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SHORT COMMUNICATION

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A mitochondrial analysis reveals distinct founder effect signatures in Canarian and Balearic goats

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Summary

In the course of human migrations, domestic animals often have been translocated to islands with the aim of assuring food availability. These founder events are expected to leave a genetic footprint that may be recognised nowadays. Herewith, we have examined the mitochondrial diversity of goat populations living in the Canarian and Balearic archipelagos. Median-joining network analysis produced very distinct network topologies for these two populations. Indeed, a majority of Canarian goats shared a single ancestral haplotype that segregated in all sampled islands, suggesting a single founder effect followed by a stepping-stone pattern of diffusion. This haplotype also was present in samples collected from archaeological assemblies at Gran Canaria and Lanzarote, making evident its widespread distribution in ancient times. In stark contrast, goats from Majorca and Ibiza did not share any mitochondrial haplotypes, indicating the occurrence of two independent founder events. Furthermore, in Majorcan goats, we detected the segregation of the mitochondrial G haplogroup that has only been identified in goats from Egypt, Iran and Turkey. This finding suggests the translocation of Asian and/or African goats to Majorca, possibly as a consequence of the Phoenician and Carthaginian colonisations of this island.

Keywords ancient DNA, mitochondrial control region, phylogeography, Tajima *D*-value

Humans often have introduced livestock into islands and archipelagos to be used as a source of food by settlers as well as by incoming exploratory and commercial maritime expeditions. The magnitude, timing and number of such founder effects may have had long-term consequences on the diversity of insular populations (Wang *et al.* 2014). In the absence of migration, founder events featured by a few individuals will produce populations that display, irrespective of their current size, a decreased variability and a marked genetic differentiation due to the impact of drift (Wang *et al.* 2014). Even more, if multiple and small founder effects occur independently in distinct islands from a given archipelago, a strong genetic differentiation amongst insular territories may emerge.

Goats display an extraordinary level of mitochondrial diversity (Luikart *et al.* 2001; Naderi *et al.* 2007) with six haplogroups that show a wide geographic distribution, that is haplogroup A (cosmopolite distribution), B1 (Far East, Indian subcontinent, southern Africa), B2 (Far East), C and D (Europe, Indian subcontinent and Far East) and G (North

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Africa and the Near East). The goal of the current study was to obtain a fine-grained perspective of the mitochondrial variability of goat breeds from the Canarian (La Palma, Tenerife, Fuerteventura, Gran Canaria) and Balearic (Majorca and Ibiza) archipelagos. This comparative analysis should allow us to evaluate whether founder effects, geographic isolation and drift have generated similar or distinct genetic signatures in the gene pools of goats from both archipelagos.

With this aim, we collected 165 and 80 blood/hair samples from Canarian and Balearic goats respectively. The number of individuals sampled per breed and the description and geographic distribution of breeds can be found in Table 1 and Fig. S1 respectively. We did our best to sample individuals without known relationships and belonging to different farms. This approach, however, was not feasible when sampling semiferal coastal goats (Pinalera, Cofete, Ajuí and Pozo Negro populations) because they live on their own for the most part of the year and, consequently, genealogical data are not available. Total DNA was isolated from hair samples with the DNeasy Blood & Tissue Kit (Qiagen Iberia SL). Blood DNA extraction was carried out in an ABI PRISM 6100 Nucleic Acid Prep Station (Applied Biosystems). A total of 628 bp of the mitochondrial control region were sequenced (GenBank accession numbers KM893154–KM893398) following the protocols described by Martínez *et al.* (2012). With the goal of having a more comprehensive view of Canarian goat diversity, in our population genetic analyses we considered 15 additional control region sequences from Palmera and Majorera goats that were previously reported by Amills *et al.* (2004). Median-joining networks were built with NETWORK v.4.6.1.2 (Bandelt *et al.* 1999) by setting the transversion/transition ratio to 3:1 (Amills *et al.* 2009). Diversity parameters, F_{ST} values and coalescent Tajima's *D* estimates were obtained with DNASP v.5.10.1 software (Librado & Rozas 2009). Neighbour-joining phylogenetic trees were built with MEGA5 (Tamura *et al.* 2011).

All sequences obtained from Canarian goats belonged to the A haplogroup, whereas Balearic goats showed a higher diversity with three segregating haplogroups: A (frequency = 0.95), C (frequency = 0.01) and G (frequency = 0.04) (Figs 1, S2 and S3, Table S1). As previously discussed, the signatures left by single and multiple founder effects in the gene pools of insular goats are usually very distinct and provide valuable clues to the genesis of these populations. In this regard, we can observe that the two median-joining networks shown in Fig. 1 are substantially different. Although goats from Majorca and Ibiza do not share a single haplotype, a feature that suggests that two independent founder effects took place in ancient times, the Canarian median-joining network has a star-shaped topology reflecting extensive haplotype sharing amongst goats from different islands. This finding is consistent with the occurrence of a single founder effect and the subsequent spread of the incoming population all over the Canarian archipelago. Furthermore, the negative and significant Tajima *D*-values observed in Palmera ($P = 0.01$) and Tinerfeña ($P = 0.02$) goats reflect an excess of low-frequency polymorphisms (Table 1). Such a pattern can be produced by either a sustained population growth (after the founder effect) or a very strong bottleneck during which no lineage escapes the extinction process (Gattepaille *et al.* 2013).

