Ribeiro’s typology, genomes, and Spanish colonialism, as viewed from Gran Canaria and Colombia

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Abstract

Four biallelic and six multiallelic Y-chromosome polymorphisms were investigated in 59 Gran Canarian, 60 North African Berber and 46 Spanish subjects. These new data were merged with equivalent literature information to obtain the parental Y-chromosomal contribution in Gran Canarians, Colombians, and Venezuelans. The results were then compared, for Gran Canarians and Colombians, to those derived from autosomal and mtDNA. In both groups, the Spanish Y-chromosome contribution was much more marked than that estimated using mtDNA. This analysis showed a usual trend in the Spanish Colonial history, characterized by a demographic collapse of the aboriginal population, but with considerable introgression of genes through native women. In accordance to D. Ribeiro’s typology for peoples subjected to Colonialism, the Y-chromosomes of these admixed populations are classified as transplanted, their mtDNA as witness, and their autosome sets as new.

Key words: Gran Canaria, Y-chromosome polymorphisms, admixture.

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Introduction

The great adventure of the maritime colonial expansion promoted by Europeans during the 15th and 16th centuries considerably changed their history and that of the other continents. The socio-cultural impact of this event has already been determined, but only more recently have the genetic aspects related to it been evaluated (Salzano and Bortolini, 2002). Present-day American populations which are directly related to this relatively recent historical event can be classified, according to Ribeiro (1970, 1977) as witness, new, transplanted and emergent peoples. Recently, we coined the expression transplanted male genome for the event of substitution of native Y-chromosomes in South America (Castro-de-Guerra et al., 2003).

The Canarian archipelago is located in the Atlantic Ocean off the southern coast of Morocco and comprises seven islands: El Hierro, La Palma, La Gomera, Fuerteventura, Lanzarote and the main islands of Tenerife and Gran Canaria. The first inhabitants of these islands arrived around the middle of the second millennium BC, and anthropological studies indicate a close relationship between these early colonizers and the North African Berbers, although this aboriginal population was probably not a homogeneous group (Murdock, 1959; Schwidetzky, 1963; Velasco-Vásquez et al., 1999; Flores et al., 2003). Although the Greeks and Romans explored the Canary Islands (giving them that name), it was not until the 15th century that the archipelago was settled by Europeans, when it was incorporated into the expanding Spanish Empire. Following the colonial settlement, the native population of the Islands (known as Guanche) declined from an estimated 60,000 at the time of first contact to complete extinction in our days (Fernandez-Armesto, 1982).

Despite the disappearance of the Guanche, genetic studies indicate that the population of the Canarian archipelago shows evidence of North African admixture, which most likely reflects intermarriage between natives and immigrants early in the colonial period (Esteban et al., 1998). Classical markers (blood groups and proteins) suggest that the genetic background of the current Canary Islanders as a whole is about 71% Spanish, 21% North African, and 8% Sub-Saharan African (Flores et al., 2001). Studies of the maternally inherited mitochondrial DNA (mtDNA) and paternal Y-chromosome markers indicate a considerably smaller and higher Spanish contribution, respectively
Period, the Spanish forcibly introduced some 25,000 indi- 
with African slaves, considering that, during the colonial 
Saharan African ancestry most likely reflects admixture 
mating pattern after the European occupation. The Sub-

Sub-Saharan African; Underhill 

Verde and the Canarian Islands (European, North African Berber and 
frequency differentials in the putative parental populations 

Subjects and Methods 

Populations studied 

Blood samples or oral swabs were collected from un-
related voluntary men from the Island of Gran Canaria (Las 
Palmas, N = 59), mainland Spain (Barcelona, N = 24; Va-
lença, N = 22) and from Moroccan Berbers (Ifani ethnic 
group, N = 60). The individuals from Barcelona had no 
Catalonian ancestry, but rather originated in various Span-
ish regions. Genomic DNA was extracted using the Nu-
cleon extraction kit according to the manufacturer’s 

