

Article

Not peer-reviewed version

The Canary Islands Aboriginal Maternal Genetic Pool: Haplotype Reanalysis, New Coalescent Ages, and the Roman Mediated Settlement Hypothesis

[Vicente M. Cabrera](#)*

Posted Date: 7 July 2023

doi: 10.20944/preprints202307.0464.v1

Keywords: Human evolution; mitochondrial DNA; phylogeography; coalescent dates; Northwest African haplogroups; Mediterranean haplogroups; Canary Islands



Preprints.org is a free multidiscipline platform providing preprint service that is dedicated to making early versions of research outputs permanently available and citable. Preprints posted at Preprints.org appear in Web of Science, Crossref, Google Scholar, Scilit, Europe PMC.

Copyright: This is an open access article distributed under the Creative Commons Attribution License which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Article

The Canary Islands Aboriginal Maternal Genetic Pool: Haplotype Reanalysis, New Coalescent Ages, and the Roman Mediated Settlement Hypothesis

Vicente M. Cabrera *

Department of Biochemistry, Microbiology, Cell Biology and Genetics, Universidad de La Laguna, 38200 San Cristobal de La Laguna, Spain; Vicente.vca811@gmail.com

* Retired

Abstract: Classic mitochondrial DNA phylogenetic and phylogeographic studies on the aboriginal, historical, and extant human populations of the Canary Islands have contributed to reconstructing the origin and settlement on the islands of the pre-European colonizers. The recent use of new ancient DNA targeted enrichment and next generation sequencing techniques on new Canary Islands samples has greatly improved these molecular results, but it has also revealed significant DNA contamination in the islands' previous aboriginal genetic pool. Following a thorough review of these cases, new phylogeographic analysis revealed the existence of a heterogeneous aboriginal population, asymmetrically distributed across the various islands, which most likely descended from a unique main settlement. These new results and new proposed coalescent ages are compatible with a Roman-mediated arrival driven by the exploitation of the purple dye on the Canary Islands.

Keywords: human evolution; mitochondrial DNA; phylogeography; coalescent dates; Northwest African haplogroups; Mediterranean haplogroups; Canary Islands

1. Introduction

The Canary Islands are Atlantic Oceanic islands located approximately 108 kms off Morocco's southwest coast. Since the European maritime expansion along the Atlantic Africa in the fourteenth century, the Canary Islands attracted special attention as the only Archipelago of the area inhabited by indigenous people with a late Neolithic culture. The numerous and multidisciplinary studies carried out on this population have recently been reviewed from archaeological¹ and genetic perspectives². Recent radiocarbon dates based on short-life samples, allowed the construction of a robust chronological model for the islands hypothesizing a permanent settlement on the Archipelago around the turn of the epoch³. On the other hand, new sequencing methodologies have revolutionized the analysis of ancient DNA, making the sequencing of mitogenomes and whole genomes from archaeological specimens a task with increasing chances of success⁴. Applying these techniques to aboriginal remains from the Canary Islands, the northern African origin of its most recent ancestors has been redefined^{5,6}. However, the bulk of the data from the aboriginal remains of the Canary Islands have been obtained with Polymerase Chain Reaction (PCR) techniques and subsequent classic Sanger sequencing⁶⁻⁹. Regrettably, these techniques are prone to contamination and sequencing artefacts¹⁰. The potential existence of such disturbing phenomena were revealed when the ancient haplotypes were contrasted with the largest (n=896) sample studied so far of extant whole mtDNA Canarian genomes¹¹. In addition, a disparity exists between archaeological and genetic ages, being the later much older¹². Perhaps, the biggest failure of the studies on the aboriginal settlement of the Canary Islands is the absence of a model capable of integrating the data gathered from the different scientific disciplines in a coherent frame.

The aims of this study are: a) To perform a critical re-analysis of the published mtDNA aboriginal haplotypes in order to clear up those contaminant types that disturb the authentic results; b) To apply updated mtDNA evolutionary rates^{13,14} towards obtaining more realistic coalescent ages

for the aboriginal lineages; c) To reformulate the time and sources of the Roman-mediated aboriginal settlement in order to incorporate the archaeological and genetic data into a congruent narrative.

2. Material and Methods

2.1. Samples

Partial and complete mtDNA sequences of the aboriginal (^{6-9,15,16}), historical (^{17,18}), and present-day Canary Islands population samples (^{11,19,20}) were compiled from prior published studies (Table S1 and supplementary bibliography). To find the closest matches to the Canarian aborigine sequences, we use nucleotide rare variants and co-occurrence among point variants to search within known haplogroups, and short sequences, including total or partial haplotypes, to query the whole dataset at the following databases: NCBI GenBank (www.ncbi.nlm.nih.gov/genbank/, (accessed on 30 December 2022)), Mitomap (www.mitomap.org/MITOMAP, (accessed on 30 December 2022))²¹, Ian Logan 2020 (www.ianlogan.co.uk/sequences_by_group/haplogroup_select.htm, (accessed on 30 December 2022)), Empop database (www.https://empop.online/haplotypes, (accessed on 30 December 2022))²², and AmtDB (www.http://amtdb.org, (accessed on 30 December 2022)). In total we have reanalyzed 336 mtDNA aboriginal sequences of which 288 are HVSI partial sequences (16000 to 16400 range) and 48 are complete mitogenomes. In addition, we screened 3246 northern African and 10960 European sequences in search of haplotype matches. Detailed sample sizes for each island and continental regions are specified in Table S1.

2.2. Sequence Classification

Sequence assignment to the corresponding haplogroup and its sub-haplogroups was confirmed using HaploGrep version 2, <https://haplogrep.i-med.ac.at>, (accessed on 30 December 2022)²³, and PhyloTree build 17 version, <http://www.phylotree.org>, (accessed on 30 December 2022)²⁴. Sequence variants were scored with respect to rCRS²⁵. The output raw trees were manually confirmed and refined. The hotspot 16,519 mutation and indels around nucleotides 309, 522, 573, and 16,193 were excluded from the trees and from the statistical analysis.

2.3. Population based statistical analyses

Due to the important genetic drift effects observed in the Canary Islands aboriginal populations⁶ and in order to compensate for the dominant influence of the most common haplotypes in the frequency-based pairwise distances, we have used a match-based distance proposed elsewhere¹¹. For statistical haplotype comparison of the western (Tenerife, La Gomera, La Palma, and El Hierro) and eastern (Lanzarote, Fuerteventura and Gran Canaria) population samples from the Canary Islands, we used a Hamming distance in which positive matches (1) were compared against negative matches (0) applying a sign test for categorical data (<https://www.graphpad.com/quickcalcs/> (accessed on 30 December 2022)). The important haplotype overlap among the northern African and the Mediterranean regions of Europe studied were graphically represented by Venn diagrams. A binary matrix indicating presence (1) or absence (0) of the aboriginal haplotypes in each island and continental regions sampled was the input for these analyses (Table S2). From a pairwise match-based distance matrix (Table S3), principal coordinates analysis was performed as implemented in the GenAIEx 6.51 web site (accessed on 30 December 2022)²⁶. Fisher's contingency tests and t-tests were calculated using the graphpad calculator (<https://www.graphpad.com/quickcalcs/> (accessed on 30 December 2022)).

