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Mitochondrial DNA and Prehistoric Settlements: Native Migrations on the Western Edge of North America

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Abstract We analyzed previously reported mtDNA haplogroup frequencies of 577 individuals and hypervariable segment 1 (HVS1) sequences of 265 individuals from Native American tribes in western North America to test hypotheses regarding the settlement of this region. These data were analyzed to determine whether Hokan and Penutian, two hypothesized ancient linguistic stocks, represent biological units as a result of shared ancestry within these respective groups. Although the pattern of mtDNA variation suggests regional continuity and although gene flow between populations has contributed much to the genetic landscape of western North America, some evidence supports the existence of both the Hokan and Penutian phyla. In addition, a comparison between coastal and inland populations along the west coast of North America suggests an ancient coastal migration to the New World. Similarly high levels of haplogroup A among coastal populations in the Northwest and along the California coast as well as shared HVS1 sequences indicate that early migrants to the New World settled along the coast with little gene flow into the interior valleys.

Before European contact, the western edge of North America exhibited an exceptionally high level of linguistic diversity (Campbell 1997; Mithun 1999), with 90 separate languages being spoken in California alone (Moratto 1984). This great diversity has been cited as evidence for a greater antiquity of human occupation in these regions than in the rest of the Americas [J. Nichols 1990; but see also Nettle (1998)]. Particular patterns of this diversity have also been used to formulate hypotheses of human migration and expansions in western North America as well as a higher-level subgrouping that is presumed to reflect closer relationships among certain groups of Native American populations.

Dixon and Kroeber (1913) first proposed the existence of the Hokan and

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Penutian language superstocks in California. California Penutian includes four language families—Wintuan, Maiduan, Yokutsan, and Utian (which itself includes the Miwok and Costanoan subfamilies)—which are further subdivided into approximately 30 distinct languages. Hokan languages include a number of language families in California, the Yuman languages in Baja and the southwestern United States, and Washo on the western edge of the Great Basin (Campbell 1997; Campbell and Mithun 1979; Mithun 1999). The notable nonrandom distribution of various Penutian and Hokan languages has long suggested to prehistorians a wave or waves of Penutian migrations into California. Penutian speakers eventually occupied the interior valley extending to the coast around the San Francisco Bay Area, whereas a number of Hokan-speaking populations occupied the periphery of the Central Valley (Moratto 1984). This ring of Hokan-speaking groups surrounding a contiguous body of Penutian-speaking tribes suggests to some that at one time the whole of California was occupied by Hokan speakers who were later displaced to the valley periphery by an expansion of Penutian speakers from a central California homeland (Kroeber 1935).

The “Hokan–Penutian” hypothesis has had considerable influence on interpretations of California prehistory (Breschini 1983; Moratto 1984). Glottochronological estimates for the age of the Utian branch of the Penutian stock (the Miwok and Costanoan language families) in California fall between 4500 and 5200 years B.P. (Callaghan 1997; Moratto 1984). This date coincides closely with the appearance of the Windmill pattern in the Central Valley, suggesting that the Windmill pattern represents the earliest presence of Penutian peoples in the area (Fredrickson 1973; Ragir 1972). Archeological characteristics of Windmill mortuary practices include extended burials, the presence of *Haliotis* and *Olivella* beads, characteristic charm stones, red ochre, and large projectile points (Ragir 1972). Similar archeological elements at the Kramer Cave site in western Nevada further suggest cultural contact between Great Basin peoples and the coeval Windmill cultures, whereas red ochre, charm stones, and large, contracting stem-and-leaf-shaped projectile points suggest links between Windmill and the Dalles sites in Oregon (9800–6000 years B.P.) on the Columbia Plateau (Hattori 1982), where other languages that are sometimes assigned to the Penutian superstock of languages are spoken (Sapir 1929). Foster (1996) associated Windmill with Proto-Utian and placed their homeland in the northwestern Great Basin or on the Columbia Plateau, as suggested by similarities in the Altithermal cultures in these regions. Mitochondrial DNA of ancient burials at Pyramid Lake and Stillwater Marsh in western Nevada closely resembles that of modern California Penutians but not that of the neighboring Washo population (a Hokan-speaking group) in the Sierra Nevada (Kaestle and Smith 2001). The argument then suggests that all these areas—the western Great Basin, the Columbia Plateau, and the California Central Valley—were once occupied by closely related people who spoke languages of the Penutian stock.

The vast majority of unadmixed modern Native Americans are members of one of five maternal founding lineages or haplogroups, designated as haplogroups

A, B, C, D, and X (Brown et al. 1998; Forster et al. 1996; Schurr et al. 1990; Torroni et al. 1993). These haplogroups are readily distinguished by the gain or loss of one or more restriction sites or, in the case of haplogroup B, by the presence or absence of a 9 base pair deletion in the COII-tRNA^{lys} intergenic region (Schurr et al. 1990) and are associated with corresponding point mutations in the control region (CR) of the mtDNA (Torroni et al. 1993). Each haplogroup can be further divided into multiple discrete haplotypes, or groups of closely related haplotypes, on the basis of additional CR mutations (Torroni et al. 1993).

