A Predominant European Ancestry of Paternal Lineages from Canary Islanders

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Summary

We genotyped 24 biallelic sites and 5 microsatellites from the non-recombining portion of the Y chromosome in 652 males from the Canary Islands. The results indicate that, contrary to mtDNA data, paternal lineages of the current population are overwhelmingly (>90%) of European origin, arguing for a highly asymmetric pattern of mating after European occupation. However, the presence of lineages of indisputable African assignation demonstrates that an aboriginal background still persists (<10%). On the basis of distribution and dating of some of these lineages we derived a genetic perspective of settlement processes of the archipelago in two stages, congruent with anthropological, archaeological and linguistic findings.

Introduction

The Canarian archipelago, formed by seven main islands, is located between latitudes 27° 37′ and 29° 25′ N and longitudes 13° 20′ and 18° 10′ W, geographically belonging to the African continent (Fig. 1). Unlike the rest of Macaronesian archipelagos, the Canary Islands were inhabited by aboriginal people, uniformly known as "Guanches," at the time of European occupation in the 15th Century (de Abreu-Galindo, 1977). From the beginning their dialects, and some cultural traits, were related, by conquest chroniclers, to the Berber population of neighbouring Africa. Since then, anthropology, archaeology and philology have bolstered the hypothesis of the North African origin of the Canarian indigenous population (Navarro, 1997). Furthermore, the different human types discovered, and the heterogeneity of cultural remains, point to successive arrivals of North African settlers (Verneau, 1887; Hooton, 1925; Fusté, 1958; Schwidetzky, 1963; Bermúdez de Castro, 1987; Arco & Navarro, 1987; Onrubia-Pintado, 1987; Navarro, 1991, 1997), with the exceptions of some western islands (Arnay & González-Reimers, 1985–87; González & Tejera, 1990). The most ancient human settlement seems to be no earlier than the 1st millennium B.C., according to absolute C^{14} dating (Billy, 1982; Onrubia-Pintado, 1987). In spite of the aggressive European conquest (Suárez *et al.* 1988), and subsequent massive immigration of Normans, Spaniards, Portuguese, and African slaves (Lobo-Cabrera, 1993), at the end of the 16th Century approximately two-thirds of the Canarian population were Africans and aborigines (Wölfel, 1930). Furthermore, osteological studies comparing aboriginal remains and modern rural populations support the persistence of indigenous traits even in the current population (Fusté, 1958; Schwidetzky, 1975).

Past demographic events can be inferred through the analysis of gene pools from modern populations. The first genetic approaches to decipher the origin of Canarian aborigines and their influence in the present-day populations date from the nineteen-fifties (Guash *et al.* 1952; Bravo & de las Casas, 1958; Roberts *et al.* 1966; Parejo, 1966; Schwarzfischer & Liebrich, 1963; Rössing, 1967). Using the so-called classical markers, such as blood groups and red-blood-cell enzyme loci, these works and subsequent studies (Martell *et al.* 1986;

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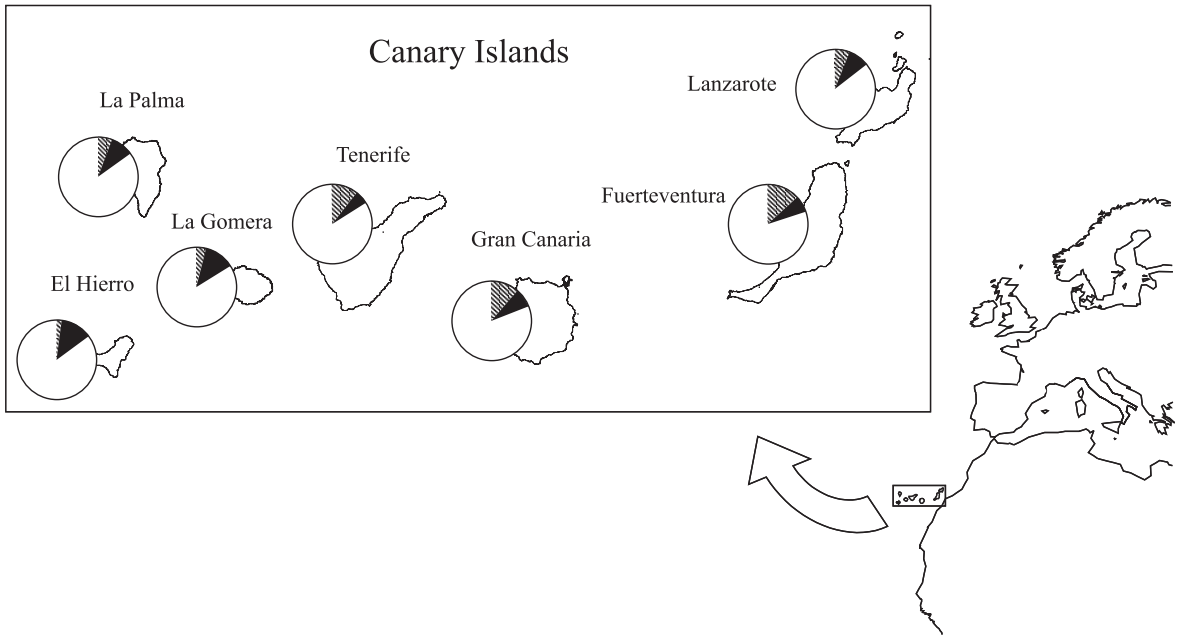

Figure 1 Map showing the location of Canary Islands and pie charts of relative frequencies for Northwest African (dashed) and Saharan (black) markers by island.

Morilla *et al.* 1988; Afonso *et al.* 1989; Pérez *et al.* 1991; Pinto *et al.* 1994, 1996b; Moral *et al.* 1997) supposed that Iberians, sub-Saharans and Northwest Africans were the most probable parental populations of current Canary Islanders, considering that the present Northwest African gene pool represents the Canarian aborigines. In general, the genes surveyed were not informative due to the absence of clear genetic differences between South Europeans and North Africans. When an unambiguous African contribution was detected, it was due to the presence of Negroid alleles. This was supposed to be from an aboriginal source, though a sub-Saharan African slave trade origin cannot be ruled out. Similar results were obtained with haplotype data from other nuclear genes (Esteban *et al.* 1998; Flores *et al.* 2001b). These markers indicated consistent admixture proportions of roughly 70% for Iberians, 20% for North Africans and 10% for Black Africans, with notable heterogeneity between islands. However, mitochondrial DNA (mtDNA) studies predicted larger maternal contributions of African descent: 25–43% for North Africans and 5–21% for Black Africans (Pinto *et al.* 1996a; Rando *et al.* 1999), although supporting a predominantly Iberian influence (36–62%). This discrepancy between admixture proportions has been interpreted in terms of unequal contributions of males and females from parental populations produced by Spanish occupation (Pinto *et al.* 1996a; Flores *et al.* 2001a). Moreover, mtDNA analysis has also clarified the aboriginal settlement process, suggesting that there was one dominant initial colonization from Northwest Africa that affected all the islands from East to West (Rando *et al.* 1999). However, Rando *et al.* (1999) did not exclude the possibility of additional immigrations from North Africa.

In this study we approach the same Canarian issues from a male perspective, using different mutability markers from the haploid part of the Y-chromosome. This analysis offers several advantages with respect to autosomal or maternal markers. As in mtDNA, the entire region is free of recombination, but the use of slowly evolving biallelic markers practically avoids problems of clade-sharing due to convergence. These markers identify well-defined composite clusters or haplogroups. Quickly evolving microsatellites further separate haplogroups into closely related lineages, enabling us to analyse population processes on a micro-evolutionary scale. Furthermore, genetic differences among human populations are greater for the Y-chromosome than for mtDNA or autosomal markers (Jorde *et al.* 2000), which

facilitates the analysis of relative affinities and more accurate admixture estimates.

