

# Mitochondrial DNA Studies of Native Americans: Conceptions and Misconceptions of the Population Prehistory of the Americas

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A decade ago, the first reviews of the collective mitochondrial DNA (mtDNA) data from Native Americans concluded that the Americas were peopled through multiple migrations from different Asian populations beginning more than 30,000 years ago.<sup>1</sup> These reports confirmed multiple-wave hypotheses suggested earlier by other sources and rejected the dominant Clovis-first archeological paradigm. Consequently, it appeared that molecular biology had made a significant contribution to the study of American prehistory. As Cann<sup>2</sup> comments, the Americas held the greatest promise for genetics to help solve some of the mysteries of prehistoric populations. In particular, mtDNA appeared to offer real potential as a means of better understanding ancient population movements. A decade later, none of the early conclusions remain unequivocal. Nevertheless, in its maturity, the study of Native American mtDNA has produced a volume of reports that still illuminate the nature and timing of the first peopling and postcolonization population movements within the New World.

For several reasons, mtDNA has been regarded as particularly useful

for studying prehistory. The human mitochondrion is an extra nuclear organelle having DNA that exists as a circular molecule 16,569 base pairs in length, in which all nucleotide positions and coding loci are known.<sup>3</sup> Because this DNA is uniquely maternally inherited and, unlike nuclear DNA, does not recombine, all changes in mtDNA sequence are the result of accumulated mutations inherited from mother to daughter. In addition, mtDNA mutates an order of magnitude faster than does nuclear DNA, with the control region mutating at an even greater rate, making it particularly useful for analyses at shallow time depths. Finally, mtDNA exists in high copy number in haploid condition. Consequently, it is easily assayed in the laboratory and can be recovered from prehistoric biological material in sufficient quantities for amplification and analysis using the polymerase chain reaction.

## HAPLOGROUPS AND HAPLOTYPES

Early studies of Native American mtDNA revealed four major clades, or haplogroups, of haplotypes.<sup>4,5</sup> Although they are broadly distributed throughout the Americas,<sup>6</sup> these four haplogroups exhibit significant re-

gional patterning among native populations of North America. All four haplogroups are shared with Asian populations, confirming the conclusions of classical genetic studies that the first Americans migrated from Asia across the Bering land bridge.<sup>4,5</sup> Early analyses of restriction fragment length polymorphism in the entire mitochondria genome showed that these four major clades could be readily distinguished by the gain or loss of one or more restriction sites or by the presence or absence of a 9 base-pair deletion in the COII-tRNA<sup>lys</sup> intergenic regions.<sup>5</sup> Torroni and coworkers<sup>7</sup> found that diagnostic mutations in the CR accompanied the restriction markers and the fragment deletion that characterize the four haplogroups, as is expected of a nonrecombining DNA molecule. Each haplogroup could be further divided into subclades or discrete haplotypes based on additional restriction fragment length polymorphisms or specific CR mutations.

Although corresponding haplogroups can be found in various Asian populations, only founding haplotypes of the New World are shared between the two continents, again confirming that the Americas were initially settled by a limited number of female immigrants from Asia whose mtDNA underwent subsequent evolution independent of its ancestral form in Asia.<sup>4</sup> The fact that shared haplotypes on both sides of the Pacific are uncommon has generated considerable debate as to the size and source of the ancestral population (or populations), as well as the number of waves of migration that came out of Asia. However, some haplogroups also share more than one haplotype with Asia, and it is not clear whether the divergence they represent occurred in

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Asia or the New World. This has made problematic the use of mtDNA diversity to estimate the time of colonization, the size and source of the ancestral population, and the number of waves of migration out of Asia.

### WAVES OF MIGRATION

Although there has been little scientific controversy about the Asian origins of Native American populations, contention surrounds the question of the number of waves of migration. The Americas are home to approximately half of the world's language stocks.<sup>8</sup> This extraordinary linguistic diversity among the indigenous groups of Native America suggests to many comparative linguists that there was either a single colonization several tens of thousands of years ago or that there were multiple colonizations by speakers of different unrelated language phyla.<sup>8</sup> There is dispute, however, about whether or not linguistic evidence supports an early<sup>8,9</sup> or later first occupation of the Americas.<sup>10</sup> The pattern of language diversity has been used to support the tripartite division of Native American groups widely popularized by Greenberg, Turner, and Zegura.<sup>11</sup> Although this division initially was suggested much earlier,<sup>12</sup> Greenberg, Turner, and Zegura<sup>11</sup> proposed that the Amerind, Na-Dene, and Eskimo-Aleut exhibit parallel genetic and morphometric differences that indicate three separate migrations to the New World. Critics noted that the agreement among linguistics, morphology and genetics was not as consistent as initially had been claimed and, indeed, the linguistic divisions themselves have not held up to persistent scrutiny.<sup>13</sup> Nonetheless, the model has strongly influenced designs for research on Native American population genetics.

Early analyses of mtDNA indicated that the distribution of haplogroups and the levels of sequence divergence among Greenberg, Turner, and Zegura's linguistic phyla were the result of multiple migrations. If the effective founding population was small, only one matriline would be likely to have survived each migration. Thus, members of different haplogroups that entered the New World at the same time should exhibit comparable levels of

within-haplogroup diversity. Torroni and colleagues<sup>7</sup> noted that sequence diversity within haplogroups A, C, and D was substantially greater than that in haplogroup B for the populations sampled. This, they argued, was evidence of a later migration of B matriline to the New World. The fact that haplogroups A, C, and D are found in Eastern Siberia, a likely staging point for any trans-Beringian migration, whereas haplogroup B is curiously absent from the region, is consistent with this argument. These two early migrations were argued to be independent of later migrations of Na-Dene. However, this model did not address the relationship of Eskimos to other American populations. Because the Eskimos represent the most recent arrivals in historical linguistic models of the settlement of the New World, the work of Torroni and coworkers<sup>7</sup> implies that there were as many as four independent migrations.

Due to the pronounced regional patterning of mtDNA haplogroup and haplotype frequency distributions in the Americas, estimates of genetic diversity are strongly influenced by sampling. Moreover, little is known about the actual number of initial colonists or the population dynamics involved in colonizing a continent free of other humans. Indeed, the degree to which Native American populations experienced an initial founder effect or subsequent genetic bottleneck is itself controversial.<sup>14</sup>

Horai and coworkers<sup>15</sup> hypothesized that each haplogroup represented an independent founding population. This view is not widely supported because a random selection of even a small group of emigrants from Eastern Siberia today would have a high probability of including members of haplogroups A, C, and D. While earlier studies of Native American mtDNA seemed to support multiple waves, in line with linguistic models of colonization, more recent studies of mtDNA have supported only a single movement out of Asia.<sup>16-19</sup>

Single-wave arguments principally emerged from analyses of larger and more diverse samples. The arguments have followed two separate lines of evidence, though they are quite compatible. Early studies of Na-Dene populations suggested that they possessed

high frequencies of haplogroup A but lacked haplogroup B and exhibited only low frequencies of haplogroups C and D, whereas Eskimo-Aleut populations appeared to have high frequencies of haplogroups A and D but lacked haplogroups B and C. However, on closer inspection of a large number of samples, Merriwether, Rothhammer, and Ferrell<sup>16</sup> demonstrated that groups traditionally classified as Eskimo and Na-Dene had measurable frequencies of all four haplogroups when larger samples were assayed. Reasoning that it is unlikely that separate migrations from Asia would have introduced exactly the same four rare Asian types,<sup>20</sup> Merriwether, Rothhammer, and Ferrell<sup>16</sup> concluded that the Americas must have been peopled from a single source. Postcolonization forces might subsequently have led to the regional patterning in the Americas that appeared to differentiate the three hypothesized linguistic phyla. Moreover, Lorenz and Smith<sup>17</sup> showed that when a larger, more regionally diverse sample of haplogroup B was analyzed, within-haplogroup diversity was not less than that for haplogroups A, C, and D. Further consideration that more than a single founding haplotype of one or more haplogroups survives in modern Native American populations<sup>14,21</sup> renders comparisons of diversity among the four haplogroups moot vis-à-vis their implications with respect to the number of independent migrations to the Americas.

