
TRANSPLANTED MALE GENOMES IN THREE VENEZUELAN POPULATIONS

DINORAH CASTRO DE GUERRA,
ESTEBAN ARROYO,
FRANCISCO MAURO SALZANO
AND MARIA CÁTIRA BORTOLINI

Since the Conquest and Colonization of the New World, Native American history has been strongly influenced by important migrations from Europe and Africa. The arrival of immigrants led to the establishment of a rapidly growing admixed population and a concomitant decline in the Amerind groups (Salzano and Bortolini, 2002). Among the Spaniard migrants, those from the Canary Islands have arrived continuously to Venezuela since the Colonial period, some Venezuelan regions having a well-known Canarian influence (Castillo Lara, 1980; Cunill Grau, 1987; Lynch, 1987). Cultural aspects of this influence have been reported (Báez Gutiérrez, 1995, Rodríguez, 1995), but little is known about their biological contribution. Recently published studies have demonstrated the maintenance of the original Canarian gene pool in three semi-isolated Venezuelan populations: San Antonio de Los Altos, San Diego de Los Altos and Hoyo de La Cumbre. Using classical genetic polymorphisms Castro de Guerra and Zambrano (2000) found that the European genetic contribution is majoritarian,

with values ranging from 78% (San Diego) to 92% (Hoyo de La Cumbre). On the other hand, genetic distance analyses suggested that this component is mainly of Canarian origin in Hoyo de La Cumbre and San Antonio, whereas in San Diego other European influences should also be considered.

Some aspects of the gender-specific gene flow from the Canary Islands to these three Canarian-derived populations were also evaluated considering the DYS19 locus (Castro de Guerra *et al.*, 2001). The results suggested that the Canarian male contribution ranged from 73% in San Diego to 100% in Hoyo de La Cumbre. The proportion of non European Y-chromosomes in San Antonio and San Diego is difficult to support historically and could be related to the known homoplasmy associated to the DYS19 locus, which leads to sharing of alleles just by recurrent mutations, not by descent (Kniff *et al.*, 1997).

The paternally inherited nonrecombining portion of the Y chromosome (NRY) includes polymorphisms that mutate relatively frequently (micro-

satellites, like the DYS19 locus) and biallelic polymorphisms (the YAP *Alu* insert and single nucleotide substitutions) that are unlikely to have arisen more than once in human evolution (Thomas *et al.*, 2000, Underhill *et al.*, 2001). In recent years, the power of the combination of these two sets of NRY polymorphisms in resolving evolutionary histories of human populations has been recognized (Carvajal-Carmona *et al.*, 2000; Mesa *et al.*, 2000; Thomas *et al.*, 2000; Bortolini *et al.*, 2002, 2003; Lell *et al.*, 2002). To obtain more precise information about the origin of the Y-chromosomes in the three above-indicated Canarian-derived populations, four biallelic and three microsatellite loci located in that region were investigated. The results were also compared with those reported in the literature, considering their potential parental groups, as well as other Latin American populations.

Subjects and Methods

Samples were collected from 53 individuals living in three small

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Dinorah Castro de Guerra. M.Sc and Ph.Sc., Instituto Venezolano de Investigaciones Científicas (IVIC). Associate Researcher, Laboratory of Human Genetics, Centro de Medicina Experimental IVIC. Address: IVIC, Apartado 21827, Caracas 1020A, Venezuela. e-mail: dcastro@ivic.ve

Esteban Arroyo. Anthropologist, Universidad Central de Venezuela (UCV). Assistant Student, Laboratory of Human Genetics IVIC. e-mail: earroyo@ivic.ve

Francisco Mauro Salzano. Ph.D., Universidade de São Paulo. Emeritus Professor, Departament of Genetics, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Brazil. e-mail: francisco.salzano@ufrgs.br

Maria Cátira Bortolini. Ph.D., UFRGS. Associate Professor, Departament of Genetics, UFRGS, Porto Alegre, Brazil. e-mail: maria.bortolini@ufrgs.br

and semi-isolated Venezuelan populations localized in the north-central region, near Caracas. Two of them (San Antonio de Los Altos and Hoyo de La Cumbre) were founded by Spanish-Canarian families at the end of the seventeenth and nineteenth centuries respectively. Previous investigations revealed that both communities have an important degree of isolation and endogamy (Villarroel, 1994; Castro de Guerra and Zambrano, 1997). San Diego de Los Altos, geographically near San Antonio, was an "encomienda town" in early times, a basically Native American settlement established by Spaniards for religious instruction. However, it also had inhabitants commonly identified as White, who came mainly from San Antonio de Los Altos and the Canary Islands, as well as a small population of African origin (initially slaves). The isolation of this population had been lower than that of the others (Chacón, 1980; Castro de Guerra and Zambrano, 1996).

