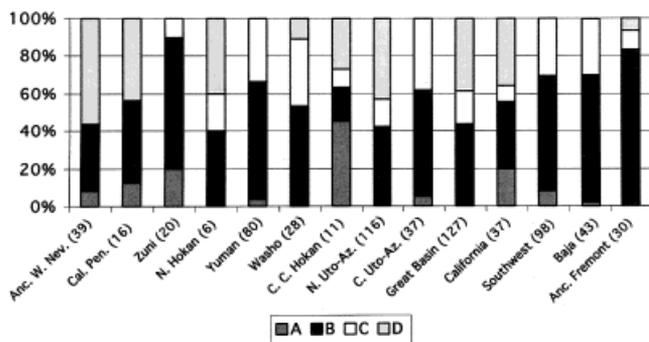


Fig. 3. Histogram of frequencies of the four most common Native American haplogroups in ancient and modern groups.

Native American haplogroups (Table 3). While testing the Stillwater Marsh samples for the markers that identify the five Native American haplogroups, it became apparent that some of these ancient samples had become contaminated with the modern DNA of one of the authors (D.G.S.), who extracted albumin from them for an earlier study (Smith et al., 1995). However, because this individual does not belong to any of the Native American haplogroups, it was still possible to identify the haplogroup for most of the Stillwater Marsh samples. Of the 21 samples from Stillwater Marsh in which the haplogroup was identified, 1 (4.8%) was A, 8 (38.1%) were B, none were C, and 12 (57.1%) were D (see Table 2). Two additional samples might belong to haplogroup X (SW9 and SW20), as they lack the *DdeI* site at np 1715 (and lack the *AluI* site at np 10028 that, in combination with the *DdeI* site loss, identifies European haplogroup I (Torroni et al., 1996), of which one of the authors (F.A.K.) is a member). However, as some DNA extracts from these samples contradict the assignment of these samples to haplogroup X, and as preliminary analyses of mitochondrial control region sequence suggest they might have been contaminated (Kaestle, 1998), they have been excluded from these analyses. Since the frequency distributions of haplogroups in these two samples (the ancient Pyramid Lake and Stillwater Marsh groups) were not statistically significantly different ($\chi^2 = 0.617$, $P = 0.735$), and there appeared to be no correlation between mtDNA haplogroup and ^{14}C dates, the two sets of samples were combined, providing a total sample size of 39; 3 (7.7%) are A, 14 (35.9%) are B, none are C, and 22 (56.4%) are D (see Table 2).

A visual comparison of the frequencies of the four most common haplogroups among the modern and ancient groups is provided by the histogram in Figure 3. The ancient Western Nevada group exhibits a very high frequency of haplogroup D, while the ancient Fremont group exhibits a very high frequency of haplogroup B, the most common haplogroup among modern Native American inhabitants of the Southwest and Baja. The haplogroup frequency distribution of the ancient Western Nevada group is statistically significantly different ($P < 0.025$) from

that of all modern language groups (excluding the Northern Hokan sample, $N = 6$) except for the California Penutians and from that of all modern geographic groups except California (Table 4).

In no case did any of the 10,000 chi-square values for the replicates in the three chi-square simulations exceed that obtained when the ancient Western Nevada group was compared to the modern group, and fewer than 5% of them exceeded a chi-square value of 11. The average of the chi-square values from the simulations was approximately 1.5 in all three cases, with an associated P value of about 0.68, suggesting that samples of 39 individuals drawn from the modern populations adequately represent the frequency distribution of their haplogroups. These results support the conclusion that the frequency distribution of haplogroups in the ancient sample is unlikely to have been sampled from a population whose haplogroup frequency distribution is similar to that of the modern Numic inhabitants of the Great Basin.

Genetic distances between the ancient sample and the modern samples clustered by language and geography are shown in Tables 5 and 6. Using these distances, all phylogenetic methods employed produced trees with the same topology. Representative phylogenetic trees depicting the relationships among both the language and the geographic groups are provided in Figure 4. In the language group tree (Fig. 4A), the ancient Western Nevada sample forms a clade with the modern California Penutian, while the ancient Fremont sample is grouped with the modern Zuni, Central Uto-Aztecan, and Yuman (all southwestern groups). The modern Northern Uto-Aztecan, Washo, and Northern Hokan are intermediate. In the geographic group tree (Fig. 4B), the ancient Western Nevada population forms a group with the modern Californians, while the ancient Fremont are grouped with the modern Southwest and Baja groups. Again, the modern Great Basin group is intermediate, although more closely allied with the modern Californians and ancient Western Nevadans.

