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Mitochondrial DNA diversity in northeast Iberians during the Iron Age

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ABSTRACT

Iberian culture emerged along the Mediterranean coast of the Iberian Peninsula between the 8th and 6th century BCE, flourishing during the 5th-3rd BCE until the Roman conquest. Iberians engaged in metallurgy, agriculture, and livestock, and actively participated in Mediterranean commercial trade networks. Despite cremation being the predominant funerary practice, advances in ancient DNA techniques have enabled the recovery of mitochondrial DNA (mtDNA) from an increasing number of Iberian individuals. Here, we analyzed the remains of 31 newborns, successfully obtaining mtDNA profiles for 21 individuals (20 Iberians and 1 Late Roman). These data were merged with 41 previously published mtDNA profiles from unrelated Iberians across different tribes of the northeast of the Iberian Peninsula. Additional prehistoric data were compiled to contextualize Iberian haplogroups. We investigated maternal lineage diversity between tribes, temporal shifts in haplogroup composition, and signatures of long-distance female mobility. Our results revealed subtle differences in mtDNA haplogroup frequencies between groups, although genetic differentiation was not statistically significant. Mitochondrial diversity remained relatively high across all tribes, consistent with patrilocal mating systems and small-distance female migration that may have prevented strong matrilineal differentiation among tribes. A predominance of haplogroups H, J, K, HV0, and U was observed, most of which were already present in the Iberian Peninsula before the Iron Age. Haplogroup diversity remained stable over time, without population differentiation, suggesting maternal genetic continuity from the Bronze Age. However, the presence of some haplogroups pointed to occasional female-mediated gene flow from North Africa, the Near East, and Central Europe. Overall, this study provides the most comprehensive NGS-based assessment of maternal ancestry in Iron Age Iberians to date, revealing a genetic landscape shaped by local continuity alongside some long-distance female mobility linked to commercial trade and cultural interaction.

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1. Introduction

The Iron Age in the Iberian Peninsula (mid-9th century BCE until the Roman conquest) was marked by the coexistence of diverse cultural groups, including the Iberians, Celts, Celtiberians, Lusitani, Vettones, Vaccaei, and Callaeci, among other indigenous populations (Sinner et al., 2024). Iberian culture emerged between the 8th and 6th century BCE in the Iberian Peninsula along the northern, eastern, and southern coasts of the Mediterranean Sea. It reached its peak between the 5th and 2nd century BCE. This culture developed a distinct identity marked by its alphabet, coinage, iron metallurgy, and economic activities like agriculture, livestock, fishing, and Mediterranean trade (Almagro et al., 2001; Jordá Cerdá et al., 1986; Sinner and Velaza, 2019). Far from being a homogenous entity, the term "Iberians" (later coined by the Romans) encompassed multiple groups — Ausetani, Cessetani, Ilergetae, Indiketes, Lacetani, Laietani, etc. — each with its own sociopolitical trajectory (Aranegui, 2012; González Reyero, 2012).

Their funeral practices were primarily based on cremation. However, cremation necropolises did not represent all types of Iberian burial (Oliver Foix, 2004), as some newborns have been found buried under the pavement of houses (Afonso et al., 2019; Crespo et al., 2011; Subirà and Molist, 2007). This funerary rite has been widely discussed in different archaeological contexts (Eng and Smith, 1976; Gowland et al., 2014; Hassan et al., 2014). Recent evidence suggests that the age profile of Iberian newborns aligns well with natural mortality causes (Martirosyan et al., 2024), and both male and female individuals have been identified (Cuesta-Aguirre et al., 2025a; Cuesta-Aguirre et al., 2025b; Sandoval-Ávila et al., 2025).

The origins of Iberian society have been broadly debated. Early theories proposed a Neolithic African substrate influenced by Greek colonists, leading to the idea of an expansive Ibero-Tartessian culture (Bosch-Gimpera, 1938). However, Maluquer de Motes and Tarradell later proposed a model of simultaneous local development, with colonial influence acting as a catalyst rather than a cause (Maluquer de Motes, 1966, 1982; Sanmartí, 2011, 2013; Tarradell, 1962). In the northeast of the Iberian Peninsula, a clear shift toward Iberian cultural traits occurred after the 6th century BCE, as seen in increased urbanization, territorial organization, and the rise of aristocratic elites (Asensio et al., 2001; Belarte, 2010; Bendala, 1998; Bosch and Santacana, 2009; Junyent, 1996a, 1996b, 2023; Sanmartí et al., 1998; Sanmartí, 2003, 2008, 2015).

From the 9th to the 6th centuries BCE, Phoenician and Greek colonization reshaped Iberian territories through the foundation of trade hubs such as Gadir, Malaka, Abdera, and Emporion. These settlements connected Iberians to wider Mediterranean economic and cultural exchanges (Dietler, 2009; S. Gitin and Bierling, 2002; Keay, 1998). Later, Carthage, founded in the 9th century BCE and expanding from the 7th century BCE, reinforced these connections. By 236 BCE, Carthaginian military campaigns brought much of the southern Iberian Peninsula under their control, establishing cities like Qart-Hadasht (Cartago Nova). However, the Roman expansion soon clashed with Carthaginian ambitions, leading to the Punic Wars (Bagnall, 1999; Carey et al., 2007; Cornell, 1995; Edwell, 2011; Feeney, 2017; Goldsworthy, 2012; Grant, 1978; Richard, 2011; Schullard, 1989; Zimmermann, 2011). In 218 BCE, Rome landed in Emporion, gaining support from some of the northeastern coastal Iberian groups (Rhys, 1905; Zimmermann, 2011). By 206 BCE, the Battle of Ilipa (near present-day Seville) secured Roman dominance (Edwell, 2011; Zimmermann, 2011), and initiated a gradual process of cultural, economic, and sociopolitical integration known as Romanization (Abad Casal et al., 2006; Blázquez, 2006; Coarelli et al., 1992; Curchin, 1991; Fear, 1996; Haley, 2003; Johnston, 2017; Keay, 1988, 1990, 1998, 2003; Rodà, 2000; Sinner, 2015).

Different Iberian populations interacted with a range of external cultures, shaping their identities in diverse ways. While archaeological evidence reveals cultural traits and trade networks, it often cannot clarify the nature or depth of these interactions, particularly whether individuals from foreign groups integrated into local communities. Paleogenetics provides a crucial complementary perspective to explore such dynamics. It offers deeper insights into processes that shaped the Iberian Peninsula over time by uncovering the genetic makeup of ancient populations.

Among genetic markers, mitochondrial DNA (mtDNA) is especially valuable in ancient DNA studies. Its molecular characteristics make it well-suited for degraded samples where whole-genome sequencing is sometimes unfeasible (Ehler et al., 2019). Unlike nuclear DNA, which exists in only two copies per cell and is more prone to post-mortem degradation, mtDNA is present in hundreds to thousands of copies, greatly increasing the chance of successful recovery from ancient remains (Gilbert et al., 2007; Pääbo et al., 2004). Its circular structure also provides stability against enzymatic degradation, aiding its long-term preservation (Krause et al., 2010). Moreover, mtDNA's strict maternal inheritance and lack of recombination simplify phylogenetic analyses (Nesheva, 2014; White et al., 2008), allowing researchers to accurately reconstruct maternal lineages. These properties enable the tracking of genetic continuity, migration events, and population admixture (Översti et al., 2019). MtDNA has also proven helpful in identifying female mobility and affinities between ancient and modern populations, shedding light on long-term demographic patterns (Achilli et al., 2008).

The study of female mobility has revealed diverse kinship and residence systems across prehistoric Europe, illustrating how social structures evolved. In Neolithic and Bronze Age contexts, many societies followed patrilocal models with widespread female exogamy (Papac et al., 2021; Simón et al., 2011; Villalba-Mouco et al., 2022). For example, in Corded Ware groups of Bohemia (2900–2400 BCE), genetic and isotopic data showed that non-local women were integrated into communities that maintained stable Y-chromosome lineages but diverse mitochondrial DNA haplogroups, indicating patrilocality and female mobility (Papac et al., 2021). A patrilocal mating system during the Bronze Age, where women moved to the husband's community after marriage, was also hypothesized in the Iberian Peninsula (Simón et al., 2011; Villalba-Mouco et al., 2022). In contrast, evidence for matrilocal or female-centered systems appeared in other contexts. In Neolithic Greece, a marked decline in mitochondrial DNA diversity during the later phases of the Neolithic (by the 4th millennium BCE) suggested increasing female sedentarism, likely associated with matrilocal residence (Silva et al., 2022). In Iron Age southern England (100 BCE - 100 CE), mitochondrial data from a Celtic community revealed that 64 % of individuals across both sexes shared a single founding maternal lineage, consistent with matrilocality. Additionally, non-local grave goods were found in male burials, suggesting that men moved into established female kin groups through biological reproductive union (Cassidy et al., 2025).

Beyond residence systems, female mobility also played a central role in cultural transmission and demographic integration. In Phoenician settlements across the Mediterranean (700-400 BCE), mitochondrial genomes from southern Sardinia and Lebanon revealed the presence of indigenous and non-local haplogroups, such as Near Eastern N1b1a5 and European W5 in Sardinia and some European lineages in Lebanon. These findings indicated bidirectional female migration between North Africa, the Levant, and Europe, demonstrating active female participation in trade and settlement networks, challenging assumptions of male-dominated migration (Matisoo-Smith et al., 2018). Together, these examples highlight how institutionalized sex-biased mobility shaped the genetic and social landscapes of past European societies, with patrilocality reinforcing male continuity and matrilocality fostering female-centered kinship systems.

