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Archaeogenetics of two subcontinents:the transition to Metal Ages in South Asia and Southwest Europe

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Archaeogenetics of two subcontinents: the transition to Metal Ages in South Asia and Southwest Europe

Marina Soares da Silva

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A thesis submitted to the University of Huddersfield in partial fulfilment of the requirements for the degree of Doctor of Philosophy

The University of Huddersfield

Main supervisor: Martin Richards

Co-supervisors: Ceiridwen Edwards; Maria Pala; Pedro Soares

Copyright statement

Declaration of authorship

I, Marina Soares da Silva, declare that the work presented in this thesis entitled "Archaeogenetics of two subcontinents: the transition to Metal Ages in South Asia and Southwest Europe", is my own. I confirm that:

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- Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.

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- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.

- I have acknowledged all main sources of help.

- Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself.

Signed: MSilva

Date: 20.02.2020

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“Time goes, you say? Ah, no!
Alas, Time stays, we go (...)”

Henry Austin Dobson, in *The Paradox Of Time*

“The past may be a foreign country, but the maps were inside us the whole time.”

Adam Rutherford, in *A Brief History Of Everyone Who Ever Lived*

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Abstract

The transition to the Metal Ages led to profound economic and social changes in Eurasian populations, as seen from the archaeological record. The spread of the Indo-European language family, from a putative origin in the Eurasian steppe, across Europe and Central and South Asia accompanied population movements and interactions during the Chalcolithic and Bronze Age. The goal of this project is to study the demographic dynamics of human populations during the transition to Metal Ages across Eurasia, by focusing on the two extremes of the Indo-European distribution: South Asia and Iberia. Additional results from a pilot study on the Medieval period in Iberia are also presented.

The comparison of uniparental markers in South Asia shows that there is a strong sex bias in the ancestry of present-day South Asian populations: while the maternal variation is mostly autochthonous (~70–90%), dating to the first settlement of the region, the paternal gene pool reflects more recent ancestry from Southwest Asia and Central Asia (~50–90%), mostly in the form of R1a branches dating to the Bronze Age.

However, despite the male-biased nature of Bronze Age movements, minor signals can also be found in the maternal gene pool. Haplogroup H is the most common mitochondrial lineage in present-day European populations (up to 45%), and is also present at considerable frequencies in other regions, such as Central and South Asia. Haplogroup H was present across continental Europe since the Neolithic, and it is possible to distinguish Late Neolithic/Bronze Age signals in some H lineages: H2 and H13 were incorporated in movements across the Steppe into Europe, in the west (mainly as H2a and H13a1a), and across Central Asia and into South Asia, in the east, mainly in the form of H2b, although a minor signal is also visible for H13a1a and in H1b. In this thesis I show how a detailed phylogeographic approach, combining both modern and ancient variation can provide additional clues into population movements, even in the case of strong male bias. An increase in Steppe-related/Central-European ancestry in Iberia in the Bronze Age coincides with a large influx of Central-European Y-chromosome R1b lineages, but the same signal is not observed in the maternal gene pool. Changes in maternal variation in Iberia are only observed later, in the Iron Age, with an increase in the frequency of haplogroup H in general (and specifically H1), coinciding with a further increase in Central-European ancestry.

The Medieval period in Iberia is characterised by a substantial arrival of people from North Africa during the Islamic period, but their potential contribution to the Iberian gene pool was largely erased by several post-Medieval events. Here, I present a pilot study on aDNA from Medieval Iberia, with particular focus on the genome of an 11th century man buried in an Islamic necropolis in Segorbe, Spain (mean average genomic coverage: 0.065x). Uniparental lineages (mtDNA U6a1a1; Y-chromosome E1b1b1b1) indicate North African ancestry. However, at autosomal level he displays both North African and European-like ancestries. Formal tests of admixture indicate that he was most likely the result of admixture between two populations, a North African and a Spanish population (although the exact populations are difficult to pinpoint, due to possible increased Levantine ancestry in one of the sources), fitting historical accounts of intermarriages during this period and recently published aDNA evidence. In addition I present two mtDNA sequences (haplogroups H5a1 and V), the former of which represents the first example of Medieval genetic data from Portugal. These two sequences fall in mostly northwest European branches and strongly contrast with the U6a haplotype retrieved from the individual found in the Islamic cemetery.

Finally, I present preliminary analyses on a low coverage (0.016-0.871x) and SNP-capture dataset of 21 individuals from (Late) Neolithic/Chalcolithic/Bronze Age sites from Portugal and eastern and southern Spain. In agreement to previous findings for this period in Iberia, all Late Neolithic/Chalcolithic males carried either an I or a G2 Y-chromosome lineage, while the maternal gene pool was much more diverse. The Bronze Age individual from Cova L'Iguala (female) carried an mtDNA H3 haplotype, which is to our knowledge the first H3 reported for this period in Iberia, and is the only individual displaying Steppe ancestry at significant proportions. However, due to low coverage (0.03x) *D*-statistics results for this sample are not significant. Instead, this individual shares the highest drift with Iberian Middle/Late Neolithic, British Neolithic and Iberian Late Neolithic/Chalcolithic groups, similarly to the majority of the samples analysed in this chapter. I detect phenotypic diversity in Late Neolithic/Chalcolithic Portugal, as well as the presence of both ancestral and derived variants in SNPs related to immunity and vitamin D metabolism.

Contributions to published work

Some of the work performed during this PhD was included in the following publications:

M. Silva*, M. Oliveira*, D. Vieira, A. Brandão, T. Rito, J.B. Pereira, et al. *A genetic chronology for the Indian Subcontinent points to heavily sex-biased dispersals.* BMC Evolutionary Biology 2017, 17:88. DOI:10.1186/s12862-017-0936-9.

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List of abbreviations

#	number of
(B)CE	(Before) Common Era
(E/M/L)BA	Early/Middle/Late Bronze Age
(E/M/L)N	Early/Middle/Late Neolithic
(un)cal.	(un)calibrated
1KGP	1000 Genomes Project
A	Adenine
aDNA	ancient DNA
AMH	anatomically modern humans
ANGSD	analysis of next generation Sequencing Data
ANI	Ancient North Indians
ASI	Anceient South Indians
BB	Bell Beaker
BEAST	Bayesian evolutionary analysis by sampling trees
BEB	Bengali from Bangladesh (1KGP population)
BMAC	Bactrian Margiana Archaeological Complex
BP	before present
bp	base pairs
BWA	Burrows-Wheeler aligner
C	Cytosine
C/Chl/CA	Chalcolithic (Copper Age)
cent.	century/centuries
CEPH	Centre d'Etude du Polymorphisme Humain/Human Polymorphism Study Center
CHB	Han Chinese in Beijing, China (1KGP population)
CHG	Caucasus hunter–gatherer
chr.	Chromosome
CNA	Centro Nacional de Aceleradores/Accelerator National Centre, Spain
del.	Deletion
DNA	Deoxyribonucleic acid
DP	Depth of position

EAGER	efficient ancient genome reconstruction
EHG	Eastern hunter-gatherers
G	Guanine
Gb	Giga basepairs
GBR	British in England and Scotland (1KGP population)
GIH	Gujarati Indian from Houston (1KGP population)
GW	genome-wide
ha	Hectare
Hel.	Hellenistic
Hg.	Haplogroup
HGDP	Human Genome Diversity Project
HVS-I/II	Hypervariable Segment I/II
IA	Iron Age
IBS	Iberian Population in Spain (1KGP population)
IGV	integrative genomics viewer
indel(s)	insertion(s)/deletion(s)
ins.	Insertion
ITU	Indian Telugu from the UK (1KGP population)
ka	thousand years
kb	kilo base pairs
Lat.	Latitude
LGM	Last Glacial Maximum
LN	Late Neolithic
Long.	Longitude
Mb	Mega basepairs
Meso.	Mesolithic
ML	Maximum likelihood
MoM	Method of moments
MSY	Male specific region of Y-chromosome
mtDNA	Mitochondrial DNA
n	Sample size
nDNA	Nuclear DNA
N_e	effective population size
NGS	next-generation sequencing
PCA	principal component analysis
PCR	Polymerase chain reaction
PJL	Punjabi from Lahore, Pakistan (1KGP population)
Pop.	Population

rCRS	Revised Cambridge Reference Sequence
RFLP	restriction-fragment length polymorphism
RomP.	Roman period
RSRS	Reconstructed Sapiens Reference Sequence
Sac	Laboratório de Datação pelo Radiocarbono/Radiocarbon Dating Laboratory, Portugal
SNP(s)	single nucleotide polymorphism(s)
std.err.	Standard error
STRs	short tandem repeats
STU	Sri Lankan Tamil from the UK (1KGP population)
T	Thymine
TMRCA	time to the most recent common ancestor
TSI	Toscani in Italy (1KGP population)
USER	Uracil-Specific Excision Reagent
WHG	Western hunter-gatherers
YRI	Yoruba in Ibadan, Nigeria (1KGP population)
ρ	Rho

Chapter I

General introduction

2

General introduction

1. Metal Ages in Eurasia

The Metal Ages in Eurasia are classified into Copper, Bronze and Iron Ages, according to the main type of metal used at each period, and although this classification can in some cases be seen as sequential that is not necessarily always the case. For example, in some regions of northern Europe there was no such period as the Copper Age, and they transitioned directly from the Neolithic to the Bronze Age (Anthony, 2010). On the other hand, since this classification takes into consideration the type of material used, contemporary archaeological cultures and/or regions can be classified as belonging to different ages. A similar logic applies for Palaeolithic, Mesolithic and Neolithic periods, which precede the Metal Ages, although in these cases it is not metal, but the mode of subsistence, the kind of stone tools and the presence or absence of ceramics that define the classification.

This model, based on the "Three Age system" (initially Stone, Bronze and Iron Ages) used by Christian J. Thomsen for the organization of an exhibition in the National Museum of Denmark in 1819, is obviously an oversimplification of prehistory. Firstly, transitions were not abrupt; instead they took quite some time (centuries or even millennia in some cases). On the other hand, similar periods might have different designations in different regions – for example, the Chalcolithic (or Copper Age) is characterized by the use of unalloyed copper in Iberia ~3250–2250 BCE (Díaz-Andreu, 1995), a definition also applied to the Eneolithic in south-eastern Europe (Anthony, 2010). Moreover, this classification does not apply worldwide and is heavily biased towards European prehistory.

The transition from the Late Neolithic to the Metal Ages was accompanied by important cultural and social changes. If agriculture was the big economic innovation of the Neolithic, then metal-working was the big advance of the Metal Ages. Metallurgy was a major milestone in human evolution with high impact on the economy of societies. Metal was important to building agricultural tools, weapons, cauldrons and other cooking utensils, and ornaments, but more importantly, the need for metal (and associated prestige) led to the establishment of trade primary between communities (Cunliffe, 2014; Kohl, 2007; Kristiansen, 2015). These new cultural and economic dynamics were ultimately responsible for a radical change in the organization of societies: from egalitarian village communities to fortified settlements ruled by powerful and wealthy elites, whose burials, rich in grave goods, bore witness to their high status in society (Cunliffe, 2014; Kristiansen, 2015).

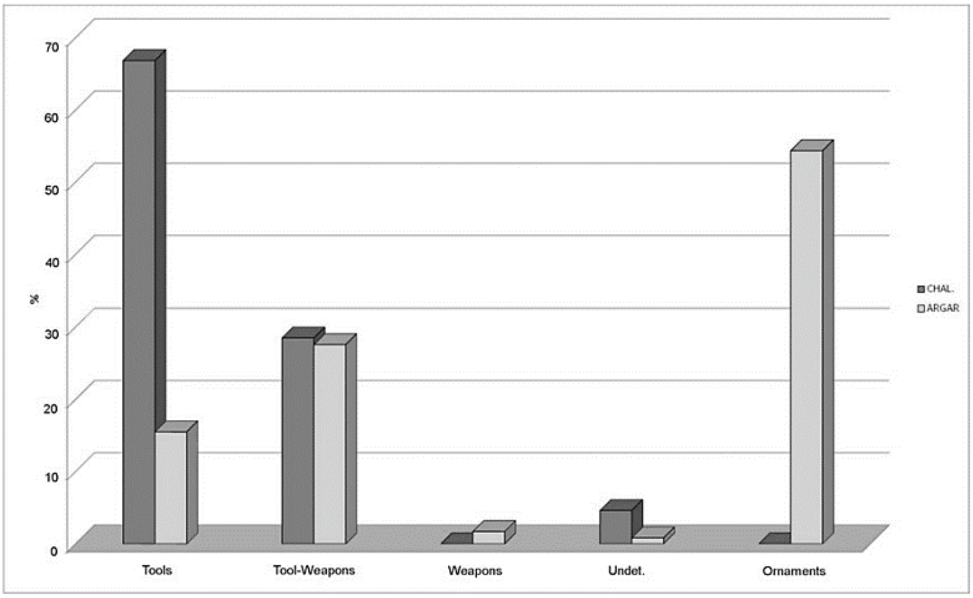
The origin of metallurgy is still uncertain. Although the first copper objects, ornamental copper beads, date to the Preceramic Neolithic (8th millennium BCE) in the site of Çäyönü Tepesi in eastern Turkey, they were probably made from hammered native (naturally-occurring) copper and do not provide direct evidence for established metallurgy (Maddin et al., 1999). The first slags (by-product waste resulting from smelting ore) testifying to copper smelting are from the sixth millennium BCE in the Near East, whereas the early attested crucibles (ceramic containers used to melt metal) date to the late sixth/early fifth millennia BCE and have been found in south-eastern Iran and Serbia (Radivojević et al., 2007; Roberts et al., 2009).

However, the first evidence of regular copper smelting comes from the Carpathians and the Balkans, a region known as the "Carpatho-Balkan Metallurgical Province" (Kohl, 2007) where mining activity was regular, and dates back to the end of the sixth millennium BCE, (Černych, 1978; Roberts et al., 2009). Copper and gold were already used in Europe for ornaments as early as ~4,400 BCE mostly as an elite commodity; the Varna culture and its rich burials on the Black Sea coast offers one of the best examples of the importance of metal in the fifth millennium BCE (Slavchev, 2010). In fact, the first metal objects were not necessarily superior to the ones produced with materials such as bone, flint or obsidian. Therefore, it seems that from very early stages, metal was used mostly for aesthetics and social purposes (Kohl, 2007; Smith, 1977).

In Iberia, the first evidence for copper ore smelting dates to the fifth millennium BCE, in a Neolithic context at Cerro Virtud in Almería (Ruiz-Taboada and Montero-Ruiz, 1999), a region rich in metal that would later harbour a rich record of Chalcolithic sites, including the well-known mega-site of Los Millares (Díaz Zorita et al., 2012). By the first half of the third millennium BCE copper metallurgy was fully established across the Peninsula, with evidence from large settlements such as Valencina de la Concepcion in Sevilla, Los Millares in Alemería (both in Spain), and Zambujal in Torres Vedras (Portugal) (Rovira and Montero-Ruiz, 2013).

The early date in Iberia in a Neolithic background hints at a possible autochthonous independent origin for metallurgy in Iberia (although not unanimously agreed amongst archaeologists (Cunliffe, 2014)). More importantly, copper metallurgy in the Iberian Chalcolithic (3200–2250 BCE) was different in its nature. While in south-eastern Europe, the Near East and the Pontic-Caspian Steppe early copper objects were mainly for ornamental use as display of status in a hierarchical society, early copper objects in Iberia were mostly tools and weapons with practical use. Metal ornaments appeared only later, with the Bronze Age Argaric (or El Argar) culture, which emerged ~2250 BC in southeast Spain (Figure 1.1) (Murillo-Barroso and Montero-Ruiz, 2012). Working of native copper and annealing technology were also uncommon in the peninsular Chalcolithic prior to the Bronze Age.

Additional differences in size, material and shape of crucibles were also observed in Iberia during the Chalcolithic (Murillo-Barroso and Montero-Ruiz, 2012).



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The transition to the Bronze Age occurred when intentional production of copper-tin alloys, with higher quality than naturally occurring copper and more suitable for the manufacture of tools and weapons, became regularly manufactured and the importance of alloyed-copper objects surpassed that of previous unalloyed artefacts. The Bronze Age started ~3700–3500 BCE in the North Caucasus mountains with the first records of arsenical bronze, and spread into the Pontic-Caspian Steppe and Eastern Europe in the following centuries, reaching the lower Danube valley ~3300–3200 BCE (Anthony, 2010). The Bronze Age, evidenced by the use of arsenical copper and bronze, spread over the following millennium into western Europe. In Iberia, the Bronze Age started only by the end of the third millennium BCE, with the onset of the Argaric culture in the southeast that broke with the previous Bell Beaker and Chalcolithic traditions, although the first objects of tin–bronze date to even later, to the beginning of the second millennium BCE (~1800–1700 BCE) (Lull et al., 2013).

Overall, the Metal Ages was a period of profound cultural and social changes across all of Eurasia, with a shift to a patriarchal society and the spread of the Indo-European language family (most likely in the form of proto-Indo-European), widespread today in Europe and some parts of Asia (Anthony, 2010). Although mobility was also important during the Late Neolithic, it not only dramatically increased in the Metal Ages, but also changed in its nature, with organized metal trade routes institutionalized across vast areas. Mining regions provided the bulk of metal to distant communities via long distance trade, connecting distinct regions, such as Mesopotamia, Europe, the Iranian Plateau, the Caucasus and the Eurasian Steppe (Cunliffe, 2014; Kohl, 2007). In Europe there were dramatic changes to the landscape during the third millennium BCE, due to the burning of large expanses of forest, with the aim of creating new pastures for herds, and to facilitate transport and communication, in agreement with the mobile lifestyle typical of pastoralist (semi-)nomadic Bronze Age Steppe societies that arrived in the region and the use of wheeled vehicles (Kristiansen, 1989, 2015). Strontium isotope analysis and specific burial goods (*e.g.* tents, mats, wagons) provide additional evidence for the mobile character of Bronze Age societies (Gerling et al., 2012; Irrgeher et al.; Kristiansen, 2015).

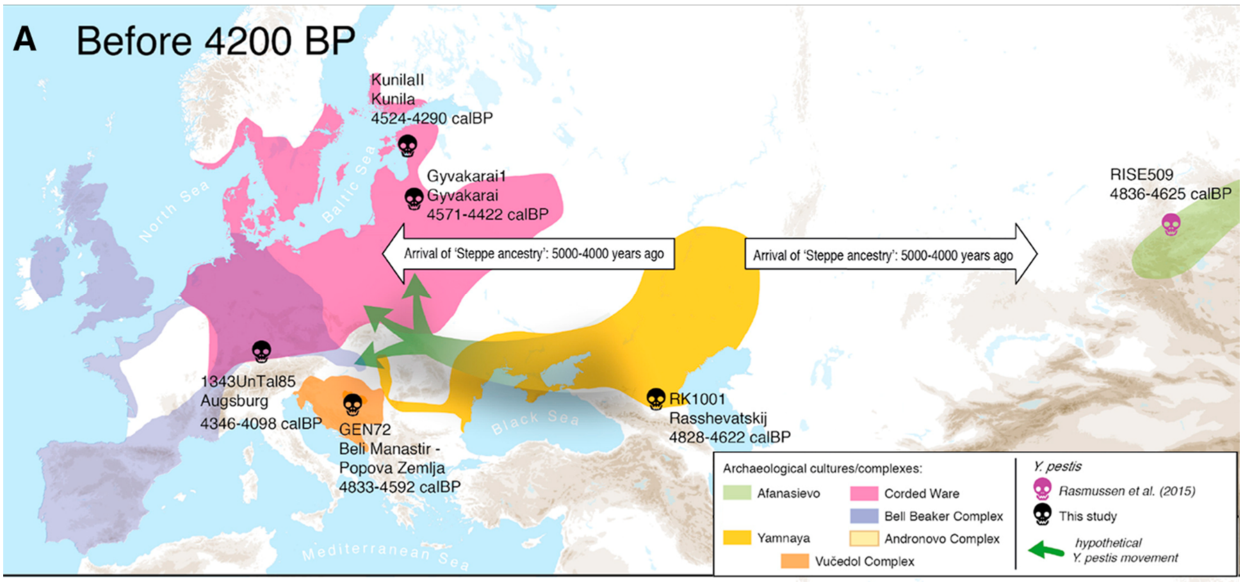

Figure 1.2. Map showing provenance of prehistoric human remains infected with *Yersinia pestis* and proposed entrance of *Y. pestis* into Europe with the expansion of Yamnaya pastoralists from the Pontic-Caspian Steppe region Figure from Andrades Valtueña et al., 2017.

Recent evidence has shown that *Yersinia pestis*, the etiological agent of plague, was widespread in the Late Neolithic and Chalcolithic across Europe (Figure 1.2) (Andrades Valtueña et al., 2017; Rasmussen et al., 2015b; Spyrou et al., 2018). The degree to which potential plague outbreaks might have influenced the population dynamics during the third and second millennia BCE is still unknown, but, even if the bacteria initially lacked the virulence genes to cause the bubonic form of plague, it is possible that the disease played an important role in the archaeological changes that took place in the transition to the Metal Ages (Rasmussen et al., 2015b). Another likely key factor in the third millennium BCE was the global climatic episode usually known as the 4.2 kiloyear event, which occurred between ~2900–2400 BCE, led to the coldest conditions since the Younger Dryas, and affected various regions in Eurasia, as described in more detail the following sections (Perry and Hsu, 2000).

1.1. The Eurasian Steppe

The Eurasian Steppe is a vast expanse of grassland that stretches ~9000 km between latitudes 40° and 55° north, from the Great Hungarian Plain in the west to Mongolia in the east (Figure 1.3). The western Steppe comprises two main regions to the west of the Altai mountains: the Pontic-Caspian Steppe, expanding from the Carpathian foothills in the present-day Ukraine and North Caucasus eastwards into the Urals; and the Kazakh steppe, from east of the Urals to the Altai, where the eastern Steppe (also known as the Mongolian Steppe) begins (Kremenetski, 2003). The west, especially the Pontic-Caspian region, is milder due to oceanic influence from the Atlantic, in comparison with the much harsher (colder and drier) eastern regions. However, climate was not stable during the Holocene, and fluctuations in precipitation levels, however minor, are thought to have had a major impact on the lifestyle of the Steppe cultures (Kohl, 2007; Kremenetski, 2003). This region, connecting Europe and Asia, has a very rich archaeological record (Kohl, 2007), which reflects its key role in shaping current Eurasian genetic variation (Allentoft et al., 2015; de Barros Damgaard et al., 2018a; Haak et al., 2015; Narasimhan et al., 2018).

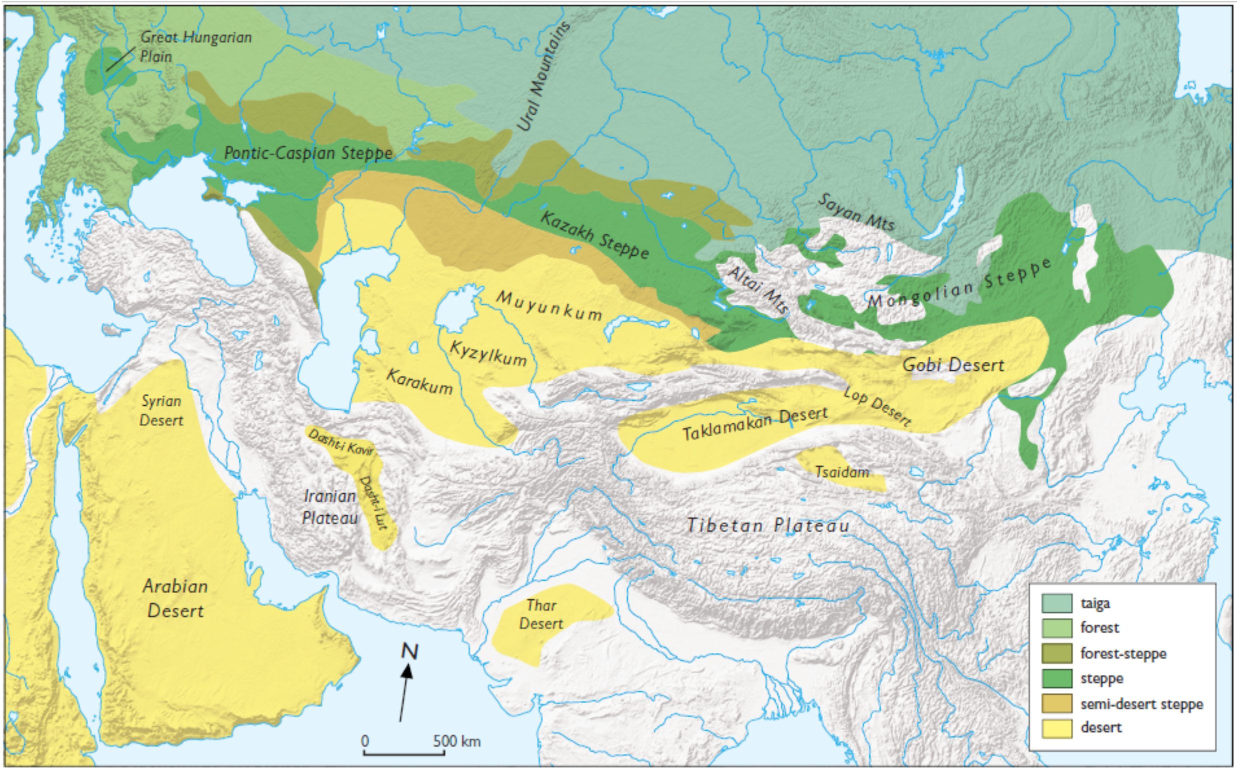

Figure 1.3. Principal ecological zones and geographic features connecting Europe and East Asia Figure from Cunliffe, 2014.

The warmer and drier conditions in the Pontic-Caspian region in the second half of the fourth millennium BCE potentiated a more mobile pastoralist way of life, moving frequently in search of water and food for flocks and herds (Cunliffe, 2014). The Yamnaya cultural complex, also referred to as the Pit Grave Culture, due to its typical burials (individual pit or shaft grave burials under a barrow, or kurgan), is a group of related cultures that emerged in the Pontic-Caspian steppe ~3300 BCE (Anthony, 2010). The Yamnaya horizon shares many of its archaeological elements with the preceding Maikop from North Caucasus, where the funerary kurgans first emerged, while maintaining the pastoralist economy and most likely hierarchical society characteristic from the Pontic-Caspian steppe (Cunliffe, 2014).

The connection between the Yamnaya and the preceding agriculturalist Cucuteni-Tripolye culture is still debatable. The Cucuteni-Tripolye people, with their distinctive decorated pottery, female figurines and architecture, thrived in the border region between Europe and the Pontic-Caspian steppe from the late fifth to the mid-fourth millennia BCE, building very large settlements (Kohl, 2002). Although the use of wheeled wagons by the Cucuteni-Tripolye is not assuredly proven, miniatures and drinking cups shaped like ox-drawn-wheeled wagons suggest that the idea of wheeled vehicles (either local or imported) was already present in the Cucuteni-Tripolye culture before 3500 BCE (Parpola, 2015). While some scholars argue that an expansion of the Cucuteni-Tripolye and their ox-drawn wagons into the steppe, where they merged with local pastoralist traditions, eventually culminated in the formation of the Yamanya (Parpola, 2015); others suggest that incursions from steppe pastoralists into Cucuteni-Tripolye areas, potentiated by the climatic conditions in the mid-fourth millennium BCE, contributed to the decline of the once prosperous Cucuteni-Tripolye mega-sites (Cunliffe, 2014). Genetic results suggest complex mechanisms of contact between early Yamnaya groups, their western agriculturalist neighbours and the Maikop (Mathieson et al., 2018; Wang et al., 2019).

The Yamnaya were the first fully pastoralist societies with a nomadic character, as testified by the virtual absence of Yamnaya settlements, suggesting that they used their ox-drawn wagons as mobile housing (Anthony, 2010). Horse riding must have been a great advantage for herding, allowing the Yamnaya to move flocks more easily. As semi-nomadic pastoralists, they exploited seasonal ecological niches, with small-scale movements between summer and winter (Kristiansen et al., 2017). Isotope analysis shows that their diet was composed of mostly meat, dairy products and fish, as well as wild seeds, with no agricultural component (except for some western sites along river valleys where there is some evidence for cereal cultivation) (Pashkevych, 2012; Schulting and Richards, 2016).

Yamnaya burial practices clearly hint at a patriarchal and highly hierarchically-structured society. The number of Yamnaya kurgans and their low rate of construction suggest that they were reserved to only a small percentage of the population. This, together with the richness of grave goods (typically metal objects) usually associated with Yamnaya burials, suggest that only a privileged elite was buried in this style, whereas the majority of the population had a different treatment, most likely excarnation (Anthony, 2010; Cunliffe, 2014). Moreover, up to 80% of the burials found in individual kurgans were male, testifying to the patriarchal character of the Yamnaya (Cunliffe, 2014).

The Yamnaya, with their wheeled ox-drawn wagons and horseback-riding, expanded westwards, to the Great Hungarian Plain and into Central Europe, in some way culminating in the formation of the Corded Ware (Kristiansen et al., 2017), and as far as to the Urals in the east between 3000–2400 BCE (Figure 1.4). They were responsible for spreading knowledge of copper production through the Steppe, and, according to recent linguistic and genetic evidence, also Indo-European languages (Allentoft et al., 2015; Anthony, 2010; Haak et al., 2015; Parpola, 2015). However, the direct connection between the Corded Ware and the Yamnaya is rather contentious (Mallory, 1989). An alternative scenario would be an infiltration of Chalcolithic Tripolye communities ~6.4 thousand years ago (ka) from southeast Europe into the Steppe and Central Europe, originating both the Yamnaya and the Corded Ware ~5.4 ka (Parpola, 2015), and thus accounting for their genetic similarities.

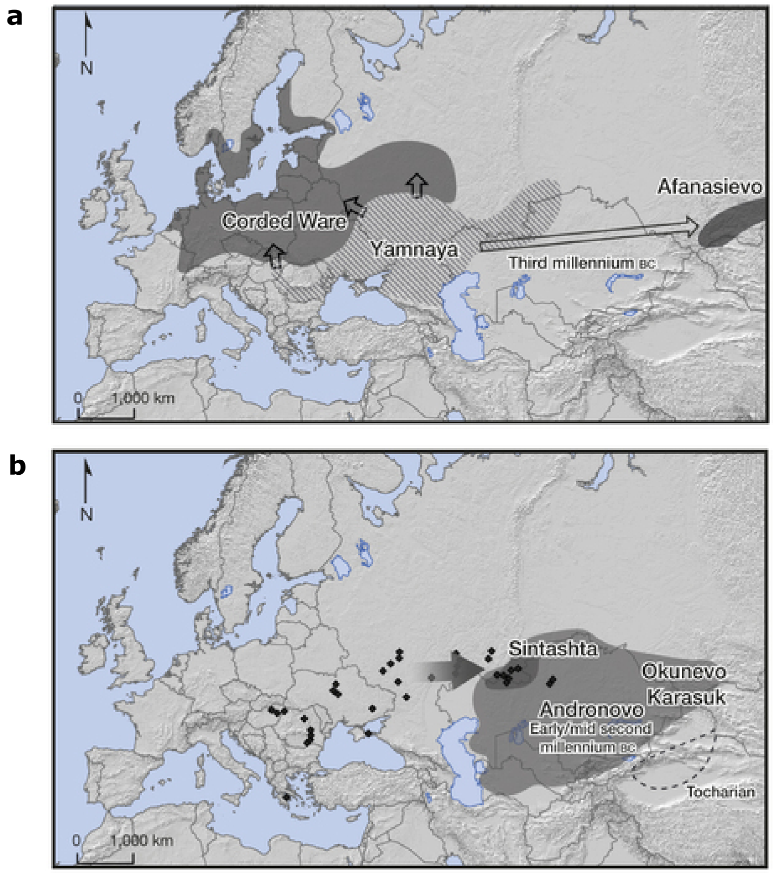

Figure 1.4. Distribution of Late Neolithic/Early Bronze Age cultures and Yamnaya movements into Central Europe and Central Asia (arrows) (**a**). Middle and Late Bronze Age cultures from Central Asia: Sintashta, Andronovo, Okunevo, and Karasuk (**b**). Black points represent chariot burials (2000–1800 BCE). Figure adapted from Allentoft et al., 2015.

To the east of the Urals the Sintashta culture, whose archaeological origin is still not clear (although it is genetically close to the Yamnaya (Allentoft et al., 2015)) emerged ~2100 BCE (Figure 1.4) (Koryakova and Epimakhov, 2007). In the southeast Urals, a region rich in copper mines, the Sintashta built closed fortified settlements, usually associated with cemeteries composed of shaft graves under barrows. Chiefs and warriors were buried with weapons and pottery, usually accompanied by horse-drawn chariots and two horses. While the Catacomb Grave culture, the successor of the Yamnaya in the western Steppe, already used ox-drawn chariots, the Sintashta were the first to use horse-drawn chariots (Koryakova and Epimakhov, 2007; Parpola, 2015). In the early second millennium BCE, Sintashta groups seem to have moved eastwards, eventually contributing to the rise of the Andronovo culture (Figure 1.4b).

1.2. South Asia

The first evidence for agriculture in South Asia was found at the site of Mehrgarh (6500–2600 BCE), which covers an area of approximately 200 ha and is located in Baluchistan, in present-day eastern Pakistan (Jarrige and Jarrige, 2006; Petrie, 2015). Despite evidence of imported Near Eastern domesticates from the Fertile Crescent, including wheat, barley, pulses, sheep and goat (Fuller, 2007; Kingwell-Banham et al., 2015), there was also an autochthonous component at Mehrgarh, the most striking example being the locally domesticated zebu cattle (Chen et al., 2010).

Mehrgarh is considered the precursor of the Harappan (or Indus Valley) Civilisation (Figure 1.5), which arose in the fertile Indus Valley region around 3200 BCE, in the intersection between the arid Iranian Plateau and the mostly tropical Indian Subcontinent (Cunliffe, 2014; Mcintosh, 2008). Many questions regarding the Indus Valley Civilisation remain unanswered. Similarly to the contemporary Proto-Elamites in Iran, the Harappans also had a writing system, and although some texts, mostly in the form of inscriptions on seals, have survived until today, the Indus script has never been properly deciphered (Parpola, 2015). The Harappans were in contact with Central Asia and Mesopotamia, including with the Proto-Elamite Culture, through trade. However, although objects of Harappan origin, including seals displaying the Indus script, have been recovered in the Persian Gulf and Mesopotamia, foreign objects were never found in the Indus Valley. There is also virtually no evidence for warfare (Parpola, 2015).

The Harappan culture flourished for over a millennium and reached its peak ~2600–1900 BCE, but it came to an end by ~1900 BCE (Parpola, 2015). This was in the wake of the climatic event generally known as the 4.2 kiloyear event, which had drastic consequences in the region, such as the increase in aridity due to the weakening of the summer monsoon ~2100 BCE, and modifications to rivers courses and change of coastlines (Dixit et al., 2014; Mcintosh, 2008). As mentioned earlier, this was a global climatic event and has been suggested as a main cause triggering the collapse of other civilisations, such as the Mesopotamian Akkadian Empire, the Old Kingdom in Egypt and the Bronze Age civilisations in the Aegean (Cullen et al., 2000; Marshall et al., 2011; Weiss and Bradley, 2001). Other anthropogenic causes might also have come into play and possibly contributed to environmental degradation. For example, deforestation and overgrazing probably caused erosion, and the canal irrigation system used in the Indus Valley may have dissolved ground salts and contributed considerably to reducing the yield of fields (Mcintosh, 2008; Parpola, 2015).

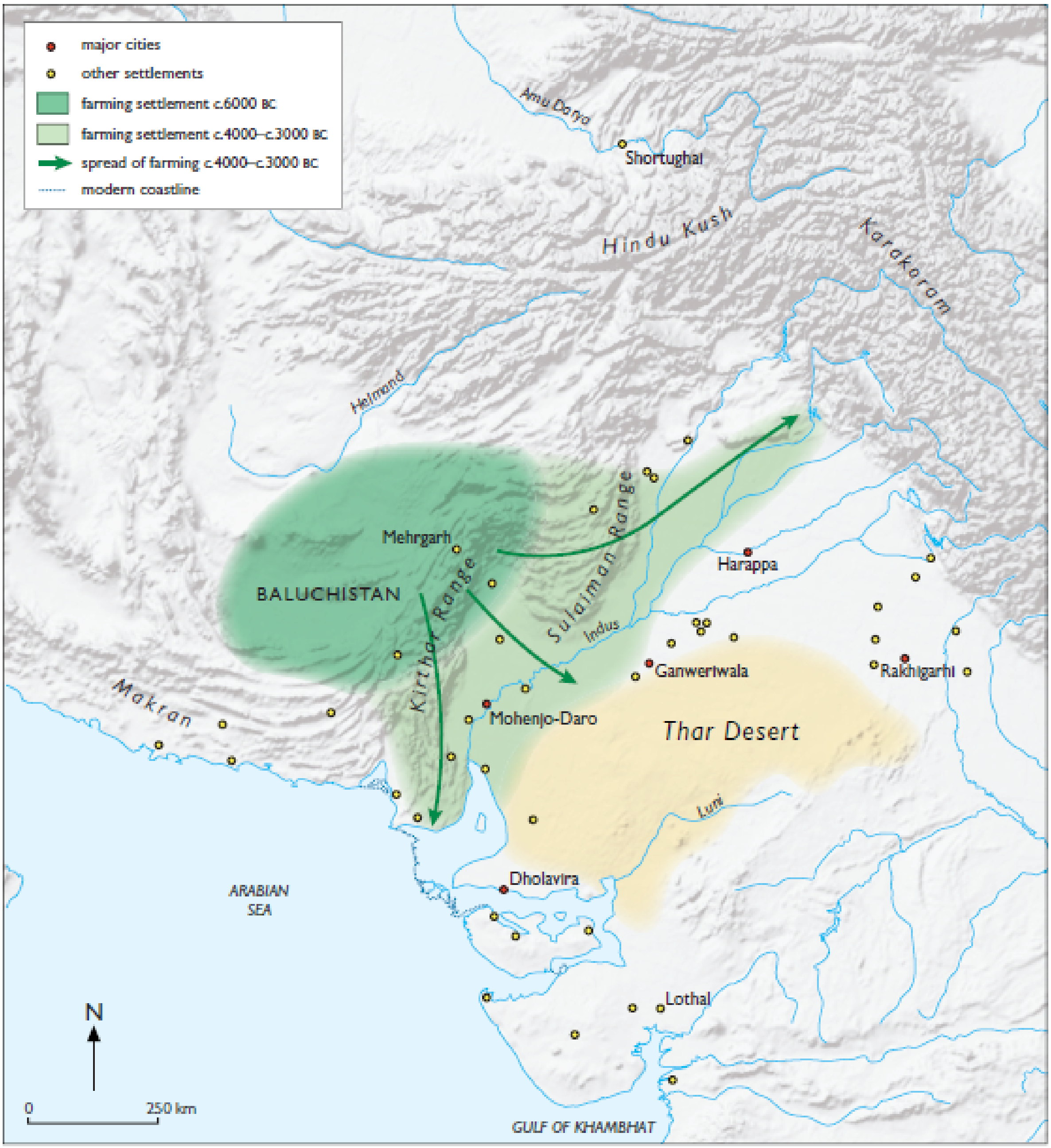

Figure 1.5. Spread of agriculture from Baluchistan ~4000–3000 BCE to the Indus Valley, and the posterior development of the Harappan/Indus Valley Civilization in the fourth millennium BCE. Figure from Cunliffe, 2014.

Although the Harappan population did not suddenly completely disappear, with some signs for regional continuity into the second millennium BCE, the once thriving Harappan cities (and the Indus script) were abandoned. This coincided with the arrival of the first Indo-European speakers to the Subcontinent, most likely speaking Indo-Aryan (a sub-branch of Indo-Iranian) (Parpola, 2015). This has led to suggestions that the Indus Valley civilisation was subjected to a massacre as a result of what has been dubbed the "Indo-Aryan invasions"

(Wheeler, 1953). However, studies on Harappan skeletons did not find evidence for violence (Parpola, 2015).

Nevertheless, archaeological evidence does show that Indo-Iranian-speaking people arrived to the Indus Valley region around the time of the downfall of the Harappan civilisation. Middle Bronze Age Andronovo descendants of the preceding Sintashta culture (known for the use of horse-drawn chariots), likely speaking an Indo-Iranian language, expanded east and southwards from the Ural Mountains region into Central Asia by the end of the second millennium BCE (Parpola, 2015). Andronovo groups, who probably controlled tin production and distribution in Central Asia (Kristiansen et al., 2018), are thought to have come into contact with the Bactrian Margiana Archaeological Complex (BMAC) in Turkmenistan and northern Afghanistan as early as 2000 BCE. Steppe elements, such as chariots, horse remains, cheek-plates in the Sintashta style and bronze pins, have been found together with BMAC ceramics in two locations in Tajikistan dating to ~2000–1800 BCE, and by the mid-first millennium BCE, BMAC settlements in south Turkmenistan were surrounded by Andronovo campsites (Parpola, 2015). However, there is no evidence of violence or systematic destruction associated with the arrival of Andronovo groups in the region (Kristiansen et al., 2018; Parpola, 2015), a central aspect of the "Indo-Aryan invasion" hypothesis (Wheeler, 1953).

In South Asia, no pottery or barrows of Steppe origin have been found. Therefore, direct contacts between Andronovo and the Indus Valley cultures seem unlikely, from an archaeological perspective (Parpola, 2015). Yet, there are striking similarities between the rites described in the Indian *Rigveda*, a series of Indo-Aryan texts thought to have been written around by middle/late second millennium BCE, and the Sintashta and Andronovo ceremonies (*e.g.* regarding horse sacrifice) (Kristiansen, 2011). On the other hand, rich BMAC cemeteries dating to ~2000 BCE were found in the Indus Valley, thus indicating that the BMAC (after infiltration by the Andronovo) moved eastwards around the beginning of the Harappan decline (Parpola, 2015). Incursions of BMAC groups moved further into South Asia, as well as westwards across northern Iran into Syria (which was dominated by the Indo-Iranian-speaking Mitanni) and Anatolia by ~1500 BCE (Anthony, 2010; Anthony et al., 1986; Kristiansen, 2011; Parpola, 2015).

1.3. Western and Central Europe

One of the most prominent events of the Late Neolithic/Chalcolithic in Europe was the expansion of the Bell Beaker cultural "package", which includes pottery (the iconic inverted-bell-shaped beakers), copper-producing techniques, archery equipment and a progressive shift from collective to single burials, showing a bigger focus on individuality. Beaker pottery had its origin in Iberia ~2800 years BCE, probably in Portuguese Estremadura along the copper-rich Tagus region where the earliest Beaker pots, known as the Maritime Beakers and characterised by impressed band decoration, have been found. It then spread into western Europe, possibly along the Mediterranean and the Atlantic façade, moving later inland into central Europe (Heyd, 2007; Kristiansen, 2015; Müller and van Willigen, 2001).

Interestingly, the early Iberian Beaker period lacks several elements of what has been proposed as the fully developed Beaker "package", such as the typical individual Beaker burial. Instead, Chalcolithic Iberian sites display variability of body treatment and burial practices, and to some extent show a continuity of Late Neolithic practices, with the use of earlier megalithic monuments, collective inhumations, deposition of partially or fully disarticulated bodies and usually fragmentary grave goods (Cleary and Gibson, 2019).

Although the Beaker "package" was widespread in western and central Europe by the mid-third millennium BCE, its distribution was not uniform, but rather organised in small discrete pockets (Vander Linden, 2007), hinting at a complex demographic history not explained by simplistic models based solely on either demic or cultural diffusion. In fact, recent genetic evidence shows no detectable expansion out of Iberia accompanying the first steps of spread of the Bell Beaker culture, whereas, at a later stage, mobility became the most likely driver for the spread of the Beaker complex in central Europe and its arrival to the British Isles (Olalde et al., 2018) and later movements into Iberia (Olalde et al., 2019).

Contemporary to the Bell Beaker, another culture emerged in the Late Neolithic in Eastern Europe – the Corded Ware (~2900–2300 BCE). The Corded Ware people were genetically descendants of the Yamnaya, who moved from the Pontic-Caspian Steppe region (or another unsampled population genetically resembling the Yamnaya), and Middle Neolithic central Europeans (Allentoft et al., 2015; Haak et al., 2015).

The Corded Ware co-existed for some time with Late Neolithic cultures in central and northern Europe, but were archaeologically distinct – they were characterised by their ceramic vases decorated with corded-impressions, and shared many archaeological aspects with the Yamnaya, especially regarding funerary practices (Furholt, 2014; Kristiansen et al., 2017). The Corded Ware from central and north Europe buried their dead in single inhumations under barrows, in the same fashion as those from the Steppe, and orientated the bodies west-east, with gender-specific deposition rules: men were buried on their right side (with the head towards the west), whereas women were laid on their left side (with the head pointing to the east), both facing south (Furholt, 2014). Male exogamy (for example due to marriage by abduction) is thought to have played an important role in maintaining Corded Ware societies and is expected in a scenario of male-dominated movements such as those postulated for Steppe pastoral cultures (Kristiansen et al., 2017; Müller et al., 2015). Strontium and diet isotope analysis show more variability on the female side, suggesting women were born and raised in a different place and most likely within a Late Neolithic (agricultural) culture, in comparison with males who seemed more local and had diets typical of pastoral societies (Haak et al., 2008; Kristiansen et al., 2017; Sjögren et al., 2016).

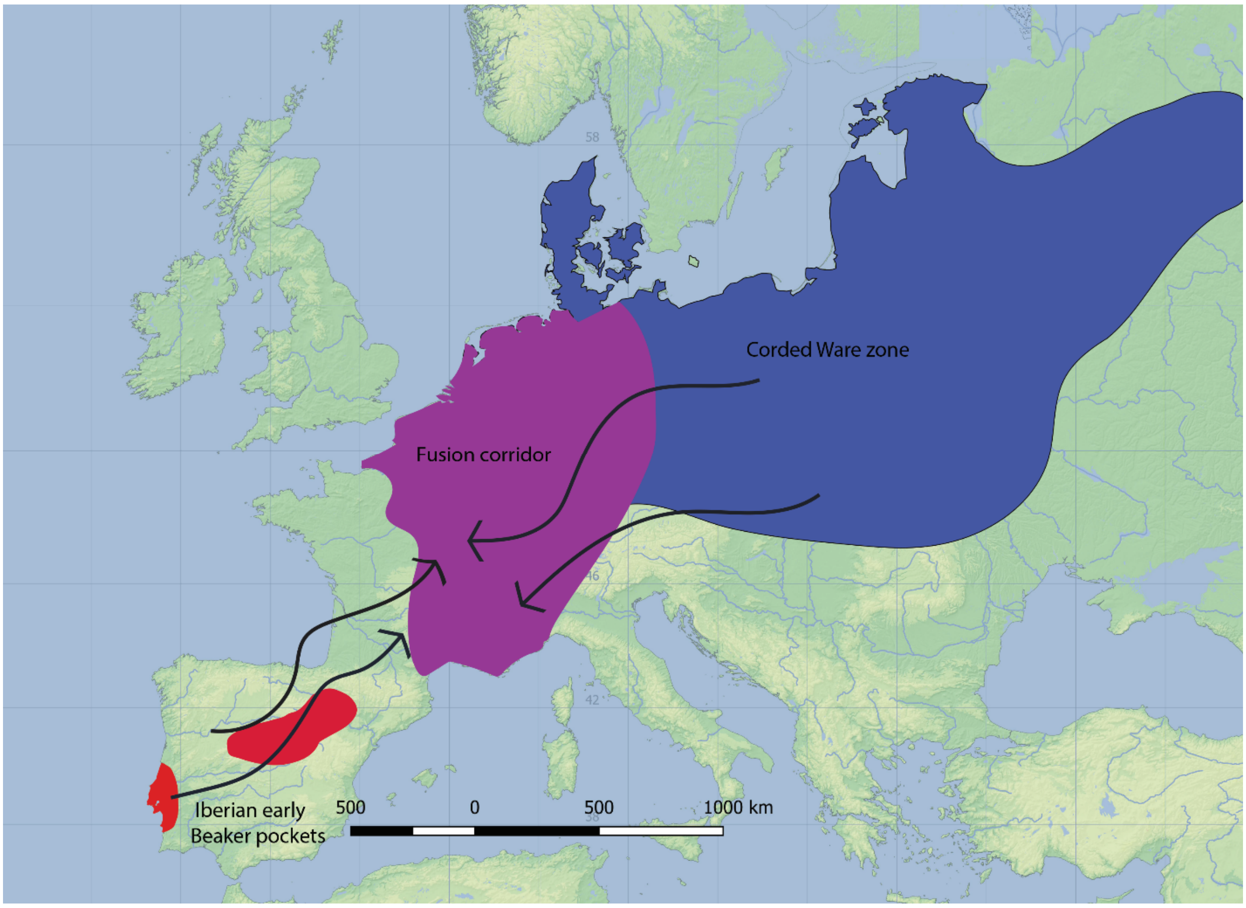

Figure 1.6. Merging of Corded Ware (blue) and Early Beaker (red) traditions in the overlap region, or fusion corridor (purple), in Central Europe. Figure from Cleary and Gibson, 2019.

Corded Ware and Bell Beaker cultures overlapped in central Europe, where they coexisted for more than three centuries (Figure 1.6) (Cleary and Gibson, 2019). Genetic evidence indicates there was admixture between the two cultures in central Europe (Brandt et al., 2015; Olalde et al., 2018). The fusion between the Maritime Beakers and Corded Ware pottery resulted in the All-Over-Ornamented (or All-Over-Corded) Beaker style, decorated with twisted cord impressions. Beaker people also adopted new burial rituals, including single inhumations (usually in a crouched positon), gender-specific body orientation and an increase and diversification of accompanying grave goods (Besse, 2014; Cleary and Gibson, 2019).

Beaker people with central European/Corded Ware-related ancestry arrived to Iberia in the second half of the third millennium BCE, and specific lineages of Y-chromosome haplogroup R1b (R1b–M269) associated with the central European Beaker burials appeared in Iberia around ~2500 BCE and quickly replaced most of the previously existing male lineages within a few centuries (Olalde et al., 2019). Around the same period, the typical Beaker cultural "package", including the emphasis on individual burials and specific body orientation according to sex, finally becomes widespread in Iberia (Cleary and Gibson, 2019;

Müller and van Willigen, 2001). However, the social and demographic dynamics responsible for the virtually complete replacement of previous Y-chromosome lineages is not presently fully understood, since there is no evidence for violence in the archaeological record of this period in Iberia. Similarly to what happened in other regions, Iberia was also affected by the environmental changes resulting from the 4.2 kiloyear event, which probably brought pressure to settlements and influenced social and cultural dynamics in the region (Mejías Moreno et al., 2014).

2. Indo-European languages

The Indo-European language family originated in Eurasia, but today is widespread around the world, being also spoken in the Americas and in large swathes of Africa and Oceania, due to colonialist and imperialist European movements in the last five centuries. The vast majority of languages presently spoken in Europe belong to the Indo-European family. The only exceptions are Basque, a linguistic isolate spoken in parts of northern Spain and southern France; Finnish, Estonian and Hungarian, which belong to Finno-Ugric, a branch of the North Eurasian Uralic family; Maltese, a derived form of Arabic (Afro-Asiatic family); and Turkish, which belongs to the Turkic family (Mallory and Adams, 2006). In Asia, Indo-European is today spoken mainly in Iran, Pakistan, India and Bangladesh. However, it was also present in Anatolia (extinct Hittite and Phrygian), Central Asia (based on archaeological similarities with other Indo-European societies) and the Tarim Basin (extinct Tocharian) before the spread of Altaic languages associated with the Turkic and Mongol movements in the Medieval period (Mallory and Adams, 2006).

In the past, languages were most likely spread through direct population contacts, and must have involved to some extent actual dispersal of people, especially before the advent of writing. The origin of Indo-European has always been a contentious topic, but two main theories were considered the most probable (Diamond and Bellwood, 2003): the Anatolian hypothesis, according to which Indo-European arrived to Europe during the Neolithic with the agricultural dispersals from the Near East (where Anatolian, the oldest Indo-European branch, was spoken) (Renfrew, 1987), and the Steppe hypothesis, which proposed a later dispersal of Indo-European, from a homeland in the Pontic-Caspian Steppe in the Bronze Age (Anthony et al., 1986; Gimbutas, 1993). The fact that earlier genetic results showed substantial movements from the Near East during the Early Neolithic, while failing to show significant influx in the Chalcolithic/Bronze Age periods, seemed to favour the Anatolian hypothesis. However, in 2015 two independent genetic studies (Allentoft et al., 2015; Haak et al., 2015) showed a migration of people with Yamnaya-related ancestry to central Europe around 4.8 ka (from a Pontic-Caspian Steppe source), adding to the linguistic and archaeological evidence supporting the Steppe hypothesis (Anthony, 2010; Anthony and Ringe, 2015; Chang et al., 2015; Kristiansen, 2011; Parpola, 2015).

Cognates (words in different languages that share the same origin) that exist in two or more branches are assumed to have been already present in the early stages of Indo-European development (Iversen and Kroonen, 2017). Diverse cognates show that Proto-Indo-European included terminology related to dairy and wool production, horse breeding and wheeled vehicles (Figure 1.7), thus suggesting that early Proto-Indo-European-speaking societies practiced pastoralism and were familiar with domesticated horses and the use of wheeled-vehicles – a description that fits the Yamnaya Steppe groups (Mallory and Adams, 2006). Examples of terms reconstructed from Proto-Indo-European include the words for "cow", "to milk", "cheese", "sheep", "lamb", "wool", "horse", "to tame", "wheel", "thill", and "axle" (Anthony and Ringe, 2015; Iversen and Kroonen, 2017). Interestingly, much of the terminology associated with "vehicle" in Uralic is borrowed from Indo-European (Parpola, 2015). On the other hand, Proto-Indo-European words for crops and land cultivation are much more difficult to reconstruct (Iversen and Kroonen, 2017).

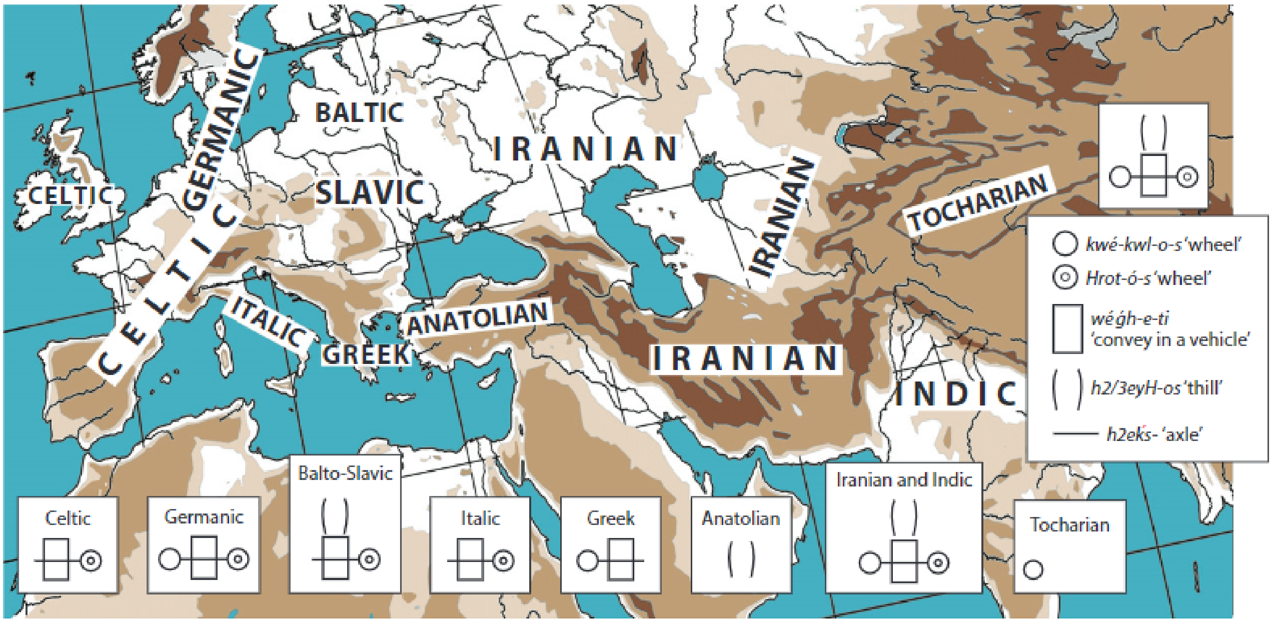

Figure 1.7. Words related to wheeled vehicles found in various Indo-European language branches. Figure from Anthony and Ringe, 2015.

2.1. Celtic languages

A currently contentious issue regarding Indo-European concerns the origins of Celtic languages, mainly due to the scarcity of early written evidence. The early written accounts of Celtic languages and associated cultures come from Greek and Roman texts, where Celtic-speakers are called *Κελτοί* and *Celtae*, respectively (Cunliffe, 2003). Celtic's past distribution seems to have been wider than the regions where it is spoken today (essentially in the British

Isles and Brittany). Several lines of evidence, such as inscriptions on funerary *stelae*, toponyms (place names), coin legends from the Roman period, or extracts of Classical and early Medieval texts, indicate that Celtic languages were once also spoken in Iberia, northern Italy, southern Gaul, central and Eastern Europe, and even in Anatolia (in the form of Galatian) (Gamito, 2005; Mallory and Adams, 2006).

Iron Age Hallstatt and the succeeding La Tène cultures in the Alps are traditionally considered as the origin of Celtic cultures, and by extent, the birthplace of Celtic languages (Cunliffe, 2003). However, the concept of shared "Celticity", *i.e.* the idea that Celtic cultures were somehow homogeneous, is erroneous. For example, Celtic-speaking groups in Iberia in the first millennium BCE, although linguistically connected, had a different material culture than that from Hallstatt and La Tène (despite some La Tène objects found in both Portugal and Spain) (Gamito, 2005; Koch, 2013a; Lorrio et al., 2005). In fact, one issue with the traditional view of Celtic origins is that it does not consider the pre-Roman Iberian Peninsula (Gamito, 2005; Koch, 2013a), mainly because the first evidence for Celtiberian (the Botorrita bronze plaque inscriptions found in Zaragoza) was only discovered in the 1970s, much later than the other Celtic languages, known since the 18th century (Lejeune, 1973). Interestingly, Celtiberian (and possibly Lusitanian, although its classification as Celtic is contentious (Cunliffe, 2003)) seems to be a more archaic branch, suggesting that Proto-Celtic could be older than 800–750 BCE, as initially established (Koch, 2013a).

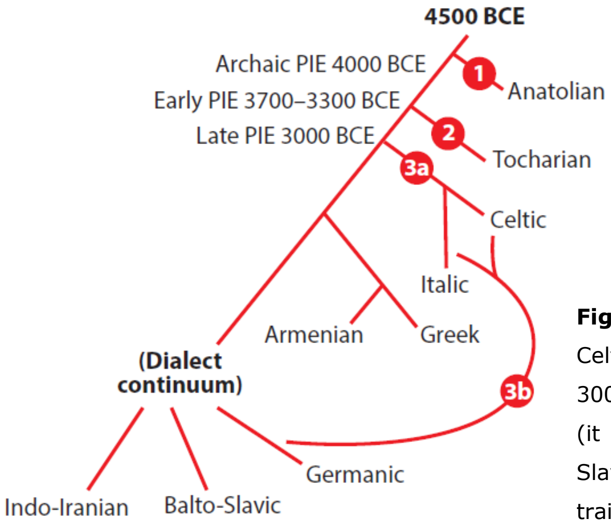

Figure 1.8. Indo-European tree diagram showing Italo-Celtic deriving from Late PIE (Proto-Indo-European) around 3000 BCE. The pre-Germanic split is currently unresolved (it either derived together with Italo-Celtic or with Balto-Slavic, since it shows a mixture of both archaic and derived traits). Figure from Anthony and Ringe, 2015.

According to a recent hypothesis, usually known as "Celtic from the West" (Koch and Cunliffe, 2013), Celtic could have originated much earlier in Iberia and spread to central Europe with the Bell Beaker radiation in the third millennium BCE, considering its recently reconstructed basal position in the Indo-European tree (Figure 1.8). This argument is heavily based on the discovery of Early Iron Age "Tartessian" inscriptions in southwest Iberia, the earliest of which, at the Medellin necropolis in Badajoz (Spain), are securely dated to the mid-seventh century BCE (Almagro-Gorbea, 2004), although the script was possibly already in use as early as the eighth century BCE (Koch, 2010, 2013b). The Southwestern script (also referred to as "Tartessian" script) was only found in some funerary *stelae* and graffiti, but it represents the first evidence for endogenous literacy in western Europe (Koch, 2019). Although regarded as a linguistic isolate with no affinity to Indo-European by some scholars (Hoz, 2011; Rodríguez Ramos, 2002), others argue that the Southwest/Tartessian inscriptions represent a form of Celtic, even though the script seems borrowed from non-Indo-European (Koch, 2019, 2010; Wikander, 1966).

However, this hypothesis is difficult to reconcile with recent genetic evidence of no movements out of Iberia in the early Beaker period (Olalde et al., 2018). Nonetheless, Italo-Celtic is indeed one of the deepest branches of Indo-European, just after Tocharian and Anatolian (Figure 1.8), which does not seem to fit with it having originated in Iron Age with the Hallstatt culture. One possibility is that Proto-Celtic could have originated as a result of Steppe expansions into central Europe and survived in the region for a few centuries before spreading into Iberia during the third millennium BCE and then diverging into regional languages or dialects. In such a scenario the use of Celtic as a *lingua franca* across Atlantic Europe as early as by the end of the Bronze Age seems plausible (Correia, 2014; Koch, 2016) and would accommodate the Southwest script and the use of Celtic in Iberia as early as the eighth or seventh century BCE.

3. From archaeogenetics to palaeogenomics

Genetics can play a very important role in answering some archaeological and linguistic questions. Although genetics alone will never be enough to answer the questions related with linguistics (*e.g.* concerning the dispersal of Indo-European in Eurasia and the spread of Celtic languages), it can still be very useful to provide insights into people's movements over time.

The first attempt to combine genetics and archaeology was made by Cavalli-Sforza and his team in the 1970s, by studying European genetic diversity based on protein markers (Menozzi et al., 1978). Later, the development of the polymerase chain reaction (PCR) (Mullis et al., 1986) and other crucial techniques, such as Sanger DNA sequencing (Sanger and Coulson, 1975; Sanger et al., 1977), revolutionised molecular genetics and greatly contributed to the development of the field of archaeogenetics (Cavalli-Sforza and Feldman, 2003) – a term coined to define the study of human evolution by means of molecular genetics (Amorim, 1999; Renfrew and Boyle, 2000).

In the following years, several studies showed that anatomically modern humans originated in Africa, from where they dispersed between 60–100 ka to settle the rest of the world (Cann et al., 1987; Maca-Meyer et al., 2001; Macaulay et al., 1999; Malaspinas et al., 2016; Mallick et al., 2016; Pagani et al., 2016). Archaeogenetics also demonstrated how the concept of human race lacks genetic grounds, by showing that most of the variation (up to 95%) is present within, rather than between, populations (Elhaik, 2012; Lewontin, 1972; Rosenberg et al., 2002), and demonstrating the existence of genetic clines (instead of abrupt changes) between different geographic regions and populations (Handley et al., 2007; Pickrell and Reich, 2014; Rosser et al., 2000).

Until recently, most of the genetic studies on prehistoric demographic events used modern genetic variation to infer past dynamics. However, with the technological advances of the past few years, especially due to the development of new sequencing techniques broadly known as next-generation sequencing (NGS), it is now easier to sequence DNA extracted post-mortem. A great advantage of using ancient DNA (aDNA) is that we can focus on a particular time period of the past, and directly compare genetic and archaeological evidence from a given location and period – an approach initially known as palaeogenetics, but which has quickly evolved to palaeogenomics (Heintzman et al., 2015).

3.1. Ancient DNA

The term ancient DNA (aDNA) refers to DNA molecules preserved in biological material and recovered post-mortem, usually from museum specimens, archaeological or fossil remains, and other unusual sources of DNA (Pääbo et al., 2004; Wayne et al., 1999). Despite evidence of successful aDNA recovery from sediments (Slon et al., 2017), ice cores (Willerslev et al., 2007), coprolites (Tito et al., 2012), a variety of human tissues (Ermini et al., 2008; Gilbert et al., 2007), and even from masticated bark pitch (Kashuba et al., 2018), DNA survival is usually highly dependent on the persistence of mineralised tissues, such as bone or teeth, and on a combination of taphonomic (post-mortem) and diagenetic (fossilization) processes (Turner-Walker, 2008). DNA is thought to be preserved in bone by adhering to the hydroxyapatite (or hydroxylapatite), or inside small hydroxyapatite crystals, where DNA is assumed to be more protected from degradation (Campos et al., 2012; Collins et al., 2002).

For preserved biological material, aDNA persistence depends not only on time and several environmental factors (*e.g.* temperature, environmental salt content, exposure to radiation, pH, humidity, availability of oxygen (Lindahl, 1993; Smith et al., 2001, 2003)), but also on post-excavation storage conditions (Pruvost et al., 2007).

3.1.1. Molecular degradation

DNA undergoes three main types of post-mortem modifications: fragmentation, blocking lesions, and deamination. Biochemical DNA degradation starts immediately post-mortem, with enzymes (nucleases) either from the organism or from microorganisms (such as fungi or bacteria present in the environment) fragmenting DNA molecules (Lindahl, 1993; Pääbo et al., 2004). This initial biochemical degradation can be retarded in cases of rapid desiccation or low temperatures (Eglinton and Logan, 1991), but overall fragmentation is not correlated with time, and is present even in young samples (Kistler et al., 2017; Sawyer et al., 2012). Other slower chemical processes inevitably act on DNA molecules, resulting in further fragmentation and chemical modifications to the DNA molecules (Lindahl, 1993; Pääbo et al., 2004), which can induce errors in sequencing and hinder sequence retrieval:

- Depurination caused by hydrolysis is the process by which the β-N-glycosyl bond between a sugar and a purine (adenine or guanine) is broken, resulting in a break in the chain, contributing to further DNA fragmentation and creating single-stranded nicks (Lindahl, 1993; Shapiro, 1981).

- Crosslinks and oxidation products of pyrimidines cause "blocking lesions", interfering with the progression of polymerases along the template strand and hampering DNA amplification (Pääbo et al., 2004).

- Deamination of cytosine to uracil caused by hydrolysis (Shapiro, 1981) is frequent at fragment ends (Figure 1.9), usually overhanging single-stranded nicks resulting from fragmentation by depurination, which are more prone to deamination by hydrolysis (Briggs et al., 2007). Unlike fragmentation, cytosine deamination, at least in mammal bones, seems to be correlated with time, as well as with temperature (Kistler et al., 2017; Sawyer et al., 2012; Skoglund et al., 2014), *i.e.* older samples and samples preserved in warmer conditions are more prone to deamination.

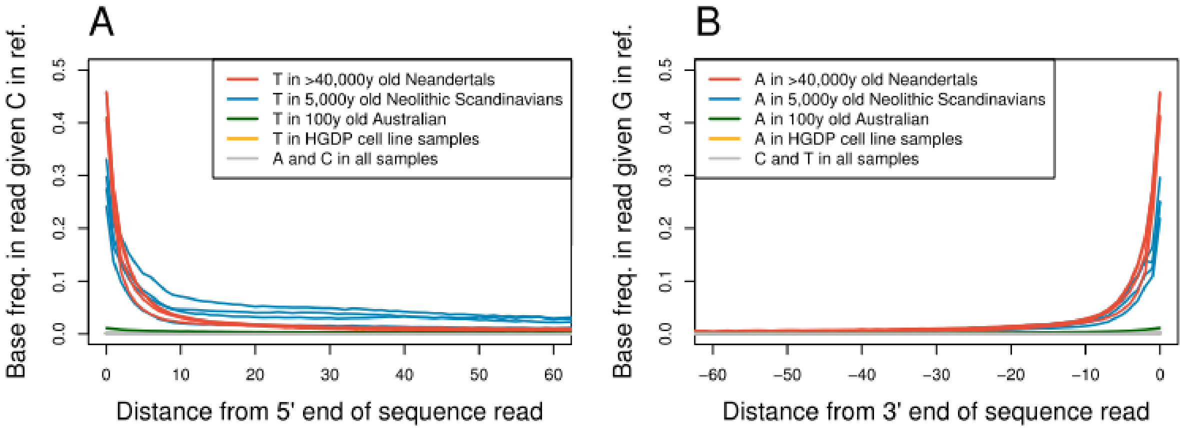

Figure 1.9. Nucleotide misincorporation patterns in ancient DNA sequences retrieved from different remains. **a)** C>T modifications at the 5'-end of sequence read and **b)** G>A modifications at the 3'-end of sequence reads. Misincorporation is more frequent in older remains. Figure from Skoglund et al., 2014.

Overall, these damage mechanisms contribute to decreasing the level of endogenous aDNA retrieved for sequencing (by increasing the chances of amplifying and sequencing contaminant sequences), but they also produce certain patterns which can be used to assess aDNA authenticity. Authentic ancient molecules are expected to be much shorter than modern ones (usually shorter than 100 bp (Sawyer et al., 2012)), and display a typical substitution pattern: C>T at the 5′-end and the complementary G>A in the reverse strand, seen at the 3′-end of fragments (Figure 1.9), due to the amplification and sequencing of artificial thymine and complementary adenine residues pairing with the uracil in the damaged aDNA molecules (Briggs et al., 2007; Green et al., 2009; Hofreiter et al., 2001).

Several precautions should be taken when performing aDNA studies (as reviewed extensively in Orlando and Cooper (2014)). Briefly, aDNA extraction and pre-PCR procedures should be performed in specialized clean-room facilities, physically separated from other molecular biology laboratories, protective clothing should be worn to avoid direct contact with the sample, additional cleaning steps should be taken to avoid contamination and negative controls should be included at different stages of the process to detect potential contamination (Fulton and Shapiro, 2019; Gilbert et al., 2005).

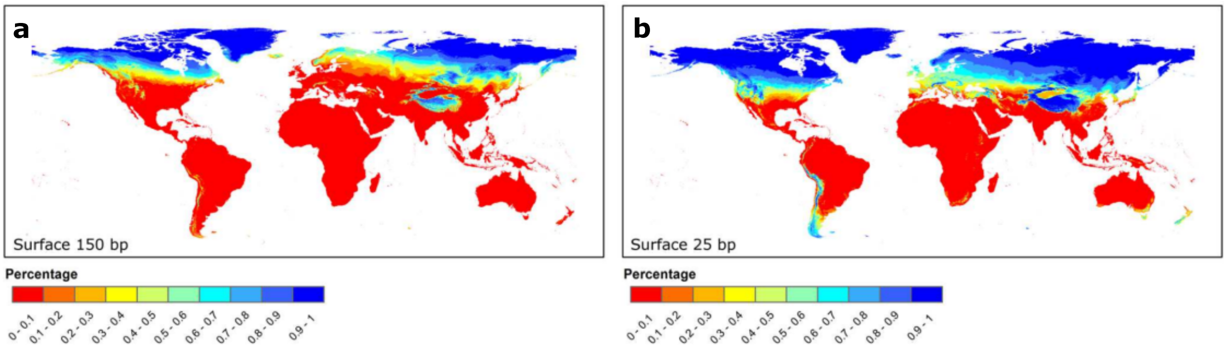

Figure 1.10. Estimation of DNA survival after 10,000 years, for **a)** 150 bp and **b)** 25 bp fragments. Figure adapted from Hofreiter et al., 2015.

Although time plays an important role in DNA degradation, the correlation between time and aDNA preservation is not straightforward (Marciniak et al., 2015). Instead, cold, dry and low-radiation conditions seem to be more important for higher aDNA survival, with temperature the most important factor (Smith et al., 2001, 2003). The oldest ancient genome, dated to 560–780 ka, was extracted from a permafrost-preserved Pleistocene horse sample (Orlando et al., 2013), testifying for the importance of low temperatures on aDNA preservation (Figure 1.10).

3.1.2. The field of ancient DNA

The earliest aDNA studies date to the 1980s and used cloning techniques (Higuchi et al., 1984; Pääbo, 1985a, 1985b). The advent of PCR-based methods allowed the amplification and sequencing of aDNA from older samples, such as the first mtDNA sequences from a Neanderthal specimen (Krings et al., 1997). In fact, the 1990s witnessed a rush to recover very old aDNA, with several high-profile publications claiming to have sequenced extremely old molecules. However, although some authors have claimed to have retrieved DNA sequences from Cretaceous bones (Woodward et al., 1994) and dinosaur eggs (An et al., 1995; Li et al., 1995), they were soon disproved (Hedges et al., 1995; Wang et al., 1997). Other several-million-year-old DNA sequences from plants, amber-preserved insects or even bacteria in salt crystals (Cano and Borucki, 1995; Cano et al., 1993; DeSalle et al., 1992; Fish et al., 2002; Golenberg et al., 1990; Vreeland et al., 2000) have been generally regarded with scepticism and failed replication (Austin et al., 1997b, 1997a; Sidow et al., 1991). Under ideal preservation conditions, DNA is not expected to survive more than one million years (Lindahl, 1993).

Nevertheless, several advances were made in the post-PCR era and contributed to maintaining the credibility of the field: for example, the retrieval of fragments of mtDNA sequences from extinct animals, such as the thylacine (the Tasmanian wolf) (Thomas et al., 1989) and moa (Cooper et al., 1992), or the first DNA from the Pleistocene, recovered from extinct mammoths (Hagelberg et al., 1994) and cave bears (Hänni et al., 1994). In the following years, aDNA was proven useful for population and ecological studies, with publications on the population dynamics of European rabbits from the Pleistocene/Holocene transition (Hardy et al., 1995), and Ice Age brown bears in North America (Leonard et al., 2000), or the study of the ground sloth diet patterns over 20,000 years using aDNA extracted from coprolites (Hofreiter et al., 2000).

Presently, the oldest reliable authentic ancient genome has been recovered from a permafrost-preserved horse sample (~560–780 ka) (Orlando et al., 2013), followed by DNA from ~430 ka hominins from Sima de los Huesos, in Atapuerca, northern Spain (Meyer et al., 2014, 2016). Milestones include the analysis of DNA from the nuclear genome of the woolly mammoth (~28 ka) (Miller et al., 2008; Poinar et al., 2006), a small number of Neanderthal genomes of varying ages (Green et al., 2006, 2008, 2010; Prüfer et al., 2014, 2017), and a Denisovan individual, described solely based on the genetic evidence recovered from a phalanx (Meyer et al., 2012; Reich et al., 2010). All of these publications were ground-breaking. For instance, the studies of Neanderthal and Denisovan genomes were seminal by demonstrating interbreeding between ancient modern humans and other hominins, by detecting introgression of Neanderthal and Denisovan DNA into modern human populations (Sankararaman et al., 2016), a signal also recovered from a ~40 ka anatomically modern human from Peştera cu Oase, in Romania, who had a recent Neanderthal ancestor (Fu et al., 2015). Interestingly, as of last year, the genome of an offspring between a Neanderthal mother and a Denisovan father has directly shown that there was also interbreeding between these two hominin species (Slon et al., 2018).

The first anatomically modern human genome from the Holocene, a ~4 ka Palaeo-Eskimo from Greenland, was published in 2010 (Rasmussen et al., 2010), two years after the first complete ancient human mtDNA sequences (Ermini et al., 2008; Gilbert et al., 2008). Since then, several prehistoric humans from diverse locations and periods have been studied (reviewed in Skoglund and Mathieson, 2018; Slatkin and Racimo, 2016; Yang and Fu, 2018). However, despite recent efforts to increase sampling in other parts of the world, such as Africa (Fregel et al., 2018; Gallego Llorente et al., 2015; van de Loosdrecht et al., 2018; Rodríguez-Varela et al., 2017; Schlebusch et al., 2017; Skoglund et al., 2017), Asia (de Barros Damgaard et al., 2018a, 2018b; Narasimhan et al., 2018), America (Moreno-Mayar et al., 2018; Posth et al., 2018; Raghavan et al., 2015; Rasmussen et al., 2015a; Scheib et al., 2018), or Oceania (Lipson et al., 2018; Skoglund et al., 2016), most of the genetic studies still focus on Holocene Europe (as reviewed in Slatkin and Racimo, 2016).

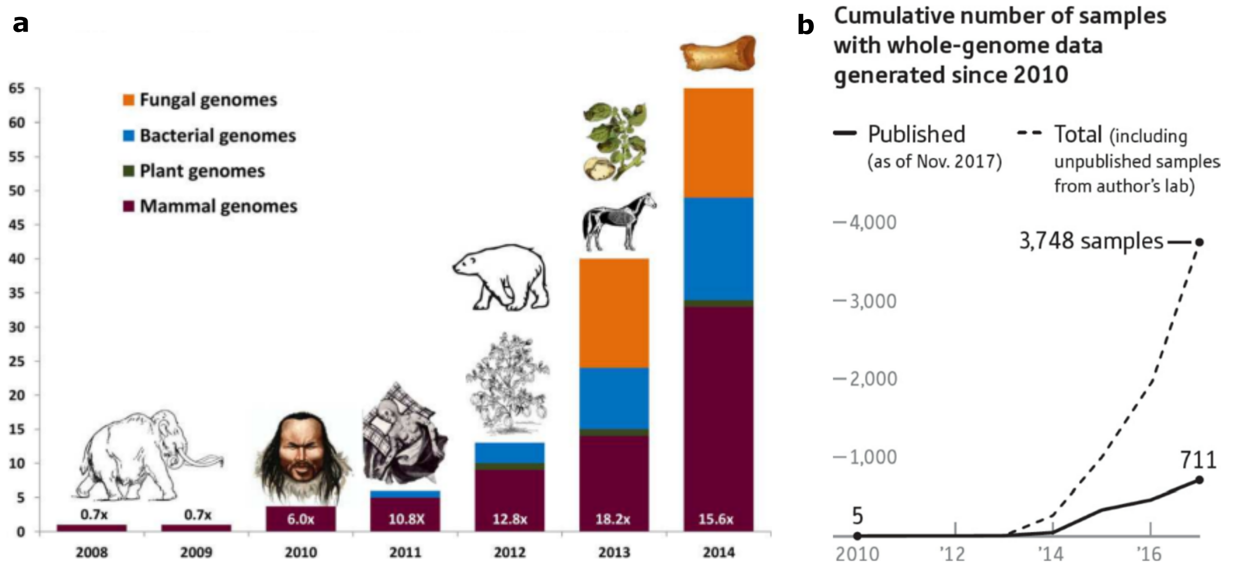

Figure 1.11. Constant increase in the number of ancient genomes published. **a**) Cumulative number of ancient genomes published since 2008, indicating the average-fold coverage. Figure from Hofreiter et al., 2015. **b**) Cumulative number of samples with genome-wide data generated since 2010: published (as of November 2017) *versus* the total number of samples studied (including unpublished samples from Reich's lab). Figure from Reich, 2018.

Nowadays the state-of-the-art for recovery of aDNA from Holocene human specimens is to target the petrous portion of the temporal bone, the densest bone in the human skeleton (Gamba et al., 2014; Pinhasi et al., 2015). This, combined with the development of NGS technologies allowed for a revolution in the field of aDNA, with an exponential growth in the number of recent publications. Published datasets are ever-increasing, from single-sample studies a decade ago, to dozens, and now hundreds of samples being analysed in a single study (Figure 1.11) (Hofreiter et al., 2015; Reich, 2018). Moreover, due to the diversification and improvement of laboratory methods, the quality of the data retrieved also increased: it is now possible to recover higher-coverage genomes, or alternatively a higher number of SNPs with SNP-capture approaches.

3.2. Next-generation sequencing

NGS allows a thorough exploration of the variation within the genome, with the possibility of sequencing entire genomes or screening thousands of single nucleotide polymorphisms (SNPs). NGS methods, require smaller amounts of template DNA and, in the case of Illumina platforms, produce very short reads, repeatedly sequenced several times, ideal for aDNA, which is naturally highly fragmented. Moreover, the inherent high depth is useful as a quality control, and the possibility of multiplexing allows the screening of multiple samples simultaneously with low risk of cross-contamination.

There are currently two main approaches to retrieve GW data from human archaeological remains (Hofreiter et al., 2015): either sequencing all the DNA present in the extract (which usually include a high proportion of contaminant DNA from environmental and pathogenic microorganisms, which are also co-amplified and sequenced), or target-enrichment capture methods, by using probes to select only the human genome (Carpenter et al., 2013), or specific portions of the genome, such as the exome (Castellano et al., 2014), individual chromosomes (Cruz-Dávalos et al., 2018; Fu et al., 2013), the mitochondrial genome (Briggs et al., 2009; Brotherton et al., 2013), or a specific set of SNPs (Elhaik et al., 2013; Haak et al., 2015).

Whole-genome shotgun sequencing (WGS) provides information regarding endogenous aDNA content and patterns of DNA fragmentation to assess authenticity, and offers an unbiased view of the genetic variation present in an individual. Moreover, it is possible to BLAST the sequencing output for pathogen DNA (Huebler et al., 2019), an approach that allowed the successful identification of, for example, *Yersinia pestis* (Andrades Valtueña et al., 2017; Rasmussen et al., 2015b; Spyrou et al., 2016, 2018), *Salmonella enterica* (Vågene et al., 2018), *Mycobacterium tuberculosis* (Bos et al., 2014), and *M. leprae* (Schuenemann et al., 2018) in ancient human remains.

However, the costs of WGS can be prohibitive, especially for poorly-preserved samples. Target-capture methods can be an alternative in such cases. One of the most commonly used approaches is the Human Origins SNP array, which allows the genotyping of hundreds of thousands of SNPs (Haak et al., 2015; Patterson et al., 2012). However, such SNP panels can be prone to ascertainment bias, which might be especially problematic when attempting to capture ancient variation, and therefore in some cases these SNPs might not be representative of past variation and lead to underestimation of ancient diversity (Hofreiter et al., 2015; Lachance and Tishkoff, 2013).

3.3. Uniparental markers

Uniparental genetic markers, mtDNA and the male-specific portion of the Y-chromosome (MSY), allow the study of sex-biased demographic events (female and male-mediated, respectively), due to their uniparental inheritance and lack of recombination (Figure 1.12). Since they are effectively haploid and have a lower effective size (N_e) than autosomal DNA (one-quarter), uniparental markers are more prone to drift (stochastic changes) and more sensitive to demographic events such as migrations, founder effects or bottlenecks (Destro-Bisol et al., 2010; Jobling, 2012).

Using these markers it is possible to reconstruct the evolution of different lineage clusters (known as haplogroups) based primarily on mutational events and build phylogenies that represent the relationship among lineages (Jobling and Tyler-Smith, 2003; Underhill and Kivisild, 2007). By applying a molecular clock to assess the age of lineages, or the time to the most recent common ancestor (TMRCA), it is possible to infer expansion times and other demographic events that contributed to shape the observed phylogeny (Underhill and Kivisild, 2007).

3.3.1. Mitochondrial DNA

Mitochondrial DNA (mtDNA) is a circular double-stranded molecule present in mitochondrial matrix, normally as a supercoiled structure. It has ~16.6 kilobase pairs (kb) in humans (<0.001% of the size of the nuclear human genome), and codes for proteins involved in oxidative phosphorylation (Jobling et al., 2014). The first complete human mtDNA sequence, mainly from a British individual, was published in 1981 (Anderson et al., 1981), but was later corrected (Andrews et al., 1999). The new corrected sequence is known as the rCRS (revised Cambridge Reference Sequence) and is still used nowadays as a reference mitochondrial genome. Although a new human mtDNA reference sequence was later proposed, the Reconstructed Sapiens Reference Sequence (RSRS) (Behar et al., 2012a), much of the software available for mtDNA analyses still uses the rCRS. Moreover, the use of RSRS is not unanimously accepted by experts in mtDNA analysis, due to issues in reconstructing the ancestral state of some of its positions (Bandelt et al., 2014; Malyarchuk, 2013).

The mtDNA molecule is very compact and mostly coding (with all the protein-coding genes lacking introns), except for a ~1200 base-pair (bp) long segment with regulatory functions (from position 16,024 to 576), known as the control region (Anderson et al., 1981), which encompasses two fast-evolving segments – hypervariable segments I and II (HVS-I and HVS-II). The mtDNA has a higher mutation rate than nuclear DNA (nDNA) (Brown et al., 1979), as it is not protected by histones and is heavily exposed to free radicals of oxygen resulting from cellular respiration (Fernández-Silva et al., 2003), but the molecule does not evolve all at the same rate – the control region (particularly the hypervariable segments) has a higher mutation rate (Pakendorf and Stoneking, 2005). Most of the early mtDNA studies relied uniquely on HVS-I (due to its higher mutation rate), or in some cases on the whole control region, due to the high costs and heavy workload involved in routinely sequencing the whole molecule using standard PCR and Sanger sequencing.

Despite some scarce and highly contentious (Lutz-Bonengel and Parson, 2019; Salas et al., 2019) evidence of paternal or biparental mitochondria transmission in a context of suspected mitochondrial disease (Luo et al., 2018; Schwartz and Vissing, 2002), mtDNA is considered a uniparental marker in healthy individuals, accounting only for the maternal variation of a population. Due to its fast mutation rate, mtDNA accumulates variation relatively rapidly and is a suitable molecular marker for a phylogeographic approach. Using reliable mtDNA mutation rates, it is possible to frame the various demographic events within distinct time periods (Soares et al., 2009). Since a eukaryotic cell has a variable number of mitochondria (mammalian cells typically contain 1000 to 10,000 organelles) and each mitochondrion contains several (2–10) copies of mtDNA molecules (Shuster et al., 1988; Wiesner et al., 1992), mtDNA is present at a much higher copy number than nDNA. This is of particular importance in aDNA studies as mtDNA is easier to recover and authenticate than nDNA, especially for poorly preserved samples. However, it is worth noting that the petrous bone, which is not very metabolically active, yields comparatively less mtDNA than, for example, tooth cementum (Hansen et al., 2017).

3.3.1.1. Mitochondrial phylogeography

Being non-recombining, mtDNA is transmitted from mothers to children as a unique locus, in a block known as haplotype. The term "haplogroup", first coined by Torroni et al. (1993), refers to a monophyletic cluster of haplotypes, *i.e.* a group of all lineages sharing a common ancestor, either extant or reconstructed. The mtDNA haplogroups are labelled with a capital letter defining the main haplogroup, with more derived branches usually named by intercalating lower-case letters and numbers (*e.g.* H, H1, H1a, H1a1, etc.) (van Oven and Kayser, 2009; Richards et al., 1998). The first haplogroups defined (A, B, C, and D) were described in Native American populations (Torroni et al., 1993), and haplogroups subsequently reported were designated with other letters of the alphabet, which do not reflect any particular evolutionary logic.

The first attempts to define a global tree for mtDNA variation were based on RFLP (restriction-fragment length polymorphism) analysis, and haplogroups were defined by specific restriction sites. Despite the low resolution associated with this type of approach, the early studies were able to identify the major basal clades (Richards et al., 1998; Torroni et al., 1996). With DNA sequencing the level of resolution of the tree has increased, and the basal clades were dissected into younger monophyletic branches, representing more restricted geographic units (Richards and Macaulay, 2001). The resolution of the worldwide mtDNA tree has increased enormously in the last decade, with the sequencing of the entire molecule becoming routinely performed. The global phylogenetic tree for human mtDNA (PhyloTree) (van Oven and Kayser, 2009) presently comprises more than 24,000 complete published mtDNA sequences (PhyloTree Build 17, as of February 2016) (van Oven, 2015). However, it lacks most of the ancient mtDNA variation reported in the last few years and the associated topology implications (*e.g.* the previously undescribed pre-N and M0 lineages (Fu et al., 2015; Posth et al., 2016)).

The phylogenetic tree of human mtDNA ultimately traces back to two basal African clades: L0 and L1′2′3′4′5′6, the latter being more widespread and comprising the majority of lineages found today both within and outside of Africa (Torroni et al., 2006). The L(xMN) haplogroups are the autochthonous African lineages and the deepest clades of the phylogeny, reflecting the African origin of *Homo sapiens*, whereas all non-African mtDNA diversity (macrohaplogroups M, N and R) descends from one specific African haplogroup (L3) (Macaulay et al., 1999; Watson et al., 1997).

The topology of the mtDNA global phylogenetic tree reflects a period of population growth between 40 and 50 ka (Miller et al., 2018), particularly visible in the lineages that directly descend from L3, and coinciding with the arrival of basal M and R lineages to South Asia (Atkinson et al., 2009; Behar et al., 2012a; Mellars et al., 2013; Soares et al., 2009). This population growth intensified in the post-glacial period in several regions of the world (Batini et al., 2017; Miller et al., 2018).

3.3.1.2. Eurasian mtDNA variation

The present-day European mitochondrial gene pool is largely characterized by derived lineages of haplogroups U, R0 (mostly H) and JT (Soares et al., 2010). The majority of Mesolithic European lineages retrieved to date belong to haplogroup U (Figure 1.12), more specifically to U5, but also U4 and U8 (Brandt et al., 2013). However, the maternal variation in the Palaeolithic was more diverse, including also U6 (Fu et al., 2016; Hervella et al., 2016), a lineage found today mostly in North Africa, and M0 (Fu et al., 2016; Posth et al., 2016), providing evidence that M lineages, nowadays restricted to Asia, were once also found in Europe (Richards et al., 2016). The current distribution of U6, with the highest frequencies in North Africa and restricted in Europe to the Mediterranean areas, and the virtual absence of M lineages in Europe reflect the importance of pre-Holocene events in shaping European genetic variation (Posth et al., 2016).

With the climate improvement in the post-LGM (Last Glacial Maximum), the current European gene pool started to form, likely with the arrival of JT lineages to Europe (Pala et al., 2012; Pereira et al., 2017) and increment in effective population sizes (N_e) (Batini et al., 2017; Miller et al., 2018). However, the most common maternal lineage found in Europe nowadays, haplogroup H (Pala et al., 2016; Soares et al., 2010), was never found in pre-Neolithic remains, suggesting instead a Neolithic origin for this lineage (Figure 1.12). Detailed information about mtDNA haplogroup H is provided in Chapter III.

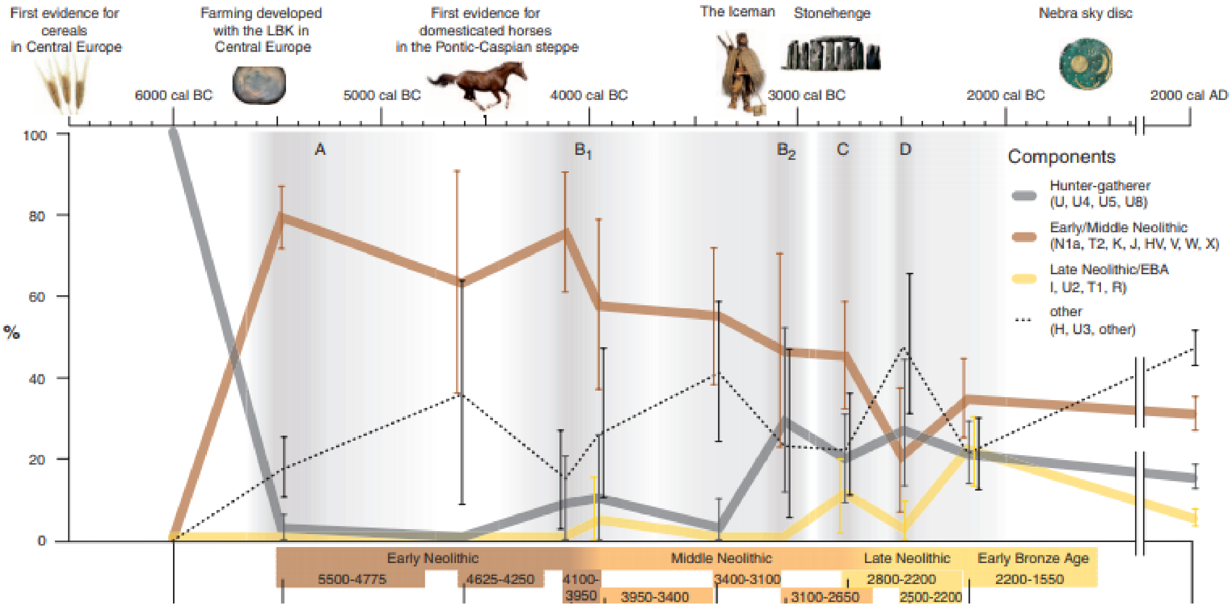

Figure 1.12. Mitochondrial variation in Central Europe through time, from the Late Mesolithic to present day. Figure from Brandt et al., 2013.

Maternal diversity in South Asia consists mostly of basal autochthonous lineages of the out-of-Africa founder haplogroups M and N (the latter largely from the derived sub-haplogroup R) (Mellars et al., 2013; Palanichamy et al., 2004; Sun et al., 2006). An overview of mitochondrial variation in South Asia is provided in Chapter II, and its detailed analysis has been published as Silva et al. (2017).

Stark differences in the patterns observed for mtDNA and Y-chromosome in Eurasia suggest sex-specific dynamics (Batini et al., 2017; Lippold et al., 2014). While a large proportion of present-day European and South Asian Y-variation dates to the last 5 ka (Batini et al., 2015; Karmin et al., 2015), most European mtDNA lineages are associated with post-glacial and Neolithic arrivals, when the bulk of the current mitochondrial European variation was established (Brandt et al., 2013; Pala et al., 2012; Posth et al., 2016). The South Asian maternal gene pool is even older, reflecting mostly the first settlement of the region (Mellars et al., 2013), but also with some evidence for post-glacial and Neolithic arrivals (discussed in detail in Chapter II, published as Silva et al. (2017)). Therefore, in contrast with the Y chromosome, Chalcolithic and Bronze Age related mtDNA lineages are much rarer (with the exception of the expansion of some specific T lineages (Figure 1.12)), a signal of male-biased demographic events during this period (Brandt et al., 2013).

3.3.2. Y chromosome

The MSY consists of about 95% of the total length of the Y chromosome in humans, corresponding to around 57 megabase pairs (Mb) in length (Hammer and Zegura, 2003; Jobling and Tyler-Smith, 2003). Initial studies of the Y chromosome focused on two distinct types of polymorphisms: bi-allelic markers (SNPs, *Alu*-insertions and insertions/deletions (indels)), and multi-allelic markers (microsatellites, also known as short tandem repeats, or STRs). Bi-allelic SNPs were used to define the main haplogroups, with additional resolution being provided by STR typing (Jobling and Tyler-Smith, 2003; The Y Chromosome Consortium, 2002).

These earlier approaches were problematic in many ways. One issue was that SNPs were often chosen from a panel of previously studied markers, which can lead to ascertainment bias and result in the systematic distortion of the results due to biases in the set of markers included in the populations used as reference (Jobling and Tyler-Smith, 2003). Additionally, age estimates based on STRs are not very robust (Carvalho-Silva et al., 1999), since they strongly depend on the choice of markers, and STRs evolve at a high rate and usually under a stepwise mutation model, which can rapidly lead to homoplasy (Jobling et al., 2014). Moreover, mutation rates vary drastically across different STRs (Carvalho-Silva et al., 1999; Jobling and Tyler-Smith, 2003). Binary markers such as SNPs, with lower mutation rates, are less prone to parallel and back mutations and are, therefore, more suitable to trace back paternal lineages over thousands of years (The Y Chromosome Consortium, 2002), but until recently it was not feasible to rely uniquely on SNPs to build and date Y-phylogenies.

Thanks to NGS methods it is now possible to sequence large portions of the MSY (Wei et al., 2013) and overcome many of the previous issues with STRs and SNP selection. Recent studies have produced high-resolution MSY phylogenies based on SNPs extracted from Y-chromosome resequencing (Batini et al., 2015; Karmin et al., 2015; Poznik et al., 2016) and proved very useful in refining the narrative of the peopling of Eurasia, especially in the last 5 ka.

3.3.2.1. Y-chromosome variation in Eurasia

Mesolithic European lineages belong mostly to haplogroup I, which was already present in Europe in the Palaeolithic (Fu et al., 2016), but the picture is not straightforward, since I (especially I2) is also associated with farmers in Europe (Gamba et al., 2014; Mathieson et al., 2015), recently suggested as a signal of male-mediated gene flow from hunter-gatherers to farmers during the Middle and Late Neolithic (Sánchez-Quinto et al., 2019). Haplogroups G and H were the most common amongst Anatolian and Iranian early farmers (Broushaki et al., 2016; Lazaridis et al., 2016). G (together with I2) is also found amongst European Early Neolithic remains (Mathieson et al., 2015), despite being rare today in most of Europe, except for some specific G2a lineages that display peaks of frequency in isolated populations in Sardinia, Corsica and the Tyrol (Berger et al., 2013; Keller et al., 2012). Haplogroup H, on the other hand, is today predominantly present in South Asia (Karmin et al., 2015; Kivisild, 2017).

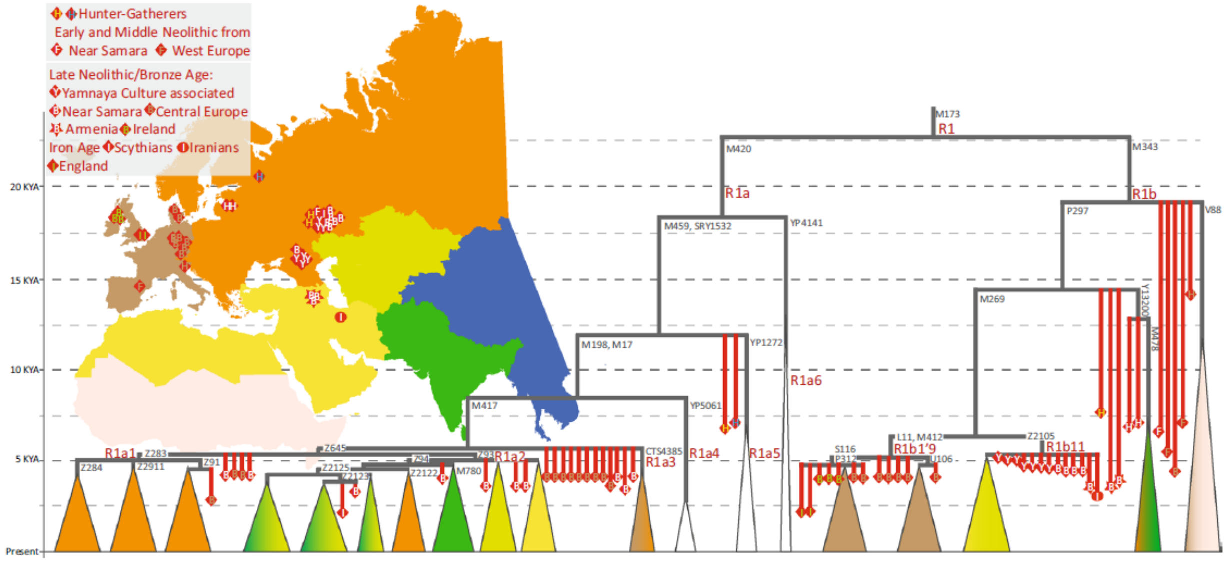

Figure 1.13. Schematic tree of Y-chromosome haplogroup R1-M173, including present-day variation and ancient samples (in red). Colours represent main geographic distribution of each branch, according to the map shown on top left. Figure from Kivisild et al., 2017.

One of the most frequent lineages in Eurasia today is R1. Y-chromosome haplogroup R is divided into two main branches, R1-M173 and R2-M479 and accounts for more than half of the European male population (Jobling and Tyler-Smith, 2003). It is also common in Western, Central and South Asia (reaching frequencies up to ~50% in some populations), as well as in some regions along the Sahel corridor in Africa (Jobling and Tyler-Smith, 2003). The main branch in Europe is R1-M173, which subdivides into R1a-M420 and R1b-M343 (Figure 1.13). While the first has a wider distribution across Eurasia, the latter is essentially restricted to western and central Europe, but also found at considerable frequencies (>5%) in other very distinct regions, such as the Balkans, Anatolia, the Caucasus, the Near East, Pakistan and North Africa (Battaglia et al., 2009; Myres et al., 2011; Robino et al., 2008). On the other hand, R2-M479 has a more restricted distribution, and is found essentially in certain regions of the Indian Subcontinent, Iran and southern Central Asia (Kivisild et al., 2003; Sahoo et al., 2006).

Even though previous studies based on a few markers argued for a postglacial expansion of Y-chromosome R1 lineages (Semino, 2000; Underhill et al., 2010), recent more precise analyses of Y-chromosome sequencing data (Batini et al., 2015; Karmin et al., 2015; Poznik et al., 2016) have shown that R1 expanded across Eurasia mainly during the Late Neolithic/Chalcolithic and Early Bronze Age, in the form of specific R1a and R1b lineages (Figure 1.13) (Karmin et al., 2015).

R1a has been found in the majority of remains analysed to date from the Bronze Age Sintashta culture (eastern of the Urals), the Sintashta-derived Andronovo horizon in Central Asia and the Late Bronze Age Srubnaya culture in the Pontic-Caspian Steppe (Allentoft et al., 2015; Mathieson et al., 2015). R1a is also predominant in kurgan burials in south-central Siberia (Keyser et al., 2009), dating from the Middle Bronze Age Andronovo horizon and to the Late Bronze and Iron Ages, which are the potential source populations for Bronze Age expansions of Indo-Iranian speakers to Iran and the Indian Subcontinent, by the end of the Indus Valley civilization, ~4.0–3.5 ka (Parpola, 2015).

Interestingly, R1a has never yet been found amongst Yamnaya remains. In contrast, they harbour R1b lineages (Allentoft et al., 2015; de Barros Damgaard et al., 2018a; Haak et al., 2015), which has a more western-central European distribution today, peaking in Ireland, Wales and the Basque region of Spain (Myres et al., 2011; Young et al., 2011). R1b (Figure 1.14) dates to the LGM (~20.9 ka (Karmin et al., 2015)), with deep pre-Neolithic and Eneolithic south Russian lineages at the root of its tree (Mathieson et al., 2015). Additionally, deep-rooting lineages have been identified in Late Glacial Italy (Villabruna, dating to ~14.0 ka) (Fu et al., 2016) and Early Neolithic Spain (~7.0 ka) (Haak et al., 2015). However, despite appearing to be present in Europe since Late Glacial times, these ancient lineages are very uncommon amongst modern Europeans (Figure 1.14). Instead, the majority of European males today belong to more recent star-like branches within R1b-M269 (dating to ~5.5 ka) (Batini et al., 2015), suggesting a rapid population growth associated with these lineages (Poznik et al., 2016): R1b-L11 (>70% frequency in west Europe (Myres et al., 2011)) and R1b-S116 (nested within R1b-L11) date to around 4.5 ka and 4.2 ka respectively (Batini et al., 2015). Although these dates coincide with the expansion of Corded Ware pastoralists in northern and central Europe, the connection between genetic and archaeological evidence is not so straightforward, since Corded Ware individuals studied to date belong mostly to other Y-chromosome lineages (namely, R1a and I2a (Allentoft et al., 2015; Mathieson et al., 2015; Olalde et al., 2018)).

Nevertheless, both R1a and R1b seem to have been involved in population movements across and out of the Eurasian Steppe, most likely associated with the spread of the Indo-European language family.

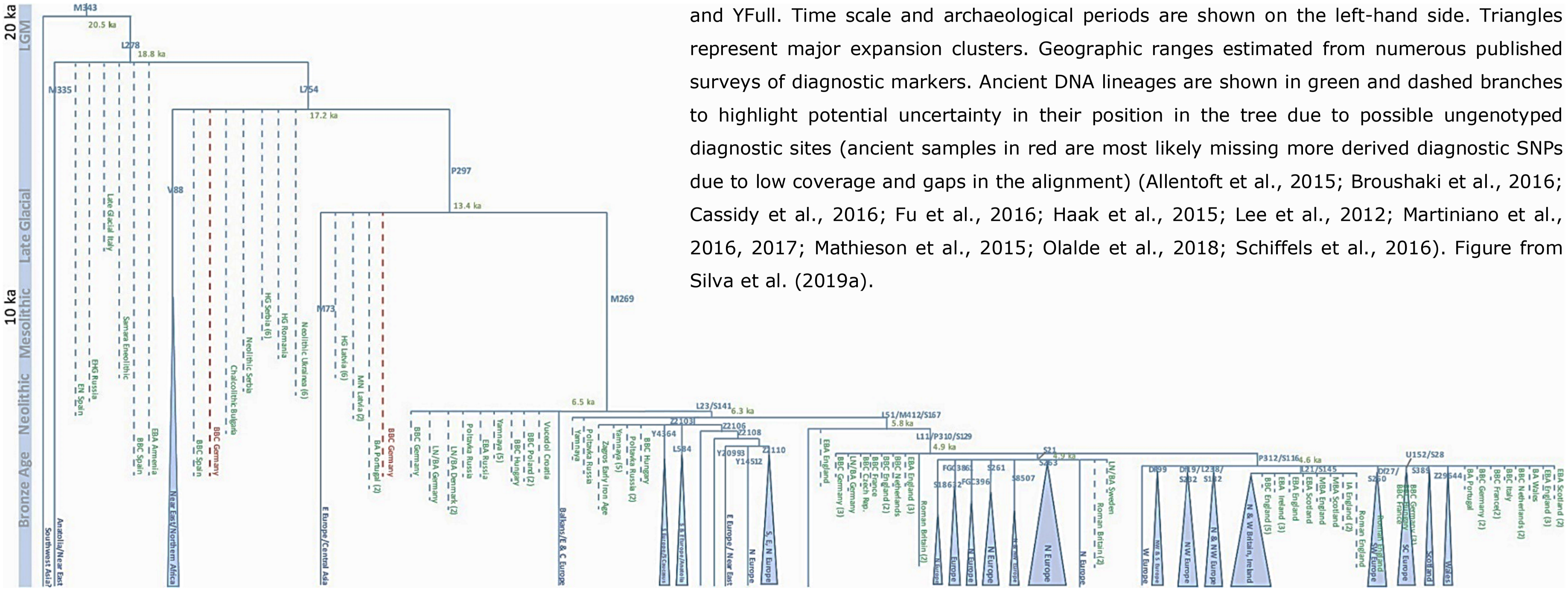

Figure 1.14. Schematic tree of Y-chromosome haplogroup R1b. Branching structure based on PhyloTree-Y, age estimates based on Batini et al., 2015; Karmin et al., 2015; Poznik et al., 2016 and YFull. Time scale and archaeological periods are shown on the left-hand side. Triangles represent major expansion clusters. Geographic ranges estimated from numerous published surveys of diagnostic markers. Ancient DNA lineages are shown in green and dashed branches to highlight potential uncertainty in their position in the tree due to possible ungenotyped diagnostic sites (ancient samples in red are most likely missing more derived diagnostic SNPs due to low coverage and gaps in the alignment) (Allentoft et al., 2015; Broushaki et al., 2016; Cassidy et al., 2016; Fu et al., 2016; Haak et al., 2015; Lee et al., 2012; Martiniano et al., 2016, 2017; Mathieson et al., 2015; Olalde et al., 2018; Schiffels et al., 2016). Figure from Silva et al. (2019a).

3.3.3. Phylogeographic approach

Phylogeography aims to apply phylogenetic methods to the study of intraspecific genetic variation, by combining geographic information with an appropriate mutation rate to the molecular marker under study, in order to date geographically specific nodes within a given phylogeny (Avise et al., 1987; Hewitt, 2001). A lineage-based approach is important to organize the phylogenetic tree of a given haplogroup, in order to overcome nomenclature issues and provide a tool for quality assessment (Bandelt et al., 2001; Behar et al., 2012a), especially useful to assess authenticity in low coverage, very fragmented and/or contaminated ancient mtDNA sequences. Although the analysis of a given lineage does not equate to the study of a population, it can provide insights into the demography of populations and reveal informative patterns that would otherwise be missed.

Some authors defend a uniquely population-based strategy (Langaney et al., 1992; Pakendorf and Stoneking, 2005; Simoni et al., 2000). However, the majority of mtDNA population studies are not based on complete sequences, relying instead on HVS-I (or the whole control region), since it accumulates mutations at a high rate (van Oven and Kayser, 2009; Pakendorf and Stoneking, 2005). This fast mutation rate can lead to homoplasy and recurrence within the control region (Underhill and Kivisild, 2007), which might result in distant lineages sharing similar diagnostic positions, or in the loss of "intermediate" polymorphic states due to back mutations. Moreover, in some cases, such as many haplogroup H lineages, diagnostic mutations would never be considered, since they are only located within the coding region. Consequently, the resolution of many population studies based only on HVS-I or control region is very low. For MSY, sequence data is even rarer, due to its size (~57 Mb) and internal organization, with long stretches of satellite DNA (tandem repetitive traits) that render more difficult the sequencing process (Bachtrog and Charlesworth, 2001), and has only become a reality in the last few years (Batini et al., 2015; Karmin et al., 2015; Poznik et al., 2016).

When studying a specific mtDNA or Y-chromosome haplogroup we are only recovering the history of that specific lineage, a small fraction of all maternal or paternal variation, which is, by itself, a small fraction of all the genetic variation contained within the population. Combining a lineage-based approach with population analysis based on GW markers allows us to confirm the patterns observed in the uniparental phylogenetic trees, and offers a population-level perspective.

3.4. Genome-wide variation

The first draft of the human genome was published in 2001, as a result of an endeavour of over 10 years and a collaboration of several laboratories and funding bodies, both public and private (International Human Genome Sequencing Consortium, 2001; Olson, 1993; Sawicki et al., 1993; Venter et al., 2001). The human nuclear genome, consisting of 23 pairs of chromosomes (22 pairs of autosomes and two sex chromosomes), comprises ~3.2 gigabases (Gb) (Jobling et al., 2014). Most of the variation found in the human genome does not result in phenotypic alterations, and does not affect evolutionary fitness – this is usually referred to as neutral variation (Jobling et al., 2014). A typical genome displays ~4.1–5.0 million variant sites relative to the human reference sequence (a composite of DNA from several individuals, except for the Y-chromosome sequence that derives mostly from one single individual) – 99.9% of these variants are SNPs and short indels, with African genomes harbouring the highest number of non-reference sites (The 1000 Genomes Project Consortium, 2015).

The average cost per genome has decreased dramatically in the last few years, with an authentic revolution in sequencing technologies – the development of NGS methods. The applications resulting from the sequencing of human genomes are countless. Genome-wide (GW) studies aim to capture and analyse the autosomal variation of the genome and have proved important not only for demographic studies of human populations, but also to assess patterns of selection and their potential biomedical implications (Collins, 1999; Prohaska et al., 2019; Rosenberg et al., 2010). A GW approach allows us to identify population structure (Figure 1.15), as well as to detect and quantify admixture between populations with distinct ancestries (Novembre and Ramachandran, 2011).

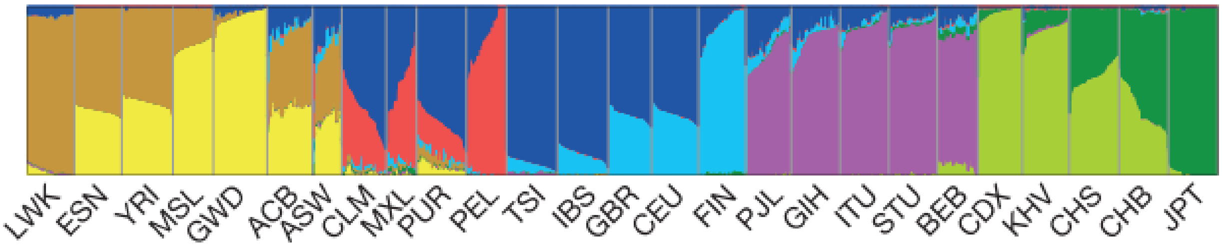

Figure 1.15. Population structure in world-wide populations with eight clusters (*K*=8). Population codes: FIN, Finnish in Finland; GBR, British in England and Scotland; CEU, Utah Residents (CEPH) with northern and western European ancestry; IBS, Iberian population in Spain; TSI, Toscani in Italia; CHS, Southern Han Chinese; CDX, Chinese Dai in Xishuangbanna, China; CHB, Han Chinese in Beijing, China; JPT, Japanese in Tokyo, Japan; KHV, Kinh in Ho Chi Minh City, Vietnam; GIH, Gujarati Indian from Houston, Texas; STU, Sri Lankan Tamil from the UK; PJL, Punjabi from Lahore, Pakistan; ITU, Indian Telugu from the UK; BEB, Bengali from Bangladesh; PEL, Peruvians from Lima, Peru; MXL, Mexican ancestry from Los Angeles USA; CLM, Colombians from Medellin, Colombia; PUR, Puerto Ricans from Puerto Rico; ASW, Americans of African ancestry in SW USA; ACB, African-Caribbeans in Barbados; GWD, Gambian in Western Divisions in the Gambia; YRI, Yoruba in Ibadan, Nigeria; LWK, Luhya in Webuye, Kenya; ESN, Esan in Nigeria; MSL, Mende in Sierra Leone. Figure adapted from The 1000 Genomes Project Consortium, 2015.

GW studies gained importance and became the state-of-the art in the last few years due to several recent methodological and technical advances: increased read length, reduced per-base error rate, paired-end sequencing, and improved data analysis tools, with the development of strategies for filtering poor-quality data, more accurate mapping and variation identification (The 1000 Genomes Project Consortium, 2015). For aDNA specifically, several tools have been developed to deal with very short reads, post-mortem damage patterns, or contamination (Jónsson et al., 2013; Renaud et al., 2014; Skoglund et al., 2014).

3.4.1. GW patterns in Eurasian populations

GW studies have shown north-south and east-west clines in Europe (Figure 1.16) (Novembre et al., 2008; The 1000 Genomes Project Consortium, 2015).

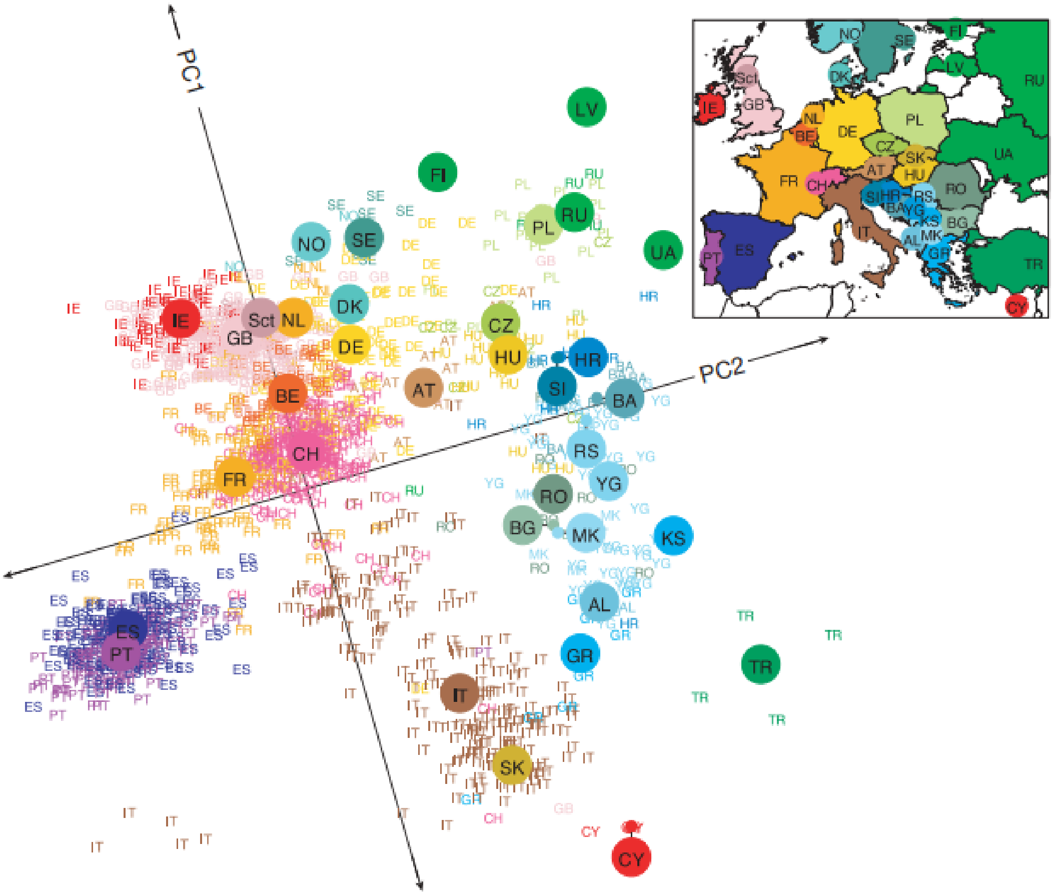

Figure 1.16. Principal component analysis based on 197,146 GW loci and 1,387 European individuals. Individuals labelled according to self-reported country of origin (large coloured points represent median PC1 and PC2 values for each country). Population codes: AL, Albania; AT, Austria; BA, Bosnia-Herzegovina; BE, Belgium; BG, Bulgaria; CH, Switzerland; CY, Cyprus; CZ, Czech Republic; DE, Germany; DK, Denmark; ES, Spain; FI, Finland; FR, France; GB, United Kingdom; GR, Greece; HR, Croatia; HU, Hungary; IE, Ireland; IT, Italy; KS, Kosovo; LV, Latvia; MK, Macedonia; NO, Norway; NL, Netherlands; PL, Poland; PT, Portugal; RO, Romania; RS, Serbia; RU, Russia, Sct, Scotland; SE, Sweden; SI, Slovenia; SK, Slovakia; TR, Turkey; UA, Ukraine; YG, former Yugoslavia. Figure from Novembre et al., 2008.

Most modern European populations display three distinct GW components (Figure 1.17a): (1) a hunter-gatherer component, common to all European populations, but present at its highest frequency in the Saami (Huyghe et al., 2011), and seen in Mesolithic individuals at ~100% (Haak et al., 2015); (2) a Neolithic component (found earliest in the early Levantine and Anatolian farmers, and Natufian Levantine hunter-gatherers) (Lazaridis et al., 2016), brought to Europe from the Near East during the agricultural expansions; and (3) a component absent before the Late Neolithic seen at high frequencies in the Bronze Age Yamnaya individuals of the Pontic-Caspian Steppe (Allentoft et al., 2015; Haak et al., 2015). This component reaches the highest frequency in Late Palaeolithic and Mesolithic individuals from the Caucasus, and has therefore been dubbed the "Caucasus hunter–gatherer" (CHG) component (Jones et al., 2015), but it is also seen at similarly high frequencies in Mesolithic and Neolithic remains found in Iran (Lazaridis et al., 2016). This CHG/Steppe-related component varies in frequency amongst present-day European populations, reaching its maximum in central and northern Europe, while being less frequent in southern Europe, especially in Sardinia (Haak et al., 2015; Marcus et al., 2019).

According to a recent study on a large dataset of ancient individuals (a total of over 640 ancient European samples) (Olalde et al., 2018), British Bell Beaker individuals trace most of their ancestry to central Europe, displaying the three aforementioned components (Figure 1.17b). This suggests a discontinuity in Britain between the Late Neolithic and the Beaker period, due to a migration from central Europe into Britain that virtually replaced the previous genetic diversity. However, in Iberia the picture is not so straightforward, with the CHG component not always present in Iberian Beaker remains, who seem to have retained more of the previous genetic variation, with most individuals resembling those from the Chalcolithic and Late Neolithic (Olalde et al., 2018). It has been recently shown that Iberian individuals started displaying the CHG component ~2500 BCE, associated with the arrival of R1b Y-chromosome lineages, which virtually replaced all the previous existing paternal variation (Martiniano et al., 2017; Olalde et al., 2019). Nevertheless the population dynamics responsible for the entrance and spread of the CHG component to Iberia are not yet completely understood, especially regarding the dissemination of Y-chromosome R1b lineages.

Present-day South Asian populations also carry the CHG component at varying proportions (de Barros Damgaard et al., 2018a). Whilst a fraction of this may be the result of agricultural dispersals into the Subcontinent from Iran, a recent study has compared the contribution of both the Iranian Neolithic and Yamnaya gene pools as proxies for the sources for modern South Asian populations and concluded that the Yamnaya/Steppe-related proportion was as great or greater than the Neolithic Iranian fraction for many Indian and Pakistani populations (Narasimhan et al., 2018). However, there was no direct contact between the Yamnaya and South Asian populations in the Early Bronze Age. Instead, the Steppe component, and by inference the Indo-European languages and associated archaeology, seem to have arrived to the Subcontinent in Late Bronze Age Steppe movements from Central Asia (Allentoft et al., 2015; de Barros Damgaard et al., 2018a; Narasimhan et al., 2018) (more details on Chapter Two).

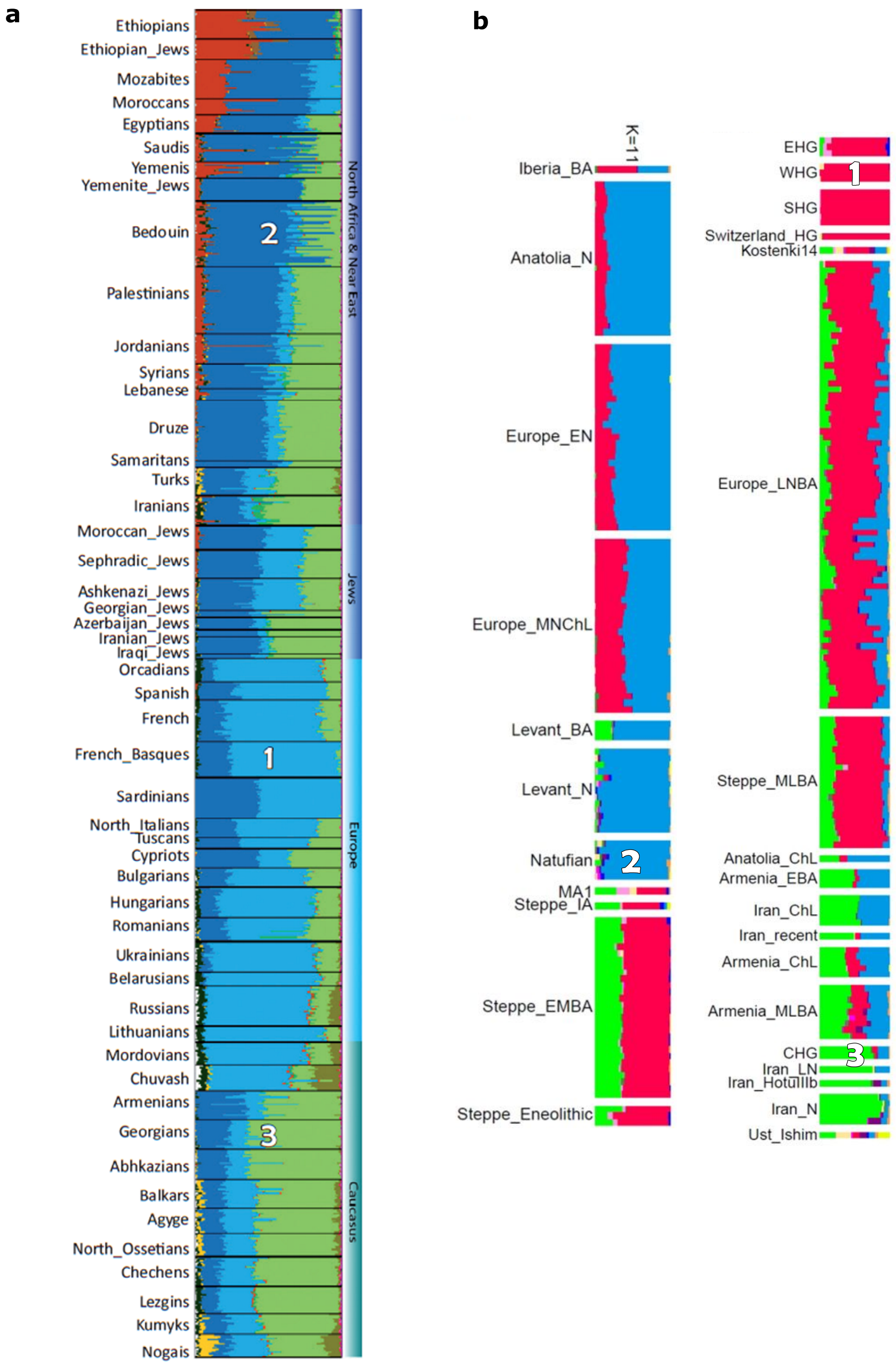

Figure 1.17. ADMIXTURE results for **a)** modern (adapted from Pala et al., 2016) and **b)** ancient populations (adapted from Lazaridis et al., 2016), showing the three components associated to European populations: 1) hunter-gatherer component, 2) Neolithic/Anatolian component, and 3) Caucasus hunter-gatherer component.

4. Objectives and thesis outline

The main goal of this project is to study the demographic dynamics of human populations that occurred at the Metal Age transition in Eurasia, focusing on the two extremes of the Indo-European distribution: South Asia and Iberia. Additionally, I also present results from a pilot study on the Medieval period in Iberia, a period of known movement of people and cultural transition in the region. The methods and results will be presented as follows:

Chapter II. A genetic chronology for the Indian Subcontinent: sex-biased dispersals in the Bronze Age

Here I present a chronology for the peopling of South Asia, combining information from uniparental markers and genome-wide patterns from the Subcontinent and neighbouring regions, and taking into consideration the most updated aDNA evidence.

Chapter III. Dissecting mtDNA haplogroups H1, H2, H11 and H13

In this chapter I assess the phylogeographic patterns of mtDNA haplogroup H, the most common maternal European lineage today, and found at minor frequencies in the Indian Subcontinent. I focus my analysis on H1, H2, H11 and H13. Additionally, I give an overview of modern Iberian mtDNA variation and present a follow-up of the work presented in Chapter II, focusing on specific H2 and H13 branches present in both Europe and South Asia.

Chapter IV. A genetic snapshot of Medieval Iberia: a pilot study

This is a pilot aDNA study in order to delineate the strategy for Chapter V. Here I focus mostly on the genomic analysis of an individual from a Spanish Islamic Necropolis (11th–13th century CE), but I also analyse mtDNA information from additional earlier (pre-Islamic) individuals. Additionally, I assess the impact of the Islamic Period in modern Iberia by focusing on the study of mtDNA haplogroup U6.

Chapter V. Transition to Metal Ages in Iberia: preliminary results

Here I present preliminary analyses on a dataset of 19 individuals from Late Neolithic/Chalcolithic/Bronze Age sites in Iberia.

Chapter II

A genetic chronology for the Indian Subcontinent: sex-biased dispersals in the Bronze Age

Most of the content of this chapter is published in:

Silva M, Oliveira M, et al. A genetic chronology for the Indian Subcontinent points to heavily sex-biased dispersals. BMC Evolutionary Biology 2017, 17:88. DOI:10.1186/s12862-017-0936-9.