DNA of 21 samples from San Antonio, 19 from Hoyo de La Cumbre, and 13 from San Diego, were isolated from 3ml of whole blood using the Debomoy and Nurnberger (1991) procedure.

Haplogroups were defined through four bi-allelic markers that were typed as reported in the following references: YAP or DYS287, Hammer and Horai (1995); sY81 or DYS271, Seielstad *et al.* (1994); 92R7, Hurles *et al.* (1999); and DYS199, Underhill *et al.* (1996). Additionally, three microsatellite loci were examined: DYS19, as reported by Castro de Guerra *et al.* (2001), while DYS390 and DYS393 were amplified using primers and conditions reported by Kayser *et al.* (1997). PCR products were loaded in 8% polyacrilamide/0.4 bisacrylamide gels in TBE buffer (50mM tris borate/EDTA 10mM, pH 8.3) and submitted to polyacrylamide gel electrophoresis (PAGE). The gel was visualized by silver-staining and fragments were identified according to previously identified allelic patterns (Ruíz-Linares *et al.*, 1999; Bortolini *et al.*, 2002). Following common usage, we refer to microsatellite lineages as haplotypes to distinguish them from biallelic haplogroups, which were defined according to the nomenclature established by the Y-Chromosome Consortium (http://ycc.biosci.arizona.edu/nomenclature_system/frontpage.html).

The ARLEQUIN program (Schneider *et al.*, 2000) was used to estimate allele and haplotype frequencies, gene diversity indices, and pairwise F_{ST} genetic distances. Admixture values were obtained using the least squares method and ADMIX computer program (Long,

TABLE I
Y-CHROMOSOME HAPLOGROUPS AS DEFINED BY ALLELES PRESENT AT FOUR BIALLELIC MARKERS (TOP) AND THEIR FREQUENCY IN THE THREE VENEZUELAN POPULATIONS AND OTHER HUMAN POPULATIONS (BOTTOM)

Markers	Haplogroups ¹					h^3
	P-M45	Null ²	YAP	E-M2	Q-M3	
92R7	T	C	C	C	T	
DYS287 (YAP)	-	-	+	+	-	
DYS271 (sY81)	A	A	A	G	A	
DYS199	C	C	C	C	T	
Population	Frequency (%)					
Hoyo de La Cumbre (N=19)	53	42	5	0	0	0.57 ± 0.06
San Antonio (N=21)	67	14	19	0	0	0.52 ± 0.10
San Diego (N=13)	77	23	0	0	0	0.38 ± 0.13
Gran Canaria (N=59)	70	15	15	0	0	0.48 ± 0.07
Spain (N=123)	80	15	5	0	0	0.33 ± 0.05
Berbers (N=104)	2	11	83	4	0	0.29 ± 0.06
Venezuelan Amerinds (N=36)	0	0	0	0	100	0
South Amerinds (N=356)	11	2	1	1	85	0.27 ± 0.03
Colombia (N= 80)	58	33	4	4	1	0.57 ± 0.04
Brazil (N=200)	58	27	13	2	0	0.58 ± 0.03
West Africa (N=56)	0	12	25	63	0	0.54 ± 0.06

¹ Haplogroup nomenclature as recommended by the Y-Chromosome Consortium (http://ycc.biosci.arizona.edu/nomenclature_system/frontpage.html).

² Ancestral alleles for the four loci.

³ Gene diversity index (Nei, 1987).

Note: Data for Gran Canaria, Spain and Berbers are from Bortolini *et al.* (2003); Western Africa and Colombia from Carvajal-Carmona *et al.* (2000); Venezuelan and other South Amerinds from Bortolini *et al.* (2002); and Brazilians from Carvalho-Silva *et al.* (2001).

