



OPEN

Middle eastern genetic legacy in the paternal and maternal gene pools of Chuetas

J. F. Ferragut¹✉, C. Ramon¹, J. A. Castro¹, A. Amorim^{2,3,4}, L. Alvarez^{2,3,5} & A. Picornell¹

Chuetas are a group of descendants of Majorcan Crypto-Jews (Balearic Islands, Spain) who were socially stigmatized and segregated by their Majorcan neighbours until recently; generating a community that, although after the seventeenth century no longer contained Judaic religious elements, maintained strong group cohesion, Jewishness consciousness, and endogamy. Collective memory fixed 15 surnames as a most important defining element of Chueta families. Previous studies demonstrated Chuetas were a differentiated population, with a considerable proportion of their original genetic make-up. Genetic data of Y-chromosome polymorphism and mtDNA control region showed, in Chuetas' paternal lineages, high prevalence of haplogroups J2-M172 (33%) and J1-M267 (18%). In maternal lineages, the Chuetas hallmark is the presence of a new sub-branching of the rare haplogroup R0a2m as their modal haplogroup (21%). Genetic diversity in both Y-chromosome and mtDNA indicates the Chueta community has managed to avoid the expected heterogeneity decrease in their gene pool after centuries of isolation and inbreeding. Moreover, the composition of their uniparentally transmitted lineages demonstrates a remarkable signature of Middle Eastern ancestry—despite some degree of host admixture—confirming Chuetas have retained over the centuries a considerable degree of ancestral genetic signature along with the cultural memory of their Jewish origin.

Jewish communities in the Balearic Islands date back to the fifth century AD¹. With the Christian conquest of Majorca in 1229, their physical survival was guaranteed, despite social and religious pressures forcing their conversion to Christianity between 1391 and 1435. Consequently, there were officially no more Jews in Majorca nearly 60 years before the Edict of Expulsion by the Catholic Kings in 1492. Many of these converted Jews were integrated in the general population; however, a few families remained in the ghetto and secretly adhered to Judaism, forming a Crypto-Jewish community which was persecuted by the Inquisition (fifteenth–seventeenth centuries)². The last “Autos de Fe” in 1691 put a stop to their hidden Jewish religious practices, and this population of convicts and their descendants came to be known as Chuetas, a word probably derived from the Catalan for Jew³, with their social stigma and segregation (imposed by their Majorcan neighbours) continuing until the mid-twentieth century. There was a definitive point of inflection when Majorca opened to tourism, as the arrival of newcomers (Spaniards or foreigners) who had no knowledge of the status of Chuetas led to a decrease in anti-Chueta prejudice. Therefore, Chuetas were an isolated population with very scarce intermarriage with the Majorcan host population until recently⁴. One of the most important defining elements of this group is that they bear one of the 15 surnames of converso lineages (Aguiló, Bonnín, Cortès, Fortesa, Fuster, Martí, Miró, Picó, Pinya, Pomar, Segura, Tarongí, Valentí, Valleriola, and Valls) targeted by the inquisitorial sentences for Crypto-Judaism in the last quarter of the seventeenth century⁵. Some of these surnames are common in other Spanish regions, where they are not related to Judaism. In Majorca, however, they have been fixed in the collective memory by their identification as Chueta families.

The rise of modern Population Genetics in the second half of the twentieth century enabled geneticists to endeavour to define the origins and relatedness of Jewish people⁶. Since then, populations with Jewish origin have been analysed by means of uniparental and recombining markers^{7–12}, and more recently also through

¹Institut Universitari d'Investigació en Ciències de la Salut (IUNICS) i Laboratori de Genètica, Departament de Biologia, Universitat de les Illes Balears, Carretera de Valldemossa, km 7.5, 07122 Palma de Mallorca, Illes Balears, Spain. ²IS-Instituto de Investigação e Inovação em Saúde, Universidade do Porto, Rua Alfredo Allen, 208, 4200-135 Porto, Portugal. ³PATIMUP-Instituto de Patologia e Imunologia Molecular da Universidade do Porto, Rua Júlio Amaral de Carvalho, 45, 4200-135 Porto, Portugal. ⁴Faculdade de Ciências da Universidade do Porto, Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal. ⁵TellmeGen, Calle Arquitecto Mora, 5-4, 46010 Valencia, Spain. ✉email: jf.ferragut@uib.es

genome-wide SNP arrays^{13–18}. The combined analysis of millions of polymorphic markers along the genome have led to greater precision in the clustering of different Jewish groups and to the ability to estimate the Middle Eastern, European, and African components in each group. These analyses reflect that each of today's Jewish populations is the result of the blending of Middle Eastern and host populations (European, Asian, or African). Regarding haploid markers, on the one hand, male lineages indicate that most Jewish communities share a common Middle Eastern ancestral origin, and remained relatively isolated from neighbouring non-Jewish communities during the Diaspora. On the other hand, mtDNA studies lead to conclude that there are differences in the demographic history of the widespread communities resulting from the Jewish Diaspora in terms of maternal ancestries, indicating different maternal founder effects.

Converted Jews have also been subject of study, either due to their contribution to the host population genetic pool^{19–21}, or owing to their isolation and differentiation from their neighbours, such as the Portuguese Crypto-Jew communities in Belmonte and Bragança^{22–24} or the Chuetas in Majorca, the subject of the present study. Chuetas have been previously studied by means of autosomal and X-chromosome markers^{25–29}. The results conducted to date demonstrate that Chuetas are a differentiated population that has kept a considerable proportion of its original genetic make-up, especially clear in some markers where Chuetas show polymorphic frequencies of alleles that are very rare in neighbour populations, but not in Middle Eastern populations³⁰. However, a certain degree of admixture from and with the host population has also been detected^{26,29}.

In this study, we focus on haploid markers in order to investigate the ancestry and demographic history of the maternal and paternal founding lineages of the Chueta population, and to analyse whether cultural isolation has led to the reduction of genetic diversity in mtDNA and Y-chromosome lineages in this population.

Materials and methods

Population sampling. For the study of the Y-chromosome, samples from 146 unrelated males were obtained: 100 from the Chueta population, and 46 from Majorca (Balearic Islands, Spain), included as the host population of Chuetas. The Majorcan samples constitute a subset of a larger sample previously genotyped for 12 Y-STRs³¹. For mtDNA analyses, 183 samples were used: 104 non-maternally related individuals from the Chueta population (some of these samples were used in a preliminary analysis in a conference contribution³²) and 79 Majorcans. All participants provided appropriate informed consent statements, approved by the "Direcció General de R + D + I" (Government of the Balearic Islands, Spain), and the University of the Balearic Islands (procedure AAEE24/2014), following the procedures approved by the Ethics Committee of the University of Porto (N102/CEUP/2012). Anonymity of the recruited samples was preserved during the study. All methods were carried out in accordance with the guidelines and regulations of the Declaration of Helsinki.

DNA extraction. DNA was extracted by standard phenol–chloroform method and quantified on a NanoVue Plus spectrophotometer (GE Healthcare Life Sciences, Cambridge, UK).

Genotyping analyses. *Y-chromosome.* Seventeen Y-chromosome STR markers were amplified using the Y-filer kit (Applied Biosystems, Foster City, CA, USA), following the manufacturer's recommendations. Thirty-eight SNPs were typed to define the major male lineages. Thirty-two of them were genotyped using SNaPshot kit (Applied Biosystems) in five multiplexes as previously described^{21,33–35} (Fig. 1). M1 and M269 were genotyped with conventional PCR followed by agarose gel electrophoresis; S116, M17, and M18 were genotyped by Sanger sequencing; and DYS458.2 was used to determine the J1 chromosomes³⁶.

Y-STR amplification products and Y-SNP purified minisequencing products were separated in an ABI PRISM 3130 Genetic Analyser, and electropherograms were analysed using GeneMapper ID software v3.2 and Peak Scanner software (Applied Biosystems). Y-STR alleles were designated according to ISFG recommendations³⁷, and Y-SNP haplogroups according to the latest ISOGG update (2019).

Mitochondrial DNA. The mitochondrial DNA control region, or D-loop (16024–576), was amplified with two overlapping fragments using mtDNA-specific primers (L15997, H016 and L16555, H639)³⁸. The amplified product was purified with the MBS Spin PCRapace kit (Invitek, Berlin, Germany), and subsequent sequencing reactions were carried out using the BigDye Terminator v3.1 Cycle Sequencing kit (Applied Biosystems), following the manufacturers' procedures. Finally, products were run in an ABI prism 3130 analyser.

Sequences were assembled and compared to the revised Cambridge Reference Sequence (rCRS) (NC_012920) using Geneious software version 7.1.3 (Biomatters, Ltd., Auckland, New Zealand). Haplogroups were classified following the updated mtDNA phylogeny, PhyloTree, mtDNA tree Build 17 (<http://www.phylotree.org/>) using HaploGrep2 tool^{39,40}, and assigned haplotypes were validated by EMPOP (<http://empop.org/>) curators.

Moreover, the entire mtDNA molecule was sequenced for six Chueta samples belonging to the modal haplogroup R0a + 60.1 T. Amplification of the whole molecule was carried out by 19 overlapping fragments, and the sequencing strategy used 31 smaller fragments, primers, and specifications as described in Ramos et al.^{41,42}. When Chueta specific mutations were identified in the complete mtDNA molecule, the status of such nucleotide positions was interrogated in the rest of the samples belonging to the haplogroup.

Data analysis. Haplogroup frequencies were estimated by gene counting. Allele and haplotype frequencies, molecular diversity indices, Analysis of Molecular Variance (AMOVA), as well as the corresponding non-differentiation p-values, and Y-chromosome pairwise F_{ST} genetic distances were assessed using Arlequin v3.5.1.2⁴³. For easier visualisation of the genetic distances observed, a multidimensional scaling (MDS) plot of the pairwise F_{ST} matrix was represented using SPSS v.15.0 (SPSS, Inc., Chicago, IL, USA).

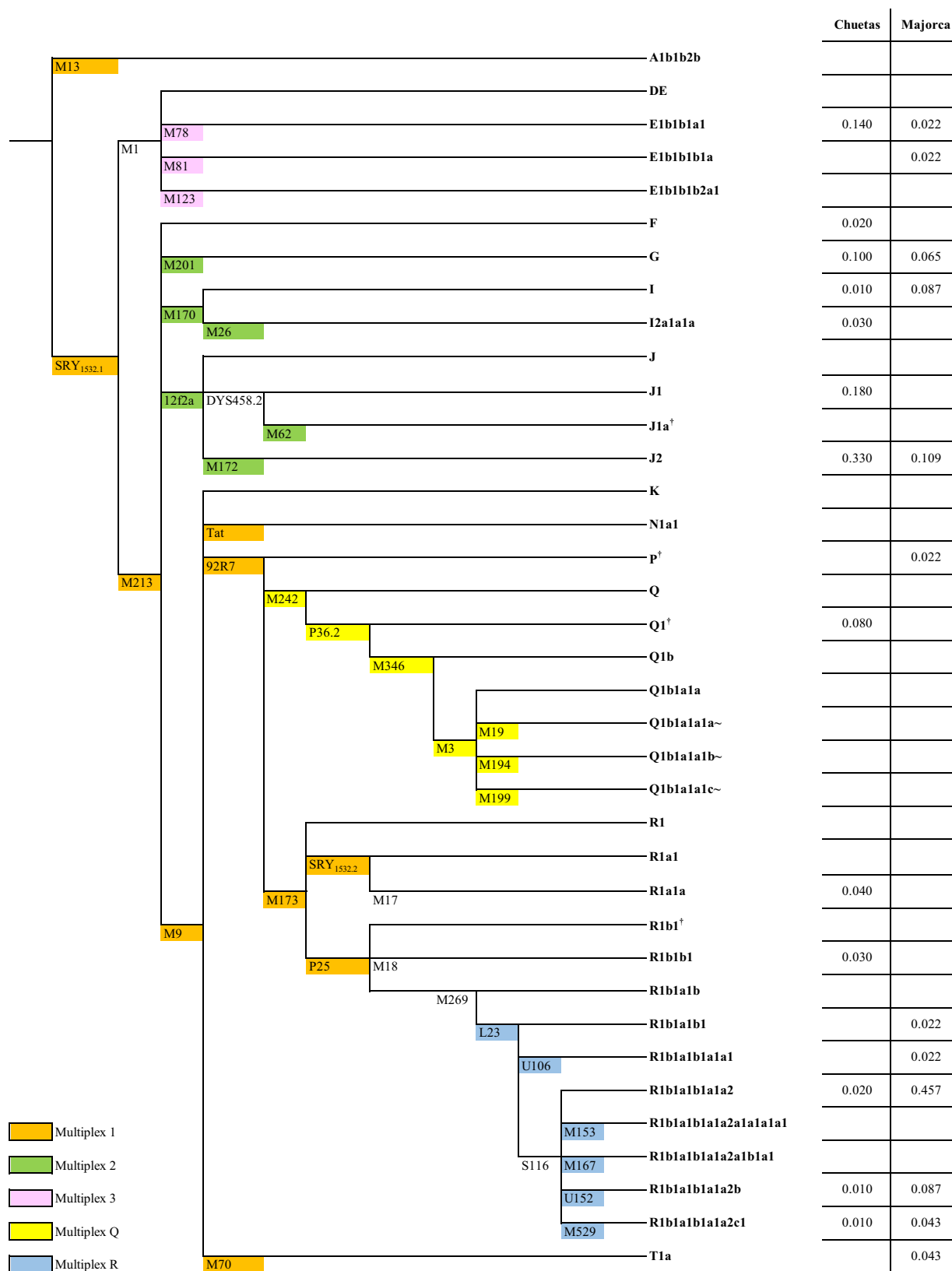


Figure 1. Phylogenetic tree of the 38 Y-SNPs typed, and haplogroup frequencies for Chuetas and Majorca populations. Haplogroups were named in accordance with the latest Update of ISOGG 2019. Haplogroups labelled with † are named as in their original description: J1a-M62, P-92R7, and R1b1-P25 (Brion et al.³⁵), and Q1-P36.2 (Roewer et al.³⁵).

	N	K	UH	HD	h	MPD
Yfiler						
Chuetas	100	53	39	0.965 ± 0.008	0.611 ± 0.311	10.387 ± 4.774
Majorca	46	44	44	0.998 ± 0.005	0.606 ± 0.312	10.308 ± 4.783
Y-SNPs						
Chuetas	100	13	3	0.827 ± 0.023	0.106 ± 0.059	4.033 ± 2.029
Majorca	47	12	5	0.771 ± 0.058	0.121 ± 0.067	4.614 ± 2.302

Table 1. Y chromosome molecular diversity indices for haplotypes and haplogroups in Chuetas and Majorcans. *N* number of individuals, *K* number of haplotypes/haplogroups, *UH* unique haplotypes/haplogroups, *HD* haplotype diversity ± SD, *h* gene diversity over loci, *MPD* mean pairwise differences.

