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A Molecular Anthropological View of the Peopling of the Americas

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Mitochondrial DNA Data

Numerous studies of mitochondrial DNA (mtDNA) variation in modern Native American populations have shown that the vast majority of their haplotypes belong to four haplogroups, or lineages (Batista et al. 1995; Fox 1996; Hoiai et al. 1993; Kolman et al. 1995, 1997; Lorenz and Smith 1996, 1997; Merriwether et al. 1994; Santos et al. 1996; Santos et al. 1994; Schurr et al. 1990; Torroni et al. 1992, 1993a, 1994b, d; Ward et al. 1991, 1993, 1996). All four of these founding haplogroups are observed in North, Central, and South American populations and can be found in the three proposed Native American linguistic groups (Amerind, Na-Dene, Eskimo-Aleut) (Greenberg 1987). This pattern implies that haplogroups A–D were present in the original migration(s) to the New World, although it is not certain that haplogroup B was present in the ancestral Na-Dene Indians and Eskimo-Aleuts. Furthermore, analyses of ancient Amerindian samples obtained from different geographic locations in the New World also reveal the same general haplogroup composition seen in modern samples (Ginther et al. 1993; Hayes 1999; Kaestle 1997; Merriwether et al. 1994; O'Rourke et al. 1999; Parr et al. 1996; Stone and Stoneking 1998). Consequently, these four haplogroups can unequivocally be considered the primary founding mtDNA lineages in all New World populations.

The four major founding haplogroups are also unevenly distributed amongst various Amerindian tribes. Specifically, there is a decreasing north-to-south frequency cline for haplogroup A and an increasing north-to-south frequency cline for haplogroups C and D. By contrast, there is no particular clinal distribution for haplogroup B, aside from being

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virtually absent in northern North America. Whether these distributions reflect the original pattern of settlement of the Americas or instead the subsequent genetic differentiation of New World populations within certain geographic regions, such as the American Southwest, has yet to be fully determined. In addition, nearly all northern Na-Dene mtDNAs belong to haplogroup A, whereas those of the southern Na-Dene also include some from haplogroups B–D (Torroni et al. 1992, 1993a). This finding is consistent with southern Na-Dene populations having experienced nontrivial admixture with neighboring Amerindian populations since their arrival in the American Southwest some 500–1000 years ago.

Various researchers have further attempted to date the antiquity of New World haplogroups A–D, using both RFLP haplotype and CR sequence data, since these kinds of dates provide a temporal yardstick by which to measure the length of human occupancy of the Americas. The average age of these haplogroups in the Americas ranges from around 40,000 to 20,000 yr B.P., and similar values were obtained for these haplogroups in Siberia and/or East Asia. These results confirm the ancient genetic links between the populations inhabiting these regions and suggest the four primary haplogroups in Native Americans were brought to the New World before the Last Glacial Maximum (ca. 18,000 yr B.P.). In addition, haplogroup A in the Chukchi, Siberian and North American Eskimos, and Na-Dene Indians shows a shallow time depth (13,000–7000 yr B.P.) (Shields et al. 1993; Starikovskaya et al. 1998; Ward et al. 1993). Thus it appears the ancient Beringian populations that gave rise to these modern circumarctic groups underwent a more recent "bottleneck," followed by the expansion of these haplogroup A mtDNAs into the Arctic and Subarctic regions of North America.