My contributions to this paper were as follows:

- Phylogeographic analysis of "non-autochthonous" lineages (*ρ* and ML);
- GW analysis (PCA and ADMIXTURE) with the dataset including the Yamnaya;
- Comparison of ancestry proportions on the 1KGP dataset;
- Y-R1a tree;
- Co-writing of first draft, editing after co-authors' contributions and submission process (including responding to referees).

A genetic chronology for the Indian Subcontinent: sex-biased dispersals in the Bronze Age

1. Introduction

South Asia (or the Indian Subcontinent, comprising India, Pakistan, Bangladesh, Sri Lanka, Nepal and Bhutan) was one of the earliest regions settled by modern humans after leaving Africa (Macaulay et al., 2005; Majumder, 2010; Mellars et al., 2013), as evinced by the high levels of genetic diversity found in the region (Majumder, 2010; Xing et al., 2010). Although the earliest modern human fossils in the region (found in Sri Lanka) date to ~36–28 ka (Kennedy and Deraniyagala, 1989; Perera et al., 2011), both genetic and archaeological evidence suggest a much earlier (>50 ka) arrival of modern humans to the Subcontinent, most likely after the eruption of Mount Toba in Sumatra ~74 ka (Malaspinas et al., 2016; Mallick et al., 2016; Mellars et al., 2013), with some evidence pointing to an even earlier initial colonisation (Pagani et al., 2016; Petraglia et al., 2007).

India is the second most populous country in the world, and harbours a high cultural diversity, translated in a myriad of religions and languages, tribal groups (corresponding to ~8% of the population and speaking hundreds of different dialects of the Austro-Asiatic, Dravidian and Tibeto-Burman language families) and non-tribal populations, most of whom practice Hinduism, based on a strictly hierarchical caste system, and speak either Indo-European or Dravidian languages. Indo-European is spoken predominantly amongst northern Indian populations, Pakistan and Bangladesh, whereas South India, is associated to the Dravidian family. The demographic events that contributed to the current language distribution in the region are still poorly known.

The so-called "Indo-Aryan invasions", traditionally associated to the arrival of Indo-European languages to South Asia from Iran ~3.5 ka and usually connected with the implementation of the caste system (Parpola, 2015; Witzel, 2005), have not been confirmed. Despite the greater genetic proximity of upper castes to populations from European and Southwest Asian ancestry in comparison to lower castes (Bamshad et al., 2001; Basu et al., 2003), genetic evidence has provided no clear evidence for these so-called "Indo-Aryan invasions" (Kivisild et al., 2003), and many archaeologists have questioned their very existence (Coningham and Young, 2015).

On the other hand, Dravidian languages seem to have dispersed to South Asia earlier, with Neolithic arrivals from Southwest Asia (Majumder, 2010; Palanichamy et al., 2015; Parpola, 2015). Despite some debate regarding the origin of agriculture in the Subcontinent, due to some degree of autochthonous domestication (*e.g*. zebu cattle (Chen et al., 2010)), archaeological and genetic evidence show that several domesticates found in the region were brought from the Fertile Crescent (Fuller, 2007; Kingwell-Banham et al., 2015).

Nowadays, Indian populations show high levels of endogamy, due to strict social rules, and high genetic drift resulting from long-term isolation (Chaubey et al., 2007) which, together with its complex history, makes the genetic study of Indian populations both challenging and appealing. South Asian mitochondrial diversity consists mostly of basal autochthonous lineages of haplogroups M and N (mostly R) tracing back to the first settlement of the region by modern humans (Endicott et al., 2007; Kivisild et al., 2003; Mellars et al., 2013; Palanichamy et al., 2004; Sun et al., 2006). On the paternal line, Y-chromosome haplogroups H, R1 (especially R1a), R2, G, L1, J2, and O (especially O2a) are present in the Subcontinent at considerable frequencies (Sahoo et al., 2006; Sengupta et al., 2006; Trivedi et al., 2008).

In this chapter, I study the maternal variation in South Asia, and explore the influence of later migrations from other regions (Southwest and Central Asia), by assessing phylogeographic patterns of several mtDNA N lineages that entered South Asia at different periods after the first settlement. I analyse the GW patterns across Southwest, Central and South Asia, and perform a revision of Y-chromosome R1a phylogeny. Finally, I compare both uniparental markers and GW variation, so as to identify sex-biased demographic events. Additionally, I include newly available aDNA evidence from the Eurasian steppe, Central and South Asia (de Barros Damgaard et al., 2018a; Narasimhan et al., 2018), to confirm the patterns observed in modern variation, and to compare with the results presented in this chapter (published in 2017 (Silva et al., 2017)).

2. Methods

2.1. Mitochondrial DNA analysis

In order to distinguish migrations into the Subcontinent at different time periods, I studied several "non-autochthonous" lineages of macro-haplogroup N which are found today in South Asia: H2b, H7b, H13, H15a, H29, HV, I1, J1b, J1d, K1a, K2a, N1a, R0a, R1a, R2, T1a, T2, U1, U7, V2a, W and X2 (corresponding to a total of 635 complete mtDNA sequences (Appendix A, Table S1)). These "non-autochthonous" lineages are subclades of West Eurasian haplogroups, shared with neighbouring regions, and were introduced in the Subcontinent towards the end of the Pleistocene and during the Holocene, in contrast to those belonging to M and R that rose in South Asia following the out-of-Africa dispersal (Endicott et al., 2007). I assigned haplogroups using HaploGrep v.2 (Kloss-Brandstätter et al., 2011), following the nomenclature in PhyloTree (Build 17, February 2016) (van Oven, 2015). I built the tree based on a reduced-median network analysis using Network v.4.611 (Bandelt et al., 1995) and estimated coalescence ages using both the ρ statistic (Forster et al., 1996) and maximum likelihood (ML). In accordance to PhyloTree recommendations, insertions at positions 309 and 315, *indels* between positions 515 and 522 and hotspot positions (16182, 16183 and 16519) were excluded from the analysis. Other indels (included for phylogenetic reconstruction) were excluded from age estimation, since this type of variation is not considered by the models used for age calculations.

I computed ρ estimates using a molecular clock of one substitution every 3,624 years further corrected for purifying selection (Soares et al., 2009), and estimated standard errors as in Saillard et al. (2000). ρ-statistics estimate node ages based on the average number of mutations from a given ancestral node to the tips of the phylogeny, using only a given mutation rate (*i.e.* no evolutionary mutation model is considered).

I performed ML analysis with baseml v.4.7 from PAML (Phylogenetic Analysis using Maximum Likelihood) package (Yang, 2007), using the molecular clock mentioned above. I employed the REV/GTR, general (time) reversible, substitution model (Tavaré, 1986) with gamma-distributed rates (discrete distribution of 32 categories), after attempts using the HKY85 (a simpler and widely used model for human mtDNA analyses previously tested on a large dataset (Soares et al., 2009)) failed to converge. I defined two partitions, in order to distinguish HVS–I and HVS–II from the rest of the molecule.

2.2. GW analysis

I performed a basic GW analysis in order to compare present-day populations from Southwest, Central and South Asia (a total of 1440 individuals from published populations) with a dataset of Yamnaya individuals (*n*=9) (Haak et al., 2015) (Appendix A, Table S2). The overlapping dataset initially comprised a total of ~250,000 SNPs, which I pruned for linkage disequilibrium (LD) using PLINK v1.07 (Purcell et al., 2007) (--*indep-pairwise* 100 1 0.25), resulting in a subset of 64,926 SNPs. This LD-pruned dataset was used to compute principal component analysis (PCA) using the standard *pca* command in EIGENSOFT v.6.0.1 (Patterson et al., 2006) (please note that no projection was used for this PCA). Three additional 1KGP (The 1000 Genomes Project Consortium, 2015) populations – Han Chinese from Beijing, China (CHB), Tuscans from Italy (TSI) and Yoruba from Nigeria (YRI) – were added for the clustering analysis with ADMIXTURE v1.23 (Alexander et al., 2009) for *K* between 2 and 10, using a total of 66,245 LD-pruned SNPs.

2.3. Assessment of sex-biased events

In order to assess potential sex-biased gene flow into the Subcontinent, I compared ancestry patterns detected at uniparental and autosomal level in the 1KGP South Asian populations. The putative source of uniparental lineages found in the 1KGP populations analysed is shown in Table 2.1. Y-chromosome lineages that entered the Subcontinent before the LGM and are most likely connected with the first settlement were considered as South Asian: H, NO (Karmin et al., 2015; Trivedi et al., 2008) and C5 (Poznik et al., 2016). Y-chromosome haplogroups G, J, L, Q, R1 and R2 seem to have entered South Asia more recently from a Western Eurasian source (Karmin et al., 2015; Sahoo et al., 2006; Trivedi et al., 2008); haplogroup L was considered as having an Western Eurasian origin due to the presence of Near Eastern (and European) sequences in deep splitting branches (Y-full v.4.10) and its oldest record dating to ~6 ka in Armenia (Lazaridis et al., 2016), following previous suggestions of a Neolithic dispersal of L lineages into the Subcontinent (Cordaux et al., 2004; Qamar et al., 2002; Thangaraj et al., 2010). Haplogroups C(xC5), O and N(xNO) probably had an eastern origin (Karmin et al., 2015; Yan et al., 2011; Zhong et al., 2010).

Table 2.1. Putative origin for the uniparental lineages present in the 1KGP South Asian populations.

	Source	**Haplogroups**
mtDNA	Africa	L2, L3
	East Asia	A4, D4, F1, G3, N21
	South Asia (pre-LGM)	M, M18, M18'38, M2, M3, M30, M33, M34, M35, M36, M37, M38, M39, M39'70, M4, M40, M41, M42, M43, M44, M45, M4'67, M49, M5, M50, M52, M53, M6, M64, M65, M66, N5, R, R30, R31, R5, R6, R7, R8, U2
	West Eurasia	H, H13, H2, H29, H6, H7, HV, HV12, HV13, HV14, HV2, I1, J1, K1, K2, N1, R0, R2, R2'JT, T1, T2, U1, U5, U7, U9, W1, W4, W6, X
	Source	**Haplogroups**
Y-chromosome	East Asia	C(xC5), N(xNO), O
	South Asia (pre-LGM)	C5, H, NO
	West Eurasia	G, J, L1, N, Q(xQ-L53), R1, R2

Additionally, in order to shed light into the dispersal patterns of the Indo-European language family into South Asia, I made a revision of the Y-chromosome haplogroup R1a phylogeny, based on recent phylogenies published (Karmin et al., 2015; Poznik et al., 2016), with special focus on the Indian Subcontinent and including all ancient samples available from the Steppe and Central Asia available to date (as of December 2016).

2.4. Recent aDNA evidence

Recently a myriad of novel ancient genomic data from Eurasia has been released. In order to compare the newly available data with my results, I have gathered autosomal information from 437 non-related ancient individuals from Anatolia, Iran, the Steppe, and Central and South Asia (Appendix A, Table S3), with particular focus on the Chalcolithic and Bronze Age (de Barros Damgaard et al., 2018a; Narasimhan et al., 2018). I extracted the autosomal SNPs present in the modern South Asian dataset used previously (composed of 1KGP populations from South Asia and other published samples (Appendix A, Table S2)) that matched the positions typed in the ancient samples with PLINK v1.07 (*--extract*), resulting in a total of ~480K autosomal SNPs. I then merged the ancient and modern datasets using *mergeit* (part of EIGENSOFT v.7.2.1 package) and projected the ancient samples onto a PCA of modern South Asian populations using *smartpca* (EIGENSOFT v.7.2.1), with the default setting for outlier removal, *shrinkmode: YES* and *lsqproject: YES*.

3. Results

3.1. West Eurasian mtDNA lineages in South Asia

Mitochondrial lineages with origin in West Eurasia account for ~20% of the overall South Asian maternal variation and document multiple events since the LGM. The node ages mentioned along the text are ML (both ρ and ML estimates are shown in Appendix A, Table S4). Arrival times were considered as ranging between node age estimates of the parent nodes and the estimates of the descendant subclades (95% confidence intervals shown in Figures 2.1–2.3).

3.1.1. LGM and Late Glacial arrivals

Lineage N1a1b1 dating to ~21 ka and with a probable origin in the Near East (Fernandes et al., 2012), displays the earliest evidence of movements into South Asia after the first settlement (Figure 2.1; Appendix A, Table S4. Pre-HV2, HV+146!, HV+9716, HV+73!, pre-U1c, U1a1, J1d and a basal clade within T2, with similar age estimates and a possible source in the Near East, may have also moved eastwards in this time frame (Figure 2.1; Appendix A, Table S4), corresponding to 2.6% in the overall South Asian 1KGP data. This was a period of short-lived relative global warmth after the peak of the last glaciation, which has been linked to possible population movements in several regions (Perry and Hsu, 2000).

Other Near Eastern lineages (W4, HV+16311!, HV12b, I1, U7a and J1b1b1, with frequencies of 4.5% in the South Asian 1KGP data) spread to the Subcontinent ~16–13 ka (Figure 2.1; Appendix A, Table S4), in the Late Glacial period. Late Glacial movements from Southwest Asian *refugia* have also been reported for Europe (Pala et al., 2012; Pereira et al., 2017).

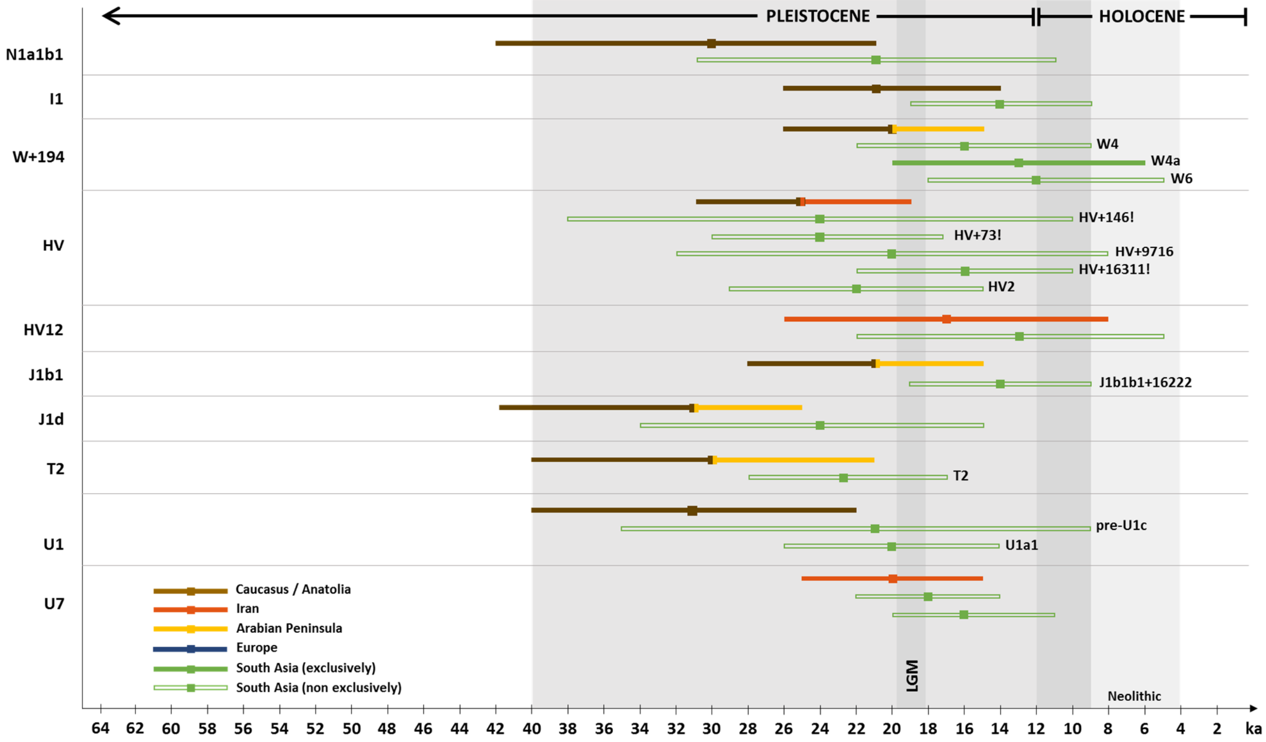

Figure 2.1. Putative source and ML node age ranges (95% confidence interval) for non-autochthonous mtDNA lineages found in South Asia dating to the Pleistocene. The colours represent the most likely geographical origin for each lineage; branches exclusively with South Asian sequences in the dataset coloured in green, whereas branches that also contain sequences from other regions in white and with green contour.

3.1.2. Early postglacial arrivals

With the end of the Younger Dryas glacial relapse, after ~12 ka, movements into South Asia seem to have intensified, with the arrival of yet more clades from Southwest Asia harbouring exclusively South Asian branches in the dataset: T2e2, T2+195+4225, W3a1+143, W3a1b, U1a3+10253, N1a2, U7a+12373 and U7a3a+6150 (Figure 2.2; Appendix A, Table S4). Additional South Asian sequences nest within several other clades with similar node age estimates (W6, T2b, T2d1a, U7b+16309! and K1a1b2a, with a frequency of 4.7% in the South Asian 1KGP dataset) (Figure 2.2; Appendix A, Table S4).

This period coincides with the expansion of several autochthonous maternal lineages across the Subcontinent, to some extent from western sources (possibly alongside dispersing Southwest Asian lineages), but primarily from the south (Silva et al., 2017). Increments in the effective population size (*Ne*) during this period are detected in the west and the south of the Subcontinent, associated to the expansion of South Asian M haplogroups, as discussed in detail in Silva et al. (2017).

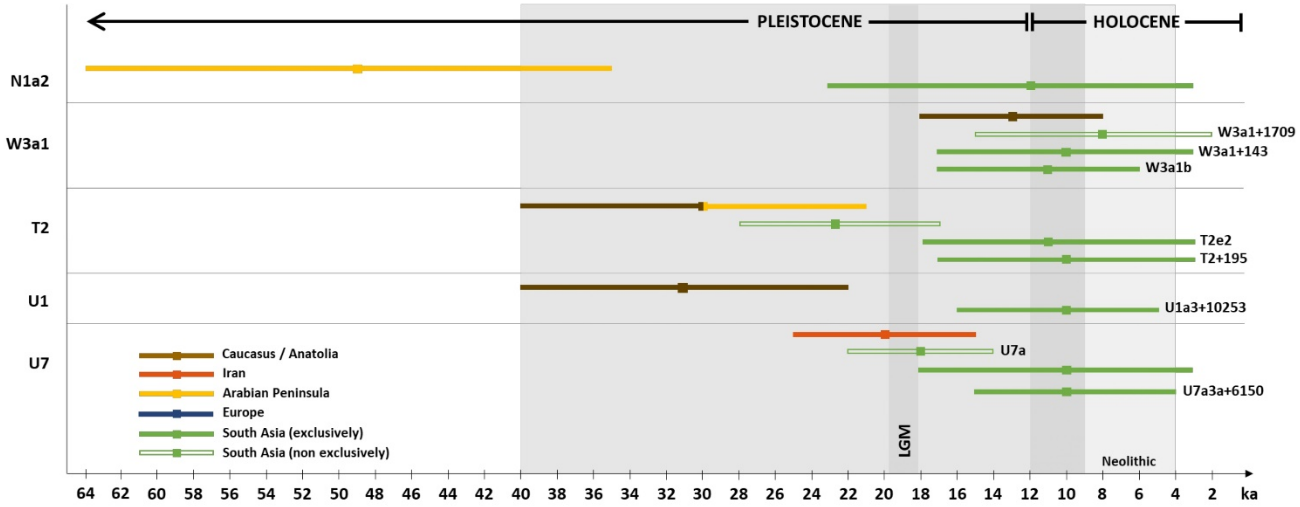

Figure 2.2. Putative source and ML node age ranges (95% confidence intervals) for non-autochthonous mtDNA lineages found in South Asia dating to the postglacial period. The colours represent the most likely origin for each lineage; branches exclusively with South Asian sequences in the dataset coloured in green, whereas branches that also contain sequences from other regions in white and with green contour.

3.1.3. Untangling Neolithic and Bronze Age dispersals

Putative Neolithic lineages likely from Anatolia, the Caucasus and Iran, seem to have entered the Subcontinent ~9–5 ka, harbouring nested South Asian subclades (K2a5+2831+189, HV14+150, H13a2a+8952, K2a5+2831, X2+153!+7109 and U1a3a, with overall frequency of 3.4%) (Figure 2.3; Appendix A, Table S4). Additional movements from Arabia and the Near East can also be inferred, with R0a2+11152 (~7.1 ka) the most striking example. One lineage, H2b, most likely traces its source to north or Eastern Europe and seems to have arrived to South Asia through Central Asia later, as discussed below.

In the last ~4 ka, the detected genetic mitochondrial influx seems restricted to the northwest of the Subcontinent (Pakistan) and traces mostly to Iran (H29+9156+4689, R2a+7142 and U1a1a2a) (frequency of 2.4% in South Asia, reaching 5.4% in the western populations) (Figure 2.3; Appendix A, Table S4). Movements at this time were clearly bidirectional, as seen in the expansion westwards of M5a2a4, U2c1b+146 and M3a1b+13105 (Silva et al., 2017). This seems to be also visible at the autosomal level, as seen in the ADMIXTURE analysis (Figure 2.5b; Appendix A, Figure S2), with the autochthonous South Asian component (green in Figure 2.5) seen at low frequency in Iran.

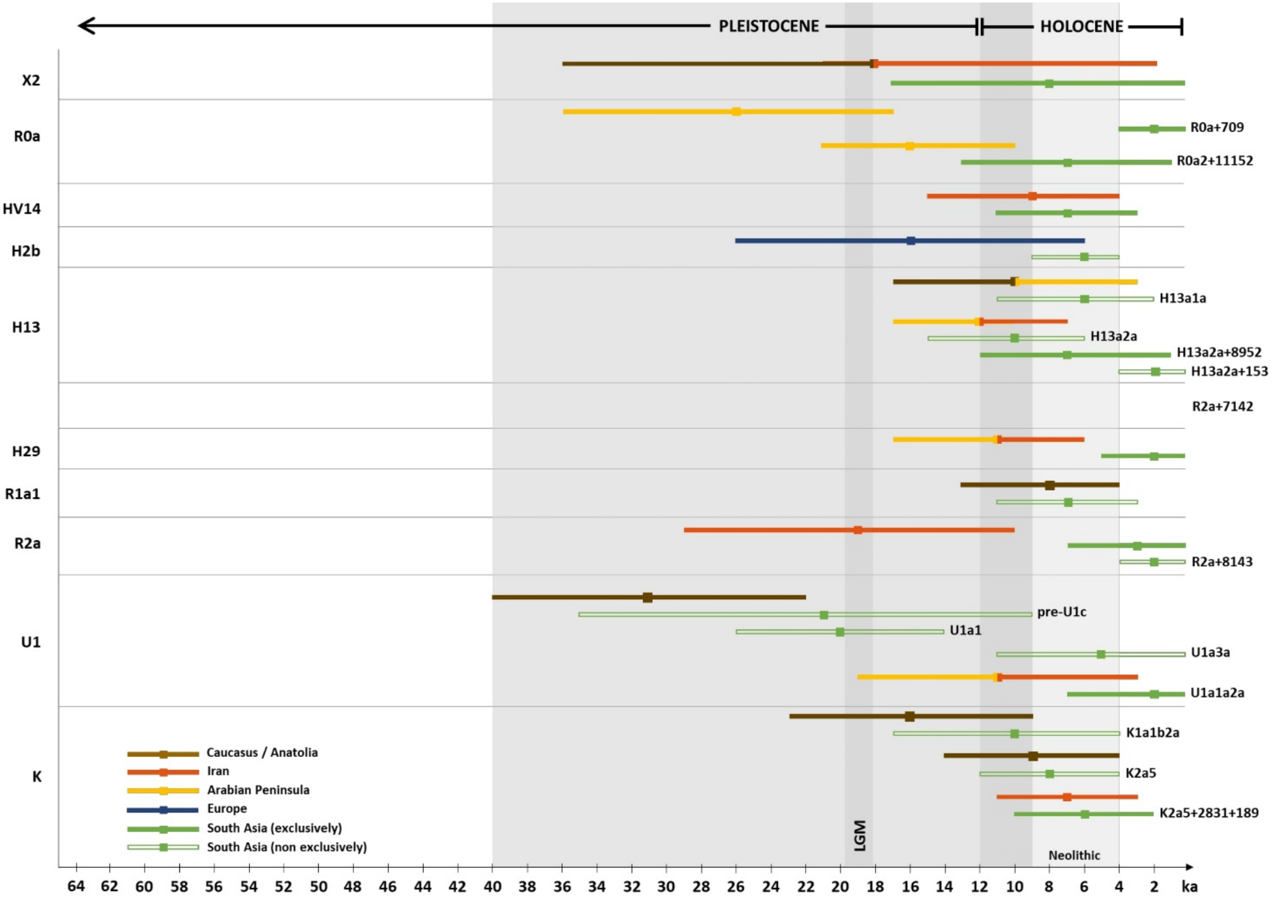

Figure 2.3. Putative source and ML node age ranges (95% confidence interval) for non-autochthonous Neolithic and Bronze Age mtDNA lineages found in South Asia. The colours represent the most likely origin for each lineage; branches exclusively with South Asian sequences in the dataset coloured in green, whereas branches that also harbour sequences from other regions in white and with green contour.

Haplogroup H2b (Figure 2.4), although with an ultimate source in Europe, probably entered the Subcontinent from Central Asia. H2b includes several South Asian lineages from across the region (Pakistan, India and Sri Lanka), and two ancient sequences (as of December 2016): one Yamnaya individual (Allentoft et al., 2015; Haak et al., 2015) and another from the Late Bronze Age Srubnaya culture (Mathieson et al., 2015). A more updated H2b tree and a detailed discussion are presented on Chapter III, in which I focus my analysis on mtDNA haplogroup H.

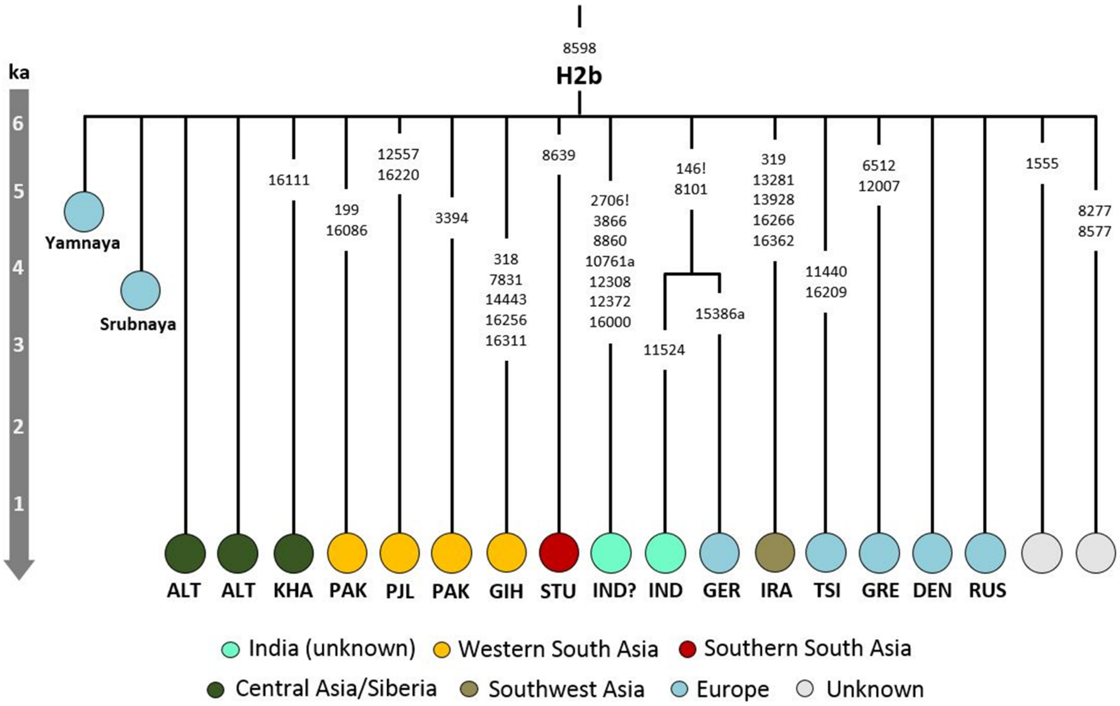

Figure 2.4. Schematic tree of mtDNA haplogroup H2b based on ML node age estimates for modern sequences (as of December 2016). Population codes: ALT, Altai, DEN, Denmark; GER, Germany; GIH, Gujarati Indian from Houston, Texas; GRE, Greece; IND, India (without more details regarding location within India; the sample marked with "?" is classified as possibly Indian); IRA, Iraq; KHA, Khamnigan; PAK, Pakistan; PJL, Punjabi from Lahore, Pakistan; RUS, Russia; TSI, Tuscans from Italy (Appendix A, Table S1). The Yamnaya sample has been radiocarbon dated to 3010–2622 cal. BCE (Haak et al., 2015); the Srubnaya sample dates to 1850–1600 BCE (Mathieson et al., 2015). An updated H2b tree is shown on Chapter III, section 3.2.1 (Figure 3.7).

3.2. Genome-wide overview of South Asia

Present-day South Asians in the PCA (Figure 2.5a) are closer to groups from Central Asia and the Caucasus than to Near Eastern populations (except for Iran). Pakistani groups occupy an intermediate position, clustering in PC1 closer to present-day Turkic-speakers from Central Asia (Turkmens, Nogais and Uzbeks) and the Tajiks (Indo-Iranian-speakers). Turkic-speaking groups are genetically similar to their Indo-European-speaking neighbours, indicating deep local ancestry and recent language shift (Yunusbayev et al., 2015).

The Yamnaya individuals plot scattered amongst the Central Asian and Pakistani groups (Figure 2.5a), pointing to similarities between Steppe groups and present-day populations from Central and South Asia. Groups from Pakistan plot much more scattered in PC1 in comparison with the other South Asian populations (from India, Bangladesh and Sri Lanka), which are better distinguishable in PC2, with the exception of the Gujaratis (from Western India) that are largely dispersed in PC1 (clustering with individuals from Punjab), the castes of Brahmins and Kshatriya (plotting together with the Punjabis and Gujaratis) and, on one extreme of PC1, some tribal groups.

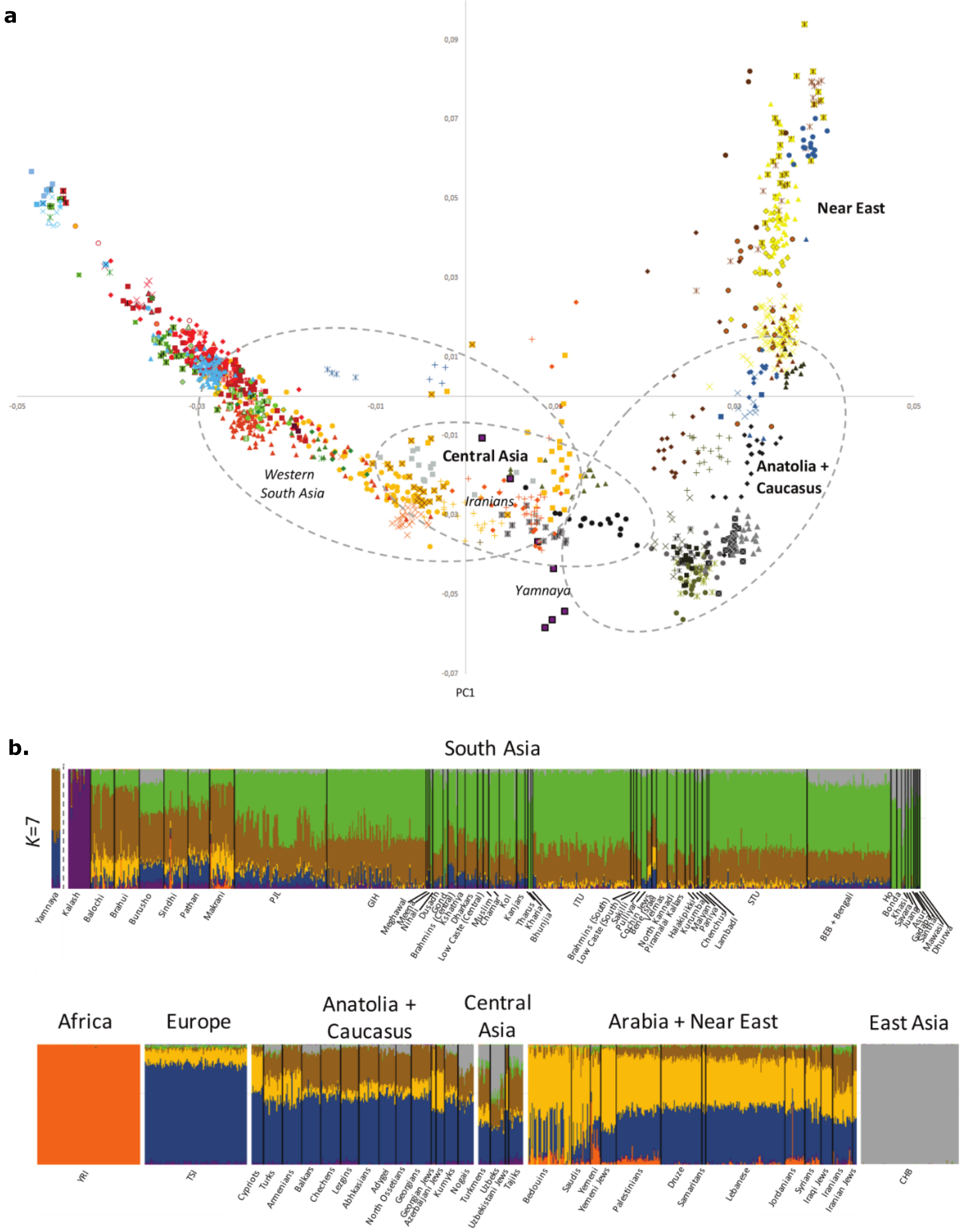

Figure 2.5. a) PCA including present-day populations and Yamnaya individuals. Detailed legend in Appendix A, Figure S1. **b)** ADMIXTURE analysis for *K*=7. Note that the three typical European components are not detected here in the Tuscans, probably due to the small overall European representation in the analysis. Plots for other *K* values and information on populations included in these analyses on Appendix A (Figure S2, Table S2).

South Asian populations are distinguishable from *K*=3 in the ADMIXTURE analysis (Appendix A, Figure S2), highlighting their distinctive genetic variation. At *K*=7 (with the lowest CV error) (Figure 2.5b; Appendix A, Figure S3), the overall pattern for South Asian groups is clinal, with a considerable autochthonous component (shown in green). The only exception is the Kalash, with a virtually exclusive component, most likely due to genetic drift in a small, isolated population (Ayub et al., 2015), a result previously observed with both ADMIXTURE (Ayub et al., 2015; Shriner et al., 2014) and STRUCTURE (Rosenberg et al., 2006) analyses (STRUCTURE is a similar clustering method, but based on Bayesian statistics rather than ML (Pritchard et al., 2000)).

A striking feature (for *K*=7) is the much higher proportion of the typical West Eurasian components (shown in brown, yellow and dark blue) in the western (particularly Pakistani) South Asian populations. Further structure in the Subcontinent is only detectable from *K*=9 (Appendix A, Figure S2), with a new component (dark green) visible amongst the Gujarati (originally from West India), but not shared among all individuals. The heterogeneity of the Gujaratis has been previously shown (Juyal et al., 2014) and is thought to be the result of marriage practices in the region (Pemberton et al., 2012).

The main non-autochthonous component in the Subcontinent (brown) exceeds 35% in Pakistani and Gujarati groups (Juyal et al., 2014; Moorjani et al., 2013; Reich et al., 2009), although it is visible across most of the groups from the Subcontinent. This Iran/Caucasus/Steppe component is known as the "Caucasus hunter–gatherer" (CHG) component, since it was detected at very high frequencies in the Late Palaeolithic and Mesolithic Caucasus (Jones et al., 2015). The CHG component is seen at ~50% in the Yamnaya (Allentoft et al., 2015; Haak et al., 2015) and was also found at high proportions in Mesolithic and Neolithic Iranian individuals (Lazaridis et al., 2016). The Pakistani Muslim Balochi, Brahui and Makrani display ~15% of the Near Eastern/Arabian component (yellow), which is also found in present-day Europe and is associated with the Early Neolithic dispersals from the Near East (Lazaridis et al., 2016). However, this component is virtually absent in other South Asian populations (including Muslims) except for Jewish groups, in agreement with previous mitochondrial evidence for little genetic input from Arabia into present-day Indian Muslims (Eaaswarkhanth et al., 2010).

The widely accepted paradigm for modern South Asian genetic structure suggests that South Asian populations are the result of admixture between two main ancestral groups, referred to as Ancient North Indians (ANI) and Ancient South Indians (ASI) (Reich et al., 2009). According to this model, the proximity of north-western South Asians (such as Pakistanis and Gujaratis) to European and Southwest Asian populations is due to high levels of ANI ancestry (Reich et al., 2009), postulated to have arrived in two waves (Moorjani et al., 2013). However, the present mtDNA results shown here suggest that the process was probably much more complex. The genetic variation seen in present-day Pakistani populations is likely the result of dispersals into the region at, at least, four different periods, involving the ancestral West Eurasian components, dating as far back as at least the LGM through into the Bronze Age. A recent analysis based on a novel software method, GLOBETROTTER, which considers haplotypes rather than independent SNPs (Hellenthal et al., 2014), supports these results with all the South Asian populations analysed showing a common autochthonous "component" and a higher contribution of Southwest Asia in Pakistani populations and Indian Jews.

3.3. Comparing marker systems

For a direct comparison, I examined ancestry patterns in the maternal, paternal and autosomal gene pools of the 1KGP populations (Figure 2.6a), which consist of unbiased population data.

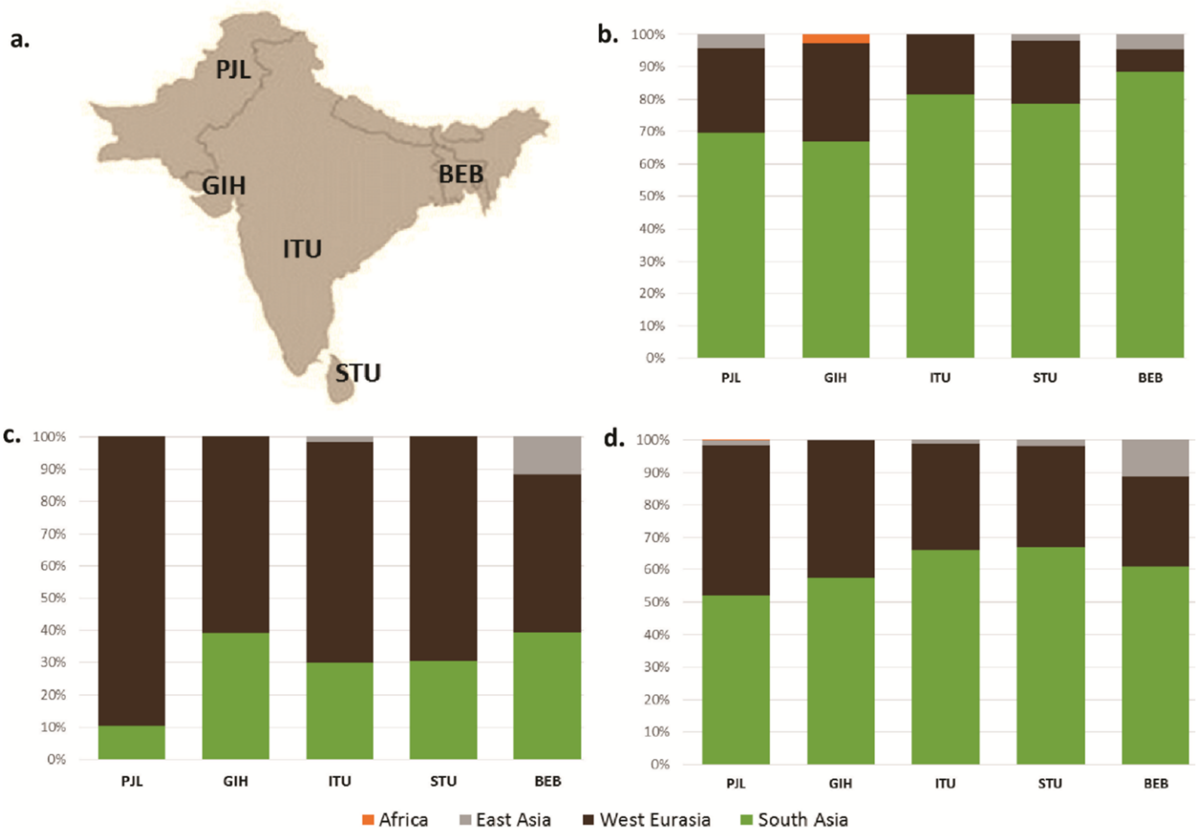

Figure 2.6. The ancestry of South Asian 1KGP populations (**a**) according to different molecular markers: **b**) mtDNA, **c**) Y-chromosome lineages and **d**) GW. Putative origin of the uniparental lineages present in the populations in Table 2.1.

The results suggest much higher levels of autochthonous variation on the maternal line (~70–90%) (Figure 2.6b) than in the overall autosomal variation (about a half to two-thirds) (Figure 2.6d). In contrast, ~50–90% of male lineages seen in these 1KGP populations are of likely West Eurasian origin (Figure 6c). A sex-biased pattern is also visible for East Asian ancestry, although much less marked, and with a much lower overall contribution (mostly restricted to Tibeto-Burman and Austroasiatic speakers (Chaubey et al., 2011)).

Y-chromosome haplogroup R1a-M17 has significantly higher frequencies in Indo-European than in Dravidian-speaking populations (Trivedi et al., 2008). The derived R1a-L657 branch, dating to ~3.9 ka (according to Y-full v.4.10), harbours the bulk of South Asian non-autochthonous male lineages (Karmin et al., 2015) (Figure 2.7a), and is more common amongst the Indo-European-speaking 1KGP populations (PJL, GIH and BEB; with frequencies ~20.9%—25.0%), than in the other Dravidian-speaking populations (ITU and STU) (Figure 2.7b), although in this case the differences are not significant ($p>0.05$). Moreover, aDNA studies show that R1a was probably present at very high frequencies in Central Asia during the Middle and Late Bronze Age, since it was detected amongst all the males analysed so far from the Sintashta, Andronovo and Srubnaya cultures ($n=9$) (as of December 2016), adding up to the previous accounts of R1a in a majority of Andronovo ($n=2$) and post-Andronovo (Tagar and Tachtyk) Iron Age ($n=6$) male individuals from southern central Siberia studied using STRs (Keyser et al., 2009). Altogether, R1a seems to be a probable marker for an Indo-European spread to South Asia in the Middle or Late Bronze Age.

Given this scenario, the spread of Indo-European within the Subcontinent seems to have been predominantly a male-mediated phenomenon, as suggested by the high frequency of West Eurasian paternal lineages across the region (Figure 2.6c), and in particular of R1a (Figure 2.7b), in contrast to the pattern seen in the maternal line. However, these movements cannot be directly correlated with language dispersal and replacement, since R1a is also found at considerable frequencies in Dravidian-speaking populations, thus suggesting some degree of contact between Indo-European and Dravidian-speaking populations in South Asia which did not always result in linguistic shifts. A similar situation is seen in Iberia, where the Basque population carry a high frequency of R1b paternal lineages (>80%), associated with the spread of Indo-European in Europe, but speak a non-Indo-European linguistic isolate (Karmin et al., 2015; Mallory and Adams, 2006; Young et al., 2011).

Archaeological evidence points to expansions of Middle Bronze Age Andronovo groups (descendants of the Early Bronze Age Sintashta) into Central Asia by ~3.8 ka. Andronovo and/or Sintashta groups are thought to have infiltrated the Bactrian Margiana Archaeological Complex (BMAC) settlements in Turkmenistan and northern Afghanistan ~3.5–4 ka, a time when there were interactions between the BMAC and the Harappan civilization in the Indus Valley, coinciding with the beginning of its decline. Pastoralist groups seem to have dispersed further into South Asia by ~3.5 ka (Kristiansen, 2015; Anthony et al. 1986; Anthony 2010; Parpola 2015).

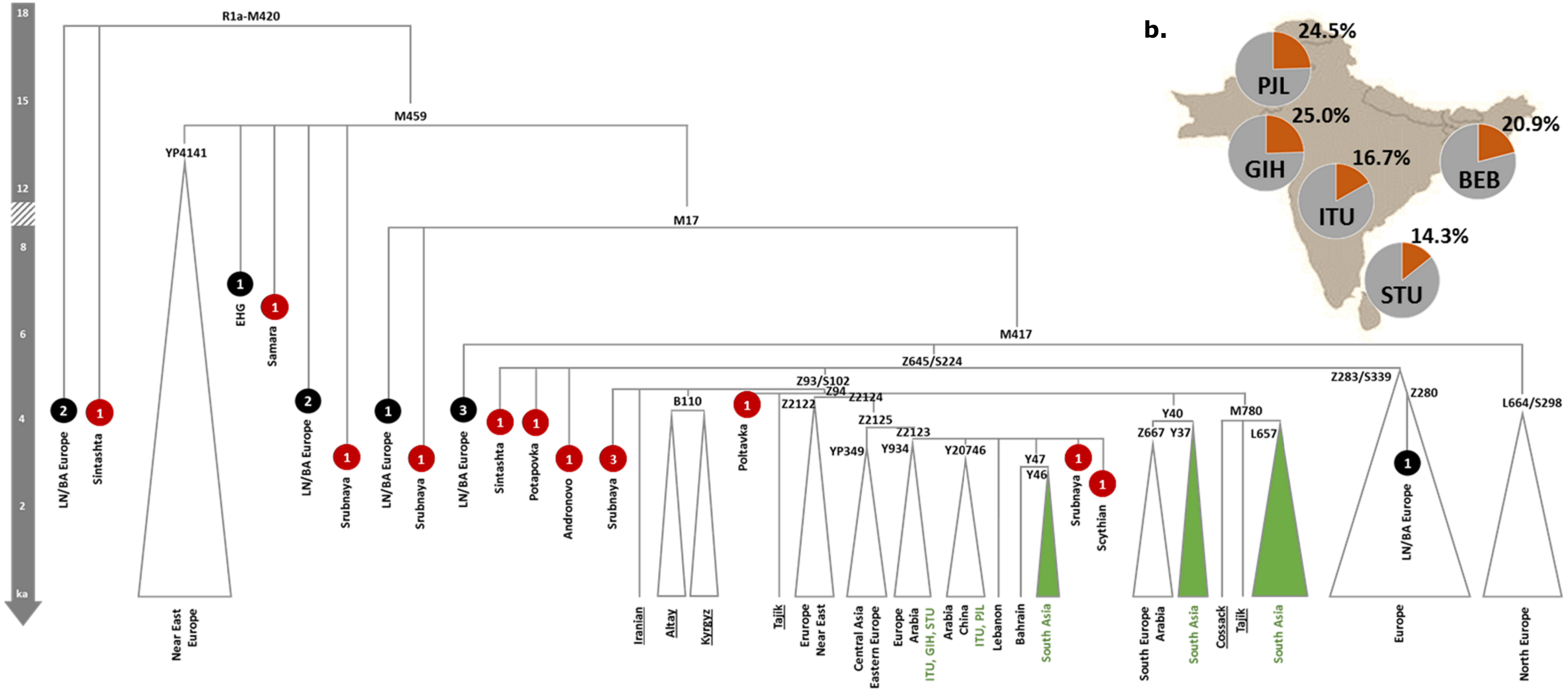

Figure 2.7. a) Schematic tree of Y-chromosome haplogroup R1a. Phylogeny and age estimates based on Yfull tree v4.10. Age estimates are corroborated by published estimates (Karmin et al., 2015) and aDNA evidence from radiocarbon and indirectly dated samples. Underlined samples and/or clades from Karmin et al. (2015). Black and red circles represent European and Steppe aDNA samples (number represents the sample size for each culture/period; LN/BA stands for Late Neolithic/Bronze Age) (Allentoft et al., 2015; Haak et al., 2015; Mathieson et al., 2015). **b)** Frequency of Y-chromosome lineage R1a-L657 in South Asian 1KGP populations.

3.4. Incorporating recent aDNA evidence

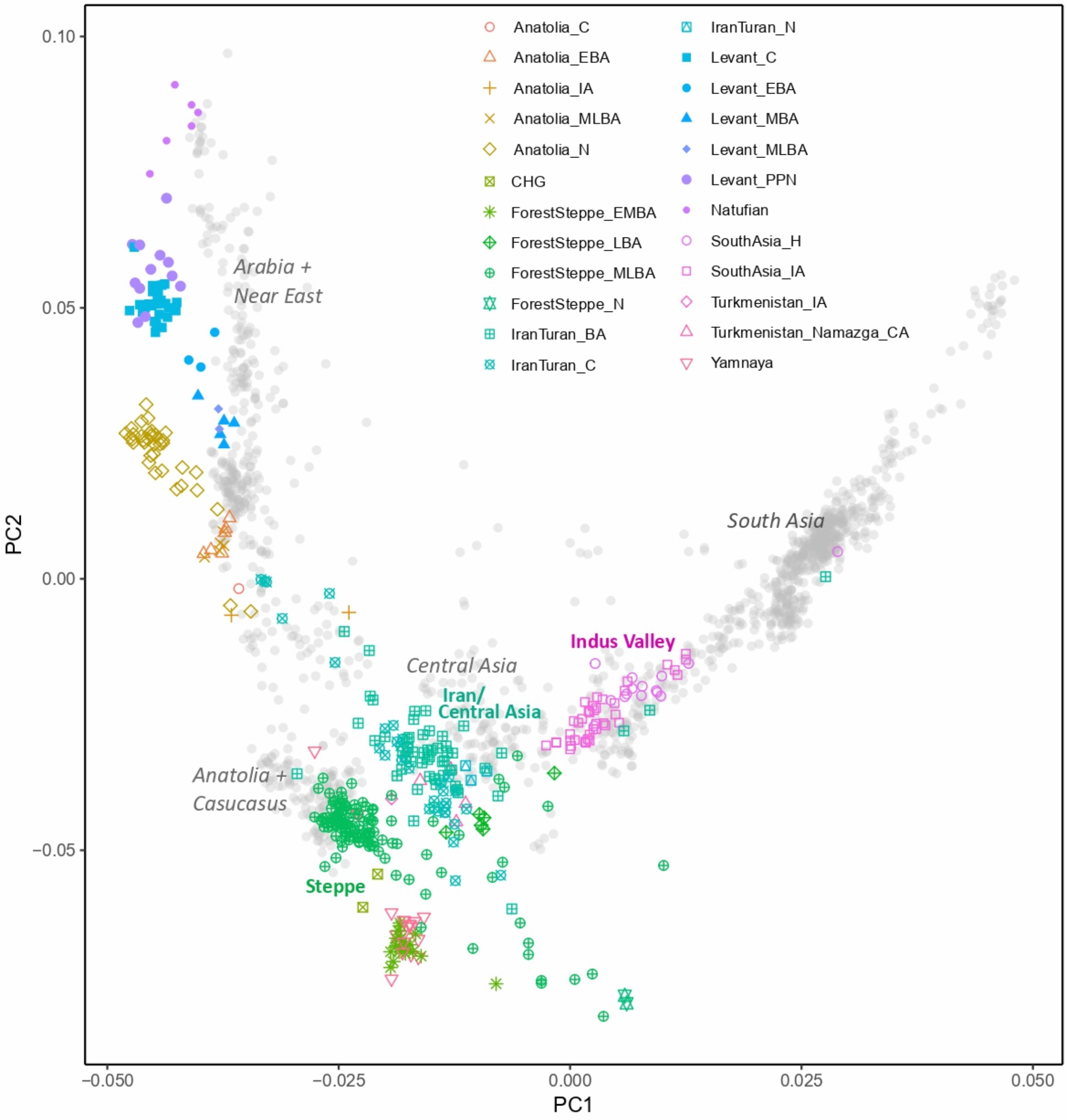

Figure 2.8. PCA based on ~480K SNPs, projecting 437 ancient individuals on the modern dataset used for the PCA on Figure 2.5a (in grey). Abbreviations: (PP)N – (Pre-pottery) Neolithic, C/CA – Chalcolithic, (E/M/L)BA – Early/Middle/Late Bronze Age, IA – Iron Age, H – Historical. More information on the ancient dataset used can be found in Appendix A, Table S3.

The recently reported Chalcolithic and Bronze Age samples from eastern Iran and southern region of Central Asia (Turkmenistan, Uzbekistan and Tajikistan – also referred to as Turan), including >60 individuals from five BMAC sites, as well as from the Kazakh Steppe (de Barros Damgaard et al., 2018a; Narasimhan et al., 2018) provide insightful clues about the prehistory of the region. No genetic information was available from Harappan or immediately posterior Bronze Age individuals from the Indus Valley when I ran this PCA. Therefore, the best proxy available was the Iron Age and "historical" populations from the

Swat Valley (Pakistan), dating to 1200 BCE–1 CE (Narasimhan et al., 2018). These individuals (*n*=55, from seven archaeological sites) cluster in the PCA together with present-day western South Asian populations (Figure 2.8), showing genetic continuity in the region since at least the Iron Age, except for one individual that clusters with southern Indians and is probably a direct migrant from a different region (Narasimhan et al., 2018).

Three genetic clusters of ancient individuals are observed in the PCA (Figure 2.8), corresponding essentially to a geographical/ecological gradient: i) Steppe, ii) Iran/Central Asia, and iii) Indus Valley. Although genomic data do not show evidence for widespread incursions of Steppe individuals to BMAC settlements of the Turan region (Narasimhan et al., 2018), the presence of outlier individuals in between each of these clusters hints at population contacts. Specifically, the fact that some Bronze Age individuals from Turan plot next to Middle/Late Bronze Age Steppe individuals, and, conversely, some Middle/Late Bronze Age Steppe individuals cluster together with both Chalcolithic and Bronze Age Turan, suggests complex interactions between Central Asian and the Steppe populations from further north. Moreover, the presence along the Indian cline of three outliers from the Iran/Turan cluster (one BMAC individual and two others from Shahr-i-Sokhta, a Bronze Age site in eastern Iran, dating to 3100–2200 BCE) could represent direct migrants from the Indus Valley region, and therefore provide an indirect look onto the genetic variation of the Indus Valley civilisation (Narasimhan et al., 2018; Shinde et al., 2019). These individuals show an increased proportion of ASI ancestry compared to the later Swat Valley individuals (Narasimhan et al., 2018). Together with these outliers, a recently published Harappan genome (not included here) – the only available to date – supports the view that the Indus Valley people lacked Steppe ancestry, unlike the later Iron Age and "historical" populations from the Swat Valley (Narasimhan et al., 2018; Shinde et al., 2019).

4. Discussion

The phylogeographic analysis of uniparental markers can complement GW patterns and provide a more nuanced and detailed picture. In particular, the directionality of gene trees, defined by how different clades nest within others, is important to identify sources of dispersals, especially when incorporating aDNA evidence. Thanks to the increasing precision of molecular clocks for uniparental markers, and the rapidly expanding aDNA evidence, it is possible to date events during the ancestry of lineages. However, such events can have had different impacts on the maternal and paternal lines. It is clear from the results presented in this chapter that there is a strong sex bias in the ancestry of present-day South Asian populations. The maternal variation is mostly autochthonous and traces back to the first settlement in the Pleistocene, whereas the paternal gene pool harbours more recent ancestry, from Southwest and Central Asia, with a high proportion of lineages associated to Bronze Age events.

By combining detailed mtDNA phylogenies with autosomal and Y-chromosome data, and in addition to archaeological and palaeoclimatological information, it is possible to reconstruct an outline demographic history of human occupancy in the Indian Subcontinent, moving beyond simplistic models of admixture between the earliest settlers and foreign Neolithic farmers or Indo-Aryan-speakers, in only two waves of admixture (Moorjani et al., 2013) (Figure 2.9).

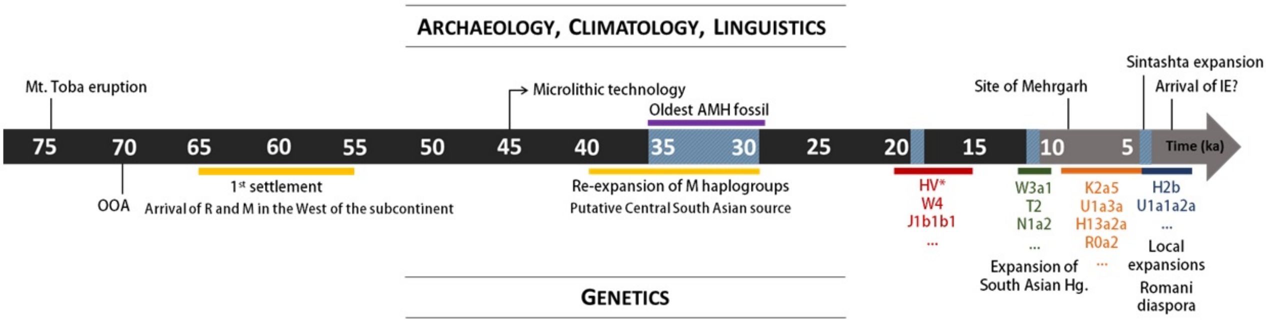

Figure 2.9. Timeline for human evolution in South Asia based on genetic, archaeological, climatological and linguistic evidence. Black and grey portions of the arrow represent Pleistocene and Holocene, respectively. Blue sections correspond to periods of important climate changes: dryer periods between 35-30 ka, LGM ~18 ka, Younger Dryas ~12 ka and the 4.2 ka event. Lineages in red stand for the putative Late Glacial/postglacial genetic influx from West Eurasia; green for movements from West Eurasia into the Subcontinent around the Pleistocene/Holocene transition, orange for the Neolithic period and blue for the mtDNA lineages arriving in the last 4 ka. Abbreviations: AMH, anatomically modern humans; Hg, haplogroup; Mt. Toba, Mount Toba; OOA, Out-of-Africa. Results on M and R South Asian lineages presented in Silva et al., 2017.

Although South Asia displays very high levels of autochthonous variation (particularly visible in the maternal gene pool and, to a lesser extent, in the autosomal diversity), the region later received substantial genetic input from both west and east, whose signal is still visible on South Asia genetic variation today. Overall, the West Eurasian populations closest to present-day South Asians are the Iranian and Central Asian groups. Western South Asians (Pakistanis and Gujaratis, in particular) carry a higher proportion of the ANI ancestry (Basu et al., 2016; Reich et al., 2009). However, results presented in this chapter show that this pattern is due to multiple dispersals from the north-west and from distinct sources, instead of only one or two major admixture events in the Neolithic/Bronze Age, as previously proposed (Moorjani et al., 2013).

In fact, mitochondrial analysis suggests that lineages originating in Southwest Asia dispersed to the Subcontinent as early as ~20 ka, a period of relative global warmth following the LGM, which might have prompted population movements in different world regions (Perry and Hsu, 2000). Several lineages from Southwest Asian sources arrived in the Late Glacial period, similarly to what is seen in Europe (Pala et al., 2012). Following the end of the Younger Dryas, ~12 ka, these movements seem to have intensified, with the arrival of additional Southwest Asian mtDNA lineages. During this period N_e increments are observed for several autochthonous M lineages across South Asia (in the west and the south) (Silva et al., 2017).

After the first settlement, the Neolithic and Bronze Age periods have been the focus of most of the genetic research in South Asia, considering their potential implications for the spread of Indo-European languages. The earliest Neolithic site was found in Baluchistan (northwest of the Subcontinent) (Chapter I, Figure 1.5) and dates to ~9 ka (in the seventh millennium BCE) (Jarrige and Jarrige, 2006; Petrie, 2015). The earliest crops in South Asia descended from Southwest Asian founder crops from the Fertile Crescent (Fuller, 2007; Kingwell-Banham et al., 2015), suggesting Neolithic dispersals into the Subcontinent. The present analysis shows that several maternal lineages appear to have entered the Subcontinent in this period from Anatolia, the Caucasus and Iran, although this signal is not visible in the only Harappan individual studied to date (Shinde et al., 2019). Instead, this individual (a female) seems to lack Iranian-farmer-related autosomal ancestry, and carried a U2b2 mtDNA haplotype. U2 is a South Asian branch, with U2b2 dating to 9.2 [6.3-12.2] ka (Silva et al., 2017).

Although some authors have favoured a co-dispersal of Indo-Aryan languages with agricultural dispersals from the Fertile Crescent (Bouckaert et al., 2012; Renfrew, 1987), others have proposed that the Dravidian family, spoken nowadays across much of central and southern India, is more likely to have dispersed with the Neolithic into South Asia (Parpola, 2015). The presently more widely accepted "Steppe hypothesis" (Anthony and Ringe, 2015; Anthony et al., 1986; Gimbutas, 1993) for the origins and spread of Indo-European has received strong support from aDNA evidence (Allentoft et al., 2015; Haak et al., 2015). Genetics suggests that the Indo-European-speaking Yamnaya pastoralists (and/or genetically similar populations) who dispersed into Europe from the Pontic-Caspian Steppe in the Late Neolithic also expanded east and later southwards into Central Asia in the Bronze Age (Allentoft et al., 2015; Anthony, 2010; Haak et al., 2015).

An influx of Steppe/Yamnaya-derived people into the Subcontinent would likely have contributed to the CHG component present across the region, as this is found at a high proportion amongst Yamnaya individuals and successor Bronze Age groups from Central Asia. Middle Bronze Age Andronovo groups (descendants of the Early Bronze Age Steppe Sintashta culture), located to the east of the Southern Ural Mountains and probably proto-Indo-Iranian-speaking, expanded into Central Asia by ~3.8 ka (Parpola, 2015). Archaeology has shown that Andronovo (and/or Sintashta) groups infiltrated and dominated the BMAC, in the vicinity of the Indus Valley, by possibly as early as 4 ka (Parpola, 2015; Sarianidi, 2001), and that there is evidence of contacts between the BMAC and the Harappans from ~4 ka onwards, coinciding with the beginning of the decline of the Indus Valley culture (Anthony, 2010; Anthony et al., 1986; Kristiansen, 2015; Parpola, 2015). However, recent aDNA data from the Steppe, Central and South Asia have shown that the interactions between Steppe pastoralists, BMAC and the Harappan Civilisation were very complex (de Barros Damgaard et al., 2018a; Narasimhan et al., 2018).

Steppe-related ancestry has been recently found in some BMAC individuals, but contrary to what could be expected based on the archaeological evidence, it does not seem to have been widespread amongst BMAC populations (Narasimhan et al., 2018). Overall, BMAC individuals lack Steppe ancestry (apart from some outlier individuals), and more importantly, no Y-chromosome R1a lineages associated to the BMAC has been found (Narasimhan et al., 2018). Therefore, while the archaeological connection between the Steppe and the Indus Valley seems to be via the BMAC (Parpola, 2015), genetic results show that direct contact between Steppe groups and South Asian populations, instead of BMAC incursions into the Indus Valley, were the most likely vehicle for the arrival of CHG ancestry to the Subcontinent (Narasimhan et al., 2018). Nevertheless, these new studies overall confirm the results presented here (published in 2017), since they directly show the presence of CHG ancestry in Indian populations tracing back to the second millennium BCE (in contrast to what is observed in a Harappan individual (Shinde et al., 2019)) and teases out the fraction of CHG component deriving from Iranian farmers and from the Steppe (Yamnaya-related) (de Barros Damgaard et al., 2018a; Narasimhan et al., 2018). The complexity of interactions at the end of Bronze Age in the Indus Valley region is reflected in the heterogeneity of present-day local populations, which harbour high variability in their proportions of steppe-related ancestry (Pathak et al., 2018).

The pastoralist early Indo-European societies are believed to have had a strong patriarchal, patrilocal and patrilineal social structure (Anthony, 2010; Anthony et al., 1986). Therefore, even though I found a potential signal for the Indo-European arrival into South Asia in the phylogeny of H2b (discussed in more detail on Chapter III), Indo-Aryan movements are expected to have been mostly male-mediated. I confirmed this hypothesis by comparing the ancestry of mtDNA and Y-chromosome lineages in five South Asian populations from the 1KGP. There are remarkable differences between the maternal and paternal gene pools of these populations: while maternal South Asian genetic diversity derives largely (~70–90%, depending on the population) from the first settlement of modern humans soon after the out-of-Africa migration (with an mtDNA pool composed essentially of basal autochthonous lineages of haplogroups M and N/R), the paternal counterpart reflects a markedly higher more recent genetic influence (~50–90%) from West Eurasia and East Asia.

Since the publication of the main results from this chapter in March 2017, several additional Y-chromosome R1a lineages have been retrieved from Middle and Late Bronze Age Steppe individuals and in one individual from Iron Age Pakistan (Narasimhan et al., 2018), as well as from the Turkmenistan Iron Age (de Barros Damgaard et al., 2018a). As a consequence, the pattern observed in Figure 2.7a is now much more compelling. The situation observed for R1a draws a parallel with the spread of haplogroup R1b, although slightly earlier in the latter case, in the Chalcolithic/Early Bronze Age of central and western Europe. The process responsible for the spread of Bronze Age male-dominated Steppe-related ancestry in Europe seems to have been especially dramatic at its westernmost edge, in the Iberian peninsula, where a virtual complete turnover of male variation ~4.5 ka (in the third millennium BCE) has recently been shown (Olalde et al., 2019, a work to which I contributed – more details in Chapter V).

Chapter III

Dissecting mtDNA haplogroups H1, H2, H11 and H13

Section 3.2.1 of this chapter is published in:

Silva M, et al. Untangling Neolithic and Bronze Age mitochondrial lineages in South Asia. Annals of Human Biology 2019. DOI: 10.1080/03014460.2019.1623319

My contributions to this paper were as follows:

- Amplification and sequencing of samples from Spain (together with fellow PhD student, Gonzalo Oteo-Garcia), including NGS data processing;
- Phylogeographic analysis of H2 and H13 (ρ and ML);
- Writing of first draft, editing after co-authors' contributions and submission process (including responding to referees).

Dissecting mtDNA haplogroups H1, H2, H11 and H13

1. Introduction

Haplogroup H is one of the most common lineages found in present-day European populations, accounting for ~40–45% of European maternal variation (Pala et al., 2016; Soares et al., 2010), but it is also present at considerable frequencies in the Near East, Central and South Asia, Siberia and North Africa (Loogväli et al., 2004). Its origin is still unknown but it was most likely in southwest Asia, where many of its sister branches (HV clades) are found (Loogväli et al., 2004; Richards et al., 2000; Roostalu et al., 2007).

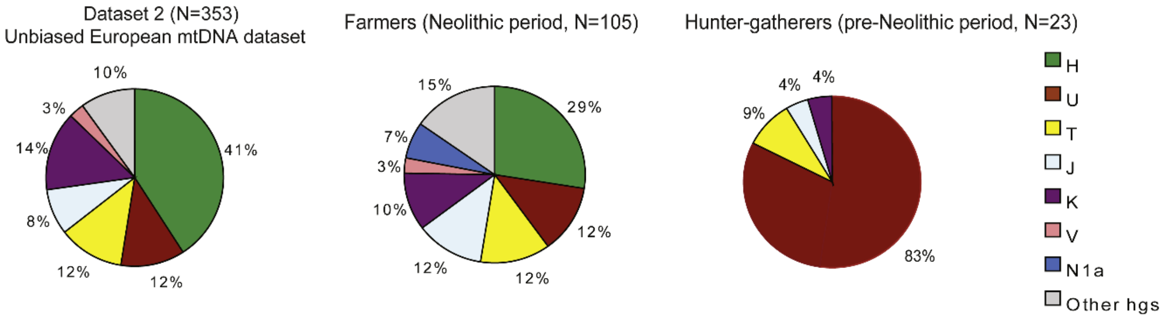

Figure 3.1. Haplogroup H frequencies amongst European hunter-gatherers and early farmers (based on short, <400 bp, mtDNA fragments) and in present-day Europe (based on an unbiased population dataset of complete mitogenomes). Figure adapted from Fu et al., 2012.

According to phylogeographic patterns of extant variation it seemed that H had entered Europe around, or even before, the LGM (Roostalu et al., 2007; Soares et al., 2010), but aDNA results have complicated the picture. The main subclades of H (H1 and H3) were thought to have originated in south Europe ~12–10 ka (possibly in the Iberian peninsula) and spread across Europe with postglacial expansions (Pala et al., 2014; Pereira et al., 2005). However, haplogroup H has rarely been identified in pre-Neolithic European remains (Figure 3.1) (Brandt et al., 2013; Brotherton et al., 2013; Fu et al., 2012), apart from some contentious non-peer-reviewed HVS–I sequences retrieved from Portuguese Mesolithic remains (Chandler et al., 2005), and two additional Upper Palaeolithic (Magdalenian) northern Spanish HVS-I sequences (Hervella et al., 2012). On the other hand, aDNA studies have shown that Bell Beaker individuals in Central Europe displayed frequencies of mtDNA haplogroup H >45%, much higher than the frequency for the previous Neolithic farmers, the contemporaneous Corded Ware culture and the following Bronze Age Unetice Culture in the same region, all with frequencies ~20% (Brandt et al., 2013; Brotherton et al., 2013). This has led to the suggestion that H expanded during the Beaker period from Iberia into Central Europe (Brotherton et al., 2013), although more recent aDNA evidence does not seem to support this scenario (Olalde et al., 2018).

Haplogroup H is defined by the transitions at the diagnostic positions 2706 and 7028 and many of its major branches (*e.g.* H1, H2, H3, H4, H7, H10, H13) are only defined by coding-region mutations, posing a problem for studies relying mostly on HVS–I and HVS–II sequencing such as the aforementioned Chandler et al. (2005) and Hervella et al. (2012). Additionally, its particular phylogenetic structure, with many clades branching out directly from the root of H, in many cases defined by variants at only one or two positions, and some degree of recurrence (*e.g.* position 3010 defines the major clade H1, but it is also diagnostic for H30b, H65a, H79a and H105a), makes the classification of haplogroup H lineages very difficult.

Considering its recurrence in European genetic record since the Neolithic (Figure 3.1) (Brandt et al., 2013), haplogroup H was probably involved in diverse population events in Eurasia. In this chapter I focus on haplogroup H1, a major H branch, which is the most common lineage in present-day Iberia and very common in southwest Europe (Achilli et al., 2004; Alvarez-Iglesias et al., 2009); haplogroup H2, present at highest frequencies in northern and eastern Europe, but also found across Central, North and South Asia (Derenko et al., 2014; Loogväli et al., 2004; Roostalu et al., 2007); the minor branch H11, with a mainly northern distribution ranging from western and Central Europe to Siberia (Alvarez-Iglesias et al., 2009; Roostalu et al., 2007); and H13, ranging from the east Mediterranean to South Asia (Derenko et al., 2013; Palanichamy et al., 2015; Pereira et al., 2005) and present in the Caucasus region since the at least the Mesolithic (Jones et al., 2015). These lineages, with a pan-Eurasian distribution, can be expected to provide insights into population movements in the Late Neolithic and Metal Ages across the continent and are an important step towards characterising the wider Eurasian maternal gene pool.

2. Methods

2.1. Modern Iberian mtDNA dataset

2.1.1. Sampling

I selected a total of 1023 Spanish and 103 Portuguese individuals for mtDNA analysis. The Spanish DNA extracts were sent by Professor Antonio Salas, a collaborator from

University of Santiago de Compostela (Spain), while the Portuguese extracts were sent by Dr Teresa Rito (University of Minho, Portugal) and by Professor Antonio Brehm (University of Madeira, Portugal). Three additional Spanish and four Portuguese samples were extracted from buccal swabs in the lab in Huddersfield, using the PureLink® Genomic DNA Mini Kit (Thermo Fisher Scientific). The Spanish samples were amplified and analysed in cooperation with Gonzalo Oteo–Garcia, a fellow PhD student in the group.

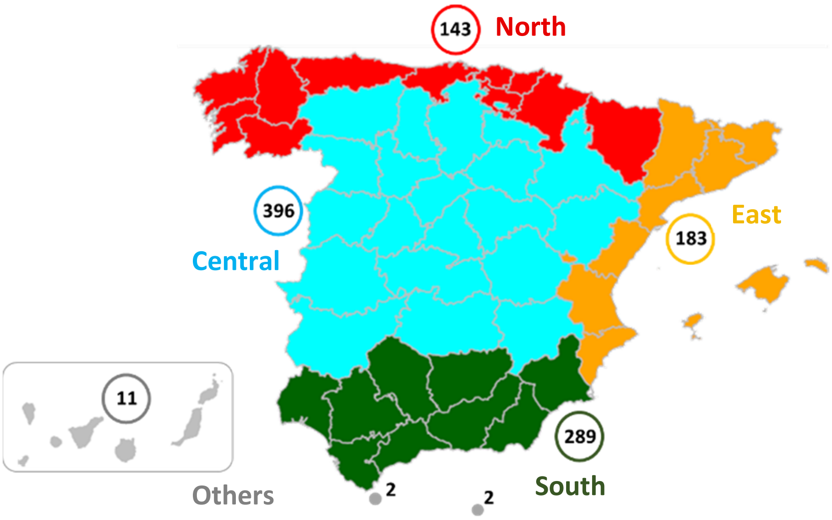

Figure 3.2. Number of complete Spanish modern mitogenomes sequenced, by region.

The sampling covers all regions of Spain (Figure 3.2) and is representative of modern Spanish populations. Unfortunately, the sampling for Portugal (classified as West Iberia) is heavily biased towards the north, with 81 sequences from the northern and central regions (corresponding to ~83% of the Portuguese dataset), and therefore it should be treated cautiously.

2.1.2. Amplification

With this long-range PCR protocol it is possible to amplify the entire mtDNA molecule with only two reactions (primers described in Table 3.1). PCR conditions were optimized according to the specifications of the GoTaq® Long PCR Master Mix Kit (commercialized by Promega Corporation), which includes a hot-start DNA polymerase (GoTaq® Hot Start Polymerase, Promega Corporation) in combination with a thermostable proofreading polymerase, allowing for the amplification of up to 30 kb of human genomic DNA. PCR reaction contained 0.5 μL of template DNA, 11 μL of nuclease-free water, 1X GoTaq® Long PCR Master Mix (Promega), and 0.2 μM of each primer (final volume 25 μL). The PCR program consisted on an initial denaturation step of 2 minutes at 94°C, followed by 30 cycles (denaturation at 94°C for 30 seconds, primer annealing at 55°C for 30 seconds, and extension for 9 minutes at 65°C) and final step of 10 minutes at 72°C (Brandini et al., 2018).

Table 3.1. List of primers forward (for) and reverse (rev) used for the long range PCR.

Fragment	Primer (position)	Reference	Sequence (5'–3')	Fragment size (bp)
1	5871for	Brandini et al., 2018	GCTTCACTCAGCCATTTTACCT	7959
	13829rev	Brandini et al., 2018	AGTCCTAGGAAAGTGACAGCGA	
2	13477for	Brandini et al., 2018	GCAGGAATACCTTTCCTCACAG	9438
	6345rev	Meierhofer et al., 2005	AGATGGTTAGGTCTACGGAGGC	

Amplification was always confirmed by 1% agarose gel electrophoresis (Cleaver Scientific Agarose), and visualized under UV light with INGENIUS 3, using GeneSys 1.2.5.0 software (both from Syngene).

2.1.3. DNA purification and quantification

I purified PCR products following Wizard® SV Gel and PCR Clean-Up System (Promega) protocol and quantified the purified DNA with Qubit™ 3.0 Fluorometer (ThermoFisher Scientific), using the Qubit® dsDNA HS Assay Kit (volume of DNA sample = 1 µL). The purified samples were then diluted to 1 ng/µL and both fragments pooled together in the same well, for a final volume of 40 µL per sample.

2.1.4. Library preparation and sequencing

The 96-well plates (each well containing 40 µL of complete amplified mtDNA sequence for one individual) were sent to the Earlham Institute, located at the Norwich Science Park, where the library preparation step was performed using an optimised protocol based on Nextera® DNA Library Prep Kit (llumina, Inc). Libraries were then pooled and sequenced with Illumina MiSeq paired-end (size of fragment: 150 bp), aiming for ~200x coverage. The company sent us the raw data as FASTQ files already demultiplexed (one file per read direction for each individual).

2.1.5. NGS data analysis

I used EAGER (efficient ancient genome reconstruction) pipeline (Peltzer et al., 2016) for many initial steps. I checked raw FASTQ files with FastQC (Andrews, 2010) and ran them through AdapterRemoval v.2.2 (Schubert et al., 2016) to remove adaptors and merge paired reads. I then aligned the reads to rCRS with BWA–MEM (Li, 2013), which is optimized for long Illumina reads, and posteriorly identified PCR duplicates with DeDup (included in EAGER pipeline). I performed quality control of the alignment with QualiMap v.2.2.1, and called variants against the rCRS using GATK v.3.7-0-gcfedb67 (McKenna et al., 2010) Indel Realigner and HaplotypeCaller.

I performed the initial SNP filtering for minimum quality (Q30) and minimum coverage (5x) using VCFtools v.0.1.11 (Danecek et al., 2011) and then handled the resultant VCF file with BCFtools v.1.4 (https://samtools.github.io/bcftools/) *view* and a shell command in order to further filter the called variants: a polymorphism was called when the minimum allele frequency was over 0.70 (MIN(AF)>0.7), discarding SNPs with frequency under 0.30, and calling all remaining variants (MIN(AF)>0.3 & MAX(AF)<0.71) to a separate file as potential heteroplasmic positions, which I later manually checked with IGV (Integrative Genomics Viewer) (Thorvaldsdottir et al., 2013). The filtered VCF files were converted into variant lists and merged into one TXT file that can be used as input for downstream analysis (such as haplogroup identification with HaploGrep) or, alternatively, easily be converted to FASTA.

I checked potential gaps in the alignments by generating a consensus sequence for each individual using a combination of SAMtools *mpileup*, BCFtools *call*, vcfutils.pl *vcf2fq,* and seqtk (Li et al., 2009, https://github.com/lh3/seqtk), in order to retrieve the mapped FASTQ reads from the sorted BAM files and generate the consensus sequences in FASTA format, which I visually checked with Geneious R6 (https://www.geneious.com) (Kearse et al., 2012). This was important in order to detect cases when one of the fragments was missing, due to pipetting errors.

Sequences were assigned to haplogroups using HaploGrep 2.0, following the nomenclature in PhyloTree (Build 17, February 2016) (van Oven, 2015). Private mutations and heteroplasmies were manually checked by visualising the alignment with IGV.

2.2. Ancient DNA data

In order to trace the presence of different H lineages in the Eurasian archaeological record though time, I computed maps using the meta-information available in the annotation file accompanying the dataset of published aDNA genotypes released by Reich's Lab on their website (v37.2.1240K, https://reich.hms.harvard.edu), which I completed with data from Wang et al. (2019), Narasimhan et al. (2018) and Olalde et al. (2019), as well as from mtDNA-only studies (Brandt et al., 2013; Brotherton et al., 2013; Juras et al., 2018; Knipper et al., 2017; Margaryan et al., 2017; Nikitin et al., 2017a; Olivieri et al., 2017; Rusu et al., 2018; Stolarek et al., 2018; Vai et al., 2019).

I mapped a total of 605 ancient H sequences using geographical coordinates in R (Appendix B, Table S1), with the packages *maps* v.3.3.0 (Brownrigg et al., 2018), *mapdata* v.2.3.0 (Brownrigg, 2018) and *ggplot2* v.3.1.1 (Wickham, 2016), and coloured the maps according to the average of 95.4% date range in calibrated (cal.) BP (defined as 1950 CE) using the colour-blind friendly *RdYlBu* pallet included in the *RColorBrewer* v.1.0-5 package

(Neuwirth, 2011). Random jitter was added so as to distinguish multiple samples sharing geographical coordinates. In addition, I also computed individual maps for lineages H1, H2, H11 and H13.

Carefully curated datasets of ancient H1, H2, H11 and H13 sequences were included in the phylogenetic trees (see section below) (Appendix B, Table S2). Sequences containing large gaps and/or missing important diagnostic positions, which therefore could not provide reliable phylogenetic information, were excluded from trees (although included in the dataset used to compile the maps whenever it was possible to confirm the main haplogroup), in order to prevent spurious basal positions within branches, which could lead to erroneous data interpretation. Special care was taken for sequences classified as H2a when compared to rCRS, to confirm if the absence of mutations in relation to the reference was not an artefact of low coverage.

2.3. Phylogenetic reconstruction

2.3.1. European population dataset

Our group is jointly conducting the analysis of the European mtDNA haplogroup H. Collectively we sequenced more than 3000 mitogenomes from several present-day European populations: Britain (*n*=584), Ireland (*n*=97), Belgium (*n*=124), France (*n*=336), Germany (*n*=213), Italy (*n*=508), Greece (*n*=134) and Cyprus (*n*=44) (amplified and sequenced by fellow PhD students in the group), in addition to the Iberian dataset described above (*n*>1100).

I also had access to additional unpublished mtDNA sequences through the groups' on-going collaborations with Professor Jim Wilson (University of Edinburgh), and with Professor Walther Parson (Institute of Legal Medicine, Innsbruck Medical University) and Dr Antònia Flaquer (Institute of Genetic Epidemiology, Ludwig Maximilians University) from KORA-gen project (Wichmann et al., 2005): Shetland, Scotland (*n*=500), Germany (*n*=2900) and the Netherlands (*n*=491). The German dataset was however considered as of unknown origin and only included in the trees for topology purposes, since there was no additional information about the background of the individuals and the dataset did not reflect German populations' haplogroup composition.

I have focused my analysis on H1 (~3500 sequences) (Appendix B, table S3), H2 (~650 sequences) (Appendix B, table S4), H11 (~200 sequences) (Appendix B, table S5) and H13 (~350 sequences) (Appendix B, table S6), for which I have combined the newly jointly generated European sequences from our lab with published ancient and modern sequences. The datasets used to compute the trees were divided into 14 different geographic regions (with a more detailed division for Europe), plus an extra category for unknown geographic origin (Table 3.2).

Table 3.2. Colour scheme used in the complete trees of haplogroup H (Appendix B, Excel files S1-S4). Please note that the colour code might slightly change in some figures for simplicity and aesthetic purposes.

Region/colour code	Countries/groups included
Europe Northwest	Austria, Belgium, Czech Republic, Denmark, France, Germany, Hungary, Ireland, Luxembourg, Netherlands, Norway, Poland, Slovakia, Sweden, Switzerland, United Kingdom
Europe Northeast	Belarus, Estonia, Finland, Latvia, Lithuania, Moldova, Romania, Ukraine, Western Russia
Europe Southeast	Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Greece, Cyprus, Italy, Macedonia, Serbia, Slovenia
Iberia	Portugal, Spain (except Basque region/Basque-speaking)
Europe Basque	Basque country; historically Basque-speaking populations
Europe/European ancestry	*e.g.:* USA, South Africa, Brazil, Argentina (with recent European ancestry)
South Asia	Indian subcontinent (Bangladesh, Bhutan, India, Nepal, Pakistan, Sri Lanka)
Asia	Central and East Asia (includes Central and Eastern Russia)
Near East	Iran, Iraq, Israel, Jordan, Kuwait, Lebanon, Oman, Qatar, Saudi Arabia, Syria, Turkey, UAE, Yemen
South Caucasus	Armenia, Azerbaijan, Georgia
North Caucasus	Adygea, Chechnya, Dagestan, Ingushetia, Kabardino–Balkaria, Karachay–Cherkessia, North Ossetia (Russia)
North Africa	Morocco, Algeria, Tunisia, Libya, Egypt, archaeological samples from Canary Islands (except clear recent European ancestry)
West/central Africa	*e.g.:* Burkina Faso, Nigeria (except clear recent European ancestry)
Eastern Africa	Sudan, South Sudan, Ethiopia, Djibouti, Somalia, Kenya (except clear recent European ancestry)
Unknown	Unknown origin; unpublished German dataset

2.3.2. Node age estimates

I built a phylogenetic tree for each haplogroup using unweighted maximum parsimony with MtPhyl v5.003 software (http://eltsov.org), and excluding indels and hotspot mutations according to PhyloTree recommendations, as explained in Chapter II (section 2.1). Node age estimates were calculated both using *ρ*-statistics and with ML, in the same fashion as in Chapter II. Ancient samples were not considered for age calculations, but included in the trees for phylogenetic support.

ρ estimates and standard errors, estimated as in Saillard et al. (2000), were calculated and converted into years using an in-house software developed by Daniel Vieira, a collaborator from the University of Minho, using a mutation rate of one substitution in every 3,624 years, correcting for purifying selection (Soares et al., 2009). ML node age calculations were performed with baseml v.4.7 from PAML package (Yang, 2007). I used the HKY85 mutation model (Hasegawa et al., 1985) with gamma-distributed rates (discrete distribution of 32 categories), and considered two partitions so as to differentiate the fast-evolving HVS–I (16024–16400 bp) and HVS–II (44–340 bp) from the rest of the mitochondrial sequence. HKY85, which distinguishes transitions from transversions and accounts for different nucleotide frequencies, has previously been successfully tested for large mtDNA datasets (Soares et al., 2009).

3. Results

3.1. Overall phylogeographic patterns: integrating the archaeological record

Note: for simplicity the node age estimates mentioned in this section are reported in ka (thousand years ago), whereas cal. BP is used when referring to archaeological samples (to allow for direct comparison with the dataset used to compute the maps). Age estimates reported here result from ML calculations, apart from H1 internal nodes, for which paml analysis is still ongoing, and thus the estimates shown here are the result of preliminary *ρ* analysis. Complete trees and node age estimates can be found in Appendix B, Excel files S1-S4. Haplogroup frequencies on the Iberian mtDNA dataset (*n*>1100) are shown in Appendix B, Table S7.

3.1.1. Haplogroup H1

Haplogroup H1, one of the major branches of haplogroup H, is defined by a transition at hotspot position 3010, which appears recurrently in the global mtDNA phylogeny (Soares et al., 2009), and is also diagnostic for other more derived H branches, such as H30b, H65a, H79a and H105a. The dataset contains 3483 modern (1048 of which newly reported) and 148 ancient sequences, spanning from the Early Neolithic to the Medieval times.

H1 is one of the most common lineages in present-day western European populations (Batini et al., 2017; Pereira et al., 2005), and it has been found numerous times in the European archaeological record of the last 8 ka, especially in the west (Figure 3.3). The oldest H1 sequence reported is from Croatian Cardial Neolithic (~7800 cal. BP) (Mathieson et al., 2015), matching well with the ML estimate for H1 (8.5 [7.1-9.8] ka). In Iberia the earliest H1 mitogenome was retrieved from an individual found in an Early Neolithic site in Burgos (north Spain), dating to ~7070 cal. BP (Lipson et al., 2017). Additional sequences of similar age were found in Central Europe ~7100-7000 cal. BP, and in Bulgaria and Ukraine in the following centuries, always associated to Y-lineages G2 and I2 (Brotherton et al., 2013; Lipson et al., 2017; Mathieson et al., 2015). The similar dates in central and southwest Europe suggest that H1 probably spread from southeast Europe with Neolithic dispersals along the Mediterranean and Danubian routes. The first instance of H1 in the British isles is from a Scottish Neolithic context in the mid-fourth millennium BCE (Olalde et al., 2018).

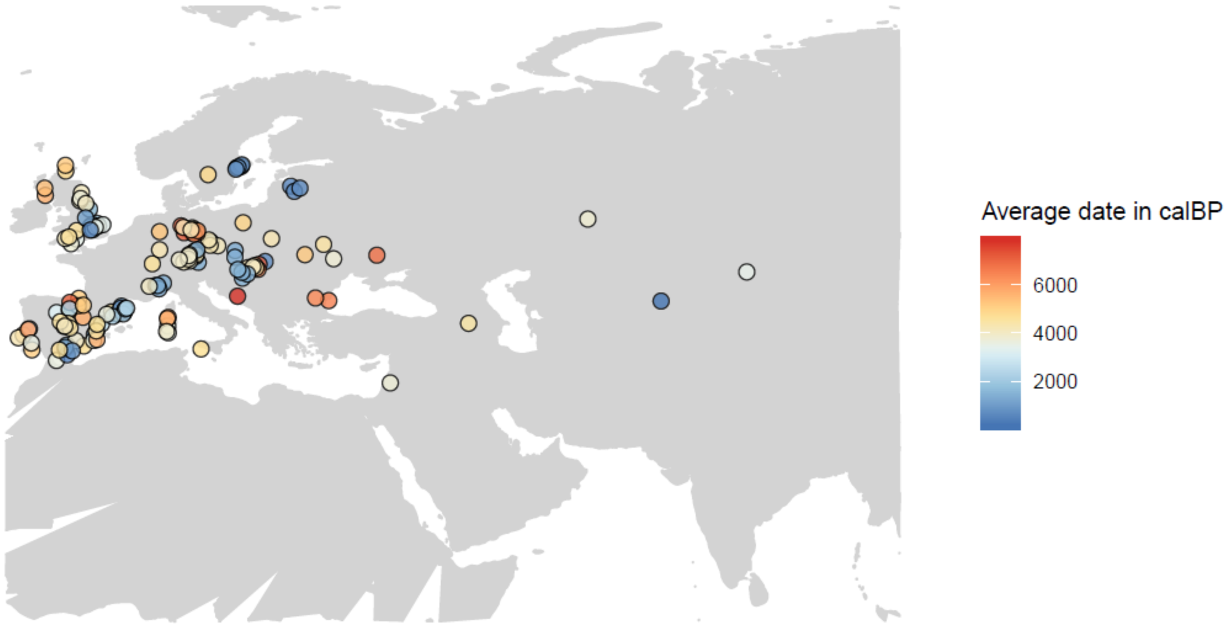

Figure 3.3. Occurrence of haplogroup H1 in the archaeological record. Each point represents one individual (with added jitter for sites with multiple individuals), coloured according to the average of 95.4% date range in cal. BP (defined as 1950 CE).

Although with a predominantly western distribution, H1 was identified in an Armenian Early Bronze Age individual from the mid-third millennium BCE, and in one individual from the Middle Bronze Age Lebanese Canaanites in the following millennium (both female) (Haber et al., 2017; Lazaridis et al., 2016). H1, in the form of H1b (7.0 [3.7-10.3] ka), was also found in one Sintashta individual and in another one from Middle Bronze Age Kazakhstan ~3800-3500 cal. BP, both males carrying R1 Y-haplogroups (R1a in the case of the latter) (Narasimhan et al., 2018). These two sequences form a cluster defined by position 11530, with no descendent modern sequences in the present dataset (Appendix B, Excel file S1).

H1b and H1b1 (5.9 [2.2-9.6] ka) are also present in Beaker and Bronze Age Central European samples (Knipper et al., 2017; Olalde et al., 2018), in addition to one Ukrainian Trypillian and Bronze Age Latvian sequences (Mittnik et al., 2018; Nikitin et al., 2017b)). H1 was present in the gene pool of southeast Europe and in the Pontic-Caspian region in the fifth and fourth millennia BCE (although probably in low frequencies, as it was only found in two Ukrainian individuals dating to ~6.8 and ~5.2 cal. BP (Mathieson et al., 2015; Nikitin et al., 2017b) (Figure 3.1). Therefore, H1b seems to also have been involved in movements of Indo-European speakers eastwards, even if its frequencies nowadays across the Steppe and Central Asia are very low (<1%) (Loogväli et al., 2004), and the phylogenetic signal in modern populations virtually disappeared.

Several major branches stem directly from the root of H1, *e.g.* H1a (7.0 [4.1-9.9] ka), H1c (7.2 [4.4-10.2] ka), H1e (10.7 [6.5-14.9] ka), H1j (7.5 [4.1-10.9] ka), H1n (10.7 [4.7-16.8] ka) and H1q (8.1 [5.3-11.0] ka) (ρ estimates). H1 harbours at its root several basal Neolithic sequences from Spain, Sardinia, Scotland and Croatia, as well as two Beaker sequences (one Spanish and one Italian), together with present-day sequences from west and south Europe (Appendix B, Excel file S1).

H1 peaks in frequency ~18-25% in Iberia and Sardinia (Alvarez-Iglesias et al., 2009; Batini et al., 2017; Olivieri et al., 2017) (Appendix B, Table S7). Many Iberian sequences are found in large branches, shared with Central Europe: *e.g.* H1b, H1c, H1e, H1ba. H1e has been found in several Neolithic and Chalcolithic Iberian individuals (Martiniano et al., 2017; Olalde et al., 2018, 2019), but has also been retrieved from Neolithic individuals from Central Europe (Brotherton et al., 2013; Lipson et al., 2017), and was recently found in Sicilian Middle Neolithic remains (not included in the present dataset) (Fernandes et al., 2019), thus further confirming its pan-European distribution in the Neolithic, and probable involvement in both the Mediterranean and Danubian routes of Neolithic dispersals. H1t (6.9 [1.1-13.0] ka), harbouring one Bell Beaker, one Chalcolithic and one Iron Age Spanish samples (Olalde et al., 2018, 2019), H1j1 (4.3 [1.9-6.6] ka), and H1av1 (2.8 [0.3-5.4] ka) are more specific Iberian branches, all with a strong Basque component. Together with H3 and some lineages of H2 (such as H2a5a1), H1 is one of the most common mtDNA lineages amongst the present-day Basque population (Behar et al., 2012b).

Several Sardinian-specific haplogroups derive directly from the root of H1 tree, with only one defining mutation (*e.g.* branches defined by positions 16319 (6.2 [1.6-11.0] ka), 7543 (3.5 [0.0-8.6] ka), 14329 (2.7 [0.0-6.5] ka), and 15217 (1.6 [0.4-2.8] ka)). The oldest H1 from Sardinia in the dataset dates to just over 6000 cal. BP (Olivieri et al., 2017), suggesting a Neolithic presence in the island.

North African branches are also visible in the tree (Appendix B, Excel file S1). H1 is present in North Africa at frequencies ranging from ~7% to >50% in certain isolated Tuareg groups (Ennafaa et al., 2009; Ottoni et al., 2010; Pereira et al., 2010a), essentially in the form of North African specific branches: H1w, H1x (both with a node age estimate of 0.9 [0.0-2.6] ka) and H1v (4.0 [1.0-7.0] ka, also including two present-day Spanish and two other western European sequences in the dataset). The age estimates of these nodes do not support a pre-Neolithic arrival in North Africa, as suggested before (Ennafaa et al., 2009; Ottoni et al., 2010). Neither do the first data from Palaeolithic and Early Neolithic Moroccan sites indicate such an early presence of H1 in North Africa (Fregel et al., 2018; van de Loosdrecht et al., 2018). Instead, although H1 itself (or any H lineage) was not identified amongst the Late Neolithic individuals of Kelif el Boroud (Morocco) (Fregel et al., 2018), the presence of other maternal lineages typically found in Anatolian and European Neolithic farmers (K1, T2, X2), as well as of European-like autosomal ancestry, indicate that the Neolithic (or later) is a more probable timeframe for the arrival of H1 to North Africa.

H1 is also found at low frequencies in present-day Near Eastern populations, varying from <1% in Jordans to ~3.4% in the Druze (Achilli et al., 2004; Roostalu et al., 2007), and present at <2% in Iranians (Derenko et al., 2013). In the present dataset, only 42 sequences (~1.2% of the modern dataset) are of Near Eastern origin, reflecting low H1 frequencies in the region. Most samples are found inside larger, mostly European, branches, except for H1ca (3.6 [0.0-8.3] ka), which is composed of one Druze, two Pakistani and five Iranian sequences. Additionally, three Near Eastern (two Levantine and one Iranian) sequences stem directly from the root of H1.

The low frequencies in the Near East, which translate into a small number of H1 Near Eastern complete sequences, make the detection of phylogeographic patterns difficult. However, the fact that H1 has been retrieved from only one Late Bronze Age Near Eastern individual (Haber et al., 2017) – an H1bc lineage in Bronze Age Canaan that has otherwise been found only within Europe – despite >100 Near Eastern ancient individuals sampled (spanning from the Palaeolithic to the Bronze Age), suggest that this haplogroup was not present in the region at earlier periods, and therefore unlikely to have originated in the region. Instead, current evidence (especially based on aDNA) points to a southeast European origin for H1, from where it was carried into the rest of Europe following Neolithic dispersal routes, and increased in frequency. In this scenario, the present-day Near Eastern H1 lineages seem to be the result of later movements from Europe.

3.1.2. Haplogroup H2

The present dataset comprises 621 present-day (171 of which unpublished) and 36 ancient H2 sequences (Figure 3.4). Haplogroup H2, with an age estimate of 14.3 [0.9–19.3] ka, is defined by position 1438. It is divided into three main branches: H2a (10.7 [7.9–13.6] ka), H2b (7.5 [4.9–10.2] ka) and H2c (8.2 [2.0–14.5] ka).

The oldest H2 sequence known is an H2a lineage dating to 6800 cal. BP and retrieved from the Russian Steppe Eneolithic (Mathieson et al., 2018). Additional H2a lineages, as well as one basal H2, dating to ~6500-6100 cal. BP, were retrieved from the Armenian Chalcolithic and from the Pontic-Caspian Steppe Eneolithic (Lazaridis et al., 2016; Mathieson et al., 2018; Wang et al., 2019). H2a was also found in the remains of a Maikop individual, dating to ~5500 cal. BP (Wang et al., 2019), and approximately two centuries later, in the Copper Age Remedello culture in Italy (Allentoft et al., 2015).

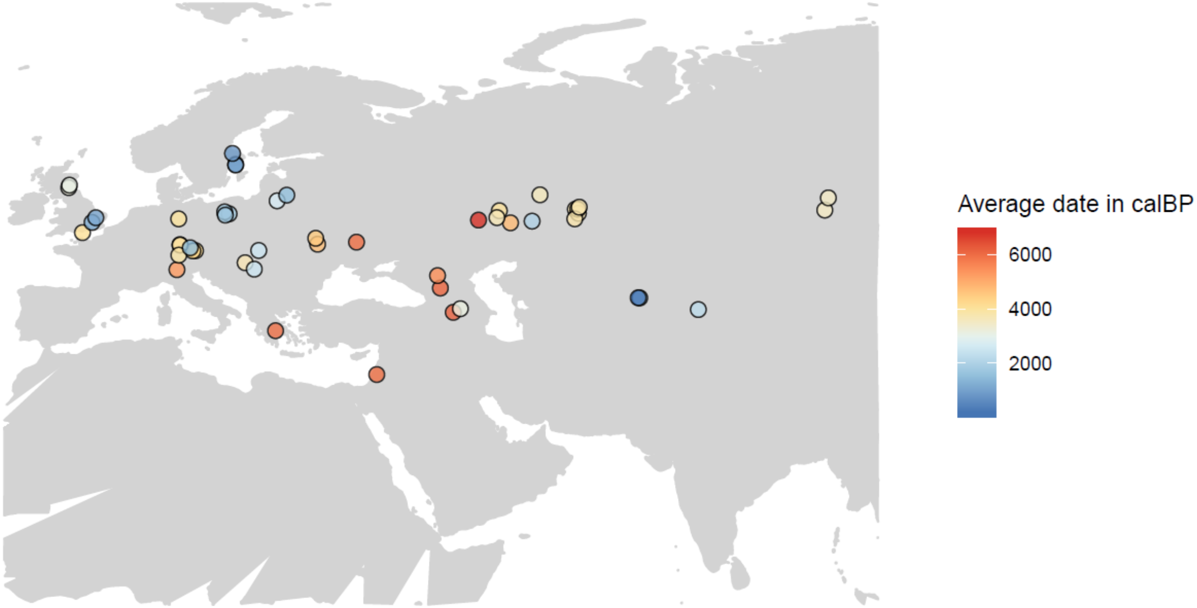

Figure 3.4. Occurrence of haplogroup H2 in the archaeological record. Each point represents one individual (with added jitter for sites with multiple individuals), coloured according to the average of 95.4% date range in cal. BP (defined as 1950 CE).

H2a is the largest and most complex of H2 branches, with ~95% of the present-day H2 sequences in the dataset. After 5000 BP, H2a was found amongst Corded Ware (Juras et al., 2018) and Bell Beaker individuals in Poland and Germany, respectively (Allentoft et al., 2015; Olalde et al., 2018), and seems to have reached western Europe with the Copper or Bronze Age at ~4000 cal. BP. Additional H2a lineages were found in Bronze and Iron Age remains from the Pontic-Caspian region (Krzewińska et al., 2018). H2 (and specifically H2a) seems to have been distributed around the Black Sea, before being taken across northern Europe from the Steppe with the Yamnaya.

To my knowledge, H2 has never been identified in the Iberian archaeological record, thus supporting a more eastern evolution of this lineage, and a more recent arrival to the western Atlantic edge of continental Europe. The bulk of present-day Iberian sequences in the H2 tree, the majority of which are from the Basque country region, cluster within H2a5a, which dates to 2.9 [0.0–7.1] ka. The derived H2a5a1 (1.8 [0.6–3.0] ka) is thought to have arisen within the Basque country region (Behar et al., 2012b). Overall H2 is found at a frequency ~2% in present-day Iberian populations (Appendix B, Table S7).

H2b is a smaller branch, and it has been found across the Eurasian steppe ~3800–3500 cal. BP, ranging from the Samara region to west Siberia (Krasnoyarsk) – a detailed description of H2b can be found later on in this chapter (section 3.2.1). Lastly, H2c is a minor European branch, with only ten present-day sequences in the present dataset. No ancient H2c sequence has ever been reported.

3.1.3. Haplogroup H11

H11 is defined by mutations at positions 8448, 13759 and 16311, as well as 195, a rapidly-evolving site (Soares et al., 2009) that is also shared with H8’31, and minor haplogroups H12, H91 and H108, potentially due to long-branch attraction.

Figure 3.5. Occurrence of haplogroup H11 in the archaeological record. Each point represents one individual (with added jitter for sites with multiple individuals), coloured according to the average of 95.4% date range in cal. BP (defined as 1950 CE).

The tree presented here includes 205 complete modern H11 mitogenomes, of which 70 are newly reported here. The majority of present-day sequences are from northern Europe, with sequences from this region accounting for ~55% of the modern dataset (~70% if taking into consideration the German sequences from KORA-gen, which I classified as of unknown geographic origin). Overall, H11 frequency peaks in Central European populations, and also has an eastern distribution (around the Baltic Sea, in the eastern Mediterranean area, and further east into central Eurasia), whereas it is virtually absent in southwest Europe (Alvarez-Iglesias et al., 2009) (~0.5% in the present Iberian dataset (Appendix B, Table S7)).

H11 has a node age estimate of 12.5 [8.4–16.7] ka, and divides into two branches: H11a (7.9 [6.1–9.8] ka) and H11b (9.0 [4.5–13.5] ka). H11 has rarely been observed in the archaeological record (Figure 3.5), and always in the form of H11a, the main branch. The oldest H11a lineage, dating to ~4300 cal. BP, was found in a Narva context in Lithuania (Mittnik et al., 2018), thus suggesting continuous presence of H11 in the Baltic region since at least Neolithic times. H11a was also present in Central Europe during the Bronze Age, although most likely in low frequencies, since it has only been recovered from one German and one Hungarian individual, associated to the Unetice and Vatya cultures, respectively (Allentoft et al., 2015; Brandt et al., 2013; Brotherton et al., 2013). Additional H11a sequences have been found in Medieval Italy (in a Lombard cemetery) and Germany (Amorim et al., 2018; Vai et al., 2019; Veeramah et al., 2018). H11b is a very small branch (with only 12 sequences in the dataset), and to date has not been retrieved from archaeological remains.

3.1.4. Haplogroup H13

H13 is defined by a single mutation at position 14872. My tree includes 348 complete sequences (325 modern, 102 of which unpublished, and 23 ancient). Despite the majority of present-day sequences being from Europe, a considerable proportion of samples come from other more easterly regions (namely, the Caucasus, the Near East and South Asia), accounting for approximately 16% of the modern dataset. H13 has a node age estimate of 18.6 [13.8–23.5] ka and is divided into three main clades: H13a (17.1 [10.3–24.1] ka) – the largest branch, comprising ~89% of modern H13 sequences in the dataset, H13b (16.7 [11.5–21.9] ka) and H13c (16.1 [10.7–21.6] ka).

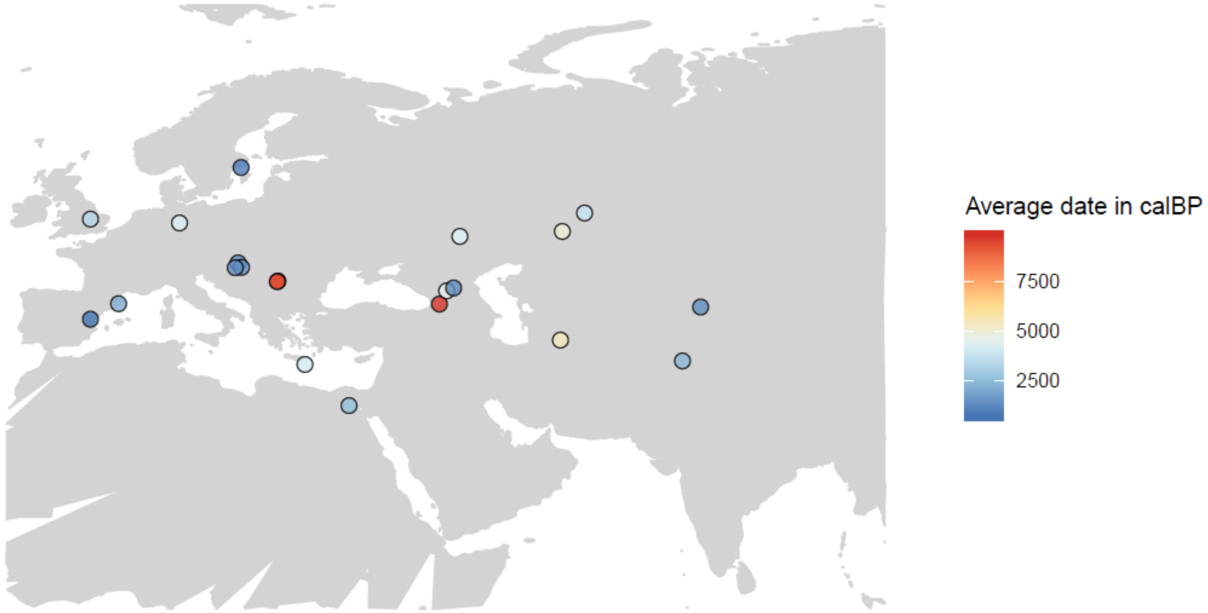

Figure 3.6. Occurrence of haplogroup H13 in the archaeological record. Each point represents one individual (with added jitter for sites with multiple individuals), coloured according to the average of 95.4% date range in cal. BP (defined as 1950 CE).

Overall, the main H13 subclades seem to have a dual west/east distribution, except for H13a1a, and H13a1a1 in particular, which are essentially European, with H13a1a1d harbouring uniquely Finnish sequences in the dataset (Appendix B, Excel file S4). Nevertheless, some non-European clusters occur within H13a1a, such as the Druze-associated H13a1a2b, or the small unnamed branch defined by the position 12771, which contains one modern Indian and one Sintashta, which will be discussed below, in section 3.2.1 of this chapter.

Despite the old age estimates based on modern variation, the oldest H13 mitogenomes (Figure 3.6) known are from the Iron Gates Mesolithic in Romania and Serbia, dating to ~9800 and ~9300 cal. BP (two sequences forming a cluster branching directly from the root of H13, with no descendants in the modern dataset (Mathieson et al., 2018)), and from Georgia, in the South Caucasus (~9720 cal. BP), in the form of H13c (Jones et al., 2015). The following oldest H13 sequence, a H13a2a lineage, has been retrieved from an individual found in the Early Neolithic site of Tepe Anau in Turkmenistan (Narasimhan et al., 2018) – more details about this branch later, in section 3.2.1 of this chapter.

H13 lineages dating between 4000 and 5500 cal. BP have been found in the North Caucasus (Wang et al., 2019), across the Eurasian Steppe (in Yamnaya and Poltavka individuals from Russia (Haak et al., 2015; Mathieson et al., 2015)), in German Bell Beaker remains (Brotherton et al., 2013; Haak et al., 2015), and in Minoan Greece (Lazaridis et al., 2017) – all belonging to the H13a1a branch, which has a node age estimate of 7.2 [5.6–8.8] ka (section 3.2.2). Strikingly, the males carry an R1b1 Y-chromosome lineage, except for the Minoan individual, whose Y-lineage belongs to J2a. H13a1a reappears in Bronze Age contexts, not only in Europe, where it has been found in England (Olalde et al., 2018), but also to the east, associated to a Sintashta individual (Narasimhan et al., 2018), again together with Y–R1b1 lineages.

In the Iberian archaeological record, H13 (in the form of H13a1a) has only been found in two individuals from Spain (Olalde et al., 2019): one individual from the Greek colony of Empúries ~2150 cal. BP, and one individual found in an Islamic burial, dating to the 11th–13th century CE (~750 cal. BP); both linking the presence of H13 lineages in the peninsula with the eastern Mediterranean and possibly North Africa. In the dataset presented here H13 has an average frequency of <1% in Iberia (Appendix B, Table S7).

3.2. Haplogroup H and the transition to the Metal Ages

3.2.1. Untangling Neolithic and Bronze Age maternal lineages in South Asia

In Chapter II I proposed a chronology for the human occupation of South Asia by combining uniparental and autosomal information. Following the initial settlement of the region in the Pleistocene, and in addition to the Late Glacial dispersal of some lineages from Near Eastern *refugia*, two important moments brought additional layers of diversity to South Asian maternal gene pool (Silva et al., 2017): (i) the Neolithic, characterised by the onset of agriculture and the rise of the Harappan (or Indus Valley) Civilisation in Baluchistan, in the northwest of the Subcontinent (Mcintosh, 2008); and (ii) the Late Bronze Age, following the 4.2 ka BP climatic event (which affected aridity levels in the Indus Valley region) (Staubwasser et al., 2003), comprising the decline of the Harappan Civilisation and the likely spread of the Indo-European language family into the region (Parpola, 2015). In this section (published recently: Silva et al., 2019b), I exploit phylogeographic patterns of two mtDNA haplogroups, whose distribution span from Europe to South Asia: H2 and H13. I use published ancient mitochondrial sequences from Eurasia, with special emphasis on the recently published sequences from Central and South Asia (Narasimhan et al., 2018), and re-examine the conclusions from Chapter II.

As mentioned above, H2a is the largest branch within H2 tree, and seems to have been distributed around the Black Sea, from where it spread with the Yamnaya movements into northern Europe. H2b, on the other hand, is a small clade (Figure 3.7). It harbours several ancient Russian samples, which are basal to the rest of the branch, including two from the Pontic-Caspian Steppe (one Yamnaya individual (~4770 cal. BP) (Haak et al., 2015) and another from the Late Bronze Age Srubnaya culture (~3680 cal. BP) (Mathieson et al., 2015)), as well as five other Bronze Age sequences from east of the Volga river: three Sintashta (dating to ~3800 cal. BP) and two from Krasnoyarsk (~3500 cal. BP) (Narasimhan et al., 2018). There are also three modern sequences from Russia (two of which from the Altai region) and one sequence from present-day Denmark, all stemming directly from the root of H2b.

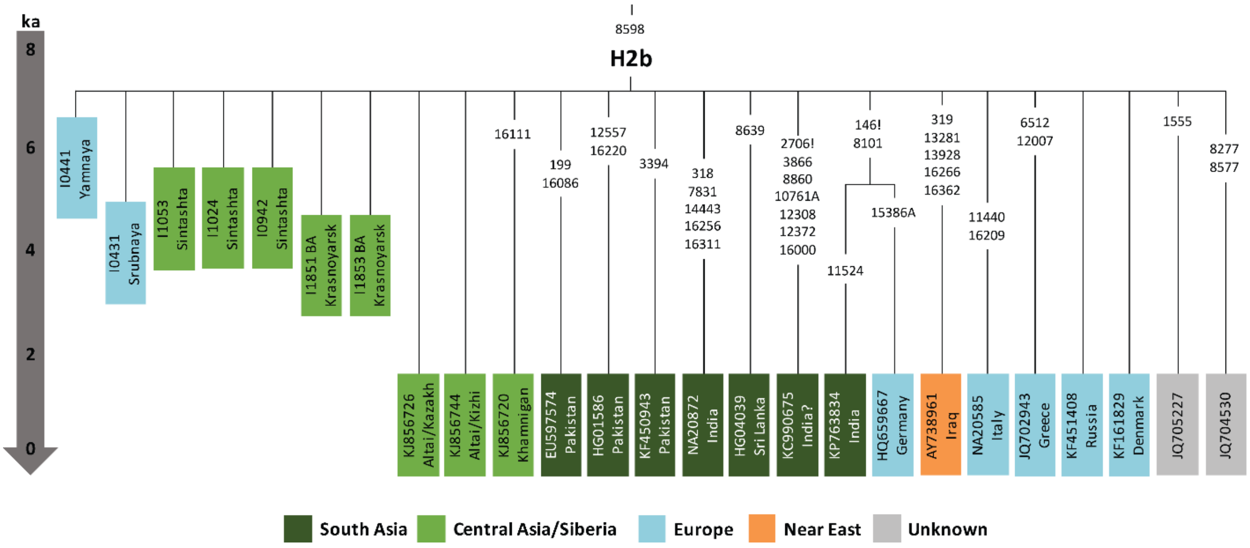

Figure 3.7. Schematic tree of mtDNA sublacde H2b. Details on these samples can be found in Appendix B, Tables S2 and S5. Complete tree in Appendix B, Excel file S2.

Although the large majority (~70%) of H2 present-day mitogenomes in the tree are from Europe, H2b shows a strong South Asian component, harbouring seven sequences from Pakistan, India and Sri Lanka. The recently released Sintashta and Middle Bronze Age Krasnoyarsk (from Russia) mitogenomes (Narasimhan et al., 2018), together with the previously published Yamnaya and Srubnaya, represent a time frame ranging from ~5 to 3.5 ka. Furthermore, three of the five males carrying the maternal H2b also carry a Y–R1a lineage (the other two are classified as R and R1, but lack the resolution necessary to determine if they are also R1a) (Narasimhan et al., 2018). These, together with the present-day South Asian sequences, support my earlier claim that H2b was included in movements into South Asia, ultimately from a source in the Pontic-Caspian Steppe (Silva et al., 2017), by showing its progress across the Eurasian Steppe, together with the Y–R1a haplogroup. As I discussed in Chapter II, the Sintashta in the Urals, or a "Sintashta-related" culture (*e.g.* the Andronovo), is thought to have expanded ~3.8 ka into Central Asia, arriving to the Indian Subcontinent in the following centuries (Anthony et al., 1986; Gimbutas, 1963) and, according to linguistic and archaeological evidence, they were most likely responsible for transmitting the Indo-European across Central and South Asia (Parpola, 2015).

Despite showing some similarities with H2, the phylogeny of haplogroup H13 provides a different overall pattern. Although the majority of present-day sequences are of European origin, ~15% of the modern dataset (20% excluding those of unknown geographic origin) is from more easterly regions (the Caucasus, the Near East and South Asia) – more than the double the case for H2.

Interestingly, a possible signal of Bronze Age events is also seen in the phylogeny of H13. Although H13a1a (~7 [5.6–8.8] ka) probably arose in the Caucasus, it is mostly a typical northern European clade: it harbours Middle Bronze Age sequences from the Poltavka Culture (the descendant to the Yamnaya in the Samara region in Russia, dating to ~4350 cal. BP) (Mathieson et al., 2015) and England (~3400 cal. BP) (Olalde et al., 2018) at its root, in addition to a Russian Yamnaya sample (Haak et al., 2015) in a deep Eastern European subclade. In the dataset, one present-day sample from India (Palanichamy et al., 2004) clusters together with a Sintashta sequence (Narasimhan et al., 2018) (H13a1a+12771) (Figure 3.8a) within H13a1a, thus showing that H13a1a (similarly to H2b) was likely included in the long-range movements associated with the Yamnaya horizon, not only across northern and Central Europe (discussed in more detail in section 3.2.2 of this chapter) but also eastwards into Central Asia. Moreover, sample I0980, the Sintashta male, carries the Y-chromosome lineage R1b1 alongside an H13a1a maternal haplotype, similarly to the northern/Central European males dating to ~5000–3000 cal. BP (section 3.2.2). H13a1a is nowadays reportedly found in India predominantly amongst the Uttar Pradesh Brahmin communities, who are Indo-Aryan-speakers (Palanichamy et al., 2015).

I focus here instead on H13a2a (Figure 3.8b), which dates to ~12 [8.1–15.5] ka, and probably arose in the region between the South Caucasus and Iran. H13a2a harbours an unusually high proportion of South Asian lineages compared to the majority of haplogroup H subclusters.

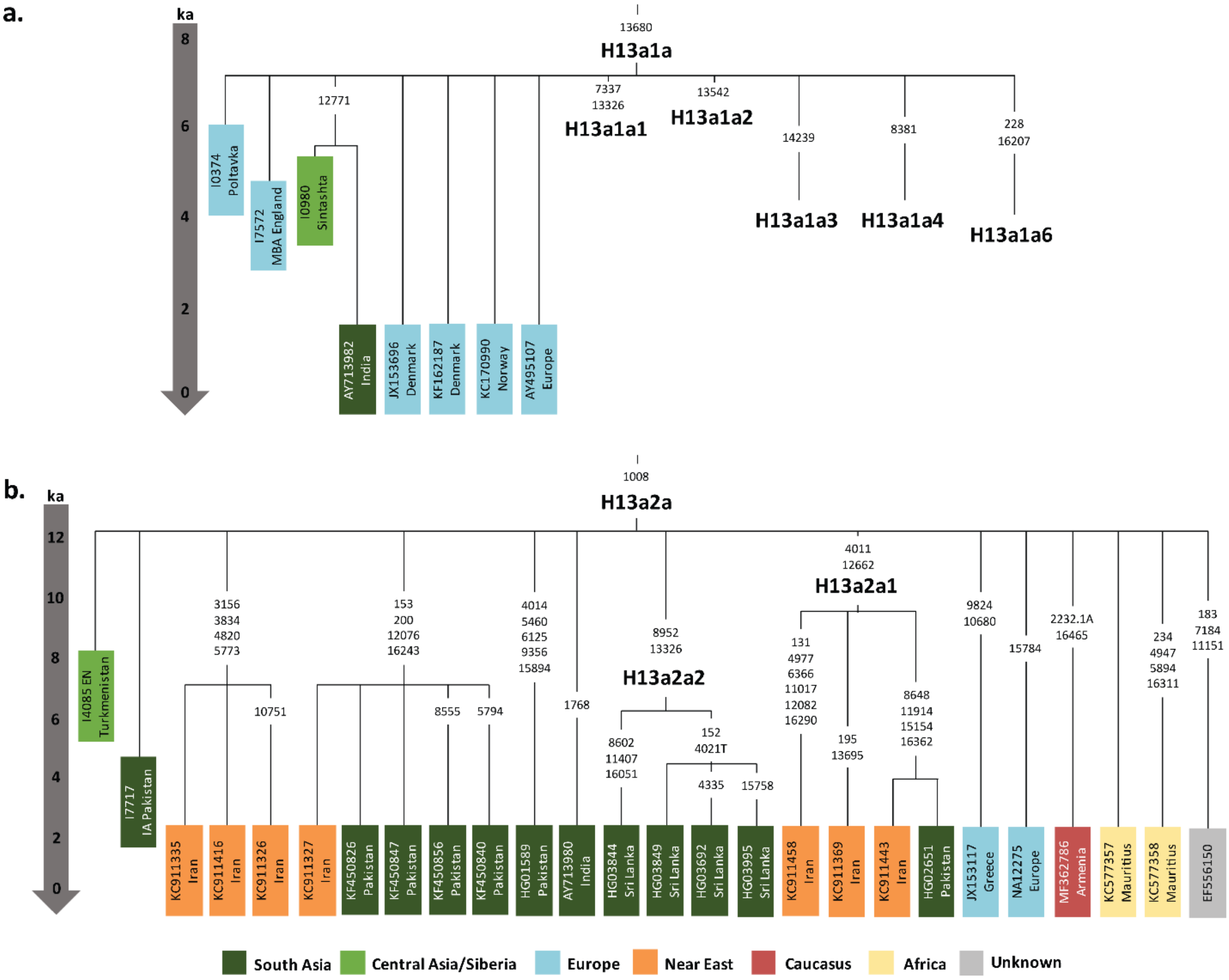

Figure 3.8. Schematic trees of mtDNA subclades **a)** H13a1a (only basal samples and H13a1a+12771 shown) and **b)** H13a2a.1. Abbreviations for ancient samples: MBA – Middle Bronze Age, EN – Early Neolithic, IA – Iron Age. Details on these samples can be found in Appendix B, Tables S2 and S6. Complete trees in Appendix B, Excel file S4.

As mentioned before, the earliest evidence of the Neolithic in South Asia dates to the 7th millennium BCE, in the site of Mehrgarh, in Baluchistan (Jarrige and Jarrige, 2006; Petrie, 2015) (Chapter I, Figure 1.5). Humidity in this region was higher in the early Holocene than nowadays, with a peak in humidity values ~8 ka (Van Campo, 1986), providing good conditions for agriculture and culminating in the eventual rise of the Indus Valley Civilisation (Coningham and Young, 2015). The analysis of non-autochthonous South Asian mtDNA haplogroups performed in Chapter II seems in agreement with archaeological evidence, with numerous lineages, including H13a2a, arriving to the Subcontinent in the Neolithic period from a putative source in the Fertile Crescent, possibly accompanying the spread of the Dravidian language family, as discussed on Chapter II (Silva et al., 2017).

H13a2a1 (~10 [5.3–13.7] ka) is shared between Iran and South Asia, whereas a previously unnamed H13a2a sub-clade, labelled here as H13a2a2 (Figure 3.8), is a Sri Lanka (more specifically Tamil, *i.e.* Dravidian-speaking) branch with an age estimate of ~7 ka [2.1–12.4] (however with wide confidence intervals, since it is a small sub-branch). H13a2a harbours two recently reported ancient mitogenomes (Narasimhan et al., 2018) that further confirm this scenario: one male from the Early Neolithic Turkmenistani site of Tepe Anau, dating to 5450 cal. BP (much earlier than the inferred pastoralist expansions from the Steppe), and another from Iron Age Pakistan (2350 cal. BP) (Narasimhan et al., 2018) (Figure 3.8b). The Early Neolithic individual's paternal lineage is R2, which I have postulated as connected to agricultural arrivals from the Near East to the Indian Subcontinent (Silva et al., 2017), based on the phylogenetic patterns seen with high-resolution Y-chromosome trees based on chromosome resequencing (Karmin et al., 2015).

Therefore, it seems that H13 arrived in the Indian Subcontinent first from Iran with Neolithic dispersals, in the form of H13a2a, and then at a later stage, in the Bronze Age, when H13a1a was incorporated into movements from the Steppe (most likely associated with Indo-European spread), in parallel to what is seen across northern and Central Europe.

3.2.2. Tracing Bronze Age movements in Europe

Mobility during Late Neolithic in Europe is known from archaeological evidence (Kristiansen, 2015), and has left recognisable signals in autosomal variation, with the spread of the Steppe/CHG component (Allentoft et al., 2015; Haak et al., 2015), and in the Y-chromosome gene pool, with drastic changes in haplogroup composition (Batini et al., 2015; Karmin et al., 2015; Poznik et al., 2016). However, a signal in the maternal variation has rarely been shown (Brandt et al., 2013). On the contrary, most of the maternal European gene pool traces back to older events in the Palaeolithic and earlier in the Holocene (Mesolithic and Neolithic periods) (Brandt et al., 2013; Pala et al., 2012; Posth et al., 2016). The high-resolution trees compiled for this chapter allow a thorough exploration of maternal lineages associated with later movements in Europe.

The oldest sequence clustering within H2a1 is a basal Eneolithic Russian Samara individual, dating to ~6800 cal. BP, followed by a ~6150 cal. BP H2a1i sample from Chalcolithic Armenia. A ~5500 cal. BP Maikop (not included in the tree due to large gaps in the mtDNA sequence) and one Eneolithic Ukrainian individual dating to ~4700 cal. BP also share a H2a1 haplotype (despite displaying many private mutations, it was still possible to confidently assign the latter to H2a1) (Juras et al., 2018; Lazaridis et al., 2016; Mathieson et al., 2015; Wang et al., 2019). Additional sequences from German Beaker and Bronze Age individuals, from one Vatya individual from Hungary, and from Russian individuals from various periods from west of the Urals (one Potapovka, one Srubnaya and one Late

Sarmatian) cluster within different branches of H2a1 (Figure 3.9a) (Allentoft et al., 2015; Knipper et al., 2017; Krzewińska et al., 2018; Narasimhan et al., 2018).

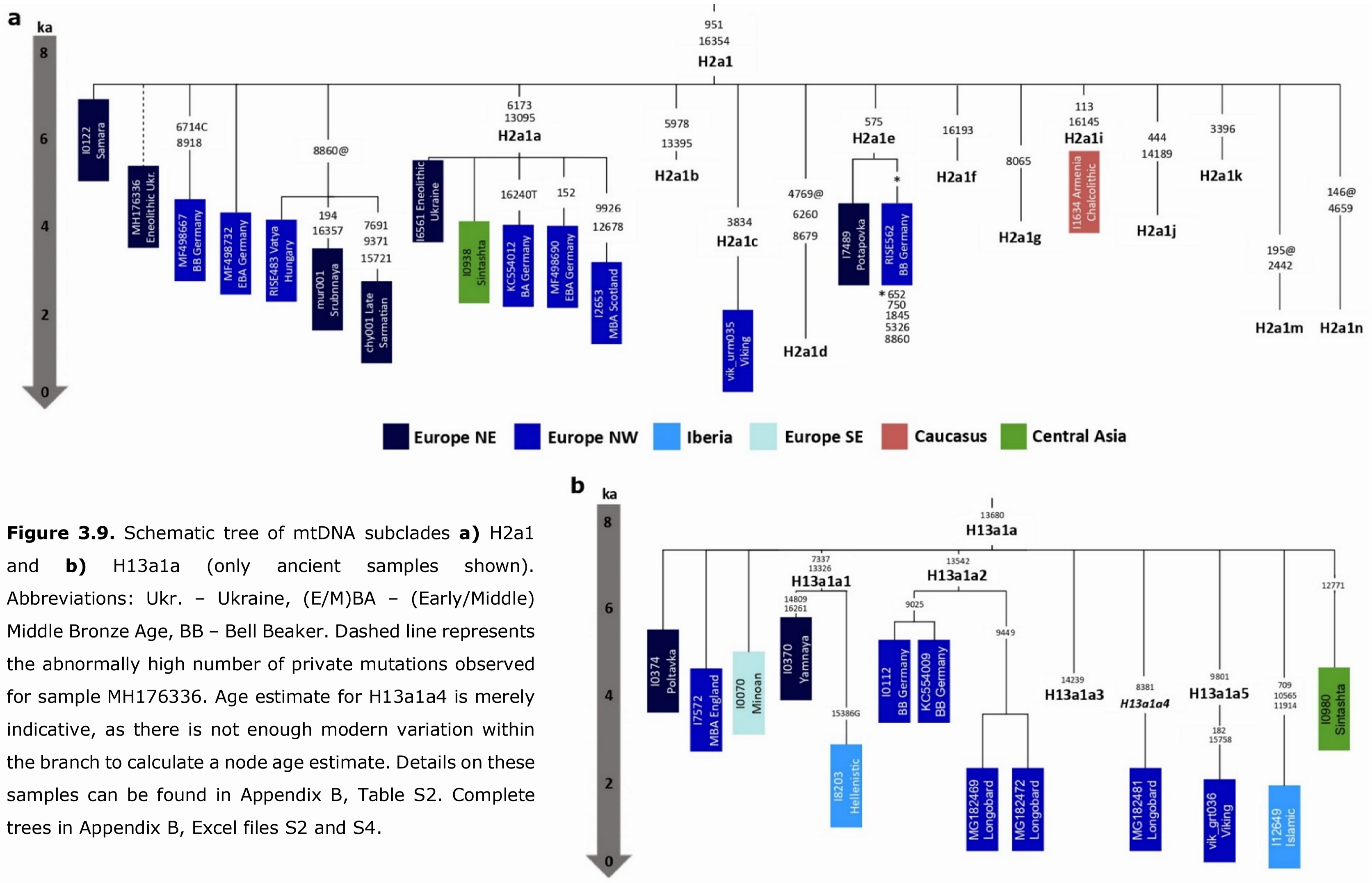

Figure 3.9. Schematic tree of mtDNA subclades **a)** H2a1 and **b)** H13a1a (only ancient samples shown). Abbreviations: Ukr. – Ukraine, (E/M)BA – (Early/Middle) Middle Bronze Age, BB – Bell Beaker. Dashed line represents the abnormally high number of private mutations observed for sample MH176336. Age estimate for H13a1a4 is merely indicative, as there is not enough modern variation within the branch to calculate a node age estimate. Details on these samples can be found in Appendix B, Table S2. Complete trees in Appendix B, Excel files S2 and S4.