1991).

Results and Discussion

The haplogroup frequencies identified in the three Venezuelan

Canarian-derived populations and in their potential parental groups, as well as in two other Latin American populations, are shown in Table I. Overall, the haplogroup frequencies in Venezuelans are closer to those seen in Gran Canaria

TABLE II
PAIRWISE F_{ST} DISTANCES BETWEEN THE THREE VENEZUELAN POPULATIONS STUDIED AND OTHER HUMAN POPULATIONS, BASED ON BIALLELIC HAPLOGROUP FREQUENCIES

Others	Venezuela		
	Hoyo de La Cumbre	San Diego	San Antonio
Hoyo de La Cumbre	0.0000		
San Diego	0.0326	0.0000	
San Antonio	0.0530	-0.0045	0.0000
Gran Canaria	0.0702	-0.0093	-0.0308
Berbers	0.5864	0.6741	0.5532
Spain	0.1508	-0.0277	0.0251
Western African	0.4077	0.4955	0.4284
Colombia	-0.0214	0.0019	0.0256
Brazil	0.0010	0.0080	-0.0037
Southern Amerinds	0.6475	0.6838	0.6533
Venezuelan Amerinds	0.7873	0.8927	0.7960

Significant P values (P<.05) in boldface. For references to the non-Venezuelan populations see footnote in Table I.

and Spain. E-M2 and Q-M3, which are unequivocally Sub-Saharan African and Amerindian markers, respectively, were not observed in the three Venezuelan communities. YAP, present in West Africa (25%), Spain (5%), and which has its highest distribution in Berbers (83%), is absent in San Diego, but was present in low (5%) and moderate frequencies (19%) in Hoyo de La Cumbre and San Antonio, respectively.

The haplogroup analysis also reveals a major genetic similarity between San Antonio and San Diego, and between these two populations and Gran Canaria and Spain, whereas Hoyo de La Cumbre shows a different distribution. This difference is mainly represented by the high frequency of Null (ancestral alleles for 92R7, DYS287, DYS271 and DYS199) and may be explained by a founder effect or genetic drift, since this population is the smallest and most isolated of the three.

Table II shows the genetic distances between these Venezuelan populations and the others, based on the above-indicated haplogroup distributions. Considering the potential parental populations, the smallest distances were observed in relation to Gran Canaria and Spain, with the exception of Hoyo de La Cumbre, which has a significant difference with these two populations. High similarity was observed with the previously tested Colombian and Brazilian mixed populations. Among Venezuelans, the smallest distance is between San Antonio and San Diego, and the highest between San Diego and Hoyo de La Cumbre, but the last number is not significantly different from zero.

Admixture estimations based on the haplogroup frequencies (Table III) suggest that the Y-chromosomes of these Venezuelan populations have an exclusively Canarian and/or Spaniard origin, while the autosome markers indicate some Amerindian and African ancestry (Castro de Guerra and Zambrano, 2000).

To refine the assessment of Y-chromosome origins in the three Venezuelan populations, the microsatellite haplotypes obtained were grouped considering simultaneously the biallelic data (Table IV). An important proportion of the haplotypes observed in Gran Canaria and Spain, 76% and 78% respectively, is present in at least one of the Venezuelan populations. Haplotype 1, the most commonly detected in Hoyo de La Cumbre and San Antonio, is also the most frequent in Gran Canaria and Spain. In San Diego, the most frequent haplotype (4) differs by just one mutational step from

TABLE III
ADMIXTURE (%) IN THE THREE VENEZUELAN POPULATIONS STUDIED
BASED ON AUTOSOMAL (CLASSICAL MARKERS)¹ AND BIALLELIC
Y-HAPLOGROUPS

Population/Marker	Admixture proportion (%)		
	Canary and Spain	Amerindian	Sub-Saharan Africa
San Antonio			
Autosomal	88	8	4
Y-Haplogroups	100	0	0
San Diego			
Autosomal	78	8	14
Y-Haplogroups	100	0	0
Hoyo de La Cumbre			
Autosomal	92	8	0
Y-Haplogroups	100	0	0

¹ Compiled from Castro de Guerra and Zambrano (2000).