Materials and Methods

Samples

A total of 652 unrelated male subjects from the Canary Islands were analysed. Samples were collected in hospitals and health care centres of the archipelago with appropriate informed consent. Paternal grandfather birthplaces were used to classify the samples as 47 individuals from El Hierro, 85 from La Palma, 92 from La Gomera, 178 from Tenerife, 78 from Gran Canaria, 97 from Lanzarote and 75 from Fuerteventura. Additionally, data on 45 Basques (Underhill *et al.* 2000) and 16 Catalans (Bosch *et al.* 2001), along with data on 568 general Iberians (non-Basque, non-Catalan), 26 Normans, 99 Northwest Africans and 90 West sub-Saharans (C. Flores, unpublished) were included for comparative analysis.

Y-Chromosome Polymorphisms

We chose 24 biallelic markers from the non-recombining portion of the Y chromosome that reflect unique events from the literature. Eight of these markers have been typed according to published protocols: *DYS287* as in Hammer & Horai (1995), p12f2 (Casanova *et al.* 1985) as in Sun *et al.* (2000), *DYS271* as in Seielstad *et al.* (1994), 92R7 as in Forster *et al.* (2000), SRY_{10831} (Whitfield *et al.* 1995) as in Kwok *et al.* (1996), SRY_{2627} as in Veitia *et al.* (1997), Tat as in Zerjal *et al.* (1997), and M9 (Underhill *et al.* 1997) as in Hurles *et al.* (1998). The remaining sixteen include: PN2 (Hammer *et al.* 1997); M13 (Underhill *et al.* 1997); M26, M67, M70, M81, M89, M170, M172, and M173 (Shen *et al.* 2000; Underhill *et al.* 2000); M34, M52, M78, M123 and M153 (Underhill *et al.* 2000); and M201 (Semino *et al.* 2000). The majority of these sixteen polymorphisms (excepting M34, M70, M78, M81 and M153) do not change sites recognized by available restriction enzymes. Consequently, we developed PCR-RFLP protocols for all of them. Primer sequences were as previously described (Underhill *et al.* 1997, 2000), or were changed by introducing a mismatched base to build a variable restriction site on amplification products. Conditions for PCR-RFLP of each of these 16 markers are shown in Table 1. For each marker, over 10% of the thermal cycling reactions were positive and negative controls to monitor the PCR-RFLP typing.

Five Y-linked tetranucleotide-repeat microsatellites were also analysed. *DYS391*, *DYS393* and *DYS434* were genotyped as previously described (Ayub *et al.* 2000; Kayser *et al.* 2001). For *DYS391*, we used another primer pair (5′-CTATTCATTCAATCATACACCCA-3′ and 5′-AGGTAGGCAGGCAGATAGGC-3′) to reduce the product length. In addition, *DYS466* and *DYS467* were also typed with a new protocol that will be described elsewhere (C. Flores, unpublished). *DYS466* was discarded for coalescence estimates, as there is evidence of stepwise mutation model violation (Flores, 2002).

PCR amplifications were carried out in an MJ Research PTC-100 thermal cycler in 10 μl reactions containing: 0.4 U Eco*Taq* DNA polymerase (Ecogen), 3 pmol of each primer, 0.2 mM dNTPs, 2.5 mM $MgCl_2$, 16.6 mM $(NH_4)SO_4$, 67 mM Tris-HCl pH = 8.8, and 10–30 ng of template DNA extracted from whole blood as in Rudbeck & Dissing (1998). For biallelic markers, cycling programs were standard three-step PCR profiles, plus a first step of 94°C for 2 min. and a final extension step of 5 min. at 72°C. Habitually, the PCR conditions were 35 cycles of 5–30 sec. at 94°C, 5–30 sec. at the adequate annealing temperature, and 5–30 sec. at 72°C. For RFLP analysis, 0.5–1 U of the appropriate restriction enzyme was used to directly digest the whole volume of PCR product under the manufacturers' recommendations. RFLP patterns and microsatellite alleles were resolved on 6% PAGE (29:1 and 19:1 acrylamide: bis-acrylamide, respectively) in 1X TBE buffer using an X-Cell™ MiniCell (NOVEX) and then stained with ethidium bromide (1 μg/ml) for 15 min. For microsatellite allele size calibration, a mixture of different sequenced alleles was included in each run.

We used the term haplogroup to designate the combination of allelic states of the biallelic markers, and reserved the term haplotype to define distinct sublineages within haplogroups characterized by variations at microsatellite loci. Haplogroup tree and nomenclature, identified by lineage, is shown in Fig. 2 on the basis

Table 1 PCR-RFLP protocols developed for sixteen biallelic markers

Marker	Primer pairs (above, forward; below, reverse)	T[b]	t[c]	Size[d]	Digestion	Fragment/s (allele)[e]
PN2	5′- AAGGAGCATTAATAAAACTAAAGC-3′[a] 5′-GAACTCCCGATTCCCCTCTA-3′	54	15	104	*Alu* I	69/35 (C) → 46/35/23 (T)
M13	[f]	54	10	231	*Nde* II	160/71 (C) → 231 (G)
M26	5′-TTTTTCTGAATTAGAATGATC-3′[a] 5′-GTACACCTTTCTTAGGTTGC-3′	48	10	239	*Bcl* I	239 (G) → 222/17 (A)
M34	5′-ATGTTAATGCCTGGCTTCCA-3′ 5′-AGTCATTCCAGGGACATCCA-3′	55	5	259	*Hin*f I	169/90 (G) → 143/90/26 (T)
M52	5′-ATACCTATAAGAATATTGCCTCCA-3′[a] 5′-GACGAAGCAAACATTTCAAG-3′	50	10	82	*Sty* I	60/22 (A) → 82 (C)
M67	5′-GACAAACTCCCCTGCACACT-3′ 5′-GTTCGTGGACCCCTCTACAT-3′[a]	58	10	264	*Nde* I	264 (A) → 243/21 (T)
M70	[g]	48	10	257	*Bsa* I	257 (A) → 218/39 (C)
M78	[g]	50	20	301	*Aci* I	196/105 (C) → 301 (T)
M81	[g]	54	20	422	*Hpy*CH4 IV	276/146 (C) → 422 (T)
M89	5′-AAGAACTCTGCCCCATTCAA-3′ 5′-CAACTCAGGCAAAGTGAGACAT-3′[a]	58	20	191	*Nla* III	93/79/19 (C) → 98/93 (T)
M123	5′-CACAGTATCTGAACTAGCATCTCA-3′[a] 5′-CAGCGAATTAGATTTTCTTGC-3′	50	20	257	*Dde* I	102/76/58/21 (G) → 123/76/58 (A)
M153	[g]	45	10	459	*Tsp* 509I	168/130/82/79 (T) → 168/130/79/48/34 (A)
M170	5′-CTATTTTATTTACTTAAAAATCATTGATC-3′[a] 5′-AGACCACACAAAAACAGGTC-3′	50	10	88	*Bcl* I	63/25 (A) → 88 (C)
M172	5′-AAATTAGGAGCCAGATGACC-3′ 5′-AATAATAATTGAAGACCTTTTGAGT-3′[a]	52	5	176	*Hin*f I	176 (T) → 151/25 (G)
M173	5′-AAGTTGATGCCACTTTTCAG-3′ 5′-TTCTGAATATTAACAGATCACAAAG-3′[a]	48	10	199	*Dra* III	178/21 (A) → 199 (C)
M201	5′-CTAATAATCCAGTACCAACTGAGG-3′[a] 5′-TGAAAGTTCAAACGTCAAACAG-3′	55	10	207	*Bsl* I	108/78/21 (G) → 129/78 (T)

[a]Mismatched primer. [b]PCR annealing temperature in °C. [c]Time (sec.) for the three PCR steps. [d]PCR product size in base pairs. [e]RFLP fragments in base pairs. [f]From Underhill *et al*. (1997). [g]From Underhill *et al*. (2000).

of those of the YCC (Y Chromosome Consortium, 2002).