The existence, in all Canary Islands, of a highly abundant mitochondrial haplotype could reflect the introduction of domestic goats by the early colonisers of this archipelago (around 2,500 YBP). In other words, this haplotype may have a pre-Hispanic origin. Alternatively, it may have been harboured by Spanish goats brought to the Canary Islands during the last centuries (i.e. Hispanic origin). Indeed, during the 15–17th centuries, the Canary Islands became an important port of call in the trade with South America, a circumstance that may have favoured the introduction of goat breeds from Spain and, in more recent times, from other countries (e.g. Majorera goats have been crossed to

Table 1 Nucleotide and haplotype diversity parameters and Tajima's *D* coefficients inferred from mitochondrial control region sequences of modern Canarian and Balearic goats.

Region	Canary Islands								Balearic Islands	
Parameter	La Palma	Fuerteventura				Tenerife		Gran Canaria	Majorca	Ibiza
Tajima *D*	−1.882*	−1.258				−1.785*		0.169	0.071	−1.349
	Palmera[1] ($n = 13$)	Majorera[1] ($n = 22$)	Ajuí ($n = 23$)	P. Negro ($n = 25$)	Cofete ($n = 24$)	N. Tin. ($n = 16$)	S. Tin. ($n = 27$)	Pinalera ($n = 30$)	Mallorquina ($n = 23$)	Pitiüsa ($n = 57$)
Nucleotide diversity	0.004	0.011	0.007	0.009	0.007	0.003	0.007	0.007	0.019	0.016
Number of haplotypes	4	7	9	13	11	7	17	7	13	28
Haplotype diversity	0.423	0.814	0.822	0.923	0.906	0.792	0.926	0.710	0.939	0.962
Detected haplogroups	A	A	A	A	A	A	A	A	A, G	A, C

P. Negro, Pozo Negro; N. Tin., North Tinerfeña; S. Tin, South Tinerfeña.

*P-value <0.05.

[1]Mitochondrial control region sequences from Palmera and Majorera goats were previously reported by Amills *et al.* (2004).

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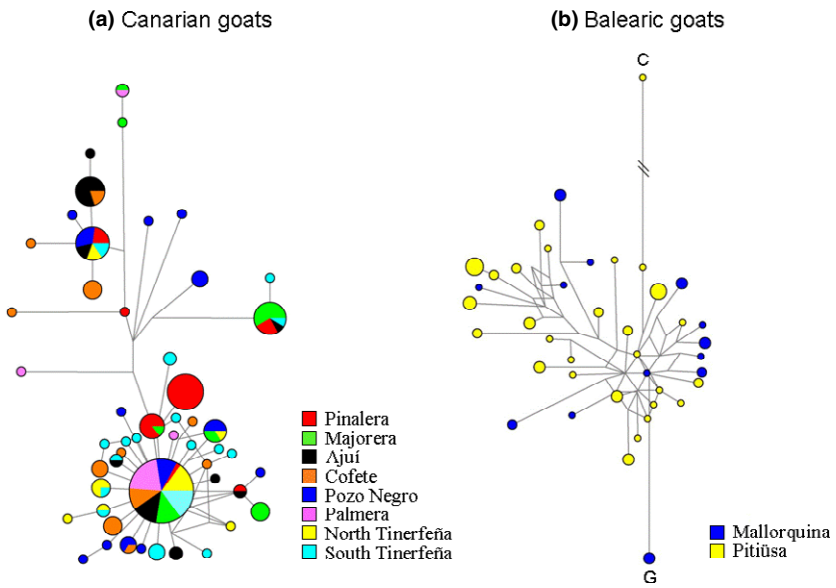

Figure 1 Median-joining network of mitochondrial control region sequences of Canarian (a) and Balearic (b) goats. All Canarian goats displayed the A haplogroup, whereas the A, C and G haplogroups were found in Pitiüsa and Mallorquina goats respectively.

some extent with Saanen bucks, Capote, personal communication). In order to discriminate between these two scenarios, we decided to survey the past diversity of Canarian goats. With this aim, 13 ancient ovicaprid remains were collected at several archaeological aboriginal assemblies and museums of the Canary Islands (Table S2).

