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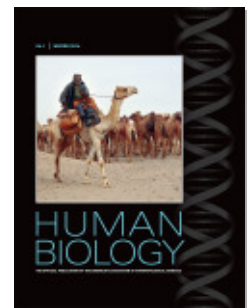
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Distribution of Mitochondrial DNA Lineages Among Native American Tribes of Northeastern North America

RIPAN S. MALHI,¹ BETH A. SCHULTZ,¹ AND DAVID G. SMITH^{1,2}

Abstract The mtDNA haplogroups of 185 individuals from Native American tribes in Northeast North America were determined. A subset of these individuals was analyzed by sequencing hypervariable segments I and II of the control region. The haplogroup frequency distributions of populations in the Northeast exhibit regional continuity that predates European contact. A large amount of gene flow has occurred between Siouan- and Algonquian-speaking groups, probably due to an Algonquian intrusion into the Northeast. The data also support both the Macro-Siouan hypothesis and a relatively recent intrusion of Northern Iroquoians into the Northeast. These conclusions are consistent with archaeological and linguistic evidence.

The Northeast culture area of North America (Driver and Massey 1957) extends from the western end of the Great Lakes to Maine. The principal language families in this area include Iroquoian in the east, Siouan in the west, and Algonquian throughout the entire region (Campbell and Mithun 1979; Campbell 1997). The distribution of these language families within and beyond the Northeast, together with the archaeological record, have fostered hypotheses about large population movements and admixture during prehistoric times (Siebert 1967; Lounsbury 1978). For example, Goddard (1994) demonstrated a west-to-east cline in declining depth of common ancestry among Algonquian languages, and this may be interpreted as evidence that Algonquians migrated eastward from a homeland in the west. The Red Ocher/Glacial Kame twin burial complex (2500–2000 ybp) in the southern Great Lakes Region might be the cultural manifestation of these recently arrived proto-Algonquian-speaking people in the east, who are hypothesized (by Denny 1991) to be descendants of the people of the Western Idaho Archaic Burial Complex located on the Columbia Plateau, between 4000 and 1000 years earlier (Pavesic 1985). Fiedel (1987) argued that the Point Peninsula

¹Department of Anthropology, University of California, Davis, CA.

²California Regional Primate Center (CRPC), University of California, Davis, CA.

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QUIAN, IROQUOIAN, SEQUENCE

culture (2200–1300 ybp) is the material manifestation of the further spread of Algonquian-speaking ancestors into the northern Great Lakes Region from southern Ontario. The replacement of dolicocephalic Otamid populations by brachycephalic Lenapid populations of the Great Lakes and Ohio Valley regions constitutes craniometric evidence for an intruding population into the Great Lakes region from the Pacific Northwest (Neumann 1952). The appearance of the Red Ocher/Glacial Kame Burial complex in the Great Lakes Region coincides with the estimated time, based on glottochronological evidence that proto-Algonquian began to diversify into its Algonquian-speaking descendants (Denny 1991). However, that there is a link between the Western Idaho Archaic Burial Complex and a proto-Algonquian population is not widely accepted among North American prehistorians.

Siouan groups that were pushed into the Plains by the expansion of Algonquian groups are closely related linguistically to groups (e.g., Biloxi, Catawba, Ofo, Tutelo) that lived in the Southeast United States at contact (Campbell and Mithun 1979; Campbell 1997). Chafe (1976) has proposed the existence of a Macro-Siouan language stock consisting of the Iroquoian, Siouan, and Caddoan language families, which might have originated in the Southeast. Populations from all three of these groups are now widely scattered throughout the Northeast, Plains, and Southeast regions.

Northern Iroquoians constitute another hypothesized immigrant population in the Northeast. During the past few decades archaeologists have used an *in situ* model of development for explaining culture change in the Northern Iroquoian region (Lounsbury 1978). Recently, however, Snow (1995) reiterated the idea of an Iroquoian intrusion and presented evidence of an Iroquoian migration into the Northeast from the southeastern United States, where other Iroquoian groups, such as the Cherokee, lived during the early historic period. Snow (1995) argued that there is a clear discontinuity in the archaeological record resulting from the intrusion of Iroquoian-speaking people into Algonquian territory approximately 1200 ybp. Such population movements, and any resulting admixture, should cause detectable patterns in the mitochondrial DNA (mtDNA) diversity in populations of this region.

All unadmixed modern Native Americans are members of one of five different maternal haplogroups: *A*, *B*, *C*, *D*, or *X*. Each haplogroup is defined by a restriction site gain or loss or by the presence of a 9 base-pair (bp) deletion, as well as by corresponding point mutations in the control region (CR) of mtDNA (Schurr et al. 1990; Torroni et al. 1993; Forster et al. 1996; Brown et al. 1998). The frequency distributions of these five haplogroups differ significantly among Native American groups in North America (Lorenz and Smith 1996; Smith et al. 1999). For example, haplogroup *A* is high in frequency in Native American populations in the northern region of North America (occupied mainly by Athapaskan and Eskimo/Aleut speakers). It is, however, nearly absent in Native American populations of the Southwest United States (except in the Navaho and Apache, Southern Athapaskan speak-

ers who are relatively recent emigrants from the North), where haplogroup *B* predominates. In at least some geographic regions this patterning of haplogroup distributions in North America appears to have prehistoric continuity as well. For example, data from ancient populations in the Southwest United States indicate that haplogroup *B* has been the most common haplogroup in the region at least as early as 3000 ybp (O'Rourke et al. 2000).

Cavalli-Sforza et al. (1992) have shown a relatively high degree of concordance between genes and language phyla on a worldwide level. However, on a more regional level there is less agreement between the distributions of genes and languages of tribes in North America (Ward et al. 1993). For example, in the Southwest United States many unrelated language groups (including the Pueblo, Uto-Aztecan, and Yuman) share similar haplogroup frequency distributions, while others (such as the Uto-Aztecs of the Southwest United States and those of Mexico), who share language and other cultural traits in common (Hale and Harris 1979), exhibit very different haplogroup frequency distributions (Lorenz and Smith 1996; Smith et al. 2000). In regions where neighboring populations exhibit markedly different haplogroup frequency distributions, the influence of population movements can account for this difference. For example, Lorenz and Smith (1996) and Smith et al. (2000) have presented evidence that haplogroup *B*, which is absent in northern Athapaskans but is present in high frequency in southwestern Athapaskan-speaking populations, resulted from a recent Athapaskan migration from Northwest North America followed by intense admixture with women from southwestern United States tribes. The presence of haplogroup *X* in Navaho, but not in Apache or northern Athapaskans, implicates Tanoan-speaking groups, such as the Jemez Pueblo, as a potential source for this admixture (Smith et al. 2000). However, it is possible, but less likely, that haplogroup *X* is indigenous to the Navaho since the haplotype is different from that found in the Jemez Pueblo.

Regions like the southwestern United States, where many genetically homogeneous populations speak distantly related languages, might have experienced periodic prehistoric population intrusions followed by admixture over a sufficient period of time for both the intruding and native populations to reach similar haplogroup frequency distributions (regional continuity) through gene flow. Language adoption could also account for such a pattern. It is possible that evidence of recent population intrusions in Native American prehistory, such as the Athapaskan migration to the Southwest cited above, persists because insufficient time has passed for regional continuity to develop through admixture with neighboring populations and, consequently, genes and language remain correlated. Even when regional continuity of haplogroup frequency distributions exists in a region, analysis of haplotype distributions among different populations in the same region can reveal evidence of population intrusions or admixture among these groups (Kaestle 1998). The purpose of this study is to examine the genetic relationships among Native Amer-

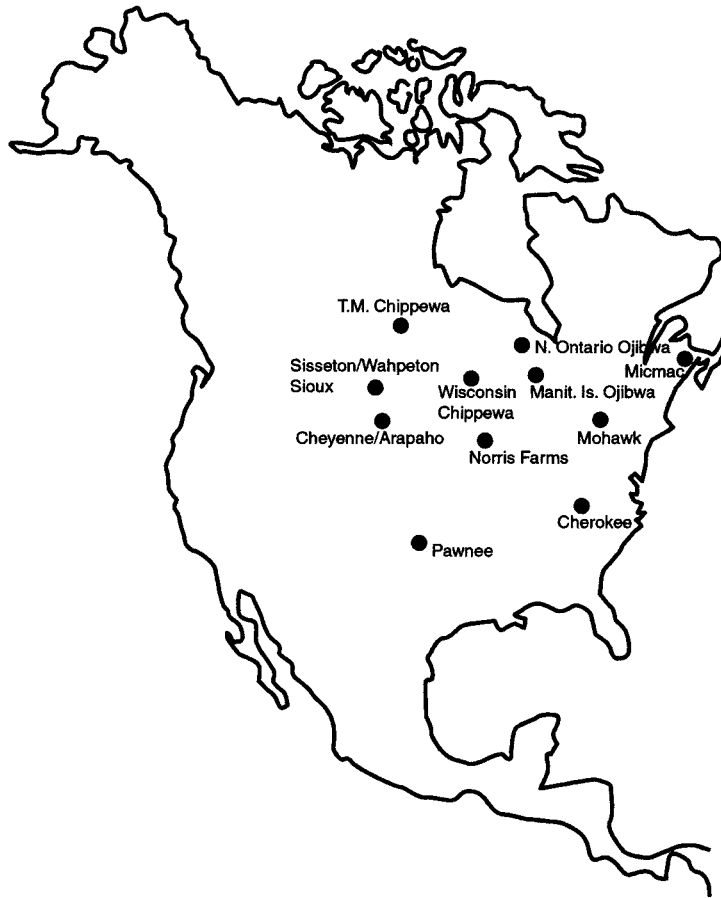


Figure 1. Geographic location of populations analyzed in this study.

ican populations in the Northeast culture area of North America in the context of linguistic and archaeological evidence of population movements or migrations.

