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The genomic history of the Iberian Peninsula over the past 8000 years

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Abstract

We assembled genome-wide data from 271 ancient Iberians of whom 176 are from the largely unsampled period after 2000 BCE, thereby providing a high resolution time transect of the Peninsula. We document high genetic substructure between northwestern and southeastern hunter-gatherers prior to the spread of farming. We reveal sporadic contacts between Iberia and North Africa by ~2500 BCE, and by ~2000 BCE the replacement of 40% of Iberia's ancestry and nearly 100% of its Y-chromosomes by people with Steppe ancestry. In the Iron Age, we show that Steppe ancestry had spread not only into Indo-European-speaking regions but also into non-Indo-European-speaking ones, and we reveal that present-day Basques are best described as a typical Iron Age population without the admixture events that later impacted the rest of Iberia. Beginning at least in the Roman period, we document how the ancestry of the Peninsula was transformed by gene flow from North Africa and the eastern Mediterranean.

The Iberian Peninsula, lying at the extreme southwestern corner of Europe, provides an excellent context in which to assess the final impact of population movements entering the continent from the east as well as interactions with North Africa. To study the genetic impact of prehistoric and historic events in Iberia, we prepared next-generation sequencing libraries treated with uracil-DNA glycosylase (UDG) (1) and enriched them for ~1.2 million single nucleotide polymorphisms (SNPs) (2, 3) to generate genome-wide data from 4 Mesolithic, 44 Neolithic, 47 Copper Age, 53 Bronze Age, 24 Iron Age, and 99 historical period Iberians (Fig. 1A-B and tables S1–2). We also generated 26 radiocarbon dates (table S3). We co-analyzed the new genomic data with previously reported data from 1107 ancient individuals, including 132 from Iberia (Fig. 1B) (2, 4–9), and 2862 present-day individuals (10). We filtered from the analysis datasets individuals covered by <10,000 single nucleotide polymorphisms (SNPs), evidence of contamination, or first-degree relatives of others (table

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S1). We analyzed the data with Principal Component Analysis (PCA) (Fig. 1C-D), *f*-statistics (11), and *qpAdm* (12), and summarize the results in Fig. 1E. We confirmed the robustness of key findings by repeating analyses after removing SNPs in CpG dinucleotides (table S5) that are susceptible to cytosine-to-thymine errors even in UDG-treated libraries (1).

Previous knowledge of the genetic structure of Mesolithic Iberia is from 3 individuals from the northwest: LaBraña1 (2), Canes1 (5) and Chan (5). We add LaBraña2, who was a brother of the previously reported LaBraña1 (figs. S1–2 and table S6), as well as Cueva de la Carigüela (fig. S10), Cingle del Mas Nou and Cueva de la Cocina from the southeast. In northwest Iberia, we document a previously unappreciated ancestry shift before the arrival of farming (Figs. 2A, S5 and table S7). The oldest individual Chan was similar to the ~17000 BCE El Mirón, whereas the La Braña brothers from ~1300 years later were closer to central European hunter-gatherers like the Hungarian KO1, with an even more extreme shift ~700 years later in Canes1. This likely reflects gene flow impacting northwest Iberia but not the southeast, where individuals remained close to El Mirón (Fig. 2A). More data from the Mesolithic period, and especially from currently unsampled areas, would provide additional insight into the geographical impact and archaeological correlates of this ancestry shift.

In the Neolithic and Copper Age, we model populations as mixtures of groups related to Anatolian Neolithic, El Mirón and KO1 (Fig. 2A and table S8). We replicate previous findings of the arrival of Anatolian Neolithic-associated ancestry in multiple regions of Iberia in the Early Neolithic (7, 8, 12); however, sampling from this period remains limited and studies of larger sample sizes and additional sites will be important in order to shed additional light on the interaction between the incoming farmers and indigenous hunter-gatherers. In the Middle Neolithic and Copper Age, we reproduce previous reports of an increase of hunter-gatherer-related ancestry after 4000 BCE (6, 7, 12, 13), with higher proportions in groups from the north and center. By using as a reference frame our observations about population substructure in the Mesolithic, we show that the hunter-gatherer-related ancestry during those periods was more closely related to later northwestern (Canes1-like) than to the El Mirón-like hunter-gatherers (Fig. 2A), providing clues about the source of this ancestry.

