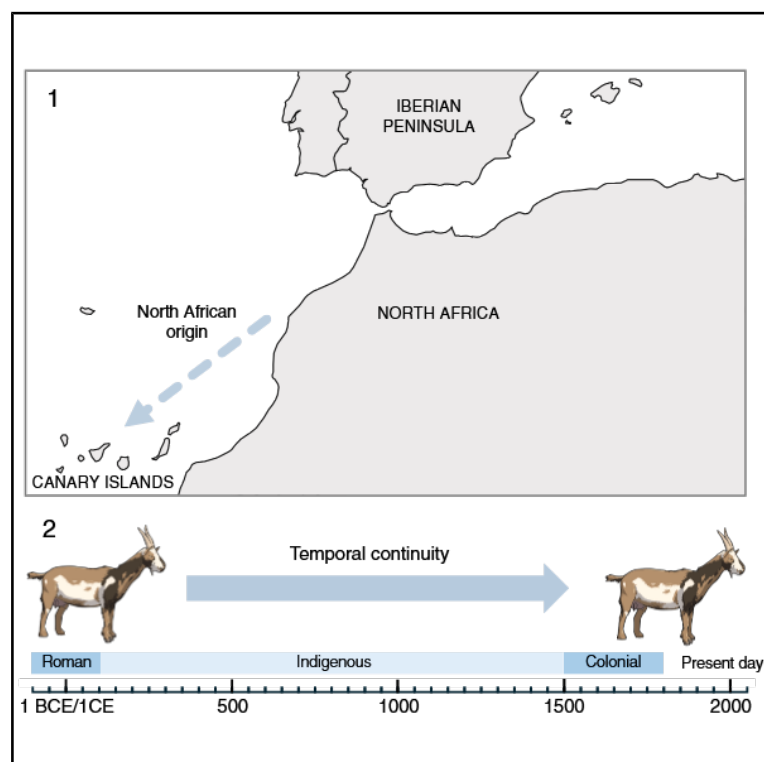


Paleogenomic evidence on the temporal continuity of indigenous goat exploitation in the Canary Islands

Graphical abstract



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In brief

Genomics; Paleobiology; Archeology

Highlights

- Mitogenomes present in indigenous goats are consistent with a North African origin
- Median-joining network suggests a founder effect in goats from the Canary Islands
- Low diversity and non-shared derived lineages point to a lack of gene flow between islands
- MtDNA data point to a temporal continuity from the Roman period to present-day goats



Article

Paleogenomic evidence on the temporal continuity of indigenous goat exploitation in the Canary Islands

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<https://doi.org/10.1016/j.isci.2025.113771>

SUMMARY

Paleogenomic and radiocarbon data indicate that, excluding the temporal occupation of the islet of Lobos by Romans, the Canary Islands were permanently colonized by North Africans around the 3rd century CE. The archipelago was seemingly forgotten in the following centuries by Western societies until the beginning of the European Age of Exploration in the 14th century. In this study, we present 52 mitogenomes of ancient Canarian goats, including samples from the Roman site of Lobos, and the indigenous and colonial periods. We observe that the mitogenomes of indigenous goats are consistent with a North African origin for the human Canarian population. Goats from Lobos share the same haplotypes as the indigenous population, indicating that both settlements briefly overlapped, and goats in Lobos were probably taken from neighboring islands. We also detect temporal continuity from the indigenous period to the colonial and present-day goats, suggesting European settlers exploited this well-adapted species.

INTRODUCTION

During the European Atlantic Expansion (14th century CE), Mediterranean sailors came across the Canary Islands,¹ an archipelago located off the southwestern coast of Morocco and the only one inhabited in the Macaronesia region at the time (Figure 1). Archaeological and linguistic evidence have confirmed that the geographic origin of the indigenous people of the Canary Islands is related to Berber populations in North Africa.^{2–4} Archaeological evidence from the islet of Lobos, at just 4 km from the island of Fuerteventura (Figure 1), has revealed that the archipelago

was already known by the Romans. The archaeological site of Lobos, dated between the 1st century BCE and the 1st century CE, has produced amphorae remains associated with the Roman province of Baetica (southern Iberian Peninsula) and numerous shells of the mollusk *Stramonite haemastoma*, used to produce purple dye.⁵ However, this workshop was abandoned after some time, leaving the Amazigh colonization as the first permanent settlement endeavor in the archipelago.⁶ The analysis of radiocarbon data using a chronometric hygiene protocol has indicated that, leaving aside the temporal settlement in Lobos,⁵ the time of the first arrival of human populations





Figure 1. Location of the archaeological sites included in the present study

Codes are as follows: 1 – Cueva de la Herradura, 2 – Belmaco, 3 – Buracas, 4 – El Tendal, 5 – Tigalate, 6 – Cuevas Herrera González, 7 – La Cañada de la Gurona, 8 – El Lomito del Medio, 9 – Cuevas de Bencomo, 10 – El Chorrillo (CH7), 11 – Los Riscos de Ifara, 12 – Tubo Volcánico-Los Roques de García, 13 – Aguadulce, 14 – Hospital de San Martín, 15 – Los Caserones, 16 – La Fortaleza, 17 – Playa Chica, 18 – Cueva de Villaverde, 19 – Punta del Mallorquín, 20 – Llano del Sombrero, 21 – Lobos, 22 – Peña de las Cucharas - Fiquineo and 23 – El Portalón. Roman, indigenous, and colonial sites are indicated with squares, circles, and triangles, respectively.

to the archipelago occurred around the beginning of the Common Era.⁶ Although ethnohistorical and archaeological evidence suggest that the indigenous people lacked navigational skills at the time of the European arrival (14th – 15th centuries CE),⁷ it is worth mentioning that they migrated with all the necessary means to survive, including domestic animals and crop plants: goat (*Capra hircus*), sheep (*Ovis aries*), pig (*Sus scrofa domesticus*), cat (*Felis catus*), dog (*Canis lupus familiaris*), barley (*Hordeum vulgare*), wheat (*Triticum durum*), lentils (*Lens culinaris*), beans (*Vicia faba*), peas (*Pisum sativum*) and, in Gran Canaria, figs (*Ficus carica*).^{8–11} Whether the Amazigh populations reached the islands by their own means or by the intervention of the Roman Empire is still a matter of contention between experts.⁴

Due to its strategic location in the Atlantic Ocean, Europeans conquered the islands, starting in 1402 when Jean de Bethencourt occupied the island of Lanzarote and ending in 1496 with the defeat of the indigenous people of Tenerife by the Crown of Castile. The military conquest and, probably, the introduction of unknown diseases to the islands carried by the Europeans produced a high mortality in the native population.¹² Additionally, the European colonization and the new sociopolitical order led to the beginning of an admixture process, which translated into a gradual loss of the indigenous culture and language.¹³ Apart from the European contribution, the forced migration of African enslaved people to work in sugar cane plantations and the intense commercial contact with the American continent produced additional admixture with African and Amerindian contingents.^{14,15}

In the past two decades, the study of DNA preserved in ancient remains (ancient DNA or aDNA) has been revolutionized by next-generation sequencing techniques, representing a powerful tool for disentangling the history of past populations and leading to the development of the paleogenomics field. The indigenous people of the Canary Islands have been the sub-

ject of several paleogenomic studies^{16–20} that have provided valuable data on their origin and evolution. These studies have indicated that ancient Canarians originated in North Africa and that insular populations were variable, both regarding their genetic composition and diversity. An alternative way of obtaining information on the origin of an ancient human population, their migration patterns, and their contacts with other geographical regions can be by analyzing the remains of their domestic animals and plants. This indirect approach has already been applied to the Canary Islands' indigenous population by retrieving aDNA from animal and plant domesticated species used in this period. For example, the analysis of mitochondrial DNA (mtDNA) on pre-Hispanic pigs from La Palma, Tenerife, Gran Canaria, and Lanzarote showed the presence of maternal lineages related to wild boars from North Africa,²¹ confirming previous results based on human aDNA. Similarly, nuclear single-nucleotide polymorphism (SNP) data from pre-Hispanic barley seeds suggested a North African origin for the crops cultivated by the indigenous people. This study also showed that the genetic composition of barley has been constant from the 7th century to the present, evidencing that the islands were not affected by gene flow after the initial colonization process.^{22,23}