Despite extensive research on the prehistory of the Iberian Peninsula (Gamba et al., 2014; Olalde et al., 2019; Roca-Rada et al., 2025; Villalba-Mouco et al., 2021, 2023), genetic studies focusing specifically on the Iron Age remain limited, particularly for Iberian culture. This scarcity is largely due to the limited availability of anthropological remains, as cremation was the predominant funerary practice among Iberian

groups. The earliest paleogenetic research on Iberian populations focused on mitochondrial DNA, particularly the hypervariable region I (Gamba et al., 2008; Sampietro et al., 2005). These initial studies aimed to identify the main mitochondrial haplogroups present in Iron Age Iberians and to compare them with those from the Chalcolithic, Bronze Age, and Roman periods (Gamba et al., 2008), as well as with culturally distinct groups like the Basques and Etruscans (Sampietro et al., 2005). These analyses, based on the remains of 27 adults from nine archaeological sites — including bone fragments from areas historically associated with Iberians, though not always of confirmed Iberian origin — revealed several key insights. The haplogroup composition of these individuals was strikingly similar to that of present-day Iberian Peninsula populations, albeit with reduced variability, suggesting a degree of genetic continuity since pre-Roman times (Sampietro et al., 2005). Importantly, no close genetic relationship was observed between the Iberians and the Etruscans, underscoring the genetic diversity of pre-Roman Western Europe. Haplogroup H was the most frequent mtDNA lineage, followed by J, T, K, U4, U5, and W (Gamba et al., 2008;

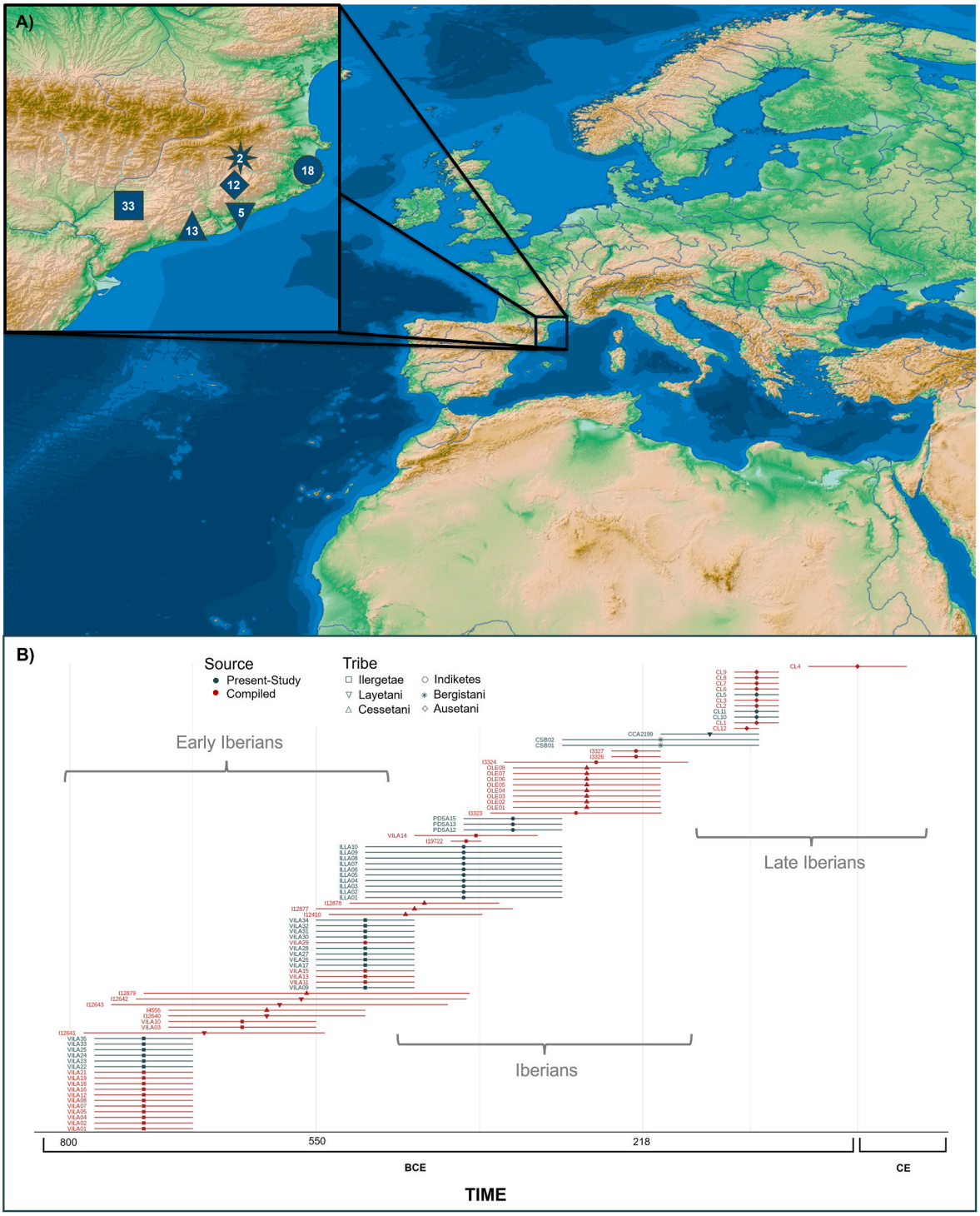

Fig. 1. Geographic (A) and temporal (B) distribution of the Iberians included in this study. The number of samples is indicated in white in panel A, and shapes correspond to the tribe each individual is associated with, as defined in panel B. Additional information on the individuals is provided in Supplementary Table S1.

Sampietro et al., 2005). An unusually high frequency of haplogroup V, a lineage often associated with Paleolithic populations in Europe (Torroni et al., 1998, 2001), was also detected (Gamba et al., 2008).

Recent methodological advances, particularly in Next-Generation Sequencing (NGS) and targeted capture techniques, have significantly improved the retrieval of ancient mitochondrial data. These newer approaches enabled the recovery of mtDNA from 16 individuals (including three newborns from Valencia and 13 adults from Catalonia) across seven Iberian archaeological sites (Olalde et al., 2019), and one additional individual also from Catalonia (Patterson et al., 2022). The results again showed a predominance of haplogroups H and J, along with lineages from HV0, K1, and X2b (Olalde et al., 2019; Patterson et al., 2022).

No systematic mitochondrial study has been conducted on Iberians who span the Early Iron Age to the Roman Conquest period. In this article, we focus on high-resolution mitochondrial DNA variation identified by us (Cuesta-Aguirre et al., 2025a) and other groups (Olalde et al., 2019; Patterson et al., 2022) in Iberian individuals from different groups, and expand our dataset by analyzing new Iberian samples. Our main objectives are to compare the mitochondrial diversity of northeastern Iberian tribes with that of earlier and later population groups from the same region, in order to trace the origins and distribution of specific mitochondrial haplogroups identified in the Iberian populations to understand their evolutionary trajectories, and to investigate maternal lineage diversity over time, with particular attention to signals of long-distance female mobility.

2. Material and methods

2.1. Sample selection

Thirty Iberian individuals from the fortress of Vilars, Sant Miquel d'Olèrdola, El Camp de les Lloses, Ullastret - Illa d'en Reixac, Ullastret - Puig de Sant Andreu, Castell de Besora, and Ilduro (Cabrera de Mar), located in Catalonia, Spain, that span the Early Iron Age to the Roman Conquest period, were analyzed. Additionally, a Late Roman individual from the fortress of Vilars was analyzed, and four Iberian individuals from Ullastret - Illa d'en Reixac were reanalyzed. All necessary permissions for the analysis of ancient human remains were obtained from the institutions responsible for the archaeological collections, which are under the authority of the Government of Catalonia, Spain. Furthermore, information from 49 published Iberians from the northeast of the Iberian Peninsula has been collected. All Iberian individuals involved in this study are represented in Fig. 1 and Table 1. In addition, 172 individuals from the Neolithic to Visigoth era (Supplementary Material, Table S1) were compiled from previous works to build the chronological framework.

A summary of the most relevant references for the archaeological context of the fortress of Vilars, Sant Miquel d'Olèrdola, and El Camp de les Lloses can be found in Cuesta-Aguirre et al., 2025a. Those for Can-Roqueta/Can Revella, Hort d'en Grimau, and Mas d'en Boixos can be found in Olalde et al. (2019). For Illa d'en Reixac and Puig de Sant Andreu, such information can be found in Sandoval-Ávila et al. (2025), and for Mas Castellar in Patterson et al. (2022).

Castell de Besora (Bergistani tribe) is located at approximately 1025 m above sea level in the municipality of Santa Maria de Besora, province of Barcelona (Catalonia, Spain). This strategically positioned site has played a crucial role in the region's history, with its occupation dating back to the Iron Age and associated with the Ausetani tribe. Although the Iron Age strata have been poorly explored, the discovery of two Iberian newborns highlights the archaeological potential (Busquets i Costa et al., 2018). The site continued to be used through various historical periods, with the first written reference to the castle dating to the late 9th century, when it served as a defensive stronghold during the early medieval era (Busquets i Costa et al., 2018).

