

Y-Chromosome Evidence for Differing Ancient Demographic Histories in the Americas

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To scrutinize the male ancestry of extant Native American populations, we examined eight biallelic and six microsatellite polymorphisms from the nonrecombining portion of the Y chromosome, in 438 individuals from 24 Native American populations (1 Na Dené and 23 South Amerinds) and in 404 Mongolians. One of the biallelic markers typed is a recently identified mutation (M242) characterizing a novel founder Native American haplogroup. The distribution, relatedness, and diversity of Y lineages in Native Americans indicate a differentiated male ancestry for populations from North and South America, strongly supporting a diverse demographic history for populations from these areas. These data are consistent with the occurrence of two major male migrations from southern/central Siberia to the Americas (with the second migration being restricted to North America) and a shared ancestry in central Asia for some of the initial migrants to Europe and the Americas. The microsatellite diversity and distribution of a Y lineage specific to South America (Q-M19) indicates that certain Amerind populations have been isolated since the initial colonization of the region, suggesting an early onset for tribalization of Native Americans. Age estimates based on Y-chromosome microsatellite diversity place the initial settlement of the American continent at ~14,000 years ago, in relative agreement with the age of well-established archaeological evidence.

Introduction

Although there is general agreement that America was first settled from Asia by people who migrated across Beringia, the pattern of migration, its timing, and the place of origin in Asia of the people(s) that migrated to the Americas remain unclear (Fiedel 1992; Crawford 1998; Jablonski 2002). Synthesizing the linguistic, dental, and genetic information available at the time, Greenberg et al. (1986) proposed that the settlement of the American continent happened in three major migratory waves. According to this model, the first migration occurred ~12,000 years ago (coinciding with the appear-

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been interpreted as indicative of more than one migratory wave during the initial colonization of the Americas (Torroni et al. 1992, 1993; Horai et al. 1993).

However, other mtDNA studies have challenged this interpretation and suggested the occurrence of a single migration into the continent, which would be at the origin of all major Native American linguistic families (Merriwether and Ferrell 1996; Bonatto and Salzano 1997, 1997; Silva et al. 2002). Interestingly, mtDNA analyses generally estimate an initial entry into the Americas prior to the last glacial maximum, ~30,000 years before present (ybp) (Torroni et al. 1994; Forster et al. 1996; Bonatto and Salzano 1997, 1997; Silva et al. 2002). These age estimates have contributed to the debate generated by archaeological and geological findings concerning the possibility of a colonization of the Americas significantly earlier than assumed in Greenberg's model (Crawford 1998; Jablonski 2002).

In the past few years, markers on the nonrecombining region of the Y chromosome have been used as a male complement to mtDNA analyses for the study of the colonization of the Americas. Initial analyses found one haplotype at high frequencies in native populations of all linguistic groups from North to South America (Pena et al. 1995; Santos et al. 1996; Underhill et al. 1996). This observation was interpreted as being indicative of a single founder Native American Y lineage, consistent with the view of a unique migratory wave into the continent. The other Y haplotypes detected in extant Native Americans were ascribed to recent admixture with non-natives (Underhill et al. 1996; Bianchi et al. 1997). This putative single founder Native American lineage is characterized by a C→T mutation at marker M3 within the P-M45 Y lineage (Karafet et al. 1997; Underhill et al. 2001).

Calling into question the proposal of a single founder Y lineage in the Americas, the analysis of microsatellite (STR) diversity in five populations from Colombia indicated that a fraction of those carrying the ancestral M3 allele are Native American in origin (Ruiz-Linares et al. 1999). Moreover, in Asia, the M3 mutation has been found only in extreme northeastern Siberia, raising the possibility that this lineage is, in fact, native to America, from which it could have back migrated into neighboring Siberia (Karafet et al. 1997; Lell et al. 1997). Genuine Native American Y founder haplogroups would thus correspond to P-M45 lineages ancestral to M3 and possibly to lineages other than P-M45. Indeed, Bergen et al. (1999) recently identified a mutation (RPS4Y