Materials and Methods

Populations Studied. The geographic locations (during early historic times) of the populations studied are depicted in Figure 1. The Northern Ontario Ojibwa located north of Lake Superior in Ontario, whose mtDNA haplogroups were analyzed by Scozzari et al. (1997), were originally studied by Szathmary et al. (1978) and Torroni et al. (1993). The Manitoulin Island

(Central) Ojibwa, originally described by Szathmary et al. (1978), were also studied by Scozzari et al. (1997). The Turtle Mountain Chippewa samples were collected by Lorenz and Smith (1996) from the Public Health Service Hospital in Belcourt, North Dakota. Chippewa is the name for Ojibwa-speaking groups south of the Canadian border. The Turtle Mountain Chippewa, a Salteaux group, arrived in their present homeland on the North Dakota/Alberta border from Sault Ste. Marie, to the east, on the southeastern tip of Lake Superior. The Wisconsin Chippewa samples were collected by Lorenz and Smith (1996) from an Indian Health Services clinic in Hayward, Wisconsin, serving a population that speaks the Southwestern Ojibwa dialect. These Ojibwa had expanded northwest and forced the original Sioux occupants of this region westward onto the Plains (Hickerson 1970). The Micmac samples were collected for Lorenz and Smith (1996) by Dr. David L. Schmidt from residents of Eskasoni, Nova Scotia.

The Micmac, whose language is classified as Eastern Algonquian, are the most northeastern Algonquian group and are located in New Brunswick, Nova Scotia, Maine, and Labrador. The Cheyenne/Arapaho samples were collected by Lorenz and Smith (1996) from the Indian Health Center in Concho, Oklahoma. Since these Cheyenne and Arapaho are both closely related and (recently) highly admixed with each other, we have treated them as a single sample. The Cheyenne and Arapaho are both Plains Algonquian groups that were located on the prairies of southern Minnesota during early historic times (Kehoe 1962) and were pushed west into the Dakotas due to warfare with the Sioux and Chippewa. In the early 19th century, the Cheyenne lived adjacent to the Comanches, horse-riding Shoshoni, and probably had considerable contact with them (Fiedel, personal communication).

Samples of Sisseton/Wapeton Sioux, a Central Siouan group, were collected by Lorenz and Smith (1996) from the Fort Totten Health Center in Fort Totten, North Dakota. During the 17th century the Sioux occupied most of Minnesota but were pushed into the Dakotas by the expansion of Southwestern Ojibwa (Wisconsin Chippewa) groups. The Norris Farms (Oneota) samples were extracted from skeletal remains collected from a pre-Columbian (approx. 700 ybp) cemetery site located in west-central Illinois and analyzed by Stone and Stoneking (1993; 1998). Based on the geographic location of this site, its inhabitants are assumed to be ancestors of modern Siouan groups.

The Mohawk samples were collected and analyzed by Merriwether and Ferrell (1996). This population speaks a language of the northern branch of Iroquoian and is located on the southeast side of Lake Ontario. The Cherokee, whose original homeland is in North Carolina, represent the southern branch of the Iroquoian language family. Most of their ancestors moved west of the Mississippi and eventually to the eastern district of Oklahoma during late historic times. The Stillwell Cherokee samples were collected by Lorenz and Smith (1996) from the Cherokee Nation Indian Health Clinic in Stillwell, Oklahoma. The Oklahoma Red Cross Cherokee samples were provided to

Lorenz and Smith (1996) by the American Red Cross in Tulsa, Oklahoma, who collected them from Cherokee individuals at various clinics throughout the designated Cherokee district in Oklahoma. Finally, the Pawnee samples were collected by Lorenz and Smith (1996) from individuals that reside on the Pawnee reservation in Oklahoma. The Pawnee are a Caddoan-speaking group that lived in Kansas before being relocated to Oklahoma in the 19th century.

Subsets of the population samples described above were sequenced as were additional samples from closely related tribes that increase the breadth of representation of each language family. They include individuals from the Sisseton/Wapeton Sioux ($n = 16$), Pawnee ($n = 4$), Ponca ($n = 3$), Quapaw ($n = 3$), Iowa ($n = 3$), Stillwell Cherokee ($n = 16$), Oklahoma Red Cross Cherokee ($n = 15$), Chippewa ($n = 29$), Micmac ($n = 4$), Cheyenne/Arapaho ($n = 4$), Kickapoo ($n = 5$), Shawnee ($n = 2$), Potowatomi ($n = 1$), Sac & Fox ($n = 1$), Delaware ($n = 1$), Yurok ($n = 2$), Siouan ($n = 1$), and Sioux/Caddoan ($n = 1$).

DNA Extraction and Typing. The haplogroups of 185 full-blooded Native Americans were determined by restriction fragment length polymorphism (RFLP) analysis and/or by sequencing of the control region of the mitochondrial genome. DNA was extracted from 200 μ L of serum or from hair follicles using the Qiagen Blood Amp Kit. Amplification reactions were carried out in a 25 μ L volume with 3 μ L of DNA template, 50 mM of each primer, 10X Buffer (50 μ M Tris, pH 8.4, 1.5 μ M $MgCl_2$, 20 μ M NaCl, 500 mg/mL BSA), 1.5 units of Platinum Taq (Gibco), 200 mM of each dNTP and ddH₂O. After an initial 4 min denaturation step at 95°C, 40 cycles were performed denaturing at 95°C for 30 sec, annealing at 52°–58°C for 30 sec, and extending at 72°C for 30 sec, ending with a final 4 min extension at 72°C. A 5 μ L-portion of amplification product was electrophoresed on a 6% polyacrylamide gel and stained with ethidium bromide to confirm the presence of polymerase chain reaction (PCR) product. In cases where PCR product was visible, the remaining 20 μ L were incubated with 10 units of the appropriate restriction enzyme overnight at 37°C. Primers used for amplification are described in Smith et al. (1999).

Hypervariable segment I (HVS I) of the control region was amplified using primers described in Smith et al. (1999). Hypervariable segment II (HVS II) of the control region was amplified using primer sequences L00017: 5'-CCCTATTAACCACTCACGGG-3' and H00350: 5'-TGGCAGAGATGTGTTTAAGTGCT-3'.

The PCR products were filtered using a Microcon 100 filter unit (Millipore) and then submitted for sequencing to the DBS Automated DNA sequencing facility on the University of California, Davis campus. Both the heavy and light strands were sequenced to preclude undetected sequencing errors. All sequences are reported in Appendix A.

Analysis of Haplogroup Frequency Distributions. The five Native American haplogroups were treated as alternate (i^{th}) alleles at a single locus. Any of the “N” individuals in a given sample determined not to belong to haplogroups A, B, C, D, or X were assumed to represent non-Native American admixture (Smith et al. 1999) and excluded from the analysis. Therefore, the samples identified as haplogroup H in the Ojibwa populations (Scozzari et al. 1997) were excluded as well as the samples identified as haplogroups X6 and X7 (Merriwether and Ferrell 1996). Heterozygosity (haplogroup diversity) was estimated (according to Nei 1987) as:

$$h = (1 - \sum [x_i]^2)N/N - 1. \quad (1)$$

Pairwise comparisons of the haplogroup frequency distributions were made between all populations using Fisher’s exact test (Weir 1990) in the Genepop software program (Raymond and Rousset 2000). The Micmac and Pawnee were excluded from this part of the analysis due to extremely small sample sizes. Each pairwise comparison was bootstrapped with 1000 iterations, and the mean p -value and standard error are reported. Genetic distance was calculated between all pairs of populations using the Chord Distance measurement of Cavalli-Sforza and Edwards (1967) in GENDIST, and trees were generated by the neighbor-joining method using NEIGHBOR and DRAWTREE in PHYLIP 3.572 software package (Felsenstein 1993). A consensus tree and phenogram constructed from 100 iterations are reported. The consensus tree was constructed using SEQBOOT and CONSENSUS in the PHYLIP software package. Principal components analysis was performed using standard correlation measures (Harpending and Jenkins 1973), and the first three components are reported.