El poblat Ibèric de Burriac (Laietani tribe) lies at the foot of Burriac Mountain in the province of Barcelona (Catalonia, Spain). This key settlement of the Laietani people reflects the political and economic complexity of Iberian societies in northeastern Iberia. Initially settled in the 6th century BCE, the site flourished in the 4th century BCE with the construction of fortifications and an urban street network. Spanning 7–10 ha, it became one of the largest Iberian urban centers, exerting control over surrounding agricultural zones until the late 3rd century BCE. Following the Second Punic War, Iberian dominance declined, and italic culture was rapidly adopted. Archaeological finds include public and private buildings, thermal baths, a wine production center from the late Republican period, and a Roman mint issuing coins with the Iberian legend "ILDURO" (Sinner, 2017), attesting to the site's continued significance under Roman rule. So far, the remains of only one newborn from the Iron Age levels of Ilduro have been available, found in one of the Late Republican houses that developed outside the walls of the oppidum (Martín i Méndez, 1998; Sinner, 2015; Sinner and Ferrer i Jané, 2016; Zamora Moreno, 2006).

Table 1
Summary of Iberian archaeological sites from the northeastern Iberian Peninsula included in this study. Sites are grouped by associated tribe, with the number of individuals analyzed, the number of mitochondrial DNA (mtDNA) sequences retained, and the corresponding reference for the mtDNA data. The number of mtDNA sequences may be lower than the number of individuals due to failed recovery or genetic relatedness.

Tribe	Site	Number of Iberians available	Number of mtDNA employed	Reference for the mtDNA data
Ilergetae	The fortress of Vilars	15 18	10 13	Present-study Cuesta-Aguirre et al., 2025a
Cessetani	Font de la Canya	1	1	Olalde et al. (2019)
	Hort d'en Grimau	1	1	Olalde et al. (2019)
	Mas d'en Boixos	3	3	Olalde et al. (2019)
	Sant Miquel d'Olèrdola	8	6	Cuesta-Aguirre et al., 2025a
Laietani	Can-Roqueta/ Can Revella	4	4	Olalde et al. (2019)
	Ilduro	1	0	Present-Study
Indiketes	Ullastret - Illa d'en Reixac	6 4	2 1	Present-study Sandoval-Ávila et al. (2025)
	Ullastret - Puig de Sant Andreu	3 4	2 4	Present-study Olalde et al. (2019)
	Mas Castellar	1	1	Patterson et al. (2022)
Bergistani	Castell de Besora	2	2	Present-Study
Ausetani	El Camp de les Lloses	3 9	3 8	Present-Study Cuesta-Aguirre et al., 2025a

2.2. Sample preparation, DNA extraction, and quantification

In this study, new mtDNA data were generated for newborns from various Iberian archaeological sites across the Northeast of the Iberian Peninsula (Table 1 and Supplementary Table S1). All processing steps further described were conducted in the Anthropology Unit's dedicated clean ancient DNA laboratory at the Universitat Autònoma de Barcelona (UAB).

When available, the petrous bone was prioritized for analysis. Vertebral hemiarches or long bones (humerus, femur, or tibia) were used for samples lacking the petrous bone. The outer surfaces of all bones were initially cleaned to remove dirt and then polished with a milling cutter to eliminate the outermost layers. Petrous bones were cut transversely near the internal acoustic opening to expose the cochlea, and a

small section was selected and pulverized using a hammer for subsequent DNA extraction. Similarly, a section of long bones was pulverized, while two vertebral hemiarches were directly pulverized after light polishing.

DNA was extracted from all samples using a protocol that involved mixing 25 μl of proteinase K with 1 ml of extraction buffer, followed by purification with the High Pure Viral Nucleic Acid Large Volume Assembly Kit (Roche). This kit employs a silica-in-HE-membrane column-based method, as described in Vinueza-Espinosa et al. (2020). Blank controls were included in each extraction batch to monitor and ensure the absence of contamination, which was further confirmed by performing quantitative PCR (qPCR) targeting the Hypervariable Region I of mitochondrial DNA (mtDNA). The DNA concentration of each sample was quantified using the Qubit® 1x dsDNA High Sensitivity (HS) Assay Kit (Thermo Fisher Scientific, 2015). The DNA fragmentation profile was assessed using the Bioanalyzer® Agilent High Sensitivity DNA Kit (Agilent Technologies, 2017).

2.3. Library preparation and sequencing

When the samples presented more than 0.05 pmol/ul of DNA (CSB01 and VILA20), Whole Genome Sequencing (WGS) was conducted. Double-strand libraries were made following the Blunt-End-Single-Tube (BEST) protocol (Carøe et al., 2018), with or without partial-UDG treatment (Rohland et al., 2015), as described in Protocol II or III from Cuesta-Aguirre et al., 2025a (see Supplementary Material, Table S2) and sequenced using the NextSeq 1000 instrument from Illumina technology.

For the rest of the samples, where WGS was not feasible, NGS libraries targeting the control region (CR) of human mtDNA were prepared using the PowerSeq CRM Nested System Custom kit (Promega), following the M3 method described by Vinueza-Espinosa et al. (2023). These libraries were sequenced on an Illumina MiSeq instrument using standard flow cells and the MiSeq Reagent Kit v2 Nano.

2.4. Bioinformatic analysis and haplogroup determination

For WGS, nf-core/eager pipeline (v2.4.6) (Ewels et al., 2020; Fellows Yates et al., 2021) was used for pre-processing the reads and aligning them to the Human Reference Genome GRCh37 (hg19, GenBank accession GCA_000001405.1). Reads mapping to mitochondrial DNA were subsequently realigned to the revised Cambridge Reference Sequence (rCRS, GenBank accession NC_012920.1) (Andrews et al., 1999) using CircularMapper (v1.0) (Peltzer et al., 2016). Haplotypes were called using freebayes (v1.3.6) (Garrison and Marth, 2012) and processed with vcflib (v1.0.3) (Garrison et al., 2022). The C-to-T misincorporation rate in the 1st base of the 5′ end was analyzed to discard contamination (a threshold higher than 10 % was considered as indicative of no contamination).

For samples in which only the CR was sequenced, the pipeline developed by Cuesta-Aguirre et al. (2024) was applied following their recommendations. Samples with a mean mapping quality lower than 25, less than 10 % of damaged reads, or mixed bases were discarded, and neither their haplotype nor haplogroup were estimated.

Visual inspection of all samples was conducted using the Integrative Genome Viewer (IGV, v2.16.1) (Robinson et al., 2011) to verify the called positions. In the low-coverage regions, the damage, mutational, and heteroplasmic profiles (Cuesta-Aguirre et al., 2025b; Li et al., 2015; Soares et al., 2009) were examined to improve the credibility of call variants. Finally, haplogroups were assigned using Haplogrep 3 (v3.2.1) (Schönherr et al., 2023), with the PhyloTree 17 - Forensic Update 1.2 (Dür et al., 2021; Weissensteiner et al., 2016).

2.5. Haplogroup diversity and genetic structure

Haplogroups were categorized according to frequency and phylogenetic significance (Supplementary Material, Table S1). Individuals were grouped according to cultural and chronological criteria (Cultural-Chronological groups) and by Iberian tribes (Supplementary Material, Table S1). Based on these groupings, haplogroup frequency tables were generated.

To investigate associations between mitochondrial haplogroups and different cultural-chronological contexts or tribes, a Correspondence Analysis (CA) was carried out. This multivariate technique enables the visualization of relationships in categorical data by reducing its dimensionality while retaining the main patterns of variation. The analysis was performed in R v4.4.2 (R Core Team, 2024) using the CA(.) function from the FactoMineR package (Lê et al., 2008), applied to the contingency table with the frequencies of mtDNA haplogroups across the defined cultural-chronological groups and Iberian tribes.

Nei's gene diversity (Nei, 1987) was estimated for each cultural-chronological group and for each tribe with more than 10 individuals using Arlequin v3.5.2.2 (Excoffier and Lischer, 2010). In addition, genetic structure analyses were conducted with Arlequin, incorporating pairwise population comparisons using F_{ST} and an exact test of population differentiation based on haplogroup frequencies (Goudet et al., 1996; Raymond and Rousset, 1995). The significance level was considered 0.05 in all the analyses.

2.6. Distribution of specific haplogroups

Haplogroups present in Iberian individuals were investigated to determine their occurrence and geographical distribution. Samples belonging to haplogroups reported in Iberian individuals were compiled from the Allen Ancient DNA Resource (AADR) database (Mallick et al., 2024) and several recent paleogenomic studies focusing on the Iberian Peninsula (Carrión et al., 2024; Papac et al., 2023; Roca-Rada et al., 2025). Only samples marked as "PASS" in the AADR database and not indicated as possibly contaminated were used. Samples with the same haplogroup and phylogenetically close haplogroups were compiled. For haplogroups that could be precisely classified and that were not exclusively from the Iberian Peninsula, heatmaps were made with QGIS v3.30 (QGIS Development Team, 2025). For this, only unrelated samples older than the Iberians were used to determine if the lineage was already present on the Iberian Peninsula before the Iron Age. Maternal relatives were removed from the analysis to avoid frequency inflation due to kinship. For cases where the haplogroup was found only in the Iberian Peninsula or when it was rare in ancient populations, the heatmaps from the present-day population were extracted from EMPOP v5/R12 (Huber et al., 2018).