This pattern is mirrored in the phylogeny of the derived H2a1a (5.8 [4.0–7.6] ka), although in this case H2a1a is also found in (ancient and present-day) individuals from further east (Appendix B, Excel file S2). H2a1a harbours one other Ukrainian Eneolithic (6000 cal. BP) and one Sintashta (3800 cal. BP) sequence at its root, as well as one Scottish and two German Bronze Age individuals (Brotherton et al., 2013; Knipper et al., 2017; Mathieson et al., 2018; Narasimhan et al., 2018; Olalde et al., 2018), together with present-day samples ranging from the west (France and British Isles) to the east (from the Altai region and one Pakistani sample).

The Chalcolithic H2a1i Armenian individual carried an L1a1 Y-chromosome lineage (Y–L haplogroup is today more common in southwest Asia and the Indian Subcontinent (Thanseem et al., 2006; Zalloua et al., 2008)), whereas the two Eneolithic males were classified as R1a (Ukrainian individual) and R1b (Russian Samara individual). As mentioned before, an increasing body of evidence has shown in the last years that both R1a and R1b expanded with the spread of Indo-European-speaking semi-nomadic pastoralists, ultimately from a source in the Eurasian Steppe (Allentoft et al., 2015; Batini et al., 2015; Haak et al., 2015; Karmin et al., 2015). Indeed, R1a looks particularly associated with Baltic, Slavic and Germanic, in agreement with linguistic evidence showing that Indo-Iranian, Balto-Slavic and Germanic split from the same ancestral node on the Indo-European tree (Figure 1.8) (Ringe et al., 2002; Silva et al., 2019b). Overall, the pattern of H2a1 points to an origin around the Pontic-Caspian Steppe region, where it evolved in the following millennia, and from where it spread with the onset of the Late Neolithic/Metal Ages transition, as evidenced by its recurrence in the archaeological record across Eurasia since the Eneolithic (especially in the west), and its association with Y-chromosome R1 haplogroup.

A similar phylogenetic signal is observed within H13. H13a1a (Figure 3.9b) seems to also have spread across northern and Central Europe during the transition from the Late Neolithic to the Metal Ages, as evidenced by its presence in Yamnaya, Poltavka, Bell Beaker and one individual from Middle Bronze Age England (Brotherton et al., 2013; Mathieson et al., 2015; Olalde et al., 2018), as well as further east, possibly associated with Sintashta movements into Central Asia, as shown above (section 3.2.1, Silva et al., 2019b).

3.2.3. Haplogroup H1 in Iberian Metal Ages

H1 is the most common single H lineage in western Europe (Batini et al., 2017), with peaks of frequency in the Iberia peninsula and Sardinia (Achilli et al., 2004; Olivieri et al., 2017). H1 contributed substantially to the Early Neolithic of Mediterranean Europe, first appearing at considerable frequencies in Iberian Middle/Late Neolithic (~13%), maintaining its frequency during the Chalcolithic (in both Beaker and non-Beaker individuals), and increasing slightly in the Bronze Age (~19%) (Figure 3.10) (Günther et al., 2015; Martiniano et al., 2017; Olalde et al., 2018, 2019; Valdiosera et al., 2018). H1 was also frequent amongst Central European Bell Beaker individuals (~15%) (Brandt et al., 2013; Haak et al., 2015; Olalde et al., 2018), but its frequency was much lower amongst British Beaker individuals (~6%) (Olalde et al., 2018).

Iberian Beaker H1 sequences (~2850–2250 BCE, *n*=4) (Olalde et al., 2018) are basal to branches (H1ax (6.4 [2.4–10.5] ka), H1+292 (2.1 [0.0–4.6] ka), H1q (8.1 [5.3–11.0] ka) and H1t (6.9 [1.1–13.0] ka)), harbouring in most cases sequences not only from modern Iberia, but also from the British Isles, Central Europe, northern Europe and the Mediterranean region. (Please note these are ρ estimates, as ML analysis is still running.)

The frequency of H1 seems unaffected by the transition from Late Neolithic to Chalcolithic in the Iberian Peninsula. Additionally, no differences in H1 frequency are observed between Beaker and non-Beaker Iberian groups, contrary to what is observed for H3, which has a frequency of ~11% in non-Beaker populations, while being absent in Beaker or the later Bronze Age datasets (Figure 3.10). Both lineages were thought to have co-evolved in Iberia, from where they would have expanded to the rest of Europe after the LGM, and would have been later involved in Beaker movements (Brotherton et al., 2013; Pala et al., 2014; Pereira et al., 2005) – a scenario that is not supported by more recent aDNA evidence (Olalde et al., 2018). Although separate origins and different evolutionary histories for H1 and H3 are plausible, considering their different age estimates (Olivieri et al., 2017), low sample sizes of Iberian Late Neolithic (*n*=47), Beaker (*n*=32) and Bronze Age (*n*=37) populations (compared to >100 non-Beaker Chalcolithic individuals) do not allow a fine comparison of maternal variation through time.

However, the frequency of H1 (and H, in general) seems to have increased in Iberia during the Iron Age (although sample size is very low, *n*=24). Curiously, an increase in Steppe/central-European-related ancestry is also observed in these Iron Age individuals, in comparison with Bronze Age (Olalde et al., 2019). Assuming a scenario of male-mediated gene flow during the Bronze Age, as shown by the virtual total replacement of Iberian Y-chromosome linages around 2,500 BCE (Martiniano et al., 2017; Olalde et al., 2019), the maternal gene pool is not expected to be significantly affected. However, the change observed during the Iron Age hints at a different mechanism operating in this period, although more sampling is needed to clarify this question.

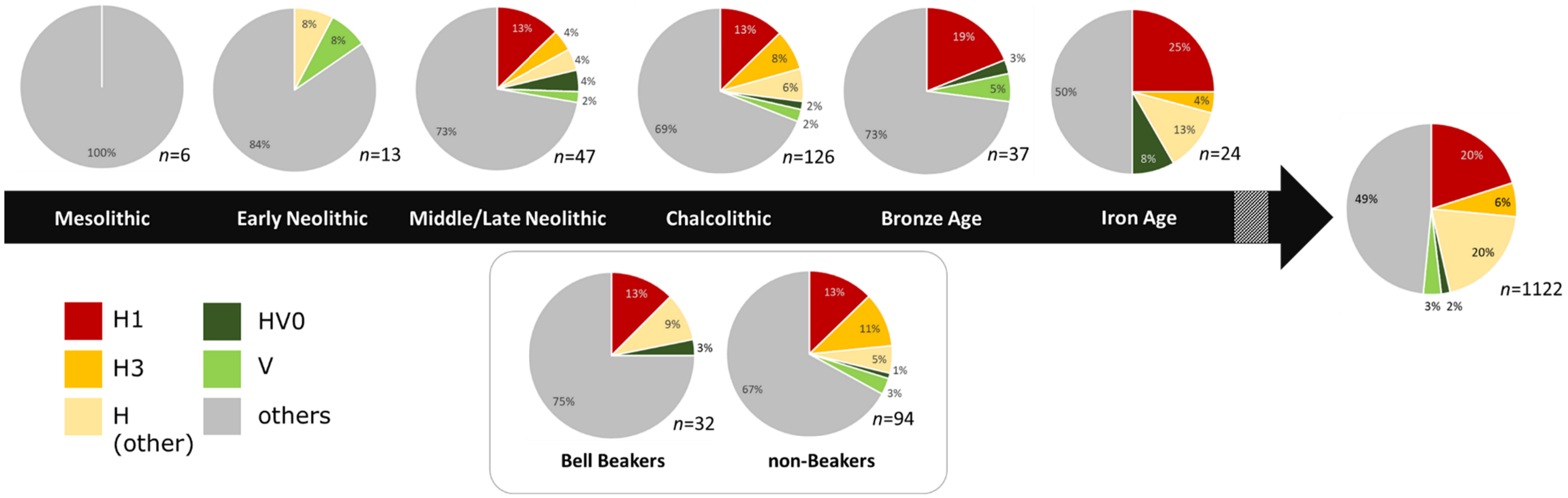

Figure 3.10. Maternal variation in Iberia through time, with focus on haplogroups H, HV0 and V. Piecharts based uniquely on complete mtDNA sequences, to ensure a correct haplogroup classification, especially for haplogroup H, whose main subclades (including H1 and H3) are classified by diagnostic positions outside the control region. Table of frequencies on the present-day mtDNA dataset (n>1100) can be found in Appendix B, Table S7.

4. Discussion

Europe – especially the western and central regions – has been the focus of most aDNA studies to date (Slatkin and Racimo, 2016). Some of the regions showing an absence of haplogroup H in the archaeological record are probably the result of lack of sampling in the area – this is most likely the case for central and northern France and most of the Fertile Crescent region, considering the presence and frequency of H lineages in the neighbouring regions over time (Figure 3.11). Nevertheless, it is still possible to track the occurrence of haplogroup H in the archaeological record, especially in Europe.

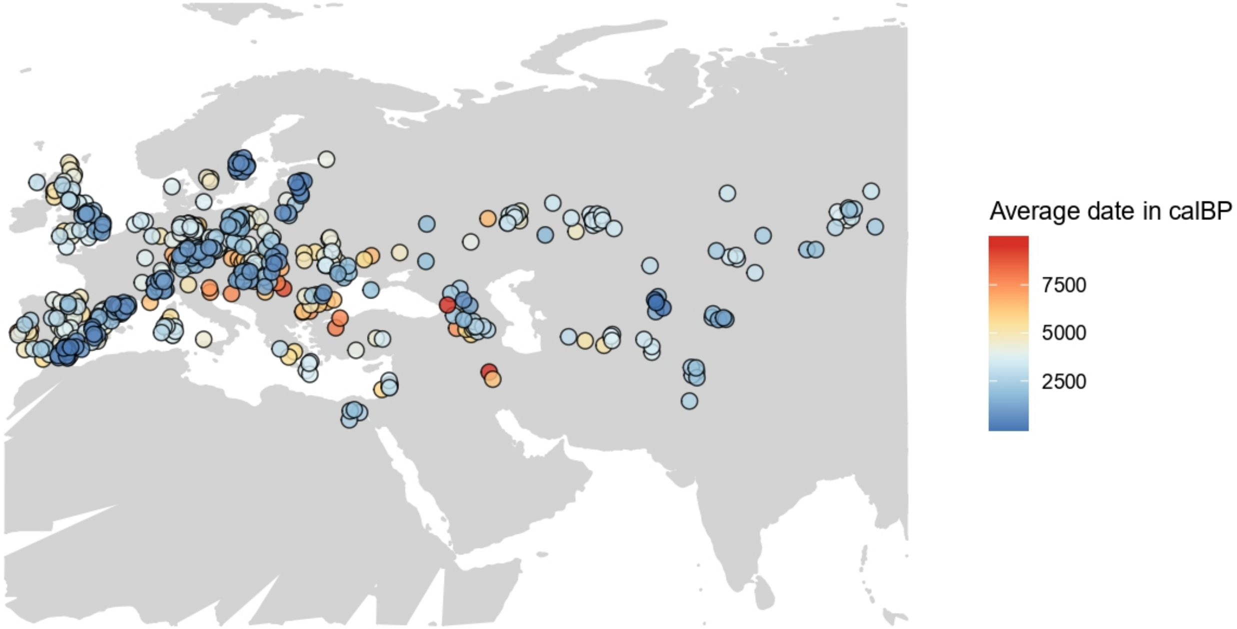

Figure 3.11. Occurrence of haplogroup H in the archaeological record. Each point represents one individual (with added jitter for sites with multiple individuals), coloured according to the average of 95.4% date range in cal. BP (defined as 1950 CE).

Although with a reduced number of Palaeolithic and Mesolithic samples (*n*<150), the ever-increasing collection of ancient European mitogenomes (*n*~2000) produced using state-of-the-art NGS approaches does not include any pre-Neolithic H lineage in central or west Europe. Previous reports of Mesolithic and Palaeolithic H lineages in Iberia (Chandler et al., 2005; Hervella et al., 2012), based on PCR-methods (which are more prone to amplify modern contaminant DNA, and do not allow reliable authenticity and contamination-screening steps (Hofreiter et al., 2015; Willerslev and Cooper, 2005)), are not supported by the most recent body of evidence. On the contrary, H seems to have first expanded in the last 10 ka in southeast Europe, as evidenced by H13 sequences retrieved from Serbia and Romania Iron Gates sites dating to ~9800–9300 cal. BP (Mathieson et al., 2018). An equally old H13 lineage was also found in South Caucasus (Jones et al., 2015).

Haplogroup H presence in southeast Europe continued in the Early Neolithic, after ~8000 cal. BP, when H also appeared in Croatian remains associated to Cardial and Impressa pottery (Mathieson et al., 2018), and in a Körös site in Hungary (Lipson et al., 2017). H seems to have been carried to the rest of Europe with Neolithic dispersals ultimately from a source in southeast Europe – through the Danubian route into Central Europe (where haplogroup H is present since at least ~7000 cal. BP in Germany, associated to LBK remains (Brotherton et al., 2013; Haak et al., 2015; Lipson et al., 2017; Mathieson et al., 2015)); and along the Mediterranean route, eventually reaching Iberia, where the oldest H lineages, in the form of H4 and H3, date to ~7300–7200 cal. BP, in the Cardial Ware (Olalde et al., 2015).

This is in agreement with genomic evidence showing a common origin for Central and southwest European early farmers (Olalde et al., 2015), but challenges the previously proposed scenario of a pre-Holocene European origin of haplogroup H and a subsequent expansion of H1 and H3 clades from a proposed Franco-Iberian refuge after the LGM (Pala et al., 2014; Pereira et al., 2005; Roostalu et al., 2007; Soares et al., 2010). The H1 node age estimate of 8.5 [7.1-9.8] ka calculated here fits well with a scenario of Neolithic expansion of H1 across Europe, and accommodates its presence in both Iberia and Central Europe ~7000 cal. BP (Brotherton et al., 2013; Lipson et al., 2017; Mathieson et al., 2015), while it seems to disprove a post-glacial out-of-Iberia dispersal. A rapid expansion of H lineages with agricultural dispersals, together with the exponential growth observed in the *Ne* associated to the haplogroup during the Neolithic period (Brotherton et al., 2013), could explain the striking star-like burst of the haplogroup H phylogeny, with many major branches stemming directly from the root of H and defined by only one or two diagnostic mutations (*e.g.* H1, H2, H3, H5′36, H7, H13).

Southwest Asia, the proposed origin for haplogroup H based on the current distribution of most of HV sister branches (Loogväli et al., 2004; Richards et al., 2000; Roostalu et al., 2007), is under-represented in aDNA studies (especially compared to Europe). The fact that the oldest confirmed H sequences were found in both southeast Europe and the South Caucasus seem to favour an origin in Anatolia or further south in the Levant. A Neolithic signal has also been found further east, in Iran, with the oldest H sequence in the region (classified as H32), dating to ~10,000 cal. BP, found in an Early Neolithic site in the Zagros Mountains (Lazaridis et al., 2016). An early expansion eastwards adds support to a possible southwest Asian origin for this haplogroup.

Since haplogroup H was present in most of continental Europe since the Neolithic, some H lineages display Late Neolithic/Bronze Age signals: H2 and H13 were incorporated in movements across the Steppe into Europe, in the west (mainly as H2a and H13a1a), and across Central Asia and into the Indian Subcontinent, in the east, in the form of H2b, although a minor signal is also visible for H13a1a (recently published as Silva et al. (2019b)). An additional signal of eastward movements from the Steppe is evident for H1b. While the spread of Y-chromosome lineages R1a and R1b during the Late Neolithic/Chalcolithic and Bronze Age has left very strong signals on their phylogenies (Batini et al., 2015; Karmin et al., 2015; Poznik et al., 2016), in a scenario of male-biased population events, such as in the case of the Late Neolithic/Chalcolithic transition in Europe, or the Late Bronze Age movements into South Asia (Martiniano et al., 2017; Narasimhan et al., 2018; Olalde et al., 2019; Silva et al., 2017), evidence in the maternal gene pool is expected to be scarce. Nevertheless, I have shown in this chapter how a high-resolution phylogeographic approach, combining both modern and ancient variation, can provide additional clues into population dynamics, even in the case of strong male bias.

On the other hand, previous suggestions that there was an expansion of maternal lineages, in particular haplogroup H1, possibly together with other sub-clusters of H (such as H3), from Chalcolithic Iberia, as a result of movements of Beaker people (Brotherton et al., 2013) are difficult to reconcile with more recent aDNA results. There are obvious differences in the frequencies of H1 and H3 between Beaker and non-Beaker individuals and for the Bronze Age dataset, and although this can be the result of sampling effect, different evolutionary histories are plausible for these haplogroups (Olivieri et al., 2017). Although archaeological evidence shows the spread of Bell Beaker pottery across western and Central Europe from a putative Iberian source (Heyd, 2007; Kristiansen, 2015; Müller and van Willigen, 2001), there is no clear genome-wide evidence of significant movements out of Iberia during this period (Olalde et al., 2018). On the other hand, an increase in Steppe-related/central-European ancestry in Iberia in the Bronze Age coincides with a large influx of Central-European Y-chromosome lineages arriving to the peninsula and dramatically increasing in frequency within a few generations (Martiniano et al., 2017; Olalde et al., 2019). The same signal is not observed in the maternal gene pool, in agreement with the proposed model of male-mediated movements across Europe during this period (Batini et al., 2017; Olalde et al., 2019).

However, changes in mtDNA frequencies in Iberia are observed later, in the Iron Age, with an increase in the frequency of haplogroup H in general, and H1 and H3 specifically, also connected with a further increase in Central-European ancestry (Olalde et al., 2019). More sampling of Iberian Iron Age sites is needed to confirm this trend and understand possible fine-scale regional differences. However, Iron Age sampling is hindered in Iberia, due to the widespread practice of cremation during this period (López-Cachero, 2011; Raquela Vilaça, 2014), which reduces the amount of archaeological material available for DNA extraction. Unfortunately, sample sizes are not uniform across time periods, with a disproportionally high number of Chalcolithic (non-Beaker) individuals. Moreover, the number of Portuguese ancient mtDNA sequences is very low (*n*=37) compared to Spain (*n*=362, plus four from Gibraltar), and no genomes are currently available from Portuguese Iron Age or later periods. Therefore, a fine assessment of regional differences in the maternal gene pool of the peninsula through time is not possible at the moment.

Chapter IV

A genetic snapshot of Medieval Iberia: a pilot study

A genetic snapshot of Medieval Iberia: a pilot study

1. Introduction

The location of Iberia, bridging the Mediterranean and the Atlantic, and its proximity to Africa, has allowed contacts with populations of distinct ancestries over time, making the Peninsula a genetic and cultural crossroads. There is both archaeological and genetic evidence of contacts between Iberia and North African populations since at least the Late Neolithic (Anderung et al., 2005; Fregel et al., 2018; González-Fortes et al., 2019; Olalde et al., 2019; Sanjuán et al., 2013; Valera, 2017). Prehistoric populations have been the focus of most of the aDNA work published on Iberia so far, including the study of Mesolithic individuals (Olalde et al., 2014; Sánchez-Quinto et al., 2012a), the impact of Neolithic migrations (Günther et al., 2015; Olalde et al., 2015), and the incursions of individuals with Pontic Steppe related ancestry at the time of the transition from the Chalcolithic to the Bronze Age (González-Fortes et al., 2019; Martiniano et al., 2017; Olalde et al., 2018; Valdiosera et al., 2018). This leaves a temporal gap, comprising historical periods of known population movements (Moorjani et al., 2011), that only very recently has started to be explored in detail (Olalde et al., 2019).

In historical times, Iberia was home to various people of diverse origins, such as Phoenicians from the Eastern Mediterranean, Sephardic Jews, Greeks, Romans, Central European Germanic tribes, Arabs from the Persian Gulf, Berbers from North Africa, and Roma people from an ultimate source in South Asia. These contacts left their marks in what is nowadays Spanish and Portuguese culture, and contributed to varying extents to the Iberian gene pool (Olalde et al., 2019).

However, it was recently shown that several post-Medieval events reshuffled Iberian genetic variation (Bycroft et al., 2019). The military expansion of the Catholic kingdoms southwards, which culminated in 1249 CE in Portugal and more than two centuries later in Spain, with the Battle of Granada in 1492 CE, progressively forced the populations under Islamic rule further south. Although different Crowns dealt with the population living in conquered territories differently, in general much of the population who was previously living under Islamic rule was expelled from the Peninsula, and replaced with people from further North, which has left a genomic signal still visible in Iberia today (Bycroft et al., 2019) (Figure 4.1). Thus, much of the existing genetic variation from both the preceding Iberian populations and the North African newcomers during Islamic rule most likely disappeared by the late 17th century CE in many regions, especially in the east and south of the Peninsula (Bycroft et al., 2019). Therefore, DNA from archaeological remains can provide an important tool to understand the demographic dynamics of Medieval Iberia before and during the Islamic period.

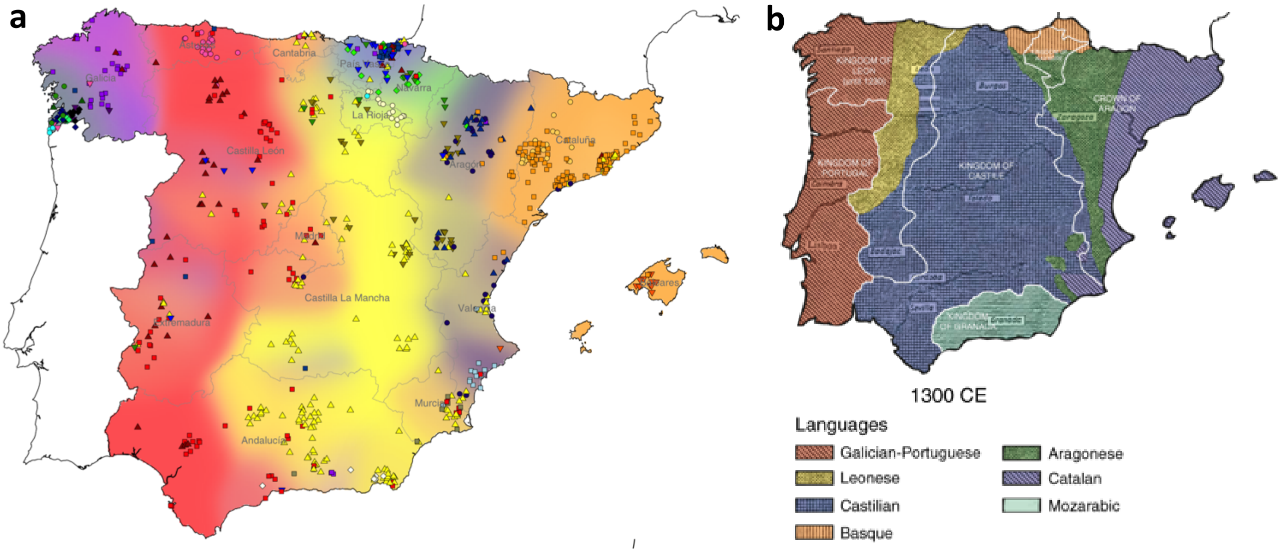

Figure 4.1. Distribution of genomic variation in present-day Iberia resembles the expansion of Catholic kingdoms southwards and respective languages: **a)** Genetic clusters of present-day Spanish individuals. **b)** Distribution of languages and political borders in Iberia around 1300 CE. Adapted from Bycroft et al., 2019.

In this chapter, I report a pilot study on Iberian aDNA, based on samples from Medieval Portugal and Spain. When I first started working on this chapter there was no aDNA data available from the Medieval period in Iberia, and thus this pilot study would provide the first insights onto this period in the region. Additionally, this study allowed me to define a strategy for ancient DNA and genomic analysis that was later employed in the study of a larger dataset (Chapter V). One of the individuals, from an Islamic necropolis, yielded enough DNA for genomic analysis. This individual was dubbed as the "Segorbe Giant", due to his unusual height compared with all the others found in the site. He was buried in an Islamic *maqbara* (necropolis) in the city of Segorbe (province of Castellón, Autonomous Region of Valencia, Spain), and was reported to have some skeletal sub-Saharan features (Barrachina, 2004). I conducted through on-going collaborations with the universities of Oxford and York an analysis of stable isotopes on twelve additional individuals and several animals from the same site in order to investigate mobility and diet patterns. Additionally, I took advantage of more than 1000 new modern Iberian whole mitochondrial genomes sequenced in our lab to assess the impact of North African mtDNA U6 lineages on the modern Iberian mitochondrial gene pool, and performed a detailed phylogeographic reanalysis of U6.

2. Methods

2.1. Archaeological samples

I selected teeth and petrous bones from five individuals from Portugal and Spain, spanning from the 8th to the 13th century CE (Table 4.1). This sampling, although modest, covers a very interesting and understudied (from a genetic point of view) period in Iberian history, especially in Portugal. To my knowledge, this is the first attempt to recover DNA from Medieval Portuguese samples. Moreover, this sampling results from a close contact with archaeologists and museum curators, and the detailed anthropological and archaeological studies already available for some of these individuals allowed for a direct comparison with the genetic results and provide additional context to the genetic data presented here.

Table 4.1. Summary of Medieval individuals targeted for aDNA analysis. Uncalibrated radiocarbon dates (in BP, with lab and sample codes) are presented here for all individuals except for MS060/Segorbe Giant.

Individual	DNA code	Dating	Site	Location	Sample
ALM/01	MS058	1200±35 BP (Sac-2430)	Alto dos Moinhos	Torres Vedras, Portugal	Tooth (premolar)
CBU/33	MS059	940 ±35 BP (Sac-2880)	Casal dos Bucículos	Torres Vedras, Portugal	Tooth (molar)
UE2298, ”Segorbe Giant”	MS060	11th cent. CE	Plaza del Almudín	Segorbe, Spain	Tooth (molar)
Menga01	MS061	1100±45 BP (CNA-1173)	Átrio de Menga	Malaga, Spain	Tooth (molar)
Menga02	MS062	1250±35 BP (CNA-1174)	Átrio de Menga	Malaga, Spain	Petrous

2.1.1. Alto dos Moinhos and Casal dos Bucículos (Torres Vedras, Portugal)

The individual from Alto dos Moinhos, ALM/01 (MS058), was found accidentally during the plantation of eucalypt trees in 1992, in the village of Maxial, ~10 km northeast from the city of Torres Vedras, on the left margin of the Alcabrichel River, in an area rich in water streams (Luna, 2008). Except for grave stones and some small fragments of roof tiles, no other grave goods were found with the remains, which were mostly fragmentary (Luna, 2008). The tiles pointed to an old manufacturing style, which was later confirmed by radiocarbon dating of the bones to the 7th-10th century CE (Table 4.1). The anthropological study concluded that the individual was most likely a 35-40 year-old female (Luna, 2008).

Casal dos Bucículos is located ~5.5 km southwest from Torres Vedras in the town of Dois Portos, on the left margin of Sizandro River, and in the eastern slope of Serra da

Archeira, next to the water stream of Ribeira dos Bucículos. There are records dating back to at least the 19th century CE of old burial grounds around the area (Torres, 1862), and accounts of vandalism and theft of grave goods, although these were never formally confirmed by official entities (Luna, 2012). I had access to a set of maxillary teeth recovered from the individual CBU/33 (MS059), a young adult of undetermined sex radiocarbon dated to the 11th-12th century CE (Table 4.1), who was found in grave 3, Sector I (Figure 4.2) in July 2009 (Luna, 2012).

The Portuguese remains were stored at Museu Municipal Leonel Trindade, in Torres Vedras. Permission for genetic analysis was granted by the City Hall (Câmara Municipal de Torres Vedras). The teeth were sent to our lab by Isabel Luna, a curator of the museum, who was involved in the excavations of both sites.

Figure 4.2. Grave 3 from Sector I, site of Casal dos Bucículos, photo from 1995 (Luna, 2012). CBU/33 (MS059) teeth belong to the skull in the middle.

2.1.2. Menga (Malaga, Spain)

Menga, a UNESCO World Heritage site since 2016, is located in Malaga (South Spain), and is a Neolithic megalithic site displaying evidence of being reused as a ritual and burial site during antiquity and Medieval times (Aranda Jiménez et al., 2015; Díaz-Zorita and García Sanjuán, 2012). The attempted genetic analysis of these two individuals aimed to complete a throughout archaeological and anthropological study (Díaz-Zorita and García Sanjuán, 2012). Both individuals were radiocarbon dated to the Medieval period (Table 4.1) (Díaz-Zorita and García Sanjuán, 2012).

Individual Menga01 (MS061) was older than 45 years when he died, whereas Menga02 (MS062) died at the age of 45-50 years old. Both were classified as male, based on the cranial and pelvis cranial dimorphic characters, albeit with a certain degree of uncertainty for Menga02 (Díaz-Zorita and García Sanjuán, 2012). I had access to a molar tooth and a portion of petrous bone, respectively, which were collected by Gonzalo Oteo-Garcia.

2.1.3. Plaza de Almudín (Segorbe, Spain)

The site of Plaza del Almudín in Segorbe (province of Castellón, Autonomous Region of Valencia, Spain) is a Medieval Islamic necropolis dated to the 11th–13th century CE (Figure

4.3). All individuals were buried according to Islamic tradition, lying on their right side, orientated northeast–southwest, and facing southeast, towards Mecca.

Figure 4.3. a) Location of Segorbe in the province of Castellón, autonomous community of Valencia (Spain) (image from Google Maps). **b)** Photo of the "Segorbe Giant" (individual UE2298/MS060) in his burial site. **c)** Medieval (post-Islamic) plan of the city of Segorbe overlapped to a satellite view of modern Segorbe. Location of the archaeological site (Plaza de Almudín) indicated by the red icon. Satellite image from Google Maps; Medieval city plan from Barrachina (2004).

For this pilot study I targeted one individual, UE2298/MS060 (dubbed the “Segorbe Giant”) (Table 4.1), excavated in 1999. This was a ~25-year-old male, whose burial stood out from the others in the cemetery in several ways. He was 184–190 cm tall, ~20-25 cm taller than any other individual buried at the same site, which led to his designation as “Giant”. His grave was the deepest found in the cemetery, and was covered by a layer of rocks that protected the grave and contributed to the particularly good anatomical preservation of his remains. This allowed for a detailed anthropological study, which concluded that he suffered from various non-lethal pathologies, impoverished nutrition and/or high-fever episodes during childhood (Barrachina, 2004). Nevertheless, these episodes of malnutrition and/or disease did not seem to handicap his well-above-average growth.

In order to investigate his diet and mobility patterns, tooth samples from twelve additional individuals from the necropolis, plus seventeen animal bones and twelve animal teeth, were also collected for stable isotopic (carbon, nitrogen and oxygen) analysis. Although the necropolis is dated to the 11th–13th century CE, the human samples collected for this study are from a context dated to the 11th century. However, the faunal assemblage might post-date the timeframe of the Islamic necropolis of Plaza de Almudín and date instead to the later Christian period. All samples have been stored in the Museo Municipal de Arqueología y Etnología de Segorbe, where the teeth were selected by Gonzalo Oteo-Garcia. Permissions for sample collection and analysis were agreed by the museum, and granted by the Direcció General de Cultura i Patrimoni (Conselleria d’Educació, Investigació, Cultura i Esport de la Generalitat Valenciana).

2.2. Ancient DNA lab protocol

2.2.1. Sample processing

I processed all the archaeological samples in clean rooms in the specialized Ancient DNA Facility at the University of Huddersfield, which is in a different building, physically separated from all the other molecular biology labs dealing with modern sources of DNA (Figure 4.4) (Fulton and Shapiro, 2019). Surfaces and tools were frequently bleached, cleaned with LookOut® DNA Erase (Sigma-Aldrich) and regularly exposed to UV-radiation. I used a full-body suit, gloves, hairnet and face mask at all stages. I subjected selected samples to UV-radiation for a total of 60 minutes (30 minutes each side), and cleaned sampling surfaces with air-abrasion using 29 μm aluminium oxide powder (OEA Labs) and a SWAM-Blaster® compressed air abrasive system (Crystal Mark, inc.). I used a Micromotor System Maxima hobby drill with a 22 mm diameter diamond cutting disc (RS Components) to sample roots of teeth and the densest portion of the petrous bone (Pinhasi et al., 2015), which were then powdered using a Mixer Mill (Retsch MM400) for 45 seconds at a frequency of 30 Hz/s, aiming for 0.10–0.20 g of fine tooth or bone powder.

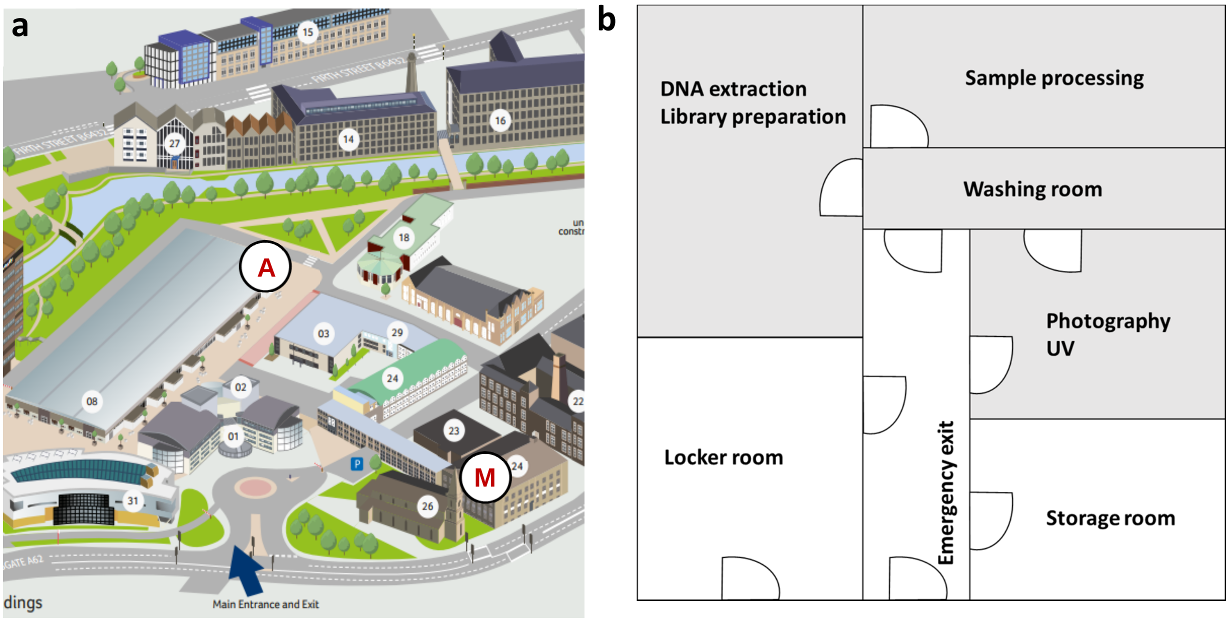

Figure 4.4. a) Campus map (source: https://www.hud.ac.uk/media/assets/document/maps/CampusMap.pdf) indicating the location of Ancient DNA Facility (A) and modern molecular biology labs (M). **b)** Plan of the Ancient DNA Facility: rooms coloured in grey are clean rooms, only accessible with suitable protective clothing and cleaned regularly with UV-radiation), separate rooms for initial sorting and UV treatment, bone processing and DNA extraction/library preparation.

Dietary isotope analysis of carbon and nitrogen was performed by Dr Peter W. Ditchfield at the Research Laboratory for Archaeology (University of Oxford), and oxygen analysis was conducted at BioArCh (University of York), through a collaboration with Dr Michelle Alexander. Further details of stable isotope analyses can be found in Appendix C, Text S1.

2.2.2. DNA extraction

I performed DNA extraction following the protocol of Yang et al. (1998) with modifications by MacHugh (2000). The three-day long protocol started with the preparation of Extraction Buffer, containing 20 mM of Tris HCL, pH 8; ~50 mM of EDTA, pH 8, filtered and autoclaved, RNase and Proteinase free; ~0.5% of SDS (DNase, RNase and protease free, warmed to 37ºC). The buffer components were exposed to UV-light for 15 minutes before the addition of ~200 µg of proteinase K. All reagents were from Fisher Bioreagents.

I added 1 mL of extraction buffer to the tooth root or bone powder, and incubated the tubes at constant rotation for approximately 24 hours at 37 ºC. After this incubation period, I centrifuged the tubes at 13,000 rpm for 15 minutes, and carefully removed the supernatant (which was retained in a separate tube in the fridge, in case I might need to repeat the extraction from the supernatants in the future). I added 1 mL of freshly prepared extraction buffer to the resultant pellet, and vortexed the tubes vigorously in order to resuspend the pellet. I again placed the tubes in the rotator and left them for another 24-hour period of incubation at 37ºC, after which I centrifuged the samples once more at 13,000 rpm for 15 minutes.

I then transferred the supernatant to 6 mL Corning® Spin-X® UF Concentrator tubes, to which I had previously added 3 mL of 10 mM Tris HCL (pH 8). I centrifuged the concentrator tubes for 20 minutes at 2,500 rpm. I discarded the flow-through, added another 3 mL of 10 mM Tris HCL to the concentrator tubes, and repeated the centrifugation at 2,500 rpm up to 30 minutes, so as to obtain a final volume of ~100 µL above the filter. I transferred the liquid above the filter to purification silica columns (MinElute® PCR Purification Kit, commercialised by Qiagen) and purified it according to the manufacturer's instructions, with the only modification being the addition of 0.05% Tween™20 (Fisher Bioreagents) to Buffer EB, in an attempt to reduce the absorption of DNA to plastics and maintain pipetting accuracy, and to guarantee long-term extract viability. I stored the DNA extracts in 2 ML O-ring tubes (Molecular Bio Products) at 4ºC.

I included four blanks (air, water and two extraction buffer controls) at different stages to control for potential sources contamination. DNA extraction was confirmed by DNA quantification with Qubit™ 3.0 Fluorometer (ThermoFisher Scientific), using the Qubit® dsDNA HS Assay Kit (Invitrogen).

2.2.3. Library preparation and sequencing

I performed library preparation according to the protocol by Meyer and Kircher (2010), modified as described in Gamba et al. (2014) and Cassidy et al. (2016) (explained in detail below). Since aDNA is already naturally fragmented, no DNA shearing step was included in the protocol. Similarly to DNA extraction, I performed all purification steps using the MinElute PCR Purification Kit, according to manufacturer instructions, and adding 0.05% of Tween™20 to Buffer EB. The library preparation protocol was as follows (Figure 4.5):

- **UDG-treatment:** For UDG-treated libraries, I added 5.0 µL of USER® (Uracil-Specific Excision Reagent) enzyme (New England BioLabs®) to 16.5 µL of DNA extract and incubated for 3 hours at 37ºC. USER is a mixture of uracil DNA glycosylase (UDG) and endonuclease VIII. UDG excises uracil residues resulting from post-mortem damage (Briggs et al., 2007; Lindahl, 1996), generating abasic (apyrimidinic) sites, whereas the endonuclease VIII cleaves the molecule on those sites, by breaking the phosphodiester backbone at the 3′ and 5′ sides of the abasic site. This process fragments the molecule into even shorter fragments, which are still suitable for sequencing, while minimizing the proportion of post-mortem damage detected during sequencing (Briggs et al., 2010).

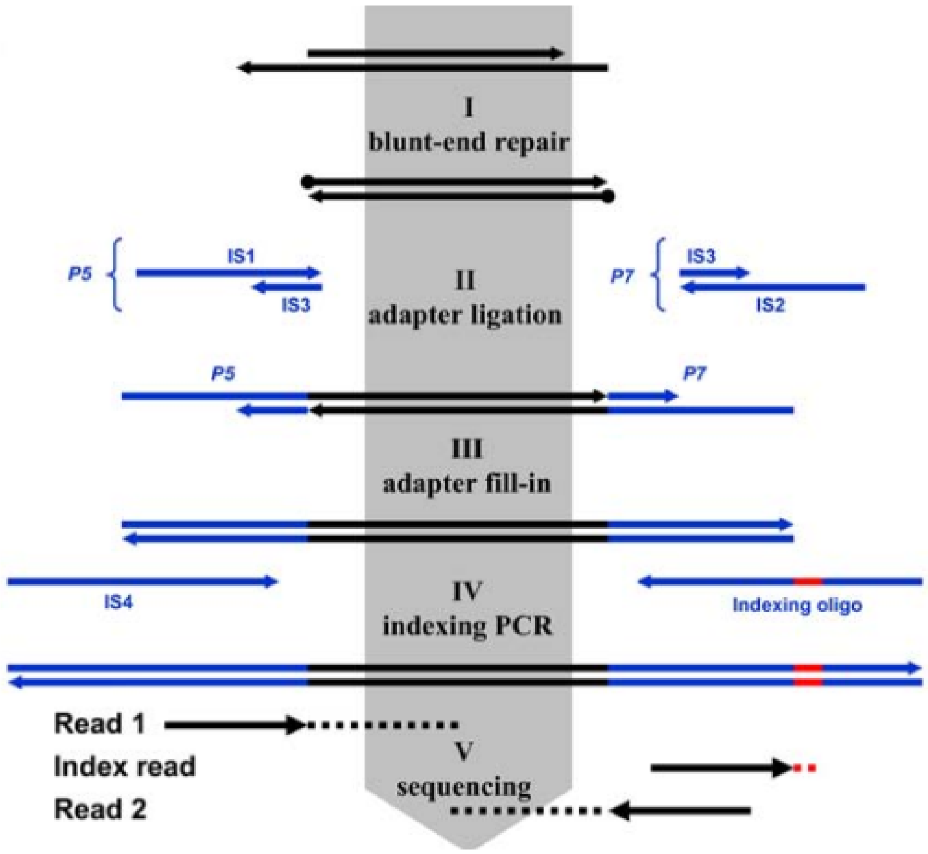

Figure 4.5. Schematic overview of the library preparation protocol (Figure from Meyer and Kircher, 2010). During blunt-end repair overhanging ends are removed by T4 DNA polymerase (I). P5 and P7 adapter ligation is potentiated by T4 DNA ligase (II), followed by an adapter fill-in reaction with *Bst* polymerase (III). Indexing oligo sequences are added by amplification with IS4 primer (IV). Indexed libraries are then pooled and sequenced (V). Intermediate clean-up steps, as well as optional initial UDG-treatment, are not shown in this

- **Blunt-end repair:** In order to remove overhangs from the DNA fragments, I added the total 21.5 µL resultant from the USER-treatment reaction (for the non-treated libraries I directly added a total of 21.5 µL of extracted DNA) to 3.5 µL of NEBNext End Prep Enzyme Mix, 1X of NEBNext End Repair Reaction Buffer (both included in the NEBNext® End Repair Module, provided commercially by New England BioLabs®), and 38 µL of distilled DNase/RNase-free water (final reaction volume of 70.0 µL, corresponding to 70% of manufacturer's guidelines). I incubated the reaction at 25ºC for 15 minutes, followed by 5 minutes at 12ºC, and purified it with MinElute PCR Purification Kit.

- **Adapter ligation:** I incubated the 40 µL reaction mix (consisting of 10 µL of distilled DNase/RNase-free water, 1X of T4 DNA ligase Buffer (Thermo Scientific), 5% of PEG-

4000 (Thermo Scientific), 2.5 µM of each adapter (custom-made by Sigma-Adrich), 0.125 U/µL of T4 DNA ligase (Thermo Scientific), and 20 µL of eluate resultant from the previous step) at 22ºC for 30 minutes. T4 DNA ligase catalyses the formation of a phosphodiester bond between adjoining 5' and 3'-ends in dsDNA, whereas PEG-4000 is necessary to ensure a successful blunt-end ligation of the adapter. After the incubation period, I purified the samples once again using the MinElute PCR Purification Kit.

- **Adapter fill-in:** Since the P5 and P7 adapters used in the previous step do not carry 5′-phosphates, they generate single-end overhangs, which have to be filled in by a reaction using *Bst* polymerase. I added 20 µL of DNA resulting from the previous step to 1X ThermoPol® Reaction Buffer, 0.3 U/µL of *Bst* polymerase, Large Fragment (both from New England BioLabs®), 0.25 mM of each dNTP, and 13.5 µL of distilled DNase/RNase-free water, for a total volume of 40 µL. The reaction incubated for 30 minutes at 37ºC, followed by an extra 20 minutes at 80ºC, in order to inactivate the *Bst* polymerase and terminate the reaction.

- **Amplification:** Finally, I added barcoding indexes to the sequences, to allow for multiplexing. The reaction consisted of 41 µL of Accuprime™ Pfx SuperMix (Thermo Scientific), 0.2 µM of primer IS4, 0.4 µM of a specific indexing oligo (both custom-made by Sigma-Aldrich) and 6 µl of sample library resulting from the previous step (total reaction volume: 50 µl). I prepared library amplification reactions in the specialized Ancient DNA Facility, and then sealed the tubes and took them to the modern lab, where I carried out the amplification reaction. The reaction consisted of an initial denaturation at 95ºC for 5 minutes, followed by 12 cycles of denaturation at 95ºC for 15 seconds, annealing at 60ºC for 30 seconds, and extension at 68ºC for 30 seconds, and a final extension at 68ºC for 5 minutes. I performed a final purification step with MinElute PCR Purification Kit.

I measured the concentration of each library with a Qubit™ 3.0 Fluorometer, using the Qubit® dsDNA HS Assay Kit, and checked fragment size distribution with a Bioanalyzer (Agilent), using the Agilent High Sensitivity DNA Kit. Successful libraries were then pooled together, aiming to normalise individual concentrations, and sent to Macrogen, inc. (Seoul, South Korea) for WGS.

Initially I sequenced one USER-treated library on a tenth of an Illumina HiSeq4000 lane (100 cycles) to screen for endogenous aDNA content. Since the individual from Plaza del Almudín (MS060/Segorbe Giant) yielded the best endogenous aDNA content (~2%), and considering its interest for the study of the Islamic period in the region of Valencia (a period that was virtually unsampled when this work was planned), I sent three additional libraries (one of which was non-USER treated) to be sequenced on half an Illumina HiSeq4000 lane for 100 cycles.

2.3. Ancient DNA analysis

2.3.1. NGS data processing

I initially checked raw FASTQ files with FastQC v.0.11.5 ((Andrews, 2010); bioinformatics.babraham.ac.uk). I then merged paired-end reads and removed sequencing adapters using leeHom (Renaud et al., 2014). Merging reads improves mappability, especially for short reads such in the case of aDNA sequencing, by extending read lengths, and therefore facilitates the detection of sequencing errors and adapters (Kircher, 2012).

I mapped reads both to the human genome reference (Hg19, but modified to include rCRS as chrM) and only to rCRS (revised Cambridge Reference Sequence) with BWA (Burrows-Wheeler Aligner) v.0.7.5a-r405 (Li, 2013) *aln* (using the optimized settings for aDNA mapping: -l 16569, -n 0.01 and -o 2), and *samse*. Although increasing runtime significantly, by disabling the seed (-l) and allowing for more differences (-n) and gap openings (-o) in the alignment, BWA is able to map reads displaying more mismatches relative to the reference in the initial nucleotides of reads, and therefore increase the number of damaged aDNA reads mapped (Schubert et al., 2012).

I used samtools v.1.4 (Li et al., 2009) to sort BAM files (*sort*), remove PCR duplicates (*rmdup*) and filter BAM files for mapping quality 30 and minimum read length of 30 base pairs (bp). In order to check mean coverage, number of mapped reads, duplication rate, mean mapping quality and average read length, I ran the BAM files through QualiMap v.2.2.1 (Okonechnikov et al., 2015) (Table 4.2).

2.3.2. Data authenticity and contamination assessment

I performed sex determination using the script by Skoglund et al. (2013) (Appendix C, Figure S1), and by karyotype comparison on all libraries (Appendix C, Figure S2), since the script by Skoglund et al. (2013) is often not conclusive for very low coverage samples.

To confirm aDNA authenticity I followed the following steps:

- confirmed post-mortem damage and DNA fragmentation with mapDamage v. 2.0.7 (Jónsson et al., 2013) and bamdamage (included in bammds package (Malaspinas et al., 2014)) for all libraries (Appendix C, Figures S3 and S4).

- confirmed one single mtDNA haplotype consistent with one single donor (and different from the people working in the lab and handling the samples), and, in the case of MS060/Segorbe Giant, consistent across all libraries;
- confirmed that all libraries from Segorbe Giant could confidently be assigned as genetically male (Appendix C, Figure S1);
- checked for contamination in the mtDNA sequence of the non-treated library of MS060/Segorbe Giant using schmutzi (Renaud et al., 2015);
- estimated contamination in the X chromosome of MS060/Segorbe Giant using ANGSD (Analysis of next generation Sequencing Data) v.0.919 (Korneliussen et al., 2014);

USER-treated libraries displayed a lower percentage of post-mortem damage (<5%), usually restricted to only the terminal two nucleotides, whereas, as expected, the non-treated library presented a higher percentage of damage (Appendix C, Figure S3b). To avoid SNP miscalls due to post-mortem damage, I downscaled base quality of positions likely affected by post-mortem misincorporations using the --*rescale* option in mapDamage (Jónsson et al., 2013). Finally, I merged all libraries from MS060/Segorbe Giant using picard MERGESAM (https://github.com/broadinstitute/picard).

2.3.3. Uniparental markers

I retrieved mtDNA variant positions with GATK v.3.7-0-gcfedb67 HaplotypeCaller (McKenna et al., 2010) and assigned haplogroups using HaploGrep 2.0 (Kloss-Brandstätter et al., 2011), according to the nomenclature in PhyloTree (Build 17, February 2016) (van Oven, 2015) where possible. All missing and private mutations detected by HaploGrep, as well as heteroplasmies, were individually checked with IGV v.2.3 (Thorvaldsdottir et al., 2013). I included the sequences in phylogenetic trees to further confirm their authenticity and compared them to mtDNA sequences from people handling the samples in our lab.

I performed Y-chromosome haplogroup classification using Yleaf (Ralf et al., 2018), and checked mutations against the ISOGG (International Society of Genetic Genealogy) SNP index (as of June 2018).

2.3.4. Autosomal analysis

2.3.4.1. 600k-SNP dataset

I called pseudo-haploid SNPs for the Segorbe Giant against the Human Origins 600k SNP list (Lazaridis et al., 2016) using a combination of samtools *mpileup* (-R, -B, -q30, -Q30) and pileupCaller v1.1.0 (https://github.com/stschiff/sequenceTools), using the default option for random calling. The total number of SNPs covered in the Segorbe Giant was of 39,795 (39,751 of which located in autosomes). I carried out PCA of autosomal SNPs using *smartpca* (included in EIGENSOFT), with the default setting for outlier removal, *shrinkmode: YES* and *lsqproject: YES* to project ancient samples on a selection of 668 modern individuals from 42 populations from North Africa, Europe, the Caucasus and the Near East (Appendix C, Table S1).

I filtered an enlarged dataset, comprising 2068 individuals from the worldwide modern dataset (Lazaridis et al., 2016), for positions in linkage disequilibrium (LD) using the command *--indep-pairwise* (200, 25, 0.4) in PLINK v.1.07 (Purcell et al., 2007), as performed before for Iberian ancient datasets (Martiniano et al., 2017; Olalde et al., 2018), resulting in a total of 298,622 SNPs (19,259 of which covered in the Segorbe Giant). This was used to run ADMIXTURE v.1.3.0 (Alexander et al., 2009) in unsupervised mode for values between *K*=2 and *K*=15 with cross-validation (*--cv*) and 10 independent replicates (using time as seed to approximate to a random seed).

2.3.4.2. 1240k-SNP dataset

I used the 1240k SNP list (v37.2.1240K, available at https://reich.hms.harvard.edu/) to call SNPs for the Segorbe Giant in the same way as described above, resulting in a total of 74,209 autosomal SNPs covered. I compiled a dataset including only ancient samples, to which I have added outgroups for the formal tests of admixture (ADMIXTOOLS v.4.1 (Patterson et al., 2012)). I ran outgroup-*f3* statistics using *qp3Pop*, testing three outgroups (Mbuti, Ju|'hoan North and Ust'-Ishim), to account for any potential African ancestry in the Segorbe Giant. I also computed *D*-statistics (using a chimpanzee genotype as outgroup) with *qpDstat*. In order to compare the Segorbe Giant with other recently published Islamic individuals from Spain (Olalde et al., 2019), I performed *D*-statistics tests to untangle Spanish, North African and Near Eastern contributions to both the Segorbe Giant and to the Islamic Valencian population from the 10th-16th century CE (Olalde et al., 2019), as follows:

- *D*(Chimp, Segorbe Giant; Iberian population, North African population);
- *D*(Chimp, Islamic Valencia; Iberian population, North African population).
- *D*(Chimp, Segorbe Giant; North African population, Levantine population);
- *D*(Chimp, Islamic Valencia; North African population, Levantine population);
- *D*(Chimp, Segorbe Giant; Iberian population, Levantine population);
- *D*(Chimp, Islamic Valencia; Iberian population, Levantine population);

In order to further investigate admixture proportions in the Segorbe Giant, I ran *qpAdm* (Haak et al., 2015) (also included in ADMIXTOOLS), testing 1-way, 2-way and 3-way combinations of Late Neolithic Morocco, Spanish and Levantine groups as source (left) populations, and using a set of outgroups (right populations) based on that used by Olalde et al. (2019) for southeast Spain in the last two millennia.

Published ancient samples were remapped to my reference sequence (Hg19, and rCRS) and reanalysed alongside Segorbe Giant to prevent possible batch effects due to differences in pipelines. I used *convertf* and *mergeit* (both included in EIGENSOFT v.7.2.1 package (Patterson et al., 2006)) to merge and convert files whenever necessary. Plots were computer either using basic R plot options (The R Development Core Team, 2008), or *ggplot2* package (Wickham, 2016).

2.4. Haplogroup U6 in modern Iberia

Here I used the Iberian mtDNA dataset described in Chapter III (*n*>1100) to assess the frequency of U6, H5 and V in present-day Iberia. I computed a frequency distribution map for U6a with Surfer® v.8 (Golden Software) using the Kriging algorithm, considering the coordinates of Spanish provincial capital cities as geographic location of the samples. For the Portuguese dataset I considered only two geographic points (Viseu and Évora) as a proxy for North (*n*=85) and South (*n*=13) Portugal, in an attempt to minimize the effects of the poor sampling distribution. Samples from Madeira and the Canary Islands, as well as from the African cities of Melilla and Ceuta, were not considered here.

2.5. Phylogeographic analysis of mtDNA haplogroup U6

I built a phylogenetic tree of mtDNA haplogroup U6 based on a total of 330 modern (36 of which are unpublished, from Iberia, Italy, and Libyan Berbers) and 30 ancient sequences (one being the Segorbe Giant) using MtPhyl v.5.003 software (http://eltsov.org) (Appendix C, Table S2), following the same steps as described in Chapter III, section 2.3.2 (HKY85 mutation model (Hasegawa et al., 1985), and two partitions to differentiate HVS-I/II from the remaining sequence for ML analysis). Most of these sequences were collected and extracted by our collaborators in Portugal, Spain and Italy, and amplified either by me or by other members of our group in a collective effort to sample European mitochondrial variation, as explained on Chapter III. The Libyan sequences were extracted and amplified by Dr Ali Madour as part of his PhD project under the supervision of Dr Dougie Clarke (University of Huddersfield).

I computed Bayesian skyline plots (BSPs) (Drummond et al., 2005) for the complete modern U6 dataset using BEAST v.1.8.0 (Drummond et al., 2012) (100,000,000 interactions with a burn-in of 10,000,000 steps), applying a relaxed molecular clock with a mutation rate of 2.514 x 10^{-8} mutations/site/year (previously calculated for U6 (Pereira et al., 2010b)), assuming a 28-year generation time (Moorjani et al., 2016), and combined three independent runs with LogCombiner v.1.8.0 (BEAST package).

3. Results

MS058, from Altar dos Moinhos, and MS062, from Atrio de Menga, failed the screening for endogenous DNA (Table 4.2), with 0.21% and 0.13% of mapped reads, respectively, corresponding to ~0.001x of mean genome coverage.

A manual check of the polymorphisms found in the mtDNA alignments allowed me to classify MS058 (0.334x mtDNA mean coverage) as haplogroup H, by confirming the presence of variant 1438G (potentially H5, although with a heteroplasmy 16304R). The manual classification of MS062 proved more contentious, due to the very low mean mtDNA coverage (0.193x), with two variants pointing to H3c3 (6776C, defining H3, and 16278T, defining H3c3), and U6a (variants 14179G and 16278T). Although the individual was not buried according to Islamic tradition, its radiocarbon date (674–875 cal. CE, using OxCal4.3/IntCal13 curve (Bronk Ramsey, 2009; Reimer et al., 2013)) overlaps with the Islamic period in southern Spain and does not allow us to exclude the possibility of a U6 sequence. Therefore, this mtDNA classification is not conclusive, and I cannot exclude the possibility of contamination.

MS058 is genetically female (Appendix C, Figure S2), as reported in the export excavation (Luna, 2008). MS062, also seems to be genetically female, contrarily to the previous classification based on skeletal features (Díaz-Zorita and García Sanjuán, 2012) (Appendix C, Figure S2).

Table 4.2. Information regarding sequencing of ancient individuals included in this chapter.

Individual	**DNA code**	**# total raw reads**	**Duplication rate**	**# mapped reads (%)**	**Mean genome coverage**	**# mapped reads rCRS**	**Mean mtDNA coverage**	**mtDNA haplogroup**	**Genetic sex**
ALM/01	MS058	26,314,391	7.41%	54,190 (0.21)	0.001x	106	0.334x	H **	XX
CBU/33	MS059	27,390,274	11.24%	92,744 (0.34)	0.002x	1094	3.534x	H5a1+152	XX
UE2298 ”Segorbe Giant”	MS060*	220,447,557	13.81%	3,709,529 (1.68)	0.065x	12,601	31.978x	U6a1a1a	XY
Menga01	MS061	38,253,581	12.83%	290,820 (0.76)	0.004x	1547	4.147x	V+72@	XY
Menga02	MS062	37,469,787	8.87%	48,072 (0.13)	0.001x	65	0.193x	H3c3/U6a **	XX

* merged libraries

** manually checked, very low coverage mtDNA sequences

3.1. Casal dos Bucículos and Menga

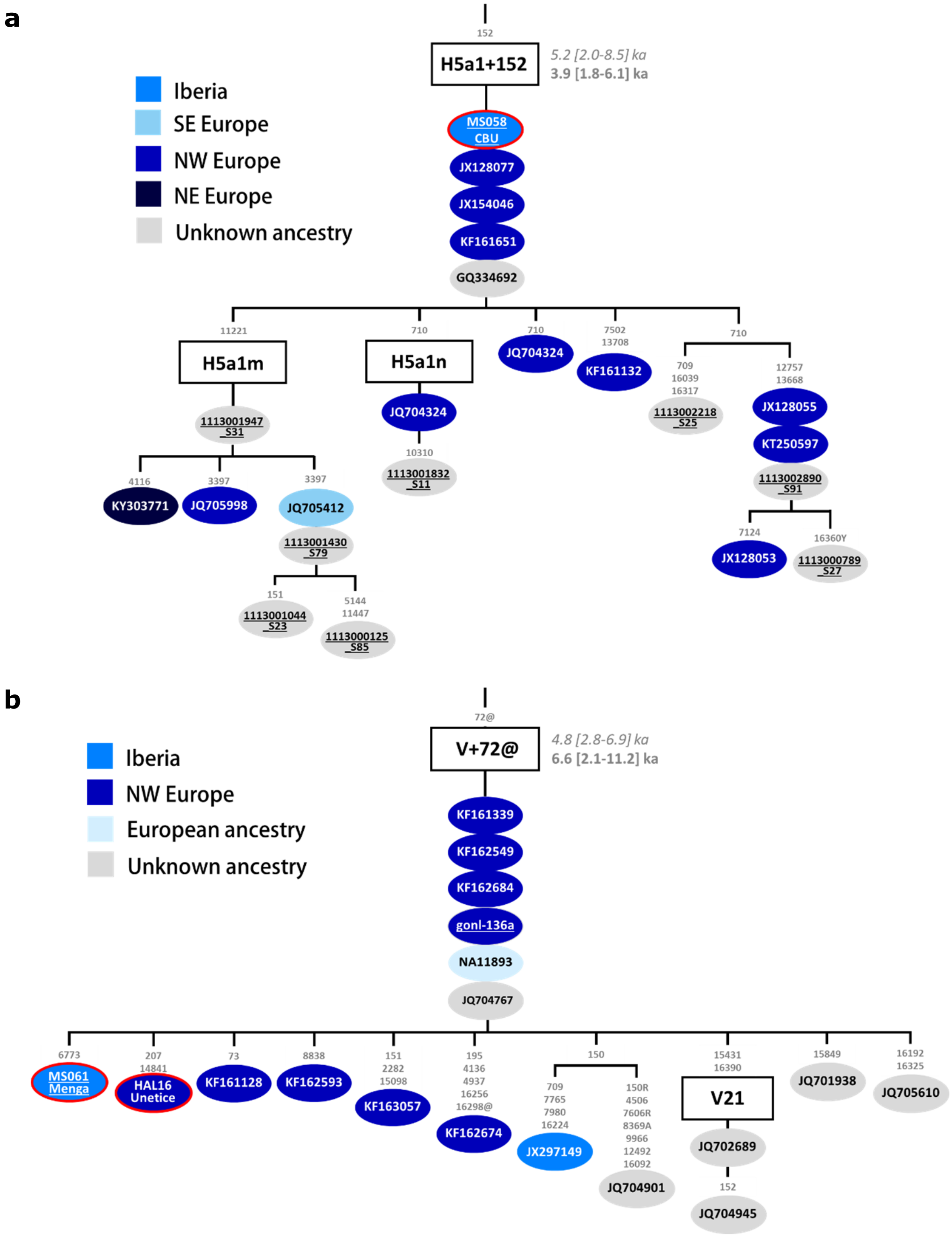

Figure 4.6. Phylogenetic trees of mtDNA lineages **a)** H5a1+152 and **b)** V+72@. ρ and maximum likelihood (ML) node age estimates shown on the branches (in italics and in bold, respectively); sequences are coloured according to geography, with sequence from ancient samples highlighted in red; underlined samples are newly reported; mutations relative to rCRS are indicated on the branches (@ indicates a back mutation). Note: complete phylogenetic trees of HV and H5, as well as node age estimate analysis, were performed by Alessandro Fichera (a fellow PhD student in the group) and Dr Francesca Gandini, respectively.

MS059, from Casal dos Bucículos (Portugal), belongs to H5a1+152 and MS061, from Menga (Spain), to V+72@. H5 and V are found in the present Iberian mtDNA dataset at a frequency of ~3% (Appendix B, Table S7), and are part of the major HV clade, which has a typically European distribution. Both sequences cluster in predominantly northwest European branches that date to around 5 ka (Figure 4.6).

Unfortunately, the low content of endogenous aDNA (<1% of mapped reads) (Table 4.2) did not allow me to conduct any genomic analysis. Nevertheless, it was possible to retrieve sex information for these two samples (Appendix C, Figure S2): MS069, previously unclassified, is genetically XX, whereas MS061 is XY, corroborating the anthropological analysis (Díaz-Zorita and García Sanjuán, 2012).

3.2. Segorbe Giant

Although with a low percentage of mapped reads (~1.68%) and low mean coverage (0.065x), the Segorbe Giant yielded enough aDNA for genomic analysis. The individual is genetically male (R_Y>0.077; Appendix C, Figures S1 and S2), thus confirming the anthropological evidence (Barrachina, 2004). The levels of contamination were low on both the X chromosome (Method 1, new_llh (MoM): 0.037142 ±3.745333^{-2}, estimated using ANGSD) and on the mtDNA sequence (0–0.005%, calculated with schmutzi).

3.2.1. Mitochondrial DNA

The Segorbe Giant belongs to mtDNA haplogroup U6a1a1a (nomenclature according to Hernández et al. (2015)). Although U6 in general, and U6a in particular, is present in higher frequencies in North and West Africa (Maca-Meyer et al., 2003; Macaulay et al., 1999; Secher et al., 2014), the complete mitochondrial genome dataset available is currently heavily biased towards Europe, and U6a1a1a, which dates to 3.5 thousand years ago (ka), appears to have a more southern European distribution (Figure 4.7a). However, in the modern Iberian mitogenome dataset presented in this thesis, U6a1a1a occurs only at 0.3%, whereas the HVS-I (hypervariable segment I) subclade U6a1a1, defined by a variant at position 16239, which nests U6a1a1a, is found at ~14% in Algerian Mozabite Berbers (Macaulay et al., 1999). Moreover, the fact that U6a1a1 was also found in two individuals from the indigenous population of the Canary Islands (Fregel et al., 2019) further supports its North African provenance.

Haplogroup U6a1 has been found in Moroccan Iberomaurusian remains dating to 14–15 ka (van de Loosdrecht et al., 2018), as well as in Early Neolithic Morocco (Fregel et al., 2018) (Figure 4.7b). Although U6 lineages have been retrieved from 15th century CE Islamic burials in Granada (Olalde et al., 2019), to my knowledge, the Segorbe Giant is the earliest documented finding of a U6 lineage in Iberia. Based on the results of the newly generated Iberian mitochondrial dataset (*n*=1107: 1011 sequences from mainland Spain and the Balearic Islands, plus 96 from mainland Portugal), U6a can be found at an average frequency of 1.6% in modern mainland Iberian populations, with a peak of >3% in the south of Spain (Figure 4.7b; Appendix B, Table S7).

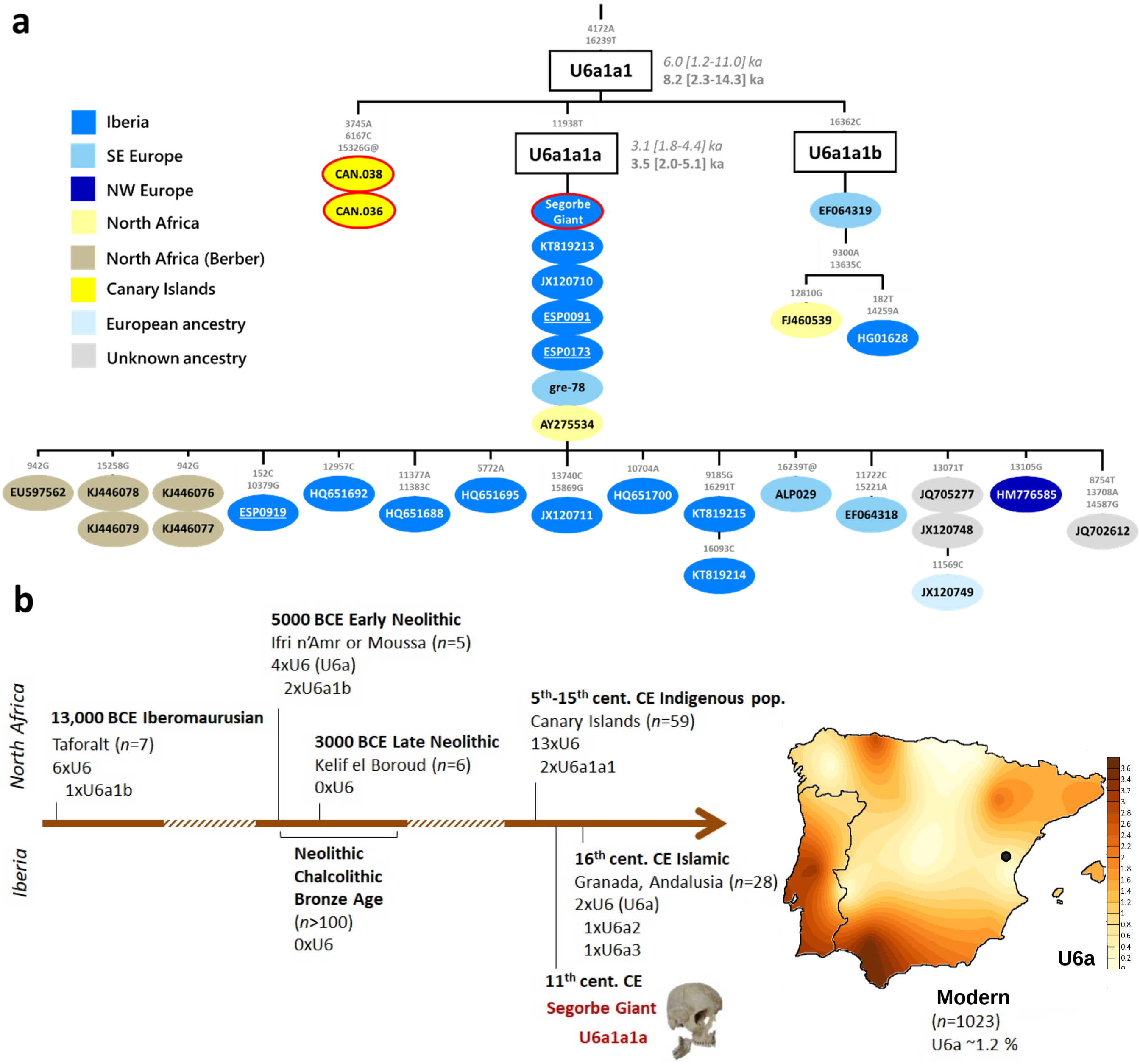

Figure 4.7. a) Phylogenetic tree of mtDNA lineage U6a1a1. ρ and maximum likelihood (ML) node age estimates shown on branches (in italics and in bold, respectively); sequences are coloured according to geography, with the aDNA sequences highlighted in red; underlined samples are newly reported; mutations relative to rCRS are indicated on the branches. The complete and more detailed tree for haplogroup U6 is shown in Appendix C, Excel file S5. Details about the sequences used to build the tree in Appendix C, Table S2. **b)** Timeline showing occurrence of haplogroup U6 in the archaeological record of North Africa and Spain through time (Fregel et al., 2018, 2019; van de Loosdrecht et al., 2018; Martiniano et al., 2017; Olalde et al., 2018, 2019; Rodríguez-Varela et al., 2017; Szécsényi-Nagy et al., 2017; Valdiosera et al., 2018), and a map of frequency distribution of U6a in present-day Iberia, with a point indicating the location of Segorbe city.

The Segorbe Giant falls outside the modern geographic distribution of U6a lineages in Spain (Figure 4.7b). A detailed description of haplogroup U6 is presented on section 3.3 of this chapter.

3.2.2. Y chromosome

The Segorbe Giant belongs to the Y-chromosome haplogroup E1b1b1b1 (E–M310), with two diagnostic SNPs (CTS6444 and CTS1243) being transversions, and therefore unlikely to be the result of post-mortem damage, although covered by only one read (Table 4.3).

Table 4.3. Diagnostic SNPs retrieved from the Segorbe Giant's Y-chromosome. SNPs that represent transversions in bold and underlined. Positions according to Hg19 reference.

Position	Marker name	Haplogroup	Ancestral	Derived	# Reads	Called base
19193159	M5272	E1b1b1b1	G	A	1	A
16899460	**<u>CTS6444</u>**	E1b1b1b1	T	G	1	G
7290454	**<u>CTS1243</u>**	E1b1b1b	G	C	1	C
22181731	M5322	E1b1b1	G	A	1	A
22671606	CTS10637	E1b1b	T	C	1	C
14718400	CTS3199	E	A	G	1	G
14329233	CTS2496	E	C	T	1	T
15809326	P174	E	G	A	1	A
19379113	CTS10296	E	T	C	1	C

E1b1b1b1 (E–M310) dates to ~13.9 [12.1–15.7] ka (Y-full, v.6.06.15) and is immediately basal to the clade nesting E–M81. E1b1b is very frequent in North Africa (>40%) (Semino et al., 2004), and has been found in North African and Levantine remains (Fregel et al., 2018; Lazaridis et al., 2016; van de Loosdrecht et al., 2018; Rodríguez-Varela et al., 2017) (Figure 4.8). The more derived E–M81 (E1b1b1b1a), dating to ~2.8 ka (YFull, v.6.06.15), has been retrieved from early Islamic remains (7th-8th cent. CE) in southern France (Gleize et al., 2016), and the more derived E1b1b1b1a1 was found in an Islamic necropolis in the city of Valencia (Olalde et al., 2019). E–M81 is predominantly found nowadays in the Maghreb (where its average frequency is >40%) and peaks in modern Berber groups, with frequencies reaching >80% (Cruciani et al., 2004; Fadhlaoui-Zid et al., 2004; Pereira et al., 2010b), being almost fixed in some groups, such as the southern Moroccan Tachlhit-speakers (Reguig et al., 2014) or the Chenini–Douiret and Jradou from Tunisia (Fadhlaoui-Zid et al., 2004). In Europe, it is found mostly in Iberia and Sicily at frequencies <5% (Semino et al., 2004), and it seems to be a marker of North African ancestry in southern Europe during the Islamic movements in Medieval times. Given that there are no reads covering any of its diagnostic positions, one cannot exclude the possibility that the Segorbe Giant could belong to the E–M81 lineage.

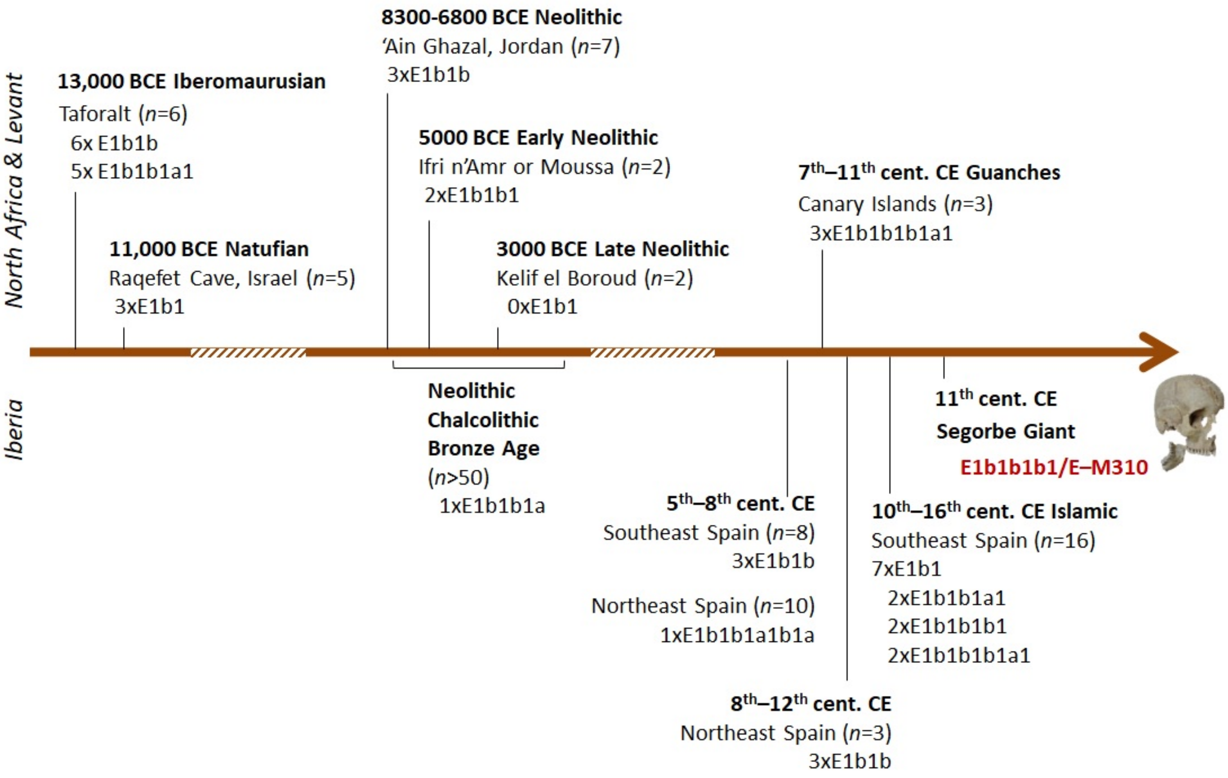

Figure 4.8. Timeline showing occurrence of Y-chromosome E1b1 lineages in the archaeological record of Spain, North Africa and Levant through time (Fregel et al., 2018; Lazaridis et al., 2016; van de Loosdrecht et al., 2018; Martiniano et al., 2017; Olalde et al., 2018; Rodríguez-Varela et al., 2017; Valdiosera et al., 2018).

3.2.3. Genomic background

The PCA (Figure 4.9a) shows that the Segorbe Giant occupies an intermediate position between North African and Iberian populations in PC1. Moreover, he does not plot together with the other contemporary Islamic samples (including those from the region of Valencia), which seem to be pushed more towards the Near East, rather than to North Africa (with the exception of individual I12644, from the site of Carrer Sagunto 49, in the city of Valencia, who displays a higher proportion of African ancestry, and I3810 and I7427 from Granada, who plot together with North African populations (Olalde et al., 2019)).

In the ADMIXTURE analysis the lowest median CV-errors were at *K*=10 (Figure 4.9b) and *K*=11 (Appendix C, Figure S5). Since the median CV error for both *K*s is not significantly different (Appendix C, Figure S6), I choose to show here *K*=10 for simplicity. Moreover, not only does the distribution of CV-errors for *K*=11 look more skewed than for *K*=10, but the addition of an 11th component seems to spuriously divide modern and ancient individuals, without adding any insight into the ancestry of the ancient populations of interest.

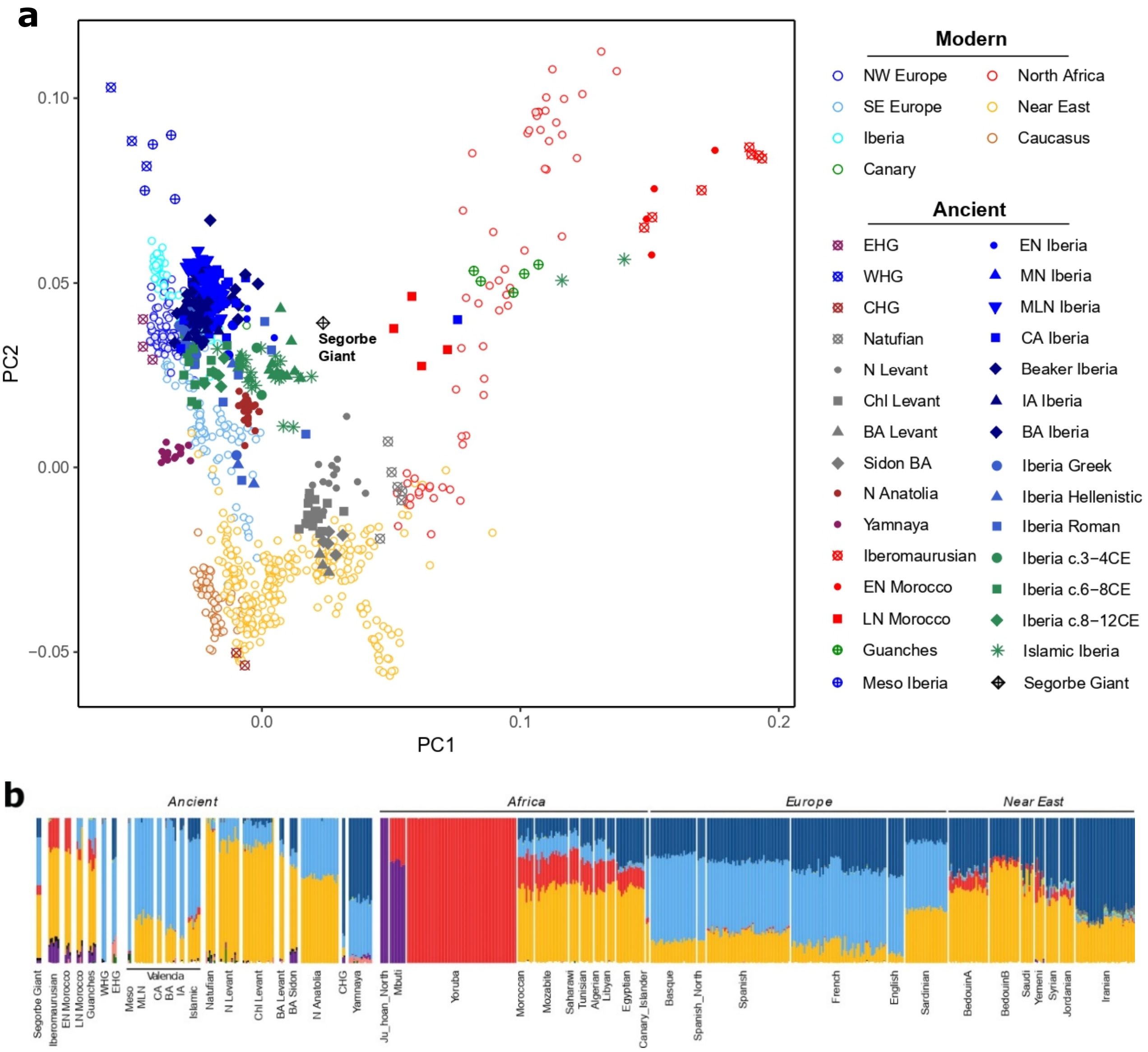

Figure 4.9. a) PCA projecting 418 ancient samples on 668 modern individuals from North African, European, Near Eastern and Caucasian populations. **b)** ADMIXTURE plot (*K*=10), showing a selection of ancient and modern African, European, Near Eastern and Caucasian populations. EHG, WHG and CHG refer to East, West and Caucasus hunter-gatherers, respectively. M, N (EN/MN/LN), CA/Chl and BA stand for Mesolithic, Neolithic (Early, Middle, Late), Copper Age/Chalcolithic and Bronze Age, respectively. Only ancient individuals from the Community of Valencia shown here, for an ADMIXTURE with ancient individuals from the whole of Iberia please refer to Appendix C, Figure S5.

For *K*=10, the Segorbe Giant displays four main components: two major ancestries (western European hunter-gatherer or "WHG", and Natufian, or Levantine hunter-gatherer/Levantine Neolithic), and two minor (Caucasus hunter–gatherer or "CHG", *i.e.* Mesolithic Caucasus component, and sub-Saharan African). These ancestry proportions seem intermediately derived from potential admixture between Spanish with Late Neolithic Morocco or Guanches. Interestingly, his profile in ADMIXTURE does not match any of the immediately preceding Spanish individuals, who also display variable African ancestry, but in lower frequencies (apart from two outlier individuals from Malaga (Figure 4.9) that have been shown to overlap with North Africans in the PCA (Olalde et al., 2019)). Overall the pattern seems consistent with contributions from two sources: one with more Iberian-like ancestry, and other resembling the Guanches and Late Neolithic Morocco.

However, formal tests of admixture suggest a more complex scenario. Outgroup-*f3* runs using different outgroups (Mbuti, Ju|'hoan and Ust'-Ishim) consistently show a higher proportion of shared drift with Middle/Late Neolithic, Chalcolithic and Bronze Age Iberian populations and with the Anatolian Neolithic (Figure 4.10a), than with North African populations – although one should note that the proximity of North African groups to the Segorbe Giant changes when using a non-Sub-Saharan African outgroup (Ust'-Ishim). *D*-statistics are consistent in showing the Segorbe Giant to be significantly closer to Iberian (Spanish) and Levantine populations than to Iberomaurusian, Early Neolithic Morocco or the Guanches, a trend also observed in the Valencian population from 10th–16th century CE (Olalde et al., 2019) (Appendix C, Figure S7 and Table S7). However, tests with Late Neolithic Morocco all failed to produce significant results, which might be an indicator that a population genetically close to Late Neolithic Morocco contributed to the ancestry of Segorbe Giant in similar proportions to Spanish and/or Levantine sources.

In agreement with this hypothesis, *qpAdm* 1-way scenarios were all rejected (Appendix C, Table S8). Instead, the Segorbe Giant can be modelled using 2-way models, with certain combinations of Late Neolithic Morocco and different Spanish populations (admixture coefficients ranging from 0.276-0.724, using the Spanish population from 8th–12th century CE, to 0.445–0.555, with Spain Iron Age), and with the combinations of Guanches plus 5th-8th century CE Spain (admixture coefficients: 0.281-0.719), and Guanches plus 8th-12th century CE Spain (admixture coefficients: 0.192-0.808), albeit with high standard errors, probably an effect of low coverage on my sample (Table 4.4; Appendix C, Table S9). Although comparisons using the Levant Chalcolithic and Middle/Late Neolithic or Bronze Age Spain cannot be statistically rejected (p>0.05) (Table 4.4), *qpAdm* with three source populations (combinations of Late Neolithic Morocco, Levant Chalcolithic and Spanish populations) failed to produce significant and plausible results (Appendix D, Table S10).

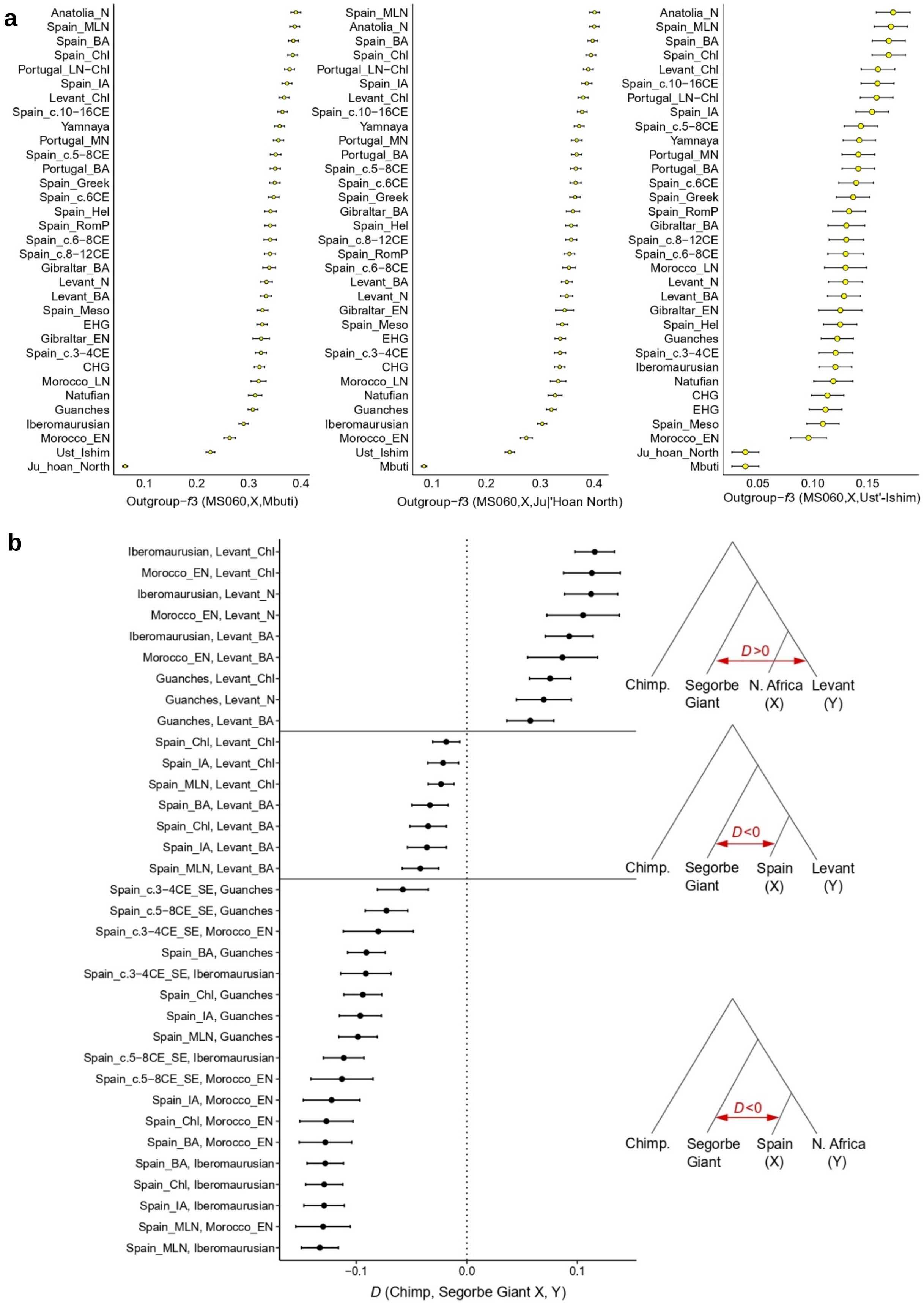

Figure 4.10. a) Outgroup-*f3* testing three different outgroups: Mbuti, Ju|'Hoan North and Ust'-Ishim, and **b)** *D*-statistics in the form *D*(Chimp, Segorbe Giant; X, Y), in which X and Y are different Spanish, North African and Levantine ancient populations (only significant tests supported by |Z|>3 are shown). All error bars correspond to 2 standard errors. Detailed output of all tests can be found in Appendix D, Tables S3-S6.

Table 4.4. *qpAdm* results modelling two populations as sources (Pop.1 and Pop.2). Only non-rejected (*p*>0.05) and plausible scenarios (admixture coefficients between 0 and 1) are shown here. The complete output can be found in Appendix D, Table S9.

Target	**Sources (left populations)**		**best coefficients**		**std.err.**	***p*-value**
	Pop.1	**Pop.2**	**Pop.1**	**Pop.2**		
SegorbeGiant	Guanches	Spain_c.8-12CE	0.192	0.808	0.262	0.353281
SegorbeGiant	Guanches	Spain_c.5-8CE	0.281	0.719	0.653	0.457149
SegorbeGiant	Morocco_LN	Spain_c.8-12CE	0.276	0.724	0.268	0.197
SegorbeGiant	Morocco_LN	Spain_c.3-4CE	0.296	0.704	0.558	0.568
SegorbeGiant	Morocco_LN	Spain_IA	0.445	0.555	0.934	0.184
SegorbeGiant	Levant_Chl	Spain_BA	0.457	0.543	0.491	0.141
SegorbeGiant	Levant_Chl	Spain_MLN	0.689	0.311	0.369	0.297

3.3. Phylogenetic analysis of mtDNA haplogroup U6

The study of the Segorbe Giant led to a renewed phylogeographic study of mtDNA haplogroup U6 (Appendix C, Excel file S5). Haplogroup U6 dates to ~39.8 [29.2-50.7] ka, based on the present maximum-likelihood (ML) analysis. Its modern distribution differs greatly from other U clades, which are mostly Eurasian lineages, with the typically European U4 and U5 (together with U8) representing the majority of Mesolithic European lineages described (Brandt et al., 2013; Malyarchuk et al., 2008, 2010), U1 and U3 present at highest frequencies in present-day Near East (Al-Zahery et al., 2011; Derenko et al., 2013), and U2 and U7 contributing considerably to Southwestern and South Asian maternal variation (Metspalu et al., 2004; Sahakyan et al., 2017). U6, on the other hand, has a broad Mediterranean distribution, with its highest extant frequencies in North Africa, and some subclades present in sub-Saharan Africa.

However, basal U6* has been retrieved from two individuals dating to 35–33 ka found in the Peştera Muierii cave in Romania (Fu et al., 2016; Hervella et al., 2016), and an additional Palaeolithic U6 lineage from the Caucasus (~27–24 ka) was recently described (Lazaridis et al., 2018), supporting the suggestion that U6, similarly to other U clades, most likely originated in Eurasia, and was later involved in a pre-Holocene back-to-Africa migration probably from Southwest Asia (Henn et al., 2012; Macaulay et al., 1999; Olivieri et al., 2006; Sánchez-Quinto et al., 2012b), which must have occurred before 14–15 ka (the age of the Iberomaurusian remains in Taforalt (Morocco), the earliest account of U6 lineages in North Africa (van de Loosdrecht et al., 2018)). The expansion of the Iberomaurusian culture into Northwest Africa dates to the early LGM or before (at least 25 ka) (Hogue and Barton, 2016).

U6a is the largest and most widespread of all U6 subclades, and the only one with a node age estimated to pre–date the LGM (26.9 [21.4–32.4] ka). U6a seems to have been restricted to the Mediterranean basin before the LGM, where its oldest branches arose: U6a1 (21.7 [14.5–29.2] ka) and U6a7 (25.2 [19.4–31.2] ka), between them harbouring the bulk of Iberomaurusian and Early Neolithic Moroccan lineages (Fregel et al., 2018; van de Loosdrecht et al., 2018). In contrast, sub-Saharan branches (either in West or in East Africa) all date to the post–LGM. U6a3 (18.7 [14.3–23.3] ka) shows a dual distribution, with lineages spanning from the east (U6a3d: 7.3 [1.2–13.5] ka) to the west Mediterranean (U6a3a: 12.9 [6.7–19.4] ka), and sub–Saharan West African lineages, with ages ranging from the Late Glacial and early postglacial to the Neolithic: U6a3f (15.4 [9.7–21.2] ka), U6a3+150 (9.8 [2.8–17.1] ka), and pre–U6a3c (5.0 [0.7–9.5] ka). U6a2a (12.3 [7.0–17.8] ka) and U6a2b (9.2 [1.9–16.9] ka) date to Late Glacial/postglacial Ethiopia. U6a8, harbouring North African and southern European sequences, also dates to post-LGM/Late Glacial period (14.9 [6.5-23.8] ka).

Haplogroup U6a1, dating to 21.7 ka, has been found in Iberomaurusian samples dating to 14–15 ka (van de Loosdrecht et al., 2018) and in Early Neolithic Morocco (Fregel et al., 2018). Many of the Iberomaurusian lineages cluster with Early Neolithic or present-day Moroccan lineages, showing a certain degree of continuity in the Maghreb on the female line of descent, despite more recent population events, such as the Arab Conquest and increase in sub-Saharan influx, that changed the autosomal variation in the region (Arauna et al., 2016). Additionally, two recently published U6a1a1 sequences have been retrieved from indigenous Canary Islanders (roughly dating to 13th–17th century CE) (Fregel et al., 2019), and two *Morisco* (Muslims forcibly converted to Christianity) U6 lineages (one U6a2 and one U6a3) from Granada, in Andalusia, south Spain, approximately five centuries later than the Segorbe Giant, have been recently reported (Olalde et al., 2019).

U6b (12.5 [8.6–16.5] ka), U6c (10.8 [5.4–16.3] ka) and U6d (12.7 [7.4–18.2] ka) are smaller subclades, dating to the Pleistocene–Holocene transition. U6c is present in the western Mediterranean region and in the Canary Islands (including in one sample dating to 13th–15th century CE (Fregel et al., 2019)), whereas U6b and U6d have a wider distribution around the Mediterranean basin, with incursions into sub-Saharan Africa, northern Europe and Arabia. U6b1a is mostly restricted to the Canary Islands, and harbours the bulk of U6 sequences retrieved from the archipelago's archaeological remains (Fregel et al., 2019; Maca-Meyer et al., 2004; Rodríguez-Varela et al., 2017). Its age estimate of 2.8 [0.9–4.6] ka suggests that this lineage was likely carried by first settlers of the islands (Secher et al., 2014).

The BSP of haplogroup U6 indicates three main moments of population increase (Figure 4.11): (1) around the LGM, just before 20 ka, most likely a trace of Iberomaurusian expansions in North Africa, as mentioned above and discussed in detail in Pereira et al. (2010); (2) in the Late Glacial (12–15 ka), coinciding with the ranges for the age estimates of the U6 branches in sub-Saharan Africa in the tree; and (3) in the last 5 ka, with an acceleration in the last ~2 ka.

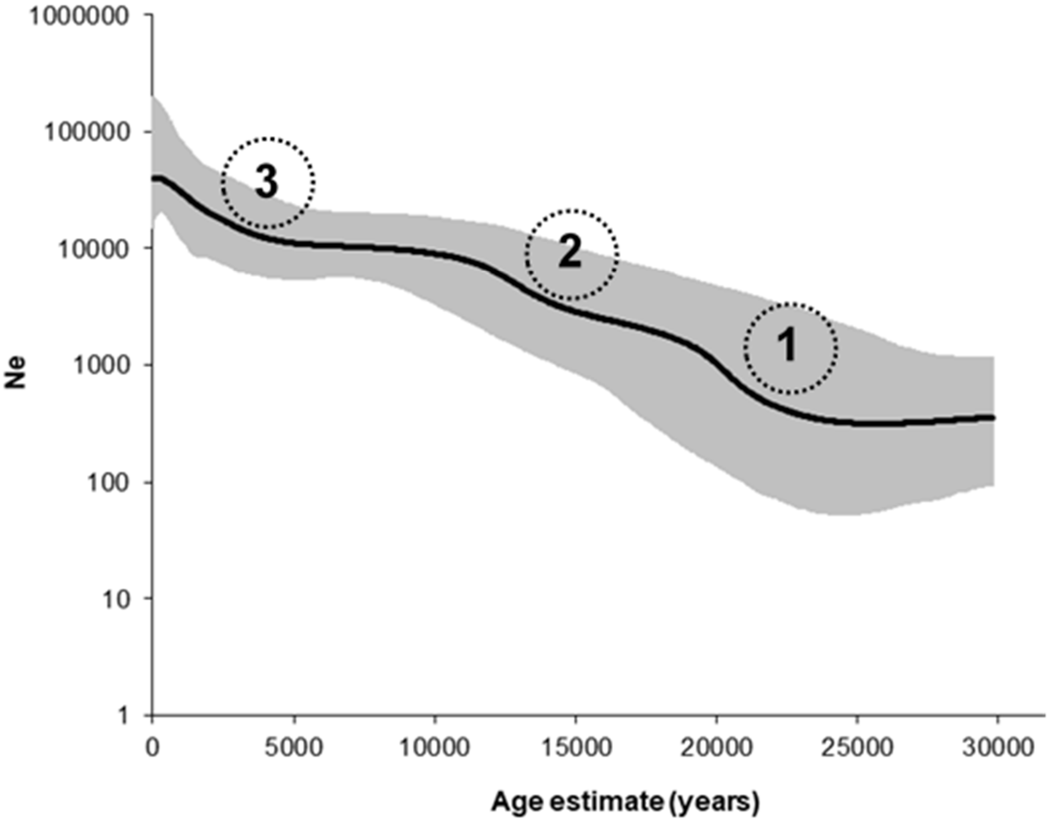

Figure 4.11. BSP indicating the median of the *Ne* associated to mtDNA haplogroup U6 through time. Three main moments of population increment: (1) around the LGM, just before 20 ka; (2) in the Late Glacial (12–15 ka) period; and (3) in the last 5 ka, with an acceleration in the last ~2 ka.

The main feature of the glacial period in Africa was high aridity, with the expansion of the Sahara hundreds of kilometres southwards (Adams and Faure, 1997). This probably prevented contacts between North African and sub-Saharan populations and explains the scarcity of evidence of human occupation during this period. During the African Humid Period (~14.7–5.5 ka) the North and Central African climate was much more moist than today (Otto-Bliesner et al., 2014; Shanahan et al., 2015). The expansion of rainforest in equatorial Africa, combined with the movement of monsoon rains northwards, resulted in the greening and occupation of the Sahara (Adams and Faure, 1997; Jousse, 2006; Kuper and Kröpelin, 2006; Nicoll, 2004), probably potentiating the *Ne* associated with U6 observed in the BSP and movements into sub-Saharan Africa, with the rise of several U6 sub-Saharan clades (*e.g.* U6a2a, U6a2b, U6a3c, U6a3f).

The 5-ka increment might correspond to the expansion of indigenous communities triggered by the spread of agriculture into the Maghreb (Fregel et al., 2018). The more recent acceleration, in the last 2 ka, coincides with the Islamic conquest of North Africa and probably corresponds to further expansions set in motion by the Arab conquest of North Africa and Iberia, which led to profound cultural, religious and linguistic changes in the region.

4. Discussion

Here I have attempted to analyse medieval human remains from Portugal and Spain. Due to the low preservation of DNA, only one individual could be studied in detail. This was an individual excavated from the Islamic necropolis of Plaza del Almudín, in Segorbe, dating to the 11th century CE. The archaeologists who were responsible for the excavation in 1999 considered this individual unusual due to his considerable height compared with other individuals found at the same site (Barrachina, 2004), and dubbed him the "Segorbe Giant". The subsequent anthropological analysis suggested some sub-Saharan African morphological features and postulated a link to the Berber-speaking populations that settled in the region in Medieval times (Barrachina, 2004).

Analysis of uniparental markers fits well with this assumption, pointing to an origin in the Maghreb, most likely from a Berber group. U6a is not only connected to modern Amazigh populations (Secher et al., 2014), but has also been found in Moroccan remains associated with the Iberomaurusian culture, in the Early Neolithic Moroccan site of Ifri n'Amr or Moussa and in archaeological remains from the Canary Islands (Fregel et al., 2018, 2019; van de Loosdrecht et al., 2018). This is in sharp contrast with two other individuals for whom I could retrieve reliable mtDNA sequences (from Casal dos Bucículos (Torres Vedras, Portugal) and Menga (Málaga, Spain)), both harbouring typically European mtDNA lineages (Figure 4.6). (Note that the other individual from Menga, MS062, could also harbour an U6a haplotype, since her mtDNA sequence contains two diagnostic mutations. However, although the date of the burial matches the Islamic period in the region, she was not buried according to the Islamic norm. Moreover, the extremely low mtDNA coverage, as well as the presence of diagnostic positions also leading to an H3 branch, render the mtDNA classification of this sequence inconclusive.)

The Segorbe Giant carries the Y-chromosome E1b1b1b1 (E–M310) lineage. E1b1b is common amongst extant North Africans and has been found in North African and Levantine remains (Fregel et al., 2018; Lazaridis et al., 2016; van de Loosdrecht et al., 2018; Rodríguez-Varela et al., 2017). He has been assigned to a basal position within E1b1b1b1, but due to low coverage, it is possible that he may belong to a more derived subclade, such as E1b1b1b1a (E–M81), which is the most common haplogroup amongst modern Berber males today (Fadhlaoui-Zid et al., 2011; Reguig et al., 2014), and has been linked to Islamic remains in southern France (Gleize et al., 2016), or to its descendant, E1b1b1b1a1-M183 lineage, identified in three Guanche males, in two Islamic individuals from Granada, and in an earlier 6th century CE male from the Visigoth site of Pla de l'Horta, in Catalonia (Olalde et al., 2019; Rodríguez-Varela et al., 2017).

However, the whole-genome evidence paints a more complex picture. The individual does not resemble any modern or ancient population from Europe, North Africa or the Near East described to date in the PCA. Rather, he is positioned mid-way between modern and ancient Spanish, and Late Neolithic Moroccan, Guanches and modern Berber individuals (Figure 4.9a). On the other hand, although he carries both uniparental markers of probable North African origin, the formal tests of admixture point to very high Iberian-like ancestry (Figure 4.10).

Three distinct scenarios could explain the observed autosomal ancestry in the Segorbe Giant. One would be to assume that this individual is a direct migrant from North Africa (whose unique genetic composition has not been studied yet), or derives from a population that migrated into Iberia but retained their genetic identity. A second scenario is that he descends from the pre-Islamic Spanish population, that already displayed higher levels of African ancestry in Medieval times (Olalde et al., 2019). Finally, the third scenario is that he is the result of admixture between Iberian and North African sources.

The first scenario would imply that pre-Islamic populations in North Africa would genomically resemble the Segorbe Giant. The nearest temporal proxy available are the Guanches (from the 7th–11th century CE), who originated in the Maghreb but have been isolated in the Canary Islands since at least the early Iron Age. However, the Guanche population is more similar to Iberomaurusian, Early Neolithic and Late Neolithic Moroccans than my sample (Rodríguez-Varela et al., 2017) and formal tests of admixture, especially *D*-statistics, suggest that Late Neolithic Morocco is genetically closer to Segorbe Giant than the Guanches (Figure 4.10). In any case, *qpAdm* rejects the hypothesis that the Segorbe Giant directly descends from a population resembling either the Guanches or the population from the Late Neolithic Moroccan Kelif el Boroud site (Appendix C, Table S8). Additionally, the oxygen analysis for the Segorbe Giant (Appendix C, Text S1) shows that he does not differ from most of the population studied, and points towards low mobility between early childhood and adolescence, suggesting that he grew up in the region. (In contrast, another individual from the same necropolis (MS075) looks non-local (Appendix C, Text S1), possibly a migrant from a hotter climate outside Europe, with oxygen values similar to those of North Africa or the Near East (Bowen and Revenaugh, 2003).)

Although North African ancestry in modern Spain is present at low values (typically between ~3–8%), with a slight southwest-to-northeast decline (Botigué et al., 2013; Bycroft et al., 2019), increased African ancestry was present in Spain since the 3th–4th century CE (Olalde et al., 2019). However, *qpAdm* also rejects the scenario of the Segorbe Giant directly descending from a previous Spanish population (Appendix C, Table S8).

The third scenario, according to which the Segorbe Giant was a result of admixture between Amazigh people who migrated from North Africa to Iberia, and the local Spanish population, at some point during either the Islamic conquest, the Caliphate period, or the Berber empires (8th–13th centuries CE), is in agreement with recent aDNA evidence from Iberia (Olalde et al., 2019). This would explain the Segorbe Giant's intermediate position in the PCA and his profile in ADMIXTURE, with WHG and Natufian ancestry shared with both Iberians and North Africans, CHG ancestry shared only with Iberians (the most plausible source, since CHG component seems to be absent in the ancient North Africans and in the Guanches reanalysed in this chapter), and sub-Saharan ancestry shared with Maghreb people. The fact that he still carried both uniparental markers of North African origin suggests that the admixture may have happened only a few generations before his time, coinciding with the zenith of Berber power, rather than earlier during the conquest, in agreement with admixture dates inferred from modern Iberian genomes from Aragon and Catalonia (Bycroft et al., 2019). However, it is not possible to entirely rule out assortative mating, allowing these uniparental markers to be retained for longer.

Again, however, *qpAdm* results are not so straightforward. Although they are consistent with admixture of a North African (either the Guanches or Late Neolithic Morocco) and a Spanish source, there also seems to be evidence of increased Levantine ancestry in Segorbe Giant (Table 4.4; Appendix C, Table S9), in agreement to what has been found in other individuals from the Islamic period (Olalde et al., 2019), despite the rejection of 3-way models including either Levant Chalcolithic or Levant Bronze Age (Appendix C, Table S10).

The date of the burial (11th century CE) (Barrachina, 2004) fit the historical narrative of Berber settlement in the region of Sharq al-Ándalus (Oliver Asín, 1974). Considering the genetic evidence, together with the stable isotope results and the historical accounts of intermarriage between local Spanish and the North African newcomers, and in agreement with recent aDNA evidence from Iberia (Olalde et al., 2019), this third scenario seems the most plausible. However, the original source populations are difficult to pinpoint. Due to lack of sampling in North Africa for this specific period, the nearest proxies available for the North African source are the Guanches (Rodríguez-Varela et al., 2017) and Late Neolithic Morocco (Fregel et al., 2018, 2019). As shown by the formal tests of admixture, the North African source seems to be closer to Late Neolithic Morocco, although possibly with increased Levantine ancestry (Olalde et al., 2019). On the other hand, the population of Valencia in the immediately preceding centuries has yet to be studied, and the closest Valencian population available prior to the Islamic period is from the Iron Age. Post-Iron Age individuals from other regions of Spain dating to Roman and post-Roman times, show a high degree of heterogeneity, especially in regards to the presence and frequency of African ancestry (Olalde et al., 2019), which would explain the discrepancies observed in *qpAdm*.

Interestingly, a recent study in modern South Americans detected North African ancestry introduced at the early stages of European colonization (Chacón-Duque et al., 2018). The presence of individuals in Medieval Spain with a genetic background similar to Segorbe Giant's would explain the source of this ancestry in America, suggesting that admixture with North Africans had impact on Medieval Spanish genetic variation, before virtually disappearing in the following centuries.

I found no U6 in the present-day whole-mtDNA dataset from the Valencia region (54 samples from Valencia), or in a larger previously published HVS-I database (123 samples from the region) (Barral-Arca et al., 2016). This absence might be an echo of the brutality of the decree of expulsion of *Moriscos* (Muslims forcibly converted to Christianity), which may have effectively erased the population carrying North African ancestry that lived in the region in the preceding centuries. They were replaced by settlers from regions further north with little North African ancestry (Bycroft et al., 2019). This is in sharp contrast with regions of the Crown of Castilla, where historical sources claim there was a better integration of the *Morisco* identity into the general population, and where no mass deportations were recorded: the frequency of U6 lineages is higher in the western part of Iberia, with a peak in the south-west (Figure 4.6b). This pattern is also visible at the genome-wide level (Bycroft et al., 2019).

This study emphasises the importance of immigration during the Islamic period, reaching territories in the hinterland. In contrast to Andalusia, the region of Valencia is not geographically close to the Maghreb, and was under Islamic rule for a much shorter time, but nonetheless developed strong links with the Arab–Berber world during the Islamic period (Coscollá Sanz, 2003; Ruggles, 2000, 2008). The Segorbe Giant's contemporary, individual MS075, is evidence of at least sporadic movement during Berber rule (Appendix C, Text S1).

The Segorbe Giant is a single, low-coverage sample and although the results cannot be extrapolated to the population as a whole, recently published results (Olalde et al., 2019) show a similar trend of admixture in Islamic Spain. More individuals and sites should be studied, in addition to a detailed comparison with present-day North African populations, in order to explore the population dynamics during the Islamic period in more detail and assess potential fine differences between geographical regions and periods of occupation.

Nonetheless, this pilot study provided an important opportunity to delineate a strategy for the genomic analysis of a larger dataset for which preliminary results are presented in the next chapter. Additionally, the mtDNA sequence of Casal dos Bucículos is to my knowledge the first aDNA retrieved from the Medieval period in Portugal.

Chapter V

Transition to Metal Ages in Iberia: preliminary results

Transition to Metal Ages in Iberia: preliminary results

1. Introduction

The Iberian Peninsula lies in the southwest extreme of continental Europe. Together with the Italian and Balkan peninsulas (and to some extent, the Carpathians), Iberia acted as a refuge for many plant and animal species, including humans, during the LGM, due to its milder climatic conditions compared to the harsh environment in the north (Gómez and Lunt, 2007; Taberlet et al., 1998; Tallavaara et al., 2015). Despite its peripheral location within Europe, Iberia connects the Mediterranean and the Atlantic worlds, and also provides a bridge to North Africa (as explored in Chapter IV), which has allowed contacts with other populations throughout time.

The phenomenon of megalithism, with an origin in the second half of the fifth millennium BCE, proliferated along coastal areas of Atlantic Europe, from Portugal and northern Spain, to the British Isles and Scandinavia, and also in the Mediterranean region, including eastern and southern Spain (Schulz Paulsson, 2019). This consisted of the construction of dolmens and passage graves, stone circles, standing stones, and other megalithic monuments. Far-flung regions shared similar geometric motifs carved in stone and architectonic features, showing a certain degree of connectivity across distant locations (Cleary and Gibson, 2019; Schulz Paulsson, 2019), also visible in the genetic make-up of Neolithic groups of European Atlantic façade (Brace et al., 2019; Cassidy et al., 2016; Sánchez-Quinto et al., 2019).

In the Chalcolithic the Bell Beaker culture emerged in western and central Europe, with a probable origin in the western façade of Iberia, most likely in Portuguese Estremadura, ~2800 BCE (more details in Chapter I, section 1.3). Although the Beaker culture was widespread across vast regions of Europe, the initial Iberian phase lacked several elements from what is considered the full Beaker "package", especially concerning burial practices, which showed a degree of continuity of some megalithic traditions (Cleary and Gibson, 2019). For example the practice of individual inhumations only became widespread in Iberia in the second half of the third millennium BCE (Cleary and Gibson, 2019; Müller and van Willigen, 2001), when genetic evidence support the arrival of Steppe-related ancestry (possibly from

Central Europe) to the peninsula (Olalde et al., 2019), coinciding with a period of strong environmental changes (Mejías Moreno et al., 2014; Perry and Hsu, 2000).

In the second half of the third millennium BCE the Iberian Bronze Age seems to have emerged on the Mediterranean coast of Spain, with the development of the Argaric (or El Argar) culture in southwest Spain (Murillo-Barroso and Montero-Ruiz, 2012). The Bronze Age period is marked by a series of social transformations, such as a further increase in the importance of individuality, and the establishment of elites (Arteaga, 1992), but the long-distant interactions between western Iberia and the British Isles seem to have persisted, and even perhaps intensified, during this period (Cleary and Gibson, 2019; Gibson, 2013).

Early studies of modern Iberian populations, based on frequencies of blood groups, enzymes and proteins, showed large genetic differences between Basque and non-Basque populations (in addition to genetic differentiation of the Pyrenees region), and a dualism between the Atlantic and Mediterranean fringes (Bertranpetit and Cavalli-Sforza, 1991). Subsequent studies using different markers have continued to support the genetic uniqueness of the Basque populations (Behar et al., 2012b; Busby et al., 2015; Rodríguez-Ezpeleta et al., 2010; Young et al., 2011), and have detected the presence of genetic clusters tracing back to the end of the Medieval period (Bycroft et al., 2019). This Atlantic/Mediterranean polarity was also visible in the linguistics of the peninsula, with Celtic (Indo-European) languages spoken in the Atlantic western and northern regions in the first millennium BCE, in contrast to the Mediterranean and Pyrenees regions, where non-Indo-European languages, from which Basque is the only surviving today, prevailed for longer, as evidenced by toponymy (Figure 5.1).

Figure 5.1. Areas of Celtic and non-Indo-European (IE) toponyms in Iberia. Figure from Koch, 2016.

In order to explore the interactions of the Atlantic and Mediterranean regions of the peninsula, I targeted Neolithic, Chalcolithic and Bronze Age archaeological sites from Portugal and eastern and southern Spain for DNA analysis. In this chapter I present preliminary analyses on this dataset.

2. Methods

2.1. Sampling and archaeological background

I had access to skeletal samples from eleven different archaeological sites in Portugal and Spain (Figure 5.2), which are broadly classified as (Late) Neolithic/Chalcolithic/Bronze Age.

Three of the Portuguese sites (Bolores, Cabeço da Arruda I, and Paimogo I) are located in the region of Estremadura (Lisbon peninsula), a region very rich in Chalcolithic sites and considered as the most probable origin for the Bell Beaker culture (Cleary and Gibson, 2019). Additionally, I targeted individuals from the site of Perdigões and Monte do Carrascal 2, both in Alentejo, south Portugal, and from the site of Covão d'Almeida in Coimbra, central Portugal. These samples were either collected by myself in July 2016 from museum and/or university collections, or sent directly by the archaeologists involved in the excavations.

Figure 5.2. Location of archaeological sites sampled in this chapter. Samples were either genotyped with 1240k SNP-capture (circles) or whole-genome shotgun sequencing (WGS) (squares).

Additionally, I had access to samples from five sites in south and east Spain: Pla de Rambla, Cova del Diablets, Costa Lloguera and Cova L'Iguala, all in the province of Castellon (region of Valencia), and Arroyo Saladillo, in Malaga. The Spanish samples were collected by Gonzalo Oteo-Garcia, a fellow PhD student in the Archaeogenetics Research Group. The required permissions to access the samples were obtained with the approval of the museums involved, the Servei de Cultura i Esport de Castello, the Direccio General de Cultura i Patrimoni, the Conselleria de Educacio, Investigacio, Cultura i Esport de la Generalitat Valenciana.

Whenever possible I targeted the petrous portion of the temporal bone, since it has been shown to yield more and better preserved DNA (Gamba et al., 2014; Pinhasi et al., 2015). However, for the sites of Paimogo I, Costa Lloguera and Cova L'Iguala petrous were not available, and I analysed teeth instead. Calibrated (cal.) BCE dates reported below were converted using OxCal 4.3 (IntCal13 curve, 95.4% probability) (Bronk Ramsey, 2009; Reimer et al., 2013).

2.1.1. Archaeological sites in Portugal

2.1.1.1. Bolores

The site of Bolores, in Torres Vedras, is located in the Sizandro river valley, approximately 15 km from the Atlantic Ocean. The semi-artificial cave was used as a collective grave, and was composed of three chambers carved into the bedrock. The minimal postdepositional disturbance and the absence of gnawing evidence indicate the space was enclosed (Lillios et al., 2014). The use of ochre (both yellow and red) together with the placement of slabs ("pillow stones", carved into trapezoidal and triangular forms) and a variety of offerings made of ceramic, stone, bone and shells suggest the occurrence of ritual practices (Lillios, 2015; Lillios et al., 2014). The site was initially excavated in 1986 but the majority of the excavation process proceeded later, between 2007 and 2012 by Professor Katina Lillios from University of Iowa and her team (Lillios, 2015). The bones were kept in Museu Municipal Leonel Trindade, in Torres Vedras, who granted permission for sampling.

Bone fragments previously radiocarbon dated range from 2920–2679 cal. BCE (4240±40 BP, Beta-249032) to 2831–2356 cal. BCE (4000±40 BP, Beta-256325) (Lillios et al., 2010, 2014). I processed 16 petrous bones from Bolores.

2.1.1.2. Cabeço da Arruda I

Cabeço da Arruda is also situated in Torres Vedras. The site is composed of two collective monuments (Cabeço da Arruda I and II) and one individual grave (Cabeço da Arruda III). Minimum number of individuals (MNI) in Cabeço da Arruda I is 19 (Silva, 2002), which is very low compared to other sites from the same period in the region (*e.g.* Paimogo, and Bolores) and with the other monument in the same site, Cabeço da Arruda II (MNI: 74) (Silva, 2002). This abnormally low MNI is believed to be a result of the poor preservation of the site, which had been damaged prior to its discovery and initial excavation in the 1930s. Previous radiocarbon dating from two bones excavated in Cabeço da Arruda I place the site at 3002–2635 cal. BCE (4240±50 BP, Beta-132975) and 3331–2885 cal. BCE (4370±70 BP, Beta-123363).

I sampled petrous from five individuals found in Cabeço da Arruda I. The samples were stored in the University of Coimbra (Portugal) and were provided by Professor Ana Maria Silva.

2.1.1.3. Paimogo I

The *tholos* (vaulted chamber grave) of Paimogo I, excavated in the 1970s and 1980s, is located ~65 km north of Lisbon, in Casal de Pai Mogo, Lourinhã. It is mainly contemporary to Bolores, but located 23 km away and two river valleys to the north, and much closer to the Atlantic Ocean (only ~1 km from the coast). The monument contains one elliptic chamber and one corridor. Inside the chamber there was a large horizontal stone (1.5m x 0.5m) on top of two smaller stones, interpreted by archaeologists as being a stool or an altar. There is some evidence for the use of red ochre in the bones, but to a small extent (Silva, 2002).

Two human bones were previously radiocarbon dated to 3261–2574 cal. BCE (4250±90 BP, Sac-1556) and 2896–2486 cal. BCE (4130±90 BP, UBAR-539). Both the chamber and the corridor contained several human and animal bones, as well as funerary goods. The archaeological record was rich and diversified, with bone, flint and metal tools, and different types of pottery, including bell beakers. In total, the *tholos* of Paimogo I contained at least 413 individuals, based on counts of MNI (Silva, 2002). I sampled teeth belonging to three individuals, which were provided by Professor Ana Maria Silva (University of Coimbra).

2.1.1.4. Covão d’Almeida

The existence of caves in the region of Condeixa (Coimbra, central Portugal) harbouring human remains and archaeological artefacts has been known since the 1800s (Costa Simões, 1854). The presence of Cardial pottery around the village of Eira Pedrinha suggest that the area was occupied since the sixth or fifth millennium BCE (Vilaça, 2016). However, the site of Covão d'Almeida (Eira Pedrinha, Condeixa-a-Velha), a system of natural caves first excavated in 1945, were used as a later burial site (Vilaça, 1990), as confirmed by the ^{14}C dating of a human bone to the Late Neolithic: 3361–2938 cal. BCE (4480±60 BP, Beta-134363). In addition, some ceramic findings indicate the re-utilisation of the site during the Late Bronze Age, but possibly with a residential, rather than funerary, purpose (Vilaça, 1990).

Artefacts dating to the third millennium BCE include Bell Beaker vessels and a metal axe. Unfortunately, the site was vandalised between 1945 and 1986 (Vilaça, 1990). Nevertheless, although Covão d’Almeida was probably not a primary burial site, the bones seemed well-preserved, with no evidence of serious taphonomic alterations, apart from some fragmentation (Gama and Cunha, 2003). The MNI calculated was ~140 individuals (Gama and Cunha, 2003; Silva, 2002). I had access to petrous from 19 individuals from Covão d’Almeida, provided by Professor Ana Maria Silva (University of Coimbra).

2.1.1.5. Perdigões

The site of Perdigões is located ~2 km north-west of Reguengos de Monsaraz, district of Évora in the region of Alentejo (south Portugal). It extends for an area of 16 ha and has a very complex, almost geometrical structure composed of at least a dozen roughly concentric ditches and thousands of pits with a long period of construction and use (Márquez-Romero and Jiménez-Jáimez, 2013). Its construction probably started ~3400–3100 BCE, during the Middle Neolithic, and developed throughout the Chalcolithic until the third millennium BCE (Valera et al., 2014a). Archaeological evidence shows that Perdigões was integrated in a complex exchange network with other regions of Iberia and North Africa, with isotopic analysis revealing a considerable percentage of individuals from external origin (Valera, 2017).

I had access to six petrous samples from the Chalcolithic context, through an ongoing collaboration with Dr António Valera (University of Algarve and Era Arqueologia S.A.), one of the archaeologists responsible for the excavations in the site. Additionally, I tested two cremated petrous bones for DNA content. These displayed a beige/brownish colour, which has been demonstrated to result from fire temperatures in the interval of 100–300ºC (Ellingham et al., 2015; Gómez Bellard, 1996).

2.1.1.6. Monte do Carrascal 2

Monte do Carrascal 2, located in Ferreira do Alentejo (south Portugal), consists of a complex assemblage of funerary structures (at least two rock-cut tombs and up to 20 ditches) dating mostly to the Chalcolithic, although with some additional structures pointing to a much older utilisation for funerary purposes in Late Mesolithic (Valera et al., 2014b). I targeted four petrous bones from the Chalcolithic context for DNA extraction. The samples were provided by Dr António Valera.

2.1.2. Archaeological sites in Spain

2.1.2.1. Arroyo Saladillo

Arroyo Saladillo is a Late Neolithic settlement (fourth millennium BCE) located ~4 km west of Antequera (Málaga), in an area very rich in Neolithic and Chalcolithic megalithic sites, such as Menga and Viera (dolmens), or El Romeral (*tholos*) (García Sanjuán et al., 2016). The large settlement, estimated to cover an area of ~124 ha, was primarily a residential area, but also harbours evidence of burial practice, and is believed to have been the home of the people who built the nearby dolmens (Rodríguezi et al., 2014). I analysed one petrous found in this settlement.

2.1.2.2. Pla de Rambla

Pla de Rambla is a looted grave in the province of Castellon, thought to date to the Neolithic/Chalcolithic. Little is known about this site, as there is currently no published information. The remains of one individual were taken to the Museo Arqueológico de Vall de Uxó, where this sample was collected. Some rock beads, possibly part of a necklace or bracelet, were found together with the individual, which led to speculation that the remains belonged to a female. I analysed one petrous sample from this individual.

2.1.2.3. Cova del Diablets

Located on Serra d'Irta, in the northeast of Castellon province, Cova del Diablets is a natural cave, 460 m above sea level (Aguilella et al., 1999). The site dates to 2890-2627 cal. BCE, based on radiocarbon dating of human bones (4197±21 BP, MAMS-18650; 4141±21 BP, MAMS-18651; 4143±21 BP, MAMS-18652 (Aguilella et al., 2014a)), and harboured remains of four human individuals: three adults (one male, one female, and one of undetermined sex), and one female adolescent, ~14–17 years old (Aguilella et al., 2014b). I targeted one petrous for analysis.

2.1.2.4. Costa Lloguera

Costa Lloguera, a natural cave also located in Castellon and first excavated in the 1920s, dates to the early Chalcolithic (Soler Díaz, 2013). Some aDNA analysis has been attempted before, but targeting only the HVS–I of mtDNA (Gamba et al., 2008). I had access to one tooth from this site.

2.1.2.5. Cova L'Iguala

Cova L'Iguala is a natural cave situated in Alcudia de Veo, Castellon. It may be part of a larger system of galleries, although no evidence for additional caves has been found to date. The scarce archaeological materials recovered from the site seem typical of Bronze Age Valencia. Although the site has not been radiocarbon dated, the ceramic style is similar to what has been found in other sites in the region of Valencia dating to ~1,400–1,300 BCE (Olaria Puyoles, 1995). The bone assemblage seems to belong mostly to one single individual (probably female, 30-40 years old), except from one fragment of humerus, which belonged to a different individual, and four animal bone fragments (Olaria Puyoles, 1995). I sampled one molar tooth.

2.2. Ancient DNA lab protocol

I subjected the bones from Monte do Carrascal 2, as well as the two tested cremated petrous samples from Perdigões, to CT-scan analysis prior to sample processing, as requested by Dr António Valera. The CT-scans were carried out in the School of Computing and Engineering (University of Huddersfield), by Dr Katie Addinall and Dr Paul Bills.