2.4. Coalescence Age Estimations

The coalescence ages for the putative autochthonous Canarian lineages were calculated using rho statistics²⁷ and a revised substitution rate of one mutation every 1,400 years (95% CI: 1,261–1,539) based on the most recent period of human demographic history¹³. Seqbot (<https://evolution.genetics.washington.edu/phylip/doc/seqboot.html>) was used to generate 3,600

bootstrapped mtDNA alignments to calculate the rho statistical error for each autochthonous founder lineage using the python-based script *'bootstrap_rho.py'* available at (<https://github.com/genomicsITER/mitogenomes/tree/main/CanarymtDNA> (accessed on 30 December 2022))¹¹.

3. Results

3.1. Contamination and sequencing artefacts in the Canary Islands aboriginal maternal genetic pool

Studies of ancient DNA (aDNA) based on the classical Polymerase Chain Reaction (PCR) and subsequent Sanger sequencing are likely to provide unreliable data¹⁰. This possibility increases when haplotypes that have never appeared previously are detected for the first time in aDNA studies. This is the case for the aboriginal mtDNA genetic pool of the Canary Islands. From the 81 different lineages found in the published studies to date, 15 (19%) have not been reported in the historical or current populations from the Canary Islands or in any of those from continental regions where the most likely ancestors originated (Table S1). Table 1, lists ten (12%) of the haplotypes that might have resulted from partial sample contamination or incomplete sequencing.

Table 1. Possibly contaminated and/or incomplected Canarian Aborigine haplotypes, based on HVSI variants (16000 to 16400 range) minus 16000. Hg 1 and Hg 2 mean haplogroup classification before and after the analysis.					
Detected	Hg 1	Most probable	Contaminator	Hg 2	Region
093 192	H/HV/U/R	093 192 (256 270 362)	Incomplete	U5a1b4	IP (68)
129 294	H/HV/U/R	(126) 129 294 (296 304)	Incomplete	T2b	IP (75)
145 213	H/HV/U/R	145 213 (223 278 294 390)	Incomplete	L2	NWA (11)
126 255 292 294	T2c1d3	126 292 294	069 126 255	T2c1d3	NWA (11)
239 278	U*	(172 219) 239 278	Incomplete	U6a1a1	NWA (30)
172 219 221 224 278	U6a	172 219 278	221 224 311	U6a7	NWA (6)
129 169 172 189 213	U6c	129 169 172 189	213	U6c1	NWA (42)
126 223 262 320	L3e2b	223 320	126 262 292 294	L3e2	NA (70)
223 239 278 292	L3	(111A 145 184) 223 239 278 292 (311 355 390)	complete	L2e	Senegal (6)
223 278 311 355 362	L3b1a12	(114A 129 213) 223 278 311 355 362	Incomplete	L2b1a	Mali (71)

The fact that the first hypervariable segment (HVSI) studied was amplified in seven overlapping small fragments⁷, favored the formation of these chimeric lineages. In order to reinforce the authenticity of the results, samples were also tested for haplogroup diagnostic positions by restriction fragment length polymorphisms (RFLPs), looking for phylogenetic consistency between HVSI sequences and RFLPs⁷. However, in the case of ambiguous HVSI haplotypes, a contaminated haplogroup RFLP assay could paradoxically misclassify that haplotype. A case in question could be the pair of transitions 16172-16278 that by RFLP (7028 Alu-; 3010 Tsp+) was classified as belonging to haplogroup H1, but it has also been found as belonging to haplogroup U6a in Morocco²⁸, on the Portuguese island of Madeira, very close to the Canary Islands¹⁹, and within the U6a7a1a Acadian clade of French origin²⁹. In addition, at least the 16213 transition was a likely sequence artefact¹⁰ as it was found in different haplotypes of independent haplogroups in which it was not previously been detected (Table S1).

3.2. Persistency and phylogeographic origin of the Canary Islands aboriginal haplotypes

It was recently found¹¹ that around 50%-60% of the Canary Islands aboriginal mtDNA lineages are extant in the current Canary Island populations. However, when we take into account all the lineages detected in the historic and present-day samples, we observed a slow decreasing trend, since the historic times aboriginal lineages represented 37.9% of the total, whereas in present-day samples they account only for 26.5% of all the lineages observed (Table S1). Because all the published results from various disciplines point to Canarian aborigines' North African origin, the abundance of exclusive matches of aboriginal haplotypes to Europeans compared to North Africans was surprising in our results ($p = 0.006$). A graphical representation, including sub-Saharan Africa populations,

showed that most aboriginal haplotypes matched to both North Africans and Europeans, while those from sub-Saharan African were in the minority (Figure 1).

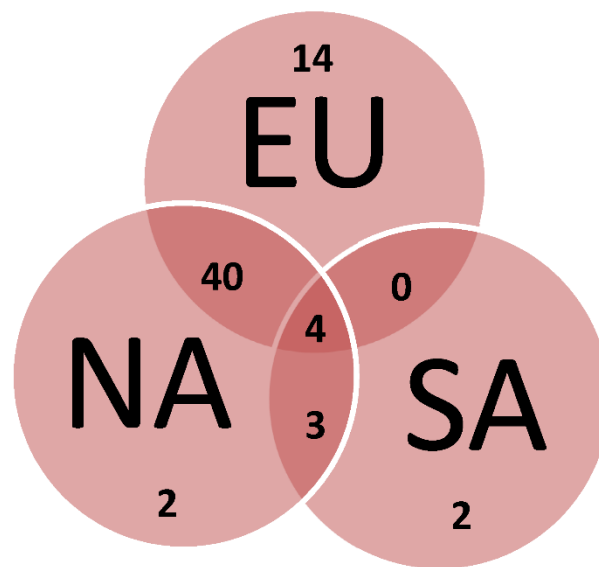


Figure 1. Venn diagram showing the aboriginal haplotype overlapping among Europe (EU), North Africa (NA) and sub-Saharan Africa (SA).

About half of the aboriginal haplotypes detected in El Hierro had matches with Europeans alone. A partition of the 14 aboriginal haplotypes shared exclusively with Europe (Figure 2) suggested that the contribution of the Iberian and Italian peninsulas pair might be greater (20.6%) than that of Iberia and France (11.5%), but was not statistically significant ($p = 0.17$).

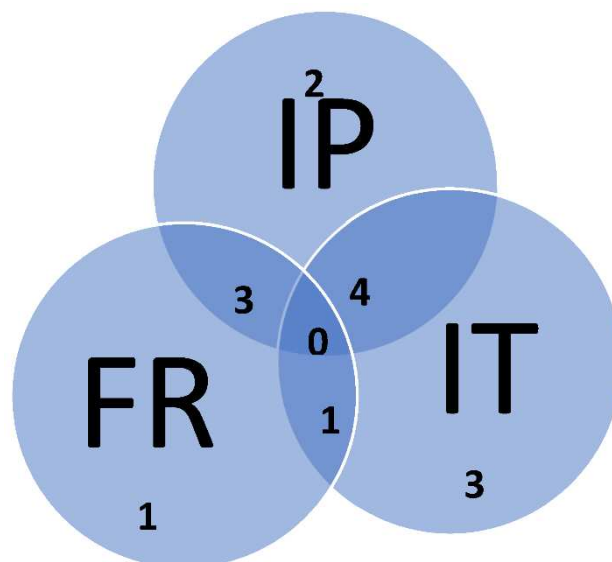


Figure 2. Venn diagram showing the aboriginal haplotype overlapping among Iberian Peninsula (IP), France (FR) and Italy (IT).

