Admixture Estimates for Caracas, Venezuela, Based on Autosomal, Y-Chromosome, and mtDNA Markers

Author(s): Helios Martínez, Alvaro Rodríguez-Larralde, Mary Helen Izaguirre, and Dinorah Castro De Guerra
Source: Human Biology, 79(2):201-213.
Published By: Wayne State University Press
DOI: http://dx.doi.org/10.1353/hub.2007.0032
URL: http://www.bioone.org/doi/full/10.1353/hub.2007.0032

Admixture Estimates for Caracas, Venezuela, Based on Autosomal, Y-Chromosome, and mtDNA Markers

HELIOS MARTÍNEZ,[1] ALVARO RODRÍGUEZ-LARRALDE,[1] MARY HELEN IZAGUIRRE,[1] AND DINORAH CASTRO DE GUERRA[1]

Abstract The present Venezuelan population is the product of admixture of Amerindians, Europeans, and Africans, a process that was not homogeneous throughout the country. Blood groups, short tandem repeats (STRs), mtDNA, and Y-chromosome markers have been used successfully in admixture studies, but few such studies have been conducted in Venezuela. In this study we aim to estimate the admixture components of samples from two different socioeconomic levels from Caracas, Venezuela's capital city, compare their differences, and infer sexual asymmetry in the European Amerindian union patterns. Gene frequencies for blood groups *ABO* and Rh (*CDE*) and for the STRs *VWA*, *F13A01*, and *FES/FPS* and mtDNA and Y-chromosome haplogroups were studied in a sample of 60 individuals living in Caracas, taken from a private clinic (high socioeconomic level), and 50 individuals, also living in Caracas, drawn from a public maternity clinic (low socioeconomic level). The admixture analysis for the five autosomal markers gives a high European component (0.78) and an almost negligible African sub-Saharan component (0.06) for the high socioeconomic level, whereas for the low socioeconomic level the sub-Saharan, European, and Amerindian components were 0.21, 0.42, and 0.36, respectively. Estimates of admixture based on mtDNA and Y-chromosome markers reveal that the Amerindian contribution to these Caracas samples is almost entirely through females, because the Y-chromosome Amerindian and African sub-Saharan chromosomes found in this study were scarce. Our study reveals that the identification of the grandparents' geographic origin is an important methodological aspect to take into account in genetic studies related to the reconstruction of historical events.

The present Venezuelan population is the product of crosses between Amerindians, Europeans, mostly Spaniards, and Africans, who entered into contact five centuries ago and then interacted and mixed. Spaniards have been coming to Venezuela continuously since the conquest, and during the last century other Europeans, mainly

[1]Laboratorio de Genética Humana, Instituto Venezolano de Investigaciones Científicas, Apdo. 21827, Caracas 1020-A, Venezuela.

Human Biology, April 2007, v. 79, no. 2, pp. 201–213.

KEY WORDS: ABO, RH, STRS, *FES/FPS*, *VWA*, *F13A01,* MTDNA, Y-CHROMOSOME MARKERS, *YAP, DYS287*, *SY81, DYS271, 92R7*, *DYS199,* GENE FREQUENCIES, ADMIXTURE, GENETIC DISTANCE, VENEZUELA.

Italians and Portuguese, have also contributed to the Venezuelan gene pool. African migration, mainly from the sub-Saharan region, was limited to the 16th, 17th, and 18th centuries, the period in which slave trade was most active. Caracas, the capital of Venezuela, was founded in 1567 and has been an important economic pole of attraction for inhabitants from the entire country and from abroad, but the admixture process within Caracas has been heterogeneous throughout the different socioeconomic levels. During the 17th century, Spanish founders and their descendants had a privileged position and kept the political domain of the city while the natives lived in the suburbs and the Africans were slaves or domestic servants (Acosta Saignes 1967). However, Spanish people of Canarian origin have also been reported as living in the suburbs (Cunill Grau 1987). During the 18th century, interethnic crossing was evident, and the *pardos*, the product of these crosses for several generations, joined the natives on the outskirts of Caracas. At the beginning of the 20th century, oil production caused a massive national immigration to the city, which had a strong influence on the socioeconomic distribution of its inhabitants; the poorer showed a tendency to settle in the western section of Caracas, and the wealthier migrants settled in the eastern section. During the 1940s and 1950s, after World War II, Spaniards, Italians, and Portuguese arrived in Caracas; most of them engaged in commercial activities. Immigration from South America, mainly from Colombia, was also important during the 1970s. Thus the population of Caracas has become strongly stratified, with evident genetic and cultural admixture.