Our Copper Age dataset includes a newly reported 2473–2030 cal BCE male (I4246) from Camino de las Yeseras (14) in central Iberia, who clusters with modern and ancient North Africans in the PCA (Fig. 1C and fig. S3), and like ~3000 BCE Moroccans (8) can be well modeled as having ancestry from both Late Pleistocene North Africans (15) and Early Neolithic Europeans (tables S9–10). His genome-wide ancestry and uniparental markers (tables S1 and S4) are unique among Copper Age Iberians, including individuals from sites with many analyzed individuals such as Sima del Ángel, and point to a North African origin. Our genetic evidence of sporadic contacts from North Africa during the Copper Age fits with the presence of African ivory at Iberian sites (16), and is confirmed by a Bronze Age individual (I7162) from Loma del Puerco in southern Iberia who had 25% ancestry related to individuals like I4246 (Fig. 1D; table S16). However, these early movements from North Africa had a limited impact on Copper and Bronze Age Iberians, as North African ancestry only became widespread in the past ~2000 years.

From the Bronze Age (~2200–900 BCE) we increase the available dataset (6, 7, 17) from 7 to 60 individuals and show how ancestry from the Pontic-Caspian steppe ("Steppe ancestry") appeared throughout Iberia in this period (Fig. 1C-D), albeit with less impact in the south (table S13). The earliest evidence is in 14 individuals dated to ~2500–2000 BCE who co-existed with local people without Steppe ancestry (Fig. 2B). These groups lived in close proximity and admixed to form the Bronze Age population after 2000 BCE with ~40% ancestry from incoming groups (Fig. 2B and fig. S6). Y-chromosome turnover was even more dramatic (Fig. 2B), as the lineages common in Copper Age Iberia (I2, G2, H) were nearly completely replaced by one lineage, R1b-M269. These patterns point to a higher contribution of incoming males than females, also supported by a lower proportion of non-local ancestry on the X-chromosome (table S14 and fig. S7), a paradigm that can be exemplified by a Bronze Age tomb from Castillejo del Bonete containing a male with Steppe ancestry and a female with ancestry similar to Copper Age Iberians. While ancient DNA can document that sex-biased admixture occurred, archaeological and anthropological research will be needed to understand the processes that generated it.

In the Iron Age, we document a consistent trend of increased ancestry related to North/Central European populations with respect to the preceding Bronze Age (Figs. 1C-D and 2B). The increase was 10–19% (95% confidence intervals given here and in what follows) in 15 individuals along the eastern Mediterranean coast where non-Indo-European Iberian languages were spoken; 11–31% in 2 individuals at the Tartessian site of La Angorrilla in the southwest with unknown language attribution; and 28–43% in 3 individuals at La Hoya in the north where Indo-European Celtiberian languages were likely spoken (fig. S6 and tables S11–12). This documents gene flow into Iberia during the Late Bronze Age or Early Iron Age, possibly associated with the introduction of the Urnfield tradition (18). Unlike central or northern Europe where Steppe ancestry likely marked the introduction of Indo-European languages (12), our results indicate that in Iberia increases in Steppe ancestry were not always accompanied by switches to Indo-European languages. This is consistent with present-day Basques who speak the only non-Indo-European language in western Europe but overlap genetically with Iron Age populations (Fig. 1D) showing substantial levels of Steppe ancestry.

In the historical period, our transect begins with 24 individuals from the Greek colony of Empúries in the northeast from 500 BCE to 600 CE (19) who fall into two ancestry groups (Fig. 1C-D and fig. S8): one similar to Bronze Age individuals from the Aegean, and the other similar to the population of Iron Age Iberia that includes the nearby non-Greek site of Ullastret, confirming historical sources indicating that this town was inhabited by a multi-ethnic population (19). The impact of mobility from the Central/Eastern Mediterranean during the Classical period is also evident in 10 individuals from the 7th-8th centuries CE site of L'Esquerda in the northeast, who show a shift from the Iron Age population in the direction of present-day Italians and Greeks (Fig. 1D), accounting for approximately one quarter of their ancestry (Fig. 2C and table S17). The same shift is also observed in present-day populations from Iberia outside the Basque area and is plausibly a consequence of the Roman presence in Iberia, which had a profound cultural impact and, according to our data, a substantial genetic impact too.

