



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.

Received: April 14, 2003; Accepted: September 8, 2003.

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 an-

thropological 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

(Flores *et al.*, 2001, 2003), suggesting a highly asymmetric mating pattern after the European occupation. The Sub-Saharan African ancestry most likely reflects admixture with African slaves, considering that, during the colonial period, the Spanish forcibly introduced some 25,000 individuals (mostly from West Africa) into Madeira, Cape Verde and the Canary Islands (Curtin, 1969).

We present here data obtained from the investigation of 4 biallelic and 6 multiallelic Y-chromosome markers in samples from the island of Gran Canaria, from Spain and from North African Berbers. This new genetic data set was analyzed in conjunction with other relevant data from the literature. Additionally, we compared our results with those obtained with the same Y-chromosome markers in Colombia and Venezuela, both former Spanish colonies. Our results show a noticeable Guanche (Berber) contribution at the Y-chromosome level in Gran Canaria, while a Sub-Saharan African ancestry is negligible, in agreement with previous inferences using other sets of Y-chromosome markers. Additionally, we extended Ribeiro's (1970, 1977) typology to characterize the genomes of these admixed populations.

Subjects and Methods

Populations studied

Blood samples or oral swabs were collected from unrelated voluntary men from the Island of Gran Canaria (Las Palmas, N = 59), mainland Spain (Barcelona, N = 24; Valencia, N = 22) and from Moroccan Berbers (Ifani ethnic group, N = 60). The individuals from Barcelona had no Catalonian ancestry, but rather originated in various Spanish regions. Genomic DNA was extracted using the Nucleon extraction kit according to the manufacturer's instructions.

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 approximation to the effect of marker polymorphism on the estimation of admixture. Y-chromosome haplogroups were defined by typing the following biallelic or SNP (single nucleotide 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 potentially 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 microsatellites DYS19, DYS388, DYS390, DYS391, DYS392, and DYS393. This set of markers has been used in numerous 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 Canarians by Flores *et al.* (2003). The other four markers (DYS19, DYS388, DYS390, and DYS392) were never investigated 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 marker 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 microsatellite haplotype frequencies. Admixture was estimated by Long's (1991) method, using the ADMIX program kindly provided by the author.

Results and Discussion

We grouped our Gran Canaria, Berber and Spanish data set (Appendix) with other information from the literature. 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 populations from areas of early Spanish colonial influence (Colombia 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 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 Berber, Sub-Saharan African and Native American ancestry, as they reach frequencies of respectively 83%, 63% and 85% in those populations and low frequencies elsewhere. Haplogroup 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 exclusion 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				
	P-92R7*	Y*	DE-YAP**	E-M2	Q-M3 ⁶
	Frequency (%)				
Gran Canarians (N = 137) ¹	62	20	17	1	NT
Colombians (N = 80) ²	58	33	4	4	1
Venezuelans (N = 53) ³	65	26	9	0	0
Spanish (N = 124) ¹	80	15	5	0	NT
North African Berbers (N = 104) ¹	2	11	83	4	NT
Sub-Saharan Africans (N = 56) ⁴	0	12	25	63	NT
Native Americans (356) ⁵	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).

^{2,3}The individuals could be classified as white (L. Carvajal-Carmona and D. Castro-de-Guerra, personal communication).

⁴Hammer *et al.* (1997).

⁵Bortolini *et al.* (2002).

⁶The 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 Berbers¹.

Haplotype	Loci ²						Population		
	1	2	3	4	5	6	Spain (124)	Gran Canaria (59)	Berbers (104)
P-92R7* haplogroup									
1	14	12	24	11	13	13	0.174	0.168	
2	14	12	24	10	13	13	0.137	0.067	
3	14	12	23	11	13	13	0.016	0.051	
4	15	12	24	11	13	13	0.024	0.034	
5	15	12	23	11	13	13	0.024	0.017	
6	15	12	24	10	13	13	0.008	0.017	
7	14	13	24	10	13	13	0.008	0.017	
8	14	12	25	10	13	13	0.016	0.017	
9	14	12	25	11	13	14	0.008	0.017	
10	14	12	24	10	11	13	0.040		
11	14	13	23	10	11	12	0.008		
12	14	12	24	11	11	13	0.089		
13	14	12	25	11	13	13	0.032		
14	14	12	23	10	13	13	0.024		
15	14	12	23	11	13	14	0.016		
16	14	17	24	10	11	12	0.008		
17	14	17	24	11	13	13	0.008		
18	13	12	24	10	13	13	0.008		
19	14	12	25	10	13	12	0.008		
20	14	12	23	10	13	14	0.008		
21	13	12	25	10	13	12	0.008		
22	14	12	24	12	13	13	0.008		
23	15	12	23	10	11	13	0.008		
24	14	12	23	10	11	13	0.008		
25	14	12	23	11	14	14	0.008		
26	14	12	24	11	12	12	0.008		
27	14	12	24	10	11	14	0.008		

Table 2 (cont.)

Haplotype	Loci ²						Population		
	1	2	3	4	5	6	Spain (124)	Gran Canaria (59)	Berbers (104)
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									
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	21	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

Table 2 (cont.)

