



## Mitochondrial DNA (mtDNA) haplogroups in 1526 unrelated individuals from 11 Departments of Colombia

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### Abstract

The frequencies of four mitochondrial Native American DNA haplogroups were determined in 1526 unrelated individuals from 11 Departments of Colombia and compared to the frequencies previously obtained for Amerindian and Afro-Colombian populations. Amerindian mtDNA haplogroups ranged from 74% to 97%. The lowest frequencies were found in Departments on the Caribbean coast and in the Pacific region, where the frequency of Afro-Colombians is higher, while the highest mtDNA Amerindian haplogroup frequencies were found in Departments that historically have a strong Amerindian heritage. Interestingly, all four mtDNA haplogroups were found in all Departments, in contrast to the complete absence of haplogroup D and high frequencies of haplogroup A in Amerindian populations in the Caribbean region of Colombia. Our results indicate that all four Native American mtDNA haplogroups were widely distributed in Colombia at the time of the Spanish conquest.

**Keywords:** admixture, Colombia, haplogroup, Mestizo, mitochondrial DNA.

Received: October 31, 2012; Accepted: June 16, 2013.

The population of Colombia is predominantly of European origin (86.1%), with most individuals being of Spanish descent; other European groups, as well as Arab and Jewish descendants, represent a minor contribution (Yunis *et al.*, 2000b; Rodríguez-Palau *et al.*, 2007). The population of African descent (10.5%) is distributed mainly in the Pacific and Caribbean coastal regions and islands. The Amerindians (~3.4%) are found mainly in the plains, Amazonian jungle and in some regions of the Colombian Andes (Rodríguez-Palau *et al.*, 2007). Different degrees of admixture have been documented in different regions of the country based on blood group analysis (Sandoval *et al.*, 1993). In the Pacific and Caribbean coastal regions there is admixture between those of African and European descent. Amerindian admixture is higher in the southwest and decreases towards the northern section of the Andes, where the European descent component is higher.

Previous mtDNA analysis in Colombian Amerindian populations revealed four distinct haplogroups referred to as A, B, C and D (Mesa *et al.*, 2000; Keyeux *et al.*, 2002; Rodas *et al.*, 2002; Torres *et al.*, 2006; Melton *et al.*, 2007; Rondon *et al.*, 2007). These results have been confirmed by our own study of Amerindian populations (Usme-Romero *et al.*, 2013) that revealed high frequencies of haplogroups

A and C and lower frequencies of haplogroups B and D in northern Colombia, while in the southeast, higher frequencies of haplogroups D and C and a lower frequency of haplogroup A were found; we also observed a higher frequency of haplogroup B in western Colombia that declined towards eastern Colombia. In a study of Mestizo populations from the Departments of Cauca and Valle del Cauca, Salas *et al.* (2008) showed that 94% of the mtDNA haplogroups were Native American. Rondón *et al.* (2006), in a sample of Mestizo individuals from Cali in Valle del Cauca, observed that 78% of the 135 individuals tested carried Amerindian haplogroups. In a study of a non-Amerindian sample from the Department of Antioquia, Mesa *et al.* (2000) reported that the mtDNA haplogroups were predominantly Amerindian while the Y-chromosome haplotypes were mainly of European origin.

The aim of this study was to use a large sample of the current Colombian population from different Departments of Colombia to confirm that the Colombian mtDNA haplogroups are predominantly of Amerindian origin. The present report represents the largest mtDNA haplogroup study of the non-Amerindian population of Colombia done to date.

We analyzed 1526 archived blood samples from individuals of unrelated maternal lineage. The samples were randomly selected from our database of referrals for paternity testing. Prior informed consent was provided by each individual at the moment of blood collection. In contrast to

other studies, we did not ask the individuals for “self-reported ancestry” (Caucasian-Mestizo, Amerindian, Afro-descendant, Mulato) since our aim was to verify the previous finding of a sex bias, with the Y-chromosome of European origin and mtDNA of Amerindian origin in present-day Mestizo populations of Colombia (Mesa *et al.*, 2000). The samples were collected in local laboratories in the capitals of 11 Departments of Colombia (Table 1) and then referred to our central laboratory for paternity testing.

