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Review Article

Uniparental genetic markers in South Amerindians

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Abstract

A comprehensive review of uniparental systems in South Amerindians was undertaken. Variability in the Y-chromosome haplogroups were assessed in 68 populations and 1,814 individuals whereas that of Y-STR markers was assessed in 29 populations and 590 subjects. Variability in the mitochondrial DNA (mtDNA) haplogroup was examined in 108 populations and 6,697 persons, and sequencing studies used either the complete mtDNA genome or the highly variable segments 1 and 2. The diversity of the markers made it difficult to establish a general picture of Y-chromosome variability in the populations studied. However, haplogroup Q1a3a* was almost always the most prevalent whereas Q1a3* occurred equally in all regions, which suggested its prevalence among the early colonizers. The STR allele frequencies were used to derive a possible ancient Native American Q-clade chromosome haplotype and five of six STR loci showed significant geographic variation. Geographic and linguistic factors moderately influenced the mtDNA distributions (6% and 7%, respectively) and mtDNA haplogroups A and D correlated positively and negatively, respectively, with latitude. The data analyzed here provide rich material for understanding the biological history of South Amerindians and can serve as a basis for comparative studies involving other types of data, such as cultural data.

Key words: genetics, language and geography, mitochondrial DNA, Native Americans, South Amerindians, Y-chromosome.

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Introduction

Native Americans have been the subject of a large number of population genetic studies because of particular characteristics: (a) there are groups among them that until recently had a hunter-gatherer way of living with only incipient agriculture, typical of our ancestors, (b) they show considerable interpopulation but low intrapopulation variability, and (c) since until recently they could not write there is no written record of their history, except for those of non-Amerindian colonizers. Biological studies can therefore be used to investigate their past.

The first genetic studies examined the variability in blood groups and proteins and have been summarized in Salzano and Callegari-Jacques (1988) and Crawford (1998). The advent of modern molecular biology, which allows direct, detailed DNA analysis, has opened new possibilities for investigating these populations.

DNA studies can basically be divided into two groups: those involving autosomal markers and those involving uniparental (Y-chromosome, mitochondrial DNA) markers. The latter are important because they can provide a clear-cut pattern of historical events that is not clouded by recombination factors. For Amerindians, the number of reviews that have dealt with these markers is not large or comprehensive. For the Y-chromosome, Bortolini *et al.* (2003) considered 438 individuals from 23 Southern and one Northern Amerindian populations who were screened for eight single nucleotide polymorphisms (SNPs) and six short tandem repeat/microsatellite (STR) loci, and Zegura *et al.* (2004) studied 63 binary polymorphisms and 10 STR regions in 2,344 persons from 15 Northern and three Southern Amerindian groups. Only a few recent studies have used all known SNPs necessary to identify the major Native American Y-haplogroups and their sublineages in Amerindian populations (Geppert *et al.*, 2011; Jota *et al.*, 2011; Bisso-Machado *et al.*, 2011).

The most recent mtDNA reviews were published four years ago and involved sequence variability in the hypervariable region 1 (Hunley *et al.*, 2007; Lewis Jr *et al.*, 2007). Schurr and Sherry (2004), on the other hand, associated data from Y-chromosome markers with mitochondrial DNA (mtDNA) results, providing a good picture of the information available at the time. No general review considering both data sets has been published since then.

This review provides a detailed, comprehensive survey of Y-chromosome haplogroup frequency variation in 68 populations involving 1,814 individuals. In addition,

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specific information on Y-STR markers for 29 populations and 590 subjects is given. The haplogroup mtDNA data included 108 populations involving a total of 6,697 persons. Geographic and linguistic factors that may have influenced this variation were carefully considered, leading to a global, overview of the genetic pattern associated with these markers in South Amerindians. Information on mtDNA sequencing studies is also supplied.

Materials and Methods

The data used in this review were obtained from 17 primary surveys of the Y-chromosome and 66 primary surveys of mtDNA. These studies were retrieved through PubMed and by searching the reference lists of the corresponding papers. Haplogroup frequencies were obtained by direct counting. Intra- and inter-populational diversity was calculated with AMOVA (Weir and Cockerham, 1984; Excoffier *et al.*, 1992; Weir, 1996) using Arlequin 3.5.1.2 software (Excoffier and Lischer, 2010). AMOVA was also used to estimate the level of differentiation between and within 17 pre-defined language and 7 geographical categories, respectively. The distribution patterns of the mtDNA haplogroup frequencies were established by generating isoline maps using IDRISI 16.0 software (IDRISI Taiga) (Eastman, 2006). Spearman's correlation coefficients were calculated with PASW Statistics 18 software. Average heterozygosity (ah) was calculated with Arlequin 3.5.1.2 software.

Results and Discussion

Table 1 gives the distribution of the Q and non-Q-chromosomes (defined by a set of SNPs), as well as linguistic and geographical information for the samples considered. The samples were distributed from latitude 11° North to 45° South and longitude 46° to 76° West, with the individuals involved speaking 23 languages. Sample sizes varied widely from 1 to 151 individuals. Twenty-two of the studies involved less than 10 persons. Unfortunately, there is no standardization on the number of SNPs studied and in most cases only the M242 and M3 markers (which define the Asian/Native American paragroup Q* and its autochthonous Native American sublineage Q1a3a*, respec-

Table 1 - The distribution of Q and non-Q lineages and linguistic and geographical information for the samples considered.

Populations (n)[1]	Haplogroup (%)		Language[2]	Geographical coordinates	References
	Q lineages / Amerindian origin	Non-Q lineages			
Wayuu (19)	69	31	Arawakan	11° N; 73° W	Bortolini *et al.* (2003)
Kogi (17)	100		Chibchan	11° N; 74° W	Rojas *et al.* (2010)
Barira (12)	100		Chibchan	10° 44' N; 71° 23' W	Bortolini *et al.* (2003)
Arsario (Wiwa) (6)	100		Chibchan	10° 25' N; 73° 05' W	Rojas *et al.* (2010)
Arhuaco (Ijka) (19)	100		Chibchan	9° 04' N; 73° 59' W	Rojas *et al.* (2010)
Warao (12)	100		Warao	9° N; 61° W	Bortolini *et al.* (2003)
Yukpa (12)	100		Carib	8° 40' N; 72° 41' W	Bortolini *et al.* (2003)
Zenu (52)	79	21	Spanish[3]	8° 30' N; 76° W	Bortolini *et al.* (2003); Rojas *et al.* (2010)
Embera (13)	92	8	Choco	7° N; 76° 30' W	Rojas *et al.* (2010)
Makiritare (25)	68	32	Carib	5° 33' N; 65° 33' W	Lell *et al.* (2002)
Kali'na (21)	81	19	Carib	5° 31' N; 53° 47' W	Mazières *et al.* (2008)
Waunana (29)	100		Choco	4° 50' N; 77° W	Rojas *et al.* (2010)
Palikur (35)	94	6	Arawakan	4° N; 51° 45' W	Mazières *et al.* (2008)
Macushi (4)	100		Carib	4° N; 60° 50' W	Lell *et al.* (2002)
Piaroa (6)	100		Salivan	3° 57' N; 66° 22' W	Lell *et al.* (2002)
Wapishana (2)	50	50	Arawakan	3° 07' N; 60° 03' W	Lell *et al.* (2002)
Emerillon (9)	100		Tupi	3° N; 53° W	Mazières *et al.* (2008)
Yanomámi (39)	38	62	Yanomam	2° 50' N; 54° W	Rodriguez-Delfin *et al.* (1997); Lell *et al.* (2002)
Tiryió (4)	100		Carib	2° N; 56° W	Bortolini *et al.* (2003)
Apalaí (57)	98	2	Carib	1° 20' N; 54° 40' W	Rodriguez-Delfin *et al.* (1997); Bortolini *et al.* (2003)
Wayampi (62)	100		Tupi	1° N; 53° W	Rodriguez-Delfin *et al.* (1997); Bortolini *et al.* (2003); Mazières *et al.* (2008)

Table 1 (cont).