Population	N	K (% K)	S	HD ± SD	Π ± SD	θ _k (95% CI)
D-loop (16,024–576)						
Chuetas	104	50 (48.08%)	110	0.950 ± 0.015	0.010 ± 0.005	37.216 (25.061; 55.103)
Majorca	79	67 (84.81%)	120	0.995 ± 0.003	0.009 ± 0.005	205.807 (117.911; 374.184)
HVRI (16,024–16,365) and HVRII (72–300)						
Chuetas	104	46 (44.23%)	74	0.948 ± 0.014	0.013 ± 0.007	31.003 (20.769; 46.042)
Bragança Jews ²⁴	57	35 (61.40%)	61	0.967 ± 0.012	0.014 ± 0.008	37.616 (22.328; 63.866)
Belmonte Jews ²²	30	2 (6.67%)	6	0.129 ± 0.115	0.001 ± 0.001	0.279 (0.065; 1.097)
Bulgarian Jews ²²	71	46 (64.79%)	70	0.982 ± 0.007	0.012 ± 0.007	55.477 (34.470; 90.159)
Turkish Jews ²²	123	85 (69.11%)	109	0.985 ± 0.005	0.013 ± 0.007	120.394 (82.638; 176.996)
Libyan Jews ²²	83	36 (43.37%)	63	0.922 ± 0.019	0.013 ± 0.007	23.631 (15.104; 36.717)
Moroccan Jews ²²	148	80 (54.05%)	92	0.979 ± 0.005	0.012 ± 0.006	70.307 (50.484; 97.941)
Tunisian Jews ²²	36	25 (69.44%)	43	0.971 ± 0.015	0.012 ± 0.007	34.939 (18.044; 69.325)
Iranian Jews ²²	82	43 (52.44%)	76	0.971 ± 0.008	0.016 ± 0.008	35.821 (23.098; 55.513)
Iraqi Jews ²²	134	48 (35.82%)	79	0.950 ± 0.009	0.016 ± 0.008	26.344 (18.151; 37.920)

Table 2. Diversity indices results calculated for the complete D-loop and for the HVRI + HVRII fragment for inter-population comparison. *K* Number of different haplotypes, *S* number of polymorphic sites, *HD* haplotype diversity, *Π* nucleotide diversity averaged over loci, *θ_k* theta estimator based on the number of different lineages.

To attain statistical significance for frequencies of putative Jewish founding lineages, Bayesian 0.90 credible region (90% CR) was calculated using SAMPLING software (Macaulay, personal communication). Furthermore, another criterion established by Behar et al.²² was to consider haplogroups with a frequency greater than 5% and TMRCA prior to 2 Kya as founder lineages.

Median joining networks of Y-STR haplotypes were constructed using Network 4.6.1.1 (www.fluxus-technology.com)⁴⁴.

In order to visualise the distribution of mtDNA haplogroup R0a frequencies in the Mediterranean geographic context, an isometric spatial frequency distribution map was constructed with the program Surfer 9 (Golden Software, <http://www.goldensoftware.com/products/surfer>).

Results and discussion

Genetic diversity. *Haplotype diversity.* Allele frequencies and gene diversities of each Y-STR of the populations under study are shown in Supplementary Table 1. The DYS385 locus showed the highest gene diversity (GD) values (>0.83) in both Chuetas and Majorcans, as expected, due to its duplicated structure, while especially low values were found at DYS389I (0.224) and DYS392 (0.288).

Amongst the 146 males analysed, 97 Y-STR haplotypes were observed (Table 1 and Supplementary Table 2), 81 of which were observed only once (singletons). The frequencies of the most common haplotypes were 12% and ~4% in Chuetas and Majorcans, respectively. No haplotype was shared between Chuetas and Majorcans. Haplotype diversity in Chuetas (0.965) was considerably lower than in Majorcans (0.998), Bragança Jews (0.987)²³, or other populations in the literature^{45,46}. These results are in accordance with the historical and demographic data of this population and with the reduced genetic diversity in some markers found in previous genetic studies^{29,47}.

Complete mitochondrial control region haplotypes for Majorcan and Chueta populations are presented in Supplementary Tables 3 and 4. In the 104 samples from the Chueta population, 50 (48.08%) different haplotypes were identified; meanwhile, in the 79 Majorcans, 67 (84.81%) different haplotypes were found. Estimated diversity parameters are summarised in Table 2. Notably, theta *k* values (θ_k) in Chuetas were much lower than in Majorcans, but within the same range as those reported for other non-Ashkenazi Jews^{22,24}. Therefore, the estimated number of putative female founders in Chuetas is similar to the one estimated in most of these Jewish groups.

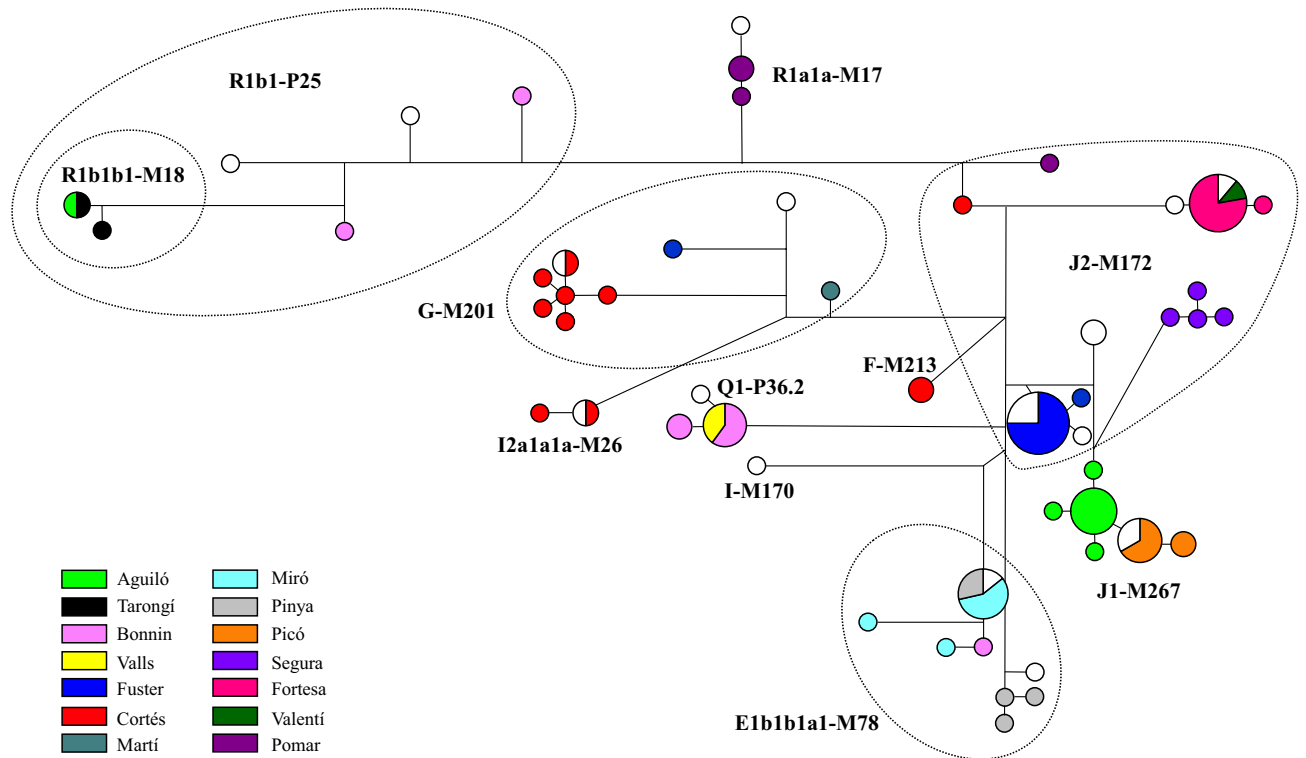


Figure 2. Median-Joining network of Chueta haplotypes. Colour code indicates the Chueta surname of the sample, the colour white is used for anonymised individuals. Smaller circles are singletons and size is proportional to haplotype frequency. Haplogroup assignment is indicated in each group of haplotypes.

Haplogroup composition. Regarding the Y-chromosome, Chueta samples were classified into 13 different haplogroups according to the 38 SNPs genotyped (Table 1 and Fig. 1). The six most frequent haplogroups ($\geq 4\%$) (E1b1b1a1-M78 (hereafter E1b-M78), G-M201, J1-DYS458.2 (used in this study as synonymous of J1-M267), J2-M172, Q1-P36.2, and R1a1a-M17) accounted together for up to 87%, with J2-M172 as the most frequent (33%). Three of the seven remaining haplogroups occurred in only one individual. For the Majorca population, 12 haplogroups were found, the most common being R1b-S116 (46%). High diversity values, based on haplogroup frequencies, were found in Chuetas (0.827 ± 0.023) in comparison with other Iberian populations and Majorca (0.771 ± 0.058), but in the same range as the Sephardic Jewish population¹⁹.

AMOVA analyses at both haplogroup and haplotype (Y-STRs) level showed significance when taking Chuetas and Majorcans as a whole ($F_{ST} = 0.196$; $p < 10^{-5}$), indicating the differentiation of the Chuetas with respect to their host population. SAMPLING software identified three differential haplogroups between Chuetas and Majorcans: R1b1a1a2-M269 (hereafter R1b-M269), J1-DYS458.2, and J2-M172, pointing towards the lack of R1b-M269 and the presence of J1-DYS458.2 and J2-M172 as Chuetas' putative founding lineages. The frequency in Chuetas of haplogroups rarely found in neighbouring populations—E1b-M78, Q1-P36.2, G-M201, and R1a1a-M17 (14, 10, 8, and 4%, respectively)—could also mean that they might have been present in the original Jewish Majorcan gene pool.

Network analyses were performed for the main haplogroups (Supplementary Fig. 1). Within networks, Majorcan and Chueta individuals did not share haplotypes. R1b-M269, found mainly in Majorcans, showed the highest diversity (0.998), while the main haplogroups in Chuetas manifested much lower haplotype diversities [ranging between 0.684 (J-12f2a) and 0.833 (R1a1-M17)], except for G-M201 (0.978).

Although studying the relationship between haplogroups and surnames was not an initial aim of our work on the Y-chromosome in Chuetas and, therefore, the sampling was not designed for it, with a median joining network we assigned and compared the haplotypes and haplogroups found with the surnames of the individuals (Fig. 2). Fourteen of the 15 Chueta surnames are represented, but not the surname Valleriola, which left no descendants. When sorted and analysed by surnames, the majority of these surname sets contained a highly reduced haplogroup diversity ($h = 0.000$ – 0.222), contrarily to that observed in Majorcan non-Chuetas surnames included in other studies⁴⁸. The surnames Bonnin and Pomar revealed two different haplogroups with intermediate h values (~ 0.500) and Cortés was the most diverse with 4 haplogroups and an h value of 0.691; although the sample size would need to be enlarged to confirm these results. Putative founding haplogroups in the Chueta population, J1-M267 and J2-M172, were found to be associated to the surnames Picó and Aguiló (J1-M267) and Segura, Fortesa, and Fuster (J2-M172). The haplotypes carried by the individuals of most surnames show a star-like distribution with only one or two mutational steps between them. Foundation of each Chueta surname by one or a very few individuals in the Christian conversions (fourteenth–fifteenth centuries) could explain these results. In a few cases, the same haplotype is shared by different surnames or, contrarily, individuals within a surname

Haplogroup	Chueta	Majorca	Haplogroup	Chueta	Majorca	Haplogroup	Chueta	Majorca
D1j	0.0096	–	K1a	0.0385	0.0380	T2b23	0.0192	–
H*	–	0.0633	K1a1b1a	0.0385	–	T2b5a1	0.0096	–
H1	0.0865	0.1772	K1a4a1a + 195	0.0096	0.0127	T2c1d	0.0481	0.0127
H2a2a	0.0385	0.0253	K1b1a1 + 199	0.0096	–	U1a1a	0.0481	–
H3	0.0288	0.0380	K1b1 + 16,093	–	0.0127	U2e1'2'3	–	0.0127
H4a1a	–	0.0253	K1c	0.0096	–	U2e1e	–	0.0127
H6a1	0.0096	0.0380	K2a5	–	0.0127	U2e2a2	–	0.0127
H11a	0.0096	0.0253	K2b1a1	0.0096	0.0506	U3	0.0192	–
HV0	–	0.0759	L2a1b + 143	–	0.0127	U3a	0.0096	–
HV0 + 195	0.0192	0.0380	L3d1b2	–	0.0127	U4b3	–	0.0127
HV15	–	0.0127	L3e2b + 152	0.0481	–	U5a2	0.0096	–
HV4a2a	–	0.0127	M1a1	0.0192	–	U5b1d2	0.0096	–
I	–	0.0127	M5a1	0.0192	–	U5b1f1a	0.0192	–
I1c1	0.0096	–	N1b1	–	0.0127	U5b2a2	–	0.0127
I2'3	–	0.0127	R0a + 60.1 T	0.2019	–	U5b2b1a1	–	0.0127
J1b1a1	–	0.0127	T	0.0288	0.0127	U5b2b3	–	0.0253
J1b1b	–	0.0127	T1a	0.0577	–	U5b3	0.0096	0.0253
J1c	–	0.0127	T1a1'3	0.0096	–	U6a	0.0096	–
J1c2o	0.0096	–	T2	0.0096	0.0127	V + 16,298	–	0.0127
J1d1	0.0096	–	T2a1b	–	0.0253	X2c	–	0.0127
J2a1a1	0.0288	–	T2b	0.0096	–	Unclassified	–	0.0127
J2b1a	0.0096	0.0127						

Table 3. Haplogroup frequencies in Chueta and Majorcan populations.

belong to very distant Y-lineages, although the scarcity of historical documents with the Christian names that converted Jews adopted does not allow us to assess the different scenarios that could explain these cases further.

Upon analysing mtDNA results (Table 3), we found the Majorcan population had haplogroup H as the most common one (39%), as was expected of a typical European population^{47,49}. Haplogroup H together with haplogroups U, K, and HV (frequencies ranging from 13 to 14%) accounted for 78% of total diversity. Other haplogroups found in this population were I, J, L, N, T, V, and X. In contrast with the Majorcan population, in the Chueta samples, haplogroup H only accounted for 17% of total diversity. The modal haplogroup in Chuetas (~20%) was found to be the Middle Eastern haplogroup R0a + 60.1 T, followed by haplogroups T, K, U, and J (19%, 12%, 8%, and 6%, respectively). Together these 5 haplogroups represented 64% of all variation. The remaining lineages were observed at frequencies ranging from ~1 to 5% (Table 3).

All in all, the mitochondrial haplogroup composition indicated that Chuetas are statistically different from their host population (Majorca) (F_{ST} p-values < 10^{-5}). By means of the SAMPLING analyses, and also with the Behar et al.²² criterion, two haplogroups showed up as the founder lineages in the Chueta population: R0a + 60.1 T (~20%) and T1a (~6%).

The presence in Chuetas of haplogroups rarely found in neighbouring populations—L3eb + 152, U1a1a, and K1a1b1a (with frequencies of 5%, 5%, and 4%, respectively)—could also mean that they might have been present in the original Jewish Majorcan gene pool.

Phylogenetic relation with other populations. *Y-chromosome.* The most frequent subclade of haplogroup R in Europe is R1b-M269, with frequencies ranging from 41 to 83%⁵⁰. Ancient DNA studies carried out in recent years^{51–54} have shown that this lineage is associated with the spread of Steppe ancestry during the Bronze Age. In Iberia former Y-chromosome lineages were nearly completely replaced by haplogroup R1b-M269⁵³, and a west-to-east gene flow from Iberia could have introduced these haplogroups into Western Mediterranean islands⁵⁴. Majorca showed similar values (63%) to the rest of Iberian populations^{19,46}, whereas the Chueta population (4%), had similar values to Middle Eastern and North African populations^{55,56}. In Jewish populations, values range between 5% and 11.5%^{19,57,58}, with the highest frequencies in Sephardim. These results support some degree of Iberian admixture in Sephardic Jews¹⁹ and important gene flow from the host population in Bragança Crypto-Jews (with an R1b-M269 frequency of 28%), as suggested by Nogueiro et al.²³.

Haplogroup J-12f2a, thought to have originated in the Fertile Crescent⁵⁹, shows an East to West gradient in Europe. Although the phylogeography of haplogroup J is complex, its radiation seems to be concentrated mainly in the Bronze Age, an essential period for the establishment of the modern European genetic pool⁶⁰. It contains two major branches, one of them, J2-M172, has its high frequencies in the Levant and is the most frequent sub-haplogroup in Europe, mainly throughout the Mediterranean basin. It was long considered to have spread across Europe with the demic diffusion of Neolithic agriculturalists^{61,62}, but ancient DNA studies contradict this hypothesis, since in early Middle Eastern farmers, and also in European Neolithic remains, haplogroup J2-M172 is only detected sporadically⁶³. Signs of population movements from the East, mainly maritime, such

as the Phoenicians^{7,56,63} have been linked to J2^{56,60} and also to the other main branch, J1-M267. This lineage has its maximum frequency in Arabia, but also high frequencies in the Middle East and in Jewish groups^{58,64}. Some of its derived lines have purportedly been associated with Arabisation in North Africa^{46,62} while others have been implicated with different expansions of Middle Eastern populations through the Mediterranean Sea⁵⁶. In most Jewish populations, J2-M172 reaches considerable frequencies^{9,14,19,57} (Fig. 3), but in Europeans it is about 10%. In the Chueta population, J2-M172 was the modal haplogroup with a frequency of 33%, while in its host population it was found in 10% of males. This value is similar to other Jewish populations and higher than the average Sephardic percentage (22%). Haplogroup J1-M267, not found in Majorca, was the second most frequent in Chuetas, with similar values (18%) to those in other Jews (Fig. 3)^{14,19}.

