Annu. Rev. Anthropol. 2004. 33:551–83
doi: 10.1146/annurev.anthro.33.070203.143932

THE PEOPLING OF THE NEW WORLD: Perspectives from Molecular Anthropology

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Key Words mtDNA, Y chromosome, Americas, migrations, Siberia

■ **Abstract** A number of important insights into the peopling of the New World have been gained through molecular genetic studies of Siberian and Native American populations. These data indicate that the initial migration of ancestral Amerindian originated in south-central Siberia and entered the New World between 20,000–14,000 calendar years before present (cal yr BP). These early immigrants probably followed a coastal route into the New World, where they expanded into all continental regions. A second migration that may have come from the same Siberian region entered the Americas somewhat later, possibly using an interior route, and genetically contributed to indigenous populations from North and Central America. In addition, Beringian populations moved into northern North America after the last glacial maximum (LGM) and gave rise to Aleuts, Eskimos, and Na-Dené Indians.

INTRODUCTION

The past decade has been an enormously productive period for research into questions concerning the peopling of the Americas. During this time, investigators from all subfields of anthropology and from many different laboratories across the world have focused their attention on determining who the First Americans were. Like their intellectual predecessors before them, these researchers have attempted to elucidate when ancestral Native Americans first arrived in the New World, how many population expansions or migrations were involved in this colonization process, and where in Asia/Eurasia these ancestral groups came from. Their efforts have yielded new insights into the origins of Native Americans, while also raising a number of additional and intriguing questions about Native American prehistory.

Until relatively recently, the dominant explanation for the colonization of the Americas was the Clovis First model. According to this model, human populations first entered the Americas around 12,900 calendar years before present (cal yr BP), after the last glacial maximum (LGM) (24,000–13,050 cal yr BP). They entered from the Beringian landmass and followed an ice-free corridor that had opened in northern North America into the interior of the continent, where they rapidly

expanded into the uninhabited areas of the Americas (Haynes 1992, 1993; Fiedel 1999; Meltzer 1997; Meltzer et al. 1997; Fagan 2000). These early pioneers were thought to be part of a cultural tradition that employed large, sophisticated bifacial points for big game hunting. Because no older Paleoindian sites had been discovered or confirmed, and because all other lithic traditions in the Americas seemed to derive from the Clovis culture, many archeologists believed that the Clovis points demarcated the earliest occupancy of the Americas by modern human groups.

However, recent archeological data have brought the Clovis First model into question. The Meadowcroft site in Pennsylvania (Adovasio et al. 1998, 2000), the Cactus Hill site in Virginia (McAvoy et al. 2000, McAvoy & McAvoy 1997), the Topper site in South Carolina (Goodyear 1999), several sites in Texas (Collins 2002), and other locations in North America (Dixon 2001, 2002) have all been dated to between 16,000–14,250 cal yr BP, times that are older than those associated with Clovis lithic sites in North America (12,900–12,550 cal yr BP). Similarly, a growing number of sites in South America, including the well-publicized Monte Verde site in southern Chile (Dillehay 1989, 1997, 1999; Dillehay et al. 1992; Keefer et al. 1998; Roosevelt et al. 1996, 2002; Sandweiss et al. 1998), are at least the same age, if not older, than Clovis sites in North America. These South American sites have yielded lithic and other cultural materials that do not appear to have been created by Clovis peoples. Their existence implies that ancestral Native Americans arrived in the New World earlier than 13,000 cal yr BP, and hence, began settling the Americas prior to the emergence of the Clovis lithic tradition in North America.

The date at which ancestral Native Americans arrived in the New World from Siberia has also come under increasing scrutiny. A problem for migration models involving very early expansion times (before the LGM) has been that these estimates approached the dates for the oldest known human occupation sites in southeastern Siberia (40,000–30,000 cal yr BP) and were older than the archeological sites in northeastern Siberia (18,000–22,000 cal yr BP) (Goebel & Aksenov 1995, Goebel 1999, Goebel et al. 2001, Hoeffecker et al. 1993, Waters et al. 1997). However, a recent study of the Yana River site has indicated that humans were living in the Arctic by ~30,000 years ago, well before the LGM (Pitulko et al. 2004). This date, as well as the fact that human groups were able to adapt to cold climates at that time, suggests that an entry from eastern Siberia shortly before the LGM might not be as implausible as once thought.

Furthermore, data from a variety of geological, archeological, and paleontological studies are now questioning the idea of an ice-free corridor in North America at the time of the emergence of the Clovis lithic tradition. These data suggest that there were no connections between Beringia and areas south of the Wisconsin and Laurentide glaciers in northern North America until ~12,550 cal yr BP (Clague et al. 1987, Jackson & Duk-Rodkin 1996). Likewise, no animal bones have been recovered from the ice-free corridor between 21,000–11,500 years BP (until 13,050 cal yr BP) (Burns 1996). Thus, it appears that glacial ice sheets blocked the movement of human groups from Beringia through the interior of

North America between ~24,000–13,000 cal yr BP (Fedje 2002, Heaton & Grady 2003, Mathewes 1989).

Given these facts, if the earliest immigrants to the Americas arrived during the LGM, then they must have followed a coastal route into the New World. This possibility had been put forward previously on the basis of geological and linguistic evidence (Fladmark 1979, 1983; Gruhn 1987, 1992). Computer simulations of a colonization process by interior and coastal routes using demographic data from hunter-gatherer groups have also suggested that the patterns of genetic diversity in Amerindian populations are more consistent with a coastal model that allowed an earlier and rapid expansion into the Southern hemisphere (Fix 2002).

However, until recently, geological evidence for the deglaciation of the Northwest Coast of North America, hence, the availability of this region as a migratory route, had been equivocal. Current studies now indicate that human occupation of these areas was possible between 16,800–14,850 cal yr BP (Blaise et al. 1990, Bobrowsky et al. 1990, Fedje 2002, Fedje & Christiansen 1999, Hetherington & Reid 2003, Jackson & Duk-Rodkin 1996, Josenhans et al. 1997, Mandryk et al. 2001, Mann & Hamilton 1995). Therefore, immigrant groups could have made use of the glacial refugia during their movements down the coast of western North America via watercraft. Once deglaciation took place around 13,000–11,000 cal yr BP, human populations would then have been free to expand into North America from the Beringia platform, as well as expand north from regions below the ice sheets.

Studies of craniometric variation in human remains from the Americas have also shed light on the biological history of these regions. These data have revealed biological differences between the earliest settlers of the Americas, the Paleoindians, and populations dating from the Archaic Period (7000 cal yr BP) to modern times (Brace et al. 2001, Jantz & Owsley 2001, Ross et al. 2002). The Paleoindian individuals show a much wider range of variation in their craniofacial features compared to later Native Americans, and they show almost no overlap in these features with these latter groups. Such differences suggest that the Paleoindians and subsequent Amerindian populations may have arisen from two temporally distinct migrations that originated in different parts of Asia. However, not all researchers think that these differences reflect two migrations and instead assert that these craniofacial differences resulted from the effects of genetic drift and adaptation over the past 10,000 years (Powell & Neves 1999). Even so, many of these Paleoindian crania, including the 9300-year-old Kennewick Man skeleton (Chatters 2001), seem to bear some resemblance to those of ancient Eurasian/East Asian populations (Brace et al. 2001; Hanihara et al. 2003, 2004).

These lines of evidence set the stage for a discussion of the molecular genetic data from Siberian and Native American populations and their implications for the peopling of the New World. In the majority of recent molecular studies, researchers have analyzed two uniparentally inherited genetic systems, the mitochondrial DNA (mtDNA) and nonrecombining portion of the Y chromosome (NRY). The mtDNA and NRY possess a series of different markers that define or identify specific genetic