DNA markers typed 

The strategy adopted for assessing the male ancestry 
of our Gran Canarian sample was to contrast results for 
biallelic and multiallelic markers. This should allow an ap-
proximation to the effect of marker polymorphism on the 
estimation of admixture. Y-chromosome haplogroups were 
deﬁned by typing the following biallelic or SNP (single nu-
cleotide polymorphism) markers: DYS271 (Hammer and 
Horai, 1995), DYS287 (Seielstad et al., 1994), M9 
(Underhill et al., 1997), and 92R7 (Hurles et al., 1998). 
These SNPs were selected based on their important allele 
frequency differentials in the putative parental populations 
of the Canary Islands (European, North African Berber and 
Sub-Saharan African; Underhill et al. 2000, 2001), thus po-
tentially being the most informative biallelic markers for 
assessing ethnic ancestry on the island. The aim was not to 
establish a ﬁne-grained SNP-Y-chromosome phylogeny, 
but rather to apportion the diversity observed on Gran 
Canaria into its three major possible ancestral lineages. 

Multiallelic marker data were obtained by typing micro-
satellites DYS19, DYS388, DYS390, DYS391, DYS392, 
and DYS393. This set of markers has been used in numer-
ous other studies (Thomas et al., 2000; Carvajal-Carmona 
et al., 2000; Bortolini et al., 2003; Kayser et al., 2003), and 
speciﬁcally DYS19 and DYS393 had been tested in Cana-
rians by Flores et al. (2003). The other four markers 
(DYS19, DYS388, DYS390, and DYS392) were never in-
vestigated in a Canarian sample. They were typed using the 
experimental conditions reported by Thomas et al. (1999). 
Following common usage, we refer to biallelic lineages as 
haplogroups, to distinguish them from microsatellite mar-
er haplotypes. Haplogroup nomenclature is based on YCC 
(Y Chromosome Consortium, 2002) recommendations. 

Data analysis 

The ARLEQUIN 2000 computer package (Schneider 
et al., 2000) was employed to obtain the six-locus microsa-
tellite haplotype frequencies. Admixture was estimated by 
Long’s (1991) method, using the ADMIX program kindly 

Results and Discussion 

We grouped our Gran Canaria, Berber and Spanish 
data set (Appendix) with other information from the litera-
ture. Table 1 summarizes the frequency of Y-chromosome 
haplogroups in Gran Canarians and their presumed parental 
populations (Spanish, North African Berber and Sub-
Saharan African), as well as in two South American popu-
lations from areas of early Spanish colonial inﬂuence (Co-
lombia and Venezuela). The Native American group was 
also included, since it is a putative parental population of 
Colombians and Venezuelans. Haplogroup P-92R7 is 
a good indicator of Spanish ancestry, as it reaches a fre-
frequency of 80% in Spain, while it is rare in the other putative 
parental populations. Similarly, haplogroups DE-YAP*, 
E-M2 and Q-M3 are good indicators of North African Ber-
ber, Sub-Saharan African and Native American ancestry, as 
they reach frequencies of respectively 83%, 63% and 85% 
in those populations and low frequencies elsewhere. Haplo-
group Y* (ancestral to all SNP markers typed here) is less 
informative in that it has a largely uniform distribution 
across the parental populations compared, with the exclu-
sion of Native Americans. In Gran Canarian chromosomes, 
P-92R7* and DE-YAP* were found at frequencies of 62% 
and 17% respectively, while the frequency detected for 
E-M2 was low (1%), suggesting a negligible Sub-Saharan 
African contribution. Comparable frequencies were found 
in Colombia and Venezuela. 