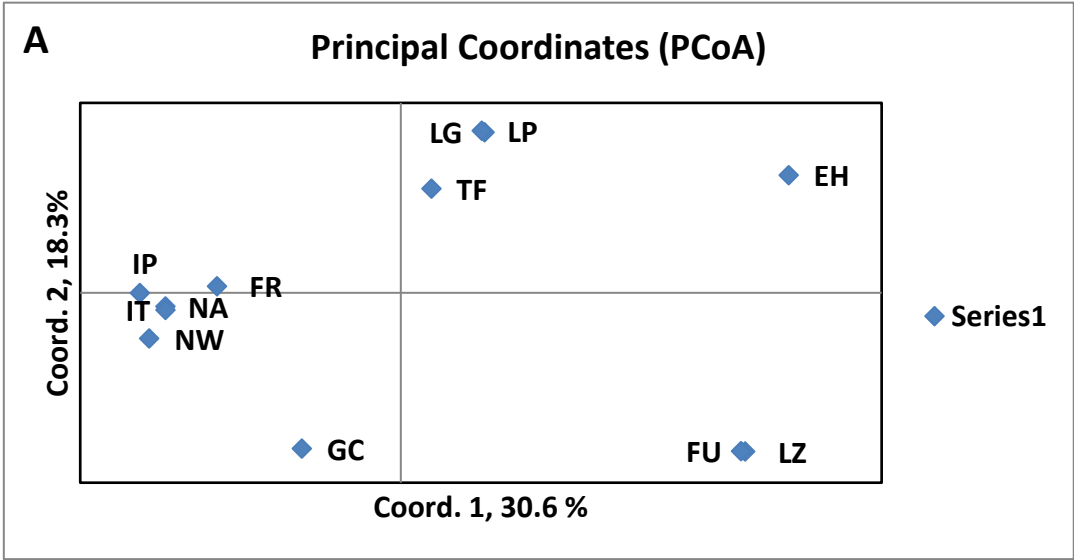
The relative affinities of the Canarian aborigines with the northern African regions (Table S1), suggested that 67.3% of the matches occur to both the northwest and northern Africa. However, exclusive matches with the northwest (26.5%) was significantly higher ($p = 0.01$) than to the northern region (6.1%). Of the 81 aboriginal haplotypes examined, 33 (41%) were not been detected in historic or contemporary samples from the Canary Islands (Table S1). Of these, 7 haplotypes (9 %) exclusively matched to European regions. Naturally, these haplotypes could have not yet been detected in

northern Africa, but also it could be assumed that they were brought to the islands by European males and, since mtDNA is only transmitted by females, they went extinct on the Canary Islands. Similarly, there are also exclusive matches of aboriginal haplotypes with the Middle East and sub-Saharan Africa that are waiting for a congruent explanation (Table S1).

Special mention deserves those haplotypes detected solely in the Canary Islands and Latin America, most likely originated from post-conquest immigration of Canary Islanders to that continent (Table S1). Another interesting case are those haplotypes derived from the autochthonous haplogroup U6b1a with prominent implantation in western islands ⁶ that although lacking exact matches, still have their closest counterparts in the Moroccan sister clade U6b1b ³⁰. Special attention also deserves those putatively sub-Saharan African haplotypes in the haplogroup L3b1a12 detected in the eastern island of Gran Canaria ^{6,15}. Attending to its HVSI region (16223-16278-16311-16362), their exact matches are found within haplogroup L3b1a11 from Madagascar ³¹. However, the complete sequencing of several L3b1a12 aboriginal mtDNA genomes ^{6,15} revealed that the Canarian haplotypes differed from their putative African counterparts by the exclusive presence of six transitions from their coding region (8697, 9947, 10646, 11257, 14136, 14553), contradicting the phylogenetic identity deduced from the HVSI analysis. Taken together, this evidence emphasizes the need to study complete mitogenomes in order to obtain truly reliable genetic matches.

3.3. Divergence of aboriginal genetic pool among islands

It has been deduced from the present-day Canary Islands insular populations' studies that the genetic differentiation detected between western (Tenerife, La Gomera, La Palma, and El Hierro) and eastern (Gran Canaria, Lanzarote, and Fuerteventura) islands may have dated back to the pre-colonial past ^{19,32,33}. This assumption has been recently corroborated by direct analyses of the aboriginal populations ⁶. A pair-wise match-distance between islands is presented in Table S3, and a graphical representation of their respective relationships and genetic affinities with their putative continental colonizers can be visualized in Figure 3.



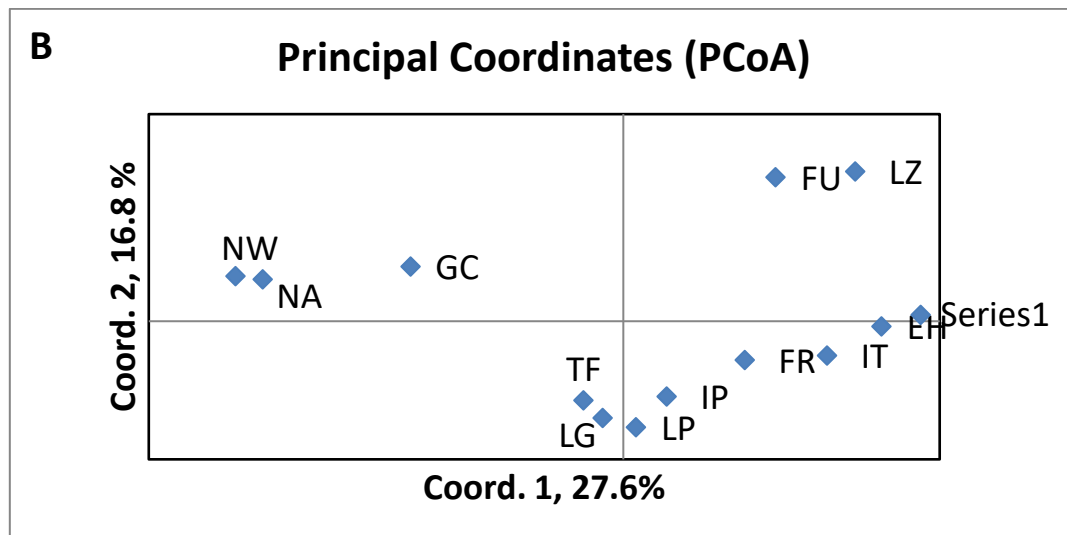


Figure 3.

Principal Coordinate Analyses showing the relative affinities among islands (LZ, Lanzarote; FU, Fuerteventura; GC, Gran Canaria; TF, Tenerife; LG, La Gomera; LP, La Palma y EH, El Hierro) and with the Continental African (NW, North West Africa; NA, Northern Africa) and European regions (IP, Iberian Peninsula; FR, France; IT, Italy) from where their putative ancestors most probably came from. A. Distances between continental regions based on their relative sharing of aboriginal haplotypes. B. Distances between continental regions based on their own haplotypal pools.