Populations (n)[1]	Haplogroup (%)		Language[2]	Geographical coordinates	References
	Q lineages / Amerindian origin	Non-Q lineages			
Yagua (7)	100		Peba-Yaguan	0° 51' N; 72° 27' W	Bortolini *et al.* (2003)
Ingano (108)	80	20	Quechuan	0° 50' N; 77° W	Bortolini *et al.* (2003); Rojas *et al.* (2010)
Wai-Wai (9)	100		Carib	0° 40' S; 58° W	Bisso-Machado *et al.* (2011)
Urubu-Kaapor (16)	100		Tupi	2° -3° S; 46° -47° W	Bortolini *et al.* (2003)
Huitoto (4)	75	25	Witotoan	2° 14' S; 72° 19' W	Bortolini *et al.* (2003)
Arara (15)	100		Carib	3° 30' -4° 20' S; 53° 0' -54° 10' W	Rodriguez-Delfin *et al.* (1997); Bianchi *et al.* (1998); Bisso-Machado *et al.* (2011)
Asurini (4)	100		Tupi	3° 35' -4° 12' S; 49° 40' -52° 26' W	Bortolini *et al.* (2003)
Ticuna (59)	93	7	Ticuna	4° S; 69° 58' W;	Bortolini *et al.* (2003); Rojas *et al.* (2010)
Parakanã (20)	100		Tupi	5° 22' S; 51° 17' W	Bortolini *et al.* (2003)
Xikrin (14)	100		Macro-Ge	5° 55' S; 51° W	Bortolini *et al.* (2003); Bisso-Machado *et al.* (2011)
Suruí (24)	96	4	Tupi	5° 58' -10° 50' S; 48° 39' -61° 10' W	Underhill *et al.* (1996); Bisso-Machado *et al.* (2011)
Araweté (4)	100		Tupi	5° 9' S; 52° 22' W	Bisso-Machado *et al.* (2011)
Munduruku (1)	100		Tupi	6° 23' S; 59° 9' W	Bisso-Machado *et al.* (2011)
Jamamadi (3)	100		Arauan	7° 15' S; 66° 41' W	Bisso-Machado *et al.* (2011)
Gorotire (19)	100		Macro-Ge	7° 44' S; 51° 10' W	Bortolini *et al.* (2003); Bisso-Machado *et al.* (2011)
Krahó (15)	93	7	Macro-Ge	8° S; 47° 15' W	Lell *et al.* (2002); Bortolini *et al.* (2003)
Kuben-Kran-Kegn (9)	100		Macro-Ge	8° 10' S; 52° 8' W	Bisso-Machado *et al.* (2011)
Tenharim (1)	100		Tupi	8° 20' S; 62° W	Bisso-Machado *et al.* (2011)
Mekranoti (9)	78	22	Macro-Ge	8° 40' S; 54° W	Bortolini *et al.* (2003)
Kayapó (10)	100		Macro-Ge	9° S; 53° W	Rodriguez-Delfin *et al.* (1997)
Karitiana (18)	100		Tupi	9° 30' S; 64° 15' W	Underhill *et al.* (1996); Bisso-Machado *et al.* (2011)
Cinta-Larga (15)	100		Tupi	9° 50' –12° 30' S; 59° 10' –60° 50' W	Bortolini *et al.* (2003)
Gavião (7)	100		Tupi	10° 10' S; 61° 8' W	Bisso-Machado *et al.* (2011)
Karipuna (1)		100	Tupi	10° 14' S; 64° 13' W	Bisso-Machado *et al.* (2011)
Zoró (6)	100		Tupi	10° 20' S; 60° 20' W	Bisso-Machado *et al.* (2011)
Matsiguenga (28)	91	9	Arawakan	10° 47' -12° 51' S; 73° 17' -70° 44' W	Mazières *et al.* (2008)
Pacaás Novos (Wari) (29)	100		Chapacura-Wanham	11° 8' S; 65° W	Bortolini *et al.* (2003)
Panoa (5)	100		Pano	12° 55' S; 65° 12' W	Lell *et al.* (2002)
Xavante (15)	100		Macro-Ge	14° S; 52° 30' W	Bisso-Machado *et al.* (2011)
Quechua (44)	73	27	Quechuan	14° 30' S; 69° W	Gayà-Vidal *et al.* (2011)
Aymara (59)	97	3	Aymaran	17° 68' S; 69° 16' W	Gayà-Vidal *et al.* (2011)
Ayoreo (9)	78	22	Zamucoan	19° S; 60° 30' W	Bailliet *et al.* (2009)
Wichí (Mataco) (151)	48	52	Mataco-Guaicuru	22° 28' S; 62° 70' W	Demarchi and Mitchell (2004); Bailliet *et al.* (2009)
Lengua (36)	97	3	Mascoian	22° 45' S; 58° 5' W	Bailliet *et al.* (2009); Bisso-Machado *et al.* (2011)
Chorote (9)	89	21	Mataco-Guaicuru	22° 90' S; 65° 40' W;	Bailliet *et al.* (2009)
Aché (54)	98	2	Tupi	23° 30' –24° 10' S; 55° 50' –56° 30' W	Bortolini *et al.* (2003)

Table 1 (cont).

Populations (n)[1]	Haplogroup (%)		Language[2]	Geographical coordinates	References
	Q lineages / Amerindian origin	Non-Q lineages			
Guarani (78)	77	23	Tupi	23° 6’ S; 55° 12’ W	Bortolini *et al.* (2003); Marrero *et al.* (2007)
Pilagá	47	53	Mataco-Guaicuru	24° S; 59° W	Demarchi and Mitchell (2004)
Colla (63)	35	65	Quechuan[3]	24° 10’ -24° 43’ S; 65° 17’ -65° 52’ W	Blanco-Verea *et al.* (2010); Toscanini *et al.* (2011)
Toba (89)	88	12	Mataco-Guaicuru	26° S; 58° W	Demarchi and Mitchell (2004); Bailliet *et al.* (2009); Toscanini *et al.* (2011)
Kaingang (59)	69	31	Macro-Ge	28° S; 51° 20’ W	Bortolini *et al.* (2003); Marrero *et al.* (2007); Bisso-Machado *et al.* (2011)
Diaguita (24)	37	63	Quechuan[4]	28° 20’ S; 67° 43’ W	Blanco-Verea *et al.* (2010)
Mocoví (40)	60	40	Mataco-Guaicuru	29° 51’ S; 59° 56’ W	Bailliet *et al.* (2009)
Pehuenche (18)	83	17	Araucanian	37° 43’ S; 71° 16’ W	Bailliet *et al.* (2009)
Mapuche (105)	36	64	Araucanian	39° 10’ -41° 20’ S; 68° 37’ -70° 22’ W	Bailliet *et al.* (2009); Blanco-Verea *et al.* (2010)
Huilliche (26)	50	50	Araucanian	41° 16’ S; 73° W	Bailliet *et al.* (2009)
Tehuelche (20)	65	35	Chon	45° S; 71° W	Bailliet *et al.* (2009)

[1]Arranged according to latitude. [2]Classification according to Lewis (2009). [3]Original language is extinct. [4]The Diaguita spoke originally Kakán, but this language became extinct and was substituted by Quechua.

tively; Pena *et al.*, 1995; Bortolini *et al.*, 2003; Seielstad *et al.*, 2003) were investigated. This fact precludes a complete, precise view of the distribution of Q1a3a sublineages and other Q clade chromosomes in South America. For this reason, the information in Table 1 was limited to the frequencies of the Q and non-Q-lineages only. Note that non-Q-chromosomes (which, for the reasons given above, could not be identified in sublineages) were identified in ~50% of the tribal groups. For some of these populations admixture with non-Indians is known and could be the source of these non-Q chromosomes (for example, Mapuche and Guarani; Marrero *et al.*, 2007; Bailliet *et al.*, 2009; Blanco-Verea *et al.*, 2010). Overall, the numbers presented in Table 1 indicate a higher presence of non-Q lineages in southern populations than in those of the northern/Amazonian region, probably because of greater admixture with non-Indians in the former than in the latter. However, for some isolated groups such as the Yanomámi, it is unlikely that admixture explains the findings. In these cases other causes are more probable, such as the presence of unknown autochthonous lineages and/or known Q lineages whose defining markers were not tested.

Despite the great variation in the number of Y-SNPs used in these studies, Figure 1 illustrates some of the trends that were observed: The autochthonous Native American Q1a3a* is almost always the most prevalent, whereas its sublineages (Q1a3a1, Q1a3a2, Q1a3a3 and Q1a3a4) seem to have more restricted geographical distributions. The second most prevalent, Q1a3*, appears to occur equally in all regions, suggesting its presence among the first settlers of South America. The other known Q clade chromosomes (Q1*, Q1a*, Q1a1, Q1a2, Q1a4, Q1a5, Q1a6 and Q1b) have not yet been identified in South America. Only one non-Q-chromosome (C3*) of probable native origin has been described in northwest South Amerindian populations (Figure 1; Geppert *et al.*, 2011).

The nature of some evolutionary and demographic scenarios, mediated by men, in native American populations has also been evaluated by using Y microsatellite markers (Y-STRs), which have a much faster evolutionary rate than SNPs. Y-STRs allow the retrieval of population and chromosome evolutionary histories. For example, STR data have been used to estimate that the mutations that gave rise to the Q1a3a1 and Q1a3a4 sublineages occurred 7,972 ± 2,916 and 5,280 ± 1,330 years ago, probably in northwest South America and the Andean region, respectively (Bortolini *et al.*, 2003; Jota *et al.*, 2011).

Table 2 shows the STR allele frequencies observed in 29 South Amerindian populations, based only on Q clade chromosomes. In this compilation, we considered only studies containing information on the allele frequencies for each population individually. There was considerable variation in the number of samples tested in each study, the number of tribes, and the number of individuals per tribe. Depending on the locus considered, the number of alleles observed ranged from one to eight, with some of them appearing in only one study while others were present in almost all populations. Based on the most prevalent alleles per locus we reconstructed a probable haplotype of the ancient Native American Q-clade chromosome (ANAQC) as: 13(DYS19)-12(DYS388)-14(DYS389I)-31(DYS389II)-2

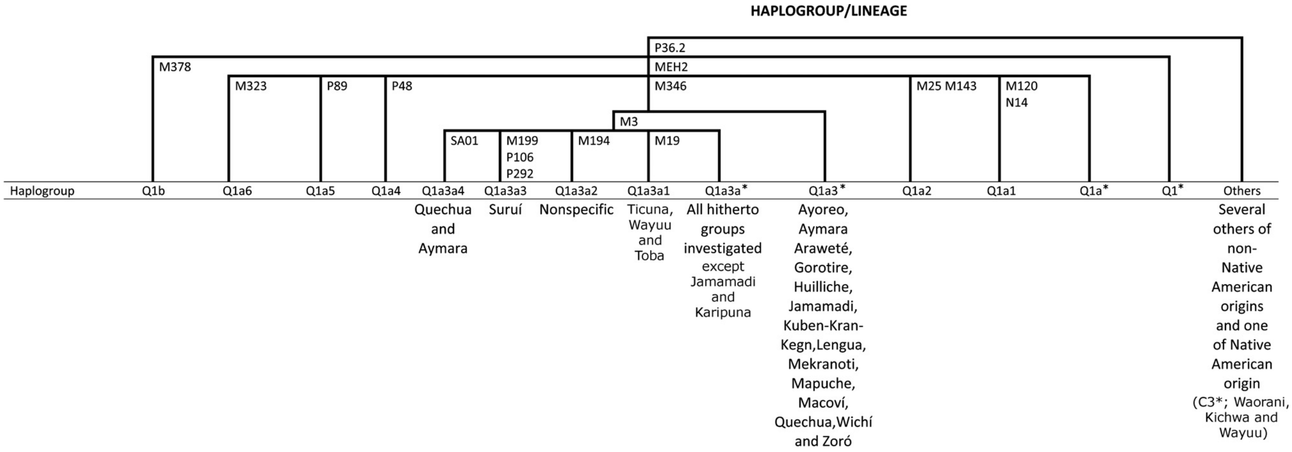

Figure 1 - Y-chromosome phylogenetic tree considering only the Q derived lineages. Note: The letters and numbers in the branches indicate the name of the loci where the mutations occurred, leading to the haplogroup classification. The data for this tree were compiled from the references in Table 1, plus Santos *et al.* (1995), Underhill *et al.* (1997, 2001), Karafet *et al.* (1997, 1999, 2008), Carvalho-Silva *et al.* (1999), Vallinoto *et al.* (1999), Bortolini *et al.* (2002), The Y-Chromosome Consortium (2002) and Geppert *et al.* (2011).