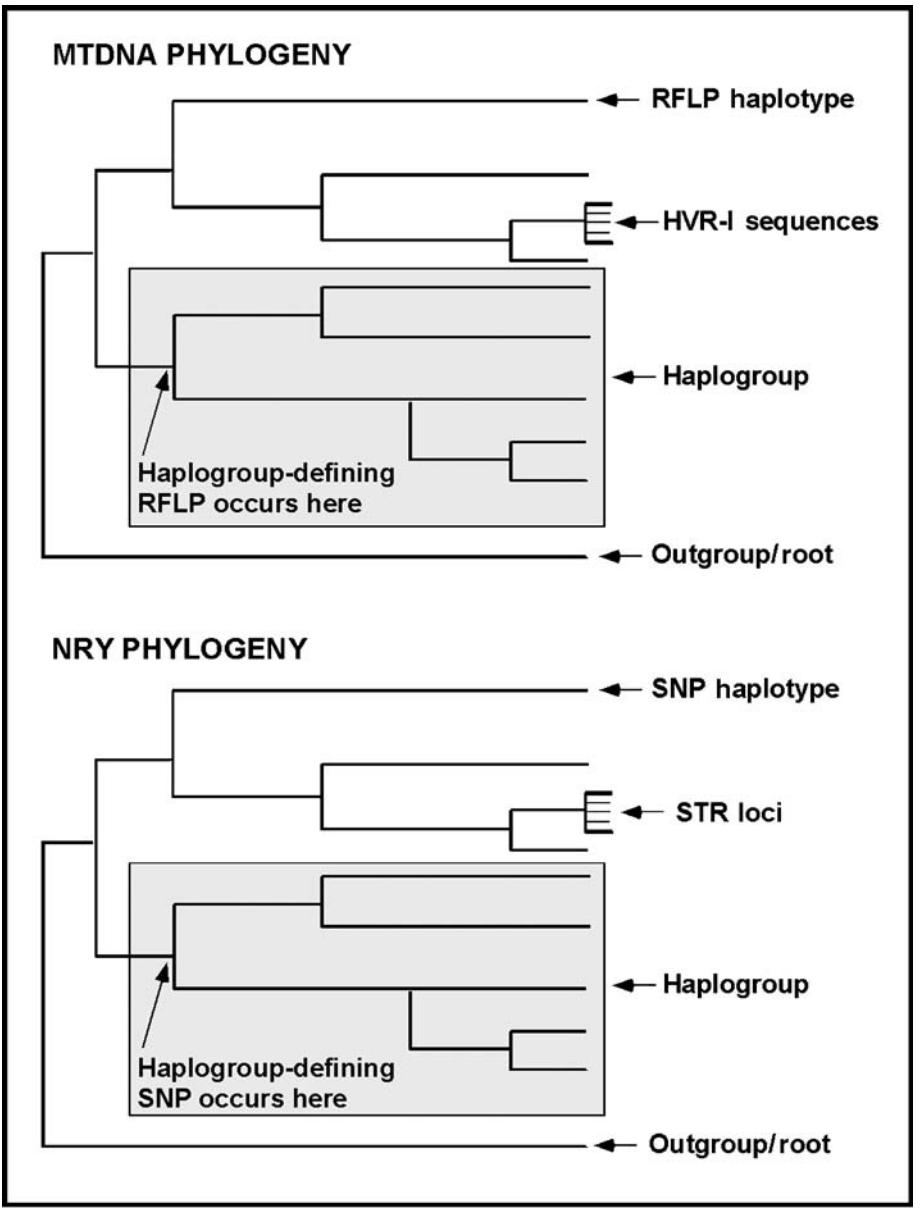

Figure 1 Mitochondrial DNA and NRY phylogenies illustrating the relationship between different kinds of mutations used in phylogenetic reconstructions.

lineages present in human populations (Figure 1). By analyzing the sequence variation in them, one can identify the maternal and paternal lineages present within populations, characterize the extent of diversity within them, and ascertain the manner in which they have been spread into neighboring groups. Other genetic loci also have been used to explore Native American origins and affinities, but they are not discussed here (Crawford et al. 1998, Rothhammer et al. 1997, Salzano 2002, Schurr 2004c).

This paper reviews the findings of molecular genetic studies of Native American and Siberian populations and explores their implications for the peopling of the New World. Several specific issues are addressed, including (*a*) the nature of genetic diversity in Native Americans and Siberians, (*b*) the timing of the initial colonization of the New World, (*c*) the number of expansions that entered the Americas, and (*d*) the source area for ancestral Native Americans. In addition, the population history of Native American tribes after the initial colonization, and the consequences of contact with Europeans since the late fifteenth century, are discussed briefly.

GENETIC DIVERSITY OF NATIVE AMERICAN POPULATIONS

mtDNA Diversity in Siberia and the Americas

Much is now known about the maternal genetic lineages present in Native American populations. Their mtDNAs belong to five founding haplogroups, which have been designated A–D and X (Brown et al. 1998; Forster et al. 1996; Schurr et al. 1990; Torroni et al. 1992, 1993a,c). Each of these maternal lineages is distinguished by a unique combination of restriction fragment length polymorphisms (RFLPs) and hypervariable region I (HVR-I) sequence polymorphisms, as well as coding region mutations (Kivisild et al. 2002, Yao et al. 2002). Together, they encompass 96%–100% of the mitochondrial haplotypes in modern indigenous populations of the New World (Schurr 2002, and references therein).

There are also several major geographic trends in the distribution of the founding mtDNA lineages in the Americas. First, haplogroups A–D are observed in Amerindian populations from North, Central, and South America (Schurr 2002, and references therein) (Figure 2). These trends also have been detected in the three Native American linguistic groups (Amerind, Na-Dené, Eskimo-Aleut) proposed by Greenberg et al. (1986) and Greenberg (1987). Investigators interpret these findings as indicating that all four mtDNA lineages were present in the original migration(s) to the New World (Kolman et al. 1996; Merriwether et al. 1994, 1995; Stone & Stoneking 1998). However, Na-Dené Indians and Eskimo-Aleuts show a different haplogroup profile than do Amerindians, one consisting largely of haplogroup A and D mtDNAs, and may have lacked haplogroup B, and possibly haplogroup C, in their original genetic makeup (Rubicz et al. 2003; Saillard et al. 2000; Shields et al. 1993; Starikovskaya et al. 1998; Torroni et al. 1992, 1993a;

Ward et al. 1993). For this reason, they may represent a different expansion into North America than that giving rise to Amerindians.

At a continental level, the five founding haplogroups are differentially distributed in the New World. Among Amerindians, haplogroup A decreases in frequency from north to south, whereas haplogroups C and D generally increase in the same direction. However, haplogroup B shows no similar clinal distribution, other than being virtually absent in northern North America (Lorenz & Smith 1996, 1997; Schurr et al. 1990; Torroni et al. 1992, 1993a, 1994a,c). Haplogroup B does appear at high frequencies in both the Southwest United States and the Andean region, probably because of recent population expansions (Malhi et al. 2001; Merriwether et al. 1994, 1995). By contrast, haplogroup X is found nearly exclusively in North America (Bolnick & Smith 2003; Brown et al. 1998; Malhi et al. 2001; Scozzari et al. 1997; Smith et al. 1999; Torroni et al. 1992, 1993a), with only trace frequencies of this mtDNA lineage possibly being seen elsewhere (Ribiero-dos-Santos et al. 1996). These distributions probably reflect the original pattern of settlement of the Americas, as well as the subsequent genetic differentiation of populations within certain geographic regions.

Although mtDNAs from haplogroups A–D commonly occur together in single populations, many tribes lack haplotypes from at least one of these haplogroups (Batista et al. 1995; Easton et al. 1996; Ginther et al. 1993; Lorenz & Smith 1996, 1997; Kolman et al. 1996; Kolman & Bermingham 1997; Rickards et al. 1999, Scozzari et al. 1997; Torroni et al. 1992, 1993a, 1994a,c). This is especially true for Central American populations, which essentially have only haplogroup A and B mtDNAs (Batista et al. 1995; Gonzalez-Oliver et al. 2004; Kolman et al. 1996; Kolman & Bermingham 1997; Melton et al. 2004; Santos et al. 1994; Torroni et al. 1993a, 1994c). Various studies have also revealed a high frequency of "private haplotypes" in individual populations or groups of related Amerindian tribes (e.g., Lorenz & Smith 1997; Malhi et al. 2001; Torroni et al. 1993a). These patterns reflect the role that genetic drift and founder effects have played in the stochastic extinction and fixation of mtDNA haplotypes in Native American populations.

A number of haplotypes not clearly belonging to these five maternal lineages have been also detected in different Native American groups (Bailliet et al. 1994; Easton et al. 1996; Lorenz & Smith 1996, 1997; Merriwether et al. 1994, 1995; Ribiero-dos-Santos et al. 1996; Rickards et al. 1999; SE Santos et al. 1996; Smith et al. 1999; Torroni et al. 1993a; Ward et al. 1991). These "other" mtDNAs have often been considered additional founding haplotypes or haplogroups in New World populations. However, most have since been shown to be derivatives of haplogroups A–D that have lost diagnostic mutations (Schurr 2002, 2004a; Schurr & Wallace 1999). The remainder appears to have been contributed to indigenous groups through nonnative admixture (see below). In addition, the "other" mtDNAs detected in archeological samples (e.g., Hauswirth et al. 1994, Parr et al. 1996, Ribiero-dos-Santos et al. 1996) may have resulted from contamination with modern mtDNAs, or were insufficiently analyzed to make a determination of their haplogroup status.

Y Chromosome Diversity in Siberia and the Americas

To characterize NRY variation in Native Americans, researchers have employed a number of different single nucleotide polymorphisms (SNPs) and short tandem repeat (STR) loci to define the paternal lineages present within them (Bianchi et al. 1997, 1998; Hammer et al. 1997; Karafet et al. 1997, 1999; Lell et al. 1997, 2002; Pena et al. 1995; Underhill et al. 1996, 1997, 2000, 2001). However, these research groups have not consistently used the same combination of genetic markers in their studies, which leads to alternative and sometimes confusing nomenclatures for NRY haplotypes and haplogroups. A recent synthesis of these data has resulted in a consensus nomenclature based on known SNPs [Y Chromosome Consortium (YCC) 2002], and it is used in this review. This system identifies an NRY haplogroup by a letter and the primary SNP that defines it (e.g., G-M201).

A variety of NRY haplogroups are present in Native American populations, with most of these also being present in Siberia (Figure 3). These haplogroups include Q-M3, R1a1-M17, P-M45, F-M89, and C-M130. Two of them, Q-M3 and P-M45, represent the majority of Native American Y chromosomes. Q-M3 haplotypes appear at significant frequencies in all Native American populations and are distributed in an increasing north-to-south cline within the New World (Bianchi et al. 1996, Karafet et al. 1997, 1999; Lell et al. 1997, 2002; Santos et al. 1999; Underhill et al. 1996, 1997) (Figure 4). In addition, the STR data from Q-M3 haplotypes reveal significant differences in haplotype distributions between North, Central, and South American populations (Bianchi et al. 1996, 1998; Karafet et al. 1999; Lell et al. 1997, 2002; Ruiz-Linares et al. 1999; Santos et al. 1996b, 1999). These data point to different population histories in the two major continental regions of the New World, a pattern also seen in the gamma globulin (GM), major histocompatibility locus antigen (HLA), and nuclear genetic data from Native American groups (Erlich et al. 1997, Rothhammer et al. 1997, Schanfield et al. 1992).