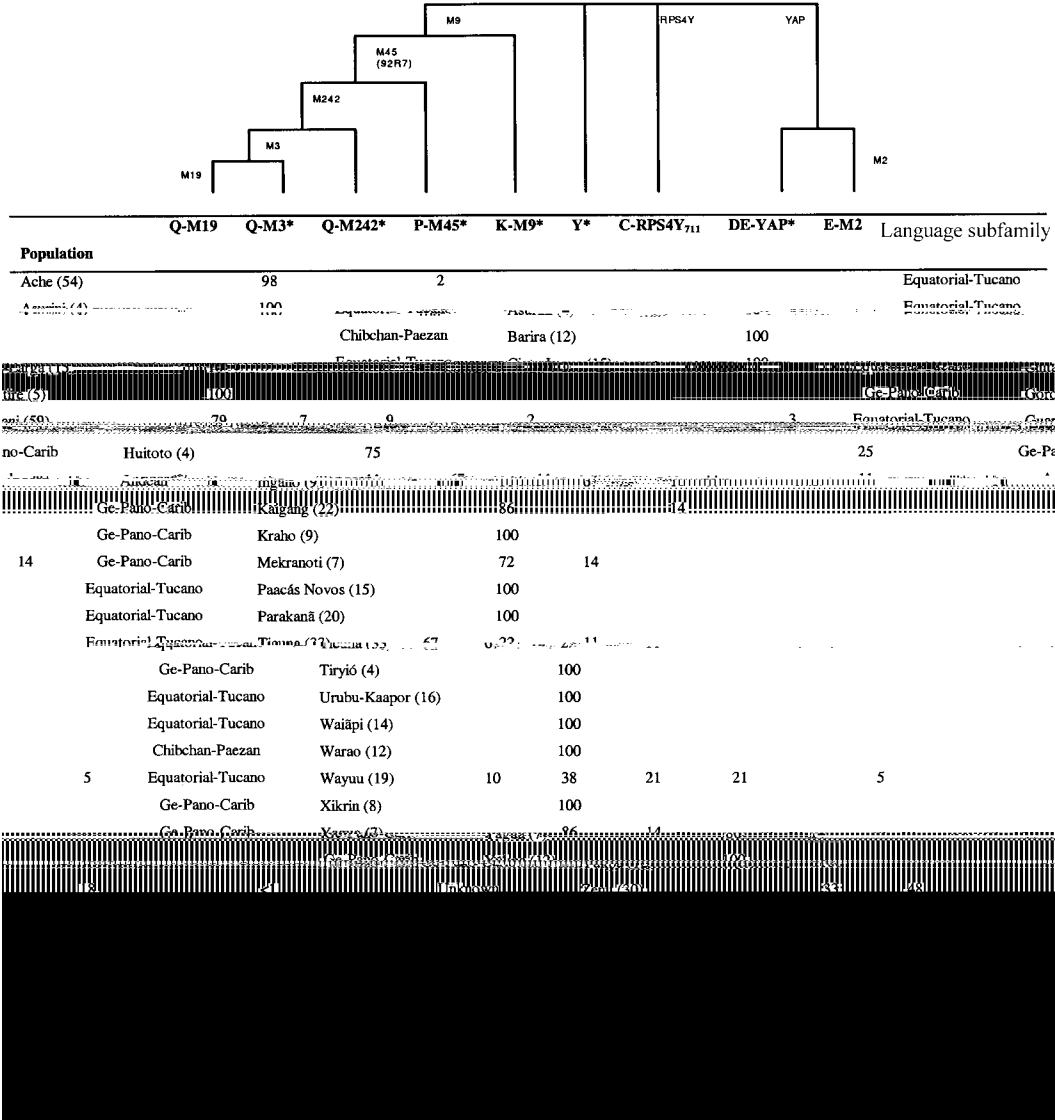


Figure 2 Phylogenetic relationship of nine Y-chromosome lineages and their frequency in Native Americans, Mongolians, Europeans, and sub-Saharan Africans. The tree at the top displays the relationship of these lineages and the markers that were examined to identify them. The lineage frequency (%) in the populations examined here (with sample size in parentheses) is indicated in the middle. The mean lineage frequencies for major population groups are given at the bottom and were calculated from the data of Karafet et al. (1999) and Lell et al. (2002) and from the data collected here (the Na Dené being represented by the Chipewayan sample). The nomenclature of lineages follows the guidelines of the Y Chromosome Consortium (2002). Asterisks indicate lineages characterized by the derived state at that marker but the ancestral state at the other loci examined within that clade. For example, "P-M45*" refers to chromosomes carrying the derived M45 allele but the ancestral allele at marker M242—that is, P-M45*(x M242)—and Y* chromosomes carry the ancestral allele at all markers examined—that is, Y*(x M9, RPS4Y₇₁₁, YAP).

ellite lineages as "haplotypes," to distinguish them from biallelic marker "haplogroups."

Data Analysis

Allele and lineage frequencies were calculated by counting, using the Arlequin package (Schneider et al. 2000). A principal-component analysis of Y-haplogroup frequencies was performed with the Ntsys (v. 2.1) program (Rohlf 2001). This analysis included data for the

populations examined here, as well as data for the Asian and Native American populations examined by Karafet et al. (1999) and Lell et al. (2002). The relatedness of microsatellite haplotypes was assessed through reduced-median networks (Bandelt et al. 1995) constructed with the Network (v. 3.1) program. Neighbor-joining trees relating haplogroups on the basis of Nei's genetic distance (Nei 1987), calculated from microsatellite allele frequencies, were obtained using programs in the Phylip