Ancient samples were processed in a dedicated laboratory (IBE-PRBB, Barcelona), where no previous work with modern goat samples had been conducted. Total DNA was isolated by performing a proteinase-K digestion followed by a phenol–chloroform extraction and a final column concentration step (Merck Millipore), as described elsewhere (Lalueza-Fox *et al.* 2007). Extracts from skin samples were subsequently purified with the DNA extraction kit (Fermentas). Goat-specific primers (F: 5′-TCCTCATGCATATAAG CATG-3; R: 5′-GATACGCATGTTGGCAAGAA-3′) were designed to amplify a 112-bp fragment of the mitochondrial control region. The amplification was carried out by following a two-step PCR protocol reported by Krause *et al.* (2006). Both steps included 2 U of AmpliTaq Gold [Applied Biosystems (ABI)], 1× AmpliTaq Gold buffer (ABI), 2.5 mM of $MgCl_2$ (ABI) and 500 μM of each dNTP. In the first multiplex step, 150 nM of each primer pair and 5 μl of DNA extract were included in a final reaction volume of 20 μl. First step amplification consisted of a 12-min activation step at 94 °C, followed by 27 cycles at 94 °C for 20 s, 50 °C for 20 s and 72 °C for 20 s. Five microlitres of a 1:10 dilution of the primary amplification product was used as a template in the second PCR. Conditions were the same as the ones employed in the first step, except that the standard primer concentration was increased to 1.5 μM and that 33 cycles of amplification were performed, followed by a final step of 11 min at 72 °C. Blank and mock PCR controls were included in each amplification to monitor against contamination. Amplicons of the expected size were extracted from the gel and purified using a silica-based method (Lalueza-Fox *et al.* 2007). Subsequently, they were cloned in plasmids with the TOPO TA cloning kit (Life Technologies). White colonies were subjected to 30 cycles of PCR with M13 universal primers (Lalueza-Fox *et al.* 2007), and inserts of the correct size were sequenced at the Servei de Seqüenciació of the Universitat Pompeu Fabra (Barcelona) using an Applied BioSystems 3100 DNA sequencer. The criteria for authenticity described by Gilbert *et al.* (2005) were strictly followed in these analyses: (i) DNA from one sample (Bebedero) was independently extracted, amplified and sequenced in two dedicated ancient DNA laboratories (Institut de Biologia Evolutiva and Universitat Pompeu Fabra); (ii) in all analyses, mock extractions and PCR blank controls were used; and (iii) about 30% of the fragments were replicated twice. Nucleotide substitutions exclusively present in one or few clones, derived from one particular PCR but not consistently found in another PCR generated from the same sample, were not taken into consideration.

Using the above methods, we determined the species origin of 10 samples, that is four corresponded to sheep, five to goats and one to deer (Table S2). The presence of a deer sample is relevant because this species cannot be found in the Canary Islands, but is relatively common in North Africa, thus suggesting a translocation event. Amongst the goat samples, we were able to identify the ancestral Canarian haplotype in specimens from Lanzarote and Gran Canaria, a finding that is consistent with a widespread distribution of this variant in pre-Hispanic times (Fig. S4).

It is also worth commenting that the neighbour-joining tree displayed in Fig. S5 evidences that coastal goat populations from Fuerteventura (Cofete, Pozo Negro and Ajuí) are more related to the Palmera and South and North Tinerfeña ecotypes than to Majorera. Whereas coastal goats graze in the mountains, for the most part of the year,

Majorera goats are usually bred in an intensive regime (Capote *et al.* 1998). These findings are relevant because, at present, coastal goats are considered to be a variety of the Majorera breed. Indeed, a microsatellite analysis revealed a weak differentiation between Majorera and Ajuí goats (Martínez *et al.* 2006). However, the mitochondrial phylogenetic tree shown in Fig. S5 is not consistent with this concept and would support growing claims, based on phenotypic data and management features, for an independent breed status for Fuerteventura coastal goats (Capote *et al.* 1998; Morales-de la Nuez *et al.* 2012). We may conclude that some degree of genetic differentiation exists between Majorera and Ajuí goats, although this is more evident at the maternal than at the autosomal level.

As a whole, our data reflect considerable differences in the patterns of maternal variation associated with the foundation of the Canarian and Balearic goat populations. The absence of shared haplotypes between Mallorquina and Pitiüsa goats would be consistent with the independent settlement of these two islands during the Bronze Age (Micó 2006). Indeed, megalithic monuments, named talaiots, can be found in Majorca and Menorca but not in Ibiza or Formentera, indicating the existence of substantial cultural differences between the Gymnesian and Pitiusan islands (Micó 2006). It is also worth mentioning that several Mallorquina goats harboured the G haplogroup that so far has been found only in specimens from the Near East and Egypt (Naderi *et al.* 2007). Majorca was colonised by the Phoenicians and the Carthaginians (Boardman & Edwards 1991), providing an opportunity for the entry of Asian and African goats. Indeed, one sheep breed from Majorca, the Roja Mallorquina, has a fat tail and a red coloration which is typical of certain African and Asian ovine breeds.

Regarding the Canarian archipelago, archaeological and linguistic records indicate that it was populated by Imazighen people around 2500 YBP (Fregel *et al.* 2009). Our findings are consistent with an initial settlement of the islands nearest to the African coast (Fuerteventura and Lanzarote). Subsequently, these first settlers would have spread westward until reaching La Palma Island. This would explain why goats from different Canarian islands share a common haplotype and also the restricted diversity of Palmeran and Tinerfeña goats. This east to west gradient of diversity, however, has not been observed in ancient samples from Canarian aborigines (Fregel *et al.* 2009), suggesting that the historical events that led to the settlement of this archipelago were much more complex than previously thought.

Acknowledgements

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Supporting information

Additional supporting information may be found in the online version of this article.

Figure S1 Geographic distribution and brief description of the Canarian and Balearic goat breeds analysed in the current work.

Figure S2 Alignment of mitochondrial control region haplotypes in Balearic goats.

Figure S3 Alignment of mitochondrial control region haplotypes in Canarian goats.