Other Y-haplogroups with differential frequency between Chuetas and their host population were E1b-M78, Q1-P36.2, G-M201, and R1a1a-M17. E1b-M78 seems to have originated in north-eastern Africa and several lines of evidence suggest that some E1b-M78 derived lines have been involved in trans-Mediterranean migrations directly from Africa to Europe⁶⁵. Chuetas showed a frequency for this haplogroup of 14%. In other populations with Jewish origin, it has been found to range from 3.5% (Bragança Crypto-Jews) to 15% (North African Jews)^{19,23,57,58,61}; and in Middle East non-Jewish populations, from 10.0 to 17.0%⁵⁷. Haplogroup Q1-P36.2 (xM346) is practically absent in Europe and Africa^{19,66}. In Chuetas it showed a frequency of 8%, while in Jewish populations, percentages ranging from < 1% to 5% have been found^{9,19,58,66}, with one branch typical of Ashkenazi Jews⁶⁶. One of the main sub-branches of haplogroup G-M201, G2a, was the predominant male lineage in early European farmers, although the important Y-chromosome turnover in the Bronze Age nearly completely replaced it with the R1b lineage^{52,53}. Nowadays haplogroup G-M201 is most common in Caucasus where the maximum frequencies are observed (> 70%), but it also occurs in the rest of the Middle East and south-western European countries at frequencies ranging from 5 to 15%⁶⁷; while in North Africa it is far lower than in any European Mediterranean population⁴⁶. In Jewish populations, Moroccan and Sephardic Jews have the highest values, 16% and 19%, respectively^{14,23,57} (Fig. 3). The existence of gene flow between Sephardim and Iberians (with frequencies reaching 5.0%) has been suggested^{19,23}, although the direction of the introgression could not be determined. Lastly, the main subclade of the typical Eastern Europe R1a-M240⁶⁸ is R1a1a-M17⁶⁹, which is found in high percentages in Ashkenazim (up to 14.5%) and is also present in other non-Ashkenazi Jewish populations, but at a much lower frequency (4.4%)^{9,70}. In Chuetas, R1a1a-M17 was found in 4% of the individuals analysed, but not in the Majorcan samples. It could be interesting to assess whether the Chueta R1a1a chromosomes belong to the subclade shared by Ashkenazim and other Middle Eastern populations (M582), but absent in Eastern Europeans⁷⁰.

All in all, the Y-chromosome haplogroup profile in Chuetas is clearly dissimilar from their neighbouring population, Majorca, and quite similar to the haplogroup frequencies found in Sephardic and other Jewish populations, evidencing a considerable frequency of J2 + J1 haplogroups and low values of R1b (Fig. 3). Therefore, it seems likely that the differential presence in the Chueta population of both haplogroups (and also of E1b-M78, Q1-P36.2, G-M201, and R1a1a-M17) results from their well-known historical Jewish origin and/or by admixture with other Jewish groups, especially with North Africans, due to commercial contact between both communities⁷¹.

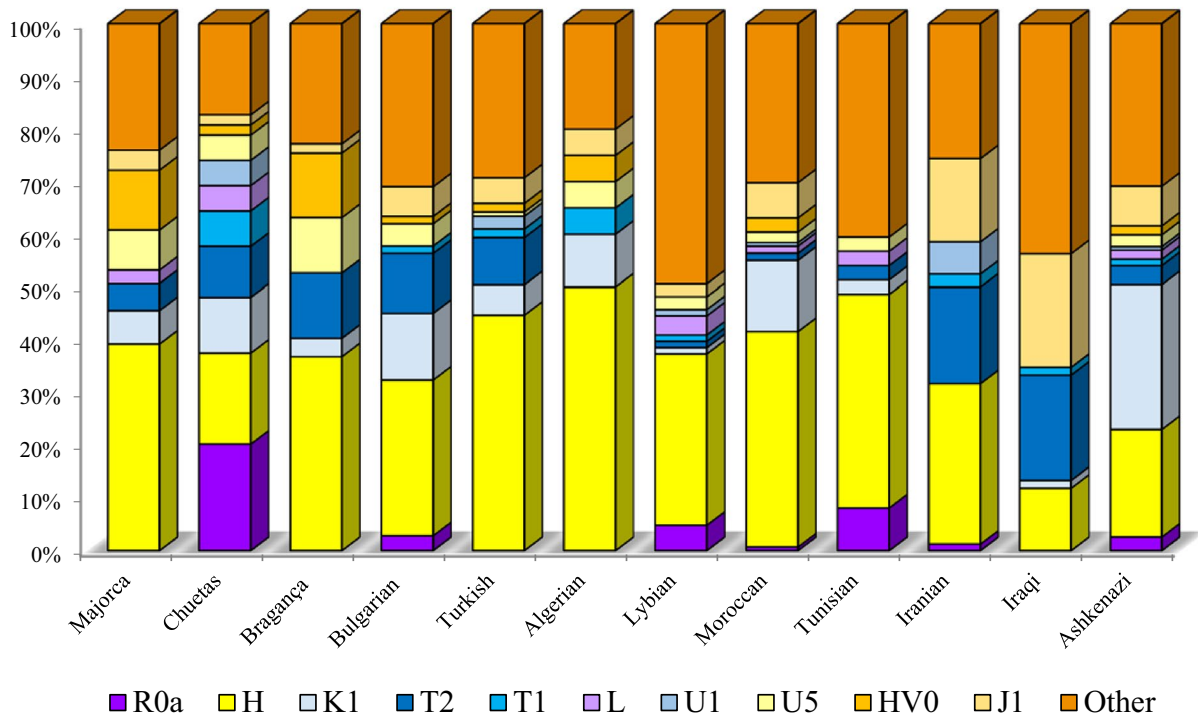
A comparison with available populations in the literature, based on both STRs and SNPs, (Fig. 4) positioned Chuetas with other Jewish and Middle Eastern populations, far from their geographical neighbours, evidencing that Chuetas maintain, in male lineages, substantial relics of their Jewish ancestry.

Mitochondrial DNA. The origin in terms of location and timescale of the Chuetas' modal haplogroup R0a has been under debate in recent years due to the geographic distribution of its frequencies^{72–74}. As shown in Fig. 5, this haplogroup is practically absent in Europe (0–2%), although some exceptions are found, such as Cappadocia village in Italy (14.6%)⁷⁵. The highest frequencies of haplogroup R0a are found in the Arabian Peninsula and the Horn of Africa, reaching values as high as ~ 25% in Soqatra Island in Yemen⁷³. Frequencies in Jewish groups^{8,22,73,76} on the whole show similar frequencies to their host populations (Fig. 5), but not in the case of Chuetas, who present a frequency of R0a of 20.2% while it is absent in their host population. The first dating of the haplogroup (~ 19 Kya) suggested an Arabian origin⁷². Later studies dated the haplogroup earlier, ~ 22.5 Kya⁷³ and ~ 30 Kya⁷⁴. Both studies discuss whether the origin could be in the Horn of Africa or the Arabian Peninsula. Phylogeographic differences in the regional distribution of R0a and the fact that the most ancient reservoir of R0a variation is found in Arabia led the authors to conclude an Arabian origin of the haplogroup. Two main branches characterise this haplogroup: R0a1 (~ 26 Kya) and R0a2'3 (~ 21 Kya). R0a2'3 is defined by the insertion 60.1 T and most of the Jewish populations where information is available show this branch. Only Yemenite Jews show both²².

Taking into account the high prevalence of this haplogroup in the Chueta population, it was considered important to delve into the phylogeny of their possible main maternal founder. Thus, the complete mtDNA genome was obtained for 6 out of the 21 R0a + 60.1 T samples, which classified the Chueta samples as R0a2m. The R0a2m branch, dated by Gandini et al.⁷⁴ to ~ 1.4 Kya, is found in just three samples in the literature, two of them from Jewish origin and the other with unknown ethnicity. In Fig. 6, it can be seen that all six complete Chueta molecules share an additional mutation (A13858G), whereas one sample has a G15734A private mutation. In all the rest of R0a + 60.1 T Chueta samples, we have checked the defining mutation of the R0a2m branch (A4767G). Besides, the two specific Chueta positions have also been examined, revealing that A13858G was present in all 21 individuals, suggesting a new R0a2m sub-branch in this population, while the G15734A mutation remained as a private variant.

The time of the appearance of haplogroup JT can be estimated at ~ 58 Kya, before the settlement of the Fertile Crescent. It has been suggested that haplogroups J and T diverged during the settlement ~ 40 Kya and ~ 30 Kya,

a) mtDNA



b) Y-chromosome

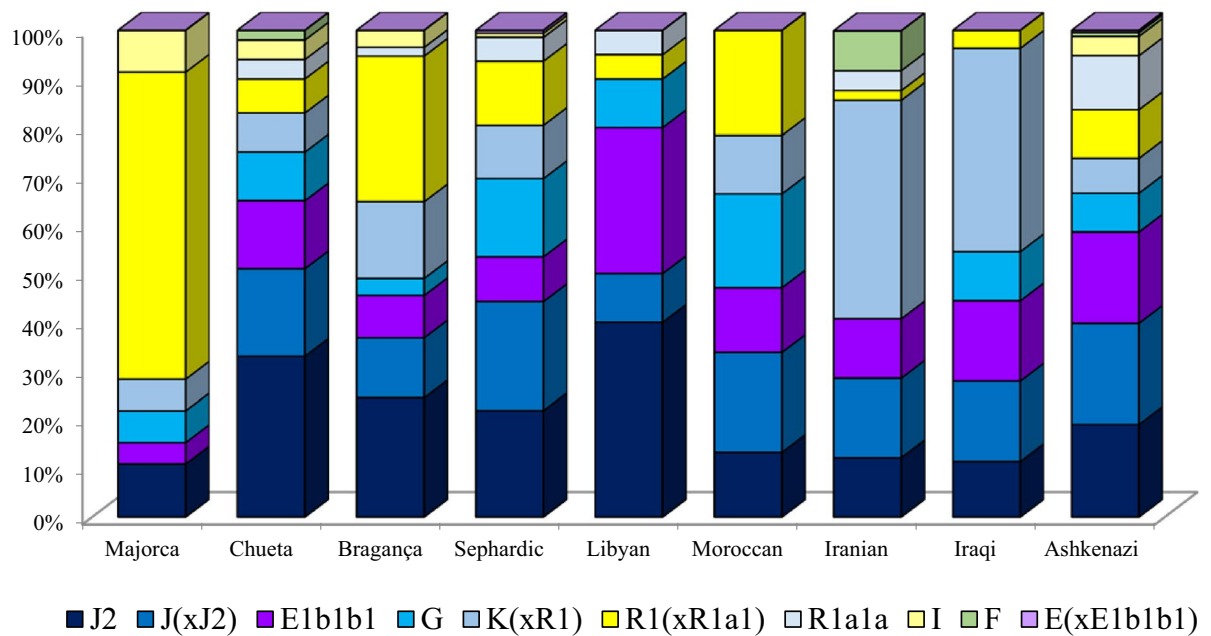


Figure 3. Haplogroup frequencies of mtDNA (a) and Y-chromosome (b) in Chuetas, Majorcans, and different populations with Jewish origin, based on data from the literature (Supplementary Table 5). Y-chromosome haplogroups are defined with the following SNPs: M172 (J2), 12f2a (J(xJ2)), M35 (E1b1b1), M201 (G), M9(xM173) K(xR1), M173(xM17) R1(xR1a1), M17 (R1a1), M170 (I), M213 (F), M1(xM35) E(xE1b1b1).

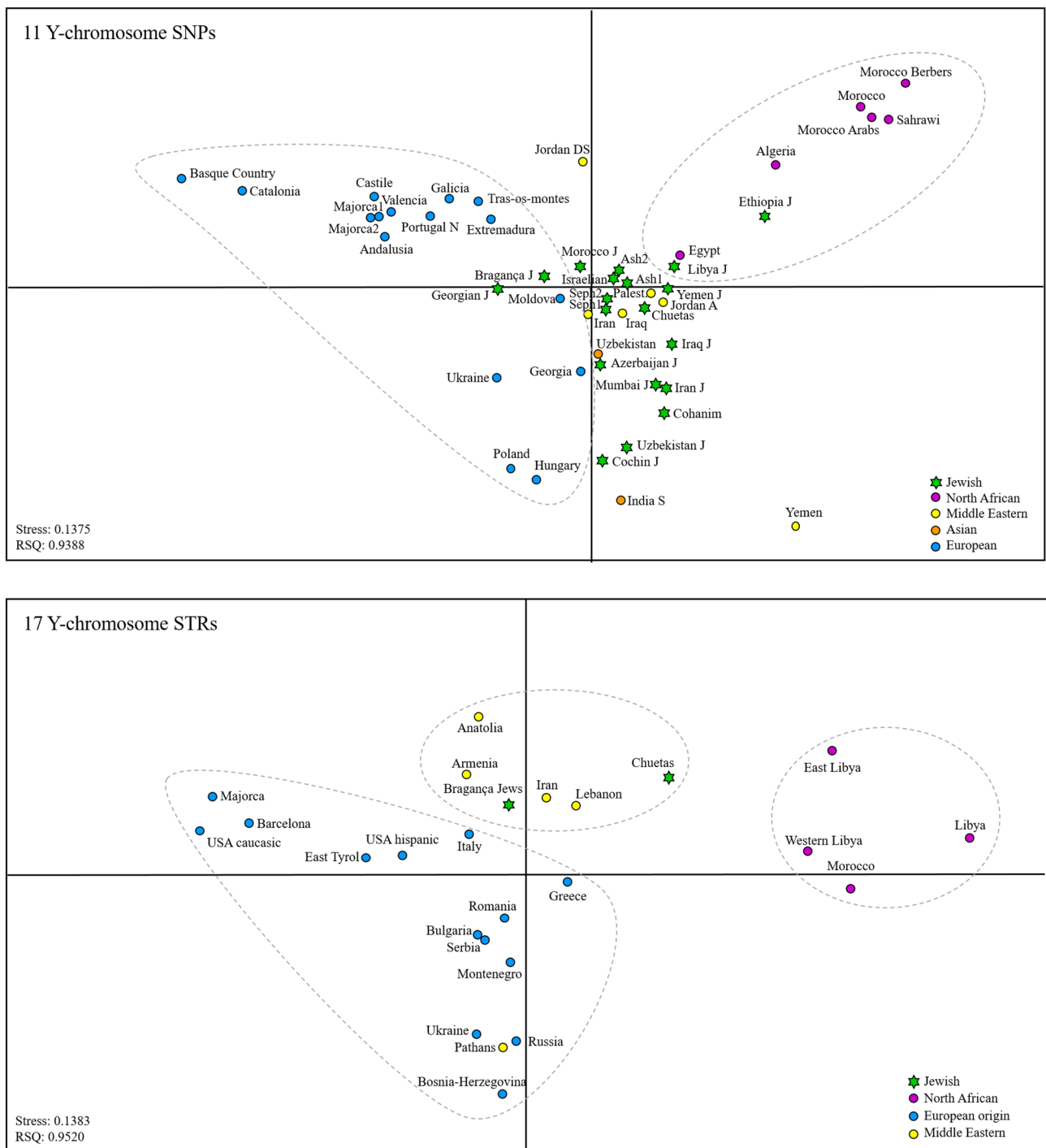


Figure 4. Multidimensional Scaling plot performed with (a) 11 SNPs: M1(xM35) E(xE1b1b1), M35 (E1b1b1), M213 (F), M201 (G), M170 (I), 12f2a (J(xJ2)), M172 (J2), M9(xM173) K(xR1), M173(xM17) R1(xR1a1), M17 (R1a1) and a final category for other haplogroups not included in these 10 SNPs and (b) Y-filer STRs. Circles defining each population are coloured following the legend code. Jewish populations are labelled with a Star of David. Populations and references are in Supplementary Table 5.

respectively⁷⁷. Haplogroup J has higher frequencies in the Middle East and Arabia than in Europe (13–20% vs. 9%), while haplogroup T shows the opposite behaviour (10% in Europe and 8% in the Middle East)^{77,78}. No significant differences were found between modern and ancient Majorcan populations regarding haplogroup frequencies since at least the Bronze Age⁷⁹. T1a (5.8%) is considered one of the founders of the Chueta population, and originated in the Near East ~ 17 Kya, although most of its sub-branches seem to be European⁷⁷.