DNA Sequence Analysis. The control regions of 110 individuals were sequenced. The HVSI is defined as nucleotide positions (nps) 16063–16520 and the HVSII is defined as nps 60–263. Mean pairwise differences, pairwise F_{ST} , Tajima’s D statistic, and mismatch distributions were calculated using the ARLEQUIN software package (Schneider et al. 1997) and Microsoft Excel. Tajima’s D , a statistical method used to test the neutral mutation hypothesis that a population is panmictic and in equilibrium, was calculated for any mismatch distribution that was Poisson-like (i.e., exhibited a unimodal mean pairwise difference that was similar to its variance). The test utilizes the difference between the average number of paired nucleotide differences (assumed to be distributed as a Poisson) and an expected value based on the number of segregating sites that is consistent with neutrality. Any significant difference between the two parameters suggests that neutrality does not apply because the population is not in equilibrium, possibly due to a recent demographic event (Tajima 1997).

Haplotype networks were formed using the Bandelt Network Program (Bandelt et al. 1999), and nested clades were constructed by hand based on guidelines proposed by Templeton et al. (1995). Mutational differences separating clades were identified with reference to the Anderson et al. (1981) sequence. Comparison of percentage sequence divergence of HVSI and HVSII confirm earlier reports that the two regions do not evolve in a similar fashion. Therefore, even though the two regions are closely linked, they are analyzed separately. Values of haplotype diversity were not used to calculate coalescence times due to uncertainties about the average mutation rate (Parsons et al. 1997), the correct model of evolution for the control region in the mitochondrial genome (Schneider et al. 1999), and the timing of population movements in the Northeast.

Results

Haplogroup Frequency Distribution. As shown in Table 1, all populations exhibit moderate-to-high frequencies of haplogroup A, except the two Cherokee populations. Haplogroup C is moderate to high in frequency in all populations, except the Northern Ontario Ojibwa (7.1% haplogroup C). The frequency of haplogroup B is high in both Iroquoian-speaking groups, moderate in the Siouan-speaking groups and the Turtle Mountain Chippewa who reside in North Dakota, and low in all other populations. Haplogroup D is uniformly low in all populations, except the Cheyenne/Arapaho (14.3% haplogroup D) and the prehistoric Norris Farms population (9.6% haplogroup D). The presence of haplogroup D in the Cheyenne/Arapaho is unusual (Lorenz and Smith 1996) and might reflect unacknowledged admixture with neighboring Shoshoni, who exhibit a high frequency of this haplogroup (Kaestle 1998). Haplogroup X is highest in frequency among Algonquian-speaking populations, reaching a maximum of 50% (albeit sampling error might have inflated the estimate) in the Micmac. It is present in low frequency in the Siouan-speaking group and the Algonquian groups located in the Midwest (Turtle Mountain Chippewa and Cheyenne/Arapaho) and is absent from the Iroquoian-speaking groups. Only haplogroups A and B were found among the five Pawnee samples; the absence of haplogroups C, D, and X in the Pawnee sample might reflect sampling error caused by the extremely small sample size. Overall, Algonquian and Siouan speakers exhibit all five haplogroups with A, C, and X being the most common; in the Iroquoian speakers, haplogroups B and C are common, and haplogroup X is absent (Table 1).

The results of Fisher's exact test (Table 2) between all pairs of populations are in agreement with the consensus tree and principal components analysis (Figures 2 and 3). Except for the Mohawk, populations in the Northeast display a pattern of regional continuity. This continuity predates European contact, as shown by the haplogroup frequency distribution of the Norris

Table 1. Haplogroup Frequency Distribution and Heterozygosity of Native American Populations

<i>Population</i>	<i>N</i>	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>X</i>	<i>h</i>	<i>Reference</i>
Micmac	6	0.333	0.000	0.167	0.000	0.500	0.713	Lorenz and Smith 1996; Smith et al. 1999; this study (1) ^a
Manitoulian Island Ojibwa	33	0.325	0.097	0.269	0.040	0.269	0.762	Scozzari et al. 1997
Northern Ontario Ojibwa	26	0.643	0.036	0.071	0.000	0.250	0.538	Scozzari et al. 1997
Turtle Mountain Chippewa	28	0.571	0.179	0.179	0.000	0.071	0.627	This study
Wisconsin Chippewa	62	0.275	0.048	0.355	0.032	0.290	0.723	This study
Cheyenne/Arapaho	35	0.343	0.114	0.343	0.143	0.057	0.749	Smith et al. 1999; this study (9)
Norris Farms	108	0.315	0.120	0.426	0.083	0.056	0.701	Stone and Stoneking 1998
Sisseton/Wapeton Sioux	45	0.556	0.200	0.178	0.044	0.022	0.631	Lorenz and Smith 1996; Smith et al. 1999; this study (15)
Pawnee	5	0.400	0.600	0.000	0.000	0.000	0.600	Lorenz and Smith 1996; this study (2)
Oklahoma Red Cross Cherokee	19	0.211	0.211	0.525	0.053	0.000	0.683	Lorenz and Smith 1996; this study (8)
Stillwell Cherokee	37	0.108	0.459	0.433	0.000	0.000	0.607	Lorenz and Smith 1996; this study (30)
Mohawk	123	0.577	0.171	0.236	0.016	0.000	0.587	Merriwether and Ferrell 1996

a. Figures in parentheses indicate number of samples analyzed in this study.

Table 2. Fisher's Exact Test (p -value and Standard Error Reported)

<i>Northern Ontario Ojibwa</i>	<i>Turtle Mountain Chippewa</i>	<i>Wisconsin Chippewa</i>	<i>Cheyenne/ Arapaho</i>	<i>Sisseton/ Wapeton Sioux</i>	<i>Norris Farms</i>	<i>Oklahoma Red Cross Cherokee</i>	<i>Stillwell Cherokee</i>	<i>Mohawk</i>	
0.090 (0.004)	0.092 (0.004)	0.850 (0.003)	0.104 (0.004)	0.005 (0.001)	0.013 (0.001)	0.022 (0.001)	0.005 (0.000)	0.000 (0.000)	Manitoulian Island Ojibwa
	0.095 (0.003)	0.008 (0.001)	0.001 (0.000)	0.005 (0.001)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	Northern Ontario Ojibwa
		0.002 (0.000)	0.085 (0.003)	0.805 (0.004)	0.021 (0.002)	0.016 (0.001)	0.000 (0.000)	0.134 (0.005)	Turtle Mountain Chippewa
			0.012 (0.001)	0.000 (0.000)	0.001 (0.000)	0.010 (0.001)	0.000 (0.000)	0.000 (0.000)	Wisconsin Chippewa
				0.085 (0.004)	0.802 (0.005)	0.403 (0.006)	0.000 (0.000)	0.001 (0.000)	Cheyenne/Arapaho
					0.007 (0.001)	0.029 (0.002)	0.000 (0.000)	0.313 (0.009)	Sisseton/Wapeton Sioux
						0.631 (0.005)	0.000 (0.000)	0.000 (0.000)	Norris Farms
							0.128 (0.004)	0.011 (0.001)	Oklahoma Red Cross Cherokee
								0.000 (0.000)	Stillwater Cherokee

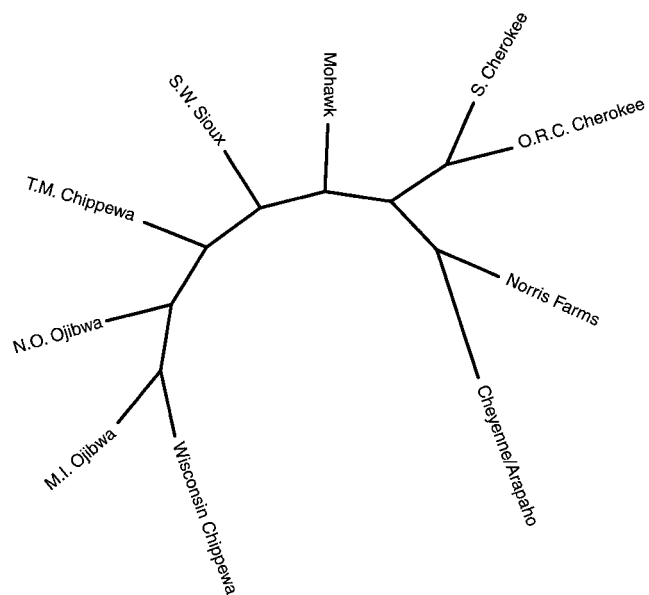


Figure 2. Consensus tree.

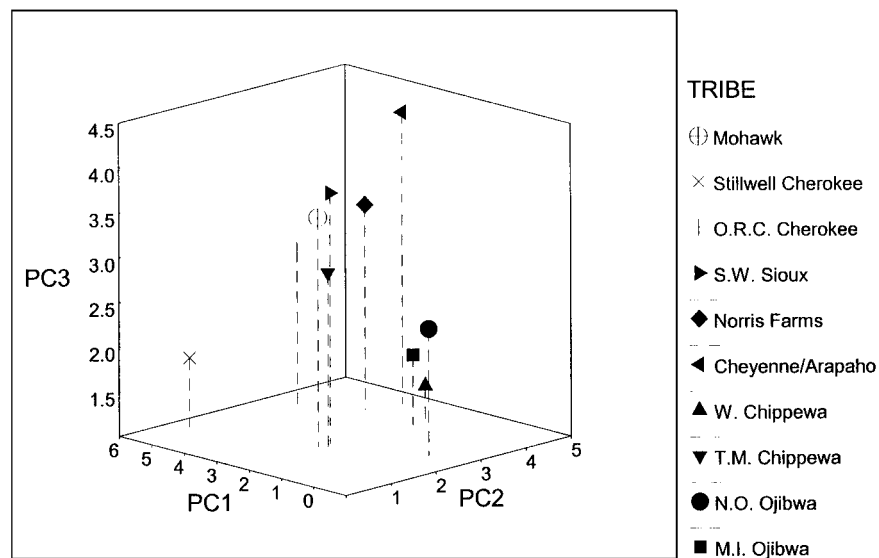


Figure 3. Principal components analysis.