Statistical Analysis

Haplogroup frequency distributions was inspected by an exact test of population differentiation (Raymond & Rousset, 1995) implemented in ARLEQUIN 2000 (Schneider *et al*. 2000). Significance of these tests were assessed by comparison of the observed frequency distributions to 10,000 explorations of Markov Chain steps. This software was also used to analyse the among population variability based on haplogroup frequencies (AMOVA), and to test for correlations between geographic and genetic distances through a Mantel test (Mantel, 1967) with 1000 permutation steps. Genetic distances, as pairwise F_{ST} from haplogroup frequencies, were calculated by means of the PHYLIP ver. 3.5 package (Felsenstein, 1993), and represented in two-dimensional space with multidimensional scaling (MDS) (Kruskal & Wish, 1978), with the program ALSCAL included in the SPSS ver. 9 package. Geographical distances were drawn from the Great Circle Distance program (http://www.mercury.demon.co.uk/dist/dodist.html) by comparison of geographical coordinates. The geographical distribution of some haplogroups was also inspected by Spearman ranked correlations, comparing major cities of the Canarian archipelago with respect to Cape Juby, the nearest African point.

Admixture estimates were calculated by two different estimators. We used Long's measure, or m_L (Long, 1991) to obtain an estimate based only on haplogroup frequencies. This also allowed us to calculate, in the absence of selection, the amount of variance in the hybrid population not explained by the admixture model. This

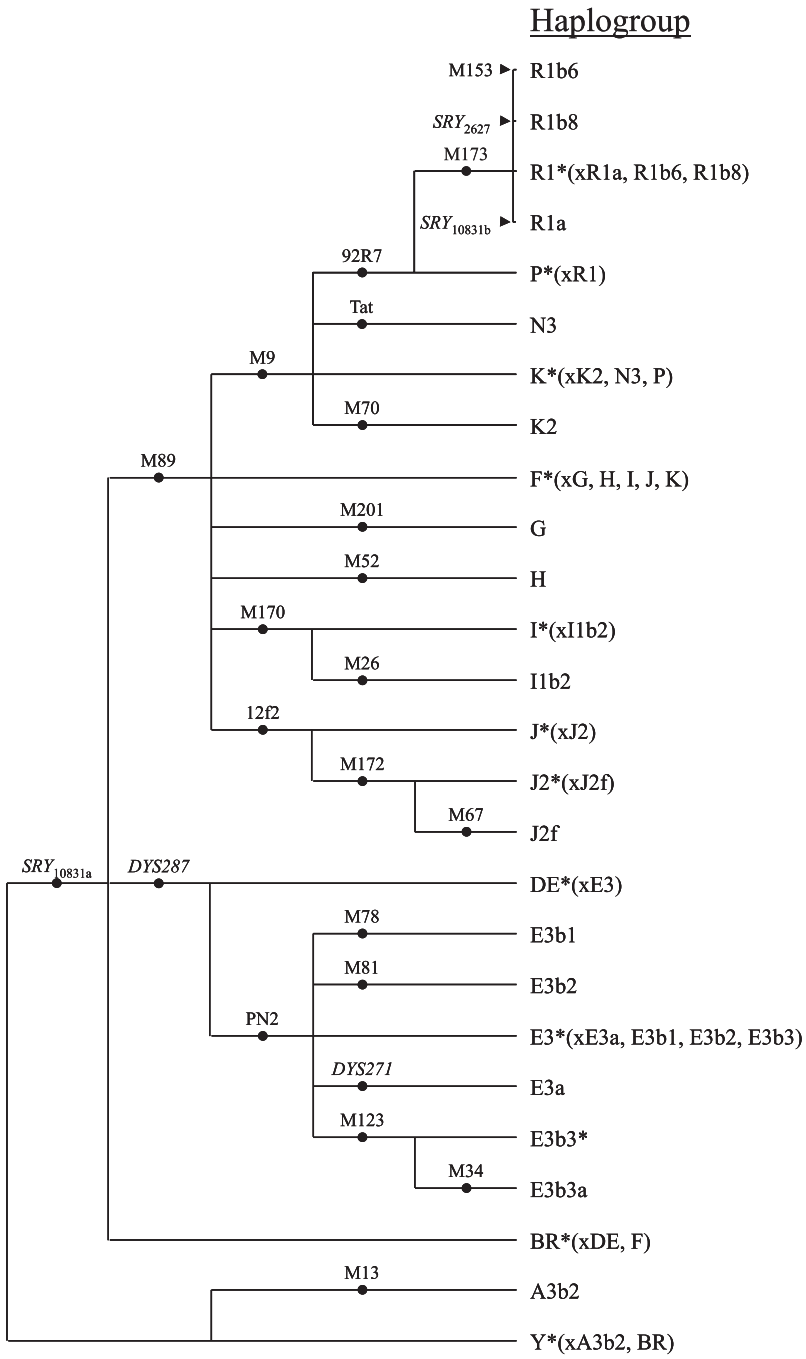

Figure 2 Phylogenetic network of 26 Y-chromosome haplogroups potentially detected by the 24 biallelic markers shown on branches.

variation was transformed to an inbreeding coefficient, an F_{ST} distance, by computing equation 9 from Long (1991) substituting 2N by N chromosomes. The second estimator was m_Y (Bertorelle & Excoffier, 1998), which also incorporates the molecular differences into calculations, counted as the number of differences for haplogroups and as squared differences in microsatellite allele sizes for haplotype data.

Haplogroup ages were calculated as follows: first, as in Bertranpetit & Calafell (1996), we computed the mean number of mutational steps from a root haplotype (chosen as the haplotype with the least number of mutational

steps from all the others); then we transformed it for haplogroup dating, assuming a generation time of 30 years and a mutation rate of 2.1×10^{-3} (95% CI 0.6–4.9 $\times$ 10^{-3} [Heyer *et al.* 1997]). Divergence percentages of haplogroups between the Canarian population and their parental populations were assessed following Hurles *et al.* (1999). By means of the Microsat 1.5d program (Minch, 1997), we computed ASD distances (Thomas *et al.* 1998) between all haplotypes within a haplogroup and the root haplotype ("ASDr"), and ASD between Canarian and European-African compound chromosomes ("ASDcr"). Dividing ASDcr by twice ASDr we obtained a percentage of divergence by haplogroup. This divergence was translated into years by multiplying it by the age of the haplogroup calculated as above.

Results and Discussion

Haplogroup Distribution

We have identified 20 different haplogroups (Table 2), of the 26 possible, in the sample from the Canary Islands, being indicative of the informativeness of the markers selected for the study of this population. Relatedness and nomenclature of haplogroups are shown in Fig. 2 based on those from the YCC (Y Chromosome Consortium, 2002). Haplogroup R1*(xR1a, R1b6, R1b8) is the most frequent in all seven islands, comprising 47% of the total sample (range 39.9–53.9%). This is, by far, also the most abundant haplogroup in the Iberian Peninsula (Bosch *et al.* 2001), reaching higher frequencies than in the Canarian population ($P < 0.05$, Mann-Whitney U-test). Excluding this haplogroup, several others are frequent (>10%), but only in some islands: haplogroup E3b2 in Tenerife, Gran Canaria and Fuerteventura; haplogroup I*(xI1b2) in La Gomera; and haplogroup R1b8 in El Hierro. Haplogroup E3b2, which has been assigned a Northwest African origin (Bosch *et al.* 2001), constitutes a clear African influence, reaching in some islands frequencies twice as high as those reported for the Iberian Peninsula (Bosch *et al.* 2001). On the other hand, haplogroups I*(xI1b2) and R1b8 are European related lineages (Semino *et al.* 2000), the latter with an Iberian assignation (Hurles *et al.* 1999). Albeit at low frequencies, we have also detected the sub-Saharan haplogroup E3a in four of the seven islands. Considering the geographical location of the populations included in this analysis, haplogroup DE*(xE3) may also be the result of