As part of a project related to the genetic structure of the Venezuelan population, we decided to estimate admixture in samples from Caracas's low and high socioeconomic levels and to evaluate their differences, using the ABO and Rh (CDE) blood groups and three autosomal short tandem repeat (STR) sequences (*FES/FPS*, *VWA*, *F13A01*). Y-chromosome and mtDNA haplogroups were also studied to detect any sexual asymmetry in the admixture process, as observed in other Latin American populations (Alves-Silva et al. 2000; Carvajal-Carmona et al. 2000; Martínez-Marignac et al. 2004; Sans 2000).

Materials and Methods

Caracas is localized in the north-central part of Venezuela, at 10° 30′ N and 66° 60′ W, with a population of 2,758,917 inhabitants in 2001 (Instituto Nacional de Estadística 2002).

Blood samples from 50 and 60 unrelated individuals up to second degree, living in Caracas, were selected in 2002 from the blood bank of the main public maternity clinic of the city (low socioeconomic level) and from the blood bank of the private clinic El Avila (high socioeconomic level), respectively. An informed consent form, approved by the Bioethics Committee of the Instituto Venezolano de Investigaciones Científicas, was signed by each individual. Socioeconomic level was measured according to Graffar's (1956) method, modified for the Venezuelan population by Mendez Castellanos and de Mendez (1994). The method takes into account four variables: profession of the head of the family, level of instruction at-

tained by the mother, main source of family income, and general conditions of the household. This method is widely used in Venezuelan social studies.

Blood samples were collected by venipuncture into tubes containing EDTA. The samples were stored at 5°C and brought to our laboratory packed in ice within three days after collection, where ABO and Rh (*CDE*) were typed based on standard immunological procedures.

DNA was extracted (Debomoy and Nurnberger 1991) and stored in alcohol until used. The microsatellites *FES/FPS*, *VWA*, and *F13A01* were amplified using a multiplex system according to the manufacturer's recommendations, using the Gene Print STR systems (Promega Corp., Madison, Wisconsin) in a MiniCycler thermocycler (M. J. Research, Waltham, Massachusetts). The PCR products were typed using vertical electrophoresis on denaturing polyacrylamide gels and silver staining.

mtDNA haplogroups were defined using the following restriction enzymes: +663 *Hae*III, +2349 *Dpn*II, +3592 *Hpa*I, –5176 *Alu*I, –7025 *Alu*I, –8616 *Dpn*II, +10394 *Dde*I, –13259 *Hin*cII, and the 9-bp deletion in the intragenic region COII/tRNA^{Lys}. These restriction enzymes allow the identification of continent-specific haplogroups: Amerindian haplogroups (A, B, C, and D), the main European (H) and sub-Saharan African haplogroups (L1 + L2, L3d, and L3e), and other haplogroups (I, J, K, T, U, V, W, X), which are also indicative of European ancestry (Table 1). Primers were synthesized according to the method of Torroni et al. (1995), Bailliet et al. (1994), and Toro-Labrador et al. (2003), and the amplification products were digested with the corresponding enzymes (New England BioLabs, Ipswich, Massachusetts). Y-chromosome haplogroups were defined with the use of four biallelic markers: *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). These markers allow the identification of North African and sub-Saharan African haplogroups D1-E* and E3a*, respectively; the Amerindian haplogroup Q3*, the European haplogroup P*, and the ancestral haplogroup Y*. Haplogroup nomenclature is as recommended by the Y-Chromosome Consortium (available at http://ycc.biosci.arizona.edu/nomenclature_system/frontpage.html).

The PCR products and digestions were typed using vertical electrophoresis on polyacrylamide gels and silver staining.

Statistical Analysis. Allele frequencies for *ABO* and Rh blood groups were estimated using the MAXLIK program, which is based on a maximum-likelihood approach (Reed and Schull 1968), and Hardy-Weinberg equilibrium was studied with the same program, using a chi-square test.

Allele frequencies for the three STRs were estimated through direct counting, and Hardy-Weinberg equilibrium was tested using likelihood ratio methods. The significance of this ratio was ascertained by generating empirical distributions using Monte Carlo procedures.