P-M45 haplotypes also are widely distributed among Native American populations and represent approximately 30% of their Y chromosomes (Lell et al. 2002,

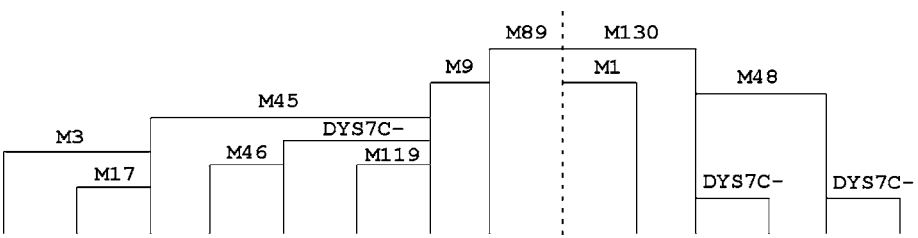

Figure 3 An NRY phylogeny that illustrates the relationships among the SNPs that define different paternal haplogroups in world populations. This is an abbreviated version of the phylogenies appearing in Underhill et al. (2001) or YCC (2002).

Ruiz-Linares et al. 1999, Santos et al. 1999). Phylogenetic analysis has revealed two distinct sets of P-M45 haplotypes in Native American populations. One of these (M45a) is more broadly distributed in populations from North, Central, and South America, whereas the second (M45b) appears in only North and Central American groups (Bortolini et al. 2003, Lell et al. 2002).

The remaining NRY haplotypes belong to one of several different haplogroups and constitute only 5% of Native American Y chromosomes. For the most part, these haplotypes have limited distribution, being present only in North and Central America. For example, C-M130 haplotypes have been detected only in Na-Dené-speaking Tanana, Navajo, and Chipewayans, and the Amerindian Cheyenne (Bergen et al. 1999, Bortolini et al. 2003, Karafet et al. 1999, Lell et al. 2002). In addition, R1a1-M17 haplotypes have been observed only in the Guaymi (Ngöbe), a Chibchan-speaking tribe from Costa Rica (Lell et al. 2002). The limited distribution of these minor haplogroups suggests that they were brought to the New World as part of a secondary expansion of ancient Asian populations.

TIMING OF THE INITIAL MIGRATION TO THE NEW WORLD

Although there is relatively little controversy now about the number and type of founding haplogroups in the New World, the ages of these maternal and paternal lineages continues to be debated. Early studies of RFLP variation in Native American mtDNAs produced time depths for haplogroups A, C, D, and X of between 35,000–20,000 cal yr BP (Torroni et al. 1992, 1993a, 1994a,c). Investigators viewed these estimates as reflecting the genetic diversity that had accumulated in the American branches of these mtDNA lineages, and hence, the time at which modern humans first entered the Americas. Additional support for these findings came from the fact that Native American and Siberian populations did not appear to share any specific haplotypes (Schurr et al. 1999, Starikovskaya et al. 1998, Torroni et al. 1993b). By contrast, Brown et al. (1998) estimates the age for haplogroup B in the New World at 17,000–13,000 cal yr BP, which suggests that haplogroup B was brought to the Americas in a later and separate migration from the earlier one(s) bringing the other four maternal lineages. The age of haplogroup X was identical to that of haplogroup B when estimated from RFLP haplotype data, although it increased when estimated from HVS-I sequence data (Brown et al. 1998).

Subsequent analyses of HVS-I sequence variation in Native Americans argued against the great antiquity of these haplogroups. They showed that haplogroups A, B, and C had roughly the same extent of genetic diversification in North America, and that haplogroup B could possibly have been present in the New World by 30,000–20,000 cal BP (Bonatto & Salzano 1997, Forster et al. 1996, Lorenz & Smith 1997, Stone & Stoneking 1998). The older date also implied that haplogroup B arrived in the Americas around the same time as did haplogroups A, C, and

D. In fact, most HVS-I studies have provided ages for the four major founding haplogroups that range between 35,000–15,000 cal BP, with the earliest dates being 14,000–12,000 cal BP (Shields et al. 1993). A recent analysis of mtDNA coding region sequences in Native American populations has also provided dates for haplogroups A–D of between 20,000–15,000 cal BP (Silva et al. 2002). Thus, most studies now favor an entry time for these mtDNA lineages that is intermediate between the earliest estimates and the dates associated with the Clovis lithic sites in North America.

Two related issues about haplogroup ages have arisen in this debate. The first issue centers on the question of whether haplogroup age estimates actually reveal the timing of human expansion(s) into the New World. Because the genetic divergence or coalescence of genetic lineages does not necessarily correspond to the timing of population splits, some scholars suggest that the older dates instead reflect the emergence of these mtDNA lineages in Asia rather than their entry into the Americas (Bonatto & Salzano 1997, Merriwether et al. 1995, Shields et al. 1993, Ward et al. 1993). On the other hand, only the founding RFLP haplotypes for haplogroups A–D and X have been shown to be present in both Siberia and the Americas (Brown et al. 1998; Schurr et al. 1999; Torroni et al. 1992, 1993a). Thus, the temporal split between the ancestral Amerindian population and its Asian precursor would appear to mirror the split in the branches of each respective haplogroup in each geographic region.

The second issue is the number of founding haplotypes that were brought with each founding haplogroup. The number of founders present in a genetic lineage will affect estimates of its age because a certain amount of the diversity present in that lineage will have accumulated from each founding type. If a haplogroup had more than one founding haplotype, then its age or entry time would need to be estimated from the diversity of haplotypes accumulating from each of its founding haplotypes. Otherwise, the estimated ages made under the assumption of a single founder might inflate the antiquity of these genetic lineages in the Americas. For Native Americans, the presence of more than one founding haplotype would imply that the ages of haplogroups A–D should be less than 30,000–25,000 cal BP, and that the colonization date for the Americas is more consistent with a late-entry, or Clovis-first migration model.

As noted above, there appears to be only one founding haplotype each for haplogroups A–D and X, on the basis of RFLP data (Brown et al. 1998; Schurr et al. 1999; Torroni et al. 1992, 1993a, 1994a,c). These founder haplotypes are the most widely distributed mtDNAs in the Americas and are central to the diversification of their respective haplogroups. However, other investigators have suggested that more than one founding haplotype from haplogroups A–D were among the original set of Native American mtDNAs (Bailliet et al. 1994; Easton et al. 1996; Merriwether et al. 1994, 1995; Rickards et al. 1999; SE Santos et al. 1996). Unfortunately, none of these studies provide additional RFLP or HVR-I sequence data to demonstrate that these are actually the same founding haplotypes defined in other studies (Schurr 2004b, Schurr & Wallace 1999).

In comparison, more than one founder HVS-I sequence from some of these haplogroups may have been brought to the Americas, with these being identical to ones present in Asian and Siberian populations (Malhi et al. 2001, Schurr et al. 1999, Torroni et al. 1993a). However, it is difficult to distinguish founding HVS-I sequences from derivatives that have lost or gained key polymorphisms that delineate American from Asian motifs. A major contributor to this problem is the fact that recurrent mutations typically occur in the mtDNA control region (Gurven 2000, Stoneking 2000). Thus, additional coding region data must be obtained from these same mtDNAs to clearly define their putative status as founder haplotypes.

A recent attempt to date the entry of ancestral Native Americans employed the mismatch analysis of mtDNA RFLP haplotypes from Amerindian populations (Schurr & Sherry 2004). This method extracts demographic information from DNA sequences that reveals episodes of population expansion and growth that can be dated using known mutation rates (Rogers & Harpending 1992, Sherry et al. 1994). This analysis distinguished between the initial expansion of these haplogroups in Siberia or Eurasia (25,000–18,000 cal yr BP) and their expansion in the New World (18,000–12,000 cal yr BP). The shape of the mismatch curve for all Native American haplogroups was generally unimodal, implying that there was an initial major expansion into the Americas. However, the mismatch curves for individual Native American tribes were often bimodal, which suggests that they had experienced at least two episodes of expansion since their ancestral populations first came to the New World.

Another intriguing line of evidence concerning the antiquity of these haplogroups comes from ancient DNA studies. On the basis of current analyses of ancient Holocene skeletal materials from North America, only haplogroups B, C, D, and X, and not haplogroup A (Smith et al. 2000a) have been identified definitively in these remains. These observations tentatively suggested that haplogroup A, rather than haplogroup B, arrived in the New World later than the other four founding mtDNA lineages. This interpretation receives some support from the higher frequencies of haplogroup A in North and Central American populations compared with South American populations. However, the aggregate mtDNA data from modern Native American populations do not support this view, nor do ancient DNA studies of other human populations in the Americas (e.g., Merriwether et al. 1994; Monsalve et al. 1996, 2002; Ribiero dos Santos et al. 1996). Thus, additional skeletal samples dating from before 7000 cal yr BP must be analyzed for genetic variation to clarify these preliminary findings.

Antiquity of Y Chromosome Haplogroups in Siberia and the Americas

The methods for dating NRY haplogroups have employed both the SNPs that define them and the STR loci that occur on each Y chromosome. Because SNPs are rare, if not unique, evolutionary events, it is difficult for investigators to estimate when they evolved in a particular paternal lineage using only this kind of data.

