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Mitochondrial DNA characterisation of European isolates: The Maragatos from Spain

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Mitochondrial DNA analysis confirms that Maragatos from Spain are a genetically isolated human group. Genetic distances between Maragatos and the comparison samples are significantly different even with the León sample ($P < 0.001$) which shares the same geographic area as the Maragatos. Although the north-African haplogroup U6 is present in them, their attributed Berber origin is weakened, as this haplogroup is also detected in surrounding populations with which, in addition, Maragatos have the smaller genetic distances. These U6 haplotypes are ascribed to a pre-historic African colonisation that influenced all the Iberian Peninsula. The presence of Neolithic haplogroups in this sample suggests that their isolation culture was not absolute until recent times. *European Journal of Human Genetics* (2001) 9, 708–716.

Keywords: human isolates; Maragatos; mtDNA; haplogroups

Introduction

The genetic characterisation of isolated populations is relevant to accomplish several scientific goals as those related to disease mapping, human diversity or human history. In Europe, the genetic heterogeneity of the Iberian Peninsula at mitochondrial DNA (mtDNA) level has been repeatedly confirmed,^{1,2} the Basques being the most outstanding and best studied population.^{2,3} The analysis of new Iberian isolates other than the Basques may help to unravel the relative influence that pre-historic and historic colonisers, with different geographic origins, had on the extant Iberian population. Here, we deal with one of these alternative groups, the Maragatos. Although very little is known outside Spain, the Maragato is one of the most interesting human cultural isolates in the Iberian Peninsula. They inhabit a western mountainous region in the province of León in the north of Spain (Figure 1). During the last century their census was steady around 10 000 inhabitants, but in the last years this number has dropped to about 3000, mainly due to emigration.⁴ Nevertheless these emigrants faithfully con-

serve their isolated and endogamic customs. That the Maragatos have developed agriculture in this area and itinerant merchant activity throughout the Iberian Peninsula since the Middle Ages are well-documented facts.⁵ Their cultural peculiarities with attributed resemblances to North African Berbers or to Near East Semitic cultures have differentiated them from their surrounding neighbours ever since. After sometimes bizarre etymological interpretations, today it is generally accepted that the name comes from their trading activity, as a popular derivative of the Latin word 'mercatores' that is merchants, and has nothing to do with their ethnic origin. However, archaeological, anthropological and ethnographical studies point to an ancient human continuity in this area.⁵ At least three different interpretations about their origins have been proposed: (1) they are descendants of North African Berbers that settled in this area after the Moslem invasion;⁶ (2) they are Goths, allied to the Moslems, that adopted the Berber culture; (3) they have a Celtic ancestry as their surrounding neighbours, but with a differential Semitic component brought by the Phoenicians in pre-Roman times. The most interesting characteristic of the Maragatos is their cultural isolation that, due to their voluntary endogamy, has created a barrier against external marriages. This behaviour has presumably caused a genetic differentiation between this group and its neighbours by genetic drift. At the same time it might keep some genetic

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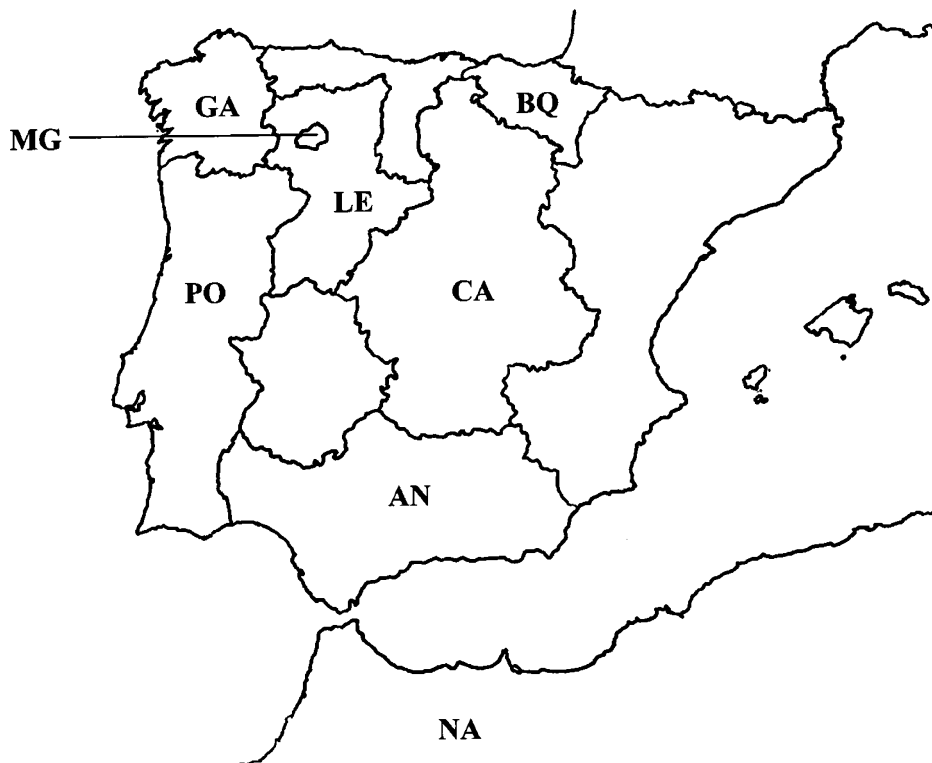