The presence of all four haplogroups in all three of Greenberg, Turner, and Zegura's<sup>11</sup> language phyla could, of course, be the result of admixture after colonization. Neighboring Algonquian and Athabaskan populations both have the rare mutation associated with Albumin Naskapi (Al\*Nas), possibly as a result of ancient admixture, given that the Athabaskan and Algonquian languages exhibit no evidence of a close or even remote linguistic relationship.<sup>22</sup> However, haplogroup frequencies alone cannot distinguish between admixture and common ancestry. Making this distinction requires a more extensive analysis of the discrete haplotypes to determine if related types are shared only between neighboring populations, suggesting admixture.

Haplotype analyses are also consis-

tent with the single-migration hypothesis. The CR sequence of the great majority of all Native American members of haplogroup A, regardless of linguistic affiliation, shares a C→T transition at np16111 that is not seen in any Asian populations except a few in Eastern Siberia, including the Chukchi.<sup>19</sup> The predominance of this marker in the Americas and its conspicuous absence from Asia supports the view that this marker originated in Beringia soon after its settlement. A characteristic Native American form of haplogroup C that includes the C→T transition at np16325 and a form of haplogroup X that includes the T→C transition at np16213 are both widespread in the Americas and absent from Asia, suggesting a Beringian source for, and a single origin of, those haplogroups as well. That a particular marker is widespread in individuals classified as Amerind, Eskimo, and Na-Dene but does not occur in any Asian source outside of eastern Siberia suggests that speakers of all three of the proposed divisions have a common New World origin.<sup>19</sup> Moreover, Bonatto and Salzano<sup>19</sup> reported that the diversity of haplogroup A among Greenberg, Turner, and Zegura's principle Native American language groupings was remarkably similar within each of the three linguistic phyla. In addition to the C→T transition at np16111, the Chukchi of Northeastern Siberia share a C→T transition at np16192 with many Na-Dene and Eskimo samples, suggesting a common ancestry for members of both language phyla.<sup>19,23</sup> The Chukchi might be a rare Asian remnant of a Beringian population that separated from all other Asian groups before emergence of the transition at np16111 and, together with the Na-Dene and Eskimo, experienced a later re-expansion during which the C→T transition at np16192 emerged, as suggested by Forster and coworkers.<sup>21</sup> Population contraction among the remnant Beringians, who presumably were isolated from the Amerind populations that had earlier moved south into North and South America, might have resulted in the dramatic reduction or extinction of members of haplogroups B, C, and D among the Beringians. This scenario is not consistent with separate migrations to the New World for the Na-Dene and Eskimo-

mos, but only with a later reexpansion out of the north.

While Bonatto and Salzano could not estimate the sequence divergence of haplogroups B, C, and D in the Na-Dene and Eskimo, in whom these haplogroups are rare, they did assess the relative diversity of haplogroups A, B, C, and D in Amerinds. As in the analysis of haplogroup distributions by

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Merriwether, Rothhammer, and Ferrell,<sup>16</sup> larger samples of haplotypes showed near-equal levels of sequence diversity in all four lineages.<sup>24</sup> Lorenz and Smith<sup>17</sup> found similar diversity levels in four haplogroups when geographically diverse samples were considered. Although some authors question whether the equal diversity estimates are a result of more com-

plete sampling or different methods of calculating diversity,<sup>25</sup> these results are consistent with a single wave of migration to the Americas. However, equal diversity within haplogroups would be expected only if the number of founding haplotypes is the same. Indeed, future clarification of this dispute will require that we consider not only the level of diversity, but also the population structure, which might give better clues to prehistoric origins.<sup>26–28</sup>

#### WHERE DID THE FOUNDING POPULATIONS ORIGINATE?

Based on geographic proximity alone, Eastern Siberia stands as a likely candidate for the source of the Native American founder population. However, while haplogroups A, C, and D are all found in Eastern Siberia, B is conspicuously absent.<sup>29,30</sup> While the absence of haplogroup B from Eastern Siberia might suggest an additional migration, presumably from southern coastal Asia or South-Central China,<sup>31</sup> where the 9 base pair deletion is more common,<sup>29</sup> it is also possible that haplogroup B was present in Eastern Siberia before the New World was colonized but has since become extinct there.<sup>30</sup> If this is not the case, Eastern Siberia is not a likely candidate for the source of a single-wave migration. In fact, the mitochondrial lineages in Siberia themselves appear to be derived from other Central East Asian populations. Moreover, population histories within Siberia probably have disrupted genetic patterning since the Americas were first colonized.<sup>25,32</sup> The restriction to eastern Siberia of some other Asian haplogroups that exhibit low levels of diversity<sup>25</sup> might suggest that most of the present populations of that region descend from a resettlement of eastern Siberia after Beringia had already been settled.

Central East Asian populations do exhibit all four lineages common in Native American populations. Populations in Tibet,<sup>33</sup> Central China (designated the Chinese Han),<sup>34</sup> and Mongolia<sup>20,35</sup> carry detectable frequencies of haplogroups A, B, C, and D. Merriwether and coworkers<sup>35</sup> and Kolman, Sambuughin, and Bermingham<sup>20</sup> cited Mongolia as a likely source for a single wave of migrations. Y-chromo-

some analysis of aboriginal populations in South-Central Siberia near Lake Baikal further support this as a likely staging ground for a Beringian migration.<sup>36</sup> Of course, just as the absence of particular haplogroups from Siberia does not mean that those haplogroups were never present there, it is entirely possible that the presence of markers elsewhere in Asia could be the product of more recent population movements in Asia.

### THE CURIOUS CASE OF HAPLOGROUP X, A FIFTH FOUNDING LINEAGE

The identification of four haplogroups found in Asia confirmed earlier evidence that Native American populations had Asian origins. Yet in several studies of modern Native American mtDNA, certain similar sequences appeared that did not fall into one of the four known lineages.<sup>7,14</sup> Undoubtedly some of these represented postcontact admixture. Ward and colleagues<sup>14</sup> reported several sequences sharing transitions at np16223 and np16278 that, in their phylogenetic analysis, did not cluster with any other Native American types. Torroni and coworkers<sup>7</sup> reported that a small number of haplotypes found in the Ojibwa shared a *DdeI* site loss at np1715, a marker also shared with a limited number of Europeans. Bailliet and coworkers<sup>37</sup> and Forster and coworkers<sup>21</sup> suggested that the C→T at np16278, coupled with the absence of mutations marking haplogroups A, B, C, or D, constituted an additional haplogroup.

Several lines of evidence now confirm haplogroup X as a fifth founding haplogroup in the Americas. In Brown and colleagues'<sup>38</sup> phylogenetic analysis, a larger sample of Native American sequences from mtDNAs containing the *DdeI* site loss at np1715 (as well as an *AccI* site gain at np14465) and the transitions at np16223 and np16278 formed a distinct clade. Although apparently sharing a matrilineal ancestor with the European haplogroup X at some point deep in time, the Native American sequences formed their own branches independent of European representatives of haplogroup X.

The distribution of haplogroup X is

also consistent with a pre-Columbian source. Though presently thought to be most common among speakers of Algonquian languages, haplogroup X, which reaches a frequency of 20% in some Algonquian populations, is geographically widespread throughout North America among groups sharing no close historic or linguistic ties.<sup>39</sup> Sequences consistent with haplogroup X also have been reported from ancient human burials in South

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America.<sup>40</sup> If the presence of these mtDNAs were the result of recent admixture with modern Europeans, other European haplogroups should also be found. However, among allegedly maternally full-blooded Native Americans, less than one-half percent (four individuals previously classified as "others" in a screening of more than 800 individuals) were shown to be members of haplogroup H,<sup>39</sup> the most common mtDNA type in Eu-

rope, where its frequency approaches 40%.<sup>41</sup> In contrast to haplogroup H, haplogroup X, still the least common Native American haplogroup (~3% of samples screened<sup>39</sup>), is relatively rare in Europe, where it accounts for only approximately 3% of the samples screened.<sup>41</sup> It is unlikely that admixture with Europeans could produce the wide distribution of haplogroup X without also resulting in significantly detectable levels of other, more common European haplogroups. The high frequency of haplogroup X among Algonquians and several other groups also indicates a prehistoric presence in the New World; as such presence reflects the result of common ancestry.<sup>39,42</sup>