In principal coordinates' analysis (Figure 3A), the genetic match distances between continental regions are based on their respective sharing of Canarian aboriginal haplotypes exclusively. The coordinate 1 axis clearly separates all samples the continental regions from those from the Canary Islands, meaning that they are mainly sharing the same ancestral haplotypes. Coordinate 2 axis, in turn, separated the western from the eastern Canary Islands, showing in each case that the least sampled eastern islands of Fuerteventura and Lanzarote and the westernmost island of El Hierro samples, having the greatest genetic drift effects ¹⁶, are clear outliers. On the other hand, we found that Gran Canaria is the island that shared the largest number of aboriginal lineages with its putative continental maternal sources. In Figure 1B, the genetic distances between samples from the continental regions were based on their respective sharing of their own lineages ¹¹. In this case, the closest affinities between samples from regions within continents were clearly reflected, anchoring Northern African regions far from European regions along the X coordinate axis. Again, the eastern and western islands were separated along the Y-axis although now Gran Canaria has the greatest genetic affinity with northern Africa while the western islands show a closer proximity to the European regions. A sign test based on the number of haplotypes shared between groups and those unique to each group showed that they are statistically different ($p=0.001$). However, due to the high haplotype diversity of the total aboriginal sample, it cannot be guaranteed that the eastern and western islands samples originated from different populations. In the following analysis of the haplotype differences between the two groups of islands, the following assumption was made: consider of northern African provenance all the haplotypes with matches in North Africa although they were also present in other regions and having European provenance those haplotypes with matches only in Europe. Prominent or exclusive haplogroups in the eastern islands are: H1 (16239), H1ao (16278), H3r (16126), H4a1e (16362), T2c1d3, U5, U6a, U6c, M1, and L3b1a12 (Table S1). It is interesting to mention that U6a, U6c and M1 have a pan-Mediterranean range and that U6a and M1 have had an implantation in Northwest Africa since the Pleistocene ³⁴, which is also extensible to H1 (16239) and H3r (16126) ³⁵. It deserves mentioning that a recent study has extended the geographic range of H4a1e to southern Egypt prior to the Roman and Greek influx in the area ³⁶. In addition, some T sequences have localized specific matches: T1a (16126-16154-16163-16186-16189-16294) in Algeria ³⁷, T2c1d3 (16092-16126-16292-16294) in Morocco ³⁸ or T2c1d3 (126-292-294-362) in the Near

East. On the contrary, the basal U5b1 haplotypes are present in an ample geographic range from the Western Sahara ³⁹ and Mauritania ⁴⁰ to Mediterranean Africa (Table S1). On the opposite side were the haplotypes of haplogroup L3b1a12, whose place of origin in Africa is still unknown ⁶. In relation to haplotypes having probable European origin, H1e1a9 (13934) and HV (16316) stand out for their exclusive matches in Italy. Nevertheless it has to be mentioned that an ancestral type of H1e1a was detected in Chalcolithic–Middle Bronze Age samples from Portugal ⁴¹. In the western group, northern African heritage was represented by several haplotypes derived from the H1 haplogroup (Table S1). A special mention deserves the H1cf type which, by sequences of the complete mtDNA, revealed its closest relative in Algeria ⁸. All the J haplotypes detected in the aboriginal population were from western islands, and the J2a2d1 branch seemed to have a northwest African origin. This type is present on all western islands except El Hierro (Table S1). However, without a doubt, the haplotypes of haplogroup U6b1a showed the most notable northern African contribution to the western islands, with the highest incidence in La Gomera ⁹ and being again absent from El Hierro. Although not detected on the African continent, it had its closest phylogenetic sister clade (U6b1b) in Morocco ³⁰. The traces left by these U6b1a haplotypes in Latin America and the Iberian Peninsula after the forced migration of Canarian aborigines following the conquest are also significant (Table S1). Regarding the European contribution, once again, the high incidence of haplogroup H types stands out (Table S1). For example, the H1 (16292) type was detected in all the western islands except La Gomera, with matches in the Iberian Peninsula and Italy. Attending to J haplotypes other than J2a2d1, the J1c3 and J1c2c2 types present in Tenerife had exact matches both in the Iberian Peninsula and in Italy and France, respectively (Table S1). La Gomera presented an enigmatic N1b1a7 lineage that had an exact match in the Middle East alone ⁴². La Palma also harbored two haplotypes belonging to macrohaplogroup N. The W1e1 type had matches in the current populations of the Iberian Peninsula and Italy, being detected since the Neolithic in Catalonia ⁴³, indicating its ancient presence in the Iberian Peninsula. The other is a specific derivative of X3a (16111-16189-16223-16278), which also had a unique match in that peninsula (Table S1). Finally, El Hierro was peculiar by having a rare U5a1b4 haplotype only found in France and a rare U7 haplotype (16309-16318T) whose nearest matches were in the Iberian Peninsula and Italy but that was also spotted in Egypt ⁴⁴.

Finally, around 12% of the aboriginal lineages traced their origins in sub-Saharan Africa despite some of them were also observed in northern Africa, and approximately 30% of them had exclusive matches within regions where the Portuguese slave trade peaked (Table S1). Notably, this result closely resembles the situation in the current populations of the Macaronesia Islands of Madeira and the Canarian archipelago, where about 40% of their sub-Saharan L sequences have exact matches in Cape Verde and Sao Tomé and Príncipe, which were main outposts of the Portuguese Atlantic slave trade ¹⁹.

3.4. New coalescence ages for the Aboriginal lineages

Some of the first radiocarbon dates placed the aboriginal settlement of the Canary Islands back to late Neolithic times, which was in agreement with the cultural level of the Canary aborigines ⁴⁵ and with the first coalescent age estimations obtained for the Canary islands mtDNA autochthonous lineages U6b1a and U6c1a around 5,000 ya ^{46,47}. However, those old radiocarbon dates have recently been considered as artefacts due to the inappropriate material used. New and revised archaeological dates and demographic inferences have concluded that, with the available data, a permanent settlement on the islands prior to the first millennium AD is highly improbable ³. In parallel, studies on the mtDNA evolutionary rate ^{14,48,48} have demonstrated that it is dependent on the population size and that a rate of one mutation every 3,624 years extensively used in phylogenetic analysis ¹² is inappropriate to apply to relatively recent events. In this study, an alternative evolutionary rate of one mutation every 1,400 years was used as is much more in line with the time frame studied here ¹³. Applying this evolutionary rate to the phylogenetic trees (Figures S1 to S6) of the 16 aboriginal lineages with a number of complete mtDNA sequences, for the indigenous ^{6,15} and current populations ¹¹ of the Canary Islands, enough to carry out a phylogenetic analysis (Table S4), the coalescence ages obtained ranged from 2,333 (95% CI: 2,300-2,368) ya for the H1cf (16260) clade to 382

(95% CI: 361-401) ya for the Gran Canaria autochthonous lineage L3b1a (@16124). It deserves mentioning that H1cf and H1e1a, the oldest lineages, both belonged to the European haplogroup H1. For the former, the closest sequence to the Canary cluster was an Algerian sequence ⁸ and for the latter an Italian sequence (Table S1). These clusters were followed by J2a2d1a and U6b1a with main introductions in the western Islands and U6c1 limited to the eastern islands, whose ages located them in the Canarian archipelago between the second and the fifth centuries AD. At first, this apparent continuous range of ages could be compatible with a permanent flux of migrants to the Archipelago. However, this is in contrast with the important genetic drift effects observed in the islands of La Gomera ⁹ and El Hierro ¹⁶ and the relatively high genetic differentiation found between the main islands of Tenerife and Gran Canaria ⁶. These results are more in line with successive but discrete migrations that did not affect all the islands equally. Thus, taking into account the relative proximity of their respective ages, we subdivided the aboriginal lineages into three discrete time intervals (Table 4). The oldest group comprised the five lineages (H1cf, H1e1a, J2a2d1, U6b1a, and U6c1) commented above. Lineages of the middle age group (W1e1, X3a, and U5a1b4) could arrive to the Archipelago at the beginning of the twelfth century affecting only to the western islands which would coincide in time with an internal population growth marked by the autochthonous U6b1a1 lineage. It should be noted that these three lineages, would have a European origin instead of Arab. The third and most recent group coincides with the period of the European colonization of the Archipelago (from 1,402 to 1,496 years). In it U6a* represents a set of current Canarian sequences belonging to subgroups U6a1a1 (16239), U6a3a1, and U6a7a1b, all detected in the aboriginal sample (Table S1). These three clades had Chalcolithic expansions in Europe ²⁹. From them, it is particularly interesting the case of U6a7a1b that is related to the Sephardic radiation and historical diffusions to the American continent ²⁹. Clades H4a1, T2c1d3 and T2c1d1c could signal the post-conquest Moorish slave trade ⁶, while the L sub-Saharan African members seem to be the result of the Atlantic slave trade practiced by Portuguese traffickers ¹¹. Predictable, age differences between groups 1 and 2 ($p = 0.0007$) and between group 2 and 3 ($p = 0.0026$) were highly significant.