Table 2 (a) - Y-Q-chromosome STR studies in distinct South Amerindian samples in which allele frequencies can be assessed (Part A).

STR (allele)	Ref. (n)														
	Aché (48)[2]	Apalaí (9)[1]	Arara (8)[1]	Aymara (57)[9]	Ayoreo (2)[7]	Barira (12)[2]	Diaguita (9)[8]	Guarani (47)[4, 5]	Ingano (8)[2]	Kaingang (17)[5]	Kayapó (10)[1]	Colla (22)[6, 8]	Lengua (6)[7]	Mapuche (24)[6, 8]	Mekranoti (5)[2]
DYS19 (12)				0.020					0.250						
DYS19 (13)	1.000			0.820		0.920	1.000	0.790	0.620	0.300		0.910	0.500	0.830	0.600
DYS19 (14)				0.160	1.000	0.080		0.190	0.130	0.300		0.090	0.330	0.040	0.400
DYS19 (15)								0.020		0.350			0.170	0.130	
DYS19 (16)										0.050					
DYS19 total															
DYS388 (12)	1.000					1.000			0.750						1.000
DYS388 (13)									0.120						
DYS388 (14)									0.130						
DYS388 (17)															
DYS388 total															
DYS389I (12)				0.020				0.280		0.180		0.040	0.160	0.040	
DYS389I (13)				0.470	0.500		0.220	0.020		0.820		0.410	0.500	0.750	
DYS389I (14)				0.510	0.500		0.780	0.550				0.550	0.170	0.210	
DYS389I (15)								0.150					0.170		
DYS389I total															
DYS389II (17)															
DYS389II (18)															
DYS389II (19)															
DYS389II (26)										0.060					
DYS389II (27)													0.160		
DYS389II (28)				0.020				0.020		0.120					
DYS389II (29)				0.090	0.500			0.150		0.290		0.090	0.500	0.290	
DYS389II (30)				0.370	0.500		0.440	0.130		0.470		0.180	0.170	0.420	
DYS389II (31)				0.450			0.560	0.620		0.060		0.500		0.250	
DYS389II (32)				0.070				0.080				0.090	0.170	0.040	
DYS389II (33)												0.140			
DYS389II (34)															
DYS389II total															

Table 2 (a) (cont.)

STR (allele)	Ref. (n)														
	Aché (48)^{2}	Apalaí (9)^{1}	Arara (8)^{1}	Aymara (57)^{9}	Ayoreo (2)^{7}	Barira (12)^{2}	Diaguita (9)^{8}	Guarani (47)$^{4, 5}$	Ingano (8)^{2}	Kaingang (17)^{5}	Kayapó (10)^{1}	Colla (22)$^{6, 8}$	Lengua (6)^{7}	Mapuche (24)$^{6, 8}$	Mekranoti (5)^{2}
DYS390 (20)															
DYS390 (21)		0.230	0.120	0.070						0.060	0.100	0.040			
DYS390 (22)		0.110						0.130						0.040	
DYS390 (23)	1.000	0.330	0.880	0.560		0.080	0.330	0.080	0.250		0.100	0.640	0.330	0.420	0.400
DYS390 (24)		0.330		0.250	1.000	0.920	0.450	0.680	0.370	0.940	0.700	0.180	0.670	0.330	0.600
DYS390 (25)				0.120			0.220	0.090	0.250		0.100			0.210	
DYS390 (26)								0.020	0.130			0.140			
DYS390 (27)															
DYS390 total															
DYS391 (9)				0.020										0.210	
DYS391 (10)	1.000			0.820	1.000	1.000	0.890	0.210	0.860			0.820	1.000	0.750	1.000
DYS391 (11)				0.140			0.110	0.790	0.140			0.180		0.040	
DYS391 (12)				0.020											
DYS391 total															
DYS392 (11)										0.060					
DYS392 (12)												0.140			
DYS392 (13)		1.000	1.000			0.920		0.070	0.120	0.350	0.700	0.050		0.170	1.000
DYS392 (14)	1.000			0.470	0.500	0.080	0.450	0.720	0.880	0.530	0.300	0.360	0.830	0.710	
DYS392 (15)				0.040	0.500		0.330	0.210		0.060		0.090	0.170	0.120	
DYS392 (16)				0.470			0.220					0.360			
DYS392 (17)				0.020											
DYS392 (18)															
DYS392 total															
DYS393 (11)								0.480							
DYS393 (12)		0.220	0.120			0.080		0.090	0.120	0.060	0.400	0.090			0.400
DYS393 (13)	1.000	0.780	0.880	0.440	1.000		0.670	0.340	0.760	0.590	0.600	0.550	1.000	1.000	0.600
DYS393 (14)				0.560		0.920	0.330	0.090	0.120	0.350		0.360			
DYS393 (15)															
DYS393 (16)															
DYS393 total															
DYS437 (8)															
DYS437 (9)															
DYS437 (11)														0.040	
DYS437 (14)				1.000			1.000	0.930		0.590		1.000		0.920	
DYS437 (15)								0.070		0.410				0.040	
DYS437 total															
DYS438 (9)															
DYS438 (10)				0.050			0.220							0.040	
DYS438 (11)				0.930			0.670	0.860		0.590		1.000		0.920	
DYS438 (12)				0.020			0.110	0.140		0.410					
DYS438 (16)														0.040	
DYS438 total															
DYS439 (9)												0.050			
DYS439 (10)										0.060				0.130	
DYS439 (11)				0.160			0.220	0.070		0.230		0.050		0.220	
DYS439 (12)				0.240			0.450	0.640		0.590		0.360		0.390	
DYS439 (13)				0.370			0.330	0.290		0.060		0.270		0.260	

Table 2 (a) (cont.)

STR (allele)	Aché (48)[2]	Apalaí (9)[1]	Arara (8)[1]	Aymara (57)[9]	Ayoreo (2)[7]	Barira (12)[2]	Diaguita (9)[8]	Guarani (47)[4, 5]	Ingano (8)[2]	Kaingang (17)[5]	Kayapó (10)[1]	Colla (22)[6, 8]	Lengua (6)[7]	Mapuche (24)[6, 8]	Mekranoti (5)[2]
DYS439 (14)				0.230						0.060		0.270			
DYS439 total															
DYS448 (18)												0.200			
DYS448 (19)				0.110											
DYS448 (20)				0.770								0.800			
DYS448 (21)				0.120											
DYS448 (22)															
DYS448 total															
DYS456 (11)				0.020											
DYS456 (13)				0.050											
DYS456 (14)				0.020											
DYS456 (15)				0.800								0.900			
DYS456 (16)				0.090								0.100			
DYS456 (17)				0.020											
DYS456 total															
DYS458 (13)				0.050								0.100			
DYS458 (15)				0.030											
DYS458 (16)				0.490								0.700			
DYS458 (17)				0.250								0.200			
DYS458 (18)				0.140											
DYS458 (19)				0.040											
DYS458 total															
DYS635 (22)				0.820								0.700			
DYS635 (23)				0.160								0.300			
DYS635 (24)															
DYS635 (26)				0.020											
DYS635 total															

[1] Rodriguez-Delfin *et al.* (1997); [2] Bortolini *et al.* (2003); [3] Demarchi and Mitchell (2004); [4] Altuna *et al.* (2006); [5] Leite *et al.* (2008); [6] Toscanini *et al.* (2008); [7] Bailliet *et al.* (2009); [8] Blanco-Verea *et al.* (2010); [9] Gayà-Vidal *et al.* (2011); [10] Jota *et al.* (2011).

Table 2 (b) – Y-Q-chromosome STR studies in distinct South Amerindian samples in which allele frequencies can be assessed (Part B).

STR (allele)	Mocoví (2)[8]	Pacaás Novos (15)[2]	Parakanã (4)[2]	Pilagá (9)[3]	Quechua (58)[10, 11]	Ticuna (36)[2]	Toba (70)[3, 7]	Warao (12)[2]	Wayampi (10)[1]	Wayuu (14)[2]	Wichí (27)[3]	Yanoma-ma (9)[1]	Yukpa (12)[2]	Zenu (28)[2]	Total (590)
DYS19 (12)							0.030				0.030				0.010
DYS19 (13)	0.500			0.790	0.950	0.850	0.870	1.000		0.790	0.640		0.550	0.650	0.890
DYS19 (14)	0.500	1.000		0.210	0.030	0.090	0.090			0.140	0.230		0.450	0.270	0.050
DYS19 (15)					0.020	0.060	0.010			0.070	0.100			0.080	0.040
DYS19 (16)															0.010
DYS19 total															474
DYS388 (12)		0.860	1.000			0.780		0.750		0.570			0.500	0.500	0.780
DYS388 (13)		0.140				0.220		0.250		0.430			0.500	0.430	0.200
DYS388 (14)															0.010
DYS388 (17)														0.070	0.040
DYS388 total															189
DYS389I (12)					0.090										0.080
DYS389I (13)	1.000				0.240		0.800								0.440

Table 2 (b) (cont.)