I performed sample processing and DNA extraction as described in Chapter IV (section 2.2). I processed and extracted DNA from a total of 60 samples (55 petrous and five teeth). I later excluded the extracts of the two cremated petrous bones from Perdigões, as they showed no DNA concentration, in line with previous attempts at DNA extraction from cremated bones from archaeological contexts (Hansen et al., 2017).

I prepared USER-treated libraries for 34 extracts, following the protocol previously described (Chapter IV, section 2.2.3), which were initially sent to Macrogen for WGS on either a twelfth or a tenth of an Illumina HiSeq4000 lane, and sequenced for 100 cycles. I later sent three additional libraries (two USER-treated and one non-treated) from the five samples with the highest percentage of mapped reads for sequencing in order to increase coverage (individuals MS033, MS036, MS037 and MS045, from Covão d'Almeida, and MS051, from Monte do Carrascal 2) – each library occupying a sixth of an Illumina HiSeq4000 lane (100 cycles).

I sent the remaining 24 extracts to Prof David Reich's Lab at the Harvard Medical School for 1240k SNP capture, where double-indexed (Kircher et al., 2012) double-stranded captured libraries were prepared and sequenced. The DNA was subjected to partial UDG-treatment, which eliminates uracil residues generated by cytosine deamination within the molecules, while keeping the damage signal in the terminal nucleotides for aDNA authentication purpose (Rohland et al., 2015). The Harvard lab enriched the libraries for human DNA with probes targeting 1,233,013 SNPs and the mitochondrial genome ("1240k SNP–capture") – for more details see the Supplementary Material of Olalde et al. (2019).

2.3. Bioinformatic analysis

2.3.1. Initial data processing and DNA authenticity

Information on sequenced libraries can be found in Appendix D, Table S1. I processed, merged and mapped raw paired-end reads resulting from WGS as previously described (Chapter IV, section 2.3.1). I performed data authenticity and contamination assessments

(Appendix D, Table S2), mapping quality control and genetic sex assignment (Appendix D, Figure S1; Tables S3 and S4) as explained in Chapter IV (section 2.3.2). In addition, I also estimated contamination in nuclear DNA with VerifyBamID v.1.1.3 (Jun et al., 2012).

USER-treated libraries sent as initial screening all displayed the expected C>T and G>A misincorporation pattern at low levels (~1-3% of reads) restricted to the initial 2-3 nucleotides (Appendix D, Figures S2-S4). For samples with multiple libraries, I merged all libraries with picard MERGESAM, similarly to what was done for the Segorbe Giant (Chapter IV). I further confirmed authenticity of aDNA for multiple library samples as follows:

- confirmation that all libraries from the same sample belong to the same individual, by means of kinship analysis with READ (see 2.3.4) (Appendix D, Figure S5).
- consistency in the sex assignment for all libraries from the same individual (Skoglund et al. (2013) (Appendix D, Table S4);
- consistency in the mtDNA haplogroup classification across all libraries from the same individual (Appendix D, Table S1);
- assessment of contamination levels on the mtDNA sequence of the non-USER-treated libraries using schmutzi (Renaud et al., 2015) (Appendix D, Table S2);
- estimation of contamination in the X-chromosome on individual libraries of males with ANGSD v.0.919 (Korneliussen et al., 2014) (Appendix D, Table S2);
- estimation of autosomal levels of contamination on individual libraries using VerifyBamID (Appendix D, Table 2).

In order to minimise the effect of post-mortem damage, I used the *--rescale* option in mapDamage to downscale base quality of positions likely affected by post-mortem C>T or G>A misincorporations (Jónsson et al., 2013).

2.3.2. 1240k SNP-capture data

I received SNP capture data for 10 individuals (out of a total of 24 sent) as BAM files. For consistency, I converted reads to FASTQ using SAMtools *bam2fq* (adapters had already been trimmed), remapped the reads to my version of the reference sequence (Hg19, and rCRS), rescaled the files using mapDamage, and treated the BAM files alongside the WGS data for all downstream analyses. Contamination and quality assessment were performed as described above (Appendix D, Table S2).

Post-mortem damage (~6.9-21.0%) was restricted to the terminal two nucleotides, as expected for partial USER-treatment (Rohland et al., 2015) (Appendix D, Figure S4). Schmutzi and ANGSD showed potential contamination for MS013 (although not detected with VerifyBamID) (Appendix D, Table S2), and the sample could not be confidently assigned to a genetic sex (Appendix D, Table S3), and thus this individual was excluded from the following analyses. MS010, from Cabeço da Arruda I is a duplicate of a previously published sample

(CabeçoArruda122A) (Martiniano et al., 2017), and was therefore also excluded from the dataset presented here. Six of these samples (MS002, MS009, MS011, MS014, MS015 and MS024) have been included in a recently published study of a temporal transect of Iberia, ranging from the Mesolithic to Medieval times (Olalde et al., 2019).

2.3.3. Uniparental markers

I classified mtDNA and Y-chromosome haplogroups as in Chapter IV (2.3.3). I checked alignments of mtDNA sequences with several missing and/or heteroplasmic positions manually on IGV.

2.3.4. Kinship analysis

I used READ (Relationship Estimation from Ancient DNA) (Monroy Kuhn et al., 2018) with the 1240k SNP dataset to determine genetic kinship amongst individuals (with >15,000 SNPs covered by at least one read) from the site of Covão d'Almeida (*n*=9), Bolores (*n*=3), Cabeço da Arruda I (*n*=4) and Paimogo (*n*=2). READ is optimized to deal with low-coverage (pseudo-)haploid data, and classifies pairs of individuals as unrelated, second-degree (*e.g.* grandparent-grandchild, half-siblings, or uncle/aunt-nephew/niece), first-degree (parent-offspring, siblings), or identical (in the case of identical twins, or the same individual).

2.3.5. Final dataset and SNP calling

I called pseudo-haploid SNPs on these individuals using the 1240k SNP list from Harvard (v37.2.1240K, https://reich.hms.harvard.edu/), as described in Chapter III, section 2.3.4. In addition to excluding relatives, only samples with more than 15,000 autosomal SNPs (Appendix D, Table S1), with low contamination estimates (Appendix D, Table S2), and confidently assigned to a genetic sex (Appendix D, Figure S1; Tables S3 and S4) were considered for analysis: 12 individuals from WGS, five of which resulted from merging multiple libraries (0.22–0.87x), and seven from 1240k SNP-capture (total of 19 samples).

2.3.6. Autosomal analysis

In an attempt to maximize both the number of SNPs and the number of individuals included in the analysis, and in order to curate the final dataset, I compiled different dataset combinations:

i) Only newly reported ancient Iberian samples and 798 individuals from Europe, Near East and Caucasus from Human Origins (~600k SNPs) (Appendix D, Table S5), as an initial sanity check on the newly produced data (Appendix D, Figure S7);

ii) Dataset i merged with previously published 180 ancient Iberian samples from Mesolithic to Bronze Age (including the recently published dataset from Olalde et al. (2019)), and 415 other ancient samples from Central Europe, British Isles and Mediterranean region, Yamnaya, eastern hunter-gatherers, Caucasus hunter-gatherers, Anatolian Neolithic, Natufians and other Levantine groups (Appendix D, Table S6);

iii) Only ancient samples from dataset ii (614 individuals), retaining a total of ~1240k SNPs (Appendix D, Table S6).

All published ancient samples were remapped to my reference (Hg19, and rCRS) and reanalysed in the same way as the newly generated data in order to prevent possible batch effects arising from different pipelines.

Datasets i and ii were used to compute a PCA of autosomal SNPs, using *smartpca* (EIGENSOFT v.7.2.1 (Patterson et al., 2006)), with the default setting for outlier removal, *shrinkmode: YES* and *lsqproject: YES*. I filtered dataset iii for positions on LD as before (Chapter IV, 2.3.4) and used the pruned dataset containing 521,527 SNPs to run ADMIXTURE v.1.3.0 (Alexander et al., 2009) (with parameters: *--cv* and *--seed time*) in supervised mode for *K*=3, using Mesolithic Spain, Natufian and Yamnaya as the three reference populations, as proxies for the three ancestral components usually found in European populations (Chapter I, section 3.4.1). I added Mbuti (v37.2.1240K, https://reich.hms.harvard.edu/) to dataset iii to serve as the outgroup population for outgroup-*f3* using *qp3Pop* (ADMIXTOOLS v.4.1 (Patterson et al., 2012)).

2.3.7. Functional SNPs and prediction of phenotypic traits

I studied loci with known phenotypic association in thirteen individuals: five resulting from multiple-library WGS and eight from 1240k SNP-capture. I organised a different dataset containing a list of positions covering the 41 SNPs included in the forensic database HIrisPlex-S (involved in hair, skin and eye pigmentation) (Chaitanya et al., 2018), positions on gene *MCM6* associated with lactase persistence in adulthood (Enattah et al., 2002), SNPs on *TLR1/TLR6/TLR10* and MHC (involved in immunity response), and on genes involved in vitamin D (*DHCL7/NADSYN1*) and fatty acids metabolism (*FADS*), using GATK Unified

Genotyper (--output_mode *EMIT_ALL_SITES*), considering only positions with quality >30 (-mbq 30).

I used HIrisPlex-S online tool (https://hirisplex.erasmusmc.nl) for phenotypic prediction, considering only variants with a minimum depth of position (DP) of two reads.

2.3.8. Metagenomics screening

I performed a preliminary metagenomics screening on the WGS USER-treated libraries sent as initial screening. I retrieved WGS-reads not mapped to Hg19 from mapped BAM files (SAMtools *view* -f4), converted to FASTQ (SAMtools *bam2fq*), filtered for minimum length of 32 bp, and subjected to a preliminary metagenomics analysis using One Codex (Minot et al., 2015), with default parameters. One Codex is a *k*-mer-based analysis: it identifies short sequences 17-31 bp long (*k*-mers) which are unique to specific taxa present in a given database. Based on the pool of *k*-mers found on a given read, that read is assigned to a specific taxon. The sample is then classified according to the proportion of reads assigned to different taxa. FASTQ files were compared against One Codex database (which comprises ~62,000 bacterial, ~48,400 viral, ~1800 fungal, ~2000 archaeal, and ~200 protozoan genomes). To visualise differences in amongst libraries, I computed a PCA based on the frequencies of families present in each library using the package *stats* v. 3.5.1 in R (The R Development Core Team, 2008).

3. Results and discussion

Although preliminary, the analysis of the present dataset allowed me to explore various aspects of genetic variation in Portugal and Spain during the Late Neolithic/Chalcolithic and Bronze Age, which will be presented and discussed in this section.

In the previous chapter, I used aDNA analysis to complement a series of archaeological and anthropological studies on Medieval individuals (*e.g*. by determining the genetic sex of unclassified remains). Here, I used genetic analysis to confirm that individuals MS065 (from Pla de Rambla) and MS068 (from Cova L'Iguala) are genetically female (Appendix D, Figure S1) – an example of how genetic analysis can provide useful insights into archaeological remains, for which no clear archaeological context is available, such as in the case of the individual from Pla de Rambla.

3.1. Kinship analysis

In addition to identifying molecular sex of human remains, aDNA can also be used to directly answer archaeological questions regarding individual remains by, for example, inferring kinship amongst individuals in a given site. Considering the high number of individuals targeted from Covão d'Almeida (*n*=19), it was my intention to assess potential familial relationships in this collective burial site, similarly to what has been done in various prehistoric contexts (Haak et al., 2008; Juras et al., 2017; Sánchez-Quinto et al., 2019; Scheib et al., 2019; Schroeder et al., 2019). However, from the 19 samples initially sent for sequencing, only eight individuals met the quality standards for autosomal analysis (>15,000 SNPs, and low contamination). From these, I identified only one pair of related individuals in this site (in addition to another kinship relation amongst two individuals from the site of Bolores).

3.1.1. Covão d'Almeida

I identified a possible first-degree kinship between two individuals (MS046 and MS049) from the site of Covão d'Almeida (Coimbra, Portugal) (Appendix D, Figure S6a), genetically classified as male and female, respectively (Appendix D, Figure S1). Considering that they do not share a mitochondrial lineage (MS046: U5b1e and MS049: K2b1a, Table 5.1), they evidently shared a father and daughter kinship, instead of being siblings or a mother–son duo. The mother, or any other potential maternally related individuals, are absent from the dataset, since no other individual harbours a K2b1a mtDNA haplotype. However, due to wide error estimates, a second-degree relationship between these two individuals cannot be disregarded. Only MS046, with a higher coverage, was included in the following population genetics analysis.

3.1.2. Bolores

Individuals MS002 and MS017 from the site of Bolores are second-degree relatives (Appendix D, Figure S6b). Both males carried a Y-chromosome I lineage, but did not share a mitochondrial haplotype (MS002: U5b2b and MS017: K1a2b) (Table 5.1), so I infer that these two individuals must be paternally related – half-brothers, grandfather–grandson or uncle–nephew. MS017 was excluded from the following autosomal population analysis.

3.2. Uniparental markers

All males belonged to haplogroup I, except for the individual from Cova del Diablets (MS066), who carried a G2 haplotype (Figure 5.3; Appendix D, Table S1), reflecting previous assessments of Iberian paternal variation in the Late Neolithic and Chalcolithic (Martiniano et al., 2017; Olalde et al., 2019; Valdiosera et al., 2018).

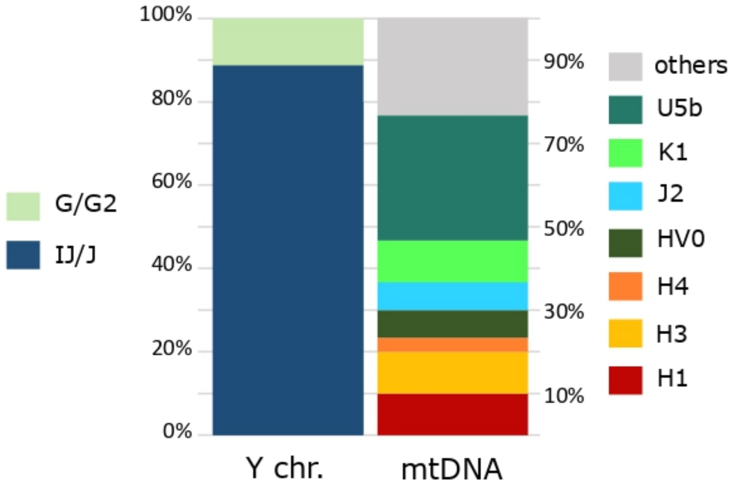

Figure 5.3. Y-chromosome (n=10) and mtDNA (n=29) frequencies amongst the Iberian Late Neolithic/Chalcolithic individuals studied in this chapter. Other mtDNA lineages present at lower frequencies and not individually represented in the plot are haplogroupsn J1, HV, R0, K2, V and X2.

On the other hand, the maternal gene pool shows more variation (Figure 5.3) (Szécsényi-Nagy et al., 2017), visible also intra-site, with the exception of Perdigões, although with only two individuals analysed (both carrying a U5b1 haplotype) (Table 5.1). The presence of U5b, a remnant from the Palaeolithic (Fu et al., 2016; Szécsényi-Nagy et al., 2017), at three Portuguese sites (Bolores, Covão d'Almeida and Perdigões), with an overall frequency of ~31% in the entire dataset, shows a significant level of continuity in the region, perhaps an effect of its role as a *refugium* during the LGM (Tallavaara et al., 2015), and evinces increased hunter–gatherer ancestry assimilated into Late Neolithic/Chalcolithic individuals reported at autosomal level (Martiniano et al., 2017; Valdiosera et al., 2018). In addition, various typically Early/Middle Neolithic lineages were also found amongst the reported individuals, such as different H lineages (H1, H3 and H4), K1, X2 and V (Brandt et al., 2013; Szécsényi-Nagy et al., 2017). Mitochondrial lineage T2, found in Portuguese Neolithic and Chalcolithic at frequencies of ~12.5% and ~7.7%, respectively (frequencies in Spain: ~11.3% and 8.9%, respectively) (Szécsényi-Nagy et al., 2017), is absent from this dataset.

The Bronze Age individual from Cova L'Iguala (MS068) carried an H3 haplotype (Table 5.1) (to my knowledge, the first H3 reported for this period in Iberia (Chapter III, Figure 3.10)), but a more refined classification is not possible. Unfortunately, it was not possible to recover a haplogroup assignment for MS063, the Neolithic individual from Arroyo Saladillo, dating to the fourth millennium BCE, the oldest individual in the present dataset.

Table 5.1. Mitochondrial variation in the archaeological sites studied in this chapter.

Country	Date	Site	DNA code	mtDNA haplogroup
Portugal	2900-2350 cal. BCE	Bolores	MS002	U5b2b
			MS017	K1a2b
			MS024	H4a1a
	3300-2600 cal. BCE	Cabeço da Arruda I	MS009	J2b1a2
			MS011	V+16298@
			MS012	J1c3
	3300-2500 cal. BCE	Paimogo I	MS014	K1a1
			MS015	HV0d
	Chalcolithic	Perdigões	MS027	U5b1
			MS029	U5b1
	3300-2900 cal. BCE	Covão d'Almeida	MS031	H3+73
			MS032	R0
			MS033	U5b1
			MS036	J2b1a
			MS037	H1e1c
			MS039	HV
			MS040	U5b1+16189+@16192
			MS041	HV0b
			MS042	U5b2
			MS043	H1e2
			MS045	U5b1e
			MS046	U5b1e
			MS047	U5b
			MS048	K1
			MS049	K2b1a
	Chalcolithic	Monte do Carrascal 2	MS050	R0
			MS051	X2b+226
Spain	Neolithic/Chalcolithic?	Pla de Rambla	MS065	H3
	2900-2600 cal. BCE	Cova del Diablets	MS066	H1q
	1400-1300 BCE	Cova L'Iguala	MS068	H3

3.3. Autosomal population analysis

All the newly sequenced individuals fall in the space occupied by other published ancient Iberians from the same period in a PCA (Figure 5.4a). MS046 (from Covão d'Almeida), although clustering with Late Neolithic/Chalcolithic Spanish individuals, appears to be an outlier in the PCA compared with other samples from the same site. The outgroup-*f3* statistics show that MS046 shares the highest drift with British Neolithic, in contrast to other individuals from Covão d'Almeida, who are closer to Iberian Late Neolithic/Chalcolithic (Appendix D, Figure S9; Table S18).

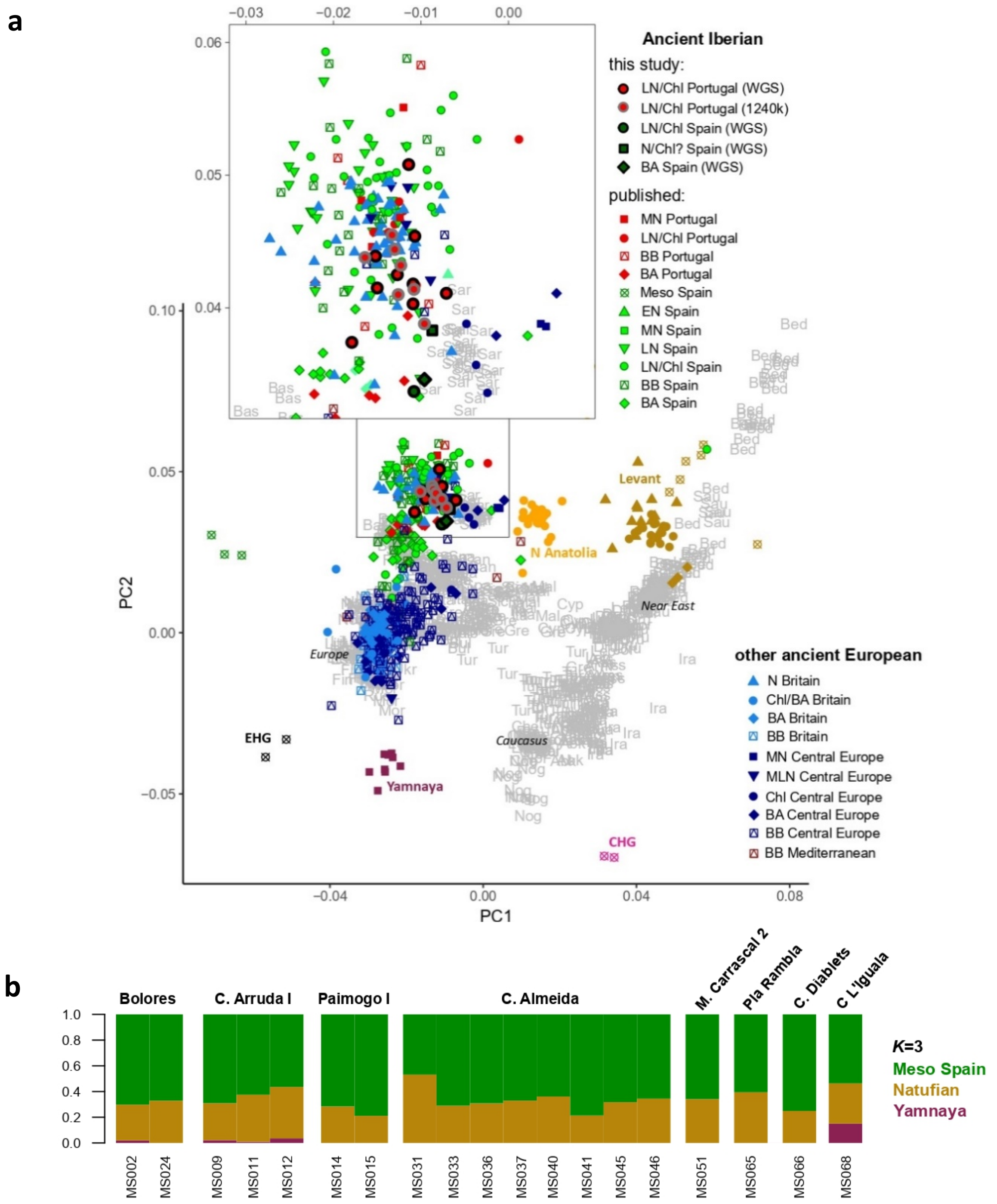

Figure 5.4. a) PCA of ancient individuals projected on modern individuals from Europe, the Near East and the Caucasus. Abbreviations: Meso – Mesolithic, (E/M/L)N – (Early/Middle/Late) Neolithic, Chl – Chalcolithic, BB – Bell Beaker, BA – Bronze Age, C/E/HG – Caucasus/Eastern hunter-gatherers. Squared area is zoomed in on top panel. **b)** Supervised ADMIXTURE (*K*=3) of newly sequences individuals, using Mesolithic Spain, Natufian and Yamnaya as reference populations, as proxies for WHG, Neolithic and Steppe components. Plot with all ancient samples included in the analysis is shown in Appendix D, Figure S8.

On the other hand, the individual from Cova L'Iguala (MS068), dating to the second millennium BCE, clusters at the edge of the space occupied by the newly reported samples, together with other Bronze Age individuals from Portugal and Spain, in agreement with a higher proportion of Steppe-like ancestry (represented by the Yamnaya in the analysis) seen in a supervised run of ADMIXTURE for $K=3$ (Figure 5.4b). However, D-statistics indicate that MS068 is significantly closer ($|Z|$-score>3) to Iberian Late Neolithic/Chalcolithic, Iberian Bronze Age and Central European Middle/Late Neolithic populations than to Central European Bronze Age and Beaker groups (Appendix D, Table S19), but with values close to zero. The test D(Mbuti, Cova L'Iguala; Iberia Bronze Age, Iberia Late Neolithic/Chalcolithic) produces a result very close to zero (-0.0007±0.0046), with a very low, non-significant, $|Z|$-score (0.158) (Appendix D, Table S19). Additional tests using the formulae (Mbuti, published population; Cova L'Iguala, other newly reported population) failed to produce significant results (Appendix D, Table S20), probably due to low coverage on this sample (0.03x).

MS066 (from Cova del Diablets), who appears to cluster together with MS068 in the PCA (Figure 5.4a), does not display any Steppe/Yamnaya-like component (Figure 5.4b). His position in the PCA is probably an artefact of low coverage (0.016x), which is also interfering with outgroup-*f3* results, with an overall low number of SNPs (<20,000) included in all comparisons, especially in the comparison with MS068 (<600 SNPs and the lowest Z-score), to whom MS066 appears to be artificially close (Figure 5.5; Appendix D, Table S13). In fact, the low coverage of the three Spanish samples, in addition to being the only representatives for each of the three sites (Pla de Rambla, Cova del Diablets and Cova L'Iguala), results in a low number of SNPs available for the tests, low Z-scores and high standard errors (Appendix D, Tables S12-S14). However, excluding the artificial proximity between MS066 and MS068 discussed above, these three samples share the highest drift with Iberian Middle/Late Neolithic and Chalcolithic and British Neolithic, with overlapping confidence intervals (Figure 5.6; Appendix D, Tables S12-S14), in line with the results for the individuals from Portuguese sites reported here.

Overall, the Late Neolithic/Chalcolithic samples lack Steppe/Yamnaya-like component, in agreement with what has been shown for other contemporary Iberian individuals (Martiniano et al., 2017; Olalde et al., 2018; Valdiosera et al., 2018), except for MS002 (Bolores) and MS009 and MS012 (Cabeço da Arruda I), from Portugal, who seem to display this component at very low levels in a supervised run of ADMIXTURE (Figure 5.4b). Nevertheless, these individuals seem to share the highest drift with British Neolithic and Iberia Late Neolithic/Chalcolithic, similarly to the other individuals from the same sites without Steppe component (Appendix D, Figure S15 and S16).

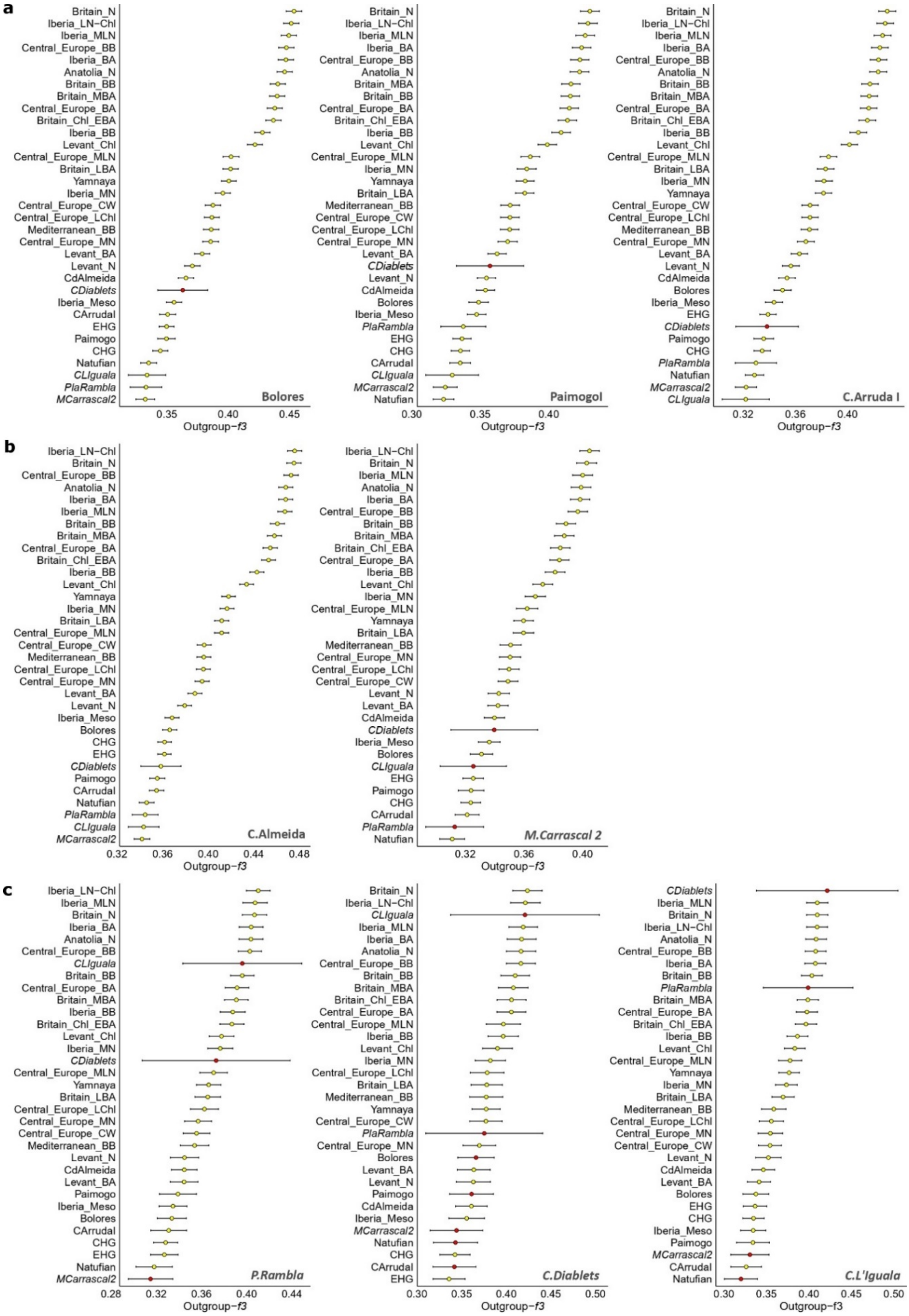

Figure 5.5. Outgroup-*f3* in the form (newly published Iberian, X, Mbuti): **a)** 1240k SNP-capture, **b)** WGS from Portugal, **c)** WGS from Spain. Populations in italics are represented by one single sample, points in red denote comparisons with <10,000 SNPs. Error bars correspond to 2 standard errors. Detailed output tables in Appendix D, Tables S7-S14. Outgroup-*f3* for each individual sample from Bolores, Paimogo I, Cabeço da Arruda I and Covão d'Almeida in Appendix D, Tables S15-18. Abbreviations as in Figure 5.4.

D-statistics comparison of different distal (CHG, Yamnaya, Natufian and Anatolia Neolithic) and proximal (Iberian, British and Central European Late Neolithic/Chalcolithic, Beaker and Bronze Age groups) populations with one individual displaying Steppe component (MS002, from Bolores, and MS009 and MS012, from Cabeço da Arruda I) and another individual from the same site without this component (MS024 and MS011, respectively) generate results very close to zero, and always non-significant (|Z|-score<3) (Appendix D, Table S21). Moreover, the two males (MS002 and MS009) carry a haplogroup I Y-chromosome lineage (Appendix D, Table S1), rather than haplogroup R1b, which typically accompanies the Steppe component in Iberia after the second half of the third millennium BCE (Olalde et al., 2019). Altogether, the minimal fraction of Steppe component observed in these individuals seems to be an artefact in the ADMIXTURE analysis. Although Bolores, Paimogo I and Cabeço da Arruda I share the highest drift with the British Neolithic, followed by the Iberian Late Neolithic/Chalcolithic, the opposite trend is seen for Covão d'Almeida and Monte do Carrascal 2. However, once again the confidence intervals are overlapping and therefore no significant differences are observed in the proximity of any of these groups to either British Neolithic or Iberian Late Neolithic/Chalcolithic individuals, in line with previous evidence of genetic proximity between Iberia and the British Isles in Neolithic and Chalcolithic times (Brace et al., 2019; Cassidy et al., 2016; Sánchez-Quinto et al., 2019).

3.4. Phenotypic traits in Late Neolithic/Chalcolithic Portugal

Although coverage is in most cases too low to determine heterozygosity, these data allow us to identify the presence of derived alleles at certain positions and detect phenotypic variability in Late Neolithic/Chalcolithic Portugal (Tables 5.3 and 5.4; Appendix D, Table S22). Please note that the interpretation of the following results demands caution due to very low coverage hampering the detection of heterozygous positions.

3.4.1. HIrisPlex-S

Variants strongly connected with light skin pigmentation in European populations are found on genes *SLC45A2*/*MATP* (rs16891982) and *SLC24A5* (rs1426654). The derived allele of rs16891982 (C) is present in four individuals (MS002, MS015, MS024 and MS051, although covered by only one read in the last two), whereas MS033 and MS036 display the ancestral state (G), but covered by only one single read. The derived allele has been found in Neolithic and Chalcolithic Iberian populations, although at frequencies much lower than nowadays (Olalde et al., 2019). The derived allele of rs1426654 is virtually fixed in modern-day European populations, and seems to have reached similar frequencies in Iberia in the Bronze

Age (Olalde et al., 2019). MS033 is heterozygous for this locus (three reads), and is the only sample in the studied dataset showing the presence of the G (ancestral) allele.

Information on rs28777 (also in *SLC45A2*) was retrieved from only one individual (MS017) carrying the ancestral (C) allele (DP=1x), which has an overall European frequency of 3% in the 1KGP dataset, but is found in IBS population at 13% (Hunt et al., 2018; The 1000 Genomes Project Consortium, 2015). This SNP is also associated with hair colour, skin pigmentation and tanning ability (Han et al., 2008).

MS017 is the only individual with derived T in position rs1220359, located in an intronic region of gene *IRF4*. This variant has been linked to slightly lighter hair and eye colour, and lower tanning in Europeans, as well as the presence of freckles (Eriksson et al., 2010; Han et al., 2008), and is present at ~13% in the IBS population (Hunt et al., 2018; The 1000 Genomes Project Consortium, 2015).

MS033 seems homozygous (although with a low number of reads covering the position, DP=3x) for the derived allele at rs1393350 (*TYR*) and rs12896399 (15.5 kb upstream of *SLC24A4)*, both linked to blue eyes (Sulem et al., 2007), and in the case of the latter also to lighter hair (Han et al., 2008).

OCA2 encodes the P protein, involved in the transport of tyrosine, a precursor of melanin. *HERC2*, located ~20 kb upstream of *OCA2* promotor, has a regulatory function upon *OCA2* expression within iris melanocytes, and is strongly associated with iris pigmentation (Han et al., 2008). All individuals with reads covering rs12913832 (*HERC2*) (MS002, MS009, MS012, MS017, MS024 and MS033), which is also involved in skin pigmentation and propensity to tan (Han et al., 2008), displayed the ancestral and dominant allele (A). The presence of the ancestral allele in rs12913832 results in a brown eye phenotype (Sturm et al., 2008; Visser et al., 2012). Although the derived form seems to have been fixed in Mesolithic Europe, its frequency dropped by half in Central European early farmers, and to lower than a quarter amongst Iberian Neolithic and Chalcolithic individuals (Mathieson et al., 2015).

Mutations in *MCR1* are known for their association with red hair and a fair skin complexion, as well being an increased risk factor for different types of skin cancer (Binstock et al., 2014; Valverde et al., 1995, 1996). SNPs on this gene are only present in the ancestral form amongst the reported individuals.

Only sites covered by at least two reads were considered for phenotype prediction with HIrisPlex-S. Since the majority of the individuals did not have coverage on most of the positions (or were covered by only one read), prediction was only possible for four samples: MS002, MS017, MS024 (from Bolores) and MS033 (from Covão d'Almeida) (Table 5.2).

There are stark differences in the phenotypes from Bolores and Covão d'Almeida. Individuals MS002 and MS024 from Bolores seem to have had brown eyes and black hair, although with probability values <0.8 for hair colour (no data for MS017 from Paimogo I in these traits). However, there is high variability in skin pigmentation amongst these three individuals: dark to black (MS002), intermediate to pale (MS017, albeit with AUC loss >0.1) and intermediate to dark (MS024). On the other hand, HIrisPlex-S calculations predict blue eyes (despite the presence of the dominant allele in rs12913832 (Appendix D, Table S22)), light shaded hair (but no hair colour) and intermediate skin colour for MS033, from Covão d'Almeida, with high probability values (>85%) for all indicators, and AUC loss <0.1 for all predicted traits.

Table 5.2. HIrisPlex-S probabilities for individuals MS002, MS017, MS024 and MS033.

Phenotypic trait		p-value (AUC loss)			
		MS002	**MS017**	**MS024**	**MS033**
Eye colour	blue	0 (0.012)	0 (0.409)	0 (0.018)	0.968 (0.005)
	intermediate	0.003 (0.033)	0 (0.206)	0.003 (0.046)	0.024 (0.019)
	brown	0.997 (0.008)	0 (0.402)	0.997 (0.014)	0.008 (0.009)
Hair colour	blond	0.006 (0.069)	0 (0.18)	0.006 (0.07)	0 (0.057)
	brown	0.33 (0.053)	0 (0.107)	0.368 (0.054)	0 (0.054)
	red	0 (0.035)	0 (0.163)	0 (0.014)	0 (0.245)
	black	0.664 (0.015)	0 (0.274)	0.626 (0.018)	0 (0.044)
Hair shade	light	0.01 (0.034)	0 (0.266)	0.012 (0.037)	0.956 (0.034)
	dark	0.99 (0.034)	0 (0.266)	0.988 (0.037)	0.044 (0.034)
Skin colour	very pale	0 (0.075)	0.111 (0.059)	0.002 (0.079)	0 (0.049)
	pale	0 (0.046)	0.639 (0.085)	0.01 (0.058)	0 (0.058)
	intermediate	0 (0.059)	0.248 (0.131)	0.256 (0.082)	0.857 (0.058)
	dark	0.01 (0.05)	0.002 (0.19)	0.516 (0.041)	0.14 (0.047)
	dark to black	0.99 (0.006)	0 (0.061)	0.217 (0.005)	0.003 (0.003)

3.4.2. Diet and immunity

The enzyme lactase-phlorizin hydrolase, essential for milk digestion, is encoded by *LCT*, located on chromosome 2. *MCM6*, upstream of *LCT*, has regulatory function upon *LCT* (Enattah et al., 2002), and therefore several *MCM6* variants resulting in lactase persistence have been identified. Two variants are associated with lactase persistence in European populations: rs4988235 and rs182549 (Bersaglieri et al., 2004; Enattah et al., 2002). Despite the low coverage, both variants display the ancestral allele in all individuals that have these positions covered (although in some cases only by one read) (Table 5.3). This is in agreement with what is expected for Late Neolithic/Chalcolithic European individuals (Burger et al., 2007), since lactase persistence was most likely introduced to Europe only in the last 4.0 ka from a putative Steppe source (Allentoft et al., 2015), and is first detected in Iberia only in historical times (Olalde et al., 2019). Three additional variants (rs41525747, rs41380347 and rs145946881), connected with lactase persistence in the Near East and sub-Saharan Africa (Enattah et al., 2008; Ingram et al., 2007; Tishkoff et al., 2007), also display the ancestral state (Table 5.3) (again covered by only one or two reads), as expected.

Table 5.3. Genotype and depth of position (DP) of SNPs associated to lactase persistence in *MCM6* gene. Individuals MS012 and MS024 did not have any of these positions covered, and thus are not included in this table. Alleles according to genomic reference sequence (in forward strand).

SNP	SNP-capture						Multiple-library WGS				
	MS002	**MS009**	**MS011**	**MS014**	**MS015**	**MS017**	**MS033**	**MS036**	**MS037**	**MS045**	**MS051**
rs41525747	G/G (3)	G/G (3)	G/- (1)	-	G/- (1)	G/G (3)	-	-	-	-	G/G (2)
rs4988235	G/G (2)	G/G (3)	G/- (1)	-	G/- (1)	G/G (3)	G/- (1)	-	-	-	G/- (1)
rs41380347	A/A (2)	A/A (3)	-	-	A/- (1)	A/A (3)	A/- (1)	-	-	-	A/- (1)
rs145946881	-	-	-	-	-	-	-	-	C/1 (1)	C/C (2)	-
rs182549	C/- (1)	-	-	C/- (1)	-	-	C/- (1)	C/- (1)	C/C (2)	-	-

Table 5.4. Genotype and depth of position (DP) of SNPs associated to genes involved in immunity (*TLR10-TLR1-TLR6* cluster and MHC complex), and in vitamin D (*DHCR7/NADSYN1*) and fatty acid (*FADS1*) metabolism. Individuals MS014, MS017, MS036 and MS045 did not have any of these positions covered, and thus are not included in this table. Alleles according to genomic reference sequence (in forward strand).

SNP	Genes	SNP-capture						Multiple-library WGS		
		MS002	**MS009**	**MS011**	**MS012**	**MS015**	**MS024**	**MS033**	**MS037**	**MS051**
rs4833103	*TLR10-TLR1-TLR6*	-	-	-	-	-	C/- (1)	C/C (2)	-	-
rs2269424	MHC	G/- (1)	-	-	-	G/- (1)	-	-	G/- (1)	A/A (2)
rs174546	*FADS1*	-	C/- (1)	C/- (1)	-	-	-	C/C (4)	-	-
rs7944926	*DHCR7/NADSYN1*	A/- (1)	-	-	-	-	-	-	-	A/- (1)
rs7940244	*DHCR7/NADSYN1*	T/C (3)	C/C (4)	-	T/- (1)	-	C/C (2)	C/C (3)	C/- (1)	-

Other genes possibly related to diet and under recent selection in European populations are *DHCR7/NADSYN1* and *FADS1*, involved in vitamin D and fatty acid metabolism, respectively (Mathieson et al., 2015). *DHCR7* mutations are linked to higher vitamin D levels (Kuan et al., 2013), an important selective trait for survival at higher latitudes that seems to have emerged earlier than reduced skin pigmentation in European groups (Hanel and Carlberg, 2019; Kuan et al., 2013; Mathieson et al., 2015). MS009, MS024 and MS033 (from Cabeço da Arruda I, Bolores and Covão d'Almeida) are homozygous for the ancestral allele of rs7940244 (in addition to MS037, with one read covering the position). However, the derived T is present in two other individuals – MS002 (from Bolores, possibly heterozygous) and MS012 (from Cabeço da Arruda I, one single read). The derived allele was inferred to be present at frequencies close to 50% in Mesolithic hunter-gatherers and Neolithic Europeans (Günther et al., 2018; Mathieson et al., 2015), while it shows an average frequency of 76% in modern European populations (Hunt et al., 2018; The 1000 Genomes Project Consortium, 2015). MS002 and MS051 harbour the derived A in rs7944926 (although only covered by one read), the most common amongst early European farmers (Mathieson et al., 2015).

MS033 seems to be homozygous (DP=4x) for the derived allele of rs174546 (*FADS1*), which is associated with lower triglyceride levels (Bokor et al., 2010), and seems to have emerged in the Neolithic, probably associated to changes in diet resulting from the shift to agriculture (Martiniano et al., 2017; Mathieson and Mathieson, 2018). The derived allele (C) is present at highest frequencies in present-day European (~65%) and South Asian (~86%) 1KGP populations (Hunt et al., 2018; The 1000 Genomes Project Consortium, 2015). Two additional individuals from Cabeço da Arruda I (MS009 and MS011) also present the derived allele, although covered only once.

The presence of both derived and ancestral variation in several immunity-related loci has been reported in a Mesolithic Iberian sample (Olalde et al., 2014), suggesting that pre-Neolithic selective constraints also shaped immunity response in Europeans. Two SNPs involved in immunity were investigated here: rs4833103 and rs2269424.

Locus rs4833103, in the *TLR10-TLR1-TLR6* cluster (chromosome 4), is under selection in Europe, possibly linked to resistance to mycobacterial diseases, such as leprosy or tuberculosis (Johnson et al., 2007; Ma et al., 2007; Wong et al., 2010). The derived allele (A) is present at ~50% in present-day European populations from 1KGP (Hunt et al., 2018; The 1000 Genomes Project Consortium, 2015), but it seems to be absent from the present dataset (although with information for only two individuals: MS024 and MS033), in agreement with previous reports of low frequency (~5%) in Neolithic and Chalcolithic Europe (Mathieson et al., 2015).

SNP rs2269424, in the major histocompatibility complex (MHC), on chromosome 6, display a strong signal of selection (Mathieson et al., 2015). The only individual with more than one read for rs2269424 (MS051) seems to be homozygous for the derived allele (A), whereas MS002, MS015 and MS037 display one read each, all with the ancestral form. The derived A was much more frequent in Mesolithic and Neolithic European groups (~80%) than in nowadays European populations (~26%) (Hunt et al., 2018; Mathieson et al., 2015; The 1000 Genomes Project Consortium, 2015), and has also been found in heterozygosity in two individuals from central Zagros (Iran) dating to the early Neolithic (Broushaki et al., 2016).

3.5. Metagenomics screening

In order to test a pipeline to identify possible pathogens, and in an attempt to categorise the biodiversity contained on each library, I performed a basic metagenomics screening. Modifications to the soil (*e.g.* agriculture) as well as environmental factors (pH, humidity, temperature, etc.) are known to impact soil microbial diversity, and microbial influence on cadaver decomposition (Hyde et al., 2015; Roesch et al., 2007). A metagenomics screening shows that all libraries analysed here display taxa commonly found in soil and involved in organic decomposition (Figure 5.6) (Pechal et al., 2014).

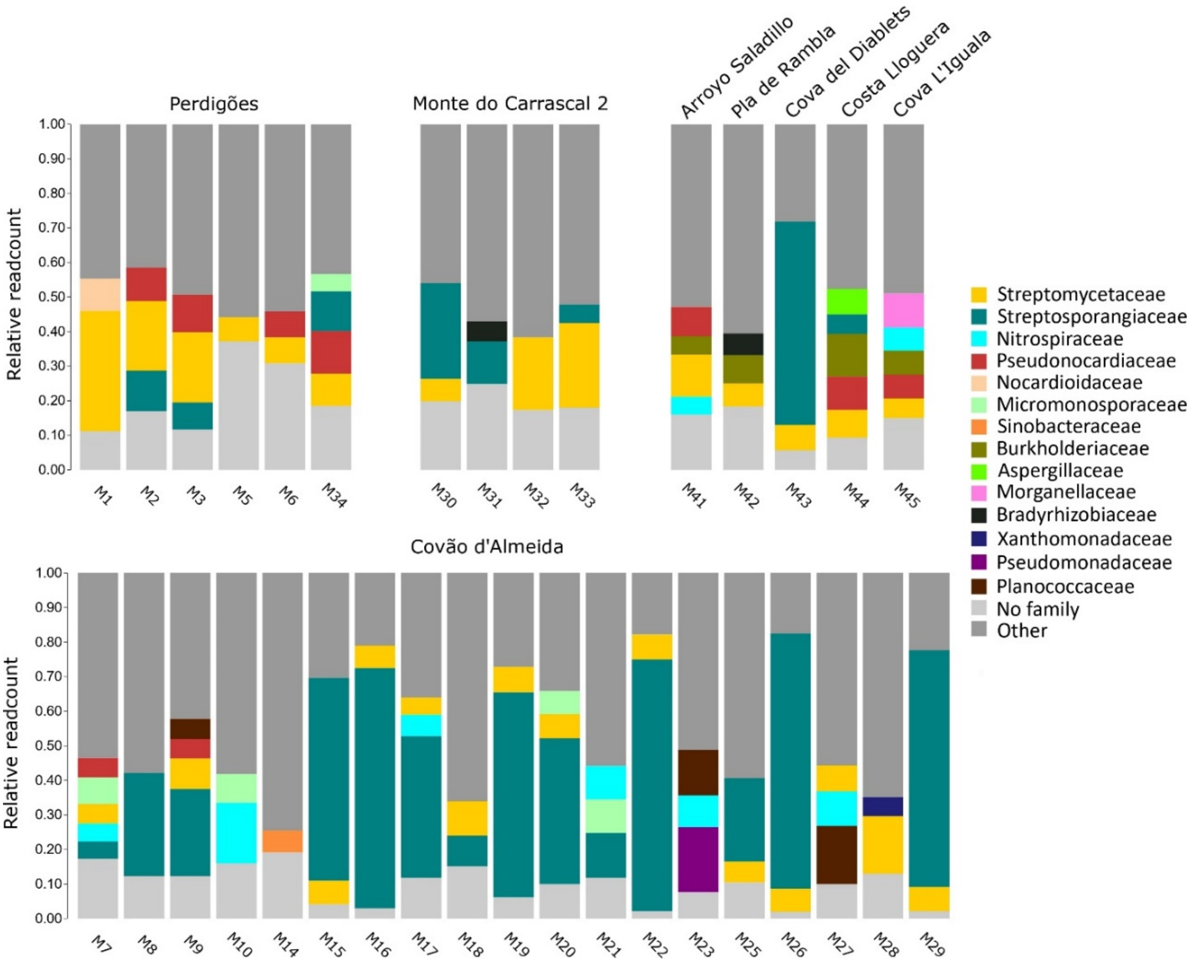

Figure 5.6. Relative read count of microorganisms (family-level) present at >5% on each WGS library.

The most represented phylum amongst the studied libraries is Actinobacteria, with at least one of the following families found at >5% in all samples apart from M14 and M23 (both from Covão d'Almeida): Streptosporangiaceae, Streptomycetaceae, Pseudonocardiaceae, Micromonosporaceae and Nocardioidaceae. There is a higher prevalence of Streptosporangiaceae in the samples from Covão d'Almeida (although with some heterogeneity, as seen in Figures 5.6), whereas extracts from samples from Perdigões show a higher proportion of Streptomycetaceae and tend to cluster closer together in the PCA (Appendix D, Figure S10). Monte do Carrascal 2 seems heterogeneous, however, sample size is low (*n*=4).

Proteobacteria were more restricted: Gammaproteobacteria (Sinobacteraceae, Pseudomonadaceae and Xanthomonadaceae) were occasionally detected above the established 5% threshold in libraries from Covão d'Almeida, whereas Burkholderiaceae (a class of Betaproteobacteria) were found in four (out of five) Spanish sites. Nitrospiraceae, involved in nitrogen cycle (Watson et al., 1986), was also commonly found in libraries from Covão d'Almeida and in two Spanish sites (Arroyo Saladillo and Cova L'Iguala). Other taxa found at considerable proportions were Planococcaceae (present in three libraries from Covão d'Almeida), Morganellaceae (in Cova L'Iguala), and Aspergillaceae, a fungal family, (in Costa Lloguera).

Although no pathogens were identified with this preliminary screening, this type of metagenomics approach can be used as an initial step to identify, for example, the presence of *Yersinia pestis*, the etiological agent of plague, which was found across Europe in the third millennium BCE (Andrades Valtueña et al., 2017; Rasmussen et al., 2015b; Spyrou et al., 2018), and possibly played an important role in the archaeological transitions of this period (Rasmussen et al., 2015b).

Chapter VI

Final remarks

Content from section 2 of this chapter was published in:

Silva M, et al. On Methodological issues in the Indo-European debate By Michel Danino. Journal of Biosciences 2019, 44, 69. DOI:10.1007/s12038-019-9890-6.

My contributions to this paper were as follows:

- Co-writing of first draft and revising drafts.

Final remarks

1. Sampling strategy

There was an authentic revolution in the field of aDNA in the last years. I started my PhD project in September 2015, just a few months after the publication of Haak et al. (2015) and Allentoft et al. (2015), both directly showing by means of aDNA the presence of Steppe-related ancestry (possibly connected with the Yamnaya) across Eurasia. Many of the key archaeological questions concerning population dynamics at the end of the Neolithic and at the onset of Copper and Bronze Ages were addressed in the following months, with an ever-increasing rate of aDNA studies published, accompanied by a dramatic increase in the number of samples and coverage achieved on each new study (Reich, 2018), as summarised by Heyd (2017). Several recent publications addressed the main archaeological questions and/or focussed on key geographical areas concerning the purpose of my PhD project – *e.g.* studies of mtDNA variation through time in Iberia (Szécsényi-Nagy et al., 2017), genome-wide analysis of Late Neolithic/Chalcolithic and Bronze Age Iberia (Martiniano et al., 2017; Valdiosera et al., 2018), the genetic origins and spread of the Bell Beaker culture in Iberia and western Europe (Olalde et al., 2018), the Islamic period in Spain (Olalde et al., 2019), and the recent studies on Central and South Asian prehistory (de Barros Damgaard et al., 2018a; Narasimhan et al., 2019; Shinde et al., 2019).

Regarding the study of Iberia, Portugal is still underrepresented in the literature. Only four studies include ancient Portuguese genomic data (González-Fortes et al., 2019; Martiniano et al., 2017; Olalde et al., 2018, 2019), representing a total of 37 individuals (six of which were collected, processed and extracted by me during the course of the PhD, and generated as part of our collaboration with Harvard (Olalde et al., 2019)). Moreover, this sampling covers only the Middle/Late Neolithic, Chalcolithic and Bronze Age periods, and are mostly from the regions of Estremadura (Lisbon peninsula) and Alentejo. On the other hand, there are 362 ancient samples from mainland Spain (plus four from Gibraltar) with genomic data available in the literature, including also Iron Age and later periods (Olalde et al., 2019). Despite their difference in land mass, even for the most extensively sampled period in the peninsula, the Late Neolithic/Chalcolithic, when key developments of the early Bell Beaker culture are thought to have taken place in Portuguese Estremadura, the difference is also obvious: 24 Portuguese (six of which generated for this thesis) *versus* 120 Spanish.

In an attempt to overcome this bias, I have targeted my sampling mostly on Portuguese archaeological sites, with a total of 57 samples from eight different Portuguese sites processed. I focussed essentially in the Late Neolithic/Chalcolithic, since the period was unsampled in 2016, when the samples were collected (Chapter V). Additionally, I presented here the first attempt to sequence Medieval Portuguese samples and one of the first studies of the Islamic period in Spain (Chapter IV).

Table 6.1. Total number of samples analysed during my PhD project.

	Portugal	Spain
Ancient samples		
Processed	57	20
DNA Extracted	57	8
WGS	31	8
1240k-SNP capture (Harvard)	24	-
Sent for isotope analysis	-	13
Modern samples		
Whole-mtDNA sequencing	103	488

In total I have processed 77 bone and tooth samples, from which I selected 63 for genetic analysis, either by WGS or by 1240k SNP-capture (Table 6.1). From these, only 22 (~14%) passed the filters for genomic analysis (>15,000 autosomal SNPs and low contamination estimates). This is in agreement with the rate of aDNA retrieval success for warm climates and expected for Iberian latitudes (Hofreiter et al., 2015).

2. Addressing the controversy concerning Indo-European dispersals in South Asia

Note: some of the content in this section was included in Silva et al., 2019c.

There has been a long-running debate regarding the origin of Indo-European languages in the Indian subcontinent, as summarised by Majumder (2018). Much of this debate is centred on the origin and dispersion of Y-chromosome haplogroup R1a1, with the methods employed in archaeogenetics sometimes deemed insubstantial (Danino, 2019). One recurrent criticism is the fact that the most recent evidence (de Barros Damgaard et al., 2018a; Lazaridis et al., 2016; Narasimhan et al., 2019; Pathak et al., 2018; Valera et al., 2014a) seems to contradict earlier conclusions (Kivisild et al., 1999, 2003; Sahoo et al., 2006; Sengupta et al., 2006), thus conveying the impression that results can be interpreted subjectively by different authors. However, these discrepancies are due mainly to two factors: i) recent years have seen the advent and constant evolution of NGS techniques, which now allow the resequencing of the MSY of modern individuals in order to overcome the weaknesses of traditional SNP/STR-typing (Wei et al., 2013); and ii) these technological advances, coupled with other methodological improvements (both in lab methods and in bioinformatic pipelines) resulted in the transformation of the field of aDNA, so that it is now possible to extract and analyse aDNA from high numbers of samples and at higher coverage, as discussed throughout this thesis (Hofreiter et al., 2015; Reich, 2018), including regions with difficult environmental conditions for DNA survival, as shown by the first aDNA recovered from the Indus Valley region, recently published (Shinde et al., 2019). As a result, more accurate Y-chromosome date estimates and more data from prehistoric Steppe and Central Asian individuals are now available, and were crucial to discern Bronze Age movements that had been dismissed by previous mtDNA-based studies. The sex-biased pattern inferred for Indo-European associated migrations is not expected to leave strong traces in the maternal variation, as explored in Chapter II (Silva et al., 2017) – although with high resolution trees, and by integrating aDNA mitogenomes, it is now possible to recover weak phylogenetic signals of these movements in both South Asians and Europeans (as shown in the case of H2b in Chapter II and explored in more detail for other H lineages in Chapter III; Silva et al., 2019b).

Y-chromosome R1a South Asian sub-clusters, dating to ~3–4 ka (YFull v.4.10), nest within Central Asian, and ultimately Eastern European, clades. Strikingly, the majority of aDNA paternal lineages recovered from the Bronze Age Steppe and Central Asia, as well as some from the Late Neolithic Corded Ware culture of northern and central Europe, belong to R1a (Allentoft et al., 2015; Keyser et al., 2009; Mathieson et al., 2015). Altogeher, this recent genetic evidence, based on Y-chromosome analysis, is strongly consistent with the linguistic argument that Indo-Iranian, Balto-Slavic and Germanic have a common origin and belong to the same branch in the Indo-European language tree (Ringe et al., 2002). However, the R1a haplogroup long predates the emergence of Proto-Indo-European, as its first occurrence in the archaeological record dates the Mesolithic (in Russia and Ukraine) (Mathieson et al., 2018). R1a probably originated in the Black Sea region in the last ice age (although an origin in Iran cannot be discarded, taking into account R1a's present-day distribution (Underhill et al., 2015)). Nevertheless, the argument that R1a dispersed from the Steppe into Central Asia with Indo-Iranian speakers, and later into the Indian Subcontinent in the Bronze Age, is very compelling from its phylogeographic pattern, especially when considering aDNA evidence.

R1a is not the only Y-chromosome lineage associated with Proto-Indo-European-speakers. Another paternal haplogroup, R1b, the most common amongst present-day western and central European males, is the main lineage associated with putative westward Indo-European dispersals (Poznik et al., 2016). Similarly to R1a, the directionality of movement is inferred from the clustering of ancient and modern sequences in the phylogeny, and, although R1b already existed long before the Metal Ages (Fu et al., 2016; Karmin et al., 2015; Mathieson et al., 2018), these more ancient lineages are extremely uncommon today (Myres et al., 2011) and evoke different demographic events from that of the younger, Indo-European-associated, clades (Chapter I, Figure 1.14) (Kivisild, 2017; Olalde et al., 2018, 2019). Parallels to the sex-bias genetic pattern mentioned above, which have been recently dismissed as discredited and echoing old 'rants on the "powerful" Aryans' (Danino, 2019), have also been recently suggested for Iberia (Olalde et al., 2019) – where, as in South Asia, non-Indo-European languages (Basque) still survive today – indicating that the proposed social implications of Bronze Age events were not unique to South Asia.

Obviously the scenario is not as simplistic as equating a particular genetic lineage one-to-one with a given language or culture. For example, the non-Indo-European-speaking Basques also harbour R1b lineages as their neighbouring Indo-European-speakers, at particularly high frequencies (Batini et al., 2015; Young et al., 2011). Nor is it the case that movements only ever occurred in one direction. In fact, South Asian lineages also dispersed both north-westwards and north-eastwards over time (Silva et al., 2017).

Another common criticism (not restricted to the Indo-Aryan debate, but broadly aimed at aDNA studies) is to target small sample sizes (Danino, 2019; Heyd, 2017), and, in the case of South Asia, the 1KGP sampling, since some populations (Gujarati, Tamil and Telugu) were sampled in diaspora communities in the USA and UK. Although these are easy targets, i) small sample sizes do not necessarily imply bias, especially in the case of autosomal analysis, which rely on the recombinant genome that has resulted from several ancestors, and therefore can provide insights into several generations in the past (Li and Durbin, 2011), and ii) 1KGP sampling required subjects to have at least three grandparents self-identified as members of a given group (The 1000 Genomes Project Consortium, 2015), therefore minimising the effect of admixture with other populations. In fact, a recent study on previously unsampled present-day groups from the Indus Valley support the presence of Steppe-related ancestry at variable proportions (Pathak et al., 2018). Nevertheless, one should point out that bias can indeed be an issue in the case of archaeological sampling. Available ancient genomes might not be representative of the diversity of a given period and location (Booth, 2019; Heyd, 2017), and therefore current sampling might not capture the heterogeneity of populations over time, as discussed in this thesis in the cases of Central/South Asia (Chapter II) and Iberia (Chapters IIII and IV).

Indo-European studies in 20th-century Europe were tragically distorted to serve as a central premise for Nazi ideology, mostly based on Gustaf Kossinna's culture-historical approach, and misused to justify acts of ethnic cleansing and war crimes perpetrated by the

Nazi regime (Arnold, 2006). This understandably leads to fears of a similar scenario arising again, with a possible misuse of archaeogenetics research by nationalist, racist or other extremist movements (Booth, 2019; Hakenbeck, 2019; Richardson and Booth, 2017). In India the topic is also sensitive, due to a recent past under colonialism and imperialism (Danino, 2019). However, this should not obscure the weight of scientific evidence pointing to a likely arrival of Indo-European (in the form of Indo-Aryan) to the Subcontinent from Central Asia in the Bronze Age, and research opportunities (preferably in an interdisciplinary environment) should not be hampered by ideological agendas.

In a broader sense, there is a clear problem with media coverage of aDNA research, usually based on sensationalism and click-bait, which is not restricted to mainstream media, but also patent in more targeted publications, such as *New Scientist* – *e.g.* Barras, 2019; Marshall, 2018. In the case of the *New Scientist* article, which conveyed the idea of violent invasions at the end of the third millennium BCE in Iberia, the piece was written and circulated months ahead of the publication of Olalde et al. (2019), whose results it was supposedly covering, and was echoed by both Portuguese and Spanish media outlets without the opportunity for contradictory views to be aired.

Additionally, now that it has been shown that migration played a significant role in late prehistory, it may be time to move away from grand narratives and continent-wide processes and start to tackle the more fine-scale interactions between populations (Veeramah, 2018), for example, by focussing on familial relationships and local interactions between sites, in an attempt to explain the social mechanisms involved at the local scale in the arrival of Indo-Aryan speakers to South Asia – an approach that should also be applied to study the arrival of Steppe-related ancestry to Iberia.

3. Ongoing and future work

Several aspects of this work could be explored in more detail. In order to do so, further analyses are either ongoing, or will be performed in the near future, as described below:

- H1 paml analysis is currently ongoing, in order to obtain ML node age estimates for this haplogroup. It would also be interesting to apply Bayesian inference (with BEAST) and use the aDNA sequences to calibrate the phylogenies and estimate variations in N_e over time (Drummond et al., 2012);

- The formal tests of admixture analysis performed in Chapter IV for the Segorbe Giant should be complemented with comparisons using present-day North African populations;

- In order to further study mitochondrial variation in Chalcolithic Iberia, I will add these sequences to haplogroup trees and check the phylogeographic patterns of the nodes in which they cluster, similarly to what has been done in Chapter IV for the Medieval individuals;

- Although post-mortem damage was accounted by rescaling the BAM files, key analyses should be repeated using only transversion positions in order to confirm that the patterns observed are not an artefact caused by damage;

- I aim to integrate the newly published data from Mediterranean islands (Fernandes et al., 2019; Marcus et al., 2019) and Atlantic regions (Brace et al., 2019; Sánchez-Quinto et al., 2019), which will allow a finer analysis of possible interactions with other regions, and explore potential different dynamics of the Atlantic and Mediterranean façades of Iberia;

- The preliminary screening of phenotypic variation amongst Portuguese Late Neolithic/Chalcolithic individuals reported here suggests variability in many traits. This requires a detailed comparison with individuals from the temporal transect recently published (Olalde et al., 2019), in order to assess allele frequencies over time in Iberia;

- One of the advantages of generating WGS data is that it is possible to conduct a metagenomics analysis for each library (as shown in Chapter V), which can be useful to detect the presence of pathogens. This has not been explored in detail in this thesis but would be an interesting approach for a future study.

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Appendix A

Supplementary material for chapter II

A genetic chronology for the Indian Subcontinent:
sex-biased dispersals in the Bronze Age

Arabia + Near East:

× Bedouins
✱ Saudis
● Yemeni
● Yemeni Jews
▲ Palestinians
▲ Druze
× Lebanese
◇ Jordanians
● Syrians
⊠ Iraqi Jews
◆ Iranians
◆ Iranian Jews

Anatolia + Caucasus:

▲ Cypriots
+ Turks
◆ Armenians
✱ Balkars
✱ Chechens
● Lezgins
⊠ Abhkasians
● Adygei
■ North Ossetians
▲ Georgians
▲ Georgian Jews
× Azerbaijani Jews
× Kumyks
● Nogais

Central Asia:

▲ Turkmens
■ Uzbeks
■ Uzbekistani Jews
⊠ Tajiks

South Asia:

+ Kalash
◆ Balochi
+ Brahui
× Burusho
⊠ Sindhi
✱ Pathan
■ Makrani
● PJL
▲ GIH+Gujaratis
● Meghawal
● Meena
■ Nihali
◇ Dusadh
✱ Gond
◆ Brahmins-Central
▲ Kshatriya
● Dharkars
△ Low Caste - Central
◇ Muslim
⊠ Chamar
⊠ Kol
⊞ Kanjars
○ Tharus
⊞ Kharia
● Bhunjia
■ ITU
■ Brahmins-South
◆ Low Caste-South
○ Sakilli
✱ Cochin Jews
+ Bene Israel
⊞ Velmas
× North Kannadi
□ Piramalai Kallars
▲ Halakipikki
⊠ Kurumba
○ Malayan
⊠ Paniya
● Chenchus
+ Lambadi
◆ STU
▲ BEB+Bengali
× Ho
■ Bonda
● Khasi
◆ Savara
+ Juang
⊠ Asur
■ Gadaba
⊠ Santhal
◇ Mawasi
△ Dhurwa

Figure S1. Detailed caption for the PCA shown in Figure 2.5.

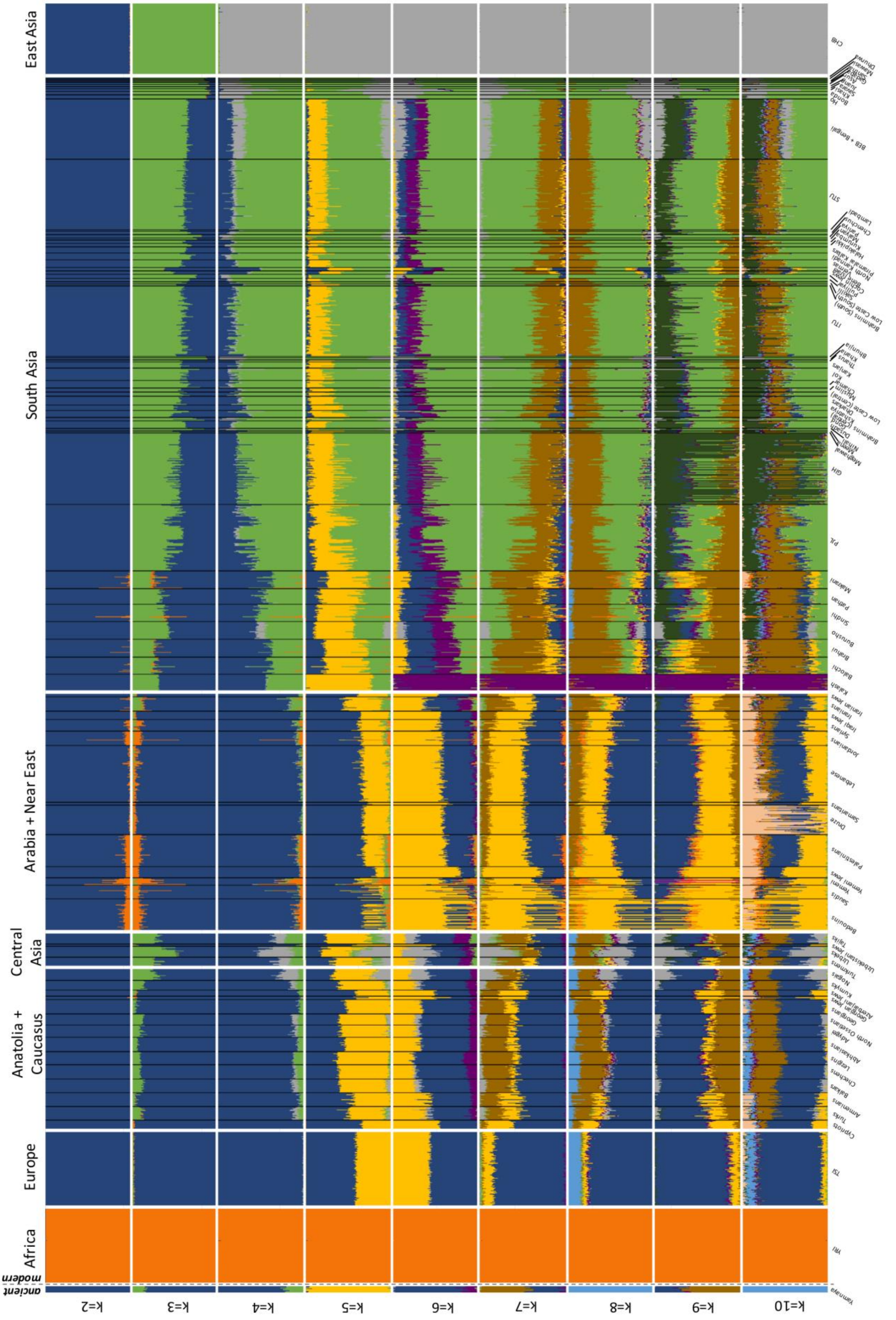
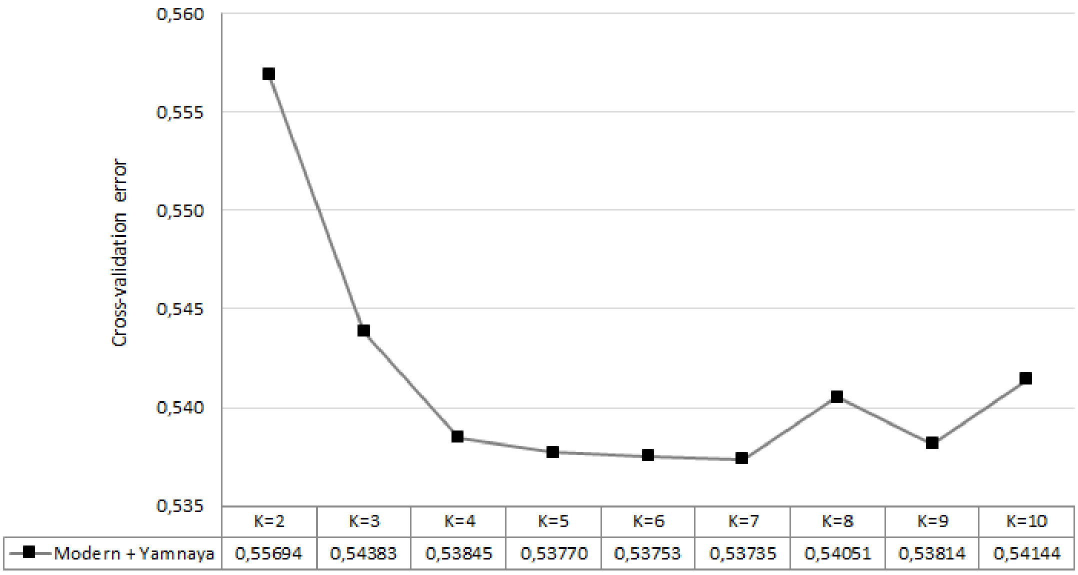


Figure S2. ADMIXTURE analysis (*K*=2 to *K*=10). Information on the populations included in Table S2.



	K=2	K=3	K=4	K=5	K=6	K=7	K=8	K=9	K=10
■ Modern + Yamnaya	0,55694	0,54383	0,53845	0,53770	0,53753	0,53735	0,54051	0,53814	0,54144

Figure S3. Cross-validation errors for different values of *K* for ADMIXTURE.

Table S1. List of non-autochthonous complete modern mtDNA sequences used in the analyses. Population codes: BEB – Bengali from Bangladesh; GIH – Gujarati Indian from Houston, Texas; ITU – Indian Telugu from the UK; PJL – Punjabi from Lahore, Pakistan; STU – Sri Lankan Tamil from the UK; TSI – Tuscans from Italy; KHV – Kinh from Ho Chi Minh City, Vietnam; CDX – Chinese Dai from Xishuangbanna, China; CEU – Utah Residents (CEPH) with Northern and Western Ancestry.

Sample	Hg.	Origin (Population)	Region	Reference
EU597524	H1	Czech Republic	Europe	Hartmann et al. (2009)
EU747355	H1	Germany	Europe	Family Tree
JQ702008	H1	Germany	Europe	Behar et al. (2012)
JQ702174	H1	unknown	unknown	Behar et al. (2012)
JQ702182	H1	unknown	unknown	Behar et al. (2012)
JQ704245	H1	Ireland	Europe	Behar et al. (2012)
JQ704536	H1	unknown	unknown	Behar et al. (2012)
JX885690	H1	England	Europe	Family Tree
AY713977	H1	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY738961	H2	Iraq	Southwest Asia	Achilli et al. (2004)
HQ659667	H2	Germany	Europe	Family Tree
JQ702621	H2	unknown	unknown	Behar et al. (2012)
JQ704274	H2	unknown	unknown	Behar et al. (2012)
JQ704530	H2	unknown	unknown	Behar et al. (2012)
NA07051	H2	CEU	Europe	Sudmant et al. (2015)
NA20585	H2	TSI	Europe	Sudmant et al. (2015)
NA20802	H2	TSI	Europe	Sudmant et al. (2015)
EU597574	H2	Pakistan: Brahui	South Asia - West	Hartmann et al. (2009)
HG01586	H2	PJL	South Asia - West	Sudmant et al. (2015)
HG04039	H2	STU	South Asia - South	Sudmant et al. (2015)
KJ446362	H2	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
KP763834	H2	India	South Asia	Palanichamy et al. (2015)
NA20872	H2	GIH	South Asia - West	Sudmant et al. (2015)
KJ856744	H2	Altai	Central Asia/Siberia	Derenko et al. (2014)
KJ856726	H2	Altai	Central Asia/Siberia	Derenko et al. (2014)
KJ856720	H2	Khamnigan	Central Asia/Siberia	Derenko et al. (2014)
KF161829	H2	Denmark	Europe	Li et al. (2014)
KJ446360	H2	Russia	Europe	HGDP - Zheng, et al. (unpublished)
KC990675	H2	Possibly India	South Asia	Ramanan et al. (unpublished)
JQ705227	H2	unknown	unknown	Behar et al. (2012)
JQ702943	H2	Greece	Europe	Behar et al. (2012)
EU600329	H6	Druze	Southwest Asia	Shlush et al. (2008)
FJ348203	H6	Hutterite	Europe	HGDP - Zheng, et al. (unpublished)
JQ702285	H6	unknown	unknown	Behar et al. (2012)
NA20850	H6	GIH	South Asia - West	Sudmant et al. (2015)
HM852826	H7	Iran	Southwest Asia	Schönberg et al. (2011)
JQ702601	H7	Germany	Europe	Behar et al. (2012)
JQ702990	H7	unknown	unknown	Behar et al. (2012)
JQ704890	H7	unknown	unknown	Behar et al. (2012)
KC911403	H7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
NA20870	H7	GIH	South Asia - West	Sudmant et al. (2015)
AY713978	H9	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY738969	H9	Italy	Europe	Achilli et al. (2004)
JQ705022	H9	Germany	Europe	Behar et al. (2012)
AY339409	H13	Finland	Europe	Finnilä et al. (2001)
AY495107	H13	Europe	Europe	Coble et al. (2004)
AY495149	H13	Europe	Europe	Coble et al. (2004)
EF556150	H13	Israel: Jew	Southwest Asia	Behar et al. (2008a)
EU597515	H13	Palestine	Southwest Asia	Hartmann et al. (2009)
AY713980	H13	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)

AY713982	H13	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
JQ702112	H13	England	Europe	Behar et al. (2012)
JQ703858	H13	Ireland	Europe	Behar et al. (2012)
KC911327	H13	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911369	H13	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911443	H13	Iran: Indian	Southwest Asia	Derenko et al. (2013)
KC911454	H13	Russia: Saratov Region	Europe	Derenko et al. (2013)
HG01589	H13	PJL	South Asia - West	Sudmant et al. (2015)
HG02651	H13	PJL	South Asia - West	Sudmant et al. (2015)
HG03692	H13	STU	South Asia - South	Sudmant et al. (2015)
HG03844	H13	STU	South Asia - South	Sudmant et al. (2015)
HG03849	H13	STU	South Asia - South	Sudmant et al. (2015)
HG03995	H13	STU	South Asia - South	Sudmant et al. (2015)
KJ446338	H13	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446339	H13	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446340	H13	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446341	H13	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
AY713995	H15	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY495146	H15	Europe	Europe	Coble et al. (2004)
HM852832	H15	Iran	Southwest Asia	Schönberg et al. (2011)
JQ704364	H15	unknown	unknown	Behar et al. (2012)
KC911289	H15	Iran: Azeri	Southwest Asia	Derenko et al. (2013)
KC911292	H15	Iran: Persian	Southwest Asia	Derenko et al. (2013)
EU600335	H29	Druze	Southwest Asia	Shlush et al. (2008)
EU600343	H29	Druze	Southwest Asia	Shlush et al. (2008)
JQ704540	H29	Italy	Europe	Behar et al. (2012)
KC911535	H29	Iran: Azeri	Southwest Asia	Derenko et al. (2013)
NA20896	H29	GIH	South Asia - West	Sudmant et al. (2015)
NA21098	H29	GIH	South Asia - West	Sudmant et al. (2015)
AY713981	HV	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
EF222251	HV	Poland	Europe	Malyarchuk et al. (2008b)
EU545435	HV	Russia	Europe	Malyarchuk et al. (2008b)
HM852792	HV	Azeri	Southwest Asia	Schönberg et al. (2011)
HM852816	HV	Iran	Southwest Asia	Schönberg et al. (2011)
HQ287727	HV	Armenia	Southwest Asia	Family Tree
HQ436102	HV	Armenia	Southwest Asia	Family Tree
JF313325	HV	Sweden	Europe	Family Tree
KC765916	HV	Bulgaria	Europe	Family Tree
KC911391	HV	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911408	HV	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911439	HV	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911472	HV	Iran: Persian	Southwest Asia	Derenko et al. (2013)
HG02491	HV	PJL	South Asia - West	Sudmant et al. (2015)
HG02661	HV	PJL	South Asia - West	Sudmant et al. (2015)
HG03235	HV	PJL	South Asia - West	Sudmant et al. (2015)
HM776579	HV	India: Tamil Nadu	South Asia - South	Family Tree
DQ523620	HV0	Sardinia	Europe	Fraumene et al. (2006)
JQ705544	HV0	unknown	unknown	Behar et al. (2012)
AY713986	HV2	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
HM852806	HV2	Azeri	Southwest Asia	Schönberg et al. (2011)
KC911372	HV2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911452	HV2	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
NA20867	HV2	GIH	South Asia - West	Sudmant et al. (2015)
AY713976	HV12	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY713987	HV12	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
HM852785	HV12	Armenia	Southwest Asia	Schönberg et al. (2011)
KC911301	HV12	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911424	HV12	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911482	HV12	Iran: Mazandarani	Southwest Asia	Derenko et al. (2013)
HG03009	HV12	BEB	South Asia - East	Sudmant et al. (2015)

NA21112	HV12	GIH	South Asia - West	Sudmant et al. (2015)
HM852828	HV13	Iran	Southwest Asia	Schönberg et al. (2011)
JF700125	HV13	Armenia	Southwest Asia	Family Tree
KC911298	HV13	Iran: Persian	Southwest Asia	Derenko et al. (2013)
HG02652	HV13	PJL	South Asia - West	Sudmant et al. (2015)
AY713988	HV14	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
KC911456	HV14	Iran: Persian	Southwest Asia	Derenko et al. (2013)
NA18743	HV14	Han Chinese	East Asia	Sudmant et al. (2015)
HG03873	HV14	ITU	South Asia - South	Sudmant et al. (2015)
HG03890	HV14	STU	South Asia - South	Sudmant et al. (2015)
HG03895	HV14	STU	South Asia - South	Sudmant et al. (2015)
HG03900	HV14	STU	South Asia - South	Sudmant et al. (2015)
HG03998	HV14	STU	South Asia - South	Sudmant et al. (2015)
HG03999	HV14	STU	South Asia - South	Sudmant et al. (2015)
HG04003	HV14	STU	South Asia - South	Sudmant et al. (2015)
HG04225	HV14	ITU	South Asia - South	Sudmant et al. (2015)
KJ446056	I	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446060	I	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
AY714041	I1	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY195769	I1	unknown	unknown	Mishmar et al. (2003)
EF556153	I1	Tunisia: Jew	Africa	Behar et al. (2008a)
FJ234984	I1	Armenia	Southwest Asia	Family Tree
JQ245776	I1	Turkey: Kurd	Southwest Asia	Fernandes et al. (2012)
JQ705376	I1	unknown	unknown	Behar et al. (2012)
JQ705840	I1	England	Europe	Behar et al. (2012)
HG03727	I1	ITU	South Asia - South	Sudmant et al. (2015)
KJ446055	I1	Pakistan: Burusho	South Asia - West	HGDP - Zheng, et al. (unpublished)
JQ245724	I5	Russia: North Ossetia	Southwest Asia	Fernandes et al. (2012)
KJ446057	I5	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
AY714033	J1	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY714034	J1	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY714035	J1	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY495202	J1	Europe	Europe	Coble et al. (2004)
AY495216	J1	Europe	Europe	Coble et al. (2004)
AY495234	J1	Europe	Europe	Coble et al. (2004)
AY495235	J1	Europe	Europe	Coble et al. (2004)
EF556155	J1	Iran: Jew	Southwest Asia	Behar et al. (2008a)
EF583177	J1	Slovakia	Europe	Malyarchuk et al. (2008a)
FJ348177	J1	Hutterite	Europe	HGDP - Zheng, et al. (unpublished)
FJ502349	J1	unknown	unknown	Family Tree
HM852779	J1	Armenia	Southwest Asia	Schönberg et al. (2011)
HM852784	J1	Armenia	Southwest Asia	Schönberg et al. (2011)
HM852838	J1	Iran	Southwest Asia	Schönberg et al. (2011)
JF929909	J1	Armenia	Southwest Asia	Family Tree
JN663354	J1	Armenia	Southwest Asia	Family Tree
JQ703029	J1	unknown	unknown	Behar et al. (2012)
JQ703802	J1	unknown	unknown	Behar et al. (2012)
JQ703825	J1	unknown	unknown	Behar et al. (2012)
JQ705141	J1	unknown	unknown	Behar et al. (2012)
JQ705164	J1	Scotland	Europe	Behar et al. (2012)
JQ797765	J1	Kuwait	Southwest Asia	Pala et al. (2012)
JQ797770	J1	Iran	Southwest Asia	Pala et al. (2012)
JQ797775	J1	Greece	Europe	Pala et al. (2012)
KC911407	J1	Iran: Armenian	Southwest Asia	Derenko et al. (2013)
KC911461	J1	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911496	J1	Iran: Gilak	Southwest Asia	Derenko et al. (2013)
KJ445884	J1	Israel: Druze	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445886	J1	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445907	J1	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
HG03744	J1	STU	South Asia - South	Sudmant et al. (2015)

HG03833	J1	BEB	South Asia - East	Sudmant et al. (2015)
HG03868	J1	ITU	South Asia - South	Sudmant et al. (2015)
HG03902	J1	BEB	South Asia - East	Sudmant et al. (2015)
KJ445885	J1	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445899	J1	Pakistan: Sindhi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445900	J1	Pakistan: Burusho	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445901	J1	Pakistan: Burusho	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445902	J1	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445904	J1	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445905	J1	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445906	J1	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
NA21126	J1	GIH	South Asia - West	Sudmant et al. (2015)
JQ704041	J2	Ireland	Europe	Behar et al. (2012)
HM852886	K	Georgia	Southwest Asia	Schönberg et al. (2011)
AY714044	K1	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AF382005	K1	Spain	Europe	Maca-Meyer et al. (2001)
EU259093	K1	unknown	unknown	Family Tree
HM852762	K1	Armenia	Southwest Asia	Schönberg et al. (2011)
HQ586011	K1	USA	America	Family Tree
JN048471	K1	Armenia	Southwest Asia	Family Tree
JQ702086	K1	unknown	unknown	Behar et al. (2012)
JQ702624	K1	unknown	unknown	Behar et al. (2012)
JQ703522	K1	Syria	Southwest Asia	Behar et al. (2012)
JQ706042	K1	Iran	Southwest Asia	Behar et al. (2012)
JX273286	K1	Russia	Europe	Costa et al. (2013)
KC911418	K1	Iran: Azeri	Southwest Asia	Derenko et al. (2013)
KC911440	K1	Iran: Persian	Southwest Asia	Derenko et al. (2013)
HG04014	K1	ITU	South Asia - South	Sudmant et al. (2015)
AY714017	K2	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
EU597528	K2	Pakistan: Pathan	South Asia - West	Hartmann et al. (2009)
AY495241	K2	Europe	Europe	Coble et al. (2004)
AY495247	K2	Europe	Europe	Coble et al. (2004)
DQ301796	K2	Yemen: Jew	Southwest Asia	Behar et al. (2006)
JQ703018	K2	Ireland	Europe	Behar et al. (2012)
JX021502	K2	Germany	Europe	Family Tree
JX273250	K2	Turkey	Southwest Asia	Costa et al. (2013)
KC911393	K2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KJ445985	K2	Pakistan: Sindhi	South Asia - West	HGDP - Zheng, et al. (unpublished)
NA20910	K2	GIH	South Asia - West	Sudmant et al. (2015)
DQ341069	L3	Ethiopia	Africa	Torroni et al. (2006)
EU092923	L3	Yemen	Southwest Asia	Behar et al. (2008b)
JN655780	L3	Ethiopia	Africa	Soares et al. (2012)
JN655785	L3	Ethiopia	Africa	Soares et al. (2012)
NA21118	L3	GIH	South Asia - West	Sudmant et al. (2015)
NA21142	L3	GIH	South Asia - West	Sudmant et al. (2015)
AY714008	N1	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
JF298212	N1	Armenia	Southwest Asia	Family Tree
JQ245734	N1	United Arab Emirates: Dubai	Southwest Asia	Fernandes et al. (2012)
JQ245766	N1	Turkey	Southwest Asia	Fernandes et al. (2012)
JQ245777	N1	Yemen	Southwest Asia	Fernandes et al. (2012)
KC911323	N1	Iran: Azeri	Southwest Asia	Derenko et al. (2013)
KJ446050	N1	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
HG03698	N1	STU	South Asia - South	Sudmant et al. (2015)
HG04238	N1	ITU	South Asia - South	Sudmant et al. (2015)
KJ446052	N1	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446053	N1	Pakistan: Burusho	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446070	N1	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KP763833	N1	India	South Asia	Palanichamy et al. (2015)
KP763844	N1	India	South Asia	Palanichamy et al. (2015)
KC911431	N2	Iran: Persian	Southwest Asia	Derenko et al. (2013)

HG04047	N5	STU	South Asia - South	Sudmant et al. (2015)
GQ301867	N21	Vietnam	Southeast Asia	Peng et al. (2010)
GQ301885	N21	Thailand	Southeast Asia	Peng et al. (2010)
GQ301887	N21	China	East Asia	Peng et al. (2010)
HG03943	N21	STU	South Asia - South	Sudmant et al. (2015)
AY713999	R0	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
EU597493	R0	Pakistan: Kalash	South Asia - West	Hartmann et al. (2009)
HG02657	R0	PJL	South Asia - West	Sudmant et al. (2015)
HG02072	R0	KHV	Southeast Asia	Sudmant et al. (2015)
HG02399	R0	CDX	East Asia	Sudmant et al. (2015)
HM185249	R0	Yemen	Southwest Asia	Cerný et al. (2011)
HM852825	R0	Iran	Southwest Asia	Schönberg et al. (2011)
KC911373	R0	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KJ446215	R0	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446216	R0	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446217	R0	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446218	R0	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446219	R0	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446220	R0	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446221	R0	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446222	R0	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446223	R0	Israel: Druze	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446225	R0	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446226	R0	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446227	R0	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446228	R0	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ446206	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446207	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446208	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446209	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446211	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446212	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446213	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446214	R0	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446224	R0	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
AY714045	R1	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AF381997	R1	Jordan	Southwest Asia	Maca-Meyer et al. (2001)
EU545437	R1	Russia	Europe	Malyarchuk et al. (2008b)
EU545445	R1	Russia	Europe	Malyarchuk et al. (2008b)
HM852786	R1	Azeri	Southwest Asia	Schönberg et al. (2011)
HQ602771	R1	Armenia	Southwest Asia	Family Tree
JQ705295	R1	Sweden	Europe	Behar et al. (2012)
JQ705561	R1	England	Europe	Behar et al. (2012)
AY714007	R2	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
EU597551	R2	Pakistan: Brahui	South Asia - West	Hartmann et al. (2009)
EF556167	R2	Yemen: Jew	Southwest Asia	Behar et al. (2008a)
HM030516	R2	Mongolian	East Asia	Kong et al. (2011)
HM852870	R2	Turk	Southwest Asia	Schönberg et al. (2011)
JN581649	R2	Italy	Europe	Bertolin et al. (2011)
JX155264	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155265	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155266	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155267	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155268	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155269	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155270	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155271	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
JX155272	R2	Oman	Southwest Asia	Al-Abri et al. (2012)
KC911280	R2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911319	R2	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)

KC911337	R2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911374	R2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911379	R2	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911485	R2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911495	R2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911541	R2	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911627	R2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KJ446063	R2	Pakistan: Makrani	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446065	R2	Pakistan: Makrani	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446066	R2	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446067	R2	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ446069	R2	Pakistan: Balochi	South Asia - West	HGDP - Zheng, et al. (unpublished)
NA20877	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA20892	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA20899	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA21086	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA21091	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA21093	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA21117	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA21123	R2	GIH	South Asia - West	Sudmant et al. (2015)
NA21141	R2	GIH	South Asia - West	Sudmant et al. (2015)
KC911379	R2'JT	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
AY714015	T1	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY714036	T1	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY495288	T1	Europe	Europe	Coble et al. (2004)
AY495289	T1	Europe	Europe	Coble et al. (2004)
AY495290	T1	Europe	Europe	Coble et al. (2004)
AY495293	T1	Europe	Europe	Coble et al. (2004)
AY495295	T1	Europe	Europe	Coble et al. (2004)
AY495296	T1	Europe	Europe	Coble et al. (2004)
AY495297	T1	Europe	Europe	Coble et al. (2004)
DQ358975	T1	unknown	unknown	Detjen et al. (2007)
FJ348197	T1	Hutterite	Europe	HGDP - Zheng, et al. (unpublished)
HM184912	T1	Czech Republic	Europe	Family Tree
HM852798	T1	Azeri	Southwest Asia	Schönberg et al. (2011)
JF831941	T1	unknown	unknown	Family Tree
JQ702340	T1	unknown	unknown	Behar et al. (2012)
JQ702556	T1	England	Europe	Behar et al. (2012)
JQ702716	T1	Ireland	Europe	Behar et al. (2012)
JQ705353	T1	unknown	unknown	Behar et al. (2012)
JQ705463	T1	unknown	unknown	Behar et al. (2012)
KC911320	T1	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911343	T1	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911473	T1	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KJ445831	T1	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
HG04093	T1	ITU	South Asia - South	Sudmant et al. (2015)
KJ445834	T1	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445835	T1	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445839	T1	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
NA20890	T1	GIH	South Asia - West	Sudmant et al. (2015)
AY714016	T2	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY714022	T2	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY714029	T2	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY714037	T2	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
HG02604	T2	PJL	South Asia - West	Sudmant et al. (2015)
HG02649	T2	PJL	South Asia - West	Sudmant et al. (2015)
HG03625	T2	PJL	South Asia - West	Sudmant et al. (2015)
HG03784	T2	ITU	South Asia - South	Sudmant et al. (2015)
HG04023	T2	ITU	South Asia - South	Sudmant et al. (2015)
AY495272	T2	Europe	Europe	Coble et al. (2004)

AY495298	T2	Europe	Europe	Coble et al. (2004)
AY495299	T2	Europe	Europe	Coble et al. (2004)
AY495301	T2	Europe	Europe	Coble et al. (2004)
AY495304	T2	Europe	Europe	Coble et al. (2004)
HG04025	T2	ITU	South Asia - South	Sudmant et al. (2015)
EF060363	T2	Italy	Europe	La Morgia et al. (2008)
FJ238094	T2	Armenia	Southwest Asia	Family Tree
FJ656215	T2	Russia	Europe	HGDP - Zheng, et al. (unpublished)
GU565218	T2	unknown	unknown	Family Tree
HM852766	T2	Armenia	Southwest Asia	Schönberg et al. (2011)
HM852781	T2	Armenia	Southwest Asia	Schönberg et al. (2011)
HM852899	T2	Georgia	Southwest Asia	Schönberg et al. (2011)
JQ702108	T2	Germany	Europe	Behar et al. (2012)
JQ702594	T2	Scotland	Europe	Behar et al. (2012)
JQ703754	T2	Scotland	Europe	Behar et al. (2012)
JQ705133	T2	Ireland	Europe	Behar et al. (2012)
KC911414	T2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911414	T2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KJ445844	T2	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445845	T2	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445849	T2	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445856	T2	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445862	T2	Russia: Adygei, Caucasus	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445863	T2	Russia: Adygei, Caucasus	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445851	T2	Pakistan: Sindhi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445855	T2	Pakistan: Burusho	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445860	T2	Pakistan: Kalash	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445861	T2	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
NA20901	T2	GIH	South Asia - West	Sudmant et al. (2015)
AY289073	U1	India: Koraga	South Asia - South	Ingman and Gyllensten 2003)
AY714038	U1	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY714042	U1	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
EF556194	U1	Cochin Jew	South Asia	Behar et al. (2008a)
HG03780	U1	ITU	South Asia - South	Sudmant et al. (2015)
HG03862	U1	ITU	South Asia - South	Sudmant et al. (2015)
HG03886	U1	STU	South Asia - South	Sudmant et al. (2015)
HG04098	U1	ITU	South Asia - South	Sudmant et al. (2015)
HM156682	U1	India	South Asia	Govindaraj et al. (2011)
AY882396	U1	Adygei	Southwest Asia	Achilli et al. (2004)
EF556161	U1	Iran: Jew	Southwest Asia	Behar et al. (2008a)
EF661008	U1	Italy	Europe	Gasparre et al. (2007)
FJ748753	U1	Tibet	East Asia	Ji et al. (2012)
GU218692	U1	Greece	Europe	Family Tree
HM852789	U1	Azeri	Southwest Asia	Schönberg et al. (2011)
HM852790	U1	Azeri	Southwest Asia	Schönberg et al. (2011)
HM852847	U1	Turk	Southwest Asia	Schönberg et al. (2011)
KC477757	U1	Iraq - Kurd	Southwest Asia	Family Tree
KC911306	U1	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911344	U1	Iran: Armenian	Southwest Asia	Derenko et al. (2013)
KC911457	U1	Iran: Azeri	Southwest Asia	Derenko et al. (2013)
KC911527	U1	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KJ445918	U1	Russia: Adygei, Caucasus	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445919	U1	Israel: Druze	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445921	U1	Palestine	Southwest Asia	HGDP - Zheng, et al. (unpublished)
KJ445920	U1	Pakistan: Hazara	South Asia - West	HGDP - Zheng, et al. (unpublished)
NA21097	U1	GIH	South Asia - West	Sudmant et al. (2015)
AY714026	U2	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY714040	U2	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
AY714049	U2	India: Andhra Pradesh	South Asia - South	Palanichamy et al. (2004)
HG03960	U2	ITU	South Asia - South	Sudmant et al. (2015)

HM156683	U2	India	South Asia	Govindaraj et al. (2011)
HM156688	U2	India	South Asia	Govindaraj et al. (2011)
AF381995	U2	Jordan	Southwest Asia	Maca-Meyer et al. (2001)
EF528162	U2	unknown	unknown	Family Tree
EF661006	U2	Italy	Europe	Gasparre et al. (2007)
FJ493504	U2	Russia	Europe	Sukernik et al. (2012)
FJ828532	U2	unknown	unknown	Family Tree
JQ701890	U2	unknown	unknown	Behar et al. (2012)
JQ701947	U2	unknown	unknown	Behar et al. (2012)
JQ702004	U2	unknown	unknown	Behar et al. (2012)
JQ702106	U2	unknown	unknown	Behar et al. (2012)
JQ702663	U2	unknown	unknown	Behar et al. (2012)
JQ705559	U2	unknown	unknown	Behar et al. (2012)
JQ705711	U2	England	Europe	Behar et al. (2012)
JQ705900	U2	England	Europe	Behar et al. (2012)
KC911479	U2	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911513	U2	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
NA20904	U2	GIH	South Asia - West	Sudmant et al. (2015)
AY714023	U3	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
HM852797	U3	Azeri	Southwest Asia	Schönberg et al. (2011)
HM852819	U3	Iran	Southwest Asia	Schönberg et al. (2011)
HM852891	U3	Georgia	Southwest Asia	Schönberg et al. (2011)
JQ704130	U3	Hungary	Europe	Behar et al. (2012)
KC911459	U3	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911334	U4	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
HG03897	U5	STU	South Asia - South	Sudmant et al. (2015)
HG04159	U5	BEB	South Asia - East	Sudmant et al. (2015)
JF906114	U5	India	South Asia	Family Tree
DQ156210	U5	Spain	Europe	Montiel-Sosa et al. (2006)
EU597527	U5	Palestine	Southwest Asia	Hartmann et al. (2009)
GU296543	U5	Poland	Europe	Malyarchuk et al. (2010b)
GU296570	U5	Czech Republic	Europe	Malyarchuk et al. (2010b)
GU296581	U5	Belarus	Europe	Malyarchuk et al. (2010b)
GU296583	U5	Belarus	Europe	Malyarchuk et al. (2010b)
HM852782	U5	Armenia	Southwest Asia	Schönberg et al. (2011)
JQ582984	U5	England	Europe	Family Tree
JQ702310	U5	unknown	unknown	Behar et al. (2012)
JQ702913	U5	unknown	unknown	Behar et al. (2012)
JQ704112	U5	Scotland	Europe	Behar et al. (2012)
JQ705429	U5	England	Europe	Behar et al. (2012)
KC569552	U5	USA	Europe	Family Tree
KC911325	U5	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911503	U5	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911532	U5	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
NA20854	U5	GIH	South Asia - West	Sudmant et al. (2015)
AY714004	U7	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY714013	U7	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY714014	U7	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY882391	U7	Pakistan	South Asia - West	Achilli et al. (2004)
GU213243	U7	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2015)
GU213244	U7	India: Tamil Nadu	South Asia - South	Palanichamy et al. (2015)
GU213245	U7	Bangladesh	South Asia - East	Palanichamy et al. (2015)
GU213246	U7	Bangladesh	South Asia - East	Palanichamy et al. (2015)
GU213247	U7	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2015)
GU213248	U7	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2015)
GU213249	U7	India: Tamil Nadu	South Asia - South	Palanichamy et al. (2015)
GU213250	U7	India: Tamil Nadu	South Asia - South	(Palanichamy et al., 2015)
GU213251	U7	India: West Bengal	South Asia - East	Palanichamy et al. (2015)
GU213252	U7	India: West Bengal	South Asia - East	Palanichamy et al. (2015)
GU213253	U7	India: Tamil Nadu	South Asia - South	Palanichamy et al. (2015)

GU213254	U7	India: Tamil Nadu	South Asia - South	Palanichamy et al. (2015)
GU480003	U7	India: Madhya Pradesh	South Asia - Central	Sharma et al. (2012)
HG02494	U7	PJL	South Asia - West	Sudmant et al. (2015)
HG02648	U7	PJL	South Asia - West	Sudmant et al. (2015)
HG02694	U7	PJL	South Asia - West	Sudmant et al. (2015)
HG02724	U7	PJL	South Asia - West	Sudmant et al. (2015)
HG02731	U7	PJL	South Asia - West	Sudmant et al. (2015)
HG02775	U7	PJL	South Asia - West	Sudmant et al. (2015)
HG03681	U7	STU	South Asia - South	Sudmant et al. (2015)
HG03696	U7	STU	South Asia - South	Sudmant et al. (2015)
HG03711	U7	STU	South Asia - South	Sudmant et al. (2015)
HG04056	U7	ITU	South Asia - South	Sudmant et al. (2015)
HG04134	U7	BEB	South Asia - East	Sudmant et al. (2015)
AF382011	U7	Spain	Europe	Maca-Meyer et al. (2001)
AY339547	U7	Finland	Europe	Finnilä et al. (2001)
AY339548	U7	Finland	Europe	Finnilä et al. (2001)
KJ445973	U7	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445974	U7	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
EF556179	U7	Iran: Jew	Southwest Asia	Behar et al. (2008a)
EU445683	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445684	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445685	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445686	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445687	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445688	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445689	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445690	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009)
EU445691	U7	Italy: Isle of Elba	Europe	Brisighelli et al. (2009), 2009
EU597503	U7	Israel: Bedouin	Southwest Asia	Hartmann et al. (2009)
FJ858878	U7	Russia: North-West Siberia	East Asia	Sukernik et al. (2012)
GQ176284	U7	Finland	Europe	Family Tree
GU213236	U7	Russia	Europe	Palanichamy et al. (2015)
GU213237	U7	Kalmyk	Europe	Palanichamy et al. (2015)
GU213238	U7	Russia	Europe	Palanichamy et al. (2015)
GU213239	U7	Iran: Persian	Southwest Asia	Palanichamy et al. (2015)
GU213240	U7	Bargut	East Asia	Palanichamy et al. (2015)
GU213241	U7	Slovakia	Europe	Palanichamy et al. (2015)
GU213242	U7	Russia	Europe	Palanichamy et al. (2015)
KJ445975	U7	Pakistan: Burusho	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445976	U7	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445977	U7	Pakistan: Hazara	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445979	U7	Pakistan: Brahui	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445980	U7	Pakistan: Burusho	South Asia - West	HGDP - Zheng, et al. (unpublished)
GU213255	U7	unknown	unknown	Palanichamy et al. (2015)
GU213256	U7	unknown	unknown	Palanichamy et al. (2015)
GU213257	U7	unknown	unknown	Palanichamy et al. (2015)
GU213258	U7	unknown	unknown	Palanichamy et al. (2015)
GU213259	U7	unknown	unknown	Palanichamy et al. (2015)
GU327373	U7	unknown	unknown	Zhang, et al. (unpublished)
HM852777	U7	Armenia	Southwest Asia	Schönberg et al. (2011)
HM852788	U7	Azeri	Southwest Asia	Schönberg et al. (2011)
HM852791	U7	Azeri	Southwest Asia	Schönberg et al. (2011)
HM852801	U7	Azeri	Southwest Asia	Schönberg et al. (2011)
HM852823	U7	Iran	Southwest Asia	Schönberg et al. (2011)
HM852853	U7	Turk	Southwest Asia	Schönberg et al. (2011)
JQ701923	U7	unknown	unknown	Behar et al. (2012)
JQ703913	U7	unknown	unknown	Behar et al. (2012)
JQ703978	U7	Poland: Ashkenazi Jew	Europe	Behar et al. (2012)
JQ704100	U7	unknown	unknown	Behar et al. (2012)
JQ705198	U7	unknown	unknown	Behar et al. (2012)

JQ705966	U7	Iraq: Kirkuk, Mizrachi	Southwest Asia	Behar et al. (2012)
KC911278	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911287	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911288	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911299	U7	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911347	U7	Iran: Lur	Southwest Asia	Derenko et al. (2013)
KC911392	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911402	U7	Iran: Lur	Southwest Asia	Derenko et al. (2013)
KC911415	U7	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911448	U7	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
KC911455	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911470	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911508	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911509	U7	Iran: Kurd	Southwest Asia	Derenko et al. (2013)
KC911526	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911553	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911563	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911615	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911620	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911622	U7	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KJ445972	U7	Israel: Bedouin	Southwest Asia	HGDP - Zheng, et al. (unpublished)
NA18130	U7	Han Chinese	East Asia	Sudmant et al. (2015)
KP763839	U7	India: Uttar Pradesh	South Asia	Palanichamy et al. (2015)
NA20862	U7	GIH	South Asia - West	Sudmant et al. (2015)
NA20889	U7	GIH	South Asia - West	Sudmant et al. (2015)
NA21107	U7	GIH	South Asia - West	Sudmant et al. (2015)
NA21113	U7	GIH	South Asia - West	Sudmant et al. (2015)
NA21130	U7	GIH	South Asia - West	Sudmant et al. (2015)
HM852759	U8	Armenia	Southwest Asia	Schönberg et al. (2011)
JQ702759	U8	unknown	unknown	Behar et al. (2012)
AY882390	U9	Pakistan	South Asia - West	Achilli et al. (2004)
EU597540	U9	Pakistan: Pathan	South Asia - West	Hartmann et al. (2009)
FJ770944	U9	India: Andhra Pradesh	South Asia	Fornarino et al. (2009)
HG03777	U9	ITU	South Asia - South	Sudmant et al. (2015)
HG03916	U9	BEB	South Asia - East	Sudmant et al. (2015)
HG04118	U9	ITU	South Asia - South	Sudmant et al. (2015)
KJ445948	U9	Pakistan: Makrani	South Asia - West	HGDP - Zheng, et al. (unpublished)
KP763838	U9	India	South Asia	Palanichamy et al. (2015)
KP763849	U9	India	South Asia	Palanichamy et al. (2015)
AY882389	U9	Ethiopia	Africa	Achilli et al. (2004)
GU990521	U9	USA	America	Family Tree
NA21108	U9	GIH	South Asia - West	Sudmant et al. (2015)
AY713979	V	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
AY195750	V	unknown	unknown	Mishmar et al. (2003)
AY495307	V	Europe	Europe	Coble et al. (2004)
AY495309	V	Europe	Europe	Coble et al. (2004)
AY495311	V	Europe	Europe	Coble et al. (2004)
AY495315	V	Europe	Europe	Coble et al. (2004)
AY495320	V	Europe	Europe	Coble et al. (2004)
AY495322	V	Europe	Europe	Coble et al. (2004)
AY495326	V	Europe	Europe	Coble et al. (2004)
JN630803	V	Spain: Jew	Europe	Family Tree
KC911406	V	Iran: Persian	Southwest Asia	Derenko et al. (2013)
JQ705658	V2	England	Europe	Behar et al. (2012)
JQ245778	W	Yemen	Southwest Asia	Fernandes et al. (2012)
KC911341	W	Iran: Persian	Southwest Asia	Derenko et al. (2013)
AY714039	W1	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
HG03228	W1	PJL	South Asia - West	Sudmant et al. (2015)
EU257638	W1	unknown	unknown	Family Tree
EU558696	W1	England	Europe	Family Tree

FJ472633	W1	unknown	unknown	Family Tree
GU123002	W1	Russia	Europe	Malyarchuk et al. (2010a)
JQ245768	W1	Turkey	Southwest Asia	Fernandes et al. (2012)
JQ702050	W1	unknown	unknown	Behar et al. (2012)
JQ702450	W1	unknown	unknown	Behar et al. (2012)
JQ706021	W1	United Kingdom	Europe	Behar et al. (2012)
JQ898579	W1	Ashkenazi Jew	Europe	Family Tree
KC911433	W1	Iran: Persian	Southwest Asia	Derenko et al. (2013)
KC911537	W1	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)
AY714043	W3	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
GU002155	W3	India: Punjab	South Asia	Family Tree
HG03778	W3	ITU	South Asia - South	Sudmant et al. (2015)
HG03785	W3	ITU	South Asia - South	Sudmant et al. (2015)
HG03786	W3	ITU	South Asia - South	Sudmant et al. (2015)
HG03815	W3	BEB	South Asia - East	Sudmant et al. (2015)
HG04026	W3	ITU	South Asia - South	Sudmant et al. (2015)
HG04156	W3	BEB	South Asia - East	Sudmant et al. (2015)
KJ445931	W3	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445932	W3	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445933	W3	Pakistan: Sindhi	South Asia - West	HGDP - Zheng, et al. (unpublished)
KJ445934	W3	Pakistan: Pathan	South Asia - West	HGDP - Zheng, et al. (unpublished)
JQ245741	W3	Azerbaijan	Southwest Asia	Fernandes et al. (2012)
JQ245760	W3	Turkey: Kurd	Southwest Asia	Fernandes et al. (2012)
JQ702421	W3	unknown	unknown	Behar et al. (2012)
JQ705313	W3	Austria	Europe	Behar et al. (2012)
AY714018	W4	India: Uttar Pradesh	South Asia - Central	Palanichamy et al. (2004)
NA20858	W4	GIH	South Asia - West	Sudmant et al. (2015)
GU045487	W4	Ulter Scots	Europe	Family Tree
JQ245758	W4	Turkey: Kurd	Southwest Asia	Fernandes et al. (2012)
HG02734	W6	PJL	South Asia - West	Sudmant et al. (2015)
HG04239	W6	ITU	South Asia - South	Sudmant et al. (2015)
NA20851	W6	GIH	South Asia - West	Sudmant et al. (2015)
JF902025	W6	England	Europe	Family Tree
JQ245723	W6	Russia: North Ossetia	Southwest Asia	Fernandes et al. (2012)
JQ245736	W6	Russia: North Ossetia	Southwest Asia	Fernandes et al. (2012)
JQ245769	W6	Turkey	Southwest Asia	Fernandes et al. (2012)
JQ705793	W6	England	Europe	Behar et al. (2012)
KC911604	W6	Iran: Persian	Southwest Asia	Derenko et al. (2013)
HG02733	X	PJL	South Asia - West	Sudmant et al. (2015)
NA20886	X	GIH	South Asia - West	Sudmant et al. (2015)
NA20898	X	GIH	South Asia - West	Sudmant et al. (2015)
EU600318	X	Druze	Southwest Asia	Shlush et al. (2008)
HM852799	X	Azeri	Southwest Asia	Schönberg et al. (2011)
JQ245765	X	Turkey	Southwest Asia	Fernandes et al. (2012)
KC911291	X	Iran: Qashqai	Southwest Asia	Derenko et al. (2013)

Table S2. Dataset used for GW analyses. **(a)** Modern dataset. Populations marked with an asterisk (*) were added to the dataset exclusively for ADMIXTURE analysis. Population codes: BEB – Bengali from Bangladesh; GIH – Gujarati Indian from Houston, Texas; ITU – Indian Telugu from the UK; PJL – Punjabi from Lahore, Pakistan; STU – Sri Lankan Tamil from the UK; CHB – Han Chinese in Beijing, China; TSI – Tuscans from Italy; IRY – Yoruba in Ibadan, Nigeria. **(b)** Yamnaya samples.

(a) Modern dataset

Region	**Population**	**Reference**	***n***
Africa	YRI*	Sudmant et al. (2015)	108
Europe	TSI*	Sudmant et al. (2015)	107
Anatolia + Caucasus	Abkhazians	Yunusbayev et al. (2012)	20
	Adygei	Li et al. (2008)	17
	Armenians	Behar et al. (2010); Yunusbayev et al. (2012)	19
	Azerbaijani Jews	Behar et al. (2010)	8
	Balkars	Yunusbayev et al. (2012)	19
	Chechens	Yunusbayev et al. (2012)	20
	Cypriots	Behar et al. (2010)	12
	Georgian Jews	Behar et al. (2010)	4
	Georgians	Behar et al. (2010)	20
	Kumyks	Yunusbayev et al. (2012)	13
	Lezgins	Behar et al. (2010)	18
	Nogais	Yunusbayev et al. (2012)	16
	North Ossetians	Yunusbayev et al. (2012)	15
	Turks	Behar et al. (2010)	19
Central Asia	Tajiks	Yunusbayev et al. (2012)	15
	Turkmens	Yunusbayev et al. (2012)	12
	Uzbekistani Jews	Behar et al. (2010)	2
	Uzbeks	Behar et al. (2010); Di Cristofaro et al. (2013)	15
Arabia + Near East	Bedouins	Li et al. (2008)	45
	Druze	Li et al. (2008)	42
	Iranian Jews	Behar et al. (2010)	20
	Iranians	Behar et al. (2010)	4
	Iraqi Jews	Behar et al. (2010)	11
	Jordanians	Behar et al. (2010)	20
	Lebanese	Haber et al. (2013)	75
	Lebanese	Behar et al. (2010)	7
	Palestinians	Li et al. (2008)	46
	Samaritans	Chaubey et al. (2011)	3
	Saudis	Behar et al. (2010)	19
	Syrians	Behar et al. (2010)	16
	Yemeni	Behar et al. (2010)	10
	Yemeni Jews	Behar et al. (2010)	15
	Asur	Chaubey et al. (2011)	2
	Balochi	Li et al. (2008)	24
	BEB + Bengali	Chaubey et al. (2011); Sudmant et al. (2015)	87 (86+1)
	Bene Israel	Chaubey et al. (2011)	4
	Bhunjia	Chaubey et al. (2011)	1
	Bonda	Chaubey et al. (2011)	4
	Brahmins_TN (South)	Chaubey et al. (2011)	2

South Asia	Brahmins_UP/UTT (Central)	Chaubey et al. (2011)	9 (8/1)
	Brahui	Li et al. (2008)	25
	Burusho	Li et al. (2008)	25
	Chamar	Chaubey et al. (2011)	10
	Chenchus	Metspalu et al. (2011)	4
	Cochin Jews	Behar et al. (2010)	4
	Dharkars	Chaubey et al. (2011)	12
	Dhurwa	Chaubey et al. (2011)	1
	Dusadh	Chaubey et al. (2011)	10
	Gadaba	Chaubey et al. (2011)	1
	GIH + Gujaratis	Altshuler et al. (2010); Sudmant et al. (2015)	103 (22+81)
	Gond	Metspalu et al. (2011)	4
	Halakipikki	Metspalu et al. (2011)	4
	Ho	Chaubey et al. (2011)	5
	ITU	Sudmant et al. (2015)	102
	Juang	Chaubey et al. (2011)	2
	Kalash	Li et al. (2008)	23
	Kanjars	Chaubey et al. (2011)	8
	Kharia	Chaubey et al. (2011)	2
	Khasi	Chaubey et al. (2011)	3
	Kol	Chaubey et al. (2011)	17
	Kshatriya	Chaubey et al. (2011)	7
	Kurumba	Metspalu et al. (2011)	4
	Lambadi	Chaubey et al. (2011)	1
	Low Caste_TN (South)	Chaubey et al. (2011)	2
	Low Caste_UP (Central)	Chaubey et al. (2011)	5
	Makrani	Li et al. (2008)	25
	Malayan	Behar et al. (2010)	2
	Mawasi	Chaubey et al. (2011)	1
	Meena	Chaubey et al. (2011)	1
	Meghwal	Chaubey et al. (2011)	1
	Muslim	Chaubey et al. (2011)	5
	Nihali	Chaubey et al. (2011)	2
	North Kannadi	Behar et al. (2010)	9
	Paniya	Behar et al. (2010)	4
	Pathan	Li et al. (2008)	22
	Piramalai Kallars	Chaubey et al. (2011)	8
	PJL	Sudmant et al. (2015)	96
	Pulliyar	Metspalu et al. (2011)	5
	Sakilli	Behar et al. (2010)	4
	Santhal	Chaubey et al. (2011)	1
	Savara	Chaubey et al. (2011)	2
	Sindhi	Li et al. (2008)	24
	STU	Sudmant et al. (2015)	102
	Tharus	Chaubey et al. (2011)	2
	Velmas	Metspalu et al. (2011)	10
East Asia	CHB*	Sudmant et al. (2015)	103

(b) Yamanaya

-	Yamanaya	Haak et al. (2015)	9

Table S3. List of ancient individuals used to compute PCA of Figure 2.8. Abbreviations: (PP)N – (Pre-pottery) Neolithic, C/CA – Chalcolithic, (E/M/L)BA – Early/Middle/Late Bronze Age, IA – Iron Age, H – Historical

SampleID	PCA label	Country	Reference
RISE240 RISE546 RISE547 RISE548 RISE550 RISE552	Yamnaya	Russia	Allentoft et al. (2015)
DA379 DA380 DA381 DA383	Turkmenistan_Namazga_CA	Turkmenistan	de Barros Damgaard et al. (2018)
DA382	Turkmenistan_IA		
MA2197 MA2198	Anatolia_IA	Turkey	
MA2200-01 MA2203-04 MA2205 MA2206 MA2208-09	Anatolia_MLBA		
MA2210 MA2212 MA2213	Anatolia_EBA		
Yamnaya	Yamnaya	Kazakhstan	
ERS1790729 ERS1790730 ERS1790731 ERS1790732 ERS1790733	Levant_MBA	Lebanon	Haber et al. (2017)
I0644 I1152 I1154 I1155 I1160 I1164 I1165 I1166 I1168 I1169 I1170 I1171	Levant_C	Israel	Harney et al. (2018)
I117C I1177 I1178 I1179 I1180 I1181 I1182 I1183 I1184 I1187	Levant_C	Israel	
Bar31 Bar8	Anatolia_N	Turkey	Hofmanová et al. (2016)
KK1 SATP	CHG	Georgia	Jones et al. (2015)
Bon001 Bon002 Bon004 Bon005 Tep001 Tep002 Tep003 Tep004 Tep006	Anatolia_N	Turkey	Kılınç et al. (2016)
I1584	Anatolia_C	Turkey	Lazaridis et al. (2016)
I1705 I1706 I1730	Levant_EBA	Jordan	
I0867	Levant_PPN	Israel	
I1414 I1415 I1679	Levant_PPN	Jordan	

I1699			
I1700			
I1701			
I1704			
I1707			
I1709			
I1710			
I1727			
I0861	Natufian	Israel	
I1069			
I1072			
I1685			
I1687			
I1690			
I2495	Anatolia_EBA	Turkey	Lazaridis et al. (2017)l
I2499			
I2683			
I0231	Yamnaya	Russia	Mathieson et al. (2015)
I0357			
I0438			
I0439			
I0441			
I0443			
I0444			
I0707	Anatolia_N	Turkey	
I0708			
I0709			
I0723			
I0724			
I0725			
I0726			
I0727			
I0736			
I0744			
I0745			
I0746			
I0854			
I1096			
I1097			
I1098			
I1099			
I1100			
I1101			
I1102			
I1103			
I1580			
I1581			
I1583			
Bul4	Yamnaya	Bulgaria	Mathieson et al. (2018)
I1917	Yamnaya	Ukraine	
I2105			
I3141			
I0244	ForestSteppe_EMBA	Russia	Narasimhan et al. (2018)
I1829			
I2071			
I3387			
I3388			
I3950			
I3952			
I3954			
I5269			
I5272			
I5273			
I5277			
I5278			
I5279			
I6294			
I6711			
I6712			
I6713			
I6715			
I7489			
I7671			
I0246			
I0419			
I3753	ForestSteppe_LBA	Kazakhstan	
I3772			
I3976			
I3977			

I4267		
I4295		
I0507	ForestSteppe_MLBA	
I1931		
I3447		
I3448		
I3763		
I3767		
I3769		
I3770		
I3788		
I3860		
I3861		
I3864		
I4262		
I4263		
I4264		
I4265		
I4318		
I4321		
I4322		
I4323		
I4566		
I4567		
I4568		
I4773		
I4774		
I4776		
I4778		
I4780		
I4782		
I4783		
I4784		
I4787		
I4789		
I4790		
I4791		
I4794		
I5761		
I6707		
I6708		
I6788		
I6789		
I6790		
I6791		
I6792		
I6793		
I6794		
I6795		
I6796		
I6797		
I6799		
I6800		
I6823		
I7059		
I7060		
I0937	ForestSteppe_MLBA	Russia
I0938		
I0939		
I0941		
I0942		
I0943		
I0944		
I0945		
I0946		
I0980		
I0982		
I0983		
I0984		
I0986		
I0989		
I1003		
I1006		
I1007		
I1008		
I1011		
I1012		
I1013		
I1017		
I1018		
I1020		
I1022		

I1024 I1027 I1028 I1029 I1053 I1057 I1060 I1061 I1062 I1063 I1064 I1065 I1082 I1084 I1088 I1089 I1090 I1821 I1828 I1851 I1852 I1853 I1856 I3389 I3390 I3391 I3392 I3394 I3395 I3396 I6716 I6717 I6718 I7480 I7670 I0232 I0354 I0358 I0359 I0360 I0422 I0430 I0431		
I4160 I4258	ForestSteppe_MLBA	Tajikistan
I4153 I4255	ForestSteppe_MLBA	Uzbekistan
I1960 I5766	ForestSteppe_N	Russia
Darra.I.Kur	IranTuran_BA	Afghanistan
I8724 I8725 I8726 I8728	IranTuran_BA	Iran
I1781 I1783 I1784 I1787 I1788 I1793 I2085 I2087 I2116 I2121 I2123 I2125 I2128 I3374 I6119 I6124 I6217 I6667 I6668 I6671 I6674 I6675	IranTuran_BA	Turkmenistan
I4156 I4157 I4159 I4161 I4163	IranTuran_BA	Uzbekistan

I4285 I4286 I4288 I4289 I4312 I4313 I4315 I4899 I4901 I5604 I5605 I5608 I7411 I7412 I7414 I7416 I7419 I7420 I7421 I7492 I7493 I7494 I7495 I7542		
I2323 I2327 I2328 I2337 I2512 I2514 I2918 I2921 I2922 I2923 I2924 I2925 I2927 I2928 I4241 I4349 I4351	IranTuran_C	Iran
I4910	IranTuran_C	Tajikistan
I4085 I4086 I4087 I4259 I4634 I4635 I6669 I8504 I8510 I8524 I8526 I8527 I8528 I8529 I8532	IranTuran_C	Turkmenistan
I1947 I1954 I7527 I1944 I1945 I1949	IranTuran_N	Iran
I6549 **I6550** **I6551** **I6888** **I6891** **I6893** **I6894** **I6896** **I7717** **I7718** **I7719** **I7720** **I7721** **I7722** **I7723**	SouthAsia_H	Pakistan
I10000 I10001	SouthAsia_IA	

I10974 I1796 I1799 I1985 I1992 I1994 I3261 I5396 I5397 I5398 I5399 I5400 I6195 I6198 I6292 I6545 I6546 I6547 I6548 I6553 I6555 I6556 I6557 I6897 I6899 I6900 I6901 I7725 I8192 I8193 I8194 I8195 I8219 I8220 I8245 I8246 I8997 I8998 I8999			
I0361 I0424	Yamnaya	Russia	
kum4 kum6	Anatolia_N	Turkey	Kılınç et al. (2016)
I1934 I2062	Levant_MLBA	Israel	van den Brink et al. (2017)

Table S4. Age estimates (in ka) of the non-autochthonous South Asian mtDNA clades mentioned in the text.

Clade	ML	ρ	Clade	ML	ρ
N1a2	12.5 [2.9–22.6]	6.5 [2.1–11.2]	T2b	10.6 [5.3–16.0]	7.1 [3.6–10.8]
N1a1b1	20.9 [11.4–30.8]	19.0 [10.4–27.9]	T2d1a	12.0 [5.0–19.3]	10.6 [4.5–16.9]
H2b	6.2 [3.8–8.7]	5.2 [3.4–7.1]	T2e2	10.6 [3.4–18.1]	12.0 [4.1–20.3]
H13a2a+8952	6.6 [1.3–12.1]	7.2 [1.0–13.6]	U1a1	20.0 [14.4–25.7]	15.2 [10.4–20.1]
H29+9156+4689	1.6 [0.0–4.7]	1.3 [0.0–3.8]	U1a1a2a	2.5 [0.0–7.3]	1.9 [0.0–4.8]
HV+73	23.7 [17.1–30.4]	30.1 [19.6–41.0]	U1a3+10253	10.3 [4.6–16.2]	8.9 [4.6–13.3]
HV+146	23.9 [10.3–38.4]	19.0 [8.8–29.8]	U1a3a	5.2 [0.0–11.0]	3.9 [0.0–8.4]
HV+9716	19.6 [8.1–31.8]	13.4 [5.0–22.2]	Pre-U1c	21.4 [9.1–34.5]	14.3 [6.7–22.2]
HV+16311	15.6 [9.9–21.5]	15.5 [7.6–23.8]	U2	52.3 [41.6–63.3]	53.8 [41.8–66.2]
HV2	21.9 [15.1–28.9]	30.7 [17.9–44.2]	U2b2	9.2 [6.3–12.2]	8.6 [6.1–11.1]
HV12b	13.3 [5.3–21.6]	12.6 [5.7–19.8]	U2c1+146	1.4 [0.0–24.8]	1.7 [0.0–5.1]
HV14+150	6.9 [2.9–11.0]	6.7 [1.0–12.6]	U7a	18.1 [14.4–22.0]	18.8 [14.5–23.2]
I1	13.8 [8.5–19.2]	10.6 [6.3–15.0]	U7a+12373	10.2 [3.0–17.6]	8.8 [2.8–15.0]
J1b1b1	13.9 [8.6–19.3]	12.6 [7.9–17.4]	U7a3a+6150	9.8 [4.4–15.4]	8.6 [3.5–13.8]
J1d	24.1 [14.9–33.7]	16.2 [10.2–22.3]	U7b+16309!	10.9 [6.1–15.9]	8.6 [3.6–13.8]
K1a1b2a	10.4 [4.0–17.0]	12.0 [4.1–20.3]	W3a1+143	9.8 [3.0–16.8]	7.9 [1.5–14.5]
K2a5	7.6 [3.6–11.7]	8.2 [3.9–12.6]	W3a1+1709	8.1 [1.6–15.0]	6.5 [0.8–12.5]
K2a5+2831	6.8 [2.9–10.7]	8.4 [3.5–13.5]	W3a1b	11.4 [6.3–16.6]	11.2 [6.1–16.3]
K2a5+2831+189	5.9 [2.1–9.8]	10.6 [3.2–18.4]	W4	15.8 [9.5–22.3]	15.5 [8.7–22.5]
R0a2+11152	7.1 [1.1–13.3]	6.5 [0.8–12.5]	W6	11.5 [5.0–18.3]	10.9 [5.7–16.3]
R2a+7142	3.2 [0.0–6.9]	2.9 [0.0–5.9]	X2+153+7109	7.7 [0.0–17.0]	4.3 [0.0–9.0]
T2+195+4225	9.7 [2.9–16.8]	6.8 [2.3–11.5]			

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Appendix B

Supplementary Material for Chapter III

Dissecting mtDNA haplogroups H1, H2, H11 and H13

Table S1. List of ancient H mtDNA sequences used to build the map shown in Figure 3.11. Dates are calculated as the average of 95.4% date range in calibrated (cal.) BP (defined as 1950 CE).