4. Discussion

4.1. Contamination problems in ancient DNA studies

Due to the availability of many human mtDNA sequences in data banks, for which the recent contribution of Canarian samples is remarkable ¹¹, rare or incomplete aboriginal haplotypes published in earlier studies on ancient DNA from the Canary Islands ⁷ appear related to lineages sampled in the current population, highlighting their potential authenticity. Paradigmatic are the cases of H* (16290) in La Palma, J1c2e2 (16069-16126-16278-16366) in Tenerife, L3d1b3a (16124-16223-16256-16311) in La Gomera, or U5a1b4 (16093-16192-16256-16270-16362) in El Hierro ¹¹. Remarkable are also other aboriginal types detected in Latin America regions with demographic ties in the Canary Islands (Table 2), and those identified in continental areas from which their potential ancestors originated (Table 3).

Table 2. Aboriginal mtDNA haplotypes present in the historic or current Canarian population but absent in North Africa. Details as in Table S1.					
Haplotype	Haplogroup	IP	FR	IT	Other
126	H3r	14	9	35	
239	H1	14	9	10	
292	H1	8	9		
316	H1bw	13		10	
192 260	H3v				Chile (67)
069 126 278 366	J1c2e2	8	9		
163 172 219 311	U6b1a	43			Pto.Rico (66)
048 163 172 219 311	U6b1a				Uruguay (65)
092 163 172 219 311	U6b1a				Chile (67)
223 292 295	W1e1	35		10	
223 278 311 362	L3b1a12				Dominican (44)

Table 3. Aboriginal mtDNA haplotypes absent in the historic and/or current Canarian population. Details as in Table S1							
Haplotype	Haplogroup	NW	NA	IP	FR	IT	Other
067	HV1	11	12	37		10	
086	H1	6	20	14	9	10	
213	H/HV/U/R	21	12	45	48	26	
223	H1		19	29	9	24	
265	HV/R	16		14	9	24	
302	H1				9	19	
172 278	H1	16		51			
145 213*	H/HV/U/R						
260 278	H1cf						Yemen (62)
129 294*	H/HV/U/R				9		Frisian (63)
316	HV						Iran (38)
189 316	HV						Iran (38)
069	J1c3			13		19	
126 294	T2e	11	19	37	9	24	
126 224 292 294	T2c1d3						Romania(58)
126 255 292 294*	T2c1d3						
126 292 294 362	T2c1d3						Iraq (57)
126 154 163 186 189 294	T1a		53				
224 235 311	K2a5a1			21		29	
270 294	U5a2a			41			
239 278*	U6a1a1						
172 219 221 224 278*	U6a						
169 172 189	U6c1	6	34	45	44		
129 169 172 189 213*	U6c1						
309 318T	U7			29		24	
145 176G 223 297 311	N1b1a7						Armenia(63)
111 189 223 278	X3a			13			
081 093 175 223 278 320	L3						Sao Tomé(69)
223 278 311 355 362*	L3b1a12						
126 223 262 320*	L3e2b						
223 278 390	L2	6	19				
223 239 278 292*	L2e						
111A 145 184 223 239 278 292 311 355 390	L2e						Senegal(6)

The absence of matches with any published mtDNA sequence of some aboriginal haplotypes may indicate contamination, mixed up types or incomplete sequencing, and has led to the identification of the most probable aboriginal haplotype and its contaminant (Table 1). Finally, some aboriginal types, with potential relatives in Europe but not detected in historical or present-day Canarian populations, may represent pre-conquest male limited incursions that did not transmit this maternal marker. Other empirical data are in support of this hypothesis. The Y-chromosome haplogroup I-M170 is a predominant European male-lineage. While it shows a frequency around 9.8% in the Iberian Peninsula, its presence in northern Africa is minority (0.002%), a difference that is statistically highly significant ($P < 0.0001$). Curiously, haplogroup I-M170 reached a frequency of 6.7% in a Canarian aboriginal sample⁴⁹ which is also significantly different from that in northern Africa ($p = 0.0097$). These results strongly support the existence of a male-mediated European gene-flow on the aboriginal population before the Spanish Conquest or, alternatively, a strong contamination/admixture of the aboriginal remains with potential European remains. Although more recent techniques of enrichment and sequencing of ancient DNA make it easier to identify contamination, the reassessment of doubtful sequences with the panel of publicly available sequences will continue to be a useful strategy.

4.2. Lack of date and context of archaeological samples

Archaeological samples are precious materials, and their preservation is a justified obsession of archaeologists. However, to be fructiferous, in collaboration with other disciplines, donated samples should be accurately dated and contextualized following precise radiocarbon hygiene protocols. Regrettably, this was not the case in the first ancient DNA studies carried out on aboriginal material,

in which the samples consisted of non-individualized, loose teeth, theoretically obtained from aboriginal sites roughly dated around 1,000 ya. Thus, in order not to duplicate samples, geneticists opted to use a single dental type, preferably the left canine ⁷ for all the DNA extractions. Although molecular results from that material yielded important information, including the presence in the aboriginal sample of several predicted founder lineages as U6b1a ²⁰, the critical re-analysis performed here clearly confirms that those putative aboriginal samples contained a jumble of samples that, in addition to aboriginal ones, included European remains from the conquest period, remains of Moorish and sub-Saharan Africans brought to the islands by the Europeans as forced labor and, probably, remains of fugitive Sephardic people. Thus, the supposedly high genetic diversity found in the Aboriginal sample ⁷ was in fact the result of heavy archaeological contamination. This appreciation seems to be confirmed in more recent studies carried out on dated and contextualized archaeological material, for which observed genetic diversity is appreciably lower ^{6,15}. Another effect of the absence of precise archaeological dating is the existence of long-debated one or more colonization waves to the Canary Islands could only be inferred from the coalescent age of those aboriginal lineages that remain represented in the current population ¹¹.

4.3. Molecular age for a permanent aboriginal settlement

The mtDNA evolutionary rate of humans appears to have accelerated in recent times ¹³. Applying this faster rate to calculate the coalescent ages for those aboriginal lineages that remain represented today (Table S4), revealed molecular ages between 2,300 and 2,185 years ago for the two oldest lineages, H1cf and H1e1a (Table S4), that is, two or three centuries BD. These molecular ages are earlier than the recent archaeological estimates, dating the first settlement of the Canary Islands to two or three centuries AD ⁵⁰, but are much closer to each other than those previously proposed ¹². On the other hand, age differences among lineages, and their heterogeneous settlements on the islands, gives us some clues to resolve other intriguing questions such as whether the Archipelago was colonized in one or several immigration waves, or whether the pre-conquest settlers arose from one or more genetically heterogeneous populations. Focusing first on the oldest group (Table 4), two lineages (H1e1e and U6c1) showed a wide Mediterranean geographic range, including Italy and northern Africa, who exclusively settled on the eastern islands. On the other side, three lineages (H1cf, J2a2d1, and U6b1a) showed a prominent or exclusive trace to the western islands, of which at least two (H1cf and U6b1a) appeared restricted to northwestern Africa.