Overall, goats represented one of the main livestock among the indigenous population of the Canary Islands. Although zooarchaeological evidence indicates sheep herding was important in the central and western islands, it did not surpass the use of goats.^{11,24–29} Goats played a key role in the human adaptation to the islands' environments, which lacked native ruminants or medium-sized mammals suitable for hunting. The indigenous people used goats for multiple purposes (e.g., meat, fat, milk, hides, and fiber production), which significantly shaped their material culture and household strategies, with dairy products playing an important role.³⁰ Zooarchaeological evidence also suggests that goats were relevant in ritual practices, as their

remains have been found among offering contexts and funerary sites.^{31–36} The importance of goats persisted into the colonial period, highlighting their enduring value in regional adaptation strategies and conditions.^{10,37} For all these reasons, paleogenomic evidence on goats could provide an excellent opportunity to deeply explore the genetic origin of the human population and the evolution and adaptation of domesticated animals in the islands.

Most aDNA studies on domesticated animals, including goats, have been performed using the mtDNA. There are several advantages of using this molecule: a) it is inherited through the maternal line without recombination, which allows for an easier reconstruction of the genealogy of a population; b) it has a relatively high mutation rate, suitable for identifying structure within populations; and c) it is a multicopy locus that provides a higher recovery of aDNA. In goats, mtDNA lineages are currently organized into six highly divergent haplogroups^{38,39}: A, B, C, D, F, and G. Haplogroup F, exclusive nowadays of the bezoar ibex (*Capra aegagrus aegagrus*), is the lineage that radiated first.³⁹ Haplogroup A, that is almost fixed in present-day goats, diversified around 12,800 years ago (ya), coinciding with the beginning of the Neolithic transition.³⁹ Paleogenomic data generated by Daly et al.,⁴⁰ including individuals from the western, eastern, and southern regions of the Fertile Crescent, indicate that goat domestication in the Near East was a process dispersed in space and time, rather than radiating from a central core. During the Neolithic, the mtDNA diversity was highly structured between western, eastern, and southern goats. This evidence suggested that domestication in the Near East happened in multiple events or involved multiple populations, producing genetically and geographically distinct Neolithic goat populations.⁴⁰ From that area, goats expanded and reached the edges of North and West Europe, as well as Asia and North and sub-Saharan Africa ~7,000 ya.^{41,42} Following the Neolithic period, mtDNA differentiation between regions decreased substantially, with haplogroup A becoming as widespread as observed in current goat populations.

Today, goats represent the most important and abundant livestock in the Canary Islands and play a crucial role in producing high-quality dairy products such as milk, cheese, butter, and yogurt.⁴³ Goats are exceptionally well adapted to the subtropical climate of the islands, including different arid and more humid microclimates.⁴⁴ There are three official breeds of Canarian goats: Palmera, Majorera, and Tinerfeña.⁴⁵ The Palmera breed is adapted to humid and abrupt areas, while the Majorera breed is adapted to arid and semiarid climates. Two different ecotypes exist for the Tinerfeña breed: South Tinerfeña, adapted to dry areas, and North Tinerfeña, adapted to humid areas.⁴⁴ Additionally, there are several semi-feral populations, including Ajúi, Esquinzo, Pozo Negro, Cofete, and Pinalera.⁴⁶ Extensive genetic analyses have been performed on present-day Canary Islands goats, focusing both on the official breeds and the semi-feral populations. The first genetic study of Canarian goats was based on the PCR amplification and Sanger sequencing of the mtDNA D-loop and showed that present-day goats from the Canary Islands belong to haplogroup A.⁴⁷ Although an introduction of Iberian goats during the colonial period could be expected, this study demonstrated that the Canarian goats are character-

ized by a strong differentiation from the rest of the Spanish breeds, with a C to T substitution at position 641 that is exclusive to the Canary Islands.⁴⁷ A more in-depth analysis showed that current insular populations exhibit extensive haplotype sharing between them, indicating a common founder effect.⁴⁸ In fact, the most common ancestral mtDNA D-loop haplotype in present-day goats was found by Ferrando et al.⁴⁸ in ancient individuals by sequencing a small portion of the D-loop (112 bp). This suggests that modern goats could have descended from those brought to the islands by the indigenous people. Low diversity values have also been observed in present-day goats for microsatellites^{46,49,50} and genome-wide data,^{51,52} which imply a lack of gene flow in the islands. Regarding their origin, genome-wide data align with results obtained from the indigenous human populations and other domesticates such as barley,²³ pointing to an affiliation of current Canarian breeds with African goats.^{51–53}

Although mtDNA data have already been obtained from indigenous goats of the Canary Islands,⁴⁸ these were generated using PCR and Sanger sequencing, and focused on a small portion of the D-loop that excluded the Canarian-specific 641C>T variant identified by Amills et al.⁴⁷ Given the high rate of parallel and back mutations in the D-loop, this small portion of the mtDNA sequence on its own does not allow for a refined classification within A sub-haplogroups,³⁹ which could be instrumental for determining the lineages' geographical origin. Instead, applying paleogenomic techniques has the advantage of providing complete mtDNA genomes that allow a better geographic assignment compared to those obtained from partial D-loop sequences. Another limitation of previously obtained aDNA data is that it only provided information on four individuals from the islands of La Palma, Gran Canaria, and Lanzarote, which is insufficient to characterize the whole population.

In this study, we performed a paleogenomic study of complete mitogenomes of ancient Canarian goats. With the aim of determining if goat insular populations were structured in the indigenous period, we obtained complete mitogenomes from goats from several archeological sites from the seven main islands. To determine if the Roman settlement produced an admixture event with the indigenous breeds, we also analyzed individuals from the islet of Lobos and another Roman site for comparison. Finally, we obtained complete mtDNA sequences from individuals excavated in colonial sites (15th to 18th centuries CE) to ascertain if Canarian breeds were used after the European conquest.

RESULTS AND DISCUSSION

DNA conservation

The average endogenous DNA content for the entire sample set is 6.30% ± 10.28% (median = 1.72%, IQR = 0.35%–6.25%), with the maximum value reaching 50.5%. We observed heterogeneity in the endogenous values for the different locations and also within archaeological sites (Table S1). Despite analyzing faunal samples that are part of waste and cooked remains, the average endogenous rate is only slightly lower than that observed for human remains.²⁰ After removing low-endogenous samples (values below 0.5%; *n* = 36), we used edit distances to classify samples at the species level, identifying 104 goats and 47 sheep

(Table S1). Among the samples classified as goats, we selected the best-preserved ones from each archaeological site for complete mtDNA enrichment and sequencing.

Enrichment

Regarding the recovery of reads mapping to the mtDNA reference genome, shotgun libraries show endogenous rates around 0.0085%. After the bleach treatment, the endogenous mtDNA rate increases almost four times, reaching an average value of 0.033%. When the mtDNA capture methodology was used, we retrieved a mean endogenous mtDNA rate of ~7% for both the libraries treated and non-treated with bleach, almost 850 times higher than the average value observed for the original shotgun libraries. As expected, the use of bleach increases the percentage of damage at the end of the molecules, but with the application of the partial uracil-DNA-glycosylase (UDG) treatment,⁵⁴ this disadvantage can be easily managed. Finally, the use of mtDNA capture dramatically increases the rates of duplicates compared to shotgun data (1.69% vs. 77.0%). However, given that the improvement in the endogenous mtDNA rate is higher than 800×, the loss of complexity is not a limitation for the recovery of high-coverage mitogenomes.