Sample	Date (cal. BP)	Country	Lat.	Long.	Reference
I1069	12750	Israel	32.65	35.07	Lazaridis et al. (2016)
I1690	12750	Israel	32.65	35.07	Lazaridis et al. (2016)
I1949	10052	Iran	34.45	48.12	Lazaridis et al. (2016)
I5407	9800	Serbia	44.55	22.03	Mathieson et al. (2018)
KK1	9720	Georgia	42.28	43.28	Jones et al. (2015)
I4081	9335	Romania	44.52	22.72	Mathieson et al. (2018)
I1580	8195	Turkey	40.30	29.57	Mathieson et al. (2018)
I4666	8017	Serbia	44.55	22.03	Mathieson et al. (2018)
I0726	7950	Turkey	40.26	29.65	Mathieson et al. (2018)
I0698	7900	Bulgaria	42.10	25.75	Mathieson et al. (2018)
I3879	7828	Bulgaria	43.98	26.40	Mathieson et al. (2018)
I1297	7817	Bulgaria	43.98	26.40	Mathieson et al. (2018)
I3433	7814	Croatia	43.59	16.65	Mathieson et al. (2018)
I2373	7700	Hungary	47.18	20.35	Lipson et al. (2017)
arm7	7700	Armenia	40.10	44.29	Margaryan et al. (2017)
arm9	7700	Armenia	40.10	44.29	Margaryan et al. (2017)
I0679	7622	Bulgaria	42.02	25.60	Mathieson et al. (2018)
I5071	7571	Croatia	44.82	13.64	Mathieson et al. (2018)
I5072	7551	Croatia	44.82	13.64	Mathieson et al. (2018)
I2521	7505	Bulgaria	43.16	25.88	Mathieson et al. (2018)
H3C6	7285	Spain	38.84	-0.37	Olalde et al. (2015)
G21	7230	Portugal	39.50	-8.62	Olalde et al. (2015)
F19	7215	Portugal	39.50	-8.62	Olalde et al. (2015)
I1895	7151	Hungary	45.60	18.28	Lipson et al. (2017)
I0797	7125	Germany	51.28	11.65	Mathieson et al. (2015)
I2030	7125	Germany	51.90	11.05	Lipson et al. (2017)
NE2.SG	7124	Hungary	47.52	21.59	Mathieson et al. (2015)
I0023	7100	Germany	48.78	9.18	Haak et al. (2015)
I0027	7100	Germany	48.78	9.18	Haak et al. (2015)
I0796	7088	Germany	51.28	11.65	Brotherton et al. (2013)
I0795	7079	Germany	51.28	11.65	Mathieson et al. (2015)
I2199	7074	Spain	42.63	-3.12	Lipson et al. (2017)
DEB9	7063	Germany	51.88	11.03	Brotherton et al. (2013)
HAL11_8201	7063	Germany	51.88	11.04	Brotherton et al. (2013)
DEB21	7060	Germany	51.88	11.03	Brotherton et al. (2013)
I2037	7056	Germany	51.90	11.05	Lipson et al. (2017)
I2357	7050	Hungary	47.46	20.51	Lipson et al. (2017)
I2375	7050	Hungary	48.00	21.18	Lipson et al. (2017)
I2743	7050	Hungary	47.18	19.86	Lipson et al. (2017)
I4181	7050	Hungary	46.74	18.96	Lipson et al. (2017)
I1891	6969	Hungary	46.42	18.92	Lipson et al. (2017)
I5205	6950	Austria	48.58	16.47	Mathieson et al. (2018)
I5207	6950	Austria	48.58	16.47	Mathieson et al. (2018)
I3719	6824	Ukraine	48.91	33.76	Mathieson et al. (2018)
I0122	6800	Russia	52.22	48.10	Mathieson et al. (2015)
I2746	6700	Hungary	46.94	21.21	Lipson et al. (2017)
I4303	6633	France	43.46	5.86	Olalde et al. (2018)
I1902	6600	Hungary	47.02	17.96	Lipson et al. (2017)
I1906	6600	Hungary	47.51	18.62	Lipson et al. (2017)
ANI163	6577	Bulgaria	43.21	27.86	Mathieson et al. (2018)
I5078	6569	Croatia	45.55	18.75	Mathieson et al. (2018)
ANI160	6550	Bulgaria	43.21	27.86	Mathieson et al. (2018)
I1661	6544	Iran	34.50	47.96	Lazaridis et al. (2016)
I1131	6483	Serbia	44.90	19.75	Mathieson et al. (2018)
I0163	6445	Germany	51.66	11.53	Brotherton et al. (2013)
I2423	6388	Bulgaria	43.06	26.98	Mathieson et al. (2018)
I0162	6388	Germany	51.67	11.53	Brotherton et al. (2013)
OSH2_4362B	6388	Germany	51.66	11.53	Brotherton et al. (2013)
OSH3_4364	6388	Germany	51.66	11.53	Brotherton et al. (2013)
I0785	6357	Bulgaria	42.23	24.26	Mathieson et al. (2018)
I2427	6340	Bulgaria	43.06	26.77	Mathieson et al. (2018)
I2793	6301	Hungary	47.19	20.40	Lipson et al. (2017)
I2394	6238	Hungary	47.10	17.91	Lipson et al. (2017)
I2395	6200	Hungary	47.46	20.51	Lipson et al. (2017)
I1166	6150	Israel	32.98	35.31	Harney et al. (2018)
I1634	6145	Armenia	39.73	45.20	Lazaridis et al. (2016)
N31	6138	Poland	52.61	18.80	Fernandes et al. (2018)
KZ3	6100	Poland	52.74	18.25	Juras et al. (2017a)
I0798	6081	Germany	51.53	11.83	Brotherton et al. (2013)
MA76	6070	Italy	40.66	8.58	Olivieri et al. (2017)
I7042	6050	Hungary	47.43	19.05	Olalde et al. (2018)
NHP1	6050	Poland	50.07	20.11	Chyleński et al. (2017)
I0799	5975	Germany	51.53	11.83	Brotherton et al. (2013)

I6561	5960	Ukraine	48.66	33.10	Mathieson et al. (2018)
I0644	5950	Israel	32.97	35.33	Harney et al. (2018)
I7679	5950	Spain	36.45	-6.21	Olalde et al. (2019)
LugarCanto42	5950	Portugal	39.41	-8.82	Martiniano et al. (2017)
LugarCanto44	5950	Portugal	39.41	-8.82	Martiniano et al. (2017)
I2318	5945	Greece	37.42	23.13	Mathieson et al. (2018)
I1407	5875	Armenia	39.73	45.20	Lazaridis et al. (2016)
I0807	5790	Germany	51.42	11.68	Mathieson et al. (2015)
I3920	5770	Greece	36.64	22.38	Mathieson et al. (2018)
I1926	5736	Ukraine	48.72	25.88	Mathieson et al. (2018)
I2788	5730	Hungary	47.19	20.00	Lipson et al. (2017)
I0406	5700	Spain	41.25	-2.33	Mathieson et al. (2015)
I2659	5652	Great Britain	56.41	-5.47	Olalde et al. (2018)
I0808	5625	Germany	51.48	12.13	Brotherton et al. (2013)
I7646	5620	Spain	38.70	-0.49	Olalde et al. (2019)
I5359	5600	Great Britain	51.45	-3.31	Olalde et al. (2018)
I5371	5600	Great Britain	56.41	-5.47	Olalde et al. (2018)
I2796	5571	Great Britain	59.31	-2.94	Olalde et al. (2018)
MA77	5568	Italy	40.66	8.58	Olivieri et al. (2017)
3.17.1	5550	Ukraine	48.78	25.84	Nikitin et al. (2017)
N20	5462	Poland	52.62	18.96	Fernandes et al. (2018)
I4085	5450	Turkmenistan	37.87	58.23	Narasimhan et al. (2018)
S8505.E1.L1	5450	Turkmenistan	37.19	61.03	Narasimhan et al. (2018)
I3136	5394	Great Britain	56.40	-5.48	Olalde et al. (2018)
I1563	5361	Germany	51.36	7.55	Lipson et al. (2017)
arm40	5250	Armenia	39.58	45.92	Margaryan et al. (2017)
RISE487	5245	Italy	45.26	10.38	Allentoft et al. (2015)
poz090	5225	Ukraine	48.24	28.28	Juras et al. (2018)
M5	5200	Ukraine	48.78	25.84	Nikitin et al. (2017)
I2980	5181	Great Britain	59.31	-2.94	Olalde et al. (2018)
I0800	5171	Germany	51.53	11.83	Lipson et al. (2017)
I0802	5163	Germany	51.53	11.83	Lipson et al. (2017)
I0552	5163	Germany	51.52	11.85	Haak et al. (2015)
I7604	5150	Spain	43.09	-2.25	Olalde et al. (2019)
I7605	5150	Spain	43.09	-2.25	Olalde et al. (2019)
I11301	5136	Spain	43.09	-2.22	Olalde et al. (2019)
I2520	5132	Bulgaria	43.16	25.88	Mathieson et al. (2018)
I5076	5131	Portugal	37.20	-8.59	Olalde et al. (2019)
I2366	5093	Hungary	47.62	19.04	Lipson et al. (2017)
Gok4	5085	Sweden	58.18	13.39	Skoglund et al. (2014)
I0444	5059	Russia	53.31	51.15	Mathieson et al. (2015)
I11600	5050	Portugal	39.11	-8.66	Martiniano et al. (2017)
I6766	5050	UnitedKingdom	57.91	-4.00	Brace et al. (2019)
I1842	5000	Spain	42.63	-2.70	Olalde et al. (2019)
I2407	4955	Poland	52.85	17.88	Mathieson et al. (2018)
I2631	4952	Great Britain	59.23	-2.57	Olalde et al. (2018)
I0370	4950	Russia	51.27	58.18	Mathieson et al. (2015)
I2433	4950	Poland	52.85	17.88	Mathieson et al. (2018)
I2435	4950	Poland	52.85	17.88	Mathieson et al. (2018)
I2440	4950	Poland	52.85	17.88	Mathieson et al. (2018)
I3141	4950	Ukraine	48.22	37.15	Mathieson et al. (2018)
poz222	4917	Ukraine	48.24	28.28	Juras et al. (2018)
I4565	4915	Spain	41.29	1.06	Olalde et al. (2019)
poz232	4912	Poland	50.45	27.79	Juras et al. (2018)
CovaMoura364	4900	Portugal	38.75	-9.22	Martiniano et al. (2017)
I10283	4900	Spain	41.44	1.57	Olalde et al. (2019)
I11303	4900	Spain	41.44	1.57	Olalde et al. (2019)
Gok2	4900	Sweden	58.18	13.39	Skoglund et al. (2014)
Gok7	4900	Sweden	58.18	13.39	Skoglund et al. (2014)
atp12-1420	4896	Spain	42.37	-3.56	Valdiosera et al. (2018)
ATP17	4889	Spain	42.37	-3.56	Günther et al. (2015)
arm2	4850	Armenia	40.87	43.75	Margaryan et al. (2017)
I2977	4836	Great Britain	58.74	-2.92	Olalde et al. (2018)
poz211	4780	Ukraine	48.24	28.28	Juras et al. (2018)
I0441	4766	Russia	52.30	52.05	Mathieson et al. (2015)
I2473	4765	Spain	42.57	-2.62	Lipson et al. (2017)
I2510	4758	Bulgaria	43.16	25.88	Mathieson et al. (2018)
CO1.SG	4750	Hungary	47.17	19.83	Mathieson et al. (2015)
poz208	4740	Ukraine	48.24	28.28	Juras et al. (2018)
I0455	4735	Spain	38.10	-1.85	Olalde et al. (2018)
I4930	4721	Italy	37.73	12.96	Olalde et al. (2018)
MA2210	4700	Turkey	38.63	34.30	de Barros Damgaard et al. (2018a)
I8569	4699	Spain	40.30	0.28	Olalde et al. (2019)
poz214	4697	Ukraine	48.24	28.28	Juras et al. (2018)
poz225	4690	Ukraine	48.19	28.45	Juras et al. (2018)
I1281	4670	Spain	42.33	-3.50	Mathieson et al. (2015)
poz224	4661	Ukraine	48.24	28.28	Juras et al. (2018)
I11614	4650	Portugal	39.08	9.27	Olalde et al. (2019)
I8155	4650	Spain	37.24	-4.24	Olalde et al. (2019)
I8158	4650	Spain	37.24	-4.24	Olalde et al. (2019)
I8197	4650	Spain	37.24	-4.24	Olalde et al. (2019)
I0126	4627	Russia	53.31	51.15	Mathieson et al. (2015)

poz220	4619	Ukraine	48.24	28.28	Juras et al. (2018)
I0826	4607	Spain	41.49	2.14	Olalde et al. (2018)
I1392	4604	France	47.34	7.31	Olalde et al. (2018)
I5374	4595	Great Britain	51.28	-2.74	Olalde et al. (2018)
I8365	4589	Spain	37.24	-4.24	Olalde et al. (2019)
I1274	4573	Spain	42.33	-3.50	Mathieson et al. (2015)
I1276	4573	Spain	42.33	-3.50	Mathieson et al. (2015)
I1282	4573	Spain	42.33	-3.50	Mathieson et al. (2015)
I1284	4573	Spain	42.33	-3.50	Mathieson et al. (2015)
I5118	4550	Hungary	47.81	20.89	Olalde et al. (2018)
I6596	4550	Spain	40.22	-3.76	Olalde et al. (2018)
I6617	4550	Spain	40.22	-3.76	Olalde et al. (2018)
I6628	4550	Spain	40.22	-3.76	Olalde et al. (2018)
poz234	4500	Poland	50.45	27.79	Juras et al. (2018)
poz235	4500	Poland	50.45	27.79	Juras et al. (2018)
poz280	4500	Poland	50.34	20.52	Juras et al. (2018)
poz281	4500	Poland	50.34	20.52	Juras et al. (2018)
poz282	4500	Poland	50.34	20.52	Juras et al. (2018)
I1553	4500	Spain	41.49	2.14	Olalde et al. (2018)
I1633	4465	Armenia	40.65	45.12	Lazaridis et al. (2016)
I8132	4450	Spain	38.98	-0.16	Olalde et al. (2019)
Sope	4413	Estonia	59.41	27.03	Saag et al. (2017)
I0257	4411	Spain	41.49	2.14	Olalde et al. (2018)
I1976	4409	Spain	42.57	-2.62	Lipson et al. (2017)
I2932	4409	Great Britain	58.74	-2.92	Olalde et al. (2018)
I1277	4407	Spain	42.33	-3.50	Mathieson et al. (2015)
N45	4405	Poland	52.62	18.96	Fernandes et al. (2018)
N49	4405	Poland	52.62	18.96	Fernandes et al. (2018)
poz221	4398	Ukraine	48.24	28.28	Juras et al. (2018)
I0108	4387	Germany	51.45	11.54	Mathieson et al. (2015)
I2495	4377	Turkey	37.92	30.71	Lazaridis et al. (2017)
I0051	4369	Germany	51.45	11.63	Haak et al. (2015)
I6605	4357	Spain	40.44	-3.50	Olalde et al. (2018)
UNTA85_1336	4353	Germany	48.32	10.89	Knipper et al. (2017)
I0258	4350	Spain	41.49	2.14	Olalde et al. (2018)
I0374	4350	Russia	49.97	44.67	Mathieson et al. (2015)
I0823	4350	Spain	41.49	2.14	Olalde et al. (2018)
I9129	4350	Greece	35.05	24.81	Lazaridis et al. (2017)
Spiginas1	4340	Lithuania	55.77	22.42	Mittnik et al. (2018)
ESP15_4408	4333	Germany	51.41	11.67	Brotherton et al. (2013)
I3238	4300	Spain	43.41	-5.98	Olalde et al. (2019)
I4947	4300	Czech Republic	50.05	14.37	Olalde et al. (2018)
I7041	4300	Hungary	47.43	19.05	Olalde et al. (2018)
RISE671	4300	Russia	53.16	90.21	de Barros Damgaard et al. (2018a)
RISE672	4300	Russia	53.16	90.21	de Barros Damgaard et al. (2018a)
poz279	4295	Poland	50.34	20.52	Juras et al. (2018)
I0111	4290	Germany	51.45	11.54	Mathieson et al. (2015)
I4131	4289	Hungary	47.60	19.05	Olalde et al. (2018)
I0460	4285	Spain	42.40	-3.75	Olalde et al. (2018)
I4124	4284	Germany	48.33	10.90	Allentoft et al. (2015)
I4143	4282	Germany	48.66	12.71	Allentoft et al. (2015)
I3592	4281	Germany	48.88	12.53	Olalde et al. (2018)
I2461	4270	Great Britain	51.13	-1.69	Olalde et al. (2018)
ALB1_4442	4258	Germany	51.44	11.61	Brotherton et al. (2013)
I2741	4256	Hungary	47.38	19.02	Olalde et al. (2018)
I0805	4255	Germany	51.79	11.14	Mathieson et al. (2015)
I5385	4252	Great Britain	58.36	-3.40	Olalde et al. (2018)
I6581	4251	Poland	50.09	18.10	Olalde et al. (2018)
I0112	4250	Germany	51.79	11.14	Mathieson et al. (2015)
I4890	4250	Czech Republic	50.12	14.46	Olalde et al. (2018)
I5376	4250	Great Britain	51.47	-0.31	Olalde et al. (2018)
I5524	4250	Germany	48.66	12.71	Olalde et al. (2018)
I5526	4250	Germany	48.66	12.71	Olalde et al. (2018)
I5836	4250	Germany	49.65	8.33	Olalde et al. (2018)
I6601	4250	Portugal	39.09	-9.29	Olalde et al. (2018)
I7195	4250	Czech Republic	50.05	14.37	Olalde et al. (2018)
I7203	4250	Czech Republic	50.05	14.37	Olalde et al. (2018)
I1530	4249	Germany	51.45	11.54	Mathieson et al. (2015)
QUEXII3_4330C	4249	Germany	51.78	11.14	Brotherton et al. (2013
I1388	4246	France	45.46	6.21	Olalde et al. (2018)
I4251	4242	Poland	50.65	20.66	Olalde et al. (2018)
I0806	4241	Germany	51.79	11.14	Mathieson et al. (2015)
ROT2_4448	4225	Germany	51.45	11.54	Brotherton et al. (2013)
I3593	4222	Germany	48.88	12.53	Olalde et al. (2018)
UNTA85_1334	4219	Germany	48.32	10.89	Knipper et al. (2017)
I4134	4200	Germany	48.69	13.02	Allentoft et al. (2015)
I5655	4200	Germany	48.84	12.75	Olalde et al. (2018)
I6584	4200	Spain	40.22	-3.76	Olalde et al. (2018)
I7205	4200	Czech Republic	50.41	14.07	Olalde et al. (2018)
I7276	4200	Czech Republic	50.19	14.16	Olalde et al. (2018)
I7279	4200	Czech Republic	50.19	14.16	Olalde et al. (2018)
I7288	4200	Czech Republic	50.41	14.07	Olalde et al. (2018)

QUEXII1_4325	4198	Germany	51.78	11.14	Brotherton et al. (2013)
I3590	4191	Germany	48.88	12.53	Olalde et al. (2018)
I4249	4189	Germany	48.84	12.75	Olalde et al. (2018)
I0059	4188	Germany	51.82	10.91	Mathieson et al. (2015)
I5757	4178	Switzerland	46.23	7.35	Olalde et al. (2018)
I3587	4175	Germany	48.88	12.53	Olalde et al. (2018)
I3588	4175	Germany	48.88	12.53	Olalde et al. (2018)
I3596	4175	Germany	48.88	12.53	Olalde et al. (2018)
I3599	4175	Germany	48.88	12.53	Olalde et al. (2018)
I3601	4175	Germany	48.88	12.53	Olalde et al. (2018)
I0059	4170	Germany	51.82	10.91	Brotherton et al. (2013)
I4945	4168	Czech Republic	50.12	14.46	Olalde et al. (2018)
E09613	4165	Germany	48.33	10.90	Olalde et al. (2018)
I0058	4165	Germany	51.82	10.91	Brotherton et al. (2013)
I6774	4150	Great Britain	50.86	-0.12	Olalde et al. (2018)
I6775	4150	Great Britain	51.12	-3.08	Olalde et al. (2018)
I7281	4150	Czech Republic	50.04	14.34	Olalde et al. (2018)
I4895	4110	Czech Republic	50.05	14.37	Olalde et al. (2018)
I4145	4106	Czech Republic	50.12	14.26	Allentoft et al. (2015)
I1381	4100	France	49.15	6.10	Olalde et al. (2018)
I6543	4100	Spain	40.44	-3.50	Olalde et al. (2018)
I5471	4096	Great Britain	55.95	-2.47	Olalde et al. (2018)
I6626	4075	Spain	40.44	-3.50	Olalde et al. (2018)
I4886	4074	Czech Republic	50.12	14.46	Olalde et al. (2018)
I2604	4070	Great Britain	51.15	-1.36	Olalde et al. (2018)
RISE516	4069	Russia	53.16	90.21	de Barros Damgaard et al. (2018a)
POST_38	4067	Germany	48.31	10.89	Knipper et al. (2017)
I6124	4062	Turkmenistan	38.19	62.03	Narasimhan et al. (2018)
RISE71	4060	Denmark	56.68	10.03	Allentoft et al. (2015)
I7210	4050	Czech Republic	50.41	14.07	Olalde et al. (2018)
I2452	4049	Great Britain	52.15	-0.38	Olalde et al. (2018)
I4074	4046	Netherlands	52.73	5.10	Olalde et al. (2018)
I7635	4037	Great Britain	54.52	-1.31	Olalde et al. (2018)
I1705	4032	Jordan	31.99	35.98	Lazaridis et al. (2016)
RISE42	4031	Denmark	55.66	12.15	Allentoft et al. (2015)
POST_24	4030	Germany	48.31	10.89	Knipper et al. (2017)
RISE145	4022	Poland	50.91	17.18	Allentoft et al. (2015)
I0804	4001	Germany	51.17	11.85	Mathieson et al. (2015)
I0070	4000	Greece	35.08	25.83	Lazaridis et al. (2017)
I0073	4000	Greece	35.08	25.83	Lazaridis et al. (2017)
I0074	4000	Greece	35.08	25.83	Lazaridis et al. (2017)
I6318	4000	Turkmenistan	38.19	62.03	Narasimhan et al. (2018)
I7043	4000	Hungary	47.43	19.05	Olalde et al. (2018)
I7489	4000	Russia	52.91	50.99	Narasimhan et al. (2018)
QUEXII2_4327B	3996	Germany	51.78	11.14	Brotherton et al. (2013)
I2618	3993	Great Britain	55.06	-2.15	Olalde et al. (2018)
MA78	3992	Italy	39.24	9.49	Olivieri et al. (2017)
I3875	3991	France	44.48	6.37	Olalde et al. (2018)
I2598	3990	Great Britain	51.16	-1.77	Olalde et al. (2018)
I0803	3987	Germany	51.17	11.85	Mathieson et al. (2015)
poz213	3984	Ukraine	48.24	28.28	Juras et al. (2018)
I4075	3979	Netherlands	52.73	5.10	Olalde et al. (2018)
RISE683	3977	Russia	53.71	90.36	de Barros Damgaard et al. (2018)
I1788	3966	Turkmenistan	38.19	62.03	Narasimhan et al. (2018)
BZH8_9417	3962	Germany	51.83	10.86	Brotherton et al. (2013)
POST_140	3944	Germany	48.31	10.89	Knipper et al. (2017)
OBKR_85	3938	Germany	48.27	10.88	Knipper et al. (2017)
POST_35	3936	Germany	48.31	10.89	Knipper et al. (2017)
UNTA58-62_147	3929	Germany	48.32	10.89	Knipper et al. (2017)
WEHR_1415child	3914	Germany	48.25	10.78	Knipper et al. (2017)
MA85	3901	Italy	39.39	9.16	Olivieri et al. (2017)
QUEVIII4_4308B	3899	Germany	51.78	11.14	Brotherton et al. (2013)
POST_1	3878	Germany	48.31	10.89	Knipper et al. (2017)
UNTA85_1163	3878	Germany	48.32	10.89	Knipper et al. (2017)
poz094	3875	Ukraine	48.24	28.28	Juras et al. (2018)
OBKR_79	3874	Germany	48.27	10.88	Knipper et al. (2017)
WEHR_1415adult	3868	Germany	48.25	10.78	Knipper et al. (2017)
UNTA58-62_146	3867	Germany	48.32	10.89	Knipper et al. (2017)
OBKR_96	3866	Germany	48.27	10.88	Knipper et al. (2017)
I5515	3856	Great Britain	56.06	-3.42	Olalde et al. (2018)
I3756	3848	Spain	38.58	-2.84	Olalde et al. (2019)
I6538	3838	Poland	50.91	16.79	Olalde et al. (2018)
BZH1_9403	3838	Germany	51.83	10.86	Brotherton et al. (2013)
WEHR_1193	3829	Germany	48.25	10.78	Knipper et al. (2017)
I7495	3827	Uzbekistan	37.42	66.83	Narasimhan et al. (2018)
I0938	3800	Russia	52.82	60.47	Narasimhan et al. (2018)
I0942	3800	Russia	52.82	60.47	Narasimhan et al. (2018)
I0980	3800	Russia	52.82	60.47	Narasimhan et al. (2018)
I0986	3800	Russia	52.82	60.47	Narasimhan et al. (2018)
I0989	3800	Russia	52.82	60.47	Narasimhan et al. (2018)
I1024	3800	Russia	52.82	60.47	Narasimhan et al. (2018)
I1061	3800	Russia	52.82	60.47	Narasimhan et al. (2018)

I1065	3800	Russia	52.82	60.47	Narasimhan et al. (2018)
MA2208	3800	Turkey	39.35	33.79	de Barros Damgaard et al. (2018)
I9005	3800	Greece	35.08	25.83	Lazaridis et al. (2017)
I1053	3793	Russia	52.82	60.47	Narasimhan et al. (2018)
I1017	3791	Russia	52.82	60.47	Narasimhan et al. (2018)
BZH14_9429	3782	Germany	51.83	10.86	Brotherton et al. (2013)
poz356	3776	Ukraine	48.24	28.28	Juras et al. (2018)
I12809	3775	Spain	38.58	-2.84	Olalde et al. (2019)
I1054	3769	Russia	52.82	60.47	Narasimhan et al. (2018)
I4884	3764	Czech Republic	50.12	14.46	Olalde et al. (2018)
burial 46	3750	Lebanon	33.56	35.40	Haber et al. (2017)
I5441	3750	Great Britain	50.43	-3.58	Olalde et al. (2018)
I4314	3743	Uzbekistan	37.75	67.00	Narasimhan et al. (2018)
I1064	3737	Russia	52.82	60.47	Narasimhan et al. (2018)
I4071	3724	Netherlands	52.73	5.10	Olalde et al. (2018)
I0358	3719	Russia	53.03	50.39	Mathieson et al. (2015)
I6680	3702	Great Britain	55.31	-1.55	Olalde et al. (2018)
RISE483	3700	Hungary	47.34	18.90	Allentoft et al. (2015)
I0421	3675	Russia	53.08	50.36	Mathieson et al. (2015)
I0430	3675	Russia	53.08	50.36	Mathieson et al. (2015)
I0431	3675	Russia	53.08	50.36	Mathieson et al. (2015)
BLA10	3668	Germany	51.36	7.55	Bollongino et al. (2013)
I6800	3663	Kazakhstan	52.61	62.69	Narasimhan et al. (2018)
kzb003	3650	Russia	53.35	57.52	Krzewińska et al. (2018a)
I7412	3646	Uzbekistan	37.75	67.00	Narasimhan et al. (2018)
I4568	3641	Kazakhstan	48.74	77.00	Narasimhan et al. (2018)
I4779	3641	Kazakhstan	48.74	77.00	Narasimhan et al. (2018)
Sardinia_8415	3638	Italy	39.87	9.22	Brotherton et al. (2013)
I4562	3631	Spain	41.29	1.06	Olalde et al. (2019)
RISE247	3629	Hungary	47.33	18.96	Allentoft et al. (2015)
I3487	3626	Spain	38.63	-0.86	Olalde et al. (2019)
mur001	3604	Russia	54.79	56.01	Krzewińska et al. (2018a)
I10940	3600	Gibraltar	36.13	-5.34	Olalde et al. (2019)
I3389	3600	Russia	56.02	92.90	Narasimhan et al. (2018)
I6048	3596	Russia	55.51	77.05	Narasimhan et al. (2018)
I4778	3587	Kazakhstan	48.78	76.45	Narasimhan et al. (2018)
I3486	3550	Spain	38.63	-0.86	Olalde et al. (2019)
I4561	3550	Spain	41.29	1.06	Olalde et al. (2019)
I4563	3550	Spain	41.29	1.06	Olalde et al. (2019)
TV3831	3550	Portugal	37.94	-7.59	Martiniano et al. (2017)
I5469	3524	Great Britain	55.97	-3.18	Olalde et al. (2018)
I1840	3507	Spain	42.57	-2.62	Olalde et al. (2019)
I1853	3507	Russia	53.87	91.46	Narasimhan et al. (2018)
I1851	3485	Russia	54.18	91.58	Narasimhan et al. (2018)
I5470	3485	Great Britain	55.97	-3.18	Olalde et al. (2018)
I4783	3482	Kazakhstan	46.95	79.99	Narasimhan et al. (2018)
I0361	3475	Russia	53.03	50.39	Mathieson et al. (2015)
MA82	3463	Italy	39.45	9.44	Olivieri et al. (2017)
I3082	3455	Great Britain	50.92	-2.02	Olalde et al. (2018)
I7572	3400	Great Britain	52.34	0.03	Olalde et al. (2018)
I7573	3400	Great Britain	52.31	0.39	Olalde et al. (2018)
I7574	3400	Great Britain	52.18	0.12	Olalde et al. (2018)
I2573	3352	Great Britain	55.98	-2.90	Olalde et al. (2018)
I5364	3350	Great Britain	51.54	-4.21	Olalde et al. (2018)
arm20	3312	Armenia	40.15	45.25	Margaryan et al. (2017)
I2655	3308	Great Britain	58.23	-6.94	Olalde et al. (2018)
I3493	3302	Spain	40.86	-5.35	Olalde et al. (2019)
I9033	3297	Greece	36.92	21.70	Lazaridis et al. (2017)
I6668	3250	Turkmenistan	38.35	56.25	Narasimhan et al. (2018)
arm15	3250	Armenia	40.15	45.25	Margaryan et al. (2017)
arm18	3250	Armenia	40.15	45.25	Margaryan et al. (2017)
I12209	3240	Spain	41.46	-5.29	Olalde et al. (2019)
I4787	3238	Kazakhstan	48.21	67.02	Narasimhan et al. (2018)
I2653	3211	Great Britain	55.98	-2.90	Olalde et al. (2018)
MA115	3204	Italy	39.96	8.45	Olivieri et al. (2017)
I2062	3197	Israel	32.66	35.23	van den Brink et al. (2017)
arm22	3150	Armenia	40.16	45.74	Margaryan et al. (2017)
RISE499	3100	Russia	51.91	88.57	Allentoft et al. (2015)
MA138	3087	Italy	39.94	8.40	Olivieri et al. (2017)
I2656	3080	Great Britain	55.97	-2.90	Olalde et al. (2018)
I1992	3037	Pakistan	34.75	72.31	Narasimhan et al. (2018)
RISE396	3014	Armenia	39.20	46.40	Allentoft et al. (2015)
RISE407	2955	Armenia	40.15	45.86	Allentoft et al. (2015)
arm37	2950	Armenia	40.16	45.74	Margaryan et al. (2017)
I7688	2900	Portugal	40.09	-8.52	Olalde et al. (2019)
I3262	2854	Pakistan	34.75	72.31	Narasimhan et al. (2018)
DA4	2850	Russia	54.68	90.85	de Barros Damgaard et al. (2018b)
I6548	2850	Pakistan	30.40	72.12	Narasimhan et al. (2018)
I2860	2843	Great Britain	57.72	-3.39	Olalde et al. (2018)
I2469	2825	Spain	42.57	-2.62	Olalde et al. (2019)
cim357	2810	Moldova	46.41	29.49	Krzewińska et al. (2018a)
JK2974	2796	Egypt	29.24	31.09	Schuenemann et al. (2017)

JK2893	2734	Egypt	29.24	31.09	Schuenemann et al. (2017)
I7689	2730	Portugal	39.67	-8.13	Olalde et al. (2019)
DA111	2702	Czech Republic	50.51	14.05	de Barros Damgaard et al. (2018b)
I6888	2700	Pakistan	34.75	72.35	Narasimhan et al. (2018)
Is_4	2700	Kazakhstan	50.30	81.43	Unterländer et al. (2017)
I0576	2650	Russia	52.10	93.71	Unterländer et al. (2017)
NOV_5	2650	Russia	44.27	43.63	Unterländer et al. (2017)
NOV_7	2650	Russia	44.27	43.63	Unterländer et al. (2017)
Turlojiske4	2647	Lithuania	54.36	23.33	Mittnik et al. (2018)
RISE598	2646	Lithuania	54.36	23.30	Allentoft et al. (2015)
DA17	2642	Kazakhstan	43.07	68.25	de Barros Damgaard et al. (2018b)
JK2962	2601	Egypt	29.24	31.09	Schuenemann et al. (2017)
I5769	2600	Bulgaria	43.16	25.88	Mathieson et al. (2018)
arm10	2577	Armenia	40.72	43.82	Margaryan et al. (2017)
I12640	2568	Spain	41.54	2.13	Olalde et al. (2019)
Latsch_4461	2566	Italy	46.62	10.86	Brotherton et al. (2013)
DA195	2553	Hungary	46.34	20.16	de Barros Damgaard et al. (2018b)
I12560	2550	Spain	37.52	-5.98	Olalde et al. (2019)
I12561	2550	Spain	37.52	-5.98	Olalde et al. (2019)
DA14	2549	Kazakhstan	49.12	75.19	de Barros Damgaard et al. (2018b)
DA191	2524	Hungary	47.56	20.71	de Barros Damgaard et al. (2018b)
I12642	2515	Spain	41.54	2.13	Olalde et al. (2019)
DA198	2514	Hungary	46.34	20.16	de Barros Damgaard et al. (2018b)
DA197	2510	Hungary	46.34	20.16	de Barros Damgaard et al. (2018b)
I3322	2500	Spain	40.51	0.43	Olalde et al. (2019)
I8344	2400	Spain	42.13	3.11	Olalde et al. (2019)
poz256	2400	Moravia (Czech Republic)	49.49	17.13	Juras et al. (2018)
poz257	2400	Moravia (Czech Republic)	49.49	17.13	Juras et al. (2018)
I12410	2394	Spain	41.36	1.67	Olalde et al. (2019)
I12878	2387	Spain	41.36	1.67	Olalde et al. (2019)
I8212	2375	Spain	42.13	3.11	Olalde et al. (2019)
I8341	2375	Spain	42.13	3.11	Olalde et al. (2019)
I6893	2350	Pakistan	34.75	72.35	Narasimhan et al. (2018)
poz286	2350	Poland	50.39	21.04	Juras et al. (2018)
poz287	2350	Poland	50.39	21.04	Juras et al. (2018)
S7717	2350	Pakistan	34.75	72.35	Narasimhan et al. (2018)
I8214	2325	Spain	42.13	3.11	Olalde et al. (2019)
DA144	2300	Russia	47.29	39.55	de Barros Damgaard et al. (2018b)
S32	2300	Russia	54.49	91.08	Keyser et al. (2009)
scy300	2253	Moldova	46.67	29.80	Krzewińska et al. (2018a)
Be_3	2250	Kazakhstan	49.30	86.20	Unterländer et al. (2017)
K_1*	2250	Russia	49.41	87.58	Unterländer et al. (2017)
SCY005	2250	Ukraine	44.95	34.04	Juras et al. (2017b)
SCY192	2250	Moldova	46.65	29.79	Juras et al. (2017b)
SCY300	2250	Moldova	46.65	29.79	Juras et al. (2017b)
SCY334	2250	Moldova	46.65	29.79	Juras et al. (2017b)
DA51	2242	Kyrgyzstan	41.43	75.33	de Barros Damgaard et al. (2018b)
I8208	2237	Spain	42.13	3.11	Olalde et al. (2019)
JK2950	2232	Egypt	29.24	31.09	Schuenemann et al. (2017)
I3759	2228	Spain	42.57	-2.59	Olalde et al. (2019)
I3324	2227	Spain	42.01	3.08	Olalde et al. (2019)
DA48	2200	Kyrgyzstan	41.43	75.33	de Barros Damgaard et al. (2018b)
I3496	2200	Spain	41.50	2.15	Olalde et al. (2019)
KOL_2	2200	Russia	51.61	39.18	Unterländer et al. (2017)
I0789	2155	Great Britain	52.10	0.28	Schiffels et al. (2016)
I8203	2150	Spain	42.13	3.11	Olalde et al. (2019)
I8204	2150	Spain	42.13	3.11	Olalde et al. (2019)
I8205	2150	Spain	42.13	3.11	Olalde et al. (2019)
I8206	2150	Spain	42.13	3.11	Olalde et al. (2019)
chy001	2022	Russia	51.07	55.07	Krzewińska et al. (2018a)
I0160	1995	Great Britain	52.08	0.18	Schiffels et al. (2016)
arm4	1950	Armenia	40.14	44.11	Margaryan et al. (2017)
PCA0027	1850	Poland	52.59	16.78	Stolarek et al. (2018)
I8216	1818	Spain	42.13	3.11	Olalde et al. (2019)
PCA0030	1815	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0049	1815	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0066	1815	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0003	1780	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0015	1780	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0038	1780	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0044	1780	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0047	1780	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0050	1780	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0061	1780	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0002	1758	Poland	52.59	16.78	Stolarek et al. (2018)
PCA0063	1758	Poland	52.59	16.78	Stolarek et al. (2018)
3DT16	1750	Great Britain	53.96	-1.08	Martiniano et al. (2016)
3DT26	1750	Great Britain	53.96	-1.08	Martiniano et al. (2016)
6DT18	1750	Great Britain	53.96	-1.08	Martiniano et al. (2016)
6DT22	1750	Great Britain	53.96	-1.08	Martiniano et al. (2016)

6DT23	1750	Great Britain	53.96	-1.08	Martiniano et al. (2016)
FN2	1650	Germany	48.14	11.40	Veeramah et al. (2018)
I4054	1650	Spain	37.18	-3.61	Olalde et al. (2019)
scy192	1650	Moldova	46.67	29.80	Krzewińska et al. (2018a)
DA121	1613	Kazakhstan	42.73	68.34	de Barros Damgaard et al. (2018b)
DA224	1613	Kazakhstan	43.07	68.25	de Barros Damgaard et al. (2018b)
I3983	1604	Spain	37.18	-3.61	Olalde et al. (2019)
DA171	1600	Lithuania	55.74	24.23	de Barros Damgaard et al. (2018b)
I6491	1600	Spain	41.27	1.18	Olalde et al. (2019)
Alh2	1553	Germany	48.59	12.20	Veeramah et al. (2018)
AED513	1528	Germany	48.28	11.90	Veeramah et al. (2018)
AEHIb	1513	Germany	48.90	12.20	Veeramah et al. (2018)
DA74	1511	Kyrgyzstan	41.50	75.79	de Barros Damgaard et al. (2018b)
Alh3a	1506	Germany	48.59	12.20	Veeramah et al. (2018)
I0773	1490	Great Britain	52.26	0.07	Schiffels et al. (2016)
I0777	1478	Great Britain	52.26	0.07	Schiffels et al. (2016)
NW255a	1476	Germany	48.99	12.14	Veeramah et al. (2018)
DA385	1467	Kyrgyzstan	41.50	75.79	de Barros Damgaard et al. (2018b)
STR241	1455	Germany	48.87	12.55	Veeramah et al. (2018)
STR316b	1455	Germany	48.87	12.55	Veeramah et al. (2018)
STR393b	1455	Germany	48.87	12.55	Veeramah et al. (2018)
I3577	1450	Spain	37.32	-4.01	Olalde et al. (2019)
I3579	1450	Spain	37.32	-4.01	Olalde et al. (2019)
I3581	1450	Spain	37.32	-4.01	Olalde et al. (2019)
I3584	1450	Spain	36.96	-4.12	Olalde et al. (2019)
DA66	1447	Kyrgyzstan	41.50	75.79	de Barros Damgaard et al. (2018b)
SZ37	1447	Hungary	46.28	17.85	Amorim et al. (2018)
AED1135b	1445	Germany	48.28	11.90	Veeramah et al. (2018)
AED432b	1445	Germany	48.28	11.90	Veeramah et al. (2018)
SZ15	1442	Hungary	46.28	17.85	Amorim et al. (2018)
SZ18	1442	Hungary	46.28	17.85	Amorim et al. (2018)
SZ23	1442	Hungary	46.28	17.85	Amorim et al. (2018)
SZ28	1442	Hungary	46.28	17.85	Amorim et al. (2018)
SZ3	1442	Hungary	46.28	17.85	Amorim et al. (2018)
SZ30	1442	Hungary	46.28	17.85	Amorim et al. (2018)
SZ32	1442	Hungary	46.28	17.85	Amorim et al. (2018)
SZ4	1442	Hungary	46.28	17.85	Amorim et al. (2018)
I3980	1432	Spain	37.18	-3.61	Olalde et al. (2019)
SZ43	1431	Hungary	46.28	17.85	Amorim et al. (2018)
STR310	1430	Germany	48.87	12.55	Veeramah et al. (2018)
STR360c	1430	Germany	48.87	12.55	Veeramah et al. (2018)
STR248b	1405	Germany	48.87	12.55	Veeramah et al. (2018)
I12031	1400	Spain	42.02	2.81	Veeramah et al. (2018)
Vim2b	1400	Serbia	44.73	21.23	Veeramah et al. (2018)
Turlojiske5	1350	Lithuania	54.36	23.33	Mittnik et al. (2018)
CL102	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL23	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL25	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL31	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL47	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL53	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL57	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL63	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL83	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL84	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL87	1345	Italy	45.08	7.58	Amorim et al. (2018)
CL92	1345	Italy	45.08	7.58	Amorim et al. (2018)
DA162	1300	Russia	43.22	44.54	de Barros Damgaard et al. (2018b)
I3775	1300	Spain	41.98	2.31	Olalde et al. (2019)
I3778	1300	Spain	41.98	2.31	Olalde et al. (2019)
1333	1250	Germany	48.55	10.19	O'Sullivan et al. (2018)
1575	1250	Germany	48.55	10.19	O'Sullivan et al. (2018)
1576	1250	Germany	48.55	10.19	O'Sullivan et al. (2018)
I4137	1235	Czech Republic	50.19	14.16	Allentoft et al. (2015)
I0157	1232	Great Britain	52.08	0.18	Schiffels et al. (2016)
I5026	1200	Czech Republic	50.19	14.16	Allentoft et al. (2015)
I3585	1178	Spain	36.96	-4.12	Olalde et al. (2019)
NO3423	1170	Great Britain	53.63	-1.18	Martiniano et al. (2016)
I0161	1165	Great Britain	52.08	0.18	Schiffels et al. (2016)
I7674	1157	Spain	41.98	2.31	Olalde et al. (2019)
vik_84035	1078	Sweden	59.62	17.72	Krzewińska et al. (2018b)
I10895	1053	Spain	42.05	2.87	Olalde et al. (2019)
CAP-M15	1050	Romania	44.50	28.09	Rusu et al. (2018)
CAP-M17	1050	Romania	44.50	28.09	Rusu et al. (2018)
K3per10	1050	Hungary	48.33	21.72	Neparáczki et al. (2017)
K3per17	1050	Hungary	48.33	21.72	Neparáczki et al. (2017)
K3per3	1050	Hungary	48.33	21.72	Neparáczki et al. (2017)
Riper10perAnc25	1050	Hungary	46.69	19.02	Neparáczki et al. (2017)
I10851	1000	Spain	42.05	2.87	Olalde et al. (2019)
I7427	1000	Spain	37.18	-3.59	Olalde et al. (2019)
Riper1perAnc2	1000	Hungary	47.03	21.46	Neparáczki et al. (2017)
vik_grt035	996	Sweden	59.62	17.72	Krzewińska et al. (2018b)

gun005	994	Canary Islands	27.97	-15.60	Rodríguez-Varela et al. (2017)
vik_84001	989	Sweden	59.62	17.72	Krzewińska et al. (2018b)
I10892	965	Spain	42.05	2.87	Olalde et al. (2019)
Turlojiske3	905	Lithuania	54.36	23.33	Mittnik et al. (2018)
I7497	900	Spain	37.81	-2.54	Olalde et al. (2019)
I7498	900	Spain	37.81	-2.54	Olalde et al. (2019)
I7499	900	Spain	37.81	-2.54	Olalde et al. (2019)
vik_84005	900	Sweden	59.62	17.72	Krzewińska et al. (2018b)
vik_bns023	900	Sweden	59.62	17.72	Krzewińska et al. (2018b)
vik_gtm021	900	Sweden	59.62	17.72	Krzewińska et al. (2018b)
vik_gtm127	900	Sweden	59.62	17.72	Krzewińska et al. (2018b)
vik_kls001	900	Sweden	59.62	17.72	Krzewińska et al. (2018b)
vik_urm045	900	Sweden	59.62	17.72	Krzewińska et al. (2018b)
I10852	888	Spain	42.05	2.87	Olalde et al. (2019)
I10854	888	Spain	42.05	2.87	Olalde et al. (2019)
vik_grt036	878	Sweden	59.62	17.72	Krzewińska et al. (2018b)
vik_urm035	874	Sweden	59.62	17.72	Krzewińska et al. (2018b)
gun002	861	Canary Islands	28.27	-16.61	Rodríguez-Varela et al. (2017)
DA164	850	Russia	43.33	44.18	de Barros Damgaard et al. (2018b)
I12515	840	Spain	39.93	-0.20	Olalde et al. (2019)
vik_urm160	821	Sweden	59.62	17.72	Krzewińska et al. (2018b)
I12647	750	Spain	39.47	-0.38	Olalde et al. (2019)
I12648	750	Spain	39.47	-0.38	Olalde et al. (2019)
I12649	750	Spain	39.47	-0.38	Olalde et al. (2019)
I12650	750	Spain	39.47	-0.38	Olalde et al. (2019)
I7457	750	Spain	37.00	-3.99	Olalde et al. (2019)
I7458	750	Spain	37.00	-3.99	Olalde et al. (2019)
DA199	715	Hungary	47.56	21.02	de Barros Damgaard et al. (2018b)
Kivutkalns42	685	Latvia	56.85	24.27	Mittnik et al. (2018)
Kivutkalns25	673	Latvia	56.85	24.27	Mittnik et al. (2018)
Kivutkalns215	663	Latvia	56.85	24.27	Mittnik et al. (2018)
Kivutkalns19	565	Latvia	56.85	24.27	Mittnik et al. (2018)
Kivutkalns207	560	Latvia	56.85	24.27	Mittnik et al. (2018)
I8145	550	Spain	37.15	-3.59	Olalde et al. (2019)
I8146	550	Spain	37.15	-3.59	Olalde et al. (2019)
I8147	550	Spain	37.15	-3.59	Olalde et al. (2019)
I3808	400	Spain	36.95	-3.55	Olalde et al. (2019)
I7423	400	Spain	36.95	-3.55	Olalde et al. (2019)
I7426	400	Spain	36.95	-3.55	Olalde et al. (2019)
DA207	200	Kazakhstan	43.07	68.25	de Barros Damgaard et al. (2018b)
DA208	200	Kazakhstan	43.07	68.25	de Barros Damgaard et al. (2018b)
DA117	144	Kyrgyzstan	43.07	68.25	de Barros Damgaard et al. (2018b)

Table S2. List of ancient sequences included in the trees (Excel files S1-S4).

H1

Sample	Reference	Sample	Reference	Sample	Reference
12884A	Schiffels et al. (2016)	I3496	Olalde et al. (2019)	KC553983	Brotherton et al. (2013)
15569A	Schiffels et al. (2016)	I3579	Olalde et al. (2019)	KC553985	Brotherton et al. (2013)
15577A	Schiffels et al. (2016)	I3585	Olalde et al. (2019)	KC553986	Brotherton et al. (2013)
15579A	Schiffels et al. (2016)	I3587	Olalde et al. (2018)	KC553990	Brotherton et al. (2013)
6DRIF-18	Martiniano et al. 2016	I3588	Olalde et al. (2018)	KC553994	Brotherton et al. (2013)
AED432b	Veeramah et al. (2018)	I3590	Olalde et al. (2018)	KC553995	Brotherton et al. (2013)
ANI160	Mathieson et al. (2015)	I3593	Olalde et al. (2018)	KC554000	Brotherton et al. (2013)
CA122A	Martiniano et al. (2017)	I3599	Olalde et al. (2018)	KC554001	Brotherton et al. (2013)
ERS1790729	Haber et al. (2017)	I3719	Mathieson et al. (2015)	KC554008	Brotherton et al. (2013)
Gok2	Skoglund et al. (2014)	I3756	Olalde et al. (2019)	KC554010	Brotherton et al. (2013)
gun002	Rodríguez-Varela et al. (2017)	I3759	Olalde et al. (2019)	KC554017	Brotherton et al. (2013)
HE576982	Schuenemann et al. (2011)	I3808	Olalde et al. (2019)	KF523403	Bollongino et al. (2013)
I0257	Olalde et al. (2018)	I3875	Olalde et al. (2018)	KY198382	Nikitin et al. (2017)
I0258	Olalde et al. (2018)	I3980	Olalde et al. (2019)	KY399152	Olivieri et al. (2017)
I0406	Haak et al. (2015)	I4131	Olalde et al. (2018)	KY399153	Olivieri et al. (2017)
I0455	Olalde et al. (2018)	I4251	Olalde et al. (2018)	KY399157	Olivieri et al. (2017)
I0823	Olalde et al. (2018)	I4562	Olalde et al. (2019)	KY399158	Olivieri et al. (2017)
I0826	Olalde et al. (2018)	I4783	Narasimhan et al. (2018)	LC44	Martiniano et al. (2017)
I0986	Narasimhan et al. (2018)	I4895	Olalde et al. (2018)	MF498681	Knipper et al. (2017)
I10854	Olalde et al. (2019)	I4930	Olalde et al. (2018)	MF498692	Knipper et al. (2017)
I10892	Olalde et al. (2019)	I5015	Olalde et al. (2018)	MF498698	Knipper et al. (2017)
I10895	Olalde et al. (2019)	I5076	Olalde et al. (2019)	MF498711	Knipper et al. (2017)
I10940	Olalde et al. (2019)	I5374	Olalde et al. (2018)	MF498722	Knipper et al. (2017)
I11301	Olalde et al. (2019)	I5441	Olalde et al. (2018)	MF498728	Knipper et al. (2017)
I12031	Olalde et al. (2019)	I5471	Olalde et al. (2018)	MG182450	Vai et al. (2019)
I12209	Olalde et al. (2019)	I5836	Olalde et al. (2018)	MG182452	Vai et al. (2019)
I12647	Olalde et al. (2019)	I6543	Olalde et al. (2018)	MG182466	Vai et al. (2019)
I12650	Olalde et al. (2019)	I6601	Olalde et al. (2018)	MG182493	Vai et al. (2019)
I1281	Mathieson et al. (2015)	I6605	Olalde et al. (2018)	MG182494	Vai et al. (2019)
I1392	Olalde et al. (2018)	I6617	Olalde et al. (2018)	MG182501	Vai et al. (2019)
I1633	Lazaridis et al. (2016)	I6626	Olalde et al. (2018)	MG182517	Vai et al. (2019)
I1842	Olalde et al. (2019)	I6628	Olalde et al. (2018)	MG182518	Vai et al. (2019)
I2199	Lipson et al. (2017)	I6680	Olalde et al. (2018)	MG182519	Vai et al. (2019)
I2357	Lipson et al. (2017)	I6775	Olalde et al. (2018)	MG182530	Vai et al. (2019)
I2427	Mathieson et al. (2018)	I7041	Olalde et al. (2018)	MG429042	Mittnik et al. (2018)
I2440	Mathieson et al. (2015)	I7043	Olalde et al. (2018)	MG429044	Mittnik et al. (2018)
I2452	Olalde et al. (2018)	I7203	Olalde et al. (2018)	MG429047	Mittnik et al. (2018)
I2618	Olalde et al. (2018)	I7288	Olalde et al. (2018)	MH176343	Juras et al. (2018)
I2659	Olalde et al. (2018)	I7427	Olalde et al. (2019)	MH176353	Juras et al. (2018)
I2741	Olalde et al. (2018)	I7573	Olalde et al. (2018)	NO3423	Martiniano et al. (2016)
I2793	Lipson et al. (2017)	I7574	Olalde et al. (2018)	RISE569	Allentoft et al. (2015)
I2977	Olalde et al. (2018)	I7604	Olalde et al. (2019)	STR241	Veeramah et al. (2018)
I2980	Olalde et al. (2018)	I7635	Olalde et al. (2018)	TV3831	Martiniano et al. (2017)
I3049	Olalde et al. (2018)	I7646	Olalde et al. (2019)	vik84005	Krzewińska et al. (2018b)
I3082	Olalde et al. (2018)	I7689	Olalde et al. (2019)	vikgtm127	Krzewińska et al. (2018b)
I3136	Olalde et al. (2018)	I8132	Olalde et al. (2019)	vikkls001	Krzewińska et al. (2018b)
I3322	Olalde et al. (2019)	I8158	Olalde et al. (2019)	vikurm045	Krzewińska et al. (2018b)
I3324	Olalde et al. (2019)	I8216	Olalde et al. (2019)	vikurm160	Krzewińska et al. (2018b)
I3433	Mathieson et al. (2018)	I8341	Olalde et al. (2019)		
I3486	Olalde et al. (2019)	I8569	Olalde et al. (2019)		

H2

Sample	Reference	Sample	Reference	Sample	Reference
12881A:HS1	Schiffels et al. (2016)	I1054	Narasimhan et al. (2018)	MF498690	Knipper et al. (2017)
12885A:HS3	Schiffels et al. (2016)	I1634	Lazaridis et al. (2016)	MF498732	Knipper et al. (2017)

Alh3a	Veeramah et al. (2018)	I1851	Narasimhan et al. (2018)	MH176336	Juras et al. (2018)
chy001	Krzewińska et al. (2018a)	I1853	Narasimhan et al. (2018)	mur001	Krzewińska et al. (2018a)
gun005	Rodríguez-Varela et al. (2017)	I2604	Olalde et al. (2018)	PCA0030	Stolarek et al. (2018)
I0122	Mathieson et al. (2015)	I2653	Olalde et al. (2018)	PCA0063	Stolarek et al. (2018)
I0431	Mathieson et al. (2015)	I2656	Olalde et al. (2018)	PCA0066	Stolarek et al. (2018)
I0441	Haak et al. (2015)	I6561	Mathieson et al. (2018)	RISE483	Allentoft et al. (2015)
I0938	Narasimhan et al. (2018)	I7489	Narasimhan et al. (2018)	RISE487	Allentoft et al. (2015)
I0942	Narasimhan et al. (2018)	KC554012	Brandt et al. (2013); Brotherton et al. (2013)	RISE562	Allentoft et al. (2015)
I1024	Narasimhan et al. (2018)	MF362704	Margaryan et al. (2017)	RISE598	Allentoft et al. (2015)
I1053	Narasimhan et al. (2018)	MF498667	Knipper et al. (2017)	vik_urm035	Krzewińska et al. (2018b)

H11

Sample	Reference	Sample	Reference	Sample	Reference
KC554011	Brandt et al. (2013); Brotherton et al. (2013)	MG182516	Vai et al. (2019)	RISE247	Allentoft et al. (2015)
MG182511	Vai et al. (2019)	MG429009	Mittnik et al. (2018)	STR248b	Veeramah et al. (2018)
MG182513	Vai et al. (2019)				

H13

Sample	Reference	Sample	Reference	Sample	Reference
I0070	Lazaridis et al. (2017)	I5407	Mathieson et al. (2018)	MF498675	Knipper et al. (2017)
I0112	Haak et al. (2015)	I7572	Olalde et al. (2018)	MF498676	Knipper et al. (2017)
I0370	Haak et al. (2015)	I7717	Narasimhan et al. (2018)	MF597777	Rusu et al. (2018)
I0374	Mathieson et al. (2015)	I8203	Olalde et al. (2019)	MG182469	Vai et al. (2019)
I0980	Narasimhan et al. (2018)	JK2962	Schuenemann et al. (2017)	MG182472	Vai et al. (2019)
I12649	Olalde et al. (2019)	KC554009	Brotherton et al. (2013)	MG182481	Vai et al. (2019)
I4081	Mathieson et al. (2018)	KK1Kotias	Jones et al. (2015)	vik_grt036	Krzewińska et al. (2018b)
I4085	Narasimhan et al. (2018)	MF362692	Margaryan et al. (2017)		

Table S3. List of modern H1 mtDNA sequences used to build the tree. Newly reported samples in bold.

Sample	Region	Geography/ Population	Additional information	Reference
10391	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
107	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
11103	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
1113000008_S31	**Unknown**	**Germany**		**This study**
1113000032_S8	**Unknown**	**Germany**		**This study**
1113000037_S2	**Unknown**	**Germany**		**This study**
1113000049-2_S96	**Unknown**	**Germany**		**This study**
1113000057_S87	**Unknown**	**Germany**		**This study**
1113000063_S51	**Unknown**	**Germany**		**This study**
1113000071_S96	**Unknown**	**Germany**		**This study**
1113000073_S28	**Unknown**	**Germany**		**This study**
1113000090_S90	**Unknown**	**Germany**		**This study**
1113000096_S31	**Unknown**	**Germany**		**This study**
1113000099_S21	**Unknown**	**Germany**		**This study**
1113000106_S47	**Unknown**	**Germany**		**This study**
1113000110_S53	**Unknown**	**Germany**		**This study**
1113000113_S8	**Unknown**	**Germany**		**This study**
1113000124_S68	**Unknown**	**Germany**		**This study**
1113000127_S34	**Unknown**	**Germany**		**This study**
1113000135_S33	**Unknown**	**Germany**		**This study**
1113000143_S94	**Unknown**	**Germany**		**This study**
1113000145_S40	**Unknown**	**Germany**		**This study**
1113000150_S11	**Unknown**	**Germany**		**This study**
1113000173_S21	**Unknown**	**Germany**		**This study**
1113000174_S86	**Unknown**	**Germany**		**This study**
1113000183_S31	**Unknown**	**Germany**		**This study**
1113000185_S80	**Unknown**	**Germany**		**This study**
1113000187_S70	**Unknown**	**Germany**		**This study**
1113000189_S17	**Unknown**	**Germany**		**This study**
1113000216_S44	**Unknown**	**Germany**		**This study**
1113000218_S58	**Unknown**	**Germany**		**This study**
1113000226_S65	**Unknown**	**Germany**		**This study**
1113000230_S59	**Unknown**	**Germany**		**This study**
1113000235_S10	**Unknown**	**Germany**		**This study**
1113000239_S49	**Unknown**	**Germany**		**This study**
1113000241_S39	**Unknown**	**Germany**		**This study**
1113000249_S5	**Unknown**	**Germany**		**This study**
1113000254_S2	**Unknown**	**Germany**		**This study**
1113000259_S42	**Unknown**	**Germany**		**This study**
1113000263_S67	**Unknown**	**Germany**		**This study**
1113000271_S92	**Unknown**	**Germany**		**This study**
1113000291_S27	**Unknown**	**Germany**		**This study**
1113000306_S24	**Unknown**	**Germany**		**This study**
1113000313_S11	**Unknown**	**Germany**		**This study**
1113000324_S42	**Unknown**	**Germany**		**This study**
1113000328_S85	**Unknown**	**Germany**		**This study**
1113000340_S54	**Unknown**	**Germany**		**This study**
1113000359_S46	**Unknown**	**Germany**		**This study**
1113000360_S77	**Unknown**	**Germany**		**This study**
1113000363_S46	**Unknown**	**Germany**		**This study**
1113000391_S85	**Unknown**	**Germany**		**This study**
1113000396_S16	**Unknown**	**Germany**		**This study**
1113000402_S86	**Unknown**	**Germany**		**This study**
1113000403_S3	**Unknown**	**Germany**		**This study**
1113000405_S17	**Unknown**	**Germany**		**This study**
1113000406_S66	**Unknown**	**Germany**		**This study**
1113000435_S35	**Unknown**	**Germany**		**This study**
1113000442_S23	**Unknown**	**Germany**		**This study**
1113000451_S49	**Unknown**	**Germany**		**This study**
1113000455_S40	**Unknown**	**Germany**		**This study**
1113000459_S93	**Unknown**	**Germany**		**This study**
1113000482_S55	**Unknown**	**Germany**		**This study**
1113000487_S92	**Unknown**	**Germany**		**This study**
1113000488_S95	**Unknown**	**Germany**		**This study**
1113000499_S19	**Unknown**	**Germany**		**This study**
1113000504-WDH_S34	**Unknown**	**Germany**		**This study**
1113000517_S32	**Unknown**	**Germany**		**This study**
1113000521_S62	**Unknown**	**Germany**		**This study**
1113000523_S17	**Unknown**	**Germany**		**This study**
1113000527_S9	**Unknown**	**Germany**		**This study**
1113000530_S63	**Unknown**	**Germany**		**This study**
1113000532_S10	**Unknown**	**Germany**		**This study**
1113000550_S82	**Unknown**	**Germany**		**This study**
1113000562_S20	**Unknown**	**Germany**		**This study**
1113000566_S28	**Unknown**	**Germany**		**This study**

1113000571_S16	**Unknown**	**Germany**	**This study**
1113000577_S7	**Unknown**	**Germany**	**This study**
1113000589_S40	**Unknown**	**Germany**	**This study**
1113000600_S39	**Unknown**	**Germany**	**This study**
1113000601_S91	**Unknown**	**Germany**	**This study**
1113000615_S40	**Unknown**	**Germany**	**This study**
1113000619_S59	**Unknown**	**Germany**	**This study**
1113000631_S11	**Unknown**	**Germany**	**This study**
1113000640_S63	**Unknown**	**Germany**	**This study**
1113000643_S16	**Unknown**	**Germany**	**This study**
1113000657_S56	**Unknown**	**Germany**	**This study**
1113000665_S45	**Unknown**	**Germany**	**This study**
1113000685_S29	**Unknown**	**Germany**	**This study**
1113000699_S39	**Unknown**	**Germany**	**This study**
1113000704_S90	**Unknown**	**Germany**	**This study**
1113000710_S25	**Unknown**	**Germany**	**This study**
1113000711_S95	**Unknown**	**Germany**	**This study**
1113000714_S43	**Unknown**	**Germany**	**This study**
1113000716_S32	**Unknown**	**Germany**	**This study**
1113000721_S37	**Unknown**	**Germany**	**This study**
1113000733_S67	**Unknown**	**Germany**	**This study**
1113000736_S45	**Unknown**	**Germany**	**This study**
1113000738_S74	**Unknown**	**Germany**	**This study**
1113000757_S20	**Unknown**	**Germany**	**This study**
1113000781_S47	**Unknown**	**Germany**	**This study**
1113000787_S6	**Unknown**	**Germany**	**This study**
1113000792_S10	**Unknown**	**Germany**	**This study**
1113000806_S85	**Unknown**	**Germany**	**This study**
1113000816_S56	**Unknown**	**Germany**	**This study**
1113000819_S17	**Unknown**	**Germany**	**This study**
1113000831_S1	**Unknown**	**Germany**	**This study**
1113000834_S90	**Unknown**	**Germany**	**This study**
1113000836_S71	**Unknown**	**Germany**	**This study**
1113000850_S15	**Unknown**	**Germany**	**This study**
1113000855_S6	**Unknown**	**Germany**	**This study**
1113000858_S20	**Unknown**	**Germany**	**This study**
1113000861_S38	**Unknown**	**Germany**	**This study**
1113000873_S90	**Unknown**	**Germany**	**This study**
1113000886_S68	**Unknown**	**Germany**	**This study**
1113000888_S43	**Unknown**	**Germany**	**This study**
1113000892_S4	**Unknown**	**Germany**	**This study**
1113000900_S48	**Unknown**	**Germany**	**This study**
1113000901_S38	**Unknown**	**Germany**	**This study**
1113000914_S83	**Unknown**	**Germany**	**This study**
1113000917_S35	**Unknown**	**Germany**	**This study**
1113000919_S70	**Unknown**	**Germany**	**This study**
1113000945_S55	**Unknown**	**Germany**	**This study**
1113000947_S12	**Unknown**	**Germany**	**This study**
1113000950_S93	**Unknown**	**Germany**	**This study**
1113000953_S27	**Unknown**	**Germany**	**This study**
1113000962_S28	**Unknown**	**Germany**	**This study**
1113000967_S19	**Unknown**	**Germany**	**This study**
1113000979_S65	**Unknown**	**Germany**	**This study**
1113000984_S20	**Unknown**	**Germany**	**This study**
1113000985_S1	**Unknown**	**Germany**	**This study**
1113000986_S66	**Unknown**	**Germany**	**This study**
1113000996_S56	**Unknown**	**Germany**	**This study**
1113000997_S60	**Unknown**	**Germany**	**This study**
1113001007_S89	**Unknown**	**Germany**	**This study**
1113001016_S92	**Unknown**	**Germany**	**This study**
1113001019_S1	**Unknown**	**Germany**	**This study**
1113001023_S77	**Unknown**	**Germany**	**This study**
1113001037_S63	**Unknown**	**Germany**	**This study**
1113001038_S7	**Unknown**	**Germany**	**This study**
1113001046_S13	**Unknown**	**Germany**	**This study**
1113001049_S41	**Unknown**	**Germany**	**This study**
1113001050_S58	**Unknown**	**Germany**	**This study**
1113001055_S30	**Unknown**	**Germany**	**This study**
1113001058_S28	**Unknown**	**Germany**	**This study**
1113001063_S35	**Unknown**	**Germany**	**This study**
1113001067_S94	**Unknown**	**Germany**	**This study**
1113001083_S26	**Unknown**	**Germany**	**This study**
1113001092_S4	**Unknown**	**Germany**	**This study**
1113001095_S26	**Unknown**	**Germany**	**This study**
1113001097_S2	**Unknown**	**Germany**	**This study**
1113001124_S13	**Unknown**	**Germany**	**This study**
1113001133_S19	**Unknown**	**Germany**	**This study**
1113001141_S50	**Unknown**	**Germany**	**This study**
1113001143_S16	**Unknown**	**Germany**	**This study**
1113001144_S4	**Unknown**	**Germany**	**This study**
1113001147_S49	**Unknown**	**Germany**	**This study**
1113001151_S84	**Unknown**	**Germany**	**This study**

1113001163_S25	**Unknown**	**Germany**	**This study**
1113001164_S76	**Unknown**	**Germany**	**This study**
1113001169_S40	**Unknown**	**Germany**	**This study**
1113001173_S59	**Unknown**	**Germany**	**This study**
1113001174_S41	**Unknown**	**Germany**	**This study**
1113001179_S3	**Unknown**	**Germany**	**This study**
1113001192_S38	**Unknown**	**Germany**	**This study**
1113001198_S33	**Unknown**	**Germany**	**This study**
1113001225_S94	**Unknown**	**Germany**	**This study**
1113001227_S86	**Unknown**	**Germany**	**This study**
1113001228_S91	**Unknown**	**Germany**	**This study**
1113001233_S96	**Unknown**	**Germany**	**This study**
1113001236_S28	**Unknown**	**Germany**	**This study**
1113001244_S66	**Unknown**	**Germany**	**This study**
1113001246_S35	**Unknown**	**Germany**	**This study**
1113001251_S5	**Unknown**	**Germany**	**This study**
1113001256_S17	**Unknown**	**Germany**	**This study**
1113001263_S16	**Unknown**	**Germany**	**This study**
1113001264_S16	**Unknown**	**Germany**	**This study**
1113001274_S34	**Unknown**	**Germany**	**This study**
1113001293_S45	**Unknown**	**Germany**	**This study**
1113001294_S38	**Unknown**	**Germany**	**This study**
1113001314_S30	**Unknown**	**Germany**	**This study**
1113001315_S77	**Unknown**	**Germany**	**This study**
1113001318_S71	**Unknown**	**Germany**	**This study**
1113001319_S34	**Unknown**	**Germany**	**This study**
1113001346_S66	**Unknown**	**Germany**	**This study**
1113001350_S2	**Unknown**	**Germany**	**This study**
1113001351_S16	**Unknown**	**Germany**	**This study**
1113001353_S43	**Unknown**	**Germany**	**This study**
1113001354_S17	**Unknown**	**Germany**	**This study**
1113001365_S30	**Unknown**	**Germany**	**This study**
1113001366_S82	**Unknown**	**Germany**	**This study**
1113001367_S89	**Unknown**	**Germany**	**This study**
1113001374_S27	**Unknown**	**Germany**	**This study**
1113001375_S73	**Unknown**	**Germany**	**This study**
1113001379_S80	**Unknown**	**Germany**	**This study**
1113001388_S8	**Unknown**	**Germany**	**This study**
1113001405_S46	**Unknown**	**Germany**	**This study**
1113001414_S37	**Unknown**	**Germany**	**This study**
1113001416_S5	**Unknown**	**Germany**	**This study**
1113001428_S40	**Unknown**	**Germany**	**This study**
1113001437_S76	**Unknown**	**Germany**	**This study**
1113001440_S36	**Unknown**	**Germany**	**This study**
1113001456_S77	**Unknown**	**Germany**	**This study**
1113001461_S73	**Unknown**	**Germany**	**This study**
1113001466_S82	**Unknown**	**Germany**	**This study**
1113001475_S69	**Unknown**	**Germany**	**This study**
1113001488_S77	**Unknown**	**Germany**	**This study**
1113001489_S46	**Unknown**	**Germany**	**This study**
1113001496_S54	**Unknown**	**Germany**	**This study**
1113001505_S71	**Unknown**	**Germany**	**This study**
1113001532_S48	**Unknown**	**Germany**	**This study**
1113001547_S17	**Unknown**	**Germany**	**This study**
1113001553_S75	**Unknown**	**Germany**	**This study**
1113001560_S69	**Unknown**	**Germany**	**This study**
1113001561_S19	**Unknown**	**Germany**	**This study**
1113001575_S37	**Unknown**	**Germany**	**This study**
1113001581_S5	**Unknown**	**Germany**	**This study**
1113001585_S60	**Unknown**	**Germany**	**This study**
1113001588_S32	**Unknown**	**Germany**	**This study**
1113001593_S25	**Unknown**	**Germany**	**This study**
1113001594_S27	**Unknown**	**Germany**	**This study**
1113001616_S16	**Unknown**	**Germany**	**This study**
1113001619_S61	**Unknown**	**Germany**	**This study**
1113001626_S82	**Unknown**	**Germany**	**This study**
1113001633_S62	**Unknown**	**Germany**	**This study**
1113001644_S88	**Unknown**	**Germany**	**This study**
1113001645_S68	**Unknown**	**Germany**	**This study**
1113001651_S38	**Unknown**	**Germany**	**This study**
1113001668_S25	**Unknown**	**Germany**	**This study**
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1113001696_S86	**Unknown**	**Germany**	**This study**
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1113001743_S23	**Unknown**	**Germany**	**This study**
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1113001818_S74	**Unknown**	**Germany**	**This study**
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1113002408_S80	**Unknown**	**Germany**	**This study**
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1113002441_S59	**Unknown**	**Germany**	**This study**
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12675	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
12682	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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13	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
1369	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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1789	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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2017	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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21336	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
2142	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
21676	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
2272	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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25437	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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28954	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
29791	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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34976	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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43076	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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5584	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
5645	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
5661	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
5688	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
5875	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
5902	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
5988	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
6057	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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7387	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
753	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
7882	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
801	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
871	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
899	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
925	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
9570	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
970	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
995	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)

A-14	**Europe NW**	**France**		**This study**
A-17	**Europe NW**	**France**		**This study**
A-19	**Europe NW**	**France**		**This study**
A-2	**Europe NW**	**France**		**This study**
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A-36	**Europe NW**	**France**		**This study**
A-38	**Europe NW**	**France**		**This study**
A-4	**Europe NW**	**France**		**This study**
A-41	**Europe NW**	**France**		**This study**
A-64	**Europe NW**	**France**		**This study**
A-67	**Europe NW**	**France**		**This study**
A-71	**Europe NW**	**France**		**This study**
A-75	**Europe NW**	**France**		**This study**
A-79	**Europe NW**	**France**		**This study**
AF346981	Europe NW	France		Ingman et al. (2000)
AF381993	North Africa	Mauritania		Maca-Meyer et al. (2001)
ALP003	**Europe SE**	**Italy**	**Abruzzo**	**This study**
ALP032	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP042	**Europe SE**	**Italy**	**Toscana**	**This study**
ALP052	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP056	**Europe SE**	**Italy**	**Liguria**	**This study**
ALP074	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP094	**Europe SE**	**Italy**	**Friuli**	**This study**
ALP103	**Europe SE**	**Italy**	**Veneto**	**This study**
ALP104	**Europe SE**	**Italy**	**Veneto**	**This study**
ALP107	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP109	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP119	**Europe SE**	**Italy**	**Calabria**	**This study**
ALP126	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP127	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP131	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP138	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP150	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP174	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP181	**Europe SE**	**Italy**	**Friuli**	**This study**
ALP182	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP184	**Europe SE**	**Italy**	**Friuli**	**This study**
ALP232	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP245	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP275	**Europe SE**	**Italy**	**Marche**	**This study**
ALP329	**Europe SE**	**Italy**	**Trentino**	**This study**
ALP346	**Europe SE**	**Italy**	**Friuli**	**This study**
ALP394	**Europe SE**	**Italy**	**Trentino**	**This study**
ALP435	**Europe SE**	**Italy**	**Friuli**	**This study**
ALP468	**Europe SE**	**Italy**	**Friuli**	**This study**
ALP575	**Europe SE**	**Italy**	**Abruzzo**	**This study**
ALP580	**Europe SE**	**Italy**	**Puglia**	**This study**
ALP582	**Europe SE**	**Italy**	**Calabria**	**This study**
ALP583	**Europe SE**	**Italy**	**Puglia**	**This study**
ALP584	**Europe SE**	**Italy**	**Abruzzo**	**This study**
ALP591	**Europe SE**	**Italy**	**Puglia**	**This study**
ALP592	**Europe SE**	**Italy**	**Puglia**	**This study**
AY195775	Unknown	Unknown		Mishmar et al. (2003)
AY339412	Europe NE	Finland		Finnilä et al. (2001)
AY339413	Europe NE	Finland		Finnilä et al. (2001)
AY339414	Europe NE	Finland		Finnilä et al. (2001)
AY339415	Europe NE	Finland		Finnilä et al. (2001)
AY339416	Europe NE	Finland		Finnilä et al. (2001)
AY339417	Europe NE	Finland		Finnilä et al. (2001)
AY339418	Europe NE	Finland		Finnilä et al. (2001)
AY339419	Europe NE	Finland		Finnilä et al. (2001)
AY339420	Europe NE	Finland		Finnilä et al. (2001)
AY339421	Europe NE	Finland		Finnilä et al. (2001)
AY339422	Europe NE	Finland		Finnilä et al. (2001)
AY339423	Europe NE	Finland		Finnilä et al. (2001)
AY339424	Europe NE	Finland		Finnilä et al. (2001)
AY339425	Europe NE	Finland		Finnilä et al. (2001)
AY495094	Europe	Europe		Coble et al. (2004)
AY495096	Europe	Europe		Coble et al. (2004)
AY495099	Europe	Europe		Coble et al. (2004)
AY495102	Europe	Europe		Coble et al. (2004)
AY495103	Europe	Europe		Coble et al. (2004)
AY495106	Europe	Europe		Coble et al. (2004)
AY495112	Europe	Europe		Coble et al. (2004)
AY495113	Europe	Europe		Coble et al. (2004)
AY495117	Europe	Europe		Coble et al. (2004)
AY495119	Europe	Europe		Coble et al. (2004)
AY495124	Europe	Europe		Coble et al. (2004)
AY495139	Europe	Europe		Coble et al. (2004)
AY495141	Europe	Europe		Coble et al. (2004)

AY495144	Europe	Europe		Coble et al. (2004)
AY495147	Europe	Europe		Coble et al. (2004)
AY495152	Europe	Europe		Coble et al. (2004)
AY495153	Europe	Europe		Coble et al. (2004)
AY495157	Europe	Europe		Coble et al. (2004)
AY495158	Europe	Europe		Coble et al. (2004)
AY495159	Europe	Europe		Coble et al. (2004)
AY495160	Europe	Europe		Coble et al. (2004)
AY495161	Europe	Europe		Coble et al. (2004)
AY495162	Europe	Europe		Coble et al. (2004)
AY495163	Europe	Europe		Coble et al. (2004)
AY495164	Europe	Europe		Coble et al. (2004)
AY495187	Europe	Europe		Coble et al. (2004)
AY495188	Europe	Europe		Coble et al. (2004)
AY495189	Europe	Europe		Coble et al. (2004)
AY495190	Europe	Europe		Coble et al. (2004)
AY495191	Europe	Europe		Coble et al. (2004)
AY495192	Europe	Europe		Coble et al. (2004)
AY495193	Europe	Europe		Coble et al. (2004)
AY495194	Europe	Europe		Coble et al. (2004)
AY738971	South Caucasus	Georgia		Achilli et al (2004)
AY738972	Europe SE	Italy		Achilli et al (2004)
AY738973	North Africa	Egypt		Achilli et al (2004)
AY738974	Europe SE	Italy		Achilli et al (2004)
AY738975	Europe SE	Italy		Achilli et al (2004)
AY738976	Europe SE	Italy		Achilli et al (2004)
AY738977	Near East	Iraq		Achilli et al (2004)
AY738978	Europe SE	Italy		Achilli et al (2004)
AY738979	Europe SE	Italy		Achilli et al (2004)
AY738980	Europe SE	Italy		Achilli et al (2004)
AY738981	Europe SE	Italy		Achilli et al (2004)
AY738982	Europe SE	Italy		Achilli et al (2004)
B-10	**Europe NW**	**France**		**This study**
B-20	**Europe NW**	**France**		**This study**
B-23	**Europe NW**	**France**		**This study**
B-26	**Europe NW**	**France**		**This study**
B-37	**Europe NW**	**France**		**This study**
B-41	**Europe NW**	**France**		**This study**
B-5	**Europe NW**	**France**		**This study**
B-55	**Europe NW**	**France**		**This study**
B-57	**Europe NW**	**France**		**This study**
B-61	**Europe NW**	**France**		**This study**
B-62	**Europe NW**	**France**		**This study**
B-80	**Europe NW**	**France**		**This study**
bas-11	Europe Basque	Spain	Basque Country	Batini et al. (2017)
bas-12	Europe Basque	Spain	Basque Country	Batini et al. (2017)
bas-19	Europe Basque	Spain	Basque Country	Batini et al. (2017)
bas-3	Europe Basque	Spain	Basque Country	Batini et al. (2017)
bas-9	Europe Basque	Spain	Basque Country	Batini et al. (2017)
bav-12	Europe NW	Germany		Batini et al. (2017)
BER	**Iberia**	**Spain**		**This study**
BG111	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BG175	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BG184	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BG56	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BG9	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BGD115	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BGD144	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BGD202	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BGD228	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
BGD46	**Europe SE**	**Italy**	**Lombardy, Bergamo**	**This study**
C-13	**Europe NW**	**France**		**This study**
C-23	**Europe NW**	**France**		**This study**
C-31	**Europe NW**	**France**		**This study**
C-36	**Europe NW**	**France**		**This study**
C-37	**Europe NW**	**France**		**This study**
C-39	**Europe NW**	**France**		**This study**
C-44	**Europe NW**	**France**		**This study**
C-51	**Europe NW**	**France**		**This study**
C-61	**Europe NW**	**France**		**This study**
Ca94_112	Europe SE	Italy(Sardinia)		**unpub**
Ca94_114	Europe SE	Italy(Sardinia)		**unpub**
Ca94_122	Europe SE	Italy(Sardinia)		**unpub**
Ca94_146	Europe SE	Italy(Sardinia)		**unpub**
Ca94_155	Europe SE	Italy(Sardinia)		**unpub**
Ca94_28	Europe SE	Italy(Sardinia)		**unpub**
CA94_38	Europe SE	Italy(Sardinia)		**unpub**
Ca94_41	Europe SE	Italy(Sardinia)		**unpub**
Ca94_48	Europe SE	Italy(Sardinia)		**unpub**
Ca94_5	Europe SE	Italy(Sardinia)		**unpub**
Ca94_52	Europe SE	Italy(Sardinia)		**unpub**
Ca94_63	Europe SE	Italy(Sardinia)		**unpub**

Ca94_76	Europe SE	Italy(Sardinia)	**unpub**
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csct_000018	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000021	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000045	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000048	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000066	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000072	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000085	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000086	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000096	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000112	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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csct_000219	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
csct_000222	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)
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csct_007575	Europe SE	Italy(Sardinia)	Olivieri et al. (2017)

csct_007579	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007589	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007591	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007617	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007637	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007639	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007681	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007685	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007689	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007711	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007743	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007763	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007785	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007797	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
csct_007801	Europe SE	Italy(Sardinia)		Olivieri et al. (2017)
den-104	Europe NW	Denmark	DNK	Batini et al. (2017)
den-207	Europe NW	Denmark	DNK	Batini et al. (2017)
den-SN	Europe NW	Denmark	DNK	Batini et al. (2017)
DQ306709	Europe NE	Russia		Malyarchuk et al. unpub.
DQ523627	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523632	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523635	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523638	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523641	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523648	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523657	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523670	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523673	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523677	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523678	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
DQ523681	Europe SE	Italy(Sardinia)	Ogliastra region (Eastern Sardinia)	Fraumene et al. (2006)
Drz27	**Near East**	**Druze**		**unpub**
Drz46	**Near East**	**Druze**		**unpub**
DUL	**Iberia**	**Portugal**		**This study**
EF177411	Iberia	Portugal		Pereira et al. (2007)
EF177421	Iberia	Portugal		Pereira et al. (2007)
EF177425	Iberia	Portugal		Pereira et al. (2007)
EF177427	Iberia	Portugal		Pereira et al. (2007)
EF177428	Iberia	Portugal		Pereira et al. (2007)
EF177432	Iberia	Portugal		Pereira et al. (2007)
EF177436	Iberia	Portugal		Pereira et al. (2007)
EF177446	Iberia	Portugal		Pereira et al. (2007)
EF177447	Iberia	Portugal		Pereira et al. (2007)
EF376015	Europe NW	Sweden		Family Tree
EF449507	Unknown	Unknown		Family Tree
EF491001	Unknown	Unknown		Family Tree
EF526076	Unknown	Unknown		Family Tree
EF556177	Unknown	Unknown		Behar et al. (2008)
EF556181	Unknown	Unknown		Behar et al. (2008)
EF556184	Unknown	Unknown		Behar et al. (2008)
EKD008	**Europe NW**	**United Kingdom**		**This study**
EKD011	**Europe NW**	**United Kingdom**		**This study**
eng-G9	Europe NW	British Isles		Batini et al. (2017)
eng-O15	Europe NW	British Isles		Batini et al. (2017)
eng-O36	Europe NW	British Isles		Batini et al. (2017)
eng-W20	Europe NW	British Isles		Batini et al. (2017)
ESP0007	**Iberia**	**Spain**	**Cuenca**	**This study**
ESP0015	**Iberia**	**Spain**	**Toledo**	**This study**
ESP0016	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0019	**Iberia**	**Spain**	**Girona**	**This study**
ESP0023	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0026	**Iberia**	**Spain**	**Badajoz**	**This study**
ESP0027	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0031	**Iberia**	**Spain**	**Burgos**	**This study**
ESP0035	**Iberia**	**Spain**	**Segovia**	**This study**
ESP0038	**Iberia**	**Spain**	**Tarragona**	**This study**
ESP0040	**Iberia**	**Spain**	**Cantabria**	**This study**
ESP0045	**Iberia**	**Spain**	**Asturias**	**This study**
ESP0047	**Iberia**	**Spain**	**Salamanca**	**This study**

ESP0048	Iberia	Spain	Burgos	This study
ESP0049	Iberia	Spain	Jaén	This study
ESP0060	Iberia	Spain	Navarra	This study
ESP0064	Iberia	Spain	Tarragona	This study
ESP0079	Iberia	Spain	Zaragoza	This study
ESP0100	Iberia	Spain	Cuidad Real	This study
ESP0105	Iberia	Spain	Navarra	This study
ESP0116	Iberia	Spain	Cantabria	This study
ESP0133	Iberia	Spain	Castellón	This study
ESP0141	Iberia	Spain	Córdoba	This study
ESP0143	Iberia	Spain	Barcelona	This study
ESP0145	Iberia	Spain	Alicante	This study
ESP0147	Iberia	Spain	Navarra	This study
ESP0151	Iberia	Spain	Badajoz	This study
ESP0157	Iberia	Spain	Jaén	This study
ESP0158	Iberia	Spain	La Rioja	This study
ESP0163	Iberia	Spain	Jaén	This study
ESP0164	Iberia	Spain	León	This study
ESP0172	Iberia	Spain	Córdoba	This study
ESP0174	Iberia	Spain	Cuenca	This study
ESP0179	Iberia	Spain	Salamanca	This study
ESP0182	Iberia	Spain	Córdoba	This study
ESP0183	Iberia	Spain	Avila	This study
ESP0188	Iberia	Spain	Ciudad Real	This study
ESP0192	Iberia	Spain	Ciudad Real	This study
ESP0195	Iberia	Spain	Murcia	This study
ESP0205	Iberia	Spain	Asturias	This study
ESP0208	Iberia	Spain	Badajoz	This study
ESP0211	Iberia	Spain	Albacete	This study
ESP0213	Iberia	Spain	Salamanca	This study
ESP0214	Iberia	Spain	Salamanca	This study
ESP0215	Iberia	Spain	Murcia	This study
ESP0216	Iberia	Spain	Jaén	This study
ESP0224	Iberia	Spain	León	This study
ESP0226	Iberia	Spain	Murcia	This study
ESP0227	Iberia	Spain	Salamanca	This study
ESP0228	Iberia	Spain	Valencia	This study
ESP0231	Iberia	Spain	Cuenca	This study
ESP0232	Iberia	Spain	Asturias	This study
ESP0233	Iberia	Spain	Badajoz	This study
ESP0240	Iberia	Spain	Córdoba	This study
ESP0257	Iberia	Spain	Cantabria	This study
ESP0261	Iberia	Spain	Murcia	This study
ESP0265	Iberia	Spain	Zaragoza	This study
ESP0285	Iberia	Spain	Murcia	This study
ESP0292	Iberia	Spain	Murcia	This study
ESP0295	Iberia	Spain	Cantabria	This study
ESP0296	Iberia	Spain	Cantabria	This study
ESP0305	Iberia	Spain	Burgos	This study
ESP0310	Iberia	Spain	Lugo	This study
ESP0324	Iberia	Spain	Huesca	This study
ESP0335	Iberia	Spain	Salamanca	This study
ESP0341	Iberia	Spain	Murcia	This study
ESP0344	Iberia	Spain	Murcia	This study
ESP0347	Iberia	Spain	Córdoba	This study
ESP0353	Iberia	Spain	Córdoba	This study
ESP0354	Iberia	Spain	Barcelona	This study
ESP0357	Iberia	Spain	Valladolid	This study
ESP0361	Iberia	Spain	Sevilla	This study
ESP0366	Iberia	Spain	Cantabria	This study
ESP0377	Iberia	Spain	Asturias	This study
ESP0378	Iberia	Spain	Badajoz	This study
ESP0382	Iberia	Spain	Barcelona	This study
ESP0395	Iberia	Spain	Alicante	This study
ESP0398	Iberia	Spain	Salamanca	This study
ESP0399	Iberia	Spain	Toledo	This study
ESP0400	Iberia	Spain	Málaga	This study
ESP0419	Iberia	Spain	Granada	This study
ESP0424	Iberia	Spain	Alicante	This study
ESP0425	Iberia	Spain	Córdoba	This study
ESP0430	Iberia	Spain	Lugo	This study
ESP0436	Iberia	Spain	Málaga	This study
ESP0439	Iberia	Spain	Salamanca	This study
ESP0440	Iberia	Spain	Asturias	This study
ESP0446	Iberia	Spain	Albacete	This study
ESP0454	Iberia	Spain	Cáceres	This study
ESP0459	Iberia	Spain	Málaga	This study
ESP0463	Iberia	Spain	Toledo	This study
ESP0465	Iberia	Spain	Ciudad Real	This study
ESP0477	Iberia	Spain	Galicia	This study
ESP0492	Iberia	Spain	Barcelona	This study
ESP0498	Iberia	Spain	Jaén	This study

ESP0500	**Iberia**	**Spain**	**Toledo**	**This study**
ESP0503	**Iberia**	**Spain**	**Granada**	**This study**
ESP0504	**Iberia**	**Spain**	**Madrid**	**This study**
ESP0509	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0511	**Iberia**	**Spain**	**Guadalajara**	**This study**
ESP0513	**Iberia**	**Spain**	**Tarragona**	**This study**
ESP0526	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0535	**Iberia**	**Spain**	**León**	**This study**
ESP0545	**Iberia**	**Spain**	**Tarragona**	**This study**
ESP0550	**Iberia**	**Spain**	**Teruel**	**This study**
ESP0552	**Iberia**	**Spain**	**Guadalajara**	**This study**
ESP0558	**Iberia**	**Spain**	**Burgos**	**This study**
ESP0561	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0567	**Iberia**	**Spain**	**Tarragona**	**This study**
ESP0571	**Iberia**	**Spain**	**Toledo**	**This study**
ESP0573	**Iberia**	**Spain**	**Cáceres**	**This study**
ESP0574	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0579	**Iberia**	**Spain**	**Cantabria**	**This study**
ESP0582	**Iberia**	**Spain**	**Castilla-La Mancha**	**This study**
ESP0583	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0596	**Iberia**	**Spain**	**Ciudad Real**	**This study**
ESP0599	**Iberia**	**Spain**	**Jaén**	**This study**
ESP0606	**Iberia**	**Spain**	**Valencia**	**This study**
ESP0611	**Iberia**	**Spain**		**This study**
ESP0616	**Iberia**	**Spain**	**Soria**	**This study**
ESP0618	**Iberia**	**Spain**	**Palencia**	**This study**
ESP0623	**Iberia**	**Spain**	**Cáceres**	**This study**
ESP0629	**Iberia**	**Spain**	**Toledo**	**This study**
ESP0634	**Iberia**	**Spain**	**La Coruña**	**This study**
ESP0637	**Europe Basque**	**Spain**	**Basque Country**	**This study**
ESP0653	**Iberia**	**Spain**	**Cantabria**	**This study**
ESP0670	**Iberia**	**Spain**	**Baleares**	**This study**
ESP0670	**Iberia**	**Spain**	**Baleares**	**This study**
ESP0671	**Iberia**	**Spain**	**Las Palmas**	**This study**
ESP0674	**Iberia**	**Spain**	**Madrid**	**This study**
ESP0680	**Iberia**	**Spain**	**Granada**	**This study**
ESP0684	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0690	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0693	**Iberia**	**Spain**		**This study**
ESP0717	**Iberia**	**Spain**	**Avila**	**This study**
ESP0728	**Iberia**	**Spain**	**Soria**	**This study**
ESP0730	**Iberia**	**Spain**	**Albacete**	**This study**
ESP0737	**Iberia**	**Spain**	**Avila**	**This study**
ESP0746	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0747	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0752	**Iberia**	**Spain**	**Sevilla**	**This study**
ESP0754	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0758	**Iberia**	**Spain**		**This study**
ESP0770	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0773	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0775	**Iberia**	**Spain**	**Salamanca**	**This study**
ESP0784	**Iberia**	**Spain**	**Asturias**	**This study**
ESP0792	**Iberia**	**Spain**	**Pontevedra**	**This study**
ESP0793	**Iberia**	**Spain**	**Badajoz**	**This study**
ESP0798	**Iberia**	**Spain**		**This study**
ESP0799	**Iberia**	**Spain**	**Cantabria**	**This study**
ESP0801	**Iberia**	**Spain**	**Granada**	**This study**
ESP0805	**Iberia**	**Spain**	**Ourense**	**This study**
ESP0809	**Iberia**	**Spain**	**Albacete**	**This study**
ESP0830	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0831	**Iberia**	**Spain**	**Huelva**	**This study**
ESP0832	**Iberia**	**Spain**	**Valencia**	**This study**
ESP0833	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0845	**Iberia**	**Spain**	**Huesca**	**This study**
ESP0849	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0854	**Iberia**	**Spain**	**Salamanca**	**This study**
ESP0856	**Iberia**	**Spain**	**Valencia**	**This study**
ESP0863	**Iberia**	**Spain**	**Coruña, La**	**This study**
ESP0865	**Europe Basque**	**Spain**	**Basque country, Vizcaya**	**This study**
ESP0870	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0877	**Iberia**	**Spain**	**Avila**	**This study**
ESP0880	**Iberia**	**Spain**		**This study**
ESP0881	**Iberia**	**Spain**	**Girona**	**This study**
ESP0883	**Iberia**	**Spain**	**Valencia**	**This study**
ESP0900	**Iberia**	**Spain**	**Granada**	**This study**
ESP0906	**Iberia**	**Spain**	**Salamanca**	**This study**
ESP0915	**Iberia**	**Spain**		**This study**
ESP0921	**Iberia**	**Spain**		**This study**
ESP0924	**Iberia**	**Spain**	**Sevilla**	**This study**
ESP0934	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0939	**Iberia**	**Spain**	**Toledo**	**This study**
ESP0945	**Iberia**	**Spain**		**This study**

ESP0946	**Iberia**	**Spain**	**Cuenca**	**This study**
ESP0947	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0959	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0960	**Iberia**	**Spain**	**León**	**This study**
ESP0962	**Iberia**	**Spain**	**Cantabria**	**This study**
ESP0964	**Iberia**	**Spain**	**Guadalajara**	**This study**
ESP0968	**Iberia**	**Spain**		**This study**
ESP0970	**Iberia**	**Spain**	**Jaén**	**This study**
ESP0981	**Iberia**	**Spain**	**Aragón**	**This study**
ESP0988	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0995	**Iberia**	**Spain**		**This study**
ESP1005	**Iberia**	**Spain**	**Canarias (Islas)**	**This study**
ESP1013	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP1016	**Iberia**	**Spain**	**Valladolid**	**This study**
ESP1017	**Iberia**	**Spain**	**León**	**This study**
ESP1020	**Iberia**	**Spain**	**Teruel**	**This study**
ESP1025	**Iberia**	**Spain**	**Asturias**	**This study**
ESP1030	**Iberia**	**Spain**	**Huesca**	**This study**
ESP1033	**Iberia**	**Spain**		**This study**
ESP1040	**Iberia**	**Spain**		**This study**
ESP1041	**Iberia**	**Spain**		**This study**
EU074158	Unknown	Unknown		Family Tree
EU080974	Unknown	Unknown		Family Tree
EU089747	Unknown	Unknown		Family Tree
EU130562	Unknown	Unknown		Family Tree
EU130942	Europe NW	England	ethnicity:English	Family Tree
EU148452	Europe NE	Lithuania	Ashkenazi	Family Tree
EU200235	Unknown	Unknown		Family Tree
EU200237	Unknown	Unknown		Family Tree
EU215517	Unknown	Unknown		Family Tree
EU219920	Unknown	Unknown		Family Tree
EU233277	Unknown	Unknown		Family Tree
EU262984	Europe NE	Belarus	Ashkenazi	Family Tree
EU369376	Europe NW	England	USA (English)	Family Tree
EU372628	Europe NW	Wales		Family Tree
EU372630	Unknown	Unknown		Family Tree
EU428754	Unknown	Unknown		Family Tree
EU555475	Europe NW	Ireland		Family Tree
EU568371	Unknown	Unknown		Family Tree
EU597509	North Caucasus	Adygei, Russia		Hartmann et al. (2009)
EU597511	Europe NW	France	NA12625	Hartmann et al. (2009)
EU597524	Europe NW	Czech Republic	NA15727	Hartmann et al. (2009)
EU597532	Europe SE	Italy(Sardinia)		Hartmann et al. (2009)
EU597560	Unknown	Unknown		Hartmann et al. (2009)
EU600345	Near East	Druze		Shlush et al (2008)
EU600348	Near East	Druze		Shlush et al (2008)
EU675941	Unknown	Unknown		Family Tree
EU687746	Europe NW	Norway	Saami	Family Tree
EU714270	Europe NW	Scotland/Ireland		Family Tree
EU715237	Unknown	Unknown		Family Tree
EU747355	Europe NW	Germany	USA (German)	Family Tree
EU768844	Europe NW	Germany	Unterfranken (Lower Franconia)	Family Tree
EU770202	Europe NW	Germany	Wuerttemberg	Family Tree
EU779660	Europe NW	Germany	Unterfranken (Lower Franconia)	Family Tree
EU828774	Unknown	Unknown		Family Tree
EU914954	Europe NW	Ireland	USA(Irish)	Family Tree
EU935845	Europe NW	Hungary	USA (ethnicity:Hungarian)	Family Tree
EU979418	Europe NW	England	USA (English)	Family Tree
EU980593	Europe NW	Norway	Sweden (ethnicity:Norwegian)	Family Tree
F12S927675	**Near East**	**Palestine**		**unpub**
F8S927862	**Near East**	**Jordan**		**unpub**
FJ156761	Europe NW	Slovakia	USA (ethnicity:Slovak)	Family Tree
FJ188716	Europe NW	Germany		Family Tree
FJ216960	Europe	Europe		Family Tree
FJ236980	North Africa	Sahara		Ennafaa et al. (2009)
FJ236981	Iberia	Spain		Ennafaa et al. (2009)
FJ236982	South Caucasus	Georgia		Ennafaa et al. (2009)
FJ236983	North Africa	Morocco		Ennafaa et al. (2009)
FJ348176	Europe NW	South Tyrol		Pichler et al. (2010)
FJ348185	Europe NW	South Tyrol		Pichler et al. (2010)
FJ348196	Europe NW	South Tyrol		Pichler et al. (2010)
FJ348199	Europe NW	South Tyrol		Pichler et al. (2010)
FJ348200	Europe NW	South Tyrol		Pichler et al. (2010)
FJ348214	Europe NW	South Tyrol		Pichler et al. (2010)
FJ460532	North Africa	Tunisia		Costa et al. (2009)
FJ460534	North Africa	Tunisia		Costa et al. (2009)
FJ460544	North Africa	Tunisia		Costa et al. (2009)
FJ460548	North Africa	Tunisia		Costa et al. (2009)
FJ711775	Unknown	Unknown		Family Tree
FJ719302	Iberia	Canary Islands		Fregel et al. (2009)
FJ719303	North Africa	Algeria		Fregel et al. (2009)
FJ719304	Iberia	Canary Islands		Fregel et al. (2009)

FJ719305	Iberia	Canary Islands		Fregel et al. (2009)
FJ798928	Europe	USA		Family Tree
FJ801039	Europe NE	Finland		Family Tree
FJ858266	Europe NW	England	ethnicity:English; origin_locality:USA	Family Tree
FJ917552	Unknown	Unknown		Family Tree
FJ940865	Europe NW	England	ethnicity:English; origin_locality:Canada: Ontario	Family Tree
FRA	**Europe SE**	**Italy**	**Northern Italy, Lombardy**	**This study**
fri-1087	Europe NW	Netherlands		Batini et al. (2017)
fri-1312	Europe NW	Netherlands		Batini et al. (2017)
fri-1324	Europe NW	Netherlands		Batini et al. (2017)
GOG	**Iberia**	**Spain**		**This study**
gonl-103a	**Europe NW**	**Netherlands**		**This study**
gonl-105b	**Europe NW**	**Netherlands**		**This study**
gonl-108a	**Europe NW**	**Netherlands**		**This study**
gonl-114a	**Europe NW**	**Netherlands**		**This study**
gonl-128b	**Europe NW**	**Netherlands**		**This study**
gonl-130a	**Europe NW**	**Netherlands**		**This study**
gonl-132a	**Europe NW**	**Netherlands**		**This study**
gonl-13b	**Europe NW**	**Netherlands**		**This study**
gonl-141b	**Europe NW**	**Netherlands**		**This study**
gonl-143a	**Europe NW**	**Netherlands**		**This study**
gonl-146b	**Europe NW**	**Netherlands**		**This study**
gonl-147b	**Europe NW**	**Netherlands**		**This study**
gonl-154a	**Europe NW**	**Netherlands**		**This study**
gonl-15a	**Europe NW**	**Netherlands**		**This study**
gonl-160a	**Europe NW**	**Netherlands**		**This study**
gonl-167b	**Europe NW**	**Netherlands**		**This study**
gonl-16a	**Europe NW**	**Netherlands**		**This study**
gonl-172a	**Europe NW**	**Netherlands**		**This study**
gonl-172b	**Europe NW**	**Netherlands**		**This study**
gonl-173b	**Europe NW**	**Netherlands**		**This study**
gonl-187a	**Europe NW**	**Netherlands**		**This study**
gonl-188b	**Europe NW**	**Netherlands**		**This study**
gonl-197a	**Europe NW**	**Netherlands**		**This study**
gonl-201a	**Europe NW**	**Netherlands**		**This study**
gonl-202a	**Europe NW**	**Netherlands**		**This study**
gonl-205b	**Europe NW**	**Netherlands**		**This study**
gonl-206a	**Europe NW**	**Netherlands**		**This study**
gonl-216b	**Europe NW**	**Netherlands**		**This study**
gonl-21a	**Europe NW**	**Netherlands**		**This study**
gonl-227b	**Europe NW**	**Netherlands**		**This study**
gonl-231b	**Europe NW**	**Netherlands**		**This study**
gonl-233b	**Europe NW**	**Netherlands**		**This study**
gonl-236b	**Europe NW**	**Netherlands**		**This study**
gonl-26a	**Europe NW**	**Netherlands**		**This study**
gonl-26b	**Europe NW**	**Netherlands**		**This study**
gonl-28b	**Europe NW**	**Netherlands**		**This study**
gonl-29b	**Europe NW**	**Netherlands**		**This study**
gonl-2b	**Europe NW**	**Netherlands**		**This study**
gonl-34b	**Europe NW**	**Netherlands**		**This study**
gonl-35a	**Europe NW**	**Netherlands**		**This study**
gonl-41a	**Europe NW**	**Netherlands**		**This study**
gonl-42a	**Europe NW**	**Netherlands**		**This study**
gonl-48a	**Europe NW**	**Netherlands**		**This study**
gonl-49a	**Europe NW**	**Netherlands**		**This study**
gonl-50a	**Europe NW**	**Netherlands**		**This study**
gonl-56a	**Europe NW**	**Netherlands**		**This study**
gonl-58a	**Europe NW**	**Netherlands**		**This study**
gonl-66b	**Europe NW**	**Netherlands**		**This study**
gonl-68a	**Europe NW**	**Netherlands**		**This study**
gonl-70a	**Europe NW**	**Netherlands**		**This study**
gonl-72a	**Europe NW**	**Netherlands**		**This study**
gonl-76b	**Europe NW**	**Netherlands**		**This study**
gonl-77b	**Europe NW**	**Netherlands**		**This study**
gonl-81a	**Europe NW**	**Netherlands**		**This study**
gonl-92a	**Europe NW**	**Netherlands**		**This study**
gonl-92b	**Europe NW**	**Netherlands**		**This study**
gonl-93b	**Europe NW**	**Netherlands**		**This study**
gonl-96b	**Europe NW**	**Netherlands**		**This study**
gonl-97b	**Europe NW**	**Netherlands**		**This study**
GP2_A6	**Europe NW**	**Germany**		**This study**
GP2_B12	**Europe NW**	**Germany**		**This study**
GP2_B6	**Europe NW**	**Germany**		**This study**
GP2_C1	**Europe NW**	**Germany**		**This study**
GP2_C12	**Europe NW**	**Germany**		**This study**
GP2_D10	**Europe NW**	**Germany**		**This study**
GP2_D3	**Europe NW**	**Germany**		**This study**
GP2_E3	**Europe NW**	**Germany**		**This study**
GP2_E5	**Europe NW**	**Germany**		**This study**
GP2_F10	**Europe NW**	**Germany**		**This study**

GP2_F3	**Europe NW**	**Germany**		**This study**
GP2_F5	**Europe NW**	**Germany**		**This study**
GP2_F7	**Europe NW**	**Germany**		**This study**
GP2_G12	**Europe NW**	**Germany**		**This study**
GP2_H2	**Europe NW**	**Germany**		**This study**
GP2_H7	**Europe NW**	**Germany**		**This study**
GP2_H8	**Europe NW**	**Germany**		**This study**
GP3_A1	**Europe NW**	**Germany**		**This study**
GP3_A6	**Europe NW**	**Germany**		**This study**
GP3_A7	**Europe NW**	**Germany**		**This study**
GP3_B2	**Europe NW**	**Germany**		**This study**
GP3_B4	**Europe NW**	**Germany**		**This study**
GP3_B8	**Europe NW**	**Germany**		**This study**
GP3_C11	**Europe NW**	**Germany**		**This study**
GP3_D6	**Europe NW**	**Germany**		**This study**
GP3_D7	**Europe NW**	**Germany**		**This study**
GP3_E12	**Europe NW**	**Germany**		**This study**
GP3_E6	**Europe NW**	**Germany**		**This study**
GP3_G4	**Europe NW**	**Germany**		**This study**
GP3_G6	**Europe NW**	**Germany**		**This study**
GP3_G8	**Europe NW**	**Germany**		**This study**
GP3_H10	**Europe NW**	**Germany**		**This study**
GQ150344	Europe NW	England		Family Tree
GQ153528	Europe NW	England		Family Tree
GQ175058	Europe	USA		Family Tree
GQ332765	Europe	USA		Family Tree
GQ334714	Iberia	Portugal	origin_locality:Portugal: The Azores	Family Tree
GQ478575	Europe NW	Sweden	origin_locality:Sweden: Vastergotland	Family Tree
GQ888707	Unknown	Unknown		Family Tree
GQ888723	Europe Basque	Spain	Basque Country	García et al. (2011)
GQ888724	Iberia	Spain	Andalusia	Garcia et al. (2011)
GQ888725	Iberia	Spain	Andalusia	Garcia et al. (2011)
GQ888726	Iberia	Spain	Asturias	Garcia et al. (2011)
GQ888727	Europe Basque	Spain	Basque Country	Garcia et al. (2011)
GR67	Europe SE	Greece		**unpub**
GR73	Europe SE	Greece		**unpub**
GR74	Europe SE	Greece		**unpub**
gre-79	Europe SE	Greece		Batini et al. (2017)
GU122983	Europe NE	Russia	Tatars, Volga-Ural Region	Malyarchuk et al. (2010)
GU122996	Europe NE	Russia	Tatars, Volga-Ural Region	Malyarchuk et al. (2010)
GU123023	Europe NE	Russia	Tatars, Volga-Ural Region	Malyarchuk et al. (2010)
GU181350	Unknown	Unknown		Family Tree
GU207871	Europe NW	Ireland		Family Tree
GU214208	Europe NW	Ireland		Family Tree
GU289555	Europe NW	England		Family Tree
GU433215	Europe NW	Scotland	ethnicity:Scottish; origin_locality:USA	Family Tree
GU461664	Europe	USA		Family Tree
GU592022	Unknown	Unknown		(Fendt et al., 2011)
GU724771	Europe NW	Poland		Family Tree
GU797136	Europe	USA		Family Tree
GU797829	Europe NW	Britain	ethnicity:British; origin_locality:USA	Family Tree
GU812902	Unknown	Unknown		Family Tree
GU981676	Europe NW	Poland		Family Tree
HG00099	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00110	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00111	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00125	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00134	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00135	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00138	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)

HG00150	Europe NW	England/Scotland	GBR		The 1000 Genomes Project Consortium (2015)
HG00152	Europe NW	England/Scotland	GBR		The 1000 Genomes Project Consortium (2015)
HG00153	Europe NW	England/Scotland	GBR		The 1000 Genomes Project Consortium (2015)
HG00158	Europe NW	England/Scotland	GBR		The 1000 Genomes Project Consortium (2015)
HG00159	Europe NW	England/Scotland	GBR		The 1000 Genomes Project Consortium (2015)
HG00180	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00182	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00189	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00232	Europe NW	England/Scotland	GBR		The 1000 Genomes Project Consortium (2015)
HG00266	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00269	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00272	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00278	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00310	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00313	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00335	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00342	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00353	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00361	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00362	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00372	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00378	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00380	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00381	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG00382	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG01167	Europe NE	Finland	FIN		The 1000 Genomes Project Consortium (2015)
HG01509	Iberia	Spain	IBS		The 1000 Genomes Project Consortium (2015)

HG01519	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HG01521	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HG01613	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HG01765	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HG01786	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HG02236	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HG02239	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HM000002	Unknown	Unknown		Family Tree
HM017858	Unknown	Unknown		Family Tree
HM027898	Europe SE	Bulgaria		Family Tree
HM060309	Europe NE	Russia	origin_locality:Moscow	Family Tree
HM100712	Europe NW	Netherlands		Family Tree
HM103354	Unknown	Unknown		Gómez-Durán et al. (2010)
HM103357	Unknown	Unknown		Gómez-Durán et al. (2010)
HM103358	Unknown	Unknown		Gómez-Durán et al. (2010)
HM119592	Europe NW	Sweden	ethnicity:Swedish; origin_locality:USA: Kansas	Family Tree
HM171270	North Africa	Libya	Tahala (Tuareg)	Ottoni et al. (2010)
HM171271	North Africa	Libya	Tahala (Tuareg)	Ottoni et al. (2010)
HM171272	North Africa	Libya	Tahala (Tuareg)	Ottoni et al. (2010)
HM171273	North Africa	Libya	Al Awayant (Tuareg)	Ottoni et al. (2010)
HM171274	North Africa	Libya	Al Awayant (Tuareg)	Ottoni et al. (2010)
HM171275	North Africa	Libya	Al Awayant (Tuareg)	Ottoni et al. (2010)
HM171276	North Africa	Libya	Al Awayant (Tuareg)	Ottoni et al. (2010)
HM171277	North Africa	Libya	Al Awayant (Tuareg)	Ottoni et al. (2010)
HM171278	North Africa	Libya	Tahala (Tuareg)	Ottoni et al. (2010)
HM171279	North Africa	Libya	Tahala (Tuareg)	Ottoni et al. (2010)
HM171280	North Africa	Libya	Tahala (Tuareg)	Ottoni et al. (2010)
HM245920	Europe NW	England/Wales	USA (English/Welsh)	Family Tree
HM462218	Europe NW	England	USA (Early Virginia, English)	Family Tree
HM488738	Europe NW	England	USA (ethnicity:English)	Family Tree
HM589042	Europe NW	England		Family Tree
HM622671	Europe	USA		Family Tree
HM628905	Europe NW	Ireland	ethnicity:Irish; origin_locality:Canada	Family Tree
HM775496	Europe NW	Sweden	ethnicity:Swedish; origin_locality:Sweden	Family Tree
HM852868	Near East	Turkey		Schönberg et al. (2011)
HQ114015	Europe NW	England	ethnicity:English; origin_locality:Canada	Family Tree
HQ114262	Europe NW	Germany		Family Tree
HQ184065	Europe NE	Belarus		Family Tree
HQ234333	Europe	USA		Family Tree
HQ268504	Unknown	Unknown		Direct submission: GENE- Nucleo de Genetica Medica
HQ284163	Europe NE	Russia		Family Tree
HQ287885	Europe NW	Europe NW	Newfoundland (English, Irish, or French ancestries)	Pope et al. (2011)
HQ287886	Europe NW	Europe NW	Newfoundland (English, Irish, or French ancestries)	Pope et al. (2011)
HQ287887	Europe NW	Europe NW	Newfoundland (English, Irish, or French ancestries)	Pope et al. (2011)
HQ287891	Europe NW	Europe NW	Newfoundland (English, Irish, or French ancestries)	Pope et al. (2011)
HQ287892	Europe NW	Europe NW	Newfoundland (English, Irish, or French ancestries)	Pope et al. (2011)
HQ287893	Europe NW	Europe NW	Newfoundland (English, Irish, or French ancestries)	Pope et al. (2011)
HQ325738	Near East	Lebanon		Family Tree
HQ336334	Europe NW	Europe NW	ethnicity:W. Euro-French	Family Tree
HQ384172	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384173	Iberia	Iberia		Gómez-Carballa et al. (2011)

HQ384174	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384175	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384176	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384177	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384178	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384179	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384180	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384181	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384182	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384183	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ384184	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ400746	Europe NW	Denmark		Family Tree
HQ588357	Europe NW	Sweden		Family Tree
HQ658133	Europe NW	Sweden		Family Tree
HQ658466	Europe NW	Ireland	origin_locality:USA	Family Tree
HQ658478	Europe	USA		Family Tree
HQ658480	Europe NW	Denmark		Family Tree
HQ658482	Europe NW	Ireland	origin_locality:USA	Family Tree
HQ658607	Europe	USA		Family Tree
HQ659685	Europe	USA		Family Tree
HQ659690	Unknown	Unknown		Family Tree
HQ659701	Unknown	Unknown		Family Tree
HQ659703	Europe NW	Germany	origin_locality:USA	Family Tree
HQ659848	Europe NW	England	origin_locality:USA	Family Tree
HQ661844	Europe	USA		Family Tree
HQ662225	Europe NW	England		Family Tree
HQ663876	Unknown	Unknown		Family Tree
HQ663877	Europe NW	Wales		Family Tree
HQ676806	Europe NW	Norway		Family Tree
HQ681884	Europe	USA		Family Tree
HQ703482	Europe NW	Ireland/England	Irish/English; origin_locality:USA	Family Tree
HQ839859	Europe NW	Germany	origin_locality:USA	Family Tree
HQ841014	Europe NW	England		Family Tree
HQ842871	Europe NW	Sweden		Family Tree
HQ843989	Unknown	Unknown		Family Tree
HQ875780	Europe NW	Slovakia		Family Tree
HQ880578	Europe NW	Belgium		Family Tree
HQ908087	Europe NE	Russia	Pskov	Family Tree
hun-25	Europe NW	Hungary		Batini et al. (2017)
hun-38	Europe NW	Hungary		Batini et al. (2017)
hun-46	Europe NW	Hungary		Batini et al. (2017)
hun-47	Europe NW	Hungary		Batini et al. (2017)
IMA	**Europe Basque**	**Spain**	**Basque Country**	**This study**
ire-0114	Europe NW	British Isles		Batini et al. (2017)
ire-0116	Europe NW	British Isles		Batini et al. (2017)
JF326185	Europe NW	England	ethnicity:English; origin_locality:Australia	Family Tree
JF825889	Europe NW	Norway		Family Tree
JF833269	Europe	USA		Family Tree
JF903928	Europe NE	Finland	origin_locality:Finland	Family Tree
JN202726	Europe NW	England	ethnicity:English; origin_locality:USA	Family Tree
JN224991	Europe SE	Italy	Calabria	Family Tree
JN400598	Europe	USA		Family Tree
JN581638	Europe SE	Italy	Chioggia, Venice	Bertolin et al. (2011)
JN581639	Europe SE	Italy	Chioggia, Venice	Bertolin et al. (2011)
JN581641	Europe SE	Italy	Chioggia, Venice	Bertolin et al. (2011)
JN581644	Europe SE	Italy	Chioggia, Venice	Bertolin et al. (2011)
JN581647	Europe SE	Italy	Chioggia, Venice	Bertolin et al. (2011)
JN581648	Europe SE	Italy	Chioggia, Venice	Bertolin et al. (2011)
JN603189	Unknown	Unknown		Family Tree
JN604117	South Caucasus	Armenia		Family Tree
JN899290	Europe NE	Russia		Family Tree
JN903384	Europe NE	Russia		Family Tree
JOA	**Iberia**	**Portugal**	**Viana do Castelo**	**This study**
JQ044904	West Africa	Burkina Faso	Mande	Barbieri et al. (2012)
JQ065050	Europe NW	Scotland	ethnicity:Scottish; origin_locality:USA	Family Tree
JQ324516	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)

JQ324517	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324520	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324521	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324523	Europe Basque	Spain	Basque Country	Behar et al. (2012a)
JQ324524	Europe Basque	Spain	Basque Country	Behar et al. (2012a)
JQ324525	Europe Basque	Spain	Basque-speaking	Behar et al. (2012a)
JQ324529	Europe Basque	Spain	Basque-speaking	Behar et al. (2012a)
JQ324530	Europe Basque	Spain	Basque-speaking	Behar et al. (2012a)
JQ324535	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324536	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324539	Europe NW	France	Basque-speaking	Behar et al. (2012a)
JQ324542	Europe NW	France	Basque-speaking	Behar et al. (2012a)
JQ324543	Europe NW	France	Basque-speaking	Behar et al. (2012a)
JQ324551	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324552	Europe Basque	Spain		Behar et al. (2012a)
JQ324554	Europe Basque	Spain		Behar et al. (2012a)
JQ324557	Europe Basque	Spain		Behar et al. (2012a)
JQ324560	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324561	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324562	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324563	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324565	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324569	Europe Basque	Spain	Navarra CW, Basque spoken up to the last century	Behar et al. (2012a)
JQ324576	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324577	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324579	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324580	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324584	Iberia	Spain	Basque Country	Behar et al. (2012a)
JQ324588	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324589	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324590	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324593	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324594	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324599	Europe Basque	Spain		Behar et al. (2012a)
JQ324602	Europe Basque	Spain		Behar et al. (2012a)
JQ324604	Europe Basque	Spain		Behar et al. (2012a)
JQ324605	Europe Basque	Spain		Behar et al. (2012a)
JQ324607	Europe Basque	Spain		Behar et al. (2012a)
JQ324609	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324614	Iberia	Spain	Burgos	Behar et al. (2012a)
JQ324615	Europe Basque	Spain	Navarra CW, Basque spoken up to the last century	Behar et al. (2012a)
JQ324624	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324626	Iberia	Spain	Cantabria	Behar et al. (2012a)
JQ324627	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324631	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324633	Iberia	Spain	Cantabria	Behar et al. (2012a)
JQ324636	Iberia	Spain	Burgos	Behar et al. (2012a)
JQ324641	Europe Basque	Spain	Navarra CW, Basque spoken up to the last century	Behar et al. (2012a)
JQ324643	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324644	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324646	Europe Basque	Spain	Navarra CW, Basque spoken up to the last century	Behar et al. (2012a)
JQ324649	Europe Basque	Spain		Behar et al. (2012a)
JQ324650	Europe Basque	Spain		Behar et al. (2012a)
JQ324653	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324655	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324656	Europe Basque	Spain		Behar et al. (2012a)
JQ324657	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324658	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324659	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324660	Iberia	Spain	Cantabria	Behar et al. (2012a)
JQ324662	Iberia	Spain	Cantabria	Behar et al. (2012a)
JQ324664	Iberia	Spain	Cantabria	Behar et al. (2012a)
JQ324667	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324669	Europe Basque	Spain		Behar et al. (2012a)
JQ324670	Europe Basque	Spain		Behar et al. (2012a)
JQ324672	Europe Basque	Spain		Behar et al. (2012a)

JQ324674	Europe Basque	Spain		Behar et al. (2012a)
JQ324681	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324683	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324686	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324688	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324689	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324690	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324691	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324698	Europe Basque	Spain		Behar et al. (2012a)
JQ324700	Europe Basque	Spain		Behar et al. (2012a)
JQ324705	Europe Basque	Spain		Behar et al. (2012a)
JQ324708	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324709	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324710	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324713	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324714	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324715	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324717	Europe Basque	Spain		Behar et al. (2012a)
JQ324719	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324720	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324721	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324722	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324723	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324726	Europe Basque	Spain		Behar et al. (2012a)
JQ324728	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324732	Europe Basque	Spain		Behar et al. (2012a)
JQ324736	Europe Basque	Spain		Behar et al. (2012a)
JQ324737	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324739	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324742	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324743	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324746	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324747	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324748	Europe Basque	Spain		Behar et al. (2012a)
JQ324751	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324752	Europe Basque	France	Basque-spealing	Behar et al. (2012a)
JQ324753	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324754	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324755	Iberia	Spain	La Rioja	Behar et al. (2012a)
JQ324756	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324760	Europe Basque	Spain		Behar et al. (2012a)
JQ324763	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324765	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324766	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324768	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324770	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324771	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324773	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324777	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324778	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324779	Europe Basque	Spain		Behar et al. (2012a)
JQ324780	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324782	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324784	Europe Basque	Spain		Behar et al. (2012a)
JQ324786	Europe Basque	Spain		Behar et al. (2012a)
JQ324787	Europe Basque	Spain		Behar et al. (2012a)
JQ324793	Europe Basque	Spain	Basque Country	Behar et al. (2012a)
JQ324796	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324797	Europe Basque	Spain		Behar et al. (2012a)
JQ324798	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)

JQ324799	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324800	Europe Basque	Spain		Behar et al. (2012a)
JQ324801	Europe Basque	Spain		Behar et al. (2012a)
JQ324802	Europe Basque	Spain		Behar et al. (2012a)
JQ324803	Europe Basque	Spain		Behar et al. (2012a)
JQ324805	Europe Basque	Spain	Basque Country	Behar et al. (2012a)
JQ324807	Europe Basque	Spain		Behar et al. (2012a)
JQ324808	Europe Basque	Spain		Behar et al. (2012a)
JQ324809	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324813	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324815	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324816	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324819	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324822	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324823	Europe Basque	Spain		Behar et al. (2012a)
JQ324824	Europe Basque	Spain		Behar et al. (2012a)
JQ324825	Europe Basque	Spain		Behar et al. (2012a)
JQ324826	Europe Basque	Spain		Behar et al. (2012a)
JQ324829	Europe Basque	Spain		Behar et al. (2012a)
JQ324830	Europe Basque	Spain		Behar et al. (2012a)
JQ324831	Europe Basque	Spain		Behar et al. (2012a)
JQ324834	Europe Basque	Spain		Behar et al. (2012a)
JQ324835	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324836	Europe Basque	Spain		Behar et al. (2012a)
JQ324837	Europe Basque	Spain		Behar et al. (2012a)
JQ324838	Europe Basque	Spain		Behar et al. (2012a)
JQ324839	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324840	Europe Basque	Spain		Behar et al. (2012a)
JQ324841	Europe Basque	Spain		Behar et al. (2012a)
JQ324842	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324843	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324844	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324849	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324850	Europe Basque	Spain		Behar et al. (2012a)
JQ324852	Europe Basque	Spain		Behar et al. (2012a)
JQ324856	Europe Basque	Spain		Behar et al. (2012a)
JQ324857	Europe Basque	Spain		Behar et al. (2012a)
JQ324859	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324860	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324862	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324863	Europe Basque	Spain		Behar et al. (2012a)
JQ324864	Europe Basque	Spain		Behar et al. (2012a)
JQ324865	Europe Basque	Spain		Behar et al. (2012a)
JQ324866	Europe Basque	Spain		Behar et al. (2012a)
JQ324867	Europe Basque	Spain		Behar et al. (2012a)
JQ324870	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324871	Europe Basque	Spain		Behar et al. (2012a)
JQ324873	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324874	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324876	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324877	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324878	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324879	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324880	Europe Basque	Spain		Behar et al. (2012a)
JQ324882	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324883	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324884	Europe Basque	Spain		Behar et al. (2012a)
JQ324885	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324886	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324887	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324888	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324889	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324890	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324892	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324893	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)

JQ324894	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324895	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324897	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324898	Europe Basque	Spain		Behar et al. (2012a)
JQ324901	Europe Basque	Spain		Behar et al. (2012a)
JQ324902	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324904	Europe Basque	Spain		Behar et al. (2012a)
JQ324905	Europe Basque	Spain		Behar et al. (2012a)
JQ324908	Europe Basque	Spain		Behar et al. (2012a)
JQ324909	Europe Basque	Spain		Behar et al. (2012a)
JQ324911	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324912	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324915	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324917	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324919	Europe Basque	Spain		Behar et al. (2012a)
JQ324920	Europe Basque	Spain		Behar et al. (2012a)
JQ324921	Europe Basque	Spain		Behar et al. (2012a)
JQ324923	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324924	Europe Basque	Spain		Behar et al. (2012a)
JQ324927	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324928	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324931	Europe Basque	France	Basque-speaking	Behar et al. (2012a)
JQ324933	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324934	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ324935	Europe Basque	Spain	Basque spoken up to the last century	Behar et al. (2012a)
JQ406575	Unknown	Unknown		Family Tree
JQ664511	Europe SE	Croatia		Fu et al. (2012)
JQ664519	Europe SE	Croatia		Fu et al. (2012)
JQ664523	Europe SE	Croatia		Fu et al. (2012)
JQ664534	Europe SE	Croatia		Fu et al. (2012)
JQ664535	Europe SE	Croatia		Fu et al. (2012)
JQ664542	Europe SE	Croatia		Fu et al. (2012)
JQ664547	Europe SE	Croatia		Fu et al. (2012)
JQ701806	Unknown	Unknown		Behar et al. (2012b)
JQ701813	Unknown	Unknown		Behar et al. (2012b)
JQ701825	Unknown	Unknown		Behar et al. (2012b)
JQ701830	Europe NW	Germany	Czech Republic, ethnic German	Behar et al. (2012b)
JQ701831	Unknown	Unknown		Behar et al. (2012b)
JQ701846	Unknown	Unknown		Behar et al. (2012b)
JQ701861	Unknown	Unknown		Behar et al. (2012b)
JQ701863	Unknown	Unknown		Behar et al. (2012b)
JQ701873	Unknown	Unknown		Behar et al. (2012b)
JQ701874	Europe NW	Germany		Behar et al. (2012b)
JQ701879	Europe NW	Austria		Behar et al. (2012b)
JQ701881	Unknown	Unknown		Behar et al. (2012b)
JQ701888	Unknown	Unknown		Behar et al. (2012b)
JQ701931	Unknown	Unknown		Behar et al. (2012b)
JQ701944	Unknown	Unknown		Behar et al. (2012b)
JQ701945	Unknown	Unknown		Behar et al. (2012b)
JQ701950	Unknown	Unknown		Behar et al. (2012b)
JQ701952	Unknown	Unknown		Behar et al. (2012b)
JQ701966	Unknown	Unknown		Behar et al. (2012b)
JQ701969	Unknown	Unknown		Behar et al. (2012b)
JQ701978	Unknown	Unknown		Behar et al. (2012b)
JQ701980	Europe NW	Germany		Behar et al. (2012b)
JQ701984	Unknown	Unknown		Behar et al. (2012b)
JQ701987	Unknown	Unknown		Behar et al. (2012b)
JQ701993	Unknown	Unknown		Behar et al. (2012b)
JQ702002	Europe NW	Belgium		Behar et al. (2012b)
JQ702005	Europe NE	Romania		Behar et al. (2012b)
JQ702006	Unknown	Unknown		Behar et al. (2012b)
JQ702007	Europe NW	United Kingdom		Behar et al. (2012b)
JQ702008	Europe NW	Germany		Behar et al. (2012b)
JQ702009	Unknown	Unknown		Behar et al. (2012b)
JQ702016	Europe NW	England		Behar et al. (2012b)
JQ702024	Iberia	Spain		Behar et al. (2012b)
JQ702028	Europe NW	Poland		Behar et al. (2012b)
JQ702034	Europe NW	United Kingdom		Behar et al. (2012b)
JQ702039	Unknown	Unknown		Behar et al. (2012b)
JQ702043	Unknown	Unknown		Behar et al. (2012b)
JQ702057	Unknown	Unknown		Behar et al. (2012b)
JQ702071	Unknown	Unknown		Behar et al. (2012b)
JQ702077	Europe NW	United Kingdom		Behar et al. (2012b)
JQ702089	Europe NW	Germany		Behar et al. (2012b)
JQ702099	Unknown	Unknown		Behar et al. (2012b)