STR (allele)	Ref. (n)														
	Mocoví (2)[8]	Pacaás Novos (15)[2]	Parakanã (4)[2]	Pilagá (9)[3]	Quechua (58)[10, 11]	Ticuna (36)[2]	Toba (70)[3, 7]	Warao (12)[2]	Wayampi (10)[1]	Wayuu (14)[2]	Wichí (27)[3]	Yanoma-ma (9)[1]	Yukpa (12)[2]	Zenu (28)[2]	Total (590)
DYS389I (14)					0.670		0.200								0.450
DYS389I (15)															0.030
DYS389I total															288
DYS389II (17)					0.270										0.020
DYS389II (18)					0.530										0.030
DYS389II (19)					0.200										0.010
DYS389II (26)															0.010
DYS389II (27)															0.010
DYS389II (28)					0.090										0.030
DYS389II (29)					0.070										0.110
DYS389II (30)					0.210		0.500								0.290
DYS389II (31)	0.500				0.540		0.320								0.390
DYS389II (32)	0.500				0.090		0.160								0.080
DYS389II (33)															0.010
DYS389II (34)							0.020								0.010
DYS389II total															288
DYS390 (20)					0.020										0.010
DYS390 (21)					0.240										0.070
DYS390 (22)					0.020		0.080				0.030	0.780			0.070
DYS390 (23)	0.500	0.450		0.210	0.450	0.060	0.110	0.080	1.000	0.220	0.070			0.250	0.320
DYS390 (24)	0.500	0.550	1.000	0.790	0.220	0.150	0.730	0.920		0.560	0.740	0.110	1.000	0.290	0.400
DYS390 (25)					0.050	0.760	0.080			0.220	0.130			0.420	0.110
DYS390 (26)											0.030				0.010
DYS390 (27)						0.030						0.110		0.040	0.010
DYS390 total															659
DYS391 (9)										0.070	0.030				0.030
DYS391 (10)	1.000	1.000		0.890	0.840	0.930	0.900	0.250		0.570	0.870		1.000	0.640	0.800
DYS391 (11)			1.000	0.110	0.160	0.070	0.100	0.750		0.360	0.100			0.360	0.160
DYS391 (12)															0.010
DYS391 total															512
DYS392 (11)							0.030			0.570	0.060				0.020
DYS392 (12)									1.000	0.070				0.130	0.030
DYS392 (13)	1.000	0.890		0.100			0.100	0.110			0.130	0.890	0.180	0.060	0.170
DYS392 (14)		0.110		0.800	0.520	0.380	0.670	0.890		0.290	0.420	0.110	0.460	0.560	0.510
DYS392 (15)				0.100	0.070	0.620	0.190			0.070	0.390		0.360	0.250	0.150
DYS392 (16)					0.290										0.100
DYS392 (17)					0.020										0.010
DYS392 (18)					0.100		0.010								0.010
DYS392 total															535
DYS393 (11)			1.000												0.040
DYS393 (12)						0.060	0.010			0.100	0.060			0.040	0.040
DYS393 (13)	1.000	0.780		1.000	0.550	0.710	0.980	0.750		0.800	0.840	0.890	0.500	0.200	0.670
DYS393 (14)		0.220			0.450	0.170	0.010	0.250	1.000	0.100	0.100	0.110	0.500	0.240	0.220
DYS393 (15)						0.030								0.480	0.020
DYS393 (16)						0.030								0.040	0.010
DYS393 total															584

Table 2 (b) (cont.)

	Ref. (n)														
STR (allele)	Mocoví (2)[8]	Pacaás Novos (15)[2]	Parakanã (4)[2]	Pilagá (9)[3]	Quechua (58)[10, 11]	Ticuna (36)[2]	Toba (70)[3, 7]	Warao (12)[2]	Wayampi (10)[1]	Wayuu (14)[2]	Wichí (27)[3]	Yanoma-ma (9)[1]	Yukpa (12)[2]	Zenu (28)[2]	Total (590)
DYS437 (8)				0.420			0.360				1.000				0.200
DYS437 (9)				0.580			0.030								0.040
DYS437 (11)															0.010
DYS437 (14)					1.000		0.500								0.700
DYS437 (15)							0.110								0.050
DYS437 total															322
DYS438 (9)					0.020										0.010
DYS438 (10)							0.050				0.160				0.050
DYS438 (11)				0.790	0.930		0.850				0.840				0.850
DYS438 (12)				0.210	0.050		0.100								0.080
DYS438 (16)															0.010
DYS438 total															322
DYS439 (9)															0.010
DYS439 (10)															0.010
DYS439 (11)					0.090		0.130				0.230				0.140
DYS439 (12)				0.320	0.240		0.500				0.710				0.400
DYS439 (13)				0.680	0.500		0.290				0.060				0.330
DYS439 (14)					0.170		0.080								0.110
DYS439 total															322
DYS448 (18)															0.010
DYS448 (19)					0.140		0.020								0.090
DYS448 (20)					0.550		0.930								0.740
DYS448 (21)					0.240		0.050								0.140
DYS448 (22)					0.070										0.020
DYS448 total															169
DYS456 (11)															0.010
DYS456 (13)															0.020
DYS456 (14)					0.230		0.020								0.090
DYS456 (15)					0.720		0.730								0.750
DYS456 (16)					0.050		0.250								0.120
DYS456 (17)															0.010
DYS456 total															169
DYS458 (13)															0.020
DYS458 (15)					0.030		0.040								0.040
DYS458 (16)					0.360		0.180								0.380
DYS458 (17)					0.520		0.550								0.410
DYS458 (18)					0.090		0.230								0.140
DYS458 (19)															0.010
DYS458 total															169
DYS635 (22)					0.950		0.950								0.890
DYS635 (23)					0.020		0.050								0.090
DYS635 (24)					0.030										0.010
DYS635 (26)															0.010
DYS635 total															169

[1]Rodriguez-Delfin *et al.* (1997); [2]Bortolini *et al.* (2003); [3]Demarchi and Mitchell (2004); [4]Altuna *et al.* (2006); [5]Leite *et al.* (2008); [6]Toscanini *et al.* (2008); [7]Bailliet *et al.* (2009); [8]Blanco-Verea *et al.* (2010); [9]Gayà-Vidal *et al.* (2011); [10]Jota *et al.* (2011).

4(DYS390)-10(DYS391)-14(DYS392)-13(DYS393)-14(DYS437)-11(DYS438)-12(DYS439)-20(DYS448)-15(DYS456)-16(DYS458)-22(DYS635). Using this information and additional data for these loci (except DYS388) reported in the Y Chromosome Haplotype Reference Database we found no matches in 36,448 haplotypes (245 populations). Although we found no complete identity with our estimated ANAQC, three one-step neighbor haplotypes were encountered, two in individuals with an admixed ancestry living in Latin American countries and one in a Native American individual (Kaqchiquel).

Table 3 shows the results of the molecular analysis of variance for populations structured by language or geography based on the data in Table 2. The estimates were calculated for each STR locus because testing heterogeneity prevented haplotype identification. As expected, most of the diversity was attributable to intrapopulation variation, with one exception (DYS437) that was explained by the fixation of allele 14 in 40% of the populations, whereas only allele 8 was found in the Wichí. In contrast, significant variation among subdivisions was detected for only six loci (DYS398I, DYS391, DYS392, DYS393, DYS437 and DYS456) and in five out of these six it was attributable to geography. There was also considerable inter-population/within subdivision variability (significant in 28 of 30 evaluations), with the average percentage being 16% for geography and 21% for language.

Table 4 summarizes the information on sequencing studies of mitochondrial DNA. The mtDNA genome of representative individuals from 35 populations has been entirely sequenced, as reported in six publications (Ingman *et al.*, 2000; Kivisild *et al.*, 2006; Tamm *et al.*, 2007; Fagundes *et al.*, 2008; Perego *et al.*, 2009, 2010). However, the analyses performed did not consider the within South Amerindian relationships and were mostly concerned with interethnic or interhaplogroup comparisons. Based on 86 complete Amerindian genomes, Fagundes *et al.* (2008) concluded that the prehistoric colonization of the Americas involved a single founding population, with an initial differentiation from Asia occurring in Beringia that ended around 19,000-23,000 years ago, with a moderate bottleneck. Expansion into the New World would have occurred about 18,000 years ago. An extensive 5.76 kb analysis by Dornelles *et al.* (2005) established that haplogroup X is not present in extant South American Indians.

The most extensive set of data involves the highly variable segment 1 (HVS-I) that has been studied in 92 populations and reported in 30 papers; surveys that have included the HVS-II region are much less common (10 articles) (Table 4). For HVS-I, Merriwether *et al.* (2000) provided an excellent example of how intrapopulation variability in the Yanomámi could be interpreted in a historical and demographical context and relating it to other Amerindian and Asian data. They studied 129 Yanomámi sequences from individuals in eight villages and compared their haplotypes with those of other Asian and New World populations, in a total of 482 unique haplotypes. Interestingly, the pairwise inter-population gene flow estimates were lower between some pairs of Yanomámi villages than between them and four other South Amerindian groups.

Table 3 - Analysis of molecular variance of the distinct alleles of the Y-Q STRs in relation to the language and geography of the populations tested.