TABLE IV
Y-CHROMOSOME MICROSATELLITE HAPLOTYPE FREQUENCIES
IN VENEZUELAN, GRAN CANARY, SPAIN AND BERBER POPULATIONS

Haplogroups and haplotypes	Loci			Populations					
	DYS19	DYS390	DYS393	San Antonio	San Diego	Hoyo Cumbre	Gran Canaria	Spain	Berbers
P-M45									
1	14	24	13	0.145	0.077	0.368	0.286	0.496	
2	14	25	13	0.047	0.077	0.053	0.034	0.048	
3	13	24	13	0.096		0.104	0.017	0.008	
4	14	23	13	0.144	0.230		0.068	0.048	
5	14	24	12	0.047	0.077		0.034	0.016	
6	14	24	14	0.047			0.051	0.008	
7	15	24	13	0.096			0.051	0.032	
8	16	23	13	0.047	0.077				
9	15	25	13		0.077				0.010
10	15	23	14		0.077			0.008	
11	14	24	15		0.077				
Null									
12	14	24	13			0.053	0.017	0.008	
13	14	23	12			0.053	0.034	0.032	0.059
14	13	24	13		0.077	0.104		0.008	
15	14	22	13	0.047		0.053		0.008	
16	14	22	12			0.053			
17	15	24	12			0.053			
18	15	24	14			0.053			
19	15	23	14		0.154				
20	14	23	13	0.047			0.017	0.016	
21	15	22	14	0.047			0.017	0.008	0.010
YAP									
22	13	25	13	0.047					0.048
23	13	25	14	0.047			0.017		0.010
24	13	24	13	0.096			0.119	0.040	0.413
25	13	24	14			0.053			0.019
Sum				1.000	1.000	1.000	0.762	0.784	0.569

Note: Allele size is indicated according to the number of repeats (Kayser *et al.*, 1997).

haplotype 1. This haplotype is also frequent in San Antonio, but it is absent or has a low frequency in the other populations. Considering haplotype 1 and its one-step derivatives (2, 3, 4, 5, 6 and 7) as a modal cluster, it can be seen that it represents more than half of the chromosomes in all populations, except for Berbers. The most frequent (47%) haplotype in Berbers (24; alleles 13, 24 and 13 for DYS19, DYS390, and DYS393, respectively), occurs in low frequency (9%) in San Antonio only. These results allow to discard an Amerindian origin for the DYS19-13 allele, as well as a Sub-Saharan Africa origin for the YAP chromosomes in these Venezuelans. In Amerindians DYS19-13 allele is associated with Q-M3 chromosomes, while in Sub-Saharan Africans they are associated to alleles with 15 or more repeats (Ruíz-Linares *et al.*, 1999; Bravi *et al.*, 2000). However, rather than any direct migration from North Africa to America, these data reveal the importance of the Berber male contribution to the formation of the Canarian population and/or of Berber Y-chromosome introgression between the VII and XV centuries, during the Muslim occupation of the Iberian Peninsula (Bortolini *et al.*, 2003). Table IV shows that about 5% and 15% of haplotypes associated with P-M45 in San Antonio and San Diego, respectively, and 15% and 16% of haplotypes identified with the Null haplogroup in San Diego and Hoyo de La Cumbre, respectively, are not shared with Spain, Gran Canaria and/or Berber populations. A distinct European and/or a low Sub-Saharan African male influence can be suggested to explain these findings.

The results presented, as a whole, suggest that the Sub-Saharan African and Amerind contributions to the three Venezuelan populations considered seem to have been introduced mainly by females, although of course, the introduction of non-Y alleles through the males cannot be excluded.

The predominantly European origin of Y-chromosomes has also been reported for other areas of America, like Antioquia in Colombia (Carvajal-Carmona *et al.*, 2000), Northern Chile (Rocco *et al.*, 2002) and Brazil in general (Carvalho-Silva *et al.*, 2001), although regional differences occur due to the different processes of conquest carried out by the Spaniards and Portuguese.

In many American countries or in areas within them, populations were subjected to the phenomena of replacement of their cultural or morphological traits by European characteristics. They were named by Ribeiro (1970) as *transplanted peoples*. Here it is proposed

that the substitution of their Y-chromosomes be characterized as cases of *transplanted male genomes*.

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