JQ702101	Unknown	Unknown	Behar et al. (2012b)
JQ702102	Unknown	Unknown	Behar et al. (2012b)
JQ702104	Europe NW	England	Behar et al. (2012b)
JQ702105	Unknown	Unknown	Behar et al. (2012b)
JQ702113	Unknown	Unknown	Behar et al. (2012b)
JQ702114	Unknown	Unknown	Behar et al. (2012b)
JQ702130	Unknown	Unknown	Behar et al. (2012b)
JQ702132	Unknown	Unknown	Behar et al. (2012b)
JQ702140	Europe NW	England	Behar et al. (2012b)
JQ702161	Europe NW	England	Behar et al. (2012b)
JQ702174	Unknown	Unknown	Behar et al. (2012b)
JQ702178	Unknown	Unknown	Behar et al. (2012b)
JQ702182	Unknown	Unknown	Behar et al. (2012b)
JQ702186	Unknown	Unknown	Behar et al. (2012b)
JQ702187	Unknown	Unknown	Behar et al. (2012b)
JQ702198	Unknown	Unknown	Behar et al. (2012b)
JQ702204	Unknown	Unknown	Behar et al. (2012b)
JQ702215	Unknown	Unknown	Behar et al. (2012b)
JQ702221	Unknown	Unknown	Behar et al. (2012b)
JQ702223	Unknown	Unknown	Behar et al. (2012b)
JQ702226	Iberia	Spain	Behar et al. (2012b)
JQ702234	Unknown	Unknown	Behar et al. (2012b)
JQ702236	Europe NW	United Kingdom	Behar et al. (2012b)
JQ702237	Unknown	Unknown	Behar et al. (2012b)
JQ702262	Unknown	Unknown	Behar et al. (2012b)
JQ702263	Unknown	Unknown	Behar et al. (2012b)
JQ702269	Unknown	Unknown	Behar et al. (2012b)
JQ702275	Unknown	Unknown	Behar et al. (2012b)
JQ702288	Unknown	Unknown	Behar et al. (2012b)
JQ702296	Europe NW	England	Behar et al. (2012b)
JQ702308	Unknown	Unknown	Behar et al. (2012b)
JQ702313	Europe SE	Italy	Behar et al. (2012b)
JQ702328	Unknown	Unknown	Behar et al. (2012b)
JQ702334	Unknown	Unknown	Behar et al. (2012b)
JQ702335	Europe NW	France	Behar et al. (2012b)
JQ702336	Unknown	Unknown	Behar et al. (2012b)
JQ702349	Unknown	Unknown	Behar et al. (2012b)
JQ702359	Unknown	Unknown	Behar et al. (2012b)
JQ702360	Unknown	Unknown	Behar et al. (2012b)
JQ702362	Unknown	Unknown	Behar et al. (2012b)
JQ702370	Europe NW	Sweden	Behar et al. (2012b)
JQ702371	Unknown	Unknown	Behar et al. (2012b)
JQ702377	Unknown	Unknown	Behar et al. (2012b)
JQ702382	Unknown	Unknown	Behar et al. (2012b)
JQ702383	Unknown	Unknown	Behar et al. (2012b)
JQ702401	Unknown	Unknown	Behar et al. (2012b)
JQ702405	Unknown	Unknown	Behar et al. (2012b)
JQ702409	Europe NE	Ukraine	Behar et al. (2012b)
JQ702415	Unknown	Unknown	Behar et al. (2012b)
JQ702433	Unknown	Unknown	Behar et al. (2012b)
JQ702436	Unknown	Unknown	Behar et al. (2012b)
JQ702455	Unknown	Unknown	Behar et al. (2012b)
JQ702458	Unknown	Unknown	Behar et al. (2012b)
JQ702474	Unknown	Unknown	Behar et al. (2012b)
JQ702478	Unknown	Unknown	Behar et al. (2012b)
JQ702480	Europe NW	England	Behar et al. (2012b)
JQ702483	Unknown	Unknown	Behar et al. (2012b)
JQ702491	Europe NW	Germany	Behar et al. (2012b)
JQ702494	Unknown	Unknown	Behar et al. (2012b)
JQ702495	Unknown	Unknown	Behar et al. (2012b)
JQ702497	Europe NW	Scotland	Behar et al. (2012b)
JQ702501	Unknown	Unknown	Behar et al. (2012b)
JQ702523	Unknown	Unknown	Behar et al. (2012b)
JQ702527	Europe NW	Austria	Behar et al. (2012b)
JQ702528	Unknown	Unknown	Behar et al. (2012b)
JQ702529	Unknown	Unknown	Behar et al. (2012b)
JQ702532	Unknown	Unknown	Behar et al. (2012b)
JQ702535	Unknown	Unknown	Behar et al. (2012b)
JQ702542	Unknown	Unknown	Behar et al. (2012b)
JQ702557	Europe NW	United Kingdom	Behar et al. (2012b)
JQ702559	Europe NW	England	Behar et al. (2012b)
JQ702565	Unknown	Unknown	Behar et al. (2012b)
JQ702566	Europe NE	Russia	Behar et al. (2012b)
JQ702570	Unknown	Unknown	Behar et al. (2012b)
JQ702575	Unknown	Unknown	Behar et al. (2012b)
JQ702577	Unknown	Unknown	Behar et al. (2012b)
JQ702584	Europe NW	Czech Republic	Behar et al. (2012b)
JQ702590	Europe NW	United Kingdom	Behar et al. (2012b)
JQ702591	Europe NW	Poland	Behar et al. (2012b)
JQ702597	Unknown	Unknown	Behar et al. (2012b)
JQ702598	Europe NW	England	Behar et al. (2012b)
JQ702602	Unknown	Unknown	Behar et al. (2012b)

JQ702607	Unknown	Unknown		Behar et al. (2012b)
JQ702608	Unknown	Unknown		Behar et al. (2012b)
JQ702623	Unknown	Unknown		Behar et al. (2012b)
JQ702628	Europe NW	Ireland		Behar et al. (2012b)
JQ702634	Europe NW	Scotland		Behar et al. (2012b)
JQ702639	Unknown	Unknown		Behar et al. (2012b)
JQ702649	Unknown	Unknown		Behar et al. (2012b)
JQ702650	Unknown	Unknown		Behar et al. (2012b)
JQ702657	Unknown	Unknown		Behar et al. (2012b)
JQ702679	Unknown	Unknown		Behar et al. (2012b)
JQ702683	Europe NW	Sweden		Behar et al. (2012b)
JQ702698	Unknown	Unknown		Behar et al. (2012b)
JQ702701	Unknown	Unknown		Behar et al. (2012b)
JQ702703	Europe SE	Italy		Behar et al. (2012b)
JQ702709	Unknown	Unknown		Behar et al. (2012b)
JQ702719	Unknown	Unknown		Behar et al. (2012b)
JQ702726	Unknown	Unknown		Behar et al. (2012b)
JQ702738	Europe NW	England		Behar et al. (2012b)
JQ702751	Unknown	Unknown		Behar et al. (2012b)
JQ702753	Unknown	Unknown		Behar et al. (2012b)
JQ702757	Europe SE	Greece	Island of Rhodes	Behar et al. (2012b)
JQ702763	Unknown	Unknown		Behar et al. (2012b)
JQ702770	Unknown	Unknown		Behar et al. (2012b)
JQ702799	Unknown	Unknown		Behar et al. (2012b)
JQ702828	Europe NW	England	Sheffield	Behar et al. (2012b)
JQ702832	Unknown	Unknown		Behar et al. (2012b)
JQ702833	Europe SE	Greece		Behar et al. (2012b)
JQ702846	Unknown	Unknown		Behar et al. (2012b)
JQ702848	Unknown	Unknown		Behar et al. (2012b)
JQ702850	Unknown	Unknown		Behar et al. (2012b)
JQ702856	Europe NW	France		Behar et al. (2012b)
JQ702867	Europe NW	United Kingdom		Behar et al. (2012b)
JQ702870	Unknown	Unknown		Behar et al. (2012b)
JQ702873	Europe SE	Italy	Tornio	Behar et al. (2012b)
JQ702881	Unknown	Unknown		Behar et al. (2012b)
JQ702899	Unknown	Unknown		Behar et al. (2012b)
JQ702907	Unknown	Unknown		Behar et al. (2012b)
JQ702971	Europe NW	England		Behar et al. (2012b)
JQ702983	Unknown	Unknown		Behar et al. (2012b)
JQ702992	Unknown	Unknown		Behar et al. (2012b)
JQ703052	Europe NW	Germany		Behar et al. (2012b)
JQ703089	Unknown	Unknown		Behar et al. (2012b)
JQ703098	Europe NW	Ireland		Behar et al. (2012b)
JQ703104	Unknown	Unknown		Behar et al. (2012b)
JQ703109	Europe NW	Czechoslovakia		Behar et al. (2012b)
JQ703112	Unknown	Unknown		Behar et al. (2012b)
JQ703115	Unknown	Unknown		Behar et al. (2012b)
JQ703121	Unknown	Unknown		Behar et al. (2012b)
JQ703125	Unknown	Unknown		Behar et al. (2012b)
JQ703126	Unknown	Unknown		Behar et al. (2012b)
JQ703129	Europe NW	Norway		Behar et al. (2012b)
JQ703132	Unknown	Unknown		Behar et al. (2012b)
JQ703135	Europe NW	United Kingdom		Behar et al. (2012b)
JQ703137	Europe NW	Germany	Ashkenazi	Behar et al. (2012b)
JQ703142	Europe NW	Scotland		Behar et al. (2012b)
JQ703143	Europe SE	Italy		Behar et al. (2012b)
JQ703147	Unknown	Unknown		Behar et al. (2012b)
JQ703148	Europe NW	France		Behar et al. (2012b)
JQ703151	Europe NW	Scotland		Behar et al. (2012b)
JQ703153	Europe NW	Germany		Behar et al. (2012b)
JQ703166	Unknown	Unknown		Behar et al. (2012b)
JQ703170	Europe NW	Ireland		Behar et al. (2012b)
JQ703174	Unknown	Unknown		Behar et al. (2012b)
JQ703176	Europe NW	Ireland		Behar et al. (2012b)
JQ703190	Europe NW	Northern Ireland		Behar et al. (2012b)
JQ703196	Unknown	Unknown		Behar et al. (2012b)
JQ703198	Europe NW	Germany		Behar et al. (2012b)
JQ703199	Unknown	Unknown		Behar et al. (2012b)
JQ703207	Europe NW	Germany		Behar et al. (2012b)
JQ703216	Europe SE	Italy	Sicily	Behar et al. (2012b)
JQ703218	Iberia	Portugal		Behar et al. (2012b)
JQ703219	Europe NW	United Kingdom		Behar et al. (2012b)
JQ703220	Near East	Iran		Behar et al. (2012b)
JQ703222	Europe NW	Sweden		Behar et al. (2012b)
JQ703224	Unknown	Unknown		Behar et al. (2012b)
JQ703226	Europe NW	Sweden		Behar et al. (2012b)
JQ703231	Unknown	Unknown		Behar et al. (2012b)
JQ703238	Unknown	Unknown		Behar et al. (2012b)
JQ703243	Europe Basque	Spain	Basque Country, Biscay	Behar et al. (2012b)
JQ703244	Unknown	Unknown		Behar et al. (2012b)
JQ703245	Europe NW	Germany		Behar et al. (2012b)
JQ703251	Unknown	Unknown		Behar et al. (2012b)

JQ703254	Unknown	Unknown		Behar et al. (2012b)
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JQ703268	Europe NW	Poland	Ashkenazi	Behar et al. (2012b)
JQ703270	Unknown	Unknown		Behar et al. (2012b)
JQ703274	Unknown	Unknown		Behar et al. (2012b)
JQ703277	Unknown	Unknown		Behar et al. (2012b)
JQ703282	Europe NW	Poland		Behar et al. (2012b)
JQ703286	Europe NW	Switzerland		Behar et al. (2012b)
JQ703305	Unknown	Unknown		Behar et al. (2012b)
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JQ703312	Unknown	Unknown		Behar et al. (2012b)
JQ703315	Europe NW	England		Behar et al. (2012b)
JQ703316	Unknown	Unknown		Behar et al. (2012b)
JQ703317	Unknown	Unknown		Behar et al. (2012b)
JQ703319	Europe NW	France		Behar et al. (2012b)
JQ703322	Unknown	Unknown		Behar et al. (2012b)
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JQ703333	Europe NW	England		Behar et al. (2012b)
JQ703336	Unknown	Unknown		Behar et al. (2012b)
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JQ703342	Europe NW	Scotland		Behar et al. (2012b)
JQ703346	Unknown	Unknown		Behar et al. (2012b)
JQ703351	Unknown	Unknown		Behar et al. (2012b)
JQ703357	Unknown	Unknown		Behar et al. (2012b)
JQ703364	Unknown	Unknown		Behar et al. (2012b)
JQ703371	Europe NW	Ireland		Behar et al. (2012b)
JQ703380	Europe NW	United Kingdom		Behar et al. (2012b)
JQ703383	Europe NW	Poland		Behar et al. (2012b)
JQ703384	Europe NE	Russia		Behar et al. (2012b)
JQ703388	Unknown	Unknown		Behar et al. (2012b)
JQ703390	Unknown	Unknown		Behar et al. (2012b)
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JQ703400	Europe NW	England	Surrey	Behar et al. (2012b)
JQ703403	Unknown	Unknown		Behar et al. (2012b)
JQ703411	Unknown	Unknown		Behar et al. (2012b)
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JQ703419	Europe NW	Czechoslovakia		Behar et al. (2012b)
JQ703420	Europe NW	Hungary		Behar et al. (2012b)
JQ703424	Unknown	Unknown		Behar et al. (2012b)
JQ703426	Unknown	Unknown		Behar et al. (2012b)
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JQ703430	Europe NW	United Kingdom		Behar et al. (2012b)
JQ703438	Europe SE	Italy		Behar et al. (2012b)
JQ703441	Europe NW	Ireland		Behar et al. (2012b)
JQ703443	Unknown	Unknown		Behar et al. (2012b)
JQ703450	Unknown	Unknown		Behar et al. (2012b)
JQ703457	Europe SE	Italy		Behar et al. (2012b)
JQ703459	Unknown	Unknown		Behar et al. (2012b)
JQ703465	Unknown	Unknown		Behar et al. (2012b)
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JQ703472	Europe NW	Scotland	Isla of Bute	Behar et al. (2012b)
JQ703473	Unknown	Unknown		Behar et al. (2012b)
JQ703476	Unknown	Unknown		Behar et al. (2012b)
JQ703477	Europe NW	Ireland		Behar et al. (2012b)
JQ703484	Europe NW	Germany		Behar et al. (2012b)
JQ703489	Europe NW	Denmark		Behar et al. (2012b)
JQ703496	Unknown	Unknown		Behar et al. (2012b)
JQ703499	Unknown	Unknown		Behar et al. (2012b)
JQ703500	Unknown	Unknown		Behar et al. (2012b)
JQ703506	Europe NW	England	south England	Behar et al. (2012b)
JQ703512	Unknown	Unknown		Behar et al. (2012b)
JQ703518	Europe NW	England		Behar et al. (2012b)
JQ703525	Unknown	Unknown		Behar et al. (2012b)
JQ703527	Europe NW	England		Behar et al. (2012b)
JQ703535	Unknown	Unknown		Behar et al. (2012b)
JQ703536	Europe NE	Lithuania		Behar et al. (2012b)
JQ703537	Unknown	Unknown		Behar et al. (2012b)
JQ703541	Europe NW	Ireland		Behar et al. (2012b)
JQ703551	Unknown	Unknown		Behar et al. (2012b)
JQ703561	Unknown	Unknown		Behar et al. (2012b)
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JQ703571	Unknown	Unknown		Behar et al. (2012b)
JQ703576	Unknown	Unknown		Behar et al. (2012b)
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JQ703603	Europe NW	England		Behar et al. (2012b)
JQ703611	Unknown	Unknown		Behar et al. (2012b)
JQ703616	Unknown	Unknown		Behar et al. (2012b)
JQ703617	Europe NW	Poland		Behar et al. (2012b)
JQ703631	Unknown	Unknown		Behar et al. (2012b)
JQ703634	Unknown	Unknown		Behar et al. (2012b)
JQ703635	Unknown	Unknown		Behar et al. (2012b)

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JQ703655	Europe NE	Ukraine	Ashkenazi	Behar et al. (2012b)
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JQ703668	Unknown	Unknown		Behar et al. (2012b)
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JQ703681	Unknown	Unknown		Behar et al. (2012b)
JQ703683	Europe NW	Germany		Behar et al. (2012b)
JQ703687	Unknown	Unknown		Behar et al. (2012b)
JQ703698	Europe NW	Germany	Hannover, Frisian	Behar et al. (2012b)
JQ703705	Unknown	Unknown		Behar et al. (2012b)
JQ703706	Unknown	Unknown		Behar et al. (2012b)
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JQ703719	Europe NW	Ireland		Behar et al. (2012b)
JQ703729	Europe NW	Wales		Behar et al. (2012b)
JQ703735	Europe NW	Germany		Behar et al. (2012b)
JQ703742	Unknown	Unknown		Behar et al. (2012b)
JQ703745	Unknown	Unknown		Behar et al. (2012b)
JQ703751	Europe NW	Ireland		Behar et al. (2012b)
JQ703756	Unknown	Unknown		Behar et al. (2012b)
JQ703758	Unknown	Unknown		Behar et al. (2012b)
JQ703759	Unknown	Unknown		Behar et al. (2012b)
JQ703765	Unknown	Unknown		Behar et al. (2012b)
JQ703787	Unknown	Unknown		Behar et al. (2012b)
JQ703788	Europe NE	Lithuania	Kovno (Kaunas), Ashkenazi	Behar et al. (2012b)
JQ703795	Europe NW	England	London	Behar et al. (2012b)
JQ703810	Europe NE	Finland		Behar et al. (2012b)
JQ703811	Europe NW	Ireland		Behar et al. (2012b)
JQ703814	Unknown	Unknown		Behar et al. (2012b)
JQ703817	Europe NW	Germany		Behar et al. (2012b)
JQ703838	Unknown	Unknown		Behar et al. (2012b)
JQ703839	Europe NW	Scotland		Behar et al. (2012b)
JQ703848	Unknown	Unknown		Behar et al. (2012b)
JQ703856	Iberia	Spain	Extremadura	Behar et al. (2012b)
JQ703869	Unknown	Unknown		Behar et al. (2012b)
JQ703879?	Europe Basque	Spain	Bilbao, possibly Basque origins	Behar et al. (2012b)
JQ703888	Iberia	Spain	Asturias	Behar et al. (2012b)
JQ703889	Unknown	Unknown		Behar et al. (2012b)
JQ703893	Europe NW	Ireland		Behar et al. (2012b)
JQ703901	Unknown	Unknown		Behar et al. (2012b)
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JQ703922	Europe NW	United Kingdom		Behar et al. (2012b)
JQ703923	Unknown	Unknown		Behar et al. (2012b)
JQ703925	Europe NW	Poland	Mlawa	Behar et al. (2012b)
JQ703938	Unknown	Unknown		Behar et al. (2012b)
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JQ703948	Near East	Israel		Behar et al. (2012b)
JQ703956	Unknown	Unknown		Behar et al. (2012b)
JQ703967	Unknown	Unknown		Behar et al. (2012b)
JQ703974	Unknown	Unknown		Behar et al. (2012b)
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JQ703998	Unknown	Unknown		Behar et al. (2012b)
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JQ704003	Unknown	Unknown		Behar et al. (2012b)
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JQ704032	Europe NW	Ireland		Behar et al. (2012b)
JQ704038	Europe NE	Finland		Behar et al. (2012b)
JQ704050	Unknown	Unknown		Behar et al. (2012b)
JQ704066	Unknown	Unknown		Behar et al. (2012b)
JQ704080	Unknown	Unknown		Behar et al. (2012b)
JQ704085	Unknown	Unknown		Behar et al. (2012b)
JQ704086	Unknown	Unknown		Behar et al. (2012b)
JQ704089	Unknown	Unknown		Behar et al. (2012b)
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JQ704095	Unknown	Unknown		Behar et al. (2012b)
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JQ704119	Unknown	Unknown		Behar et al. (2012b)
JQ704122	Unknown	Unknown		Behar et al. (2012b)
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JQ704134	Unknown	Unknown		Behar et al. (2012b)
JQ704138	West Africa	Nigeria		Behar et al. (2012b)
JQ704139	Unknown	Unknown		Behar et al. (2012b)
JQ704141	Europe NW	Germany	Ladbergen, Westfalen	Behar et al. (2012b)
JQ704154	Europe NW	England		Behar et al. (2012b)
JQ704156	Unknown	Unknown		Behar et al. (2012b)
JQ704157	Unknown	Unknown		Behar et al. (2012b)
JQ704158	Europe NW	Scotland		Behar et al. (2012b)
JQ704159	Europe NW	England	Middlesex	Behar et al. (2012b)
JQ704162	Unknown	Unknown		Behar et al. (2012b)
JQ704163	Unknown	Unknown		Behar et al. (2012b)

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JQ704175	Europe NW	England		Behar et al. (2012b)
JQ704177	Europe NW	Scotland		Behar et al. (2012b)
JQ704186	Europe NW	Ireland		Behar et al. (2012b)
JQ704191	Europe NW	Poland	Vilnius	Behar et al. (2012b)
JQ704193	Europe NW	England		Behar et al. (2012b)
JQ704194	Unknown	Unknown		Behar et al. (2012b)
JQ704196	Europe NW	Germany		Behar et al. (2012b)
JQ704199	Europe NW	Germany	Rhineland-Pfalz	Behar et al. (2012b)
JQ704200	Unknown	Unknown		Behar et al. (2012b)
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JQ704203	Unknown	Unknown		Behar et al. (2012b)
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JQ704212	Unknown	Unknown		Behar et al. (2012b)
JQ704219	Europe NW	Sweden		Behar et al. (2012b)
JQ704223	Unknown	Unknown		Behar et al. (2012b)
JQ704226	Europe NW	England		Behar et al. (2012b)
JQ704230	Unknown	Unknown		Behar et al. (2012b)
JQ704235	Unknown	Unknown		Behar et al. (2012b)
JQ704240	Europe NW	Czech Republic	Kozolupy (Beroun, Bohemia)	Behar et al. (2012b)
JQ704242	Unknown	Unknown		Behar et al. (2012b)
JQ704243	Europe NW	England		Behar et al. (2012b)
JQ704245	Europe NW	Ireland		Behar et al. (2012b)
JQ704250	Europe NW	France		Behar et al. (2012b)
JQ704257	Europe NW	Scotland		Behar et al. (2012b)
JQ704258	Unknown	Unknown		Behar et al. (2012b)
JQ704259	Europe NW	Poland		Behar et al. (2012b)
JQ704263	Unknown	Unknown		Behar et al. (2012b)
JQ704265	Unknown	Unknown		Behar et al. (2012b)
JQ704267	Unknown	Unknown		Behar et al. (2012b)
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JQ704279	Unknown	Unknown		Behar et al. (2012b)
JQ704282	Europe NW	England		Behar et al. (2012b)
JQ704285	Unknown	Unknown		Behar et al. (2012b)
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JQ704292	Unknown	Unknown		Behar et al. (2012b)
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JQ704294	Unknown	Unknown		Behar et al. (2012b)
JQ704298	Unknown	Unknown		Behar et al. (2012b)
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JQ704311	Unknown	Unknown		Behar et al. (2012b)
JQ704312	Unknown	Unknown		Behar et al. (2012b)
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JQ704317	Unknown	Unknown		Behar et al. (2012b)
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JQ704327	Europe NW	Norway		Behar et al. (2012b)
JQ704329	Unknown	Unknown		Behar et al. (2012b)
JQ704336	Unknown	Unknown		Behar et al. (2012b)
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JQ704352	Europe NW	Scotland		Behar et al. (2012b)
JQ704356	Unknown	Unknown		Behar et al. (2012b)
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JQ704368	Europe NW	Germany		Behar et al. (2012b)
JQ704369	Unknown	Unknown		Behar et al. (2012b)
JQ704370	Unknown	Unknown		Behar et al. (2012b)
JQ704373	Europe NW	France	St-Thomas-de-Conac, Charente-Maritime	Behar et al. (2012b)
JQ704378	Unknown	Unknown		Behar et al. (2012b)
JQ704381	Unknown	Unknown		Behar et al. (2012b)
JQ704382	Unknown	Unknown		Behar et al. (2012b)
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JQ704392	Europe NW	Poland		Behar et al. (2012b)
JQ704398	Europe NW	England		Behar et al. (2012b)
JQ704400	Europe NW	Germany		Behar et al. (2012b)
JQ704402	Europe NW	Ireland		Behar et al. (2012b)
JQ704407	Unknown	Unknown		Behar et al. (2012b)
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JQ704412	Europe NW	Ireland		Behar et al. (2012b)
JQ704413	Europe NW	Ireland	Dublin	Behar et al. (2012b)
JQ704414	Unknown	Unknown		Behar et al. (2012b)
JQ704418	Unknown	Unknown		Behar et al. (2012b)
JQ704419	Europe NW	Germany		Behar et al. (2012b)
JQ704424	Unknown	Unknown		Behar et al. (2012b)
JQ704429	Unknown	Unknown		Behar et al. (2012b)

JQ704431	Unknown	Unknown		Behar et al. (2012b)
JQ704433	Unknown	Unknown		Behar et al. (2012b)
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JQ704438	Unknown	Unknown		Behar et al. (2012b)
JQ704439	Europe NW	Germany	East Frieland, Hannover	Behar et al. (2012b)
JQ704444	Europe NW	British Isles		Behar et al. (2012b)
JQ704446	Unknown	Unknown		Behar et al. (2012b)
JQ704447	Unknown	Unknown		Behar et al. (2012b)
JQ704448	Unknown	Unknown		Behar et al. (2012b)
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JQ704459	Europe NW	Ireland		Behar et al. (2012b)
JQ704462	Europe NW	United Kingdom		Behar et al. (2012b)
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JQ704465	Unknown	Unknown		Behar et al. (2012b)
JQ704466	Europe NW	Ireland		Behar et al. (2012b)
JQ704470	Unknown	Unknown		Behar et al. (2012b)
JQ704481	Iberia	Spain		Behar et al. (2012b)
JQ704485	Unknown	Unknown		Behar et al. (2012b)
JQ704486	Europe NW	Poland	Jawornik Ruski	Behar et al. (2012b)
JQ704487	Unknown	Unknown		Behar et al. (2012b)
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JQ704502	Europe NW	Germany	Waldeck	Behar et al. (2012b)
JQ704507	Europe NW	United Kingdom		Behar et al. (2012b)
JQ704509	Europe NW	United Kingdom		Behar et al. (2012b)
JQ704511	Unknown	Unknown		Behar et al. (2012b)
JQ704513	Europe NW	Mennonite	Mennonite	Behar et al. (2012b)
JQ704516	Unknown	Unknown		Behar et al. (2012b)
JQ704519	Europe NW	Germany	Allgau	Behar et al. (2012b)
JQ704522	Europe NW	England		Behar et al. (2012b)
JQ704525	Europe NW	Ireland		Behar et al. (2012b)
JQ704536	Unknown	Unknown		Behar et al. (2012b)
JQ704538	Unknown	Unknown		Behar et al. (2012b)
JQ704544	Unknown	Unknown		Behar et al. (2012b)
JQ704551	Unknown	Unknown		Behar et al. (2012b)
JQ704553	Europe NW	France		Behar et al. (2012b)
JQ704557	Unknown	Unknown		Behar et al. (2012b)
JQ704558	Europe NW	Germany		Behar et al. (2012b)
JQ704562	Europe NW	United Kingdom		Behar et al. (2012b)
JQ704564	Europe NW	England		Behar et al. (2012b)
JQ704566	Europe NW	Scotland		Behar et al. (2012b)
JQ704567	Europe NW	Sweden		Behar et al. (2012b)
JQ704571	Unknown	Unknown		Behar et al. (2012b)
JQ704575	Europe NW	Germany		Behar et al. (2012b)
JQ704585	Iberia	Portugal	Madeira	Behar et al. (2012b)
JQ704587	Unknown	Unknown		Behar et al. (2012b)
JQ704588	Europe NE	Romania		Behar et al. (2012b)
JQ704589	Europe NW	Germany		Behar et al. (2012b)
JQ704593	Europe NW	England		Behar et al. (2012b)
JQ704601	Europe NW	France		Behar et al. (2012b)
JQ704606	Europe NW	Germany		Behar et al. (2012b)
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JQ704618	Unknown	Unknown		Behar et al. (2012b)
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JQ704630	Unknown	Unknown		Behar et al. (2012b)
JQ704636	Unknown	Unknown		Behar et al. (2012b)
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JQ704639	Unknown	Unknown		Behar et al. (2012b)
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JQ704655	Unknown	Unknown		Behar et al. (2012b)
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JQ704657	Europe NW	United Kingdom		Behar et al. (2012b)
JQ704659	Unknown	Unknown		Behar et al. (2012b)
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JQ704669	Unknown	Unknown		Behar et al. (2012b)
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JQ704685	Unknown	Unknown		Behar et al. (2012b)
JQ704693	Unknown	Unknown		Behar et al. (2012b)
JQ704702	Unknown	Unknown		Behar et al. (2012b)
JQ704709	Unknown	Unknown		Behar et al. (2012b)
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JQ704717	Europe NW	Norway		Behar et al. (2012b)
JQ704718	Europe NW	England		Behar et al. (2012b)
JQ704719	Unknown	Unknown		Behar et al. (2012b)
JQ704720	Europe NW	England		Behar et al. (2012b)
JQ704721	Europe NW	Ireland		Behar et al. (2012b)
JQ704731	Europe NW	France		Behar et al. (2012b)
JQ704743	Europe NW	Ireland		Behar et al. (2012b)
JQ704744	Europe NE	Russia		Behar et al. (2012b)
JQ704756	Unknown	Unknown		Behar et al. (2012b)
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JQ704781	Unknown	Unknown		Behar et al. (2012b)

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JQ704810	Unknown	Unknown		Behar et al. (2012b)
JQ704819	Unknown	Unknown		Behar et al. (2012b)
JQ704824	Europe NW	Germany		Behar et al. (2012b)
JQ704832	Europe NW	England		Behar et al. (2012b)
JQ704838	Europe NW	England		Behar et al. (2012b)
JQ704839	Unknown	Unknown		Behar et al. (2012b)
JQ704844	Europe NW	Germany		Behar et al. (2012b)
JQ704849	Europe NW	Sweden		Behar et al. (2012b)
JQ704852	Europe NW	Germany		Behar et al. (2012b)
JQ704861	Unknown	Unknown		Behar et al. (2012b)
JQ704872	Unknown	Unknown		Behar et al. (2012b)
JQ704877	Europe NW	Denmark		Behar et al. (2012b)
JQ704880	Europe NW	Germany		Behar et al. (2012b)
JQ704881	Europe NW	England	Greater London	Behar et al. (2012b)
JQ704882	Unknown	Unknown		Behar et al. (2012b)
JQ704894	Unknown	Unknown		Behar et al. (2012b)
JQ704905	Europe NW	France		Behar et al. (2012b)
JQ704909	Unknown	Unknown		Behar et al. (2012b)
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JQ704927	Unknown	Unknown		Behar et al. (2012b)
JQ704934	Unknown	Unknown		Behar et al. (2012b)
JQ704943	Europe NW	Germany		Behar et al. (2012b)
JQ704954	Unknown	Unknown		Behar et al. (2012b)
JQ704957	Europe NW	United Kingdom		Behar et al. (2012b)
JQ704980	Unknown	Unknown		Behar et al. (2012b)
JQ704994	Europe NW	Netherlands		Behar et al. (2012b)
JQ705011	Unknown	Unknown		Behar et al. (2012b)
JQ705013	Europe NW	Germany		Behar et al. (2012b)
JQ705024	Europe SE	Italy(Sicily)	Sicily	Behar et al. (2012b)
JQ705027	Unknown	Unknown		Behar et al. (2012b)
JQ705028	Unknown	Unknown		Behar et al. (2012b)
JQ705039	Unknown	Unknown		Behar et al. (2012b)
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JQ705052	Europe SE	Serbia		Behar et al. (2012b)
JQ705076	Unknown	Unknown		Behar et al. (2012b)
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JQ705102	Europe NW	Denmark		Behar et al. (2012b)
JQ705107	Unknown	Unknown		Behar et al. (2012b)
JQ705125	Europe SE	Albania		Behar et al. (2012b)
JQ705126	Unknown	Unknown		Behar et al. (2012b)
JQ705135	Unknown	Unknown		Behar et al. (2012b)
JQ705138	Unknown	Unknown		Behar et al. (2012b)
JQ705157	Unknown	Unknown		Behar et al. (2012b)
JQ705159	Unknown	Unknown		Behar et al. (2012b)
JQ705167	Unknown	Unknown		Behar et al. (2012b)
JQ705169	Unknown	Unknown		Behar et al. (2012b)
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JQ705171	Europe NW	United Kingdom		Behar et al. (2012b)
JQ705182	Europe NE	Finland		Behar et al. (2012b)
JQ705195	Unknown	Unknown		Behar et al. (2012b)
JQ705205	Unknown	Unknown		Behar et al. (2012b)
JQ705210	Unknown	Unknown		Behar et al. (2012b)
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JQ705216	Unknown	Unknown		Behar et al. (2012b)
JQ705231	Europe NW	Germany		Behar et al. (2012b)
JQ705235	Europe NW	United Kingdom		Behar et al. (2012b)
JQ705236	Europe NW	Germany	Ashkenazi	Behar et al. (2012b)
JQ705238	Unknown	Unknown		Behar et al. (2012b)
JQ705239	Unknown	Unknown		Behar et al. (2012b)
JQ705252	Unknown	Unknown		Behar et al. (2012b)
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JQ705306	Europe NW	England		Behar et al. (2012b)
JQ705311	Europe SE	Italy		Behar et al. (2012b)
JQ705330	Unknown	Unknown		Behar et al. (2012b)
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JQ705343	Europe NE	Estonia		Behar et al. (2012b)
JQ705350	Europe NW	United Kingdom		Behar et al. (2012b)
JQ705362	Europe NW	Germany		Behar et al. (2012b)
JQ705367	Unknown	Unknown		Behar et al. (2012b)
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JQ705383	Unknown	Unknown		Behar et al. (2012b)
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JQ705395	Unknown	Unknown		Behar et al. (2012b)
JQ705426	Europe NW	United Kingdom		Behar et al. (2012b)

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JQ705436	Unknown	Unknown		Behar et al. (2012b)
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JQ705894	Unknown	Unknown		Behar et al. (2012b)
JQ705903	Unknown	Unknown		Behar et al. (2012b)
JQ705914	Europe	Europe	Mexico (European)	Behar et al. (2012b)
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JQ705987	Unknown	Unknown		Behar et al. (2012b)
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JQ706009	Europe NW	England		Behar et al. (2012b)
JQ706010	Unknown	Unknown		Behar et al. (2012b)
JQ724862	Europe NW	Poland	origin_locality: Warsaw	Family Tree
JQ735910	Europe NW	Norway		Family Tree
JQ801295	Europe	Europe	German, Spanish; origin_locality:USA; DE	Family Tree
JQ898578	Europe NW	Norway		Family Tree
JX021621	Europe NE	Lithuania	ethnicity:Lithuanian; origin_locality:USA: NJ	Family Tree
JX021729	Europe NW	Scotland		Family Tree
JX092101	Iberia	Spain	Barcelona	Family Tree
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JX152784	Europe NE	Finland		Raule et al. (2014)
JX152791	Europe NW	Denmark		Raule et al. (2014)
JX152798	Europe NW	Denmark		Raule et al. (2014)
JX152803	Europe NW	Denmark		Raule et al. (2014)
JX152804	Europe NW	Denmark		Raule et al. (2014)

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JX152821	Europe NW	Denmark		Raule et al. (2014)
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JX152984	Europe NE	Finland		Raule et al. (2014)
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JX153000	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153009	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153012	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153023	Europe SE	Italy	Calabria	Raule et al. (2014)
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JX153082	Europe NE	Finland		Raule et al. (2014)
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JX153088	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153093	Europe SE	Italy	Calabria	Raule et al. (2014)
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JX153270	Europe NE	Finland		Raule et al. (2014)
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JX171102	Unknown	unknown		Soini et al. (2012)
JX171103	Unknown	unknown		Soini et al. (2012)
JX171104	Unknown	unknown		Soini et al. (2012)
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JX171108	Unknown	unknown		Soini et al. (2012)
JX297151	Europe Basque	Spain	Basque Country, northern Navarre	Cardoso et al. (2013)
JX297155	Europe Basque	Spain	Basque Country, Biscay	Cardoso et al. (2013)
JX297157	Europe Basque	Spain	Basque Country, northern Navarre	Cardoso et al. (2013)
JX297158	Europe Basque	Spain	Basque Country, northern Navarre	Cardoso et al. (2013)
JX297161	Iberia	Spain	Cantabria, Pas Valley	Cardoso et al. (2013)
JX297162	Iberia	Spain	Cantabria, Pas Valley	Cardoso et al. (2013)
JX297163	Europe Basque	Spain	Basque Country, Guipuzcoa	Cardoso et al. (2013)
JX297164	Europe Basque	Spain	Basque Country, Guipuzcoa	Cardoso et al. (2013)
JX297180	Iberia	Spain	Cantabria, Pas Valley	Cardoso et al. (2013)
JX297181	Europe Basque	Spain	Basque Country, Guipuzcoa	Cardoso et al. (2013)
JX297199	Europe Basque	Spain	Basque Country, Biscay	Cardoso et al. (2013)
JX885690	Europe NW	England	ethnicity:English	Family Tree
KC121273	Europe NW	Sweden	ethnicity:Swedish	Family Tree
KC158585	Europe NW	Scotland	ethnicity:Scottish	Family Tree
KC175606	Europe NW	England	ethnicity:English; origin_locality:USA	Family Tree
KC409356	Europe NW	England	ethnicity:English; origin_locality:USA	Family Tree
KC763373	Europe NE	Finland		Soini et al. (2013)
KC763374	Europe NE	Finland		Soini et al. (2013)
KC763375	Europe NE	Finland		Soini et al. (2013)

KC763376	Europe NE	Finland		Soini et al. (2013)
KC763377	Europe NE	Finland		Soini et al. (2013)
KC763379	Europe NE	Finland		Soini et al. (2013)
KC763381	Europe NE	Finland		Soini et al. (2013)
KC763382	Europe NE	Finland		Soini et al. (2013)
KC763384	Europe NE	Finland		Soini et al. (2013)
KC763394	Europe NE	Finland		Soini et al. (2013)
KC763397	Europe NE	Finland		Soini et al. (2013)
KC763401	Europe NE	Finland		Soini et al. (2013)
KC763445	Europe NE	Finland		Soini et al. (2013)
KC763448	Europe NE	Finland		Soini et al. (2013)
KC785095	Europe NE	Finland	ethnicity:Finnish	Family Tree
KC911277	Near East	Iran		Derenko et al. (2013)
KC911283	Near East	Iran		Derenko et al. (2013)
KC911297	Near East	Iran		Derenko et al. (2013)
KC911318	Near East	Iran		Derenko et al. (2013)
KC911376	Near East	Iran		Derenko et al. (2013)
KC911429	Near East	Iran		Derenko et al. (2013)
KC911510	Near East	Iran		Derenko et al. (2013)
KC911534	Near East	Iran		Derenko et al. (2013)
KC911554	Near East	Iran		Derenko et al. (2013)
KC911565	Near East	Iran		Derenko et al. (2013)
KC911611	Near East	Iran		Derenko et al. (2013)
KF052033	Europe NW	Sweden	ethnicity:Swedish	Family Tree
KF055316	Unknown	unknown		Collins et al. (2013)
KF055863	Iberia	Spain	Romani	Gómez-Carballa et al. (2013)
KF161062	Europe NW	Denmark		Li et al. (2014)
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KF161074	Europe NW	Denmark		Li et al. (2014)
KF161076	Europe NW	Denmark		Li et al. (2014)
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KF161087	Europe NW	Denmark		Li et al. (2014)
KF161094	Europe NW	Denmark		Li et al. (2014)
KF161096	Europe NW	Denmark		Li et al. (2014)
KF161097	Europe NW	Denmark		Li et al. (2014)
KF161101	Europe NW	Denmark		Li et al. (2014)
KF161104	Europe NW	Denmark		Li et al. (2014)
KF161120	Europe NW	Denmark		Li et al. (2014)
KF161123	Europe NW	Denmark		Li et al. (2014)
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KF162913	Europe NW	Denmark		Li et al. (2014)
KF162919	Europe NW	Denmark		Li et al. (2014)
KF162923	Europe NW	Denmark		Li et al. (2014)
KF162928	Europe NW	Denmark		Li et al. (2014)
KF162936	Europe NW	Denmark		Li et al. (2014)
KF162945	Europe NW	Denmark		Li et al. (2014)
KF162949	Europe NW	Denmark		Li et al. (2014)
KF162950	Europe NW	Denmark		Li et al. (2014)
KF162954	Europe NW	Denmark		Li et al. (2014)
KF162963	Europe NW	Denmark		Li et al. (2014)
KF162968	Europe NW	Denmark		Li et al. (2014)
KF162969	Europe NW	Denmark		Li et al. (2014)
KF163002	Europe NW	Denmark		Li et al. (2014)
KF163007	Europe NW	Denmark		Li et al. (2014)
KF163008	Europe NW	Denmark		Li et al. (2014)
KF163010	Europe NW	Denmark		Li et al. (2014)
KF163011	Europe NW	Denmark		Li et al. (2014)
KF163014	Europe NW	Denmark		Li et al. (2014)
KF163017	Europe NW	Denmark		Li et al. (2014)
KF163018	Europe NW	Denmark		Li et al. (2014)
KF163020	Europe NW	Denmark		Li et al. (2014)
KF163029	Europe NW	Denmark		Li et al. (2014)
KF163037	Europe NW	Denmark		Li et al. (2014)
KF163040	Europe NW	Denmark		Li et al. (2014)
KF163043	Europe NW	Denmark		Li et al. (2014)
KF163046	Europe NW	Denmark		Li et al. (2014)
KF163048	Europe NW	Denmark		Li et al. (2014)
KF163052	Europe NW	Denmark		Li et al. (2014)
KF163056	Europe NW	Denmark		Li et al. (2014)
KF429262	Europe NW	England	ethnicity:British	Family Tree
KF450827	South Asia	Pakistan	Brahui	Lippold et al. (2014)
KF450909	South Asia	Pakistan	Makrani	Lippold et al. (2014)
KF451050	Europe NW	France		Lippold et al. (2014)
KF451061	Europe NW	France		Lippold et al. (2014)
KF451092	Near East	Israel	Druze	Lippold et al. (2014)
KF451111	Near East	Israel	Druze	Lippold et al. (2014)
KF451114	Near East	Israel	Druze	Lippold et al. (2014)
KF451124	Near East	Israel	Druze	Lippold et al. (2014)
KF451152	Near East	Israel	Bedouin	Lippold et al. (2014)
KF451160	Near East	Israel	Bedouin	Lippold et al. (2014)
KF451401	Europe NE	Russia		Lippold et al. (2014)
KF451405	Europe NE	Russia		Lippold et al. (2014)
KF451415	Europe NE	Russia		Lippold et al. (2014)
KF451587	Europe SE	Italy	Sardinia	Lippold et al. (2014)
KF451706	North Africa	Algeria	Mozabite	Lippold et al. (2014)
KF451711	North Africa	Algeria	Mozabite	Lippold et al. (2014)
KF451717	North Africa	Algeria	Mozabite	Lippold et al. (2014)
KF451720	North Africa	Algeria	Mozabite	Lippold et al. (2014)
KF451814	Europe Basque	France	Basque	Lippold et al. (2014)
KF451816	Europe Basque	France	Basque	Lippold et al. (2014)

KF451862	Near East	Israel	Druze	Lippold et al. (2014)
KF466257	Europe SE	Serbia	origin_locality:Serbia: Novi Kazarci	Family Tree
KF493878	Europe NW	England/Ireland	ethnicity:Anglo-Irish; origin_locality:USA	Family Tree
KF562342	Europe NW	Sweden		Family Tree
KJ198894	Europe NW	Sweden		Family Tree
KJ446294	Europe SE	Italy	Italy	Zheng et al. unpub.
KJ446295	Europe NW	France		Zheng et al. unpub.
KJ446296	Europe NW	France		Zheng et al. unpub.
KJ446298	Europe SE	Italy	Sardinia	Zheng et al. unpub.
KJ446301	Europe Basque	France		Zheng et al. unpub.
KJ446302	Europe Basque	France		Zheng et al. unpub.
KJ446303	Europe Basque	France	Basque	Zheng et al. unpub.
KJ446304	Europe SE	Italy	Tuscan	Zheng et al. unpub.
KJ446305	Near East	Israel	Druze	Zheng et al. unpub.
KJ446307	Near East	Israel	Bedouin	Zheng et al. unpub.
KJ446317	Europe NW	France		Zheng et al. unpub.
KJ446318	Europe SE	Italy	Sardinia	Zheng et al. unpub.
KJ446319	Europe SE	Italy	Sardinia	Zheng et al. unpub.
KJ446325	Europe SE	Italy	Sardinia	Zheng et al. unpub.
KJ446329	Europe NE	Russia		Zheng et al. unpub.
KJ446343	Europe SE	Italy	North	Zheng et al. unpub.
KJ446358	Europe NW	France		Zheng et al. unpub.
KJ486159	Unknown	Unknown		Family Tree
KJ486160	Europe NW	England	ethnicity:English; origin_locality:Canada	Family Tree
KJ487971	Europe NE	Finland	ethnicity:Finnish; origin_locality:Sweden	Family Tree
KJ742712	Unknown	Unknown		López-Gallardo et al. (2014)
KJ742713	Unknown	Unknown		Lopez-Gallardo et al. (2014)
KJ742715	Unknown	Unknown		Lopez-Gallardo et al. (2014)
KJ786931	Europe NW	Ireland		Family Tree
KJ856682	Asia	China	China: Inner Mongolia, Hulun Buir Aimak	Derenko et al. (2014)
KJ856706	Asia	Russia(Altai)	Altai Republic	Derenko et al. (2014)
KJ856715	Asia	Russia(Altai)	Altai Republic	Derenko et al. (2014)
KJ856728	Asia	Russia(Altai)	Altai Republic	Derenko et al. (2014)
KJ856732	Asia	Russia(Altai)	Altai Republic	Derenko et al. (2014)
KJ856753	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ856763	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ856765	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ856770	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ856773	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ856777	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ856778	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ856786	Asia	Russia(Buryat)	Buryat	Derenko et al. (2014)
KJ857245	Europe NW	Germany	ethnicity:German; origin_locality:Germany	Family Tree
KJ871653	Europe	USA		Family Tree
KJ882848	Europe NW	England		Family Tree
KM047188	Europe NW	Poland	normal colon tissue	Skonieczna et al. (2015)
KM047190	Europe NW	Poland	normal colon tissue	Skonieczna et al. (2015)
KM047216	Europe NW	Poland	normal colon tissue	Skonieczna et al. (2015)
KM047222	Europe NW	Poland	normal colon tissue	Skonieczna et al. (2015)
KM047225	Europe NW	Poland	normal colon tissue	Skonieczna et al. (2015)
KM062183	Europe	USA	origin_locality:USA	Family Tree
KM062185	Europe NW	Sweden		Family Tree
KM101740	Europe	USA		Just et al. (2015)
KM101764	Europe	USA		Just et al. (2015)
KM101770	Europe	USA		Just et al. (2015)
KM101775	Europe	USA		Just et al. (2015)
KM101776	Europe	USA		Just et al. (2015)
KM101783	Europe	USA		Just et al. (2015)
KM101786	Europe	USA		Just et al. (2015)
KM101791	Europe	USA		Just et al. (2015)
KM101792	Europe	USA		Just et al. (2015)
KM101799	Europe	USA		Just et al. (2015)
KM101800	Europe	USA		Just et al. (2015)
KM101804	Europe	USA		Just et al. (2015)
KM101824	Europe	USA		Just et al. (2015)
KM101827	Europe	USA		Just et al. (2015)
KM101828	Europe	USA		Just et al. (2015)
KM101831	Europe	USA		Just et al. (2015)

KM101833	Europe	USA		Just et al. (2015)
KM101874	Europe	USA		Just et al. (2015)
KM101880	Europe	USA		Just et al. (2015)
KM101899	Europe	USA		Just et al. (2015)
KM101912	Europe	USA		Just et al. (2015)
KM101920	Europe	USA		Just et al. (2015)
KM101929	Europe	USA		Just et al. (2015)
KM101934	Europe	USA		Just et al. (2015)
KM101949	Europe	USA		Just et al. (2015)
KM101952	Europe	USA		Just et al. (2015)
KM101958	Europe	USA		Just et al. (2015)
KM101963	Europe	USA		Just et al. (2015)
KM101965	Europe	USA		Just et al. (2015)
KM101970	Europe	USA		Just et al. (2015)
KM101971	Europe	USA		Just et al. (2015)
KM101989	Europe	USA		Just et al. (2015)
KM101991	Europe	USA		Just et al. (2015)
KM101994	Europe	USA		Just et al. (2015)
KM101997	Europe	USA		Just et al. (2015)
KM102015	Europe	USA/Hispanic		Just et al. (2015)
KM102044	Europe	USA/Hispanic		Just et al. (2015)
KM102045	Europe	USA/Hispanic		Just et al. (2015)
KM102068	Europe	USA/Hispanic		Just et al. (2015)
KM102075	Europe	USA/Hispanic		Just et al. (2015)
KM102091	Europe	USA/Hispanic		Just et al. (2015)
KM102151	Europe	USA/Hispanic		Just et al. (2015)
KM102152	Europe	USA/Hispanic		Just et al. (2015)
KM102154	Europe	USA/Hispanic		Just et al. (2015)
KM213522	Europe NE	Finland		Family Tree
KM213526	Unknown	Unknown		Family Tree
KM233204	Europe NW	Sweden		Family Tree
KM252727	Europe SE	Italy	Apulia	Bodner et al. (2015)
KM252731	Europe SE	Italy	Tuscany	Bodner et al. (2015)
KM252732	Europe SE	Italy	Tuscany	Bodner et al. (2015)
KM252737	Europe SE	Italy	Sardinia	Bodner et al. (2015)
KM252738	Europe SE	Italy	Sardinia	Bodner et al. (2015)
KM252740	Europe SE	Italy	Marche	Bodner et al. (2015)
KM252741	Europe SE	Italy	Sicily	Bodner et al. (2015)
KM252744	Europe SE	Italy	Sicily	Bodner et al. (2015)
KM252750	Europe SE	Italy	Liguria	Bodner et al. (2015)
KM252751	Europe SE	Italy	Liguria	Bodner et al. (2015)
KM252752	Europe SE	Italy	Liguria	Bodner et al. (2015)
KM252753	Europe SE	Italy	Liguria	Bodner et al. (2015)
KM252755	Europe SE	Italy	Emilia-Romagna	Bodner et al. (2015)
KM267903	Europe	USA		Family Tree
KM267905	Europe NW	Poland	ethnicity:Polish	Family Tree
KM582873	Europe NW	Scotland	ethnicity:Scottish	Family Tree
KP116293	Europe NW	Germany		Family Tree
KP215448	Europe NW	Norway		Family Tree
KR758762	Europe NE	Finland	origin_locality:Finland Sievi	Family Tree
KR858775	Europe NW	Ireland/Scotland	ethnicity:Irish/Scot; origin_locality:USA	Family Tree
KR902536	Unknown	Unknown		Family Tree
KT153530	Europe NW	England	ethnicity:English; origin_locality:Essex	Family Tree
KT625440	Europe	USA		Family Tree
KT827363	Europe NE	Russia	ethnicity:Russian; origin_locality:Moscow	Family Tree
KT827380	Unknown	Unknown		Family Tree
KT833130	Europe NW	Ireland		Family Tree
KT833146	Europe	USA		Family Tree
KT851984	Unknown	Unknown		Family Tree
KT861626	Europe	USA		Family Tree
KT868948	Europe	USA		Family Tree
KT892948	Europe NE	Finland		Family Tree
KT901290	Europe SE	Bosnia and Herzegovina	Bosnia and Herzegovina: Sarajevo	Family Tree
KT936634	Europe NW	Germany	origin_locality:Germany: Danish German border, region: Fahrtoft	Family Tree
LIE007	**Europe NW**	**Belgium**		**This study**
LIE015	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE022	**Europe NW**	**Belgium**	**Limburg**	**This study**
LIE033	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE037	**Europe NW**	**Belgium**	**Walloon Brabant**	**This study**
LIE040	**Europe NW**	**Belgium**	**Hainaut**	**This study**
LIE046	**Europe NW**	**Belgium**	**Bruxelles**	**This study**
LIE055	**Europe NW**	**Belgium**	**East Flanders**	**This study**
LIE059	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE061	**Europe NW**	**Belgium**	**Bruxelles**	**This study**
LIE064	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE071	**Europe NW**	**Belgium**	**Walloon Brabant**	**This study**
LIE095	**Europe NW**	**Belgium**	**Liege**	**This study**

LIE100	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE108	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE116	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE120	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE191	**Europe NW**	**Belgium**	**Hainaut**	**This study**
LIE194	**Europe NW**	**Belgium**	**Namur**	**This study**
LIE204	**Europe NW**	**Belgium**	**Luxembourg**	**This study**
LIE226	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE245	**Europe NW**	**Canada**	**Alberta**	**This study**
M1180	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M1198_S	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1230	**Europe NW**	**United Kingdom**	**England_Yorkshire**	**This study**
M1287	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M1291	**Europe NW**	**United Kingdom**	**England_Yorkshire**	**This study**
M1296	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1297	**Europe NW**	**United Kingdom**	**England_Yorkshire**	**This study**
M1308	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1678	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
M1684	**Europe NW**	**United Kingdom**	**England_N**	**This study**
M1726	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M1735	**Europe NW**	**United Kingdom**	**England_N**	**This study**
M1751	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M1752	**Europe NW**	**United Kingdom**	**England_C**	**This study**
M1790	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1807	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1841	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
M1861	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M1888	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M1956	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1959	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M1962	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
M1966	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2038	**Europe NW**	**United Kingdom**	**Scotland_NE**	**This study**
M2039	**Europe NW**	**United Kingdom**	**England_C**	**This study**
M2045	**Europe NW**	**United Kingdom**	**England_Yorkshire**	**This study**
M2054	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M2116	**Europe NW**	**United Kingdom**	**England_Yorkshire**	**This study**
M2147	**Europe NW**	**United Kingdom**	**Scotland_SW**	**This study**
M2178	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
M2200	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2243	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
M2246	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2299	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2349	**Europe NW**	**United Kingdom**	**Scotland_SW**	**This study**
M2368	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M2411	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M2419	**Europe NW**	**United Kingdom**	**England_SW**	**This study**
M2462	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
M2471	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2543	**Europe NW**	**United Kingdom**	**Scotland_SW**	**This study**
M2549	**Europe NW**	**United Kingdom**	**Scotland_C**	**This study**
M2553	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M2554	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2575	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M2589	**Europe NW**	**United Kingdom**	**Scotland_NE**	**This study**
M2601	**Europe NW**	**United Kingdom**	**England_C**	**This study**
M2640	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2642	**Europe NW**	**United Kingdom**		**This study**
M2649	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M2662	**Europe NW**	**United Kingdom**	**Scotland_SE**	**This study**
M2672	**Europe NW**	**United Kingdom**	**England_E**	**This study**
M2681	**Europe NW**	**United Kingdom**	**Scotland_SE**	**This study**
M2698	**Europe NW**	**United Kingdom**		**This study**
M2700	**Europe NW**	**United Kingdom**	**England_N**	**This study**
M2703	**Europe NW**	**United Kingdom**	**England_N**	**This study**
M2706	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M3071	**Europe NW**	**United Kingdom**	**England_SW**	**This study**
M4031	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M5984	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M6006	**Europe NW**	**United Kingdom**	**Scotland_SE**	**This study**
M6314	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
M6596	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M8170	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M8988	**Europe NW**	**United Kingdom**	**Scotland_SW**	**This study**
M9319	**Europe NW**	**United Kingdom**	**England_E**	**This study**
MIR04	**Europe NW**	**Ireland**		**This study**
MIR22	**Europe NW**	**Ireland**		**This study**
MIR28	**Europe NW**	**Ireland**		**This study**
MIR36	**Europe NW**	**Ireland**		**This study**
NA07345	Europe	CEPH		The 1000 Genomes Project Consortium (2015)

NA07347	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA11881	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA11919	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA11920	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA11930	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12144	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12249	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12341	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12399	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12716	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12717	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12748	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12777	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12812	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12890	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA12891	Europe	CEPH		The 1000 Genomes Project Consortium (2015)
NA19648	Europe	Mexico	MXL	The 1000 Genomes Project Consortium (2015)
NA19655	Europe	Mexico	MXL	The 1000 Genomes Project Consortium (2015)
NA20504	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20509	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20513	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20514	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20525	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20526	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20531	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20535	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20541	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)

NA20543	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20586	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20767	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20768	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20769	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20790	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20792	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20803	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20810	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20811	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
NA20832	Europe SE	Italy	Tuscany	The 1000 Genomes Project Consortium (2015)
OL24	**Europe SE**	**Italy**	**Lazio**	**This study**
OL3	**Europe SE**	**Italy**	**Lazio**	**This study**
OL51	**Europe SE**	**Italy**	**Lazio**	**This study**
OL63	**Europe SE**	**Italy**	**Calabria**	**This study**
OL79	**Europe SE**	**Italy**	**Marche**	**This study**
P10D6	**Europe NW**	**Germany**		**This study**
P10G7	**Europe NW**	**Germany**		**This study**
pal-5341	Near East	Palestine		Batini et al. (2017)
PalAo2065	Near East	Palestine		**unpub**
PalAo830	Near East	Palestine		**unpub**
PU100	**Europe SE**	**Italy**	**Puglia**	**This study**
PU30	**Europe SE**	**Italy**	**Puglia**	**This study**
PU41	**Europe SE**	**Italy**	**Puglia**	**This study**
PU44	**Europe SE**	**Italy**	**Puglia**	**This study**
PU83	**Europe SE**	**Italy**	**Puglia**	**This study**
ROM-MM98	**Europe NE**	**Romania**		**This study**
S366	**Europe NW**	**British Isles**		**This study**
S368	**Europe NW**	**British Isles**		**This study**
ser-5	Europe SE	Serbia		Batini et al. (2017)
snia_012758	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
spa-15	Iberia	Spain		Batini et al. (2017)
spa-20	Iberia	Spain		Batini et al. (2017)
spa-26u	Iberia	Spain		Batini et al. (2017)
spa-40	Iberia	Spain		Batini et al. (2017)
spa-63	Iberia	Spain		Batini et al. (2017)
SS84III18	Europe SE	Italy	Sardinia	**unpub**
T-1	**Europe NW**	**France**		**This study**
T-105	**Europe NW**	**France**		**This study**
T-109	**Europe NW**	**France**		**This study**
T-114	**Europe NW**	**France**		**This study**
T-118	**Europe NW**	**France**		**This study**
T-123	**Europe NW**	**France**		**This study**
T-13	**Europe NW**	**France**		**This study**
T-2	**Europe NW**	**France**		**This study**
T-20	**Europe NW**	**France**		**This study**
T-23	**Europe NW**	**France**		**This study**
T-39	**Europe NW**	**France**		**This study**
T-63	**Europe NW**	**France**		**This study**
T-7	**Europe NW**	**France**		**This study**
T-74	**Europe NW**	**France**		**This study**
T-77	**Europe NW**	**France**		**This study**
T-9	**Europe NW**	**France**		**This study**
TurAT16	Near East	Turkey		**unpub**
TurAT7	Near East	Turkey		**unpub**
TurAT9	Near East	Turkey		**unpub**
TurAT95	Near East	Turkey		**unpub**
TurATb14	Near East	Turkey		**unpub**
TurTT27	Near East	Turkey		**unpub**
TurTT3	Near East	Turkey		**unpub**

TurTT73	Near East	Turkey		**unpub**
VDS17	**Europe SE**	**Italy**	**Val di Susa, Piemonte**	**This study**
VDS21	**Europe SE**	**Italy**	**Val di Susa, Piemonte**	**This study**
VDS41	**Europe SE**	**Italy**	**Val di Susa, Piemonte**	**This study**
VIKI5019	**Europe NW**			**This study**
VIKI5052	**Europe NW**			**This study**
VIKI5069	**Europe NW**			**This study**
VIKI5079	**Europe NW**			**This study**
VIKI5106	**Europe NW**			**This study**
VIKI5123	**Europe NW**			**This study**
VIKI5128	**Europe NW**			**This study**
VIKI5144	**Europe NW**			**This study**
VIKI5181	**Europe NW**			**This study**
VIKI5195	**Europe NW**			**This study**
VIKI5213	**Europe NW**			**This study**
VIKI5226	**Europe NW**			**This study**
VIKI5241	**Europe NW**			**This study**
VIKI5249	**Europe NW**			**This study**
VIKI5253	**Europe NW**			**This study**
VIKI5257	**Europe NW**			**This study**
VIKI5288	**Europe NW**			**This study**
VIKI5295	**Europe NW**			**This study**
VIKI5303	**Europe NW**			**This study**
VIKI5343	**Europe NW**			**This study**
VIKI5357	**Europe NW**			**This study**
VIKI5360	**Europe NW**			**This study**
VIKI5375	**Europe NW**			**This study**
VIKI5386	**Europe NW**			**This study**
VIKI5389	**Europe NW**			**This study**
VIKI5415	**Europe NW**			**This study**
VIKI5418	**Europe NW**			**This study**
VIKI5446	**Europe NW**			**This study**
VIKI5460	**Europe NW**			**This study**
VIKI5462	**Europe NW**			**This study**
VIKI5477	**Europe NW**			**This study**
VIKI5484	**Europe NW**			**This study**
VIKI5489	**Europe NW**			**This study**
VIKI5516	**Europe NW**			**This study**
VIKI5527	**Europe NW**			**This study**
VIKI5559	**Europe NW**			**This study**
VIKI5571	**Europe NW**			**This study**
VIKI5572	**Europe NW**			**This study**
VIKI5594	**Europe NW**			**This study**
VIKI5643	**Europe NW**			**This study**
VIKI5648	**Europe NW**			**This study**
VIKI5652	**Europe NW**			**This study**
VIKI5675	**Europe NW**			**This study**
VIKI5708	**Europe NW**			**This study**
VIKI5710	**Europe NW**			**This study**
VIKI5729	**Europe NW**			**This study**
VIKI5752	**Europe NW**			**This study**
VIKI5786	**Europe NW**			**This study**
VIKI5842	**Europe NW**			**This study**
VIKI5875	**Europe NW**			**This study**
VIKI5885	**Europe NW**			**This study**
VIKI5918	**Europe NW**			**This study**
VIKI5924	**Europe NW**			**This study**
VIKI5927	**Europe NW**			**This study**
VIKI5936	**Europe NW**			**This study**
VIKI5964	**Europe NW**			**This study**
VIKI5981	**Europe NW**			**This study**
VIKI6009	**Europe NW**			**This study**
VIKI6016	**Europe NW**			**This study**
VIKI6041	**Europe NW**			**This study**
VIKI6068	**Europe NW**			**This study**
VIKI6079	**Europe NW**			**This study**
VIKI6083	**Europe NW**			**This study**
VIKI6106	**Europe NW**			**This study**
VIKI6157	**Europe NW**			**This study**
VIKI6163	**Europe NW**			**This study**
VIKI6172	**Europe NW**			**This study**
VIKI6177	**Europe NW**			**This study**
VIKI6216	**Europe NW**			**This study**
VIKI6231	**Europe NW**			**This study**
VIKI6234	**Europe NW**			**This study**
VIKI6248	**Europe NW**			**This study**
VIKI6257	**Europe NW**			**This study**
VIKI6300	**Europe NW**			**This study**
VIKI6303	**Europe NW**			**This study**
VIKI6313	**Europe NW**			**This study**
VIKI6321	**Europe NW**			**This study**
VIKI6386	**Europe NW**			**This study**

VIKI6466	**Europe NW**	**This study**
VIKI6476	**Europe NW**	**This study**
VIKI6493	**Europe NW**	**This study**
VIKI6495	**Europe NW**	**This study**
VIKI6516	**Europe NW**	**This study**
VIKI6551	**Europe NW**	**This study**
VIKI6593	**Europe NW**	**This study**
VIKI6607	**Europe NW**	**This study**
VIKI6611	**Europe NW**	**This study**
VIKI6637	**Europe NW**	**This study**
VIKI6704	**Europe NW**	**This study**
VIKI6736	**Europe NW**	**This study**
VIKI6751	**Europe NW**	**This study**
VIKI6763	**Europe NW**	**This study**
VIKI6765	**Europe NW**	**This study**
VIKI6857	**Europe NW**	**This study**
VIKI6886	**Europe NW**	**This study**
VIKI6899	**Europe NW**	**This study**
VIKI6902	**Europe NW**	**This study**
VIKI6925	**Europe NW**	**This study**
VIKI6934	**Europe NW**	**This study**
VIKI6976	**Europe NW**	**This study**
VIKI6998	**Europe NW**	**This study**
VIKI7010	**Europe NW**	**This study**
VIKI7014	**Europe NW**	**This study**
VIKI7018	**Europe NW**	**This study**
VIKI7040	**Europe NW**	**This study**
VIKI7082	**Europe NW**	**This study**
VIKI7090	**Europe NW**	**This study**
VIKI7119	**Europe NW**	**This study**
VIKI7120	**Europe NW**	**This study**
VIKI7148	**Europe NW**	**This study**
VIKI7189	**Europe NW**	**This study**
VIKI7221	**Europe NW**	**This study**
VIKI7260	**Europe NW**	**This study**
VIKI7264	**Europe NW**	**This study**

Table S4. List of modern H2 mtDNA sequences used to build the tree. Newly reported samples in bold.

Sample	Region	Geography/ Population	Additional information	Reference
109	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
1113000038_S9	**Unknown**	**Germany**		**This study**
1113000084_S29	**Unknown**	**Germany**		**This study**
1113000103_S3	**Unknown**	**Germany**		**This study**
1113000149_S70	**Unknown**	**Germany**		**This study**
1113000163_S55	**Unknown**	**Germany**		**This study**
1113000169_S74	**Unknown**	**Germany**		**This study**
1113000181_S60	**Unknown**	**Germany**		**This study**
1113000231_S90	**Unknown**	**Germany**		**This study**
1113000248_S16	**Unknown**	**Germany**		**This study**
1113000282_S39	**Unknown**	**Germany**		**This study**
1113000329_S20	**Unknown**	**Germany**		**This study**
1113000472_S37	**Unknown**	**Germany**		**This study**
1113000496_S82	**Unknown**	**Germany**		**This study**
1113000505_S69	**Unknown**	**Germany**		**This study**
1113000569_S7	**Unknown**	**Germany**		**This study**
1113000570_S33	**Unknown**	**Germany**		**This study**
1113000585_S48	**Unknown**	**Germany**		**This study**
1113000703_S6	**Unknown**	**Germany**		**This study**
1113000718_S81	**Unknown**	**Germany**		**This study**
1113000719_S13	**Unknown**	**Germany**		**This study**
1113000741_S88	**Unknown**	**Germany**		**This study**
1113000758_S70	**Unknown**	**Germany**		**This study**
1113000763_S34	**Unknown**	**Germany**		**This study**
1113000780_S84	**Unknown**	**Germany**		**This study**
1113000833_S36	**Unknown**	**Germany**		**This study**
1113000898_S87	**Unknown**	**Germany**		**This study**
1113000928_S64	**Unknown**	**Germany**		**This study**
1113000974_S43	**Unknown**	**Germany**		**This study**
1113001022_S48	**Unknown**	**Germany**		**This study**
1113001030_S18	**Unknown**	**Germany**		**This study**
1113001056_S84	**Unknown**	**Germany**		**This study**
1113001107_S15	**Unknown**	**Germany**		**This study**
1113001182_S9	**Unknown**	**Germany**		**This study**
1113001220_S91	**Unknown**	**Germany**		**This study**
1113001247_S54	**Unknown**	**Germany**		**This study**
1113001281_S45	**Unknown**	**Germany**		**This study**
1113001310_S83	**Unknown**	**Germany**		**This study**
1113001377_S15	**Unknown**	**Germany**		**This study**
1113001435_S36	**Unknown**	**Germany**		**This study**
1113001457_S30	**Unknown**	**Germany**		**This study**
1113001464_S3	**Unknown**	**Germany**		**This study**
1113001516_S12	**Unknown**	**Germany**		**This study**
1113001533_S30	**Unknown**	**Germany**		**This study**
1113001541_S56	**Unknown**	**Germany**		**This study**
1113001574_S67	**Unknown**	**Germany**		**This study**
1113001598_S15	**Unknown**	**Germany**		**This study**
1113001603_S26	**Unknown**	**Germany**		**This study**
1113001650_S76	**Unknown**	**Germany**		**This study**
1113001686_S7	**Unknown**	**Germany**		**This study**
1113001703_S39	**Unknown**	**Germany**		**This study**
1113001765_S28	**Unknown**	**Germany**		**This study**
1113001826_S90	**Unknown**	**Germany**		**This study**
1113001830_S14	**Unknown**	**Germany**		**This study**
1113001854_S80	**Unknown**	**Germany**		**This study**
1113001887_S42	**Unknown**	**Germany**		**This study**
1113001931_S76	**Unknown**	**Germany**		**This study**
1113002009_S56	**Unknown**	**Germany**		**This study**
1113002016_S3	**Unknown**	**Germany**		**This study**
1113002024_S45	**Unknown**	**Germany**		**This study**
1113002045_S48	**Unknown**	**Germany**		**This study**
1113002176_S95	**Unknown**	**Germany**		**This study**
1113002197_S47	**Unknown**	**Germany**		**This study**
1113002222_S46	**Unknown**	**Germany**		**This study**
1113002249_S89	**Unknown**	**Germany**		**This study**
1113002261_S89	**Unknown**	**Germany**		**This study**
1113002280_S16	**Unknown**	**Germany**		**This study**
1113002291_S88	**Unknown**	**Germany**		**This study**
1113002323_S72	**Unknown**	**Germany**		**This study**
1113002354_S36	**Unknown**	**Germany**		**This study**
1113002382_S41	**Unknown**	**Germany**		**This study**
1113002546_S34	**Unknown**	**Germany**		**This study**
1113002562_S48	**Unknown**	**Germany**		**This study**
1113002610_S32	**Unknown**	**Germany**		**This study**
1113002712_S73	**Unknown**	**Germany**		**This study**
1113002729_S33	**Unknown**	**Germany**		**This study**

1113002732_S62	**Unknown**	**Germany**		**This study**
1113002768_S40	**Unknown**	**Germany**		**This study**
1113002818_S66	**Unknown**	**Germany**		**This study**
1113002858_S90	**Unknown**	**Germany**		**This study**
1113002865_S76	**Unknown**	**Germany**		**This study**
1113002938_S30	**Unknown**	**Germany**		**This study**
1113003020_S58	**Unknown**	**Germany**		**This study**
1113003036_S18	**Unknown**	**Germany**		**This study**
1113003075_S90	**Unknown**	**Germany**		**This study**
A-3	**Europe NW**	**France**		**This study**
A-48	**Europe NW**	**France**		**This study**
ALP008	**Europe SE**	**Italy**	**Veneto**	**This study**
ALP037	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP055	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP225	**Europe SE**	**Italy**	**Valle d'Aosta**	**This study**
ALP302	**Europe SE**	**Italy**	**Lazio**	**This study**
ALP338	**Europe SE**	**Italy**	**Liguria**	**This study**
ALP503	**Europe SE**	**Italy**	**Abruzzo**	**This study**
ALP570	**Europe SE**	**Italy**	**Sicilia**	**This study**
AM263179	Caucasus North	Russia	Dargin	Roostalu et al. (2007)
AM263180	Caucasus North	Russia	Dargin	Roostalu et al. (2007)
AM263181	Caucasus North	Russia	Dargin	Roostalu et al. (2007)
AY339426	Europe NE	Finland	Finland	Finnilä et al. (2001)
AY339427	Europe NE	Finland	Finland	Finnilä et al. (2001)
AY339428	Europe NE	Finland	Finland	Finnilä et al. (2001)
AY339429	Europe NE	Finland	Finland	Finnilä et al. (2001)
AY738961	Near East	Iraq		Achilli et al. (2004)
AY738962	Europe SE	Italy	Italy	Achilli et al. (2004)
AY738963	Iberia	Spain	Spain	Achilli et al. (2004)
B-4	**Europe NW**	**France**		**This study**
B-59	**Europe NW**	**France**		**This study**
bas-10	Europe Basque	Spain		Batini et al. (2017)
bas-5	Europe Basque	Spain		Batini et al. (2017)
bas-6	Europe Basque	Spain		Batini et al. (2017)
bas-7	Europe Basque	Spain		Batini et al. (2017)
bav-30	Europe NW	Germany		Batini et al. (2017)
bav-8	Europe NW	Germany		Batini et al. (2017)
BG135	**Europe SE**	**Italy**	**Lombardy**	**This study**
BG74	**Europe SE**	**Italy**	**Lombardy**	**This study**
BGD220	**Europe SE**	**Italy**	**Lombardy**	**This study**
C-16	**Europe NW**	**France**		**This study**
C-65	**Europe NW**	**France**		**This study**
C-91	**Europe NW**	**France**		**This study**
csct_000241	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_000375	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_007094	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
EF418606	Unknown	Unknown		Family Tree
eng-W13	Europe NW	British Isles		Batini et al. (2017)
ESP0034	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0041	**Iberia**	**Spain**	**Madrid**	**This study**
ESP0071	**Iberia**	**Spain**	**Zaragoza**	**This study**
ESP0088	**Iberia**	**Spain**	**San Sebastian**	**This study**
ESP0099	**Iberia**	**Spain**		**This study**
ESP0185	**Iberia**	**Spain**	**Jaén**	**This study**
ESP0269	**Iberia**	**Spain**	**Girona**	**This study**
ESP0273	**Iberia**	**Spain**	**Sevilla**	**This study**
ESP0311	**Iberia**	**Spain**	**Madrid**	**This study**
ESP0315	**Iberia**	**Spain**	**Cádiz**	**This study**
ESP0332	**Iberia**	**Spain**	**Sevilla**	**This study**
ESP0371	**Iberia**	**Spain**	**Badajoz**	**This study**
ESP0496	**Iberia**	**Spain**	**Cáceres**	**This study**
ESP0564	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0570	**Iberia**	**Spain**	**Cuenca**	**This study**
ESP0786	**Iberia**	**Spain**	**Salamanca**	**This study**
ESP0835	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0941	**Iberia**	**Spain**	**Barcelona**	**This study**
EU130575	Europe	Canada	French Canadian	Family Tree
EU157923	Europe NW	Sweden	Sweden	Family Tree
EU233278	Unknown	Unknown		Family Tree
EU284181	Unknown	Unknown		Family Tree
EU330412	Europe NE	Finland		Family Tree
EU443605	Europe	USA	USA	Family Tree
EU444119	Europe NE	Russia	Russian	Family Tree
EU597492	South Asia	Pakistan	Sindhi, HGDP00163	Hartmann et al. (2009)
EU597521	Caucasus North	Adygei, Russia	HGDP01404	Hartmann et al. (2009)
EU597574	South Asia	Pakistan	Brahui	Hartmann et al. (2009)
EU714299	Unknown	Unknown		Family Tree
EU716647	Unknown	Unknown		Family Tree
EU719115	Europe	USA		Family Tree
EU780223	Europe NW	Sweden	ethnicity: Swedish	Family Tree
EU795361	Europe	USA		Family Tree
FJ161702	Unknown	Unknown		Family Tree

FJ238053	Europe NW	Germany	ethnicity: German	Family Tree
FJ496869	Europe	USA		Family Tree
FJ527772	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ527773	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ527774	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ527775	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ527776	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ527777	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ527778	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ527779	Europe Basque	Spain	Basque Country	Alvarez-Iglesias et al. (2009)
FJ668389	Europe	USA		Family Tree
FJ800808	Europe NW	Ireland	ethnicity: Irish	Family Tree
FJ842614	Europe NW	Denmark	ethnicity: Danish, Northern Jutland	Family Tree
GFM020	**Europe SE**	**Greece**	**Patsos, Amari, Rethymnon**	**This study**
gonl-122b	**Europe NW**	**Netherlands**		**This study**
gonl-126b	**Europe NW**	**Netherlands**		**This study**
gonl-192a	**Europe NW**	**Netherlands**		**This study**
gonl-193b	**Europe NW**	**Netherlands**		**This study**
gonl-212a	**Europe NW**	**Netherlands**		**This study**
gonl-229a	**Europe NW**	**Netherlands**		**This study**
gonl-232a	**Europe NW**	**Netherlands**		**This study**
gonl-39a	**Europe NW**	**Netherlands**		**This study**
gonl-88b	**Europe NW**	**Netherlands**		**This study**
GP2_C2	**Europe NW**	**Germany**		**This study**
GP2_H6	**Europe NW**	**Germany**		**This study**
GP3_A2	**Europe NW**	**Germany**		**This study**
GP3_E8	**Europe NW**	**Germany**		**This study**
GU122997	Europe NE	Russia	Mishars	Malyarchuk et al. (2010)
GU123009	Europe NE	Russia	Mishars	Malyarchuk et al. (2010)
GU592029	Unknown	Unknown		Fendt et al. (2011)
GU903055	Central Asia	Russia	Sakha Republic, Chokurdakh Village	Sukernik et al. (2010)
HG00123	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00127	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00131	Europe NW	England/Scotland	GBR	The 1000 Genomes Project Consortium (2015)
HG00304	Europe NE	Finland	FIN	The 1000 Genomes Project Consortium (2015)
HG00360	Europe NE	Finland	FIN	The 1000 Genomes Project Consortium (2015)
HG01586	South Asia	Pakistan	PJL	The 1000 Genomes Project Consortium (2015)
HG02224	Iberia	Spain	IBS	The 1000 Genomes Project Consortium (2015)
HG04039	South Asia	Sri Lanka	STU	The 1000 Genomes Project Consortium (2015)
HM107111	Europe	USA	origin_locality: USA, Los Angeles	Family Tree
HM589044	Europe NW	Norway	origin_locality: Norway, Telemark	Family Tree
HM852771	Caucasus South	Armenia		Schönberg et al. (2011)
HM852854	Near East	Turkey	Ankara	Schönberg et al. (2011)
HM991709	Europe NW	Germany	ethnicity: German	Family Tree
HQ153430	Europe NW	Norway	ethnicity: Norwegian	Family Tree
HQ336422	Europe NW	England	origin_locality: England, Exeter	Family Tree
HQ659667	Europe NW	Germany	ethnicity: German	Family Tree
HQ659684	Europe NW	England	ethnicity: English	Family Tree
HQ659870	Europe	USA	origin_locality: USA	Family Tree
HQ667351	Europe NE	Lithuania	ethnicity: Lithuanian	Family Tree
HQ670226	Europe NW	England	ethnicity: English	Family Tree
HQ686079	Europe	USA		Family Tree
HQ698266	Europe	Canada		Family Tree
HQ914650	Europe NW	England	ethnicity: English	Family Tree
hun-27	Europe NW	Hungary		Batini et al. (2017)
JF284816	Europe	Argentina	Argentina	Catelli et al. 2011)

JF284817	Europe	Argentina	Argentina	Catelli et al. 2011)
JF284818	Europe	Argentina	Argentina	Catelli et al. 2011)
JF742199	South Asia	Nepal	Kathmandu	Wang et al. (2012)
JN810911	Europe NW	England	ethnicity: English	Family tree
JQ324555	Europe Basque	Spain	Basque	Behar et al. (2012a)
JQ324582	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324606	Europe Basque	Spain	Biscaye	Behar et al. (2012a)
JQ324632	Europe Basque	Spain	Navarra CW, Basque spoken up to the last century	Behar et al. (2012a)
JQ324651	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324654	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324673	Europe Basque	Spain	Biscaye	Behar et al. (2012a)
JQ324675	Europe Basque	Spain	Biscaye	Behar et al. (2012a)
JQ324677	Europe Basque	Spain	Biscaye	Behar et al. (2012a)
JQ324679	Europe Basque	Spain	Biscaye	Behar et al. (2012a)
JQ324680	Europe Basque	France	Labourdin	Behar et al. (2012a)
JQ324685	Europe Basque	France	Soule, Basque-speaking regions located in France	Behar et al. (2012a)
JQ324703	Europe Basque	Spain	Navarra NW	Behar et al. (2012a)
JQ324733	Europe Basque	France	Soule, Basque-speaking regions located in France	Behar et al. (2012a)
JQ324738	Europe Basque	France	Soule, Basque-speaking regions located in France	Behar et al. (2012a)
JQ324744	Europe Basque	Spain	Navarra NW	Behar et al. (2012a)
JQ324758	Europe Basque	Spain	Navarra NW	Behar et al. (2012a)
JQ324761	Europe Basque	Spain	Guipuscoa SW	Behar et al. (2012a)
JQ324764	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324772	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324781	Europe Basque	Spain	Guipuscoa SW	Behar et al. (2012a)
JQ324846	Europe Basque	France	Labourdin, Basque-speaking regions located in France	Behar et al. (2012a)
JQ324853	Europe Basque	Spain	Guipuscoa SW	Behar et al. (2012a)
JQ324896	Europe NW	France	Historically Gascon-speaking region	Behar et al. (2012a)
JQ324899	Europe Basque	Spain	Guipuscoa	Behar et al. (2012a)
JQ324922	Europe Basque	France	Navarra-France, Basque-speaking regions located in France	Behar et al. (2012a)
JQ324929	Europe NW	France	Bigorre: French-speaking regions that historically spoke Gascon	Behar et al. (2012a)
JQ701812	Unknown	Unknown		Behar et al. (2012b)
JQ701819	Unknown	Unknown		Behar et al. (2012b)
JQ701826	Unknown	Unknown		Behar et al. (2012b)
JQ701836	Europe NW	Ireland		Behar et al. (2012b)
JQ701848	Unknown	Unknown		Behar et al. (2012b)
JQ701885	Europe NW	England		Behar et al. (2012b)
JQ701899	Europe NW	England		Behar et al. (2012b)
JQ701904	Unknown	Unknown		Behar et al. (2012b)
JQ702029	Unknown	Unknown		Behar et al. (2012b)
JQ702059	Unknown	Unknown		Behar et al. (2012b)
JQ702171	Europe NW	Ireland		Behar et al. (2012b)
JQ702205	Europe NW	Slovakia		Behar et al. (2012b)
JQ702287	Unknown	Unknown		Behar et al. (2012b)
JQ702309	Unknown	Unknown		Behar et al. (2012b)
JQ702368	Unknown	Unknown		Behar et al. (2012b)
JQ702397	Unknown	Unknown		Behar et al. (2012b)
JQ702426	Europe NW	Poland		Behar et al. (2012b)
JQ702473	Unknown	Unknown		Behar et al. (2012b)
JQ702514	Unknown	Unknown		Behar et al. (2012b)
JQ702890	Unknown	Unknown		Behar et al. (2012b)
JQ702900	Europe NW	England		Behar et al. (2012b)
JQ702943	Europe SE	Greece	Rhodes	Behar et al. (2012b)
JQ702974	Unknown	Unknown		Behar et al. (2012b)
JQ703017	Unknown	Unknown		Behar et al. (2012b)
JQ703020	Europe NW	Germany	Bavaria, Upper Palatinate	Behar et al. (2012b)
JQ703056	Europe NW	Germany		Behar et al. (2012b)
JQ703068	Europe NW	Norway		Behar et al. (2012b)
JQ703080	Europe NW	Scotland		Behar et al. (2012b)
JQ703081	Europe NW	Germany		Behar et al. (2012b)
JQ703144	Unknown	Unknown		Behar et al. (2012b)
JQ703145	Europe NW	Germany		Behar et al. (2012b)
JQ703156	Europe NW	Czech Republic	Bohemia	Behar et al. (2012b)
JQ703173	Europe NW	Ireland		Behar et al. (2012b)
JQ703191	Unknown	Unknown		Behar et al. (2012b)
JQ703192	Unknown	Unknown		Behar et al. (2012b)
JQ703204	Europe NW	Scotland		Behar et al. (2012b)
JQ703209	Europe NW	Poland		Behar et al. (2012b)
JQ703213	Near East	Iran		Behar et al. (2012b)

JQ703214	Unknown	Unknown		Behar et al. (2012b)
JQ703223	Europe NW	Denmark		Behar et al. (2012b)
JQ703290	Unknown	Unknown		Behar et al. (2012b)
JQ703328	Unknown	Unknown		Behar et al. (2012b)
JQ703344	Near East	Turkey		Behar et al. (2012b)
JQ703355	Europe NW	Ireland		Behar et al. (2012b)
JQ703362	Europe NW	Ireland	Ballitore	Behar et al. (2012b)
JQ703366	Europe NW	Ireland		Behar et al. (2012b)
JQ703374	Unknown	Unknown		Behar et al. (2012b)
JQ703397	Unknown	Unknown		Behar et al. (2012b)
JQ703413	Unknown	Unknown		Behar et al. (2012b)
JQ703414	Europe NW	Austria-Hungary		Behar, AJHG 2012
JQ703433	Unknown	Unknown		Behar et al. (2012b)
JQ703449	Europe NW	Ireland		Behar et al. (2012b)
JQ703471	Europe NW	Scotland	Isla of Bute	Behar et al. (2012b)
JQ703509	Europe NW	France		Behar et al. (2012b)
JQ703554	Europe NW	Ireland		Behar et al. (2012b)
JQ703582	Unknown	Unknown		Behar et al. (2012b)
JQ703641	Europe NW	Poland		Behar et al. (2012b)
JQ703760	Europe SE	Italy		Behar et al. (2012b)
JQ703854	Europe NE	Finland		Behar et al. (2012b)
JQ703864	Unknown	Unknown		Behar et al. (2012b)
JQ703881	Europe NW	Sweden		Behar et al. (2012b)
JQ703954	Europe NE	Finland		Behar et al. (2012b)
JQ704025	Unknown	Unknown		Behar et al. (2012b)
JQ704058	Unknown	Unknown		Behar et al. (2012b)
JQ704123	Unknown	Unknown		Behar et al. (2012b)
JQ704140	Europe NW	France		Behar et al. (2012b)
JQ704173	Europe NW	Norway		Behar et al. (2012b)
JQ704189	Europe NW	Northern Ireland	Presbyterian	Behar et al. (2012b)
JQ704198	Europe NW	Ireland		Behar et al. (2012b)
JQ704214	Europe NW	Norway		Behar et al. (2012b)
JQ704220	Europe NW	France		Behar et al. (2012b)
JQ704224	Unknown	Unknown		Behar et al. (2012b)
JQ704262	Europe NE	Finland		Behar et al. (2012b)
JQ704269	Europe NW	Scotland		Behar et al. (2012b)
JQ704274	Unknown	Unknown		Behar et al. (2012b)
JQ704288	Unknown	Unknown		Behar et al. (2012b)
JQ704297	Europe NW	England		Behar et al. (2012b)
JQ704337	Unknown	Unknown		Behar et al. (2012b)
JQ704346	Europe NE	Finland		Behar et al. (2012b)
JQ704361	Europe NW	Germany		Behar et al. (2012b)
JQ704425	Europe NW	Germany		Behar et al. (2012b)
JQ704434	Europe NW	Germany		Behar et al. (2012b)
JQ704478	Unknown	Unknown		Behar et al. (2012b)
JQ704488	Europe NW	Poland	Wielkapolska	Behar et al. (2012b)
JQ704492	Europe NW	Germany	Hanover	Behar et al. (2012b)
JQ704496	Europe NW	France		Behar et al. (2012b)
JQ704499	Europe NW	Germany		Behar et al. (2012b)
JQ704503	Europe NW	Scotland		Behar et al. (2012b)
JQ704520	Unknown	Unknown		Behar et al. (2012b)
JQ704530	Unknown	Unknown		Behar et al. (2012b)
JQ704532	Europe NW	Denmark		Behar et al. (2012b)
JQ704533	Unknown	Unknown		Behar et al. (2012b)
JQ704563	Europe NW	Germany		Behar et al. (2012b)
JQ704565	Unknown	Unknown		Behar et al. (2012b)
JQ704579	Europe NW	France		Behar et al. (2012b)
JQ704673	Unknown	Unknown		Behar et al. (2012b)
JQ704686	Europe NW	England		Behar et al. (2012b)
JQ704687	Europe NW	Slovakia	Sedlak (Szedlak) Presov	Behar et al. (2012b)
JQ704698	Europe NW	England		Behar et al. (2012b)
JQ704774	Unknown	Unknown		Behar et al. (2012b)
JQ704802	Unknown	Unknown		Behar et al. (2012b)
JQ704842	Europe NW	Sweden		Behar et al. (2012b)
JQ704847	Unknown	Unknown		Behar et al. (2012b)
JQ704874	Near East	Cyprus		Behar et al. (2012b)
JQ704939	Europe NW	Poland		Behar et al. (2012b)
JQ705139	Unknown	Unknown		Behar et al. (2012b)
JQ705201	Europe NE	Russia		Behar et al. (2012b)
JQ705223	Europe NW	England		Behar et al. (2012b)
JQ705227	Unknown	Unknown		Behar et al. (2012b)
JQ705262	Europe NW	Sweden		Behar et al. (2012b)
JQ705265	Unknown	Unknown		Behar et al. (2012b)
JQ705365	Europe NW	France		Behar et al. (2012b)
JQ705370	Unknown	Unknown		Behar et al. (2012b)
JQ705385	Europe NW	Germany		Behar et al. (2012b)
JQ705408	Unknown	Unknown		Behar et al. (2012b)
JQ705411	Unknown	Unknown		Behar et al. (2012b)
JQ705413	Europe NE	Finland		Behar et al. (2012b)
JQ705443	Unknown	Unknown		Behar et al. (2012b)
JQ705457	Unknown	Unknown		Behar et al. (2012b)
JQ705471	Unknown	Unknown		Behar et al. (2012b)

JQ705510	Unknown	Unknown		Behar et al. (2012b)
JQ705532	Unknown	Unknown		Behar et al. (2012b)
JQ705563	Unknown	Unknown		Behar et al. (2012b)
JQ705578	Unknown	Unknown		Behar et al. (2012b)
JQ705734	Europe NW	Ireland		Behar et al. (2012b)
JQ705806	Europe NW	Denmark		Behar et al. (2012b)
JQ705837	Unknown	Unknown		Behar et al. (2012b)
JQ705842	Europe NW	France		Behar et al. (2012b)
JQ705852	Unknown	Unknown		Behar et al. (2012b)
JQ705878	Unknown	Unknown		Behar et al. (2012b)
JQ705949	Unknown	Unknown		Behar et al. (2012b)
JQ705956	Europe NW	Ireland		Behar et al. (2012b)
JQ705978	Unknown	Unknown		Behar et al. (2012b)
JQ706011	Europe NW	Ireland		Behar et al. (2012b)
JQ706018	Unknown	Unknown		Behar et al. (2012b)
JQ724861	Europe NW	Poland		Family Tree
JX082002	Europe	Europe		Pacheu-Grau et al. (2013)
JX152789	Europe NW	Denmark		Raule et al. (2014)
JX152802	Europe NW	Denmark		Raule et al. (2014)
JX152807	Europe NW	Denmark		Raule et al. (2014)
JX152816	Europe NW	Denmark		Raule et al. (2014)
JX152847	Europe NW	Denmark		Raule et al. (2014)
JX152855	Europe NW	Denmark		Raule et al. (2014)
JX152856	Europe NW	Denmark		Raule et al. (2014)
JX152900	Europe NW	Denmark		Raule et al. (2014)
JX152911	Europe NW	Denmark		Raule et al. (2014)
JX152950	Europe NW	Denmark		Raule et al. (2014)
JX152962	Europe SE	Greece		Raule et al. (2014)
JX153100	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153119	Europe NE	Finland		Raule et al. (2014)
JX153159	Europe NW	Denmark		Raule et al. (2014)
JX153181	Europe NE	Finland		Raule et al. (2014)
JX153250	Europe NE	Finland		Raule et al. (2014)
JX153256	Europe NE	Finland		Raule et al. (2014)
JX153259	Europe NE	Finland		Raule et al. (2014)
JX153262	Europe NE	Finland		Raule et al. (2014)
JX153268	Europe NE	Finland		Raule et al. (2014)
JX153306	Europe NW	Denmark		Raule et al. (2014)
JX153324	Europe NW	Denmark		Raule et al. (2014)
JX153337	Europe NW	Denmark		Raule et al. (2014)
JX153346	Europe NW	Denmark		Raule et al. (2014)
JX153414	Europe NW	Denmark		Raule et al. (2014)
JX153451	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153460	Europe NW	Denmark		Raule et al. (2014)
JX153474	Europe NW	Denmark		Raule et al. (2014)
JX153477	Europe NW	Denmark		Raule et al. (2014)
JX153478	Europe NW	Denmark		Raule et al. (2014)
JX153491	Europe NW	Denmark		Raule et al. (2014)
JX153547	Europe NE	Finland		Raule et al. (2014)
JX153560	Europe NE	Finland		Raule et al. (2014)
JX153588	Europe NE	Finland		Raule et al. (2014)
JX153614	Europe NE	Finland		Raule et al. (2014)
JX153643	Europe NW	Denmark		Raule et al. (2014)
JX153659	Europe NW	Denmark		Raule et al. (2014)
JX153667	Europe NW	Denmark		Raule et al. (2014)
JX153695	Europe NW	Denmark		Raule et al. (2014)
JX153707	Europe NW	Denmark		Raule et al. (2014)
JX153746	Europe NW	Denmark		Raule et al. (2014)
JX153748	Europe NW	Denmark		Raule et al. (2014)
JX153752	Europe NW	Denmark		Raule et al. (2014)
JX153769	Europe NW	Denmark		Raule et al. (2014)
JX153776	Europe NW	Denmark		Raule et al. (2014)
JX153782	Europe NW	Denmark		Raule et al. (2014)
JX153810	Europe NW	Denmark		Raule et al. (2014)
JX153827	Europe NE	Finland		Raule et al. (2014)
JX153838	Europe NE	Finland		Raule et al. (2014)
JX153842	Europe NE	Finland		Raule et al. (2014)
JX153890	Europe NW	Denmark		Raule et al. (2014)
JX153949	Europe NW	Denmark		Raule et al. (2014)
JX153957	Europe NW	Denmark		Raule et al. (2014)
JX153982	Europe NW	Denmark		Raule et al. (2014)
JX154017	Europe NW	Denmark		Raule et al. (2014)
JX154026	Europe NW	Denmark		Raule et al. (2014)
JX154030	Europe NW	Denmark		Raule et al. (2014)
JX154035	Europe NW	Denmark		Raule et al. (2014)
JX154052	Europe NW	Denmark		Raule et al. (2014)
JX154053	Europe NW	Denmark		Raule et al. (2014)
JX171094	Europe NE	Finland		Soini et al. (2012)
JX171096	Europe NE	Finland		Soini et al. (2012)
JX297140	Europe Basque	Spain	Northern Spain	Cardoso et al. (2013)
KC763372	Europe NE	Finland		Soini et al. (2013)

KC763378	Europe NE	Finland		Soini et al. (2013)
KC763380	Europe NE	Finland		Soini et al. (2013)
KC763388	Europe NE	Finland		Soini et al. (2013)
KC763392	Europe NE	Finland		Soini et al. (2013)
KC763449	Europe NE	Finland		Soini et al. (2013)
KC866614	Europe	USA		Family Tree
KC907350	Europe NW	Slovakia	Carpathian Mountains	Family Tree
KC911386n	Caucasus South	Armenian (Iran)	Armenian	Derenko et al. (2013)
KC911598	Near East	Iran	Qashqai	Derenko et al. (2013)
KC911617	Near East	Iran	Persian	Derenko et al. (2013)
KC990675	Unknown	Unknown	Possibly Indian	Ramanan et al. unpub.
KF161066	Europe NW	Denmark		Li et al. (2014)
KF161133	Europe NW	Denmark		Li et al. (2014)
KF161138	Europe NW	Denmark		Li et al. (2014)
KF161155	Europe NW	Denmark		Li et al. (2014)
KF161175	Europe NW	Denmark		Li et al. (2014)
KF161204	Europe NW	Denmark		Li et al. (2014)
KF161261	Europe NW	Denmark		Li et al. (2014)
KF161288	Europe NW	Denmark		Li et al. (2014)
KF161311	Europe NW	Denmark		Li et al. (2014)
KF161356	Europe NW	Denmark		Li et al. (2014)
KF161364	Europe NW	Denmark		Li et al. (2014)
KF161381	Europe NW	Denmark		Li et al. (2014)
KF161394	Europe NW	Denmark		Li et al. (2014)
KF161399	Europe NW	Denmark		Li et al. (2014)
KF161406	Europe NW	Denmark		Li et al. (2014)
KF161413	Europe NW	Denmark		Li et al. (2014)
KF161436	Europe NW	Denmark		Li et al. (2014)
KF161492	Europe NW	Denmark		Li et al. (2014)
KF161540	Europe NW	Denmark		Li et al. (2014)
KF161682	Europe NW	Denmark		Li et al. (2014)
KF161688	Europe NW	Denmark		Li et al. (2014)
KF161694	Europe NW	Denmark		Li et al. (2014)
KF161696	Europe NW	Denmark		Li et al. (2014)
KF161701	Europe NW	Denmark		Li et al. (2014)
KF161709	Europe NW	Denmark		Li et al. (2014)
KF161749	Europe NW	Denmark		Li et al. (2014)
KF161772	Europe NW	Denmark		Li et al. (2014)
KF161793	Europe NW	Denmark		Li et al. (2014)
KF161815	Europe NW	Denmark		Li et al. (2014)
KF161829	Europe NW	Denmark		Li et al. (2014)
KF161877	Europe NW	Denmark		Li et al. (2014)
KF161916	Europe NW	Denmark		Li et al. (2014)
KF161917	Europe NW	Denmark		Li et al. (2014)
KF161930	Europe NW	Denmark		Li et al. (2014)
KF161947	Europe NW	Denmark		Li et al. (2014)
KF161977	Europe NW	Denmark		Li et al. (2014)
KF162060	Europe NW	Denmark		Li et al. (2014)
KF162066	Europe NW	Denmark		Li et al. (2014)
KF162141	Europe NW	Denmark		Li et al. (2014)
KF162181	Europe NW	Denmark		Li et al. (2014)
KF162222	Europe NW	Denmark		Li et al. (2014)
KF162233	Europe NW	Denmark		Li et al. (2014)
KF162234	Europe NW	Denmark		Li et al. (2014)
KF162237	Europe NW	Denmark		Li et al. (2014)
KF162239	Europe NW	Denmark		Li et al. (2014)
KF162242	Europe NW	Denmark		Li et al. (2014)
KF162252	Europe NW	Denmark		Li et al. (2014)
KF162256	Europe NW	Denmark		Li et al. (2014)
KF162258	Europe NW	Denmark		Li et al. (2014)
KF162270	Europe NW	Denmark		Li et al. (2014)
KF162273	Europe NW	Denmark		Li et al. (2014)
KF162285	Europe NW	Denmark		Li et al. (2014)
KF162320	Europe NW	Denmark		Li et al. (2014)
KF162330	Europe NW	Denmark		Li et al. (2014)
KF162336	Europe NW	Denmark		Li et al. (2014)
KF162345	Europe NW	Denmark		Li et al. (2014)
KF162357	Europe NW	Denmark		Li et al. (2014)
KF162392	Europe NW	Denmark		Li et al. (2014)
KF162412	Europe NW	Denmark		Li et al. (2014)
KF162435	Europe NW	Denmark		Li et al. (2014)
KF162460	Europe NW	Denmark		Li et al. (2014)
KF162472	Europe NW	Denmark		Li et al. (2014)
KF162510	Europe NW	Denmark		Li et al. (2014)
KF162544	Europe NW	Denmark		Li et al. (2014)
KF162576	Europe NW	Denmark		Li et al. (2014)
KF162589	Europe NW	Denmark		Li et al. (2014)
KF162623	Europe NW	Denmark		Li et al. (2014)
KF162636	Europe NW	Denmark		Li et al. (2014)
KF162706	Europe NW	Denmark		Li et al. (2014)
KF162720	Europe NW	Denmark		Li et al. (2014)
KF162760	Europe NW	Denmark		Li et al. (2014)

KF162786	Europe NW	Denmark		Li et al. (2014)
KF162806	Europe NW	Denmark		Li et al. (2014)
KF162813	Europe NW	Denmark		Li et al. (2014)
KF162824	Europe NW	Denmark		Li et al. (2014)
KF162828	Europe NW	Denmark		Li et al. (2014)
KF162877	Europe NW	Denmark		Li et al. (2014)
KF162899	Europe NW	Denmark		Li et al. (2014)
KF162914	Europe NW	Denmark		Li et al. (2014)
KF162941	Europe NW	Denmark		Li et al. (2014)
KF162955	Europe NW	Denmark		Li et al. (2014)
KF162987	Europe NW	Denmark		Li et al. (2014)
KF162999	Europe NW	Denmark		Li et al. (2014)
KF163035	Europe NW	Denmark		Li et al. (2014)
KF450943	South Asia	Pakistan	Pathan, HGDP00224	Lippold et al. (2014)
KF450963	South Asia	Pakistan	Kalash, HGDP00274	Lippold et al. (2014)
KF451168	Near East	Israel (Bedouin)	HGDP00645	Lippold et al. (2014)
KF451408	Europe NE	Russia-HGDP00894	HGDP00894	Lippold et al. (2014)
KF451414	Europe NE	Russia - HGDP00900	HGDP00900	Lippold et al. (2014)
KF451817	Europe Basque	France	HGDP01365	Lippold et al. (2014)
KF451840	Caucasus North	Russia Caucasus (Adygei)	HGDP01388	Lippold et al. (2014)
KF466258	Europe NW	Poland		Family Tree
KF723706	Europe NE	Hungary/Romania	ethnicity: Carpathian; Hungarian/Romanian	Family Tree
KJ856689	Central Asia	Russia (Khamnigan)	Buryat Republic / Khamnigan	Derenko et al. (2014)
KJ856717	Central Asia	Russia (Altai/Kazakh)	Altai Republic / Altaian Kazakh	Derenko et al. (2014)
KJ856720	Central Asia	Russia (Khamnigan)	Buryat Republic / Khamnigan	Derenko et al. (2014)
KJ856726	Central Asia	Russia (Altai/Kazakh)	Altai Republic / Altaian Kazakh	Derenko et al. (2014)
KJ856744	Central Asia	Russia (Altai/Kizhi)	Altai Republic / Altaian-Kizhi	Derenko et al. (2014)
KJ856745	Central Asia	Russia (Altai/Kizhi)	Altai Republic / Altaian-Kizhi	Derenko et al. (2014)
KM016488	Europe NW	Ireland	Clough	Family Tree
KM047201	Europe NW	Poland		Skonieczna et al. (2015)
KM047218	Europe NW	Poland		Skonieczna et al. (2015)
KM101809	Europe	USA		Just et al. (2015)
KM101856	Europe	USA		Just et al. (2015)
KM101895	Europe	USA		Just et al. (2015)
KM102063	Europe	USA/Hispanic		Just et al. (2015)
KM102077	Europe	USA/Hispanic		Just et al. (2015)
KM267907	Europe NW	Sweden	Vasterbotten, Skeleftea	Family Tree
KP722565	Europe NW	Czech Republic		Family Tree
KP763834	South Asia	India		Palanichamy et al. (2015)
KP763853	South Asia	India		Palanichamy et al. (2015)
KT390701	Europe NW	Sweden		Family Tree
LIE065	**Europe NW**	**Belgium**	**Hainaut**	**This study**
LIE067	**Europe NW**	**Belgium**	**Liege**	**This study**
M1579	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M2301	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2820	**Europe NW**	**United Kingdom**	**England_C**	**This study**
M2841	**Europe NW**	**United Kingdom**	**Scotland_SE**	**This study**
M2846	**Europe NW**	**United Kingdom**	**Scotland_NE**	**This study**
M2856	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M2859	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M2888	**Europe NW**	**United Kingdom**	**England_E**	**This study**
M2905	**Europe NW**	**United Kingdom**	**England_SW**	**This study**
M2907	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M2912	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2913	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2914	**Europe NW**	**United Kingdom**	**England_SW**	**This study**
M2948	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M2984	**Europe NW**	**United Kingdom**	**Scotland_NE**	**This study**
M2985	**Europe NW**	**United Kingdom**	**Scotland_NW**	**This study**
M3004	**Europe NW**	**United Kingdom**	**Scotland_C**	**This study**
M3015	**Europe NW**	**United Kingdom**	**Scotland_NE**	**This study**
M3022	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M3036	**Europe NW**	**United Kingdom**	**Scotland_NW**	**This study**
M6580	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M7400	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
MF362866	South Caucasus	Armenia	Artsakh_78	Margaryan et al. (2017)
MF362942	South Caucasus	Armenia	Erzrum_75	Margaryan et al. (2017)
MIR07	**Europe NW**	**Ireland**		**This study**
NA07048	Europe	CEPH	CEPH individuals	The 1000 Genomes Project Consortium (2015)
NA07346	Europe	CEPH	CEPH individuals	The 1000 Genomes Project Consortium (2015)

NA11832	Europe	CEPH	CEPH individuals	The 1000 Genomes Project Consortium (2015)
NA11918	Europe	CEPH	CEPH individuals	The 1000 Genomes Project Consortium (2015)
NA19682	Europe	Mexico	MXL	The 1000 Genomes Project Consortium (2015)
NA20585	Europe SE	Italy (Tuscany)	Toscan individuals	The 1000 Genomes Project Consortium (2015)
NA20872	South Asia	India	GIH	The 1000 Genomes Project Consortium (2015)
NC_012920	Europe NW	United Kingdom	rCRS	Andrews et al. (1999)
nor-16	Europe NW	Norway		Batini et al. (2017)
nor-27	Europe NW	Norway		Batini et al. (2017)
P10C4	**Europe NW**	**Germany**		**This study**
P10H5	**Europe NW**	**Germany**		**This study**
PU76	**Europe SE**	**Italy**	**Puglia**	**This study**
T-14	**Europe NW**	**France**		**This study**
T-35	**Europe NW**	**France**		**This study**
T-47	**Europe NW**	**France**		**This study**
VB21	**Europe SE**	**Italy**	**Val Borbera, Piemonte**	**This study**
VDS52	**Europe SE**	**Italy**	**Val di Susa, Piemonte**	**This study**
VIKI5697	**Europe NW**	**Shetland**		**This study**
VIKI5711	**Europe NW**	**Shetland**		**This study**
VIKI6101	**Europe NW**	**Shetland**		**This study**
VIKI6210	**Europe NW**	**Shetland**		**This study**
VIKI6315	**Europe NW**	**Shetland**		**This study**
VIKI6754	**Europe NW**	**Shetland**		**This study**
VIKI6806	**Europe NW**	**Shetland**		**This study**

Table S5. List of modern H11 mtDNA sequences used to build the tree. Newly reported samples in bold.

Sample	Region	Geography/ Population	Additional information	Reference
1113000033_S74	**Unknown**	**Germany**		**This study**
1113000179_S75	**Unknown**	**Germany**		**This study**
1113000286_S21	**Unknown**	**Germany**		**This study**
1113000418_S57	**Unknown**	**Germany**		**This study**
1113000419_S23	**Unknown**	**Germany**		**This study**
1113000473_S4	**Unknown**	**Germany**		**This study**
1113000537_S10	**Unknown**	**Germany**		**This study**
1113000578_S63	**Unknown**	**Germany**		**This study**
1113000599_S64	**Unknown**	**Germany**		**This study**
1113000634_S3	**Unknown**	**Germany**		**This study**
1113000869_S79	**Unknown**	**Germany**		**This study**
1113000897_S69	**Unknown**	**Germany**		**This study**
1113000999_S6	**Unknown**	**Germany**		**This study**
1113001009_S53	**Unknown**	**Germany**		**This study**
1113001261_S56	**Unknown**	**Germany**		**This study**
1113001277_S36	**Unknown**	**Germany**		**This study**
1113001614_S37	**Unknown**	**Germany**		**This study**
1113001624_S29	**Unknown**	**Germany**		**This study**
1113002046_S37	**Unknown**	**Germany**		**This study**
1113002088_S15	**Unknown**	**Germany**		**This study**
1113002091_S58	**Unknown**	**Germany**		**This study**
1113002219_S1	**Unknown**	**Germany**		**This study**
1113002266_S6	**Unknown**	**Germany**		**This study**
1113002516_S61	**Unknown**	**Germany**		**This study**
1113002578_S60	**Unknown**	**Germany**		**This study**
1113002587_S92	**Unknown**	**Germany**		**This study**
1113002642_S48	**Unknown**	**Germany**		**This study**
1113002871_S17	**Unknown**	**Germany**		**This study**
1113003025_S17	**Unknown**	**Germany**		**This study**
1113003065_S79	**Unknown**	**Germany**		**This study**
ALP005	**Europe SE**	**Italy**	**Veneto**	**This study**
ALP039	**Europe SE**	**Italy**	**Piemonte**	**This study**
ALP079	**Europe SE**	**Italy**	**Veneto**	**This study**
ALP310	**Europe SE**	**Italy**	**Piemonte**	**This study**
AY195751	Unknown	Unknown		Mishmar et al. (2003)
AY738958	Europe SE	Italy		Achilli et al. (2004)
B-28	**Europe NW**	**France**		**This study**
BGD56	**Europe SE**	**Italy**	**Lombardy**	**This study**
C-35	**Europe NW**	**France**		**This study**
csct_000097	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_000351	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_007112	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
den-176	Europe NW	Denmark		Batini et al. (2017)
den-183	Europe NW	Denmark		Batini et al. (2017)
EF545566	Unknown	Unknown		Whyte, direct submission
ESP0058	**Iberia**	**Spain**	**Lleida**	**This study**
ESP0175	**Iberia**	**Spain**	**Albacete**	**This study**
ESP0350	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0355	**Iberia**	**Spain**	**Madrid**	**This study**
ESP0557	**Iberia**	**Spain**	**Barcelona**	**This study**
FJ560912	Europe NW	England		Family Tree
FJ705060	Europe	Canada		Family Tree
fri-1319	Europe NW	Netherlands		Batini et al. (2017)
fri-1718	Europe NW	Netherlands		Batini et al. (2017)
gonl-125b	**Europe NW**	**Netherlands**		**This study**
gonl-158a	**Europe NW**	**Netherlands**		**This study**
gonl-161b	**Europe NW**	**Netherlands**		**This study**
gonl-165a	**Europe NW**	**Netherlands**		**This study**
gonl-227a	**Europe NW**	**Netherlands**		**This study**
gonl-241a	**Europe NW**	**Netherlands**		**This study**
gonl-47a	**Europe NW**	**Netherlands**		**This study**
GP2_F9	**Europe NW**	**Germany**		**This study**
GP3_C10	**Europe NW**	**Germany**		**This study**
GU122994	Asia	Russia (Volga-Urals)		Malyarchuk et al. (2010)
GU592023	Unknown	Unknown		Fendt et al. (2011)
GU592038	Unknown	Unknown		Fendt et al. (2011)
GU945760	Europe	USA		Family Tree
GU949563	Europe NE	Finland		Family Tree
HQ219084	Europe	USA		Family Tree
HQ257449	Europe NW	England		Family Tree
HQ659686	Europe	USA		Family Tree
HQ681883	Europe	USA		Family Tree
HQ707396	Europe NW	England		Family Tree
HQ843503	Europe NW	England/Germany		Family Tree

hun-39	Europe NW	Hungary		Batini et al. (2017)
JN581651	Unknown	Unknown		Bertolin et al. (2011)
JQ702044	Europe NE	Finland		Behar et al. (2012b)
JQ702051	Unknown	Unknown		Behar et al. (2012b)
JQ702388	Unknown	Unknown		Behar et al. (2012b)
JQ702396	Europe NW	England		Behar et al. (2012b)
JQ702966	Europe NW	Germany		Behar et al. (2012b)
JQ703071	Europe NW	Poland		Behar et al. (2012b)
JQ703163	Unknown	Unknown		Behar et al. (2012b)
JQ703167	Europe NW	Germany		Behar et al. (2012b)
JQ703172	Europe NW	England		Behar et al. (2012b)
JQ703175	Unknown	Unknown		Behar et al. (2012b)
JQ703183	Unknown	Unknown		Behar et al. (2012b)
JQ703235	Unknown	Unknown		Behar et al. (2012b)
JQ703253	Europe NW	Norway		Behar et al. (2012b)
JQ703259	Europe NW	Poland		Behar et al. (2012b)
JQ703343	Unknown	Unknown		Behar et al. (2012b)
JQ703451	Europe NW	Germany		Behar et al. (2012b)
JQ703453	Unknown	Unknown		Behar et al. (2012b)
JQ703510	Unknown	Unknown		Behar et al. (2012b)
JQ703543	Unknown	Unknown		Behar et al. (2012b)
JQ703593	Unknown	Unknown		Behar et al. (2012b)
JQ703676	Europe NE	Finland		Behar et al. (2012b)
JQ703678	Europe NE	Finland		Behar et al. (2012b)
JQ703684	Europe NW	Poland		Behar et al. (2012b)
JQ703688	Europe NE	Finland		Behar et al. (2012b)
JQ703733	Unknown	Unknown		Behar et al. (2012b)
JQ703781	Europe NW	Austria		Behar et al. (2012b)
JQ703949	Europe NW	Hungary		Behar et al. (2012b)
JQ704081	Europe NE	Ukraine	Ashkenazi	Behar et al. (2012b)
JQ704101	Unknown	Unknown		Behar et al. (2012b)
JQ704164	Europe NW	England		Behar et al. (2012b)
JQ704166	Europe SE	Italy		Behar et al. (2012b)
JQ704185	Europe NW	England		Behar et al. (2012b)
JQ704280	Europe NW	Ireland		Behar et al. (2012b)
JQ704286	Europe NW	Scotland		Behar et al. (2012b)
JQ704395	Europe NW	Germany		Behar et al. (2012b)
JQ704427	Europe NE	Ukraine	Ashkenazi	Behar et al. (2012b)
JQ704664	Unknown	Unknown		Behar et al. (2012b)
JQ704846	Europe NW	France		Behar et al. (2012b)
JQ705459	Europe NW	Scotland		Behar et al. (2012b)
JQ705580	Unknown	Unknown		Behar et al. (2012b)
JQ705643	Unknown	Unknown		Behar et al. (2012b)
JQ705740	Unknown	Unknown		Behar et al. (2012b)
JQ705807	Unknown	Unknown		Behar et al. (2012b)
JQ705898	Unknown	Unknown		Behar et al. (2012b)
JQ705928	Europe NW	Germany		Behar et al. (2012b)
JQ705954	Europe NW	Ireland		Behar et al. (2012b)
JQ705984	Unknown	Unknown		Behar et al. (2012b)
JQ706003	Europe NW	England		Behar et al. (2012b)
JX152946	Europe NW	Denmark		Raule et al. (2014)
JX152992	Europe NE	Finland		Raule et al. (2014)
JX153177	Europe NE	Finland		Raule et al. (2014)
JX153368	Europe NW	Denmark		Raule et al. (2014)
JX153417	Europe NW	Denmark		Raule et al. (2014)
JX153466	Europe NW	Denmark		Raule et al. (2014)
JX153476	Europe NW	Denmark		Raule et al. (2014)
JX153483	Europe NW	Denmark		Raule et al. (2014)
JX153516	Europe NW	Denmark		Raule et al. (2014)
JX153570	Europe NE	Finland		Raule et al. (2014)
JX153593	Europe NE	Finland		Raule et al. (2014)
JX153711	Europe NW	Denmark		Raule et al. (2014)
JX153761	Europe NW	Denmark		Raule et al. (2014)
JX153771	Europe NW	Denmark		Raule et al. (2014)
JX154068	Europe NE	Finland		Raule et al. (2014)
JX306646	Europe	USA		Family Tree
KC286597	Europe NW	Austria		Kloss-Brandstätter et al. (2015)
KC286601	Europe NW	Austria		Kloss-Brandstätter et al. (2015)
KC763447	Europe NE	Finland		Soini et al. (2013)
KF161209	Europe NW	Denmark		Li et al. (2014)
KF161213	Europe NW	Denmark		Li et al. (2014)
KF161435	Europe NW	Denmark		Li et al. (2014)
KF161563	Europe NW	Denmark		Li et al. (2014)
KF161565	Europe NW	Denmark		Li et al. (2014)
KF161727	Europe NW	Denmark		Li et al. (2014)
KF161732	Europe NW	Denmark		Li et al. (2014)
KF162198	Europe NW	Denmark		Li et al. (2014)
KF162267	Europe NW	Denmark		Li et al. (2014)
KF162294	Europe NW	Denmark		Li et al. (2014)
KF162388	Europe NW	Denmark		Li et al. (2014)

KF162478	Europe NW	Denmark		Li et al. (2014)
KF162553	Europe NW	Denmark		Li et al. (2014)
KF162555	Europe NW	Denmark		Li et al. (2014)
KF162617	Europe NW	Denmark		Li et al. (2014)
KF162655	Europe NW	Denmark		Li et al. (2014)
KF162803	Europe NW	Denmark		Li et al. (2014)
KF451057	Europe NW	France	HGDP00522	Lippold et al. (2014)
KF451406	Europe NE	Russia	HGDP00892	Lippold et al. (2014)
KF451844	Caucasus North	Adygei (Russia)	HGDP01399	Lippold et al. (2014)
KF765775	Europe NW	England		Family Tree
KJ361861	Europe NE	Russia		Family Tree
KJ816751	Europe SE	Croatia		Family Tree
KJ831815	Europe NW	Netherlands		Loe, direct submission
KJ856713	Asia	Russia (Altai)		Derenko et al. (2014)
KJ856767	Asia	Russia (Buryatia)		Derenko et al. (2014)
KJ856774	Asia	Russia (Buryatia)		Derenko et al. (2014)
KJ856785	Asia	Russia (Buryatia)		Derenko et al. (2014)
KJ856795	Europe NW	Poland		Derenko et al. (2014)
KJ856810	Europe NW	Poland		Derenko et al. (2014)
KJ856811	Europe NW	Poland		Derenko et al. (2014)
KJ856816	Europe NW	Poland		Derenko et al. (2014)
KJ856825	Europe NW	Poland		Derenko et al. (2014)
KJ868087	Europe	USA		Family Tree
KJ920748	Europe	USA		Family Tree
KM047214	Europe NW	Poland		Skonieczna et al. (2015)
KM101842	Europe	USA		Just et al. (2015)
KM101911	Europe	USA		Just et al. (2015)
KM101966	Europe	USA		Just et al. (2015)
KM576772	Europe NE	Lithuania		Family Tree
LIE053	**Europe NW**	**Belgium**	**Namur**	**This study**
LIE093	**Europe NW**	**Belgium**	**Walloon Brabant**	**This study**
LIE203	**Europe NW**	**Belgium**	**Walloon Brabant**	**This study**
M1406	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1438	**Europe NW**	**United Kingdom**	**Scotland_NW**	**This study**
M1440	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1441	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
M1481	**Europe NW**	**United Kingdom**	**Ireland_Ulster**	**This study**
M1491	**Europe NW**	**United Kingdom**	**Scotland_SE**	**This study**
M2739	**Europe NW**	**United Kingdom**	**Wales_N**	**This study**
M4323	**Europe NW**	**United Kingdom**	**England_C**	**This study**
M5331	**Europe NW**	**United Kingdom**	**Scotland_SE**	**This study**
M8398	**Europe NW**	**United Kingdom**	**England_SE**	**This study**
MF362825	South Caucasus	Armenia	Artsakh_31	Margaryan et al. (2017)
NA11995	Europe	CEPH	CEPH individuals	The 1000 Genomes Project Consortium (2015)
NA12873	Europe	CEPH	CEPH individuals	The 1000 Genomes Project Consortium (2015)
PU12	**Europe SE**	**Italy**	**Puglia**	**This study**
T-11	**Europe NW**	**France**		**This study**
VIKI5075	**Europe NW**	**Shetland**		**This study**
VIKI5469	**Europe NW**	**Shetland**		**This study**
VIKI5723	**Europe NW**	**Shetland**		**This study**
VIKI5776	**Europe NW**	**Shetland**		**This study**

Table S6. List of modern H13 mtDNA sequences used to build the tree. Newly reported samples in bold.