Figure 1 Geographic location of the populations sampled. Population codes as in Materials and methods

clues from their unknown ancestors. Fortunately, it is possible to test these suppositions from a molecular genetics perspective. Recent studies of maternally inherited mtDNA, based on restriction fragment length polymorphisms (RFLPs) and on sequences of the mtDNA hypervariable regions HVI and HVII, have revealed the sequence motifs which define the most common haplogroups and subhaplogroups.⁷ Some of them have their geographic origin well established^{8,9} and, therefore, can be used to reconstruct the genetic history and composition of extant carrier populations. The application of this type of analysis to find out the genetic structure and possible origin of the Maragatos is the principal aim of this study.

Materials and methods

Population samples

A total of 198 unrelated individuals natural from different Iberian regions (Figure 1) voluntarily and anonymously donated blood for this study. Their origins were as follows: 49 Maragatos (Mg) from the Astorga district, 61 individuals from the province of León (Le) (42 of them also from the Astorga district), 38 from Castile (Ca) and 50 from Andalusia (An). In addition, published and unpublished data from other populations as detailed in their references, were incorporated in the analysis: 353 Portuguese (Po)² (González

et al, personal communication), 135 Galicians (Ga)¹⁰ (González *et al*, personal communication), 167 Basques (Bq)^{2,3,11,12} (Larruga, personal communication), 349 North Africans (Na)^{2,8,13} (Larruga, personal communication), and 15 Andalusians.²

Sequencing

Total DNA was isolated from 5 µl of blood,¹⁴ PCR amplified,¹⁵ and directly sequenced for both complementary strands.⁸ The sequences of 403 bp of the first hypervariable segment (HVSI) of the control region of the mtDNA, from position 15997 to 16399,¹⁶ were determined and aligned. To discriminate for ambiguous haplogroup classification, all individuals, sorted by sequence motif as H or U¹⁷ were also analysed by restriction for the polymorphic site 12308¹⁷ and for site 73,¹⁸ the latter characterised using the L29 (5'-gTCTATCACCCTATTAACCAC-3') and H408 (5'-TgTTAAAAGTgCATACCGCCA-3') primers and the Alw44 I restriction enzyme. When ambiguity in haplogroup sorting persisted, the following additional sites were tested: 7025 *AhaI*,¹⁷ 14766 *MseI*,¹⁹ 4577 *NlaIII*,¹⁷ 4216 *NlaIII*,⁷ and 10871 *MnII*.²⁰

Phylogenetic analyses

Gene diversity was measured as H values.²¹ Pairwise population comparisons were estimated as linearized Fst

distances as implemented in the ARLEQUIN program, considering mtDNA as one locus with as many alleles as different haplotypes detected.

Phylogeographic analyses

All the sequences used in this study have been sorted into molecular clusters (haplogroups).⁷ Relative frequency of identical sequences (matches) among and between areas, within haplogroups with assigned geographic origin,⁷ has been used to refine the global affinities obtained from *Fst* distances.