3. Results

The Supplementary Material (Table S2) presents information about each library for the samples analyzed in the present study. All 38 CR-mtDNA libraries, obtained from 33 individuals (two libraries were made for some of the individuals), presented a percentage of damage over 10 %. However, thirteen libraries belonging to nine individuals were discarded due to mixed bases in their profiles. In addition, three additional libraries were removed from downstream analysis due to low mean mapping quality (lower than 25). All four WGS BEST libraries presented a level of damage over 10 % and were retained for further analysis.

A total of 21 new mtDNA sequences were generated, twenty come from the Iberian period (Table 1), one of them a reanalyzed individual from Sandoval-Ávila et al. (2025), and one was from the Roman period. Table S3 provides more information about haplotypes and haplogroups for present-study individuals and those from Sandoval-Ávila et al. (2025).

Additionally, mtDNA information from 41 unrelated Iberian individuals (Fig. 1, Table 1, and Supplementary Material, Table S1) and 172 unrelated individuals from the Neolithic to Visigoth era, all from the

Northeast of the Iberian Peninsula, was used in further analysis.

3.1. Haplogroup diversity and genetic structure

Mitochondrial haplogroups were categorized into 17 groups based on frequency and phylogenetic relevance (Supplementary Material, Table S1).

Table 2 (and Supplementary Material, Table S1) presents the frequency of haplogroups for each cultural-chronological group. The most common lineages across all periods are H and U, although their frequencies fluctuate over time. Lineages of H are present in 22.73 % of Neolithic-Bronze Age individuals and increase throughout the Iron Age, reaching their highest frequency among the Late Iberians (72.73 %). The U lineage (excluding U6), which encompasses several haplogroups, including U5a, U5b, and K, is particularly frequent in the Neolithic-Bronze Age (43.18 %) and remains present in subsequent periods. The U5b subclade is more common in earlier populations, while U5a increases during the Iron Age. An elevated frequency of HV0 lineages is observed among the Early Iberians and Iberians, a pattern also reflected in the Greek-Hellenistic group. The values of Nei Gene diversity can be considered high and were similar between populations from different periods, overlapping in all cases.

To assess genetic structure, a Correspondence Analysis (CA) was performed (Fig. 2), revealing that the first dimension (31.94 % explained) separated prehistoric populations chronologically, while dimension 2 (23.25 % explained) separated all populations chronologically, except for the Greek-Hellenistic population, which presented a wide chronological range. Along the first dimension, we observed the increase of subhaplogroup U5b and haplogroup X, and a decrease in H3, HV0, and African haplogroups (L, M1, and U6). In the second dimension, the frequency of X and U5b haplogroups decreased and increased for haplogroups T, J2, U5a, H5, V, and Others (R0 group, C4, and W). Although some chronological structuring can be deduced, globally, a small degree of differentiation is evidenced, with only pairwise F_{ST} between Neolithic-Bronze Age compared to Greek-Hellenistic being significant ($F_{ST} = 0.05185$; p-value $= 0.02734 \pm 0.0051$), and the exact test of population differentiation not showing significant differences.

Table 3 presents the haplogroup frequencies for the 61 Iberian individuals analyzed, including Early Iberians, Iberians, and Late Iberians, and the frequency for each Iberian tribe. Among the Iberian individuals, the most frequent haplogroup was H, accounting for 39.34 %

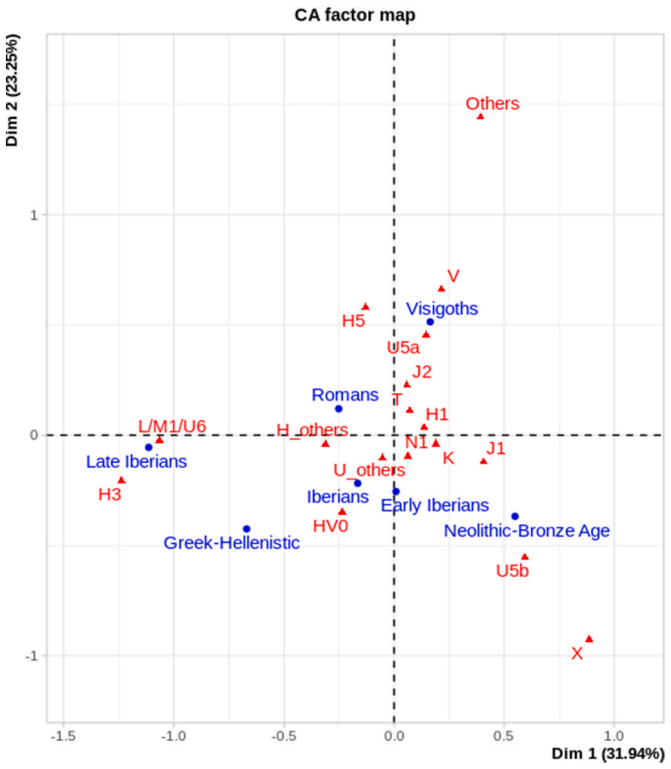

Fig. 2. Correspondence Analysis (CA) based on mitochondrial haplogroup frequencies across cultural-chronological groups. Blue labels represent population groups, while red labels correspond to mitochondrial haplogroups. Dimensions 1 and 2 explain 31.94 % and 22.35 % of the total variance, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Haplogroup frequency (%) for all the cultural-chronological groups. The total sample size is indicated in parentheses next to the population's name. Nei's gene diversity ± standard deviation is also indicated for each group. "All H" includes individuals assigned to haplogroup H without subclade resolution; "Others H″ includes subclades of H not individually listed in the table. The same applies to "All U″, which includes individuals assigned to haplogroups U without subclade resolution (including haplogroups K) and "Other U" (U subclades not separately listed).

	Neolithic-Bronze Age (5500-1400 BCE) (N = 44)	Early Iberians (775-450 BCE) (N = 28)	Iberians (450-200 BCE) (N = 22)	Late Iberians (200 BCE – 50 CE) (N = 11)	Greek-Hellenistic (750-50 BCE) (N = 13)	Romans (50 BCE – 700 CE) (N = 37)	Visigoths (200–800 CE) (N = 58)
All H	22.73	35.71	27.27	72.73	61.54	29.73	34.48
H1	13.64	7.14	4.55	18.18	7.69	2.70	12.07
H3	0.00	3.57	4.55	27.27	15.38	5.41	1.72
H5	2.27	0.00	0.00	9.09	0.00	2.70	5.17
Others H	6.82	25.00	18.18	18.18	38.46	18.92	15.52
V	2.27	0.00	0.00	0.00	0.00	5.41	5.17
HV0	2.27	10.71	13.64	0.00	15.38	2.70	3.45
J1	13.64	7.14	9.09	0.00	0.00	8.11	6.90
J2	2.27	3.57	9.09	0.00	0.00	5.41	5.17
T	4.55	10.71	9.09	0.00	0.00	10.81	6.90
L/M1/U6	0.00	0.00	4.55	9.09	0.00	5.41	0.00
N1	2.27	0.00	9.09	0.00	0.00	2.70	1.72
All U	43.18	32.14	13.64	18.18	23.08	29.73	27.59
U5a	2.27	3.57	4.55	0.00	0.00	5.41	6.90
U5b	13.64	10.71	0.00	0.00	7.69	0.00	3.45
Others U	9.09	0.00	0.00	9.09	7.69	10.81	3.45
K	18.18	17.86	9.09	9.09	7.69	13.51	13.79
X	6.82	0.00	4.55	0.00	0.00	0.00	0.00
Others (R0, C4, W)	0.00	0.00	0.00	0.00	0.00	0.00	8.62
Nei gene diversity	0.9091 ± 0.0186	0.8889 ± 0.0328	0.9394 ± 0.0277	0.9091 ± 0.0656	0.8462 ± 0.0854	0.9234 ± 0.0209	0.9244 ± 0.0134

Table 3
Haplogroup frequencies across Iberian tribal groups and the whole culture. Sample sizes are shown in parentheses next to each group's name. Tribes with fewer than 10 individuals are shown in *italics*. For each tribe, the haplogroup frequency that most differs from the other groups is highlighted in grey. Nei's gene diversity ± standard deviation is reported for groups with more than 10 individuals. "All H" includes individuals assigned to haplogroup H without subclade resolution; "Others H" includes subclades of H not individually listed in the table. The same applies to "All U", which includes individuals assigned to haplogroups U without subclade resolution (including haplogroups K) and "Other U" (U subclades not separately listed).

	Iberians (N=61)	Ilergetae (N=23)	Cessetani (N=11)	*Laietani (N=4)*	Indiketes (N=10)	*Bergistani (N=2)*	Ausetani (N=11)
All H	39.34	34.78	18.18	*50.00*	30.00	*50.00*	72.73
H1	8.20	4.35	0.00	*25.00*	10.00	*0.00*	18.18
H3	8.20	4.35	9.09	*0.00*	0.00	*0.00*	27.27
H5	1.64	0.00	0.00	*0.00*	0.00	*0.00*	9.09
Others H	21.31	26.09	9.09	*25.00*	20.00	*50.00*	18.18
HV0	9.84	4.35	27.27	*25.00*	0.00	*50.00*	0.00
J1	6.56	8.70	9.09	*0.00*	10.00	*0.00*	0.00
J2	4.92	0.00	9.09	*25.00*	10.00	*0.00*	0.00
T	8.20	13.04	0.00	*0.00*	20.00	*0.00*	0.00
L/M1/U6	3.28	0.00	9.09	*0.00*	0.00	*0.00*	9.09
N1	3.28	0.00	9.09	*0.00*	10.00	*0.00*	0.00
All U	22.95	39.13	18.18	*0.00*	10.00	*0.00*	18.18
U5a	3.28	8.70	0.00	*0.00*	0.00	*0.00*	0.00
U5b	4.92	13.04	0.00	*0.00*	0.00	*0.00*	0.00
Others U	1.64	0.00	0.00	*0.00*	0.00	*0.00*	9.09
K	13.11	17.39	18.18	*0.00*	10.00	*0.00*	9.09
X	1.64	0.00	0.00	*0.00*	10.00	*0.00*	0.00
Nei Gene Diversity	0.9093 ± 0.0176	0.8854 ±0.0379	0.9273 ± 0.0665	*NA*	0.9556 ± 0.0594	*NA*	0.9091 ± 0.0656

of the total. This was followed by haplogroup U (excluding U6) lineages, with a frequency of 22.95 %. Other haplogroups were present at lower frequencies, such as J, HV0, and T. N1 and African lineages, specifically M1, were identified in two individuals. Finally, haplogroup X appeared in only one Iberian (Table 3).