Farms population. When all samples were sorted according to language group, the haplogroup frequency distributions of both the Siouan and Algonquian groups appeared statistically significantly different from those of the Iroquoian group ($p = 0.00$, 100%), but did not differ from each other ($p = 0.135$, 54%).

The consensus tree (Figure 2) reveals that all Ojibwa/Chippewa-speaking groups cluster together, while the remaining Algonquian-speaking group, Cheyenne/Arapaho, clusters with the Norris Farms population. The two Cherokee populations cluster together but are separate from the remaining Iroquoian-speaking group, the Mohawk. The Sisseton/Wapeton Sioux, Mohawk, and Turtle Mountain Chippewa, the three groups that resembled each other in the chi-square analysis, occupy a central position in the tree between the Ojibwa/Chippewa-speaking group and the Cherokee-speaking group.

The first three principal components (Figure 3) explain 97% of the variation in the data and align the populations in a manner similar to that illustrated by the consensus tree in Figure 2 and by the results of the chi-square analysis in Table 2. There are two main groups in the analysis. The Sisseton/Wapeton Sioux, Mohawk, and Turtle Mountain Chippewa form the tightest cluster ($p = 0.257$, $SE = 0.010$), and the Wisconsin Chippewa, Manitoulin Island Ojibwa, and Northern Ontario Ojibwa cluster together ($p = 0.057$, $SE = 0.004$). The Norris Farms population does not significantly cluster with any of these groups, but lies closest to the Oklahoma Red Cross (ORC) Cherokee. The Stillwell Cherokee and Cheyenne/Arapaho populations are clear outliers. The Stillwell Cherokee is closest to the ORC Cherokee population and the Cheyenne/Arapaho is closest to the Norris Farms population.

DNA Sequence Analysis for HVSI. Contrary to earlier studies based on different Native American samples (Torroni et al. 1992; Torroni and Wallace 1995), all haplogroups show approximately the same amount of diversity (as shown in Table 3) when all Northeast populations are combined. However, haplogroup A haplotypes exhibit more diversity in the Siouan and Algonquian groups than in the Cherokee and the Norris Farms populations. The Algonquians also exhibit the most diversity, and the Cherokee and Norris Farms populations display the least diversity for haplogroup C, with the Siouan group falling in between. Algonquians and Siouans show a larger and smaller amount of diversity, respectively, in haplogroup B compared to the rest of the groups. Siouan might lack diversity in haplogroup B due to the small sample size. Finally, the Algonquian haplogroup X markers show a high amount of diversity, but the paucity of these lineages in other groups precludes comparisons. In general, Algonquians exhibit a level of diversity nearly twice that exhibited by the Cherokee and Norris Farms populations.

Pairwise F_{ST} comparisons show that the Siouan and Iroquoian groups are the least divergent of the three groups ($F_{ST} = 0.04$). The Algonquian and

Iroquoian groups are the most divergent ($F_{ST} = 0.14$), with the Algonquian and Siouan groups showing an intermediate level of divergence ($F_{ST} = 0.10$).

The haplogroup A network in Figure 4A has two centers, separated by a single mutation at np 16519. One center consists solely of Iroquoian haplotypes, while the other contains both Algonquian and Siouan haplotypes. Algonquian haplotypes are distributed throughout the network, suggesting admixture, intermingled with Siouan and Iroquoian haplotypes, but there is also a cluster of only Algonquian haplotypes. All haplogroup A haplotypes are grouped in a 3-step clade, and two 1-step clades contain only Algonquian haplotypes. The haplogroup B network (Figure 4B) shows that Siouan, Iroquoian, and Caddoan haplotypes are closely related, supporting the Macro-Siouan hypothesis, and that Algonquian haplotypes cluster together but are distant from the Siouan/Iroquoian/Caddoan cluster. The Yurok haplotype, from a language distantly related to Algonquian, clusters with the Algonquian haplotypes. All haplogroup B haplotypes are included in a 3-step clade, in which one 2-step clade contains only Algonquian haplotypes and the two remaining 2-step clades contain both Siouan and Iroquoian haplotypes, suggesting separate ancestries of Algonquians and the other groups. The haplogroup C network (Figure 4C) is intermingled with haplotypes from all language groups, with the most common haplotype being represented by Iroquoian, Algonquian, and Siouan haplotypes. All haplogroup C haplotypes show a large amount of diversity and are grouped into a 4-step clade. Finally, the haplogroup X network (not shown) shows three centers consisting only of Algonquian haplotypes (including the Blackfeet haplotype). Siouan haplotypes are randomly distributed throughout the peripheries of the network, suggesting their acquisition through admixture with Algonquians.

While the mean pairwise differences between haplotypes of haplogroups A, B, C, and X do not differ (Table 3), their modes do differ (Figure 5). Haplogroups B and X resemble each other with a unimodal distribution and a peak (or mode) at 3-pairwise differences. Haplogroup A shows a unimodal distribution with a peak at 4-pairwise differences. Haplogroup C shows a peak at 2-pairwise differences, but also has a distribution that is more markedly skewed to the left than the other haplogroup distributions. All haplogroups contain a significantly negative Tajima's D value (Table 3), suggesting that the haplogroup distributions are derived from expanding populations (Slatkin and Hudson 1991; Bonatto and Salzano 1997).

As illustrated in Figure 6A, the Siouan HVSI sequence shows a bumpy haplogroup A mismatch distribution (a mode of 4-pairwise differences), whereas the Algonquian group illustrates a unimodal distribution with a mode at 4-pairwise differences. The Algonquian haplogroup A mismatch distribution does not give a significant value for Tajima's D , despite ethnographic, linguistic, and archaeological evidence of rapid growth and spread of Algonquians. For the haplogroup C mismatch distributions (Figure 6B), the Algonquian group is trimodal and shows signs of three types of haplogroup C (with

Table 3. Table of Genetic Diversity

<i>Haplogroup</i>	<i>Nucleotide Site</i>	<i>N^a</i>	<i>No. of Lineages</i>	<i>Mean Pairwise Difference</i>	<i>Variance</i>	<i>Tajima's D</i>	<i>Mean % Sequence Divergence^b</i>
<i>A</i>							
Total	HVSI	47	30	3.47	3.31	−1.685 ($p = 0.04$)	0.759
	HVSII	34	18	3.52	3.53	−0.260 ($p = 0.189$)	1.734
Algonquian	HVSI	19	14	3.71	3.98	−1.425 ($p = 0.08$)	—
	HVSII	17	9	3.00	2.99	0.087 ($p = 0.186$)	—
Siouan	HVSI	11	8	4.04	—	—	—
	HVSII	10	8	3.71	—	—	—
Cherokee	HVSI	5	3	1.67	—	—	—
	HVSII	5	4	1.67	—	—	—
Norris Farms	HVSI	11	8	2.25	—	—	—
	HVSII	—	—	—	—	—	—
<i>B</i>							
Total	HVSI	28	18	3.02	2.74	−1.975 ($p = 0.01$)	0.661
	HVSII	20	9	2.50	2.19	−1.128 ($p = 0.154$)	1.232
Algonquian	HVSI	4	4	4.50	—	—	—
	HVSII	—	—	—	—	—	—
Siouan	HVSI	4	3	1.33	—	—	—
	HVSII	10	—	—	—	—	—
Cherokee	HVSI	10	6	2.73	—	—	—
	HVSII	7	7	2.67	—	—	—
Norris Farms	HVSI	—	4	2.00	—	—	—
	HVSII	—	—	—	—	—	—

<i>C</i>							
Total	HVSI	60	23	3.70	3.76	− 1.705 (<i>p</i> = 0.04)	0.810
	HVSII	34	10	2.98	2.89	− 1.048 (<i>p</i> = 0.067)	1.468
Algonquian	HVSI	10	8	5.79	—	—	—
	HVSII	9	5	3.00	—	—	—
Siouan	HVSI	10	8	3.32	—	—	—
	HVSII	10	4	2.00	—	—	—
Cherokee	HVSI	15	5	2.20	2.10	0.680 (<i>p</i> = 0.74)	—
	HVSII	15	3	—	—	—	—
Norris Farms	HVSI	25	7	2.29	2.02	− 1.035 (<i>p</i> = 0.18)	—
	HVSII	—	—	—	—	—	—
<i>X</i>							
Total	HVSI	29	10	3.56	3.89	− 1.899 (<i>p</i> = 0.01)	0.779
	HVSII	26	6	3.27	3.80	—	1.611

a. N = number of individuals.

b. The percentage of sequence divergence is based on the mean pairwise difference divided by the number of nucleotide sites examined (457 and 203 for HVSI and HVSII, respectively). Published sequences used in the analysis are from Brown et al. 1998; Lorenz and Smith; and Smith et al. 1999. Groups with fewer than three lineages were not analyzed.