Table 2 Y-chromosome haplogroup frequencies (%) in the Canary Islands

	Populations							
Haplogroup	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria	Lanzarote	Fuerteventura	Total
DE*(xE3)						1.0	2.7	0.5
E3*(xE3a, E3b1, E3b2, E3b3)				0.6				0.2
E3a	4.3	2.4			1.3	1.0		0.9
E3b1	6.4	2.4	4.3	3.4	3.8	3.1	2.7	3.5
E3b2	2.1	5.9	4.3	10.7	11.6	6.2	13.3	8.3
E3b3*				1.7				0.5
E3b3a	2.1	3.5	2.2	2.2	2.6			1.8
G	4.3	2.4	5.4	3.9	3.8	5.2	2.7	4.0
I*(xI1b2)	2.1	4.7	12.0	5.6	5.1	7.2	2.7	6.0
I1b2		4.7	8.7	1.7	1.3	6.2	2.7	3.7
J*(xJ2)	6.4	7.0	7.6	2.2	3.8	5.2	4.0	4.8
J2*(xJ2f)	8.5	7.0	3.3	5.1	3.8	7.2	6.7	5.7
J2f	4.3	2.4	7.6	1.1	1.3	3.1	8.0	3.5
K*(Xk2, N3, P)				0.6		1.0		0.3
K2		3.5	1.1	5.6	5.1		1.3	2.9
N3		1.2						0.2
R1*(xR1a, R1b6, R1b8)	44.7	47.0	41.3	50.0	53.9	49.5	39.9	47.0
R1a	2.1	2.4	2.2	2.2	1.3	4.1	5.3	2.8
R1b6				1.7				0.5
R1b8	12.7	3.5		1.7	1.3		8.0	2.9
Sample size	47	85	92	178	78	97	75	652

African influence. It must be noted that haplogroups E3a and DE*(xE3) have not been detected in Iberian samples to date (Semino *et al.* 2000; Bosch *et al.* 2001). Also, it is striking that both an Iberian haplogroup (R1b8) and a sub-Saharan African haplogroup (E3a) were at their highest frequencies in the archipelago in El Hierro. The presence of some haplogroups of widespread distribution in Europe, in combination with others of clear Northwest and sub-Saharan African assignation, reflect the complex demographic patterns that have shaped the current Canarian population.

Population Structure and Affinities

Haplogroup distribution in the archipelago is heterogeneous ($P = 0.001$), although few (29%) pairwise comparisons gave results at a significant level (Table 3). Furthermore, when we carried out an AMOVA analysis, a low amount (0.3%) of variance was attributed to differences between populations within the archipelago. This value is 4.5 and 8 times lower than that obtained for the European and Northwest African populations considered here, respectively, although Canarian populations are distributed with a mean distance of 228 km, those of Europe with a mean of 587 km, and Northwest Africans with a mean of 668 km. This result could be perfectly explained by the way that European occupation occurred, with groups of people of mixed origin (Suárez *et al.* 1988). This event, and subsequent gene flow, would have reduced the between island variance. Even though some neighbouring islands were also genetically related (Table 3), a Mantel test revealed that genetic and geographic distances are not correlated ($r = -0.081$, $P = 0.612$).

Table 4 Percentages of variation among different geographical areas resulting from the AMOVA analysis

	Europe	Northwest Africa	sub-Saharan Africa
El Hierro	**0.005**	0.344	0.371
La Palma	**0.000**	0.319	0.371
La Gomera	0.014	0.308	0.362
Tenerife	**0.001**	0.299	0.380
Gran Canaria	**0.000**	0.327	0.412
Lanzarote	**0.000**	0.328	0.386
Fuerteventura	0.015	0.258	0.361
Europe	—	—	—
Northwest Africa	0.323	—	—
Sub-Saharan Africa	0.373	0.503	—
Canary Islands	0.003	0.279	0.342

$P > 0.05$ in bold.

When AMOVA was calculated between populations pooled by geographical areas (Table 4), the lowest, although significant, level of variation was observed in the European-Canarian comparison, being two orders of magnitude lower than the comparison with both African groups. This clearly indicates that Canarian populations have greater differences from Africans than from Europeans. Even so, the percentage of variance between Canarians and Africans is lower than percentages between Europeans and Africans, showing again an African paternal influence on the archipelago populations. Looking at each island, all are significantly different from both African groups, but only La Gomera and Fuerteventura are significantly different from the European pool (Table 4). More precisely, these two islands have the lowest differentiation values from both, Northwest and sub-Saharan Africans.

Genetic affinities were also inspected from a MDS plot of F_{ST} genetic distances between populations

Table 3 F_{ST} distances (below diagonal) and exact probability values of differentiation (above diagonal) between Canarian populations

	El Hierro	La Palma	La Gomera	Tenerife	G. Canaria	Lanzarote	Fuerteventura
El Hierro	—	0.637	**0.008**	**0.008**	0.089	**0.042**	0.353
La Palma	0.012	—	0.273	0.295	0.886	0.525	0.307
La Gomera	0.026	0.012	—	**0.003**	0.064	0.522	**0.004**
Tenerife	0.023	0.007	0.020	—	0.997	0.075	**0.019**
G. Canaria	0.027	0.009	0.026	0.002	—	0.249	0.164
Lanzarote	0.020	0.005	0.010	0.008	0.010	—	0.120
Fuerteventura	0.016	0.014	0.020	0.017	0.023	0.018	—

$P < 0.05$ in bold.

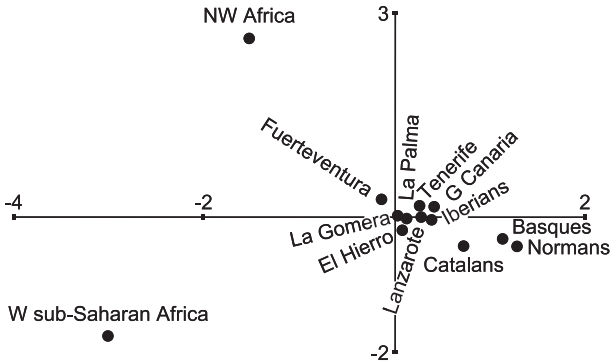

Figure 3 Two-dimensional MDS plot relating Canarian and continental populations.

(Fig. 3). The correlation between F_{ST} and the new distances derived from a two-dimensional plot was very high ($r = 0.971$). In the same way, the obtained stress value (0.127) indicates that the chosen dimensionality is appropriate, and that a plot in a higher dimension is not necessary (http://www.analytictech.com/borgatti/mds.htm). Europeans, Northwest and sub-Saharan African populations constituted three different clusters. The Canarian populations formed a relatively tight cluster near the European group, but with some islands dispersed towards Northwest Africans. From the European group, clearly the general Iberians have the highest affinities with Canarian populations.

Admixture Estimates

In previous genetic approaches, to explain the colonisation of the Canary Islands admixture proportions have been inferred considering the extant people on the islands as a hybrid population with a Northwest African ancestry, contributed, most probably, by Berber aboriginal founders and, to a lesser degree, by sub-Saharan Africans introduced after the conquest as a result of slave trade. The other main contribution is from the European population that, since the beginning of the occupation, was steadily colonising the islands. However, the high paternal differentiation between these clusters of populations makes it possible to estimate their contributions to the current Canarian populations more accurately. Our admixture results (Table 5) were similar when m_L or m_Y estimators were used, although African m_Y estimates always gave slightly higher values. For all comparisons the highest paternal contribution resulted from European descent. Northwest Africans would have also contributed significantly, but the sub-Saharan African contribution was almost negligible, excepting the case of El Hierro island. Differences between islands are evident, as the Northwest African contribution diminishes towards the westernmost islands, being insignificant in El Hierro. The opposite occurs for European contributions. As suggested from results on AMOVA

Table 5 Relative admixture contributions to the Canarian populations inferred from haplogroup frequencies

Population	Estimator	Europe	Northwest Africa	sub-Saharan Africa	F_{ST}[a]
El Hierro	m_L	0.957 ± 0.036	—	0.043 ± 0.036	0.003
	m_Y	0.959 ± 0.063	—	0.041 ± 0.063	—
La Palma	m_L	0.961 ± 0.053	0.019 ± 0.049	0.021 ± 0.024	0.007
	m_Y	0.929 ± 0.054	0.051 ± 0.049	0.021 ± 0.027	—
La Gomera	m_L	0.997 ± 0.057	0.003 ± 0.057	—	0.019
	m_Y	0.899 ± 0.050	0.092 ± 0.051	0.009 ± 0.024	—
Tenerife	m_L	0.926 ± 0.041	0.074 ± 0.041	—	0.003
	m_Y	0.894 ± 0.044	0.097 ± 0.040	0.009 ± 0.013	—
G. Canaria	m_L	0.897 ± 0.043	0.093± 0.041	0.010 ± 0.012	-0.005
	m_Y	0.885 ± 0.063	0.096± 0.059	0.019 ± 0.023	—
Lanzarote	m_L	0.956 ± 0.046	0.035 ± 0.044	0.009 ± 0.015	0.003
	m_Y	0.940 ± 0.049	0.051 ± 0.046	0.009 ± 0.022	—
Fuerteventura	m_L	0.832 ± 0.107	0.171 ± 0.107	—	0.006
	m_Y	0.877 ± 0.069	0.123 ± 0.069	—	—
Canary Is. Total	m_L	0.934 ± 0.030	0.059 ± 0.029	0.006 ± 0.008	0.003
	m_Y	0.910 ± 0.026	0.082 ± 0.026	0.008 ± 0.011	—