In North America the distribution of the five haplogroups is decidedly non-random, and significant regional patterning exists (Lorenz and Smith 1996; Smith et al. 1999). Studies of ancient mtDNA diversity in North America reveal that Native American haplogroup frequency distributions in some regions exhibit marked temporal and regional continuity (Carlyle et al. 2000; O'Rourke et al. 2000). Carlyle et al. (2000) demonstrated that the haplogroup frequency distribution of ancient human remains associated with the Anasazi cultural tradition in the American Southwest is not significantly different from that of modern Pueblo populations, such as the Zuni. This study provides biological and cultural evidence for unbroken ancestor or descendant relationships in the American Southwest, spanning at least the last 2000 years. In contrast, Kaestle and Smith (2001) demonstrated that ancient western Great Basin populations are genetically dissimilar to modern populations in the same region, probably because of a population spread of Numic speakers into the Great Basin from Southern California approximately 1000 years B.P. (Bettinger and Baumhoff 1982).

Although on a general worldwide level there is a relatively high correspondence between genes and language (Cavalli-Sforza et al. 1992), this relationship might not hold on more local levels (Shields et al. 1993; Ward et al. 1993). Some Native American populations that lack close linguistic ties in the Pacific Northwest share similar haplogroup frequency distributions and several distinct mtDNA haplotypes (Ward et al. 1993), but most Native American populations in western North America have not been studied. Similarly, Uto-Aztecan-speaking and Yuman-speaking populations in the Southwest share similarities in their mtDNA without any apparent close linguistic ties (Lorenz and Smith 1996; Malhi et al. 2003).

The present study uses mtDNA to investigate the genetic relationships among a broader range of populations in western North America, an area that exhibited considerable linguistic diversity at the time of European contact. Because the patterning of this linguistic diversity has been used to generate hypotheses of prehistoric population movements and expansions, we examine the distribution of mtDNA haplogroups and haplotypes in the context of this linguistic diversity and the archeological record.

Subjects and Methods

Haplogroup identities of 584 Native Americans, representing 11 populations, and sequences from a segment of the first hypervariable region (HVS1) of

the control region (np 16,090–16365) of 265 of these individuals were gathered from previously published sources, cited in Table 1 (Kaestle and Smith 2001; Johnson and Lorenz 2003; Malhi 2001; Malhi et al. 2003; Shields et al. 1993; Ward et al. 1991, 1993). Sequences that could not be assigned to one of the five known Native American founding haplogroups were not included in these analyses. Although some unassigned sequences might represent yet undocumented founding Native American mtDNA types, the frequency of “other” types is rather low and likely represents recent admixture (Huoponen et al. 1997; Smith et al. 1999; Torroni et al. 1993, 1994). The populations, their sample sizes, and their relative haplogroup frequencies are summarized in Table 1, and their geographic locations are given in Figure 1. Samples from Yokuts, Miwok, and Costanoan (Ohlone) individuals—all hypothesized to be members of the Penutian language stock—were included in a single Yok–Utian population. The Yok–Utian subgrouping within Penutian follows the linguistic classification proposed by Callaghan (1997).

Comparisons between the haplogroup frequency distributions of all population pairs were made using Fisher’s exact test (Weir 1990) using a Markov chain method to estimate the exact p value over 1000 iterations. Calculations were performed using the Genepop on the Web software package (Raymond and Rousset 2002), and mean probability and standard error are reported. Three measures of genetic distance—Nei’s D (Nei 1972), the chord distance of Cavalli-Sforza and Edwards (1967), and the Reynolds et al. (1983) distance measure—were calculated between members of all population pairs using Gendist in the PHYLIP (version 3.6a2) software package (Felsenstein 2001) and treating the five haplogroups as alleles at a single locus. From each of these distance estimates, trees were generated using the Fitch and Neighbor algorithms (Felsenstein 2001). The default settings were used for each tree-building algorithm, except that taxa input order was randomized for all trees. A consensus tree was created from the six trees using Consense and was plotted using Drawtree in PHYLIP.

A matrix of linear geographic distances (see Table 4) was created between all pairs of populations by estimating distance between the centers of the hypothesized homelands of all populations, as depicted in the *Handbook of North American Indians* (Sturtevant 1978, v. 17) and from Kroeber (1939). Mantel’s test of matrix correlation, using 1000 random permutations of the original matrices, was performed on the geographic and genetic distances matrices using the Arlequin software package, version 2.000 (Schneider et al. 1997). Subsets of the matrix, including the coastal groups (Chumash, Nu-Chah-Nulth, Bella Coola, and Haida), the “Penutian” groups (Wishram, Yakama, and Yok–Utian), and the Northwest groups (Haida, Bella Coola, Nu-Chah-Nulth, Wishram, and Yakama), were also analyzed for correspondence between genetic and geographic distance.