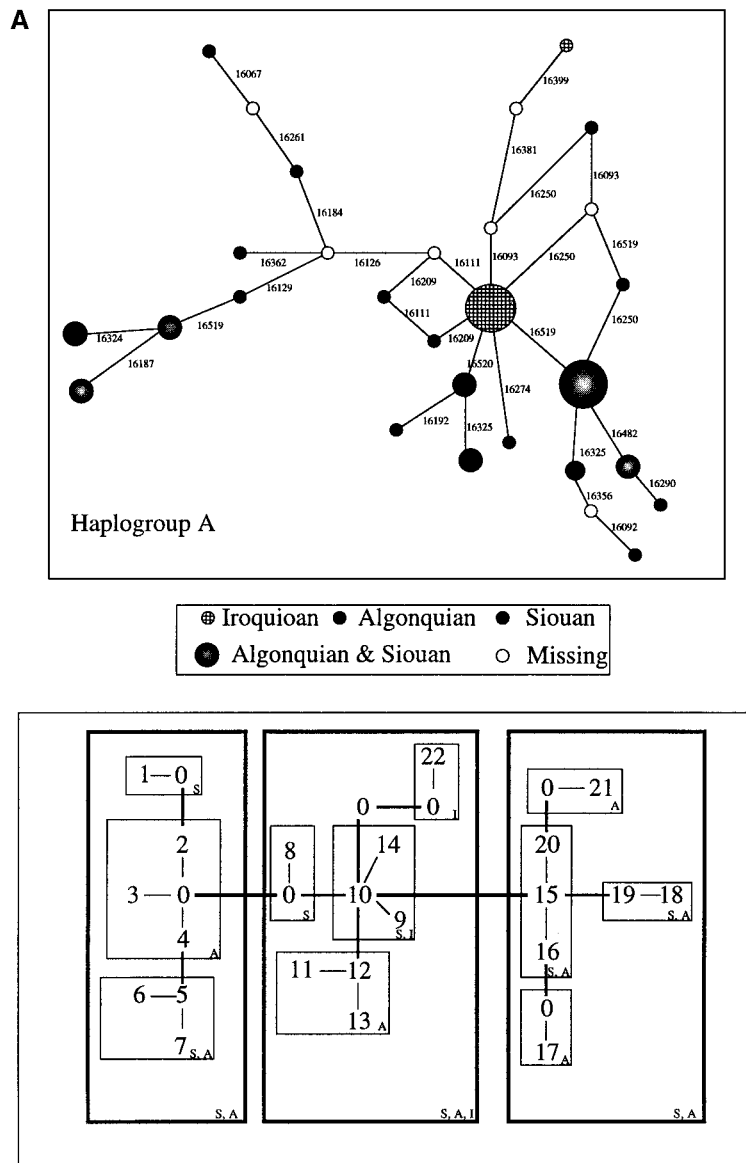


Figure 4. Haplotype networks. The size of the circle corresponds to the frequency of the haplotype. Nested clade analysis based on haplotype networks. Larger clades represent internal nodes of the network.