[a]Variation not explained by the model (Long, 1991).

analyses and genetic distances, the Europeans were the major contributors to the current Canarian paternal gene pool, explaining about 90% of its whole variability, while Northwest and sub-Saharan Africans contributed no more than 6–8%, and less than 1%, respectively (Table 5). Clearly, there is a sharp contrast between paternal admixture results and those from mtDNA and autosomal loci. As mentioned above, the higher African contribution to the Canarian mtDNA pool compared to the contribution estimated from the autosomal loci has been explained by an asymmetry of female and male aboriginal contribution to the current Canarian population (Pinto *et al.* 1996a; Flores *et al.* 2001a). During the Spanish conquest the European migration was constituted mainly of soldiers, who displaced autochthonous males by death or deportation, but mixed with aborigine females. A corollary of these results is that the aboriginal Y-chromosome contribution to the present-day Canarians has to be lower than those estimated from autosomal and mtDNA polymorphisms. This is exactly what we found with our experimental data. Although with stronger directional mating, similar results have been obtained for Amerind populations, which were also profoundly influenced by Iberian conquerors (Carvajal-Carmona *et al.* 2000; Sans, 2000; Carvalho-Silva *et al.* 2001).

Regarding the portion of variance not explained by the admixture model (Table 5), and so due to genetic drift, the highest value, by one order of magnitude, was obtained for La Gomera, the second smallest island. Precisely, for mtDNA data La Gomera is the only island significantly different to the others and characterized by the highest frequency of the North African U6 cluster (Rando *et al.* 1998, 1999). In this regard, genetic drift could be responsible for the contrasting difference in African ancestry detected with maternal (51% of African lineages) and paternal markers (0.3–10% of African lineages). Alternatively, it could reflect the dramatic way the island was conquered, producing the strongest sexual asymmetry in the archipelago (Suárez *et al.* 1988).

Aborigine Settlement Process

Three lineages deserve special attention due to their distribution in the archipelago and in populations from South western Europe and Africa: haplogroups J* (xJ2), E3b1 and E3b2. Haplogroup J* (xJ2) has been suggested to have originated in Middle East populations and spread to Europe with the dispersion of farming during the Neolithic period (Semino *et al.* 2000; Rosser *et al.* 2000; Bosch *et al.* 2001; Nebel *et al.* 2001). Its arrival to Northwest Africa could have occurred at the same time as in Mediterranean Europe (Bosch *et al.* 2001) or more recently, during the Islamization of the area (Nebel *et al.* 2002). Nevertheless, it reaches higher frequencies in North Africa than in the Iberian Peninsula (Bosch *et al.* 2001), being especially high in Ethiopians (Semino *et al.* 2002). Although a clear North African origin has been assigned to haplogroup E3b1 (Bosch *et al.* 2001), it also characterizes most of the European YAP+ haplogroups, as pointed out by Semino *et al.* (2002). Again, it reaches the highest frequencies in Ethiopians (Underhill *et al.* 2000; Semino *et al.* 2002). Strikingly, both haplogroups are coincidentally distributed in the Canary Islands, reaching highest frequencies in western islands and decreasing eastwards (Fig. 1). Furthermore, they appeared in higher frequencies in the archipelago than in the European populations considered. On the other hand, for haplogroup E3b2 an unambiguous Northwest African origin has also been suggested (Bosch *et al.* 2001). It has been detected in Iberian populations (Bosch *et al.* 2001; Flores, 2002), but never in frequencies so high as those reported for Northwest Africa. Moreover, its frequency in Canarians as a whole is nearly double those for the European populations considered, being particularly abundant in eastern islands (Fig. 1). At this point, there are at least three different explanations for the appearance of these three haplogroups in Canary Islands in such relatively high frequencies with respect to continental populations. First, they arrived in the archipelago with Iberian colonizers, as they are also influenced by Africans (Flores *et al.* 2000, 2001c; Bosch *et al.* 2001), and then augmented in frequency by genetic drift. Second, some could have come with Iberian populations and some directly from Northwest African influence. And third, they are an exclusive contribution from aboriginal inhabitants. Genetic drift could hardly explain a simultaneous increase of frequency for the three haplogroups, considering that they are precisely the three major haplogroups within North Africa (Underhill *et al.* 2000; Bosch *et al.* 2001). Furthermore, STR diversity within haplogroups by area (Table 6)

Table 6 STR diversity within haplogroups by area and m_Y haplotype contributions to the Canary Islands

	Haplogroup		
Population	E3b1	E3b2	J*(xJ2)
Northwest Africa	1.83 ± 1.31	0.66 ± 0.51	1.12 ± 0.78
Europe	0.93 ± 0.68	0.54 ± 0.46	0.58 ± 0.50
Canary Islands	1.33 ± 0.86	0.75 ± 0.56	1.37 ± 0.87
C/NWA[a]	0.168 ± 0.131	0.551 ± 0.677	0.334 ± 0.127
C/E[b]	0.832 ± 0.131	0.449 ± 0.677	0.666 ± 0.127

[a]Contributions from Northwest Africa.
[b]Contributions from Europe.

argues against drift being the only factor responsible for that increase. Note that Canarian diversities, calculated from STR haplotypes (Appendix I), are always higher than those of Iberians and, in two instances, even than those of Northwest Africans. However, we must note that the particular comparison with Northwest African samples could be biased by the comparatively low number of samples used. We then applied m_Y estimator, using STR haplotypes and their molecular differences, to clarify the percentage of influence by which an area has contributed to Canarians for these haplogroups. The results (Table 6) supported a compound origin of these three haplogroups in the Canary Islands, making the second scenario more likely. Although J*(xJ2) is not considered a genuine African marker, it seems that its presence in the Canary Islands has an important African cause. Even though it simplified the picture, we have considered haplogroups J*(xJ2) and E3b1 as indicators of a movement of people coming from Southern parts of North Africa ("Saharan marker"), and haplogroup E3b2 as their Northwest African counterpart ("Northwest African marker"). In fact, the Saharan marker showed a trend of increasing frequencies westwards ($r_s = 0.714$, $P = 0.072$, two-tailed test), and the contrary is observed for the Northwest African marker ($r_s = -0.857$, $P = 0.014$, two-tailed test). Similar clinal patterns have been found for unlinked loci, such as mtDNA (Rando *et al.* 1999) and CD4/Alu haplotypes (Flores *et al.* 2001b), pointing to demographic events as a major cause, as selection would affect single genes. Even though the aboriginal population that occupied the archipelago was probably not a homogeneous group, the discrepant distribution of these haplogroups in relation to their distribution in Africa could be compatible with the hypothesis of more than one prehistoric settlement, particularly in the eastern islands (Onrubia-Pintado, 1987). Congruent with this hypothesis, cultural (Onrubia-Pintado, 1987; Navarro, 1992; Martínez, 1996) and dialectal (Reyes-García, 2000) aborigine heterogeneities have been revealed within islands, supporting more than one arrival from Africa. Furthermore, linguistic investigation supports the idea that major dialectal influence in aborigines, common to all the islands, could have come from southern Algeria, but was also notably affected by Central Moroccan dialects (Reyes-García, pers. comm.). However, this possibility could not be confirmed in a previous mtDNA analysis (Rando *et al.* 1999), as the significant westward decrease of diversity and number of mtDNA African lineages was considered concordant to one dominant initial settlement from the African shore following a westward stepping-stone process.