After enrichment, we obtained a total of 74 complete mitogenomes from 23 different archaeological sites (Table S2). Mitogenomes show an average depth value of $63.9 \times \pm 52.7 \times$ (median = $46.6 \times$, IQR = $32.9\text{--}78.1 \times$), with the maximum value reaching $306.4 \times$ and the minimum $15.5 \times$ (Table S2). Successfully analyzed Roman individuals come from both Lobos ($n = 17$) and El Portalón (Spain; $n = 1$) sites. 53 complete mitogenomes derived from the Indigenous period (Figure 1): three from El Hierro (Cueva de la Herradura site), six from La Palma (Belmaco, Buracas, El Tendal and Tegalate sites), nine from La Gomera (Cuevas de Herrera González, Lomito del Medio and Cañada de la Gurona sites), four from Tenerife (Cuevas de Bencomo, El Chorrillo, Los Riscos de Ifara and Tubo Volcánico-Los Roques de García sites), 10 from Gran Canaria (Aguadulce, Los Caserones, La Fortaleza and Playa Chica sites), 20 from Fuerteventura (Cueva de Villaverde, Llano del Sombrero and Punta del Mallorquín) and one from Lanzarote (Fiquiníneo site). Finally, three colonial-era mitogenomes were successfully recovered from Hospital de San Martín in Gran Canaria.

Data authentication

All samples meet the standard aDNA authentication criteria, including DNA fragmentation and damage patterns due to cytosine deamination toward the 5' ends of molecules (Table S2). The average contamination rate is $3.48\% \pm 2.63\%$ (median = 3.06% , IQR = $1.82\%\text{--}4.53\%$) (Table S2). All individuals show contamination rates below 10%, except for CHIC-0026 from Hospital de San Martín (10.47%) and CHIC-0051 from Punta del Mallorquín (14.47%). After carefully reviewing the samples by visual inspection, the haplotypes for those two individuals were retained in the dataset. Briefly, we inspected the BAM file using Tablet⁵⁵ to explore the potential effect of contamination site by site. Based on the phylogenetic reconstruction of the goat's mitogenomes, we confirmed that all the mutations leading to the individuals' haplogroup were present, and those characteristic of other lineages were absent or minoritarian.

Mitochondrial DNA network reconstruction

We then reviewed the samples' haplotypes and available archaeological data (Table S1) and removed potential duplicated specimens, leaving a total of 53 mitogenomes for haplotype network building and genetic diversity estimation (Data S1, Table S2). Phylogenetic analyses of the Canarian ancient goat mitogenomes (Data S1) indicate that they belong to two different clades. Two samples from Fuerteventura (one from Cueva de Villaverde and one from Llano del Sombrero), one from La Palma (Belmaco), and two from the Roman site of Lobos belong to the A2a clade, defined by the 7213 mutation.³⁹ It is interesting that both goats from Lobos and Fuerteventura share the 257 and 14750 mutations (defining the new clade A2a2), while the individual from La Palma is classified within A2a* with five private mutations (Data S1). The remaining Canarian goats are classified within the newly defined clade A8, characterized by mutations 1237, 1541, and 6504 (Data S1). Within A8, individuals are classified into two groups. Seventeen goats belong to the A8* clade, including two from La Palma, two from La Gomera, two from Tenerife, six from Gran Canaria (one from the colonial site), and five from Fuerteventura, while it is absent in Lobos. The remaining 30 individuals are classified within the newly identified A8a clade, characterized by a transversion in 1119. This lineage is observed in the indigenous populations of most islands and the islet of Lobos. Remarkably, while Roman individuals from Lobos show lineages similar to those in the Canary Islands, the individual from El Portalón in the Iberian Peninsula belongs to the A4 clade defined by Colli et al.,³⁹ which has been observed exclusively in European goats (Data S1).

Phylogenetic analysis of indigenous individuals

The reduced-median network, including our dataset and previously published present-day and ancient sequences from clades A2, A4 and A8, is shown in Figure 2. As mentioned above, most indigenous samples belong to the A8* and A8a clades, while some individuals are in the A2 cluster (Figure 2, Data S1). Haplogroup A2 has been observed mostly in present-day goats from the Middle East and North Africa, and once in the Iberian Peninsula.³⁹ Additionally, A2a was present in Middle Eastern individuals from the Bronze and Iron Age periods.⁴⁰ Haplogroup A8* has also been observed in present-day goats from the Middle East³⁹ and one Middle Eastern sample from the Chalcolithic period,⁴⁰ while A8a seems to be restricted to the Canary Islands. The presence of A2 and A8 in a North African archipelago can be explained by the expansion of goats, along with Neolithic people, coming from the Near East since the second half of the 8th millennium cal BP,^{41,56} and later with the subsequent colonization of the islands by a North African population. This would be consistent with previous evidence from genome-wide data from present-day goats from the Canary Islands, which found a closer affinity with populations from North Africa.⁵³ It also mirrors paleogenomic evidence obtained for the indigenous people of the Canary Islands, which show that they were similar to Late Neolithic populations from Morocco.²⁰

Phylogenetic analysis of colonial individuals

The colonial individuals from the Hospital de San Martín site analyzed in the present study belong to two different periods.¹⁰

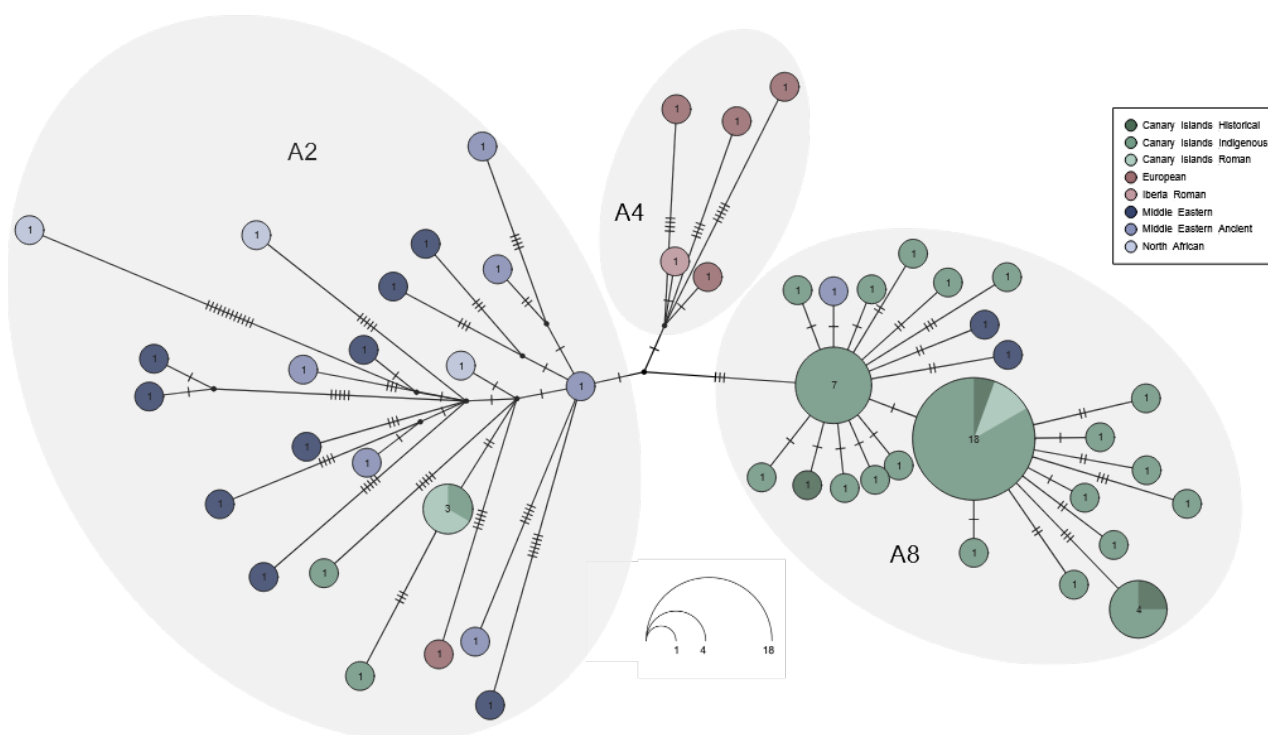


Figure 2. Mitogenome median-joining network of ancient and present-day individuals belonging to haplogroups A2, A4, and A8