(v. 3.5) package (Felsenstein 2001). The age of Y-chromosome haplogroups was estimated by calculating the mean average square distance (ASD) between the inferred ancestral haplotype of a haplogroup and all its observed descendants (Goldstein et al. 1995; Slatkin 1995; Ruiz-Linares et al. 1999). If we assume a generation time (t) of 25 years and a mean mutation rate (μ) for Y microsatellites of 0.18% per generation (Kayser et al. 2000), the age of a haplogroup can be estimated as $ASD \times t / \mu$. SEs for haplogroup age were obtained by bootstrapping the sample of observed haplotypes 1,000 times.

Results

Geographic Distribution of Y-Chromosome Haplogroups

The biallelic markers typed identified nine Y haplogroups in the populations examined (fig. 2). Four of these haplogroups (Q-M19, Q-M3*, Q-M242*, and C-RPS4Y₇₁₁) are restricted to the Americas and/or Asia. The most derived haplogroup (Q-M19) was found only in the Ticuna and in the Wayuu of northwestern South America. Its parental haplogroup (Q-M3) was detected in all of the South Amerind populations tested, where it is markedly predominant (with a mean frequency of 77%). This haplogroup was also observed, albeit at a low frequency (6%), in the Chipewyan but was not found in Mongolia. Haplogroup Q-M242* (the immediate ancestor of Q-M3) is the second most prevalent in the Chipewyan, where it was observed at a frequency of 25%. This haplogroup has a wide distribution in South Amerinds (with a mean frequency of 9%), and its highest prevalence is in populations from northwestern South America (Ingano, Wayuu, and Zenu; figs. 1 and 2). Q-M242* was also detected at a low frequency (4%) in Mongolia. Haplogroup C-RPS4Y₇₁₁ was not found in South Amerinds, has a low frequency (6%) in the Chipewyan, and is the lineage most commonly observed in Mongolia (56%).

The other five lineages detected (P-M45*, K-M9*, Y*, DE-YAP, and E-M2) are observed outside the Americas and Asia (fig. 2). Lineage P-M45* was found at a low frequency in South Amerinds (4%) and Mongolia (6%) but is the most common in Europe (52%) and the Chipewyan (63%). Lineage K-M9* has low frequencies in Europe and Africa, is the second most frequent in Mongolia (30%), and was not observed in Native Americans. Lineages Y*, DE-YAP, and E-M2 are mostly restricted to Europe or Africa. They were not observed in the Chipewyan, and their low frequency in South Amerinds (~4%) is likely to reflect recent admixture.