Regarding the other mtDNA haplogroups with differential frequencies between Chuetas and their host population, Haplogroup U is the second most frequent in modern Europeans and was predominant in pre-agricultural

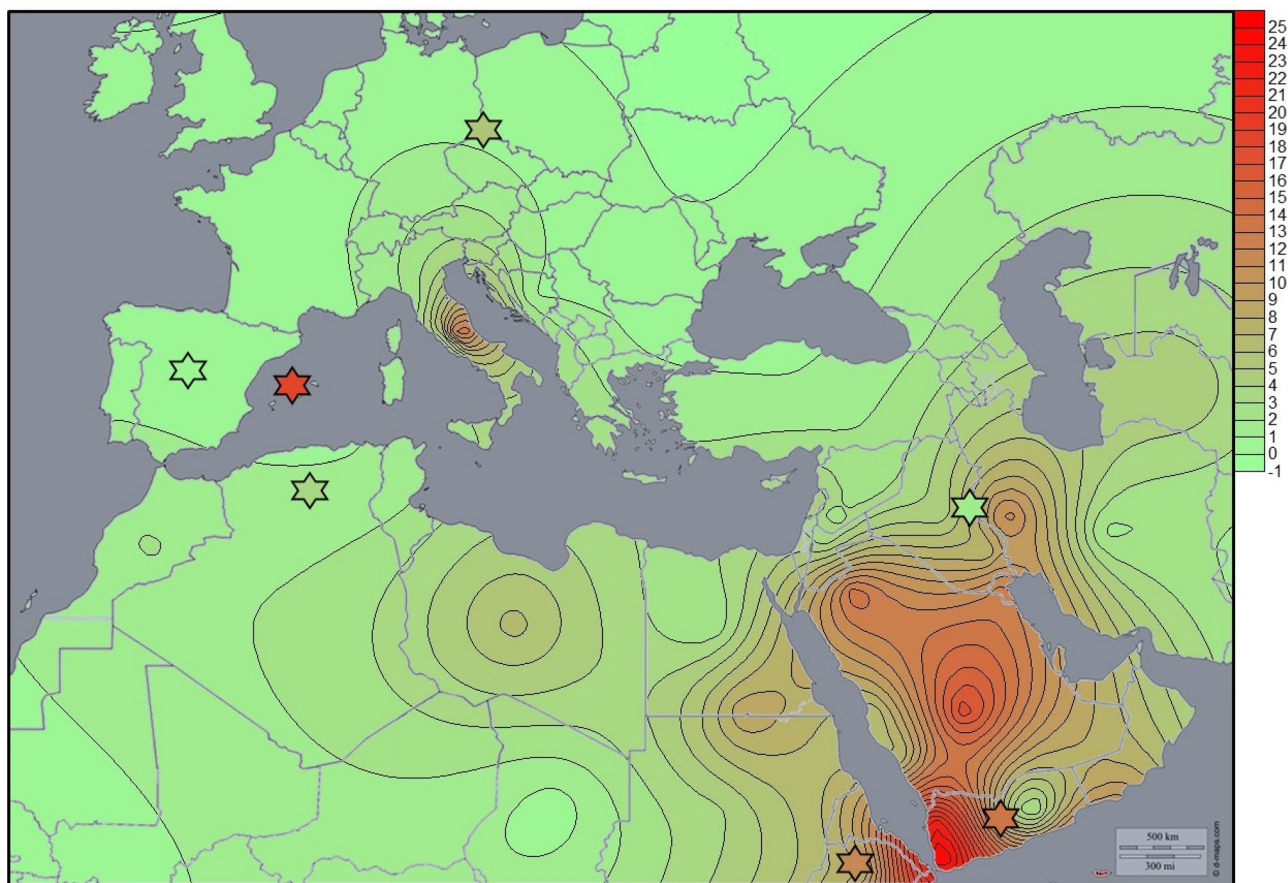


Figure 5. Isofrequency map of haplogroup R0a based on data from the literature (Supplementary Table 5) generated by Surfer v.8 (Golden Software Inc., Golden, Colorado) using a base map image (<http://d-maps.com>). Jewish populations are indicated with a Star of David.

Europe⁸⁰. The U1a sub-haplogroup is dated at ~13–15 Kya and is present in Southwest and South Asia, the Caucasus, and Europe. Five U1a1a1 samples were found in the Chueta population, whereas no U1 sub-haplogroup was observed in the host population. Haplogroup K origin has been dated to ~36 Kya and, although the place of origin is still under discussion^{81,82}, a Levantine origin seems the most likely. Sub-haplogroup K1a1b1a (dated to ~4.4 Kya⁸²), found in four Chueta samples, is a founder lineage in Ashkenazim⁸¹ and also present in Sephardic communities²², but not in non-European Jews, which can be seen as evidence of its European origin⁸².

Haplogroup L3e is widespread in Africa but practically absent in Eurasia (except in neighbouring areas due to genetic exchange). Its origin is situated in Central or Eastern Africa about 46 Kya⁸³ and one of its most frequent lineages in West-Central Africa is L3e2b (7%)⁸⁴. Five Chueta samples showed haplogroup L3e2b, while in the host population just one sample presented one African haplogroup L3, but belonging to another subclade, L3d.

Founding lineages in Chuetas, R0a + 60.1 T (~20%) and T1a (~6%), are different from those of other Sephardic populations, which also show important dissimilarity between each other. For instance, while HV0b is found as a founder in the Portuguese Crypto-Jewish communities from Belmonte and Bragança^{22–24}, this haplogroup is absent or very uncommon in Chuetas and other Sephardic groups; additionally, haplogroup K1a1b1a, which is a founder (8.5%) in the Iberian Exile Jewish community from Bulgaria, has a lower frequency in other populations with Sephardic origin (4% in Chuetas and 0.8% in Turkish Jews)²².

Conclusions

Genetic diversity in both paternal and maternal lineages in the Chueta population was higher than expected for a small, endogamous population. Comparable high diversity values were observed in the Portuguese Crypto-Jewish communities of Bragança^{23,24}. These results reveal that demographic processes more complex than the loss of genetic diversity expected under conditions of extreme inbreeding and drift, have shaped the gene pool of both isolated populations. Ongoing data from recombinant markers, together with classical genealogical studies, will help to explain what mating strategies were undertaken by these communities to avoid the expected reduction of diversity, and also whether other factors, such as high heterogeneity in founder populations, could have contributed to the diversity observed.

The composition of the Chuetas' uniparentally transmitted lineages indicates a remarkable signature of Middle Eastern ancestry. In recent years, archaeogenetic research has shed light on the history of European and Middle Eastern populations, revealing a greater degree of population movements and interactions in the past than previously considered. In this context, from the analysis of current populations, it is difficult to infer what the genetic

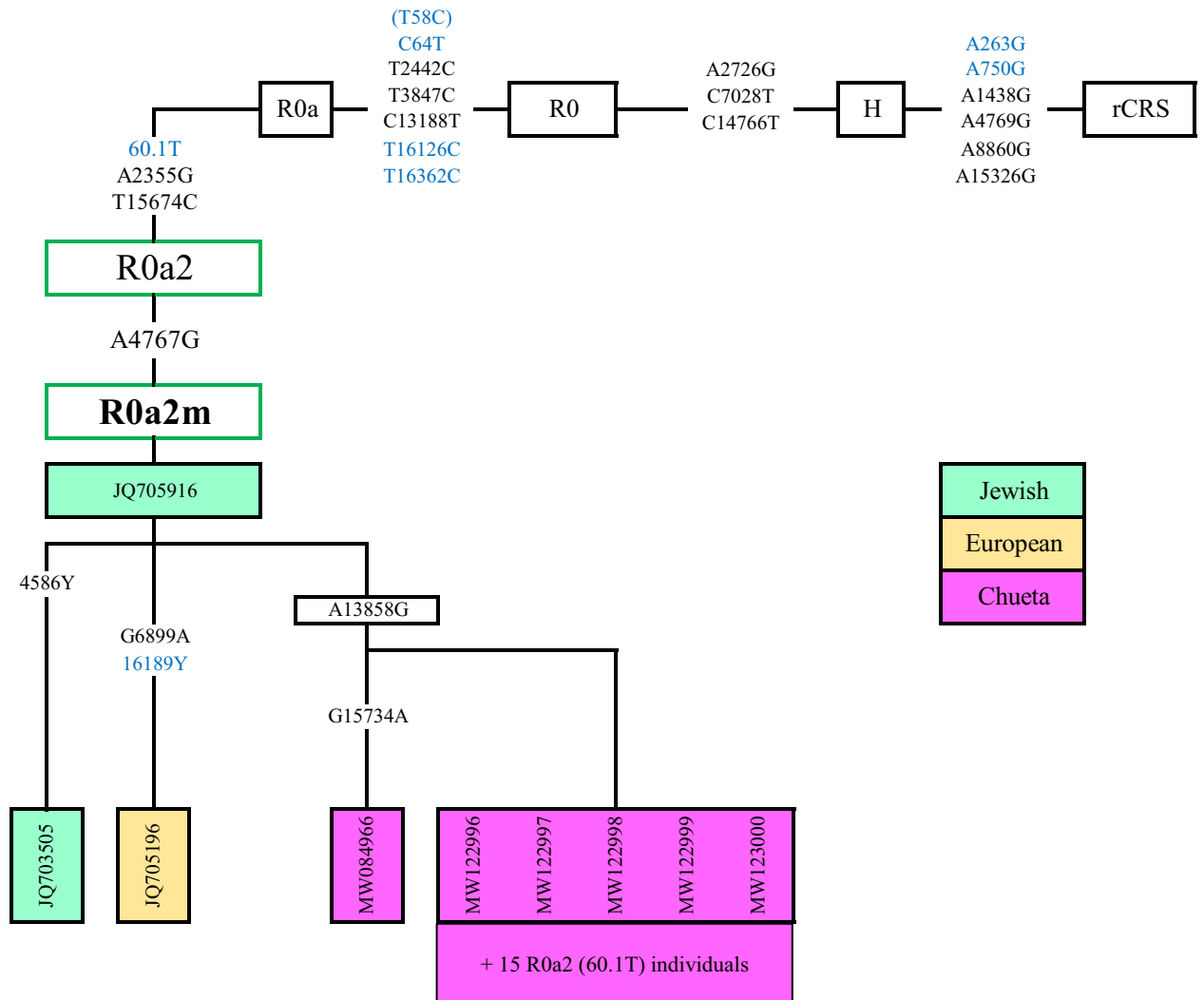


Figure 6. Phylogenetic tree of the completed mtDNA sequences belonging to haplogroup R0a2m. Mutations relative to the revised Cambridge Reference Sequence (rCRS) (NC_012920) are shown. Mutations coloured in blue correspond to the D-loop. The origin of the samples in the haplogroup are labelled in colours. In green, two Jewish samples from the Czech Republic and Ukraine (JQ705916 and JQ705196); and in yellow, one sample from Poland with unknown ethnicity (JQ703505). Finally, Chueta samples, with their corresponding GenBank accession numbers, are labelled in pink. The remaining 15 R0a + 60.1 T Chueta samples were found to be R0a2m (A4767G). Presence of the A13858G mutation was confirmed in all, whereas the G15734A mutation remained as a private variant of the MW084966 sample.

profile of the parental populations that gave rise to the Chuetas was exactly, and therefore precise inferences of the original source of the haplogroups found in this population, since there are no reasons to assume or assess the degree of genetic continuity. However, the most reasonable explanation for the differences found between Chuetas and their host population seems to be the Jewish origin of the Chuetas, considering the unquestionable historical evidence relating them with the Jewish populations who settled in Majorca long ago in the past. Therefore, our results would confirm that Chuetas have kept not only the cultural memory of their Jewish origin over centuries, but also a substantial degree of ancestral genetic signature.

In terms of paternal lineages, the results show that most Jewish communities are more similar to each other and to Middle Eastern populations than to their host populations. The Chueta population has the same behaviour, which can be observed by the high prevalence of haplogroups J2-M172 and J1-M267, and the lack of R1b-M269. Haplogroup distribution in Chuetas is very similar to other Sephardic communities, although in their gene pool there might be signatures of other Jewish communities' contribution, such as North African and Ashkenazim, which can be inferred from the presence of haplogroups such as E1b1b1a1-M78, Q1-P36.2, and R1a1a-M17.

The hallmark in the maternal gene pool in Chuetas is the presence of a new sub-branching of the rare Middle Eastern haplogroup R0a + 60.1 T as their modal haplogroup, and the low frequency of H. The presence of other haplogroups found in Jewish/Middle Eastern populations (K1a1b1a and U1a1a1) is also noteworthy. Current Jewish populations do not usually share modal maternal lineages, unlike the situation on the paternal side; not even populations with a supposed common ancestry, such as the Sephardic branch^{8,22}. Various scenarios could explain this dissimilarity found in maternal founder lineages in distinct current populations with Sephardic

origin: differences in gene flow from and admixture with other populations resulting from the contrasting history of each community; a lack of homogeneity in maternal lineages of the original Sephardic groups that settled in different areas of the Iberian Peninsula (and Balearic Islands); or genetic drift in the current populations, resulting in a lack of lineages that do not allow us to infer the original mtDNA composition of the Sephardic Jews that lived in Spain and Portugal in the middle ages from the surviving lines. Tests based on genome-wide data that enable a greater genetic resolution, such as analysis of Runs of Homozygosity (ROH), together with ancient DNA analysis, could help to solve this question.