DISCUSSION AND CONCLUSIONS

The lack of any correlation between the ^{14}C dates of the samples and their haplogroup affiliations is consistent with our hypotheses, also supported by morphometric data (Kelly, 1995), that the 39 ancient individuals studied can be regarded as a population and that their mtDNA haplogroup frequency distributions have not been influenced significantly by genetic drift. If the frequencies of the haplogroups in modern tribal groups reflect those of their ancestors, the comparison of the haplogroup frequency distribution of the ancient Western Nevada group with those of the modern groups provides additional support for the Numic Expansion Hypothesis. To the authors' knowledge, the Pyramid Lake samples reported here include the oldest published examples of each of the common Native American haplogroups,

TABLE 4. Chi-square values for test of homogeneity of frequencies of four most common Native American haplogroups between ancient Western Nevadan group and modern language group, geographic group, and Ancient Fremont group¹

	Group	Subgroup	N	Chi square	P
Language	Penutian	California Penutian	57	0.92	0.631
		Zuni	59	20.11	0.000
	Hokan	Yuman	119	62.55	0.000
		Washo	67	26.38	0.000
		Central Coast Hokan	50	13.49	0.004
	Uto-Aztecan	Northern Uto-Aztecan	155	16.04	0.001
		Central Uto-Aztecan	76	37.57	0.000
Geographic	Great Basin		166	15.69	0.000
	Southwest		137	70.54	0.000
	Baja		82	41.14	0.000
	California		75	6.84	0.077
Ancient	Fremont		69	25.02	0.000

¹ Degrees of freedom (d.f.) are three except for California Penutian when d.f. = 2. N = number of modern (or Fremont) individuals plus number of ancient Western Nevada individuals (39).

TABLE 5. Cavalli-Sforza and Edwards chord-distances between ancient groups and modern language groups

	Ancient Western Nevada	California Penutian	Northern Uto-Aztecan	Northern Hokan	Central Coast Hokan	Fremont	Washo	Zuni	Yuman	Central Uto-Aztecan
Ancient Western Nevada	0.0	0.011	0.159	0.193	0.223	0.341	0.420	0.500	0.630	0.648
California Penutian	0.011	0.0	0.180	0.200	0.185	0.294	0.396	0.387	0.545	0.562
Northern Uto-Aztecan	0.159	0.180	0.0	0.007	0.358	0.152	0.104	0.447	0.352	0.363
Northern Hokan	0.193	0.200	0.007	0.0	0.370	0.098	0.063	0.371	0.270	0.283
Central Coast Hokan	0.223	0.185	0.358	0.370	0.0	0.508	0.452	0.329	0.474	0.458
Fremont	0.341	0.294	0.152	0.098	0.508	0.0	0.079	0.184	0.131	0.156
Washo	0.420	0.396	0.104	0.063	0.452	0.079	0.0	0.268	0.103	0.107
Zuni	0.500	0.387	0.447	0.371	0.329	0.184	0.268	0.0	0.090	0.098
Yuman	0.630	0.545	0.352	0.270	0.474	0.131	0.103	0.090	0.0	0.002
Central Uto-Aztecan	0.648	0.562	0.363	0.283	0.458	0.156	0.107	0.098	0.002	0.0

TABLE 6. Cavalli-Sforza and Edwards chord-distances between ancient groups and modern geographic groups

	Ancient Western Nevada	California	Great Basin	Fremont	Southwest	Baja
Ancient Western Nevada	0.0	0.088	0.178	0.354	0.605	0.622
California	0.088	0.0	0.148	0.270	0.330	0.383
Great Basin	0.178	0.148	0.0	0.124	0.337	0.303
Fremont	0.354	0.270	0.124	0.0	0.134	0.087
Southwest	0.605	0.330	0.337	0.134	0.0	0.015
Baja	0.622	0.383	0.303	0.087	0.015	0.0

except for haplogroup B, which was found in an 8,000-year-old individual from Colorado (Stone and Stoneking, 1996), and haplogroup X, whose presence has not been confirmed in the samples studied. While all four common Native American haplogroups (A, B, C, and D) were present in Western Nevada before 4500 yBP, the frequency of haplogroup D is unusually high compared to that of modern groups (Lorenz and Smith, 1996). Thus, a high frequency of haplogroup D, otherwise the least common of the four haplogroups, might have characterized the prehistoric population of Western Nevada until the last millennium. The haplogroup frequency distribution of the ancient Western Nevada group is statistically significantly different from those of the modern Northern Uto-Aztecan language group, the