Table 2 lists the six-locus microsatellite haplotypes 
detected in Gran Canarians, as well as in Spaniards and 
North African Berbers, grouped according to their biallelic 
lineage background. About 47% of the haplotypes, which 
represent 63% of the chromosomes seen in Gran Canarians, 
are present in Spanish or Berber subjects. None of the Gran
### Table 1 - Y-chromosome biallelic haplogroups and their frequency in Gran Canarians and other human populations.

| Population                      | SNP-Haplogroup | Frequency (%) |
|---------------------------------|----------------|---------------|
|                                 | P-92R7* Y* DE-YAP** E-M2 Q-M3 |               |
| Gran Canarians (N = 137)        | 62 20 17 1 NT |               |
| Colombians (N = 80)             | 58 33 4 4 1   |               |
| Venezuelans (N = 53)            | 65 26 9 0 0   |               |
| Spanish (N = 124)               | 80 15 5 0 NT  |               |
| North African Berbers (N = 104) | 2 11 83 4 NT  |               |
| Sub-Saharan Africans (N = 56)    | 0 12 25 63 NT |               |
| Native Americans (356)          | 11 2 1 1 85   |               |

1The samples include individuals typed by us (59 Canarians, 60 North African Berbers, and 46 Spanish) and data (78 Gran Canarians, 44 North African Berbers, and 78 Spanish) reported by Pérez-Lezaun et al. (1997), Bosch et al. (1999), and Flores et al. (2003).
2Samples collected in Medellín (Carvajal-Carmona et al., 2000).
3Samples obtained from individuals living in three small communities located near Caracas, basically founded by Spanish-Canarian families at the end of the seventeenth and nineteenth centuries (Castro-de-Guerra et al., 2003).
4The individuals could be classified as white (L. Carvajal-Carmona and D. Castro-de-Guerra, personal communication).
5Hammer et al. (1997).
6Bortolini et al. (2002).
7The DYS199-T mutation, which defines this haplogroup, was not tested in the Gran Canarian, African and European samples, but earlier results indicate that it is restricted to Amerindians and a few populations of northeast Siberia. To stress the testing differences, 0 was employed when the DYS199-T mutation was searched and not found, while NT (not tested) indicates that such tests had not been performed. The assumption of Q-M3 absence in the indicated groups, used for the present admixture study, is validated by analyses such as those performed by Underhill et al. (2000).

### Table 2 - Y-chromosome microsatellite haplotype frequencies in Spain, Gran Canaria and North African Berbers.

| Haplotype | Loci | Population |
|-----------|------|------------|
|           | 1 2 3 4 5 6 | Spain (124) Gran Canaria (59) Berbers (104) |

1The samples include individuals typed by us (59 Canarians, 60 North African Berbers, and 46 Spanish) and data (78 Gran Canarians, 44 North African Berbers, and 78 Spanish) reported by Pérez-Lezaun et al. (1997), Bosch et al. (1999), and Flores et al. (2003).
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| Haplotype | Loci | Population |
|-----------|------|------------|
| 1         | 2    | 3          | 4  | 5 | 6 |
| 28        | 15   | 12         | 23 | 11 | 13 | 14 | 0.008 |
| 29        | 14   | 13         | 24 | 11 | 13 | 13 | 0.008 |
| 30        | 15   | 12         | 22 | 9  | 11 | 13 | 0.008 |
| 31        | 15   | 12         | 24 | 11 | 13 | 12 | 0.008 |
| 32        | 14   | 12         | 24 | 11 | 14 | 13 | 0.008 |
| 33        | 12   | 13         | 24 | 11 | 13 | 13 | 0.008 |
| 34        | 13   | 12         | 23 | 11 | 13 | 14 | 0.008 |
| 35        | 14   | 12         | 24 | 11 | 13 | 14 | 0.034 |
| 36        | 14   | 12         | 22 | 11 | 13 | 13 | 0.034 |
| 37        | 16   | 9          | 24 | 11 | 13 | 13 | 0.017 |
| 38        | 15   | 12         | 23 | 10 | 13 | 13 | 0.017 |
| 39        | 14   | 12         | 26 | 11 | 13 | 12 | 0.017 |
| 40        | 14   | 14         | 24 | 10 | 13 | 13 | 0.017 |
| 41        | 16   | 12         | 24 | 10 | 11 | 14 | 0.017 |
| 42        | 13   | 12         | 24 | 11 | 13 | 13 | 0.017 |
| 43        | 14   | 12         | 24 | 10 | 13 | 14 | 0.017 |
| 44        | 14   | 12         | 24 | 9  | 12 | 13 | 0.017 |
| 45        | 14   | 12         | 25 | 11 | 14 | 13 | 0.017 |
| 46        | 14   | 12         | 23 | 11 | 14 | 13 | 0.017 |
| 47        | 15   | 12         | 25 | 10 | 11 | 13 | 0.010 |
| 48        | 16   | 12         | 25 | 11 | 13 | 13 | 0.010 |
| 49        | 13   | 12         | 23 | 10 | 11 | 14 | 0.010 |