Results

Global analysis

Table 1 lists our 198 analysed sequences according to their haplogroup status. The number of different sequences to the sample size rate is the lowest in Maragatos (0.49) and the highest in Andalusian (0.92) reaching habitual levels in León (0.69) and Castile (0.76). In a similar vein, values of gene diversity (*H*) are significantly lower in Maragatos (0.87) than in any other population (0.9460 ± 0.0066) confirming at genetic level the historic endogamy attributed to the Maragatos. Table 2 shows the pairwise *Fst* distances between all the samples used in this study. The CRS sequence accounts for 91% of all matches. Differences in frequency for this haplotype, that ranges from Maragatos (0.31) to Andalusian (0.14) and North Africans (0.12) play a determinant role on the *Fst* values, for this, distances have been calculated with (above the diagonal) and without (below diagonal) CRS. Three populations are significantly well differentiated: North Africans for which geographic and cultural barriers with the Iberian Peninsula have always existed, and the two Iberian recognised outlayers: Basques and Maragatos. The latter has smaller distances with the geographically closer populations of León, Galicia and Portugal (Figure 1) than with Andalusia or North Africa, weakening the hypothesis of a Berber origin for the Maragatos. On the other hand, although the lowest distance of Maragatos is with León, this is the highest distance that León has with any other Iberian population. This data can be taken as the second proof of the genetic isolation of Maragatos. As from now, due to the lack of significance and relative geographic proximity (Figure 1), Galicia and Portugal will be merged as West Peninsula (WP) and León-Castile as Center Peninsula (CP).

Phylogeographic analyses

Table 3 presents the relative frequency by area of haplogroups with geographic and/or temporal founder assignation.^{7,11,22} Both frequencies and the distribution of matches among them give new insights into the nature of the maternal genetic affinities among areas. In the Iberian Peninsula, Maragatos have the greatest frequencies for U5a1a, J* and, excepting Basques, H/HV*/U*/R*, but this is due to the presence of only one or a few haplotypes in high frequency

(Table 1), which, again supports their genetic isolation, as the lack of representation for some widespread sub-haplogroups as V. The distribution of U6 deserves special comment. This sub-haplogroup has a putative North African origin.^{2,8} In Europe it has only been detected in the Iberian Peninsula but with higher frequencies in northern than southern areas (González *et al*, personal communication) (Table 3). This distribution and its high diversity in Iberia has ruled out that historic events such as the Moslem occupation⁶ are the main causes of its presence in the Peninsula which has been attributed to a pre-historic African colonisation. Again its high frequency in Maragatos is due to only one haplotype that differs by five mutations from the one detected in neighbouring León. The same sequence has not been found in North Africa but is present once in our small Andalusian sample. Apart from H/HV*/U*/R*, that represents 98.26% of all matches with greater mean values with northern (23.59 ± 0.80) than southern (13.74 ± 1.58) populations, Maragatos present other interesting matches. They share exclusively with Basques the widespread haplotype T* 126, 294, 296, and the infrequent T* 294, 296, 304 that apart from this area has only been detected in Sardinia. Other matches with northern, including Basques, but not southern areas include widespread haplotypes within U2 and W. Matches, in which Basques are excluded, are within the relatively recent sub-haplogroups U5a1* and J*. Haplogroup frequencies in the other Iberian regions also show interesting clues about their relative influences. Andalusia and its neighbouring area in West Peninsula show the greatest sub-Saharan African influences. The high frequency of M1 haplotypes in Andalusia is worthy of mention. Haplogroup M had a probable East African origin from where it expanded to the East to India.²⁰ However, the distribution of sub-haplogroup M1 is mainly African. It spread northwards to Egypt²³ and west to Morocco and Senegal.²⁴

The small number of haplotypes sampled does not allow an estimation of the time of arrival in southern Iberia. Other characteristics of Andalusia are its moderate frequency of CRS and in general of H/HV*/U*/R* (Table 3) more similar to North Africa than to northern Iberia, and the high contribution of lineages with a Neolithic arrival to Europe (T1, J1a*, J1b* and J2), some of them (J1b* and J2) characteristic of the Mediterranean area.²² Similarly, derivatives of the European haplogroup U5 with strong Mediterranean implantation have also relatively high frequencies in Andalusia. The opposite happens with Basques, where the absence of Neolithic representatives is outstanding. They lack T1, U3 and the majority of J, although the basal J* is present. On the other hand, cluster U5 is well represented in its basal branches U5* and U5a* but the more derived ones are absent. Relative sequence sharing with the other areas relates Basques first with Central Peninsula (*Fst*=0.0016) and second with West Peninsula (0.0060), showing more divergent values with Andalusia (0.0084) and North Africa (0.0139). Basques share with Central Peninsula-Andalusia mainly

Table 1 HVS I haplotypes and RFLPs in Maragatos, Leonese, Castile and Andalusia samples