Because of the polyphyletic nature of mtDNA lineages in the Americas (Schurr et al. 1990), we performed all analyses of discrete haplotype variations separately for each haplogroup. Molecular diversity for the control region sequences of 265 individuals from the region was estimated by θ_S . θ_S is calculated as (Watterson 1975)

Table 1. Samples and Haplogroup Frequency Distributions

<i>Population</i>	<i>Linguistic Stock</i>	<i>N</i>	<i>Haplogroup A</i>	<i>Haplogroup B</i>	<i>Haplogroup C</i>	<i>Haplogroup D</i>	<i>Haplogroup X</i>	<i>References</i>
Chumash	Isolate?	21	0.524	0.000	0.143	0.333	0.000	Johnson and Lorenz (2003)
Bella Coola	Salish	84	0.655	0.107	0.095	0.143	0.000	Malhi (2001); Ward et al. (1993)
Nuu-Chah-Nulth	Wakashan	102	0.451	0.069	0.157	0.255	0.069	Ward et al. (1991, 1993)
Haida	Isolate?	41	0.854	0.024	0.073	0.049	0.000	Ward et al. (1993)
Yok-Utian	Penutian	17	0.118	0.294	0.118	0.471	0.000	Johnson and Lorenz (2003)
Northern Paiute	Uto-Aztecan	94	0.000	0.426	0.096	0.479	0.000	Kaestle and Smith (2001)
Washo	Hokan	28	0.000	0.536	0.357	0.107	0.000	Kaestle and Smith (2001)
Yakama	Penutian	42	0.048	0.667	0.071	0.167	0.048	Shields et al. (1993)
Wishram	Penutian	33	0.212	0.515	.0000	0.273	0.000	Malhi (2001)
Takic	Uto-Aztecan	15	0.000	0.200	0.533	0.267	0.000	Johnson and Lorenz (2003)
Yuman	Hokan	100	0.030	0.590	0.380	0.000	0.000	Malhi et al. (2003)
Total		577	0.277	0.324	0.173	0.211	0.015	

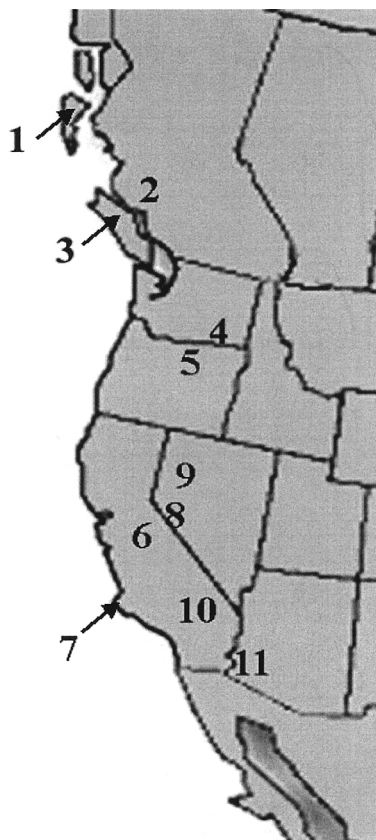


Figure 1. Geographic locations of populations analyzed in this study. (1) Haida (isolate); (2) Bella Coola (Salish); (3) Nuu-Chah-Nulth (Wakashan); (4) Yakama (Penutian superstock); (5) Wishram (Penutian superstock); (6) Yok-Utian (Miwok, Costanoan, and Yokuts; Penutian superstock); (7) Chumash (isolate); (8) Washo (Hokan superstock); (9) Northern Paiute (Uto-Aztecan language family); (10) Takic (subfamily of Uto-Aztecan language family); (11) Yuman (Hokan superstock).

$$\theta_s = \frac{S}{\sum_{i=1}^{n-1} \frac{1}{i}},$$

where S is the number of segregating sites among the approximately 270 base pairs studied and n is the sample size. θ_s is less likely to be influenced by sampling error or genetic drift than are other measures of nucleotide diversity, and, consequently, it reflects a long-term average estimate of diversity (Ewens 1983).

We estimated Tajima's D statistic to test whether or not populations were at equilibrium (Tajima 1989). Because the segment of the studied control region

appears to be selectively neutral (Di Rienzo and Wilson 1991), statistically significant values of D indicate that the population is not at equilibrium as a result of past demographic events, such as population expansions or bottlenecks.

Both θ_s and Tajima's D were calculated using the Arlequin software package (Schneider et al. 1997).