DNA was extracted with the DNA Wizard genomic DNA extraction kit (Promega Corporation, Madison, WI, USA), following the manufacturer’s recommendations. mtDNA haplogroups were determined after electrophoresis of PCR-RFLP products (haplogroups A, C, D and L) or of undigested PCR products (haplogroup B), according to Parra *et al.* (1988) (Table 2). Haplogroup L was determined in samples that tested negative for haplogroups A, B, C and D. Samples that did not carry any of the tested haplogroups were classified as “other”. Each amplification reaction consisted of 2.5  $\mu$ L of DNA (25–50 ng), 1.25  $\mu$ L of the proper set of primers (10 nmol/ $\mu$ L), 2  $\mu$ L of dNTPs (10 mM), 1.5  $\mu$ L of MgCl<sub>2</sub> (25 mM) for haplogroup A or 2  $\mu$ L for the other haplogroups, and 0.125  $\mu$ L of DNA *Taq* polymerase (Promega), in a final volume of 25  $\mu$ L. The amplification conditions consisted of a first denaturing step at 94 °C for 5 min, followed by 34 cycles of denaturing at 94 °C for 30 s, annealing at 50 °C (haplogroups B and D) or 55 °C (haplogroups A and C) for 30 s, extension at 72 °C for 30 s and a final extension step at 72 °C for 5 min. Prior to electrophoresis, 15  $\mu$ L of the amplified products were digested with appropriate restriction enzymes for 3 h at 37 °C, except for haplogroup B (Table 2). The products were electrophoresed on a 3% Nusieve/Seakem agarose gel (FMC Corporation, Philadelphia, PA, USA) in 1X TBE buffer at 100 V for 1 h, stained with ethidium bromide and photographed. As a control, samples that had been typed for each of the A–D mtDNA haplogroups by restriction enzyme digestion and sequencing of mtDNA HV1 and HV2 regions were always included. The haplogroup frequencies for each population sample were estimated by direct counting.

The mtDNA haplogroups (A, B, C or D) were present in 73.9–96.5% of the samples tested (Table 1). The lowest Amerindian mtDNA haplogroup frequencies were found in the Departments of Atlántico (73.9%) and Córdoba/Sucre (74.8%) in the Caribbean region of Colombia. The highest frequency was found in Boyacá (96.5%), followed by Nariño (91.1%). The mtDNA L haplogroup was most frequent in the Departments of Córdoba/Sucre (25%) followed by Antioquia (9.6%), Atlántico (9.3%) and Valle del Cauca (5.3%). In all other Departments, the frequencies of this haplogroup were  $\leq$  3.3%. The highest frequencies of “other” mtDNA haplogroups were found in Atlántico (16.6%), Santander (8.6%), Cundinamarca and Meta (13.3% each), Valle del Cauca (12.6%), Norte de Santander

(8.6%) and Tolima and Nariño (8% each). Frequencies < 4% were found in Boyacá (2.6%), Córdoba/Sucre (2.7%) and Antioquia (3.8%). Overall, haplogroup A was present in 529/1526 individuals (34.7%), haplogroup B in 455/1526 (29.8%), haplogroup C in 177/1526 (11.6%) and haplogroup D in 138/1526 (9%), with an overall Amerindian haplogroup frequency of 85%; haplogroup L occurred in 76/1526 (5%) and “other” haplogroups, in 151/1526 (10%). These results were compared with reports of mtDNA haplogroups in samples of Colombian Mestizos and African descendants described by others (Table 3).

Based on official records (Rodríguez-Palau *et al.*, 2007), the Colombian population is composed of Caucasian descendants (86.1%), African-descent Colombians (10.5%), Amerindians (3.4%) and gypsies (0.1%). Spaniards represent the main Caucasian ancestral population that arrived soon after the discovery of America by Columbus in 1492 (Sandoval *et al.*, 1993; Mesa *et al.*, 2000; Yunis *et al.*, 2000a, 2005a,b; Salas *et al.*, 2008). Other Europeans (German, Italian and French, among others) as well as Arab and Jewish populations have also contributed to the admixture in different regions of present-day Colombia (Yunis *et al.*, 2000a, 2005a). The Spanish conquerors started to populate the Caribbean region, the Andean mountain range and the Pacific region of Colombia soon after their arrival (Salas *et al.*, 2008). The first cities were established in 1510 (Santa María Antigua del Darien), 1525 (Santa Marta) and 1533 (Cartagena). Bogotá, the capital of Colombia was founded in 1538 (Salas *et al.*, 2008). Africans started to arrive during the slave trade that began in the 16th century and lasted until the 17th century. The current populations of African descent (10.5% in present-day Colombia) are distributed mainly in the Pacific and Caribbean coastal regions and islands (Figure 1).