To get around this problem, Underhill et al. (2001) used an average mutation rate estimated from SNP variation in three NRY genes (Thomson et al. 2000) to date the various branches (haplogroups) of their phylogeny. This estimate of 1.24×10^{-9} produced an age of ~59,000 cal BP for the major expansion of modern humans out of Africa. Using this date for the most recent common ancestor (MRCA) of their SNP phylogeny, Underhill et al. (2000) estimated an average evolution rate of 1 SNP per every 6900 years. With this rate, it is possible to tentatively date the major branches of the NRY phylogeny, as well as other points of SNP haplotype diversification.

An alternative strategy for dating the ages of NRY haplogroups is to analyze variation in the faster-evolving STR loci that co-occur on each SNP haplotype. In this case, the extent of allelic diversity of a set of STR loci are measured and averaged over all loci, with the average then being multiplied by an STR mutation rate to determine the actual age of the NRY lineage. Recent mutation rates have been estimated across multiple generations of males (meiotic transmissions) in human families. Although these rates vary somewhat depending on the type of STR used for the estimates (di-, tri-, tetra-), most studies have found that the average mutation rate of NRY STRs is around 2.80×10^{-3} per generation (Bianchi et al. 1998; Heyer et al. 1997; Kayser et al. 1997, 2000; Thomson et al. 2000). This rate can be used to date both the major SNP haplogroups and their smaller branches, which have arisen more recently in evolutionary time.

Considerable effort has been made to estimate the age of Q-M3 haplotypes because they appear to signal the initial entry of ancestral populations into the New World. Using the SNP mutation rate from Underhill et al. (2000), one obtains an age for haplogroup Q-M3 of ~13,800 cal yr BP (Schurr 2004b). The estimates made with STR mutation rates are somewhat broader, ranging from 30,000–7600 cal BP (Bianchi et al. 1998, Forster et al. 2000, Hammer et al. 1998, Karafet et al. 1999, Underhill et al. 1996). Together, these analyses tend to favor a later entry of the Q-M3 lineage into the New World, or perhaps the time at which it evolved and expanded in the Americas.

Recent efforts to date the NRY haplotypes in Native American populations have utilized a newly identified SNP called Q-M242 (Bortolini et al. 2003, Seielstad et al. 2003). The Q-M242 marker occurred within haplogroup P-M45 in Central Asia prior to the emergence of the Q-M3 SNP and the expansion of its haplotypes in the Americas. For this reason, the Q-242 marker appears to demarcate the initial human entry into the Americas somewhat more precisely than does the Q-M3 marker. Using a standard STR mutation rate, Bortolini et al. (2003) and Seielstad et al. (2003) have estimated its entry time at ~18,000–15,000 cal yr BP.

The P-M45 lineage is considerably older than the Q-M3/Q-M242 lineage, which derives from it. Using the SNP mutation rate from Underhill et al. (2000), P-M45 haplotypes were estimated to be at least 30,000 years old (Schurr 2004b). This degree of antiquity is also reflected by their widespread distribution in Siberia and Eurasia (Lell et al. 2002, Underhill et al. 2000). As noted above, the P-M45 lineage has been present in Siberia long enough to diversify into different

subgroups. Its antiquity is indicated by the presence of two different sets of NRY haplotypes in Native Americans: a central Siberian set (P-M45a) that is present in all Native American populations, and an eastern Siberian set (P-M45b) that appears only in Native Americans from North and Central America (Lell et al. 2002).

Researchers have also estimated the ages of several other NRY lineages present in Siberia and the Americas. One of the older lineages in Siberia, K-M9, has been dated at >50,000 cal yr BP (Karafet et al. 1999, Underhill et al. 2000). The antiquity of the K-M9 lineage is consistent with the presence of this SNP in a sizeable majority of Siberian Y chromosomes (Karafet et al. 1999, Lell et al. 2002, Santos et al. 1999, Underhill et al. 2000). An older SNP in the Eurasian branch of the NRY phylogeny, F-89, can be dated to ~62,000 cal BP. F-89 predates the occurrence of the K-M9 lineage because it appears in all haplotypes bearing the latter mutation. Its age also likely reflects the time at which modern human populations began expanding out of East Africa because it demarcates the majority of all non-African NRY haplotypes in the Old World.

The C-M130 lineage is somewhat younger than the F-M89 or K-M9 lineages, having been dated at ~30,000–25,000 cal BP (Karafet et al. 1999, Underhill et al. 2000). This date is generally consistent with the broad distribution of C-M130 in East Asia, where it appears to have originated, and with its considerable haplotypic diversity in eastern Siberian and East Asian populations (Lell et al. 2002, Su et al. 1999). In fact, the C-M130 lineage is quite widespread, being found in India, Australia, Papua New Guinea, and Melanesia (Underhill et al. 2000, 2001, Su et al. 1999), and may be more ancient than previously estimated because researchers associate it with the earliest expansions into East Asia.

The estimated age of haplogroup R1a1-M17 is also intriguing. Using the SNP evolution rate from Underhill et al. (2000), one obtains an age of 13,800 cal yr BP for this lineage, which falls toward the end of the LGM. These haplotypes also constitute a distinct branch within R1a and are not especially common in Siberian populations, although they do occur across a broad geographic area (Lell et al. 2002). Such data suggest that R1a1-M17 haplotypes did not emerge in Siberia until after the Americas had already been settled, and they, along with C-M130 and P-M45b haplotypes, were brought to the New World through a secondary expansion of ancient Asian populations (Lell et al. 2002).

NUMBER OF MIGRATIONS TO THE NEW WORLD

One of the most hotly debated issues concerning the peopling of the Americas has been about the number of migrations that reached the New World and gave rise to ancestral Native Americans. On the basis of nonmolecular data, this number has ranged from one to eight or more, depending on the data set being examined (craniometric, dental, blood group markers, GM allotypes, HLA haplotypes). There is general agreement that the Eskimo-Aleuts and Na-Dené Indians represent the last significant population expansion into the New World. However, investigators still

do not agree on the number of population movements that generated the genetic diversity in Amerindian groups, although a growing consensus for a single major expansion is developing.

Number of Migrations Based on mtDNA Haplogroup Data

Over the past decade, several different models for the peopling of the New World have been proposed on the basis of mtDNA data. Many researchers have asserted that haplogroups A–D were brought to the New World in a single migratory event (Figure 5). This view is based on the fact that all four of them are present throughout the Americas (Forster et al. 1996; Kolman et al. 1996; Merriwether et al. 1995, 1996) and on statistical analyses of their HVR-I sequences that indicates similar levels of diversity in each mtDNA lineage (Bonatto & Salzano 1997, Silva et al. 2002, Stone & Stoneking 1998). According to this view, the pattern of genetic variation seen in modern Native American groups is largely attributed to in situ differentiation and population movements occurring after the initial colonization of the New World, rather than as a consequence of sequential expansions.

Other investigators have argued for the occurrence of two or more migrations to the Americas. In one such model, ancestral Amerindian populations brought haplogroup A, C, and D mtDNAs from Siberia during the initial colonization(s) of the New World, whereas haplogroup B possibly represented a second independent migration. This view was based on the facts that haplogroup B appeared to be younger than the other founding lineages, was absent from most of northern Asia from East Asia to the Americas, and was widely distributed in East and Southeast Asia (Derenko et al. 2000; Schurr 2003; Schurr et al. 1999; Starikovskaya et al. 1998; Torroni et al. 1993a,b). However, evidence indicating similar levels of diversity in haplogroups A–D in the Americas weakens this interpretation.

In contrast, haplogroup X may represent a separate migration from somewhere in Eurasia. It is absent in nearly all indigenous Siberian populations except Altaian groups (Derenko et al. 2000, 2001; Schurr 2003; Schurr et al. 1998, 2000, 2004d; Schurr & Wallace 2003; Starikovskaya et al. 1998; Torroni et al. 1993b) and appears only in North American Amerindian populations (Bolnick 2004; Bolnick et al. 2003; Brown et al. 1998; Huoponen et al. 1997; Malhi et al. 2001, 2003; Scozzari et al. 1997; Smith et al. 1999; Torroni et al. 1992, 1993a). Its estimated age in Eurasia ranges from 35,000–20,000 cal yr BP (Richards et al. 1998, 2000), and its age in the Americas is somewhat younger (30,000–13,000 cal yr BP) (Brown et al. 1998, Reidla et al. 2003).

Haplogroup X is most strongly associated with the expansion of Algonquian-speaking populations (Bolnick & Smith 2003, Malhi et al. 2001, Schultz et al. 2001, Smith et al. 1999), although it seems to have arrived in North America prior to this time. It may have been brought to the Americas with ancestral Na-Dené Indians and subsequently disseminated into Amerindian populations through contact between these groups. Such a scenario is suggested by the distribution of the albumin Naskapi variant in native North American populations (Smith et al.

2000b). However, at present, there are insufficient genetic data from Na-Dené Indian groups to test this hypothesis.

An alternative scenario is that haplogroup X was contributed to the Native American gene pool by ancient European peoples (Stanford 1999, 2000) (Figure 6). According to this model, bearers of the Solutrean culture left Western Europe during the LGM (18,000–16,000 cal yr BP) and navigated their way across the Atlantic Ocean along the existing ice sheet until reaching North America. Once settled, their descendants eventually developed the Clovis lithic technology that spread across North America between 13,500–12,100 cal yr BP. This process would explain the lack of an obvious Siberian precursor to the Clovis lithic culture (Boldurian & Cotter 1999, Goebel 1999, Haynes 1982), the European appearance of these projectile points (Stanford & Bradley 2000), and the greater antiquity, density, and diversity of fluted points in the American Southeast (Anderson 2004).