Table 4. Settlements on the Canary Islands based on coalescence age and phylogeography of aboriginal mtDNA lineages

Lineages	Period	Mean Age	95% CI	Islands' Group	Origin
H1cf				Western	Algeria
H1e1a				Eastern	Italy
J2a2d1	124 AD	1,876	1,426 - 2,325	Western	Tunisia
U6b1a				Western	Morocco
U6c1				Eastern	Italy, Morocco
W1e1				Western	Italy
X3a	1,117 AD	883	809 - 956	Western	North Africa
U5a1b4				Western	France
U6b1a1				Canarian	Autochthonous
U6a*				Eastern	North Africa
H4a1				Eastern	North Africa
L2e				Western	Senegal
T2c1d3	1,430 AD	570	435 - 704	Eastern	North Africa
L3d1b3a				Western	Morocco
T2c1d1c				Eastern	Autochthonous
L3b1a				Eastern	Unknown

As the range of their ages did not allow us to significantly separate these lineages, alternative possibilities may involve only a single heterogeneous wave, or coetaneous heterogeneous waves, of settlers who colonized different groups of islands. This contradicts an earlier suggestion that the H1e1a, H4a1e, L3b1a, and U6c1 clades having an asymmetrical implantation in the eastern islands may signal a late secondary settlement on these islands ⁶. It further was deduced that most sites from

which these lineages were sampled had radiocarbon dates placed around the thirteenth century. However, the late age of the sites sampled does not guarantee that the lineages did not settle on the islands earlier, as their coalescence ages indicate (Table S4). The second group of lineages indeed could point to the existence of a second wave of colonizers affecting the western islands in an interval from the end of the tenth to the beginning of the twelfth centuries albeit, if it really occurred, it had a minor impact on the maternal genetic pool of the islands. However, the incorporation of those maternal lineages, into the western islands may have been due to early pre-conquest European sporadic landings. The third group is a set of lineages that likely became incorporated into the Canarian population during the European colonization period. As previously mentioned, the clades T2c1d3 and T2c1d1c although not detected in aboriginal remains showed an autochthonous radiation, which could signal the post-conquest forced Moorish incorporation in the eastern islands⁶, while the sub-Saharan African L haplotypes during the same period could have result from the Portuguese Atlantic slave trade¹¹. Note, however, that the eastern islands L3b1a lineage likely should be excluded from this post-conquest input as it was detected in individualized remnants radiocarbon-dated to $1,116 \pm 26$ years BP¹⁵. Because of this, the shallow age of coalescence obtained for the clade (Table S4) may be attributed to a possible loss of some divergent haplotypes due to genetic drift. Future knowledge of the place from which the L3b1a and U6b1a lineages came to the islands will help to resolve the precise origin of the aboriginal Canarian settlers. Finally, since the lineages of the second and third groups mainly belonged to the western islands, their relative genetic closeness to those from European regions (Figure 3B) should not be taken as a differentiation between aboriginal populations but as a result of the contamination of the provided archaeological samples.

With the available ancient mtDNA data, it could not be discerned whether more than one wave of pre-conquest colonizers occurred as some archaeological investigations suggested⁵¹, but it does seem that a genetically heterogeneous population or populations likely colonized the Canary Islands in an asymmetric way around the first millennium AD. Earlier studies about physical anthropology of the Canary Islands aborigines already pointed to the existence of a physically heterogeneous population. In one of those, a clear Negroid component was detected⁵² although it was ruled out after the analyses of dermatoglyphics and haptoglobin types in the extant population, which did not reveal any Negroid affinities. To explain the discrepancy, it was suggested that some sub-Saharan African skulls, from the post-conquest slave trade, could have been included in the analysis inadvertently⁵³. However, in this regard, it should be noted that, due to genetic recombination, a sub-Saharan African immigrant genome would have been diluted into the recipient population in a few generations, whereas a mtDNA lineage would retain its African roots without modification. More thorough analyses concluded that the skulls of the first islanders might be explained as mixtures, in varying proportions, of two ancestral types: the robust Cromagnoid from northwestern Africa and the gracile Mediterranean Capsian⁵⁴. Both types were present in the main islands of Tenerife and Gran Canaria, with the Cromagnoid features being more prominent in the northern and mountainous regions and the Mediterranean along the coasts; in addition, the Cromagnoid type was best preserved in La Gomera⁵⁴. However, on the contrary, a more recent study based on dental morphological measures for the same aboriginal populations of La Gomera, Gran Canaria, and Tenerife found that inter-island dental differentiation was so minor that it did not require any hypothesis of separate founding populations⁵⁵. The accumulated biological data on the first islanders is still far from forming a coherent body, and their coupling with the archaeological data only reaches some specific agreements, such as that their ancestors came from northern Africa and that a permanent settlement on the islands cannot go back much further than the beginning of the first millennium AD. Nevertheless, the ancient mtDNA information reanalyzed here is already enough to support some of the several hypotheses formulated to explain where the first settlers originated, how they arrived at the archipelago, and how they settled on the different islands.

4.4. In support of a Roman-mediated aboriginal settlement of the Canary Islands

The first question about the aboriginal Canarian population that seems to be resolved is when they arrived on the islands since both the archaeological and genetic data place it around the first

millennium AD, questioning previous hypotheses proposing Neolithic or Phoenician-Punic settlements⁵⁶. The genetic support for settlement in Roman times is the lack of indigenous lineages in the aboriginal⁶, historical^{17,18}, and current Canarian population¹¹ with coalescent ages older than this epoch. However, earlier arrivals to the islands that did not leave a genetic trace cannot be ruled out. Indeed, there are archaeological evidences that Romanized people landed on the eastern islands and established, at least, a purple dye extraction workshop on the islet of Lobos⁵⁷. The high economic benefit that the purple trade achieved in Roma, gives an additional argument to explain the far-flung and costly maritime voyages carried out by those daring entrepreneurs. However, for this business to be profitable, the production of a small workshop like the one discovered on the islet of Lobos would not be enough. *Stramonita haemastoma*, the mollusk from which the purple was extracted in Lobos, is also abundant and easy to collect on some coasts of the other Canary Islands⁵⁸. Thus, although the main exploitation centers must have been in the eastern Islands, where the frequency of the mtDNA Mediterranean lineages was greater, it seems most likely that other purple workshops, still not detected, were established along the Archipelago at the same time. Furthermore, due to the depletion of the raw material, this exploitation had to be itinerant, facilitating migration between islands. That said, it must be recognized that there is no trace of Roman culture in the Canarian aborigines. Because the coalescent ages (Table 4) of mtDNA haplotypes from concentrated ancestry in Northwest Africa (H1cf and U6b1a) are similar to those in the Mediterranean range (H1e1a and U6c1), they might have coexisted on the islands with little cultural or genetic exchange, which raises the possibility of independent arrivals for each group at the same time. However, from the beginning of the conquest, it was observed that the native islanders, although good swimmers, appeared to lack navigation skills and that there was no communication between islands⁵⁹. This led to the widespread idea that they might have been voluntarily or involuntarily transported to the islands by people with the maritime capacity to do so⁶⁰. In favor of the first option is the fact that these island settlers brought livestock and seeds with them for their future subsistence, implying that it was a programmed migration, which presupposes previous knowledge of its destination. But if this was the case, why did they not bring with them other technological advances already in use in northern Africa at that time? This includes bronze or iron tools and weapons, the Roman plow, or the ceramic lathe, just to mention a few. The second option, that they were forced to migrate, resolves these questions and could explain the genetic heterogeneity of the aboriginal population. The exploitation of purple was a hierarchical business. At the top was the elite, which has the economic and technological power to carry out this undertaking. Following are the artisans specialized in dyeing the fabrics, then the workforce capable of extracting the dye, and, finally, the slaves that have to collect the mollusk; both of last likely were brought to the Canary Islands. Most likely, the dye extractors were recruited from the already settled Mediterranean purple dye workshops, while the slaves, for economic reasons, would have been captured or bought in the vicinity of the Archipelago in places such as the Atlantic Moroccan port of Mogador. When the purple industry ceased being profitable, those people likely were left to fend for themselves on the islands. For subsistence reasons, goats and barley accompanied people on their previous inter-island transfers, making their subsequent adaptation possible. Notably, the fact that the indigenous barley has been continuously cultivated since the pre-Hispanic colonization of the islands⁶¹ and the persistence of indigenous goat breeds⁶² suggest that there were no major intrusions into the islands until their European conquest.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org, Figure S1: Phylogenetic tree for mtDNA haplogroup H complete sequences in the Canary Islands; Figure S2: Phylogenetic tree for mtDNA haplogroup J2a2d1a complete sequences in the Canary Islands; Figure S3: Phylogenetic tree for mtDNA haplogroup L complete sequences in the Canary Islands; Figure S4: Phylogenetic tree for mtDNA haplogroup T complete sequences in the Canary Islands; Figure S5: Phylogenetic tree for mtDNA U complete sequences in the Canary Islands; Figure S6: Phylogenetic tree for mtDNA haplogroup W1e1 and X3a complete sequences in the Canary Islands; Table S1: Indigenous mtDNA haplotypes detected in the Canary Islands and their continental matches; Table S2: Binary matrix indicating presence (1) or absence (0) of aboriginal haplotypes in each island and continental region; Table S3: Match-based distance Matrix; Table S4: Coalescence ages of the putative Canarian Aboriginal founder mtDNA lineages; Supplementary Bibliography.