The ancestral Amerindian populations were distributed throughout the country when the Spaniards arrived. Most of the original cultures, such as the Muisca, Quimbaya, Calima, Pijaos and Tayrona that inhabited the Colombian Andes and the Caribbean region no longer exist. During the Spanish conquest and subsequent colonization the original Amerindian populations were enslaved, exterminated or displaced to their current distribution. These Amerindian populations (~3.4% of the current Colombian population) occur mainly in the Amazonian and Orinoquian regions, and at a few locations in the Colombian Andes, Department of Chocó, Sierra Nevada de Santa Marta and Guajira peninsula (Figure 1). During the Spanish conquest and period of colonization, the Mestizo population was formed by the admixture of Amerindians and Spaniards. Admixture between Spaniards and African slaves (Mulatos) occurred in the Caribbean and Pacific regions. Consequently, the resulting pattern of admixture is not homogeneous in Colombia and different degrees of admixture are present in different regions of the country. A study based on blood group markers in a large sample of about

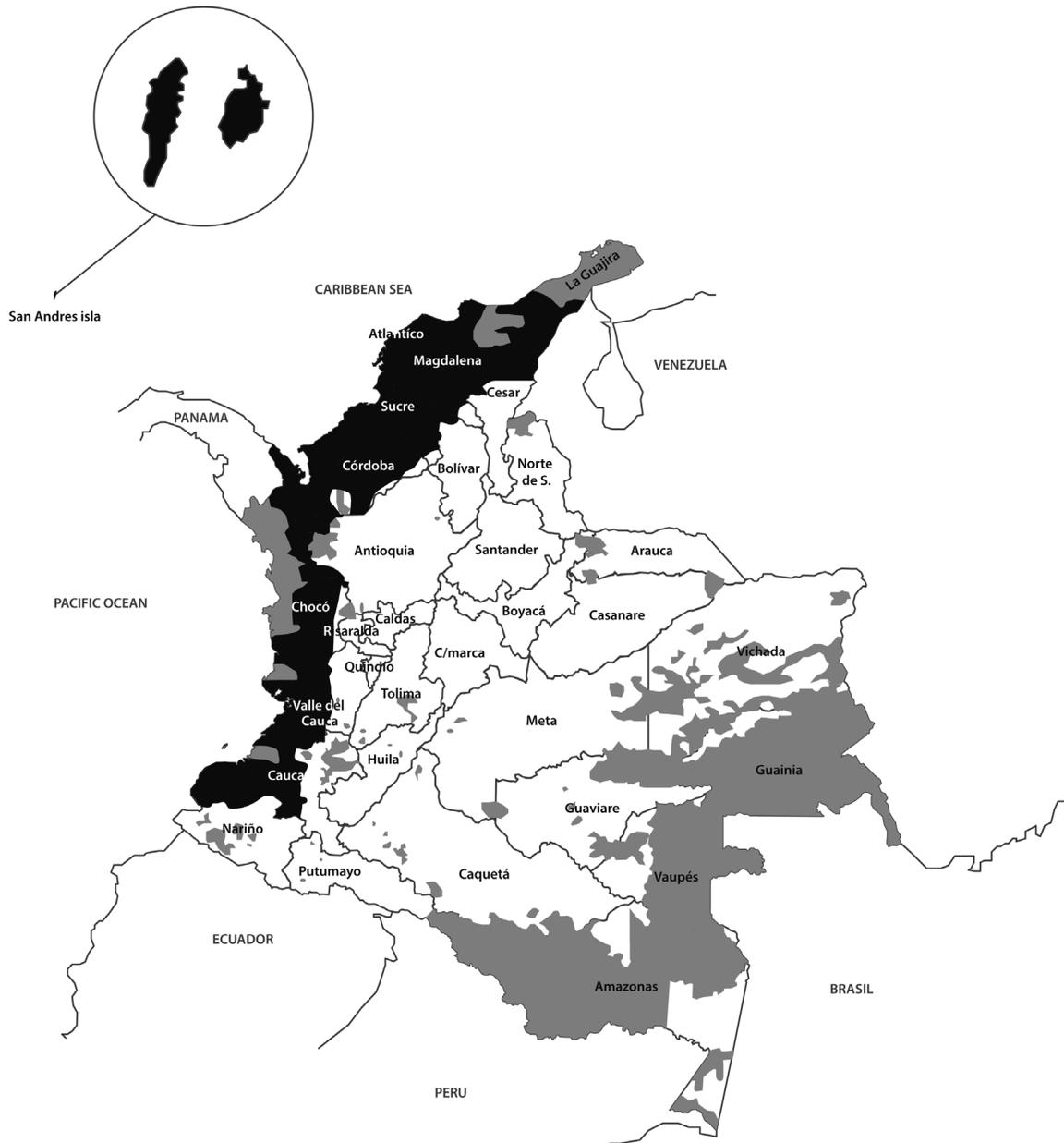
**Table 1** - mtDNA haplogroup frequencies for 1,526 present-day unrelated Colombian individuals from 11 Departments.