However, this scenario is problematic for several reasons. First, the apparent homology between the Clovis and the Solutrean lithic traditions may be circumstantial, the reflection of parallel innovations in lithic manufacturing. In addition, it is not entirely certain that Solutrean groups in Iberia were coastally adapted people, as the archeological record suggests they hunted mostly wild horses, red deer, and reindeer (Klein 1999, Strauss 2000). In fact, Strauss (2000) views the Solutrean culture as having arisen in response to the climatic changes of the LGM, and its restricted geographic distribution as evidence of a human refugium in southwestern Europe. Furthermore, there is no clear reason why this trans-Atlantic migration would involve a haplogroup (X) that typically comprises no more than 2% of the mtDNAs in modern European populations to the exclusion of another such as haplogroup H, which represents ~40% of mtDNAs in all of these groups (Comas et al. 1997, 1998; Macaulay et al. 1999; Richards et al. 1998, 2000; Sajantila et al. 1995; Torroni et al. 1994b, 1996). Thus, at best, current mtDNA data provide modest support for an ancient Solutrean migration to the New World.

It remains possible that haplogroups A–D were introduced into the Americas more than once in separate expansion events. This scenario receives tentative support from the fact that, in addition to the consensus founder haplotypes for these haplogroups, there are other HVS-I sequences shared between Asian/Siberian and Native American populations that could potentially be additional founder mtDNAs (see above). These putative founder haplotypes are not widespread in Asia and the Americas, but they appear in populations living in the vicinity of the hypothesized source area or migration route for ancestral Native Americans (Malhi et al. 2002, 2003; Schurr et al. 2000; Schurr & Wallace 1999). However, additional HVR-I sequence and coding region sequence data from both Siberian and Native American populations will be needed to confirm this interpretation.

Some scholars have suggested also that expanding Austronesian speakers, the ancestors of modern Polynesians, genetically contributed to the founding Amerindian populations of South America (Lum et al. 1994, 1998; Rickards et al. 1999). This idea was suggested by the sharing of certain linguistic and cultural

features between Polynesians and Andean populations, as well as the finding that agriculture foodstuffs cultivated in South America also were present in Polynesia. In addition, genetic data from Andean Indians do not clearly show the presence of haplogroup B mtDNAs possessing the Polynesian motif, something that would be expected if there was any significant maternal gene flow between Austronesian speakers and Andean Indian groups (Bonatto et al. 1996). In addition, a recent NRY study of the Polynesian slave trade suggests that the shared paternal haplotypes and cultural contacts between these cultures were a consequence of South American Indians being enslaved, not the result of a trans-Pacific voyage to the New World (Hurles et al. 2003). Thus, the existing genetic data do not support ancient contacts between Polynesia and South America.

Number of Migrations Based on NRY Haplogroup Data

To date, researchers have identified six major paternal SNP haplogroups that are shared between Siberian and the American populations (DE-M1, Q-M3, R1a1-M17, P-M45, N3-M46, and C-M130). Only two of these, P-M45 and Q-M3, were part of the initial peopling of the New World, either through single (Bianchi et al. 1998, Santos et al. 1999, Underhill et al. 1996) or multiple (Bortolini et al. 2003, Karafet et al. 1999, Lell et al. 2002) migrations (Figure 7). The Q-M3 haplogroup is the most frequent paternal lineage in Native American populations and is widely distributed throughout the New World (Bianchi et al. 1998, Bortolini et al. 2003, Karafet et al. 1999, Lell et al. 2002). In addition, the ancestral P-M45a haplogroup, the direct ancestor to the Q-M3 lineage, has the widest geographic distribution of all of those present in the Americas, occurring in populations from central Siberia to South America (Bortolini et al. 2003, Lell et al. 2002).

A second and later expansion(s) of human groups from Beringia appears to have brought a different set of P-M45 haplotypes to the Americas. These P-M45b haplotypes show a different array of STR alleles than do the Q-M3/P-M45a haplotypes that arrived in the initial expansion into the New World, and they also possess the M173 SNP. This second set of P-M45b haplotypes is also shared between eastern Siberian and North and Central American groups but is absent in those groups from central Siberia and South America (Lell et al. 2002). This secondary expansion may also have contributed the R1a1-M17 and C-M130 haplotypes to Amerindian populations. On the basis of their distribution in Siberia, P-M45b and C-M130 haplotypes were suggested to have come from the Amur River region (Karafet et al. 1999, Lell et al. 2002).

Bortolini et al. (2003) supports the proposal that there were two major expansions of NRY haplogroups into the New World. However, they interpret these data as showing that both NRY migrations came from southern/central Siberia to the Americas. In their view, the interpretation that the second migration came from the Amur River region is inconsistent with the generally high frequency of haplogroup K-M9 in eastern Siberia and its absence in the Americas. In addition, they detected

shared ancestry in Central Asia for some of the initial migrants to Europe and the Americas. In either case, south-central Siberia appears to have played a major role in the peopling of the New World, as well as the expansion of many indigenous groups into different parts of Siberia itself.

Expansion of Circumarctic Peoples

Recent work has provided new information about the expansion of Native American populations from the circumarctic region. All circumarctic populations have primarily haplogroup A mtDNAs that possess the 16192T mutation, with these haplotypes being absent in Amerindian groups. This is also true of the Navajo and Apache tribes of the American Southwest, who arose out of a southern expansion of Na-Dené groups some 500–1000 years ago (Budowle et al. 2002; Lorenz & Smith 1996; Malhi et al. 2001; Torroni et al. 1992, 1993a). The dating of the 16192T branch of haplogroup A suggests that the populations ancestral to the Aleuts, Eskimos, and Na-Dené Indians emerged between 13,120–10,000 cal yr BP (Rubicz et al. 2003, Starikovskaya et al. 1998). These circumarctic groups share only certain founding haplotypes from haplogroups A and D, and have become genetically differentiated from each other, as evidenced by the presence of population-specific sublineages within them (Derbeneva et al. 2002b, Rubicz et al. 2003, Schurr et al. 1999, Starikovskaya et al. 1998). The most recent expansion across the Canadian Arctic by the Inuit or Thule people took place between 4000–1000 cal yr BP and reached Greenland by around 1000 A.D. (Saillard et al. 2000).

Ancient DNA studies of archeological populations of the Canadian Arctic also have added new information about the colonization of this region. Ongoing analyses of mtDNA variation in the Dorset, Sadlermuit, and Thule populations suggest that these groups expanded into this region in a sequential fashion. The earliest settlers, the Dorset, who date to 1250 BP, had predominantly haplogroup D mtDNAs. The related Sadlermuit culture showed roughly similar frequencies of haplogroups A and D, whereas the later Thule people had exclusively haplogroup A mtDNAs (O'Rourke et al. 2000b). This series of cultural expansions is further supported by stable isotope work, which shows dietary differences between the Dorset and Thule peoples based on their consumption of marine and terrestrial species (Hayes et al. 2003).

Molecular studies also are providing a more complete picture of the settlement of the Aleutian Islands. Similar to other circumarctic groups, Aleuts have only haplogroup A and D mtDNAs (Derbeneva et al. 2002b, Merriwether et al. 1994, Rubicz et al. 2003). However, unlike Eskimos and Na-Dené Indians, Aleuts have predominantly haplogroup D mtDNAs. Although sharing several haplotypes with other circumarctic groups, Aleuts have mostly unique HVS-I sequences, including those belonging to two distinct sublineages of A and D. These Aleut-specific sublineages have been dated to 6540 and 6035 years BP, respectively, with these estimates being generally congruent with the earliest archeological dates for the colonization of the Aleutian archipelago (Rubicz et al. 2003). In addition, Aleuts lack haplogroup A mtDNAs, with the 16265G mutations that are specific to Eskimo

populations (Saillard et al. 2000, Shields et al. 1993, Starikovskaya et al. 1998), as well as mtDNAs with the 16331G mutations that are specific to Na-Dené Indian groups (Shields et al. 1993; Starikovskaya et al. 1998; Torroni et al. 1992, 1993). Overall, Aleuts are genetically closer to Chukotkan groups (Chukchi and Siberian Yupik) rather than to Alaskan Eskimos, Native Americans, or Kamchatkan populations (Koryaks and Itel'men) (Rubicz et al. 2003).

With regard to Na-Dené Indians, some scholars suggest, on the basis of linguistic data, that Na-Dené and Yeniseian (Kets) speakers have a common phylogenetic origin (Greenberg 1987, Greenberg et al. 1986, Ruhlen 1994). This idea receives some support from the presence of certain NRY haplogroups thought to be ancestral to those in northern Native American populations, including Na-Dené Indians, in Kets and Sel'kups, as well as in Altaian groups (Bianchi et al. 1998, Bortolini et al. 2003, Karafet et al. 2001, Santos et al. 1999). However, the mtDNA haplogroup profiles for Kets and Na-Dené Indians are quite different from each other, with Kets having largely haplogroups C, F, and U mtDNAs and Athapaskan Indians having mostly haplogroup A mtDNAs (Derbeneva et al. 2002b; Schurr & Wallace 1999, 2003; Shields et al. 1993; Torroni et al. 1992, 1993a). In fact, when genetic data from indigenous Siberian and Native American populations were analyzed, the Na-Dené Indians clustered with other Native American populations, whereas the Kets genetically resembled surrounding Siberian groups (Rubicz et al. 2002). Whether this discrepant pattern is related to the differential distribution of male- and female-mediated haplotypes in the Americas during its colonization remains to be determined.