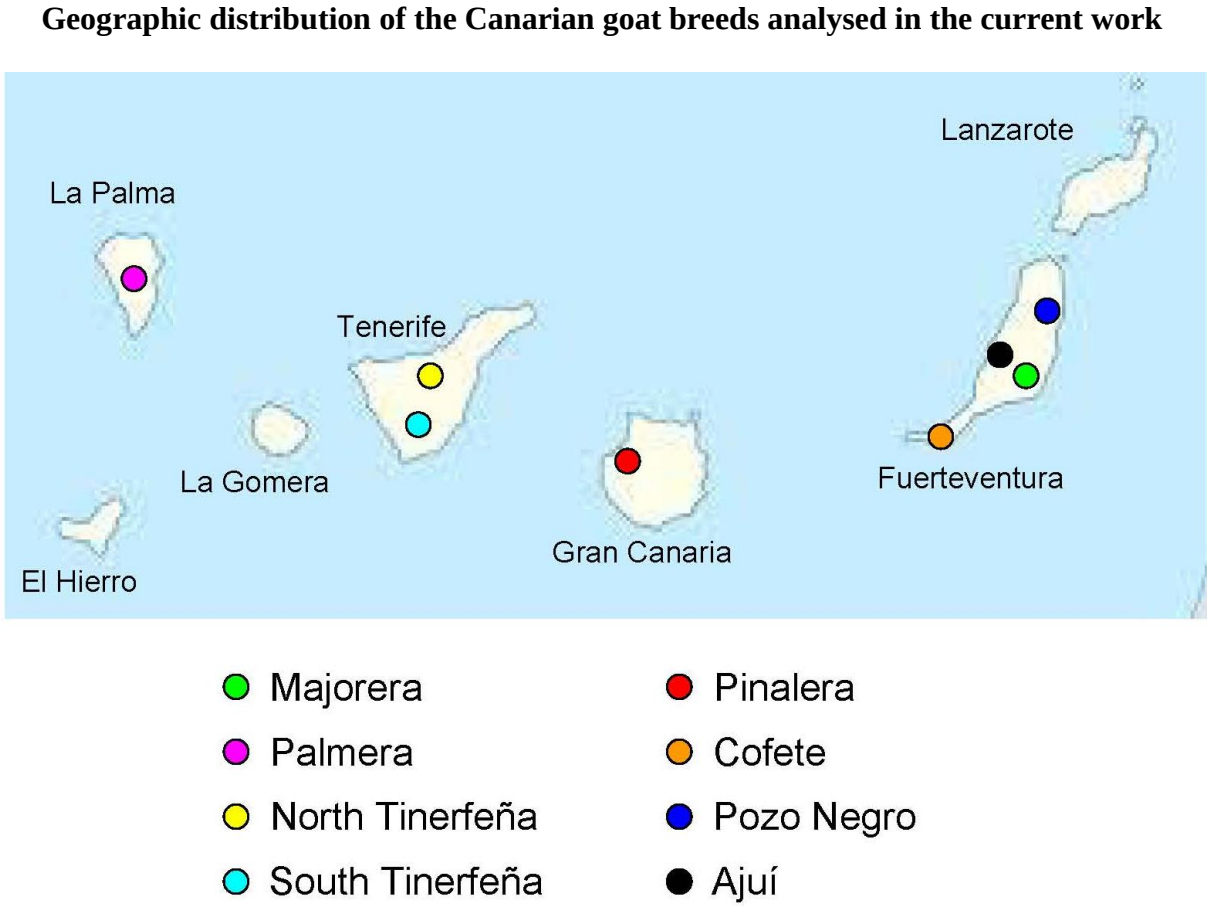
Figure S4 Median joining network depicting the relationships between mitochondrial sequences obtained from a set of modern (Amills *et al.* 2004, current work) and ancient (black color) Canarian goat samples. The origin of ancient DNA samples is shown in Table S2.

Figure S5 Neighbour-joining tree of Canarian goat populations based on F_{ST}-coefficients calculated with DNASP v.5.10.1 (Librado & Rozas 2009) and built with MEGA5 (Tamura *et al.* 2011).

Table S1 Haplotype frequencies in absolute (N) and relative (FREQ) terms.

Table S2 List of ovicaprid remains found at aboriginal Canarian assemblies that were used in the ancient mitochondrial DNA sequencing protocols.

Figure S1 Geographic distribution and brief description of the Canarian goat breeds analysed in the current work



Brief description of the Canarian goat breeds analysed in the current work

Breed	Census	Management[3]	Type	Main color coat	Main productive aptitude[4]
Majorera[1]	12,832	Intensive	Variable	Polychromous	Dairy (478 kg milk /lactation, 4.77% FC, 4.12% PC)
Palmera[1]	9,158	Extensive	Eumetric	Red	Dairy (326 kg milk /lactation, 4.06% FC, 4.21% PC)
South Tinerfeña[1]	4,705	Extensive	Eumetric	Polychromous	Dairy (363 kg milk /lactation, 5.01% FC, 4.17% PC)
North Tinerfeña[1]		Extensive	Sub-hiper metric	Black/brown	
Pinalera[2]	500	Semiferal	Eumetric	Polychromous	Meat (lack of phenotypic registers)
Cofete[2]	1100	Semiferal	Hypometric	Polychromous	Meat (lack of phenotypic registers)
Pozo Negro[2]	800	Semiferal	Hypometric	Polychromous	Meat (lack of phenotypic registers)
Ajuí[2]	1700	Semiferal	Hypometric	Polychromous	Meat (lack of phenotypic registers)

[1] Source: Catalog of Spanish breeds elaborated by the Spanish Ministry of Agriculture, Food and Environment.
[2] Source: Juan Capote, personal communication.
[3] A semiferal management means that goats are raised in the mountains, without any human intervention, for the most part of their productive cycle. Once a year, thousands of goats are gathered by shepherds and kept in big enclosures (*gambuesa*), where kids are either marked or slaughtered. This practice (*apañada*) has a prehispanic origin (2,000 YBP).
[4] FC: fat content (%), PC: protein content (%)