Sequence Type HVS-I (16...)	00073	14766u	Additional Sites ¹ 12308G	other	Mg	Populations ² Le	Ca	An
H/HV*/U*/R*								
CRS	A	—	—	—7025a	13	14		7
CRS	G	—	—	—7025a	1		7	
CRS			—					
CRS	G	+	+	+7025a	1	1	1	
093			—					
129	A	—	—			2		1
140	G	—	—	—7025a		1		
145	A		—			1		
176	A		—					1
179	A		—					1
187	A		—			1		
188	A		—			1		
188A	A	—			1			
188G	A	—		—7025a		1		
189	A	—				2		
192			—				1	
209	A		—					1
221	A	—	—	—7025a				1
240	A		—			1		
259	A	—			1			
265C	A	—				1		
286			—				1	
291	A	—				1		
293	A	—	—					1
304	A	—	—		1	1		
305	A		—					1
320A	A	—			1			
320	A	—			1			
354	A	—				1		
355	A	—			1			
362	A	—	—		1			1
362	A	—	—	—7025a		1		
362			—				1	
069 304			—				1	
093 126	A	—	—	—7025a		1		1
093 129	A		—			1		
093 251	A	—			1			
145 222	A		—					1
189 265C	A	—		—7025a		1		
207 286	A	—			2	1		
222 301	A	—			1			
239 242	A		—	—7025a				2
249 362	A		—					1
304 325			—				1	
311 362			—				3	
086 189 356	A	—		—7025a		1		
093 251 311	A	—			2			
114 217 218	A	—	—			1		
176 218 234	A		—			1		
189 255 278			—				1	
189 255 278	G	+	—	—4216q				1
218 328A 362			—				1	
304 320 335	A		—					1
311 319 321	G	+	+	+7025a				1
					28	37	18	23
V (298)								
298				—4577q		1		1
093 298				—4577q				1
153 298							1	
192 298				—4577q				1
291 298	A	—		+7025a —4577q		1		

Continued

Table 1 (Continued)

Sequence Type HVS-I (16...)	00073	14766u	Additional Sites ¹ 12308G	other	Mg	Populations ² Le	Ca	An
292 298							1	
234 274 298 311				−4577q	0	1	2	3
U2 (129C 189)								
051 129C 189 362	G		+		1	2		
051 129C 189 319 362	G		+			1		
051 092 129C 183C 189 362				+7025a	1	3	0	1
U3 (343)								
172 343 362					0	0	1	0
U4 (356)								
179 356								1
265 356 362					0	0	1	1
U5* (270)								
129 270					0	1	0	0
U5a* (192 270)								
067 192 270	G		+			1		
114G 189 192 270								1
189 192 270 311	G		+			1		
189 192 270 311 336								1
192 251 259 270 304					0	2	0	3
U5a1* (192 256 270)								
192 256 270	G		+		1		1	
104 189 192 256 270								1
148 192 196 256 270	G		+		1	1	1	1
U5a1a (256 270)								
256 270 293 304	G		+		3		1	
256 270 294 391					3	0	1	0
U6 (172 219)								
092 172 219 278							1	
172 174 219 311	G	+	+	+7025a				1
172 174 219 311	G		+		4			
172 189 219 239 278	G		+		4	1	1	1
K (224 311)								
224 311	G	+	+			2	1	
093 224 311	G		+			1	1	
129 224 311							1	
145 224 311	G	+	+			1		
224 311 320								1
224 311 362								1
093 167 224 311	G	+	+	+7025a				
				−4216q	1			
025 093 224 266 311	G	+	+	−4216q	1	1	3	2
T* (126 294)								
126 153 294	G	+		+4216q		1		
126 294 296	G	+			1			
294 296 304	G	+		+4216q	1			
126 266 294 304							1	
126 294 296 304							1	
126 147 294 296 304								2
126 243 278 292 294 296					2	1	2	3
T1 (126 163 186 189 294)								
126 163 186 189 294	G	+	—			1	1	2
126 163 186 189 289 294	G	+				1		
					0	2	1	2

Continued

Table 1 (Continued)