Sample CHIC-0024 belongs to Phase I, corresponding to the initial construction of the hospital from 1480 to the first half of the 17th century, while samples CHIC-0025 and CHIC-0026 belong to Phase II, from the second half of the 17th century to 1780. All colonial samples fall within A8, pointing to temporal continuity within indigenous and colonial times and up to the 18th century. This result is consistent with the maintenance of the indigenous caprine herds after the European conquest, with the new colonizers taking advantage of the fact that indigenous goats were adapted to the islands' environment.⁴⁴ Actually, Brito et al.¹⁰ determined that goats were one of the main sources of meat in the Hospital de San Martín. This pattern diverges from contemporary sites in the Caribbean, where meat production from native fauna and cattle outweighs that of caprines. The importance of goat consumption during the colonial period demonstrates that European settlers exploited this well-adapted species and the indigenous management knowledge.¹⁰ Moreover, the inclusion of indigenous domesticates into the colonial economy by Europeans has already been observed for other species such as barley^{22,23} and lentils.⁵⁷

Phylogenetic analysis of Roman individuals

Regarding the Roman goats, individuals from Lobos belong to the same clades as the indigenous Canarian goats, while the Iberian goat from El Portalón falls within the European A4 clade (Figure 2, Data S1). The haplotype sharing between Roman goats from Lobos and the indigenous goats from the Canary Islands points to a common North African origin for both populations. This could be the result of the contribution of Roman goats

from Lobos to the indigenous herds or vice versa, or due to a shared geographic origin for both populations in North Africa. The analysis of ceramic remains in Lobos has determined that the most abundant types are classified within the Dressel 7–11 amphorae.⁵ These cylindrical two-handed amphorae were produced in southern Spain and distributed around the western Mediterranean and across the north-west provinces during the 1st and 2nd centuries CE.⁵⁸ In addition, there has been evidence of the production of this type of amphorae in North Africa, more concretely in the Thamusida site (Sidi Ali ben Ahmed, present-day Morocco), a Roman city in the province of Mauretania Tingitana.⁵⁹ The second most-frequent typology of amphorae in Lobos is Haltern-70.⁵ These amphorae were widespread in the western Mediterranean and North Atlantic, from Portugal and Spain to Britain, Germany, France, Italy, and North Africa.⁵⁸ The fact that the lineages observed for Lobos cluster with Middle Eastern, North African, and Canarian populations implies that, regardless of the geographical origin of the Roman individuals who operated the purple dye workshop in Lobos, the goats they consumed had a North African origin. Interestingly, archaeologists have found evidence of surface accumulations of *Stramonita haemastoma* shells, occasionally associated with unequivocally Roman ceramics, along the Moroccan coastline between Agadir and Fum Asaca.⁶⁰ At the latter site, indications suggest that *S. haemastoma* was exploited by the Romans in a context dated between the 2nd century BCE and the 1st century CE, contemporaneous with the site of Lobos.⁶¹ This evidence implies that the Romans were present not only in the Canary Islands at these latitudes but also along the nearby African coast.

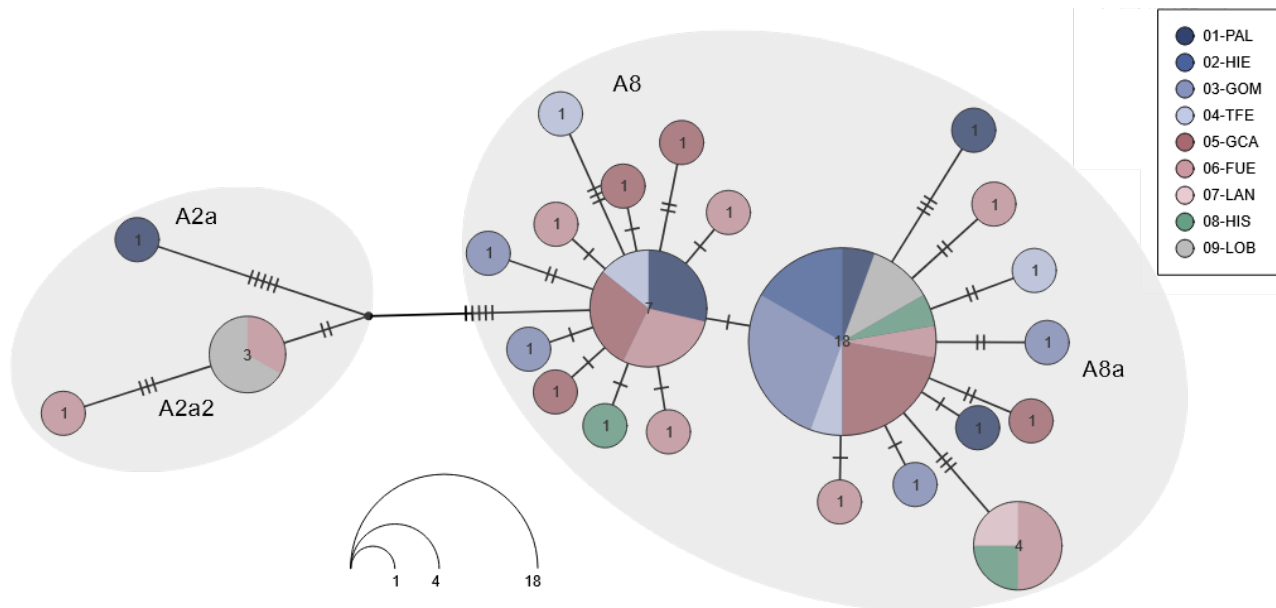


Figure 3. Mitogenome median-joining network of all Canarian individuals

A recent radiocarbon data analysis using strict radiometric hygiene methods and Bayesian methodologies has determined that the dye workshop and the indigenous occupation phase of the islands could have overlapped.⁶ Moreover, the discovery of potential Roman artifacts at the indigenous sites of El Bebedero and Buenavista in Lanzarote suggests interactions between Roman and Amazigh populations.⁶² Although it would be plausible that the goats in the main Canary Islands and the islet of Lobos had a common origin in North Africa and resulted from independent arrivals to the archipelago, it is more probable that both Roman and Amazigh settlements briefly overlapped, and the goats in Lobos were taken from the neighboring islands. This represents a more likely scenario as it would be easier for the Romans to take the goats from Fuerteventura or Lanzarote (2 and 8 km away, respectively), than to transport them 100 km from the North African coast. In favor of this hypothesis, there is evidence of the seasonal workers in Lobos taking advantage of local resources by consuming the eggs of shearwaters.⁶³