Dating the Aboriginal Colonisations

Assuming that more than one aborigine settlement dispersed part of these three haplogroups in the archipelago, we tentatively tried to date those processes. Considering all the chromosomes from the Canary Islands, Europe and Northwest Africa, haplogroup J*(xJ2) would have originated ≈3760 (CI 1610–13147) years ago, haplogroup E3b1 ≈6060 (CI 2598–22221) years ago, and haplogroup E3b2 ≈1840 (CI 788–6433) years ago. We then calculated divergence percentages of haplogroups between the Canarian population and their parental populations. The results showed again congruent values for haplogroup J*(xJ2) and E3b1, 52.7 and 52.6% respectively, bolstering the hypothesis of their coincident dispersal in the Canarian archipelago. Translating into years, haplogroup J*(xJ2) gave an age of ≈2000 years and haplogroup E3b1 ≈3200 years. These estimates match perfectly with the most ancient age of

human occupation in the Canary Islands as deduced from C^{14} dating (Onrubia-Pintado, 1987), and that deduced from mtDNA (Rando *et al*. 1999). The divergence for haplogroup E3b2 gave only 31.6%, which means ≈600 years, placing this colonization just before the European conquest. However, these coalescence time estimates must be interpreted with caution. They are highly influenced by demographic processes and are based on many assumptions of microsatellite mutation rates that could be erroneous (Stumpf & Goldstein, 2001).

In summary, our Y-chromosome analysis supports the hypothesis that the current paternal pool from the Canarian population is, to a great extent, of Iberian descent. The male aboriginal influence has been estimated to be less than 10%, whereas aboriginal mtDNA lineages represent ≈45%, reflecting the aggressive way the islands were conquered. Nevertheless, with such a low number of aboriginal lineages, we detected and dated two prehistoric settlement processes, bolstered by osteological, cultural and linguistic data: the first one, with a Saharan substrate, arriving during the 1st millennium B.C., and the second, with a Northwest African ancestry, spreading just prior to the European conquest.

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Appendix I

Haplogroup	*DYS391*	*DYS393*	*DYS434*	*DYS466*	*DYS467*	Freq.
E3b1 (N = 23)	10	12	9	7	14	1
	10	13	8	7	12	2
	10	13	9	7	11	9
	10	13	9	7	12	2
	10	13	9	7	13	3
	10	13	9	7	15	1
	10	14	9	7	11	1
	10	14	9	7	13	1
	10	15	9	7	13	1
	11	13	9	7	11	2
E3b2 (N = 54)	9	13	8	7	14	1
	9	13	9	7	12	1
	9	13	9	7	13	12
	9	13	9	7	14	30
	9	13	9	7	15	5
	9	14	9	7	13	2
	9	14	9	7	14	3
J*(xJ2) (N = 31)	10	12	9	6	12	1
	10	12	9	6	13	1
	10	12	9	7	12	11
	10	12	9	7	13	4
	10	12	9	7	14	1
	10	12	9	7	15	1
	10	13	9	7	14	1
	10	13	10	7	12	1
	10	14	9	7	12	2
	11	12	9	7	11	2
	11	12	9	7	12	4
	11	12	10	7	13	1
	12	12	9	7	11	1

Table A1 Y STR haplotypes observed in haplogroups E3b1, E3b2 and J*(xJ2) in Canary Islands. Alleles are indicated by the corresponding number of repetitions

References

Afonso, J. M., Hernández, M., Larruga, J. M., Cabrera, V. M. & González, A. M. (1989) Human enzyme polymorphism on the Canary Islands. III. Tenerife Island population. *Hum Biol* **61**, 542–549.

Arco, M. C. & Navarro, J. F. (1987) *Historia popular de Canarias. Vol. 1. Los aborígenes*. Tenerife, Centro de la Cultura Popular Canaria.

Arnay, M. & González-Reimers, E. (1985–1987) La cerámica decorada prehispánica de Tenerife. *Tabona* **6**, 241–277.

Ayub, Q., Mohyuddin, A., Qamar, R., Mazhar, K., Zerjal, T., Mehdi, S. Q. & Tyler-Smith, C. (2000) Identification and characterisation of novel human Y-chromosomal microsatellites from sequence database information. *Nucleic Acids Res* **28**, e8.

Bermúdez de Castro, J. M. (1987) Quantitative analysis of the molar-size sequence in human prehistoric populations of the Canary Isles. *Am J Phys Anthropol* **47**, 81–86.

Bertorelle, G. & Excoffier, L. (1998) Inferring admixture proportions from molecular data. *Mol Biol Evol* **15**, 1298–1311.

Bertranpetit, J. & Calafell, F. (1996) Genetic and geographic variability in cystic fibrosis: evolutionary considerations. In: *Variation in the human genome* (eds. D. Chadwick & G. Cardew), pp. 97–118. Chichester, John Wiley and Sons.

Billy, G. (1982) Le peuplement prehistorique de l'Archipel Canarien. *El Museo Canario* **41**, 59–74.

Bosch, E., Calafell, F., Comas, D., Oefner, P. J., Underhill, P. A. & Bertranpetit, J. (2001) High-resolution analysis of human Y-chromosome variation shows a sharp discontinuity and limited gene flow between Northwestern Africa and the Iberian Peninsula. *Am J Hum Genet* **68**, 1019–1029.

Bravo, A. M. & de las Casas, M. T. (1958) Distribución de grupos sanguíneos en los habitantes de la isla de La Palma. *Acta Médica de Tenerife* **10**, 114–117.

Carvajal-Carmona, L. G., Soto, I. D., Pineda, N., Ortiz-Barrientos, D., Duque, C., Ospina-Duque, J., McCarthy, M., Montoya, P., Alvarez, V. M., Bedoya, G. & Ruiz-Linares, A. (2000) Strong Amerind/white sex bias and a possible Sephardic contribution among the founders of a population in Northwestern Colombia. *Am J Hum Genet* **67**, 1287–1295.

Carvalho-Silva, D. R., Santos, F. R., Rocha, J. & Pena, S. D. J. (2001) The phylogeography of Brazilian Y-chromosome lineages. *Am J Hum Genet* **68**, 281–286.

Casanova, M., Leroy, P., Boucekkine, C., Weissenbach, J., Bishop, C., Fellous, M., Purrello, M., Fiori, G. & Siniscalco, M. A. (1985) Human Y-linked DNA polymorphism and its potential for estimating genetic and evolutionary distance. *Science* **230**, 1403–1406.

de Abreu-Galindo, F. J. (1977) *Historia de la conquista de las siete Islas de Canarias*. Tenerife, Goya.

Esteban, E., Dugoujon, J. M., Valveny, N., González-Reimers, E. & Moral, P. (1998) Spanish and African contribution to the genetic pool of the Canary islanders: data from GM and KM haplotypes and RFLPs in the immunoglobulin IGHG loci. *Ann Hum Genet* **62**, 33–45.

Felsenstein, J. (1993) *Phylogeny inference package (PHYLIP), version 3.5*. Seattle, University of Washington.

Flores, C. (2002) *Composición genética y posible origen paterno de las poblaciones humanas canarias, deducidos de su polimorfismo en el cromosoma Y*. Ph.D. diss. Tenerife, Universidad de La Laguna.

Flores, C., Hernández, M., González, A. M. & Cabrera, V. M. (2000) Genetic affinities among human populations inhabiting the sub-Saharan area, Northwest Africa and the Iberian Peninsula. In: *Prehistoric Iberia: Genetics, Anthropology and Linguistics* (ed. A. Arnaiz-Villena), pp. 33–50. New York: Kluwer Academic/Plenum Press.

Flores, C., Larruga, J. M., González, A. M., Hernández, M., Pinto, F. M. & Cabrera, V. M. (2001a) The origin of the Canary Island aborigines and their contribution to the modern population: a molecular genetics perspective. *Curr Anthropol* **42**, 749–755.

Flores, C., Maca-Meyer, N., Pérez, J. A. & Cabrera, V. M. (2001b) The peopling of the Canary Islands: a CD4/Alu microsatellite haplotype perspective. *Hum Immunol* **62**, 949–953.