Figure 3 shows a principal-component analysis of the frequency of six Y-chromosome haplogroups in the pop-

ulations typed here and in the Asian and Native American populations examined by Karafet et al. (1999) and Lell et al. (2002). The first principal component separates Native American from Asian populations, with the Chipewyan, the Cheyenne, and several populations from northern Asia occupying intermediate positions on this axis. The second principal component separates populations within America and Asia, with the Chipewyan, the Cheyenne, and some northern Asian populations (Selkup, Yakut, and Kets) maintaining a close genetic affinity. The spread of Native American populations on the principal-component graph correlates mostly with the frequency of haplogroups Q-M3 and P-M45* (data not shown), with populations from South America generally having the highest frequencies of Q-M3, whereas some populations from North America show increased frequencies of P-M45* and also show the presence of haplogroup C-RPS4Y₇₁₁. Similarly, the Asian populations closest to Native Americans are characterized by a predominance of lineage P-M45* and low frequencies of C-RPS4Y₇₁₁. Northeastern Asian populations generally appear closely related to central Asians, reflecting the generally high frequency of haplogroups K-M9* and C-RPS4Y₇₁₁ in most of these populations (data not shown).

STR Diversity of Y-Chromosome Haplogroups

Haplogroups Q-M3* and Q-M19.—A total of 36 Q-M3* STR haplotypes were identified in South Amerinds (table 1). Twenty-two of these haplotypes were seen only once. Of the 14 haplotypes seen multiple times, 9 were seen in only one population, and two or three populations share the other 5. The high frequency of haplotype 1 is mostly due to this being the only haplotype observed in the Ache ($n = 54$), a population with a marked reduction in Y-chromosome diversity. A median-joining network relating Q-M3* haplotypes detected more than once is shown in figure 4 . At the center of this network is haplotype 5. This haplotype contains the most frequent allele at the six STR loci tested (table 2). The data of Lell et al. (2002) for four of the six STR loci examined here (DYS19, DYS388, DYS390, and DYS391) show that a haplotype characterized by alleles 13-12-24-10 (included in haplotype 5 in table 1) has a wide distribution in North and Central Amerinds. These observations confirm our previous results (Ruiz-Linares et al. 1999) identifying haplotype 5 as the most likely ancestor of Q-M3* chromosomes and lead to an estimated age for this haplogroup of 7,570 years (SE 681).

Table 1 also shows the 13 Q-M19 haplotypes observed in the Ticuna and the Wayuu. Haplotype 15 (seen four times and present in two Ticuna settlements) is the most frequent and is identical to an Q-M3* chromosome also found in the Ticuna. This haplotype includes the

Table 1
Q-M3* and Q-M19 Haplotypes in Native Americans

HAPLOTYPE	ALLELE AT						FREQUENCY	
	DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	Q-M3* (n = 117)	Q-M19 (n = 18)
1	13	12	23	10	14	13	.265	.056
2	13	12	24	10	13	14	.094	0
3	13	12	24	10	15	12	.086	0
4	14	12	23	10	14	13	.051	0
5	13	12	24	10	14	13	.051	0
6	14	13	24	10	14	13	.043	0
7	13	12	24	10	15	14	.034	0
8	14	12	23	10	13	13	.034	0
9	13	12	24	11	14	13	.034	0
10	13	12	24	10	13	12	.026	0
11	14	12	24	10	14	13	.026	0
12	14	12	24	10	13	14	.026	0
13	13	14	24	10	14	14	.026	0
14	13	12	25	10	14	13	.017	.056
15	13	12	25	10	15	13	.009	.222
16	13	12	24	10	15	13	.009	.056
17	13	13	25	10	14	13	.009	.056
18	13	12	25	11	11	13	.009	0
19	13	13	24	10	11	13	.009	0
20	13	12	24	10	13	13	.009	0
21	12	12	25	10	14	13	.009	0
22	13	11	24	10	16	16	.009	0
23	14	9	24	10	16	13	.009	0
24	13	13	24	10	14	13	.009	0
25	13	12	24	10	14	14	.009	0
26	14	12	24	11	14	13	.009	0
27	14	14	24	10	14	14	.009	0
28	13	12	24	9	15	12	.009	0
29	14	12	25	11	16	13	.009	0
30	14	15	23	10	16	14	.009	0
31	13	13	24	11	14	11	.009	0
32	13	12	22	10	14	13	.009	0
33	13	12	23	10	14	14	.009	0
34	14	13	24	10	13	13	.009	0
35	13	12	24	11	13	13	.009	0
36	13	12	23	11	14	13	.009	0
37	13	12	24	10	14	12	0	.111
38	13	12	25	11	15	13	0	.111
39	14	12	25	10	14	16	0	.056
40	15	13	25	10	14	14	0	.056
41	14	13	25	10	14	14	0	.056
42	13	12	25	10	15	12	0	.056
43	13	12	25	10	15	14	0	.056
44	15	12	25	10	11	14	0	.056