Analysis of ancient DNA also demonstrates the presence of haplogroup X but, as yet, no other European haplogroups in the New World before European contact. CR mutations at np16223 and np16278 have been reported from two samples dating to 4000 years BP and another sample dating to 1,000 years BP from lowland South America.<sup>40</sup> CR mutations consistent with haplogroup X also have been found in two individuals from the Norris Farms Oneota burials, a 700-year-old cemetery in west-central Illinois.<sup>18</sup> Because the transitions at np16223 and np16278 are also found in several mtDNA types not associated with haplogroup X, sequence data alone do not provide incontrovertible evidence of the haplogroup. However, the Norris Farms sequences are virtually identical to those of modern Algonquians from the Great Lakes region confirmed to be members of haplogroup X.<sup>42</sup> Malhi has also found individuals with both CR mutations and the *AccI* site gain at np14465 in remains dated to 1340 ± 40 years BP discovered near Vantage, Washington, on the Columbia Plateau. The haplotype of this sample included the C→T transition at np16213 that uniquely characterizes most CR sequences of members of haplogroup X from the New World.<sup>43</sup>

Although haplogroup X is now accepted as a pre-Columbian Native American haplogroup, controversy still surrounds its origin. While the other Native American haplogroups are found in Central East Asia, haplogroup X had not, until quite recently, been identified that far east,<sup>44</sup> occur-

ring in highest frequencies in Europe and Western Asia.<sup>41</sup> This has led to the hypothesis, fueled by morphometric studies of the Kennewick Man remains in Washington State and other Paleo-Indian remains,<sup>45,46</sup> that there was a prehistoric migration of Europeans to the New World. These remains, some dated to more than 9,000 years BP, are morphologically distinct from most modern Native American and Central Eastern Asian populations. The case for repatriation of the Kennewick skeleton received considerable media attention, driven in large part by popular accounts stating that Kennewick man has typically Caucasoid features.<sup>47</sup> Osteological analyses of these early Paleo-Indians actually suggest closer affinities to Polynesian populations and the Ainu of Japan than to typical Europeans.<sup>48</sup> They also indicate that, as a group, the earliest Americans are also more varied than modern Native American groups.<sup>49,50</sup>

While this morphological heterogeneity could reflect multiple origins, it might also reflect a more generalized adaptation of the earliest colonists before the emergence of specialized adaptations reflected by later archaic traditions. Although DNA analysis did not produce amplifiable ancient DNA from Kennewick Man,<sup>51–53</sup> verifiable DNA from other Paleo-Indian samples belongs to typically Native American haplogroups.<sup>54–56</sup> Nevertheless, the popular depiction of Kennewick Man as a pre-Columbian Caucasoid in the New World, coupled with the discovery of haplogroup X as a founding Native American lineage, fueled premature speculation about early European migrations to the New World.<sup>57</sup> Genetic evidence does not support such a migration. Furthermore, the lack of other more common European haplogroups (or other nonmitochondrial genetic markers) in unadmixed Native Americans makes this scenario unlikely.

Haplogroup X might have originated in Europe or West Asia. It is also possible that this haplogroup was once present in a Central East Asian population that gave rise to founders of the New World and subsequently all but disappeared from Eastern Asia. Some of the mystery surrounding haplogroup X seems to have been solved by the recent detection of this haplogroup, assessed by both restric-

tion fragment length polymorphism and corresponding CR mutations, in Altaian individuals of South-Central Siberia.<sup>44</sup> Haplogroup X is not as common in Native Americans as are the other four haplogroups. Accordingly, there is no reason to believe that it need ever have been common in Asia in order to achieve its present distribution in the Americas. It is noteworthy that Y chromosome haplotype 1C is also found in Europe, the Lake Baikal region, and the Americas.<sup>36</sup> Haplogroup X might once have been present closer to Lake Baikal as well, and spread both east to Europe and west to the Americas in the same

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migrations that spread Y chromosome haplotype 1C before becoming rarer still in the Baikal region.

The Altaians of South-Central Asia have been identified as one population outside the Americas that contains all five of the founding Native American haplogroups. They may well be descendants of the same source population that lived in Southern Siberia before both eastern Siberia and Beringia were colonized. However, it is highly unlikely that a single source population has remained stable and unchanged over many thousands of years. Indeed, there is substantial evidence to the contrary. Certainly pop-

ulation structure and gene pools in the Americas appear to have been influenced by population expansions and intracontinental migrations since settlement.<sup>22,42,54,58</sup> As a consequence, it seems unreasonable to identify any extant group in the Old World, itself a product of many millennia of history, as the single parent population.

## HOW OLD ARE THE FIRST AMERICANS?

A molecular clock, first suggested by Zuckerkandl and Pauling in the 1960s, has been employed to use molecular divergence to date prehistoric events. The rapid mutation rate and unilateral maternal descent of mtDNA appear to make it particularly useful for dating events in recent prehistory. Various estimates for the peopling of the New World drawn from mtDNA data, summarized in Table 1, range broadly from about 11,000 to over 40,000 years BP based on mtDNA divergences. This variation results in part from sampling haplotypes used to estimate diversity and in part from variation in the methods used to calculate molecular divergence. When they are presented, the standard errors of these estimates and the range of the estimates themselves are rather large, thus minimizing the utility of such measures for evaluating different scenarios in prehistory. It should be noted also that these dates do not necessarily indicate the establishment of any population in the New World, but only the separations between New World and Old World lineages, which may well have begun in Asia.

Archeological evidence has established that humans were present in North America ~11,500 years ago when the widely distributed and well-dated Clovis culture appeared. The earliest known human skeletal remains date to this time. Although there has long been tantalizing evidence of earlier occupations, little of it has withstood the close scrutiny necessary to establish an early human presence in the New World.<sup>59,60</sup> Adding to the controversy surrounding pre-Clovis sites is the apparent lack of a suitable migratory route out of Beringia. While the Bering Land Bridge was open throughout the last glaciation, an ice-free corridor between the Laurentide and Cordilleran ice

TABLE 1. Divergence Dates From mtDNA Data

Study	Divergence Range (Years Before Present; Error and/or Confidence Intervals Where Reported)
Torrioni and co-workers, 1994 <sup>66</sup>	
A	25,862–34,091
B	11,724–15,456
C	33,105–43,636
D	18,276–24,091
Schurr and co-workers, 1999 <sup>25</sup>	
A	26,969–35,550
B	13,483–17,773
C	40,972–54,009
D	19,483–25,682
Forster and co-workers, 1996 <sup>21</sup> (haplogroups A, B, C, and D)	20,180 ± 1,000
Horai and co-workers, 1993 <sup>15</sup> (haplogroups A, B, C, and D)	14,000–21,000
Brown and co-workers, 1998 <sup>38</sup> (haplogroup X only)	12,00–17,000 or 23,000–36,000
Stone and Stoneking, 1998 <sup>18</sup>	
A	19k (95% CI 12k–30k) or 37k (25k–57k)
B	12k (8k–21k) or 25k (16k–41k)
C	11k (6k–21k) or 22k (13k–40k)
D	15k (9k–27k) or 31k (19k–51k)

masses was apparently impassible from 30,000 years BP until perhaps 11,000 years BP.<sup>61</sup> Thus, pre-Clovis people would have to have migrated southward out of Beringia via the ice-free corridor before 30,000 years BP.

It now appears that a 12,500 year-old occupation level at Monte Verde in south-central Chile establishes the presence of humans in the Americas before Clovis.<sup>62,63</sup> This favors a migratory route to the New World other than the ice-free corridor. Recent analysis indicates that a coastal passage, open as early as 14,000 years BP, was a likely entry point to North America.<sup>61</sup> Similarities in mtDNA among populations of the west coast of North America also appear to support the hypothesis of population expansion out of Beringia associated with gene flow along the west coast.<sup>64</sup> On its own, this is not conclusive evidence of an early coastal entry into New World and, indeed, such an expansion might have postdated the earliest migrations southward out of Beringia. Nevertheless, this evidence raises the possibility of such movement and should provide fuel for archeological and linguistic investigations of such a claim. In addition, genetic data indicate that populations of North American brown bears first reached the modern boundary of the

continental United States via coastal refugia during the terminal Pleistocene rather than through the ice-free corridor.<sup>65</sup> This, at the very least, raises the possibility that humans also could have traveled south of the ice sheets via a similar route at this time. Consequently, Monte Verde's pre-Clovis occupation lends no support to the hypothesis that the Americas were colonized as early as 30,000 years BP.