A CA was also performed for the Iberian groups (Fig. 3). The Ilergetae

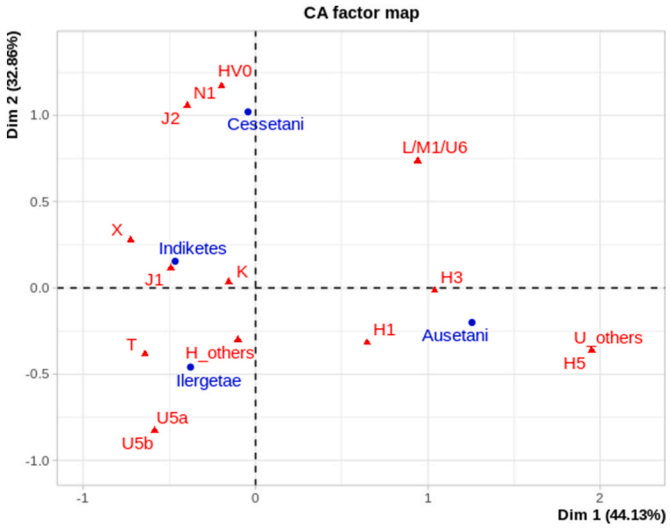

Fig. 3. Correspondence Analysis (CA) based on mitochondrial haplogroup frequencies across Iberian tribes. Blue labels represent tribes, while red labels correspond to mitochondrial haplogroups. Dimensions 1 and 2 explain 44.13 % and 32.86 % of the total variance, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

are notable for carrying U5 sublineages, which are absent in the other tribes. The Cessetani exhibit an elevated frequency of haplogroup HV0 (27.27 %) compared to the other groups with more than 10 individuals. Among the Indiketes, haplogroups T and X are more frequent than in other tribes. The Ausetani showed an increased prevalence of haplogroup H (72.73 %), particularly subclades H1 (18.18 %) and H3 (27.27 %). Despite these variations in haplogroup composition, no significant genetic differentiation was detected. Pairwise F_{ST} values were not significant, and the exact test of population differentiation did not reveal statistically significant differences. All these results could be affected by the small sample size. Nei's gene diversity values are high, comparable across tribes, and overlap in all cases.

3.2. *Distribution of Iberian haplogroups before and during the Iron Age*

To better understand the origin and persistence of the observed haplogroups, we analyzed their temporal distribution in the Iberian Peninsula, Eurasia, and Africa before and during the Iron Age. Most haplogroups found in Iberians were already present in the Iberian Peninsula and Europe before the Iron Age. However, some haplogroups were either rare or absent in the Iberian Peninsula during earlier periods, while others were exclusive to the region before the Iron Age (Table 4).

For the H lineages observed in the Iberians, haplogroups H1, H1t, H3, H3+152, H4a1, and H5 (Supplementary Material, Tables S4–S8) were already present in the Iberian Peninsula before the Iron Age. Interestingly, haplogroup H1t was exclusively found in the Iberian Peninsula until 50 CE (Supplementary Material, Table S5). Haplogroups H3am, H4a1a5, H6a1b2, and H33c (Fig. 4) had not been previously detected in the Iberian Peninsula, but their parent lineages (H3, H4a1a, H6ba1b, and H33) were already present during the Iron Age (Supplementary Material, Tables S6, S7, S9, and S10). On the other hand, haplogroup H1at1 has only been found in Iron Age individuals from Italy

Table 4
Presence of detected haplogroups in the Iberian Peninsula during or before the Iron Age for each tribe.

Tribe	Present in the Iberian Peninsula by the Iron Age	Absent in the Iberian Peninsula, but ancestral and/or sublineages present by the Iron Age	Absent in the Iberian Peninsula by the Iron Age	Never reported by the Iron Age
Illergetae	H1, HV0b, J1c, T2b3+151, T2c1d, K1a+195, U5b1b1g, U5b1f1a, K1a3a, K1a13	H, H3am, H4, H4a1a5, J1c3e, U5a, U5a1c1, K		
Cessetani	H3, HV0, HV0+195, J1c1, J2a1a1, K1a+195	H	K1a12a, N1a1a1a3, M1b	
Laietani	H1t, HV0d	H, J2a1a1c		
Indiketes	H1, H4a1, J1c, J2b1a, K1a, I1a1, X2b	H, T2		T1a1′3
Bergistani	HV0	H6a1b2		
Ausetani	H3, H3+152, H5, K1b1a	H, H33c	H1at1, U4d2	H1n2*, M1a3a

and England, with its parent haplogroup only found in the Bronze Age in Croatia and Montenegro (Fig. 5 and Supplementary Material, Table S11). Additionally, haplogroup H1n2* had not been previously detected, though its parent lineage, H1n+146, was found in an Iron Age individual from Macedonia (Supplementary Material, Table S12).

All HV0 lineages (HV0, HV0+195, HV0b, and HV0d) and the X2b haplogroup were present in the Iberian Peninsula before the Iron Age (Supplementary Material, Tables S13 and S14).

Regarding the JT lineages, haplogroups J1c, J1c1, J2a1a1, J2b1a, T2b3+151, and T2c1d were already present in the Iberian Peninsula before the Iron Age (Supplementary Material, Tables S15–S19). Haplogroups J1c3e and J2a1a1c had not been previously identified in the Iberian Peninsula, but their parent haplogroups (J1c3 and J2a1a1) were already present (Supplementary Material, Tables S15 and S16). Haplogroup T2 had not been detected, but the T2+16189 sublineage was found in a Bronze Age sample from the Iberian Peninsula (Supplementary Material, Table S20). The T1a1′3 lineage had never been observed in the Iberian Peninsula, although the T1a haplogroup was detected in France by the Bronze Age (Fig. 5 and Supplementary Material, Table S21).

For the U group (including K), haplogroups K1a, K1a+195, K1a3a, K1a13, and K1b1a were present in the Iberian Peninsula by the Iron Age (Supplementary Material, Tables S22–24). U5a1c1 had not been detected in the region, but its ancestral haplogroup (U5a1c) and subhaplogroup (U5a1c1a) were identified in Chalcolithic samples from the southeastern Iberian Peninsula (Supplementary Material, Table S25). Haplogroups U5b1f1a and U5b1b1g were found exclusively in the Iberian Peninsula, in very low frequencies (Supplementary Material, Tables S26 and S27). While K, U5a, and U5b2 haplogroups have not been detected in the Iberian Peninsula, several of their sublineages have been found in prehistoric individuals from the Iberian Peninsula (Supplementary Material, Tables S25 and S28). U4d2, a haplogroup with no known presence in Western Europe, was present in Eastern and Northern Europe during prehistory (Fig. 5 and Supplementary Material, Table S29). Similarly, K1a12 was previously found only in Iran, Armenia, and Turkey since the Neolithic, though a sample was also detected in France during the early Neolithic (Fig. 5 and Supplementary Material, Table S30).

Despite its higher frequency in Central Europe, haplogroup I1a1 was already present in the Iberian Peninsula by the Bronze Age (Supplementary Material, Table S31). While also common in Central Europe, N1a1a1a3 has not been detected in the Iberian Peninsula outside of our sample (Fig. 4 and Supplementary Material, Table S32).

Two M lineages were identified in Iberians: M1a3a and M1b. M1a3a was found in a Roman sample from the Iberian Peninsula but had not been detected before (Fig. 4 and Supplementary Material, Table S33). M1b lineages, however, were found in Morocco (Northwest Africa) before the Neolithic and in an Islamic sample from the Iberian Peninsula (Fig. 4 and Supplementary Material, Table S34).