Frequencies for mtDNA and Y-chromosome haplogroups were also estimated using the counting method. The ethnic degree of admixture for autosomal and Y-chromosome markers was estimated with a least-squares method (Long

Table 1. Mitochondrial Haplogroup Origin and Specific Markers

Haplogroup	*Origin*	*Specific Markers*
mtDNA haplogroups		
A	Amerindian	–10394 *Dde*I, +663 *Hae*III
B	Amerindian	–10394 *Dde*I, 9-bp deletion, Region V
C	Amerindian	+10394 *Dde*I, –13259 *Hin*cII
D	Amerindian	+10394 *Dde*I, –5176 *Alu*I
H	European	–10394 *Dde*I, –7025 *Alu*I
L1 + L2	Sub-Saharan African	+10394 *Alu*I, +3592 *Hpa*I
L3e	Sub-Saharan African	+10394 *Dde*I, –3592 *Hpa*I, +2349 *Dpn*II
L3d	Sub-Saharan African	+10394 *Dde*I, –3592 *Hpa*I, –8616 *Dpn*II
T, U, V, W, X	European	–10394 *Dde*I, +7025 *Alu*I, –663 *Hae*III, no 9-bp deletion
I, J, K	European	+10394 *Dde*I, –3592 *Hpa*I, –2349 *Dpn*II, +5176 *Alu*I, +8616 *Dpn*II, +13259 *Hin*cII
Y-chromosome haplogroups		
P*	European	(–) YAP, *92R7*T*, *DYS199*C*
Y*	Ancestral	(–) YAP, *92R7*C*
Q3*	Amerindian	(–) YAP, *92R7*T*, *DYS199*T*
D1-E*	North African	(+) YAP, *DYS271*A*
E3a*	Sub-Saharan African	(+) YAP, *DYS271*G*

1991), using the Admix program. For this analysis the frequencies of the parental populations (Spanish, sub-Saharan African, and Amerindian) were built as the weighted mean by sample size of several populations. Table 2 gives the populations used and the corresponding references to build the parental frequencies for each genetic marker. Because the African slaves that came to the South American continent originated from the sub-Saharan region, our aim in the admixture analysis was to estimate the contribution of Africans from this region to the Venezuelan gene pool. Thus the frequencies of the parental African population used by us and the haplogroups identified as Africans in our samples are from sub-Saharan Africa. Admixture estimates for mtDNA were obtained by direct counting of the continent-specific haplogroups.

Results

Phenotype frequencies of blood groups *ABO* and Rh were found to be in Hardy-Weinberg equilibrium for both samples, with a p value higher than 0.50. Allele frequencies and their standard errors for these markers are given in Table 3. Allele *ABO*O*, which is monomorphic in Amerindians, has a higher frequency (0.800) in the low socioeconomic level, whereas allele *ABO*A*, which has high frequencies in Spain, is higher in the high socioeconomic level, suggesting a higher Amerindian contribution in the public maternity clinic sample and a higher European contribution in the sample from the private clinic. Haplotype *cDe*, an African marker, is higher in the public maternity clinic sample.

Table 2. Samples Used to Obtain the Frequencies of the Parental Populations for Each Genetic System

System	*Spanish*	*Sub-Saharan African*	*Amerindian*
ABO and Rh	Andalucia, Aragon, Castilla, Cataluña (Castellano Arroyo and Martínez Jarreta 1991); Canary Islands (Pinto et al. 1996)	Ghana, Nigeria, Senegal, Costa de Marfil (Mourant et al. 1976)	Panare, Maquiritare, Pemon (Mourant et al. 1976)
VWA	Central and northern Spain (Martin et al. 1995)	Bamileke, Ewondo, Sanga (Destro-Bisol et al. 2000); Príncipe and São Tomé (Gusmao et al. 2001); Bubi (Gené et al. 2001)	Wichi (Sala et al. 1998); Haichol and Tarahumara (Rangel-Villalobos et al. 2000)
FES/FPS and *F13A01*	Central and northern Spain (Martin et al. 1995)	Bamileke, Ewondo, Sanga (Destro-Bisol et al. 2000); Príncipe and São Tomé (Gusmao et al. 2001)	Wichi (Sala et al. 1998); Amerindians (Perez-Lezaun et al. 1997)
Y chromosome	Spain and Gran Canaria (Bortolini et al. 2004)	West Africa (Carvajal-Carmona et al. 2000)	Venezuelan Amerindians (Bortolini et al. 2002)