Received: 24 April 2020; Accepted: 19 November 2020

Published online: 08 December 2020

References

1. Cortés, G. *Historia de los judíos mallorquines y sus descendientes cristianos*. (ed. Font, M.) (Palma, 1985).
2. Braunstein, B. *The Chuetas of Majorca. Conversos and the Inquisition of Majorca* (Ktav Pub Inc., New York, 1936).
3. de Muntaner, P. *Martí: Una família del brazo noble mallorquín durante el siglo XVII en Homenaje a Guillem Rosselló Bordoy*. Vol. 2. (Govern de les Illes Balears, Palma 2002).
4. Porqueres, E. *Lendogàmia dels xuetes de Malloca. Identitat i matrimoni en una comunitat de conversos (1435–1750)*. (ed. Lleopard, M.) (Palma, 2001).
5. Forteza, M. *Els descendents dels jueus conversos de Mallorca* (Moll, Palma, 1972).
6. Ostrer, H. & Skorecki, K. The population genetics of the Jewish people. *Hum. Genet.* **132**(2), 119–127 (2013).
7. Hammer, M. F. *et al.* Jewish and Middle Eastern non-Jewish populations share a common pool of Y-chromosome biallelic haplotypes. *Proc. Natl. Acad. Sci. U. S. A.* **97**(12), 6769–6774 (2000).
8. Thomas, M. G. *et al.* Founding mothers of Jewish communities: Geographically separated Jewish groups were independently founded by very few female ancestors. *Am. J. Hum. Genet.* **70**(6), 1411–1420 (2002).
9. Behar, D. M. *et al.* Contrasting patterns of Y chromosome variation in Ashkenazi Jewish and host non-Jewish European populations. *Hum. Genet.* **114**(4), 354–365 (2004).
10. Behar, D. M. *et al.* MtDNA evidence for a genetic bottleneck in the early history of the Ashkenazi Jewish population. *Eur. J. Hum. Genet.* **12**(5), 355–364 (2004).
11. Listman, J. B. *et al.* Identification of population substructure among Jews using STR markers and dependence on reference populations included. *BMC Genet.* **11**, 48 (2010).
12. Tian, J. Y. *et al.* A genetic contribution from the Far East into Ashkenazi Jews via the ancient Silk Road. *Sci. Rep.* **5**, 8377 (2015).
13. Atzmon, G. *et al.* Abraham's children in the genome era: Major Jewish diaspora populations comprise distinct genetic clusters with Shared Middle Eastern Ancestry. *Am. J. Hum. Genet.* **86**(6), 850–859 (2010).
14. Behar, D. M. *et al.* The genomewide structure of the Jewish people. *Nature* **466**(7303), 238–242 (2010).
15. Behar, D. M. *et al.* No evidence from genome-wide data of a Khazar origin for the Ashkenazi Jews. *Hum. Biol.* **85**(6), 859–900 (2013).
16. Waldman, Y. Y. *et al.* The genetic history of Cochin Jews from India. *Hum. Genet.* **135**(10), 1127–1143 (2016).
17. Xue, J. *et al.* The time and place of European admixture in Ashkenazi Jewish history. *PLoS Genet.* **13**(4), e1006644 (2017).
18. Gladstein, A. L. & Hammer, M. F. Substructured population growth in the Ashkenazi Jews inferred with approximate bayesian computation. *Mol. Biol. Evol.* **36**(6), 1162–1171 (2019).
19. Adams, S. M. *et al.* The genetic legacy of religious diversity and intolerance: Paternal lineages of Christians, Jews, and Muslims in the Iberian Peninsula. *Am. J. Hum. Genet.* **83**(6), 725–736 (2008).
20. Velez, C. *et al.* The impact of Converso Jews on the genomes of modern Latin Americans. *Hum. Genet.* **131**(2), 251–263 (2012).
21. Marques, S. L. *et al.* Y chromosome diversity in a linguistic isolate (Mirandese, NE Portugal). *Am. J. Hum. Biol.* **28**(5), 671–680 (2016).
22. Behar, D. M. *et al.* Counting the founders: The matrilineal genetic ancestry of the Jewish Diaspora. *PLoS ONE* **3**(4), e2062 (2008).
23. Nogueiro, I. *et al.* Phylogeographic analysis of paternal lineages in NE Portuguese Jewish communities. *Am. J. Phys. Anthropol.* **141**(3), 373–381 (2010).
24. Nogueiro, I. *et al.* Echoes from Sepharad: Signatures on the maternal gene pool of crypto-Jewish descendants. *Eur. J. Hum. Genet.* **23**(5), 693–699 (2015).
25. Picornell, A. *et al.* Genetics of the Chuetas (Majorcan Jews): A comparative study. *Hum. Biol.* **69**(3), 313–328 (1997).
26. Tomás, C. *et al.* Genetic variability at nine STR loci in the Chueta (Majorcan Jews) and the Balearic populations investigated by a single multiplex reaction. *Int. J. Leg. Med.* **113**(5), 263–267 (2000).
27. Cambra, A. *et al.* MICA-HLA-B haplotype diversity and linkage disequilibrium in a population of Jewish descent from Majorca (the Balearic Islands). *Hum. Immunol.* **70**(7), 513–517 (2009).
28. Ferragut, J. F. *et al.* Genetic diversity of 38 insertion–deletion polymorphisms in Jewish populations. *Forensic Sci. Int. Genet.* **21**, 1–4 (2016).
29. Ferragut, J. F. *et al.* Genetic portrait of Jewish populations based on three sets of X-chromosome markers: Indels, Alu insertions and STRs. *Forensic Sci. Int. Genet.* **31**, e5–e11 (2017).
30. Nevo, S. *et al.* Orosomuroid (ORM1) polymorphism in Arabs and Jews of Israel: More evidence for a Middle Eastern origin of the Jews. *Hum. Biol.* **68**(2), 217–229 (1996).
31. Rodríguez, V. *et al.* Genetic substructure in western Mediterranean populations revealed by 12 Y-chromosome STR loci. *Int. J. Leg. Med.* **123**(2), 137–141 (2009).
32. Ferragut, J. F. *et al.* Founding mothers of Chueta population. *Forensic Sci. Int. Genet. Suppl. Ser.* **5**, e492–e494 (2015).
33. Brion, M. *et al.* Hierarchical analysis of 30 Y-chromosome SNPs in European populations. *Int. J. Leg. Med.* **119**(1), 10–15 (2005).
34. Gomes, V. *et al.* Digging deeper into East African human Y chromosome lineages. *Hum. Genet.* **127**(5), 603–613 (2010).
35. Roewer, L. *et al.* Continentwide decoupling of Y-chromosomal genetic variation from language and geography in native South Americans. *PLoS Genet.* **9**(4), e1003460 (2013).
36. Myres, N. M. Y chromosome short tandem repeat DYS458.2 non-consensus alleles occur independently in both binary haplogroups J1–M267 and R1b3–M405. *Croat. Med. J.* **48**(4), 450–459 (2007).
37. Gusmão, L. *et al.* DNA Commission of the International Society of Forensic Genetics (ISFG): An update of the recommendations on the use of Y-STRs in forensic analysis. *Int. J. Leg. Med.* **120**(4), 191–200 (2006).
38. Marques, S. L. *et al.* Portuguese mitochondrial DNA genetic diversity—An update and a phylogenetic revision. *Forensic Sci. Int. Genet.* **15**, 27–32 (2015).
39. van Oven, M. PhyloTree Build 17: Growing the human mitochondrial DNA tree. *Forensic Sci. Int. Genet. Suppl. Ser.* **5**, e392–e394 (2015).

40. Weissensteiner, H. *et al.* HaploGrep 2: Mitochondrial haplogroup classification in the era of high-throughput sequencing. *Nucleic Acids Res.* **44**(W1), W58–W63 (2016).
41. Ramos, A. *et al.* Human mitochondrial DNA complete amplification and sequencing: A new validated primer set that prevents nuclear DNA sequences of mitochondrial origin co-amplification. *Electrophoresis* **30**(9), 1587–1593 (2009).
42. Ramos, A. *et al.* Validated primer set that prevents nuclear DNA sequences of mitochondrial origin co-amplification: A revision based on the New Human Genome Reference Sequence (GRCh37). *Electrophoresis* **32**(6–7), 782–783 (2011).
43. Excoffier, L. & Lischer, H. E. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**(3), 564–567 (2010).
44. Bandelt, H. J. *et al.* Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* **16**(1), 37–48 (1999).
45. Tokdemir, M. & Tunçez, F. T. Genetic polymorphisms of 17 Y-STR loci in Eastern Turkey population. *Gene Rep.* **6**, 15–18 (2017).
46. Hernández, C. L. *et al.* Paternal lineages in southern Iberia provide time frames for gene flow from mainland Europe and the Mediterranean world. *Ann. Hum. Biol.* **46**(1), 63–76 (2019).
47. Picornell, A. *et al.* Mitochondrial DNA HVRI variation in Balearic populations. *Am. J. Phys. Anthropol.* **128**(1), 119–130 (2005).
48. Solé-Morata, N. *et al.* Y-chromosome diversity in Catalan surname samples: Insights into surname origin and frequency. *Eur. J. Hum. Genet.* **23**(11), 1549–1557 (2015).
49. Roostalu, U. *et al.* Origin and expansion of haplogroup H, the dominant human mitochondrial DNA lineage in West Eurasia: The Near Eastern and Caucasian perspective. *Mol. Biol. Evol.* **24**, 436–448 (2007).
50. Myres, N. M. *et al.* A major Y-chromosome haplogroup R1b Holocene era founder effect in Central and Western Europe. *Eur. J. Hum. Genet.* **19**(1), 95–101 (2011).
51. Haak, W. *et al.* Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**(7555), 207–211 (2015).
52. Olalde, I. *et al.* The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature* **555**(7695), 190–196 (2018).
53. Olalde, I. *et al.* The genomic history of the Iberian Peninsula over the past 8000 years. *Science* **363**(6432), 1230–1234 (2019).
54. Fernandes, D. M. *et al.* The spread of steppe and Iranian-related ancestry in the islands of the western Mediterranean. *Nat. Ecol. Evol.* **4**(3), 334–345 (2020).
55. Bosch, E. *et al.* 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**(4), 1019–1029 (2001).
56. Zalloua, P. A. *et al.* Identifying genetic traces of historical expansions: Phoenician footprints in the Mediterranean. *Am. J. Hum. Genet.* **83**(5), 633–642 (2008).
57. Shen, P. *et al.* Reconstruction of patrilineages and matrilineages of Samaritans and other Israeli populations from Y-chromosome and mitochondrial DNA sequence variation. *Hum. Mutat.* **24**(3), 248–260 (2004).
58. Hammer, M. F. *et al.* Extended Y chromosome haplotypes resolve multiple and unique lineages of the Jewish priesthood. *Hum. Genet.* **126**(5), 707–717 (2009).
59. Cinnioglu, C. *et al.* Excavating Y chromosome haplotype strata in Anatolia. *Hum. Genet.* **114**(2), 127–148 (2004).
60. Finocchio, A. *et al.* A finely resolved phylogeny of Y chromosome Hg J illuminates the processes of Phoenician and Greek colonizations in the Mediterranean. *Sci. Rep.* **8**(1), 1–9 (2018).
61. Semino, O. *et al.* Origin, diffusion, and differentiation of Y-chromosome haplogroups E and J: Inferences on the neolithization of Europe and later migratory events in the Mediterranean area. *Am. J. Hum. Genet.* **74**(5), 1023–1034 (2004).
62. Francalacci, P. & Sanna, D. History and geography of human Y-chromosome in Europe: A SNP perspective. *J. Anthropol. Sci.* **86**, 59–89 (2008).
63. Manco, L. *et al.* The Eastern side of the Westernmost Europeans: Insights from subclades within Y-chromosome haplogroup J-M304. *Am. J. Hum. Biol.* **30**(2), e23082 (2018).
64. El-Sibai, M. *et al.* Geographical structure of the Y-chromosomal genetic landscape of the Levant: A coastal-inland contrast. *Ann. Hum. Genet.* **73**(6), 568–581 (2009).
65. Cruciani, F. *et al.* Tracing past human male movements in northern/eastern Africa and western Eurasia: New clues from Y-chromosomal haplogroups E-M78 and J-M12. *Mol. Biol. Evol.* **24**(6), 1300–1311 (2007).
66. Balanovsky, O. *et al.* Phylogeography of human Y-chromosome haplogroup Q3–L275 from an academic/citizen science collaboration. *BMC Evol. Biol.* **17**(1), 18 (2017).
67. Rootsi, S. *et al.* Distinguishing the co-ancestries of haplogroup G Y-chromosomes in the populations of Europe and the Caucasus. *Eur. J. Hum. Genet.* **20**(12), 1275 (2012).
68. Kayser, M. *et al.* Significant genetic differentiation between Poland and Germany follows present-day political borders, as revealed by Y-chromosome analysis. *Hum. Genet.* **117**(5), 428–443 (2005).
69. Underhill, P. A. *et al.* Separating the post-Glacial coancestry of European and Asian Y chromosomes within haplogroup R1a. *Eur. J. Hum. Genet.* **18**(4), 479–484 (2010).
70. Rootsi, S. *et al.* Phylogenetic applications of whole Y-chromosome sequences and the Near Eastern origin of Ashkenazi Levites. *Nat. Commun.* **4**, 2928 (2013).
71. Chacón, J. M. Los judíos mallorquines en el comercio y en las redes de intercambio valencianas y mediterráneas del medievo. *Anales de la Universidad de Alicante. Revista de Historia Medieval* **15**, 75–85 (2009).
72. Abu-Amero, K. K. *et al.* Eurasian and African mitochondrial DNA influences in the Saudi Arabian population. *BMC Evol. Biol.* **7**(1), 32 (2007).
73. Černý, V. *et al.* Internal diversification of mitochondrial haplogroup R0a reveals post-last glacial maximum demographic expansions in South Arabia. *Mol. Biol. Evol.* **28**(1), 71–78 (2011).
74. Gandini, F. *et al.* Mapping human dispersals into the Horn of Africa from Arabian Ice Age refugia using mitogenomes. *Sci. Rep.* **6**, 25472 (2016).
75. Messina, F. *et al.* Traces of forgotten historical events in mountain communities in Central Italy: A genetic insight. *Am. J. Hum. Biol.* **27**(4), 508–519 (2015).
76. Picornell, A. *et al.* Mitochondrial DNA sequence variation in Jewish populations. *Int. J. Leg. Med.* **120**(5), 271–281 (2006).
77. Pala, M. *et al.* Mitochondrial DNA signals of late glacial recolonization of Europe from near eastern refugia. *Am. J. Hum. Genet.* **90**(5), 915–924 (2012).
78. Fernandes, V. *et al.* Genetic stratigraphy of key demographic events in Arabia. *PLoS ONE* **10**(3), e0118625 (2015).
79. Simón, M. *et al.* Dissecting mitochondrial DNA variability of balearic populations from the bronze age to the current era. *Am. J. Hum. Biol.* **29**(1), e22883 (2017).
80. Davidovic, S. *et al.* Mitochondrial super-haplogroup U diversity in Serbians. *Ann. Hum. Biol.* **19**, 1–11 (2017).
81. Behar, D. M. *et al.* The matrilineal ancestry of Ashkenazi Jewry: portrait of a recent founder event. *Am. J. Hum. Genet.* **78**(3), 487–497 (2006).
82. Costa, M. D. *et al.* A substantial prehistoric European ancestry amongst Ashkenazi maternal lineages. *Nat. Commun.* **4**, 2543 (2013).
83. Bandelt, H. J. *et al.* Phylogeography of the human mitochondrial haplogroup L3e: A snapshot of African prehistory and Atlantic slave trade. *Ann. Hum. Genet.* **65**(6), 549–563 (2001).
84. Cerezo, M. *et al.* Comprehensive analysis of Pan-African mitochondrial DNA variation provides new insights into continental variation and demography. *J. Genet. Genom.* **43**(3), 133–143 (2016).

Acknowledgements

This work was partially supported by grant AAEE246/2014 from the Direcció General de R + D + I (Comunitat Autònoma de les Illes Balears) and European Regional Development Fund (ERDF) and FCT, Portuguese Foundation for Science and Technology PTDC/ATP-DEM/4545/2012 project financed by European Social Funds (COMPETE-FEDER). We are grateful to Maria Trinidad Garcia (from the Serveis Científicotècnics of the Universitat de les Illes Balears) for her assistance and help with capillary electrophoresis procedures, María Luz Gómez-Barbeito for her help in mtDNA sequencing and Meryl Wyn Jones for the English language corrections. We would also like to sincerely thank all the people who volunteered to participate in this study.

Author contributions

J.F.F. collected the samples, conducted laboratory analysis, analysed data, and participated in drawing figures; C.R. participated in the discussion and reviewing the manuscript; C.R. and L.A. provided financial support; J.A.C. help with the statistical analyses; A.A. and L.A. participated in the design and coordination of the study. A.P. participated in the design and coordination of the study and wrote the manuscript with support from J.F.F.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41598-020-78487-9>.