Haplotype	Loci ²						Population		
	1	2	3	4	5	6	Spain (124)	Gran Canaria (59)	Berbers (104)
DE-YAP* haplogroup									
84	13	12	24	9	11	13	0.024	0.068	0.274
85	13	12	24	10	11	13	0.016	0.051	0.038
86	13	12	23	9	11	13		0.017	0.100
87	13	12	25	10	11	14		0.017	0.010
88	14	15	22	10	11	12	0.008		0.010
89	14	12	24	10	11	13			0.010
90	13	12	23	10	11	13	0.008		
91	14	12	24	11	13	13	0.008		
92	13	13	24	9	11	13			0.067
93	13	12	25	9	11	13			0.038
94	13	12	22	9	11	13			0.038
95	13	12	24	9	11	14			0.019
96	16	12	24	10	11	13			0.019
97	12	12	24	10	11	13			0.010
98	13	13	23	9	11	13			0.010
99	13	13	22	9	11	13			0.010
100	13	12	25	9	11	12			0.010
101	13	12	24	9	11	12			0.010
102	14	12	22	9	11	13			0.010
103	14	12	24	9	11	13			0.038
104	13	12	23	8	11	13			0.010
105	15	12	24	10	11	13			0.010
106	13	13	25	10	11	13			0.010
107	16	12	24	9	11	13			0.010
108	16	12	21	10	11	14			0.010
109	13	12	24	10	10	13			0.010
110	13	12	24	11	11	13			0.010
111	13	12	23	10	11	14			0.010
112	13	12	25	10	11	13			0.010
113	15	12	25	10	11	13			0.010
114	14	12	22	10	11	13			0.010
E-M2 haplogroup									
115	17	12	21	10	11	14			0.010
116	16	12	21	10	11	14			0.010
117	16	12	21	10	11	15			0.010
118	14	12	21	10	11	13			0.010

¹North African Berber and Spanish samples include individuals typed by us (60 North African Berbers and 46 Spanish) and data (44 North African Berbers, and 78 Spanish) reported by Pérez-Lezaun *et al.* (1997) and Bosch *et al.* (1999).

²1 = DYS19, 2 = DYS388, 3 = DYS390, 4 = DYS391, 5 = DYS392, 6 = DYS393). Alleles are numbered according to the number of repeats (Kayser *et al.* 1997). In five instances identical haplotypes occurred in a different haplogroup background: 1 (P-92R7*) = 71 (Y*) = 91 (DE-YAP*); 10 (P-92R7*) = 89 (DE-YAP*); 11 (P-92R7*) = 82 (Y*); 47 (P-92R7*) = 113 (DE-YAP*); and 55 (Y*) = 114 (DE-YAP*).

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-haplotype frequencies to be used in the admixture analysis, using 10 haplotype groups defined as detailed above. Parental contributions in Gran Canarians are $82\% \pm 6\%$ Spanish and $18\% \pm 6\%$ 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 another set of Y-markers but with the same admixture analysis method, which estimated these contributions as being $90\% \pm 4\%$, $9\% \pm 4\%$, and $1\% \pm 1\%$, respectively (Flores *et al.*, 2003).

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 $45\% \pm 20\%$ Spanish and $55\% \pm 20\%$ 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

Table 3 - Parental contribution in Gran Canarian and Colombian populations based on autosomal, Y-chromosome and mtDNA data sets.

Population	Parental contribution		
	Spain	Natives ¹	Sub-Saharan Africa
Gran Canaria			
Autosomes ²	72	22	6
MtDNA ³	45	55	0
Y-chromosomes ⁴	86	14	<1
Colombia ⁵			
Autosomes	75	15	15
mtDNA	1	91	8
Y-chromosomes	93	4	3

¹Guanche (Berber) for Gran Canarians, and Native Americans for Colombian populations.

²Compiled from Roberts *et al.* (1966).

³Values calculated by us from mtDNA haplogroup frequencies furnished by Flores *et al.* (2001), using Long's least square method.

⁴Arithmetic mean values calculated from our admixture numbers and those obtained by Flores *et al.* (2003).

⁵Data of Carvajal-Carmona *et al.* (2000) and Carvajal-Carmona *et al.* (unpublished).

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 autosome 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

part of the lost 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.

Acknowledgements

We are very grateful to the individuals who donated samples for this study, and thank Luis G. Carvajal-Carmona for stimulating discussions. Special acknowledgement is due to F. Sánchez-García, J.C. Rodríguez-Gallego and M.C. Déniz-Naranjo for the Gran Canarian, and J.M. Soria, J.L. Pérez-Arellano and A.S. Auñón for the Spanish samples. MCB was a Wellcome Trust Travelling Research Fellow (Grant 059763 to M-C B and A. R-L) during 2000-2001. LC is supported by a BBSRC grant (31/G13580) to Ziheng Yang (University College London).

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Editor: Angela M. Vianna-Morgante

Appendix - Data obtained in the present study.

Population	SNP-haplogroup	No. of chromosomes	STR-haplotypes ¹ (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); 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)

¹Haplotype numbers according to Table 2.