Table 3. Allele Frequencies ± Standard Error for Blood Groups *ABO* and Rh in the Private Clinic and the Public Maternity Clinic

Allele	*Private Clinic*	*Public Maternity Clinic*
ABO		
**A*	0.205 ± 0.039	0.117 ± 0.033
**B*	0.088 ± 0.026	0.084 ± 0.028
**O*	0.707 ± 0.044	0.800 ± 0.041
n[a]	120	100
Rh		
CDE	0.012 ± 0.0120	0.000 ± 0.0001
CDe	0.435 ± 0.053	0.440 ± 0.050
CdE	0.000 ± 0.0001	0.000 ± 0.0001
Cde	0.045 ± 0.0033	0.000 ± 0.0001
cDE	0.180 ± 0.036	0.200 ± 0.0040
cDe	0.073 ± 0.041	0.132 ± 0.058
cdE	0.000 ± 0.0001	0.000 ± 0.0001
cde	0.256 ± 0.053	0.228 ± 0.063
n[a]	120	100

a. Number of chromosomes.

Table 4. Allele Frequencies, Number of Chromosomes Studied, and Probability of Adjustment to Hardy-Weinberg Equilibrium for Genetic Systems *VWA*, *FES/FPS*, and *F13A01* in the Private Clinic and in the Public Maternity Clinic

VWA			*FES/FPS*			*F13A01*		
Allele	*Private Clinic*	*Public Clinic*	*Allele*	*Private Clinic*	*Public Clinic*	*Allele*	*Private Clinic*	*Public Clinic*
11	0.008	–	7	–	0.022	3.2	0.102	0.170
14	0.067	0.050	8	0.009	0.056	4	0.068	0.075
15	0.083	0.120	9	–	0.033	5	0.144	0.277
16	0.267	0.360	10	0.375	0.233	6	0.322	0.106
17	0.333	0.270	11	0.357	0.433	7	0.314	0.298
18	0.150	0.130	12	0.214	0.178	8	0.025	0.021
19	0.083	0.060	13	0.027	0.022	11	–	0.021
20	0.008	0.010	14	0.018	0.022	12	0.009	–
						13	0.009	–
						15	–	0.011
						16	0.009	0.021
n[a]	120	100		112	90		118	94
H-W[b]	0.787	0.267		0.516	0.031		0.368	0.342

a. Number of chromosomes.

b. Probability of adjustment to Hardy-Weinberg equilibrium.

Table 5. Frequency ± Standard Error of mtDNA Haplogroups in the Private Clinic and in the Public Maternity Clinic

Haplogroup	*Ethnic Origin*	*Private Clinic, N (Frequency* ± SE)	*Public Maternity Clinic, N (Frequency* ± SE)
A	Amerindian	12 (0.235 ± 0.059)	19 (0.380 ± 0.069)
B	Amerindian	1 (0.020 ± 0.02)	8 (0.160 ± 0.052)
C	Amerindian	6 (0.118 ± 0.045)	7 (0.140 ± 0.049)
D	Amerindian	3 (0.059 ± 0.033)	2 (0.040 ± 0.028)
L1 + L 2	Sub-Saharan African	2 (0.039 ± 0.027)	4 (0.080 ± 0.038)
L3e	Sub-Saharan African	2 (0.039 ± 0.027)	3 (0.060 ± 0.034)
H	European	7 (0.137 ± 0.048)	3 (0.060 ± 0.034)
I, J, K	European	9 (0.176 ± 0.053)	3 (0.060 ± 0.034)
T, U, V, W, X	European	9 (0.176 ± 0.053)	1 (0.020 ± 0.02)
Total *N*		51	50

In Table 4 we find the allele frequencies of the STRs for the high and low socioeconomic levels, respectively, as well as the number of chromosomes studied and the probability of adjustment to Hardy-Weinberg equilibrium. The number of different alleles varies from 9 for *F13A01* in both samples to 6 for *FES/FPS* in the private clinic, whereas the number of different alleles is 8 at the maternity clinic. The highest unbiased heterozygosity was shown by *VWA* in the private clinic sample and by *F13A01* in the public maternity clinic sample. Genotype frequencies for all markers were in Hardy-Weinberg equilibrium, except for *FES/FPS* in the public maternity clinic sample, where the probability of adjustment was 0.031, probably because of allele 14, which appears in only one homozygous individual.