Results

Haplogroup Frequency Analysis. The distributions of the five haplogroups varied significantly between populations (Table 1). Haplogroup A, the most common haplogroup in North America (Lorenz and Smith 1996) was found in high frequency among the Bella Coola, Chumash, Haida, and Nuu-Chah-Nulth, populations located along the coastal margin of the continent. Elsewhere, haplogroup A was rare or absent, although the lone Esselen sequence examined was also a member of haplogroup A and haplogroup A has also been identified in reasonably high frequencies in the Salinan (Lorenz and Smith 1996). In contrast, haplogroup B was rare among coastal populations but common among all other populations. Haplogroup X was detected only in the Nuu-Chah-Nulth and the Yakama. In western North America haplogroup X has also been reported in the Pomo, Navajo, and Jemez (Smith et al. 1999).

Figure 2 displays a consensus tree produced in PHYLIP from six trees using three different distance measures and two tree-building algorithms. A clade containing four coastal populations, the Haida, Bella Coola, Nuu-Chah-Nulth, and Chumash (H-BC-NCN-C), was supported using all three distance measures and both tree-building algorithms. A second clade containing the Takic, Yuman, and Washo (T-Y-W) was supported in five of the six reconstructions, each of which also supported a Washo–Yuman clade.

Chord distance (Cavalli-Sforza and Edwards 1967) and Fisher's exact test between all population pairs are reported in Table 2, whereas Nei's D and the Reynolds distance measure are reported in Table 3. Similar to the results of the consensus tree, the Chumash fall closer to the Nuu-Chah-Nulth and Bella Coola than to any other populations in all distance measures analyzed. The haplogroup frequency distribution of the Chumash did not differ statistically significantly from that of either population at the 0.05 level of probability using Fisher's exact test, despite the great geographic distance between them. However, the Bella Coola and Nuu-Chah-Nulth were statistically different from each other. Because Fisher's exact test is heavily influenced by sample size, some similarities are likely to be the result of small samples. The Yok–Utians were not statistically significantly different from either the Wishram or the Takic groups at the 0.05 level of probability, although all were different at the 0.10 level of probability. The Washo and Yuman groups were distinguishable, whereas the Takic and Washo were not, contrary to the pairings favored in the consensus tree. However,

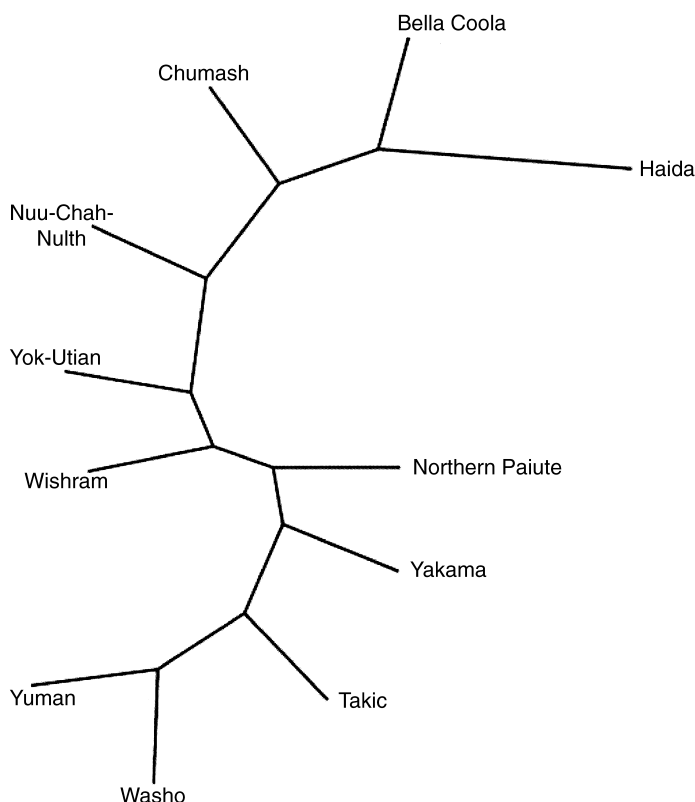


Figure 2. Consensus tree of western North American populations based on genetic distances constructed with mtDNA haplogroup frequencies.

the samples of Washo and Takic ($n = 28$ and $n = 15$, respectively) were relatively small compared to the Yuman ($n = 100$). The distance measures used to produce the trees do not consider sample size, whereas Fisher's exact test is sensitive to small samples.

The Mantel test of matrix correspondence revealed a significant positive correlation ($p < 0.02$) between geographic distance and each of the measures of genetic distance between pairs of all 11 populations (Table 4). Although geographic and genetic distances showed a statistically significant positive correlation among the populations of the Northwest group, no significant relationship occurred among the "Penutian" populations or among the populations in either of the two clades [the coastal group (H-BC-NCN-C) or the T-Y-W group] supported in all trees.