Haplogroup distribution analysis in Canarian goats

When considering the Canarian populations exclusively (Figure 3), the network shows that the A8 is the most frequent clade in all islands, pointing to a common founder event. The basal A8a haplotype appears at the highest frequency, and it is present in all islands, except for Lanzarote. Given that the sample size for Lanzarote is just one, this result is not conclusive. The second most frequent haplotype is the basal A8*, and it is present in both the western islands of La Palma and Tenerife, and the eastern islands of Gran Canaria and Fuerteventura. As previously mentioned, lineages in Lobos belong exclusively to basal haplotypes (Figure 3), attesting to the short period during which the dye workshop was operated. Conversely, A8* and A8a have a star-like shape when considering the indigenous goats, indi-

cating that both lineages radiated after their arrival on the islands (Figure 3). It is possible that both A8* and A8a were the founder lineages in the indigenous population. However, as only A8* has been observed outside of the Canary Islands, it is also possible that the mutation leading to A8a arose locally. However, A8 individuals from Lobos belong exclusively to the basal A8a haplogroup, pointing to the existence of this lineage already between the 1st century BCE and the 1st century CE.⁵ It is also worth noting that lineages derived from the basal motifs are not shared between different islands, except for a haplotype shared by Lanzarote and Fuerteventura (Figure 3). Although a larger sample size would be needed to confirm this result, it could point to the absence of domesticates' gene flow among islands during the indigenous period, with the exception of the two easternmost islands. This scenario aligns with the broader archaeological record, which documents frequent inter-island interactions between Lanzarote and Fuerteventura,⁶⁴ but the relative isolation of the remaining islands following their initial colonization.³

The A2a2 clade is only represented in individuals from Lobos and Fuerteventura, with the sequences from Lobos also restricted to the basal haplotype (Figure 3, Data S1). The absence in our sample of A2a2 in other islands would agree with a connection between the indigenous goats from Fuerteventura and those from Lobos. As stated before, it is possible to explain this result by the Roman purple dye workers taking goats from the North African settlers in the neighboring islands. However, another scenario would be that the Romans also introduced goats—intentionally or accidentally—to Fuerteventura, leaving feral descendants that the Amazigh encountered in the 2nd–3rd century CE. A similar pattern is documented in the Mediterranean,^{65,66} where feral goats of Near Eastern origin were found on uninhabited islands. Explorers commonly left goats in remote territories for food: Captain Cook introduced them to

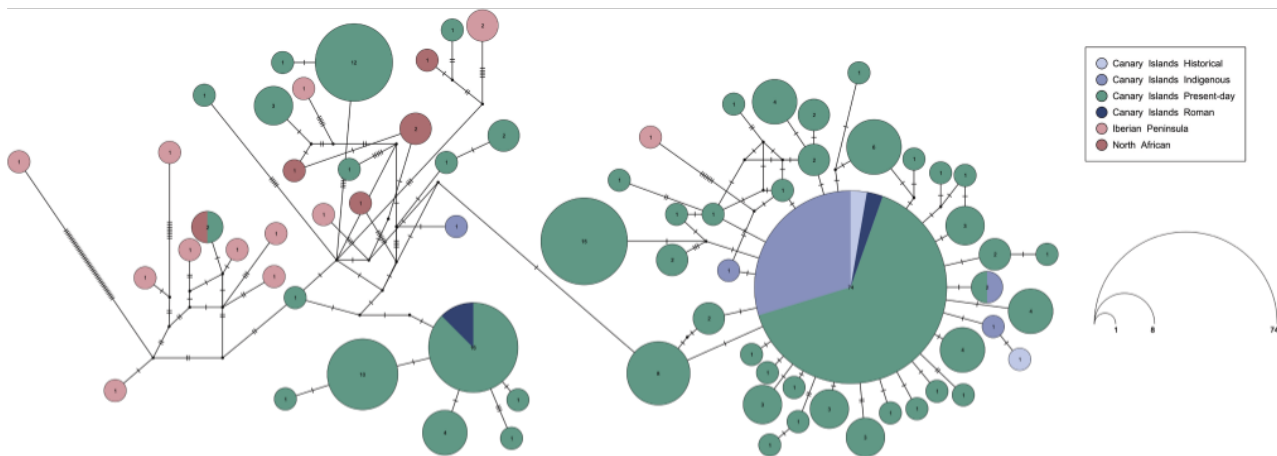


Figure 4. D-loop median-joining network of ancient and present-day individuals from the Canary Islands, and present-day individuals from North Africa and the Iberian Peninsula

New Zealand and Hawaii in the late 18th century, and Admiral Perry abandoned goats on the Ogasawara islands in 1853.^{67,68} Although larger sample sizes would be needed to confirm this result, the sharing of A2a2 exclusively in the eastern islands could be reflecting the same phenomenon observed for humans. Briefly, the human indigenous populations of the western and eastern islands showed similar genetic backgrounds but with slight differences, with the eastern islands showing a higher contribution from a component associated with Bronze Age expansions in Europe.²⁰

Comparison of ancient and present-day goats from the Canary Islands

One limitation of this study is that previously generated data from ancient and present-day goats from the Canary Islands was based on the sequencing of the mtDNA D-loop, while our analysis was directed at the mtDNA coding region following Colli et al.³⁹ To overcome this limitation, we obtained the D-loop haplotype from mitogenomes with high coverage and compared them to the data generated by Amills et al.^{47,69} and Ferrando et al.,⁴⁸ including present-day goats from the Canary Islands, the Iberian Peninsula and North Africa. In total, we obtained D-loop data from 26 indigenous goats (two from El Hierro, five from La Palma, five from La Gomera, two from Tenerife, six from Gran Canaria, five from Fuerteventura, and one from Lanzarote), three from colonial goats, and five from the Roman site of Lobos. When compared with previously published data (Figure 4), we determined that the most frequent lineage in present-day goats is the basal A8 haplotype, coinciding with the most frequent D-loop motif in the indigenous goats and with one sequence from the colonial period. This comparison also allows us to confirm that the polymorphism specific to Canarian breeds identified by Amills et al.⁴⁷ corresponds with a mutation that is present in goats belonging to the A8 haplogroup, which is also the founder haplotype identified by Ferrando et al.⁴⁸ in both modern and ancient Canarian goats. The only A2a2 individual analyzed for the D-loop (from Lobos) shares the same D-loop haplotype with 14 present-day samples, demonstrating the

presence of sequences related to A2a2 in the current population. Finally, the A2a lineage observed in an ancient goat from La Palma does not share the same motif with any present-day individual, but it is two mutations away from a present-day goat from the Canary Islands. All these results allow us not only to attest to the temporal continuity of indigenous goat lineages from the initial colonization until colonial times, but also to confirm the sharing of mtDNA lineages between indigenous and present-day goat herds as previously proposed by Ferrando et al.⁴⁸ This scenario, corroborated by archaeological findings and primary written sources,¹⁰ posits that incoming European settlers utilized indigenous caprine herds to enhance their livestock over the following centuries. Their choice was likely driven by the animals' adaptive traits,⁵³ which made them particularly well-suited to the Canary Islands' semiarid environment.

One characteristic of the present-day goat populations in the Canary Islands is a low genetic diversity, a strong differentiation, and high inbreeding values.^{49,50,53,69} Both the coding region and D-loop networks indicate an extensive haplotype sharing in ancient and present-day goat populations. The haplotypic diversity based on the D-loop sequence for the present-day population of the Canary Islands reaches a value of 0.9115 ± 0.0002 when all breeds are considered together, which is slightly lower than that of North Africa (0.9333 ± 0.0099) and the Iberian Peninsula (0.9848 ± 0.0009). The indigenous goats present an even lower value of just 0.2892 ± 0.0133 , pointing to the effects of isolation during the indigenous period. The colonial goats show an intermediate value between pre-conquest and present-day times (0.6667 ± 0.0740), although this value is based on only three sequences.