Flores, C., Maca-Meyer, N., Pérez, J. A., Hernández, M. & Cabrera, V. M. (2001c) Y-Chromosome differentiation in Northwest Africa. *Hum Biol* **73**, 513–524.

Forster, P., Röhl, A., Lünnemann, P., Brinkmann, C., Zerjal, T., Tyler-Smith, C. & Brinkmann, B. A. (2000) Short tandem repeat-based phylogeny for the human Y chromosome. *Am J Hum Genet* **67**, 182–196.

Fusté, A. M. (1958) *Algunas observaciones acerca de la antropología de las poblaciones prehistóricas y actual de Gran Canaria*. Las Palmas, Publicaciones del Museo Canario.

González, R. & Tejera, A. (1990) *Los aborigenes canarios. Gran Canaria y Tenerife*. Oviedo, Ediciones Istmo.

Guasch, J., Florensa, G., Diaz de Yraola, G., Gavilanes, C., Rio, R., Tabuenca, J. & Raichs, A. (1952) Los factores hemáticos en España, excepto en el País Vasco. *Medicina Clínica* **18**, 268–271.

Hammer, M. F. & Horai, S. (1995) Y chromosomal DNA variation and the peopling of Japan. *Am J Hum Genet* **56**, 951–962.

Hammer, M. F., Spurdle, A. B., Karafet, T., Bonner, M. R., Wood, E. T., Novelletto, A., Malaspina, P., Mitchell, R. J., Horai, S., Jenkins, T. & Zegura, S. L. (1997) The geographic distribution of human Y chromosome variation. *Genetics* **145**, 787–805.

Heyer, E., Puymirat, J., Dieltjes, P., Bakker, E. & de Knijff, P. (1997) Estimating Y chromosome specific microsatellite

mutation frequencies using deep rooting pedigrees. *Hum Mol Genet* **6**, 799–803.

Hooton, E. A. (1925) The ancient inhabitants of the Canary Islands. *Harvard African Studies*, 7.

Hurles, M. E., Irven, C., Nicholson, J., Taylor, P. G., Santos, F. R., Loughlin, J., Jobling, M. A. & Sykes, B. C. (1998) European Y-chromosomal lineages in Polynesians: A contrast to the population structure revealed by mtDNA. *Am J Hum Genet* **63**, 1793–1806.

Hurles, M. E., Veitia, R., Arroyo, E., Armenteros, M., Bertranpetit, J., Pérez-Lezaun, A., Bosch, E., Shlumukova, M., Chambón-Thomsen, A., McElreavey, K., López de Munain, A., Röhl, A., Wilson, I. J., Singh, L., Pandya, A., Santos, F. R., Tyler-Smith, C. & Jobling, M. A. (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* **65**, 1437–1448.

Jorde, L. B., Watkins, W. S., Bamshad, M. J., Dixon, M. E., Ricker, C. E., Seielstad, M. T. & Batzer, M. A. (2000) The distribution of human genetic diversity: a comparison of mitochondrial, autosomal, and Y-chromosome data. *Am J Hum Genet* **66**, 979–988.

Kayser, M., Krawczak, M., Excoffier, L., Dieltjes, P., Corach, D., Pascali, V., Gehrig, C., Bernini, L. F., Jespersen, J., Bakker, E., Roewer, L. & de Knijff, P. (2001) An extensive analysis of Y-chromosomal microsatellite haplotypes in globally dispersed human populations. *Am J Hum Genet* **68**, 990–1018.

Kruskal, J. B. & Wish, M. (1978) *Multidimensional scaling*. Beverly Hills, CA, Sage Publications.

Kwok, C., Tyler-Smith, C., Mendonca, B. B., Hughes, I., Berkovitz, G. D., Goodfellow, P. N. & Hawkins, J. R. (1996) Mutation analysis of the 2 kb 5′ to SRY in XY females and XY intersex subjects. *J Med Genet* **33**, 465–468.

Lobo-Cabrera, M. (1993) La esclavitud en Fuerteventura en los Siglos XVI y XVII. *V Jornadas de estudios sobre Fuerteventura y Lanzarote* **I**, 13–40.

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

Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* **27**, 209–220.

Martell, M., Padrón, G., Hernández, M., Afonso, J. M. & Cabrera, V. M. (1986) Human enzyme polymorphism on the Canary Islands I. Gran Canaria Island population. *Hum Hered* **36**, 41–44.

Martínez, V. M. F. (1996) *Arqueología prehistórica de África*. Madrid, Editorial Síntesis.

Minch, E. (1997) *Microsat 1.5d*. Stanford, Department of Genetics, University of Stanford.

Moral, P., Esteban, E., Vives, S., Valveny, N., Toja, D. I. & González, D. (1997) Genetic study of the population of Tenerife (Canary Islands, Spain): protein markers and review of classical polymorphisms. *Am J Phys Anthopol* **102**, 337–349.

Morilla, J. M., Afonso, J. M., Hernández, M., Pestano, J. M. & Larruga, J. M. (1988) Human enzyme polymorphism on the Canary Islands II. African influence. *Hum Hered* **38**, 101–105.

Navarro, J. F. (1991) El poblamiento prehistórico. In: *Historia de Canarias* (ed. F. Morales Padrón), pp. 41–60. Madrid, Editorial Prensa Ibérica.

Navarro, J. F. (1992) *La prehistoria de Canarias. Vol. 5. La Gomera y Los Gomeros*. Tenerife, Centro de la Cultura Popular Canaria.

Navarro, J. F. (1997) Arqueología de las Islas Canarias. *Espacio, Tiempo y Forma: Prehistoria y Arqueología* **10**, 201–232.

Nebel, A., Filon, D., Brinkmann, B., Majumder, P. P., Faerman, M. & Oppenheim, A. (2001) The Y chromosome pool of Jews as a part of the Genetic Landscape of the Middle East. *Am J Hum Genet* **69**, 1095–1112.

Nebel, A., Landau-Tasseron, E., Filon, D., Oppenheim, A. & Faerman, M. (2002) Genetic evidence for the expansion of Arabian tribes into the Southern Levant and North Africa. *Am J Hum Genet* **70**, 1594–1596.

Onrubia-Pintado, J. (1987) Les cultures préhistoriques des Îles Canaries état de la question. *L'Anthropologie* **91**, 653–678.

Parejo, M. (1966) El sistema AB0 en la poblacion actual de las Islas Canarias. *Actas del V Congreso Panafricano de prehistoria y estudios del Cuaternario* **II**, 213–217.

Pérez, M. J., Hierro, J. M., Marrero, M. J., González, A. M. & Cabrera, V. M. (1991) Human enzyme polymorphism on the Canary Islands. IV. Eastern Islands. *Hum Hered* **41**, 385–390.

Pinto, F., Cabrera, V., González, A. M., Larruga, J. M., Noya, A. & Hernández, M. (1994) Human enzyme polymorphism in the Canary Islands. VI. Northwest African influence. *Hum Hered* **44**, 156–161.

Pinto, F., González, A. M., Hernández, M., Larruga, J. M. & Cabrera, V. M. (1996a) Genetic relationship between the Canary Islanders and their African and Spanish ancestors inferred from mitochondrial DNA sequences. *Ann Hum Genet* **60**, 321–330.

Pinto, F., Rando, J. C., López, M., Morilla, J. M. & Larruga, J. M. (1996b) Blood group polymorphisms in the Canary Islands. *Gene Geography* **10**, 171–179.

Rando, J. C., Cabrera, V. M., Larruga, J. M., Hernández, M., González, A. M., Pinto, F. & Bandelt, H. J. (1999) Phylogeographic patterns of mtDNA reflecting the colonization of the Canary Islands. *Ann Hum Genet* **63**, 413–428.

Rando, J. C., Pinto, F., González, A. M., Hernández, M., Larruga, J. M., Cabrera, V. M. & Bandelt, H. J. (1998) Mitochondrial DNA analysis of northwest African populations reveals genetic exchanges with European, near-eastern, and sub-Saharan populations. *Ann Hum Genet* **62**, 531–550.