REGIONAL POPULATION HISTORIES

As ancestral Native American populations expanded into the New World, they began colonizing the new environments they encountered. This process has been modeled using the patterns of genetic diversity present in these groups. According to one model, ancestral groups settled at particular locations very early in the colonization process and remained in those areas since that time. This pattern would lead to significant biological and cultural continuity between the ancient groups and their modern antecedents. Alternatively, the genetic composition of ancient populations occupying the same geographic region as extant groups might not be the same because population relocations, mergers of adjacent tribes, genetic drift, or other stochastic processes could have altered patterns of biological diversity in them over time. In this case, there would likely be reduced biological continuity between ancient and modern Native American groups.

Malhi et al. (2002) suggest that the initial colonization process involved the prehistoric spread of small bands of people from west to east across the North American continent. This idea is supported by the greater diversity of language families along the west coast of North America compared to that in its interior regions (Gruhn 1987, 1992; Nichols 1990, 1994). A similar colonization process took place in South America but probably involved a bidirectional settlement

pattern using both Andean and Amazonian routes (Keyeux et al. 2002, Salzano & Callegari-Jacques 1988, Tarazona-Santos et al. 2001). Under this scenario, the colonizing groups would have initially experienced significant drift effects because of their relative isolation from one another but would have remained part of the same gene pool owing to gene flow across the region. Relatively soon after occupying these regions, however, native populations underwent a tribalization process, with this stage being marked by a significant reduction in gene flow among them (Salzano & Callegari-Jacques 1988, Malhi et al. 2002, Torroni et al. 1993a). This transition may be seen at archeological sites from the Archaic Period, where evidence for the specialization and intensification of local resource use appears (Dillehay 1999, Fiedel 1999, Fagan 2000, Roosevelt et al. 1996). The increased population growth and sedentarization of these groups that accompanied these changes would have reduced the effects of genetic drift in these populations and increased gene flow within local groups, thereby contributing to the formation of regional gene pools (Malhi et al. 2002).

In large part, the ancient DNA (aDNA) data support this perspective. They indicate that Amerindian populations, or groups of related populations, maintained their genetic integrity within a particular region for thousands of years, once becoming genetically distinct from surrounding groups (O'Rourke et al. 2000a,b). Patterns of continuity are seen in the American Southwest between Anasazi and modern Puebloan groups (Carlyle et al. 2000, Parr et al. 1996), ancient Tainos and modern Puerto Ricans whose ancestors trace to Carib Indian populations (Martinez-Crusado et al. 2001, Lalueza-Fox et al. 2001), and ancient and modern populations from southern Chile and Patagonia (Fox 1996, Lalueza et al. 1997, Moraga et al. 2000). By contrast, the expansion of Numic peoples in the Great Basin led to genetic discontinuity between ancient and historical populations from that region (Kaestle & Smith 2001). There are also intriguing differences in haplogroup frequencies between ancient and modern Maya populations (González-Oliver et al. 2001; Torroni et al. 1992, 1993a). Ongoing studies of ancient populations in Peru, Chile, and Argentina should also illuminate the relationships between ancient and modern groups in those regions (Adachi et al. 2004, Cabana & Merriwether 2000; McKenney et al. 2000; Williams et al. 2000).

Molecular data have also helped to reveal regional patterns of population settlement and movement in the Americas. In the southeastern United States, there are significant differences in mtDNA haplotype diversity between Muskogean and Iroquian groups (Bolnick & Smith 2003). This difference is attributable to the Iroquoian Cherokee having moved to the U.S. Southeast from the Great Lakes region in the recent past. All these populations show reduced genetic diversity, which probably reflects a genetic bottleneck related to their historical population decline (Bolnick & Smith 2003). Algonquian speakers are also known to have expanded into the Great Lakes region ~2500–3000 years ago, which is reflected by the high frequencies of haplogroup X there, and show affinities with Siouan-speaking populations of the northern United States (Malhi et al. 2001, Schultz et al. 2001, Shook 2004). In addition, aDNA studies of Hopewell and Adena remains have

revealed ties between these archeological populations from the Ohio Valley and Great Lakes tribes (Mills 2003).

Another region that has been the focus of numerous genetic studies, the U.S. Southwest, is also one of the most genetically diverse regions of North America, largely because of the number of population expansions it has experienced throughout its long history. Interestingly, the tribal haplogroup frequencies in the southwest United States are structured more by the archeological traditions in the area than by the linguistic affiliation of its extant groups (Malhi et al. 2002, 2003). Although the Uto-Aztecan languages prevalent in the region are thought to have arisen in northern Mexico, there is no evidence of maternal gene flow north from Mexico to the U.S. Southwest. This finding suggests that males disseminated Uto-Aztecan languages north into the U.S. Southwest (Malhi et al. 2002, 2003). Further evidence for the expansion of haplogroup B mtDNAs in the Southwest exists (Torroni et al. 1993a; Lorenz & Smith 1996, 1997; Malhi et al. 2002), probably in association with maize agriculture. This recent re-expansion of haplogroup B might explain its lower age estimate relative to those of the other four founding lineages (e.g., Torroni et al. 1993a), as most of its haplotypes would be derived recently, and hence, limited in genetic diversity.

Overall, the extent of language and gene association varies from region to region in the Americas. In the Pacific Northwest, there is only a modest association between language and genes (Shields et al. 1993; Ward et al. 1991, 1993). Lorenz & Smith (1997) later observed a general concordance between genetic and linguistic diversity in many North American populations. However, Hunley & Long (2004) recently showed that, within North America, there is a weak correlation between patterns of linguistic and mtDNA variation in Native American groups. Conversely, the linguistically related Chibchan-speaking populations of Costa Rica share a number of mtDNA haplotypes in common (Batista et al. 1995; Kolman et al. 1995; Kolman & Bermingham 1997; Torroni et al. 1993a, 1994c). There is a similar correspondence between mtDNA haplogroup frequencies and linguistic affiliations in Bolivian Amerindian tribes speaking Andean, Equatorial-Tucanoan, and Ge-Pano-Carib languages (Bert et al. 2001). In fact, when Fagundes et al. (2002) reanalyzed genetic data from a number of loci in South American Indian tribes, they found that mtDNA variation correlated significantly with language when geography was held constant. Thus, differences exist in language-gene covariance between the continental regions of the Americas.

Various investigators are also using molecular approaches to explore the kinship and population affinities of individuals buried at archeological sites or mound complexes in different parts of the Americas. This approach was taken at the Norris Farms site in the Illinois Valley, where patterns of haplotypic diversity were detailed in different burials around the cemetery (Stone & Stoneking 1998). Studies of human remains from the Mochica and Middle Sican cultures in Peru have also revealed genetic differences between these cultures, as well as between high-status males and the lower-status males and females who were sacrificed and buried with them in mound tombs (Shimada et al. 2004a,b). Researchers are also undertaking

similar kinds of comparisons between ancient Aztec and Toltec individuals and those from living indigenous groups of central Mexico (Kemp et al. 2004). These kinds of studies will help elucidate the interactions between ancient populations of Mesoamerican and the Andean regions and the population structure and diversity of state-level societies in the Americas.

POST-CONTACT AMERICAS

The entry of Europeans into the New World brought about a number of significant changes for Native American populations. For one thing, warfare and epidemic disease killed huge numbers of individuals from various tribal populations, sometimes leading to the extinction of particular ethnic groups. This demographic decline likely led to a reduction in the genetic diversity of these populations, as well as the formation of new populations from the remnants of tribes affected by colonizing Europeans and their microbes (Crawford 1998, Thornton & Marsh-Thornton 1981, Ubelaker 1988). Increasing interactions with peoples of European descent, as well as the introduction of African slaves from the sixteenth through the nineteenth centuries, generated many mestizo populations in different parts of the Americas. As a consequence of these events, the indigenous American gene pool has been substantially remodeled over the past 500 years.

Admixture can be seen in several forms, depending on the genetic system being used. Previous work utilized classical blood group markers and immune system genes to assess admixture levels. Current molecular genetic studies screen populations for markers defining West Eurasian H-K and T-X and African L1-L3 (Chen et al. 1995, 2000) mtDNA haplogroups, and those defining European and African M1, K-M9, M173, and other non-native NRY haplogroups (Hammer et al. 1997, 1998; Underhill et al. 1999, 2001; YCC 2002).

On the basis of these molecular data, differences exist in the extent of non-native gene flow in different parts of the Americas. Several mtDNA studies have revealed low levels of European maternal gene flow into North American Indian populations in the form of West Eurasian haplogroup H, J, and K mtDNAs (Scozzari et al. 1997, Smith et al. 1999, Torroni et al. 1993a). Evidence of European paternal gene flow has also been seen in studies of blood group markers and NRY variation in these populations (Bolnick 2004, Huoponen et al. 1997, Kaspirin et al. 1987, Pollitzer et al. 1962). In fact, nearly 60% of Greenlandic Inuit Y chromosomes may have European origins, with these most likely coming from Norse settlers who were assimilated into Inuit groups some 500 years ago (Bosch et al. 2003).