Correspondence and requests for materials should be addressed to J.F.F.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2020

MIDDLE EASTERN GENETIC LEGACY IN THE PATERNAL AND MATERNAL GENE POOLS OF CHUETAS

Ferragut JF^a; Ramon C^a; Castro JA^a; Amorim A^{b,c,d}; Alvarez L^{b,c,e}; Picornell A^a

^aInstitut Universitari d'Investigació en Ciències de la Salut (IUNICS) i Laboratori de Genètica, Departament de Biologia, Universitat de les Illes Balears, Carretera de Valldemossa, km 7.5, 07122, Palma de Mallorca, Illes Balears, Spain

^bi3S - Instituto de Investigação e Inovação em Saúde, Universidade do Porto, Rua Alfredo Allen, 208, 4200-135 Porto, Portugal

^cIPATIMUP - Instituto de Patologia e Imunologia Molecular da Universidade do Porto, Rua Júlio Amaral de Carvalho, 45, 4200-135 Porto, Portugal

^dFaculdade de Ciências da Universidade do Porto, Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal

^eTellmeGenTM, Calle Arquitecto Mora, 5 – 4, 46010, Valencia, España

Supplementary Table 1. Allele frequencies for 17 Y-chromosome STR loci in Chueta (CHU) and Majorcan (MAJ) populations.

Allele	DYS456		DYS389I		DYS390		DYS389II		DYS458		DYS19		DYS393		DYS391		DYS439		DYS635		DYS392		Y GATA H4		DYS437		DYS438		DYS448		Alleles	DYS385	
	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ	CHU	MAJ		N	CHU
8																						0.022								13-18	0.230		
9															0.180	0.087											0.320	0.130		13-16	0.110	0.065	
10			0.040										0.010		0.720	0.543	0.050	0.022									0.490	0.196		14-16	0.240	0.028	
11													0.010		0.090	0.370	0.400	0.283			0.840	0.261	0.510	0.413			0.150	0.043		11-14	0.050	0.391	
12	0.010		0.030	0.239									0.420	0.196	0.010		0.430	0.543			0.010	0.065	0.320	0.500			0.030	0.609		16-16	0.120		
13	0.090	0.021	0.880	0.521							0.172	0.043	0.460	0.696			0.120	0.130			0.070	0.630	0.070	0.043			0.010	0.022		13-13	0.050		
14	0.140	0.043	0.040	0.239			0.110		0.465	0.674	0.090	0.109						0.022			0.043	0.010		0.630	0.370				12-12	0.050	0.022		
15	0.370	0.587	0.010						0.090	0.043	0.253	0.261												0.260	0.500				11-15	0.030	0.087		
16	0.290	0.326							0.130	0.283	0.071	0.022									0.060			0.110	0.130				13-15	0.010			
17	0.100	0.021							0.420	0.326	0.040										0.020								11-12	0.010			
17.2									0.100																				14-14	0.020	0.022		
18									0.050	0.326																		0.130		19-19	0.010		
18.2									0.060																				13-14	0.010	0.043		
19									0.020	0.022																	0.280	0.587		15-15	0.010	0.022	
19.2									0.020																				15-16	0.010	0.022		
20																	0.080	0.043								0.420	0.130		18-19	0.030			
21																	0.510	0.196								0.300	0.065		12-13	0.010			
22					0.220	0.109											0.270	0.109										0.087		12-14		0.043	
23					0.540	0.217											0.140	0.500												14-20		0.022	
24					0.190	0.565																								11-13		0.087	
25					0.050	0.087																								13-17		0.065	
26						0.022																								18-21		0.022	
27							0.040																							10-14		0.022	
28							0.150	0.174																						11-16		0.022	
29							0.190	0.478																						14-18		0.022	
30							0.320	0.326																									
31							0.220																										
32							0.080	0.022																									
NA	6	5	5	3	4	5	6	4	9	5	5	4	5	3	4	3	4	5	4	6	5	4	5	5	3	3	5	5	3	5	NA	17	17
D	0.749	0.558	0.224	0.627	0.628	0.627	0.791	0.648	0.777	0.721	0.691	0.486	0.600	0.476	0.445	0.573	0.645	0.620	0.647	0.700	0.288	0.540	0.631	0.589	0.529	0.610	0.640	0.585	0.662	0.623	D	0.861	0.833

N: Number of individuals, NA: number of different alleles, D: Gene Diversity

Supplementary Table 2. Y-chromosome STR haplotype (Ht) distribution found in Chueta (CHU) (YHRD: YA004701) and Majorcan (MAJ) populations (YHRD: YA004702).

Ht	Haplogroup	CHU	MAJ	DYS456	DYS389I	DYS390	DYS389II	DYS458	DYS19	DYS385a	DYS385b	DYS393	DYS391	DYS439	DYS635	DYS392	Y GATA H4	DYS437	DYS438	DYS448
01	E1b1b1a1-M78	1	-	15	13	23	29	17	14	18	19	13	10	13	20	11	12	14	10	21
02	E1b1b1a1-M78	1	-	15	13	23	30	17	14	18	19	13	10	13	20	11	12	14	10	21
03	E1b1b1a1-M78	1	-	15	13	23	30	17	14	18	19	13	11	13	20	11	12	14	10	21
04	E1b1b1a1-M78	1	-	16	13	24	30	16	13	16	16	13	10	11	22	11	12	14	10	20
05	E1b1b1a1-M78	1	-	17	13	24	30	16	13	15	16	13	10	11	22	11	12	14	10	20
06	E1b1b1a1-M78	1	-	17	15	24	32	16	13	16	16	13	10	11	23	11	12	14	10	20
07	E1b1b1a1-M78	1	-	15	13	23	30	17	14	19	19	13	10	12	20	11	12	14	10	21
08	E1b1b1a1-M78	7	-	17	13	24	30	16	13	16	16	13	10	11	22	11	12	14	10	20
09	E1b1b1a1-M78	-	1	15	14	24	32	18	14	18	21	12	10	12	20	13	13	14	10	20
10	E1b1b1b-M81	-	1	15	14	24	30	18	13	13	16	13	9	10	21	11	11	14	10	20
11	F-M213	2	-	15	14	22	30	18	15	16	16	12	10	11	20	11	12	14	9	20
12	G-M201	1	-	13	13	22	32	17	15	13	13	14	9	11	22	11	11	16	10	21
13	G-M201	1	-	12	13	22	32	17	15	13	13	14	9	11	22	11	11	16	10	21
14	G-M201	1	-	13	13	22	30	17	15	13	13	14	9	11	22	11	11	16	10	21
15	G-M201	1	-	13	13	22	32	17	15	13	13	13	9	11	22	11	11	16	10	21
16	G-M201	2	-	13	13	22	32	17	15	13	13	14	9	11	23	11	11	16	10	21
17	G-M201	1	-	13	13	22	32	18	15	13	13	14	9	11	22	11	11	16	10	21
18	G-M201	1	-	14	12	22	29	17	15	14	14	14	10	10	21	11	12	15	9	20
19	G-M201	1	-	15	12	22	29	16	15	14	14	14	10	12	20	11	12	16	10	21
20	G-M201	1	-	15	12	22	29	18	15	14	14	10	10	11	20	11	12	16	10	21
21	G-M201	-	1	14	12	22	29	17	15	15	15	14	10	12	20	11	11	16	11	21
22	G-M201	-	1	15	12	22	28	16	15	15	16	12	10	12	21	11	11	16	10	22
23	G-M201	-	1	15	12	23	28	17	15	13	14	14	10	12	21	12	11	16	10	22
24	I-M170	1	-	15	14	23	32	16	17	15	15	14	10	12	21	12	11	14	10	20
25	I-M170	-	1	13	12	26	28	16	15	13	17	13	10	11	21	11	10	15	10	19
26	I-M170	-	1	14	12	22	28	15	14	13	14	13	10	11	21	11	11	15	10	20
27	I-M170	-	2	15	14	23	30	18	15	11	13	13	11	11	21	11	11	16	10	20
28	I2a1a1-M26	1	-	14	13	23	28	17	17	11	12	13	10	11	21	11	13	15	10	21
29	I2a1a1-M26	2	-	14	13	23	29	17	17	12	12	13	10	11	21	11	13	15	10	21
30	J1-DYS458.2	1	-	16	13	23	30	17.2	14	13	18	12	10	12	21	11	11	14	10	20
31	J1-DYS458.2	1	-	16	13	23	31	17.2	14	13	18	11	10	12	21	11	11	14	10	20
32	J1-DYS458.2	7	-	16	13	23	31	17.2	14	13	18	12	10	12	21	11	11	14	10	20
33	J1-DYS458.2	1	-	16	13	23	31	17.2	14	13	18	12	10	12	21	11	11	14	10	21
34	J1-DYS458.2	6	-	16	13	23	31	18.2	14	13	18	12	10	13	21	11	11	14	10	20

35	J1-DYS458.2	2	-	16	13	23	31	19.2	14	13	18	12	10	13	21	11	11	14	10	20
36	J2-M172	1	-	15	13	22	31	15	16	13	14	12	10	11	23	11	10	15	9	21
37	J2-M172	2	-	15	13	23	30	17	14	13	18	12	10	11	22	11	11	16	9	20
38	J2-M172	9	-	14	13	23	28	14	15	13	16	13	9	12	21	11	12	14	9	21
39	J2-M172	1	-	14	13	23	28	14	16	13	16	13	9	12	21	11	12	14	9	21
40	J2-M172	1	-	15	13	22	31	15	16	13	15	12	10	11	21	11	12	14	9	21
41	J2-M172	1	-	15	13	23	28	14	15	13	16	13	9	12	21	11	12	14	9	21
42	J2-M172	1	-	15	13	23	29	17	14	14	16	12	10	11	21	11	11	15	9	19
43	J2-M172	12	-	15	13	23	30	17	14	14	16	12	10	11	21	11	11	15	9	19
44	J2-M172	1	-	15	13	23	30	17	14	14	16	12	10	12	21	11	11	15	9	19
45	J2-M172	1	-	16	10	24	27	17	14	13	18	12	10	12	21	11	11	15	10	20
46	J2-M172	1	-	16	10	24	27	17	14	13	18	12	10	12	22	11	11	15	10	20
47	J2-M172	1	-	16	10	24	27	18	14	13	18	12	10	12	22	11	11	15	10	20
48	J2-M172	1	-	16	10	25	27	17	14	13	18	12	10	12	22	11	11	15	10	20
49	J2-M172	-	1	15	14	24	30	16	14	14	18	12	10	11	22	11	11	16	10	20
50	J2-M172	-	1	16	12	22	30	18	14	13	17	12	9	11	22	11	12	15	9	22
51	J2-M172	-	1	16	12	22	30	18	14	13	17	12	10	11	22	11	12	15	9	22
52	J2-M172	-	1	16	13	23	29	16	15	13	16	12	9	12	22	11	12	14	9	21
53	J2-M172	-	1	16	13	23	29	17	15	13	16	12	9	12	22	11	12	14	9	21
54	P-92R7	-	1	15	14	23	30	16	14	14	20	13	10	11	25	12	11	15	11	19
55	Q1-P36.2	1	-	15	13	22	28	17	13	14	16	13	10	12	22	16	10	14	11	19
56	Q1-P36.2	4	-	15	13	22	29	17	13	14	16	13	10	12	22	16	10	14	11	19
57	Q1-P36.2	2	-	15	13	22	29	17	13	14	16	13	10	12	22	17	10	14	11	19
58	Q1-P36.2	1	-	15	13	22	29	17	?	14	16	13	10	12	22	16	10	14	11	19
59	R1a1a-M17	1	-	16	13	25	30	15	16	11	14	13	11	10	23	11	14	14	11	20
60	R1a1a-M17	2	-	16	13	25	31	15	16	11	14	13	11	10	23	11	13	14	11	20
61	R1a1a-M17	1	-	16	13	25	31	15	16	11	15	13	11	10	23	11	13	14	11	20
62	R1b1a2a-M18	2	-	13	13	24	28	15	15	12	12	13	11	12	23	13	11	14	11	19
63	R1b1a2a-M18	1	-	13	14	24	29	15	15	12	12	13	11	12	23	13	11	14	11	19
64	R1b1a1a2a-L23	-	1	15	13	24	29	16	15	11	15	13	11	11	23	13	13	15	12	19
65	R1b1a1a2a1a1-U106	-	1	15	13	23	29	18	14	11	14	13	10	12	23	14	12	15	12	19
66	R1b1a1a2a1a2-S116	1	-	16	13	23	29	19	14	11	14	13	12	12	21	13	12	15	12	19
67	R1b1a1a2a1a2-S116	1	-	16	13	24	29	17	14	11	14	12	10	12	23	13	11	14	12	19
68	R1b1a1a2a1a2-S116	-	1	15	12	24	28	16	14	11	15	13	10	12	23	13	12	15	12	19
69	R1b1a1a2a1a2-S116	-	1	15	12	25	28	17	14	11	13	13	10	14	24	13	11	15	12	19
70	R1b1a1a2a1a2-S116	-	1	15	12	25	28	17	14	11	13	13	11	13	24	13	11	15	12	19
71	R1b1a1a2a1a2-S116	-	1	15	13	24	29	16	14	11	14	13	11	12	23	13	11	14	12	18
72	R1b1a1a2a1a2-S116	-	1	15	13	24	29	16	14	11	15	13	11	12	23	13	12	15	12	19

73	R1b1a1a2a1a2-S116	-	1	15	13	24	29	17	14	11	14	14	10	12	25	13	11	14	12	18
74	R1b1a1a2a1a2-S116	-	1	15	13	24	29	18	14	11	14	13	10	12	23	13	12	14	12	19
75	R1b1a1a2a1a2-S116	-	1	15	13	24	30	16	14	11	14	13	11	13	23	13	12	15	12	19
76	R1b1a1a2a1a2-S116	-	1	15	13	24	30	16	16	11	14	13	11	12	24	13	12	15	12	19
77	R1b1a1a2a1a2-S116	-	1	15	13	24	30	18	14	11	14	12	10	11	23	13	11	14	12	18
78	R1b1a1a2a1a2-S116	-	1	15	14	24	29	17	14	11	14	13	10	12	23	13	11	14	12	18
79	R1b1a1a2a1a2-S116	-	1	15	14	24	30	17	14	11	15	13	11	12	23	13	12	15	12	19
80	R1b1a1a2a1a2-S116	-	1	16	12	25	28	17	14	11	14	13	10	12	23	13	12	15	13	19
81	R1b1a1a2a1a2-S116	-	1	16	13	23	29	17	15	10	14	13	10	12	23	13	12	14	12	19
82	R1b1a1a2a1a2-S116	-	1	16	13	24	29	16	14	11	14	12	11	12	23	13	11	14	12	19
83	R1b1a1a2a1a2-S116	-	1	16	13	24	29	17	14	12	14	13	11	13	23	13	11	14	12	18
84	R1b1a1a2a1a2-S116	-	1	16	13	24	29	18	14	11	14	13	11	12	23	13	12	15	12	19
85	R1b1a1a2a1a2-S116	-	1	16	13	24	29	19	14	11	14	13	11	13	23	13	12	15	12	19
86	R1b1a1a2a1a2-S116	-	1	16	13	24	30	18	14	11	14	14	10	12	23	12	12	15	12	19
87	R1b1a1a2a1a2-S116	-	1	16	14	24	30	17	14	11	16	13	11	13	23	13	12	14	12	18
88	R1b1a1a2a1a2-S116	-	1	17	13	24	29	18	14	11	14	13	11	11	23	13	12	14	12	19
89	R1b1a1a2a1a2b-U152	1		15	13	24	29	16	14	11	15	13	10	13	23	13	13	15	13	20
90	R1b1a1a2a1a2b-U152	-	1	15	13	25	29	18	14	12	14	13	10	12	23	13	12	14	12	19
91	R1b1a1a2a1a2b-U152	-	1	15	14	24	30	18	14	12	12	14	11	12	24	13	12	15	12	19
92	R1b1a1a2a1a2b-U152	-	2	16	13	24	29	17	14	11	14	13	10	12	23	13	12	15	12	19
93	R1b1a1a2a1a2c1-M529	1	-	17	13	24	29	19	14	12	13	13	11	12	23	13	11	15	12	19
94	R1b1a1a2a1a2c1-M529	-	1	15	13	24	29	17	15	11	14	13	10	13	23	13	12	15	12	19
95	R1b1a1a2a1a2c1-M529	-	1	16	13	24	29	16	14	11	14	13	11	11	24	13	8	15	12	19
96	T-M70	-	1	15	13	23	29	18	15	14	16	13	10	11	21	13	11	14	9	19
97	T-M70	-	1	15	14	23	30	15	13	14	14	13	10	12	21	14	11	14	9	19

Supplementary Table 3. Mitochondrial D-loop haplotypes and haplogroups of the 104 Chueta samples (EMPOP*: EMP00672), classified according to HaploGrep2 (Build 17, PhyloTree).