STR loci (structured by)	Among subdivisions	Among populations within subdivisions	Within populations
DYS19 (Language)[1]	0	0.311*	0.689*
DYS19 (Geography)[2]	0	0.332*	0.668*
DYS388 (Language)[1]	0.045	0.317*	0.638*
DYS388 (Geography)[2]	0.091	0.240*	0.669*
DYS389I (Language)[1]	0.227*	0.030	0.743*
DYS389I (Geography)[2]	0.116	0.148*	0.736*
DYS389II (Language)[1]	0.036	0.077*	0.887*
DYS389II (Geography)[2]	0	0.125*	0.875*
DYS390 (Language)[1]	0.008	0.326*	0.666*
DYS390 (Geography)[2]	0	0.359*	0.642*
DYS391 (Language)[1]	0	0.385*	0.615*
DYS391 (Geography)[2]	0.253*	0.131*	0.616*
DYS392 (Language)[1]	0.005	0.319*	0.676*
DYS392 (Geography)[2]	0.007*	0.262*	0.661*
DYS393 (Language)[1]	0	0.331*	0.669*
DYS393 (Geography)[2]	0.177*	0.167*	0.656*
DYS437 (Language)[1]	0.289	0.273*	0.438*
DYS437 (Geography)[2]	0.390*	0.213*	0.397*
DYS438 (Language)[1]	0.048	0.025	0.927*
DYS438 (Geography)[2]	0.023	0.054*	0.923*
DYS439 (Language)[1]	0.019	0.054*	0.929*
DYS439 (Geography)[2]	0.055	0.034*	0.911*
DYS448 (Language)[1]	0	0.148*	0.852*
DYS448 (Geography)[2]	0	0.073*	0.927*
DYS456 (Language)[1]	0	0.078*	0.922*
DYS456 (Geography)[2]	0.017*	0.044*	0.939*
DYS458 (Language)[1]	0	0.144*	0.856*
DYS458 (Geography)[2]	0.043	0.069*	0.888*
DYS635 (Language)[1]	0	0.278*	0.722*
DYS635 (Geography)[2]	0	0.128*	0.872*

[1] Language: Tupi: Aché, Guarani, Parakanã, Wayampi; Carib: Apalaí, Arara, Yukpa; Macro-Ge: Kaingang, Kayapó, Mekranoti; Quechua: Diaguita, Quechua, Ingano; Mataco-Guaicuru: Mocoví, Toba, Wichí, Pilagá; Isolated languages and others with only one population were included as a sixth group.

[2] Geography: Amazonia/Central Brazilian Plateau: Apalaí, Arara, Kayapó, Mekranoti, Pacaás Novos, Parakanã, Ticuna, Warao, Wayampi, Yanomámi; Southern Brazil: Guarani and Kaingang; Chaco: Ache, Ayoreo, Lengua, Mocoví, Pilagá, Toba, Wichí; Andes: Aymara, Barira, Diaguita, Kolla, Quechua, Wayuu, Yukpa, Zenu.

*Significant values (p = 0.05). Negative values were adjusted to zero.

With regard to intrapopulation variability, as measured by Θ_k, Fuselli *et al.* (2003) and Corella *et al.* (2007) reported extensive variation for 14 and 27 Central and

Table 4 - Mitochondrial DNA sequencing studies in South Amerindian populations.

Population	HVS-I	HVS-II	Complete mt genome	References
Aché	X	X	X	Schmitt *et al.* (2004); Dornelles *et al.* (2005); Fagundes *et al.* (2008); Yang *et al.* (2010)
Ancash	X		X	Lewis Jr *et al.* (2005); Perego *et al.* (2009)
Andean	X			García-Bour *et al.* (2004)[1]
Apalaí	X			Lobato-da-Silva *et al.* (2001); Mazières *et al.* (2008)
Arara	X		X	Santos *et al.* (1996); Lobato-da-Silva *et al.* (2001); Ribeiro-dos-Santos *et al.* (2001); Silva Jr *et al.* (2002, 2003)[2]; Fagundes *et al.* (2008)
Araweté	X			Lobato-da-Silva *et al.* (2001)
Arequipa	X		X	Fuselli *et al.* (2003); Perego *et al.* (2009)
Arhuaco	X	X	X	Melton *et al.* (2007); Tamm *et al.* (2007); Yang *et al.* (2010)
Arsario	X		X	Melton *et al.* (2007); Tamm *et al.* (2007)
Asurini	X	X		Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005)
Auca			X	Kivisild *et al.* (2006)
Awa-Guajá	X			Santos *et al.* (1996); Lobato-da-Silva *et al.* (2001)
Awa-Juriti	X			Lobato-da-Silva *et al.* (2001)
Aymara	X	X		Corella *et al.* (2007); Lewis Jr *et al.* (2007); Yang *et al.* (2010); Barbieri *et al.* (2011)
Ayoreo	X	X		Dornelles *et al.* (2004, 2005)
Catamarca			X	Tamm *et al.* (2007)
Cayapa	X	X	X	Rickards *et al.* (1999); Tamm *et al.* (2007)
Chimane	X			Corella *et al.* (2007)
Chilean North Coast	X			Moraga *et al.* (2005)[1]
Cinta Larga	X	X		Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005)
Coreguaje			X	Tamm *et al.* (2007)
Coya	X	X		Alvarez-Iglesias *et al.* (2007)
Cubeo	X	X		Torres *et al.* (2006)
Curripaco	X	X		Torres *et al.* (2006)
Desano	X	X		Torres *et al.* (2006)
Diaguita			X	Perego *et al.* (2010)
Embera	X	X	X	Torres *et al.* (2006); Tamm *et al.* (2007)
Emerillon	X			Mazières *et al.* (2008)
Gavião	X		X	Ward *et al.* (1996); Fagundes *et al.* (2008)
Gorotire	X	X		Dornelles *et al.* (2005)
Guahibo	X	X		Vona *et al.* (2005); Torres *et al.* (2006)
Guarani	X	X	X	Ingman *et al.* (2000); Silva Jr *et al.* (2002, 2003)[2]; Dornelles *et al.* (2005); Kivisild *et al.* (2006); Marrero *et al.* (2007); Fagundes *et al.* (2008); Sala *et al.* (2010); Yang *et al.* (2010)
Huilliche	X	X		Yang *et al.* (2010)
Huitoto	X	X		Monsalve *et al.* (1994); Torres *et al.* (2006)
Içana River Indians	X	X		Dornelles *et al.* (2005)
Ignaciano	X			Bert *et al.* (2004)
Inga	X	X		Torres *et al.* (2006); Yang *et al.* (2010)
Jaqaru	X			Lewis Jr *et al.* (2007)
Jamamadi	X			Lobato-da-Silva *et al.* (2001)
Jebero	X	X		Monsalve *et al.* (1994); Torres *et al.* (2006)
Kaingang	X	X		Dornelles *et al.* (2005); Marrero *et al.* (2007); Yang *et al.* (2010)
Kali'na	X			Mazières *et al.* (2008)
Karitiana	X			Lobato-da-Silva *et al.* (2001);

Table 4 (cont.)

Population	HVS-I	HVS-II	Complete mt genome	References
Katuena	X		X	Santos *et al.* (1996); Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2002, 2003)^2; Fagundes *et al.* (2008)
Kayapó	X			Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2002, 2003)^2
Kawéskar	X			García-Bour *et al.* (2004)^1
Kogi	X	X	X	Melton *et al.* (2007); Tamm *et al.* (2007); Yang *et al.* (2010)
Kolla			X	Perego *et al.* (2010)
Krahô	X	X		Dornelles *et al.* (2005)
Kikretun	X		X	Santos *et al.* (1996); Fagundes *et al.* (2008)
Kubenkokre	X		X	Santos *et al.* (1996); Fagundes *et al.* (2008)
Kuben-Kran-Kegn	X	X		Dornelles *et al.* (2005)
Lengua	X	X		Dornelles *et al.* (2005)
Mapuche	X	X		Ginther *et al.* (1993); Moraga *et al.* (2000); Dornelles *et al.* (2005)
Mekranoti	X	X		Dornelles *et al.* (2005)
Mocovi			X	Tamm *et al.* (2007)
Movima	X			Bert *et al.* (2004); Melton *et al.* (2007)
Munduruku	X			Lobato-da-Silva *et al.* (2001);
Mura	X	X		Dornelles *et al.* (2005)
Ocaina	X	X		Monsalve *et al.* (1994); Torres *et al.* (2006)
Pacaás Novos	X	X		Dornelles *et al.* (2005)
Paez	X	X		Torres *et al.* (2006)
Palikur	X			Lobato-da-Silva *et al.* (2001); Mazières *et al.* (2008)
Parakanã	X	X		Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005)
Pehuenche	X	X		Merriwether *et al.* (1994, 1995); Merriwether and Ferrell (1996); Moraga *et al.* (1997, 2000); García *et al.* (2006)
Peruvian Andes	X	X		Shinoda *et al.* (2006)^1; Fehren-Schmitz *et al.* (2011)^1
Peruvian Southern Coast	X			Fehren-Schmitz *et al.* (2010)^1
Piapoco	X	X		Torres *et al.* (2006)
Pilagá	X			Cabana *et al.* (2006)
Poturujara	X		X	Santos *et al.* (1996); Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2002, 2003)^2; Fagundes *et al.* (2008)
Puinave	X	X		Torres *et al.* (2006)
Puno	X			Lewis Jr *et al.* (2007)
Quechua	X	X	X	Monsalve *et al.* (1994); Silva Jr *et al.* (2002, 2003)^2; Fuselli *et al.* (2003); Dornelles *et al.* (2005); Kivisild *et al.* (2006); Corella *et al.* (2007); Lewis Jr *et al.* (2007); Fagundes *et al.* (2008); Yang *et al.* (2010); Barbieri *et al.* (2011)
Saliva	X	X		Torres *et al.* (2006)
Salta			X	Tamm *et al.* (2007)
Sateré Mawé	X	X		Dornelles *et al.* (2005)
Selknam	X			García-Bour *et al.* (2004)^1
Sicán	X			Shimada *et al.* (2004)^1
Suruí	X		X	Lobato-da-Silva *et al.* (2001); Fagundes *et al.* (2008)
Tayacaja	X			Bert *et al.* (2004)
Ticuna	X	X		Monsalve *et al.* (1994); Torres *et al.* (2006); Rojas *et al.* (2010); Yang *et al.* (2010)
Tiriyó	X	X	X	Santos *et al.* (1996); Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2002, 2003)^2; Dornelles *et al.* (2005); Fagundes *et al.* (2008)
Toba	X			Cabana *et al.* (2006)

Table 4 (cont.)