Table 5 gives the mtDNA haplogroup distribution. For both samples the most frequent haplogroup is A, which has an Amerindian origin. Strangely, the most frequent haplogroup in Europe (H) is not the most frequent haplogroup in either of the Caracas samples. Haplogroups of African origin, represented by L1 + L2, L3d, and L3e, are scarce or absent, although with a slightly higher frequency in the public maternity clinic sample. Haplogroup L3d was absent in both samples.

Haplogroups of the Y chromosome are given in Table 6. Haplogroup P*, of European origin, is the most frequent in both samples. The Amerindian haplogroup Q3* is absent in the private clinic sample, and only two individuals with this haplogroup were found in the public maternity clinic sample.

Admixture estimates based on the five autosomal systems and the mtDNA and Y-chromosome haplogroups are given in Table 7. Different tendencies can be observed. Regarding the autosomal markers, the highest ethnic component in the private clinic sample is the Spanish (0.75), followed by the Amerindian and a small sub-Saharan component (0.168 and 0.082, respectively). On the other hand, the Amerindian and sub-Saharan components have high contributions in the public maternity clinic sample (0.397 and 0.275, respectively), and the Spanish component (0.328) is less than half of that observed in the private clinic sample. For the

Table 6. Frequency ± Standard Error of Y-Chromosome Haplogroups in the Private Clinic and in the Public Maternity Clinic

	*P**	*Y**	*D1-E**	*E3a**	*Q3**	*Total*
Private clinic, *N* (frequency ± SE)	15 (0.518 ± 0.093)	9 (0.31 ± 0.086)	4 (0.138 ± 0.064)	1 (0.034 ± 0.034)	0 (0)	29
Public maternity clinic, *N* (frequency ± SE)	18 (0.622 ± 0.09)	6 (0.207 ± 0.075)	1 (0.034 ± 0.034)	2 (0.068 ± 0.047)	2 (0.068 ± 0.047)	29

Table 7. Admixture Proportions ± Standard Errors with Autosomal, mtDNA, and Y-Chromosome Markers in the Private Clinic and in the Public Maternity Clinic

	Private Clinic			*Public Maternity Clinic*		
Contribution	*Autosomal*	*mtDNA*	*Y Chromosome*	*Autosomal*	*mtDNA*	*Y Chromosome*
Sub-Saharan	0.082 ± 0.045	0.078 ± 0.038	0.073 ± 0.089	0.275 ± 0.067	0.140 ± 0.049	0.097 ± 0.061
Spanish	0.750 ± 0.082	0.490 ± 0.07	0.927 ± 0.089	0.328 ± 0.089	0.140 ± 0.049	0.837 ± 0.072
Amerindian	0.168 ± 0.072	0.431 ± 0.069	0 ± 0.009	0.397 ± 0.075	0.720 ± 0.063	0.066 ± 0.042

mtDNA markers we observe a high Amerindian component in the public maternity clinic sample (0.72), followed by the European and African components (0.14 each), whereas in the private clinic sample the European component is the highest (0.49), closely followed by the Amerindian component (0.43). Regarding the Y chromosome, the estimates of admixture show a high European component in both samples, and the sub-Saharan and Amerindian components are small, with the Amerindian component being absent in the private clinic sample.

Discussion

In Caracas, as in most of Latin America, the continuous gene and cultural flow between the different groups during the last five centuries has given rise to the Mestizos or *criollos*. This is evident in the diversity of phenotypes observed in men and women of the city, a product of the European and African contribution to the native Amerindian population.

The conquest and colonization process was responsible for a drastic reduction in the native population that inhabited the region where Caracas was founded, and those who survived were confined to the *encomiendas*, Indian settlements established by the Spaniards for religious instruction. Caracas was founded in 1567, and there are references that by 1578, in addition to the Spanish founders, there were some natives working in domestic service, some black slaves, and some poor Spaniards (Guerra Cedeño 1996), evidence of the presence of social classes during the first decade of the city's existence.