Haplotype Analysis. Molecular diversity, measured with θ_S , the standard deviation of θ_S , and Tajima's D , are reported in Table 5. The diversity estimates for

Table 2. Fisher's Exact Probabilities (Above the Diagonal) and Chord Distances^a Between Population Pairs (Below the Diagonal)

Population	Chumash	Yok-Utian	Washo	Takic	Yuman	Yakama	Haida	Bella Coola	Nuu-Chah-Nulth	Wishram	Northern Paiute
Chumash											
Yok-Utian	0.2254										
Washo	0.5853	0.1733									
Takic	0.4257	0.1521	0.0674								
Yuman	0.6415	0.3123	0.0693	0.2064							
Yakama	0.5048	0.1099	0.1092	0.2291	0.1705						
Haida	0.1011	0.3538	0.6527	0.6191	0.5544	0.5086					
Bella Coola	0.0794	0.1792	0.4527	0.4333	0.4186	0.3189	0.0344				
Nuu-Chah-Nulth	0.0726	0.1442	0.4058	0.3323	0.4377	0.2699	0.1199	0.0575			
Wishram	0.3652	0.0941	0.3037	0.4091	0.369	0.0995	0.3477	0.195	0.2384		
Northern Paiute	0.4835	0.0637	0.1106	0.1243	0.3077	0.1016	0.662	0.4293	0.3563	0.17	

a. Cavalli-Sforza and Edwards (1967).

Table 3. Nei's *D* Results Between Population Pairs (Above the Diagonal) and Reynolds Distances Between Population Pairs (Below the Diagonal)

<i>Population</i>	<i>Chumash</i>	<i>Yok-Utian</i>	<i>Washo</i>	<i>Takic</i>	<i>Yuman</i>	<i>Yakama</i>	<i>Haida</i>	<i>Bella Coola</i>	<i>Nuu-Chah-Nulth</i>	<i>Wishram</i>	<i>Northern Paiute</i>
Chumash											
Yok-Utian	0.1772										
Washo	0.3606	0.1748									
Takic	0.2821	0.1572	0.1257								
Yuman	0.4082	0.2479	0.0144	0.1823							
Yakama	0.3885	0.1694	0.0893	0.2844	0.114						
Haida	0.1855	0.4618	0.5626	0.5404	0.5877	0.5805					
Bella Coola	0.0563	0.2654	0.3822	0.3624	0.4117	0.3955	0.0658				
Nuu-Chah-Nulth	0.016	0.1361	0.2774	0.2197	0.3205	0.3059	0.1855	0.0496			
Wishram	0.2422	0.0797	0.1442	0.2599	0.1868	0.057	0.4468	0.2534	0.1787		
Northern Paiute	0.29	0.025	0.1593	0.195	0.2372	0.1277	0.561	0.3671	0.2337	0.0804	

Table 4. Geographic Distances (km) Between Population Centers Used to Calculate Mantel Test of Matrix Correlation

<i>Population</i>	<i>Chumash</i>	<i>Yok- Utian</i>	<i>Washo</i>	<i>Takic</i>	<i>Yuman</i>	<i>Yakama</i>	<i>Haida</i>	<i>Bella Coola</i>	<i>Nuu-Chah- Nulth</i>	<i>Wishram</i>	<i>Northern Paiute</i>
Chumash											
Yok-Utian	188										
Washo	493	329									
Takic	242	271	588								
Yuman	477	552	867	281							
Yakama	1389	1219	897	1452	1716						
Haida	2242	2116	1796	2382	2663	1091					
Bella Coola	2038	1890	1562	2146	2422	755	394				
Nuu-Chah-Nulth	1716	1575	1249	1836	2115	537	570	443			
Wishram	1314	1151	823	1396	1667	132	1068	765	499		
Northern Paiute	706	274	221	765	1035	691	1606	1389	1042	632	

Table 5. Molecular diversity (θ_s) and Tajima's D for Haplogroups A, B, C, and D

<i>Haplogroup</i>	<i>Haplotype</i>	θ_s	<i>Standard Deviation</i> <i>of θ_s</i>	<i>Tajima's D</i>	<i>P</i>
A	43	6.702501	2.237482	− 1.92941	0.01574
B	37	6.707294	2.300276	− 2.04577	0.00969
C	48	8.562485	2.714194	− 1.86218	0.02012
D	45	8.00416	2.588121	− 2.22183	0.00394

haplogroups A and B appear slightly lower than those for haplogroups C and D. Tajima's D was statistically significantly negative at or below the 0.02 level of probability for all four haplogroups.