Population	HVS-I	HVS-II	Complete mt genome	References
Trinitario	X			Bert *et al.* (2004)
Tucuman			X	Tamm *et al.* (2007)
Tupe	X			Lewis Jr *et al.* (2007)
Txukahamãe	X	X		Dornelles *et al.* (2005)
Uro	X			Barbieri *et al.* (2011)
Urubu Kaapor	X	X		Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005)
Vaupe			X	Tamm *et al.* (2007)
Wai-wai			X	Fagundes *et al.* (2008)
Wayampi	X	X	X	Santos *et al.* (1996); Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2002, 2003)[2]; Dornelles *et al.* (2005); Fagundes *et al.* (2008); Mazières *et al.* (2008)
Warao			X	Ingman *et al.* (2000)
Waunana			X	Tamm *et al.* (2007)
Wayuu	X	X	X	Torres *et al.* (2006); Melton *et al.* (2007); Tamm *et al.* (2007); Yang *et al.* (2010)
Wichí	X			Cabana *et al.* (2006)
Xavante	X	X	X	Ward *et al.* (1996); Dornelles *et al.* (2005); Fagundes *et al.* (2008)
Xikrin	X	X		Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005)
Yagua	X	X		Monsalve *et al.* (1994); Torres *et al.* (2006)
Yámana	X			García-Bour *et al.* (2004)[1]
Yanomámi	X	X	X	Easton *et al.* (1996); Santos *et al.* (1996); Merriwether *et al.* (2000); Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2002, 2003)[2]; Williams *et al.* (2002); Dornelles *et al.* (2005); Fagundes *et al.* (2008)
Yungay	X			Lewis Jr *et al.* (2007)
Yuracare	X			Bert *et al.* (2004)
Zenu	X	X		Torres *et al.* (2006)
Zoró	X		X	Ward *et al.* (1996); Fagundes *et al.* (2008)

[1]Ancient DNA. [2]Sequencing included almost half of the genome (sites 7,148-15,976).

Southern Amerindian populations, respectively (*e.g.*, from 0.659 for the Quechua of Peru to 0.011 for the Xavante of the Brazilian Mato Grosso). Intra- and intergroup nucleotide diversity was calculated by Melton *et al.* (2007) for 20 of these Amerindian groups, whereas Barbieri *et al.* (2011) compared the sources of variation among North, Central and South Amerindians in 51 populations; the latter authors observed 3% variation among the three sets, 21% variation among populations within the subcontinent and 76% variation within populations.

To explore the mtDNA data further we compiled the prevalences of haplogroups A-D for 109 populations, in a total of 6,697 individuals distributed between latitude 11° North and 54° South, and longitude 46° to 78° West (Table 5). Sample sizes varied widely, from only one subject tested (Jebero) up to 491 (Yanomámi). The haplogroup frequencies reported in 52 articles also varied widely. The presence of mtDNA genomes of probable non-Amerindian origin was rare in all regions and populations, in contrast to the Y-SNP data (Table 1). Asymmetrical sex-mediated admixture was common during the first centuries of South American colonization, and involved mostly European men and Amerindian/African women. The main consequences of this historical contact was the formation of mestizos and the present-day national societies; the former are characterized by a composite genome, with the majority of Y-chromosomes being of European origin, while their mtDNA derives from Amerindian or African sources (Bortolini *et al.*, 1999; Alves-Silva *et al.*, 2000; Carvalho-Silva *et al.*, 2001; Salzano and Bortolini, 2002). Asymmetrical mating could also explain the introduction of non-Amerindian Y-chromosomes into the tribes, while the autochthonous mtDNA genomes were preserved. However, the admixture dynamics are probably different from those observed in urban groups since they normally involve Amerindian women who live on reservations and men who live near the border of the reservations. In this situation, the children normally remain with their mothers. This phenomenon has been described for Guarani Indians (Marrero *et al.*, 2007), but the data presented here indicate that it could be much more common than previously thought.

Table 5 - Mitochondrial DNA haplogroup and linguistic and geographical information for the samples considered.

Population (n)[1]	Haplogroups (%)					Language	Geographical coordinates	References
	A	B	C	D	Others[2]			
Wayuu (89)	26	28	45	0	1	Arawakan	11° N; 73° W	Mesa *et al.* (2000); Keyeux *et al.* (2002); Melton *et al.* (2007)
Kogi (153)	67	0	33	0	0	Chibchan	11° N; 74° W	Keyeux *et al.* (2002); Melton *et al.* (2007); Rojas *et al.* (2010)
Arsario (Wiwa) (76)	63	0	37	0	0	Chibchan	10° 25' N; 73° 05' W	Keyeux *et al.* (2002); Melton *et al.* (2007); Rojas *et al.* (2010)
Chimila (35)	88	0	3	6	3	Chibchan	10° 16' N; 74° 4' W	Keyeux *et al.* (2002)
Arhuaco (Ijka) (134)	87	1	12	0	0	Chibchan	9° 04' N; 73° 59' W	Keyeux *et al.* (2002); Melton *et al.* (2007); Rojas *et al.* (2010)
Yukpa (88)	0	100	0	0	0	Carib	8° 40' N; 72° 41' W	Keyeux *et al.* (2002)
Zenu (107)	19	38	36	5	2	Spanish	8° 30' N; 76° W	Mesa *et al.* (2000); Keyeux *et al.* (2002); Torres *et al.* (2006)
Embera (43)	53	35	2	5	5	Choco	7° N; 76° 30' W	Mesa *et al.* (2000); Keyeux *et al.* (2002)
Tule-Cuna (30)	50	27	20	0	3	Chibchan	6° 56' N; 76° 45' W	Keyeux *et al.* (2002)
Guane-Butaregua (33)	12	64	0	24	0	Chibchan	6° 15' N; 73° 15' W	Keyeux *et al.* (2002)
Cubeo (22)	27	18	50	5	0	Tucanoan	5° 9' N; 70° 18W	Torres *et al.* (2006)
Makiritare (10)	20	0	70	10	0	Carib	5° 33' N; 65° 33' W	Torroni *et al.* (1993)
Kali' na (Galibi) (29)	7	41	38	7	7	Carib	5° 31' N; 53° 47' W	Mazières *et al.* (2008)
Guahibo (99)	52	3	33	0	12	Guahiban	5° N; 69° W	Keyeux *et al.* (2002); Vona *et al.* (2005); Torres *et al.* (2006)
Waunana (161)	21	49	16	14	0	Choco	4° 50' N; 77° W	Keyeux *et al.* (2002); Tamm *et al.* (2007); Rojas *et al.* (2010)
Palikúr (64)	1	47	4	47	1	Arawakan	4° N; 51° 45' W	Lobato-da-Silva *et al.* (2001); Mazières *et al.* (2008)
Macushi (10)	10	20	30	40	0	Carib	4° N; 60° 50' W	Torroni *et al.* (1993)
Páez (51)	59	12	27	2	0	Páez	3° 9' N; 75° 28' W	Keyeux *et al.* (2002); Torres *et al.* (2006)
Ocaina (2)	0	0	100	0	0	Witotoan	3° 58' N; 68° 2' W	Torres *et al.* (2006)
Jebero (1)	0	0	100	0	0	Cahuapanan	3° 58' N; 68° 2' W	Torres *et al.* (2006)
Piaroa (28)	36	11	21	32	0	Salivan	3° 57' N; 66° 22' W	Torroni *et al.* (1993); Keyeux *et al.* (2002)
Desano (2)	50	0	0	50	0	Tucanoan	3° 24' N; 69° 40' W	Torres *et al.* (2006)
Wapishana (12)	0	25	8	67	0	Arawakan	3° 07' N; 60° 03' W	Torroni *et al.* (1993)
Emerillon (30)	30	70	0	0	0	Tupi	3° N; 53° W	Mazières *et al.* (2008)
Guambiano (23)	4	4	79	13	0	Barbacoan	2° 6' N; 76° 23' W	Keyeux *et al.* (2002)
Yanomámi (491)	2	25	50	19	4	Yanomam	2° 50' N; 54° W	Torroni *et al.* (1992, 1993); Easton *et al.* (1996); Merriwether *et al.* (2000); Williams *et al.* (2002); Silva Jr *et al.* (2003)
Guayabero (30)	50	17	13	0	20	Guahiban	2° 25' N; 71° 4' W	Keyeux *et al.* (2002)
Curripaco (22)	41	36	23	0	0	Arawakan	2° 10' N; 68° 54' W	Keyeux *et al.* (2002); Torres *et al.* (2006)
Tiriyó (32)	9	19	22	47	3	Carib	2° N; 56° W	Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2003)
Nukak (20)	0	20	80	0	0	Maku	1° 44' N; 70° 44' W	Keyeux *et al.* (2002)
Apalaí (120)	37	1	30	32	0	Carib	1° 20' N; 54° 40' W	Lobato-da-Silva *et al.* (2001); Mazières *et al.* (2008)
Cayapa (120)	29	40	9	22	0	Barbacoan	1° 17' N; 78° 50' W	Rickards *et al.* (1999)
Wayampi (99)	62	11	8	19	0	Tupi	1° N; 53° W	Santos *et al.* (1996); Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2003); Mazières *et al.* (2008)
Siona (12)	75	17	8	0	0	Tucanoan	0° 6' N; 75° 36' W	Keyeux *et al.* (2002)

Table 5 (cont.)