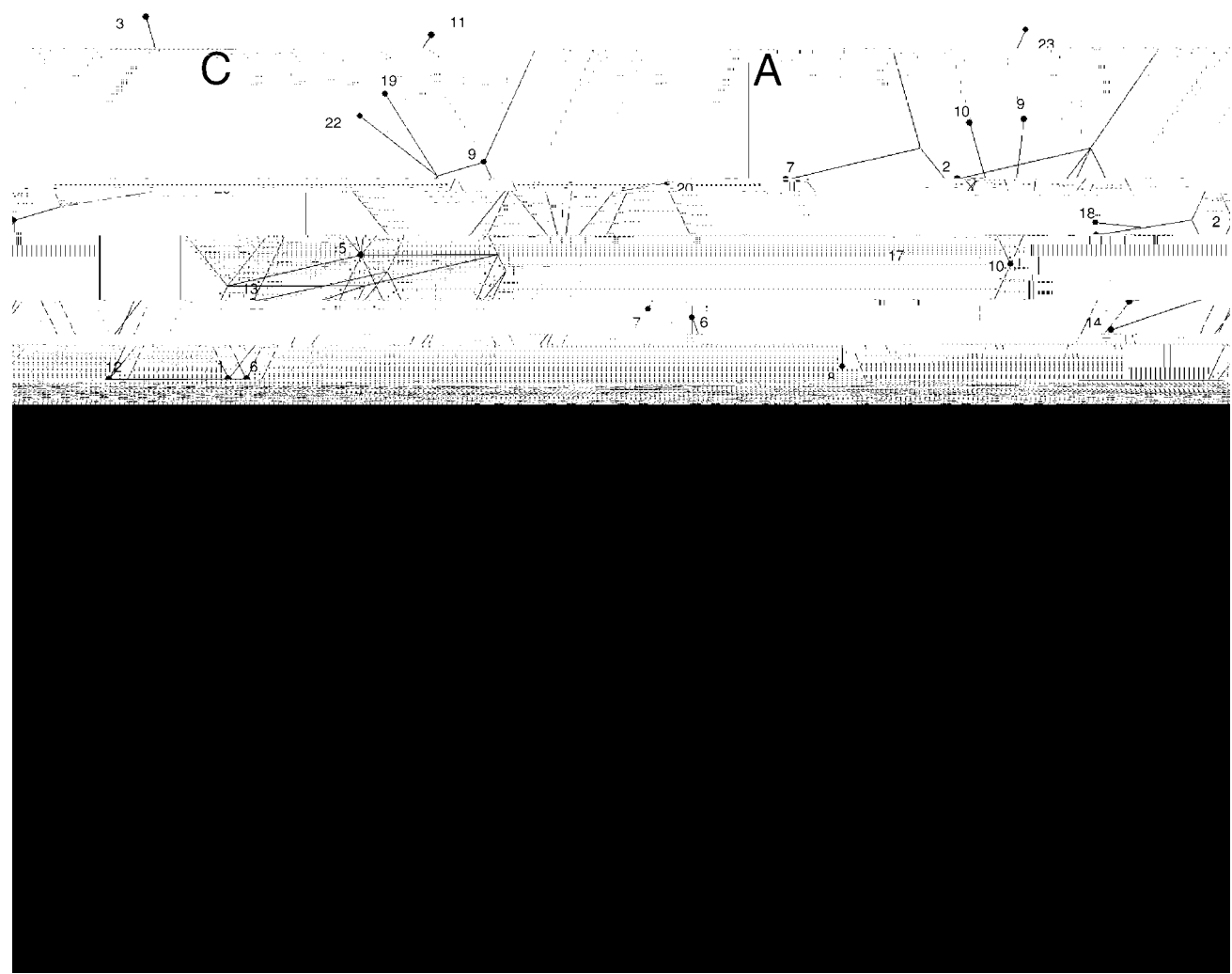


Figure 4 Median-joining networks relating haplotypes within lineages Q-M3* (), Q-M19 (), Amerind Q-M242* (), and P-M45* ()

Allele Frequencies at Six Microsatellite Loci in Lineages within the P-M45 Haplogroup in Amerindians, Chipechuan, and Mongolians

Locus and Allele	Allele Frequency							
	Q-M19 Amerindian (n = 18)	Q-M3* Amerindian (n = 117)	Q-M242*			P-M45*		
			Amerindian (n = 17)	Chipewyan (n = 10)	Mongolian (n = 15)	Amerindian (n = 10)	Chipewyan (n = 21)	Mongolian (n = 23)
DYS19:								
12	0	.009	.059	0	0	0	0	0
13	.778	.761	.647	.900	.867	.100	.048	0
14	.111	.231	.235	0	.067	.900	.714	.348
15	.111	0	.059	.100	.067	0	.238	.217
16	0	0	0	0	0	0	0	.261
17	0	0	0	0	0	0	0	.174
DYS388:								
9	0	.009	0	0	0	0	0	0
11	0	.009	0	0	0	0	0	0
12	.833	.855	.765	.900	1.000	1.000	1.000	.913
13	.167	.086	.177	.100	0	0	0	.087
14	0	.034	.059	0	0	0	0	0