Discussion

Regional Patterning of mtDNA and Language Groups. Although marked by considerable language diversity and sharp divisions among apparently unrelated language stocks, the distribution of mtDNA types follows a pattern of regional continuity and isolation by distance as a result of restricted gene flow throughout the western edge of North America. Significantly negative values of Tajima's D indicate departures from neutrality. Although significantly negative values of Tajima's D could also result from selection on the mitochondria, it seems unlikely that similar selection would be seen in all four lineages. Negative values of Tajima's D also could be a product of higher levels of heterogeneity in mutation rates within the control region, as has been observed elsewhere (Stoneking 2000) or, alternatively, from population expansions in prehistory. This latter possibility stands in contrast to the conclusions of Malhi et al. (2002) that haplogroups C and D show less evidence of expansion across the North American continent than haplogroups A and B based on analyses of haplotype networks for all four haplogroups. Although it is possible that regional expansions of haplogroups C and D in the West account for this discrepancy, it is also possible that the significantly negative values for Tajima's D are the result of other processes. In general, both the Fisher's exact test of homogeneity and the Mantel test support the observation that neighboring populations are less differentiated than more geographically distant pairs, suggesting that substantial gene flow has occurred. That geographic neighbors are generally less likely to show statistical differentiation through Fisher's exact test and the Mantel test indicates that genetic distance strongly correlates with geographic distance throughout western North America. Regional continuity and isolation by distance have been reported elsewhere in North America (Carlyle et al. 2000; Lorenz and Smith 1996; Malhi et al. 2001, 2002, 2003; O'Rourke et al. 2000).

Despite the strong regional patterning and notwithstanding that languages are not inherited in the same manner as mtDNA, some evidence supports distant genetic relationships between groups hypothesized to share common ancestry

based on linguistic similarities. Kroeber (1915) and Dixon and Kroeber (1919) hypothesized that Washo and Yuman languages are related within the Hokan language stock. Although this linguistic relationship is itself problematic [see Campbell (1997)], the mtDNA haplogroup frequency distributions from Yuman and Hokan groups do show similarities; both groups exhibit high frequencies (>50%) of haplogroup B with secondarily high frequencies (>35%) of haplogroup C. However, this is broadly characteristic of most other populations in the Southwest (Malhi et al. 2003). All three measures of genetic distance indicate that Yuman is more closely related to Washo. Such close genetic ties over a great geographic distance could indicate common ancestry at some distant point in time, consistent with the inclusion of Washo and Yuman into Hokan and, by extension, with the existence of Hokan as a meaningful entity.

The consensus tree generated from pairwise genetic distances places Takic as a sister taxon to a Washo–Yuman clade; in agreement with this, Takic is not statistically differentiated from Washo based on Fisher's exact test, although this is likely due to the relatively small sample size of both populations. In fact, unlike Nei's *D* and the Reynolds distance, chord distance places Takic marginally closer to Washo than Washo is to Yuman. The close genetic ties between Takic, a subgroup within northern Uto-Aztecan languages, and the Hokan populations stands in contrast to the linguistic evidence, which shows no apparent linguistic genetic ties between Hokan languages and Uto-Aztecan languages (Campbell 1997; Campbell and Mithun 1979). Similarly, the mtDNA of speakers of the Numic languages, another group of northern Uto-Aztecan languages, more closely resembles that of non-Uto-Aztecan-speaking groups than other northern Uto-Aztecan-speaking groups, such as Takic. Hill (2001) recently hypothesized that the northern branch of the Uto-Aztecan language family, including Takic, spread northward with the spread of maize agriculture. However, Malhi et al. (2003) showed that the mtDNA haplogroup frequencies and discrete sequence variation in haplogroup C among Uto-Aztecs in the Southwest are not consistent with such a spread. Moreover, M.J.P. Nichols (1981) cited linguistic evidence of an earlier presence of Uto-Aztecan speakers in California before a southward movement of Uto-Aztecs. According to this scenario, the progenitors of Takic speakers would long have been neighbors of Hokan populations in California, and subsequent mtDNA gene flow could account for the similarities between these neighbors.

Alternatively, the Washo, Yuman, and Takic similarities may be seen as more generally similar of Southwestern desert populations, which likewise share relatively high frequencies of haplogroup C (Malhi et al. 2003). The Washo likely inhabited parts of the southern Sierra Nevada and Great Basin, closer to Yuman populations, before the Numic spread (V. Golla, personal communication, 2002). If so, regional patterning would explain the similarities.

No close genetic ties are evident between Chumashan peoples and either Yuman or Washo, although all were once hypothesized to be linguistically related within the wider scope of Hokan (Dixon and Kroeber 1919; Sapir 1929). That

Chumashan–Hokan language ties have largely been dismissed (Campbell 1997; Mithun 1999) is consistent with the mitochondrial evidence, which shows sharp divides between the Chumash on the one hand and the Washo and Yumans on the other. The mtDNA diversity of Northern Hokan populations is known only through a limited sample ($n = 6$) (Kaestle and Smith 2001; Lorenz and Smith 1996) but appears rather divergent from the Chumash, because haplogroup A, the frequency of which approaches 50% in the Chumash, is yet unknown among the Northern Hokan. If both the Northern Hokan and Chumash were members of a common mtDNA gene pool in which the frequency of haplogroup A was 0.5, then the probability of sampling 6 individuals, none of whom were members of haplogroup A, is $(0.5)^6$, or less than 0.016. Although the Washo, Yuman, and Northern Hokan groups might descend from a common genetic stock consistent with the Hokan language hypothesis, it is unlikely that the Chumash are closely related to any of these populations.