Unfortunately, this has not discouraged attempts to seek molecular evidence of an early human presence in the Americas. Great variation in divergence estimates among molecular studies results from uncertainties regarding the proper calibration of mutation and divergence rates, the error estimates associated with these rates, and the events that genetic divergence may actually reflect. Attempts to calibrate a mitochondrial mutation rate have employed divergences dates that themselves are uncertain, as is the case with the *Homo-Pan* split, the emergence of modern *Homo sapiens*, and the linguistic break-up of the Chibcha language phylum.<sup>15,66</sup> The calculation of mutation rates has achieved certain tautological qualities as well: Attempts to calculate a rate of mtDNA sequence divergence used the peopling of the Americas, assumed to have occurred between 12,000 and

20,000 years BP as a benchmark at a time when relatively few Native American samples had been analyzed.<sup>67</sup>

Other estimates are based not on divergence from an Asian source, but instead on the accumulated diversity in the New World using coalescent theory.<sup>19,21,24</sup> Such estimates exhibit a variability that in all probability is too large to be useful for selecting among alternative hypotheses regarding the initial peopling of the Americas.<sup>68</sup> While the observed high mutation rates in mtDNA do make them particularly useful for analyses at shallow time depths such as those involving the evolution of human populations, such rapid rates of change can also add to the error associated with using molecular divergence to date prehistoric events.

It has been demonstrated that molecular estimates do not always match the empirical data. A recent molecular analysis of modern populations hypothesized the presence of haplogroup V in the Basque region of Spain by approximately 10,000 years BP based on the diversity exhibited by modern members of this haplogroup.<sup>69</sup> However, subsequent analysis of 92 ancient human remains in that region failed to confirm any signs of this haplogroup in the region as recently as 4,000 years BP.<sup>70</sup> This discrepancy between the molecular estimates and the molecular archeological record provides no confidence in molecular estimates of the times of past events when those estimates are derived solely from studies of living populations. Unlike the case of *Ramapithecus*, in which molecular data showing a later divergence of humans and the African apes led paleontologists to reconsider fossil evidence of an early split for the human line, molecular data suggesting an early occupation of the Americas have not led to discoveries of an early occupation. However, molecular evidence is still best used as part of a holistic approach to such inquiries alongside traditional archeological evidence of human presence.

### ANCIENT DNA AND THE PEOPLING OF THE NEW WORLD

The analysis of ancient DNA in the New World has largely confirmed the

**TABLE 2. Applications of mtDNA Data to Native American Migration Hypotheses**

Hypotheses Regarding Migration in North America	MtDNA Support
Athapaskan Migration to the Southwest	Positive <sup>6,78</sup>
Neo-Eskimo Migration	Positive <sup>87</sup>
Iroquian Migration	Equivocal <sup>42</sup>
Numic Spread	Positive <sup>54</sup>
Uto-Aztecan Migration and spread of Maize Agriculture	Negative <sup>78</sup>
Penutian Migration into California	Equivocal <sup>6,64</sup>
Proto-Algonquian Migration and spread	Positive <sup>42,88</sup>

findings of studies of modern DNA and other genetic polymorphism. Haplogroups A, B, C, and D have been identified through analyses of both restriction fragment length polymorphism and CR sequencing in many prehistoric samples in both North and South America.<sup>18,40,54,58,71,72</sup> Similarities in both haplogroup frequencies and specific haplotypes from ancient DNA also indicate that, for the most part, European contact did not significantly affect mtDNA diversity in the Americas.<sup>18,54,72</sup>

The presence of haplogroup X has been confirmed in prehistoric and protohistoric burials on the Columbia Plateau,<sup>73</sup> while sequence data suggest its presence in the prehistoric Onetota population<sup>18</sup> and pre-Columbian South America.<sup>40</sup> Hauswirth and co-workers<sup>74</sup> also reported haplogroup X from Windover pond skeletons (7,000 to 8,000 years BP), although other sequences generated in the study suggest the possibility of contamination in some samples.

While haplogroups B, C, and D have all been identified in Paleo-Indian skeletal remains,<sup>54,55,56</sup> the oldest reported member of haplogroup A, the most common haplogroup in North America and the New World, dates only to  $4,504 \pm 105$  years BP.<sup>75</sup> However, relatively few Paleo-Indian samples have been analyzed and a majority of these have come from the western United States, where haplogroup A is rare in modern populations except along the coast. In a preliminary restriction analysis of 18 samples dating to before 6,500 years of age, no members of haplogroup A were reported.<sup>56</sup> The binomial probability of identifying no members of haplogroup A among 18 samples, given the present distribution of haplogroups within the continental United States, is 0.0017.

Finally, in almost all studies of ancient Native American populations, individuals have been discovered who do not appear to belong to one of the five founding lineages. In many cases, this is undoubtedly a result of external contamination of samples lacking DNA or in which the DNA is inhibited from amplifying using the polymerase chain reaction. Nonetheless, the possibility remains that additional haplogroups may be discovered by studies of ancient DNA in the Americas. Such a lineage may have either become extinct or be a yet-undiscovered lineage persisting at low levels in modern populations.

#### POSTCOLONIZATION PREHISTORY WITHIN THE AMERICAS

Studies of mtDNA diversity have demonstrated that the multidisciplinary approach that uses genetic data in conjunction with cultural, archaeological, and linguistic patterns can provide significant insight into the population prehistory of the Americas (Table 2). Ward and co-workers<sup>76</sup> examined haplotype diversity within three tribes from the Pacific Northwest region, the Nuu-Chah-Nulth, the Bella Coola, and the Haida. They concluded that these tribes share a recent ancestry because the genetic boundaries among Native American groups in this region do not coincide with the boundaries described by Greenberg, Turner, and Zegura<sup>11</sup> based on language differences. However, recent re-examination of language stocks in North America suggests that the Haida probably do not belong to the Na-Dene language family and therefore did not represent a linguistic phylum that is separate from the one to which Nuu-Chah-

Nulth and Bella Coola belong.<sup>77</sup> Therefore, sample design probably accounts for the lack of genetic correlation with language in this particular study.

On a continent-wide level, Lorenz and Smith<sup>6</sup> demonstrated that mtDNA haplogroup frequency distributions often do correlate with language or geography or both.<sup>6</sup> In the north, correlations with geography were high, as were both linguistic and geographic correlations in western North America. The significant levels of correlation between language and

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**It now appears that a 12,500 year-old occupation level at Monte Verde in south-central Chile establishes the presence of humans in the Americas before Clovis. This favors a migratory route to the New World other than the ice-free corridor. Recent analysis indicates that a coastal passage, open as early as 14,000 years BP, was a likely entry point to North America.**

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mtDNA haplogroup distribution among native North Americans suggests that prehistoric population movements, especially in western North America, were not negligible events. Lorenz and Smith<sup>6</sup> also demonstrated that geographic regions of North America exhibit differences in haplogroup frequency distributions. Although haplogroup frequency distributions vary significantly across North America, regional studies of mtDNA diversity in the Northeast<sup>42</sup> and the Southwest<sup>78</sup> have confirmed a pattern of within-region similarities

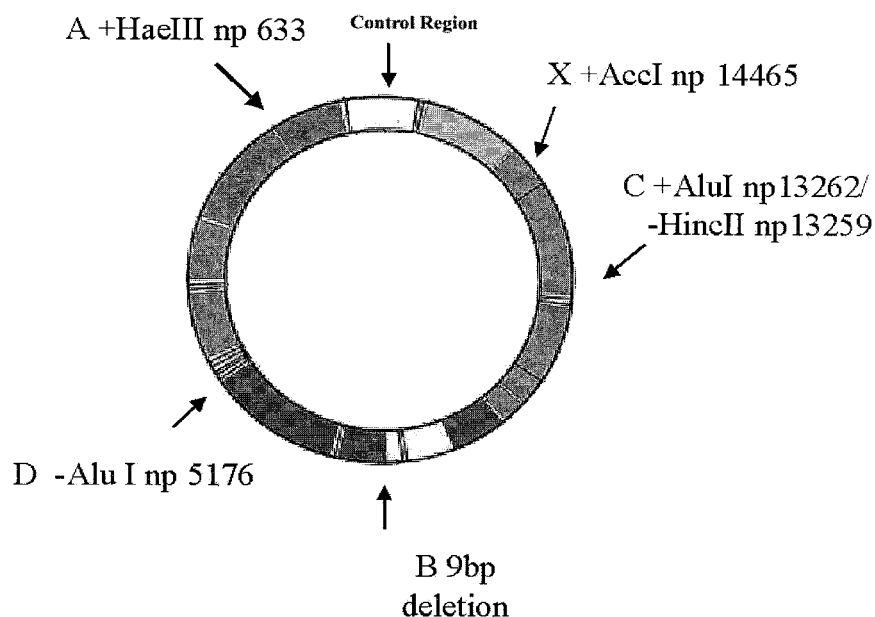


Figure 1. Map of human mitochondrion showing locations of the control region and of polymorphic sites marking 5 known Native American founding haplogroups.