In addition to these studies, recent work has shown that the majority of the mtDNAs that could not be assigned to haplogroups A–D belong to a divergent branch of haplogroup X (Brown et al. 1998; Forster et al. 1996), an mtDNA lineage that is also seen in European populations (Torroni et al. 1996, 1998). All Amerindian haplogroup X mtDNAs share a common set of RFLP and CR sequence mutations with European haplogroup X mtDNAs, but otherwise differ from them by at least several CR sequence mutations (Brown et al. 1998). Furthermore, in contrast with the distribution of haplogroups A–D, haplogroup X is found nearly exclusively in North American populations. It occurs at its highest frequencies among Algonkian-speaking groups such as the Ojibwa (Brown et al. 1998; Smith et al. 1999) and has also been detected in a pre-Columbian North American population (Stone and Stoneking 1998). Haplogroup X may also possibly be present in a few ancient Brazilian samples (Ribeiro-dos-Santos et al. 1996), although the identity of the latter mtDNAs is not entirely clear. These data imply that haplogroup X was present in the New World before Europeans first arrived in the New World. Indeed, the sequence divergence time for this mtDNA lineage in Amerindians ranges between 13,000 and 35,000 yr B.P., depending on the number of founding haplotypes (1–2) that are assumed to have been present in the ancestral population bearing this mtDNA lineage to the Americas and on whether RFLP or CR sequence data are used to make these estimates (Brown et al. 1998). Thus haplogroup X is now considered a fifth but minor founding mtDNA lineage in Native American populations.

There has been considerable speculation about the source area(s) from which the ancestral Paleoamerican populations emerged and expanded into the Americas. Recent studies

have suggested that northern China (Torroni et al. 1993a), southeastern Siberia (Derenko et al. 1999; Sukernik et al. 1996), and Mongolia (Kolman et al. 1996; Merriwether et al. 1996) are possible source areas because of the presence of haplogroups A–D in those regions. The highest frequencies of these four haplogroups appear to be found in the Altai Mountain/Tuva/Lake Baikal region (Derenko et al. 1999; Kolman et al. 1996; Merriwether et al. 1996; Sukernik et al. 1996), implying this general region gave rise to the founders of Native American populations. Otherwise, haplogroup B is absent in the vast majority of native Siberian populations, haplogroup A occurs at very low frequencies outside of Chukotka, and haplogroups C and D are the predominant mtDNA lineages in northern Asia (Derenko and Shields 1998; Petrishchev et al. 1993; Schurr et al. 1999; Shields et al. 1992, 1993; Starikovskaya et al. 1998; Sukernik et al. 1996; Torroni et al. 1993b).

However, the presence of a certain CR mutation in haplogroups C and D may point to other potential source areas for the founding New World populations. This mutation, the np 16325 T→C (16325C) transition, appears in the majority of both haplogroup C and D mtDNAs in modern Native American populations and hence appears to be part of the original sequence motifs for both of them. However, among all Asian and Siberian mtDNAs, the 16325C polymorphism occurs in haplogroup C mtDNAs of Mongolians (Kolman et al. 1996) and the Ulchi-Nanai of the Amur River region (Schurr et al. 2000), and in haplogroup D mtDNAs of the Japanese, Koreans, and Ainu of East Asia (Horai et al. 1996) and the Ulchi-Nanai of the Amur River region (Schurr et al. 2000). This distribution of the 16325C mutation suggests East Asia as well as southeast Siberia/Mongolia could have been the source area(s) for the two respective haplogroups (Schurr 1998; Schurr and Wallace 2000), although the exact role of Amur River in the peopling of the New World as revealed by mtDNA data is currently being worked out (Schurr et al. 2000).

By contrast, the origin of haplogroup X mtDNAs remains somewhat ambiguous. Judging from its sequence divergence or coalescence time values, haplogroup X could have arrived in the New World either before or after the last glacial maximum (ca. 18,000 yr B.P.). Irrespective of when it was brought to the Americas, however, the apparent absence of haplogroup X mtDNAs in Asian and Siberian groups (Schurr et al. 1999; Starikovskaya et al. 1998; Torroni et al. 1993b) and its presence in European and Middle Eastern populations (Torroni et al. 1994c, 1996, 1998) suggest that haplogroup X originated in a region outside eastern Siberia. These data further imply that haplogroup X was brought to the New World by one or several ancient Eurasian populations in a migratory event distinct from that/those bringing the other four mtDNA lineages to the Americas.