In contrast to the demographic changes in the Classical period, movements into Iberia during the decline of the Roman Empire had less long-term demographic impact. Nevertheless, individual sites bear witness to events in this period, for example at the 6th century site of Pla de l'Horta in the northeast. These individuals, archaeologically interpreted as Visigoths, are shifted from those at L'Esquerda in the direction of north/central Europe (Figs. 1D, 2C and table S18), and we observe the Asian mtDNA haplogroup C4a1a also found in Early Medieval Bavaria (20), supporting a recent link with groups with ultimate ancestry from central/eastern Europe.

In the southeast, we recovered genomic data from 45 individuals dated between the 3rd-16th centuries CE. All the analyzed individuals fell outside the genetic variation of preceding Iberian Iron Age populations (Figs. 1C-D and S3) and harbored ancestry from both southern European and North African populations (Fig. 2D), as well as additional Levantine-related ancestry that could reflect Jewish contributions (21). These results demonstrate that by the Roman period, southern Iberia had experienced a major influx of North African ancestry, probably related to the well-known mobility patterns during the Roman Empire (22) or the earlier Phoenician-Punic presence (23); the latter is also supported by the observation of the Phoenician-associated Y-chromosome J2 (24). Gene flow from North Africa continued into the Muslim period, as is clear from Muslim burials with elevated North African and sub-Saharan African ancestry (Figs. 2D, S4 and table S22), and uniparental markers typical of North Africa not present among pre-Islamic individuals (Figs. 2D and S11). Present-day populations from southern Iberia harbor less North African ancestry (25) than the ancient Muslim burials, plausibly reflecting expulsion of *moriscos* (former Muslims converted to Christianity) and repopulation from the north, as supported by historical sources and genetic analysis of present-day groups (25). The impact of Muslim rule is also evident in northeast Iberia in seven individuals from Sant Julià de Ramis from the 8–12th centuries CE who, unlike previous ancient individuals from the same region, show North African-related ancestry (Fig. 2C and table S19) and a complete overlap in PCA with present-day Iberians (Fig. 1D).

Our time transect allowed us to track frequency changes of phenotypically important variants over the last 4,000 years (fig. S9), a period which has been minimally sampled in the ancient DNA literature not just of Iberia but of Europe more generally. Prior to this work, it was known that the lactase persistence allele at (rs4988235), which is present at moderate or high frequencies in most European populations today and is one of the strongest known signals of selection in Europeans (26), occurred at extremely low frequencies in Europe through the Bronze Age (2), raising the question of when it became common. Here we show that in Iberia the allele continued to be at low frequency in the Iron Age (fig. S9), and only approached present-day frequencies in the last 2,000 years, pointing to recent strong selection.