15	0	.009	0	0	0	0	0	0
DYS390:								
21	0	0	0	0	0	0	0	.130
22	0	.009	0	.100	.067	.100	.048	.044
23	.056	.376	.177	.800	.333	.400	.143	.174
24	.167	.556	.471	.100	.600	.300	.810	.174
25	.778	.060	.235	0	0	.200	0	.478
26	0	0	.059	0	0	0	0	0
27	0	0	.059	0	0	0	0	0
DYS391:								
5	0	0	0	0	.067	0	0	0
6	0	0	0	0	.133	0	0	0
9	0	.009	0	.100	.200	0	.048	.044
10	.889	.906	.882	.300	.467	.400	.095	.565
11	.111	.086	.118	.600	.067	.600	.857	.391
12	0	0	0	0	.067	0	0	0
DYS392:								
10	0	0	0	0	0	0	0	.174
11	.056	.017	0	.100	0	0	0	.478
12	0	0	.059	0	0	0	0	.044
13	0	.205	.118	0	0	.600	.571	.304
14	.444	.598	.588	.700	.800	.300	.429	0
15	.500	.145	.177	.200	.067	0	0	0
16	0	.034	.059	0	.067	.100	0	0
17	0	0	0	0	.067	0	0	0
DYS393:								
11	0	.009	0	0	0	0	0	0
12	.167	.120	.059	.100	0	0	0	.044
13	.556	.650	.824	.900	.533	.800	.667	.696
14	.222	.214	.118	0	.467	.200	.333	.261
16	.056	.009	0	0	0	0	0	0