Not surprisingly, many rural and urban mestizo groups show differing degrees of female and male genetic contributions from non-native populations, with most European genotypes being introduced by males. These differences reflect a historically documented colonial policy of European males taking indigenous mates as part of the settlement process in various parts of the Americas (Alves-Silva et al. 2000, Bortolini et al. 1997, Bravi et al. 1997, Carvajal-Carmona et al. 2000, Mesa et al. 2000, Rodas et al. 2003, Rodriguez-Delfin et al. 1997). One can see similar

patterns in North America with Mexican Americans, with the extent of Native American ancestry varying depending on their geographic location in the United States (e.g., Merriwether et al. 1997). For these populations, there is usually a much greater Native American maternal and greater European paternal contribution to their genetic makeup.

Likewise, investigators have observed African admixture in a number of Native American groups. Haplogroup L mtDNAs have been detected in several tribal populations from the American Southeast (Huoponen et al. 1997, Smith et al. 1999). In addition, several Central American populations have African-derived DE-M1 NRY haplotypes, including the Mixe from southern Mexico (Karafet et al. 1999, Lell et al. 1997). Generally speaking, Mexico shows regional patterns of genetic variation that reflect its history of colonial settlement. European genetic influence is stronger in the northern part of the country, African influence is stronger along coastal areas, and Amerindian influence is stronger in the central/southeast region (Gorodezky et al. 2001, Green et al. 2000).

A study of the Garifuna (Black Caribs) further confirms the complex history of Mesoamerica and the Caribbean. The majority of Garifuna mtDNA haplotypes are African in origin, but some belong to haplogroups B, C, and D (Monsalve & Hagelberg 1997). These Amerindian mtDNAs likely originated with Arawak and Carib Indians who lived in this region prior to the entry of Europeans. The mixed ancestry of the Garifuna people is also evident in their nuclear gene data, which show a stronger African than European or Amerindian genetic component (Crawford 1986; Crawford et al. 1981, 1982).

Overall, Caribbean populations show a pattern of genetic variation similar to that of the Garifuna, as seen in Cubans (Torroni et al. 1995) and Puerto Ricans (Martinez-Crusado et al. 2001). However, the relative contributions of maternal and paternal genotypes by African, European, and Amerindian populations vary from island to island. These patterns reflect the distinct history of prehistoric settlement and later European colonization of the Caribbean region.

SUMMARY

Both mtDNA and NRY data now provide an initial entry time of ancestral Native Americans of between 20,000–15,000 cal yr BP. This date favors a relatively late expansion of the First Americans, which, while being more consistent with current archeological data from the New World, supports a pre-Clovis entry time. Because these dates fall in the middle of the LGM, before the earliest time at which an ice-free corridor was available for passage by modern human populations, the colonizing groups must have used a coastal route during their initial movement into North America.

The early immigrants apparently brought with them to the Americas mtDNA haplogroups A–D (maybe X) and NRY haplogroups P-M45a and Q-242/M3 haplotypes, with these being dispersed throughout the continental areas of the New World. A subsequent expansion may have brought mtDNA haplogroup X (maybe

more A–D haplotypes) and contributed NRY haplogroups P-M45b, C-M130, and R1a1-M17 to Native American populations, with these being disseminated in only North and Central America. This expansion may have coincided with the opening of the ice-free corridor around 12,550 cal yr BP.

A somewhat later expansion likely involved the ancestors of modern circumarctic populations, such as the Yupik and Inupik Eskimos, Aleuts, and Na-Dené Indians. These populations show some similarities to Amerindians living south of Canada, which suggests that their founders may have shared a common ancestral population with Amerindians. However, they have since become distinct from Amerindians in terms of the types and frequencies of genetic haplotypes and lineages they possess.

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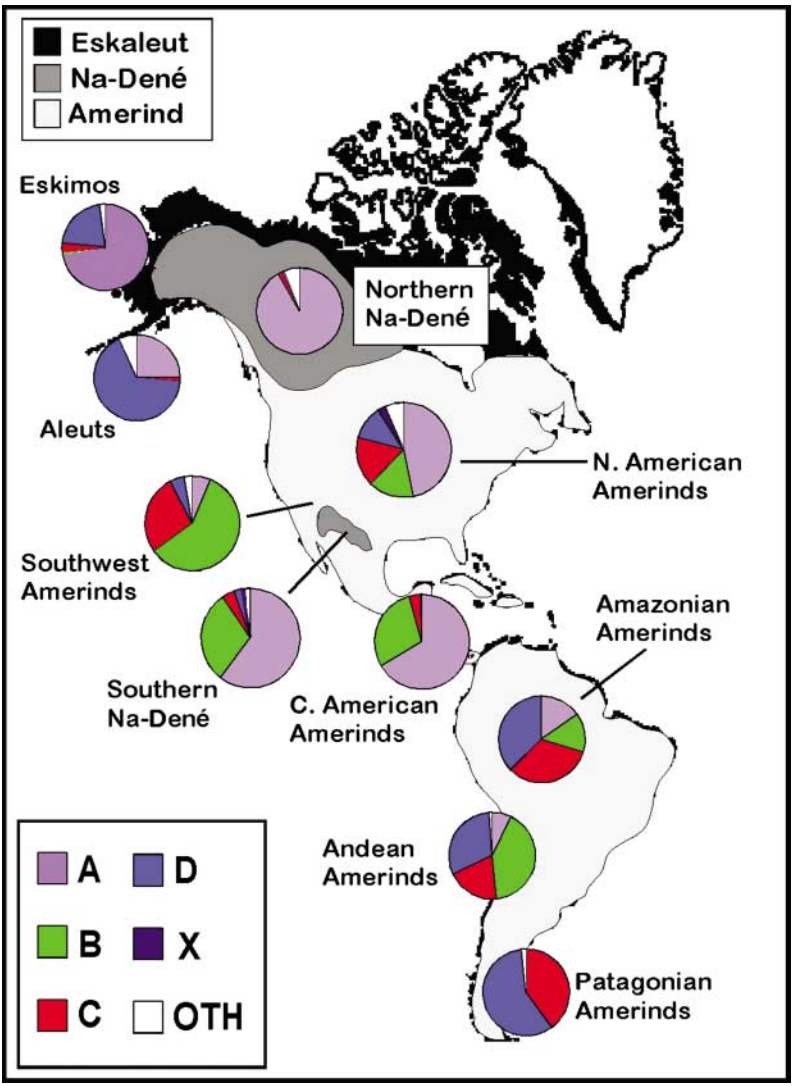

Figure 2 Distribution of mtDNA haplogroups in Native American populations. The key for Native American language groups is indicated in the upper left-hand corner of the figure, whereas the color key for the haplogroups is indicated in the lower left-hand corner. The OTH category represents "other" mtDNAs that do not belong to haplogroups A–D and X, i.e., they come from African or European populations. The frequencies shown for different parts of the Americas represent summaries of mtDNA diversity across broad geographic areas and may not reflect the regional diversity occurring at more local levels. Data for individual populations can be found in the references listed in the Literature Cited.

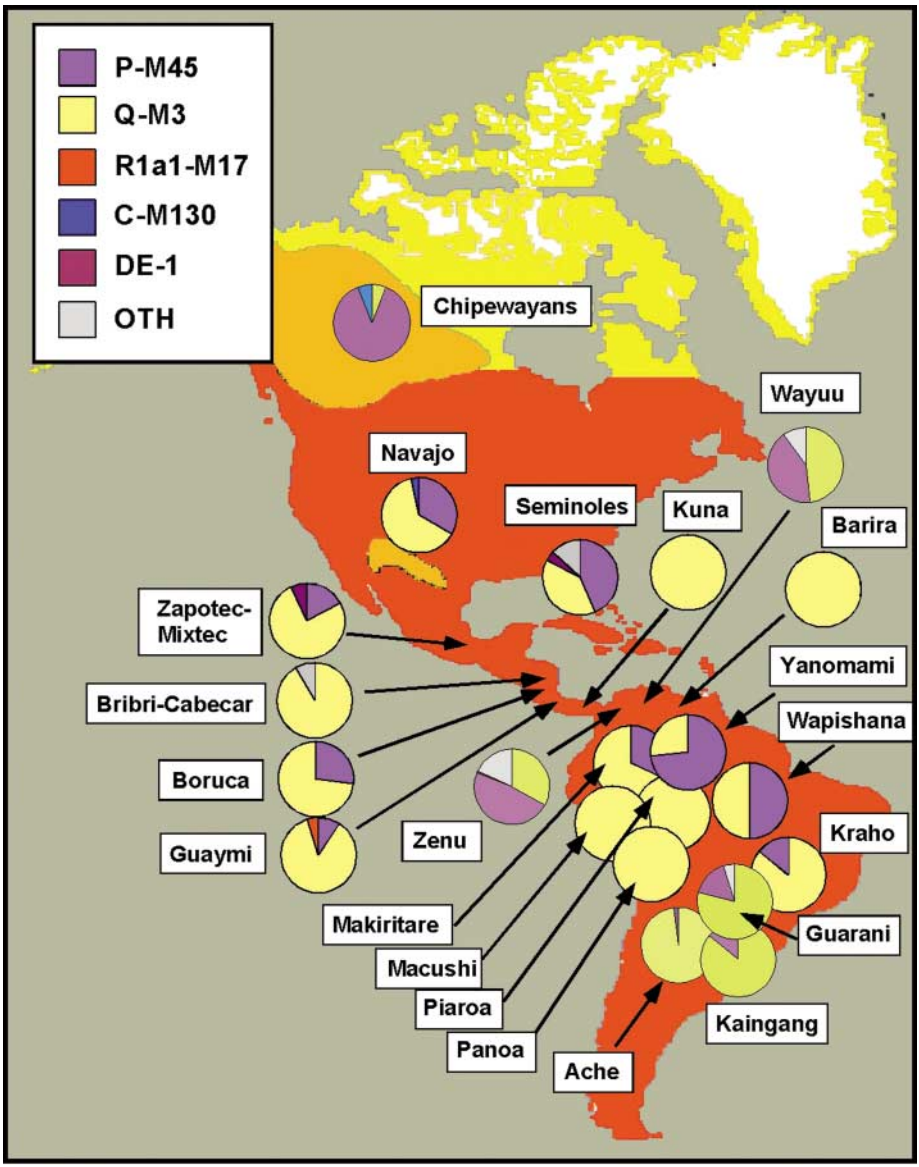

Figure 4 Distribution of NRY haplogroups in Native American populations. The color key for the haplogroups is indicated in the upper left-hand corner. The OTH category represents NRY haplotypes that do belong to "other" haplogroups, i.e., those contributed by African or European populations. The data shown here were taken from Lell et al. (2002) and Bortolini et al. (2003). For the Bortolini et al. (2003) data, the Q-M242 frequencies were added to the P-M45 frequency totals to make the distributions equivalent to those appearing in Lell et al. (2002), who did not screen their samples for the M242 SNP.