in haplogroup frequency distributions. In the Southwest, these similarities cross-cut the boundaries among different unrelated languages, suggesting considerable admixture among them. These conclusions are consistent with the results of earlier studies based on both morphology (for example, dental variation<sup>79</sup>) and blood group phenotypes.<sup>80,81</sup> The Southeast region of North America does not display a homogeneous pattern of haplogroup frequency distributions, probably due to genetic bottlenecks caused by the high impact of European contact in this region followed by genetic drift.<sup>82</sup>

Studies of ancient mtDNA diversity in most regions of North America reveal that Native American haplogroup frequency distributions often exhibit temporal as well as regional continuity.<sup>72,83</sup> In addition to regional studies, analyses of mtDNA have been used in direct tests of specific hypotheses of population movement proposed by traditional North American prehistorians (archeologists and linguists) as shown in Table 2. Carlyle and colleagues<sup>72</sup> have demonstrated that the haplogroup frequency distribution of an ancient population that practiced the Anasazi cultural tradition in the American Southwest is not significantly different from that in modern Pueblo populations. This study provides biological as well as cultural

evidence of unbroken ancestor and descendant relationships in the American Southwest during the last two millennia. Malhi<sup>73</sup> has shown that

high frequencies of haplogroups B and D have been characteristic of populations of the Columbia Plateau for at least eight millennia. In contrast, Kaestle and Smith<sup>54</sup> have demonstrated that ancient Western Great Basin populations are statistically significantly different from modern populations in the same region, probably due to a population spread of Numic speakers into the Great Basin from southern California approximately 1,000 years BP.<sup>84</sup>

Recent regional studies of mtDNA diversity within North America have shown that detailed analyses of haplotypes can provide better evidence of ancient shared ancestry than do haplogroup frequency distributions alone, which can be similar in two populations due to chance alone. For example, Malhi, Schultz, and Smith<sup>42</sup> have provided evidence from polymorphic sites in the control region of a more recent shared ancestry among speakers of Iroquoian, Caddoan, and Siouan languages than between any of the three and speakers of Algonquian languages of Eastern North Ameri-

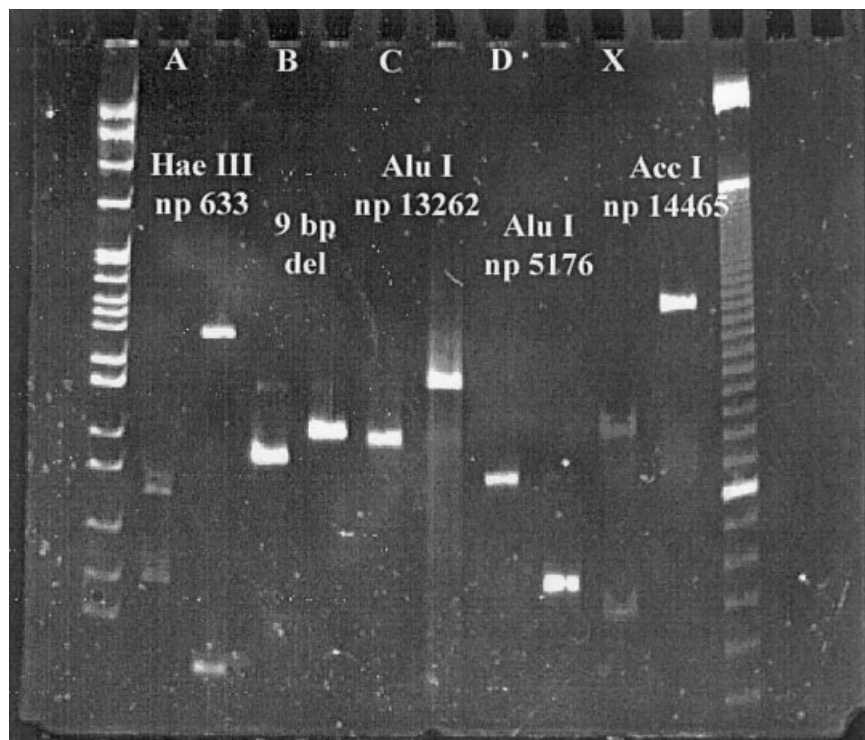


Figure 2. Electrophoretic gel showing PCR fragments amplified and digested to reveal polymorphic sites marking 5 known Native American founding haplogroups.



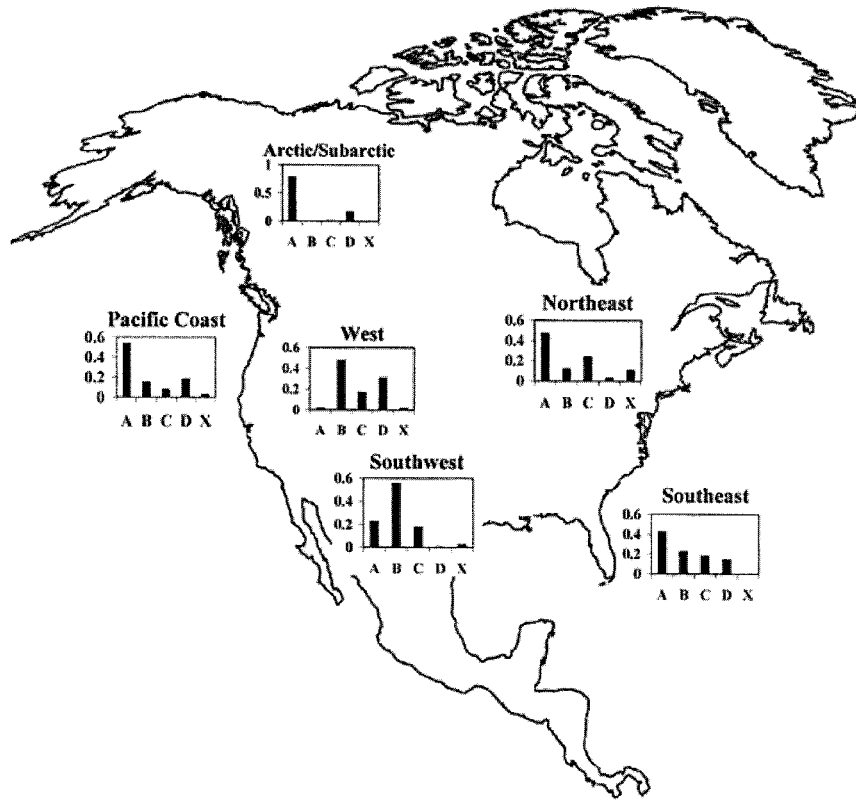


Figure 3. Regional distribution of mtDNA haplogroup frequencies in North America. Adapted from Lorenz and Smith, 1996.<sup>6</sup>

timing of these migrations.<sup>80,81</sup> This does not undermine the utility of genetic data, and mtDNA in particular, for future research. While our knowledge of the mtDNA diversity among many tribal and language groups remains limited, the growing mtDNA databases both within and outside the Americas offer a wonderful comparative tool. However, it is important to remember that mtDNA is but one marker, and one that is solely maternally inherited, and is unlikely to answer all questions regarding the origins of Native Americans.<sup>86</sup> While Y-chromosome markers have been employed to address the peopling of the Americas, they have not yet been specifically used to address postcolonization events. Like mtDNA, Y-chromosome data have not on their own conclusively answered questions regarding either source populations within Asia or the number of migrations out of Asia into the New World. Clearly, nuclear markers from more populations should be examined to provide additional data relevant to these controversies, even though it is unlikely that additional data will significantly simplify what is a convoluted and complex scenario of migra-

ca.<sup>42,85</sup> Weiss and Smith<sup>82</sup> have shown shared mutations in the control region that suggest shared ancestry among speakers of the Muskogean languages in the Southeast, even though haplogroup frequency distributions among these groups are significantly different. Thus, while genetic boundaries do not always coincide with boundaries based on the distribution of languages and culture, the latter provide hypotheses about prehistory that can be tested using modern and prehistoric populations. It is important to note that hypotheses based on genetic evidence must be consistent with evidence derived from historical linguistic and archaeological studies.