Raymond, M. & Rousset, F. (1995) An exact test of population differentiation. *Evolution* **49**, 1280–1283.

Reyes-García, I. (2000) *Consideraciones metodológicas en torno al estudio de la antigua lengua de Canarias*. Las Palmas, Cabildo de Gran Canaria, Acta del XIII coloquio de Historia Canario Americana.

Roberts, D. F., Evans, M., Ikin, E. W. & Mourant, A. E. (1966) Blood groups and the affinities of the Canary Islanders. *Man* **1**, 512.

Rösing, I. S. (1967) AB0-blutgruppen und Rh-Faktoren auf Teneriffa unter besonderer Berücksichtigung des Vergleichs zwischen vorspanischer und heutiger Bevölkerung. *Homo* **18**, 96–104.

Rosser, Z. H., Zerjal, T., Hurles, M. E., Adojaan, M., Alavantic, D., Amorim, A., Amos, W., Armenteros, M., Arroyo, E., Barbujani, G., Beckman, G., Beckman, L., Bertranpetit, J., Bosch, E., Bradley, D. G., Brede, G., Cooper, G., Côrte-Real, H. B. S. M., Knijff, P., Decorte, R., Dubrova, Y. E., Evgrafov, O., Gilissen, A., Glisic, S., Gölge, M., Hill, E. W., Jeziorowska, A., Kalaydjieva, L., Kayser, M., Kivisild, T., Kravchenco, S. A., Krumina, A., Kučinskas, V., Lavinha, J., Livshits, L. A., Malaspina, P., Maria, S., McElreavey, K., Meitinger, T. A., Mikelsaar, A.-V., Mitchell, R. J., Nafa, K., Nicholson, J., Nørby, S., Pandya, A., Parik, J., Patsalis, P. C., Pereira, L., Peterlin, B., Pielberg, G., Prata, M. J., Previderé, C., Roewer, L., Rootsi, S., Rubinsztein, D. C., Saillard, J., Santos, F. R., Stefanescu, G., Sykes, B. C., Tolun, A., Villems, R., Tyler-Smith, C. & Jobling, M. A. (2000) Y-chromosomal diversity in Europe is clinal and influenced primarily by geography, rather than by language. *Am J Hum Genet* **67**, 1526–1543.

Rudbeck, L. & Dissing, J. (1998) Rapid, simple alkaline extraction of human genomic DNA from whole blood, buccal epithelial cells, semen and forensic stains for PCR. *BioTechniques* **25**, 588–590.

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

Schneider, S., Roessli, D. & Excoffier, L. (2000) *Arlequin ver. 2000: A software for population genetics data analysis*. Switzerland, Genetics and Biometry Laboratory, University of Geneva.

Schwarzfischer, F. & Liebrich, K. (1963) Serologische untersuchungen an prähistorische bevölkerungen insbesondere an altkanarischen Mumien. *Homo* **14**, 129–133.

Schwidetzky, I. (1963) *La población prehispánica de las Islas Canarias*. Tenerife, Publicaciones del Museo Arqueológico de Tenerife.

Schwidetzky, I. (1975) *Investigaciones antropológicas en las Islas Canarias: estudio comparativo entre la población actual y la prehispánica*. Tenerife, Publicaciones del Museo Arqueológico de Tenerife.

Seielstad, M. T., Hebert, J. M., Lin, A. A., Underhill, P. A., Ibrahim, M., Vollrath, D. & Cavalli-Sforza, L. L. (1994) Construction of human Y-chromosomal haplotypes using a new polymorphic A to G transition. *Hum Mol Genet* **3**, 2159–2161.

Semino, O., Passarino, G., Oefner, P. J., Lin, A. A., Arbuzova, S., Beckman, L. E., De Benedictis, G., Francalacci, P., Kouvatsi, A., Limborska, S., Marcikiae, M., Mika, A., Mika, B., Primorac, D., Santachiara-Benerecetti, A. S., Cavalli-Sforza, L. L. & Underhill, P. A. (2000) The genetic legacy of Paleolithic Homo sapiens sapiens in extant Europeans: a Y chromosome perspective. *Science* **290**, 1155–1159.

Semino, O., Santachiara-Benerecetti, A. S., Falaschi, F., Cavalli-Sforza, L. L. & Underhill, P. A. (2002) Ethiopians and Khoisan share the deepest clades of the human Y-chromosome phylogeny. *Am J Hum Genet* **70**, 265–268.

Shen, P., Wang, F., Underhill, P., Franco, C., Yang, W.-H., Roxas, A., Sung, R., Lin, A. A., Hyman, R. W., Vollrath, D., Davis, R. W., Cavalli-Sforza, L. L. & Oefner, P. (2000) Population genetic implications from sequence variation in four Y chromosome genes. *Proc Natl Acad Sci USA* **97**, 7354–7359.

Stumpf, M. P. H. & Goldstein, D. B. (2001) Genealogical and evolutionary inference with the human Y chromosome. *Science* **291**, 1738–1742.

Suárez, J. J., Rodríguez, F. & Quintero, C. L. (1988) *Historia popular de Canarias. Vol. 2. Conquista y colonización*. Tenerife, Centro de la Cultura Popular Canaria.

Sun, C., Skaletsky, H., Rozen, S., Gromoll, J., Nieschlag, E., Oates, R. & Page, D. C. (2000) Deletion of azoospermia factor a (AZFa) region of human Y chromosome caused by recombination between HERV15 proviruses. *Hum Mol Genet* **9**, 2291–2296.

Thomas, M. G., Skorecki, K., Ben-Ami, H., Parfitt, T., Bradman, N. & Goldstein, D. B. (1998) Origins of Old Testament priests. *Nature* **394**, 138–140.

Underhill, P. A., Jin, L., Lin, A. A., Mehdi, S. Q., Jenkins, T., Vollrath, D., Davis, R. W., Cavalli-Sforza, L. L. & Oefner, P. J. (1997) Detection of numerous Y chromosome biallelic polymorphisms by denaturing high-performance liquid chromatography. *Genome Res* **7**, 996–1005.

Underhill, P. A., Shen, P., Lin, A. A., Jin, L., Passarino, G., Yang, W. H., Kauffman, E., Bonne-Tamir, B., Bertranpetit, J., Francalacci, P., Ibrahim, M., Jenkins, T., Kidd, J. R., Mehdi, S. Q., Seielstad, M. T., Wells, R. S., Piazza, A., Davis, R. W., Feldman, M. W., Cavalli-Sforza, L. L. & Oefner, P. J. (2000) Y chromosome sequence variation and the history of human populations. *Nat Genet* **26**, 358–361.

Veitia, R., Ion, A., Barbaux, S., Jobling, M. A., Souleyreau, N., Ennis, K., Ostrer, H., Tosi, M., Meo, T., Chibani, J., Fellous, M. & McElreavey, K. (1997) Mutations and sequence variants in the testis-determining region of the Y chromosome in individuals with a 46,XY female phenotype. *Hum Genet* **99**, 648–652.

Verneau, R. (1887) Rapport d'une mission scientifique dans l'Archipel Canarien. *Archives des Missions Sc. et Litté* (3er sér) **XVIII**, 567–817.

Whitfield, L. S., Sulston, J. E. & Goodfellow, P. N. (1995) Sequence variation of the human Y chromosome. *Nature* **378**, 379–380.

Wölfel, D. J. (1930) Sind die Ureinwohner der Kanaren ausgestorben? *Zeitschrift für Ethnologie* **62**, 282–302.

Y Chromosome Consortium (2002) A nomenclature system for the tree of human Y-chromosomal binary haplogroups. *Genome Res* **12**, 339–348.

Zerjal, T., Dashnyam, B., Pandya, A., Kayser, M., Roewer, L., Santos, F. R., Schiefenhovel, W., Fretwell, N., Jobling, M. A., Harihara, S., Shimizu, K., Semjidmaa, D., Sajantila, A., Salo, P., Crawford, M. H., Ginter, E. K., Evgrafov, O. V. & Tyler-Smith, C. (1997) Genetic relationships of Asians and Northern Europeans, revealed by Y-chromosomal DNA analysis. *Am J Hum Genet* **60**, 1174–83.

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