During the 17th century the intense admixture process in Caracas was evident, and a new group, the *pardos*, appeared. The *pardos* were the product of crosses for several generations between Spaniards, Africans, Amerindians, and their descendants. The composition of Caracas's population at the beginning of the 19th century was 25% European, 30% African, 5% Amerindian, and 40% *pardos* (González de Rodríguez et al. 1967). By the beginning of the 20th century, the population of Caracas had decreased enormously as a result of wars and epidemics. This population decrease caused different governments to take concrete actions to populate the country. Thus immigration laws, such as those of 1831, 1837, and 1936, were dictated in order to colonize different regions of Venezuela with European populations (Berglund 1982; Cunill Grau 1987). These laws served as a framework for what is known as the first massive immigration in Venezuelan history, between 1948 and 1961, in which 800,000 foreigners, mostly from Spain, Italy, Portugal, and Central Europe, arrived in Venezuela. Most of these immigrants settled in new residential areas in Caracas and other cities. The natural growth experimented with by the Venezuelan population during the 1950s made it unnecessary to continue the immigration policies, but during the 1970s, because of political instability in Latin America and oil prosperity in Venezuela, important immigration from South America and the Caribbean occurred. In addition, internal migrations show a growing effect by the mid 1920s. In 1920, 96% of the population resided in their

place of birth. By 1936 the urban population represented 34.7% of the total, and this changed to 77% in 1971 (Suárez and Torrealba 1979).

These demographic phenomena have made Caracas a stratified city with important evidence of admixture, historical events that help to explain our results. Estimation of admixture through biparental markers shows that an evident genetic structure resulting from socioeconomic differences is present in Caracas: The high socioeconomic level is similar to Latin American cities of typical European descent, such as Montevideo and Buenos Aires (Avena et al. 2001; Sans 2000), and the low socioeconomic level is more admixed, with the Amerindian contribution being slightly higher than that of Europeans and the European contribution being higher than the sub-Saharan African contribution.

Greater differences between the estimates of the parental contributions are observed with uniparental markers than with biparental markers. Thus admixture estimates obtained with mtDNA show the same tendency as discussed earlier, but the Amerindian contribution is much higher: 43% and 72% in the high and low socioeconomic levels, respectively. On the other hand, the Y chromosome has almost an entirely European contribution (92%), with a null Amerindian component and 8% sub-Saharan contribution in the high socioeconomic level. At the low socioeconomic level the European component is also the most important (84%), followed by a 9% sub-Saharan component and a small 7% Amerindian contribution.

Despite the small sample size, particularly for the Y chromosome, our results are in concordance with tendencies observed in other Latin American countries in relation to an important sexual asymmetry, with a prevalence of Amerindian mtDNA haplogroups and of European Y-chromosome haplogroups.

The European contribution to Caracas's gene pool seems to have been an ongoing process, mainly through the male line, as suggested by the Y-chromosome haplogroups. In relation to this, historical evidence speaks of an important decrease in the male population by the end of the 19th century as a result of independence and civil wars. By 1873 the population of Caracas was 56% female (Guerra Cedeño 1996). For that year, 58.6% of the foreign population living in the city was male, suggesting a slow process of both substitution of native Y chromosomes by the Europeans, as reported previously (Castro de Guerra et al. 2003), and dilution of the native component at the biparental level through a recombination process. On the other hand, the relatively high female Amerindian component observed in both samples suggests that the original gene contribution from native women during the conquest, because of the scarcity of European females, is still present in the population of Caracas. Thus the Amerindian contribution to the Venezuelan population is almost entirely through females, because the Amerindian Y-chromosomes are scarce.

Interviews conducted with the blood donors of this study reveal that close to 40% of the grandparents at the private clinic were born in Europe and the rest are from Venezuela, mainly Caracas. In the public maternity clinic, close to 90% of grandparents were born in Venezuela, mainly from the interior of the country. Thus admixture estimates for the high socioeconomic level reflect recent European mi-

grations, mainly after World War II. Many of these migrants, mostly Spaniards, Italians, and Portuguese, helped to develop economic activities related to commerce and construction, activities that rapidly introduced them to the high socioeconomic level. On the other hand, most of those individuals at the low socioeconomic level are a consequence of rural-urban internal migration; they seem to be more representative of the traditional Venezuelan population. This reveals that the identification of the grandparents' geographic origin is an important methodological aspect to take into account in genetic studies related to the reconstruction of historical events. Our study indicates that the results from the sample with most grandparents born in Venezuela (i.e., the sample from the low socioeconomic level) are more in agreement with Venezuelan remote genetic history than results from the high socioeconomic level.

In this study we have shown the advantages of studying admixture processes through markers with different types of inheritance, biparental and uniparental, because the information obtained gives a more complete view of the genetic process of constitution of the population under study. The differences between the results in the two socioeconomic levels reveal that these levels can differ according to the sample selection criteria used, and interpretations of the genetic history of the population may vary. It is thus important to know the origins of the sample under study and to have adequate selection criteria to allow for a solid historical interpretation of the results.