**CONCLUSIONS**

It is not surprising that mitochondrial DNA has largely confirmed the findings of classical genetic markers regarding genetic relationships among Native American tribal groups and yet has not conclusively resolved raging debates regarding number of migrations, source populations, and the

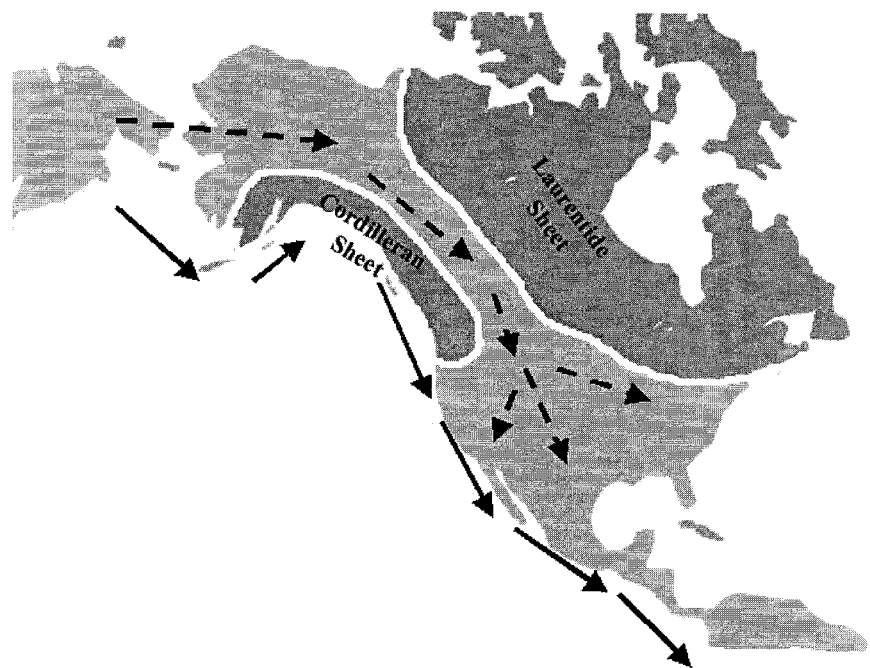


Figure 4. Alternative routes from Asia into the New World. Dotted lines represents a possible path through the ice free corridor as Cordilleran and Laurentide ice sheets separated. Solid line of arrows represents a coastal route around edge using ice-free refugia along Pacific coast.

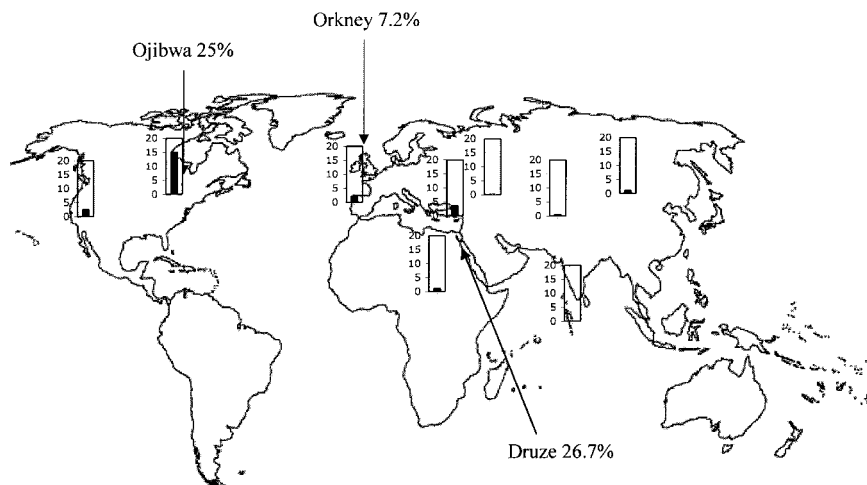


Figure 5. World wide distribution of Haplogroup X frequencies.<sup>39,41,89</sup>

tions and postmigrational evolutionary forces.

Although it is possible that nuclear genes may someday be more easily recovered from ancient human remains, as of now population-level studies of single-copy genes remain prohibitively difficult with ancient DNA. The scale of the questions most readily addressed by ancient mtDNA is different from that of questions addressed by the earliest mtDNA studies. While a decade ago research focused on the Asian affinities and principle migrations to the New World, little light was shed upon, nor interested exhibited in, postcolonization movements and interactions. The sampling necessary for addressing continent-wide phenomena is different from that necessary for characterizing the relationships between local groups. Yet the population dynamics at local levels have contributed to the current genetic diversity witnessed on a continental scale. Identification of such population dynamics can contribute significantly to our understanding of the broader questions pertaining to the settlement of the New World. Further, while critics of ancient DNA may charge that small samples limit the power of the conclusions drawn, ancient DNA remains the only direct way of detecting temporal change in the genetic composition of a population. MtDNA should be seen as another tool with which to formulate and test hypotheses about demic events such as migrations, expansions, and continuity through

time. Together with historical linguistics, ethnographic comparisons, and archeological investigations, mtDNA retains real power to illuminate prehistory.

## REFERENCES

- Wallace DC, Torroni A. 1992. American Indian prehistory as written in the mitochondrial DNA: a review. *Hum Biol* 64:403–416.
- Cann RL. 2001. Genetic clues to dispersal in human populations: retracing the past from the present. *Science* 291:1742–1748.
- Anderson S, Bankier AT, Barrell BG, de Bruijn MHL, Coulson AR, Drouin J, Eperon IC, Nierlich B, Roe A, Sanger F, Schrier PH, Smith AJH, Staden R, Young C. 1981. Sequence and organization of the human mitochondrial genome. *Nature* 290:457–465.
- Wallace DC, Garrison K, Knowler WC. 1985. Dramatic founder effects in Amerindian mitochondrial DNA species. *Am J Phys Anthropol* 68:149–156.
- Schurr TG, Ballinger SW, Gan YY, Hodge JA, Merriwether DA, Lawrence DN, Knowler WC, Weiss KM, Wallace DC. 1990. Amerindian mitochondrial DNAs have rare Asian mutations at high frequencies, suggesting they derived from four primary maternal lineages. *Am J Hum Genet* 46:613–623.
- Lorenz JG, Smith DG. 1996. Distribution of four founding mtDNA haplogroups among Native North Americans. *Am J Phys Anthropol* 101:307–323.
- Torroni A, Schurr TG, Cabell MF, Brown MD, Neel JV, Larsen M, Smith DG, Vullo CM, Wallace DC. 1993. Asian affinities and continental radiation of the four founding Native American mtDNAs. *Am J Hum Genet* 53:563–590.
- Nichols J. 1990. Linguistic diversity and the 1st settlement of the New World. *Language* 66:475–521.
- Rogers RA, Martin LD, Nicklas TD. 1990. Ice-Age geography and the distribution of native North American languages. *J Biogeogr* 17:131–143.
- Nettle D. 1998. Explaining global patterns of language diversity. *J Anthropol Archaeol* 17:354–374.
- Greenberg JH, Turner CGI, Zegura SL. 1986. The settlement of the Americas: a comparison of linguistic, dental and genetic evidence. *Curr Anthropol* 27:477–497.
- Sapir E. 1929. Central and North American Indian languages. London: Encyclopedia Britannica Company, Ltd. Encyclopedia Britannica 14th ed, vol 5, p 138–141.
- Bateman R, Goddard I, Ogrady R, Funk VA, Mooi R, Kress WJ, Cannell P. 1990. Speaking of forked tongues: the feasibility of reconciling human phylogeny and the history of language. *Curr Anthropol* 31:1–24.
- Ward RH, Frazier BL, Dew-Jager K, Paabo S. 1991. Extensive mitochondrial diversity within a single Amerindian tribe. *Proc Nat Acad Sci USA* 88:8720–8724.
- Horai S, Kondo R, Nakagawa-Hattori Y, Hayashi S, Sonoda S, Tajima K. 1993. Peopling of the Americas founded by four major lineages of mitochondrial DNA. *Mol Biol Evol* 10:23–47.
- Merriwether DA, Rothhammer F, Ferrell RE. 1995. Distribution of the four founding lineage haplotypes in native Americans suggests a single wave of migration for the New World. *Am J Phys Anthropol* 98:411–430.
- Lorenz JG, Smith DG. 1997. Distribution of sequence variation in the mtDNA control region of native North Americans. *Hum Biol* 69:749–776.
- Stone AC, Stoneking M. 1998. mtDNA analysis of a prehistoric Oneota population: implications for the peopling of the New World. *Am J Hum Genet* 62:1153–1170.
- Bonatto SL, Salzano FM. 1997. A single and early migration for the peopling of the Americas supported by mitochondrial DNA sequence data. *Proc Nat Acad Sci USA* 94:1866–1871.
- Kolman CJ, Sambuughin N, Bermingham E. 1996. Mitochondrial DNA analysis of mongolian populations and implications for the origin of New World founders. *Genetics* 142:1321–1334.
- Forster P, Harding R, Torroni A, Bandelt HJ. 1996. Origin and evolution of native American mtDNA variation: a reappraisal. *Am J Hum Genet* 59:935–945.
- Smith DG, Lorenz J, Rolfs BK, Bettinger RL, Green B, Eshleman J, Schultz B, Malhi R. 2000. Implications of the distribution of Albumin Naskapi and Albumin Mexico for new world prehistory. *Am J Phys Anthropol* 111:557–572.
- Starikovskaya YB, Sukernik RI, Schurr TG, Kogelnik AM, Wallace DC. 1998. mtDNA diversity in Chukchi and Siberian Eskimos: implications for the genetic history of ancient Beringia and the peopling of the New World. *Am J Hum Genet* 63:1473–1491.
- Bonatto SL, Salzano FM. 1997. Diversity of age of the four major mtDNA haplogroups, and their implications for the peopling of the New World. *Am J Hum Genet* 61:1413–1423.
- Schurr TG, Sukernik RI, Starikovskaya YB, Wallace DC. 1999. Mitochondrial DNA variation in Koryaks and Itel'men: population replacement in the Okhotsk Sea-Bering Sea region during the Neolithic. *Am J Phys Anthropol* 108:1–39.
- Excoffier L, Langaney A. 1989. Origin and differentiation of human mitochondrial DNA. *Am J Hum Genet* 44:73–85.
- Szathmary EJE. 1993. mtDNA and the peopling of the Americas (editorial). *Am J Hum Genet* 53:793–799.
- Templeton AR. 1998. Human races: a genetic and evolutionary perspective. *Am Anthropol* 100:632–650.
- Shields GF, Hecker K, Voevoda MI, Reed JK. 1992. Absence of the Asian-specific region V mitochondrial marker in native Beringians. *Am J Hum Genet* 50:758–765.
- Torroni A, Sukernik RI, Schurr TG, Starik-