Y* haplogroup

| Haplotype | Loci | Population |
|-----------|------|------------|
| 50        | 14   | 16         | 23 | 10 | 11 | 12 | 0.008 | 0.017 | 0.010 |
| 51        | 14   | 17         | 23 | 11 | 11 | 12 | 0.017 | 0.019 |
| 52        | 15   | 12         | 22 | 10 | 11 | 14 | 0.017 | 0.010 |
| 53        | 14   | 14         | 23 | 10 | 11 | 13 | 0.008 | 0.017 |
| 54        | 14   | 15         | 23 | 10 | 11 | 12 | 0.016 | 0.010 |
| 55        | 14   | 12         | 22 | 10 | 11 | 13 | 0.008 |
| 56        | 15   | 13         | 25 | 10 | 11 | 13 | 0.008 |
| 57        | 13   | 13         | 24 | 12 | 11 | 13 | 0.008 |
| 58        | 17   | 13         | 23 | 10 | 11 | 13 | 0.008 |
| 59        | 17   | 13         | 24 | 9  | 11 | 13 | 0.008 |
| 60        | 14   | 11         | 25 | 10 | 11 | 12 | 0.008 |
| 61        | 15   | 13         | 22 | 10 | 11 | 14 | 0.008 |
| 62        | 15   | 15         | 23 | 9  | 11 | 13 | 0.008 |
| 63        | 15   | 12         | 22 | 10 | 11 | 13 | 0.008 |
| 64        | 16   | 12         | 22 | 10 | 10 | 14 | 0.008 |
| 65        | 14   | 13         | 25 | 8  | 11 | 13 | 0.008 |
| 66        | 13   | 12         | 23 | 10 | 11 | 13 | 0.008 |
| 67        | 17   | 14         | 23 | 10 | 11 | 13 | 0.008 |
| 69        | 14   | 12         | 23 | 10 | 12 | 13 | 0.008 |
| 70        | 14   | 15         | 23 | 9  | 9  | 12 | 0.008 |
| 71        | 14   | 12         | 24 | 11 | 13 | 13 | 0.008 |
| 72        | 14   | 14         | 24 | 10 | 11 | 12 | 0.034 |
| 73        | 14   | 14         | 24 | 10 | 11 | 13 | 0.017 |
| 74        | 15   | 12         | 24 | 10 | 11 | 15 | 0.017 |
| 75        | 15   | 15         | 23 | 11 | 11 | 12 | 0.017 |
| 76        | 15   | 15         | 23 | 10 | 11 | 12 | 0.017 |
| 77        | 15   | 15         | 24 | 9  | 11 | 13 | 0.017 |
| 78        | 13   | 14         | 25 | 10 | 10 | 13 | 0.017 |
| 79        | 15   | 17         | 23 | 11 | 11 | 12 | 0.010 |
| 80        | 14   | 15         | 24 | 10 | 11 | 12 | 0.010 |
| 81        | 14   | 16         | 23 | 11 | 11 | 12 | 0.010 |
| 82        | 14   | 13         | 23 | 10 | 11 | 12 | 0.010 |
| 83        | 14   | 18         | 24 | 11 | 11 | 12 | 0.010 |
Canarian haplotypes shown in Table 2 is found in the available data for Sub-Saharan Africans (Jorde et al., 2000), which refers mostly to Bantu-speaking populations. Among the haplotypes classified as belonging to haplogroup P-92R7*, n. 1 is the most frequent in both Gran Canarian and Spanish individuals, whereas it was not observed in the Berber sample. This haplotype and its one-step derivatives represent 32% of the chromosomes typed in Gran Canarians, and 35% of the Spanish chromosomes, but no such chromosomes were found among the North African Berbers. Haplotype 84 and its one-step neighbors, on aggregate, have a frequency of 41% among North African Berbers, 14% in Gran Canarians, and 4% in Spaniards. In the Y* haplogroup, no haplotype presents a frequency higher than 3.5% in the three populations. However, a pair-wise comparison of haplotypes within this lineage revealed a cluster of one-step neighbors characterized by more than 14 repeat number alleles at locus DYS388. This group of haplotypes has a frequency of 4% in Spanish, 8% in Canarian, and 8% among the Berber subjects.