Table 3
Q-M242* Haplotypes in Mongolians, Chipewyan, and Amerindians

HAPLOTYPE	ALLELE AT						FREQUENCY IN		
	DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	Mongolian (n = 15)	Chipewyan (n = 10)	Amerindian (n = 17)
1	13	12	23	10	14	13	.332	.100	0
2	13	12	24	10	14	13	0	.100	.292
3	13	12	24	10	14	14	.067	0	0
4	13	12	23	11	14	13	0	.400	0
5	13	12	22	10	14	13	0	.100	0
6	14	12	23	10	14	13	0	0	.059
7	13	12	24	10	15	14	0	0	.059
8	14	12	23	10	13	13	0	0	.059
9	13	13	25	10	14	13	0	0	.059
10	13	12	24	10	15	13	0	0	.059
11	13	12	24	9	14	14	.200	0	0
12	13	12	24	6	14	14	.133	0	0
13	14	12	24	11	16	13	.067	0	0
14	15	12	24	12	17	13	.067	0	0
15	13	12	22	10	15	13	.067	0	0
16	13	12	24	5-4031.9(17)-4031.9(13)-4450.7(.067)-4060.4(01i8t1-(170r(032.1(1419.4(13)-3756.9(12)-4031.8(24)					

Table 4**P-M45* Haplotypes in Mongolians, Chipewyan, and Amerindians**

HAPLOTYPE	ALLELE AT						FREQUENCY IN		
	DYS19	DYS388	DYS390	DYS391	DYS392	DYS393	Mongolian (n = 23)	Chipewyan (n = 21)	Amerindian (n = 10)
1	14	12	25	11	13	13	0	0	.200
2	14	12	24	10	13	13	.044	.048	.100
3	14	12	24	11	13	13	0	.286	.100
4	14	12	24	11	16	13	0	0	.100
5	14	12	22	11	13	14	0	0	.100
6	14	12	23	10	14	13	0	0	.200
7	13	12	23	11	14	14	0	0	.100
8	14	12	23	10	13	13	0	0	.100
9	14	12	24	11	14	14	0	.190	0
10	15	12	23	11	13	13	0	.095	0
11	14	12	24	11	14	13	0	.048	0
12	15	12	24	11	14	13	0	.095	0
13	14	12	24	11	13	14	0	.095	0
14	15	12	23	11	14	13	0	.048	0
15	14	12	24	9	13	13	0	.048	0
16	13	12	22	10	14	14	0	.048	0
17	15	12	24	10	13	12	.044	0	0
18	14	12	19	10	13	13	.130	0	0
19	16	12	23	11	10	14	.044	0	0
20	15	12	24	10	13	13	.044	0	0
21	14	13	23	10	10	14	.044	0	0
22	14	12	23	10	10	14	.044	0	0
23	17	12	25	10	11	13	.044	0	0
24	15	12	25	10	11	13	.087	0	0
25	14	12	23	9	10	14	.044	0	0
26	14	13	22	11	13	13	.044	0	0
27	16	12	24	10	11	13	.044	0	0
28	16	12	25	11	11	14	.087	0	0
29	15	12	25	11	11	13	.044	0	0
30	17	12	25	11	11	13	.087	0	0
31	16	12	25	11	11	13	.087	0	0
32	17	12	25	10	12	13	.044	0	0
Variance ^a							1.218	.213	.409

^a Mean variance in repeat score.

of Lell et al. (2002). Tarazona-Santos and Santos (2002) questioned the idea that M45b constitutes a Native American founder lineage, since haplotype 3 (characterized by alleles 14-12-24-11-13-13) is common in European populations (Weale et al. 2002), and its presence in Native Americans could be the result of recent admixture.

tected in North American populations of the Amerind linguistic group (Bergen et al. 1999; Karafet et al. 1999; Lell et al. 2002). The principal-component graph in figure 3 illustrates that the haplogroup distribution in the Chipewyan and the Cheyenne is very similar. At the mtDNA level, it has also been shown that haplogroup X is present both in Na Dené and in North American Amerinds (Brown et al. 1998). These findings do not evidence a close correspondence between the second wave of Asian colonization and the Na Dené linguistic family, as proposed in the model of Greenberg et al. (1986). However, some level of admixture between the Na Dené and North Amerinds is likely and is well documented for the Navajo (Cavalli-Sforza et al. 1994).