Department	Geographic location	Number of individuals	Haplogroup												
			Amerindian					Non-Amerindian							
			A		B		C	D		L		Others			
N	%	N	%	N	%	N	%	Total %	N	%	N	%			
Atlántico	Caribbean	150	38	25.3	48	32.0	12	8.0	13	8.6	73.9	14	9.3	25	16.6
Córdoba/Sucre	Caribbean	124	35	29.6	24	20.3	18	14.8	14	10.1	74.8	30	25.0	3	2.7
Norte de Santander	Andes	150	65	43.3	37	24.6	8	5.3	24	16.0	89.2	3	2.0	13	8.6
Santander	Andes	150	45	30.0	48	32.0	9	6.0	22	14.6	82.6	5	3.3	21	14.0
Boyacá	Andes	150	76	50.6	41	27.3	15	10.0	13	8.6	96.5	1	0.6	4	2.6
Cundinamarca	Andes	151	61	40.6	53	35.3	5	3.3	8	5.3	84.5	4	2.7	20	13.3
Antioquia	Andes	51	17	32.6	21	40.4	4	7.6	2	3.8	84.4	5	9.6	2	3.8
Tolima	Andes	150	38	25.3	52	34.6	29	19.3	14	9.3	88.5	5	3.3	12	8.0
Meta	Andes/Orinoquian	150	61	40.6	46	30.6	13	8.6	10	6.6	86.4	0	0.0	20	13.3
Valle del Cauca	Andes/Pacific	150	46	30.6	42	28.0	24	16.0	11	7.3	81.9	8	5.3	19	12.6
Nariño	Andes/Pacific	150	47	31.3	43	28.6	40	26.6	7	4.6	91.1	1	0.6	12	8.0

60,000 individuals in Colombia (Sandoval *et al.*, 1993) showed that admixture between individuals of African descent and Mestizos/Caucasians was predominant in the Pacific and Caribbean coastal regions and islands, while Amerindian admixture was higher in the southwest and decreased towards the northern section of the Andes, where the Mestizo component was stronger; the analysis did not include populations living in the Orinoquian and Amazonian regions.

A few studies have examined the mtDNA haplogroups in present-day Colombian populations (Table 3). Carvajal-Carmona *et al.* (2000) studied 80 individuals from Medellín (Department of Antioquia in the Colombian Andes) and found haplogroup A, B, C and D frequencies of 45%, 37%, 6% and 1%, respectively; an overall frequency of 90% was observed for Native American haplogroups. In another study (Salas *et al.*, 2008), 185 individuals from the Departments of Cauca and Valle del Cauca (Andes/Pacific) were analyzed; 67 of them were “self-classified” as Mestizos, with 94% of them carrying Native American mtDNA haplogroups (A 40%, B 13%, C 34% and D 7%). Rondón *et al.* (2006) reported an overall frequency of 78% for Native American haplogroups (A 34%, B 27%, C 13%, D 2% and E 2%) among 135 mestizo individuals from Cali in the Department of Valle del Cauca. Rodas *et al.* (2002) analyzed 91 Mestizos from Bogotá and found that 78% carried Native American haplogroups (A 37.4%, B 26.4%, C 7.7% and D 6.6%), 1.1% carried haplogroup L and 18.7% carried “other” mtDNA haplogroups.