4. Discussion

The analyses of haplogroup diversity and genetic structure suggested a gradual shift in maternal lineages throughout pre-Roman times, consistent with the smooth transition between the Bronze and Iron Ages proposed for the northeastern Iberian Peninsula (Cuesta-Aguirre et al., 2025a; Olalde et al., 2019). This pattern suggests that while there were genetic influences from external contacts, particularly through Mediterranean trade and interactions, the core maternal ancestry remained largely continuous during this period (Cuesta-Aguirre et al., 2025a; Olalde et al., 2019). These results provide a framework to understand how local populations evolved before the more pronounced genetic changes introduced during the Roman period. The Correspondence Analysis supports this interpretation, with the first dimension reflecting a chronological gradient from Neolithic to later periods in haplogroup composition, showing a decline in U5b and X (typically associated with earlier periods) and an increase in H3, HV, and African lineages (such as L, M1, and U6), which become more prominent in later phases. Despite these gradual changes, population differentiation was generally low, aligning with nuclear DNA results for Iberians (Cuesta-Aguirre et al.,

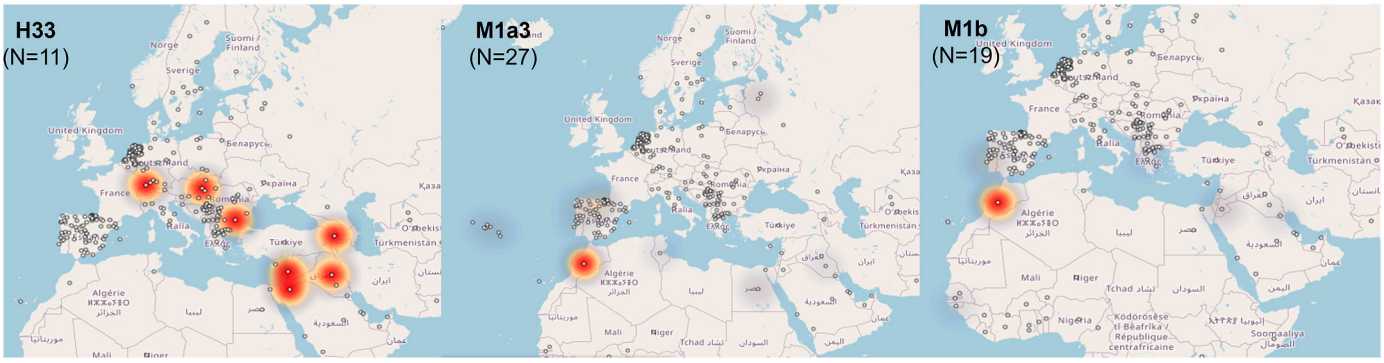

Fig. 4. Present-day distribution of haplogroups H33, M1a, and M1b based on data from EMPOP v5/R12 (N = 48,572; Huber et al., 2018). The map is centered on Europe and the Mediterranean regions. The number of individuals is indicated in parentheses, although a few individuals with haplogroups H33 and M1a3 are also found in America.

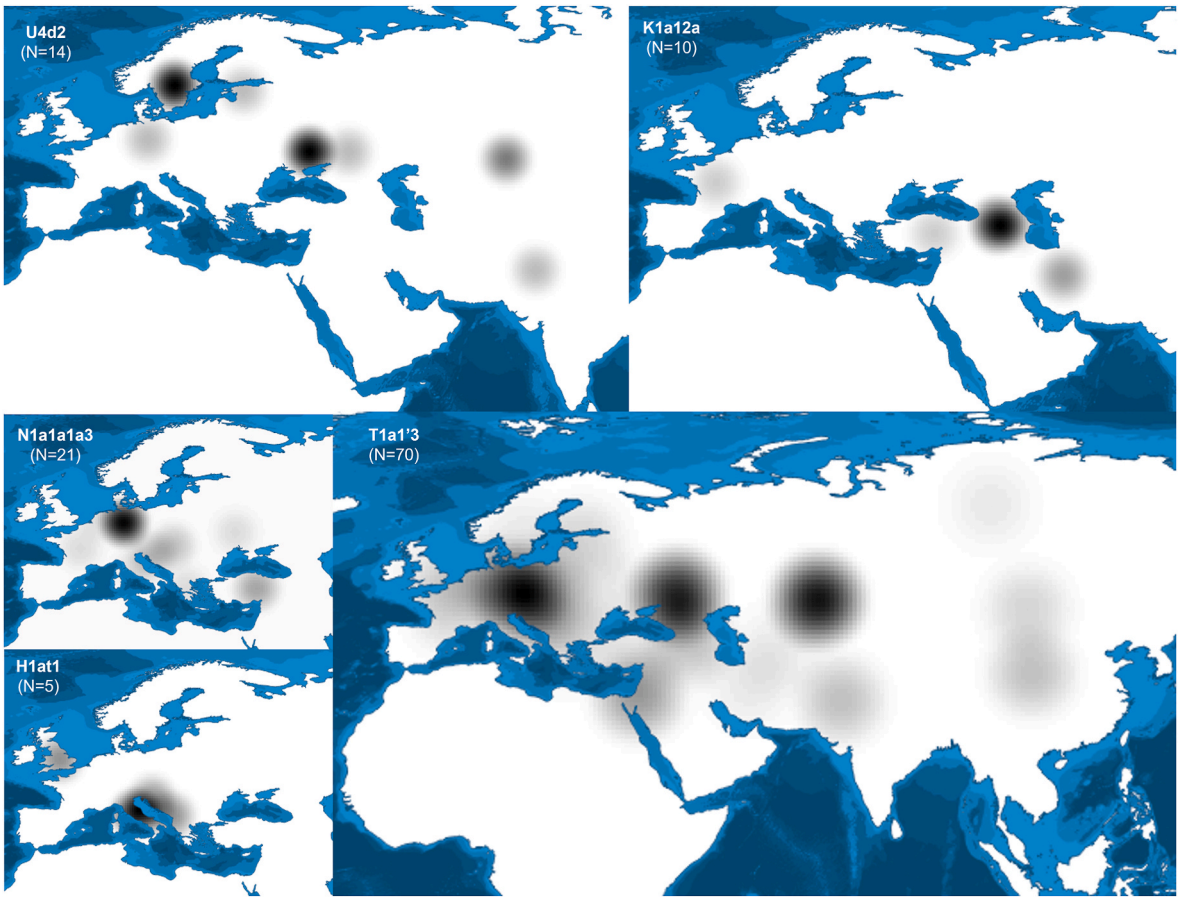

Fig. 5. Heatmaps showing the distribution of ancient samples, predating the Iron Age, carrying haplogroups U4d2 (including U4d), K1a12a (including K1a12), N1a1a1a3 (including N1a1a1a), H1at1 (including H1at), and T1a1′3 (including both its sublineages and ancestral lineage, T1a). Ancient DNA data were obtained from the Ancient Allen database, Carrión et al. (2024), Papac et al. (2023), and Roca-Rada et al. (2025). Maps were generated using QGIS v3.30. Details on the samples used are available in the Supplementary Material (Tables S11, S21, S29, S30, and S32), where the employed samples are highlighted in italics.

2025a), and overall genetic diversity (Nei's diversity) remained relatively stable across periods.

Our results revealed a high frequency of haplogroups H and U (including K but excluding U6), along with a moderate representation of J, T, and HV0, and low frequencies of M1, N1, and X. These findings broadly align with those of Sampietro et al. (2005), who examined 17 Iberians from the Northeast of the Iberian Peninsula. In their study, H was found in 52.9 % of individuals, U (including K) in 23.5 %, and J, T, and Pre-HV in smaller proportions (11.8 %, 5.9 %, and 5.9 %, respectively). It is important to note that their samples consisted exclusively of adult males, analyzed using cloning technology on fragmentary cranial remains not associated with funerary contexts. In contrast, Gamba et al. (2008) reported different haplogroup frequencies among Iberians from the central-eastern Iberian Peninsula (modern-day Valencian Community), with H (36.4 %), V (27.3 %), and W (18.2 %) being the most frequent, along with additional instances of T1 and K. We did not detect any individuals belonging to haplogroup V in our dataset. However, the study of Gamba et al. (2008) predates the redefinition of some haplogroup classifications. Specifically, the mutation at position 16298C, previously used to define haplogroup V, is now recognized as a marker of haplogroup HV0 (van Oven and Kayser, 2009), with V being considered a subclade of HV0. The HV0 frequency we observed in the Cessetani tribe (St. Miquel d'Olérdola), geographically the closest tribe to the area studied by Gamba et al. (2008), is comparable to their reported frequency of haplogroup V.

Although no statistically significant genetic differentiation was detected between the Iberian groups in our study, differences in haplogroup frequencies suggest some degree of biological distinction. The absence of significant results could be related to the still limited sample size available for each tribe. This observation is consistent with archaeological interpretations of tribal diversity in the region (Aranegui, 2012; González Reyero, 2012). Moreover, values of mtDNA diversity are slightly higher, supporting a patrilocal mating system during the Iron Age, as suggested for Bronze Age communities of the same region (Simón et al., 2011). Under this scenario, small distance female migration could have prevented high differentiation among groups in female lineages.

Most of the haplogroups identified in Ilergetae individuals from the fortress of Vilars were already present in the Iberian Peninsula before the onset of the Iron Age. In some cases, the lineages observed in Iberian individuals, such as H3am, H4a1a5, J1c3e, U5a1c1, and U5b1b1g1, had not previously been detected in the region; however, their ancestral haplogroups were already present before the Iron Age. These local haplogroups and the slightly higher mtDNA diversity support a scenario of genetic continuity from the Bronze Age (Cuesta-Aguirre et al., 2025a; Olalde et al., 2019). They also suggest that female mobility occurred largely within the Iberian Peninsula, as happened during the Bronze Age (Simón et al., 2011; Villalba-Mouco et al., 2022).