Acknowledgments We thank all the individuals who volunteered to participate in this study. We also thank Aixa Müller, of the private clinic El Avila, and Concepción Martínez, of the public maternity clinic Concepción Palacios, and the personnel of the blood banks from both institutions for allowing us to use their equipment and for their help taking the blood samples. We thank FUNDACREDESA for the information regarding Graffar's modified method. Marina Florez, Luis Jose Diaz, and Neida Gonzalez assisted in the laboratory work and data manipulation. Eleonora Garcia-Larralde revised the English. This work was partially supported by FONACIT (Venezuela) through project PI-200001829.

Received 16 May 2006; revision received 16 November 2006.

Literature Cited

Acosta Saignes, M. 1967. *La vida de los esclavos negros en Venezuela.* Caracas, Venezuela: Ediciones Hespérides.

Alves-Silva, J., M. S. Santos, P. E. M. Guimaraes et al. 2000. The ancestry of Brazilian mtDNA lineages. *Am. J. Hum. Genet.* 67:444–461.

Avena, S., A. Goicoechea, J. Dugoujon et al. 2001. Estimación de los aportes europeo, indígena y africano en poblaciones cosmopolitas de Buenos Aires a partir de la determinación de los sistemas *GM* y *KM*. In *Antropología y Biodiversidad,* P. Luja, A. Malgosa, and R. Nogués, eds. Bellaterra, Spain: Edicions Bellaterra, 41–47.

Bailliet, G., F. Rothhammer, F. Carnese et al. 1994. Founder mitochondrial haplotypes in Amerindian populations. *Am. J. Hum. Genet.* 54:27–33.

Berglund, S. 1982. Las bases sociales y económicas de las leyes de inmigración venezolanas, 1831–1935. *Bol. Acad. Nac. Hist. Caracas* 65(260):951–962.

Bortolini, M. C., F. M. Salzano, C. Bau et al. 2002. Y-chromosome polymorphisms and Native American population structure. *Ann. Hum. Genet.* 66:255–259.

Bortolini, M. C., M. Thomas, L. Chikhi et al. 2004. Ribeiro's typology, genomes, and Spanish colonialism, as viewed from Gran Canaria and Colombia. *Genet. Mol. Biol.* 27:1–8.

Carvajal-Carmona, L. G., I. D. Soto, N. Pineda et al. 2000. Strong Amerind/White sex bias and a possible Sephardic contribution among the founders of a population in northwest Colombia. *Am. J. Hum. Genet.* 67:1287–1295.

Castellano Arroyo, M., and M. Martínez Jarreta. 1991. *Distribución de frecuencias de marcadores genéticos moleculares en la población española.* Zaragoza, Spain: Edicions Consejo Asesor de Investigación (CONAI) de la Diputación General de Aragón, Cooperativa de Artes Gráficas Librería General.

Castro de Guerra, D., E. Arroyo, F. M. Salzano et al. 2003. Transplanted male genomes in three Venezuelan populations. *Interciencia* 28:197–201.

Cunill Grau, P. 1987. *Geografía del poblamiento venezolano en el siglo XIX.* Caracas, Venezuela: Ediciones de la Presidencia de la República.

Debomoy, L., and J. Nurnberger Jr. 1991. A rapid nonenzymatic method for the preparation of HMW DNA from blood for RFLP studies. *Nucleic Acids Res.* 19:5444.

Destro-Bisol, G., I. Boschi, A. Caglia et al. 2000. Microsatellite variation in Central Africa: An analysis of intrapopulational and interpopulational genetic diversity. *Am. J. Phys. Anthropol.* 112:319–337.

Gené, M., P. Moreno, N. Borrego et al. 2001. The Bubi population of Equatorial Guinea characterized by *HUMTH01*, *HUMVWA31A*, *HUMCSF1PO*, *HUMTPOX*, *D3S1358*, *D8S1179*, *D18S51*, and *D19S253* STR polymorphisms. *Int. J. Legal Med.* 114:298–300.

González de Rodríguez, M. E., L. C. Rodríguez, and G. Carrera Damas. 1967. Principales momentos del desarrollo histórico de Caracas. In *Estudio de Caracas: Historia, tecnología, economía y trabajo.* Caracas, Venezuela: Ediciones de la Biblioteca, Universidad Central de Venezuela, v. 2, bk. 1, 33–102.