Great Basin geographic group, and the modern Numic-speaking groups (i.e., the Northern Uto-Aztecan language group, excluding Tubatulabalic, Takic, and Hopic speakers), at least at the 0.001 level of probability. This outcome is consistent with a recent expansion of the Numic-speaking group into the Great Basin, leading to a replacement of the pre-Numic inhabitants. The chi-square simulation results support statistical elimination of the modern Great Basin group as a probable descendant of the ancient Nevadans. Although current evidence suggests that genetic drift has not had a large effect on mitochondrial haplogroup frequencies in recent North American prehistory (O'Rourke et al., 2000), it is possible that the differences in haplogroup frequencies between the ancient Nevadans and modern

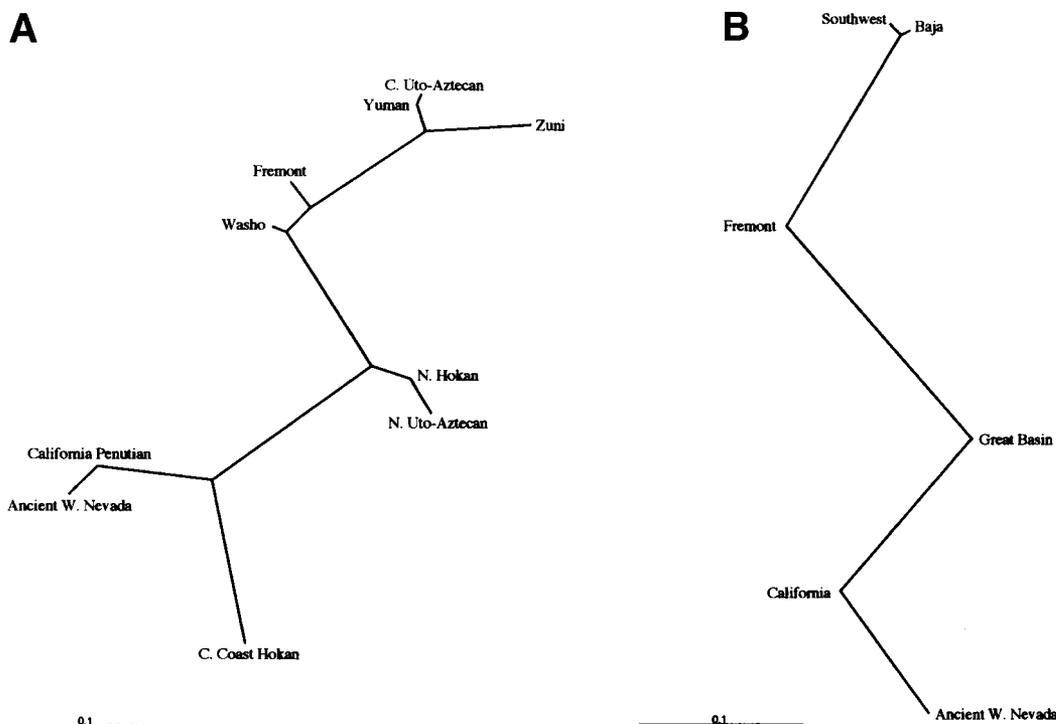


Fig. 4. Phylogenetic dendrograms of ancient and modern groups. A: Language group dendrogram generated from chord distances of Cavalli-Sforza and Edwards (1967), using the neighbor-joining method (Felsenstein, 1998). B: Geographic group dendrogram generated from chord distances of Cavalli-Sforza and Edwards (1967), using the Fitch-Margoliash method (Felsenstein, 1998).

Numic groups have been influenced by the stochastic effect of drift. These effects are mediated by a number of factors, including population size, structure, and other demographic and reproductive factors. Because a chi-square test cannot incorporate the possible effects of drift as mediated by the above factors, we are currently developing a simulation model that does, based loosely on the model by Wobst (1974, 1976) of hunter-gatherer social systems as multitiered, hexagonally organized collectives of tribes (Cabana et al., 2000). Preliminary results, using ethnographic data from modern hunter-gatherers for the relevant parameters, indicate that at the smallest tribal sizes, below approximately $N = 245$, the effects of genetic drift cannot be eliminated as the cause of the difference in haplogroup frequencies between the ancient Nevadans and modern Great Basin inhabitants ($P < 0.05$) (Cabana et al., 2000a). However, at larger tribal sizes the effects of genetic drift appear to be inadequate to cause the degree of difference observed between the haplogroup frequencies in the ancient and modern populations ($P < 0.05$) (Cabana et al., 2000a). Because the lowest estimates of tribal size derive from modern Australian and Arctic hunter-gatherers who had a significantly lower population density than is estimated for prehistoric peoples of the Great Basin (Birdsell, 1958, 1968; Wobst, 1974; Leland, 1986; Ubelaker, 1988; Crawford, 1998), it is unlikely that the ancient Nevadan tribal groups fell within this low end of the range. In the future, we will explore further the factors that would affect this

conclusion, including migration rates between populations and the number of generations of genetic drift allowed (Cabana et al., 2000b).