Beyond the specific insights about Iberia, this study serves as a model for how a high-resolution ancient DNA transect continuing into historical periods can be used to provide a detailed description of the formation of present-day populations (Fig. 1E); future application of similar strategies will provide equally valuable insights in other world regions.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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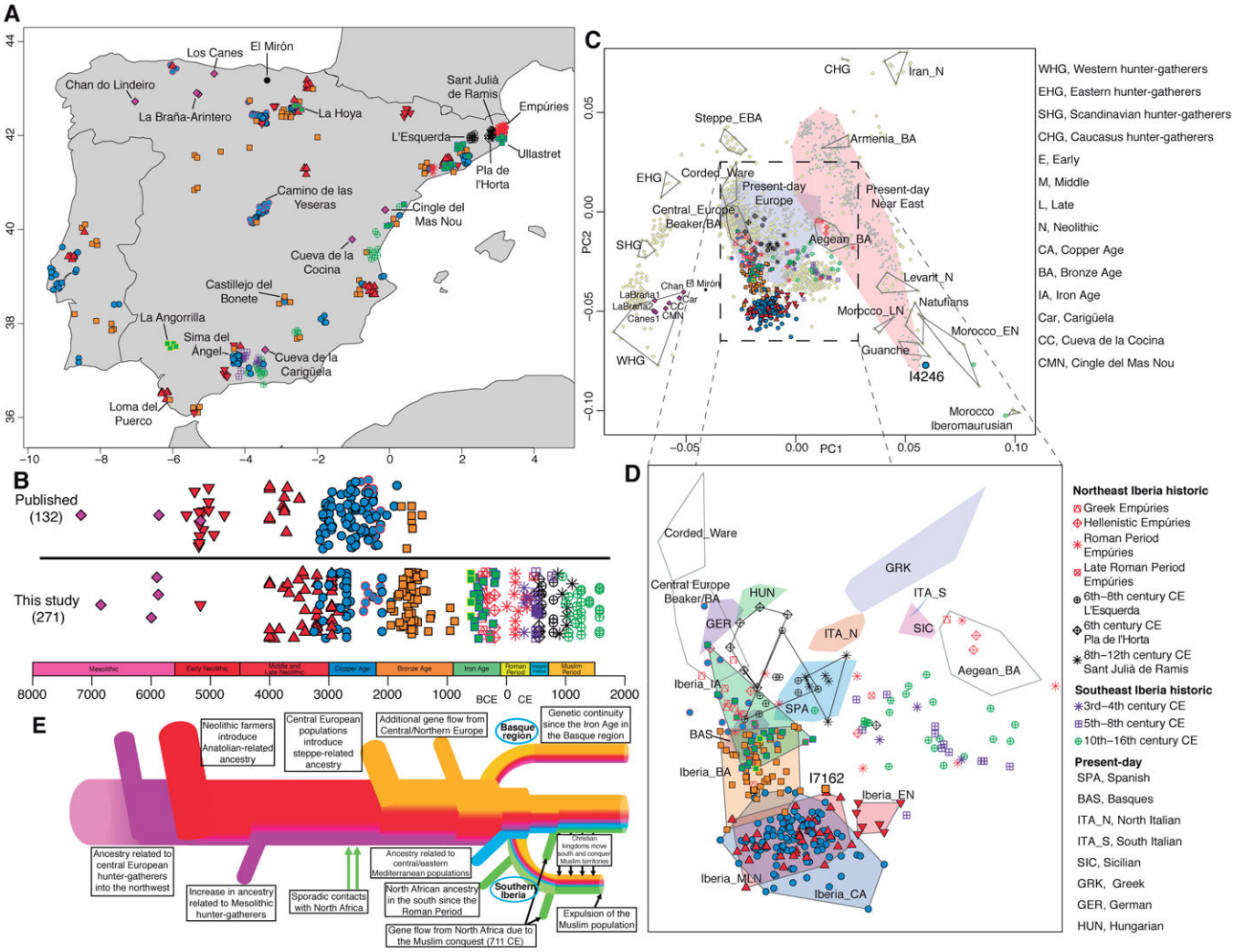

Fig. 1. Overview of the Ancient Iberian Genetic Time Transect.

(**A**) Geographic distribution and (**B**) dates of new and previously reported samples. Random jitter is added for sites with multiple individuals. Sites mentioned in the text are labeled. (**C**) Principal Component Analysis of 989 present-day west Eurasian individuals (grey dots), with ancient individuals from Iberia and other regions (pale yellow) projected onto the first two principal components. (**D**) Section of the PCA in (**C**). (**E**) Schematic representation of events documented in this study.