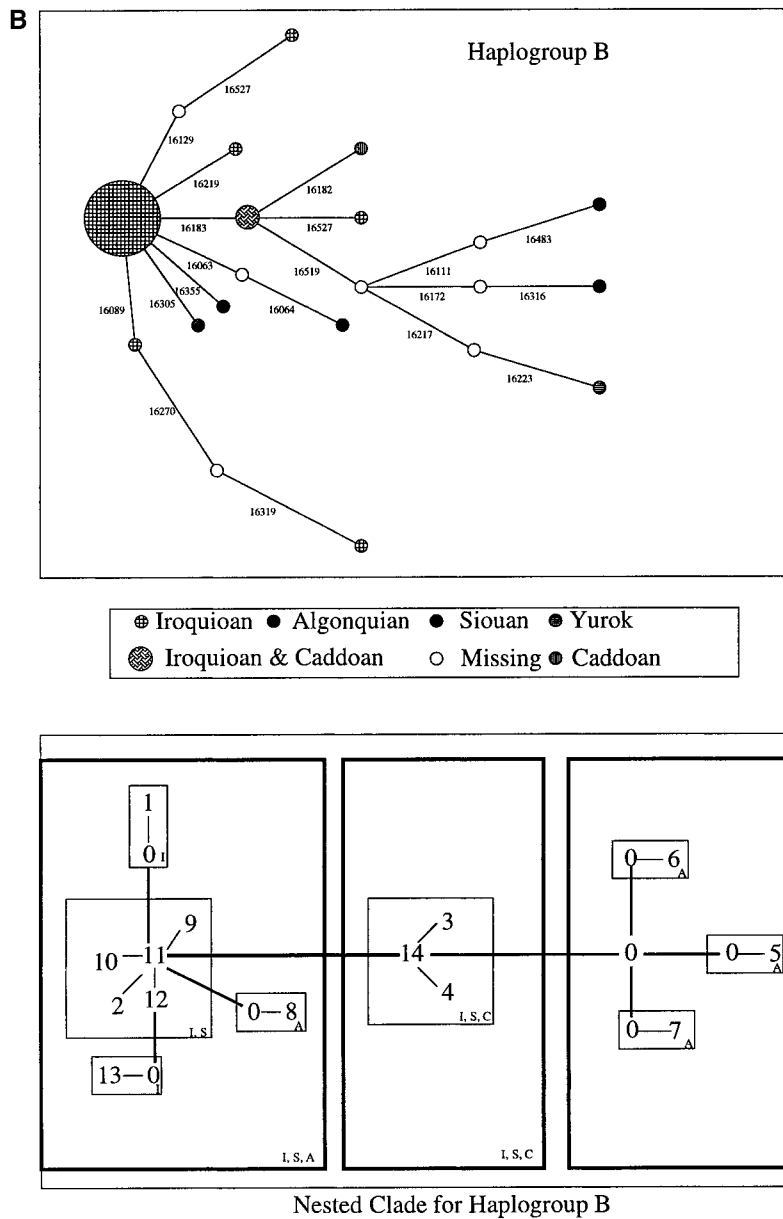


Figure 4. Continued

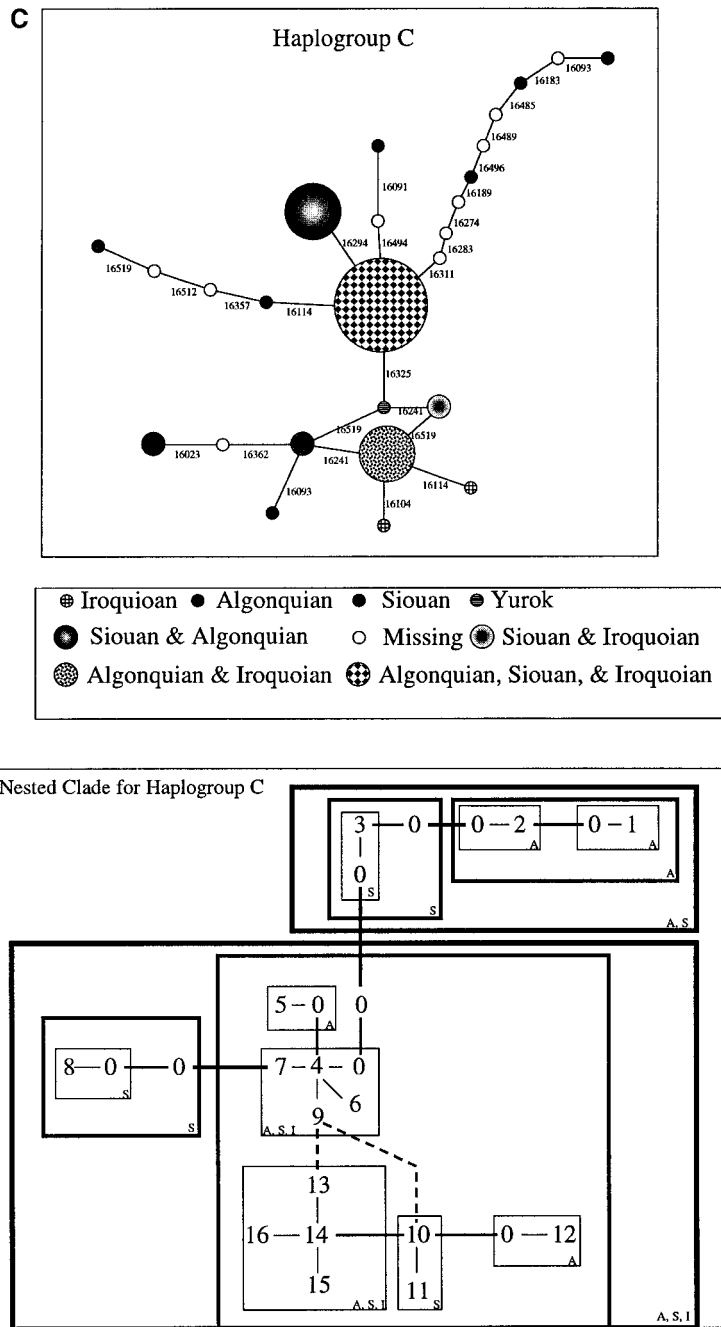


Figure 4. Continued

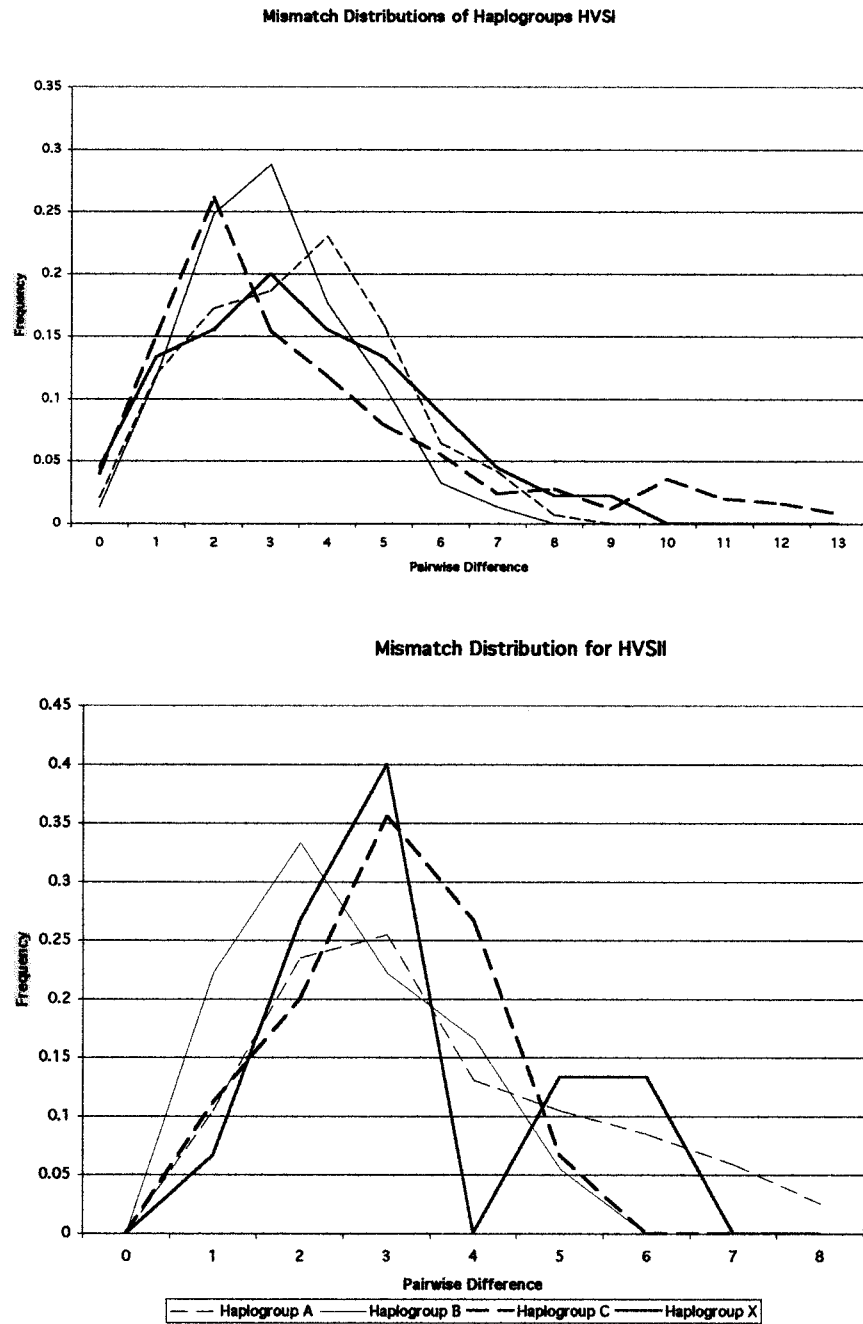


Figure 5. Mismatch distribution of haplogroups in Northeast populations for HVSI and HVSI.

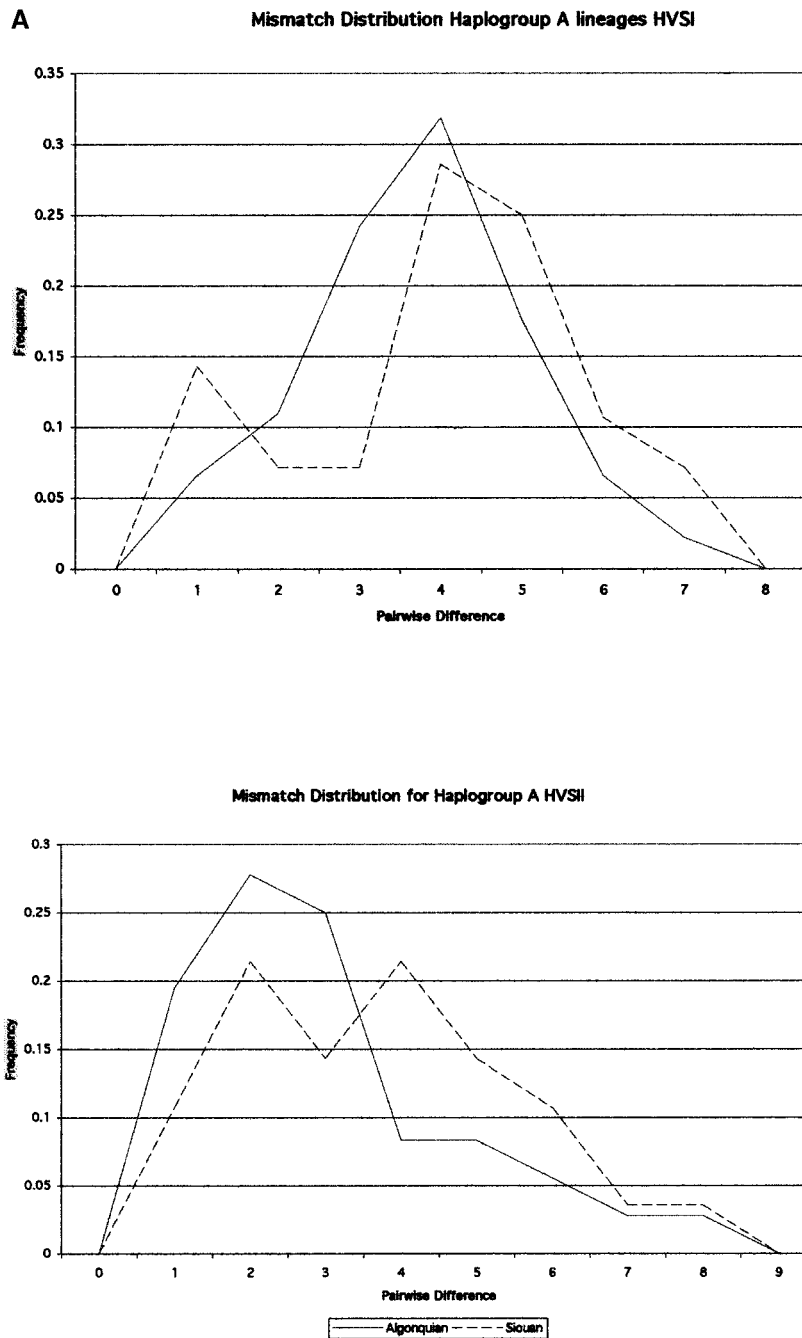


Figure 6. Mismatch distributions of haplogroups A and C for Algonquian- and Siouan-speaking populations.