Sample	Haplogroup	Haplotypes																	
CHU2	U1a1a1	16182C	16183C	16189C	16249C	73G	263G	285T	309.1C	309.2C	315.1C	385G	d523	d524	573.1C	573.2C	573.3C		
CHU3	H1a3	16051G	16162G	16519C	73G	263G	315.1C	534T											
CHU4	U5b1f1a	16192T	16270T	16319A	73G	150T	263G	315.1C	533G										
CHU10	H1bo	16189C	16519C	263G	267C	315.1C	485C												
CHU11	U5b3	16192T	16270T	16304C	16526A	73G	150A	228A	263G	309.1C	315.1C								
CHU12	H1+152	152C	263G	309.1C	309.2C	315.1C	466C												
CHU15	K1a1b1a	16223T	16224C	16234T	16311C	16519C	73G	114T	263G	315.1C	497T								
CHU16	K1a	16129A	16224C	16256T	16311C	16519C	73G	263G	315.1C	497T									
CHU17	H66a	16172C	16519C	263G	315.1C														
CHU19	H2a2a	16519C	263G	315.1C															
CHU21	T1a	16126C	16163G	16186T	16189C	16294T	16298C	16319A	16519C	73G	263G	309.1C	315.1C						
CHU22	H66a	16172C	16519C	263G	315.1C														
CHU23	M5a1	16129A	16223T	16291T	16298C	16519C	73G	263G	315.1C	489C	524.1A	524.2C							
CHU24	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU25	K1c	16224C	16311C	16519C	73G	146C	152C	263G	309.1C	315.1C	d498								
CHU26	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU27	H1+152	152C	263G	309.1C	309.2C	315.1C	466C												
CHU28	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU29	U3	16343G	73G	150T	263G	309.1C	315.1C												
CHU30	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU31	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU32	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU33	H2a2a	16519C	263G	309.1C	315.1C														
CHU34	T2b	16126C	16294T	16296T	16304C	16519C	73G	263G	309.1C	309.2C	315.1C								
CHU35	T2c1d	16126C	16292T	16294T	16519C	73G	146C	263G	279C	309.1C	315.1C								
CHU36	H	16223T	16519C	263G	315.1C														
CHU37	J1d1	16069T	16126C	16193T	16300G	73G	152C	195C	263G	295T	309.1C	315.1C	462T	489C					
CHU38	H2a2a	16519C	263G	309.1C	315.1C	d523	d524												
CHU39	H1j8	16129A	16240G	16519C	152C	185A	263G	309.1C	315.1C										
CHU40	U6a	16092C	16172C	16219G	16278T	73G	263G	315.1C											
CHU42	T	16126C	16294T	16304C	16519C	73G	263G	309.1C	309.2C	315.1C									
CHU43	H11a2	16092C	16169T	16293G	16298C	16311C	263G	315.1C											
CHU45	T2c1d	16126C	16292T	16294T	16519C	73G	146C	263G	279C	309.1C	309.2C	315.1C							
CHU46	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU47	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU48	I1c1	16129A	16223T	16264T	16270T	16311C	16319A	16362C	16391A	16519C	73G	199C	204C	250C	263G	309.1C	315.1C	455.1T	573.1C
CHU49	M5a1	16129A	16223T	16291T	16298C	16519C	73G	263G	315.1C	489C	524.1A	524.2C							
CHU52	M1a1	16129A	16183C	16189C	16193.1C	16223T	16249C	16311C	16359C	16519C	73G	195C	263G	315.1C	489C				

CHU53	J2a1a1	16069T	16126C	16145A	16231C	16261T	73G	150T	152C	195C	203A	215G	263G	295T	315.1C	319C	489C	513A
CHU54	K1a	16129A	16224C	16256T	16311C	16519C	73G	263G	315.1C	497T								
CHU55	J2a1a1	16069T	16126C	16145A	16231C	16261T	73G	150T	152C	195C	203A	215G	263G	295T	315.1C	319C	489C	513A
CHU56	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU57	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU58	K1a1b1a	16223T	16224C	16234T	16311C	16519C	73G	114T	263G	309.1C	315.1C	497T						
CHU59	L3e2b+152	16172C	16183C	16189C	16320T	16519C	73G	150T	152C	195C	263G	315.1C						
CHU60	H1e1a6	16147T	16264T	16519C	150T	263G	315.1C											
CHU61	T	16126C	16294T	16304C	16519C	73G	263G	309.1C	315.1C									
CHU62	K1a	16129A	16224C	16256T	16311C	16519C	73G	263G	315.1C	497T								
CHU63	U1a1a1	16182C	16183C	16189C	16193.1C	16249C	73G	263G	285T	309.1C	309.2C	315.1C	385G	d523	d524	573.1C	573.2C	
CHU64	D1j	16223T	16242T	16311C	16325C	16362C	73G	152C	235G	263G	309.1C	315.1C	489C					
CHU65	U3	16343G	73G	150T	263G	315.1C												
CHU66	K1b1a1+199	16093C	16224C	16311C	16319A	16463G	16519C	73G	152C	199C	263G	309.1C	315.1C	524.1A	524.2C	524.3A	524.4C	
CHU67	U3a	16343G	16390A	16519C	73G	150T	263G	309.1C	309.2C	315.1C								
CHU68	H	16223T	16519C	263G	315.1C													
CHU69	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU70	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU71	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU104	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU105	L3e2b+152	16172C	16183C	16189C	16223T	16320T	16519C	73G	150T	152C	195C	263G	315.1C					
CHU106	U5b1d2	16239T	16270T	73G	150T	263G	315.1C											
CHU107	K1a	16129A	16224C	16311C	16519C	73G	263G	315.1C	497T									
CHU108	T2c1d	16126C	16292T	16294T	16519C	73G	146C	263G	279C	309.1C	315.1C							
CHU109	U1a1a1	16182C	16183C	16189C	16249C	73G	263G	285T	309.1C	309.2C	315.1C	385G	d523	d524	573.1C	573.2C		
CHU110	L3e2b+152	16172C	16183C	16189C	16223T	16320T	16519C	73G	150T	152C	195C	263G	315.1C					
CHU111	T2b23	16126C	16147T	16294T	16296T	16297C	16304C	16519C	73G	263G	309.1C	309.2C	315.1C					
CHU112	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU113	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU115	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU117	M1a1	16129A	16183C	16189C	16223T	16249C	16311C	16359C	16519C	73G	195C	263G	315.1C	489C				
CHU118	K1a4a1	16129A	16224C	16256T	16311C	16519C	73G	263G	315.1C	497T								
CHU120	U1a1a1	16182C	16183C	16189C	16249C	73G	263G	285T	309.1C	309.2C	315.1C	385G	d523	d524	573.1C	573.2C		
CHU126	H1j8	16129A	16240G	16519C	152C	185A	263G	309.1C	315.1C									
CHU127	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU128	T2c1d	16126C	16292T	16294T	16519C	73G	146C	263G	279C	309.1C	315.1C							
CHU129	T1a	16126C	16163G	16186T	16189C	16294T	16298C	16301T	16319A	16519C	73G	263G	309.1C	315.1C				
CHU130	T1a	16126C	16163G	16186T	16189C	16294T	16298C	16319A	16519C	73G	263G	309.1C	315.1C					
CHU131	HV0+195	16298C	72C	195C	263G	309.1C	309.2C	315.1C										
CHU132	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C								
CHU133	K1a1b1a	16223T	16224C	16234T	16311C	16519C	73G	114T	263G	315.1C	497T							

CHU134	U5b1f1a	16192T	16270T	16319A	73G	150T	263G	315.1C	533G										
CHU135	T1a	16126C	16163G	16186T	16189C	16294T	16298C	16319A	16519C	73G	263G	309.1C	315.1C						
CHU136	H66a	16172C	16519C	263G	315.1C														
CHU137	J2b1a	16069T	16126C	16193T	16278T	73G	150T	152C	263G	295T	315.1C	489C	523d	524d					
CHU139	T2c1d	16126C	16292T	16294T	16519C	73G	146C	263G	279C	309.1C	315.1C								
CHU140	T1a1'3	16126C	16163G	16186T	16189C	16294T	16519C	16527T	73G	152C	195C	263G	309.1C	315.1C	573.1C				
CHU141	K2b1a1a	16222T	16224C	16270T	16311C	16519C	73G	146C	195C	263G	315.1C								
CHU142	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									
CHU143	T2b23	16126C	16147T	16294T	16296T	16297C	16304C	73G	263G	309.1C	309.2C	315.1C							
CHU144	U5a2	16192T	16256T	16270T	16526A	73G	263G	309.1C	315.1C										
CHU145	L3e2b+152	16172C	16183C	16189C	16223T	16320T	16335G	16519C	73G	150T	152C	195C	263G	315.1C					
CHU146	H6	16126C	16362C	16482G	16519C	239C	263G	309.1C	315.1C										
CHU147	T1a	16126C	16163G	16186T	16189C	16294T	16298C	16319A	16519C	73G	263G	309.1C	315.1C						
CHU148	T2b5a1	16126C	16294T	16304C	16519C	73G	152C	263G	309.1C	309.2C	315.1C	573.1C							
CHU149	H1n6	16519C	263G	309.1C	315.1C	552A													
CHU150	J2a1a1	16069T	16126C	16145A	16231C	16261T	73G	150T	152C	195C	203A	215G	263G	295T	315.1C	319C	489C	513A	
CHU151	T2	16093C	16126C	16294T	16296T	16519C	73G	263G	315.1C										
CHU153	J1c2o	16069T	16126C	16163G	16266T	16311C	16519C	73G	185A	188G	204C	228A	263G	295T	315.1C	462T	489C		
CHU154	T	16126C	16294T	16304C	16519C	73G	263G	309.1C	309.2C	315.1C									
CHU155	K1a1b1a	16223T	16224C	16234T	16311C	16519C	73G	114T	263G	315.1C	497T								
CHU156	T1a	16126C	16163G	16186T	16189C	16294T	16298C	16319A	16519C	73G	263G	309.1C	315.1C						
CHU157	U1a1a1	16182C	16183C	16189C	16249C	16545C	73G	263G	285T	309.1C	309.2C	315.1C	385G	523d	524d	573.1C	573.2C	573.3C	
CHU199	HV0+195	16298C	72C	195C	263G	309.1C	315.1C												
CHU200	L3e2b+152	16172C	16183C	16189C	16223T	16320T	16519C	73G	150T	152C	195C	263G	315.1C						
CHU201	R0a+60.1T	16126C	16362C	16519C	58C	60.1T	64T	263G	309.1C	315.1C									

*Parson, W. and A. Dür (2007). EMPOP--a forensic mtDNA database. *Forensic Sci Int Genet* 1(2): 88-92.

MAJ44	J1b1b	16069T	16126C	16145A	16261T	16263C	16519C	73G	263G	271T	295T	309.1C	315.1C	462T	489C	d523	d524	
MAJ45	HV0	16298C	16311C	72C	73G	263G	309.1C	309.2C	315.1C									
MAJ46	H2a2a	16519C	263G	315.1C														
MAJ47	J1c	16069T	16126C	73G	228A	263G	295T	309.1C	315.1C	462T	489C							
MAJ48	HV15	16129A	16234T	16311C	16519C	263G	309.1C	315.1C										
MAJ49	U5b3	16270T	16304C	16399G	64T	73G	150T	204C	228A	263G	315.1C							
MAJ50	H24	16293G	309.1C	315.1C														
MAJ51	K1a	16224C	16304C	16311C	16519C	73G	263G	315.1C	497T									
MAJ52	K2a5	16224C	16311C	16519C	73G	146C	152C	263G	315.1C	324T								
MAJ53	T2a1b	16126C	16218T	16294T	16296T	16324C	16519C	73G	263G	315.1C								
MAJ54	N1b1	16145A	16176G	16187T	16223T	16311C	16390A	16519C	73G	152C	263G	315.1C						
MAJ55	L3d1b2	16124C	16223T	16519C	73G	150T	152C	263G	309.1C	315.1C	d523	d524						
MAJ56	T	16126C	16294T	16304C	16519C	73G	93G	199C	263G	315.1C								
MAJ57	L2a1b +143	16189C	16192T	16223T	16278T	16294T	16309G	16390A	73G	143A	146C	152C	195C	263G	309.1C	315.1C		
MAJ58	H5s	16111T	16304C	16311C	16391A	16519C	263G	309.1C	309.2C	315.1C	456T							
MAJ59	H3ak	16519C	143A	263G	309.1C	309.2C	315.1C											
MAJ60	U4b3	16278T	16356C	16519C	73G	195C	215G	263G	309.1C	315.1C	499A	524.1A	524.2C					
MAJ61	H11a2	16092C	16257T	16293G	16311C	93G	195C	263G	315.1C									
MAJ62	K2b1a1a	16222T	16224C	16270T	16311C	16519C	73G	146C	195C	263G	315.1C							
MAJ63	HV0	16298C	72C	263G	309.1C	315.1C												
MAJ64	K1b1 (+16093)	16093C	16192T	16224C	16311C	16319A	16519C	73G	152C	263G	309.1C	315.1C	524.1A	524.2C				
MAJ65	H1m1	16519C	146C	263G	315.1C													
MAJ66	H1e +16129	16129A	16311C	152C	263G	309.1C	315.1C	d523	d524									
MAJ67	HV0 +195	16298C	72C	195C	263G	309.1C	315.1C											
MAJ68	H24	16293G	309.1C	315.1C														
MAJ69	HV0	16298C	72C	263G	309.1C	315.1C												
MAJ70	H1j8	16129A	16240G	16519C	152C	185A	263G	309.1C	315.1C									
MAJ71	H6	16362C	16482G	16545C	239C	263G	309.1C	315.1C										
MAJ72	HV0 +195	16298C	72C	195C	228A	263G	309.1C	315.1C										
MAJ73	J1b1a1	16069T	16092C	16126C	16145A	16172C	16222T	16261T	73G	146C	242T	263G	295T	315.1C	462T	489C		
MAJ74	H1e +16129	16129A	16519C	263G	315.1C													
MAJ75	H1m1	16519C	146C	263G	315.1C													
MAJ76	U2e1'2'3	16051G	16129C	16183C	16189C	16274A	16362C	16519C	73G	152C	217C	263G	309.1C	309.2C	315.1C	508G	524.1A	524.2C
MAJ77	T2a1b	16092C	16126C	16294T	16296T	16324C	16519C	73G	263G	315.1C								
MAJ78	H2a5a1	16291T	16519C	217C	263G	315.1C												
MAJ79	H6	16362C	16482G	239C	263G	309.1C	315.1C											
MAJ80	HV4a2a	16287T	16519C	263G	309.1C	315.1C												
MAJ81	H6	16362C	16482G	239C	263G	315.1C												
MAJ104	H1e +16129	16129A	16311C	152C	263G	309.1C	315.1C	d523	d524									
MAJ198	U5b3	16192T	16270T	16304C	16526A	73G	150T	228A	263G	309.1C	315.1C							

*Parson, W. and A. Dür (2007). EMPOP--a forensic mtDNA database. *Forensic Sci Int Genet* 1(2): 88-92.