- ovskaya YB, Cabell MF, Crawford MH, Comuzzie AG, Wallace DC. 1993. mtDNA variation of aboriginal Siberians reveals distinct genetic affinities with Native Americans. *Am J Hum Genet* 53:591–608.
- 31 Yao YG, Watkins WAS, Zhang YP. 2000. Evolutionary history of the mtDNA 9-bp deletion in Chinese populations and its relevance to the peopling of east and southeast Asia. *Hum Genet* 107:504–512.
- 32 Crawford MH, Williams JT, Duggirala R. 1997. Genetic structure of the indigenous populations of Siberia. *Am J Phys Anthropol* 104:177–192.
- 33 Torroni A, Miller JA, Moore LG, Zamudio S, Zhuang J, Droma T, Wallace DC. 1994. Mitochondrial DNA analysis in Tibet: implications for the origin of the Tibetan population and its adaptation to high altitude. *Am J Phys Anthropol* 93:189–199.
- 34 Ballinger SW, Schurr TG, Torroni A, Gan YY, Hodge JA, Hassan K, Chen KH, Wallace DC. 1992. Southeast Asian mitochondrial DNA analysis reveals genetic continuity of ancient Mongoloid migrations. *Genetics* 130:139–152.
- 35 Merriwether DA, Hall WW, Vahne A, Ferrell RE. 1996. MtDNA variation indicates Mongolia may have been the source for the founding population for the New World. *Am J Hum Genet* 59:204–212.
- 36 Karafet TM, Zegura SL, Posukh O, Osipova L, Bergen A, Long J, Goldman D, Klitz W, Harihara S, de Knijff P, Wiebe V, Griffiths RC, Templeton AR, Hammer MF. 1999. Ancestral Asian source(s) of New World Y-chromosome founder haplotypes. *Am J Hum Genet* 64:817–831.
- 37 Bailliet G, Rothhammer F, Carnese FR, Bravi CM, Bianchi NO. 1994. Founder mitochondrial haplotypes in Amerindian populations. *Am J Hum Genet* 55:27–33.
- 38 Brown MD, Hosseini SH, Torroni A, Bandelt H-J, Allen JC, Schurr TG, Scozzari R, Cruciani F, Wallace DC. 1998. mtDNA haplogroup X: an ancient link between Europe/Western Asia and North America? *Am J Hum Genet* 63:1852–1861.
- 39 Smith DG, Malhi RS, Eshleman J, Lorenz JG, Kaestle FA. 1999. Distribution of mtDNA haplogroup X among Native North Americans. *Am J Phys Anthropol* 110:271–284.
- 40 Ribeiro-Dos-Santos AKC, Santos SEB, Machado AL, Guapindaia V, Zago MA. 1996. Heterogeneity of mitochondrial DNA haplotypes in Pre-Columbian natives of the Amazon region. *Am J Phys Anthropol* 101:29–37.
- 41 Torroni A, Huoponen K, Francalacci P, Petrozzi M, Morelli L, Scozzari R, Obinu D, Savontaus ML, Wallace DC. 1996. Classification of European mtDNAs from an analysis of three European populations. *Genetics* 144:1835–1850.
- 42 Malhi RS, Schultz BA, Smith DG. 2001. Distribution of mitochondrial DNA lineages among native American tribes of northeastern North America. *Hum Biol* 73:17–55.
- 43 Malhi RS, Smith DG. 2002. Brief communication: haplogroup X confirmed in prehistoric North America. *Am J Phys Anthropol* 119:84–86.
- 44 Derenko MV, Grzybowski T, Malyarchuk BA, Czarny J, Miscicka-Sliwka D, Zakharov IA. 2001. The presence of Mitochondrial haplogroup X in Altaians from South Siberia. *Am J Hum Genet* 69:237–241.
- 45 Jantz RL, Owsley DW. 2001. Variation among early North American crania. *Am J Phys Anthropol* 114:146–155.
- 46 Steele DG, Powell JF. 1997. Biological affinities of the oldest recovered North Americans: the Spirit Cave and Pyramid Lakes data. *Am J Phys Anthropol Supplement* 24:218.
- 47 Preston D. 1997. The lost man. *The New Yorker*, June 16, 1997 p. 70.
- 48 Powell JF, Rose JC. 1999. Report on the non-destructive examination, description, and analysis of the human remains from Columbia Park, Kennewick, Washington: report on the osteological assessment of the “Kennewick Man” skeleton (CENWW.97.Kennewick). Chapter 2: National Park Service.
- 49 Powell JF, Neves WA. 1999. Craniofacial morphology of the first Americans: pattern and process in the peopling of the New World. *Yearbook Phys Anthropol* 110, Supp 29:153–188.
- 50 Neves WA, Munford D, do Carmo Zanini M, Pucciarelli HM. 1999. Cranial morphological variation in South America and the colonization of the New World: towards a four migration model? *Ciencia e Cultura (Sao Paulo)* 51:151–165.
- 51 Smith DG, Malhi R, Eshleman JA, Kaestle FA. 2000. Report on DNA analysis of the remains of “Kennewick Man” from Columbia Park, Washington: National Park Service.
- 52 Kaestle FA. 2000. Report on DNA analysis of the remains of “Kennewick Man” from Columbia Park, Washington: National Park Service.
- 53 Merriwether DA, Cabana GS. 2000. Kennewick Man ancient DNA analysis: final report submitted to the Department of the Interior: National Park Service.
- 54 Kaestle FA, Smith DG. 2001. Ancient mitochondrial DNA evidence for prehistoric population movement: the Numbic expansion. *Am J Phys Anthropol* 115:1–12.
- 55 Stone AC, Stoneking M. 1996. Genetic analyses of an 8000 year-old Native American skeleton. *Ancient Biomolecules* 1:83–87.
- 56 Smith DG, Malhi RS, Eshleman JA, Kaestle FA. 2002. Mitochondrial DNA haplogroups of Paleoamericans in North America. In: Bonnichsen R, Gruhn R, Steele DG, Stanford D, Lepper B, Warren CN editors. *Beyond Clovis: where we have been, where we are, and where we are going*. College Station, TX: Texas A & M University Press.
- 57 Morell V. 1998. Human genetics: genes may link ancient Eurasians, Native Americans. *Science* 280:520–520.
- 58 Parr RL, Carlyle SW, O'Rourke DH. 1996. Ancient DNA analysis of Fremont Amerindians of the Great Salt Lake Wetlands. *Am J Phys Anthropol* 99:507–518.
- 59 Meltzer DJ. 1993. Pleistocene peopling of the Americas. *Evol Anthropol* 1:157–169.
- 60 Dixon EJ. 2001. Human colonization of the Americas: timing, technology and process. *Quaternary Sci Rev* 20:277–299.
- 61 Mandryk CAS, Josenhans H, Fedje DW, Mathewes RW. 2001. Late Quaternary paleoenvironments of Northwestern North America: implications for inland versus coastal migration routes. *Quaternary Sci Rev* 20:301–314.
- 62 Dillehay TD. 1997. Monte Verde: a Late Pleistocene settlement in Chile, vol. 2: The archaeological context. Washington, D.C.: Smithsonian Institution Press.
- 63 Dillehay TD. 1999. The Late Pleistocene cultures of South America. *Evol Anthropol* 7:206–216.
- 64 Eshleman JA. 2002. Mitochondrial DNA and prehistoric population movements in Western North America. University of California, Davis. Doctoral dissertation, Dept. of Anthropology.
- 65 Leonard JA, Wayne RK, Cooper A. 2000. Population genetics of ice age brown bears. *Proc Nat Acad Sci USA* 97:1651–1654.
- 66 Torroni A, Neel JV, Barrantes R, Schurr TG, Wallace DC. 1994. Mitochondrial DNA “clock” for the Amerinds and its implications for timing their entry into North America. *Proc Nat Acad Sci USA* 91:1158–1162.
- 67 Stoneking M, Bhatia K, Wilson AC. 1986. Rate of sequence divergence estimated from restriction maps of mitochondrial DNAs from Papua New Guinea Cold Spring Harbor Symp Quant Biol 51(Part I):433–439.
- 68 Tavaré S, Balding DJ, Griffiths RC, Donnelly P. 1997. Inferring coalescence times from DNA sequence data. *Genetics* 145:505–518.
- 69 Torroni A, Bandelt HJ, D'Urbano L, Lahermo P, Moral P, Sellitto D, Rengo C, Forster P, Savontaus ML, Bonne-Tamir B, Scozzari R. 1998. mtDNA analysis reveals a major late Paleolithic population expansion from southwestern to northeastern Europe. *Am J Hum Genet* 62:1137–1152.
- 70 Izagirre N, de la Rua C. 1999. An mtDNA analysis in ancient Basque populations: implications for haplogroup V as a marker for a major Paleolithic expansion from Southwestern Europe. *Am J Hum Genet* 65:199–207.
- 71 Lalueza C, Perez-Perez A, Prats E, Cornudella L, Turbon D. 1997. Lack of founding Amerindian mitochondrial DNA lineages in extinct aborigines from Tierra del Fuego-Patagonia. *Hum Mol Genet* 6:41–46.
- 72 Carlyle SW, Parr RL, Hayes MG, O'Rourke DH. 2000. Context of maternal lineages in the Greater Southwest. *Am J Phys Anthropol* 113:85–101.
- 73 Malhi RS. 2001. Investigating prehistoric population movements in North America with ancient and modern mtDNA. University of California, Davis. Doctoral dissertation, Dept. of Anthropology.
- 74 Hauswirth WW, Dickel CD, Rowold DJ, Hauswirth MA. 1994. Inter- and intrapopulation studies of ancient humans. *Experientia (Basel)* 50:585–591.
- 75 Kaestle FA. 1998. Molecular evidence for prehistoric Native American population movement: the numic expansion. University of California, Davis. Doctoral dissertation, Dept. of Anthropology.
- 76 Ward RH, Redd A, Valencia D, Frazier B, Paabo S. 1993. Genetic and linguistic differentiation in the Americas. *Proc Nat Acad Sci USA* 90:10663–10667.
- 77 Campbell I. 1997. American Indian languages: the historical linguistics of Native America. New York: Oxford University Press.
- 78 Malhi RS, Mortensen HM, Eshleman JA, Lorenz JG, Kaestle FA, Johnson JR, Gorodetzky C, Smith DG. 2002. Native American mtDNA in the American Southwest. *Am J Phys Anthropol*, in press.
- 79 Turner CGI. 1993. Southwest Indian teeth: Southwest Indians: Prehistory through dentition. *Res Exploration* 9:32–53.
- 80 Brown KS, Hanna BL, Dahlberg AA, Strandskov HH. 1958. The distribution of blood group alleles among Indians of Southwest North America. *Am J Hum Genet* 10:175–195.
- 81 Spuhler JN. 1979. Genetic distances, trees and maps of North American Indians. In: Laughlin WAS, Harper AB, editors. *The first Americans: origins, affinities, and adaptations*. New York: Gustav Fischer. p 135–184.
- 82 Weiss DA, Smith DG. n.d. Evidence for a recent mtDNA bottleneck among Native Americans from the Southeastern United States. Submitted. *Am J Phys Anthropol*.
- 83 O'Rourke DH, Hayes MG, Carlyle SW. 2000. Spatial and temporal stability of mtDNA haplogroup frequencies in native North America. *Hum Biol* 72:15–34.
- 84 Bettinger RL, Baumhoff MA. 1982. The Numic spread: Great Basin cultures in competition. *Am Antiquity* 47:485–503.
- 85 Chafe WL. 1976. *The Caddoan, Iroquoian and Siouan languages*. The Hague: Mouton.