Population (n)[1]	Haplogroups (%)					Language	Geographical coordinates	References
	A	B	C	D	Others[2]			
Pasto (9)	67	33	0	0	0	Barbacoan	0° 58’ N; 77° 44’ W	Keyeux *et al.* (2002)
Yagua (12)	25	0	67	8	0	Peba-Yaguan	0° 51’ N; 72° 27’ W	Torres *et al.* (2006)
Ingano (111)	18	38	42	0	2	Quechuan	0° 50’ N; 77° W	Mesa *et al.* (2000); Keyeux *et al.* (2002); Torres *et al.* (2006); Rojas *et al.* (2010)
Tucano (17)	0	18	47	35	0	Tucanoan	0° 42’ N; 69° 53’ W	Keyeux *et al.* (2002)
Coreguaje (69)	4	20	66	6	4	Tucanoan	0° 38’ N; 76° 8’ W	Keyeux *et al.* (2002); Tamm *et al.* (2007)
Awa-Juriti (18)	0	72	11	0	17	Tucanoan	0° 16’ N; 70° 45’ W	Lobato-da-Silva *et al.* (2001)
Muinane (19)	11	21	37	26	5	Witotoan	0° 11’ N; 73° 25’ W	Keyeux *et al.* (2002)
Poturujara (23)	44	0	26	30	0	Tupi	0° 18’ S; 55° 18’ W	Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2003)
Katuena (23)	26	9	35	30	0	Carib	0° 40’ S; 57° 30’ W	Lobato-da-Silva *et al.* (2001); Silva Jr *et al.* (2003)
Wai-wai (26)	15	15	43	27	0	Carib	0° 40’ S; 58° W	Bonatto and Salzano (1997)
Urubu Kaapor (42)	21	31	14	29	5	Tupi	2° -3° S; 46° -47° W	Torroni *et al.* (1992, 1993); Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005)
Huitoto (35)	23	3	25	46	3	Witotoan	2° 14’ S; 72° 19’ W	Keyeux *et al.* (2002); Torres *et al.* (2006)
Arara (70)	54	20	26	0	0	Carib	3° 30’ -4° 20’ S; 53° 0’ -54° 10’ W	Lobato-da-Silva *et al.* (2001); Ribeiro-dos-Santos *et al.* (2001); Silva Jr *et al.* (2003); Bisso-Machado (2010, MSc Dissertation, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil.)
Awa-Guajá (53)	13	87	0	0	0	Tupi	3° 30’ S; 46° 40’ W	Lobato-da-Silva *et al.* (2001)
Asurini (24)	4	54	17	21	4	Tupi	3° 35’ -4° 12’ S; 49° 40’ -52° 26’ W	Lobato-da-Silva *et al.* (2001)
Piapoco (39)	18	3	15	5	59	Arawakan	3° 36’ S; 70° 23’ W	Torres *et al.* (2006)
Puinave (19)	5	16	58	16	5	Puinave	3° 36’ S; 70° 23’ W	Torres *et al.* (2006)
Sáliba (13)	15	0	55	15	15	Salivan	3° 49’ S; 70° 9’ W	Torres *et al.* (2006)
Ticuna (371)	20	11	35	33	1	Ticuna	4° S; 69° 58’ W	Schurr *et al.* (1990); Mesa *et al.* (2000); Torres *et al.* (2006); Mendes-Junior and Simões (2009); Rojas *et al.* (2010)
Parakanã (31)	6	39	32	23	0	Tupi	5° 22’ S; 51° 17’ W	Lobato-da-Silva *et al.* (2001); Bisso-Machado (2010, MSc Dissertation)
Xikrin (33)	30	64	3	3	0	Macro-Ge	5° 55’ S; 51° W	Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005); Bisso-Machado (2010, MSc Dissertation)
Suruí (44)	7	4	0	89	0	Tupi	5° 58’ -10° 50’ S; 48° 39’ -61° 10’ W	Bonatto and Salzano (1997); Lobato-da-Silva *et al.* (2001)
Araweté (18)	39	0	50	11	0	Tupi	5° 9’ S; 52° 22’ W	Lobato-da-Silva *et al.* (2001)
Munduruku (92)	12	17	9	58	4	Tupi	6° 23’ S; 59° 9’ W	Torroni *et al.* (1992, 1993); Lobato-da-Silva *et al.* (2001); Marrero *et al.* (2007); Bisso-Machado (2010, MSc Dissertation)
Marubo (10)	10	0	60	30	0	Panoan	6° 47’ S; 72° 80’ W	Torroni *et al.* (1993)
Jamamadi (23)	0	0	96	4	0	Arauan	7° 15’ S; 66° 41’ W	Lobato-da-Silva *et al.* (2001); Bisso-Machado (2010, MSc Dissertation)
Yungay (38)	5	45	34	16	0	Quechuan	7° 26’ S; 77° 4’ W	Lewis Jr *et al.* (2007)
Ancash (33)	9	52	18	21	0	Quechua	7° 41’ S; 77° 6’ W	Lewis Jr *et al.* (2005)
Gorotire (11)	28	18	18	36	0	Macro-Ge	7° 44’ S; 51° 10’ W	Bisso-Machado (2010, MSc Dissertation)
Krahó (14)	29	57	14	0	0	Macro-Ge	8° S; 47° 15’ W	Torroni *et al.* (1993)
Kuben-Kran-Kegn (19)	58	26	6	10	0	Macro-Ge	8° 10’ S; 52° 8’ W	Bisso-Machado (2010, MSc Dissertation)

Table 5 (cont.)

Population (n)[1]	Haplogroups (%)					Language	Geographical coordinates	References
	A	B	C	D	Others[2]			
Mekranoti (19)	26	63	11	0	0	Macro-Ge	8° 40’ S; 54° W	Dornelles *et al.* (2005); Bisso-Machado (2010, MSc Dissertation)
Kubenkokre (4)	0	100	0	0	0	Macro-Ge	8° 43’ S; 53° 23’ W	Marrero *et al.* (2007)
Kayapó (13)	46	54	0	0	0	Macro-Ge	9° S; 53° W	Lobato-da-Silva *et al.* (2001)
Karitiana (19)	0	11	0	89	0	Tupi	9° 30’ S; 64° 15’ W	Lobato-da-Silva *et al.* (2001)
Cinta-Larga (45)	25	0	20	53	2	Tupi	9° 50’ –12° 30’ S; 59° 10’ –60° 50’ W	Lobato-da-Silva *et al.* (2001); Dornelles *et al.* (2005); Bisso-Machado (2010, MSc Dissertation)
Gavião (27)	15	15	0	70	0	Tupi	10° 10’ S; 61° 8’ W	Ward *et al.* (1996)
Tupe (16)	0	69	31	0	0	Aymaran	10° 16’ S; 75° 47’ W	Lewis Jr *et al.* (2007)
Txukahamãe (2)	100	0	0	0	0	Macro-Ge	10° 20’ S; 53° 5’ W	Dornelles *et al.* (2005)
Zoró (30)	20	7	13	60	0	Tupi	10° 20’ S; 60° 20’ W	Ward *et al.* (1996)
Matsiguenga (38)	5	92	0	3	0	Arawakan	10° 47’ -12° 51’ S; 73° 17’ -70° 44’ W	Mazières *et al.* (2008)
Kokraimoro (2)	50	50	0	0	0	Macro-Ge	10° 49’ S; 55° 27’ W	Marrero *et al.* (2007)
Pacaás Novos (Wari) (30)	40	30	27	3	0	Chapacura-Wanham	11° 8’ S; 65° W	Bisso-Machado (2010, MSc Dissertation)
Tayacaja (61)	21	33	13	30	3	Quechuan	12° 24’ S; 74° 34’ W	Fuselli *et al.* (2003)
Arequipa (22)	9	68	14	9	0	Quechua	13° 13’ S; 72° 11’ W	Fuselli *et al.* (2003)
Trinitario (35)	14	40	37	3	6	Arawakan	14° S; 65° W	Bert *et al.* (2001)
Xavánte (25)	16	84	0	0	0	Macro-Ge	14° S; 52° 30’ W	Ward *et al.* (1996)
Movima (22)	9	9	64	18	0	Movima	14° 26’ S; 65° 53’ W	Bert *et al.* (2001)
Quechua (232)	14	62	15	9	0	Quechuan	14° 30’ S; 69° W	Merriwether *et al.* (1995); Bert *et al.* (2001); Silva Jr *et al.* (2003); Lewis Jr *et al.* (2007); Corella *et al.* (2007); Barbieri *et al.* (2011); Gayà-Vidal *et al.* (2011)
Chimane (Moseten) (71)	39	54	3	0	4	Chimane	14° 41’ S; 66° 50’ W	Bert *et al.* (2001); Corella *et al.* (2007);
Ignaciano (22)	18	36	41	0	5	Arawakan	15° 1’ S; 66° 4’ W	Bert *et al.* (2001)
Uro (64)	11	69	9	11	0	Uru-Chipaya	15° 45’ S; 69° 53’ W	Barbieri *et al.* (2011)
Yuracare (28)	39	32	21	4	4	Yuracare	17° S; 65° W	Bert *et al.* (2001)
Aymara (411)	4	76	8	11	1	Aymaran	17° 68’ S; 69° 16’ W	Merriwether *et al.* (1995); Easton *et al.* (1996); Bert *et al.* (2001); Lewis Jr *et al.* (2007); Corella *et al.* (2007); Barbieri *et al.* (2011); Gayà-Vidal *et al.* (2011)
Ayoreo (91)	0	0	83	17	0	Zamucoan	19° S; 60° 30’ W	Dornelles *et al.* (2004)
Wichí (199)	12	51	7	29	1	Mataco-Guaicuru	22° 28’ S; 62° 70’ W	Torroni *et al.* (1993); Bianchi *et al.* (1995); Bravi *et al.* (1995); Demarchi *et al.* (2001); Cabana *et al.* (2006)
Chorote (34)	15	44	23	18	0	Mataco-Guaicuru	22° 90’ S; 65° 40’ W	Bianchi *et al.* (1995); Bravi *et al.* (1995)
Humahuaca (46)	11	68	17	4	0	Spanish	23° 11’ S; 65° 20’ W	Dipierri *et al.* (1998)
Aché (63)	10	90	0	0	0	Tupi	23° 30’ –24° 10’ S; 55° 50’ –56° 30’ W	Schmitt *et al.* (2004)
Atacameño (79)	13	73	10	4	0	Atacama	23° 50’ S; 68° W	Baillliet *et al.* (1994); Merriwether *et al.* (1995); Merriwether and Ferrell (1996)
Guarani (249)	77	6	9	6	2	Tupi	23° 6’ S; 55° 12’ W	Silva Jr *et al.* (2003); Marrero *et al.* (2007); García and Demarchi (2009)
Pilagá (41)	5	37	27	29	2	Mataco-Guaicuru	24° S; 59° W	Demarchi *et al.* (2001); Cabana *et al.* (2006)
Coya (60)	13	57	23	5	2	Coya	25° 30’ S; 67° 28’ W	Álvarez-Iglesias *et al.* (2007)

Table 5 (cont.)