Sample	Region	Geography/ Population	Additional information	Reference
1113000158_S96	**Unknown**	**unknown**		**This study**
1113000168_S48	**Unknown**	**unknown**		**This study**
1113000200_S19	**Unknown**	**unknown**		**This study**
1113000236_S53	**Unknown**	**unknown**		**This study**
1113000274_S82	**Unknown**	**unknown**		**This study**
1113000277_S36	**Unknown**	**unknown**		**This study**
1113000390_S92	**Unknown**	**unknown**		**This study**
1113000462_S4	**Unknown**	**unknown**		**This study**
1113000540_S2	**Unknown**	**unknown**		**This study**
1113000586_S40	**Unknown**	**unknown**		**This study**
1113000590_S94	**Unknown**	**unknown**		**This study**
1113000598_S88	**Unknown**	**unknown**		**This study**
1113000705_S32	**Unknown**	**unknown**		**This study**
1113000730_S55	**Unknown**	**unknown**		**This study**
1113000740_S70	**Unknown**	**unknown**		**This study**
1113000756_S85	**Unknown**	**unknown**		**This study**
1113000907_S54	**Unknown**	**unknown**		**This study**
1113000910_S73	**Unknown**	**unknown**		**This study**
1113001077_S84	**Unknown**	**unknown**		**This study**
1113001118_S74	**Unknown**	**unknown**		**This study**
1113001191_S45	**Unknown**	**unknown**		**This study**
1113001250_S70	**Unknown**	**unknown**		**This study**
1113001296_S19	**Unknown**	**unknown**		**This study**
1113001324_S32	**Unknown**	**unknown**		**This study**
1113001459_S75	**Unknown**	**unknown**		**This study**
1113001493_S31	**Unknown**	**unknown**		**This study**
1113001531_S5	**Unknown**	**unknown**		**This study**
1113001600_S94	**Unknown**	**unknown**		**This study**
1113001657_S28	**Unknown**	**unknown**		**This study**
1113001702_S10	**Unknown**	**unknown**		**This study**
1113001751_S70	**Unknown**	**unknown**		**This study**
1113001786_S36	**Unknown**	**unknown**		**This study**
1113001789_S40	**Unknown**	**unknown**		**This study**
1113001825_S78	**Unknown**	**unknown**		**This study**
1113001855_S86	**Unknown**	**unknown**		**This study**
1113001978_S58	**Unknown**	**unknown**		**This study**
1113001991_S94	**Unknown**	**unknown**		**This study**
1113002003_S32	**Unknown**	**unknown**		**This study**
1113002020_S53	**Unknown**	**unknown**		**This study**
1113002060_S22	**Unknown**	**unknown**		**This study**
1113002129_S75	**Unknown**	**unknown**		**This study**
1113002143_S15	**Unknown**	**unknown**		**This study**
1113002169_S2	**Unknown**	**unknown**		**This study**
1113002223_S46	**Unknown**	**unknown**		**This study**
1113002310_S91	**Unknown**	**unknown**		**This study**
1113002378_S20	**Unknown**	**unknown**		**This study**
1113002494_S10	**Unknown**	**unknown**		**This study**
1113002594_S43	**Unknown**	**unknown**		**This study**
1113002691_S43	**Unknown**	**unknown**		**This study**
1113002692_S40	**Unknown**	**unknown**		**This study**
1113002702_S28	**Unknown**	**unknown**		**This study**
1113002916_S70	**Unknown**	**unknown**		**This study**
1113002956_S75	**Unknown**	**unknown**		**This study**
1113002957_S40	**Unknown**	**unknown**		**This study**
1113002979_S51	**Unknown**	**unknown**		**This study**
5809	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
A-34	**Europe NW**	**France**		**This study**
A-43	**Europe NW**	**France**		**This study**
ALP095	**Europe SE**	**Italy**	**Veneto**	**This study**
ALP128	**Europe SE**	**Italy**	**Emilia Romagna**	**This study**
ALP309	**Europe SE**	**Italy**	**Calabria**	**This study**
ALP325	**Europe SE**	**Italy**	**Calabria**	**This study**
ALP596	**Europe SE**	**Italy**	**Calabria**	**This study**
ALP597	**Europe SE**	**Italy**	**Calabria**	**This study**
AM263186	Caucasus North	Lezgin		Roostalu et al. (2007)
AM263187	Caucasus North	Tabasaran		Roostalu et al. (2007)
AM263188	Caucasus South	Mingrelian		Roostalu et al. (2007)
AM263189	Near East	Jordanian		Roostalu et al. (2007)
AM263190	Near East	Turk		Roostalu et al. (2007)
AM263191	Caucasus North	Abazin		Roostalu et al. (2007)
AY339409	Europe NE	Finland		Finnilä et al. (2001)
AY339410	Europe NE	Finland		Finnilä et al. (2001)
AY495107	Europe	Europe		Coble et al. (2004)
AY495129	Europe	Europe		Coble et al. (2004)

AY495149	Europe	Europe		Coble et al. (2004)
AY713980	South Asia	India		Palanichamy et al. (2004)
AY713982	South Asia	India		Palanichamy et al. (2004)
AY738995	Europe SE	Italy		Achilli et al. (2004)
AY738996	Europe SE	Italy		Achilli et al. (2004)
AY738997	Europe SE	Italy		Achilli et al. (2004)
B-15	**Europe NW**	**France**		**This study**
BG110	**Europe SE**	**Italy**	**Lombardy**	**This study**
C-96	**Europe NW**	**France**		**This study**
csct_000111	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_000448	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_003759	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_004110	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_004157	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_005748	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_007248	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
csct_007276	Europe SE	Italy (Sardinia)		Olivieri et al. (2017)
den-152	Europe NW	Denmark		Batini et al. (2017)
den-189	Europe NW	Denmark		Batini et al. (2017)
EF556150	Unknown	unknown		Behar et al. (2008)
EF556156	Unknown	unknown		Behar et al. (2008)
ESP0011	**Iberia**	**Spain**	**Córdoba**	**This study**
ESP0543	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0771	**Iberia**	**Spain**	**Orense**	**This study**
ESP0866	**Iberia**	**Spain**	**Valencia**	**This study**
ESP0876	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP1021	**Iberia**	**Spain**	**Cantabria**	**This study**
ESP1032	**Iberia**	**Spain**	**Jaén**	**This study**
ESP1035	**Iberia**	**Spain**		**This study**
EU052289	Unknown	unknown		Family Tree
EU370982	Europe SE	Italy	Calabria	Family Tree
EU597515	Near East	Palestinian	HGDP00675	Hartmann et al. (2009)
EU600346	Near East	Druze		Shlush et al. (2008)
EU600347	Near East	Druze		Shlush et al. (2008)
EU684448	Europe NW	Norway		Whyte, direct submission
FJ560455	Europe NW	France		Family Tree
GFM034	**Europe SE**	**Greece**	**Paleoloutra, Rethymnon**	**This study**
GFM035	**Europe SE**	**Greece**	**Koumi, Rethymnon**	**This study**
gonl-158b	**Europe NW**	**Netherlands**		**This study**
gonl-195b	**Europe NW**	**Netherlands**		**This study**
gonl-19b	**Europe NW**	**Netherlands**		**This study**
GP2_D6	**Europe NW**	**Germany**		**This study**
GP2_E12	**Europe NW**	**Germany**		**This study**
GQ478574	Europe NW	Norway		Family Tree
GU228506	Caucasus South	Armenia	Armenian (Turkey)	Family Tree
GU945543	Europe SE	Italy	Sicily	Family Tree
HG00178	Europe NE	Finland		The 1000 Genomes Project Consortium (2015)
HG00233	Europe NW	England/Scotland		The 1000 Genomes Project Consortium (2015)
HG00324	Europe NE	Finland		The 1000 Genomes Project Consortium (2015)
HG01173	Europe	Puerto Rico		The 1000 Genomes Project Consortium (2015)
HG01510	Iberia	Spain		The 1000 Genomes Project Consortium (2015)
HG01589	South Asia	Pakistan		The 1000 Genomes Project Consortium (2015)
HG02651	South Asia	Pakistan		The 1000 Genomes Project Consortium (2015)
HG03692	South Asia	India		The 1000 Genomes Project Consortium (2015)
HG03844	South Asia	India		The 1000 Genomes Project Consortium (2015)
HG03849	South Asia	India		The 1000 Genomes Project Consortium (2015)
HG03995	South Asia	India		The 1000 Genomes Project Consortium (2015)

HM044302	Europe	USA		Family Tree
HM852757	Caucasus South	Armenia		Schönberg et al. (2011)
HM852889	Caucasus South	Georgia		Schönberg et al. (2011)
HQ234355	Caucasus South	Armenia		Family Tree
HQ658464	Europe NE	Finland		Family Tree
JF828090	Europe SE	Greece	Kalamata	Family Tree
JN712772	Near East	Turkey		Family Tree
JQ324527	Europe NW	France	Southwest	Behar et al. (2012a)
JQ324531	Europe NW	France	Southwest	Behar et al. (2012a)
JQ324538	Europe NW	France	Southwest	Behar et al. (2012a)
JQ324583	Europe NW	France	Southwest	Behar et al. (2012a)
JQ324598	Iberia	Spain	North (La Rioja)	Behar et al. (2012a)
JQ664536	Europe SE	Croatia		Fu et al. (2012)
JQ664541	Europe SE	Croatia		Fu et al. (2012)
JQ701816	Near East	Iraq		Behar et al. (2012b)
JQ701818	Europe NW	Hungary	Ashkenazi	Behar et al. (2012b)
JQ701842	Europe NE	Russia		Behar et al. (2012b)
JQ701948	Unknown	unknown		Behar et al. (2012b)
JQ702022	Europe NW	Poland		Behar et al. (2012b)
JQ702112	Europe NW	England		Behar et al. (2012b)
JQ702303	Unknown	unknown		Behar et al. (2012b)
JQ702399	Unknown	unknown		Behar et al. (2012b)
JQ702582	Europe NW	United Kingdom		Behar et al. (2012b)
JQ702658	Unknown	unknown		Behar et al. (2012b)
JQ702829	Europe NE	Finland		Behar et al. (2012b)
JQ702835	Europe NE	Finland		Behar et al. (2012b)
JQ703035	Unknown	unknown		Behar et al. (2012b)
JQ703053	Unknown	unknown		Behar et al. (2012b)
JQ703169	Europe NW	France		Behar et al. (2012b)
JQ703193	Europe NW	Poland		Behar et al. (2012b)
JQ703208	Unknown	unknown		Behar et al. (2012b)
JQ703373	Unknown	unknown		Behar et al. (2012b)
JQ703386	Europe NW	Germany		Behar et al. (2012b)
JQ703421	Unknown	unknown		Behar et al. (2012b)
JQ703650	Unknown	unknown		Behar et al. (2012b)
JQ703657	Near East	UAE	United Arab Emirates	Behar et al. (2012b)
JQ703808	Europe NE	Finland		Behar et al. (2012b)
JQ703858	Europe NW	Ireland		Behar et al. (2012b)
JQ703863	Unknown	unknown		Behar et al. (2012b)
JQ703878	Europe NW	United Kingdom		Behar et al. (2012b)
JQ704072	Unknown	unknown		Behar et al. (2012b)
JQ704111	Unknown	unknown		Behar et al. (2012b)
JQ704113	Unknown	unknown		Behar et al. (2012b)
JQ704147	Unknown	unknown		Behar et al. (2012b)
JQ704176	Europe NW	United Kingdom		Behar et al. (2012b)
JQ704218	Europe NW	Norway		Behar et al. (2012b)
JQ704234	Europe NW	Poland		Behar et al. (2012b)
JQ704313	Unknown	unknown		Behar et al. (2012b)
JQ704316	Europe NW	Scotland		Behar et al. (2012b)
JQ704351	Unknown	unknown		Behar et al. (2012b)
JQ704375	Europe NW	Ireland		Behar et al. (2012b)
JQ704475	Europe NW	Wales		Behar et al. (2012b)
JQ704483	Europe SE	Italy	Sicily	Behar et al. (2012b)
JQ704549	Unknown	unknown		Behar et al. (2012b)
JQ704682	Unknown	unknown		Behar et al. (2012b)
JQ704814	Europe NW	Scotland		Behar et al. (2012b)
JQ704841	Europe NE	Finland		Behar et al. (2012b)
JQ704928	Unknown	unknown		Behar et al. (2012b)
JQ705098	Europe NW	England		Behar et al. (2012b)
JQ705194	Unknown	unknown		Behar et al. (2012b)
JQ705345	Unknown	unknown		Behar et al. (2012b)
JQ705399	Iberia	Spain		Behar et al. (2012b)
JQ705423	Unknown	unknown		Behar et al. (2012b)
JQ705508	Europe NW	Ireland		Behar et al. (2012b)
JQ705524	Unknown	unknown		Behar et al. (2012b)
JQ705699	Unknown	unknown		Behar et al. (2012b)
JQ705726	Europe NW	Ireland		Behar et al. (2012b)
JQ705780	Unknown	unknown		Behar et al. (2012b)
JQ705796	Unknown	unknown		Behar et al. (2012b)
JQ705981	Unknown	unknown		Behar et al. (2012b)
JQ706004	Unknown	unknown		Behar et al. (2012b)
JX153013	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153111	Europe SE	Italy	Calabria	Raule et al. (2014)
JX153117	Europe SE	Greece		Raule et al. (2014)
JX153198	Europe NE	Finland		Raule et al. (2014)
JX153299	Europe NW	Denmark		Raule et al. (2014)
JX153335	Europe NW	Denmark		Raule et al. (2014)
JX153480	Europe NW	Denmark		Raule et al. (2014)
JX153573	Europe NE	Finland		Raule et al. (2014)
JX153617	Europe NE	Finland		Raule et al. (2014)
JX153624	Europe NE	Finland		Raule et al. (2014)
JX153688	Europe NW	Denmark		Raule et al. (2014)

JX153696	Europe NW	Denmark		Raule et al. (2014)
JX153809	Europe NW	Denmark		Raule et al. (2014)
JX153825	Europe NE	Finland		Raule et al. (2014)
JX153866	Europe NW	Denmark		Raule et al. (2014)
JX153945	Europe NW	Denmark		Raule et al. (2014)
JX171087	Europe NE	Finland		Soini et al. (2012)
JX944820	Europe NW	England		Family Tree
KC170990	Europe NW	Norway		Family Tree
KC577357	Africa	Mauritius		Fregel et al. (2014)
KC577358	Africa	Mauritius		Fregel et al. (2014)
KC763387	Europe NE	Finland		Soini et al. (2013)
KC763390	Europe NE	Finland		Soini et al. (2013)
KC763391	Europe NE	Finland		Soini et al. (2013)
KC763400	Europe NE	Finland		Soini et al. (2013)
KC765915	Europe SE	Bulgaria		Family Tree
KC911276	Near East	Iran	Kurd	Derenko et al. (2013)
KC911290	Europe NE	Russia	Belgorod Region , ear border with Ukraine	Derenko et al. (2013)
KC911295	Near East	Iran	Qashqai	Derenko et al. (2013)
KC911326	Near East	Iran	Qashqai	Derenko et al. (2013)
KC911327	Near East	Iran	Persian	Derenko et al. (2013)
KC911335	Near East	Iran	Qashqai	Derenko et al. (2013)
KC911338	Near East	Iran	Persian	Derenko et al. (2013)
KC911361	Near East	Iran	Persian	Derenko et al. (2013)
KC911369	Near East	Iran	Qashqai	Derenko et al. (2013)
KC911416	Near East	Iran	Qashqai	Derenko et al. (2013)
KC911443	Near East	Iran	Indian	Derenko et al. (2013)
KC911454	Europe NE	Russia	Saratov Region, border with W. Kazakhstan	Derenko et al. (2013)
KC911458	Near East	Iran	Persian	Derenko et al. (2013)
KC911462	Europe NE	Russia	Belgorod Region, near border with Ukraine	Derenko et al. (2013)
KC911469	Near East	Iran	Persian	Derenko et al. (2013)
KC911555	Near East	Iran	Qashqai	Derenko et al. (2013)
KC911600	Near East	Iran	Persian	Derenko et al. (2013)
KF161108	Europe NW	Denmark		Li et al. (2014)
KF161167	Europe NW	Denmark		Li et al. (2014)
KF161603	Europe NW	Denmark		Li et al. (2014)
KF161699	Europe NW	Denmark		Li et al. (2014)
KF161731	Europe NW	Denmark		Li et al. (2014)
KF161775	Europe NW	Denmark		Li et al. (2014)
KF161847	Europe NW	Denmark		Li et al. (2014)
KF162025	Europe NW	Denmark		Li et al. (2014)
KF162062	Europe NW	Denmark		Li et al. (2014)
KF162093	Europe NW	Denmark		Li et al. (2014)
KF162138	Europe NW	Denmark		Li et al. (2014)
KF162171	Europe NW	Denmark		Li et al. (2014)
KF162187	Europe NW	Denmark		Li et al. (2014)
KF162247	Europe NW	Denmark		Li et al. (2014)
KF162279	Europe NW	Denmark		Li et al. (2014)
KF162291	Europe NW	Denmark		Li et al. (2014)
KF162311	Europe NW	Denmark		Li et al. (2014)
KF162456	Europe NW	Denmark		Li et al. (2014)
KF162567	Europe NW	Denmark		Li et al. (2014)
KF162585	Europe NW	Denmark		Li et al. (2014)
KF162595	Europe NW	Denmark		Li et al. (2014)
KF162691	Europe NW	Denmark		Li et al. (2014)
KF162893	Europe NW	Denmark		Li et al. (2014)
KF162907	Europe NW	Denmark		Li et al. (2014)
KF162940	Europe NW	Denmark		Li et al. (2014)
KF162974	Europe NW	Denmark		Li et al. (2014)
KF162982	Europe NW	Denmark		Li et al. (2014)
KF163001	Europe NW	Denmark		Li et al. (2014)
KF260957	Europe SE	Bulgaria		Family Tree
KF450826	South Asia	Pakistan	Brahui, HGDP00025	Lippold et al. (2014)
KF450840	South Asia	Pakistan	Balochi, HGDP00054	Lippold et al. (2014)
KF450847	South Asia	Pakistan	Balochi, HGDP00066	Lippold et al. (2014)
KF450856	South Asia	Pakistan	Balochi, HGDP00086	Lippold et al. (2014)
KF451105	Near East	Israel (Druze)	HGDP00571	Lippold et al. (2014)
KF451109	Near East	Israel (Druze)	HGDP00575	Lippold et al. (2014)
KF451123	Near East	Israel (Druze)	HGDP00592	Lippold et al. (2014)
KF451623	Europe SE	Italy	Tuscan, HGDP01164	Lippold et al. (2014)
KF451624	Europe SE	Italy	Tuscan, HGDP01166	Lippold et al. (2014)
KF889440	Europe SE	Bulgaria		Family Tree
KJ733699	Caucasus South	Armenia	ethnicity: Armenian	Family Tree
KM047189	Europe NW	Poland	normal colon tissue	Skonieczna et al. (2015)
KM047215	Europe NW	Poland	normal colon tissue	Skonieczna et al. (2015)
KM101884	Europe	USA		Just et al. (2015)
KP638565	Europe NE	Russia		Family Tree
KP733894	Europe NW	Czech Republic		Family Tree
KR271612	Europe NW	Germany		Family Tree
KR712271	Europe NE	Finland		Family Tree

LIE004	**Europe NW**	**Belgium**	**Liege**	**This study**
LIE051	**Europe NW**	**Belgium**	**Liege**	**This study**
LK02_19	**Europe SE**	**Cyprus**		**This study**
LK20	**Europe SE**	**Cyprus**		**This study**
LK25	**Europe SE**	**Cyprus**		**This study**
LK33	**Europe SE**	**Cyprus**		**This study**
M1473	**Europe NW**	**United Kingdom**	**Scotland_C**	**This study**
M1504	**Europe NW**	**United Kingdom**	**Scotland_SE**	**This study**
M1540	**Europe NW**	**United Kingdom**	**England_Yorkshire**	**This study**
M1553	**Europe NW**	**United Kingdom**	**England_N**	**This study**
M3465	**Europe NW**	**United Kingdom**	**Wales_S**	**This study**
MF362786	Caucasus South	Armenia	Ararat_49	Margaryan et al. (2017)
MF362874	Caucasus South	Armenia	Artsakh_86	Margaryan et al. (2017)
MF362897	Caucasus South	Armenia	Erzrum_20	Margaryan et al. (2017)
MF362902	Caucasus South	Armenia	Erzrum_28	Margaryan et al. (2017)
NA12275	Europe	Europe	CEPH	The 1000 Genomes Project Consortium (2015)
NA12878	Europe	Europe	CEPH	The 1000 Genomes Project Consortium (2015)
NA20771	Europe SE	Italy	Tuscan	The 1000 Genomes Project Consortium (2015)
NA20806	Europe SE	Italy	Tuscan	The 1000 Genomes Project Consortium (2015)
nor-2	Europe NW	Norway		Batini et al. (2017)
OL11	**Europe SE**	**Italy**	**Lazio**	**This study**
OL17	**Europe SE**	**Italy**	**Lazio**	**This study**
OL44	**Europe SE**	**Italy**	**Lazio**	**This study**
OL71	**Europe SE**	**Italy**	**Lazio**	**This study**
OL86	**Europe SE**	**Italy**	**Calabria**	**This study**
PU89	**Europe SE**	**Italy**	**Puglia**	**This study**
ROM-MM25	**Europe NE**	**Romania**		**This study**
ser-9	Europe SE	Serbia		Batini et al. (2017)
spa-51	Iberia	Spain		Batini et al. (2017)
tur-11	Near East	Turkey		Batini et al. (2017)
VIKI5478	**Europe NW**	**Shetland**		**This study**
VIKI6435	**Europe NW**	**Shetland**		**This study**
VIKI7072	**Europe NW**	**Shetland**		**This study**

Table S7. Frequency of main mtDNA haplogroups in mainland Iberia.Regions as indicated in Fgure 3.2.

Haplogroup	North		Central		South		East		West		Iberia	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
H1	35	24.48	82	20.71	58	20.07	34	18.58	19	19.79	228	20.60
H2	2	1.40	10	2.53	6	2.08	4	2.19	0	0.00	22	1.99
H3	8	5.59	29	7.32	19	6.57	9	4.92	7	7.29	72	6.50
H5	5	3.50	14	3.54	10	3.46	6	3.28	1	1.04	36	3.25
H11	0	0.00	2	0.51	1	0.35	2	1.09	0	0.00	5	0.45
H13	2	1.40	0	0.00	2	0.69	4	2.19	1	1.04	9	0.81
other H	19	13.29	53	13.38	40	13.84	24	13.11	14	14.58	150	13.55
HV0	0	0.00	4	1.01	5	1.73	8	4.37	1	1.04	18	1.63
V	5	3.50	14	3.54	11	3.81	5	2.73	3	3.13	38	3.43
other HV	2	1.40	4	1.01	3	1.04	2	1.09	2	2.08	13	1.17
J1	10	6.99	31	7.83	16	5.54	12	6.56	4	4.17	73	6.59
J2	2	1.40	9	2.27	5	1.73	4	2.19	2	2.08	22	1.99
T1	2	1.40	7	1.77	3	1.04	5	2.73	7	7.29	24	2.17
T2	9	6.29	33	8.33	19	6.57	14	7.65	7	7.29	82	7.41
K1	9	6.29	21	5.30	19	6.57	13	7.10	7	7.29	69	6.23
K2	1	0.70	4	1.01	5	1.73	3	1.64	2	2.08	15	1.36
X	5	3.50	10	2.53	7	2.42	2	1.09	1	1.04	25	2.26
U1	0	0.00	3	0.76	1	0.35	0	0.00	0	0.00	4	0.36
U2	1	0.70	6	1.52	2	0.69	2	1.09	2	2.08	13	1.17
U3	0	0.00	6	1.52	3	1.04	3	1.64	1	1.04	13	1.17
U4	1	0.70	4	1.01	4	1.38	4	2.19	1	1.04	14	1.26
U5	10	6.99	30	7.58	21	7.27	12	6.56	4	4.17	77	6.96
U6	1	0.70	3	0.76	9	3.11	2	1.09	3	3.13	18	1.63
U8	2	1.40	0	0.00	2	0.69	2	1.09	0	0.00	6	0.54
others	12	8.39	17	4.29	18	6.23	7	3.83	7	7.29	61	5.51
total	143	100	396	100	289	100	183	100	96	100	1107	100

Excel file S1. Most parsimonious phylogeny of mtDNA haplogroup H1, based on 3483 modern and 148 ancient sequences (Tables S2 and S3). Ancient samples in yellow, newly reported sequences in bold. Cells coloured according to geographic origin (Table 3.2). *ρ* node age estimates shown. Mutations relative to rCRS (position and base present in the sequence) are shown along the branches. Inverted mutations represented by a "@", insertions and deletions indicated by "ins" and "del", respectively.

Excel file S2. Most parsimonious phylogeny of mtDNA haplogroup H2, based on 621 modern and 36 ancient sequences (Tables S2 and S4). Ancient samples in yellow, newly reported sequences in bold. Cells coloured according to geographic origin (Table 3.2). *ρ* and Maximum Likelihood (ML) node age estimates shown. Mutations relative to rCRS (position and base present in the sequence) are shown along the branches. Inverted mutations represented by a "@", insertions and deletions indicated by "ins" and "del", respectively.

Excel file S3. Most parsimonious phylogeny of mtDNA haplogroup H11, based on 205 modern and 7 ancient sequences (Tables S2 and S5). Ancient samples in yellow, newly reported sequences in bold. Cells coloured according to geographic origin (Table 3.2). *ρ* and Maximum Likelihood (ML) node age estimates shown. Mutations relative to rCRS (position and base present in the sequence) are shown along the branches. Inverted mutations represented by a "@", insertions and deletions indicated by "ins" and "del", respectively.

Excel file S2. Most parsimonious phylogeny of mtDNA haplogroup H13, based on 325 modern and 23 ancient sequences (Tables S2 and S6). Ancient samples in yellow, newly reported sequences in bold. Cells coloured according to geographic origin (Table 3.2). *ρ* and Maximum Likelihood (ML) node age estimates shown. Mutations relative to rCRS (position and base present in the sequence) are shown along the branches. Inverted mutations represented by a "@", insertions and deletions indicated by "ins" and "del", respectively.

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Appendix C

Supplementary information for chapter IV

A genetic snapshot of Medieval Iberia: a pilot study

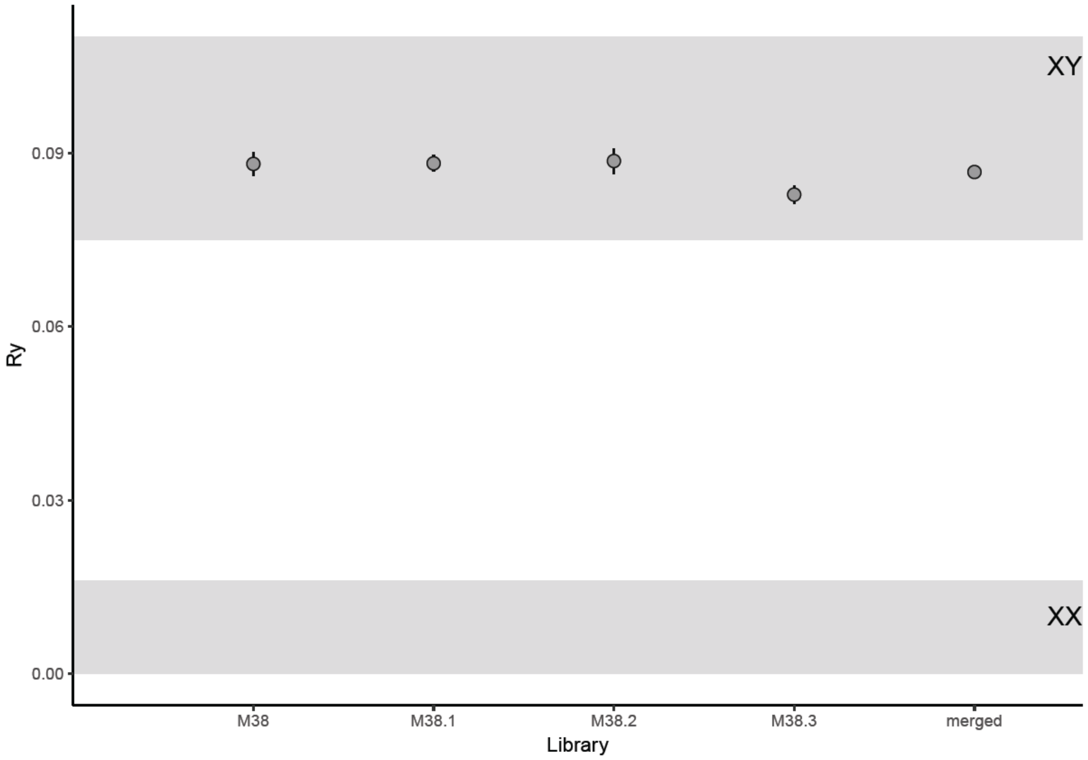


Figure S1. Sex assignment plot for all libraries of MS060/Segorbe Giant (error bars represent 95% confidence intervals). On the x-axis the name of each library for the Segorbe Giant, on the y-axis the *Ry* score used to determine the genetic sex.

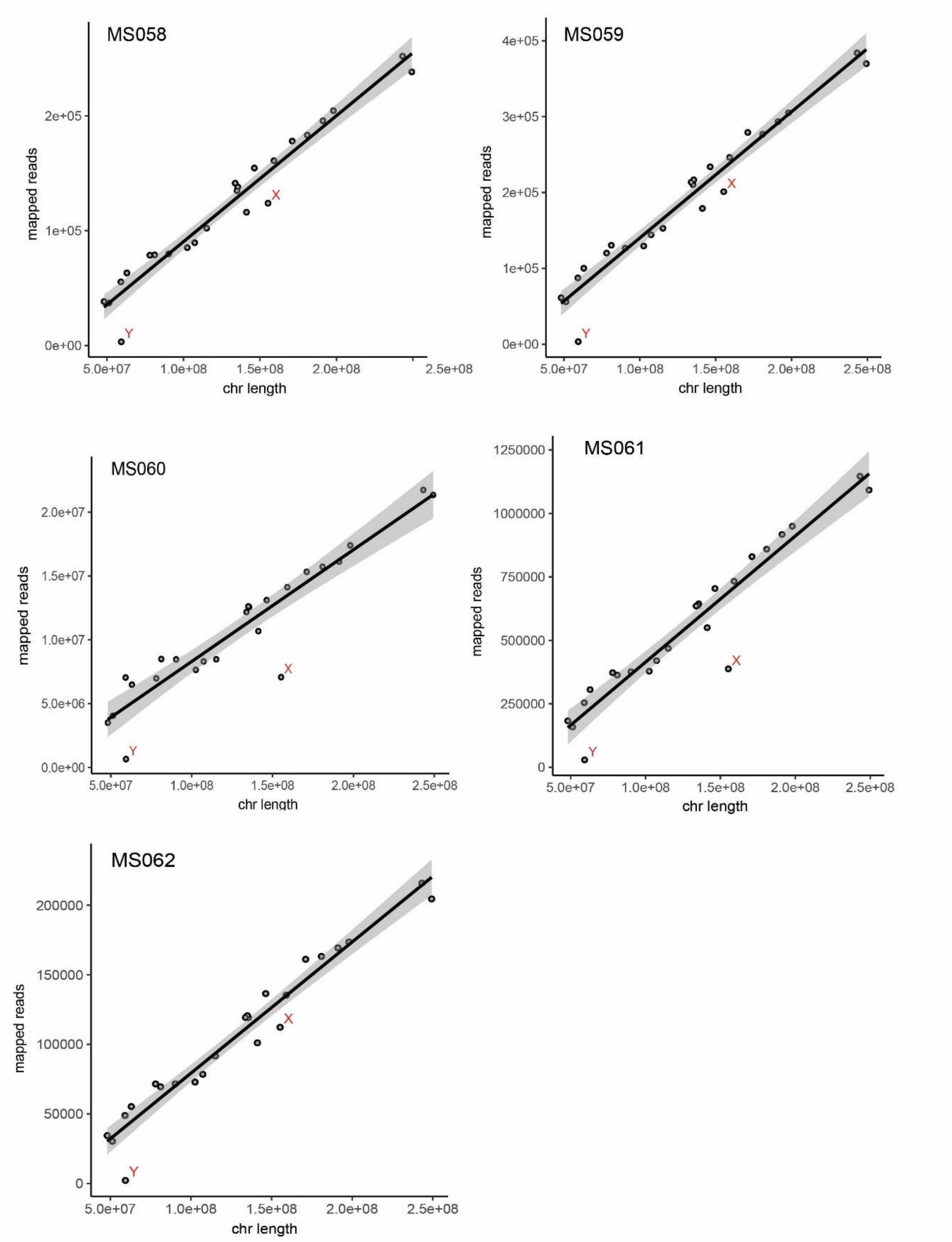
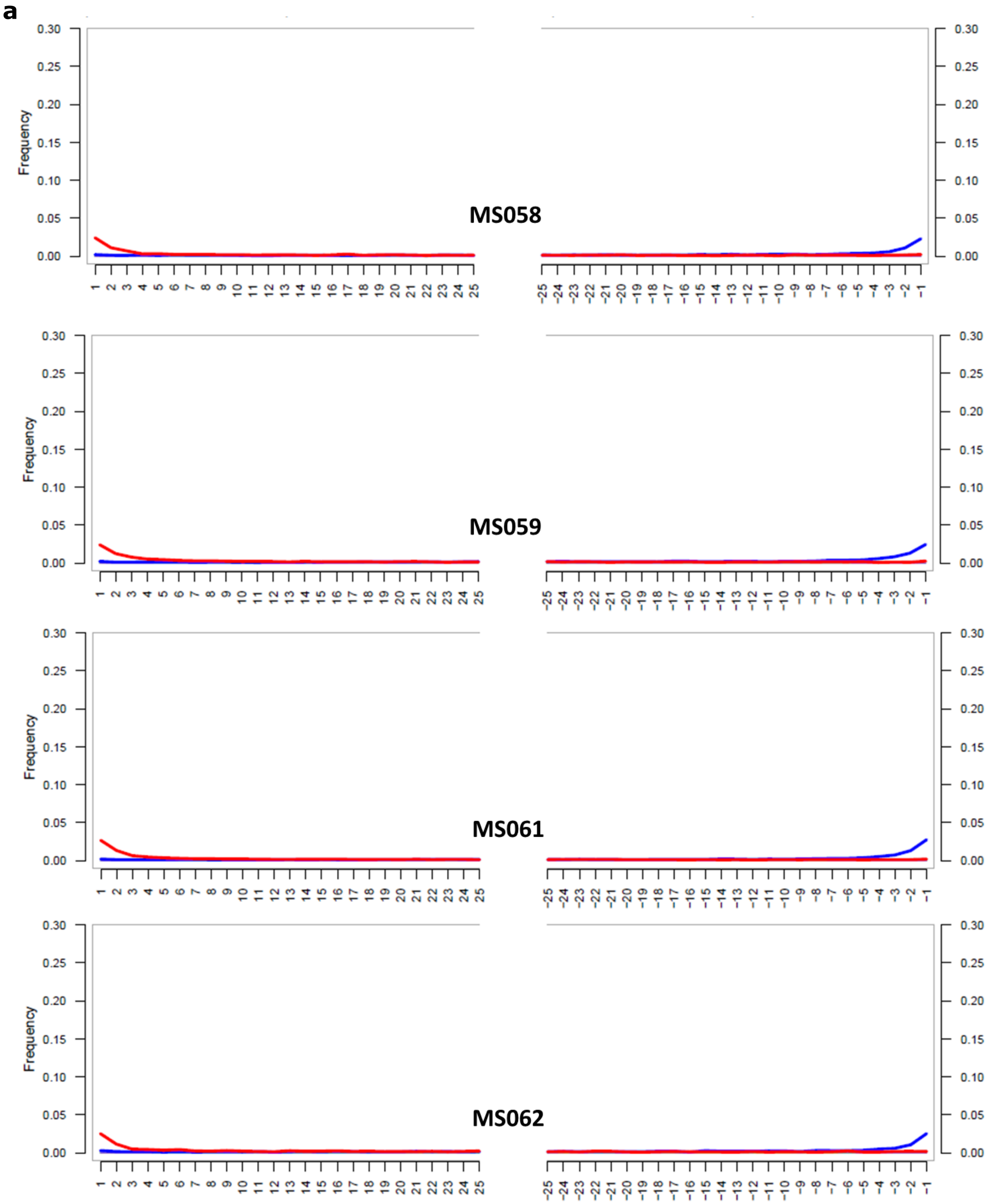


Figure S2. Sex determination by comparing chromosome lengths (chr length, x-axis) and number of mapped reads for each chromosome (y-axis). Individuals are classified as genetically male if the number of mapped reads for the X chromosome is much lower than what is expected for diploid autosomes, thus suggesting that the X chromosome is only present in one copy. Individuals are classified as genetically female if the proportion of mapped reads for the X chromosome is similar to that of diploid autosomes.


a
Frequency
0.30
0.25
0.20
0.15
0.10
0.05
0.00
MS058
MS059
MS061
MS062
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
-25 -24 -23 -22 -21 -20 -19 -18 -17 -16 -15 -14 -13 -12 -11 -10 -9 -8 -7 -6 -5 -4 -3 -2 -1

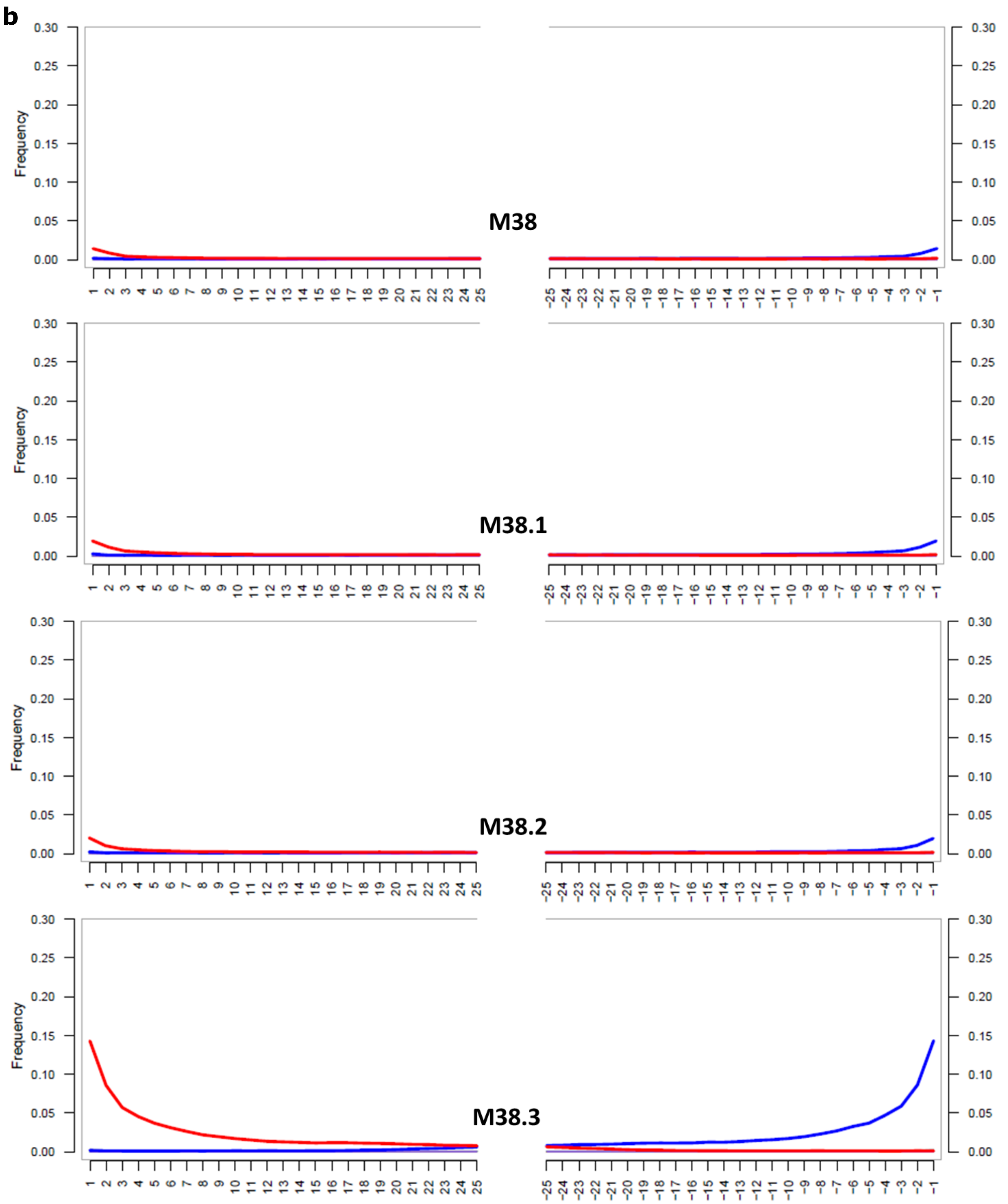


Figure S3. Damage pattern showing the typical C>T (5'end, in red) and G>A (3'end, in blue) misincorporations for **a)** USER-treated libraries of low coverage samples and **b)** for multiple libraries of sample MS060/Segorbe Giant: M38, M38.1 and M38.2 are USER-treated, M38.3 is non-treated. Plots from mapDamage.

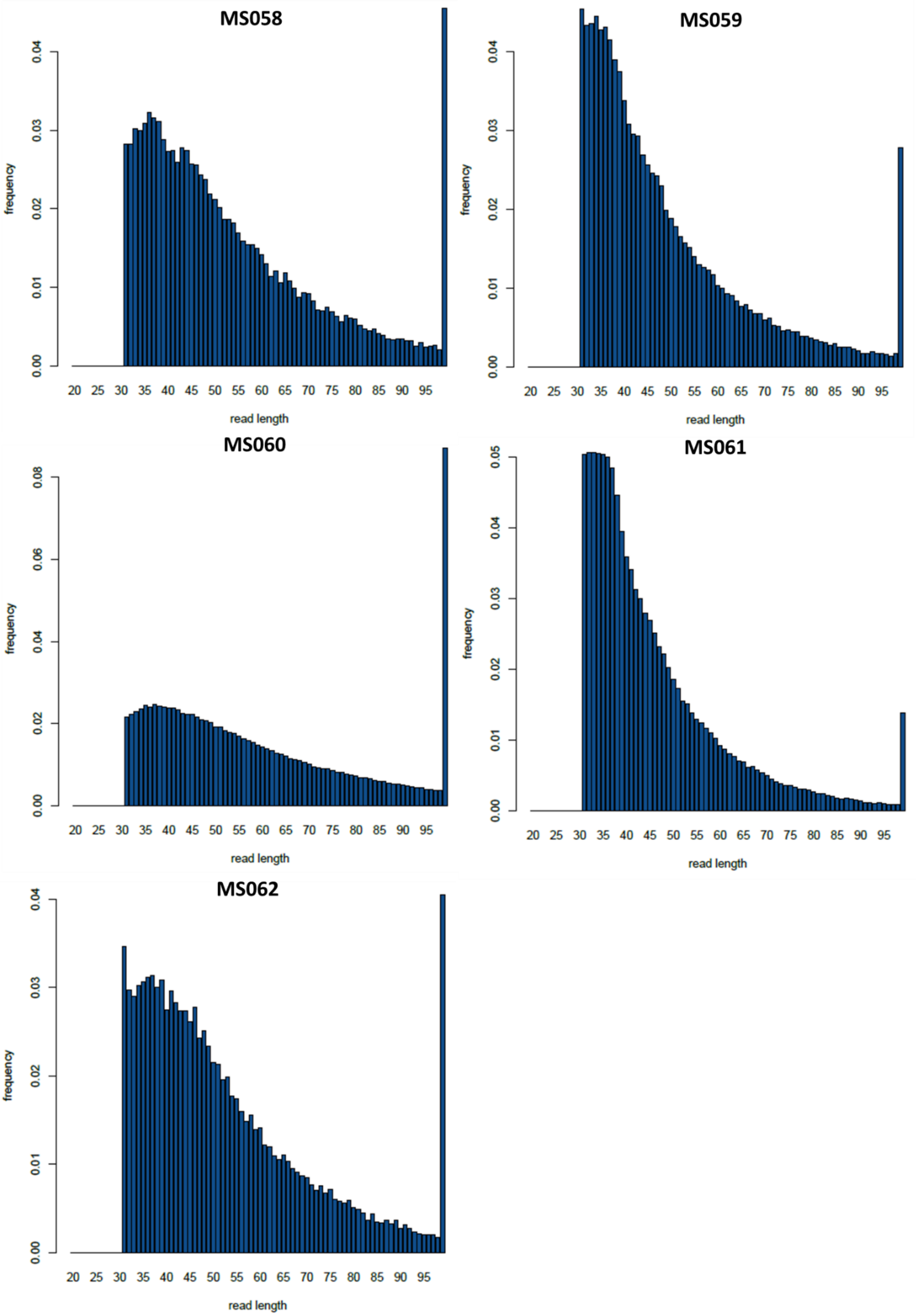


Figure S4. Read length distribution of libraries sent for screening. Plots from bamdamage

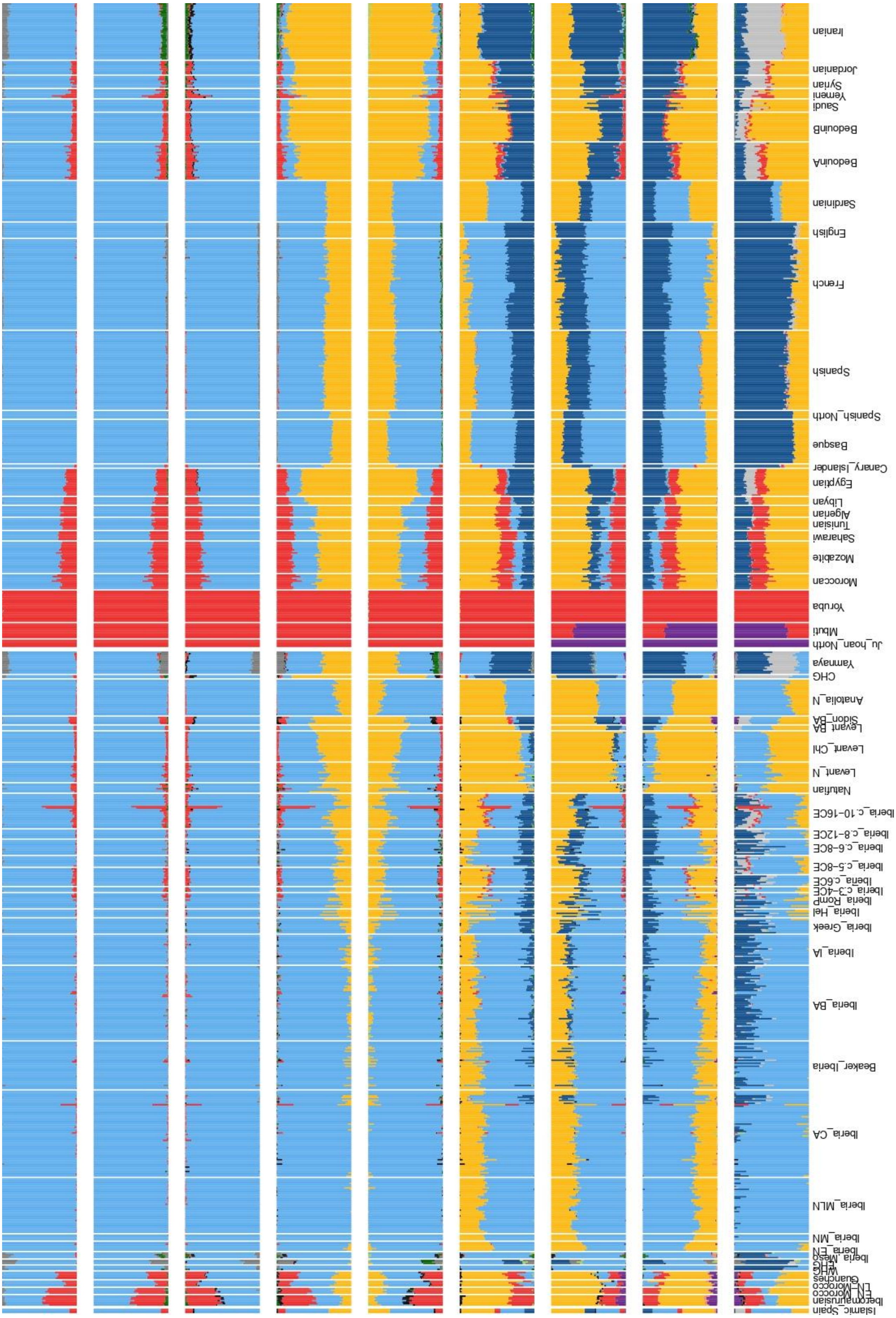

Islamic_Spain
Iberomaurusian
EN_Morocco
LN_Morocco
Guanches
WHG
EHG
Iberia_Meso
Iberia_EN
Iberia_MN
Iberia_MLN
Iberia_CA
Beaker_Iberia
Iberia_BA
Iberia_IA
Iberia_Greek
Iberia_Hel
Iberia_RomP
Iberia_c.3–4CE
Iberia_c.6CE
Iberia_c.5–8CE
Iberia_c.6–8CE
Iberia_c.8–12CE
Iberia_c.10–16CE
Natufian
Levant_N
Levant_Chl
Levant_BA
Sidon_BA
Anatolia_N
CHG
Yamnaya
Ju_hoan_North
Mbuti
Yoruba
Moroccan
Mozabite
Saharawi
Tunisian
Algerian
Libyan
Egyptian
Canary_Islander
Basque
Spanish_North
Spanish
French
English
Sardinian
BedouinA
BedouinB
Saudi
Yemeni
Syrian
Jordanian
Iranian

Figure S5. ADMIXTURE plot from *K*=2 to *K*=10 showing all ancient populations included in the analysis and a selection of modern African, European and Near Eastern populations. EHG, WHG and CHG refer to East, West and Caucasus hunter-gatherers, respectively. N (EN/MN/LN), CA/Chl, BA, IA, Hel. and RomP. stand for Neolithic (Early, Middle, Late), Chalcolithic, Bronze Age, Iron Age, Hellenistic and Roman Period, respectively.

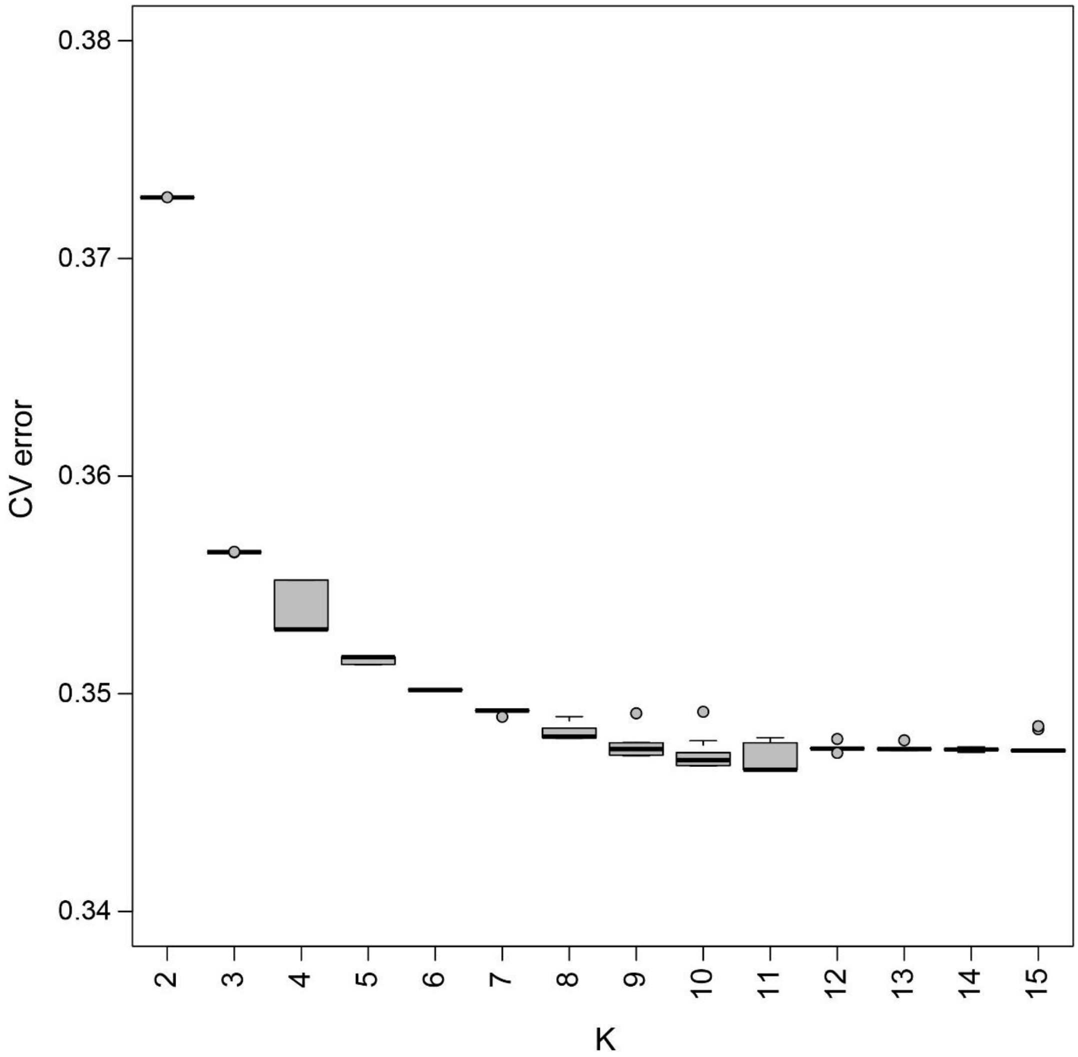


Figure S6. CV-error plot for 10 independent ADMIXTURE runs (from *K*=2 to *K*=15).

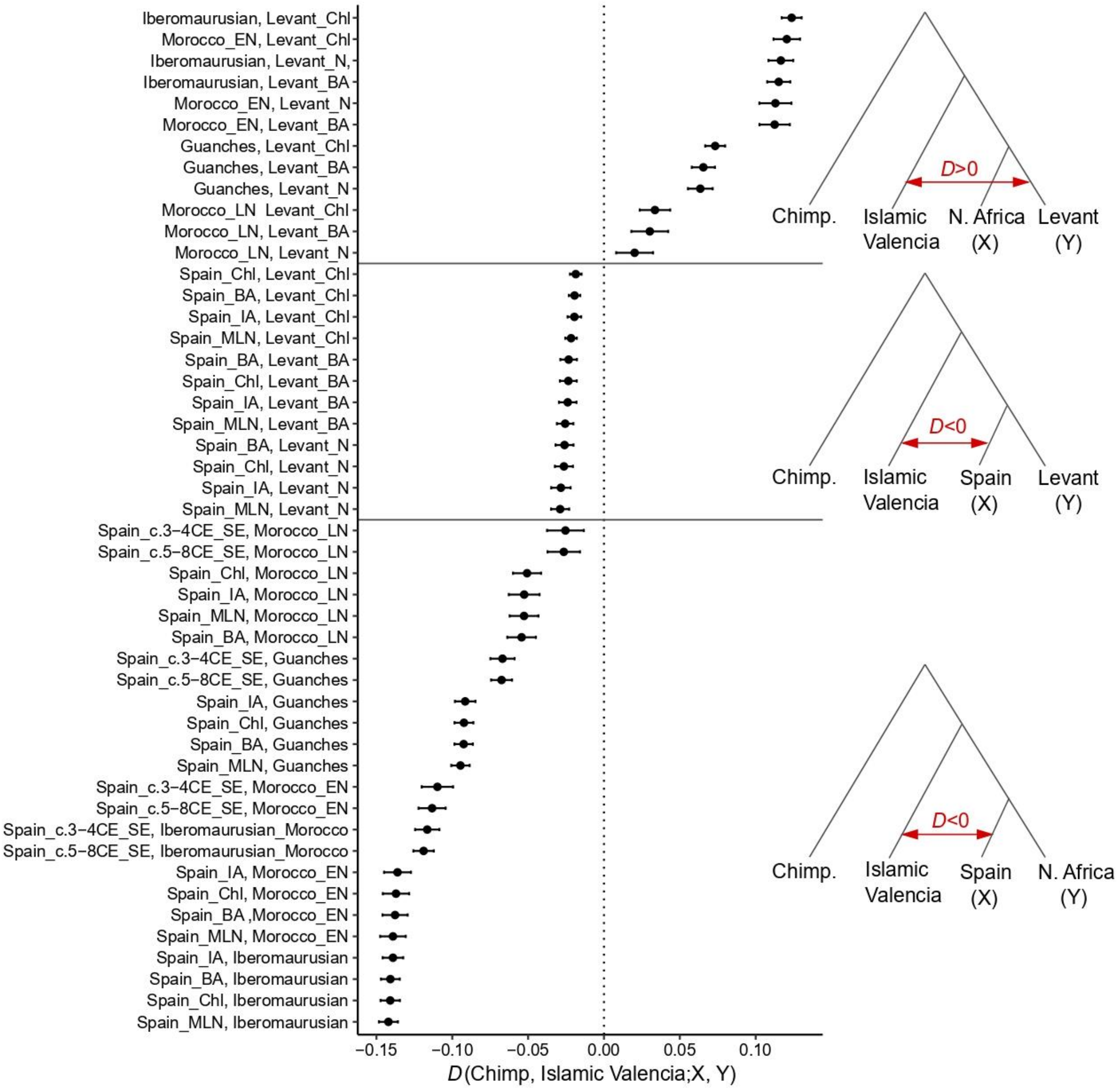


Figure S7. *D*-statistics in the form *D*(Chimp, Islamic Valencia; X, Y), in which X and Y are different Spanish, North African and Levantine ancient populations (only significant tests supported by |Z|>3 are shown). Error bars correspond to 2 standard errors. Detailed output of all testes can be found in Table S7.

Table S1. Dataset of samples used for GW analysis. Ancient samples underlined. C/E/WHG, Meso, (E/M/L)N, CA/Chl, BB, BA, IA, Hel. And RomP. stand for Caucasus/Eastern/Western hunter-gatherers Meso, (E/M/L)N , CA/Chl, BA, IA, Hel. And RomP. stand for Mesolithic, (Early/Middle/Late) Neolithic, Copper Age/Chalcolithic, Bronze Age, Iron Age, Helenistic and Roman Period, respectively.

Sample	Population label	Reference
MS060	Segorbe Giant	This study
TAF010	Iberomaurusian_Morocco	van de Loosdrecht et al. (2018)
TAF013	Iberomaurusian_Morocco	van de Loosdrecht et al. (2018)
TAF009	Iberomaurusian_Morocco	van de Loosdrecht et al. (2018)
TAF012	Iberomaurusian_Morocco	van de Loosdrecht et al. (2018)
TAF011	Iberomaurusian_Morocco	van de Loosdrecht et al. (2018)
TAF014	Iberomaurusian_Morocco	van de Loosdrecht et al. (2018)
TAF015	Iberomaurusian_Morocco	van de Loosdrecht et al. (2018)
IAM.5	EN_Morocco	Fregel et al. (2018)
IAM.7	EN_Morocco	Fregel et al. (2018)
IAM.6	EN_Morocco	Fregel et al. (2018)
IAM.4	EN_Morocco	Fregel et al. (2018)
KEB.6	LN_Morocco	Fregel et al. (2018)
KEB.1	LN_Morocco	Fregel et al. (2018)
KEB.8	LN_Morocco	Fregel et al. (2018)
KEB.4	LN_Morocco	Fregel et al. (2018)
gun012	Guanches	Rodríguez-Varela et al. (2017)
gun002	Guanches	Rodríguez-Varela et al. (2017)
gun008	Guanches	Rodríguez-Varela et al. (2017)
gun005	Guanches	Rodríguez-Varela et al. (2017)
gun011	Guanches	Rodríguez-Varela et al. (2017)
I0211	EHG	Mathieson et al. (2015)
I0061	EHG	Mathieson et al. (2015)
I0124	EHG	Mathieson et al. (2015)
I0585	WHG	Mathieson et al. (2015)
I1507	WHG	Mathieson et al. (2015)
Loschbour	WHG	Lazaridis et al. (2014)
I0409	Iberia_EN	Mathieson et al. (2015)
I0412	Iberia_EN	Mathieson et al. (2015)
CB13	Iberia_EN	Olalde et al. (2015)
I0410	Iberia_EN	Mathieson et al. (2015)
I0413	Iberia_EN	Mathieson et al. (2015)
I0405	Iberia_MN	Mathieson et al. (2015)
I0407	Iberia_MN	Mathieson et al. (2015)
I0408	Iberia_MN	Mathieson et al. (2015)
I0406	Iberia_MN	Mathieson et al. (2015)
I6630	Iberia_CA	Olalde et al. (2018)
I6613	Iberia_CA	Olalde et al. (2018)
I6612	Iberia_CA	Olalde et al. (2018)
I6628	Iberia_CA	Olalde et al. (2018)
I6596	Iberia_CA	Olalde et al. (2018)
I6543	Iberia_CA	Olalde et al. (2018)
I6605	Iberia_CA	Olalde et al. (2018)
I6604	Iberia_CA	Olalde et al. (2018)
I6608	Iberia_CA	Olalde et al. (2018)
I6609	Iberia_CA	Olalde et al. (2018)
I6629	Iberia_CA	Olalde et al. (2018)
I6617	Iberia_CA	Olalde et al. (2018)
I0453	Iberia_CA	Olalde et al. (2018)
I0457	Iberia_CA	Olalde et al. (2018)
I0456	Iberia_CA	Olalde et al. (2018)
I0455	Iberia_CA	Olalde et al. (2018)
I6601	Iberia_CA	Olalde et al. (2018)
I6584	Beaker_Iberia	Olalde et al. (2018)
I6622	Beaker_Iberia	Olalde et al. (2018)
I0840	Beaker_Iberia	Olalde et al. (2018)
I0823	Beaker_Iberia	Olalde et al. (2018)
I1553	Beaker_Iberia	Olalde et al. (2018)
I0460	Beaker_Iberia	Olalde et al. (2018)
I0462	Beaker_Iberia	Olalde et al. (2018)
I0263	Beaker_Iberia	Olalde et al. (2018)
I6588	Beaker_Iberia	Olalde et al. (2018)
I0459	Beaker_Iberia	Olalde et al. (2018)
I6587	Beaker_Iberia	Olalde et al. (2018)
I0260	Beaker_Iberia	Olalde et al. (2018)
I6539	Beaker_Iberia	Olalde et al. (2018)
I0258	Beaker_Iberia	Olalde et al. (2018)
I0461	Beaker_Iberia	Olalde et al. (2018)
I1970	Beaker_Iberia	Olalde et al. (2018)
I6475	Beaker_Iberia	Olalde et al. (2018)

I6542	Beaker_Iberia	Olalde et al. (2018)
I4245	Beaker_Iberia	Olalde et al. (2018)
I0262	Beaker_Iberia	Olalde et al. (2018)
I6471	Beaker_Iberia	Olalde et al. (2018)
I0825	Beaker_Iberia	Olalde et al. (2018)
I0826	Beaker_Iberia	Olalde et al. (2018)
I0839	Beaker_Iberia	Olalde et al. (2018)
I5665	Beaker_Iberia	Olalde et al. (2018)
I6623	Beaker_Iberia	Olalde et al. (2018)
I0261	Beaker_Iberia	Olalde et al. (2018)
I4229	Beaker_Iberia	Olalde et al. (2018)
I0257	Beaker_Iberia	Olalde et al. (2018)
I6467	Beaker_Iberia	Olalde et al. (2018)
I6472	Beaker_Iberia	Olalde et al. (2018)
I4247	Beaker_Iberia	Olalde et al. (2018)
I1690	Natufian	Lazaridis et al. (2016)
I1687	Natufian	Lazaridis et al. (2016)
I1072	Natufian	Lazaridis et al. (2016)
I0861	Natufian	Lazaridis et al. (2016)
I1685	Natufian	Lazaridis et al. (2016)
I1069	Natufian	Lazaridis et al. (2016)
I1699	Levant_N	Lazaridis et al. (2016)
I1415	Levant_N	Lazaridis et al. (2016)
I1416	Levant_N	Lazaridis et al. (2016)
I1701	Levant_N	Lazaridis et al. (2016)
I1727	Levant_N	Lazaridis et al. (2016)
I1414	Levant_N	Lazaridis et al. (2016)
I0867	Levant_N	Lazaridis et al. (2016)
I1700	Levant_N	Lazaridis et al. (2016)
I1710	Levant_N	Lazaridis et al. (2016)
I1709	Levant_N	Lazaridis et al. (2016)
I1707	Levant_N	Lazaridis et al. (2016)
I1679	Levant_N	Lazaridis et al. (2016)
I1704	Levant_N	Lazaridis et al. (2016)
I1184	Levant_Chl	Harney et al. (2018)
I1154	Levant_Chl	Harney et al. (2018)
I1152	Levant_Chl	Harney et al. (2018)
I0644	Levant_Chl	Harney et al. (2018)
I1177	Levant_Chl	Harney et al. (2018)
I1170	Levant_Chl	Harney et al. (2018)
I1164	Levant_Chl	Harney et al. (2018)
I1155	Levant_Chl	Harney et al. (2018)
I1182	Levant_Chl	Harney et al. (2018)
I1171	Levant_Chl	Harney et al. (2018)
I1168	Levant_Chl	Harney et al. (2018)
I1181	Levant_Chl	Harney et al. (2018)
I1183_d	Levant_Chl	Harney et al. (2018)
I1169	Levant_Chl	Harney et al. (2018)
I1178	Levant_Chl	Harney et al. (2018)
I1179	Levant_Chl	Harney et al. (2018)
I1160	Levant_Chl	Harney et al. (2018)
I1187	Levant_Chl	Harney et al. (2018)
I1172	Levant_Chl	Harney et al. (2018)
I1165	Levant_Chl	Harney et al. (2018)
I1705	Levant_BA	Lazaridis et al. (2016)
I1706	Levant_BA	Lazaridis et al. (2016)
I1730	Levant_BA	Lazaridis et al. (2016)
ERS1790729	Sidon_BA	Haber et al. (2017)
ERS1790730	Sidon_BA	Haber et al. (2017)
ERS1790733	Sidon_BA	Haber et al. (2017)
ERS1790732	Sidon_BA	Haber et al. (2017)
ERS1790731	Sidon_BA	Haber et al. (2017)
I1579	Anatolia_N	Mathieson et al. (2015)
I1581	Anatolia_N	Mathieson et al. (2015)
I0744	Anatolia_N	Mathieson et al. (2015)
I0727	Anatolia_N	Mathieson et al. (2015)
I0723	Anatolia_N	Mathieson et al. (2015)
I1580	Anatolia_N	Mathieson et al. (2015)
I1097	Anatolia_N	Mathieson et al. (2015)
I1101	Anatolia_N	Mathieson et al. (2015)
I1100	Anatolia_N	Mathieson et al. (2015)
I1585	Anatolia_N	Mathieson et al. (2015)
I1096	Anatolia_N	Mathieson et al. (2015)
I0736	Anatolia_N	Mathieson et al. (2015)
I0724	Anatolia_N	Mathieson et al. (2015)
I1583	Anatolia_N	Mathieson et al. (2015)
I0708	Anatolia_N	Mathieson et al. (2015)
I1098	Anatolia_N	Mathieson et al. (2015)
I1103	Anatolia_N	Mathieson et al. (2015)
I0709	Anatolia_N	Mathieson et al. (2015)
I1099	Anatolia_N	Mathieson et al. (2015)
I1102	Anatolia_N	Mathieson et al. (2015)

I0726	Anatolia_N	Mathieson et al. (2015)
I0745	Anatolia_N	Mathieson et al. (2015)
I0707	Anatolia_N	Mathieson et al. (2015)
I0746	Anatolia_N	Mathieson et al. (2015)
KK1	CHG	Jones et al. (2015)
SATP	CHG	Jones et al. (2015)
I0443	Yamnaya	Mathieson et al. (2015)
I0370	Yamnaya	Mathieson et al. (2015)
RISE550	Yamnaya	Allentoft et al. (2015)
RISE548	Yamnaya	Allentoft et al. (2015)
I0429	Yamnaya	Mathieson et al. (2015)
I0441	Yamnaya	Mathieson et al. (2015)
RISE552	Yamnaya	Allentoft et al. (2015)
RISE547	Yamnaya	Allentoft et al. (2015)
RISE546	Yamnaya	Allentoft et al. (2015)
I0357	Yamnaya	Mathieson et al. (2015)
I0439	Yamnaya	Mathieson et al. (2015)
I0444	Yamnaya	Mathieson et al. (2015)
I0438	Yamnaya	Mathieson et al. (2015)
I0231	Yamnaya	Mathieson et al. (2015)
RISE240	Yamnaya	Allentoft et al. (2015)
CabecoArruda117B	Portugal_LN-Chl	Martiniano et al. (2017)
CabecoArruda122A	Portugal_LN-Chl	Martiniano et al. (2017)
CovaMoura364	Portugal_LN-Chl	Martiniano et al. (2017)
CovaMoura9B	Portugal_LN-Chl	Martiniano et al. (2017)
DolmenAnsiao96B	Portugal_LN-Chl	Martiniano et al. (2017)
MonteCanelas337A	Portugal_LN-Chl	Martiniano et al. (2017)
LugarCanto41	Portugal_MN	Martiniano et al. (2017)
LugarCanto42	Portugal_MN	Martiniano et al. (2017)
LugarCanto44	Portugal_MN	Martiniano et al. (2017)
LugarCanto45	Portugal_MN	Martiniano et al. (2017)
MonteGato104	Portugal_MBA	Martiniano et al. (2017)
ValeOuro10207	Portugal_MBA	Martiniano et al. (2017)
TV32032	Portugal_MBA	Martiniano et al. (2017)
TV3831	Portugal_MBA	Martiniano et al. (2017)
I0843	Spain_Meso	Olalde et al. (2019)
I10277	Spain_MLN	Olalde et al. (2019)
I10278	Spain_MLN	Olalde et al. (2019)
I10280	Spain_MLN	Olalde et al. (2019)
I10283	Spain_MLN	Olalde et al. (2019)
I10285	Spain_MLN	Olalde et al. (2019)
I10287	Spain_MLN	Olalde et al. (2019)
I10851	Spain_c.8-12CE	Olalde et al. (2019)
I10852	Spain_c.8-12CE	Olalde et al. (2019)
I10853	Spain_c.8-12CE	Olalde et al. (2019)
I10865	Spain_RomP	Olalde et al. (2019)
I10866	Spain_RomP	Olalde et al. (2019)
I10892	Spain_c.8-12CE	Olalde et al. (2019)
I10895	Spain_c.8-12CE	Olalde et al. (2019)
I10897	Spain_c.8-12CE	Olalde et al. (2019)
I10899	Spain_Meso	Olalde et al. (2019)
I10939	Gibraltar_BA	Olalde et al. (2019)
I10940	Gibraltar_BA	Olalde et al. (2019)
I10941	Gibraltar_BA	Olalde et al. (2019)
I10942	Gibraltar_EN	Olalde et al. (2019)
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I11306	Spain_MLN	Olalde et al. (2019)
I12030	Spain_c.6CE	Olalde et al. (2019)
I12031	Spain_c.6CE	Olalde et al. (2019)
I12032	Spain_c.6CE	Olalde et al. (2019)
I12033	Spain_c.6CE	Olalde et al. (2019)
I12034	Spain_c.6CE	Olalde et al. (2019)
I12162	Spain_c.6CE	Olalde et al. (2019)
I12163	Spain_c.6CE	Olalde et al. (2019)
I12208	Spain_BA	Olalde et al. (2019)
I12209	Spain_BA	Olalde et al. (2019)
I12410	Spain_IA	Olalde et al. (2019)
I12515	Spain_c.10-16CE	Olalde et al. (2019)
I12516	Spain_c.10-16CE	Olalde et al. (2019)
I12640	Spain_IA	Olalde et al. (2019)
I12641	Spain_IA	Olalde et al. (2019)
I12642	Spain_IA	Olalde et al. (2019)
I12644	Spain_c.10-16CE	Olalde et al. (2019)
I12645	Spain_c.10-16CE	Olalde et al. (2019)
I12647	Spain_c.10-16CE	Olalde et al. (2019)
I12648	Spain_c.10-16CE	Olalde et al. (2019)

I12649	Spain_c.10-16CE	Olalde et al. (2019)
I12809	Spain_BA	Olalde et al. (2019)
I12877	Spain_IA	Olalde et al. (2019)
I12878	Spain_IA	Olalde et al. (2019)
I12879	Spain_IA	Olalde et al. (2019)
I1310	Spain_BA	Olalde et al. (2019)
I1836	Spain_BA	Olalde et al. (2019)
I1840	Spain_BA	Olalde et al. (2019)
I1842	Spain_Chl	Olalde et al. (2019)
I1845	Spain_Chl	Olalde et al. (2019)
I1846	Spain_Chl	Olalde et al. (2019)
I1977	Spain_BA	Olalde et al. (2019)
I1978	Spain_Chl	Olalde et al. (2019)
I1982	Spain_BA	Olalde et al. (2019)
I2469	Spain_BA	Olalde et al. (2019)
I2470	Spain_BA	Olalde et al. (2019)
I2471	Spain_BA	Olalde et al. (2019)
I2472	Spain_BA	Olalde et al. (2019)
I3209	Spain_Meso	Olalde et al. (2019)
I3214	Spain_MLN	Olalde et al. (2019)
I3238	Spain_Chl	Olalde et al. (2019)
I3239	Spain_Chl	Olalde et al. (2019)
I3243	Spain_Chl	Olalde et al. (2019)
I3320	Spain_IA	Olalde et al. (2019)
I3321	Spain_IA	Olalde et al. (2019)
I3322	Spain_IA	Olalde et al. (2019)
I3323	Spain_IA	Olalde et al. (2019)
I3324	Spain_IA	Olalde et al. (2019)
I3326	Spain_IA	Olalde et al. (2019)
I3327	Spain_IA	Olalde et al. (2019)
I3432	Portugal_Chl	Olalde et al. (2019)
I3484	Spain_Chl	Olalde et al. (2019)
I3485	Spain_Chl	Olalde et al. (2019)
I3486	Spain_BA	Olalde et al. (2019)
I3487	Spain_BA	Olalde et al. (2019)
I3488	Spain_BA	Olalde et al. (2019)
I3490	Spain_BA	Olalde et al. (2019)
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I3492	Spain_BA	Olalde et al. (2019)
I3493	Spain_BA	Olalde et al. (2019)
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VAD001	Spain_BA	Olalde et al. (2019)
VAD002	Spain_BA	Olalde et al. (2019)
VAD003	Spain_BA	Olalde et al. (2019)
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EHU001	Spain_Chl	Olalde et al. (2019)
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MCA24	Moroccan	Lazaridis et al. (2016)
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SAH21	Saharawi	Lazaridis et al. (2016)
SAH27	Saharawi	Lazaridis et al. (2016)
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Tunisian20D1	Tunisian	Lazaridis et al. (2016)
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Tunisian20C1	Tunisian	Lazaridis et al. (2016)
Tunisian20A5	Tunisian	Lazaridis et al. (2016)
Tunisian20B4	Tunisian	Lazaridis et al. (2016)
Tunisian200000	Tunisian	Lazaridis et al. (2016)
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Egypt3AQ172	Egyptian	Lazaridis et al. (2016)
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Egypt11	Egyptian	Lazaridis et al. (2016)
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Egypt9AQ172	Egyptian	Lazaridis et al. (2016)
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Egypt12	Egyptian	Lazaridis et al. (2016)

Egypt8AT113	Egyptian	Lazaridis et al. (2016)
Egypt7AQ172	Egyptian	Lazaridis et al. (2016)
Egypt1	Egyptian	Lazaridis et al. (2016)
Egypt15AQ172	Egyptian	Lazaridis et al. (2016)
Egypt12AQ172	Egyptian	Lazaridis et al. (2016)
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HG00232	English	Lazaridis et al. (2016)
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NOR126	Norwegian	Lazaridis et al. (2016)
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NOR101	Norwegian	Lazaridis et al. (2016)
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NOR146	Norwegian	Lazaridis et al. (2016)
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HGDP01172	Italian_North	Lazaridis et al. (2016)
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HGDP01163	Italian_North	Lazaridis et al. (2016)
HGDP01161	Italian_North	Lazaridis et al. (2016)
HGDP01157	Italian_North	Lazaridis et al. (2016)
HGDP01174	Italian_North	Lazaridis et al. (2016)
HGDP01167	Italian_North	Lazaridis et al. (2016)
HGDP01151	Italian_North	Lazaridis et al. (2016)
HGDP01169	Italian_North	Lazaridis et al. (2016)
HGDP01153	Italian_North	Lazaridis et al. (2016)
HGDP01171	Italian_North	Lazaridis et al. (2016)
HGDP01152	Italian_North	Lazaridis et al. (2016)
HGDP01147	Italian_North	Lazaridis et al. (2016)
ITS5	Italian_South	Lazaridis et al. (2016)
ITS4	Italian_South	Lazaridis et al. (2016)
ITS7	Italian_South	Lazaridis et al. (2016)
BEL57	Italian_South	Lazaridis et al. (2016)
ITS2	Italian_South	Lazaridis et al. (2016)
SR44	Sicilian	Lazaridis et al. (2016)
TP25	Sicilian	Lazaridis et al. (2016)
SR48R	Sicilian	Lazaridis et al. (2016)
TP06	Sicilian	Lazaridis et al. (2016)
TP05	Sicilian	Lazaridis et al. (2016)
TP07	Sicilian	Lazaridis et al. (2016)
TP08	Sicilian	Lazaridis et al. (2016)
TP04	Sicilian	Lazaridis et al. (2016)
SR23	Sicilian	Lazaridis et al. (2016)
SR64	Sicilian	Lazaridis et al. (2016)
SR60	Sicilian	Lazaridis et al. (2016)
HGDP01066	Sardinian	Lazaridis et al. (2016)
HGDP01064	Sardinian	Lazaridis et al. (2016)
HGDP01074	Sardinian	Lazaridis et al. (2016)
HGDP01068	Sardinian	Lazaridis et al. (2016)
HGDP01065	Sardinian	Lazaridis et al. (2016)

HGDP00673	Sardinian	Lazaridis et al. (2016)
HGDP01075	Sardinian	Lazaridis et al. (2016)
HGDP01063	Sardinian	Lazaridis et al. (2016)
HGDP00671	Sardinian	Lazaridis et al. (2016)
HGDP01062	Sardinian	Lazaridis et al. (2016)
HGDP00666	Sardinian	Lazaridis et al. (2016)
HGDP01076	Sardinian	Lazaridis et al. (2016)
HGDP01072	Sardinian	Lazaridis et al. (2016)
HGDP00667	Sardinian	Lazaridis et al. (2016)
HGDP01071	Sardinian	Lazaridis et al. (2016)
HGDP00672	Sardinian	Lazaridis et al. (2016)
HGDP01077	Sardinian	Lazaridis et al. (2016)
HGDP00669	Sardinian	Lazaridis et al. (2016)
HGDP01079	Sardinian	Lazaridis et al. (2016)
HGDP00670	Sardinian	Lazaridis et al. (2016)
HGDP01067	Sardinian	Lazaridis et al. (2016)
HGDP01069	Sardinian	Lazaridis et al. (2016)
HGDP00668	Sardinian	Lazaridis et al. (2016)
HGDP01073	Sardinian	Lazaridis et al. (2016)
HGDP00674	Sardinian	Lazaridis et al. (2016)
HGDP01078	Sardinian	Lazaridis et al. (2016)
HGDP01070	Sardinian	Lazaridis et al. (2016)
Malta17AM91	Maltese	Lazaridis et al. (2016)
Malta7AM91	Maltese	Lazaridis et al. (2016)
Malta2AM91	Maltese	Lazaridis et al. (2016)
Malta16AM91	Maltese	Lazaridis et al. (2016)
Malta8AM91	Maltese	Lazaridis et al. (2016)
Malta15AM91	Maltese	Lazaridis et al. (2016)
Malta12AM91	Maltese	Lazaridis et al. (2016)
Malta4AM91	Maltese	Lazaridis et al. (2016)
CRO47	Croatian	Lazaridis et al. (2016)
CRO53	Croatian	Lazaridis et al. (2016)
CRO66	Croatian	Lazaridis et al. (2016)
CRO103	Croatian	Lazaridis et al. (2016)
CRO48	Croatian	Lazaridis et al. (2016)
CRO107	Croatian	Lazaridis et al. (2016)
CRO93	Croatian	Lazaridis et al. (2016)
CRO153	Croatian	Lazaridis et al. (2016)
CRO41	Croatian	Lazaridis et al. (2016)
CRO31	Croatian	Lazaridis et al. (2016)
ALB212	Albanian	Lazaridis et al. (2016)
ALB213	Albanian	Lazaridis et al. (2016)
ALB191	Albanian	Lazaridis et al. (2016)
ALB220	Albanian	Lazaridis et al. (2016)
ALB202	Albanian	Lazaridis et al. (2016)
ALB230	Albanian	Lazaridis et al. (2016)
NA17373	Greek	Lazaridis et al. (2016)
NA17377	Greek	Lazaridis et al. (2016)
GREEKGRALPOP16	Greek	Lazaridis et al. (2016)
GREEKGRALPOP14	Greek	Lazaridis et al. (2016)
GREEKGRALPOP4	Greek	Lazaridis et al. (2016)
GREEKGRALPOP5	Greek	Lazaridis et al. (2016)
GREEKGRALPOP11	Greek	Lazaridis et al. (2016)
GREEKGRALPOP13	Greek	Lazaridis et al. (2016)
NA17372	Greek	Lazaridis et al. (2016)
GREEKGRALPOP3	Greek	Lazaridis et al. (2016)
NA17376	Greek	Lazaridis et al. (2016)
GREEKGRALPOP8	Greek	Lazaridis et al. (2016)
NA17375	Greek	Lazaridis et al. (2016)
GREEKGRALPOP15	Greek	Lazaridis et al. (2016)
GREEKGRALPOP12	Greek	Lazaridis et al. (2016)
NA17374	Greek	Lazaridis et al. (2016)
GREEKGRALPOP10	Greek	Lazaridis et al. (2016)
GREEKGRALPOP17	Greek	Lazaridis et al. (2016)
GREEKGRALPOP18	Greek	Lazaridis et al. (2016)
GREEKGRALPOP9	Greek	Lazaridis et al. (2016)
Cyprus24AJ19	Cypriot	Lazaridis et al. (2016)
Cyprus22AJ19	Cypriot	Lazaridis et al. (2016)
Cyprus2AJ19	Cypriot	Lazaridis et al. (2016)
CYP19	Cypriot	Lazaridis et al. (2016)
CYP5	Cypriot	Lazaridis et al. (2016)
Cyprus21AJ19	Cypriot	Lazaridis et al. (2016)
Cyprus13AJ19	Cypriot	Lazaridis et al. (2016)
CYP2	Cypriot	Lazaridis et al. (2016)
Yemen2	Yemeni	Lazaridis et al. (2016)
Yemenese1529	Yemeni	Lazaridis et al. (2016)
Yemen9	Yemeni	Lazaridis et al. (2016)
Yemen10	Yemeni	Lazaridis et al. (2016)
Yemen3	Yemeni	Lazaridis et al. (2016)
Yemen5	Yemeni	Lazaridis et al. (2016)
HGDP00622	BedouinA	Lazaridis et al. (2016)
HGDP00619	BedouinA	Lazaridis et al. (2016)

HGDP00626	BedouinA	Lazaridis et al. (2016)
HGDP00620	BedouinA	Lazaridis et al. (2016)
HGDP00642	BedouinA	Lazaridis et al. (2016)
HGDP00614	BedouinA	Lazaridis et al. (2016)
HGDP00637	BedouinA	Lazaridis et al. (2016)
HGDP00625	BedouinA	Lazaridis et al. (2016)
HGDP00609	BedouinA	Lazaridis et al. (2016)
HGDP00613	BedouinA	Lazaridis et al. (2016)
HGDP00611	BedouinA	Lazaridis et al. (2016)
HGDP00615	BedouinA	Lazaridis et al. (2016)
HGDP00654	BedouinA	Lazaridis et al. (2016)
HGDP00628	BedouinA	Lazaridis et al. (2016)
HGDP00647	BedouinA	Lazaridis et al. (2016)
HGDP00638	BedouinA	Lazaridis et al. (2016)
HGDP00646	BedouinA	Lazaridis et al. (2016)
HGDP00635	BedouinA	Lazaridis et al. (2016)
HGDP00629	BedouinA	Lazaridis et al. (2016)
HGDP00632	BedouinA	Lazaridis et al. (2016)
HGDP00634	BedouinA	Lazaridis et al. (2016)
HGDP00645	BedouinA	Lazaridis et al. (2016)
HGDP00639	BedouinA	Lazaridis et al. (2016)
HGDP00640	BedouinA	Lazaridis et al. (2016)
HGDP00644	BedouinA	Lazaridis et al. (2016)
HGDP00610	BedouinB	Lazaridis et al. (2016)
HGDP00618	BedouinB	Lazaridis et al. (2016)
HGDP00649	BedouinB	Lazaridis et al. (2016)
HGDP00612	BedouinB	Lazaridis et al. (2016)
HGDP00616	BedouinB	Lazaridis et al. (2016)
HGDP00653	BedouinB	Lazaridis et al. (2016)
HGDP00701	BedouinB	Lazaridis et al. (2016)
HGDP00636	BedouinB	Lazaridis et al. (2016)
HGDP00623	BedouinB	Lazaridis et al. (2016)
HGDP00651	BedouinB	Lazaridis et al. (2016)
HGDP00648	BedouinB	Lazaridis et al. (2016)
HGDP00650	BedouinB	Lazaridis et al. (2016)
HGDP00643	BedouinB	Lazaridis et al. (2016)
HGDP00630	BedouinB	Lazaridis et al. (2016)
HGDP00608	BedouinB	Lazaridis et al. (2016)
HGDP00624	BedouinB	Lazaridis et al. (2016)
HGDP00607	BedouinB	Lazaridis et al. (2016)
HGDP00631	BedouinB	Lazaridis et al. (2016)
HGDP00641	BedouinB	Lazaridis et al. (2016)
Jordan214	Jordanian	Lazaridis et al. (2016)
Jordan543	Jordanian	Lazaridis et al. (2016)
Jordan646	Jordanian	Lazaridis et al. (2016)
Jordan503	Jordanian	Lazaridis et al. (2016)
Jordan62	Jordanian	Lazaridis et al. (2016)
Jordan445	Jordanian	Lazaridis et al. (2016)
Jordan603	Jordanian	Lazaridis et al. (2016)
Jordan307	Jordanian	Lazaridis et al. (2016)
Jordan384	Jordanian	Lazaridis et al. (2016)
Lebanon3	Lebanese	Lazaridis et al. (2016)
Lebanon7	Lebanese	Lazaridis et al. (2016)
Lebanon5	Lebanese	Lazaridis et al. (2016)
Lebanon1	Lebanese	Lazaridis et al. (2016)
Lebanon4	Lebanese	Lazaridis et al. (2016)
Lebanon6	Lebanese	Lazaridis et al. (2016)
Lebanon8	Lebanese	Lazaridis et al. (2016)
Lebanon2	Lebanese	Lazaridis et al. (2016)
Lebanese6AQ170	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese1AQ170	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese15AR37	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese1AQ127	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese6AQ115	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese10AR37	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese4AQ115	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese8AS15	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese22BA23	Lebanese_Christian	Lazaridis et al. (2016)
Lebanese7AR20	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese20AR21	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese30AR21	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese7AR23	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese11AS14	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese10AQ127	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese7AQ150	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese2AQ127	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese6AS15	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese24AR27	Lebanese_Muslim	Lazaridis et al. (2016)
Lebanese2AQ121	Lebanese_Muslim	Lazaridis et al. (2016)
HGDP00732	Palestinian	Lazaridis et al. (2016)
HGDP00726	Palestinian	Lazaridis et al. (2016)
HGDP00725	Palestinian	Lazaridis et al. (2016)

HGDP00736	Palestinian	Lazaridis et al. (2016)
HGDP00688	Palestinian	Lazaridis et al. (2016)
HGDP00722	Palestinian	Lazaridis et al. (2016)
HGDP00729	Palestinian	Lazaridis et al. (2016)
HGDP00731	Palestinian	Lazaridis et al. (2016)
HGDP00734	Palestinian	Lazaridis et al. (2016)
HGDP00687	Palestinian	Lazaridis et al. (2016)
HGDP00735	Palestinian	Lazaridis et al. (2016)
HGDP00683	Palestinian	Lazaridis et al. (2016)
HGDP00741	Palestinian	Lazaridis et al. (2016)
HGDP00700	Palestinian	Lazaridis et al. (2016)
HGDP00733	Palestinian	Lazaridis et al. (2016)
HGDP00745	Palestinian	Lazaridis et al. (2016)
HGDP00677	Palestinian	Lazaridis et al. (2016)
HGDP00727	Palestinian	Lazaridis et al. (2016)
HGDP00730	Palestinian	Lazaridis et al. (2016)
HGDP00740	Palestinian	Lazaridis et al. (2016)
HGDP00698	Palestinian	Lazaridis et al. (2016)
HGDP00675	Palestinian	Lazaridis et al. (2016)
HGDP00686	Palestinian	Lazaridis et al. (2016)
HGDP00724	Palestinian	Lazaridis et al. (2016)
HGDP00680	Palestinian	Lazaridis et al. (2016)
HGDP00689	Palestinian	Lazaridis et al. (2016)
HGDP00679	Palestinian	Lazaridis et al. (2016)
HGDP00684	Palestinian	Lazaridis et al. (2016)
HGDP00739	Palestinian	Lazaridis et al. (2016)
HGDP00676	Palestinian	Lazaridis et al. (2016)
HGDP00699	Palestinian	Lazaridis et al. (2016)
HGDP00685	Palestinian	Lazaridis et al. (2016)
HGDP00697	Palestinian	Lazaridis et al. (2016)
HGDP00690	Palestinian	Lazaridis et al. (2016)
HGDP00737	Palestinian	Lazaridis et al. (2016)
HGDP00696	Palestinian	Lazaridis et al. (2016)
HGDP00694	Palestinian	Lazaridis et al. (2016)
HGDP00691	Palestinian	Lazaridis et al. (2016)
SaudiA9	Saudi	Lazaridis et al. (2016)
saudi1424	Saudi	Lazaridis et al. (2016)
SaudiA5	Saudi	Lazaridis et al. (2016)
saudi1403	Saudi	Lazaridis et al. (2016)
SaudiA1	Saudi	Lazaridis et al. (2016)
SaudiA6	Saudi	Lazaridis et al. (2016)
saudi1434	Saudi	Lazaridis et al. (2016)
SaudiA7	Saudi	Lazaridis et al. (2016)
syria461	Syrian	Lazaridis et al. (2016)
syria4	Syrian	Lazaridis et al. (2016)
syria464	Syrian	Lazaridis et al. (2016)
syria361	Syrian	Lazaridis et al. (2016)
syria6	Syrian	Lazaridis et al. (2016)
syria520	Syrian	Lazaridis et al. (2016)
syria485	Syrian	Lazaridis et al. (2016)
syria7	Syrian	Lazaridis et al. (2016)
HGDP00575	Druze	Lazaridis et al. (2016)
HGDP00567	Druze	Lazaridis et al. (2016)
HGDP00566	Druze	Lazaridis et al. (2016)
HGDP00558	Druze	Lazaridis et al. (2016)
HGDP00557	Druze	Lazaridis et al. (2016)
HGDP00565	Druze	Lazaridis et al. (2016)
HGDP00579	Druze	Lazaridis et al. (2016)
HGDP00559	Druze	Lazaridis et al. (2016)
HGDP00560	Druze	Lazaridis et al. (2016)
HGDP00573	Druze	Lazaridis et al. (2016)
HGDP00562	Druze	Lazaridis et al. (2016)
HGDP00564	Druze	Lazaridis et al. (2016)
HGDP00580	Druze	Lazaridis et al. (2016)
HGDP00577	Druze	Lazaridis et al. (2016)
HGDP00568	Druze	Lazaridis et al. (2016)
HGDP00583	Druze	Lazaridis et al. (2016)
HGDP00572	Druze	Lazaridis et al. (2016)
HGDP00571	Druze	Lazaridis et al. (2016)
HGDP00586	Druze	Lazaridis et al. (2016)
HGDP00587	Druze	Lazaridis et al. (2016)
HGDP00582	Druze	Lazaridis et al. (2016)
HGDP00599	Druze	Lazaridis et al. (2016)
HGDP00574	Druze	Lazaridis et al. (2016)
HGDP00561	Druze	Lazaridis et al. (2016)
HGDP00569	Druze	Lazaridis et al. (2016)
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HGDP00578	Druze	Lazaridis et al. (2016)
HGDP00606	Druze	Lazaridis et al. (2016)
HGDP00563	Druze	Lazaridis et al. (2016)
HGDP00602	Druze	Lazaridis et al. (2016)
HGDP00600	Druze	Lazaridis et al. (2016)

HGDP00594	Druze	Lazaridis et al. (2016)
HGDP00588	Druze	Lazaridis et al. (2016)
HGDP00595	Druze	Lazaridis et al. (2016)
HGDP00604	Druze	Lazaridis et al. (2016)
HGDP00598	Druze	Lazaridis et al. (2016)
HGDP00601	Druze	Lazaridis et al. (2016)
HGDP00597	Druze	Lazaridis et al. (2016)
HGDP00591	Druze	Lazaridis et al. (2016)
PV014	Iranian	Lazaridis et al. (2016)
PV033	Iranian	Lazaridis et al. (2016)
iran11	Iranian	Lazaridis et al. (2016)
iran14	Iranian	Lazaridis et al. (2016)
iran19	Iranian	Lazaridis et al. (2016)
iran20	Iranian	Lazaridis et al. (2016)
PV019	Iranian	Lazaridis et al. (2016)
PV015	Iranian	Lazaridis et al. (2016)
PV031	Iranian	Lazaridis et al. (2016)
PV027	Iranian	Lazaridis et al. (2016)
PV032	Iranian	Lazaridis et al. (2016)
PV028	Iranian	Lazaridis et al. (2016)
PV020	Iranian	Lazaridis et al. (2016)
PV013	Iranian	Lazaridis et al. (2016)
iran16	Iranian	Lazaridis et al. (2016)
PV016	Iranian	Lazaridis et al. (2016)
PV017	Iranian	Lazaridis et al. (2016)
PV030	Iranian	Lazaridis et al. (2016)
iran17	Iranian	Lazaridis et al. (2016)
PV018	Iranian	Lazaridis et al. (2016)
PV038	Iranian	Lazaridis et al. (2016)
PV009	Iranian	Lazaridis et al. (2016)
PV035	Iranian	Lazaridis et al. (2016)
PV012	Iranian	Lazaridis et al. (2016)
iran2	Iranian	Lazaridis et al. (2016)
PV025	Iranian	Lazaridis et al. (2016)
PV029	Iranian	Lazaridis et al. (2016)
PV011	Iranian	Lazaridis et al. (2016)
PV010	Iranian	Lazaridis et al. (2016)
PV022	Iranian	Lazaridis et al. (2016)
iran3	Iranian	Lazaridis et al. (2016)
PV037	Iranian	Lazaridis et al. (2016)
PV023	Iranian	Lazaridis et al. (2016)
PV024	Iranian	Lazaridis et al. (2016)
PV026	Iranian	Lazaridis et al. (2016)
PV034	Iranian	Lazaridis et al. (2016)
PV021	Iranian	Lazaridis et al. (2016)
PV036	Iranian	Lazaridis et al. (2016)
Adana23136	Turkish	Lazaridis et al. (2016)
Turkish4BA57	Turkish	Lazaridis et al. (2016)
Istanbul20040	Turkish	Lazaridis et al. (2016)
Istanbul15781	Turkish	Lazaridis et al. (2016)
Turkish7BA57	Turkish	Lazaridis et al. (2016)
Balikesir16837	Turkish	Lazaridis et al. (2016)
Balikesir16790	Turkish	Lazaridis et al. (2016)
Trabzon21174	Turkish	Lazaridis et al. (2016)
Aydin18873	Turkish	Lazaridis et al. (2016)
Balikesir16675	Turkish	Lazaridis et al. (2016)
Kayseri24032	Turkish	Lazaridis et al. (2016)
Istanbul19185	Turkish	Lazaridis et al. (2016)
Adana23133	Turkish	Lazaridis et al. (2016)
Adana23108	Turkish	Lazaridis et al. (2016)
Trabzon21177	Turkish	Lazaridis et al. (2016)
Aydin18636	Turkish	Lazaridis et al. (2016)
Trabzon21515	Turkish	Lazaridis et al. (2016)
Kayseri24392	Turkish	Lazaridis et al. (2016)
Aydin18784	Turkish	Lazaridis et al. (2016)
Trabzon21557	Turkish	Lazaridis et al. (2016)
Istanbul19810	Turkish	Lazaridis et al. (2016)
Trabzon21173	Turkish	Lazaridis et al. (2016)
Turkish9BA57	Turkish	Lazaridis et al. (2016)
Kayseri23892	Turkish	Lazaridis et al. (2016)
Kayseri24075	Turkish	Lazaridis et al. (2016)
Istanbul25098	Turkish	Lazaridis et al. (2016)
Istanbul20010	Turkish	Lazaridis et al. (2016)
Turkish8BA62	Turkish	Lazaridis et al. (2016)
Istanbul17778	Turkish	Lazaridis et al. (2016)
Balikesir17006	Turkish	Lazaridis et al. (2016)
Aydin18419	Turkish	Lazaridis et al. (2016)
Kayseri24276	Turkish	Lazaridis et al. (2016)
Kayseri23967	Turkish	Lazaridis et al. (2016)
Adana23150	Turkish	Lazaridis et al. (2016)
Balikesir16887	Turkish	Lazaridis et al. (2016)
Istanbul25095	Turkish	Lazaridis et al. (2016)

Kayseri24402	Turkish	Lazaridis et al. (2016)
Istanbul25081	Turkish	Lazaridis et al. (2016)
Adana23147	Turkish	Lazaridis et al. (2016)
Adana23117	Turkish	Lazaridis et al. (2016)
Adana23113	Turkish	Lazaridis et al. (2016)
Trabzon21575	Turkish	Lazaridis et al. (2016)
Istanbul19708	Turkish	Lazaridis et al. (2016)
Trabzon21534	Turkish	Lazaridis et al. (2016)
Trabzon21544	Turkish	Lazaridis et al. (2016)
Kayseri24266	Turkish	Lazaridis et al. (2016)
Adana23112	Turkish	Lazaridis et al. (2016)
Adana23114	Turkish	Lazaridis et al. (2016)
Balikesir16653	Turkish	Lazaridis et al. (2016)
Aydin18112	Turkish	Lazaridis et al. (2016)
Aydin18483	Turkish	Lazaridis et al. (2016)
Kayseri23549	Turkish	Lazaridis et al. (2016)
Kayseri23271	Turkish	Lazaridis et al. (2016)
Aydin18596	Turkish	Lazaridis et al. (2016)
Adana23144	Turkish	Lazaridis et al. (2016)
Trabzon21645	Turkish	Lazaridis et al. (2016)
Assyrian160	Assyrian	Lazaridis et al. (2016)
Assyrian161	Assyrian	Lazaridis et al. (2016)
Assyrian155	Assyrian	Lazaridis et al. (2016)
Assyrian159	Assyrian	Lazaridis et al. (2016)
Assyrian164	Assyrian	Lazaridis et al. (2016)
Assyrian165	Assyrian	Lazaridis et al. (2016)
Assyrian162	Assyrian	Lazaridis et al. (2016)
Assyrian163	Assyrian	Lazaridis et al. (2016)
Assyrian151	Assyrian	Lazaridis et al. (2016)
Assyrian152	Assyrian	Lazaridis et al. (2016)
Assyrian153	Assyrian	Lazaridis et al. (2016)
abh27	Abkhasian	Lazaridis et al. (2016)
abh133	Abkhasian	Lazaridis et al. (2016)
abh119	Abkhasian	Lazaridis et al. (2016)
abh24	Abkhasian	Lazaridis et al. (2016)
abh41	Abkhasian	Lazaridis et al. (2016)
abh107	Abkhasian	Lazaridis et al. (2016)
abh154	Abkhasian	Lazaridis et al. (2016)
abh122	Abkhasian	Lazaridis et al. (2016)
abh147	Abkhasian	Lazaridis et al. (2016)
HGDP01396	Adygei	Lazaridis et al. (2016)
HGDP01399	Adygei	Lazaridis et al. (2016)
HGDP01397	Adygei	Lazaridis et al. (2016)
HGDP01383	Adygei	Lazaridis et al. (2016)
HGDP01402	Adygei	Lazaridis et al. (2016)
HGDP01400	Adygei	Lazaridis et al. (2016)
HGDP01387	Adygei	Lazaridis et al. (2016)
HGDP01381	Adygei	Lazaridis et al. (2016)
HGDP01382	Adygei	Lazaridis et al. (2016)
HGDP01385	Adygei	Lazaridis et al. (2016)
HGDP01403	Adygei	Lazaridis et al. (2016)
HGDP01401	Adygei	Lazaridis et al. (2016)
HGDP01404	Adygei	Lazaridis et al. (2016)
HGDP01386	Adygei	Lazaridis et al. (2016)
NA13626	Adygei	Lazaridis et al. (2016)
HGDP01398	Adygei	Lazaridis et al. (2016)
armenia279	Armenian	Lazaridis et al. (2016)
armenia191	Armenian	Lazaridis et al. (2016)
armenia86	Armenian	Lazaridis et al. (2016)
armenia162	Armenian	Lazaridis et al. (2016)
armenia102	Armenian	Lazaridis et al. (2016)
armenia176	Armenian	Lazaridis et al. (2016)
armenia106	Armenian	Lazaridis et al. (2016)
armenia91	Armenian	Lazaridis et al. (2016)
armenia293	Armenian	Lazaridis et al. (2016)
armenia139	Armenian	Lazaridis et al. (2016)
bal45	Balkar	Lazaridis et al. (2016)
bal22	Balkar	Lazaridis et al. (2016)
bal42	Balkar	Lazaridis et al. (2016)
bal136	Balkar	Lazaridis et al. (2016)
bal41	Balkar	Lazaridis et al. (2016)
bal97	Balkar	Lazaridis et al. (2016)
bal102	Balkar	Lazaridis et al. (2016)
bal50	Balkar	Lazaridis et al. (2016)
bal124	Balkar	Lazaridis et al. (2016)
bal64	Balkar	Lazaridis et al. (2016)
ch193	Chechen	Lazaridis et al. (2016)
ch113	Chechen	Lazaridis et al. (2016)
ch16	Chechen	Lazaridis et al. (2016)
ch21	Chechen	Lazaridis et al. (2016)
ch31	Chechen	Lazaridis et al. (2016)
ch174	Chechen	Lazaridis et al. (2016)

ch179	Chechen	Lazaridis et al. (2016)
ch126	Chechen	Lazaridis et al. (2016)
ch3	Chechen	Lazaridis et al. (2016)
mg31	Georgian	Lazaridis et al. (2016)
mg43	Georgian	Lazaridis et al. (2016)
mg49	Georgian	Lazaridis et al. (2016)
mg27	Georgian	Lazaridis et al. (2016)
mg34	Georgian	Lazaridis et al. (2016)
mg47	Georgian	Lazaridis et al. (2016)
mg40	Georgian	Lazaridis et al. (2016)
mg23	Georgian	Lazaridis et al. (2016)
mg22	Georgian	Lazaridis et al. (2016)
mg62	Georgian	Lazaridis et al. (2016)
lez36	Lezgin	Lazaridis et al. (2016)
lez40	Lezgin	Lazaridis et al. (2016)
lez37	Lezgin	Lazaridis et al. (2016)
lez38	Lezgin	Lazaridis et al. (2016)
lez33	Lezgin	Lazaridis et al. (2016)
lez7	Lezgin	Lazaridis et al. (2016)
lez31	Lezgin	Lazaridis et al. (2016)
lez49	Lezgin	Lazaridis et al. (2016)
lez9	Lezgin	Lazaridis et al. (2016)
nogay25	Nogai	Lazaridis et al. (2016)
nogay35	Nogai	Lazaridis et al. (2016)
nogay46	Nogai	Lazaridis et al. (2016)
nogay24	Nogai	Lazaridis et al. (2016)
nogay33	Nogai	Lazaridis et al. (2016)
nogay42	Nogai	Lazaridis et al. (2016)
nogay34	Nogai	Lazaridis et al. (2016)
nogay44	Nogai	Lazaridis et al. (2016)
nogay45	Nogai	Lazaridis et al. (2016)
NorthOssetia11	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia2	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia9	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia12	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia19	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia17	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia8	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia3	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia14	North_Ossetian	Lazaridis et al. (2016)
NorthOssetia5	North_Ossetian	Lazaridis et al. (2016)

Table S2. List of mtDNA U6 sequences used to build the tree. Ancient samples underlined (not used for node age calculations). Newly reported samples in bold.

Sample	Region	Geography/ Population	Additional information	Reference
1113000357_S74	**Unknown**	**Germany**		**This study**
1113001079_S53	**Unknown**	**Germany**		**This study**
1113001817_S2	**Unknown**	**Germany**		**This study**
1113002343_S91	**Unknown**	**Germany**		**This study**
AF382008	North Africa	Morocco		Maca-Meyer et al. (2001)
ALP029	**Europe SE**	**Italy**		**This study**
ALP129	**Europe SE**	**Italy**		**This study**
ALP266	**Europe SE**	**Italy**		**This study**
AY275527	North Africa Berber	Morocco_Berber	Berber	Maca-Meyer et al. (2003)
AY275528	Canary / Madeira Islands	Spain	Canary Islands	Maca-Meyer et al. (2003)
AY275529	West/Central Africa	Senegal	Wolof	Maca-Meyer et al. (2003)
AY275530	Iberia	Spain	Galicia	Maca-Meyer et al. (2003)
AY275531	North Africa	Mauritania		Maca-Meyer et al. (2003)
AY275532	Iberia	Spain	Leon	Maca-Meyer et al. (2003)
AY275533	Canary / Madeira Islands	Spain	Canary Islands	Maca-Meyer et al. (2003)
AY275534	North Africa	Morocco		Maca-Meyer et al. (2003)
AY275535	North Africa	Mauritania		Maca-Meyer et al. (2003)
AY275536	North Africa Berber	Morocco_Berber	Berber	Maca-Meyer et al. (2003)
AY275537	Canary / Madeira Islands	Spain	Canary Islands	Maca-Meyer et al. (2003)
AY882416	Eastern Africa	Ethiopia		Achilli et al. (2005)
AY882417	Iberia	Spain		Achilli et al. (2005)
DQ523663	Europe SE	Italy	Sardinia	Fraumene et al. (2006)
DQ856317	Europe NE	Ukraine	Jewish	Family Tree
EF064317	North Africa	Morocco_Berber	Asni	Olivieri et al. (2006)
EF064318	Europe SE	Italy		Olivieri et al. (2006)
EF064319	Europe SE	Italy	Campania, Naples	Olivieri et al. (2006)
EF064320	Europe SE	Italy	Campania, Naples	Olivieri et al. (2006)
EF064321	North Africa	Algeria		Olivieri et al. (2006)
EF064322	Europe SE	Italy	Tuscany, Casentino	Olivieri et al. (2006)
EF064323	Eastern Africa	Ethiopia		Olivieri et al. (2006)
EF064324	West/Central Africa	Nigeria_Songhai	Songhai	Olivieri et al. (2006)
EF064325	North Africa Berber	Morocco_Berber	Asni	Olivieri et al. (2006)
EF064326	North Africa Berber	Morocco_Berber	Asni	Olivieri et al. (2006)
EF064327	Near East	Iraq		Olivieri et al. (2006)
EF064328	Europe SE	Italy	Marche	Olivieri et al. (2006)
EF064329	Europe SE	Italy	Tuscany, Murlo	Olivieri et al. (2006)
EF064330	North Africa	Nigeria		Olivieri et al. (2006)
EF064331	North Africa	Tunisia		Olivieri et al. (2006)
EF064332	Europe SE	Italy	Sicily	Olivieri et al. (2006)
EF064333	North Africa	Tunisia		Olivieri et al. (2006)
EF064334	North Africa Berber	Morocco_Berber	Berber, Asni	Olivieri et al. (2006)
EF064335	Europe SE	Italy	Sardinia	Olivieri et al. (2006)

EF064336	Europe SE	Italy	Campania, Naples	Olivieri et al. (2006)
EF064337	Europe SE	Italy	Puglia	Olivieri et al. (2006)
EF064338	Europe SE	Italy	Puglia grecanica	Olivieri et al. (2006)
EF064339	Europe NW	France		Olivieri et al. (2006)
EF064340	Unknown	Spain		Olivieri et al. (2006)
EF064341	Europe SE	Italy	Sicily, Trapani	Olivieri et al. (2006)
EF064342	North Africa Berber	Morocco_Berber	Berber, Asni	Olivieri et al. (2006)
EF064343	Eastern Africa	Ethiopia	Jewish	Olivieri et al. (2006)
EF064344	Europe SE	Italy	Campania, Naples	Olivieri et al. (2006)
ESP0091	**Iberia**	**Spain**	**Sevilla**	**This study**
ESP0173	**Iberia**	**Spain**	**Jaen**	**This study**
ESP0238	**Iberia**	**Spain**	**Salamanca**	**This study**
ESP0254	**Iberia**	**Spain**	**Murcia**	**This study**
ESP0281	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0351	**Iberia**	**Spain**	**Cordoba**	**This study**
ESP0536	**Iberia**	**Spain**	**Cadiz**	**This study**
ESP0584	**Iberia**	**Spain**	**Barcelona**	**This study**
ESP0716	**Iberia**	**Spain**	**Zaragoza**	**This study**
ESP0732	**Iberia**	**Spain**	**Malaga**	**This study**
ESP0749	**Iberia**	**Spain**	**Granada**	**This study**
ESP0919	**Iberia**	**Spain**	**Burgos**	**This study**
ESP0933	**Iberia**	**Spain**	**Almeria**	**This study**
ESP0965	**Iberia**	**Spain**	**Asturias**	**This study**
ESP0966	**Iberia**	**Spain**	**Sevilla**	**This study**
EU597562	North Africa Berber	Algeria_Mozabite		Hartmann et al. (2009)
FJ460538	North Africa	Tunisia		Costa et al. (2009)
FJ460539	North Africa	Tunisia		Costa et al. (2009)
FJ939330	Unknown	Unknown		Family Tree
FJ979865	Europe NW	France		Family Tree
gre-78	Europe SE	Greece		Batini et al. (2017)
GU366066	Unknown	Unknown		Family Tree
GU433197	Europe/USA/South America	Canada		Family Tree
GU967378	Europe/USA/South America	Canada	French origin	Family Tree
HG01628	Iberia	IBS	Iberian populations in Spain (IBS)	1000 Genome Project
HG02621	West/Central Africa	GWD		1000 Genome Project
HG02763	West/Central Africa	GWD		1000 Genome Project
HG02816	West/Central Africa	GWD		1000 Genome Project
HG02884	West/Central Africa	GWD		1000 Genome Project
HG03060	West/Central Africa	MSL		1000 Genome Project
HG03258	West/Central Africa	GWD		1000 Genome Project
HG03538	West/Central Africa	GWD		1000 Genome Project
HM641132	Europe NW	France	French	Family Tree
HM775494	Europe NW	France	French	Family Tree
HM775953	Iberia	Portugal	Almeirim	Family Tree
HM776585	Europe NW	Germany	German	Family Tree
HM804485	Europe NW	British Isles	England	Family Tree
HM804488	European ancestry	USA	french origine	Family Tree

HQ025914	Unknown	USA		Family Tree
HQ161773	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Family Tree
HQ286322	Europe NW	Sweden	Swedish	Family Tree
HQ287880	European ancestry	British Isles/France	Newfoundland (English, Irish, or French ancestries)	Pope et al. (2011)
HQ384209	Iberia	Iberia		Gómez-Carballa et al. (2011)
HQ585390	Unknown	USA		Family Tree
HQ592783	European ancestry	USA		Family Tree
HQ651676	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Pereira et al. (2010)
HQ651677	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Pereira et al. (2010)
HQ651678	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Pereira et al. (2010)
HQ651679	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Pereira et al. (2010)
HQ651680	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Pereira et al. (2010)
HQ651681	Iberia	Portugal		Pereira et al. (2010)
HQ651682	Iberia	Portugal		Pereira et al. (2010)
HQ651683	Iberia	Portugal		Pereira et al. (2010)
HQ651684	Iberia	Portugal		Pereira et al. (2010)
HQ651685	Iberia	Portugal		Pereira et al. (2010)
HQ651686	Iberia	Portugal		Pereira et al. (2010)
HQ651687	Iberia	Portugal		Pereira et al. (2010)
HQ651688	Iberia	Portugal		Pereira et al. (2010)
HQ651689	Iberia	Portugal		Pereira et al. (2010)
HQ651690	Iberia	Portugal		Pereira et al. (2010)
HQ651691	Iberia	Portugal		Pereira et al. (2010)
HQ651692	Iberia	Portugal		Pereira et al. (2010)
HQ651693	Iberia	Portugal		Pereira et al. (2010)
HQ651694	Iberia	Portugal		Pereira et al. (2010)
HQ651695	Iberia	Portugal		Pereira et al. (2010)
HQ651696	Iberia	Portugal		Pereira et al. (2010)
HQ651697	Iberia	Portugal		Pereira et al. (2010)
HQ651698	Iberia	Portugal		Pereira et al. (2010)
HQ651699	Iberia	Portugal		Pereira et al. (2010)
HQ651700	Iberia	Portugal		Pereira et al. (2010)
HQ651701	Iberia	Portugal		Pereira et al. (2010)
HQ651702	Iberia	Portugal		Pereira et al. (2010)
HQ651703	North Africa	Morocco		Pereira et al. (2010)
HQ651704	Near East	Turkey	Jewish	Pereira et al. (2010)
HQ651705	North Africa	Morocco	Jewish ancestry	Pereira et al. (2010)
HQ651706	Europe NW	Poland	Jewish	Pereira et al. (2010)
HQ651707	Europe NE	Russia	Jewish	Pereira et al. (2010)
HQ651708	North Africa	Morocco	Jewish ancestry	Pereira et al. (2010)
HQ651709	North Africa	Tunisia	Jewish ancestry	Pereira et al. (2010)
HQ651710	Eastern Africa	Ethiopia	Jewish	Pereira et al. (2010)
HQ651711	Near East	Palestine	Palestinian	Pereira et al. (2010)
HQ651712	Near East	Palestine	Palestinian	Pereira et al. (2010)
HQ651713	Europe NW	Bulgaria	Jewish	Pereira et al. (2010)

HQ651714	Europe NW	Bulgaria	Jewish	Pereira et al. (2010)
HQ843176	European ancestry	USA		Family Tree
HQ848079	Europe NW	British Isles	Enlgand, Jewish	Family Tree
hun-3	Europe NW	Hungary		Batini et al. (2017)
IRQ184	Near East	Iraq		Costa (2013)/ Hernández et al. (2015)
JF734845	Europe NW	British Isles	Ireland	Family Tree
JQ044807	West/Central Africa	Burkina Faso	Bisa	Barbieri et al. (2012)
JQ044946	West/Central Africa	Burkina Faso	Mossi	Barbieri et al. (2012)
JQ045003	West/Central Africa	Burkina Faso	Samo	Barbieri et al. (2012)
JQ045007	West/Central Africa	Burkina Faso	Samo	Barbieri et al. (2012)
JQ629405	North Africa	Tunisia		Family Tree
JQ702118	Unknown	Unknown		Behar et al. (2012)
JQ702612	Unknown	Unknown		Behar et al. (2012)
JQ702816	North Africa	Algeria		Behar et al. (2012)
JQ703902	Unknown	USA		Behar et al. (2012)
JQ704008	Iberia	Spain		Behar et al. (2012)
JQ704030	Unknown	Unknown		Behar et al. (2012)
JQ704099	European ancestry	USA	unknown European origin	Behar et al. (2012)
JQ704539	Europe NW	Netherlands		Behar et al. (2012)
JQ704749	Iberia	Portugal	Azores, S. Miguel	Behar et al. (2012)
JQ704800	Unknown	Unknown		Behar et al. (2012)
JQ704896	Unknown	Cuba		Behar et al. (2012)
JQ705277	Europe NW	Unknown		Behar et al. (2012)
JX120708	Iberia	Spain	Madrid	Secher et al. (2014)
JX120709	Iberia	Spain	Asturias	Secher et al. (2014)
JX120710	Iberia	Spain	Leon	Secher et al. (2014)
JX120711	Iberia	Spain	Malaga	Secher et al. (2014)
JX120712	Iberia	Spain	Sevilla	Secher et al. (2014)
JX120713	Eastern Africa	Ethiopia		Secher et al. (2014)
JX120714	Eastern Africa	Ethiopia		Secher et al. (2014)
JX120715	Eastern Africa	Ethiopia		Secher et al. (2014)
JX120716	Eastern Africa	Ethiopia		Secher et al. (2014)
JX120717	North Africa Berber	Morocco_Berber	Ifrane	Secher et al. (2014)
JX120718	West/Central Africa	Ghana		Secher et al. (2014)
JX120719	West/Central Africa	Ghana		Secher et al. (2014)
JX120720	Iberia	Spain	Galicia	Secher et al. (2014)
JX120722	West/Central Africa	Cameroon		Secher et al. (2014)
JX120723	West/Central Africa	Nigeria		Secher et al. (2014)
JX120724	North Africa	Morocco	Arab	Secher et al. (2014)
JX120725	Iberia	Spain	Asturias	Secher et al. (2014)
JX120726	North Africa	Morocco	Arab	Secher et al. (2014)
JX120727	North Africa	Algeria		Secher et al. (2014)
JX120728	European ancestry	Europe	unknown European origin	Secher et al. (2014)
JX120729	European ancestry	Europe	unknown European origin	Secher et al. (2014)
JX120730	Unknown	USA		Secher et al. (2014)
JX120731	North Africa	Algeria		Secher et al. (2014)
JX120732	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Secher et al. (2014)

JX120733	Iberia	Spain	Navarra	Secher et al. (2014)
JX120734	West/Central Africa	Ghana		Secher et al. (2014)
JX120735	North Africa Berber	Morocco_Berber	Berber	Secher et al. (2014)
JX120736	Near East	Oman		Secher et al. (2014)
JX120737	Near East	Saudi Arabia		Secher et al. (2014)
JX120738	Near East	Sudan		Secher et al. (2014)
JX120739	West/Central Africa	Chad	Lake Chad	Secher et al. (2014)
JX120740	Eastern Africa	Cameroon		Secher et al. (2014)
JX120741	North Africa Berber	Morocco_Berber	Berber	Secher et al. (2014)
JX120742	Iberia	Spain	Leon	Secher et al. (2014)
JX120743	North Africa Berber	Morocco_Berber	Ifrane, Berber	Secher et al. (2014)
JX120744	Iberia	Spain	Cordoba	Secher et al. (2014)
JX120745	Canary / Madeira Islands	Spain	Canary Islands	Secher et al. (2014)
JX120746	North Africa	Algeria		Secher et al. (2014)
JX120747	North Africa	Algeria		Secher et al. (2014)
JX120748	Unknown	USA		Family Tree
JX120749	European ancestry	USA	unknown European origin	Family Tree
JX120750	Europe NW	Germany	Jewish	Family Tree
JX120751	Iberia	Spain	Jaen	Family Tree
JX120752	Unknown	Mexico		Family Tree
JX120753	Europe NW	Poland		Family Tree
JX120754	Europe NW	France		Family Tree
JX120755	Canary / Madeira Islands	Spain	Canary Islands, Tenerife	Family Tree
JX120756	Europe SE	Italy	Sicily	Family Tree
JX120757	Unknown	Cuba	Havana	Family Tree
JX120758	Europe NW	France		Family Tree
JX120759	Europe NW	France		Family Tree
JX120760	Europe NW	British Isles		Family Tree
JX120761	European ancestry	USA	unknown European origin	Family Tree
JX120762	Europe NW	British Isles		Family Tree
JX120763	Canary / Madeira Islands	Spain	Canary Islands, Gran Canaria	Family Tree
JX120764	Iberia	Spain	Malaga	Family Tree
JX120765	European ancestry	USA	unknown European origin	Family Tree
JX120766	Europe NW	France		Family Tree
JX120767	Europe NW	France		Family Tree
JX120768	African origin	USA	unknown African origin	Family Tree
JX120769	African origin	USA	unknown African origin	Family Tree
JX120770	Europe SE	Italy		Family Tree
JX120771	Unknown	Canada		Family Tree
JX120772	Europe NE	Finland		Family Tree
JX120773	Unknown	Canada		Family Tree
JX120774	Europe NW	France		Family Tree
JX120775	Europe NW	Poland		Family Tree
JX120776	Eastern Africa	Ethiopia	Guna	Family Tree
JX153008	Europe SE	Italy		Raule et al. (2014)
JX153033	Europe SE	Italy		Raule et al. (2014)
JX153040	Europe SE	Italy		Raule et al. (2014)

JX153102	Europe SE	Italy		Raule et al. (2014)
JX297143	Iberia	Spain	Basque Country, northern Navarre	Cardoso et al. (2013)
KC152538	North Africa	Morocco		Pennarun et al. (2012)
KC152539	North Africa	Morocco		Pennarun et al. (2012)
KC152540	North Africa	Morocco		Pennarun et al. (2012)
KC152541	North Africa	Morocco		Pennarun et al. (2012)
KC152543	North Africa	Morocco		Pennarun et al. (2012)
KC152547	North Africa	Tunisia		Pennarun et al. (2012)
KC152548	North Africa	Tunisia		Pennarun et al. (2012)
KC152549	North Africa	Tunisia		Pennarun et al. (2012)
KC152550	North Africa	Tunisia		Pennarun et al. (2012)
KC152552	North Africa	Tunisia		Pennarun et al. (2012)
KC152553	North Africa	Tunisia		Pennarun et al. (2012)
KC152555	North Africa	Tunisia		Pennarun et al. (2012)
KC152558	North Africa	Tunisia		Pennarun et al. (2012)
KC152559	North Africa	Morocco		Pennarun et al. (2012)
KC152561	North Africa	Morocco		Pennarun et al. (2012)
KC152562	North Africa	Morocco		Pennarun et al. (2012)
KC152564	North Africa	Morocco		Pennarun et al. (2012)
KC152565	North Africa	Morocco		Pennarun et al. (2012)
KC152567	North Africa	Morocco		Pennarun et al. (2012)
KC152568	North Africa	Morocco		Pennarun et al. (2012)
KC152569	North Africa	Egypt		Pennarun et al. (2012)
KC152574	North Africa	Egypt		Pennarun et al. (2012)
KC152576	Eastern Africa	Ethiopia		Pennarun et al. (2012)
KC152577	Eastern Africa	Ethiopia		Pennarun et al. (2012)
KC152578	North Africa	Morocco		Pennarun et al. (2012)
KC152579	Europe SE	Italy	Sicily	Pennarun et al. (2012)
KC152580	Europe NW	Ukraine		Pennarun et al. (2012)
KC152581	Europe NW	France		Pennarun et al. (2012)
KC152584	West/Central Africa	Guinea-Bassau		Pennarun et al. (2012)
KC152585	West/Central Africa	Guinea-Bassau		Pennarun et al. (2012)
KC152589	Near East	Kuwait		Pennarun et al. (2012)
KC152590	South Caucasus	Armenia	Armenian	Pennarun et al. (2012)
KC152592	North Africa	Algeria		Pennarun et al. (2012)
KF055292	Unknown	Unknown		Collins et al. (2013)
KF161249	Europe NW	Denmark	Danish	Li et al. (2014)
KF161849	Europe NW	Denmark	Danish	Li et al. (2014)
KF451248	Near East	Palestinian		Lippold et al. 2014
KJ446071	Near East	Palestine	Palestinian	Zheng et al. 2014 unpublished
KJ446072	Near East	Palestine	Palestinian	Zheng et al. 2014 unpublished
KJ446073	North Africa Berber	Algeria_Mozabite	Mozabite	Zheng et al. 2014 unpublished
KJ446074	North Africa Berber	Algeria_Mozabite	Mozabite	Zheng et al. 2014 unpublished
KJ446075	North Africa Berber	Algeria_Mozabite	Mozabite	Zheng et al. 2014 unpublished
KJ446076	North Africa Berber	Algeria_Mozabite		Zheng et al. 2014 unpublished
KJ446077	North Africa Berber	Algeria_Mozabite	Mozabite	Zheng et al. 2014 unpublished

KJ446078	North Africa Berber	Algeria_Mozabite	Mozabite	Zheng et al. 2014 unpublished
KJ446079	North Africa Berber	Algeria_Mozabite	Mozabite	Zheng et al. 2014 unpublished
KM013404	Europe SE	Italy	Sicily	Family Tree
KM101832	European ancestry	USA	Caucasian	Just et al. (2015)
KM101973	European ancestry	USA	Caucasian	Just et al. (2015)
KT779171	Near East	Lebanon		Matisoo-Smith et al. (2016)
KT779184	Near East	Lebanon		Matisoo-Smith et al. (2016)
KT799679	Iberia	Spain	Zalamea La Real	Family Tree
KT819213	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819214	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819215	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819216	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819217	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819218	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819219	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819220	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819221	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819222	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819223	Iberia	Spain	Andalusia, Huelva	Hernández et al. (2015)
KT819232	Iberia	Spain	Andalusia, Granada	Hernández et al. (2015)
KT819233	Iberia	Spain	Andalusia, Granada	Hernández et al. (2015)
KT819234	Iberia	Spain	Andalusia, Granada	Hernández et al. (2015)
KT819235	Iberia	Spain	Andalusia, Granada	Hernández et al. (2015)
KT819236	Iberia	Spain	Andalusia, Granada	Hernández et al. (2015)
KT819243	North Africa Berber	Morocco_Berber	Berber, Asni	Hernández et al. (2015)
KT819250	North Africa Berber	Morocco_Berber	Berber, Bouhria	Hernández et al. (2015)
KT819265	North Africa Berber	Morocco_Berber	Berber, Figuig	Hernández et al. (2015)
KT819266	North Africa Berber	Morocco_Berber	Berber, Figuig	Hernández et al. (2015)
KY408742	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
KY409061	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
KY409633	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
KY409669	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
KY409857	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
KY410107	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
KY410139	Europe SE	Italy	Sardinia	Olivieri et al. (2017)
LBG00333	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBG00334	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBG00335	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBG00336	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBG00337	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBN00097	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBZ00055	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBZ00056	**North Africa Berber**	**Libya**	**Berber**	**This study**
LBZ00057	**North Africa Berber**	**Libya**	**Berber**	**This study**
NA19179	West/Central Africa	YRI		1000 Genome Project
NA19652	America	MXL		1000 Genome Project
NA20356	African American	ASW		1000 Genome Project

pal-4919	Near East	Palestine		Batini et al. (2017)
PALAO727	Near East	Palestine		Costa (2013)/ Hernández et al. (2015)
POR-89	**Iberia**	**Portugal**	**Porto**	**This study**
PT-03	**Iberia**	**Portugal**	**Beja**	**This study**
PT-05	**Canary / Madeira Islands**	**Portugal**	**Madeira Island**	**This study**
PT-17	**Iberia**	**Portugal**	**Setúbal**	**This study**
SICTR48	Europe SE	Italy	Sicily, Trapani	Costa (2013)/ Hernández et al. (2015)
SJSb4	Near East	Syria		Costa (2013)/ Hernández et al. (2015)
SJSb46	Near East	Syria		Costa (2013)/ Hernández et al. (2015)
gun012	Canary / Madeira Islands	Canary Islands	Tenerife, Guanche	Rodríguez-Varela et al. (2017)
gun001	Canary / Madeira Islands	Canary Islands	Tenerife, Guanche	Rodríguez-Varela et al. (2017)
gun013	Canary / Madeira Islands	Canary Islands	Tenerife, Guanche	Rodríguez-Varela et al. (2017)
gun014	Canary / Madeira Islands	Canary Islands	Tenerife, Guanche	Rodríguez-Varela et al. (2017)
TAF009	North Africa	Morocco	Taforalt, Iberomaurusian	van de Loosdrecht et al. (2018)
TAF010	North Africa	Morocco	Taforalt, Iberomaurusian	van de Loosdrecht et al. (2018)
TAF011	North Africa	Morocco	Taforalt, Iberomaurusian	van de Loosdrecht et al. (2018)
TAF012	North Africa	Morocco	Taforalt, Iberomaurusian	van de Loosdrecht et al. (2018)
TAF013	North Africa	Morocco	Taforalt, Iberomaurusian	van de Loosdrecht et al. (2018)
TAF015	North Africa	Morocco	Taforalt, Iberomaurusian	van de Loosdrecht et al. (2018)
IAM.4	North Africa	Morocco	Ifrin’Amro’Moussa, Early Neolithic	Fregel et al. (2018)
IAM.5	North Africa	Morocco	Ifrin’Amro’Moussa, Early Neolithic	Fregel et al. (2018)
IAM.6	North Africa	Morocco	Ifrin’Amro’Moussa, Early Neolithic	Fregel et al. (2018)
IAM.7	North Africa	Morocco	Ifrin’Amro’Moussa, Early Neolithic	Fregel et al. (2018)
PM1	Europe NE	Romania	Pestera Muierii, Early Upper Paleolithic	Hervella et al. (2016)
Muierii2	Europe NE	Romania	Pestera Muierii, Early Upper Paleolithic	Fu et al. (2016)
JK2888	North Africa	Egypt	Ptolemaic Period	Schuenemann et al. (2017)
JK2973	North Africa	Egypt		Schuenemann et al. (2017)
CAN.008	Canary / Madeira Islands	Canary Islands	Gran Canaria, indigenous population	Fregel et al. (2019)
CAN.013	Canary / Madeira Islands	Canary Islands	Gran Canaria, indigenous population	Fregel et al. (2019)
CAN.020	Canary / Madeira Islands	Canary Islands	Gran Canaria, indigenous population	Fregel et al. (2019)
CAN.027	Canary / Madeira Islands	Canary Islands	La Gomera, indigenous population	Fregel et al. (2019)
CAN.028	Canary / Madeira Islands	Canary Islands	La Gomera, indigenous population	Fregel et al. (2019)
CAN.029	Canary / Madeira Islands	Canary Islands	La Gomera, indigenous population	Fregel et al. (2019)
CAN.030	Canary / Madeira Islands	Canary Islands	La Gomera, indigenous population	Fregel et al. (2019)
CAN.038	Canary / Madeira Islands	Canary Islands	Lanzarote, indigenous population	Fregel et al. (2019)
CAN.046	Canary / Madeira Islands	Canary Islands	Tenerife, indigenous population	Fregel et al. (2019)
I3809	Iberia	Spain	Andalusia, Morisco, 1500–1600 CE	Olalde et al. (2019)
I3807	Iberia	Spain	Andalusia, Morisco, 1500–1600 CE	Olalde et al. (2019)
MS060/Segorbe Giant	**Iberia**	**Spain**	**Plaza del Almudin, Segorbe, 11th cent. CE**	**This Study**

Table S3. Outgroup-f3 output table, using Mbuti as outgroup. M, (E/M/L)N , Chl, BA and IA stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Iron Age, respectively.

Source1	**Source2**	**Target**	***f3***	**std.err.**	**Z**	**SNPs**
Anatolia_N	SegorbeGiant	Mbuti	0.374176	0.004703	79.568	59469
Spain_MLN	SegorbeGiant	Mbuti	0.372136	0.004773	77.968	56862
Spain_BA	SegorbeGiant	Mbuti	0.369345	0.004713	78.374	58178
Spain_Chl	SegorbeGiant	Mbuti	0.368219	0.004729	77.871	56592
Portugal_LN-Chl	SegorbeGiant	Mbuti	0.362203	0.004704	76.996	57167
Spain_IA	SegorbeGiant	Mbuti	0.357343	0.004766	74.979	51963
Levant_Chl	SegorbeGiant	Mbuti	0.351769	0.004823	72.932	53101
Spain_c.10-16CE	SegorbeGiant	Mbuti	0.34853	0.004763	73.181	54535
Yamnaya	SegorbeGiant	Mbuti	0.343107	0.004713	72.795	54740
Portugal_MN	SegorbeGiant	Mbuti	0.340764	0.004997	68.197	53056
Spain_c.5-8CE	SegorbeGiant	Mbuti	0.335461	0.005053	66.393	47491
Portugal_BA	SegorbeGiant	Mbuti	0.334657	0.004946	67.657	49450
Spain_Greek	SegorbeGiant	Mbuti	0.333766	0.005022	66.463	47068
Spain_c.6CE	SegorbeGiant	Mbuti	0.331807	0.005213	63.652	41179
Spain_Hel	SegorbeGiant	Mbuti	0.325703	0.005548	58.706	39290
Spain_RomP	SegorbeGiant	Mbuti	0.325057	0.005243	61.994	44782
Spain_c.6-8CE	SegorbeGiant	Mbuti	0.324952	0.005995	54.203	32023
Spain_c.8-12CE	SegorbeGiant	Mbuti	0.324572	0.005196	62.463	40576
Gibraltar_BA	SegorbeGiant	Mbuti	0.323053	0.006092	53.031	26521
Levant_N	SegorbeGiant	Mbuti	0.317757	0.005548	57.275	39374
Levant_BA	SegorbeGiant	Mbuti	0.317164	0.005139	61.712	41833
Spain_Meso	SegorbeGiant	Mbuti	0.310201	0.005189	59.785	45441
EHG	SegorbeGiant	Mbuti	0.309557	0.005027	61.577	45641
Gibraltar_EN	SegorbeGiant	Mbuti	0.307719	0.007948	38.716	16537
Spain_c.3-4CE	SegorbeGiant	Mbuti	0.307427	0.005307	57.925	42289
CHG	SegorbeGiant	Mbuti	0.30435	0.004941	61.601	51347
Morocco_LN	SegorbeGiant	Mbuti	0.302731	0.007254	41.732	18016
Natufian	SegorbeGiant	Mbuti	0.296251	0.0065	45.578	23474
Guanches	SegorbeGiant	Mbuti	0.291783	0.00474	61.554	51794
Iberomaurusian	SegorbeGiant	Mbuti	0.274003	0.004453	61.528	51539
Morocco_EN	SegorbeGiant	Mbuti	0.247179	0.005458	45.289	31221
Ust_Ishim	SegorbeGiant	Mbuti	0.210424	0.004293	49.013	52103
Ju_hoan_North	SegorbeGiant	Mbuti	0.046921	0.00239	19.636	60264

Table S4. Outgroup-f3 output table, using Ju|'Hoan North as outgroup. M, (E/M/L)N , Chl, BA and IA stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Iron Age, respectively.