Geographic distribution and brief description of the Balearaic goat breeds analysed in the current work

Brief description of the Balearic goat breeds analysed in the current work

Breed	Census	Management	Type	Main color coat	Main productive aptitude
Mallorquina[1]	236	Extensive	Eumetric	Brown and black	Meat (also used for hunting)
Pitiüsa[1]	225	Extensive	Eumetric	Polychromous	Meat (also used for milk production)

[1] Source: Catalog of Spanish breeds elaborated by the Spanish Ministry of Agriculture, Food and Environment

Figure S2. Alignment of mitochondrial control region haplotypes in Balearic goats

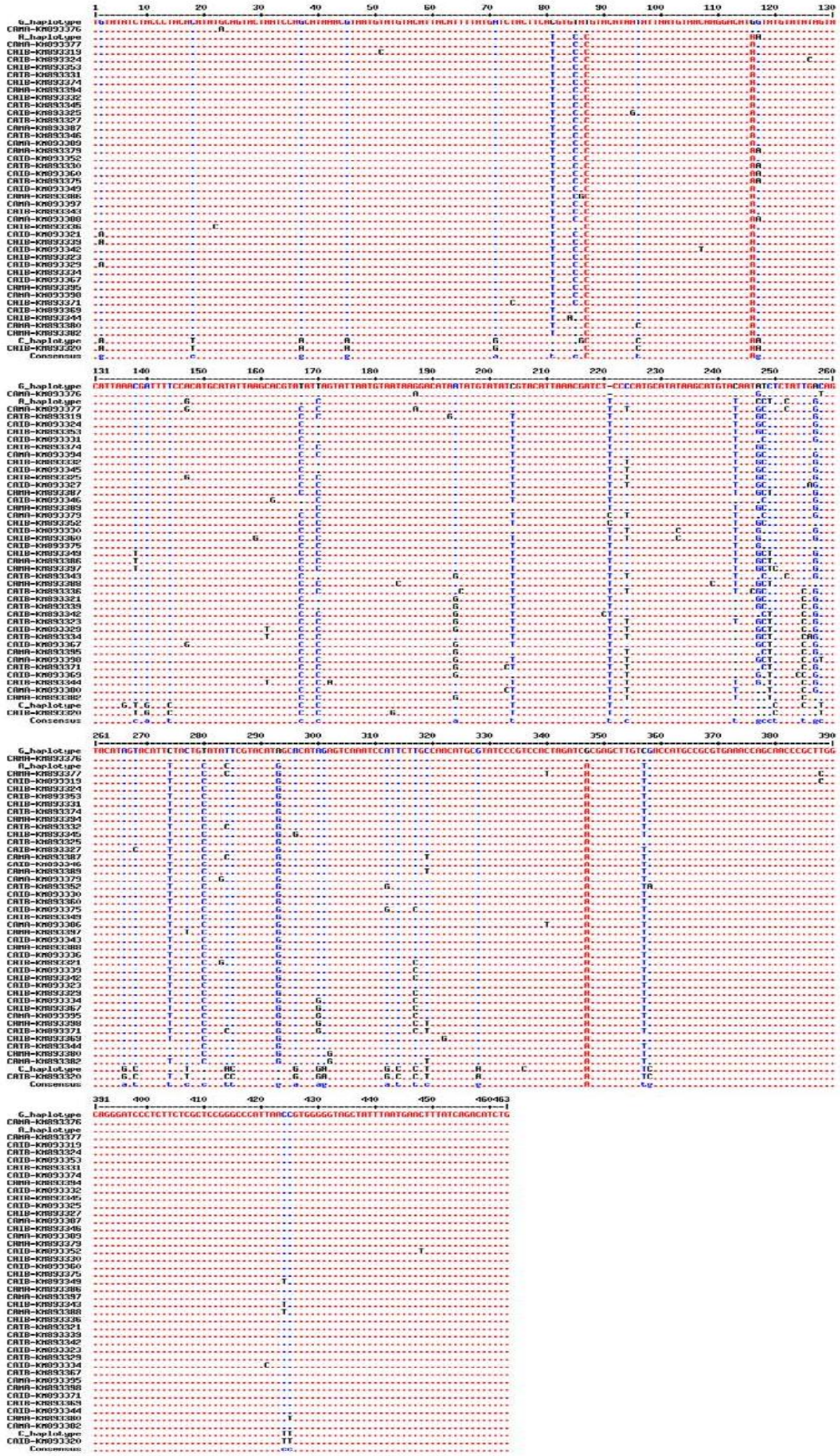


Figure S3 Alignment of mitochondrial control region haplotypes in Canarian goats

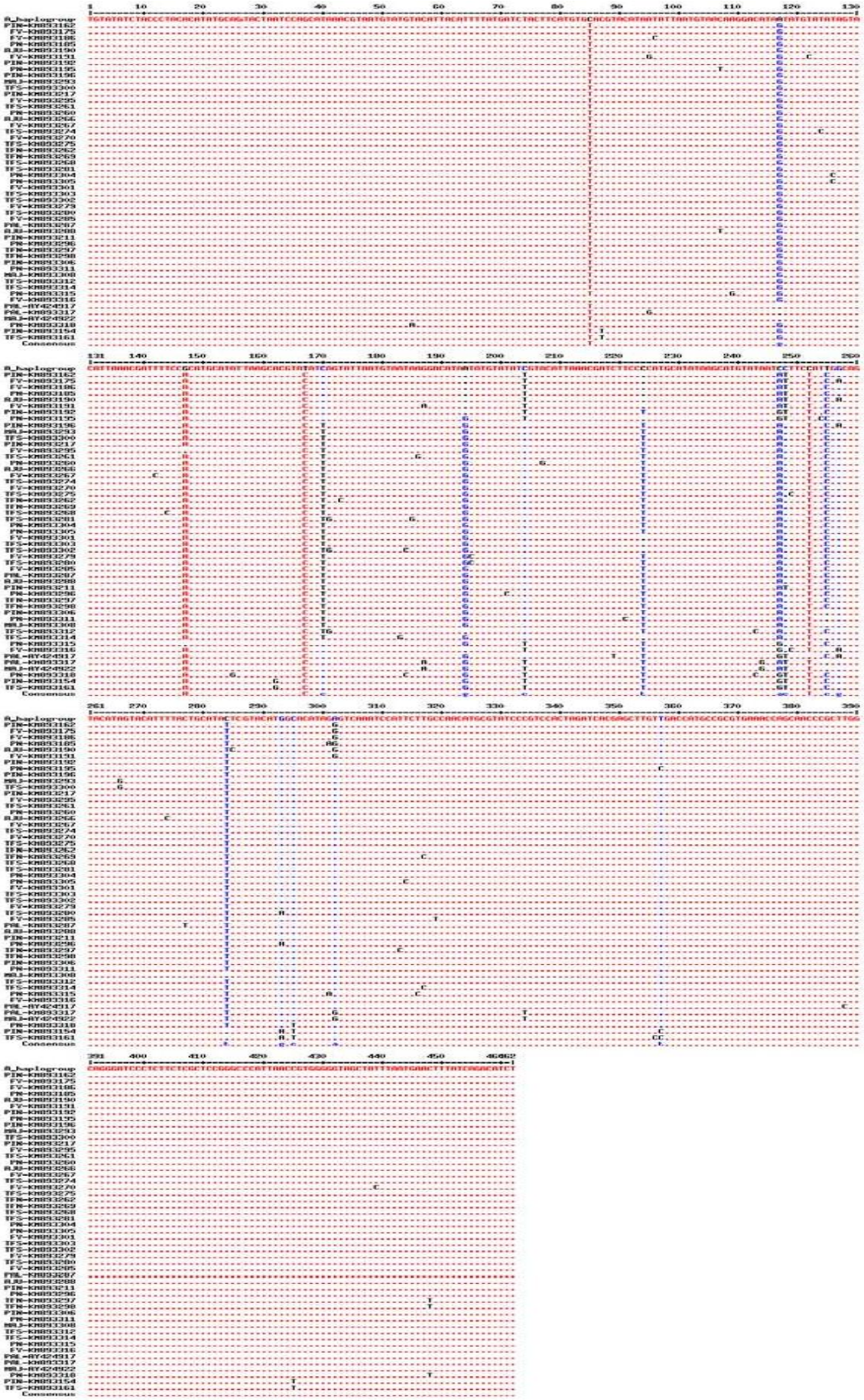


Figure S4. Median joining network depicting the relationships between mitochondrial sequences obtained from a set of modern (Amills et al. 2004, current work) and ancient (black color) Canarian goat samples. The origin of ancient DNA samples is shown in Table S2.