The modern California Penutian language group and the California geographic group have haplogroup distributions that are not statistically significantly different from that of the ancient Western Nevada group. Both groups are therefore plausible descendants of the ancient Pyramid Lake (presumably non-Numic) group. Hattori (1982) and Moratto (1984) have suggested that some California Penutian speakers originated in northwestern Nevada, while ancestors of the Hokan speakers have probably inhabited California continuously for perhaps 10,000 years. Although the correlation between language and genetics is problematic, the linguistic evidence suggests it is more likely that the California Penutians, rather than the Central Coast or Northern Hokans, are the modern descendants of the ancient Pyramid Lake group. Given that the Hokan and the Penutian-speaking groups have long inhabited adjacent geographic regions (Moratto, 1984), it is possible that admixture, or even common ancestry, is responsible for the genetic similarities observed between the modern Californian Penutian and Hokan-speaking groups.

Haplogroup X is absent in modern Numic speakers (Smith et al., 1999), but has been reported in both the Yakima (Forster et al., 1996; Brown et al., 1998), members of the Plateau Penutian language group who many believe to be related to the California Penutian speakers (Silverstein, 1979; Foster,

1996; but see Campbell, 1997), and the Pomo, Northern Hokan speakers (Smith et al., 1999a). Because haplogroup X is the rarest of the five Native American haplogroups, it is possible that modern California Penutians also possess the marker for haplogroup X in frequencies too low to be detected in the small sample examined thus far. Additional evidence for a recent Numic expansion and a connection between the pre-Numic inhabitants of the Great Basin and the Californians would exist if the presence of haplogroup X is confirmed among the ancient Western Nevada group.

While caution must be exercised when genetic distances and phylogenetic trees are generated from a single locus and those generated from multiple loci are preferable (Avice, 1994), the present study supports the connection between the ancient Western Nevadans and the Californians. However, these results suggest that the ancient Western Nevada group, while most similar to the California groups, might be more distantly related to the Northern Uto-Aztecan language group and/or the Great Basin geographic group (see Tables 5 and 6). The placement of the Northern Uto-Aztecan language group and the Great Basin geographic group near the California/Ancient Western Nevada clade in phylogenetic analyses is further support of this relationship (Fig. 4A). These data, in combination with the chi-square results, suggest an alternative hypothesis involving admixture. If the ancient Western Nevada population were early Penutian inhabitants of the western Great Basin with a haplogroup frequency distribution resembling that of modern California Penutians (high frequencies of B and D, but very low frequencies of A and C), while the haplogroup frequency distribution of the proto-Numic group expanding into the region resembled that of the modern California Uto-Aztecan (moderate frequencies of B, C, and D, and the absence of A), random admixture between the pre-Numic residents and the Numic immigrants could have produced the frequency distribution seen in the modern Numic inhabitants (high frequencies of B and D, a low frequency of C, and the absence of A). This hypothesis has received support from studies of the frequencies of an albumin variant, albumin Mexico (Al^{Me}), in these groups (Kaestle et al., 1999; Smith et al., 2000).

A final alternative is that the pre-Numic inhabitants of the Great Basin, represented by the ancient Western Nevada individuals, left no modern descendants, and any similarities in haplogroup frequencies to modern groups such as the California Penutians are due simply to chance. If that is the case, studies of other genetic markers such as nuclear microsatellite alleles should eliminate both the California Penutians and Northern Hokans as probable descendants of the ancient Western Nevada population.

It is noteworthy that these prehistoric inhabitants of the western Great Basin, with a high frequency of

haplogroup D, differed significantly from the ancient Fremont people of the eastern Great Basin who themselves resemble the ancient Anasazi, south of them (Carlyle, personal communication), and modern groups in the American Southwest. These prehistoric western groups also all differed from the prehistoric groups of the midwest who themselves resembled modern Siouan living near that region (Stone and Stoneking, 1998). This continuity of regional variation over time and its correlation with population movements hypothesized from linguistics and archaeological studies suggest that genetic drift has not obscured haplogroup frequency distributions sufficiently to preclude the identification of ancestor/descendant relationships, given sufficient sample sizes.

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