Evidence of genetic ties within Penutian is also equivocal but suggestive of common ancestry. Unlike Hokan, within which populations are argued to have diversified largely in situ, the distribution of the Penutian languages is thought to have resulted from multiple interregional migration(s) and demic spreads encompassing populations of California, the Great Basin, and the Columbia Plateau (DeLancey and Golla 1997). Languages as far north as British Columbia and as far south as southern Mexico have at one time or another been argued to belong to the Penutian stock of languages (Sapir 1929). The genetic distance between the Central Valley Yok–Utians and the Yakama of the Columbia Plateau in itself does not offer overwhelming support for a Penutian hypothesis, and the small genetic distance between the Wishram and Yakama, both languages of neighboring tribes assigned to the Plateau group of Penutian languages, could easily be explained by gene flow resulting from their geographic proximity. Haplogroup D does appear to unite groups on the Columbia Plateau with the Central Valley Yok–Utians; however, it is also found in the Chumash. It is possible that the Chumash acquired haplogroup D from neighboring Yok–Utians, who themselves entered California as part of a migration of Penutian speakers from either the Great Basin or the Columbia Plateau, although Chumash D lineages include specific derived types not shared with the Yok–Utians (Johnson and Lorenz 2003). The haplogroup frequency distribution of the Plateau Wishram and the Central Valley Yok–Utians, both of whom have high frequencies of haplogroup D, are not distinguishable at the 0.05 level of probability, and the genetic distances between the two are relatively small. Because high frequencies of haplogroup D are not common in either alleged Hokan group and, in fact, haplogroup D is relatively rare throughout North America, its presence in Wishram and Yakama of the Plateau and Yok–Utians of the Central Valley of California might reflect a distant genetic relationship consistent with the Penutian language hypothesis. Curiously, this high frequency of haplogroup D is also shared with the Northern Paiute, speakers of a Numic language within the Uto-Aztecan language family

that has no close connection with Penutian. Kaestle and Smith (2001) demonstrated that mtDNA analyzed from ancient samples in the western Great Basin is not consistent with an early occupation of this region by Numic speakers, suggesting that the Numic people arrived in this region recently. Linguistic (Lamb 1958) and archeological evidence (Bettinger and Baumhoff 1982) supports a recent Numic expansion into the Great Basin. Although the mtDNA haplogroup frequencies of the ancient inhabitants of the western Great Basin do not resemble those of the modern inhabitants of the western Great Basin, they are statistically indistinguishable from a California Penutian population (Kaestle and Smith 2001). The contrast between mtDNA haplogroup frequencies among modern Numic speakers and the ancient inhabitants of the western Great Basin is consistent with a recent Numic spread, but Kaestle and Smith (2001) indicated that this spread may not have involved a complete replacement of older populations. The high frequency of haplogroup D among the Numic may have resulted from admixture between Numic and pre-Numic populations, among whom the frequency of haplogroup D was also high. If the pre-Numic population was ancestral to modern Penutians in California (Breschini 1983; Moratto 1984) or part of a larger Penutian population that was once spread throughout California, the western Great Basin, and the Columbia Plateau, the mtDNA of the Numic might now resemble that of the modern Penutian populations as a result of admixture with the ancient inhabitants of the Great Basin.

MtDNA Affinities Among Coastal Populations. Regional continuity dominates the mtDNA landscape, but there is a sharp contrast between coastal and interior populations. Haplogroup A, the most common haplogroup among the Haida, Bella Coola, Nuuchah-Nulth, and Chumash, is rare or absent in all other populations of western North America. In addition to the nodal haplotype of haplogroup A, which is widely spread throughout North America (Malhi et al. 2002), two additional nonnodal haplotypes are shared between the central California coast and the Northwestern populations (although one is shared uniquely with the Yakama on the Columbia Plateau) (Johnson and Lorenz 2003; Shields et al. 1993; Ward et al., 1991, 1993). Although shared haplotypes in haplogroup A would appear to indicate a range expansion among the Northwest coastal populations, which could account for the similarities in the Northwest, this does not immediately explain similarities with Chumash. Chance alone might result in similar haplogroup frequency distributions among Chumash and populations of the Northwest, but it does not explain the shared haplotypes between the Northwest and the central California coast. Likewise, inland neighbors of the Chumash possess little or no haplogroup A. Haplogroup A is rare or absent among both modern and ancient samples from the Southwest (Carlyle et al. 2000), the Great Basin (Kaestle and Smith 2001), and California's Central Valley (Eshleman 2001, 2002). In contrast, haplogroup A is found to the north of the Chumash among coastal populations (Lorenz and Smith 1996) and in three ancient skeletal

samples from Monterey County, south of the San Francisco Bay Area (Eshleman 2002).