Interestingly, an ancestral lineage of haplogroup H4a1a5 (VILA12 775-675 BCE) was found in the Indiketes individual from Mas Castellar (I19722, 413-382 calBCE). The other site analyzed within the Indiketes territory was the city of Ullastret, which was composed of two urban centers, both of which reflected Mediterranean architectural influences (López i Melcion et al., 1989; Martín i Ortega, 1985; Martín i Ortega et al., 2016). In Illa d'en Reixac, the haplogroups of three individuals could be determined: H2a2a1, I1a1, and T1a1′3. H2a1a1 has already

been detected in the Iberian Peninsula with a much higher frequency than I1a1. The haplogroup I originated in the Near East 19,000–15,000 years ago as part of the N1a1b lineage, diverging into I1 — a haplogroup linked to postglacial re-peopling, including Indo-European associated groups — around 16,000 years ago (Olivieri et al., 2013). I1a1, which is restricted to Europe, emerged 7000 years ago and is associated with the Neolithic agricultural expansion (Olivieri et al., 2013). Notably, haplogroup I1 has been detected in an Iberian newborn from the central-eastern of the Iberian Peninsula (Olalde et al., 2019).

Haplogroup T is estimated to have originated approximately 28,000 years ago in the Near East, followed by a significant post-glacial expansion (Pala et al., 2012), like J and I (Olivieri et al., 2013). T1a1, the most common lineage within T1a* (comprising about 80 % of samples), is linked to early agricultural communities and emerged around 15,500 years ago. Its subclade T1a1a1, dating back roughly 6800 years, represents approximately 70 % of T1a1 samples and is prevalent in regions with high frequencies of Y-haplogroup R1a, suggesting a possible connection to Indo-European migrations during the Bronze Age (Pala et al., 2012).

Determining whether ILLA04 belongs to a sublineage associated with Bronze Age migrations is challenging, as it requires unavailable coding region mutations for our sample. However, analyzing the compiled dataset of T1a lineages may offer insights. T1a has been found as early as the Neolithic in Southeastern Europe (Bulgaria, 5723-5571 calBCE) (Lazaridis et al., 2022), while the first appearance of the T1a1 lineage was in Chalcolithic Croatia (4300-3900 BCE) (Lazaridis et al., 2022). During the Bronze Age (3500-1600 BCE), T1a1 frequency was elevated in Central Europe, the Pontiac Steppe, and Central Asia. The first appearance in Western Europe was in France (1891-1743 calBCE) (Patterson et al., 2022), after which a few samples appeared in England and France during the Bronze Age. The relatively late appearance of these lineages in Western Europe raises questions about their origin and dispersal. It is possible that T1a1′3 may have arrived in Western Europe during the Neolithic expansion but remained at low frequencies, making it difficult to detect in previous archaeological samples. However, it is also possible that it was introduced in Europe during the Neolithic, and later migrations from the Steppe during the Bronze Age may have increased the frequency of T1a1′3 sublineages across Europe, ultimately leading to their spread into the Iberian Peninsula. The absence of earlier detections in the Iberian Peninsula could be due to several factors: limited sampling, localized founder effects, or the influx of the lineage during the Iron Age from regions with stronger Steppe influences. It's also important to consider that T1a has a low overall frequency in present-day samples (Pala et al., 2012), rising to about 5 % in the South Caucasus (Alfonso-Sánchez et al., 2006; Comas et al., 2000; Quintana-Murci et al., 2004; Richards et al., 2000), 6 % in northeastern Iran (Derenko et al., 2007; Metspalu et al., 2004; Pala et al., 2012), 8 % in Tunisia (Fadhlaoui-Zid et al., 2004; Plaza et al., 2003; Turchi et al., 2009), and 9 % in Romania (Richards et al., 2000). T1a1a1 is present-day shared between geographically distant individuals from Scandinavia, the Baltic, the North Caucasus, Anatolia, and Morocco (Pala et al., 2012). This wide European and Mediterranean distribution in the present day could be explained by later migrations, such as Roman, Germanic, or Viking expansions.

In the other settlement of the dipolis of Ullastret, Puig de Sant Andreu, several haplogroups commonly found in the Iberian Peninsula were identified, including H1, J1c, J2b1a, K1a, and X2b. One exception is haplogroup T2b4+152, detected in the individual PDSA12, which is rare in prehistoric contexts. Its presence in a Neolithic individual from France (Rivollat et al., 2020) suggests it may have arrived following the same Neolithic migration routes as haplogroups like T1a1′3 or I1a1. Overall, the haplogroup profiles identified at Ullastret (including both Puig de Sant Andreu and Illa d'en Reixac) suggest that the female individuals were local. Among the four individuals with available nuclear data (I3323, I3324, I3326, and I3327) (Olalde et al., 2019), only I3327 showed minor traces of Mediterranean ancestry (Cuesta-Aguirre et al., 2025a).

Among the Laietani people, at Can Roqueta-Can Revella, haplogroups H, H1t, HV0d, and J2a1a1c were identified in Iberian individuals dated between 786 and 416 calBCE. Haplogroup H, due to its wide distribution across Western Eurasia, offers limited information on maternal origin (Hernández et al., 2017; Roostalu et al., 2007). In contrast, HV0d and H1t appear to be local, with H1t detected exclusively within the Iberian Peninsula until the Iron Age. Notably, this haplogroup was detected in an Iberian newborn from the central-eastern coast of the Iberian Peninsula (Olalde et al., 2019). Although J2a1a1c has not previously been reported in ancient samples, its ancestral haplogroup (J2a1a1) was present at high frequency in the Iberian Peninsula since the Neolithic. Taken together, these findings suggest a predominantly local maternal ancestry, consistent with the local genetic affinities inferred from nuclear genome data (Cuesta-Aguirre et al., 2025a; Olalde et al., 2019).

In the Cessetani site of Font de la Canya (700-500 BCE), the female individual analyzed was carrying haplogroup K1a12a. This lineage had not previously been reported in the Iberian Peninsula, but has been observed in regions such as Turkey, Iran, Azerbaijan, and Armenia from the Neolithic through the Iron Age (Kılınç et al., 2016; Lazaridis et al., 2016, 2022; Skourtanioti et al., 2020). Its ancestral lineage was also identified in a Neolithic individual from France, although it was later classified as K1a2 when capture-based methods were applied (Brunel et al., 2020). While nuclear data placed this individual within the genetic variability of other Iron Age Iberians in Principal Component Analyses (Cuesta-Aguirre et al., 2025a; Olalde et al., 2019), and showed similar admixture proportions to other contemporary samples (Olalde et al., 2019), her ancestry could not be successfully modeled using the same qpAdm frameworks applied to other Iberian individuals (Cuesta-Aguirre et al., 2025a). Several factors complicate the interpretation of her origins. First, the published study provides limited information about the context and condition of the remains analyzed (Olalde et al., 2019). Second, given that cremation was the dominant funerary practice among the Iberians, the preservation of her remains does not align with local traditions, raising questions about her cultural affiliation. Third, Font de la Canya maintained early and sustained contact with Phoenician groups since its foundation (Olalde et al., 2019), making the presence of non-local individuals plausible. These lines of evidence suggest that this individual may have been non-local or had mixed ancestry. While definitive conclusions cannot be drawn, the presence of K1a12a could reflect the introduction of this haplogroup into the Iberian Peninsula via Phoenician female mobility during the Late Bronze Age or Early Iron Age.

In contrast, other sites within the Cessetani territory, such as Horta d'en Grimau (725-394 BCE) and Mas d'en Boixos (550-350 BCE), revealed only local maternal lineages (e.g., H, H3, HV0+195, and J1c1), and nuclear DNA data supported a local genetic profile (Cuesta-Aguirre et al., 2025a; Olalde et al., 2019). However, the small number of individuals analyzed may influence the apparent absence of non-local ancestry at these sites.

In the most recent Cessetani site, Sant Miquel d'Olèrdola (350-200 BCE), four haplogroups, namely HV0, HV0+195, J2a1a1, and K1a+195, out of the six determined haplogroups, were most probably local. However, the other two could have a non-local origin, since they have never been detected in the Iberian Peninsula. OLE04 presented haplogroup N1a1a1a3. Limited information is available regarding N1a lineages, a relatively rare group in present-day Europeans (approximately 0.2 %) that is believed to have originated in the Near East, potentially the Arabian Peninsula, between 12,000 and 32,000 years ago (Palanichamy et al., 2010). During the Neolithic, N1a appeared at low frequency in the Iberian Peninsula (3.7 %) compared to Central Europe (9.4 %) (Szécsényi-Nagy et al., 2017). Today, N1a1a1 reaches its highest frequency in Eastern Europe and Central Asia, decreasing towards Central and Northern Europe, Anatolia, and the Caucasus (Havaš Auguštin et al., 2023; Palanichamy et al., 2010; Pimenoff et al., 2008).

Furthermore, the subclade N1a1a1a, with a proposed expansion from the Near East to Europe through Eastern Europe around 9000–11,000 years ago, has a restricted distribution in Central Asia (Kazakhstan, the Altai region, and the Buryat Republic) and the Pontiac Steppe (Havaš Auguštin et al., 2023; Palanichamy et al., 2010; Pimenoff et al., 2008). The ancient dataset compiled for N1a1a1a and N1a1a1a3 supports this origin and expansion theory. Early samples are found around 6000 BCE in Anatolia (Lazaridis et al., 2022), followed by a presence in Germany between 5500 and 4700 BCE (Childebayeva et al., 2022; Lipson et al., 2017; Rivollat et al., 2020). From the Middle Neolithic to the Chalcolithic, this haplogroup was detected in a wide range of European regions, such as France (Rivollat et al., 2020), Italy (Antonio et al., 2019), Croatia (Freilich et al., 2021; Novak et al., 2021), Hungary (Gamba et al., 2014; Mathieson et al., 2015), Ukraine (Gelabert et al., 2022), and Turkey (Skourtanioti et al., 2020). Notably, this haplogroup appears absent from the archaeological record between 3000 and 1200 BCE until its detection in a Greek sample from the Mycenaean culture (Lazaridis et al., 2022). The identification of N1a1a1a3 in OLE04 (350-200 BCE) helps bridge this long gap, providing the first evidence of this lineage in Western Europe during the Iron Age. A second occurrence is found in a Netherlandish individual (356-57 calBCE) (Patterson et al., 2022). Gaps in the archaeological record may suggest the low frequency of this haplogroup, while the presence of its ancestral haplogroup (N1a1a1a) in France could indicate the arrival of this lineage in the Iberian Peninsula during the Neolithic.