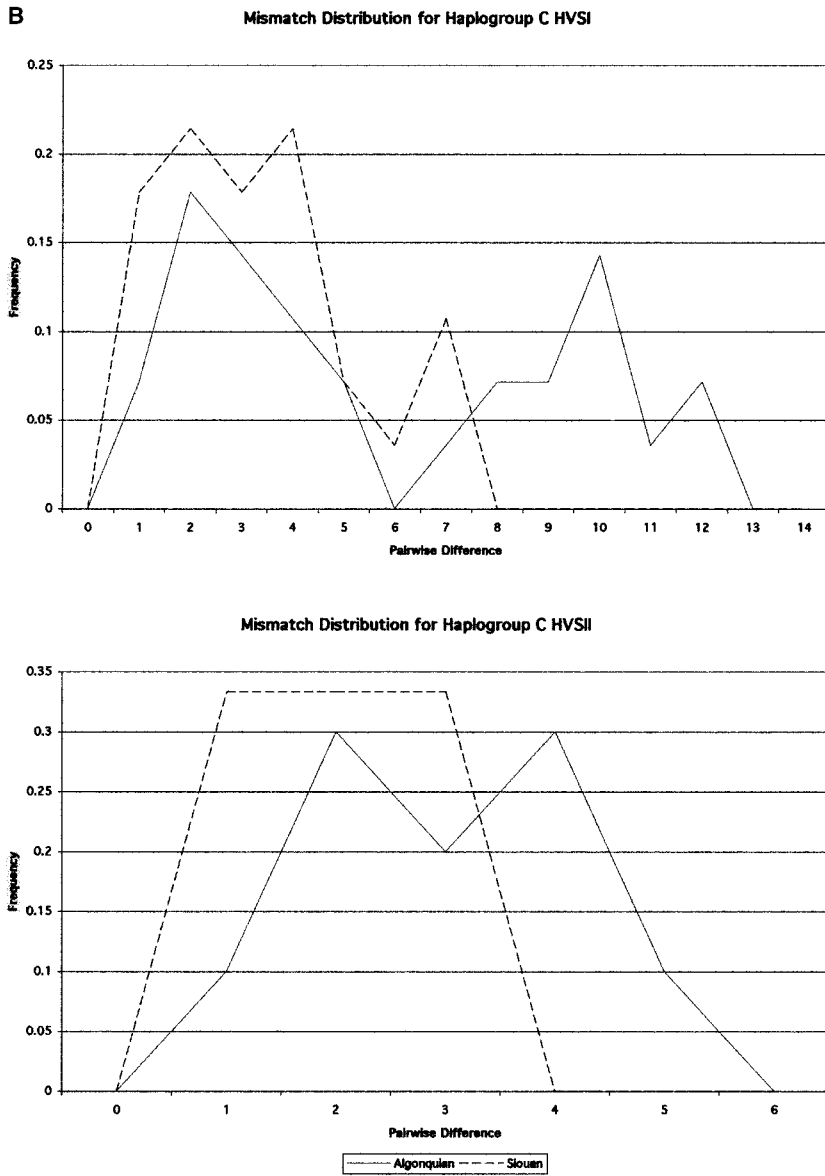


Figure 6. Continued

modes at 2-, 10-, and 12-pairwise differences). The Siouan group also shows signs of a bumpy mismatch distribution for haplogroup *C*, with modes at 2-, 4-, and 7-pairwise differences. The Cherokee group (not shown) displays a bimodal distribution for haplogroup *C* with modes at 2- and 4-pairwise differences. Finally, the Norris Farms population displays a unimodal distribution for haplogroup *C* and generates a nonsignificant Tajima's *D* value. The mismatch distribution for haplogroup *X* is heavily skewed to the left (Figure 5) and gives a nonsignificant negative Tajima's *D* value. One sample (SWO 97) lacked both of the control region markers for the Native American clade of haplogroup *X* (Brown et al. 1998) and was therefore excluded from the mismatch analysis.

DNA Sequence Analysis for HVSII. The HVSII region consistently shows higher rates of substitution and percentage sequence divergence when compared to HVSI (Table 3; Figure 7). The exception is haplogroup *C*, where the variation in substitutions is higher in HVSI, even though the mean percentage sequence divergence is still greater in HVSII. The mismatch distributions for haplogroups *A*, *B*, and *C* are all unimodal with modes at 3-, 2-, and 3-pairwise differences, respectively (Figure 5), but they are associated with nonsignificant negative Tajima's *D* values (Table 3). In contrast, the mismatch distribution for haplogroup *X* is bimodal with modes at 3- and 5.5-pairwise differences.

The mismatch distribution for haplogroup *A* is unimodal and skewed left for Algonquian speakers, but it is bimodal for Siouan speakers with modes at 2- and 4-pairwise differences (Figure 6A). The mismatch distribution for haplogroup *B* shows a bimodal distribution for Cherokee-speaking populations (not shown). For haplogroup *C*, both Siouan and Algonquian are bimodal (Figure 6B).

Discussion

Native American populations in the Northeast display a general pattern of regional continuity featuring high frequencies of haplogroups *A* and *C*, and variable frequencies of haplogroup *X*. That the Mohawk more closely resemble surrounding Algonquian and Siouan populations than they do the Cherokee, to whose language their own is closely related, underscores the strength of this regional continuity. If Algonquian speakers did migrate to the southern Great Lakes and subsequently spread from this region throughout the Northeast, the movement occurred sufficiently early in North American prehistory that no signature of a genetic intrusion survives, because the haplogroup frequency distributions of most groups in the Northeast are in equilibrium. Previous studies have shown that Algonquian speakers and Siouan speakers, but not the Iroquoian, carry the protein-coding mutation Albumin Naskapi

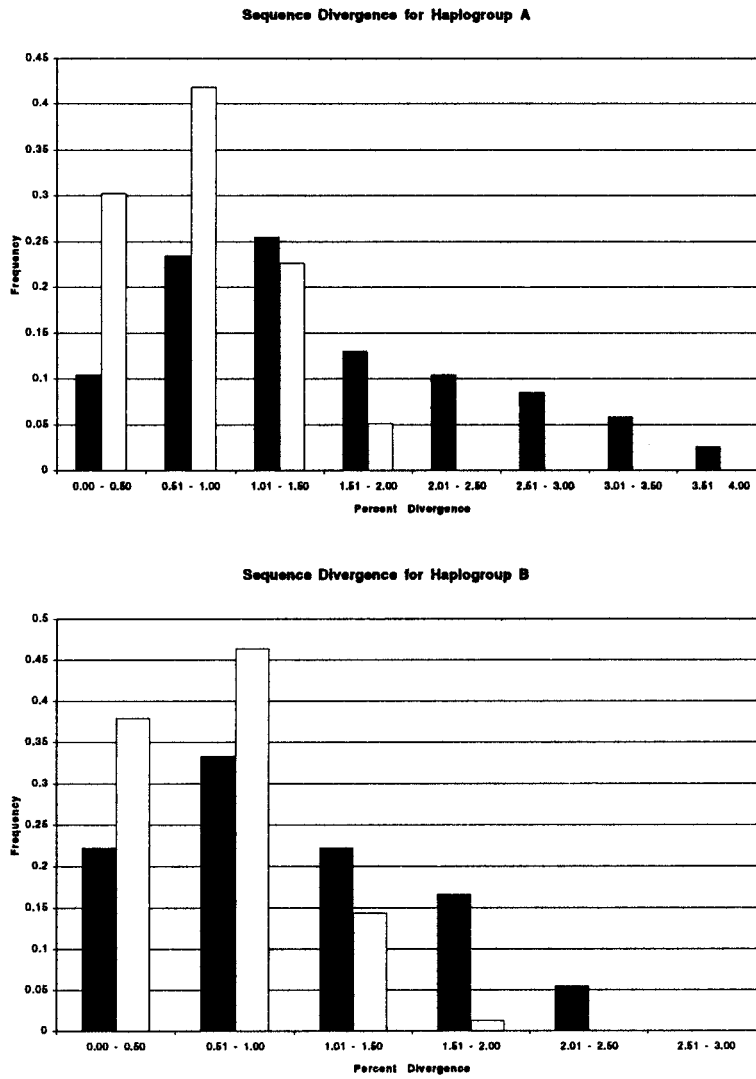


Figure 7. Mismatch distributions based on percentage of sequence divergence for haplogroups A, B, C, and X for populations in the Northeast.

(A1*Naskapi; Smith et al. 2000). The presence of both A1*Naskapi and haplogroup X in the same Algonquian and Siouan samples has been interpreted as the result of either a recent common ancestry or very early prehistoric contact and admixture (Smith et al. 2000). The extremely high level of sequence divergence in both Algonquian- and Siouan-speaking groups in com-