Funding: This study has not had any funding.

Institutional Review Board Statement: This study underwent formal review and was approved by the Ethics Committee for Human Research at the University of La Laguna as proposal NR157.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data present in this study are available in the article and Supplementary Materials.

Acknowledgments: This study would not have been possible without the DNA sequence availability and the computation support of the Instituto Tecnológico y de Energías Renovables (ITER). I thank Carlos Flores, José M. Lorenzo and Víctor M. García for their advices and English improvement.

Conflict of Interest: The author declares no conflict of interest.

References:

1. Blench R. The peopling of the Canaries by the Berbers: new data and new hypotheses. *Études et documents berbères*. 2022;45(2):149-173.
2. Fregel R, Ordóñez AC, Serrano JG. The demography of the Canary Islands from a genetic perspective. *Human Molecular Genetics*. 2021;30(R1):R64-R71.
3. Vázquez JV, Barroso VA, Darias TD, Benítez MM, Lecuyer C, Richardin P. Poblamiento, colonización y primera historia de Canarias: El C14 como paradigma/Settlement, colonization and early history of The Canary Islands: The C14 as a paradigm. *Anuario de Estudios Atlánticos*. 2020;(66):24-24.
4. Orlando L, Allaby R, Skoglund P, et al. Ancient DNA analysis. *Nature Reviews Methods Primers*. 2021;1(1):14.
5. Rodríguez-Varela R, Günther T, Krzewińska M, et al. Genomic analyses of pre-European conquest human remains from the Canary Islands reveal close affinity to modern North Africans. *Current Biology*. 2017;27(21):3396-3402.
6. Fregel R, Ordóñez AC, Santana-Cabrera J, et al. Mitogenomes illuminate the origin and migration patterns of the indigenous people of the Canary Islands. *PloS one*. 2019;14(3):e0209125.
7. Maca-Meyer N, Arnay M, Rando JC, et al. Ancient mtDNA analysis and the origin of the Guanches. *European Journal of Human Genetics*. 2004;12(2):155-162.
8. Fregel R, Pestano J, Arnay M, Cabrera VM, Larruga JM, González AM. The maternal aborigine colonization of La Palma (Canary Islands). *European Journal of Human Genetics*. 2009;17(10):1314-1324.
9. Fregel R, Cabrera VM, Larruga JM, et al. Isolation and prominent aboriginal maternal legacy in the present-day population of La Gomera (Canary Islands). *European Journal of Human Genetics*. 2015;23(9):1236-1243.
10. Bandelt H-J, Quintana-Murci L, Salas A, Macaulay V. The fingerprint of phantom mutations in mitochondrial DNA data. *The American Journal of Human Genetics*. 2002;71(5):1150-1160.
11. García-Olivares V, Rubio-Rodríguez LA, Muñoz-Barrera A, et al. Digging into the admixture strata of current-day Canary Islanders based on mitogenomes. *iScience*. 2022;105907.
12. Soares P, Ermini L, Thomson N, et al. Correcting for purifying selection: an improved human mitochondrial molecular clock. *The American Journal of Human Genetics*. 2009;84(6):740-759.
13. Cabrera VM. Human molecular evolutionary rate, time dependency and transient polymorphism effects viewed through ancient and modern mitochondrial DNA genomes. *Scientific Reports*. 2021;11(1):1-8.
14. Cabrera VM. Counterbalancing the time-dependent effect on the human mitochondrial DNA molecular clock. *BMC Evolutionary Biology*. 2020;20(1):1-9.
15. MISSING:berbersgenomic. MISSING:berbersgenomic. 2023.
16. Ordóñez AC, Fregel R, Trujillo-Mederos A, Hervella M, de-la-Rúa C, Arnay-de-la-Rosa M. Genetic studies on the prehispanic population buried in Punta Azul cave (El Hierro, Canary Islands). *Journal of Archaeological Science*. 2017;78:20-28.
17. Maca-Meyer N, Cabrera VM, Arnay M, et al. Mitochondrial DNA diversity in 17th-18th century remains from Tenerife (Canary Islands). *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*. 2005;127(4):418-426.
18. Santana J, Fregel R, Lightfoot E, et al. The early colonial Atlantic world: New insights on the African diaspora from isotopic and ancient DNA analyses of a multiethnic 15th-17th century burial population from the Canary Islands, Spain. *American Journal of Physical Anthropology*. 2016;159(2):300-312.