Sequence Type HVS-I (16...)	00073	14766u	Additional Sites ¹ 12308G	other	Mg	Populations ² Le	Ca	An
J* (069 126)								
069 126	G	+		+4216q	1		2	
069 126 189	G	+	—	+4216q	4			
069 126 148 189	G	+			2			
069 126 278 366						1	1	1
069 126 148 278 366					7	1	3	1
J1a* (069 126 145 231 261)								
069 126 145 231 261								1
069 126 145 189 231 261							1	
069 126 145 171 189 231 261								1
					0	0	1	2
J2 (069 126 193)								
069 126 193	G	+				1		1
069 126 193 278						1		
069 126 193 300	G	+		+4216q	1			
069 093 126 193 311					1	2	0	2
								3
I (129 223)								
129 148 223 391	G	+		+10871m		1		
					0	1	0	0
W (223 292)								
223 292	G			—8994e +10871m	1		1	
							1	1
223 292 295							1	
223 292 311					1	0	3	1
M1 (129 189 223 249 311)								
129 189 223 249 311								1
129 183C 189 223 249 311								1
					0	0	0	2
L1b (126 187 189 223 264 270 278 311)								
126 187 189 223 264 270 278 293 311	G			+3592h	0	1	0	0
L2 (223 278 390)								
223 278 294 390					0	0	0	1
								1
Total					49	61	38	50

¹a = *AluI*; e = *HaeIII*; h = *HpaI*; m = *MnII*; q = *NlaIII*; u = *MseI*; ²population codes as in Materials and methods.

Table 2 Linearized F_{ST} obtained when comparing the populations analysed for all the haplotypes (above the diagonal) and for all the haplotypes except the CRS (below the diagonal), and their signification. Population codes as in Materials and methods

	Po	Ga	Mg	Le	Ca	Bq	An	NA
Po		0.00000	0.00863*	0.00000	0.00024	0.00655**	0.00444	0.00954***
Ga	0.00031		0.01016*	0.00000	0.00000	0.00409*	0.00299	0.00837***
Mg	0.01588***	0.01720***		0.00535	0.01211	0.01707**	0.01950**	0.02728***
Le	0.00000	0.00000	0.01461***		0.00082	0.00278	0.00344	0.00977***
Ca	0.00212	0.00223	0.01597**	0.00370		0.00715	0.00000	0.00449
Bq	0.01100***	0.00814***	0.02689***	0.00653*	0.01443**		0.00839*	0.01392***
An	0.00200*	0.00216	0.01557***	0.00006	0.00112	0.01110***		0.00343
NA	0.00488***	0.00580***	0.02101***	0.00433*	0.00622*	0.01516***	0.00556**	

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

haplotypes belonging to J*, J1a* and U5a*, whereas with Central and West Peninsula they have the highest proportion of matches within H/HV*/U*/R*, all within U2 and X and the basal haplotype (223, 292) of W, all of them having a pre-Neolithic expansion in Europe. Finally, Central Peninsula

seems to be well connected by maternal gene flow with the Atlantic area and with Andalusia. In fact, it is not significantly different from either of them (Table 2). The three areas account for all the matches in T1, U5a1*, J2 and derived haplotypes within W, all with a probable Neolithic

Table 3 Percentage of haplogroups and CRS in the different regions analysed. Population codes as in Materials and methods and Results

Population	NA	AN	WP	MG	CP	BQ
Sample	349	65	488	49	99	167
CRS	11.75	13.85	22.34	30.61	22.22	20.96
H/HV*/U*/R*	30.95	41.54	54.10	57.14	55.56	62.28
pre-*HV (126 362)	0.86		1.02			
V (298)	5.16	4.62	3.48		5.05	10.18
U1 (249)	0.29					
U2 (129C 189)		1.54	1.02	2.04	3.03	0.60
U3 (343)	3.15		1.02		1.01	
U4 (356)		1.54	1.43		1.01	
U5* (270)	0.57				1.01	0.60
U5a* (192 270)	1.15	4.62	1.43		2.02	11.38
U5a1* (192 256 270)	0.86	3.08	0.82	2.04	2.02	
U5a1a (256 270)			0.41	6.12	1.01	
U5b (189 270)	1.15		0.61			
U6 (172 219)	14.90	1.54	2.05	8.16	2.02	0.60
U7 (309 318T)						0.60
K (224 311)	3.44	7.69	6.15	2.04	8.08	3.59
T* (126 294)	2.87	4.62	5.74	4.08	3.03	4.79
T1 (126 163 186 189 294)	2.29	4.62	2.46		3.03	
J* (069 126)	3.15	1.54	4.51	14.29	4.04	1.80
J1* (069 126 261)	0.29					
J1a (069 126 145 231 261)	0.57	3.08			1.01	0.60
J1b* (069 126 145 222 261)	0.29	3.08	0.20			
J1b1 (069 126 145 172 222 261)			0.61			
J2 (069 126 193)		4.62	1.23	2.04	2.02	
N1b (145 176G 223)	0.29		0.20			
I (129 223)		1.54	0.82		1.01	
W (223 292)	0.29	3.08	2.46	2.04	3.03	1.20
X (189 223 278)	1.15	1.54	1.23			1.20
L3* (223)	2.29		1.23			0.60
L3b (124 223 278 362)	2.29		0.61			
L3d (124 223)	0.86					
L3e (172 223 320)	1.15		1.02			
M1 (129 189 223 249 311)	2.29	4.62	0.41			
L1a (129 148 172 187 188G 189 223 230 311)	0.57					
L1b (126 187 189 223 264 270 278 311)	6.59		1.23		1.01	
L1c (129 189 223 278 294 311 360)	0.57		0.20			
L2 (223 278 390)	9.74	1.54	2.25			