Y-Chromosome Data

From a Y-chromosome perspective, two genetically related paternal lineages appear to have been part of the initial colonization of the New World. The first of these is defined by a C→T transition at the M3 locus, hereafter called the M3 lineage, whereas the second lineage has the ancestral M45 polymorphism. The M3 lineage has been found in a significant proportion of modern New World native populations and is present in all three putative Native American linguistic stocks, Amerind, Na-Dene, and Eskimo-Aleut (Bianchi et al. 1998; Karafet et al. 1997, 1999; Lell et al. 1997a, b; Santos et al. 1996, 1998; Underhill et al. 1996), with the M45 lineage constituting most of the rest of their Y-chromosomes. These data were

interpreted as indicating a single origin for the founding New World populations, followed by the subsequent differentiation of indigenous populations. The time depth of this Y lineage in the New World has also been estimated at 30,000 yr B.P. (Underhill et al. 1997), although further inquiries into its antiquity are currently being made. In contrast, only the ancestral M45 lineage was detected in Siberian and Asian populations, the exceptions being the Siberian Eskimos and the Chukchi, who represent the remnants of the original founding population(s) that colonized the Americas (Karafet et al. 1997, 1999; Lell et al. 1997). The presence of the M45 lineage in all Siberian ethnic groups and its apparent origin in southeastern Siberia suggest that the M3 lineage arose in the putative founding New World population(s) shortly before or just after it left this geographic area.

Several other Y-chromosome lineages are present in Asia and Siberia (Jobling et al. 1996; Zerjal et al. 1997), but only two appear to have been brought to the Americas, and then after its initial colonization. The first, defined by the M17 1-bp deletion (Underhill et al. 1997), is present at low frequencies in a small but not insignificant number of Siberian populations and occurs at the highest frequency among the Itel'men, whereas it is absent from the neighboring Koryaks (Lell et al. 1997a, b, 1998, 1999). However, the M17 lineage is virtually absent from Native American populations; the only group in which it appears is the Guaymi, a Chibchan-speaking tribe from Costa Rica. Because the Y-chromosome STR pattern for this Guaymi haplotype is consistent with those present in Siberian groups, it appears it was brought to the Americas through a later, secondary expansion of ancient Asian peoples, rather than with the initial immigrants to the New World.

The second Y lineage, defined by the RPS4Y 711 T→C mutation (Bergen et al. 1996), is quite ancient and widespread in East and Southeast Asia, appearing in populations as far apart as Australia and Chukotka. In addition, contrary to the other Asian Y lineages, which are thought to have arisen somewhere in the Altai-Sayan/Lake Baikal region, the RPS4Y lineage appears to have an East Asian origin. Its probable origin in this region is reflected in part by the high frequencies of this lineage and the greatest genetic diversity of its constituent haplotypes in the Amur River region and northeastern Siberia (Lell et al. 1998, 1999). Interestingly, the RPS4Y lineage is not present in any Native American populations, with the exception of the Athapaskan-speaking Tanana and Navajo, and also the Cheyenne, in whom it appears at trace frequencies (Karafet et al. 1999; Lell et al. 1998, 1999). This finding suggests RPS4Y haplotypes were dispersed into Na-Dene-speaking groups through the secondary expansion of Beringian populations into North America, rather than with the initial immigrants to the New World, and that they were passed on to other Amerindian groups during the southward expansion of Na-Dene populations ancestral to modern Navajo and Apache tribes.

In summary, these molecular genetic data suggest the initial colonization of the New World took place well before the emergence of the Clovis culture (ca. 11,500 yr B.P.), probably within the 20,000–35,000 yr B.P. time range. It also appears that multiple distinct mtDNA and Y-chromosome lineages were brought to the Americas during this interval, although not all appear to derive from the same source area in Asia/Siberia and not all have the same antiquity. There is further evidence that ancient Beringian peoples re-expanded into North America after the last major glaciation period, with these populations representing the remnants of the earlier migration(s) into the Americas. Overall, these data imply the colonization of Siberia and the Americas was a more complex process than suggested by some recent

models, one in which multiple expansions of ancient peoples contributed to the genetic diversity observed in aboriginal Siberian and Native American populations.

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