Our estimates of admixture were based on the information furnished in Table 2 and on the least squares ap-
proximation (Long, 1991). Due to the large number of microsatellite haplotypes identified, the data of Table 2 could not be used directly for this purpose. Instead, we defined ten categories of Y-haplotypes for this analysis. Two categories were defined from each of haplogroups P-92R7* and DE-YAP*, one including the modal haplotypes and their one-step neighbors, and another including all the other haplotypes detected in each haplogroup. In haplogroup Y* no modal haplotype was identified, however five haplotype clusters could be defined by grouping together one-step neighbors. Finally, the four chromosomes distinguished in haplogroup E-M2 were considered as a single category.

Combining our data with that reported in the literature (Pérez-Lezaun et al., 1997; Bosch et al., 1999; Jorde et al., 2000), we obtained the parental population Y-haplotypes frequencies to be used in the admixture analysis, using 10 haplotype groups defined as detailed above. Parental contributions in Gran Canarians are 82% ± 6% Spanish and 18% ± 6% Berber; a Sub-Saharan African contribution was not detectable. These values are of the same order of magnitude as those obtained in an earlier study carried out with the 16th century (Carvajal-Carmona, al., 2000), we obtained the parental population Y-haplotypes frequencies to be used in the admixture analysis, using 10 haplotype groups defined as detailed above. Parental contributions in Gran Canarians are 82% ± 6% Spanish and 18% ± 6% Berber; a Sub-Saharan African contribution was not detectable. These values are of the same order of magnitude as those obtained in an earlier study carried out with the 16th century (Carvajal-Carmona, 2000), using Long’s least square method.

Table 3 shows a compilation of admixture results, using bi and uniparental markers for Gran Canaria and Colombia, another population showing native-immigrant admixture as a result of the Spanish colonial expansion of the 16th century (Carvajal-Carmona et al., 2000). The values for the Y-chromosomes of Gran Canarian islanders are about 86% Spanish, 14% Berber, and 1% Sub-Saharan African, whereas for mtDNA the numbers are 45% ± 20% Spanish and 55% ± 20% Berber. An earlier study also employing mtDNA haplogroup frequencies and a similar least-squares method (Elston, 1971) obtained similar estimates for Canarian islanders as a whole, namely 43% from the Iberian Peninsula and 57% from North African Berbers (Flores et al., 2001).

It is interesting to contrast the admixture history of Gran Canarians with that of Colombians. In these two populations, the estimates of Spanish ancestry are much higher for the Y-chromosome (85%, 93%) than for mtDNA (45%, 1%), indicating a preferential mating between Spanish men and native women. This pattern seems to represent a general one at the founding of the colonial populations of the former Spanish Empire, and most likely relates to the preferentially male migration from Spain to the colonies, particularly during the early stages of the Empire (Boyd-Bowman, 1976). Although in both Colombia and Gran Canaria the mtDNA markers reveal a larger native component than the Y-chromosome, this relationship is much more marked in Colombians. The larger proportion of Spanish mtDNA lineages in Gran Canarians suggests that a relatively larger fraction of Spanish women arrived there than in Colombia. This is consistent with a scenario of Spanish women concentrating in areas of easier access during the colonial expansion, particularly along the maritime travel routes (the Colombian sample was obtained in the state of Antioquia, a mountainous inland region of Colombia). Furthermore, the greater geographic proximity of the Canary Islands to the Spanish mainland and its continuing political integration with Spain are likely to have facilitated more recent migrations, with a higher proportion of women as compared to earlier periods. On the other hand, Colombia separated from Spain in the early 19th century and has received little foreign immigration since then.