Conclusions

In this study, we applied paleogenomic techniques to analyze goat populations in the Canary Islands across a temporal transect ranging from the 2nd century CE to the 18th century CE. The indigenous goat samples are classified into two distinct clades, A2 and A8, mainly observed in ancient and/or current populations from the Middle East, which agrees with a North

African origin for the Canarian goat populations. The same clades are present in the Roman workshop in Lobos, while the Roman sample from the Iberian Peninsula is similar to lineages observed in European individuals. This suggests a shared origin between the goat populations of the islet of Lobos and the other Canary Islands. Colonial and present-day individuals belong to the A8 haplogroup, indicating temporal continuity in the management of livestock herds from indigenous to colonial and modern-day periods, as has been observed in other species.

In the Canarian indigenous goat populations, haplogroup A8 is the most prevalent, with the basal autochthonous A8a subclade being present in all the islands except for Lanzarote (but from a sample size of 1), while A8* is found on both eastern and western islands of the archipelago. The star-shaped median-joining network suggests an initial introduction of the A8a and A8* lineages, followed by subsequent radiation. Additionally, the presence of unique haplotypes on individual islands, except for Lanzarote and Fuerteventura, indicates genetic isolation across the archipelago after the initial colonization event. The sharing of haplogroup A2a2 by Fuerteventura and Lobos indicates a possible connection, but it may also reflect a different genetic background between eastern and western islands, as it has been observed for human populations. Low diversity values in the indigenous goats compared to the colonial and contemporary samples from the Canary Islands and North Africa are suggestive of the extreme isolation of indigenous goat herds.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact: Rosa Fregel (rfregel@ull.edu.es).

Materials availability

This study did not generate new reagents.

Data and code availability

- Raw sequencing data generated in this study have been deposited at the European Nucleotide Archive (ENA) under accession number PRJEB90261 and are publicly available as of the date of publication.
- This article analyzes existing, publicly available genotype data, accessible at ENA: <https://www.ebi.ac.uk/ena/browser/home>.
- This article analyzes existing mtDNA sequence data, accessible at NCBI: <https://www.ncbi.nlm.nih.gov/>.
- This article does not report original code.
- Any additional information required to reanalyze the data reported in this article is available from the [lead contact](#) upon request.

ACKNOWLEDGMENTS

This research was financed by the European Research Council under the European Union's Horizon 2020 research and innovation program (grant agreement number 851733) and the Spanish Ministry of Science, Innovation, and Universities grants PGC2018-094101-A-I00, PID2021-123080NB-I00, and PID2021-122355NB-C31, funded by MCIN/AEI/10.13039/501100011033; the "ERDF A way of making Europe" project. CDP and SBAQ were funded by fellowships (TESIS2022010015 and FPI2024010099, respectively) co-financed by the Canarian Agency for Research, Innovation and Information Society of the Counseling of Universities, Science and Innovation and Culture and by the European Social Fund Plus (ESF+) Integrated Operational Program of the Canary Islands 2021–2027, Axis 3 Priority Theme 74 (85%). JS was also funded by the Spanish Ministry of Science, Innovation, and Universities grants RYC2019-028346 and CNS2022-136039. KD conducted research with the

financial support of Taighde Éireann – Research Ireland under Grant number 21/PATH-S/9515(T). TG and PMM were supported by a grant from the Swedish Research Council (2017-05267). Ancient DNA data generation for APOR012 was performed by the SciLifeLab Ancient DNA unit, and the sequencing of APOR012 was carried out by the SNP&SEQ Technology Platform in Uppsala, part of the National Genomics Infrastructure (NGI), Sweden, and Science for Life Laboratory. The SNP&SEQ Platform is also supported by the Swedish Research Council and the Knut and Alice Wallenberg Foundation. JM work was carried out in the frame of the project PID2023-151226NB-I00 funded by MICIU/AEI/10.13039/501100011033 and by FEDER, UE. We want to acknowledge Juan Capote for fruitful discussions about goats from the Canary Islands. We thank M^a del Carmen del Arco Aguilar, Mercedes del Arco Aguilar, and Celia Siverio-Batista for providing samples from the sites of Lobos and Villaverde. Per their request, we declare that, although invited to participate in this study, they declined due to methodological disagreements regarding radiocarbon data analyses. Specifically, they do not agree with us on the need to apply strict chronometric hygiene to the study of the chronology of the human colonization of the Canary Islands. We thank the companies Servicios Integrales de Patrimonio Histórico S.L.U. (Arqueometra) and Prored Sociedad Cooperativa for their technical assistance. Most of the computing analyses were conducted using the Teide High-Performance Computing facilities (TeideHPC), provided by the Instituto Tecnológico y de Energías Renovables (ITER), S.A., thanks to the agreement between Universidad de La Laguna and Cabildo de Tenerife. We sincerely thank the three anonymous reviewers for their insightful and constructive comments.

AUTHOR CONTRIBUTIONS

Conceptualization: RF and JS; supervision: RF, MH, and MA; selection of archaeological samples: JS, ACO, CDP, EVF, ABM, SPG, JM, EMS, JCH, VA, MM, CV, and MA; archaeological and anthropological contextualization: JS, ACO, EVF, ABM, SPG, JM, EMS, JCH, VA, MM, CV, and MA; laboratory work: CDP, RF, JGS, SBAQ, ACO, and PMM; data analysis: CDP, RF, KGD, JGS, TG, CV, and PMM; funding acquisition: RF, JS, JM, TG, and CV; writing – original draft: CDP, RF, and JS; writing – review and editing: All authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2025.113771>.

Received: June 9, 2025

Revised: August 10, 2025

Accepted: October 10, 2025

Published: October 13, 2025

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Ancient fauna skeletal element	This study	Cueva de la Herradura - PGULL-1962
Ancient fauna skeletal element	This study	Cueva de la Herradura - PGULL-1965
Ancient fauna skeletal element	This study	Cueva de la Herradura - PGULL-2202
Ancient fauna skeletal element	This study	Cueva de la Herradura - PGULL-2203
Ancient fauna skeletal element	This study	Belmaco - PGULL-2197
Ancient fauna skeletal element	This study	Burracas - PGULL-2201
Ancient fauna skeletal element	This study	El Tendal - PGULL-1964
Ancient fauna skeletal element	This study	El Tendal - PGULL-2228
Ancient fauna skeletal element	This study	El Tendal - PGULL-2230
Ancient fauna skeletal element	This study	Salto de Tígalate - PGULL-2146
Ancient fauna skeletal element	This study	Cuevas de Herrera González - PGULL-0529
Ancient fauna skeletal element	This study	El Lomito del Medio - PGULL-0515
Ancient fauna skeletal element	This study	El Lomito del Medio - PGULL-0518
Ancient fauna skeletal element	This study	El Lomito del Medio - PGULL-0523
Ancient fauna skeletal element	This study	La Cañada de la Girona - PGULL-0533
Ancient fauna skeletal element	This study	La Cañada de la Girona - PGULL-0535
Ancient fauna skeletal element	This study	La Cañada de la Girona - PGULL-0537
Ancient fauna skeletal element	This study	La Cañada de la Girona - PGULL-0539
Ancient fauna skeletal element	This study	La Cañada de la Girona - PGULL-0540
Ancient fauna skeletal element	This study	Cueva de Bencomo - PGULL-1786
Ancient fauna skeletal element	This study	El Chorrillo - PGULL-2220
Ancient fauna skeletal element	This study	Los Riscos de Ifara - PGULL-2143
Ancient fauna skeletal element	This study	Tubo Volcánico - Los Roques de García - PGULL-2131
Ancient fauna skeletal element	This study	Agua Dulce - PGULL-1960
Ancient fauna skeletal element	This study	Agua Dulce - PGULL-1961
Ancient fauna skeletal element	This study	Caserones - PGULL-2144
Ancient fauna skeletal element	This study	Caserones - PGULL-2145
Ancient fauna skeletal element	This study	Hospital de San Martín - PGULL-1664
Ancient fauna skeletal element	This study	Hospital de San Martín - PGULL-1677
Ancient fauna skeletal element	This study	Hospital de San Martín - PGULL-1688
Ancient fauna skeletal element	This study	La Fortaleza - PGULL-1404
Ancient fauna skeletal element	This study	Playa Chica - PGULL-1968
Ancient fauna skeletal element	This study	Playa Chica - PGULL-2205
Ancient fauna skeletal element	This study	Playa Chica - PGULL-2207
Ancient fauna skeletal element	This study	Playa Chica - PGULL-2208
Ancient fauna skeletal element	This study	Playa Chica - PGULL-2210
Ancient fauna skeletal element	This study	Playa Chica - PGULL-2211
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1233
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1235
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1236
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1238
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1239
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1240