Graffar, M. 1956. Une methode de classification sociales d'echantillons de population. *Courrier* 6:445–459.

Guerra Cedeño, F. 1996. Perfil histórico-antropológico de la población urbana de Caracas. In *Polimorfismo génico HLA en poblaciones hispanoamericanas,* A. Martín Municio and A. García Barrero, eds. Madrid, Spain: Real Academia de Ciencias Exactas, Físicas y Naturales, 129–147.

Gusmao, L., M. J. Prata, C. Miranda et al. 2001. STR data from S. Tomé e Príncipe (Gulf of Guinea, West Africa). *Forensic Sci. Int.* 116:53–54.

Hammer, M. F., and S. Horai. 1995. Y-chromosome DNA variation and the peopling of Japan. *Am. J. Hum. Genet.* 56:951–962.

Hurles, M. E., R. Veitia, E. Arroyo et al. 1999. Recent male-mediated gene flow over a linguistic barrier in Iberia, suggested by analysis of a Y-chromosomal DNA polymorphism. *Am. J. Hum. Genet.* 64:817–831.

Instituto Nacional de Estadística. 2002. *2001 Census.* Available at http://www.ine.gov.ve/censo/censo.htm

Long, J. C. 1991. The genetic structure of admixed populations. *Genetics* 127:417–428.

Martin, P., A. Alonso, B. Bruce et al. 1995. Spanish population data on 7 tetrameric short tandem repeat loci. *Int. J. Legal Med.* 108:145–149.

Martínez-Marignac, V., B. Bertoni, E. Parra et al. 2004. Characterization of admixture in an urban sample from Buenos Aires, Argentina, using uniparentally and biparentally inherited genetic markers. *Hum. Biol.* 76:543–557.

Mendez Castellanos, H., and M. C. de Mendez. 1994. *Sociedad y Estratificación.* Caracas, Venezuela: FUNDACREDESA.

Mourant, A. E., A. C. Kopec, and K. Domaniewska-Sobczack. 1976. *The Distribution of the Human Blood Groups.* New York: Oxford University Press.

Perez-Lezaun, A., F. Calafell, E. Mateu et al. 1997. Allele frequencies for 20 microsatellites in a world-wide population survey. *Hum. Hered.* 47:189–196.

Pinto, F., J. C. Rando, M. López et al. 1996. Blood group polymorphisms in the Canary Islands. *Gene Geogr.* 10:171–179.

Rangel-Villalobos, H., F. Rivas, L. Sandoval et al. 2000. Genetic variation among four Mexican populations (Huichol, Purepecha, Tarahumara, and Mestizo) revealed by two VNTRs and four STRs. *Hum. Biol.* 72:983–995.

Reed, T. E., and W. J. Schull. 1968. A general maximum likelihood method estimation program. *Am. J. Hum. Genet.* 20:579–580.

Sala, A., G. Penacino, and D. Corach. 1998. Comparisons of allele frequencies of eight loci from Argentinian Amerindian and European populations. *Hum. Biol.* 70:937–947.

Sans, M. 2000. Admixture studies in Latin America: From the 20th to the 21st century. *Hum. Biol.* 72:155–177.

Seielstad, M. T., J. M. Hebert, A. A. Lin et al. 1994. Construction of human-chromosome haplotypes using a new polymorphic A to G transition. *Hum. Mol. Genet.* 3:2159–2161.

Suárez, M. M., and R. Torrealba. 1979. Internal migration in Venezuela. *Urban Anthropol.* 8:291–311.

Toro-Labrador, G., O. Wever, and J. C. Martínez-Cruzado. 2003. Mitochondrial DNA analysis in Aruba: Strong maternal ancestry of closely related Amerindians and implications for the peopling of northwestern Venezuela. *Carib. J. Sci.* 39:11–22.

Torroni, A., M. Brown, M. Lott et al. 1995. African, Native American, and European mitochondrial DNAs in Cubans from Pinar del Rio Province and implications for recent epidemic neuropathy in Cuba. *Hum. Mutat.* 5:310–317.

Underhill, P. A., L. Jin, R. Zemans et al. 1996. A pre-Columbian Y-chromosome-specific transition and its implications for human evolutionary history. *Proc. Natl. Acad. Sci. USA* 93:196–200.