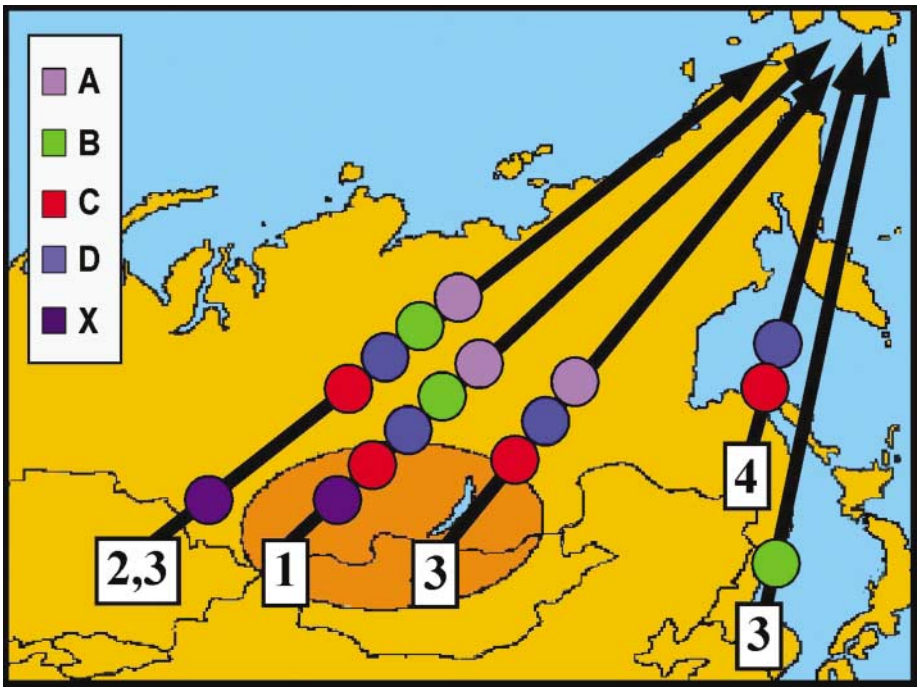

Figure 5 Migration models based on mtDNA haplogroup data. The models are as follows: (1) haplogroups A–D and X were brought together in single migration from central Siberia; (2) haplogroups A–D came with the initial migration, and haplogroup X represents a separate migration; (3) haplogroups A, C, and D were part of the initial migration, with haplogroups B and X representing separate migrations from different regions of Siberia/East Asia; (4) haplogroups C and D may have been reintroduced into the Americas as part of a secondary expansion of ancestral groups. Currently, the data support some form of model 1 or 2.

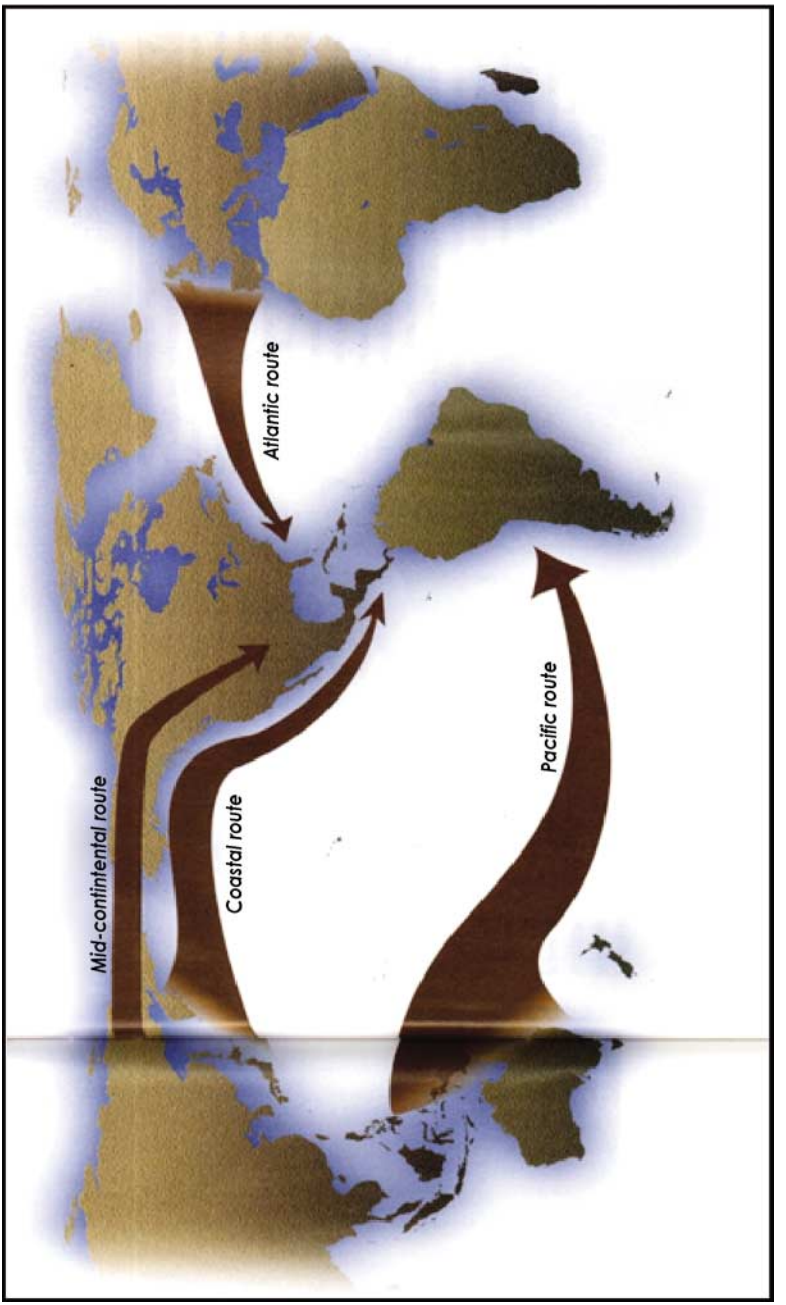

Figure 6 Possible migration pathways to the Americas. From *Sci. Am. Disc. Archeol.* Jan./Feb. 2000, pp. 34–35. Leach publ. Group Ltd.

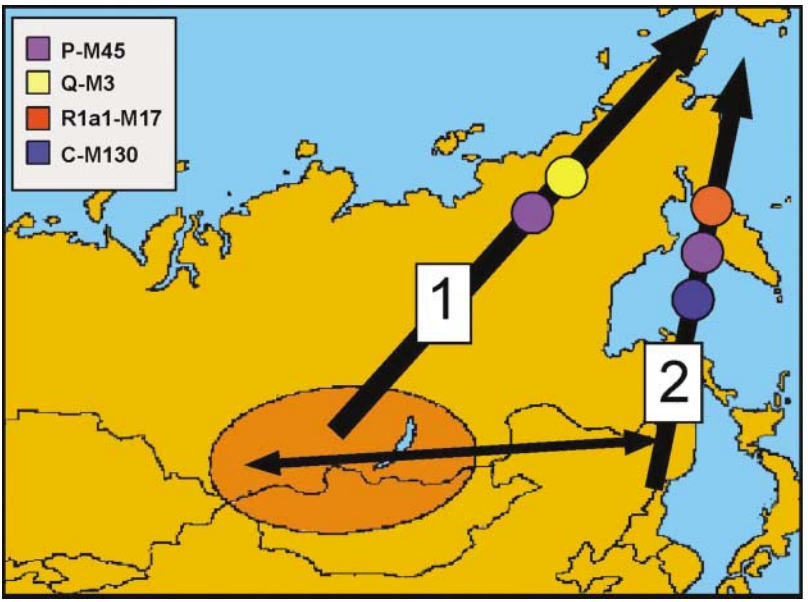

Figure 7 Migration model based on NRY haplogroup data. This model involves the following stages: (1) Haplogroups P-M45 and Q-M3 (M242) were initially brought to the Americas from central Siberia; alternatively, Q-M3 arose in the Americas shortly after human populations arrived there; (2) a secondary expansion from either central or eastern Siberia brought additional P-M45 haplotypes, along with those from C-M130 and R1a1-M17.