The mtDNA haplogroups in Afro-Colombian populations have been determined in a few studies (Rodas *et al.*, 2002; Rondon *et al.*, 2007; Salas *et al.*, 2008). Rodas *et al.* (2002) studied 159 Afro-Colombians from different locations – 40 individuals from Providencia island, 38 from San Basilio de Palenque (Caribbean coast), 28 from Quibdó (capital of the Department of Chocó), 33 from Nuquí and 20 from Cauca Department. The geographic distribution of these samples means that they have had different admixture histories. In the sample from Providencia (a Colombian island in the Caribbean Sea off the coast of Nicaragua) the frequency of haplogroup L was 52%, that of haplogroup A was 10% and that of “other” haplogroups was 32.5%. The authors suggested that the L3 haplogroup could be present among the “other” haplotypes and that the total frequency for the L macrohaplogroup would be 82.5%. In the sample from San Basilio de Palenque the frequency of haplogroup L was 44.7%, haplogroups A and B each occurred with a frequency of 5.3% and the “other” haplogroups had a frequency of 34.5%, with an overall macrohaplogroup L frequency of 76.2%. The populations of Quibdó, Nuquí and Cauca (Pacific region of Colombia) showed somehow different results. In Quibdó, haplogroup L was present only in 21.4% of the sample; the frequencies of haplogroups A, B, C and “other” haplogroups were 7.1%, 32.1%, 3.7% and 25%, respectively, with an overall frequency of 46% for



**Figure 1** - Geographic location of the Amerindian reservations (gray) and territories with a high frequency of African descendants (black) in Colombia. Inset in the upper left corner shows the San Andres (larger) and Providencia (smaller) Islands in the Caribbean Sea. Modified from Rodriguez-Palau *et al.* (2007).

**Table 2** - Fragment patterns for determining mtDNA haplogroups.

Haplogroup	Fragment patterns*				
	663 <i>Hae</i> III Primers 577F - 743R	9 bp deletion Primers 8195F - 8317R	13259 <i>Hinc</i> II Primers 13208F - 13413R	5176 <i>Alu</i> I Primers 5099F - 5274R	3592 <i>Hpa</i> I Primers 3457F - 3661R
A	+	-	+	+	-
B	-	+	+	+	-
C	-	-	-	+	-
D	-	-	+	-	-
L	-	-	+	+	+

\*Parra *et al.* (1998). (+) present, (-) absent.

**Table 3** - Frequencies of mtDNA haplogroups in studies of Colombian populations.

Populations	Number of individuals		Amerindian				Non-Amerindian				Reference						
			A		B		C		D			L		Others*			
			N	%	N	%	N	%	N	%		N	%	N	%	N	%
Admixed	1526	529	34.7	455	29.8	177	11.6	138	9.0	76	5.0	151	9.9	9.9	Present study		
Mestizo																	
Medellín	80		45.0		37.0		6.0		1.0					?	Carvajal-Carmona <i>et al.</i> (2000)		
Cauca/Valle del Cauca	67		40.0		13.0		34.0		7.0					?	Salas <i>et al.</i> (2008)		
Bogotá	91		37.4		26.4		7.7		6.6					1.1	18.7	Rodas <i>et al.</i> (2002)	
Cali	135		34.0		27.0		13.0		2.0					?	22**	Rondón <i>et al.</i> (2006)	
African descent																	
Providencia	40		10.0		?		?		?					82.5	?	Rodas <i>et al.</i> (2002)	
Providencia														16.0		Baldrich (2005)	
San Basilio de Palenque	38		5.3		5.3		?		?					76.2	?	Rodas <i>et al.</i> (2002)	
San Basilio de Palenque	35													20.0		Baldrich (2005)	
Quibdó	28		7.1		32.1		3.7		?					46.0	?	Rodas <i>et al.</i> (2002)	
Quibdó														31.0		Baldrich (2005)	
Nuquí	33		15.1		6.1		?		?					63.6	?	Rodas <i>et al.</i> (2002)	
Cauca	20				10.0									?		?	Rodas <i>et al.</i> (2002)
Cauca/Valle del Cauca	151		6.0		6.0		3.0		0.0					?	85*	Rondón <i>et al.</i> (2006)	

\*Tested negative for haplogroups A, B, C, D and L.