The Chumash do show reasonably close genetic ties to neighboring Yok-Utians and Takic populations, but both of the latter populations exhibit rather low frequencies of haplogroup A. If these similarities result from mitochondrial gene flow, female migration toward the coast must have been considerably more common than movement away from the coast. Ornamental shell beads from the Pacific Ocean, dating back to archaic periods (greater than 4000 years B.P.), have been found in the Great Basin, indicating contact with coastal people through trade (Bennyhoff and Hughes 1987). Although some mate exchange might have solidified such trade networks, it does not appear that modern coastal populations spread inland. Mitochondrial gene flow from the interior may have influenced the haplogroup frequency distribution of the Chumash, but it cannot account for either the high frequency of haplogroup A or for shared haplotypes between the Northwest and the central California coast.

For years, the Clovis-first dogma held that the Americas were first settled by trans-Beringian migrants from Asia who traveled south through an ice-free corridor between the Cordilleran and Laurentide ice masses [see Dixon (2001)]. Unless humans entered North America before the last glacial maximum, such passage into the Americas would not have been possible until after about 11,000 years B.P. (Mandryk et al. 2001). There is little or no good evidence of occupation of the Americas as early as some linguistic (J. Nichols 1990; Rogers et al. 1990, 1991) and genetic (Bonatto and Salzano 1997a; Stone and Stoneking 1998; Torroni et al. 1994) arguments suggest, but the apparent occupation of Monte Verde in southern Chile some 12,500 years B.P. (Meltzer et al. 1997) indicates that humans must have either occupied the Americas while remaining archeologically invisible for several thousand years after moving south of the ice masses or else entered through some alternative route. Mounting evidence indicates that a coastal route through the Pacific Northwest would have been passable as early as 14,000 years B.P. (Leonard et al. 2000; Mandryk et al. 2001).

The high frequency of haplogroup A and the corresponding low frequency of haplogroup B among coastal populations is consistent with a migration along the Pacific coast at some point in time. The presence of human remains on Santa Rosa Island off the southern California coast, dating in excess of 10,000 years B.P. (Johnson et al. 2002), indicates that ocean-going people had occupied this territory near the time of the earliest known human occupation of North America. The presence of early ocean-going adaptations along the Pacific coast further supports a coastal migration route into the New World.

The antiquity of such a coastal migration is difficult to ascertain. The relative diversity of haplogroup A in the West is similar in magnitude to that found in haplogroups B, C, and D. This alone does not imply a coastal expansion of haplogroup A equal in age to the expansion of the other haplogroups because the accumulated diversity of all haplogroups probably includes diversification, which occurred in Beringia before a migration south of the ice sheets. A transition at

np 16192, argued to be an Eskimo and Na-Dene specific marker within haplogroup A (Bonatto and Salzano 1997b; Schurr et al. 1999; Starikovskaya et al. 1998), was not detected among the Chumash haplotypes, nor was the Na-Dene specific *RsaI* site loss at np 16329 (Torroni et al. 1993). Consequently, any coastal migration likely would have occurred before the emergence of these markers and the more recent expansions of Na-Dene and Eskimo populations (Bonatto and Salzano 1997b; Schurr et al. 1999; Starikovskaya et al. 1998).

Archeological evidence is also equivocal. The Chumash have almost certainly occupied the Southern California coast for the last 2000 years and perhaps considerably longer (Moratto 1984). Although Harrison (1964) noted links between the prehistoric cultures of the Alaskan coast and the Chumash, King (1990) believed that the cultural chronology of the Chumashan region indicates a long in situ development. There are no apparent linguistic ties between Chumashan languages and any of the languages of the Northwest within the limits of linguistic recoverability (approximately 6000 to 8000 years) (V. Golla, personal communication, 2001; K. Whistler, personal communication, 2001). Although not conclusive, these factors leave us with the real possibility that the genetic similarities between the Chumash and the peoples of the Northwest Coast are the vestige of a very early coastal migration into the New World.

Summary and Conclusions

The results of this study provide genetic support for two hypothesized language stocks. Similarities between Yuman and Washo suggest common ancestry consistent with their affiliation within the Hokan language stock, although these similarities may also be the result of regional continuity within Southwestern desert populations. However, speakers of Chumash languages, once held by some to be members of the Hokan language phylum, exhibit no genetic evidence of such membership. Likewise, genetic evidence provides support for the Penutian language hypothesis based on similar haplogroup frequency distributions among populations of the Columbia Plateau and the Central Valley of California. Mitochondrial DNA haplogroup frequencies also provide support for a prehistoric occupation of the western Great Basin by individuals related to Penutian speakers both on the Columbia Plateau and in California's Central Valley, consistent with archeological and linguistic hypotheses placing Penutian speakers in the Great Basin before the more recent expansion of Uto-Aztecan speakers in the region.

This study also provides evidence of an early coastal migration into the New World. Mounting archeological evidence of a pre-Clovis occupation of the New World combined with climatological evidence further supports a coastal route for the first human migrations into the New World. Evidence of genetic similarities between the Northwest and coastal California presented in this study is indicative of a spread along the western edge of North America that remained in place without substantial female gene flow from any interior populations, who likely arrived later.

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