The other probable non-local haplogroup found in Sant Miquel d'Olèrdola was M1b, which was identified in OLE06.Its origin was previously proposed in Cuesta-Aguirre et al., 2025a. This haplogroup, primarily found in North Africa (González et al., 2007; Winters, 2010), was associated with an individual exhibiting high Mediterranean ancestry, potentially linking this newborn to North Africa or the eastern Mediterranean. We suggested that a woman with Punic/Carthaginian ancestry may have introduced it to Sant Miquel d'Olèrdola during the Iron Age. Ancient DNA evidence for M1b was limited to three records: two from Moroccan Paleolithic (van de Loosdrecht et al., 2018) and Early Neolithic (Fregel et al., 2018) samples and one from an Islamic-period individual in the Iberian Peninsula (Olalde et al., 2019). Today, according to EMPOP v5/R12 (Huber et al., 2018) (N = 19), its distribution is largely restricted to Morocco. The rarity of this lineage should be noted. However, its presence in an Iron Age individual from the northeastern Iberian Peninsula may reflect previously underappreciated female mobility linked to Mediterranean exchange networks, further highlighting the complex genetic landscape of the region during this period.

Two local haplogroups were detected in Castell de Besora (Bergistani tribe): HV0 and H6a1b2. By visualizing the heatmap, haplogroup H6a1b is a lineage that migrated to Western Europe during the Bronze Age. Despite appearing at low frequency, its ancestral haplogroup H6a1b was present at the Iberian Peninsula before Iberian culture was developed.

Out of the ten different haplogroups detected in the Ausetani site of El Camp de les Lloses (125 BCE – 50 CE), half of them, namely H, H3, H3+152, H5, and K1b1a, were already present in the Iberian Peninsula before the Iron Age started. However, several rare haplogroups were detected, including H33c, in CL11 (125-80 BCE). The H33 lineage was previously identified in an Aegean Hellenistic individual from Empuries (Girona, Northeast Iberian Peninsula) dating to approximately 376-201 BCE (Olalde et al., 2019) and is also present in modern-day populations across Central Europe, Southeast Europe, and Southwest Asia. Today, H33 remains extremely rare, with a broad yet low-frequency distribution, according to EMPOP v5/R12 (Huber et al., 2018) (N = 11). Given this information, it is tempting to associate the arrival of this haplogroup with the Aegean populations. This raises an important question: Was the H33 lineage introduced into the Iberian world through trade with the Greeks, or did it arrive later with the Romans? The Roman-influenced Iberian settlement of El Camp de les Lloses has yielded Greek and Roman coins, underscoring the region's strong Mediterranean connections (Duran i Caixal et al., 2017). Yet, without nuclear DNA data, determining the exact source remains speculative, and even with such data, fully resolving this question may prove impossible. Nevertheless, it is clear that this newborn's maternal lineage provides undeniable evidence of Mediterranean influence.

Another rare haplogroup found in El Camp de les Lloses was M1a3a, detected in CL2. In contrast to M1b, M1a lineages are typical of Northeast Africa and have been identified in Neolithic individuals from Kenya (Prendergast et al., 2019) and Mediterranean regions, including the Iberian Peninsula (Olalde et al., 2019), Sardinia (Fernandes et al., 2020), and Egypt (Fernandes et al., 2020). However, all these individuals carried M1a1 lineages. The present-day distribution of M1a3, according to EMPOP v5/R12 (Huber et al., 2018) (N = 27), differs from the M1a distribution and closely resembles M1b′s distribution, but with a slightly higher frequency. Interestingly, the exact M1a3a haplogroup was later identified by Roca-Rada et al. (2025) in a Roman-era female from the western Iberian Peninsula (ID_25522; 257–531 CE). Nuclear DNA analysis of the CL2 individual did not indicate North African ancestry (Cuesta-Aguirre et al., 2025a), suggesting that haplogroup M1a3a may have entered the Iberian Peninsula before the foundation of El Camp de les Lloses, remaining at such a low frequency that it had not been detected previously.

The sisters from El Camp de les Lloses (CL6 and CL7, 125-80 BCE) shared the same haplotype, belonging to haplogroup H1at1 (Cuesta-Aguirre et al., 2025a). The information about this haplogroup is scarce. It has only been identified in two Iron Age Etruscans from Italy (775-201 calBCE) (Posth et al., 2021) and a Middle Iron Age individual from England (372-197 calBCE) (Patterson et al., 2022), despite its ancestral haplogroup being present in two individuals from Croatia and Montenegro during the Middle Bronze Age (1500-1000 BCE) (Lazaridis et al., 2022). Its low frequency makes it difficult to trace its exact origin, but the most probable source is the Italian Peninsula. Whether it was introduced into the Iberian Peninsula by Etruscans or later by Romans remains uncertain.

Finally, the U4d2 haplogroup was found in CL4 (50 BCE - 50 CE) (Cuesta-Aguirre et al., 2025a). U4d lineages had previously been detected in the Pontiac Steppe during the Neolithic and in North and Central Europe during the Bronze Age (Mittnik et al., 2018; Olalde et al., 2018; Skoglund et al., 2014). Since the Pontiac Steppe was the source of Steppe-related expansions into Western Europe during the Bronze Age, these migrations likely introduced the haplogroup at a low frequency, making it undetectable until the Iron Age. Given the high proportion of Italian ancestry in CL4's nuclear DNA, it is plausible that Romans introduced this haplogroup to El Camp de les Lloses. However, the possibility that U4d2 was already present in the Iberian Peninsula since the Bronze Age, remaining undetected, cannot be ruled out.

Although genetic evidence revealed a mixture of Mediterranean and local ancestries in the nuclear DNA of the Ausetani individuals of El Camp de les Lloses (Cuesta-Aguirre et al., 2025a), the most probable scenario is that almost all mitochondrial haplogroups detected were already present in the region before the arrival of the Romans. This aligns with the interpretation of the site as a Roman military vicus associated with metallurgical workshops and logistical support for the army (Duran i Caixal et al., 2017; Duran et al., 2015, 2017). Within the context of El Camp de les Lloses' military function, this pattern supports the hypothesis that, while male soldiers or artisans likely came from outside the Iberian Peninsula, perhaps from other parts of the Mediterranean, the women connected to the settlement were likely local inhabitants.

5. Conclusions

In summary, the gradual shift in haplogroup frequencies observed until the Roman period supports a generally smooth transition between the Bronze and Iron Ages, highlighting the complex interplay of migration, commercial trade, and cultural interactions that shaped the

genetic heritage of the region. While no statistically significant genetic differentiation was detected between Iberian tribes, subtle differences in haplogroup frequencies suggest that these groups maintained a certain degree of autonomy. The mtDNA analysis of Iberians from the Northeast of the Iberian Peninsula reveals a dynamic genetic landscape influenced by both local continuity and short-distance female migration, probably linked to patrilocal mating systems and external inputs evidenced by non-local mtDNA lineages. Most of the detected haplogroups, or their ancestral lineages, were already present in the Iberian Peninsula during the Iron Age, suggesting that most Iberian women were of local origin. However, signs of Mediterranean female influence are evident during the Iron Age, pointing to potential gene flow from other regions and the role of women in commercial trade and cultural interaction. The genetic analysis of the Ausetani individuals from El Camp de les Lloses showed a mix of Mediterranean and local ancestries in their nuclear DNA, with almost all mitochondrial haplogroups likely pre-dating the Roman arrival, suggesting they were already present in the region. These findings support the idea that while male soldiers or artisans may have come from outside the Iberian Peninsula, the women from this site were likely local inhabitants.

CRediT authorship contribution statement

Daniel R. Cuesta-Aguirre: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Rosa Campoy-Caballero:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Carolina Sandoval-Ávila:** Writing – review & editing, Resources, Data curation. **Cesc Busquets i Costa:** Writing – review & editing, Resources. **Marta Fàbregas i Espadaler:** Writing – review & editing, Resources. **Alejandro G. Sinner:** Writing – review & editing, Resources. **Gabriel de Prado:** Writing – review & editing, Resources. **Nuria Molist Capella:** Writing – review & editing, Resources. **Montserrat Duran i Caixal:** Writing – review & editing, Resources. **Imma Mestres Santacreu:** Writing – review & editing, Resources. **Natalia Alonso:** Writing – review & editing, Resources. **Maria Pilar Aluja:** Writing – review & editing, Formal analysis. **Assumpció Malgosa:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Cristina Santos:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of generative AI in scientific Writing

During the preparation of this work, the authors used ChatGPT and Grammarly in order to improve the structure, clarity, and order of some paragraphs. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2025.106390.

Data availability

The raw sequencing data are available through the European Nucleotide Archive (ENA), BioProject: PRJEB97056.

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