\*\*Includes Caucasian and Afro-descendant haplogroups.

macrohaplogroup L. In Nuquí, haplogroups L, A, B and “other” haplogroups had frequencies of 39.4%, 15.1%, 6.1% and 33.3%, respectively, with an overall macrohaplogroup L frequency of 63.6%. Little can be concluded about the Department of Cauca since only haplogroup B was investigated, with a frequency of 10%.

In a study by Baldrich (2005) based on restriction enzyme digestion and sequencing, 35 individuals from San Basilio de Palenque, 26 from Quibdó and 19 from Providencia were analyzed. Haplogroup L (L1, L2 and L3) was found with frequencies of 80% in San Basilio de Palenque, 69% in Quibdó and 84% in Providencia, the remaining being Amerindian haplogroups with frequencies of 20%, 31% and 16, respectively; no European haplogroups were found. Rondón *et al.* (2006) reported a frequency of 15% for Amerindian haplogroups among 151 Afro-descendants in the Departments of Cauca and Valle del Cauca; however, the remaining 85% haplogroups were not determined. Salas *et al.* (2008) classified 95 individuals as “Afro-Colombians” and 11 as “Mulatos”; 72.6% of the African-Colombians carried the haplogroup L and 23.2% had Native American haplogroups. Among the “Mulatos”, haplogroup L was found in 81% of the individuals. Taken together, these studies indicate that admixture patterns between Afro-Colombians, Caucasian-Mestizos and Amerindians vary considerably in different regions of the country.

Other studies in Colombia have focused mainly on Amerindian populations (Mesa *et al.*, 2000; Keyeux *et al.*, 2002; Torres *et al.*, 2006; Melton *et al.*, 2007). We compared the results obtained in this report with the mtDNA haplogroups found in a sample of 424 unrelated Amerindian individuals from 21 tribes belonging to different linguistic families in present-day Colombia (Usme-Romero *et al.*, 2013). In that sample, the most frequent haplogroup was A (31%) followed by haplogroups C (30%), B (22.4%) and D (13.4%). Remarkably, present-day Amerindian populations inhabiting the Caribbean region of Colombia did not carry haplogroup D and showed lower frequencies of haplogroup B (Kogui 0%, Arhuaco and Chimila 4.8%, Arsario 12.5% and Wayuu 17.6%), while the predominant haplogroup was A followed by haplogroup C. These results contrasted with data obtained for the Departments of Atlántico and Córdoba/Sucre where haplogroup D had frequencies of 8.6% and 10.1%, respectively, and haplogroup B had frequencies of 32% and 20.3%, respectively. These results indicate that the Amerindian populations inhabiting the Caribbean region of Colombia at the time of the Spanish conquest carried all four Native American haplogroups and that the admixture that occurred at that time is reflected in the current Mestizo and Mulato populations. The first city built in Colombia during the Spanish conquest was Santa Maria la Antigua del Darién in 1510, later destroyed by the Amerindians in 1524. Present-day Amerindian populations living in geographic proximity to this city include the Embera in the Darién region of Colombia (studied by us

and others) and the Zenú (Mesa *et al.*, 2000), who currently speak only Spanish (in the Departments of Córdoba/Sucre). All four haplogroups are present in the Embera tribe studied by us (A 9.5%, B 52%, C 28.6% and D 9.5%) and are also present in the Zenú community (A 19%, B 41%, C 30% and D 5%).

The presence of the classic Native American mtDNA haplogroups A, B, C and D in all the Departments of Colombia examined indicates that during the Spanish conquest and period of colonization the Amerindian populations found in the Caribbean, Andean and Pacific regions of Colombia carried all four haplogroups, thus corroborating historical data of female Amerindian admixture with European males. The lowest frequencies of Amerindian mtDNA were found in Departments that historically had an important genetic influx from African populations, with the latter contributing to the admixture process, while the highest frequencies of Amerindian mtDNA haplogroups were found in Departments that historically had a strong Amerindian heritage, such as Nariño and Boyacá.

## Acknowledgments

This research was funded by the Instituto de Genética, Servicios Médicos Yunis Turbay y Cia. and done at this same institute. The authors have no conflict of interest related to this work.

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*Associate Editor: Angela M. Vianna-Morgante*

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