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1241
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1244
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1246
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1247
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1249
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1251
Ancient fauna skeletal element	This study	Cueva de Villaverde - PGULL-1256
Ancient fauna skeletal element	This study	Llano del Sombrero - PGULL-1969
Ancient fauna skeletal element	This study	Llano del Sombrero - PGULL-1971
Ancient fauna skeletal element	This study	Llano del Sombrero - PGULL-1972
Ancient fauna skeletal element	This study	Llano del Sombrero - PGULL-2235
Ancient fauna skeletal element	This study	Punta del Mallorquín - PGULL-1974
Ancient fauna skeletal element	This study	Punta del Mallorquín - PGULL-2217
Ancient fauna skeletal element	This study	Punta del Mallorquín - PGULL-2218
Ancient fauna skeletal element	This study	Punta del Mallorquín - PGULL-2219
Ancient fauna skeletal element	This study	Fiquiníneo - PGULL-1963
Ancient fauna skeletal element	This study	Lobos - PGULL-1295
Ancient fauna skeletal element	This study	Lobos - PGULL-1296
Ancient fauna skeletal element	This study	Lobos - PGULL-1299
Ancient fauna skeletal element	This study	Lobos - PGULL-1300
Ancient fauna skeletal element	This study	Lobos - PGULL-1301
Ancient fauna skeletal element	This study	Lobos - PGULL-1302
Ancient fauna skeletal element	This study	Lobos - PGULL-1304
Ancient fauna skeletal element	This study	Lobos - PGULL-1305
Ancient fauna skeletal element	This study	Lobos - PGULL-1307
Ancient fauna skeletal element	This study	Lobos - PGULL-1308
Ancient fauna skeletal element	This study	Lobos - PGULL-1309
Ancient fauna skeletal element	This study	Lobos - PGULL-1314
Ancient fauna skeletal element	This study	Lobos - PGULL-1315
Ancient fauna skeletal element	This study	Lobos - PGULL-1316
Ancient fauna skeletal element	This study	Lobos - PGULL-1317
Ancient fauna skeletal element	This study	Lobos - PGULL-1319
Ancient fauna skeletal element	This study	Lobos - PGULL-1868
Ancient fauna skeletal element	This study	El Portalón - APOR012

Chemicals, peptides, and recombinant proteins

2-Propanol	Merck	Cat#1.09634.1000
Absolute ethanol molecular biology grade	Merck	Cat#493546
AmpliTaq Gold® DNA Polymerase	Applied Biosystems	Cat#N8080247
ATP Solution (100 mM)	Thermo Scientific	Cat#R044
Bst DNA Polymerase	New England Biolabs	Cat#M0275L
dNTPs mix (25 mM each)	Thermo Scientific	Cat#R1121
PE buffer	QIAGEN	Cat#19065
PEG 4000	Thermo Scientific	Cat#EL0012
Proteinase K	Fisher BioReagents	Cat#BP1700-500
Sodium Acetate (3 M), pH 5.5, RNase-free	Invitrogen	Cat#AM9740
Sodium Hypochlorite Solution 6–14%	Merck	Cat#13440-500 ML
T4 DNA ligase	Thermo Scientific	Cat#EL0012
T4 DNA Polymerase	Thermo Scientific	Cat#P0062

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
T4 Polynucleotide Kinase	Thermo Scientific	Cat#M0201L
Tango Buffer (10X)	Thermo Scientific	Cat#BY5
ThermoPol® Reaction Buffer	New England Biolabs	Cat#B9004S
Tween® 20	VWR Chemicals	Cat#437082Q
UltraPure™ 0.5M EDTA, pH 8.0	Invitrogen	Cat#15575020
UltraPure™ 1M Tris-HCl Buffer, pH 7,5	Invitrogen	Cat#15567027
UltraPure™ DNase/RNase-Free Distilled Water	Invitrogen	Cat#10977015
UltraPure™ Guanidine Hydrochloride	Invitrogen	Cat#15502016
Uracil Glycosylase Inhibitor	New England Biolabs	Cat#M0281L
USER® Enzyme	New England Biolabs	Cat#M5505L
KAPA HiFi HotStart ReadyMix	Roche	Cat#7958935001
Critical commercial assays		
myBaits Mito Goat	Arbor Biosciences	Cat#303008
MinElute PCR Purification Kit	QIAGEN	Cat#28006
QIAquick Nucleotide Removal Kit	QIAGEN	Cat#28306
Select-a-Size DNA Clean & Concentrator MagBead Kit	Zymo Research	Cat#D4085
Qubit™ 1X High sensitivity dsDNA quantitation kit	Invitrogen™	Cat#Q33231
Deposited data		
Sequencing data	This study	European Nucleotide Archive (ENA) - Project: PRJEB90261
Curated haplotype data	This study	Table S1
Oligonucleotides		
IS1 adapter: A*C*A*C*TCTTCCCTA CACGACGCTC	Kircher et al. ⁷⁰	Macrogen
IS2 adapter: G*T*G*A*CTGGAGTTC AGACGTGTGCT	Kircher et al. ⁷⁰	Macrogen
IS3 adapter: A*G*A*T*CGGAA*G*A*G*C	Kircher et al. ⁷⁰	Macrogen
IS4: AATGATACGGCGACCACCGAGATC TACACTCTTCCCTACACGACGCTCTT	Kircher et al. ⁷⁰	Macrogen
IS5: AATGATACGGCGACCACCGA	Kircher et al. ⁷⁰	Macrogen
IS6: CAAGCAGAAGACGGCATACGA	Kircher et al. ⁷⁰	Macrogen
Software and algorithms		
AdapterRemoval v2.3.3	Schubert et al. ⁷¹	https://github.com/MikkelSchubert/adapterremoval ; RRID: SCR_011834
bamUtil v1.0.15	Jun et al. ⁷²	https://github.com/statgen/bamUtil
BCFtools v0.1.19	Li et al. ⁷³	https://www.htslib.org ; RRID: SCR_002105
bcl2fastq v2.19.1	N/A	https://support.illumina.com/content/dam/illumina-support/documents/downloads/software/bcl2fastq/bcl2fastq-2-19-1-release-notes-1000000035330-00.pdf ; RRID: SCR_015058
BWA v0.7.17-r1188	Li and Durbin ⁷⁴	https://github.com/lh3/bwa ; RRID: SCR_010910
iTaxoTools v0.1	Vences et al. ⁷⁵	https://github.com/iTaxoTools/iTaxoTools-Executables/releases
MapDamage v2.2.1	Jónsson et al. ⁷⁶	https://github.com/ginolhac/mapDamage/releases ; RRID: SCR_001240
R v4.3.2	R Core Team ⁷⁷	https://www.r-project.org/ ; RRID: SCR_001905
Samtools v1.15.1	Li et al. ⁷³	https://www.htslib.org ; RRID: SCR_002105
Tablet v1.17.08.17	Milne et al. ⁵⁵	https://ics.hutton.ac.uk/tablet/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Permissions needed to analyze ancient faunal remains were granted by the local authority (Dirección General de Patrimonio Cultural del Gobierno de Canarias; ref. 51/2020–0717115014). Fauna samples consisted of well-preserved teeth, bone and horn remains obtained in excavations at indigenous and colonial sites across the Canary Islands and in two Roman sites (Lobos and El Portalón). Given the difficulties in differentiating goat and sheep remains, most of the samples were first labeled as *Ovis/Capra*. In collaboration with local zooarchaeologists, we examined 271 well-preserved *Ovis/Capra* remains and selected 190 for aDNA analyses (Table S1). Among them, 32 samples come from the Roman sites of Lobos⁵ ($n = 31$) and El Portalón⁷⁸ in Burgos (Iberian Peninsula, $n = 1$). The Canarian Indigenous sample consisted of 142 samples from 34 different archaeological sites from the seven main islands (Table S1). Finally, we included 16 colonial samples from the Canary Islands. Most of them were obtained from the archaeological site of the old Hospital de San Martín in Gran Canaria ($n = 13$). This site is dated from the late 15th to the 18th centuries and it is characterized by high *Ovis/Capra* consumption.¹⁰ In addition, samples were collected from the European occupation phase of the indigenous sites of Cueva de Herrera González (La Gomera; $n = 2$)²⁷ and Peña de las Cucharas - Fiquineo (Lanzarote; $n = 1$) (Gilson, personal communication).