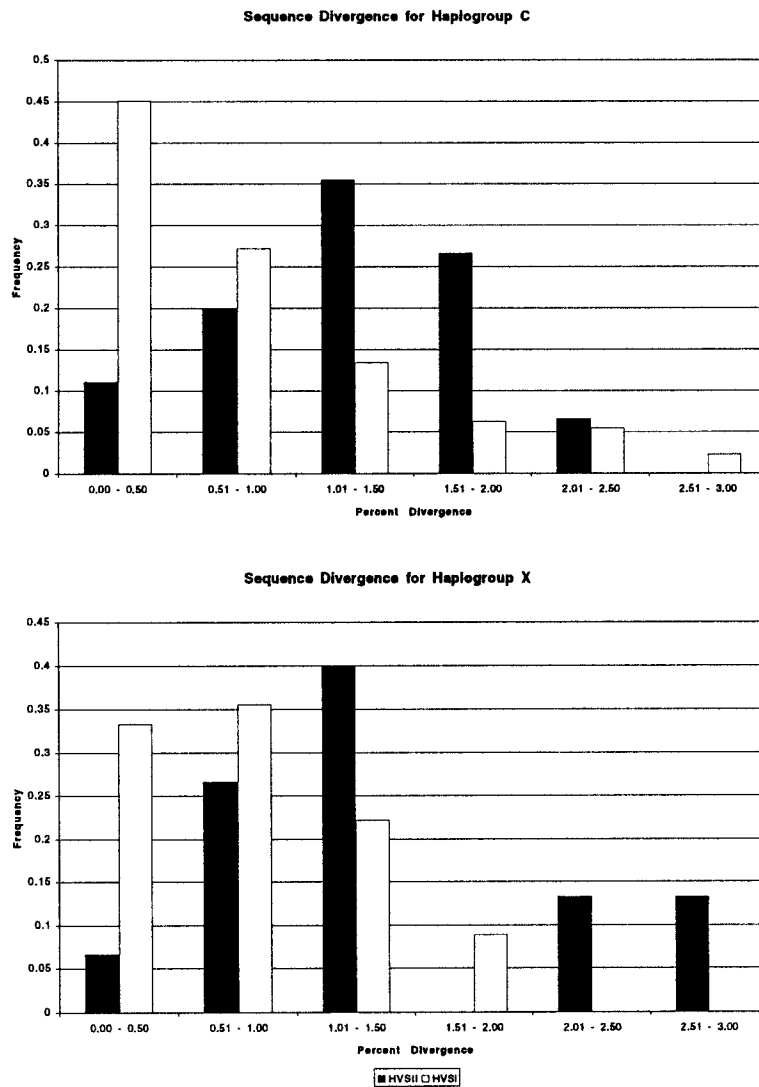


Figure 7. Continued

parison to those of the Cherokee or other previously studied groups (Lorenz and Smith 1997) is consistent with admixture between the two groups. The presence of a high level of mtDNA variation in the pre-Columbian Norris Farms population suggests that this admixture was a prehistoric event.

Populations with different demographic histories display different mismatch distributions (Harpending et al. 1998; Mountain et al. 1995). For ex-

ample, expanding populations that have been isolated from other groups exhibit smooth unimodal mismatch distributions, while stationary populations typically exhibit bumpy multimodal mismatch distributions (Harpending et al. 1998). If a population is conceived from a polymorphic ancestral population, all mismatch distributions within a haplogroup should be similar, having experienced the same demographic events. If population structure was developed through admixture events, the haplogroup mismatch distributions will likely show different patterns reflecting the various population histories of the ancestral groups that admixed to form the current population. Our data presented above confirm the general observation that HVSII evolves at a faster rate than HVSI and therefore mismatch distributions for HVSII should pass through the Poisson distribution characteristic of an expanding population faster than HVSI. While HVSI shows signs of an expanding population for the peopling of the Americas, HVSII has evolved at a faster rate and shows Native American populations as a stationary, nongrowing group. Overall, inferences drawn from mismatch distribution patterns for HVSII are compatible with those for HVSI.

Even while growing rapidly, populations that have experienced a large amount of recent admixture can also exhibit multimodal mismatch distributions. The mismatch distributions for haplogroups A, C, and X in Algonquian and Siouan speakers are multimodal. It is unlikely that these multimodal distributions result from multiple origins of haplogroups in the New World, because those for haplogroups A, B, C, and X (for all Northeastern populations) show signs of an expanding population that has experienced a genetic bottleneck in its recent history. Therefore, we hypothesize that either (1) these groups have a recent common ancestor and were not expanding or (2) these groups admixed in the past causing them to equilibrate genetically, but maintain their linguistic separation. The geographic distribution of the Algonquian languages and archaeological evidence suggest that Algonquian speakers expanded dramatically during the last three millennia (Fiedel 1987; Denny 1991). For example, material culture believed to be related to proto-Algonquian populations, such as the Wright's Laurel complex, shows signs of rapid spread into the Great Lakes Region at approximately the same time that glottochronological data estimate the divergence among Algonquian languages to have occurred (Fiedel 1987). Therefore, the mismatch distributions, based on control region sequence variation, indicate the intrusion of a growing Algonquian population and its prehistoric admixture with Siouan speakers. As with both Athapaskan and Uto-Aztecan intruders in the American Southwest (Smith et al. 2000), admixture of the Algonquian immigrants with the extant Northeastern tribes probably facilitated, and might even have made possible, this population expansion.

The haplogroup networks in Figure 3 suggest that the proto-Algonquian speakers probably contributed some haplotypes of haplogroups A, C, and X to modern populations in the Northeast. A majority of haplogroup A haplo-

types in modern populations in the Northeast might descend from a proto-Algonquian population. Algonquian haplotypes are distributed throughout the haplogroup *C* network, suggesting that proto-Algonquians also contributed some haplogroup *C* haplotypes to modern Northeast populations. The distribution of haplogroup *X* in North America suggests for it a Pacific Northwest homeland, since it is found in many distantly related Native American populations in that region (Smith et al. 1999). Since haplogroup *X* is both especially common and ubiquitous in Algonquian populations (Brown et al. 1998; Smith et al. 1999), it was probably introduced to Siouan populations by admixture with proto-Algonquian emigrants from the Pacific Northwest.

The haplogroup *B* network (and, though less clearly, the haplogroup *C* network) provide support for Chafe's (1976) Macro-Siouan hypothesis. This network portrays Siouan, Iroquoian, and Caddoan control region sequences as closely related and distant from Algonquian and Yurok sequences. This view is consistent with both the pairwise F_{ST} estimates for these groups and the principal components analysis. The genetic relationship of Algonquian and Yurok has only recently been convincingly documented (Goddard 1975), and the clustering of the Yurok with Algonquian haplotypes in this network provides genetic confirmation of this relationship.

Algonquians introduced significant numbers of haplogroups *A*, *C*, and *X* haplotypes to the prehistoric Northeast populations. Based on ancient DNA studies of an archaic maritime population in Labrador (Jelsma et al., personal communication), these populations already carried these haplogroups (especially haplogroup *C*). The mtDNA haplotype networks thus suggest that the spreading Algonquian population absorbed Siouan females, whereas Cherokee populations, possibly due to their matrilineal social structure and/or geographic location, did not absorb as large a proportion of Algonquian females into their population.

The Mohawk, an Iroquoian-speaking group, show some discontinuity with other Northeast populations. Like other northeastern tribes, the Mohawk exhibit a high frequency of haplogroup *A*. However, like the Cherokee, another Iroquoian-speaking group, they also have a high frequency of haplogroup *B* and lack haplogroup *X*. The Mohawk display a haplogroup frequency distribution resembling a mixture of the Cherokee in the southeastern United States and of non-Iroquoian northeastern groups. Genetic evidence from this study is consistent with archaeological evidence of a cultural intrusion into the Northeast by Iroquoians (Clemson Island culture, circa 1300 ybp) and linguistic evidence for the simultaneous divergence of both the Algonquian and the Iroquoian language families (Fiedel 1987). This evidence suggests that Iroquoian presence in the Northeast resulted from a population movement from the south (which geographically divided the central and eastern Algonquians) rather than a cultural (or linguistic) diffusion. The fact that the mtDNA haplogroup frequency distribution of the Mohawk has not reached equilibrium with that of other Northeast populations is consistent with a rela-

tively recent population intrusion. The matrilineal social system of Iroquoian-speaking populations might also have delayed the equilibration of the mtDNA haplogroup distribution of the Northern Iroquois with that of other neighboring groups, since socioeconomic benefits would favor female philopatry. Analysis of Y-chromosome variation among these populations might clarify this issue.

Genetic evidence presented in this study is also consistent with a recent Iroquoian (Cherokee) intrusion into the Southeast. The Iroquoian presence also conforms with Cherokee oral tradition that their ancestors were the builders of the Hopewell Earthmounds in the Ohio Valley (approximately 2000 ybp) (Mooney 1900). In analyzing eight ancient samples from the Fort Ancient culture (1000–450 ybp) that followed the Hopewell tradition in the Ohio River Valley, Merriwether et al. (1995) found that none of the samples were members of haplogroup *B*, which is common in modern Cherokee. Using the binomial probability distribution, the probability of obtaining at least one member of haplogroup *B* from eight randomly selected members of a group with haplogroup frequencies identical to those of the Cherokee studied here is 0.973. Thus, this preliminary data suggest that it is unlikely that the Fort Ancient individuals analyzed by Merriwether et al. (1995) are ancestral to the Cherokee. Furthermore, if the ancestors of the Cherokee were the Ohio Valley Hopewell Moundbuilders, another population must have replaced them before the onset of the Fort Ancient Culture period. It is also possible that the populations of the Hopewell culture were descendants of proto-Algonquians, as suggested by Denny (1991), and that the Cherokee descend from the earlier inhabitants of the Ohio Valley, who might have been displaced to the southeastern United States by the proto-Algonquians. Studies of the ancient mtDNA of Hopewell, Adena, and late Archaic populations in the Ohio Valley, which are currently being planned, are needed to select among these alternative hypotheses.

Finally, the pairwise F_{ST} comparisons and the haplogroup *B* network provide evidence for the existence of a Macro-Siouan population, ancestral to Iroquoians, Siouans, and Caddoans, early in the prehistory of eastern North America. Algonquian-speaking populations display genetic markers (e.g., Al*Naskapi and Haplogroup *X*) that are common among populations in the Pacific Northwest but absent among all other eastern groups. Proto-Algonquian populations probably invaded the Northeast from the Pacific Northwest, admixing with the prehistoric residents of the Northeast and introducing new forms of haplogroups *A*, *C*, and *X*.

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