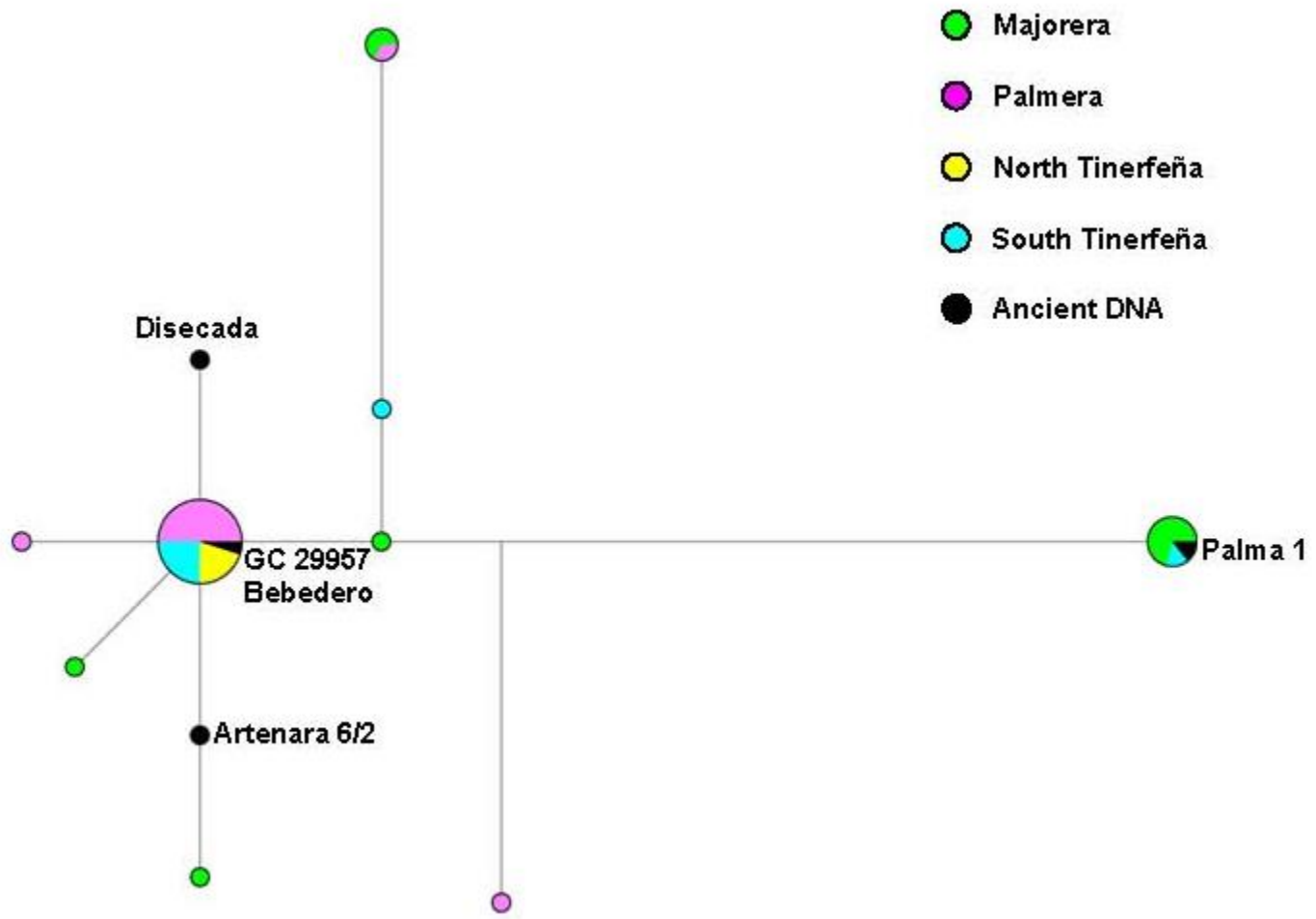


Figure 5. Neighbour-joining tree of Canarian goat populations based on FST-coefficients calculated with DNASP v.5.10.1 (Librado & Rozas 2009) and built with MEGA5 (Tamura et al. 2011).

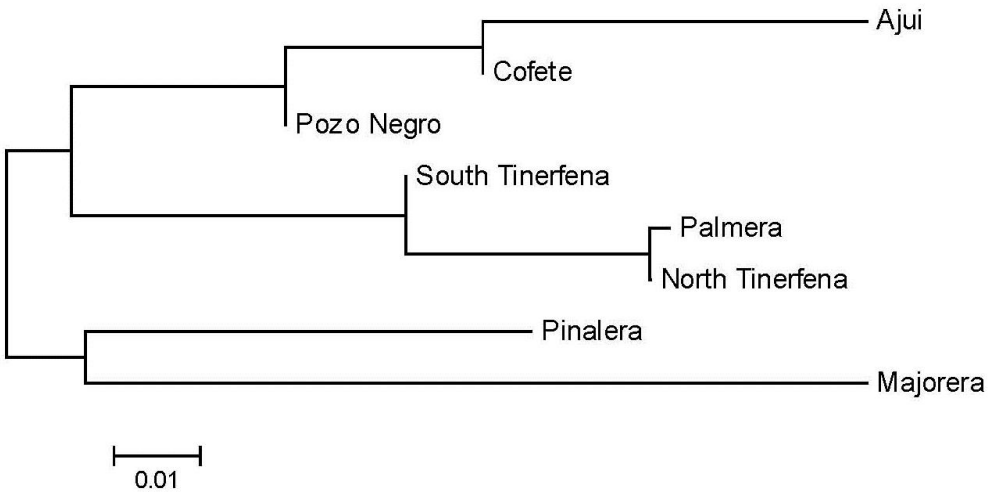


Table S1. Haplotype frequencies in absolute (N) and relative (FREQ) terms

HAPLOTYPE	N	FREQ	HAPLOGROUP
	CANARIAN GOATS		
PIN-KM893154	12	0.07	A haplogroup
PIN-KM893162	13	0.07	A haplogroup
PIN-KM893196	15	0.08	A haplogroup
PIN-KM893211	7	0.04	A haplogroup
PIN-KM893306	2	0.01	A haplogroup
PIN-KM893192	1	0.01	A haplogroup
MAJ-KM893293	6	0.03	A haplogroup
FV-KM893285	3	0.02	A haplogroup
MAJ-KM893308	4	0.02	A haplogroup
PAL-KM893317	2	0.01	A haplogroup
MAJ-AY424922	1	0.01	A haplogroup
PAL-AY424917	1	0.01	A haplogroup
PAL-KM893287	1	0.01	A haplogroup
FV-KM893279	3	0.02	A haplogroup
FV-KM893175	10	0.06	A haplogroup
FV-KM893186	4	0.02	A haplogroup
FV-KM893267	1	0.01	A haplogroup
FV-KM893301	1	0.01	A haplogroup
FV-KM893270	4	0.02	A haplogroup
FV-KM893316	1	0.01	A haplogroup
FV-KM893191	1	0.01	A haplogroup
FV-KM893295	1	0.01	A haplogroup
TFN-KM893262	4	0.02	A haplogroup
TFN-KM893297	1	0.01	A haplogroup
TFN-KM893298	2	0.01	A haplogroup
TFN-KM893269	1	0.01	A haplogroup
TFS-KM893161	1	0.01	A haplogroup
TFS-KM893261	1	0.01	A haplogroup
TFS-KM893300	1	0.01	A haplogroup
TFS-KM893302	1	0.01	A haplogroup
TFS-KM893268	1	0.01	A haplogroup
TFS-KM893280	1	0.01	A haplogroup
TFS-KM893281	3	0.02	A haplogroup
TFS-KM893303	1	0.01	A haplogroup
TFS-KM893314	1	0.01	A haplogroup
TFS-KM893275	2	0.01	A haplogroup