METHOD DETAILS

Ancient DNA laboratory work

DNA extraction and library preparation steps were performed in the clean lab facilities at the Paleogenomics Lab at Universidad de La Laguna (Canary Islands, Spain), except for those of the APOR012 sample that were carried out in the SciLifeLab Ancient DNA unit at Uppsala University (Sweden). Measures to avoid and monitor contamination from modern DNA were applied during sample manipulation. Ancient DNA was extracted from teeth, bones or horns following Dabney et al.⁷⁹ and built into double-stranded indexed libraries following Kircher et al.⁷⁰

Shotgun sequencing data processing

Ancient DNA libraries were sequenced on an Illumina NextSeq 550 using a paired-end protocol, except for the APOR012 sample that was sequenced as part of an Illumina NovaSeq SP flow cell. Paired-end reads were merged and trimmed to remove adapters and low-quality bases (BASEQ <20) using AdapterRemoval v2.3.3.⁷¹ Reads shorter than 30 bp were also discarded during the adapter removal step. Merged reads were then mapped to the goat (RefSeq: GCF_001704415.2) and sheep (RefSeq: GCA_000298735.2) reference genomes using BWA v0.7.17.⁷⁴ Low quality (MAPQ < 30) and duplicate reads were removed using SAMtools v1.15.1.⁷³ The percentage of endogenous DNA was calculated by dividing the number of reads remaining after filtering by the total number of trimmed reads. Duplicate rates were assessed by comparing reads before and after the duplicate removal step. Finally, MapDamage v2.2.1⁷⁶ was used to visualize misincorporation and fragmentation patterns. MtDNA contamination estimates were calculated based on the average number of mismatches observed in basal variable positions within our dataset. Briefly, we prepared a list of all the mutations considered as basal for the A8 and A2 lineages (194, 257, 1119, 1237, 1541, 6594, 7117, 7213 and 14740). Then, we performed SNP calling on all the samples using SAMtools mpileup, filtering the list of positions previously mentioned. Genotyping data were used for estimating the mismatch rate per site, calculated as the number of reads with the minor allele (or alleles) divided by the total number of reads. The mean contamination value considering all sites and the 95% confidence interval were estimated using R v4.3.2.⁷⁷ To minimize the effect of postmortem damage on the contamination estimation, we use the trimBam option from BamUtil⁷² to trim 3 bp at both ends of the ancient DNA reads before the SNP calling step. In spite of that, we must acknowledge that this method potentially produces an overestimation of the real contamination value, as the observed mismatches can also be caused by postmortem damage and sequencing errors.

Species assignment was performed by calculating the edit distance of mapped reads to the goat and sheep genomes and choosing the species with the lowest value. Briefly, we used SAMtools view to generate the number of mismatches per read and then calculated the mean value using AWK. All individuals classified as goats with endogenous DNA rates higher than 0.5% were selected for downstream mtDNA analyses.

Library enrichment

Given that the remains of domesticated animals usually appear highly fragmented and could have been subjected to thermal alteration from food processing or other human activities, we anticipated low percentages of endogenous DNA due to DNA degradation. To overcome these limitations, we applied two different methods to enrich for goat mtDNA reads: one capture method targeting the whole goat mitogenome (myBaits Expert Mito kit; User Manual v5.00; Arbor Biosciences) and a bleach treatment prior to extraction to reduce exogenous DNA,⁸⁰ followed by a partial UDG treatment to repair deaminated cytosines.⁵⁴ The treatment applied to each sample is detailed in Table S2. After the enrichment steps, the libraries were sequenced to saturation in an Illumina NextSeq 550 using a paired-end protocol. To explore the performance of the two enrichment methods, we compared the results obtained for the samples that were subjected to the mtDNA capture, the bleach treatment and the two protocols combined.

QUANTIFICATION AND STATISTICAL ANALYSES

Mitochondrial DNA analysis

We observed a high divergence between the mtDNA reference and our samples that affected the mapping of endogenous reads to the control region. To overcome that limitation, we created an ancestral A mitogenome by combining the mutations expected for a basal A lineage in the coding region based on Colli et al.³⁹ with the ones observed in the control regions for the Canarian indigenous goats by Ferrando et al.⁴⁸ and used it as the reference sequence for mapping.

For those individuals with a coverage higher than 15×, mtDNA consensus sequences were generated using SAMtools and BCFtools v0.1.19.⁷³ A list of variants was then obtained using SAMtools mpileup, with a minimum depth of 5. MtDNA haplotypes were manually curated by visual inspection using Tablet v1.17.08.17.⁵⁵ Haplogroup classification was performed by phylogenetic analysis based on the complete mtDNA tree published by Colli et al.,³⁹ which was built using mutations observed in the coding region. Briefly, after retrieving all available mtDNA genomes belonging to the haplogroups of interest from the NCBI (<https://www.ncbi.nlm.nih.gov>), median-joining networks were obtained using iTaxoTools v0.1.⁷⁵ Haplotypic diversity at population level was calculated according to Nei and Tajima⁸¹ using the hap.div function from the pegas package (v0.14).⁸² Sampling the same bone or tooth was not always possible as, in most cases, remains were fragmented. Because of that, our strategy was focused on selecting the best-preserved remains rather than ensuring all samples corresponded with different individuals (although we tried to select remains from well-defined stratigraphic positions when possible). Given this, when constructing networks and calculating diversity values, we considered samples from the same archaeological site and the same stratigraphic unit with identical haplotypes as belonging to the same individual (Table S2). To take advantage of previously generated data from the Canary Islands, we retained the D loop haplotype of high-coverage mitogenomes, in such a way that D loop information was only considered for samples with a coverage higher than 99.5% and a depth higher than 30× in that region. D loop sequences were then combined with sequencing data from present-day goats generated by Amills et al.^{47,69} and Ferrando et al.⁴⁸ and constructed median-joining networks as previously discussed.