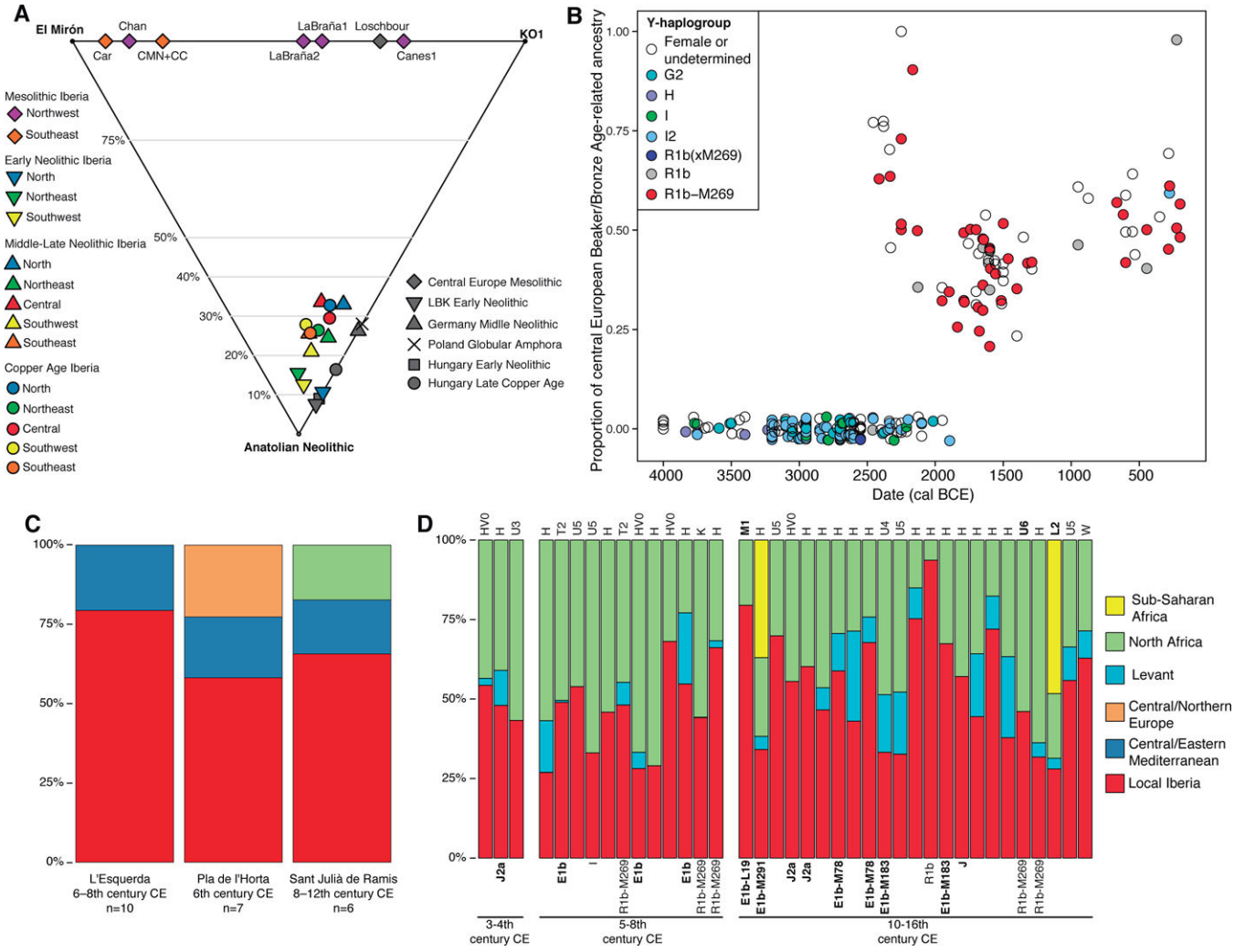

Fig. 2. Genome-wide admixture proportions using *qpAdm*.

(**A**) Modeling Mesolithic, Neolithic and Copper Age populations as a mixture of Anatolia_N, El Mirón and KO1. Percentages indicate proportion of El Mirón + KO1 ancestry. (**B**) Proportion of ancestry derived from central European Beaker/Bronze Age populations in Iberians from the Middle Neolithic to the Iron Age (table S15). Colors indicate the Y-chromosome haplogroup for each male (table S4). (**C**) Ancestry proportions for individuals from three sites in northeast Iberia dated between the 6th and 12th centuries CE. (**D**) Ancestry proportions for individuals from southeast Iberia from the 3–16th centuries CE (tables S20-S21). Each bar represents one individual with associated mtDNA (top) and Y-chromosome (bottom). In bold, haplogroups with a likely recent non-local origin.