19. Santos C, Fregel R, Cabrera VM, González AM, Larruga JM, Lima M. Mitochondrial DNA patterns in the Macaronesia islands: Variation within and among archipelagos. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*. 2010;141(4):610-619.
20. Rando J, Cabrera V, Larruga J, et al. Phylogeographic patterns of mtDNA reflecting the colonization of the Canary Islands. *Annals of human genetics*. 1999;63(5):413-428.
21. Kogelnik AM, Lott MT, Brown MD, Navathe SB, Wallace DC. MITOMAP: a human mitochondrial genome database. *Nucleic acids research*. 1996;24(1):177-179.
22. Huber N, Parson W, Dür A. Next generation database search algorithm for forensic mitogenome analyses. *Forensic Science International: Genetics*. 2018;37:204-214.
23. Weissensteiner H, Pacher D, Kloss-Brandstätter A, et al. HaploGrep 2: mitochondrial haplogroup classification in the era of high-throughput sequencing. *Nucleic acids research*. 2016;44(W1):W58-W63.
24. Van Oven M, Kayser M. Updated comprehensive phylogenetic tree of global human mitochondrial DNA variation. *Human mutation*. 2009;30(2):E386-E394.
25. Andrews RM, Kubacka I, Chinnery PF, Lightowlers RN, Turnbull DM, Howell N. Reanalysis and revision of the Cambridge reference sequence for human mitochondrial DNA. *Nature genetics*. 1999;23(2):147-147.
26. Peakall R, Smouse PE. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular ecology notes*. 2006;6(1):288-295.
27. Forster P, Harding R, Torroni A, Bandelt HJ. Origin and evolution of Native American mtDNA variation: a reappraisal. *Am J Hum Genet*. 1996;59(4):935-45.
28. Coudray C, Olivieri A, Achilli A, et al. The complex and diversified mitochondrial gene pool of Berber populations. *Annals of Human Genetics*. 2009;73(2):196-214.
29. Secher B, Fregel R, Larruga JM, et al. The history of the North African mitochondrial DNA haplogroup U6 gene flow into the African, Eurasian and American continents. *BMC evolutionary biology*. 2014;14(1):1-17.
30. Pennarun E, Kivisild T, Metspalu E, et al. Divorcing the Late Upper Palaeolithic demographic histories of mtDNA haplogroups M1 and U6 in Africa. *BMC evolutionary biology*. 2012;12(1):1-12.
31. Pierron D, Heiske M, Razafindrazaka H, et al. Genomic landscape of human diversity across Madagascar. *Proceedings of the National Academy of Sciences*. 2017;114(32):E6498-E6506.
32. Pino-Yanes M, Corrales A, Basaldúa S, et al. North African influences and potential bias in case-control association studies in the Spanish population. *PLoS One*. 2011;6(3):e18389.
33. Flores C, Maca-Meyer N, Perez J, Gonzalez A, Larruga J, Cabrera V. A predominant European ancestry of paternal lineages from Canary Islanders. *Annals of human genetics*. 2003;67(2):138-152.
34. Van de Loosdrecht M, Bouzouggar A, Humphrey L, et al. Pleistocene North African genomes link near Eastern and sub-Saharan African human populations. *Science*. 2018;360(6388):548-552.
35. Kefi R, Hechmi M, Naouali C, et al. On the origin of Iberomaurusians: new data based on ancient mitochondrial DNA and phylogenetic analysis of Afalou and Taforalt populations. *Mitochondrial DNA Part A*. 2018;29(1):147-157.
36. Drosou K, Collin TC, Freeman PJ, Loynes R, Freemont T. The first reported case of the rare mitochondrial haplotype H4a1 in ancient Egypt. *Scientific Reports*. 2020;10(1):1-8.
37. Plaza S, Calafell F, Helal A, et al. Joining the pillars of Hercules: mtDNA sequences show multidirectional gene flow in the western Mediterranean. *Annals of human genetics*. 2003;67(4):312-328.
38. Aboukhalid R, Sturk-Andreaggi K, Bouabdellah M, Squalli D, Irwin JA, Amzazi S. Mitochondrial DNA control region variation from samples of the Moroccan population. *International journal of legal medicine*. 2013;127:757-759.
39. Rando JC, Pinto F, González AM, et al. Mitochondrial DNA analysis of northwest African populations reveals genetic exchanges with European, near-eastern, and sub-Saharan populations. *Annals of human genetics*. 1998;62(6):531-550.
40. González AM, García O, Larruga JM, Cabrera VM. The mitochondrial lineage U8a reveals a Paleolithic settlement in the Basque country. *BMC genomics*. 2006;7(1):1-7.
41. Martiniano R, Cassidy LM, Ó'Maoldúin R, et al. The population genomics of archaeological transition in west Iberia: Investigation of ancient substructure using imputation and haplotype-based methods. *PLoS genetics*. 2017;13(7):e1006852.
42. Richards M, Macaulay V, Hickey E, et al. Tracing European founder lineages in the Near Eastern mtDNA pool. *Am J Hum Genet*. 2000;67(5):1251-76.

43. Sampietro ML, Lao O, Caramelli D, et al. Palaeogenetic evidence supports a dual model of Neolithic spreading into Europe. *Proceedings of the Royal Society B: Biological Sciences*. 2007;274(1622):2161-2167.
44. Krings M, Bauer K, Geisert H, et al. mtDNA analysis of Nile River Valley populations: A genetic corridor or a barrier to migration? *The American Journal of Human Genetics*. 1999;64(4):1166-1176.
45. Del Arco M, Del Arco M, Atiénzar E, et al. Dataciones absolutas en la prehistoria de Tenerife. 1997.
46. Maca-Meyer N, González AM, Pestano J, Flores C, Larruga JM, Cabrera VM. Mitochondrial DNA transit between West Asia and North Africa inferred from U6 phylogeography. *BMC genetics*. 2003;4(1):1-11.
47. Pereira L, Silva NM, Franco-Duarte R, et al. Population expansion in the North African late Pleistocene signalled by mitochondrial DNA haplogroup U6. *BMC evolutionary biology*. 2010;10(1):1-10.
48. Henn BM, Gignoux CR, Feldman MW, Mountain JL. Characterizing the time dependency of human mitochondrial DNA mutation rate estimates. *Molecular biology and evolution*. 2009;26(1):217-230.
49. Fregel R, Gomes V, Gusmão L, et al. Demographic history of Canary Islands male gene-pool: replacement of native lineages by European. *BMC evolutionary Biology*. 2009;9(1):1-14.
50. Velasco-Vázquez J, Alberto-Barroso V, Delgado-Darias T, Moreno-Benítez M. A propósito del poblamiento aborigen en Gran Canaria. *Demografía, dinámica social y ocupación del territorio. Complutum*. 2021.
51. Navarro Mederos JF. *Arqueología de las islas Canarias*. 1997.
52. Hooton EA. The Ancient Inhabitants of the Canary Islands, Harvard. *African Studies, Cambridge*. 1925;7:261-267.
53. Fuste M. Physical anthropology of the Canary Islands: old and new views. *American Journal of Physical Anthropology*. 1965;23(3):285-291.
54. Schwidetzky I. *La población prehispánica de las Islas Canarias: investigaciones antropológicas*. Museo arqueológico; 1963.
55. Guatelli-Steinberg D, Irish J, Lukacs J. Canary islands-north African population affinities: measures of divergence based on dental morphology. *Homo*. 2001;52(2):173-188.
56. Atoche Peña P, Ramírez Rodríguez MÁ. El yacimiento de Buenavista, un asentamiento fenicio púnico en Lanzarote, Islas Canarias (circa 960-360 a.n.e.). 2019.
57. Fidel DR, del Arco Aguilar M del C. Desde el taller de púrpura romano de Lobos 1, una mirada a las actividades haliéuticas/From the roman purple workshop of Lobos 1, a look at halieutic activities. *Coloquios de Historia Canario Americana*. 2020.
58. Martín AM, Cobo GE. Mare purpureum. Producción y comercio de la púrpura en el litoral atlántico norteafricano. *Rivista di studi fenici*. 2006;34:71-96.
59. Mercer J. *The Canary Islanders: their prehistory, conquest, and survival*. London: Collings; 1980.
60. Padilla AP. El poblamiento prehistórico de las islas Canarias. *El Museo Canario*. 2009;64:79-97.
61. Hagenblad J, Morales J, Leino MW, Rodríguez-Rodríguez AC. Farmer fidelity in the Canary Islands revealed by ancient DNA from prehistoric seeds. *Journal of Archaeological Science*. 2017;78:78-87.
62. Amills M, Capote J, Tomàs A, et al. Strong phylogeographic relationships among three goat breeds from the Canary Islands. *Journal of Dairy Research*. 2004;71(3):257-262.

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.