In both Gran Canaria and Colombia, the autosomal estimates of parental contributions showed in general the expected intermediate values from the other two, although they do not show exactly midpoint numbers, probably due to sampling or other random factors.

These data demonstrate that, although some heterogeneity can exist, there is a usual trend in the Spanish colonial history, characterized by a demographic collapse of the aboriginal population, but with considerable introgression of genes through native women. Similar results were observed with regard to the Portuguese conquest of Brazil (Alves-Silva et al., 2000; Carvalho-Silva et al., 2001). These events caused the contemporary hybrid people subjected to this process to present a mosaic genome. Their Y-chromosomes have mainly been transplanted from outside; their mtDNA, however, received much less outside influences, like the witness people in Ribeiros (1970, 1977) typology, who had not been much influenced by the conquerors. The witness mtDNA genome terminology is also adequate, since it indicates a unique possibility of rescuing

| Population       | Type of marker | Spain | Natives | Sub-Saharan Africa |
|------------------|----------------|-------|---------|--------------------|
| Gran Canaria     | Autosomes      | 72    | 22      | 6                  |
|                  | mtDNA          | 45    | 55      | 0                  |
|                  | Y-chromosomes  | 86    | 14      | <1                 |
| Colombia         | Autosomes      | 75    | 15      | 15                 |
|                  | mtDNA          | 1     | 91      | 8                  |
|                  | Y-chromosomes  | 93    | 4       | 3                  |

1 Guanche (Berber) for Gran Canarians, and Native Americans for Colombian populations.
2 Compiled from Roberts et al. (1966).
3 Values calculated by us from mtDNA haplogroup frequencies furnished by Flores et al. (2001), using Long’s least square method.
4 Arithmetic mean values calculated from our admixture numbers and those obtained by Flores et al. (2003).
5 Data of Carvajal-Carmona et al. (2000) and Carvajal-Carmona et al. (unpublished).
part of the last history of the extinct aboriginal groups. Finally, their autosome sets were considerably shuffled, as the new peoples arose by a process of acculturation and fusion of European, native and African contributions.

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Appendix - Data obtained in the present study.

| Population | SNP-haplogroup | No. of chromosomes | STR-haplotypes† (no. of chromosomes) |
|------------|----------------|--------------------|-------------------------------------|
| Gran Canaria | P-92R7* | 38 | 1 (10); 2(4); 3(3); 4(2); 5(1); 6(1); 7(1); 8(1); 9(1); 10(2); 2(2); 35(2); 36(2); 37(1); 38(1); 39(1); 40(1); 41(1); 42(1); 43(1); 44(1); 45(1); 46(1) |
| | Y* | 12 | 50(1); 51(1); 52(1); 53(1); 72(2); 73(1); 74(1); 75(1); 76(1); 77(1); 78(1) |
| | DE-YAP* | 9 | 84(4); 85(3); 86(1); 87(1) |
| Spain | P-92R7* | 31 | 1(5); 2(5); 5(2); 7(1); 9(1); 10(3); 11(1); 12(2); 13(3); 14(1); 28(1); 29(1); 30(1); 31(1); 32(1); 33(1); 34(1) |
| | Y* | 10 | 50(1); 53(1); 54(2); 55(1); 64(1); 65(1); 67(1); 69(1); 70(1) |
| | DE-YAP* | 5 | 84(2); 85(1); 90(1); 91(1) |
| Berber | P-92R7* | 1 | 47(1) |
| | Y* | 4 | 52(1); 79(1); 81(1); 82(1) |
| | DE-YAP* | 51 | 84(21); 85(2); 86(5); 87(1); 88(1); 89(1); 92(6); 93(3); 94(1); 95(1); 96(2); 97(1); 98(1); 99(1); 100(1); 101(1); 102(1); 114(1) |
| | E-M2 | 4 | 115(1); 116(1); 117(1); 118(1) |

†Haplotype numbers according to Table 2.