TFS-KM893312	2	0.01	A haplogroup
TFS-KM893274	1	0.01	A haplogroup
AJU-KM893288	2	0.01	A haplogroup
AJU-KM893190	1	0.01	A haplogroup
AJU-KM893266	1	0.01	A haplogroup
PN-KM893195	3	0.02	A haplogroup
PN-KM893315	1	0.01	A haplogroup
PN-KM893296	1	0.01	A haplogroup
PN-KM893304	1	0.01	A haplogroup
PN-KM893311	1	0.01	A haplogroup
PN-KM893185	1	0.01	A haplogroup
PN-KM893305	1	0.01	A haplogroup
PN-KM893318	1	0.01	A haplogroup
PN-KM893260	1	0.01	A haplogroup
PIN-KM893217	47	0.26	A haplogroup
BALEARIC GOATS			
CAMA-KM893376	3	0.04	G haplogroup
CAIB-KM893320	1	0.01	C haplogroup
CAIB-KM893319	1	0.01	A haplogroup
CAIB-KM893321	7	0.09	A haplogroup
CAIB-KM893323	2	0.03	A haplogroup
CAIB-KM893324	1	0.01	A haplogroup
CAIB-KM893325	1	0.01	A haplogroup
CAIB-KM893327	2	0.03	A haplogroup
CAIB-KM893329	3	0.04	A haplogroup
CAIB-KM893330	2	0.03	A haplogroup
CAIB-KM893331	1	0.01	A haplogroup
CAIB-KM893332	3	0.04	A haplogroup
CAIB-KM893334	4	0.05	A haplogroup
CAIB-KM893336	3	0.04	A haplogroup
CAIB-KM893339	2	0.03	A haplogroup
CAIB-KM893342	1	0.01	A haplogroup
CAIB-KM893343	3	0.04	A haplogroup
CAIB-KM893344	1	0.01	A haplogroup
CAIB-KM893345	1	0.01	A haplogroup
CAIB-KM893346	1	0.01	A haplogroup
CAIB-KM893349	1	0.01	A haplogroup
CAIB-KM893352	6	0.08	A haplogroup
CAIB-KM893353	1	0.01	A haplogroup
CAIB-KM893360	1	0.01	A haplogroup
CAIB-KM893367	2	0.03	A haplogroup
CAIB-KM893369	2	0.03	A haplogroup
CAIB-KM893371	2	0.03	A haplogroup

CAIB-KM893374	1	0.01	A haplogroup
CAIB-KM893375	1	0.01	A haplogroup
CAMA-KM893377	2	0.03	A haplogroup
CAMA-KM893379	1	0.01	A haplogroup
CAMA-KM893380	3	0.04	A haplogroup
CAMA-KM893382	1	0.01	A haplogroup
CAMA-KM893386	3	0.04	A haplogroup
CAMA-KM893387	1	0.01	A haplogroup
CAMA-KM893388	3	0.04	A haplogroup
CAMA-KM893389	2	0.03	A haplogroup
CAMA-KM893394	1	0.01	A haplogroup
CAMA-KM893395	1	0.01	A haplogroup
CAMA-KM893397	1	0.01	A haplogroup
CAMA-KM893398	1	0.01	A haplogroup

Table S2. List of ovicaprid remains found at aboriginal Canarian assemblies that were used in the ancient mitochondrial DNA sequencing protocols

Museum	Sample ID	Assembly	Type of sample	Dating	Species[1]
Lanzarote	Bebedero	El Bebedero	Secondary phalanx	330-345 AD	Goat
La Palma	UAB_1	El Espigón	Mummified skin	200 BC-400 AD	Deer
La Palma	UAB_2	El Espigón	Mummified skin	200 BC-400 AD	NA
La Palma	Palma 1	El Espigón	Mummified skin	200 BC-400 AD	Goat
La Palma	2	El Espigón	Mummified skin	200 BC-400 AD	NA
La Palma	3	El Espigón	Mummified skin	200 BC-400 AD	NA
La Palma	7	Cueva del Tendal	Teeth	400-650 AD	Sheep
La Palma	13	Cueva del Rincón	Teeth	1150-1493 AD	Sheep
Gran Canaria	Artenara	Acusa	Mummified skin	Unknown	Goat
Gran Canaria	8/3	Unknown	Mummified skin	415-560 AD	Sheep
Gran Canaria	29959	Risco Chimirique	Mummified skin	1025-1255 AD	Sheep
Gran Canaria	GC 29957	San Antón	Teeth	990-1260 AD	Goat
Gran Canaria	Disecada	Caldera de Taburiente	Embalmed hair	1935 AD	Goat

[1]Inferred from mitochondrial sequencing data generated in the current work. NA: no amplification