Population (n)[1]	Haplogroups (%)					Language	Geographical coordinates	References
	A	B	C	D	Others[2]			
Toba (80)	15	43	5	37	0	Mataco-Guaicuru	26° S; 58° W	Bianchi *et al.* (1995); Demarchi *et al.* (2001); Goicoechea *et al.* (2001); Cabana *et al.* (2006)
Jujuy (19)	16	58	16	10	0	Spanish	27° 27' S; 58° 59' W	Dipierri *et al.* (1998)
Kaingang (79)	47	4	48	0	1	Macro-Ge	28° S; 51° 20' W	Dornelles *et al.* (2005); Marrero *et al.* (2007)
Mocoví (5)	80	0	0	20	0	Mataco-Guaicuru	29° 51' S; 59° 56' W	Tamm *et al.* (2007)
Pehuenche (205)	2	9	40	49	0	Araucanian	37° 43' S; 71° 16' W	Merriwether *et al.* (1995); Moraga *et al.* (1997, 2000)
Mapuche (314)	5	23	32	36	4	Araucanian	39° 10' -41° 20' S; 68° 37' -70° 22' W	Ginther *et al.* (1993); Horai *et al.* (1993); Bailliet *et al.* (1994); Bianchi *et al.* (1995); Moraga *et al.* (2000)
Huilliche (207)	4	28	20	48	0	Araucanian	41° 16' S; 73° W	Bailliet *et al.* (1994); Merriwether *et al.* (1995); Merriwether and Ferrell (1996)
Aónikenk[3, 4] (15)	0	0	27	73	0	Chon	45° S; 71° W	Lalueza (1995, PhD thesis, Universitat de Barcelona, Barcelona, Spain)
Tehuelche[4] (29)	0	20	24	56	0	Chon	45° S; 71° W	Moraga *et al.* (2000)
Yámana[3] (Yaghan) (32)	0	0	63	37	0	Yámana	47° S; 74° W	Lalueza (1995, PhD thesis); Moraga *et al.* (1997, 2000)
Kawéskar[2] (Alacaluf) (19)	0	0	16	84	0	Alacalufan	49° S; 74° W	Lalueza (1995, PhD thesis)
Selknam[2] (Ona) (16)	0	0	56	38	6	Chon	54° S; 74° W	Lalueza (1995, PhD thesis); García-Bour *et al.* (2004)

[1] Arranged according to latitude. [2] Probably of non-Amerindian origin. [3] Ancient DNA. [4] Aónikenk and Tehuelche are the same tribe separated by time. Aónikenk refers to ancient DNA.

Table 6 summarizes the influence of geography. In the seven regions that were defined, 74% of the variation occurred within populations, 6% among geographic divisions and 20% among populations within divisions. To analyze this variability further, the isolated frequencies of haplogroups A to D were plotted as shown in Figure 2. High frequencies of haplogroup C were observed in specific regions along the northwestern portion of the continent, with additional high spots in southern Brazil and northern Argentina. The prevalences of haplogroups B and D showed a clear east-west separation, while for haplogroup A there were three main high prevalence nuclei in the north, center and south of the continent. Spearman's correlation coefficient between haplogroup frequencies and latitude yielded a positive value (0.27; $p < 0.01$) for haplogroup A, with a corresponding negative one (-0.25; $p < 0.01$) for haplogroup D. The coefficients for haplogroups B and C were not significant.

Table 6 - Mitochondrial DNA haplogroup frequencies by geography[1].

Geographic divisions	No. of populations	No. of individuals	Haplogroups (%)				
			A	B	C	D	Other
Amazonia	55	2410	20	21	31	25	3
Central Plateau	2	39	21	74	5	0	0
Southern Brazil	2	328	70	6	18	4	2
Chaco	6	479	10	43	22	24	1
Southern South America	3	726	4	20	31	43	2
Tierra del Fuego	5	111	0	5	39	55	1
Andes	35	2604	27	45	20	7	1
Total	108	6697					

[1] AMOVA results: (a) Among geographic divisions: 6.2%; (b) Among populations within geographic divisions: 19.5%; (c) Within populations: 74.3%. The three values are statistically significant.

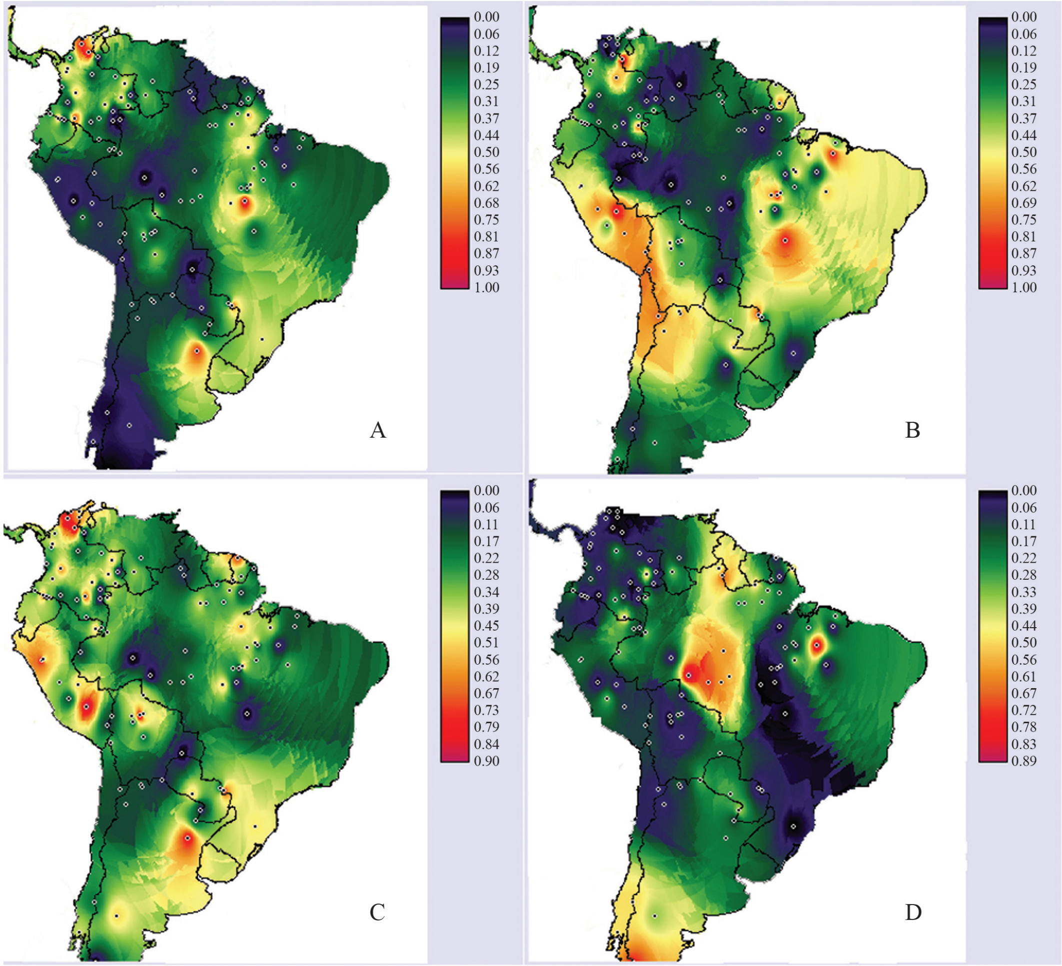

Figure 2 - Isoline map distribution showing the geographic pattern of the four (A-D) mtDNA haplogroups in South Amerindians. The dots indicate the locations of the populations sampled. As indicated in the scales given at right of each map, the colors represent the haplogroup frequencies, from dark blue (0.00) to red (1.00).

Table 7 summarizes the influence of language. Sixteen main language groups were considered, plus a composite set of "others". The AMOVA results indicated that 73% of the haplogroup prevalence variability occurred within populations, with 7% of it being attributable to languages. However, there was considerable heterogeneity (20%) within the language categories established. Overall, the variability was similar to that obtained for geography.

Table 7 - Mitochondrial DNA haplogroup frequencies by language[1].

Language	No. of populations	No. of individuals	Haplogroups (%)				
			A	B	C	D	Other
Tupi	16	889	38	24	10	27	1
Macro-Ge	11	221	37	38	21	3	1
Carib	9	408	24	32	25	18	1
Chibchan	6	461	69	6	22	2	1
Mataco-Guaicuru	5	359	13	46	11	29	1
Arawakan	8	321	16	38	24	13	9
Araucanian	3	726	4	20	31	43	2
Choco	2	204	28	46	13	12	1
Chon	3	60	0	10	33	55	2
Tucanoan	6	140	14	26	48	8	4

Table 7 (cont.)

Language	No. of populations	No. of individuals	Haplogroups (%)				
			A	B	C	D	Other
Aymaran	2	427	4	76	9	10	1
Barbacoan	3	152	28	34	19	19	0
Guahiban	2	129	51	6	29	0	14
Witotoan	3	56	18	9	32	37	4
Salivan	2	41	29	7	32	27	5
Quechuan	6	497	14	51	23	11	1
Other	21	1606	13	26	40	19	2
Total	108	6697					

[1] AMOVA results: (a) Among language groups: 6.6%; (b) Among populations within language groups: 20.1%; (c) Within populations: 73.3%. The three values are statistically significant.

Conclusion

South Amerindians have been extensively studied with regard to the Y-chromosome, as well as and especially so for mtDNA markers. In agreement with studies from other regions, by far most of the mtDNA variability (73%-74%) is intrapopulational. Geographical and linguistic factors influenced the patterns of mtDNA diversity to a similar extent, while geography was apparently more important than language in explaining the data for the Y chromosome Q clade-STRs. Additional factors that may have influenced these results include distinct male and female migration patterns, as well as cultural and other characteristics. The fact that most studies have generally dealt with small populations, in which genetic drift may be important, could also have influenced the results.

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