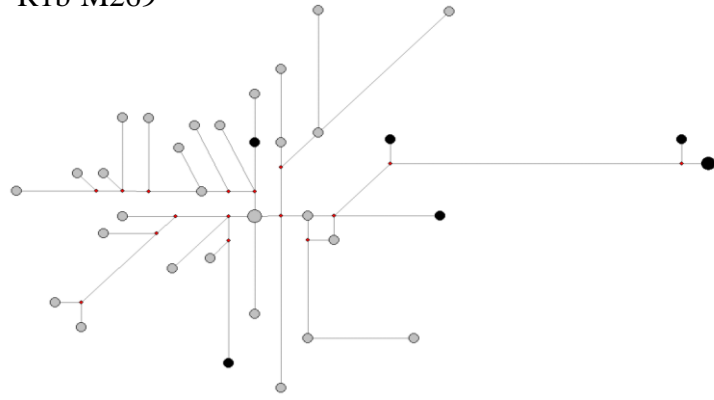
Supplementary Table 5. Populations and references used for the different analysis performed in this work.

Marker	Population	Reference
Y-SNPs	Chuetas	Present Study
	Sephardic 1	Behar et al. (2010) Nature 466: 238–242
	Sephardic 2	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Bragança Jews	Nogueiro et al. (2010) Am. J. Phys. Anthropol. 141: 373–381
	Ashkenazi 1	Behar et al. (2010) Nature 466: 238–242
	Ashkenazi 2	Behar et al. (2004) Hum. Genet. 114: 354–365
	Azerbaijan Jews	Behar et al. (2010) Nature 466: 238–242
	Cochin Jews	Chaubey et al. (2016) Sci. Rep. 6: 19166
	Cohanim	Hammer et al. (2009) Hum. Genet. 126: 707–717
	Ethiopia Jews 1	Cruciani et al. (2002) Am. J. Hum. Genet. 70(5): 1197–1214
	Ethiopia Jews 2	Behar et al. (2010) Nature 466: 238–242
	Georgia Jews	Behar et al. (2010) Nature 466: 238–242
	Iran Jews	Behar et al. (2010) Nature 466: 238–242
	Iraq Jews	Behar et al. (2010) Nature 466: 238–242
	Israelian	Hammer et al. (2009) Hum. Genet. 126: 707–717
	Libya Jews	Shen et al. (2004) Hum. Mutat. 24:248–260
	Morocco Jews	Behar et al. (2010) Nature 466: 238–242
	Mumbai Jews	Behar et al. (2010) Nature 466: 238–242
	Uzbekistan Jews	Behar et al. (2010) Nature 466: 238–242
	Majorca 1	Present Study
	Majorca 2	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Andalusia	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Basque Country	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Castile	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Catalonia	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Extremadura	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Galicia	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Valencia	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Portugal North	Adams et al. (2008) Am. J. Hum. Genet. 83: 725–736
	Tras-os-montes	Nogueiro et al. (2010) Am. J. Phys. Anthropol. 141: 373–381
	Georgia	Bataglia et al. (2009) Eur. J. Hum. Genet. 17: 820–830
	Hungary	Bataglia et al. (2009) Eur. J. Hum. Genet. 17: 820–830
	Moldova	Varzaki et al. (2013) PLoS One, 8(1): e53731
	Poland	Bataglia et al. (2009) Eur. J. Hum. Genet. 17: 820–830
	Ukraine	Varzaki et al. (2013) PLoS One, 8(1): e53731
	Iran	Crugni et al. (2012) PLoS One, 7(7): e41252
	Iraq	Al-Zahery et al. (2011) BMC Evol. Biol. 11(1): 1–16
	Jordan (Ammam)	Flores et al. (2005) J. Hum. Genet. 50(9): 435–441
	Jordan (Death Sea)	Flores et al. (2005) J. Hum. Genet. 50(9): 435–441
	Palestinian 1	Flores et al. (2005) J. Hum. Genet. 50(9): 435–441
	Palestinian 2	Behar et al. (2010) Nature 466: 238–242
	Yemen	Cadenas et al. (2008) Eur. J. Hum. Genet. 16: 374–386
	Uzbekistan	Behar et al. (2010) Nature 466: 238–242
	India (South)	Behar et al. (2010) Nature 466: 238–242
	Algeria	Bekada et al. (2015) PLoS One, 10(9): e0138453
	Egypt	Luis et al. (2004) Am. J. Hum. Genet. 74: 532–544
	Morocco	Bosch et al. (2001) Am. J. Hum. Genet. 68(4): 1019–1029
	Morocco (Arabs)	Cruciani et al. (2002) Am. J. Hum. Genet. 70(5): 1197–1214
	Morocco (Berbers)	Cruciani et al. (2002) Am. J. Hum. Genet. 70(5): 1197–1214
	Sahrawi	Bosch et al. (2001) Am. J. Hum. Genet. 68(4): 1019–1029
Y-STR	Chuetas	Present Study
	Bragança Jews	Nogueiro et al. (2010) Am. J. Phys. Anthropol. 141: 373–381
	Majorca	Present Study
	Barcelona	Sánchez et al. (2007) Forensic Sci. Int. 172: 211–217
	Bosnia-Herzegovina	Kovacekic et al. (2013) Croat. Med. J. 54: 286–290
	Bulgaria	Karachanak et al. (2013) PLoS One, 8(3): e56779
	East Tyrol	Niedersttater et al. (2012) PLoS One, 7(7): e41885
	Greece	Kovatsi et al. (2013) Forensic Sci. Int. Genet. 4: e21–e22
	Italy	Onofri et al. (2007) Int. J. Legal Med. 121: 234–237
	Montenegro	Mirabal et al. (2010) Am. J. Phys. Anthropol. 142: 380–390
	Romania	Stanciu et al. (2010) Leg. Med. 12: 259–264
	Russia	Roewer et al. (2008) Int. J. Legal Med. 122: 219–223
	Serbia	Vaselinovik et al. (2008) Forensic Sci. Int. 176: e23–e28
	Ukraine	Mielnik-Sikorska et al. (2013) Forensic Sci. Int. Genet. 7: 200–203

	USA caucasic	Coble et al. (2013) <i>Forensic Sci. Int. Genet.</i> 7: e66–e68
	USA hispanic	Coble et al. (2013) <i>Forensic Sci. Int. Genet.</i> 7: e66–e68
	Anatolia	Alakoc (2010) <i>Forensic Sci. Int. Genet.</i> 4: e135–e137
	Armenia	Lowery et al. (2013) <i>Legal Med.</i> 15: 85–90
	Iran	Roewer et al. (2009) <i>Forensic Sci. Int. Genet.</i> 4: e53–e55
	Lebanon	Haber et al. (2011) <i>J. Hum. Genet.</i> 56(1): 29–33
	Pathans	Lee et al. (2014) <i>Forensic Sci. Int. Genet.</i> 11:111–116
	Libya	Fadhlaoui-Zid et al. (2013) <i>PLoS One</i> 8(11): e80293
	East Libya	Elmrghni et al. (2012) <i>Forensic Sci. Int. Genet.</i> 6(2): 224–227
	West Libya	Triki-Fendry et al. (2013) <i>Forensic Sci. Int. Genet.</i> 7: e59–e61
	Morocco	Fadhlaoui-Zid et al. (2013) <i>PLoS One</i> 8(11): e80293
mtDNA	Chuetas	Present Study
	Sephardic Jews	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	Bragança Jews	Nogueiro et al. (2015) <i>Eur. J. Hum. Genet.</i> 23(5): 693–699
	Ashkenazi 1	Behar et al. (2006) <i>Am. J. Hum. Genet.</i> 78(3): 487–497
	Ashkenazi 2	Picornell et al. (2006) <i>Int. J. Legal Med.</i> 120(5): 271–281
	Iran Jews	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	Yemen Jews 1	Thomas et al. (2002) <i>Am. J. Hum. Genet.</i> 70(6): 1411–1420
	Yemen Jews 2	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	Yemen Jews 3	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78
	Ethiopia Jews 1	Thomas et al. (2002) <i>Am. J. Hum. Genet.</i> 70(6): 1411–1420
	Ethiopia Jews 2	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	North Africa Jews 1	Picornell et al. (2006) <i>Int. J. Legal Med.</i> 120(5): 271–281
	North Africa Jews 1 Majorca	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	Valencia	Present Study
	Galicía	Santos et al. (2014) <i>Am. J. Hum. Biol.</i> 26(2):130–141
	Portugal 1	Santos et al. (2014) <i>Am. J. Hum. Biol.</i> 26(2):130–141
	Portugal 2	Santos et al. (2014) <i>Am. J. Hum. Biol.</i> 26(2):130–141
	Italy	Marques et al. (2015) <i>Forensic Sci. Int. Genet.</i> 15:27–32
	Italy (Tuscany)	Messina et al. (2015) <i>Am. J. Hum. Boil.</i> 27(4): 508–519
	Bulgaria	Achilli et al (2007) <i>Am. J. Hum. Genet.</i> 80(4): 759–768
	France	Karachanak et al. (2012) <i>Int. J. Legal Med.</i> 126 (4): 497–503
	Greece	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Georgia 1	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Georgia 2	Thomas et al. (2002) <i>Am. J. Hum. Genet.</i> 70(6): 1411–1420
	Balkans	Quintana-Murci et al. (2004) <i>Am. J. Hum. Genet.</i> 74(5): 827–845
	Turkey 1	González et al. (2008) <i>Ann. Hum. Biol.</i> 35(2) 212–231
	Turkey 2	Quintana-Murci et al. (2004) <i>Am. J. Hum. Genet.</i> 74(5): 827–845
	Jordania (Ammam)	González et al. (2008) <i>Ann. Hum. Biol.</i> 35(2) 212–231
	Jordania	González et al. (2008) <i>Ann. Hum. Biol.</i> 35(2) 212–231
	Bedouins 1	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Bedouins 2	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	Druze 1	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78
	Druze 2	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	Lebanon	González et al. (2008) <i>Ann. Hum. Biol.</i> 35(2) 212–231
	Iran	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Iran (Zagros Mountains)	Derenko et al. (2013) <i>PLoS One</i> 8(11): e80673
	Iraq 1	Quintana-Murci et al. (2004) <i>Am. J. Hum. Genet.</i> 74(5): 827–845
	Iraq 2	Al-Zahery et al. (2011) <i>BMC Evol. Biol.</i> 11(1): 1–16
	Palestine 1	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Palestine 2	Behar et al (2008) <i>PLoS One</i> 3(4): e2062
	Palestine 3	González et al. (2008) <i>Ann. Hum. Biol.</i> 35(2) 212–231
	Syria 1	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Syria 2	Thomas et al. (2002) <i>Am. J. Hum. Genet.</i> 70(6): 1411–1420
	Pakistan	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Turkmenistan	Quintana-Murci et al. (2004) <i>Am. J. Hum. Genet.</i> 74(5): 827–845
	Kuwait	González et al. (2008) <i>Ann. Hum. Biol.</i> 35(2) 212–231
	Arabia Saudi 1	Sheible et al. (2011) <i>Forensic Sci. Int. Genet.</i> 5(4): e112–e113
	Arabia Saudi 1	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78
	Yemen 1	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
	Yemen 2	Thomas et al. (2002) <i>Am. J. Hum. Genet.</i> 70(6): 1411–1420
Yemen 3	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78	
Ethiopia 1	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616	
Ethiopia 2	Thomas et al. (2002) <i>Am. J. Hum. Genet.</i> 70(6): 1411–1420	
Ethiopia 3	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78	
Sudan	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616	
		Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78

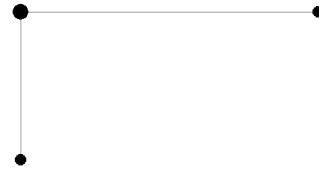
Sudan (Nubia)	González et al. (2008) <i>Ann. Hum. Biol.</i> 35(2) 212–231
Chad	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78
Egypt 1	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
Egypt 2	Elmadawy et al. (2013) <i>Legal Med.</i> 15(6): 338–341
Libya	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616
Tunisia	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78
Morocco 1	Černý et al. (2011) <i>Mol. Biol. Evol.</i> 28(1): 71–78
Morocco 2	Aboukhalid et al. (2013) <i>Int. J. Legal Med.</i> 127(4): 757–759
Morocco 3	Badro et al. (2013) <i>PLoS One</i> 8(1): e54616

R1b-M269



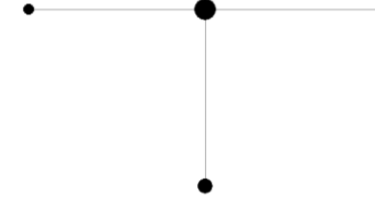
hC= 0.9524 +/- 0.0955
 hM= 0.9975 +/- 0.0099
 hT= 0.9978 +/- 0.0075

R1a1-M17



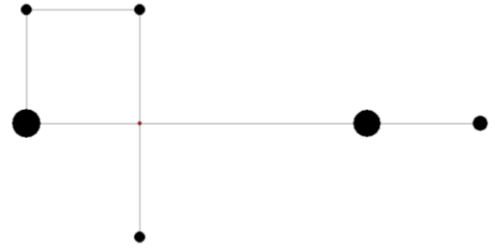
hC= 0.8333 +/- 0.2224
 hM= ---
 hT= 0.8333 +/- 0.2224

Q-P36.2

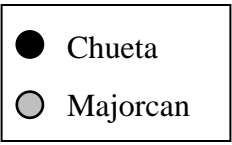


hC= 0.7500 +/- 0.1391
 hM= ---
 hT= 0.7500 +/- 0.1391

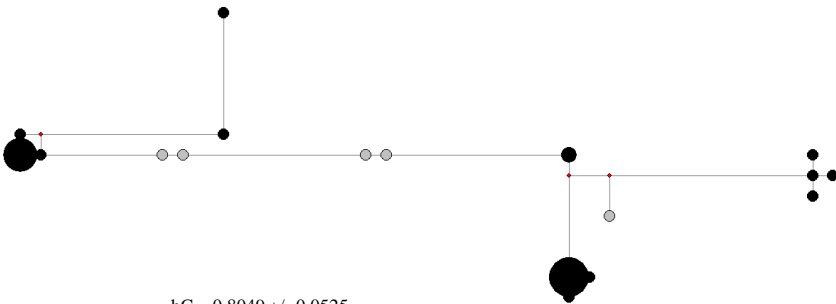
J-12f2a



hC= 0.6838 +/- 0.0805
 hM= ---
 hT= 0.6838 +/- 0.0805

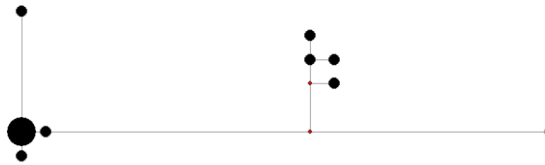


J2-M172



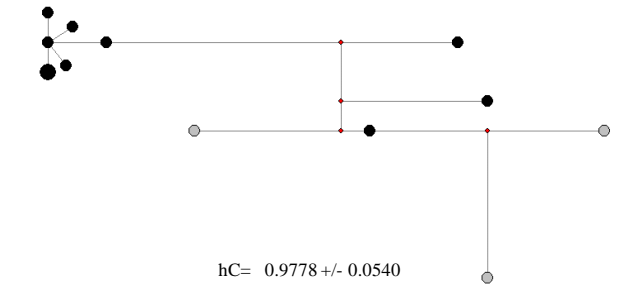
hC= 0.8049 +/- 0.0525
 hM= 1.0000 +/- 0.1265
 hT= 0.8535 +/- 0.0436

E-M78



hC= 0.7692 +/- 0.1198
 hM= 1.0000 +/- 0.2722
 hT= 0.8000 +/- 0.1080

G-M201



hC= 0.9778 +/- 0.0540
 hM= 1.0000 +/- 0.2722
 hT= 0.9872 +/- 0.0354

Supplementary Figure 1. Networks based on Y-STR haplotypes of the main haplogroups found in Chuetan (black) and Majorcan (grey) populations, as one of their parental populations. Haplotype diversities (HD) in each haplogroup are shown as follows; hC: HD in Chuetans, hM: HD in Majorcans, and finally hT: total HD within each haplogroup. No putative parental Jewish population was used in these analyses due to the lack of data for this set of markers in any proper population.