86 Szathmary EJE. 1993. Genetics of aboriginal North Americans. *Evol Anthropol* 1:202–220.

87 Hayes MG, O'Rourke DH. 2001. Genetic signatures of migrations and population replacements during human colonization of the North American Arctic. *Am J Hum Genet* 69:179.

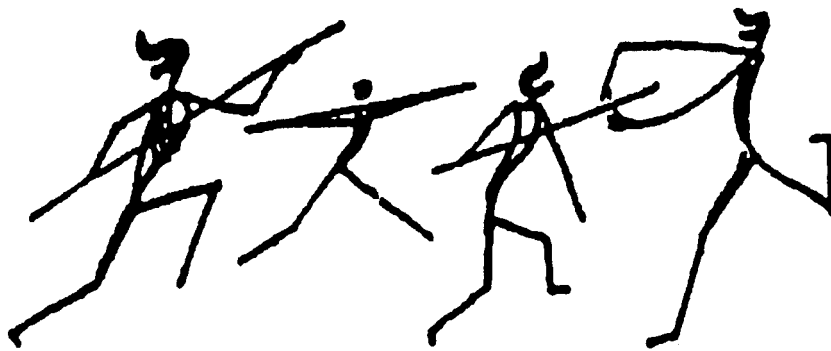
88 Schultz BA, Malhi RS, Smith DG. 2001. Examin-

ing the Proto-Algonquian migration: analysis of mtDNA. *Papers of the 32nd Algonquian Conference*. Manitoba: University of Manitoba Press. p 470–492.

89 Reidla M, Kivisild T, Metspalu E, Kaldma K, Tambets K, Tolk H-V, Parik J, Bermisheva M, Zhadanov S, Pennarun E, Gubina M, Golubenko M, Damba L, Fedorova S, Gusar V, Ge-

berhiwot T, Moisan JP, Khunsnutdinova E, Ossipova L, Stepanov V, Torroni A, Rickards O, DeStefano GF, Papiha S, Beckman L, Rudan P, Angnou NP, Koziel S, Usanga E, Villems R. 2002. Early postglacial spread of haplogroup X from Eurasia to America. In Preparation.

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