expansion. On the other hand, matches between West and Central Peninsula with Andalusia excluded, are within T* and J*.

Discussion

It is confirmed at genetic level that the Maragato is a divergent human isolate in the Iberian Peninsula. Genetic drift due to small population size and voluntary endogamy seems to be the main cause of this isolation. As a consequence, rare haplotypes have reached notable frequencies in this population. In relation to its origin some hypotheses may be discarded. The presence of sub-haplogroup U6 of North African ascription does not make them different from their Iberian neighbours that also have U6 representatives, in fact an identical sequence has been found in Andalusia but not in North Africa. Therefore, a recent

origin of the Maragatos as descendants of North African Berbers established in the Iberian Peninsula after the Moslem invasion and remaining since then isolated can be ruled out, at least for the ancestral maternal component of the population. However, what seems to be true is that Maragatos share with the majority of the Iberians an ancient North African influence. The fact that this North African input did not go beyond the Pyrenees is also against the hypothesis that the Maragatos were Goths that helped the Moslem invaders and assumed the Berber culture. Certainly Goths conquered the Iberian Peninsula around 600 A.D. after the fall of the Roman Empire but they were only a dominant elite with small demographic impact on the indigenous Iberian population. In spite of important drift effects it has been demonstrated that the Maragatos share a common genetic background with their surrounding neighbours, mainly from León but also from Galicia and Portugal. Haplotypes with a

Neolithic dispersion are present in the Maragatos. This proves that their ancestors were a permeable group in Neolithic times, however we have not detected any haplotype with an exclusive Near East ascription, which could support a differential Semitic component with its neighbours. What genetics cannot explain is from where, when and why the Maragatos adopted their peculiar and isolated culture.

The analyses of new Iberian samples has also helped to clarify the nature and level of the previously detected mtDNA regional heterogeneity in Iberia.^{2,3} The Basque is another Iberian outlier better studied than Maragatos. Our comparative analysis is in agreement with the hypothesis that they represent a Palaeolithic isolate with little Neolithic demic input as deduced from the shortage of Neolithic lineages (2.4%). It is also in favour of the existence of a common genetic background between Basques and other Iberian populations as has been repeatedly proposed^{2,25,26} and against the Georgian connection suggested on the basis of language concordances²⁷ and on the relative sharing of some nuclear markers.²⁸ Within the Iberian Peninsula, Basques have the smallest distances with their nearby populations of Central Peninsula and Galicia. With the same method employed here and using published sequences^{9,29–31} we calculated distances of Basques to Germans ($F_{st}=0.016$) and British ($F_{st}=0.017$) which are at least four times greater than those of Basques with León (0.003) or Galicia (0.004) and significantly different ($P<0.01$) to them. Furthermore, it has recently been demonstrated, using mtDNA sequences, that Basques do not present a closer relation to Georgians than to the rest of European populations.³² Finally, the comparatively higher diversity of Andalusia that was previously detected in a small sample² is confirmed here. Due to its geographical localisation, Andalusia has been a permanently open door to human movements since the Palaeolithic and this seems to be the most probable cause of its genetic complexity. In addition to the Palaeolithic substrate, Andalusia has by far the highest frequency (17%) in the Iberian Peninsula of lineages expanded with the Neolithic (J+T1+U3) and a noticeable African influence (7.7%) detected by the presence of lineages (L2+M1+U6) originated in that continent.

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