Regarding the Asian ancestry of South Amerinds, the high frequency and haplotype diversity of haplogroup P-M45* in southern/central Siberia has led to the proposal of this region as the region of origin for the initial male migration to the Americas (Karafet et al. 1999; Santos et al. 1999; Lell et al. 2002). Consistent with this scenario, the limited microsatellite data available show that Q-M242 chromosomes related to haplotype 13-12-24-10-14-13 (in which the M3 mutation presumably occurred; tables 1 and 3) are found in central Asia, including Mongolia (table 3), and in the Tuvan population (Seielstad et al. 2003 [in this issue]).

Globally, Y-chromosome data therefore emphasize the critical role of southern/central Siberia in the peopling of the Americas, since this region appears to be at the origin of two major male migratory waves of colonization. The data presented here are also consistent with the intriguing possibility of ancient links between proto-Europeans and proto-Native Americans, an idea that has been put forward in previous Y-chromosome studies (Karafet et al. 1999; Santos et al. 1999; Wells et al. 2001; Lell et al. 2002). An ancestral connection between these groups has also been suggested on the basis of morphological (Brace et al. 2001) and mtDNA (Brown et al. 1998) data and could ultimately trace back to ancient east/west human dispersals from a common source in central Asia. In agreement with this scenario, the P-M45 lineage has been found to be oldest in central Asia (Wells et al. 2001; Zerjal et al. 2002), where the Tuvan population includes haplogroups M242, M45, M173, and Tat, which are now dispersed in Europe and/or America.

Lineage Q-M19 had previously been detected in the Ticuna of the upper Amazon and in the Wayuu, a population living in the Guajira peninsula on the extreme north of Colombia's Caribbean coast (Ruiz-Linares et al. 1999). Both populations have been classified in the Equatorial-Tucano linguistic family (Ruhlen 1991). The Q-M19 lineage was not detected in any of the other South Amerind populations examined here. Our survey included several populations occupying areas interme-

diate between the Ticuna and the Wayuu and comprises eight additional representatives of the Equatorial-Tucano linguistic family (figs. 1 and 2). The restricted distribution of Q-M19 chromosomes would suggest that this lineage has a recent origin. However, the estimated age for Q-M19 is similar to the one obtained for its parental haplogroup Q-M3 (~7,000–8,000 ybp). This observation suggests that population isolation and possibly the process of tribalization of Native Americans started soon after the initial human dispersal in the region. Evidence suggestive of an early onset of tribalization in the Americas has also been provided by mtDNA studies that have documented an ancient origin for some private allelic variants (Torroni et al. 1993) and is consistent with the strong genetic drift generally observed in Native American populations (Bortolini et al. 2002). Such an ancient origin for some extant native American populations could be a contributing factor to the great linguistic diversification of Amerinds and their disputed grouping into a single linguistic family (Cavalli-Sforza et al. 1994).

The age calculated for the Q-M242* lineage in Amerinds (13,611 years) and in Mongolia (15,416 years) points to a relatively recent colonization of the Americas. These dates are similar to those obtained with 16 Y-STR markers in a wide sample of Asian Q-M242 chromosomes (Seielstad et al. 2003 [in this issue]). The Asian estimates represent an upper limit for the time of entry into the Americas, and the similarity in age obtained for Q-M242 in Asia and Amerinds is suggestive of an entry soon after the occurrence of this mutation (assuming that entrance in the Americas was associated with an important population bottleneck). Although lineage dating is subject to large error margins, these Y-chromosome estimates are considerably more recent than the ~20,000–30,000 years calculated for initial entry into America on the basis of mtDNA data (Torroni et al. 1994; Forster et al. 1996; Bonatto and Salzano 1997, 1997; Silva et al. 2002). Interestingly, the Y-based dates are comparable to the age estimated for the oldest (well-established) archaeological sites in the Americas (~12,500 radiocarbon years old [Roosevelt et al. 2002]). Y-chromosome data are thus consistent with a relatively late colonization of the Americas followed by a rapid human population dispersal, as suggested by various archaeological studies (Jablonski 2002).

The discrepancy between the Y-chromosome and mtDNA estimates for the time of initial colonization could have several explanations, of which only two are

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