Source1	**Source2**	**Target**	**f_3**	**std.err.**	**2std.err.**	**Z**	**SNPs**
Spain_MLN	SegorbeGiant	Ju_hoan_North	0.385302	0.004647	0.009294	82.912	59390
Anatolia_N	SegorbeGiant	Ju_hoan_North	0.384613	0.004517	0.009034	85.142	61980
Spain_BA	SegorbeGiant	Ju_hoan_North	0.38179	0.004547	0.009094	83.969	60788
Spain_Chl	SegorbeGiant	Ju_hoan_North	0.378565	0.00459	0.00918	82.471	59145
Portugal_LN-Chl	SegorbeGiant	Ju_hoan_North	0.373593	0.004546	0.009092	82.182	59622
Spain_IA	SegorbeGiant	Ju_hoan_North	0.370919	0.004701	0.009402	78.908	54316
Levant_Chl	SegorbeGiant	Ju_hoan_North	0.364215	0.004666	0.009332	78.063	55480
Spain_c.10-16CE	SegorbeGiant	Ju_hoan_North	0.362293	0.004568	0.009136	79.31	56955
Yamnaya	SegorbeGiant	Ju_hoan_North	0.356656	0.004578	0.009156	77.911	57318
Portugal_MN	SegorbeGiant	Ju_hoan_North	0.352074	0.004949	0.009898	71.136	55367
Portugal_BA	SegorbeGiant	Ju_hoan_North	0.351968	0.004846	0.009692	72.634	51663
Spain_c.5-8CE	SegorbeGiant	Ju_hoan_North	0.350495	0.004816	0.009632	72.775	49729
Spain_c.6CE	SegorbeGiant	Ju_hoan_North	0.350145	0.005124	0.010248	68.34	43069
Spain_Greek	SegorbeGiant	Ju_hoan_North	0.349238	0.004908	0.009816	71.153	49247
Gibraltar_BA	SegorbeGiant	Ju_hoan_North	0.345249	0.006052	0.012104	57.043	27432
Spain_Hel	SegorbeGiant	Ju_hoan_North	0.342078	0.005377	0.010754	63.621	41068
Spain_c.8-12CE	SegorbeGiant	Ju_hoan_North	0.341956	0.005204	0.010408	65.706	42250
Spain_RomP	SegorbeGiant	Ju_hoan_North	0.338733	0.004946	0.009892	68.484	46679
Spain_c.6-8CE	SegorbeGiant	Ju_hoan_North	0.337838	0.005878	0.011756	57.478	33382
Levant_BA	SegorbeGiant	Ju_hoan_North	0.333937	0.005012	0.010024	66.625	43680
Levant_N	SegorbeGiant	Ju_hoan_North	0.333687	0.00558	0.01116	59.802	41080
Gibraltar_EN	SegorbeGiant	Ju_hoan_North	0.329749	0.008324	0.016648	39.614	17116
Spain_Meso	SegorbeGiant	Ju_hoan_North	0.325398	0.005094	0.010188	63.879	47462
EHG	SegorbeGiant	Ju_hoan_North	0.321602	0.004945	0.00989	65.032	47953
Spain_c.3-4CE	SegorbeGiant	Ju_hoan_North	0.321354	0.005181	0.010362	62.021	44325
CHG	SegorbeGiant	Ju_hoan_North	0.320758	0.004763	0.009526	67.348	53675
Morocco_LN	SegorbeGiant	Ju_hoan_North	0.317846	0.00727	0.01454	43.72	18593
Natufian	SegorbeGiant	Ju_hoan_North	0.312037	0.006468	0.012936	48.246	24412
Guanches	SegorbeGiant	Ju_hoan_North	0.305155	0.004492	0.008984	67.937	54149
Iberomaurusian	SegorbeGiant	Ju_hoan_North	0.288407	0.00429	0.00858	67.224	53879
Morocco_EN	SegorbeGiant	Ju_hoan_North	0.258951	0.005536	0.011072	46.774	32569
Ust_Ishim	SegorbeGiant	Ju_hoan_North	0.228166	0.004377	0.008754	52.134	54472
Mbuti	SegorbeGiant	Ju_hoan_North	0.069587	0.002453	0.004906	28.371	60264

Table S5. Outgroup-f3 output table, using Ust'-Ishim as outgroup. M, (E/M/L)N , Chl, BA and IA stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Iron Age, respectively.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Anatolia_N	SegorbeGiant	Ust_Ishim	0.16258	0.007685	21.156	47108
Spain_MLN	SegorbeGiant	Ust_Ishim	0.160592	0.007547	21.278	44218
Spain_BA	SegorbeGiant	Ust_Ishim	0.158606	0.007499	21.15	45669
Spain_Chl	SegorbeGiant	Ust_Ishim	0.158547	0.007589	20.893	43867
Levant_Chl	SegorbeGiant	Ust_Ishim	0.148742	0.007643	19.46	40105
Spain_c.10-16CE	SegorbeGiant	Ust_Ishim	0.148351	0.007508	19.759	41792
Portugal_LN-Chl	SegorbeGiant	Ust_Ishim	0.147519	0.007438	19.832	42746
Spain_IA	SegorbeGiant	Ust_Ishim	0.143464	0.007398	19.391	38593
Spain_c.5-8CE	SegorbeGiant	Ust_Ishim	0.133165	0.00756	17.615	34501
Yamnaya	SegorbeGiant	Ust_Ishim	0.131731	0.007336	17.956	40354
Portugal_MN	SegorbeGiant	Ust_Ishim	0.130931	0.007464	17.542	36810
Portugal_BA	SegorbeGiant	Ust_Ishim	0.130875	0.00743	17.615	33859
Spain_c.6CE	SegorbeGiant	Ust_Ishim	0.128868	0.007899	16.314	28869
Spain_Greek	SegorbeGiant	Ust_Ishim	0.126067	0.007613	16.56	32496
Spain_RomP	SegorbeGiant	Ust_Ishim	0.122413	0.007497	16.328	30841
Gibraltar_BA	SegorbeGiant	Ust_Ishim	0.119987	0.008401	14.283	17593
Spain_c.8-12CE	SegorbeGiant	Ust_Ishim	0.119949	0.007893	15.198	27972
Spain_c.6-8CE	SegorbeGiant	Ust_Ishim	0.119335	0.008171	14.605	21708
Morocco_LN	SegorbeGiant	Ust_Ishim	0.11922	0.009622	12.391	11680
Levant_N	SegorbeGiant	Ust_Ishim	0.119125	0.007761	15.348	26772
Levant_BA	SegorbeGiant	Ust_Ishim	0.117842	0.007576	15.555	29319
Gibraltar_EN	SegorbeGiant	Ust_Ishim	0.114424	0.0099	11.558	10772
Spain_Hel	SegorbeGiant	Ust_Ishim	0.11433	0.007584	15.076	26388
Guanches	SegorbeGiant	Ust_Ishim	0.111676	0.007324	15.249	35984
Spain_c.3-4CE	SegorbeGiant	Ust_Ishim	0.110237	0.007749	14.227	28635
Iberomaurusian	SegorbeGiant	Ust_Ishim	0.109976	0.007463	14.736	37587
Natufian	SegorbeGiant	Ust_Ishim	0.108048	0.008883	12.163	15266
CHG	SegorbeGiant	Ust_Ishim	0.102704	0.007429	13.824	34358
EHG	SegorbeGiant	Ust_Ishim	0.100936	0.00746	13.53	29972
Spain_Meso	SegorbeGiant	Ust_Ishim	0.09854	0.007376	13.36	29702
Morocco_EN	SegorbeGiant	Ust_Ishim	0.085398	0.008131	10.503	20463
Ju_hoan_North	SegorbeGiant	Ust_Ishim	0.027846	0.00613	4.543	54472
Mbuti	SegorbeGiant	Ust_Ishim	0.027835	0.006133	4.539	52103

Table S6. *D*-statistics output table for Segorbe Giant (target). Rows in bold showing results with a |Z|-score >3, which are considered significant. Negative *D*-stats values show higher affinity with Pop. X (in red) than with Pop Y. Positive *D*-stats values show higher affinity with Pop. Y (in blue) than with Pop. X. M, (E/M/L)N, Chl, BA and IA stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Iron Age, respectively.

Outg.	Target	Pop. X	Pop. Y	*D*-stat	std.err.	|Z|	BABA	ABBA	SNPs
Chimp	**SegorbeGiant**	**Spain_MLN**	**Iberomaurusian**	**-0.133**	**0.008372**	**15.892**	**2840**	**3711**	**65378**
Chimp	**SegorbeGiant**	**Spain_MLN**	**Morocco_EN**	**-0.1301**	**0.012333**	**10.547**	**1794**	**2331**	**41532**
Chimp	**SegorbeGiant**	**Spain_IA**	**Iberomaurusian**	**-0.1292**	**0.009152**	**14.112**	**2739**	**3552**	**62545**
Chimp	**SegorbeGiant**	**Spain_Chl**	**Iberomaurusian**	**-0.1291**	**0.008399**	**15.371**	**2826**	**3664**	**65543**
Chimp	**SegorbeGiant**	**Spain_BA**	**Iberomaurusian**	**-0.1281**	**0.008254**	**15.525**	**2866**	**3709**	**66173**
Chimp	**SegorbeGiant**	**Spain_BA**	**Morocco_EN**	**-0.128**	**0.011891**	**10.761**	**1822**	**2356**	**42154**
Chimp	**SegorbeGiant**	**Spain_Chl**	**Morocco_EN**	**-0.1271**	**0.012053**	**10.541**	**1788**	**2309**	**41663**
Chimp	**SegorbeGiant**	**Spain_IA**	**Morocco_EN**	**-0.1224**	**0.012822**	**9.542**	**1749**	**2237**	**39608**
Chimp	**SegorbeGiant**	**Spain_c.5-8CE_SE**	**Morocco_EN**	**-0.113**	**0.014052**	**8.042**	**1659**	**2081**	**37415**
Chimp	**SegorbeGiant**	**Spain_c.5-8CE_SE**	**Iberomaurusian**	**-0.1114**	**0.009173**	**12.144**	**2619**	**3275**	**59211**
Chimp	**SegorbeGiant**	**Spain_MLN**	**Guanches**	**-0.0985**	**0.008707**	**11.314**	**2861**	**3486**	**65876**
Chimp	**SegorbeGiant**	**Spain_IA**	**Guanches**	**-0.0964**	**0.009494**	**10.156**	**2772**	**3364**	**62675**
Chimp	**SegorbeGiant**	**Spain_Chl**	**Guanches**	**-0.0941**	**0.008585**	**10.959**	**2863**	**3458**	**66094**
Chimp	**SegorbeGiant**	**Spain_c.3-4CE_SE**	**Iberomaurusian**	**-0.0914**	**0.011419**	**8.007**	**2547**	**3060**	**55353**
Chimp	**SegorbeGiant**	**Spain_BA**	**Guanches**	**-0.0909**	**0.008505**	**10.69**	**2919**	**3503**	**66915**
Chimp	**SegorbeGiant**	**Spain_c.3-4CE_SE**	**Morocco_EN**	**-0.0801**	**0.015846**	**5.058**	**1604**	**1884**	**34980**
Chimp	**SegorbeGiant**	**Spain_c.5-8CE_SE**	**Guanches**	**-0.0727**	**0.009634**	**7.542**	**2676**	**3095**	**59114**
Chimp	**SegorbeGiant**	**Spain_c.3-4CE_SE**	**Guanches**	**-0.0579**	**0.011511**	**5.027**	**2568**	**2883**	**55273**
Chimp	**SegorbeGiant**	**Spain_MLN**	**Levant_BA**	**-0.042**	**0.008271**	**5.077**	**2378**	**2586**	**54639**
Chimp	**SegorbeGiant**	**Spain_IA**	**Levant_BA**	**-0.0361**	**0.008818**	**4.091**	**2381**	**2559**	**53777**
Chimp	**SegorbeGiant**	**Spain_Chl**	**Levant_BA**	**-0.035**	**0.008263**	**4.235**	**2396**	**2570**	**54698**
Chimp	**SegorbeGiant**	**Spain_BA**	**Levant_BA**	**-0.0333**	**0.008218**	**4.055**	**2393**	**2557**	**54812**
Chimp	**SegorbeGiant**	**Spain_MLN**	**Levant_Chl**	**-0.0233**	**0.005859**	**3.969**	**2812**	**2946**	**64846**
Chimp	**SegorbeGiant**	**Spain_IA**	**Levant_Chl**	**-0.0214**	**0.006992**	**3.056**	**2774**	**2895**	**62591**
Chimp	**SegorbeGiant**	**Spain_Chl**	**Levant_Chl**	**-0.0186**	**0.006126**	**3.038**	**2820**	**2927**	**64925**
Chimp	**SegorbeGiant**	**Guanches**	**Levant_BA**	**0.0575**	**0.010637**	**5.405**	**2760**	**2460**	**53544**

Chimp	**SegorbeGiant**	**Guanches**	**Levant_N**	**0.0697**	**0.012428**	**5.605**	**2657**	**2311**	**51353**
Chimp	**SegorbeGiant**	**Guanches**	**Levant_Chl**	**0.0754**	**0.009311**	**8.099**	**3343**	**2874**	**63764**
Chimp	**SegorbeGiant**	**Morocco_EN**	**Levant_BA**	**0.0866**	**0.015819**	**5.473**	**1817**	**1528**	**33820**
Chimp	**SegorbeGiant**	**Iberomaurusian**	**Levant_BA**	**0.0927**	**0.01079**	**8.593**	**2946**	**2446**	**53805**
Chimp	**SegorbeGiant**	**Morocco_EN**	**Levant_N**	**0.1052**	**0.016396**	**6.416**	**1728**	**1399**	**32522**
Chimp	**SegorbeGiant**	**Iberomaurusian**	**Levant_N**	**0.1125**	**0.012037**	**9.344**	**2812**	**2244**	**51558**
Chimp	**SegorbeGiant**	**Morocco_EN**	**Levant_Chl**	**0.1132**	**0.012828**	**8.823**	**2212**	**1762**	**40259**
Chimp	**SegorbeGiant**	**Iberomaurusian**	**Levant_Chl**	**0.1158**	**0.008978**	**12.895**	**3506**	**2778**	**63594**
Chimp	SegorbeGiant	Spain_MLN	Levant_N	-0.0284	0.00958	2.967	2268	2401	52242
Chimp	SegorbeGiant	Spain_Chl	Levant_N	-0.0283	0.009693	2.92	2283	2416	52297
Chimp	SegorbeGiant	Spain_BA	Levant_Chl	-0.0151	0.005627	2.687	2855	2943	65362
Chimp	SegorbeGiant	Spain_BA	Levant_N	-0.0255	0.009771	2.607	2302	2422	52414
Chimp	SegorbeGiant	Spain_IA	Levant_N	-0.0271	0.010436	2.595	2267	2394	51330
Chimp	SegorbeGiant	Spain_c.3-4CE_SE	Levant_Chl	0.0166	0.00976	1.703	2603	2518	55360
Chimp	SegorbeGiant	Spain_c.5-8CE_SE	Levant_BA	-0.0151	0.009558	1.584	2384	2457	52165
Chimp	SegorbeGiant	Spain_c.3-4CE_SE	Morocco_LN	0.03	0.021153	1.416	991	933	19937
Chimp	SegorbeGiant	Spain_Chl	Morocco_LN	-0.02	0.016253	1.229	1074	1117	23605
Chimp	SegorbeGiant	Spain_BA	Morocco_LN	-0.0172	0.015725	1.095	1091	1129	23868
Chimp	SegorbeGiant	Spain_MLN	Morocco_LN	-0.0178	0.016498	1.076	1073	1112	23536
Chimp	SegorbeGiant	Spain_IA	Morocco_LN	-0.0168	0.017652	0.954	1033	1068	22495
Chimp	SegorbeGiant	Spain_c.3-4CE_SE	Levant_N	0.0122	0.013115	0.929	2221	2167	47118
Chimp	SegorbeGiant	Morocco_LN	Levant_N	-0.0203	0.022477	0.903	841	876	18526
Chimp	SegorbeGiant	Spain_c.5-8CE_SE	Morocco_LN	0.0139	0.017547	0.791	1031	1003	21263
Chimp	SegorbeGiant	Morocco_LN	Levant_Chl	0.0116	0.016686	0.694	1082	1058	22821
Chimp	SegorbeGiant	Morocco_LN	Levant_BA	-0.0131	0.019872	0.66	906	930	19326
Chimp	SegorbeGiant	Spain_c.3-4CE_SE	Levant_BA	-0.0035	0.011141	0.312	2317	2333	49320
Chimp	SegorbeGiant	Spain_c.5-8CE_SE	Levant_N	-0.0022	0.010691	0.204	2263	2273	49764
Chimp	SegorbeGiant	Spain_c.5-8CE_SE	Levant_Chl	0.0007	0.007508	0.09	2701	2697	59421

Table S7. *D*-statistics output table for the Valencian population from 10th-16th cent.CE (target). Rows in bold showing results with a |Z|-score >3, which are considered significant. Negative *D*-stats values show higher affinity with Pop. X (in red) than with Pop Y. Positive *D*-stats values show higher affinity with Pop. Y (in blue) than with Pop. X. M, (E/M/L)N, Chl, BA and IA stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Iron Age, respectively.

Outg.	Target	Pop. X	Pop. Y	*D*-stat	std.err.	|Z|	BABA	ABBA	SNPs
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_MLN**	**Iberomaurusian**	**-0.1421**	**0.003127**	**45.444**	**28968**	**38563**	**679441**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_Chl**	**Iberomaurusian**	**-0.1409**	**0.003185**	**44.248**	**28717**	**38140**	**679405**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_BA**	**Iberomaurusian**	**-0.1408**	**0.00309**	**45.58**	**28950**	**38441**	**682494**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_IA**	**Iberomaurusian**	**-0.1391**	**0.00339**	**41.034**	**28460**	**37656**	**659401**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_MLN**	**Morocco_EN**	**-0.1391**	**0.004218**	**32.97**	**18020**	**23842**	**412508**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_BA**	**Morocco_EN**	**-0.1377**	**0.004152**	**33.166**	**18023**	**23780**	**414561**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_Chl**	**Morocco_EN**	**-0.1371**	**0.004342**	**31.57**	**17892**	**23576**	**412797**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_IA**	**Morocco_EN**	**-0.1361**	**0.00443**	**30.719**	**17729**	**23315**	**400861**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.5-8CE_SE**	**Iberomaurusian**	**-0.1189**	**0.003369**	**35.292**	**27739**	**35224**	**630592**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.3-4CE_SE**	**Iberomaurusian**	**-0.1165**	**0.004003**	**29.106**	**26355**	**33305**	**586547**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.5-8CE_SE**	**Morocco_EN**	**-0.1133**	**0.004466**	**25.363**	**17292**	**21710**	**383880**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.3-4CE_SE**	**Morocco_EN**	**-0.1098**	**0.00517**	**21.233**	**16396**	**20440**	**359377**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_MLN**	**Guanches**	**-0.0946**	**0.003027**	**31.255**	**29469**	**35629**	**673064**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_BA**	**Guanches**	**-0.0925**	**0.003031**	**30.53**	**29676**	**35728**	**676590**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_Chl**	**Guanches**	**-0.0923**	**0.00311**	**29.687**	**29432**	**35419**	**673274**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_IA**	**Guanches**	**-0.0915**	**0.003382**	**27.06**	**28984**	**34824**	**652591**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.5-8CE_SE**	**Guanches**	**-0.0675**	**0.003449**	**19.57**	**28649**	**32796**	**623368**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.3-4CE_SE**	**Guanches**	**-0.0669**	**0.003991**	**16.773**	**27093**	**30980**	**581134**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_BA**	**Morocco_LN**	**-0.0543**	**0.00471**	**11.53**	**10720**	**11951**	**237445**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_MLN**	**Morocco_LN**	**-0.0527**	**0.004736**	**11.131**	**10665**	**11852**	**236310**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_IA**	**Morocco_LN**	**-0.0526**	**0.005068**	**10.383**	**10558**	**11731**	**229915**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_Chl**	**Morocco_LN**	**-0.0507**	**0.004632**	**10.941**	**10661**	**11799**	**236526**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.5-8CE_SE**	**Morocco_LN**	**-0.0265**	**0.005343**	**4.951**	**10503**	**11074**	**220102**

Chimp	**Spain_c.10-16CE_Valencia**	**Spain_c.3-4CE_SE**	**Morocco_LN**	**-0.0254**	**0.006059**	**4.197**	**9924**	**10442**	**206303**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_MLN**	**Levant_N**	**-0.0289**	**0.002974**	**9.725**	**24581**	**26045**	**558797**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_IA**	**Levant_N**	**-0.0284**	**0.003192**	**8.892**	**24560**	**25995**	**550673**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_Chl**	**Levant_N**	**-0.0264**	**0.002975**	**8.881**	**24587**	**25922**	**558622**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_BA**	**Levant_N**	**-0.026**	**0.002952**	**8.802**	**24776**	**26098**	**559768**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_MLN**	**Levant_BA**	**-0.0256**	**0.002723**	**9.394**	**26310**	**27692**	**593878**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_IA**	**Levant_BA**	**-0.0239**	**0.00288**	**8.315**	**26192**	**27477**	**585581**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_Chl**	**Levant_BA**	**-0.0235**	**0.002783**	**8.452**	**26278**	**27543**	**593673**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_BA**	**Levant_BA**	**-0.0233**	**0.002727**	**8.557**	**26300**	**27556**	**594855**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_MLN**	**Levant_Chl**	**-0.0217**	**0.001894**	**11.478**	**29773**	**31097**	**692053**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_IA**	**Levant_Chl**	**-0.0195**	**0.002242**	**8.713**	**29462**	**30636**	**672237**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_BA**	**Levant_Chl**	**-0.0194**	**0.001876**	**10.347**	**30007**	**31195**	**694482**
Chimp	**Spain_c.10-16CE_Valencia**	**Spain_Chl**	**Levant_Chl**	**-0.0186**	**0.001902**	**9.778**	**29786**	**30915**	**691528**
Chimp	**Spain_c.10-16CE_Valencia**	**Morocco_LN**	**Levant_N**	**0.0202**	**0.006073**	**3.318**	**9428**	**9055**	**192365**
Chimp	**Spain_c.10-16CE_Valencia**	**Morocco_LN**	**Levant_BA**	**0.0302**	**0.006072**	**4.979**	**10183**	**9585**	**202368**
Chimp	**Spain_c.10-16CE_Valencia**	**Morocco_LN**	**Levant_Chl**	**0.0336**	**0.005021**	**6.702**	**11538**	**10787**	**232306**
Chimp	**Spain_c.10-16CE_Valencia**	**Guanches**	**Levant_N**	**0.0635**	**0.004075**	**15.593**	**28340**	**24954**	**540519**
Chimp	**Spain_c.10-16CE_Valencia**	**Guanches**	**Levant_BA**	**0.0655**	**0.003818**	**17.163**	**30077**	**26378**	**571466**
Chimp	**Spain_c.10-16CE_Valencia**	**Guanches**	**Levant_Chl**	**0.0733**	**0.003289**	**22.286**	**34429**	**29727**	**660132**
Chimp	**Spain_c.10-16CE_Valencia**	**Morocco_EN**	**Levant_BA**	**0.1125**	**0.005007**	**22.466**	**19759**	**15763**	**351960**
Chimp	**Spain_c.10-16CE_Valencia**	**Morocco_EN**	**Levant_N**	**0.113**	**0.005286**	**21.385**	**18505**	**14746**	**334663**
Chimp	**Spain_c.10-16CE_Valencia**	**Iberomaurusian**	**Levant_BA**	**0.1152**	**0.003794**	**30.368**	**32253**	**25590**	**578371**
Chimp	**Spain_c.10-16CE_Valencia**	**Iberomaurusian**	**Levant_N**	**0.1166**	**0.004082**	**28.572**	**30165**	**23864**	**546361**
Chimp	**Spain_c.10-16CE_Valencia**	**Morocco_EN**	**Levant_Chl**	**0.1205**	**0.00437**	**27.568**	**22821**	**17913**	**405511**
Chimp	**Spain_c.10-16CE_Valencia**	**Iberomaurusian**	**Levant_Chl**	**0.1237**	**0.00328**	**37.713**	**36911**	**28784**	**667060**
Chimp	Spain_c.10-16CE_Valencia	Spain_c.3-4CE_SE	Levant_N	-0.0038	0.003949	0.952	23855	24035	504174
Chimp	Spain_c.10-16CE_Valencia	Spain_c.5-8CE_SE	Levant_N	-0.0024	0.003317	0.722	24912	25032	535076
Chimp	Spain_c.10-16CE_Valencia	Spain_c.3-4CE_SE	Levant_BA	-0.002	0.003698	0.552	25299	25402	533918
Chimp	Spain_c.10-16CE_Valencia	Spain_c.5-8CE_SE	Levant_BA	0	0.003119	0.014	26474	26472	569324
Chimp	Spain_c.10-16CE_Valencia	Spain_c.5-8CE_SE	Levant_Chl	0.0035	0.002436	1.435	29323	29119	642632
Chimp	Spain_c.10-16CE_Valencia	Spain_c.3-4CE_SE	Levant_Chl	0.0033	0.00317	1.055	27841	27655	594220

Table S8. All 1-way *qpAdm* models tested.

Target	**Source (left population)**	**best coefficients**	**std.err.**	***p*-value**
	Pop.1	**Pop.1**		
SegorbeGiant	Guanches	0	0	0
	Morocco_LN	0	0	0
	Spain_c.8-12CE	0	0	0
	Spain_c.5-8CE	0	0	0
	Spain_c.3-4CE	0	0	0
	Spain_IA	0	0	0
	Spain_BA	0	0	0
	Spain_Chl	0	0	0
	Spain_MLN	0	0	0
	Levant_BA	0	0	0
	Levant_Chl	0	0	0

Table S9. All 2-way *qpAdm* models tested.

Target	Sources (left populations)		best coefficients		std.err.	*p*-value
	Pop.1	**Pop.2**	**Pop.1**	**Pop.2**		
SegorbeGiant	Guanches	Spain_c.8-12CE	0.192	0.808	0.262	0.353281
		Spain_c.5-8CE	0.281	0.719	0.653	0.457149
		Spain_c.3-4CE	-0.049	1.049	0.414	-nan
		Spain_IA	0.472	0.528	0.165	0.001194
		Spain_BA	0.508	0.492	0.155	0.002256
		Spain_Chl	0.606	0.394	0.177	0.023515
		Spain_MLN	0.633	0.367	0.129	0.007049
		Levant_BA	0.035	0.965	0.424	-nan
		Levant_Chl	0.979	0.021	0.629	-nan
SegorbeGiant	Morocco_LN	Spain_c.8-12CE	0.276	0.724	0.268	0.196721
		Spain_c.5-8CE	-0.377	1.377	0.586	0.220891
		Spain_c.3-4CE	0.296	0.704	0.558	0.568084
		Spain_IA	0.445	0.555	0.934	0.184443
		Spain_BA	1.07	-0.07	767.346	-nan
		Spain_Chl	8.266	-7.266	108.43	-nan
		Spain_MLN	3.112	-2.112	5868.908	-nan
		Levant_BA	-3.268	4.268	24.475	-nan
		Levant_Chl	12.644	-11.644	68.481	0.05011
SegorbeGiant	Levant_Chl	Spain_c.8-12CE	-0.389	1.389	1.542	0.638949
		Spain_c.5-8CE	-1.49	2.49	0.933	0.000859
		Spain_c.3-4CE	-1.001	2.001	1.136	0.05115
		Spain_BA	0.457	0.543	0.491	0.140526
		Spain_Chl	1.528	-0.528	0.758	0.238596
		Spain_MLN	0.689	0.311	0.369	0.297336
SegorbeGiant	Levant_BA	Spain_c.8-12CE	2.967	-1.967	2.648	0.004545
		Spain_c.5-8CE	3.583	-2.583	3.325	0.007539
		Spain_c.3-4CE	8.831	-7.831	28.983	0.000535
		Spain_BA	2.62	-1.62	1.171	0.003709
		Spain_Chl	2.622	-1.622	0.839	0.000358
		Spain_MLN	1.858	-0.858	0.62	0.023412

Table S10. All 3-way *qpAdm* models tested.

Target	Source (left population)			best coefficients			std.err.		
	Pop.1	**Pop.2**	**Pop.3**	**Pop.1**	**Pop.2**	**Pop.3**	**Pop.1**	**Pop.2**	**Pop.3**
SegorbeGiant	Guanches	Spain_c.8-12CE	Levant_BA	2.448	8.472	-9.92	31.366	116.383	147.656
		Spain_c.8-12CE	Levant_Chl	0.374	1.086	-0.46	0.308	0.374	0.43
		Spain_c.5-8CE	Levant_BA	0.054	-2.432	3.378	0.648	3.154	3.32
		Spain_c.5-8CE	Levant_Chl	0.333	2.162	-1.495	0.478	0.985	0.914
		Spain_c.3-4CE	Levant_BA	0.514	-23.235	23.721	24.953	687.985	664.339
		Spain_c.3-4CE	Levant_Chl	0.235	2.073	-1.308	0.404	0.884	0.88
		Spain_IA	Levant_BA	-6.275	-10.483	17.759	763.187	1276.98	2040.155
		Spain_IA	Levant_Chl	0.799	0.935	-0.734	0.319	0.321	0.525
		Spain_BA	Levant_BA	-3.045	-4.884	8.93	15.92	23.851	39.727
		Spain_BA	Levant_Chl	0.855	0.917	-0.773	0.329	0.317	0.549
		Spain_Chl	Levant_BA	-0.581	-1.505	3.085	1.054	1.548	2.514
		Spain_Chl	Levant_Chl	1.109	1.288	-1.398	0.479	0.652	1.036
		Spain_MLN	Levant_BA	-0.908	-1.121	3.029	1.983	1.888	3.833
		Spain_MLN	Levant_Chl	1.289	1.159	-1.448	0.465	0.457	0.856
SegorbeGiant	Morocco_LN	Spain_c.8-12CE	Levant_BA	-0.419	8.637	-7.219	1.937	18.476	17.403
		Spain_c.8-12CE	Levant_Chl	0.053	1.199	-0.252	1.123	0.959	1.901
		Spain_c.5-8CE	Levant_BA	11.555	-85.503	74.949	134994.5	1052881	917886.8
		Spain_c.5-8CE	Levant_Chl	0.328	3.165	-2.493	1.658	3.97	5.39
		Spain_c.3-4CE	Levant_BA	0.229	-4.635	5.406	2.954	30.448	28.041
		Spain_c.3-4CE	Levant_Chl	-35.985	-59.231	96.216	3710.211	6124.092	9834.081
		Spain_IA	Levant_BA	-2.806	-17.252	21.058	763.117	5080.42	5843.11
		Spain_IA	Levant_Chl	13.355	10.942	-23.297	9582.576	7512.452	17094.82
		Spain_BA	Levant_BA	-0.012	-1.239	2.25	0.751	4.416	4.801
		Spain_BA	Levant_Chl	-2.534	-0.953	4.487	5.698	4.124	9.63
		Spain_Chl	Levant_BA	0.129	-1.688	2.559	0.637	2.941	2.962
		Spain_Chl	Levant_Chl	-2.631	-2.891	6.522	4.414	5.525	9.682
		Spain_MLN	Levant_BA	-0.012	-0.136	1.147	0.502	0.922	1.266
		Spain_MLN	Levant_Chl	1.289	1.159	-1.448	0.465	0.457	0.856

Excel file S5. Most parsimonious phylogeny of mtDNA haplogroup U6, based on 330 modern and 30 ancient sequences (Table S2). Ancient samples in red, newly reported sequences underlined. Cells coloured according to geographic origin. *ρ* and Maximum Likelihood (ML) node age estimates shown. Mutations relative to rCRS (position and base present in the sequence) are shown along the branches. Inverted mutations represented by a "@", insertions and deletions indicated by "ins" and "del", respectively.

Text S1.

Diet and mobility in Islamic Segorbe: stable isotope analysis

The results presented and discussed in this section were produced and analysed by co-authors of the manuscript Silva, Gonzalo-Garcia et al. (*in prep*.). Please note that most of this section was written by other co-authors, however, since the isotope results complement the genetic analysis presented in chapter IV and provide important archaeological context to the discussion of the genetic results, this text is included in this Appendix.

The analysis of carbon and nitrogen was performed by Dr Peter W. Ditchfield at the Research Laboratory for Archaeology (University of Oxford), whereas the oxygen analysis was conducted at BioArCh (University of York), through a collaboration with Dr Michelle Alexander. We selected teeth from a total of 13 individuals from the necropolis, including Segorbe Giant. These included three incisors, two premolars and eight molars (Table S11). We also included in this analysis of 17 bone fragments from various animals.

Table S11. Tooth identification for 13 individuals from the Islamic necropolis of Plaza de Almudín, in Segorbe.

Sample	Context	Tooth	Dentine	Enamel
MS060/ Segorbe Giant	UE2298	Lower 1st/2nd molar (left)	Y	Y
		Lower 1st/2nd molar (right)	-	Y
		Upper 3rd molar	-	Y
MS069	UE2297, 2266	Upper 1st Incisor	Y	-
MS070	UE2237 (S-1)	Upper 1st incisor	Y	-
MS071	UE2102 (S-3)	Upper 2nd molar	Y	Y
MS072	UE2085	Lower canine	Y	-
MS073	UE2196 (S-3)	Upper 1st molar	Y	-
MS074	UE2019	Lower 1st molar	Y	-
MS075	UE2173	Lower 2nd molar	Y	Y
MS076	UE2029	Upper 2nd molar	Y	Y
MS077	UE2083	Upper 2nd molar	Y	Y
MS078	UE2217	Lower 1st/2nd premolar	Y	-
MS079	UE2244	Upper 2nd molar	Y	Y
MS080	UE2083	Lower 1st/2nd premolar	Y	-

1.1. Dietary isotope analysis

The values for $\delta^{15}N$ and $\delta^{13}C$ dietary isotopes in the Islamic necropolis in Segorbe range between 10.7 to 13.2‰ and from −17.8 to −11‰, respectively, for 13 individuals studied (Figure S8). Segorbe Giant has a $\delta^{15}N$ value of 11.3‰ and a $\delta^{13}C$ value of −17.41‰.

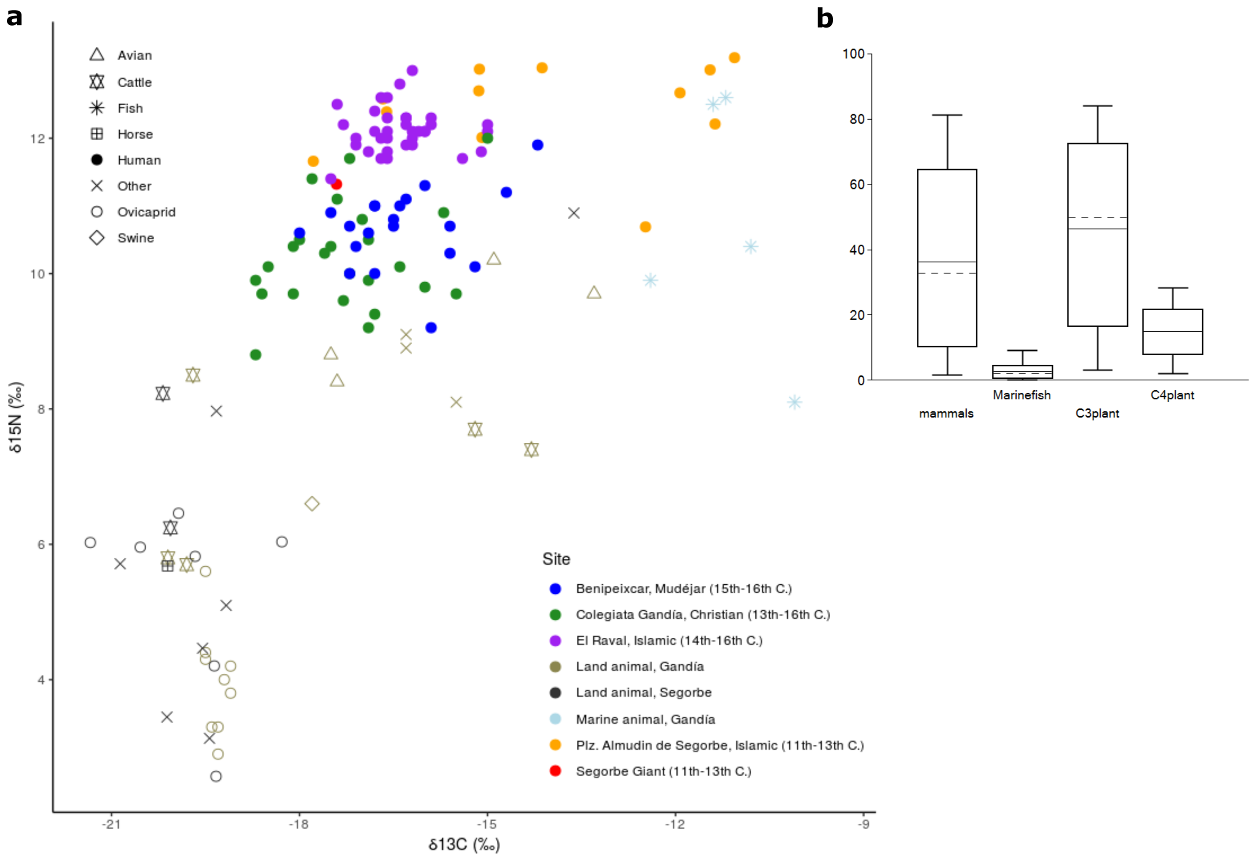

Figure S8. a) Dietary isotopes (carbon and nitrogen) values from the site of Plaza de Almudin, Segorbe compared to other Medieval Spanish sites (Alexander et al., 2015; Salazar-García et al., 2014). Animal data from the sites of Plaza de Almudin (Segorbe) and Benipeixcar (Gandia, Valencia)(Alexander et al., 2015). **b)** Proportions of terrestrial mammal, marine fish, C3 plant and C4 plant intake in the diet of MS060/Segorbe Giant, calculated using FRUITS (Fernandes et al., 2014).

The possibility of C3 and C4 plants being available for human and animal consumption coupled with the availability of marine derived protein in the human diet create potentially confounding effects when trying to understand archaeological human diet in the Mediterranean (Alexander et al., 2015). Segorbe is 35 km from the port city of Sagunto and well connected through the old Roman road communicating the valley. In the Middle Ages (14th century CE) fish arrived from the Moncófar port (Planillo Portolés, 2018). Therefore, it is not unreasonable to expect fish contribution to the diets of the Islamic inhabitants of Segorbe. Other contemporary sites in Spain such as El Raval (Salazar-García et al., 2014) show evidence for a significant C4 plant input into the human diet. Similarly high δ^{15}N values may reflect aridity in the local area, as reported from Tauste in northern Spain (Guede et al., 2017). Thus, the consumption of marine foods, C4 or C3-fed terrestrial animal protein, or a combination of all three could all play a role in the human collagen dietary isotopic signal.

Preliminary analysis of archaeological faunal collagen from Segorbe (*n*=17 mostly sheep/goat and cattle) strongly suggests that domestic animals were foddered on a largely

C3 based regime and that local aridity was not driving elevation in nitrogen isotopic composition (δ^{13}C=-19.5 VPDB, δ^{5}N=5.8 AIR). If these faunal values are representative of the terrestrial fauna available to the humans represented in the Segorbe necropolis it would suggest that the elevated carbon and nitrogen isotopic values seen in the human collagen are likely to reflect a significant but varying component of marine derived protein in the human diet.

The collagen the Segorbe Giant shows more negative δ^{13}C and lower δ^{15}N values than the majority of the humans from this assemblage and thus it is likely that the diet of this individual had a lower input of marine derived protein and/or C4 compared to others among the Segorbe population (Figure S8).

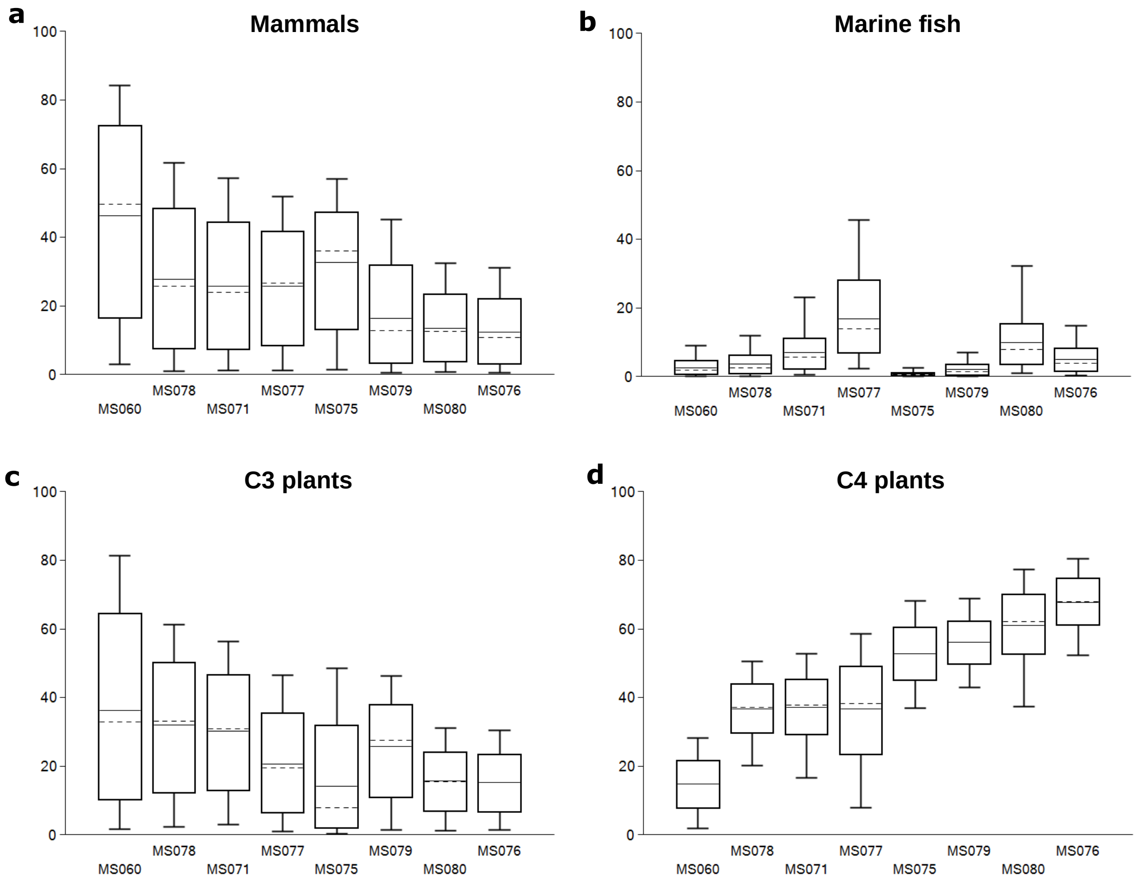

Figure S9. Proportions of terrestrial mammals **(a)**, marine fish **(b)**, C3 plants **(c)** and C4 plants **(d)** intake for each of the individuals analysed, calculated using FRUITS (Fernandes et al., 2014).

FRUITS (Food Reconstruction Using Isotopic Transferred Signals) analysis (Fernandes et al., 2014) allowed to calculate the probability of the proportions of C3 plants, C4 plants, marine fish and terrestrial mammals (using isotopic values from the literature and the terrestrial animals from Sergobe) in the diets of the individuals in Sergorbe for whom we have both bone collagen and tooth carbonate data (Figure S9). The model shows that C4 plants likely played a substantial part in the diet of some individuals and that marine fish consumption was variable. Segorbe Giant seems to have consumed very limited amounts of C4-pants (most probability between 0-30% of the diet) and marine food (most probably <15%) compared to the rest of the population analysed. On the other hand, he seems to have the highest levels of mammal and C3-plant consumption amongst the analysed individuals.

1.2. Mobility isotope analysis: oxygen

Tooth enamel carbonate data is presented in Table S12. For the purposes of comparison between Segorbe Giant and the remainder of the population, raw values were used as due to an absence of an oxygen baseline for the area, considering that this analysis is treated as an individual dataset to determine whether the enamel carbonate δ^{18}OV-PDB possessed by Segorbe Giant sets him apart from other individuals sampled from the same cemetery, which would identify him as a potential first generation migrant (Lightfoot and O'Connell, 2016). Raw δ^{18}OV-PDB values are converted δ^{18}OV-VSMOW and to drinking water (dw) values for the purposes of interpretation (Chenery et al., 2012), although it is acknowledged that there are various issues in equation selection and error propagation when converting oxygen isotope values to drinking water (see Pederzani and Britton (2019) for discussion).

Table S12. Tooth enamel carbonate and Oxygen values for all the teeth analysed from Plaza de Almudin (MS060=Segorbe Giant).

Sample	Tooth	Mineralisation time (years)*	$\delta^{13}C_{V-PDB}$ (‰)	$\delta^{18}O_{V-PDB}$ (‰)
MS060a	Lower 1st/2nd molar (right)	2.5 to 8	-10.3	-3.6
MS060b	Upper 3rd molar	7 to 16	-10.9	-4.4
MS071	Upper 2nd molar	2.5 to 8	-3.9	-8.0
MS075	Lower 2nd molar	2.5 to 8	-0.3	-4.8
MS076	Upper 2nd molar	2.5 to 8	-4.6	-3.9
MS077	Upper 2nd molar	2.5 to 8	-3.9	-7.6
MS078	Lower 1st/2nd premolar	1.5 to 7	-4.2	-8.1
MS079	Upper 2nd molar	2.5 to 8	-3.2	-4.7
MS080	Lower 1st/2nd premolar	1.5 to 7	-4.2	-4.4

*Crown enamel formation ages taken from Nelson (2014).

The δ^{18}OV-PDB values for Segorbe Giant range from -4.6 to -3.2‰ (range=1.4‰, *n*=7), with a mean of -4.1 ± 0.4‰ (1σ). The δ^{18}OV-PDB results are in keeping with a warm European climate (Lightfoot and O'Connell, 2016). The converted δ^{18}Odw values here fit with the drinking water values for eastern Iberian coast (-8 to -4 ‰ (Lightfoot and O'Connell, 2016)). The δ^{18}OV-PDB value for Segorbe Giant places him amongst the majority of the other individuals from the cemetery who have a narrow range of values between around -3 and -

5‰. The $\delta^{18}O$ value for the second molar (M2) of Segorbe Giant is -3.6‰, which only differs from the third molar (M3) by 0.7‰ (Table S12), providing little indication of movement between early childhood and adolescence.

One other individual in the population (MS075) possesses a $\delta^{18}O_{V\text{-}PDB}$ value of -0.3‰, which is more than 1.5 times the interquartile range above quartile 3. Even taking the small sample size ($n<25$), this sample can be identified as an outlier (Lightfoot and O'Connell, 2016) and therefore a potential migrant from a hot environment. Consumption of a local but differing water source in childhood cannot be ruled out but the magnitude of the difference makes this scenario unlikely. When MS075 carbonate value is converted to phosphate for comparison with published data (following the equation of Chenery et al. (2012)) the $\delta^{18}O$ phosphate value of 21.9‰ is slightly less than that reported for Nubian mummies (White et al., 2004) and the $\delta^{18}O_{dw}$ value is in keeping with Africa or the Middle East (Bowen and Revenaugh, 2003). Interestingly, this individual also displays the lowest probability (close to zero) of marine fish consumption in the population studied (Figure Sx), and signals of a mixed C3/C4 diet, which is also possibility for North Africa (Turner et al., 2007).

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Appendix D

Supplementary information for chapter V

Transition to Metal Ages in Iberia:
preliminary results

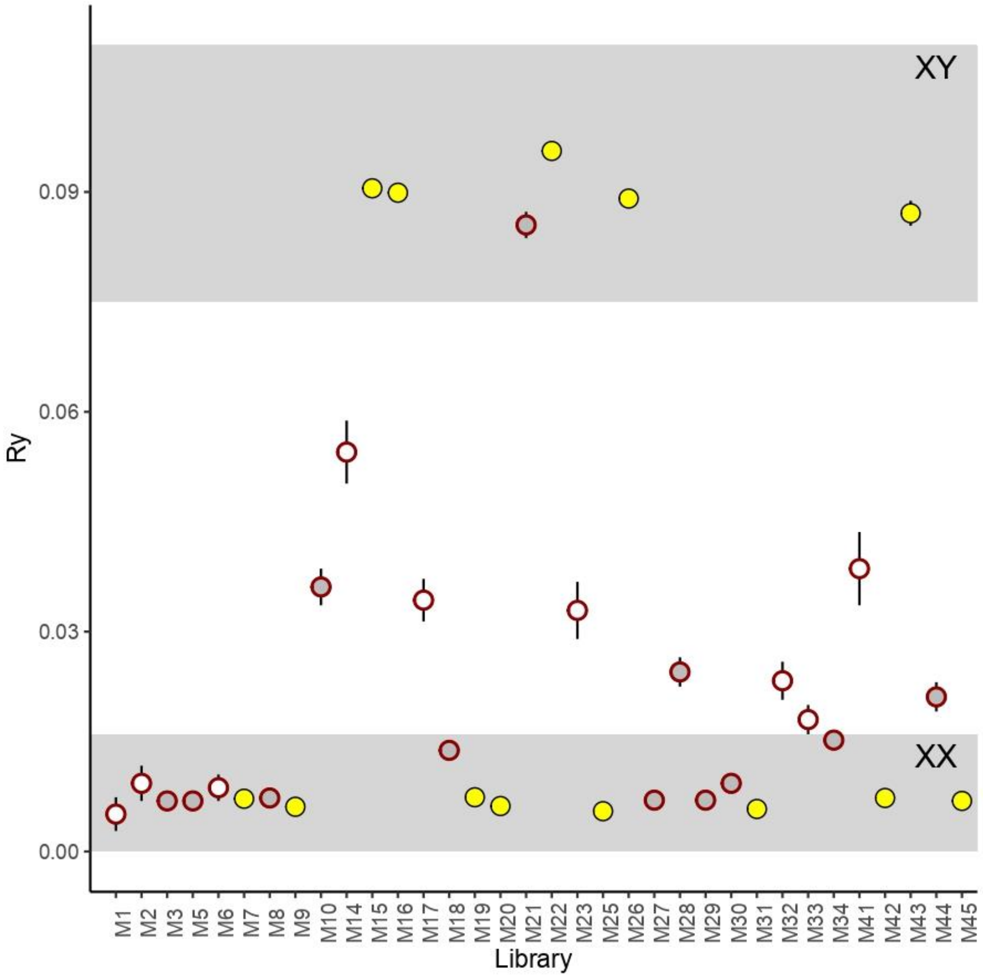

Figure S1. Sex assignment plots for libraries sent for initial screening (error bars represent 95% confidence intervals). On the x-axis the name of each library, on the y-axis the Ry score used to determine the genetic sex, calculated using the script by Skoglund et al. (2013). White and grey points with red stroke represent libraries with fewer than 100k and 1M reads, respectively.

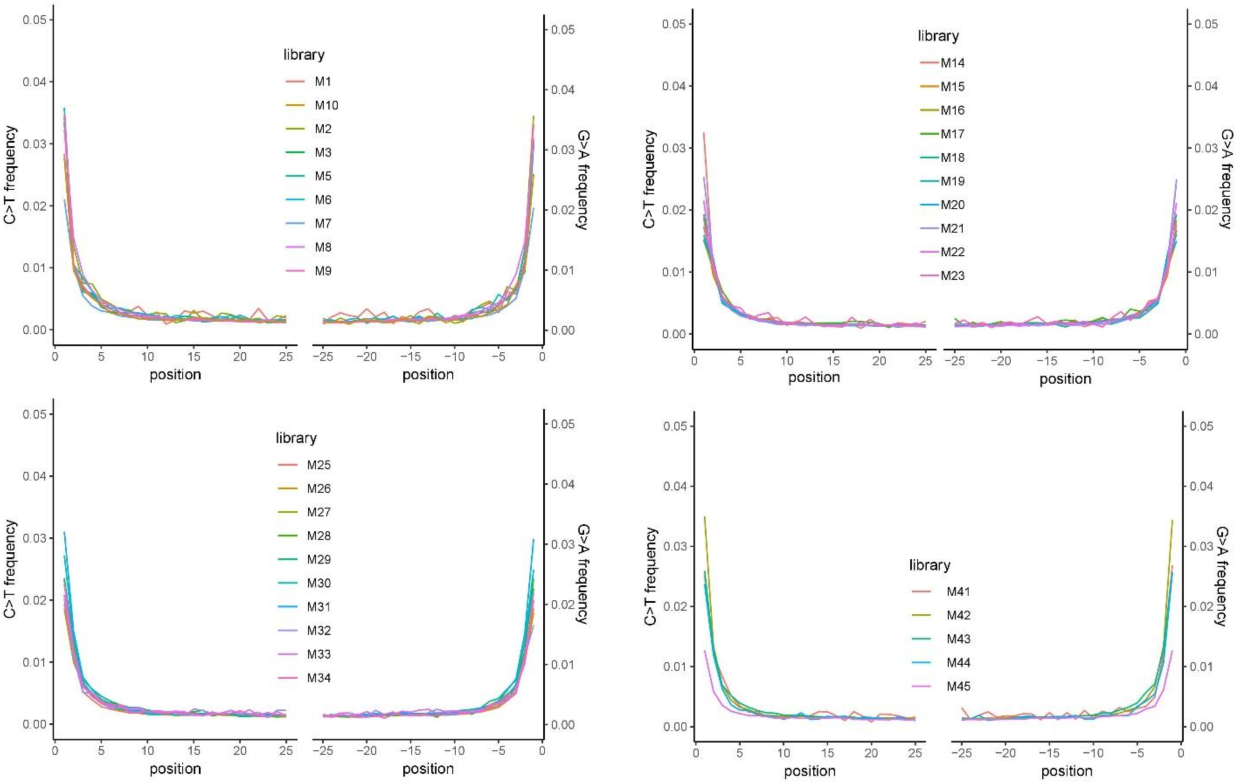

Figure S2. Damage patterns showing the typical C>T (5'end) and G>A (3'end) misincorporations for USER-treated libraries sent as initial screening (sequenced on four different lanes).

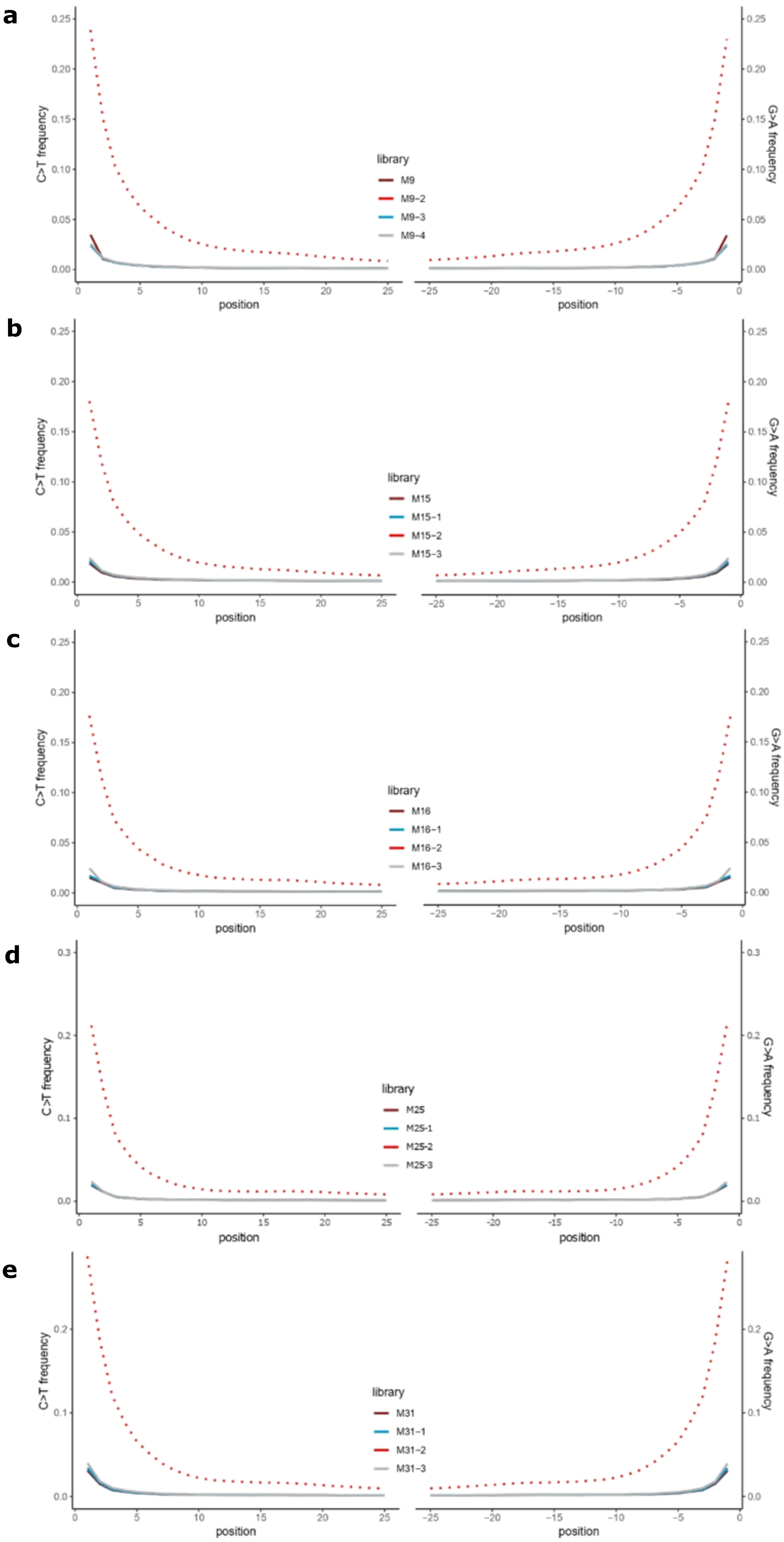

Figure S3. Damage patterns for different libraries of **a)** MS033, **b)** MS036, **c)** MS037, **d)** MS045 and **e)** MS051 (non-USER-treated library: dashed red line).

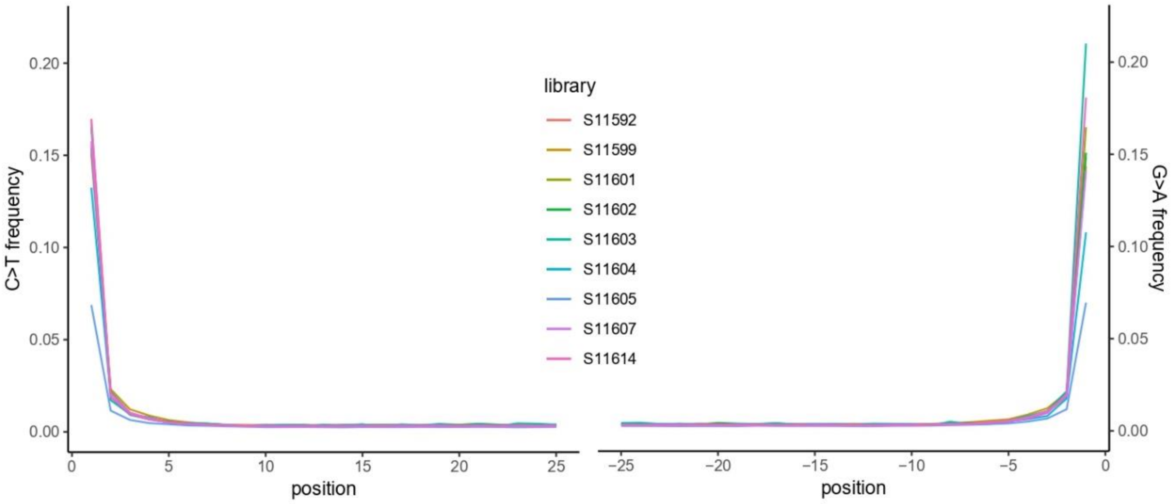

Figure S4. Damage patterns showing the typical C>T (5’end) and G>A (3’end) misincorporations for partially USER-treated 1240k-SNP enriched libraries, generated and sequenced at Harvard Medical School.

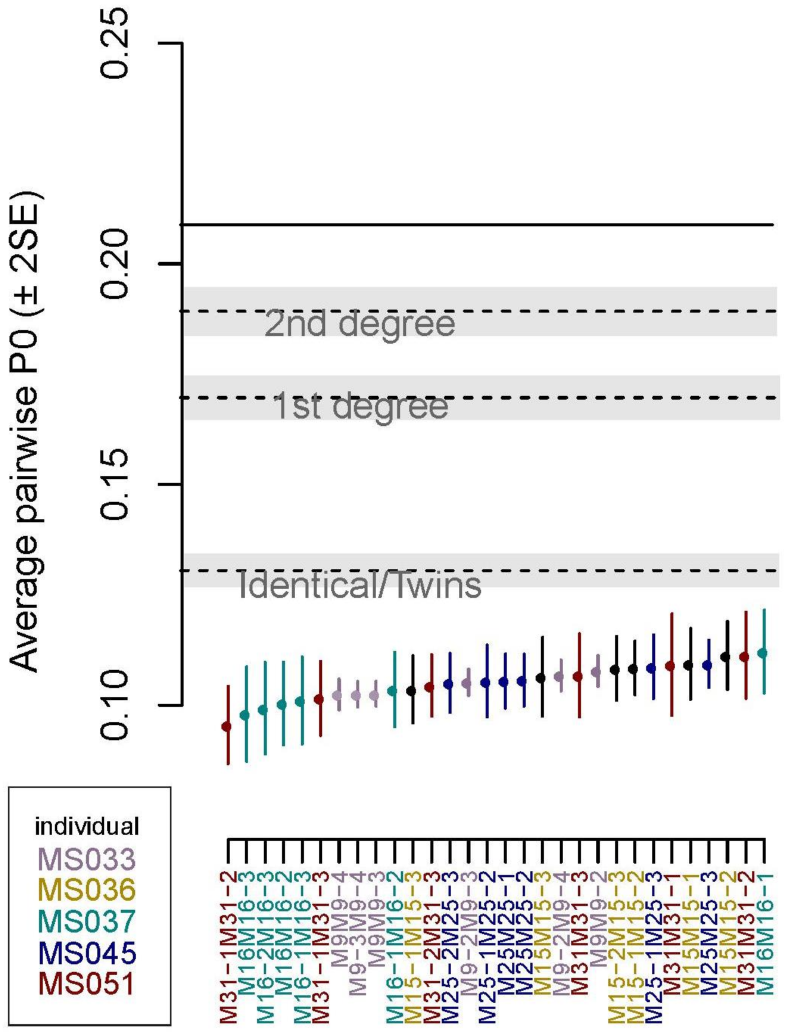

Figure S5. READ kinship analysis confirming that multiple libraries of the same sample (MS033, MS036, MS037, MS045 and MS051) correspond to the same individual.

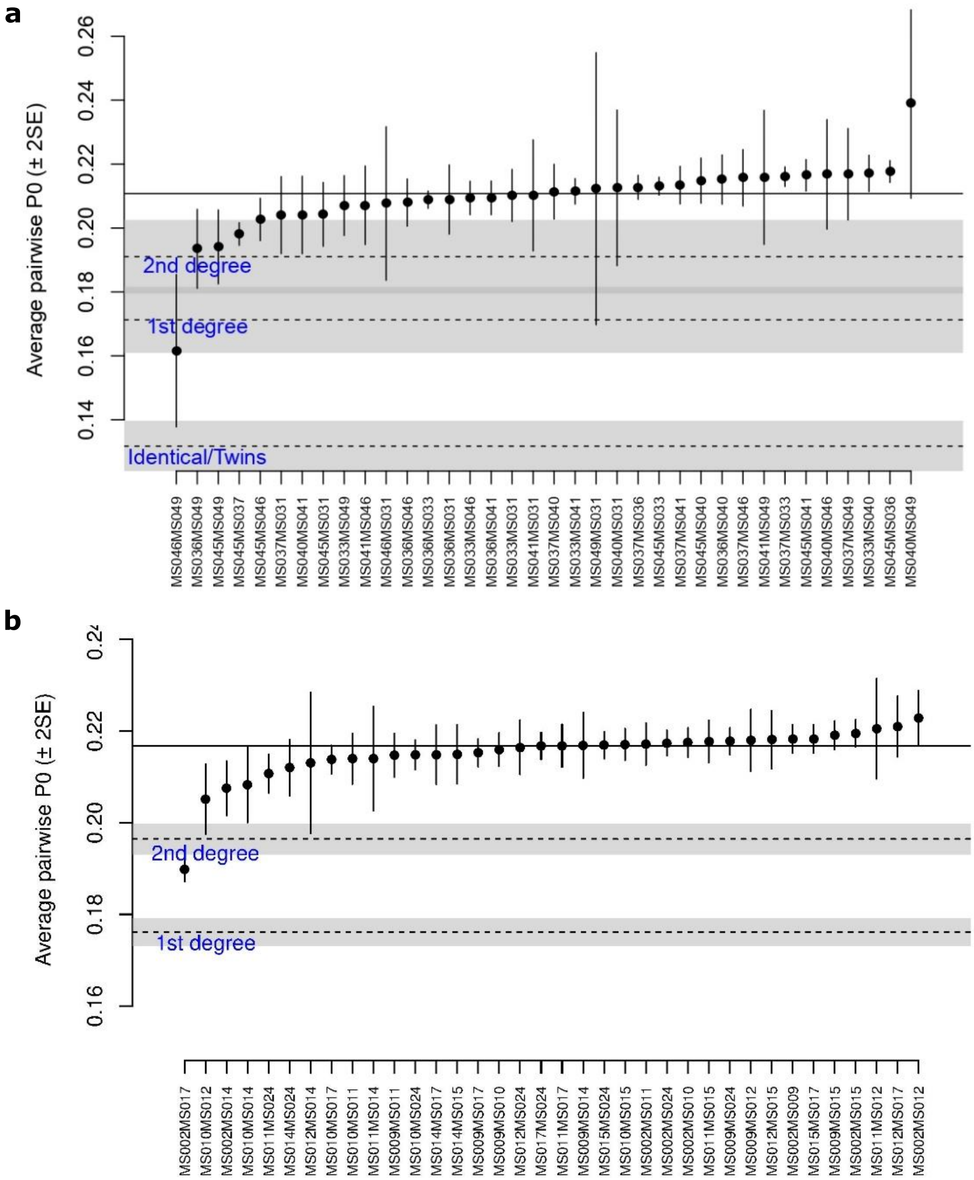

Figure S6. READ kinship analysis **a)** amongst individuals from Covão d'Almeida, and **b)** amongst individuals from Bolores, Paimogo I and Cabeço da Arruda I (1240k-SNP capture).

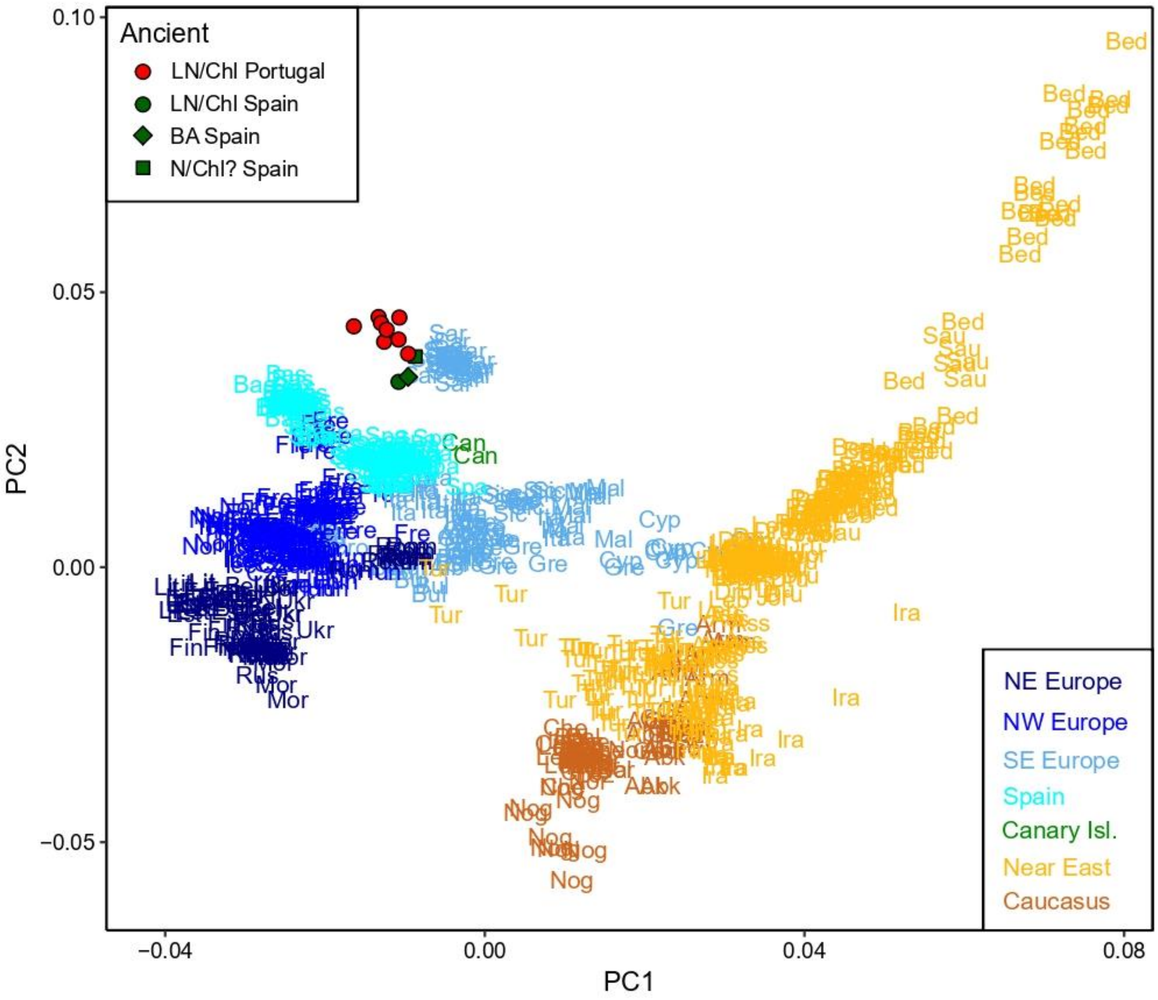

Figure S7. PCA of newly sequenced Iberian individuals projected on modern individuals from Europe, the Near East and the Caucasus (dataset i, ~600k SNPs). Abbreviations: (L)N – (Late) Neolithic, Chl – Chalcolithic, BA – Bronze Age, NE – Northeast, NW – Northwest, SE – Southeast, Isl. – Islands.

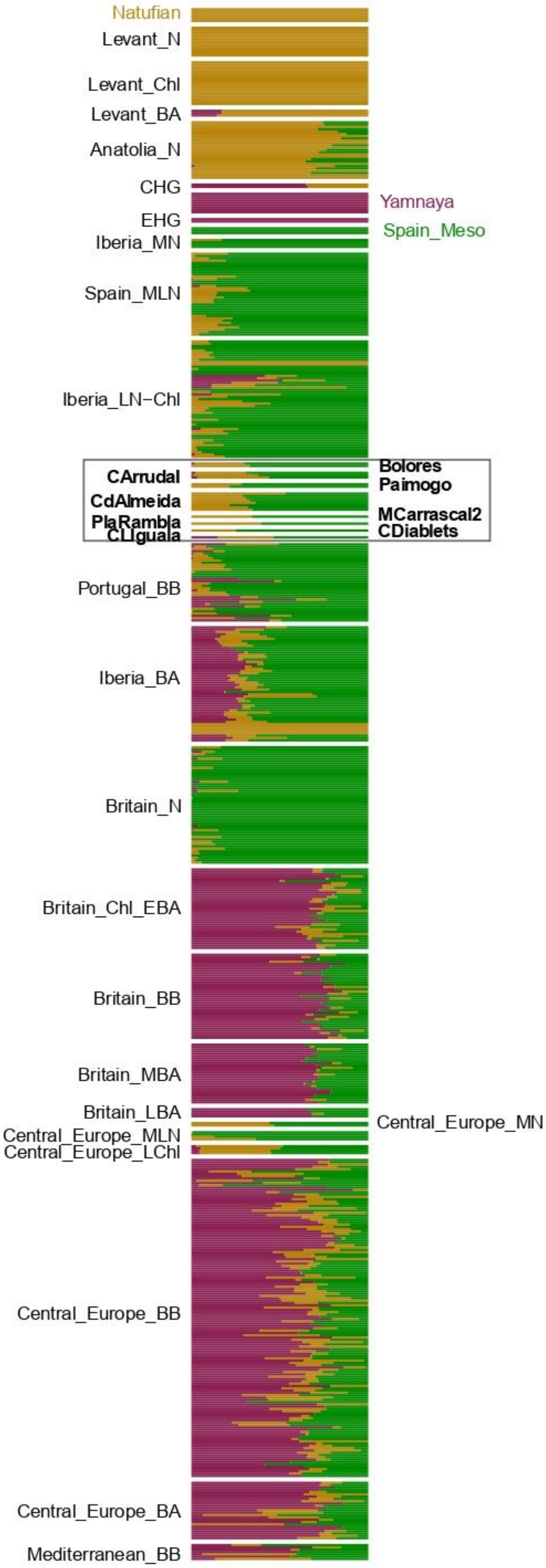

Figure S8. Supervised ADMIXTURE (K=3) of ancient individuals, using Mesolithic Spain, Natufian and Yamnaya as reference populations, as proxies for WHG, Neolithic and Steppe components. Squared area zoomed-in in Figure 5.4b.

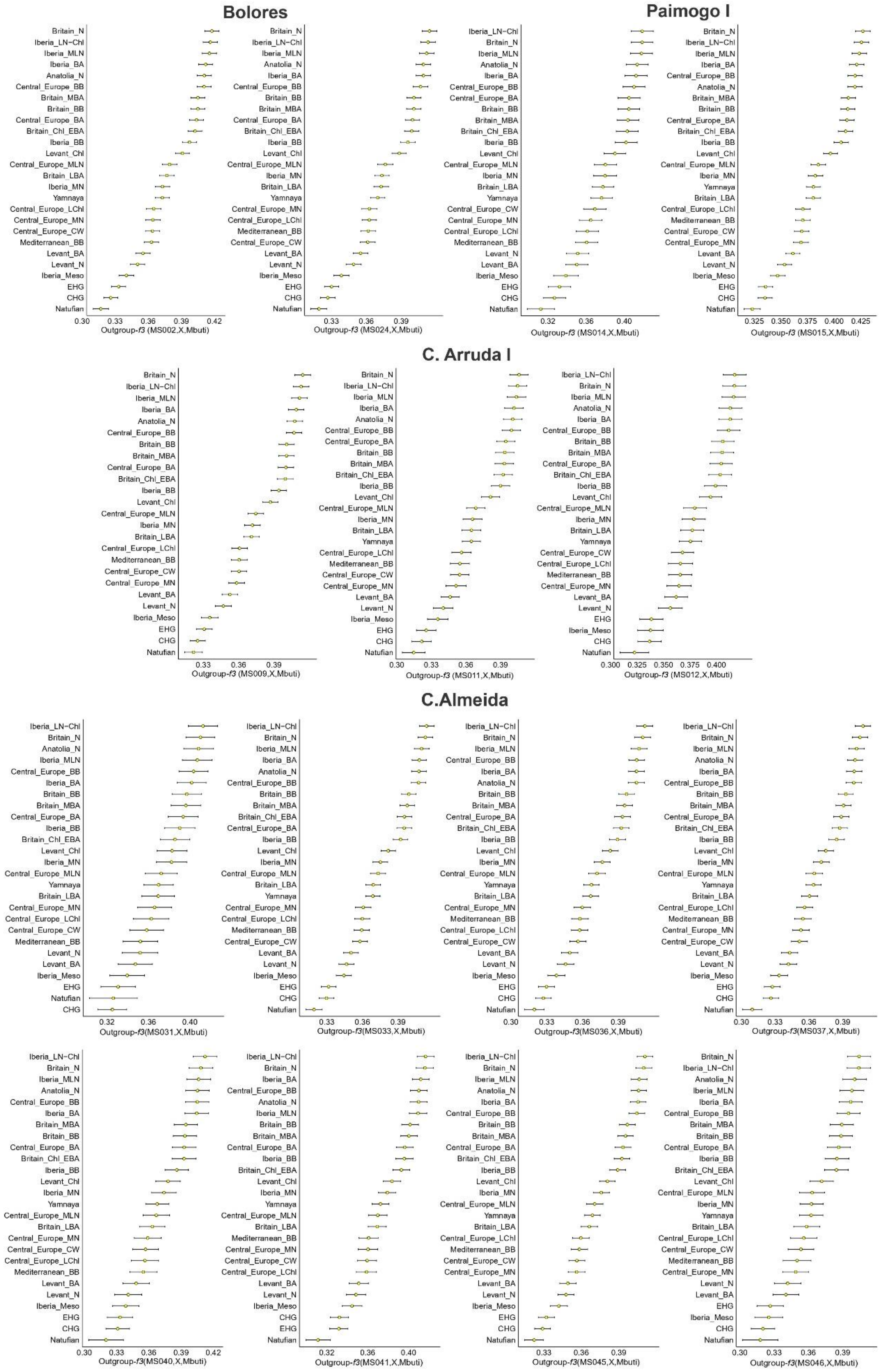

Figure S9. Outgroup-f3 (newly published Iberian, X, Mbuti) for each sample from the sites of Bolores, Paimogo I, Cabeço da Arruda I and Covão d'Almeida. Error bars correspond to 2 standard errors. Complete output in Tables S11-S18.

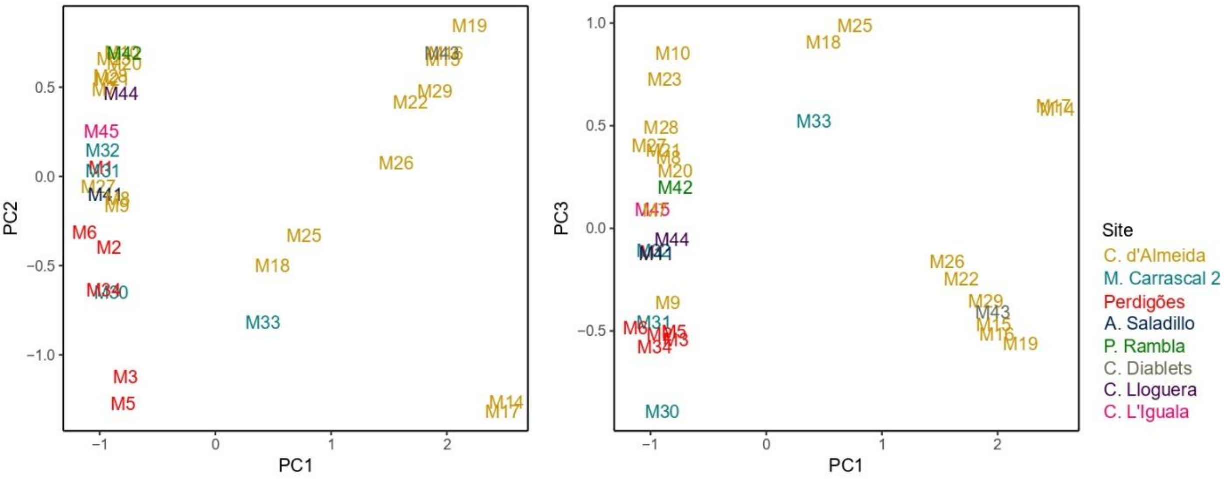

Figure S10. PCA based on frequencies of families present on each WGS library: **a)** PC1 versus PC2, **b)** PC1 versus PC3.

Table S1. Information regarding sequencing of ancient individuals included in this chapter. Libraries included in the analysis indicated in bold. Libraries in red are possibly contaminated (Table S2) and were excluded. Libraries in italics correspond to individuals who are related to others (Figure S5) and were excluded from population analysis.

library ID	DNA code	site	country	method	# total raw reads	# mapped reads (%)	Mean genome coverage	# mapped reads (rCRS)	mean mtDNA coverage	USER	# autosomal SNPs (1240k)	mtDNA Hg.	Y-chr Hg.
S11592.E1.L1	**MS002**	**Bolores**	**Portugal**	**1240k**	**.**	**3135366**	**0.058**	**19615**	**74.450**	**partial**	**445625**	**U5b2b**	**I**
S11599.E1.L1	**MS009**	**Cabeço da Arruda I**	**Portugal**	**1240k**	**.**	**1909324**	**0.034**	**19108**	**66.375**	**partial**	**335254**	**J2b1a2**	**I**
S11601.E1.L1	**MS011**	**Cabeço da Arruda I**	**Portugal**	**1240k**	**.**	**536925**	**0.009**	**4966**	**14.565**	**partial**	**109296**	**V+16298@**	**.**
S11602.E1.L1	**MS012**	**Cabeço da Arruda I**	**Portugal**	**1240k**	**.**	**190501**	**0.004**	**2881**	**9.100**	**partial**	**50868**	**J1c3**	**.**
S11603.E1.L1	MS013	Cabeço da Arruda I	Portugal	1240k	.	**55822**	0.001	317	0.984	partial	15246	J1	.
S11604.E1.L1	**MS014**	**Paimogo I**	**Portugal**	**1240k**	**.**	**197838**	**0.004**	**19056**	**68.513**	**partial**	**46794**	**K1a1**	**.**
S11605.E1.L1	**MS015**	**Paimogo I**	**Portugal**	**1240k**	**.**	**2984871**	**0.062**	**24827**	**104.938**	**partial**	**400776**	**HV0d**	**I**
S11607.E1.L1	*MS017*	*Bolores*	*Portugal*	*1240k*	*.*	**3389794**	*0.061*	*13478*	*46.844*	*partial*	*405878*	*K1a2b*	*I*
S11614.E1.L1	**MS024**	**Bolores**	**Portugal**	**1240k**	**.**	**4210104**	**0.069**	**22608**	**79.922**	**partial**	**450203**	**H4a1a**	**.**
M1	MS025	Perdigões	Portugal	WGS	26364795	20953 (0.079)	0.000	24	0.066	yes	357	.	.
M2	MS026	Perdigões	Portugal	WGS	25071502	33923 (0.135)	0.001	48	0.130	yes	538	.	.
M3	MS027	Perdigões	Portugal	WGS	8685557	256280 (2.951)	0.004	391	1.124	yes	4502	U5a'b	.
M34	MS028	Perdigões	Portugal	WGS	19606903	220056 (1.122)	0.004	180	0.587	yes	3970	H2a2a?	.
M5	MS029	Perdigões	Portugal	WGS	14657860	81902 (0.559)	0.001	109	0.300	yes	1515	U5b1	.
M6	MS030	Perdigões	Portugal	WGS	27468844	51736 (0.188)	0.001	90	0.255	yes	943	U5b1	.
M7	**MS031**	**Covão d'Almeida**	**Portugal**	**WGS**	**25052846**	**1253533 (5.004)**	**0.023**	**797**	**2.347**	**yes**	**22965**	**H3+73**	**.**
M8	MS032	Covão d'Almeida	Portugal	WGS	21478568	690414 (3.214)	0.012	426	1.271	yes	12401	R0	.
M9	MS033	Covão d'Almeida	Portugal	WGS	48904179	13294785 (27.185)	0.220	13524	41.954	yes	.	U5b1	.
M9-2	MS033	Covão d'Almeida	Portugal	WGS	42605851	10905253 (25.596)	0.199	10842	36.581	no	.	U5b1	.
M9-3	MS033	Covão d'Almeida	Portugal	WGS	76497105	19719667 (25.778)	0.358	17085	58.952	yes	.	U5b1	.
M9-4	MS033	Covão d'Almeida	Portugal	WGS	59664907	13435298 (22.518)	0.234	13683	44.788	yes	.	U5b1	.
MS033_merged	**MS033**	**Covão d'Almeida**	**Portugal**	**WGS**	**.**	**57355003**	**0.871**	**55093**	**182.153**	**.**	**618273**	**U5b1**	**.**
M10	MS034	Covão d'Almeida	Portugal	WGS	28553407	143491 (0.503)	0.002	163	0.457	yes	2558	X	.
M14	MS035	Covão d'Almeida	Portugal	WGS	61402876	78021 (0.127)	0.001	45	0.134	yes	1402	.	.
M15	MS036	Covão d'Almeida	Portugal	WGS	35110562	3587709 (10.218)	0.074	2977	10.225	yes	.	J2b1a	.
M15-1	MS036	Covão d'Almeida	Portugal	WGS	70007750	5625754 (8.036)	0.102	5271	16.545	yes	.	J2b1a	.

M15-2	MS036	Covão d'Almeida	Portugal	WGS	81590760	5812956 (7.125)	0.122	4498	16.245	no	.	J2b1a	.
M15-3	MS036	Covão d'Almeida	Portugal	WGS	57178902	3743627 (6.547)	0.072	3688	12.226	yes	.	J2b1a	.
MS036_merged	**MS036**	**Covão d'Almeida**	**Portugal**	**WGS**	**.**	**18770046**	**0.315**	**16417**	**55.192**	**.**	**325583**	**J2b1a**	**I**
M16	MS037	Covão d'Almeida	Portugal	WGS	32734136	3156433 (9.643)	0.063	1881	6.153	yes	.	H1e1c	.
M16-1	MS037	Covão d'Almeida	Portugal	WGS	55464473	4361816 (7.864)	0.081	2902	9.000	yes	.	H1e1c	.
M16-2	MS037	Covão d'Almeida	Portugal	WGS	51150674	3280277 (6.413)	0.069	2137	7.546	no	.	H1e1c	.
M16-3	MS037	Covão d'Almeida	Portugal	WGS	66427140	2587839 (3.896)	0.046	2098	6.248	yes	.	H1e1c	.
MS037_merged	**MS037**	**Covão d'Almeida**	**Portugal**	**WGS**	**.**	**13386365**	**0.224**	**9007**	**28.915**	**.**	**242670**	**H1e1c**	**I**
M17	MS038	Covão d'Almeida	Portugal	WGS	37568727	90002 (0.24)	0.002	62	0.204	yes	1784	.	.
M18	MS039	Covão d'Almeida	Portugal	WGS	30930664	656573 (2.123)	0.011	344	0.989	yes	10913	HV	.
M19	**MS040**	**Covão d'Almeida**	**Portugal**	**WGS**	**34983162**	**2432737 (6.954)**	**0.049**	**1528**	**5.385**	**yes**	**49172**	**U5b1+16189+@16192**	**.**
M20	**MS041**	**Covão d'Almeida**	**Portugal**	**WGS**	**35869137**	**5529272 (15.415)**	**0.115**	**2823**	**9.554**	**yes**	**104889**	**HV0b**	**.**
M21	MS042	Covão d'Almeida	Portugal	WGS	35374523	863783 (2.442)	0.014	438	1.217	yes	14471	U5b2	IJ/I?
M22	MS043	Covão d'Almeida	Portugal	WGS	38304504	2416129 (6.308)	0.040	1991	5.759	yes	43004	H1e2	IJ/I?
M23	MS044	Covão d'Almeida	Portugal	WGS	33960017	48649 (0.143)	0.001	26	0.077	yes	911	.	.
M25	MS045	Covão d'Almeida	Portugal	WGS	88067913	9305632 (10.566)	0.181	4504	14.981	yes	.	U5b1e	.
M25-1	MS045	Covão d'Almeida	Portugal	WGS	47005042	4500814 (9.575)	0.083	2559	8.232	yes	.	U5b1e	.
M25-2	MS045	Covão d'Almeida	Portugal	WGS	67542571	4266604 (6.317)	0.090	2354	8.438	no	.	U5b1e	.
M25-3	MS045	Covão d'Almeida	Portugal	WGS	90456277	6203651 (6.858)	0.116	3752	12.220	yes	.	U5b1e	.
MS045_merged	**MS045**	**Covão d'Almeida**	**Portugal**	**WGS**	**.**	**24276701**	**0.417**	**13147**	**43.800**	**.**	**366668**	**U5b1e**	**.**
M26	**MS046**	**Covão d'Almeida**	**Portugal**	**WGS**	**28013954**	**2766642 (9.876)**	**0.049**	**2772**	**8.643**	**yes**	**51736**	**U5b1e**	**I**
M27	MS047	Covão d'Almeida	Portugal	WGS	39731468	446913 (1.125)	0.008	714	2.086	yes	7752	U5b	.
M28	MS048	Covão d'Almeida	Portugal	WGS	40276617	147124 (0.365)	0.003	291	0.840	yes	2490	K1	.
M29	*MS049*	*Covão d'Almeida*	*Portugal*	*WGS*	*34230379*	922453 (2.695)	*0.015*	*872*	*2.429*	*yes*	*14959*	*K2b1a*	.
M30	MS050	Monte do Carrascal 2	Portugal	WGS	16746609	658410 (3.932)	0.011	447	1.296	yes	11393	R0	.
M31	MS051	Monte do Carrascal 2	Portugal	WGS	21959995	3404338 (15.502)	0.058	2742	7.884	yes	.	X2b+226	.
M31-1	MS051	Monte do Carrascal 2	Portugal	WGS	26634401	3659636 (13.74)	0.057	3285	8.935	yes	.	X2b+226	.
M31-2	MS051	Monte do Carrascal 2	Portugal	WGS	44948152	5075409 (11.292)	0.088	4335	13.231	no	.	X2b+226	.

M31-3	MS051	Monte do Carrascal 2	Portugal	WGS	63989857	5909561 (9.235)	0.091	5433	15.131	yes	.	X2b+226	.
MS051_merged	**MS051**	**Monte do Carrascal 2**	**Portugal**	**WGS**	**.**	**18048944**	**0.235**	**15781**	**45.142**	**.**	**263772**	**X2b+226**	**.**
M32	MS054	Monte do Carrascal 2	Portugal	WGS	30031398	77120 (0.257)	0.001	68	0.189	yes	1308	.	.
M33	MS055	Monte do Carrascal 2	Portugal	WGS	28970126	93786 (0.324)	0.002	77	0.227	yes	1722	.	.
M41	MS063	Arroyo Saladillo	Spain	WGS	33373782	37446 (0.112)	0.001	57	0.176	yes	683	.	.
M42	**MS065**	**Pla de Rambla**	**Spain**	**WGS**	**41963494**	**2774964 (6.613)**	**0.048**	**1676**	**5.059**	**yes**	**48794**	**H3**	**.**
M43	**MS066**	**Cova del Diablets**	**Spain**	**WGS**	**37262460**	**1035878 (2.78)**	**0.016**	**1222**	**3.397**	**yes**	**18507**	**H1q**	**G2?**
M44	MS067	Costa Lloguera	Spain	WGS	11998997	125606 (1.047)	0.002	344	0.979	yes	2273	.	.
M45	**MS068**	**Cova L'Iguala**	**Spain**	**WGS**	**28245766**	**1625879 (5.756)**	**0.031**	**4136**	**12.657**	**yes**	**32288**	**H3**	**.**

Table S2. Contamination estimates. Individuals included in the analysis indicated in bold. Libraries in red display evidence of contamination. Libraries in italics correspond to individuals who are related to others (Figure S5) and were excluded from population analysis. Some libraries did not have enough coverage on chromosome X to run ANGSD.

library ID	DNA code	verifyBamID				ANGSD: Method1 new_llh					schmutzi
		#SNPS	#READS	AVG_DP	FREEMIX	SNPs on X	MoM	SE (MoM)	ML	SE (ML)	
M1	MS025	13536013	4677	0	0.1259	*female*	.	.	.	.	*USER-treated*
M2	MS026	13536013	6933	0	0.0000	*female*	.	.	.	.	*USER-treated*
M3	MS027	13536013	57460	0	0.0000	*female*	.	.	.	.	*USER-treated*
M5	MS029	13536013	18442	0	0.0000	*female*	.	.	.	.	*USER-treated*
M6	MS030	13536013	11670	0	0.0000	*female*	.	.	.	.	*USER-treated*
M7	**MS031**	13536013	304781	0.02	0.0119	*female*	.	.	.	.	*USER-treated*
M8	MS032	13536013	162848	0.01	0.0106	*female*	.	.	.	.	*USER-treated*
M9	MS033	13536013	3030828	0.22	0.0015	*female*	.	.	.	.	*USER-treated*
M9-2	MS033	13536013	2766339	0.2	0.0019	*female*	.	.	.	.	0.01 (0-0.02)
M9-3	MS033	13536013	5059673	0.37	0.0005	*female*	.	.	.	.	*USER-treated*
M9-4	MS033	13536013	3365895	0.25	0.0006	*female*	.	.	.	.	*USER-treated*
MS033_merged	**MS033**	13536013	14210546	1.05	0.0015	*female*	.	.	.	.	*USER-treated*
M10	MS034	13536013	33276	0	0.0867	*female*	.	.	.	.	*USER-treated*
M14	MS035	13536013	19227	0	0.0000	*female*	.	.	.	.	*USER-treated*
M15	MS036	13536013	1044691	0.08	0.0070	<200	0.0448	0.0452	0.0444	0.0000	*USER-treated*
M15-1	MS036	13536013	1442339	0.11	0.0047	<200	0.0347	0.0246	0.0339	0.0000	*USER-treated*
M15-2	MS036	13536013	1747765	0.13	0.0057	<200	0.0608	0.0296	0.0576	0.0000	0.01 (0-0.02)
M15-3	MS036	13536013	1039455	0.08	0.0033	<200	0.0218	0.0254	0.0238	0.0000	*USER-treated*
MS036_merged	**MS036**	13536013	5267284	0.39	0.0022						*USER-treated*
M16	MS037	13536013	884887	0.07	0.0077						*USER-treated*
M16-1	MS037	13536013	1125634	0.08	0.0103	<200	0.0530	0.0367	0.0521	0.0000	*USER-treated*
M16-2	MS037	13536013	985892	0.07	0.0138	<200	-0.0046	0.0048	-0.0019	0.0000	0.01 (0-0.02)
M16-3	MS037	13536013	662040	0.05	0.0104						*USER-treated*
MS037_merged	**MS037**	13536013	3653222	0.27	0.0032						*USER-treated*
M17	MS038	13536013	24308	0	0.0000						*USER-treated*
M18	MS039	13536013	143688	0.01	0.0833	*female*	.	.	.	.	*USER-treated*
M19	**MS040**	13536013	673226	0.05	0.0089	*female*	.	.	.	.	*USER-treated*
M20	**MS041**	13536013	1570886	0.12	0.0046	*female*	.	.	.	.	*USER-treated*

M21	MS042	13536013	189134	0.01	0.0184						*USER-treated*
M22	MS043	13536013	556440	0.04	0.0079	<200	0.1558	0.1614	0.1503	0.0000	*USER-treated*
M23	MS044	13536013	12856	0	0.0000						*USER-treated*
M25	MS045	13536013	884887	0.07	0.0077	*female*	.	.	.	.	*USER-treated*
M25-1	MS045	13536013	1115046	0.08	0.0015	*female*	.	.	.	.	*USER-treated*
M25-2	MS045	13536013	1239792	0.09	0.0096	*female*	.	.	.	.	0.01 (0-0.02)
M25-3	MS045	13536013	1600450	0.12	0.0022	*female*	.	.	.	.	*USER-treated*
MS045_merged	**MS045**	13536013	6391515	0.47	0.0013						*USER-treated*
M26	**MS046**	13536013	690978	0.05	0.0071	<200	0.0602	0.0612	0.0560	0.0000	*USER-treated*
M27	MS047	13536013	104140	0.01	0.0587	*female*	.	.	.	.	*USER-treated*
M28	MS048	13536013	34192	0	0.0000						*USER-treated*
M29	*MS049*	13536013	200886	0.01	0.0215	*female*	.	.	.	.	*USER-treated*
M30	MS050	13536013	150865	0.01	0.0266	*female*	.	.	.	.	*USER-treated*
M31	MS051	13536013	788690	0.06	0.0097	*female*	.	.	.	.	*USER-treated*
M31-1	MS051	13536013	764181	0.06	0.0032	*female*	.	.	.	.	*USER-treated*
M31-2	MS051	13536013	1202559	0.09	0.0047	*female*	.	.	.	.	0.01 (0-0.02)
M31-3	MS051	13536013	1263541	0.09	0.0017	*female*	.	.	.	.	*USER-treated*
MS051_merged	**MS051**	13536013	4014944	0.3	0.0011						*USER-treated*
M32	MS054	13536013	19070	0	0.0726						*USER-treated*
M33	MS055	13536013	23100	0	0.0000	*consistent with XX but not XY*					*USER-treated*
M34	MS028	13536013	54313	0	0.0364	*consistent with XX but not XY*					*USER-treated*
M41	MS063	13536013	8464	0	0.0000						*USER-treated*
M42	**MS065**	13536013	653553	0.05	0.0098	*female*	.	.	.	.	*USER-treated*
M43	**MS066**	13536013	230275	0.02	0.0088	*female*	.	.	.	.	*USER-treated*
M44	MS067	13536013	29723	0	0.1218						*USER-treated*
M45	**MS068**	13536013	419635	0.03	0.0224						*USER-treated*
S11592	**MS002**	13536013	1851919	0.14	0.0017	1718	0.0130	0.0033	0.0143	0.0000	0.04 (0.03-0.05)
S11599	**MS009**	13536013	1067861	0.08	0.0000	625	0.0052	0.0041	0.0042	0.0000	0.01 (0-0.02)
S11601	**MS011**	13536013	266267	0.02	0.0000	*female*	.	.	.	.	0.01 (0-0.02)
S11602	**MS012**	13536013	111437	0.01	0.0207	*female*	.	.	.	.	0.06 (0.04-0.08)
S11603	MS013	13536013	31303	0	0.0000	*consistent with XX but not XY*					0.99 (0.98-0.99)
S11604	**MS014**	13536013	111174	0.01	0.0000						0.01 (0-0.02)
S11605	**MS015**	13536013	1611816	0.12	0.0000	986	0.0067	0.0038	0.0079	0.0000	0.01 (0-0.02)
S11607	*MS017*	13536013	1613850	0.12	0.0001	1015	0.0137	0.0044	0.0133	0.0000	0.01 (0-0.02)
S11614	**MS024**	13536013	1924998	0.14	0.0007	*female*	.	.	.	.	0.01 (0-0.02)

Table S3. Genetic sex assignment of libraries subjected to 1240k-SNP capture at Harvard Medical School.

DNA code	library	Nseqs	NchrY+ NchrX	NchrY	R_y	SE	95% CI	Assignment
MS002	S11592	3135366	86010	22398	0.2604	0.0015	0.2575-0.2633	XY
MS009	S11599	1909324	52500	13569	0.2585	0.0019	0.2547-0.2622	XY
MS011	S11601	536925	21495	236	0.011	0.0007	0.0096-0.0124	XX
MS012	S11602	190501	7585	88	0.0116	0.0012	0.0092-0.014	XX
MS013	S11603	55822	2159	28	0.013	0.0024	0.0082-0.0177	consistent with XX but not XY
MS014	S11604	197838	5188	1255	0.2419	0.0059	0.2303-0.2536	XY
MS015	S11605	2984871	82465	17559	0.2129	0.0014	0.2101-0.2157	XY
MS017	S11607	3389794	93270	19537	0.2095	0.0013	0.2069-0.2121	XY
MS024	S11614	4210104	178703	1583	0.0089	0.0002	0.0084-0.0093	XX

Table S4. Genetic sex assignment for multiple WGS libraries of the same individual.

DNA code	library	Nseqs	NchrY+NchrX	NchrY	R_y	SE	95% CI	Assignment
MS033	M9	13294785	648650	3966	0.0061	0.0001	0.0059-0.0063	XX
	M9-2	10905253	519462	3597	0.0069	0.0001	0.0067-0.0071	XX
	M9-3	19719667	927918	6448	0.0069	0.0001	0.0068-0.0071	XX
	M9-4	13435298	613866	4935	0.008	0.0001	0.0078-0.0083	XX
MS036	M15	3587709	100585	9099	0.0905	0.0009	0.0887-0.0922	XY
	M15-1	5625754	157631	13999	0.0888	0.0007	0.0874-0.0902	XY
	M15-2	5812956	160616	14637	0.0911	0.0007	0.0897-0.0925	XY
	M15-3	3743627	100990	9069	0.0898	0.0009	0.088-0.0916	XY
MS037	M16	3156433	91159	8195	0.0899	0.0009	0.088-0.0918	XY
	M16-1	4361816	124944	11116	0.089	0.0008	0.0874-0.0905	XY
	M16-2	3280277	91040	8522	0.0936	0.001	0.0917-0.0955	XY
	M16-3	2587839	69929	6480	0.0927	0.0011	0.0905-0.0948	XY
MS045	M25	9305632	475370	2612	0.0055	0.0001	0.0053-0.0057	XX
	M25-1	4500814	226159	1508	0.0067	0.0002	0.0063-0.007	XX
	M25-2	4266604	212860	1420	0.0067	0.0002	0.0063-0.007	XX
	M25-3	6203651	302541	2180	0.0072	0.0002	0.0069-0.0075	XX
MS051	M31	3404338	171685	989	0.0058	0.0002	0.0054-0.0061	XX
	M31-1	3659636	182445	1040	0.0057	0.0002	0.0054-0.006	XX
	M31-2	5075409	247587	1643	0.0066	0.0002	0.0063-0.007	XX
	M31-3	5909561	280874	1975	0.007	0.0002	0.0067-0.0073	XX

Table S5. Dataset of present-day samples used for GW analysis, included in datasets i and ii.

Sample	Population label	Sample	Population label	Sample	Population label
HGDP00511	French	HungarianC5	Hungarian	HG01673	Spanish
HGDP00512	French	hungary7	Hungarian	HG01695	Canary_Islander
HGDP00513	French	lithuania10	Lithuanian	HG01694	Canary_Islander
HGDP00514	French	iran3	Iranian	HG01761	Spanish
HGDP00515	French	Lebanon7	Lebanese	HG01770	Spanish
HGDP00516	French	SaudiA6	Saudi	HG01762	Spanish
HGDP00517	French	Jordan445	Jordanian	HG01773	Spanish
HGDP00518	French	BulgarianB1	Bulgarian	HG02220	Spanish
HGDP00519	French	HungarianE5	Hungarian	HG02238	Spanish
HGDP00522	French	HungarianH3	Hungarian	HG01678	Spanish
HGDP00523	French	lithuania9	Lithuanian	HG01699	Spanish
HGDP00524	French	Lebanon8	Lebanese	HG01697	Spanish
HGDP00525	French	SaudiA7	Saudi	HG00160	English
HGDP00526	French	Jordan62	Jordanian	Malta4AM91	Maltese
HGDP00527	French	BulgarianC1	Bulgarian	Malta8AM91	Maltese
HGDP00528	French	hungary15	Hungarian	CRO53	Croatian
HGDP00529	French	LithuanianA1	Lithuanian	NOR119	Norwegian
HGDP00531	French	LithuanianE2	Lithuanian	NOR124	Norwegian
HGDP00533	French	iran11	Iranian	CRO103	Croatian
HGDP00534	French	Lebanon1	Lebanese	CRO107	Croatian
HGDP00535	French	saudi1434	Saudi	TP08	Sicilian
HGDP00536	French	Jordan603	Jordanian	GREEKGRALPOP18	Greek
HGDP00537	French	BulgarianF1	Bulgarian	BEL57	Italian_South
HGDP00538	French	hungary20	Hungarian	BAS35	Basque
HGDP00539	French	lithuania1	Lithuanian	SR23	Sicilian
HGDP00557	Druze	lithuania8	Lithuanian	CRO47	Croatian
HGDP00558	Druze	iran16	Iranian	NOR106	Norwegian
HGDP00559	Druze	Lebanon2	Lebanese	CRO41	Croatian
HGDP00560	Druze	saudi1424	Saudi	Malta7AM91	Maltese
HGDP00561	Druze	SaudiA9	Saudi	NOR101	Norwegian
HGDP00562	Druze	Jordan307	Jordanian	TP05	Sicilian
HGDP00563	Druze	BulgarianH2	Bulgarian	Kayseri24392	Turkish
HGDP00564	Druze	hungary2	Hungarian	SR60	Sicilian
HGDP00565	Druze	lithuania2	Lithuanian	NOR146	Norwegian
HGDP00566	Druze	iran17	Iranian	TP06	Sicilian
HGDP00567	Druze	Lebanon3	Lebanese	NOR108	Norwegian
HGDP00568	Druze	Jordan503	Jordanian	CRO66	Croatian
HGDP00569	Druze	BulgarianF2	Bulgarian	NOR126	Norwegian
HGDP00571	Druze	HungarianD1	Hungarian	GREEKGRALPOP13	Greek
HGDP00572	Druze	LithuanianD1	Lithuanian	TP07	Sicilian
HGDP00573	Druze	Lebanon4	Lebanese	BAS31	Basque
HGDP00574	Druze	SaudiA1	Saudi	ALB191	Albanian
HGDP00575	Druze	Jordan646	Jordanian	GREEKGRALPOP15	Greek
HGDP00577	Druze	Jordan384	Jordanian	NOR107	Norwegian
HGDP00578	Druze	bal102	Balkar	GREEKGRALPOP5	Greek
HGDP00579	Druze	bal64	Balkar	CRO153	Croatian
HGDP00580	Druze	mg43	Georgian	NOR109	Norwegian
HGDP00582	Druze	NorthOssetia19	North_Ossetian	SouthFrench3326	French
HGDP00583	Druze	ch126	Chechen	GREEKGRALPOP9	Greek
HGDP00584	Druze	abh27	Abkhasian	TP04	Sicilian
HGDP00586	Druze	armenia176	Armenian	CRO31	Croatian
HGDP00587	Druze	lez38	Lezgin	TP25	Sicilian
HGDP00588	Druze	nogay42	Nogai	GREEKGRALPOP4	Greek
HGDP00591	Druze	bal124	Balkar	CRO93	Croatian
HGDP00594	Druze	bal97	Balkar	Malta17AM91	Maltese
HGDP00595	Druze	mg47	Georgian	SouthFrench3947	French
HGDP00597	Druze	NorthOssetia2	North_Ossetian	SouthFrench1323	French
HGDP00598	Druze	ch16	Chechen	SR48R	Sicilian
HGDP00599	Druze	abh107	Abkhasian	Balikesir16675	Turkish
HGDP00600	Druze	abh41	Abkhasian	SR44	Sicilian
HGDP00601	Druze	armenia191	Armenian	SR64	Sicilian
HGDP00602	Druze	lez40	Lezgin	NOR148	Norwegian
HGDP00604	Druze	nogay35	Nogai	CYP19	Cypriot
HGDP00606	Druze	nogay34	Nogai	CRO48	Croatian
HGDP00607	BedouinB	bal136	Balkar	GREEKGRALPOP17	Greek

HGDP00608	BedouinB	mg22	Georgian	ALB213	Albanian
HGDP00609	BedouinA	mg49	Georgian	Turkish7BA57	Turkish
HGDP00610	BedouinB	NorthOssetia3	North_Ossetian	BAS22	Basque
HGDP00611	BedouinA	ch174	Chechen	GREEKGRALPOP16	Greek
HGDP00612	BedouinB	abh119	Abkhasian	Balikesir16790	Turkish
HGDP00613	BedouinA	armenia86	Armenian	NOR111	Norwegian
HGDP00614	BedouinA	armenia279	Armenian	SouthFrench3951	French
HGDP00615	BedouinA	nogay24	Nogai	BAS25	Basque
HGDP00616	BedouinB	bal22	Balkar	BAS32	Basque
HGDP00618	BedouinB	mg23	Georgian	GREEKGRALPOP11	Greek
HGDP00619	BedouinA	mg62	Georgian	GREEKGRALPOP10	Greek
HGDP00620	BedouinA	NorthOssetia5	North_Ossetian	Malta2AM91	Maltese
HGDP00622	BedouinA	ch179	Chechen	GREEKGRALPOP3	Greek
HGDP00623	BedouinB	abh122	Abkhasian	Malta16AM91	Maltese
HGDP00624	BedouinB	armenia91	Armenian	GREEKGRALPOP8	Greek
HGDP00625	BedouinA	armenia293	Armenian	Turkish8BA62	Turkish
HGDP00626	BedouinA	lez49	Lezgin	CYP5	Cypriot
HGDP00628	BedouinA	nogay25	Nogai	SouthFrench3068	French
HGDP00629	BedouinA	bal41	Balkar	Cyprus13AJ19	Cypriot
HGDP00630	BedouinB	mg27	Georgian	Malta15AM91	Maltese
HGDP00631	BedouinB	NorthOssetia11	North_Ossetian	Istanbul20010	Turkish
HGDP00632	BedouinA	NorthOssetia8	North_Ossetian	BAS30	Basque
HGDP00634	BedouinA	ch193	Chechen	Cyprus24AJ19	Cypriot
HGDP00635	BedouinA	abh133	Abkhasian	Turkish4BA57	Turkish
HGDP00636	BedouinB	armenia102	Armenian	ALB202	Albanian
HGDP00637	BedouinA	lez31	Lezgin	GREEKGRALPOP12	Greek
HGDP00638	BedouinA	lez7	Lezgin	SouthFrench1112	French
HGDP00639	BedouinA	nogay33	Nogai	CYP2	Cypriot
HGDP00640	BedouinA	bal42	Balkar	Cyprus2AJ19	Cypriot
HGDP00641	BedouinB	mg31	Georgian	Adana23114	Turkish
HGDP00642	BedouinA	NorthOssetia12	North_Ossetian	GREEKGRALPOP14	Greek
HGDP00643	BedouinB	NorthOssetia9	North_Ossetian	SouthFrench4018	French
HGDP00644	BedouinA	ch21	Chechen	Trabzon21177	Turkish
HGDP00645	BedouinA	abh147	Abkhasian	BAS28	Basque
HGDP00646	BedouinA	armenia106	Armenian	Aydin18784	Turkish
HGDP00647	BedouinA	lez33	Lezgin	Istanbul19810	Turkish
HGDP00648	BedouinB	lez9	Lezgin	Trabzon21557	Turkish
HGDP00649	BedouinB	nogay44	Nogai	ALB212	Albanian
HGDP00650	BedouinB	bal45	Balkar	ALB220	Albanian
HGDP00651	BedouinB	mg34	Georgian	Cyprus22AJ19	Cypriot
HGDP00653	BedouinB	NorthOssetia14	North_Ossetian	Malta12AM91	Maltese
HGDP00654	BedouinA	ch3	Chechen	Trabzon21534	Turkish
HGDP00666	Sardinian	abh154	Abkhasian	BAS27	Basque
HGDP00667	Sardinian	armenia139	Armenian	Cyprus21AJ19	Cypriot
HGDP00668	Sardinian	lez36	Lezgin	Turkish9BA57	Turkish
HGDP00669	Sardinian	nogay45	Nogai	Kayseri24075	Turkish
HGDP00670	Sardinian	bal50	Balkar	ALB230	Albanian
HGDP00671	Sardinian	mg40	Georgian	Adana23108	Turkish
HGDP00672	Sardinian	NorthOssetia17	North_Ossetian	Balikesir16887	Turkish
HGDP00673	Sardinian	ch113	Chechen	BAS33	Basque
HGDP00674	Sardinian	ch31	Chechen	Kayseri24266	Turkish
HGDP00675	Palestinian	abh24	Abkhasian	Balikesir16653	Turkish
HGDP00676	Palestinian	armenia162	Armenian	Istanbul25095	Turkish
HGDP00677	Palestinian	lez37	Lezgin	Aydin18112	Turkish
HGDP00679	Palestinian	nogay46	Nogai	Kayseri24402	Turkish
HGDP00680	Palestinian	bel43s	Belarusian	Istanbul25081	Turkish
HGDP00683	Palestinian	UkrBel618	Ukrainian	Aydin18596	Turkish
HGDP00684	Palestinian	UkrLv240	Ukrainian	Istanbul17778	Turkish
HGDP00685	Palestinian	Est393	Estonian	Istanbul15781	Turkish
HGDP00686	Palestinian	Mordovians27	Mordovian	Adana23136	Turkish
HGDP00687	Palestinian	bel30s	Belarusian	Adana23113	Turkish
HGDP00688	Palestinian	UkrBel620	Ukrainian	Trabzon21575	Turkish
HGDP00689	Palestinian	Est375	Estonian	Aydin18636	Turkish
HGDP00690	Palestinian	Est380	Estonian	Istanbul20040	Turkish
HGDP00691	Palestinian	Mordovians28	Mordovian	Balikesir16837	Turkish
HGDP00694	Palestinian	bel72c	Belarusian	Adana23144	Turkish
HGDP00696	Palestinian	UkrBel622	Ukrainian	Kayseri23967	Turkish
HGDP00697	Palestinian	Est391	Estonian	Trabzon21174	Turkish
HGDP00698	Palestinian	Est377	Estonian	Aydin18873	Turkish
HGDP00699	Palestinian	Mordovians30	Mordovian	Kayseri23892	Turkish

HGDP00700	Palestinian	bel93c	Belarusian	Istanbul19185	Turkish
HGDP00701	BedouinB	UkrBel733	Ukrainian	Istanbul25098	Turkish
HGDP00722	Palestinian	Est372	Estonian	Adana23133	Turkish
HGDP00724	Palestinian	Mordovians4	Mordovian	Trabzon21515	Turkish
HGDP00725	Palestinian	Mordovians31	Mordovian	Kayseri24032	Turkish
HGDP00726	Palestinian	bel110c	Belarusian	Kayseri23549	Turkish
HGDP00727	Palestinian	UkrBel736	Ukrainian	Trabzon21544	Turkish
HGDP00729	Palestinian	Est358	Estonian	Adana23150	Turkish
HGDP00730	Palestinian	Mordovians17	Mordovian	Kayseri23271	Turkish
HGDP00731	Palestinian	Mordovians1	Mordovian	Trabzon21645	Turkish
HGDP00732	Palestinian	bel8s	Belarusian	Adana23147	Turkish
HGDP00733	Palestinian	belarusian23vp	Belarusian	Aydin18483	Turkish
HGDP00734	Palestinian	Est400	Estonian	Balikesir17006	Turkish
HGDP00735	Palestinian	Mordovians22	Mordovian	Aydin18419	Turkish
HGDP00736	Palestinian	bel23s	Belarusian	Kayseri24276	Turkish
HGDP00737	Palestinian	belarusian47zp	Belarusian	Istanbul19708	Turkish
HGDP00739	Palestinian	UkrLv228	Ukrainian	Trabzon21173	Turkish
HGDP00740	Palestinian	Est397	Estonian	Adana23112	Turkish
HGDP00741	Palestinian	Mordovians32	Mordovian	Adana23117	Turkish
HGDP00745	Palestinian	bel82s	Belarusian	Lebanese1AQ127	Lebanese_Christian
HGDP00794	Orcadian	UkrBel614	Ukrainian	Lebanese1AQ170	Lebanese_Christian
HGDP00796	Orcadian	UkrLv237	Ukrainian	Lebanese2AQ121	Lebanese_Muslim
HGDP00797	Orcadian	Est394	Estonian	Lebanese2AQ127	Lebanese_Muslim
HGDP00798	Orcadian	Mordovians5	Mordovian	Lebanese4AQ115	Lebanese_Christian
HGDP00799	Orcadian	saudi1403	Saudi	Lebanese6AQ115	Lebanese_Christian
HGDP00800	Orcadian	NA15202	Hungarian	Lebanese6AQ170	Lebanese_Christian
HGDP00802	Orcadian	NA15725	Czech	Lebanese6AS15	Lebanese_Muslim
HGDP00803	Orcadian	NA15733	Czech	Lebanese7AQ150	Lebanese_Muslim
HGDP00805	Orcadian	NA15762	Icelandic	Lebanese7AR20	Lebanese_Muslim
HGDP00806	Orcadian	NA17373	Greek	Lebanese7AR23	Lebanese_Muslim
HGDP00807	Orcadian	NA15203	Hungarian	Lebanese8AS15	Lebanese_Christian
HGDP00808	Orcadian	NA15726	Czech	Lebanese10AQ127	Lebanese_Muslim
HGDP00810	Orcadian	NA15755	Icelandic	Lebanese10AR37	Lebanese_Christian
HGDP00879	Russian	NA15763	Icelandic	Lebanese11AS14	Lebanese_Muslim
HGDP00880	Russian	NA17374	Greek	Lebanese15AR37	Lebanese_Christian
HGDP00882	Russian	NA15204	Hungarian	Lebanese20AR21	Lebanese_Muslim
HGDP00883	Russian	NA15727	Czech	Lebanese22BA23	Lebanese_Christian
HGDP00884	Russian	NA15756	Icelandic	Lebanese24AR27	Lebanese_Muslim
HGDP00887	Russian	NA15764	Icelandic	Lebanese30AR21	Lebanese_Muslim
HGDP00888	Russian	NA17375	Greek	French23812	French
HGDP00889	Russian	NA15205	Hungarian	French23814	French
HGDP00890	Russian	NA15728	Czech	French23821	French
HGDP00891	Russian	NA15757	Icelandic	French23830	French
HGDP00892	Russian	NA15765	Icelandic	French23833	French
HGDP00893	Russian	NA17376	Greek	French23862	French
HGDP00894	Russian	NA15206	Hungarian	French23915	French
HGDP00895	Russian	NA15729	Czech	French23919	French
HGDP00896	Russian	NA15758	Icelandic	French23989	French
HGDP00897	Russian	NA15766	Icelandic	French24061	French
HGDP00898	Russian	NA17377	Greek	French24075	French
HGDP00899	Russian	NA15199	Hungarian	French24076	French
HGDP00900	Russian	NA15207	Hungarian	French24090	French
HGDP00901	Russian	NA15730	Czech	French24118	French
HGDP00902	Russian	NA15759	Icelandic	French24120	French
HGDP00903	Russian	NA15200	Hungarian	French24124	French
HGDP01062	Sardinian	NA15208	Hungarian	French24144	French
HGDP01063	Sardinian	NA15731	Czech	French24148	French
HGDP01064	Sardinian	NA15760	Icelandic	French24178	French
HGDP01065	Sardinian	NA15201	Hungarian	French24247	French
HGDP01066	Sardinian	NA15724	Czech	French24381	French
HGDP01067	Sardinian	NA15732	Czech	French24400	French
HGDP01068	Sardinian	NA15761	Icelandic	French24408	French
HGDP01069	Sardinian	NA17372	Greek	French24433	French
HGDP01070	Sardinian	HG00103	Scottish	French24434	French
HGDP01071	Sardinian	HG00104	Scottish	French24437	French
HGDP01072	Sardinian	HG00105	Scottish	French24690	French
HGDP01073	Sardinian	HG00106	Scottish	French24817	French
HGDP01074	Sardinian	HG00128	English	French25068	French
HGDP01075	Sardinian	HG00129	English	PV001	Iranian_Bandari
HGDP01076	Sardinian	HG00130	English	PV002	Iranian_Bandari

HGDP01077	Sardinian
HGDP01078	Sardinian
HGDP01079	Sardinian
HGDP01147	Italian_North
HGDP01151	Italian_North
HGDP01152	Italian_North
HGDP01153	Italian_North
HGDP01155	Italian_North
HGDP01156	Italian_North
HGDP01157	Italian_North
HGDP01161	Italian_North
HGDP01162	Italian_North
HGDP01163	Italian_North
HGDP01164	Italian_North
HGDP01166	Italian_North
HGDP01167	Italian_North
HGDP01168	Italian_North
HGDP01169	Italian_North
HGDP01171	Italian_North
HGDP01172	Italian_North
HGDP01173	Italian_North
HGDP01174	Italian_North
HGDP01177	Italian_North
HGDP01357	Basque
HGDP01358	Basque
HGDP01359	Basque
HGDP01360	Basque
HGDP01362	Basque
HGDP01363	Basque
HGDP01364	Basque
HGDP01365	Basque
HGDP01366	Basque
HGDP01367	Basque
HGDP01368	Basque
HGDP01370	Basque
HGDP01371	Basque
HGDP01373	Basque
HGDP01374	Basque
HGDP01375	Basque
HGDP01377	Basque
HGDP01378	Basque
HGDP01379	Basque
HGDP01380	Basque
BulgarianD6	Bulgarian
BulgarianA4	Bulgarian
hungary3	Hungarian
LithuanianF1	Lithuanian
iran19	Iranian
iran14	Iranian
Lebanon5	Lebanese
Jordan543	Jordanian
BulgarianE2	Bulgarian
BulgarianB4	Bulgarian
hungary6	Hungarian
lithuania3	Lithuanian
iran2	Iranian
iran20	Iranian
Lebanon6	Lebanese
SaudiA5	Saudi
Jordan214	Jordanian
BulgarianA1	Bulgarian
HG00131	English
HG00233	English
HG00234	English
HG00232	English
HG01500	Spanish
HG01501	Spanish
HG01503	Spanish
HG01504	Spanish
HG01506	Spanish
HG01507	Spanish
HG01509	Spanish
HG01510	Spanish
HG01512	Spanish
HG01513	Spanish
HG01515	Spanish_North
HG01516	Spanish_North
HG01518	Spanish_North
HG01524	Spanish
HG01527	Spanish
HG01528	Spanish
HG01530	Spanish
HG01536	Spanish
HG01537	Spanish
HG01605	Spanish
HG01606	Spanish
HG01607	Spanish
HG01608	Spanish
HG01613	Spanish
HG01615	Spanish
HG01617	Spanish
HG01618	Spanish
HG01619	Spanish
HG01620	Spanish
HG01623	Spanish
HG01624	Spanish
HG01625	Spanish
HG01626	Spanish
HG00171	Finnish
HG00174	Finnish
HG00190	Finnish
HG00266	Finnish
HG00231	English
HG00183	Finnish
HG00126	English
HG00173	Finnish
HG00182	Finnish
HG01747	Spanish
HG01746	Spanish
HG01675	Spanish
HG01680	Spanish
HG01682	Spanish
HG01700	Spanish_North
HG01679	Spanish
HG01702	Spanish_North
HG01676	Spanish
HG01684	Spanish
HG01705	Spanish
HG01707	Spanish
HG01685	Spanish
HG01686	Spanish
HG01704	Spanish
PV003	Iranian_Bandari
PV004	Iranian_Bandari
PV005	Iranian_Bandari
PV006	Iranian_Bandari
PV007	Iranian_Bandari
PV008	Iranian_Bandari
PV019	Iranian
PV020	Iranian
PV021	Iranian
PV022	Iranian
PV023	Iranian
PV024	Iranian
PV025	Iranian
PV026	Iranian
PV027	Iranian
PV028	Iranian
ITS2	Italian_South
ITS4	Italian_South
ITS5	Italian_South
ITS7	Italian_South
PV009	Iranian
PV010	Iranian
PV011	Iranian
PV012	Iranian
PV013	Iranian
PV014	Iranian
PV015	Iranian
PV016	Iranian
PV017	Iranian
PV018	Iranian
PV029	Iranian
PV030	Iranian
PV031	Iranian
PV032	Iranian
PV033	Iranian
PV034	Iranian
PV035	Iranian
PV036	Iranian
PV037	Iranian
PV038	Iranian
A306	Romanian
A325	Romanian
A343	Romanian
A362	Romanian
A374	Romanian
Assyrian151	Assyrian
Assyrian152	Assyrian
Assyrian153	Assyrian
Assyrian155	Assyrian
Assyrian159	Assyrian
Assyrian160	Assyrian
Assyrian161	Assyrian
Assyrian162	Assyrian
Assyrian163	Assyrian
Assyrian164	Assyrian
Assyrian165	Assyrian
G408	Romanian
G421	Romanian
G428	Romanian
G429	Romanian
G434	Romanian

Table S6. Dataset of ancient samples used for GW analysis, included in datasets ii and iii. C/EHG, Meso, (E/M/L)N, CA/Chl, BB, BA, IA, Hel. And RomP. stand for Caucasus/Easter hunter-gatherers, Mesolithic, (Early/Middle/Late) Neolithic, Copper Age/Chalcolithic, Bell Beaker, Bronze Age, Iron Age, Helenistic and Roman Period, respectively.

Sample	Population label	Reference
I0644	Levant_Chl	Harney et al. (2018)
I1152	Levant_Chl	Harney et al. (2018)
I1154	Levant_Chl	Harney et al. (2018)
I1155	Levant_Chl	Harney et al. (2018)
I1160	Levant_Chl	Harney et al. (2018)
I1164	Levant_Chl	Harney et al. (2018)
I1165	Levant_Chl	Harney et al. (2018)
I1168	Levant_Chl	Harney et al. (2018)
I1169	Levant_Chl	Harney et al. (2018)
I1170	Levant_Chl	Harney et al. (2018)
I1171	Levant_Chl	Harney et al. (2018)
I1172	Levant_Chl	Harney et al. (2018)
I1177	Levant_Chl	Harney et al. (2018)
I1178	Levant_Chl	Harney et al. (2018)
I1179	Levant_Chl	Harney et al. (2018)
I1181	Levant_Chl	Harney et al. (2018)
I1182	Levant_Chl	Harney et al. (2018)
I1184	Levant_Chl	Harney et al. (2018)
I1187	Levant_Chl	Harney et al. (2018)
KK1	CHG	Jones et al. (2015)
SATP	CHG	Jones et al. (2015)
I1705	Levant_BA	Lazaridis et al. (2016)
I1706	Levant_BA	Lazaridis et al. (2016)
I1730	Levant_BA	Lazaridis et al. (2016)
I0867	Levant_N	Lazaridis et al. (2016)
I1414	Levant_N	Lazaridis et al. (2016)
I1415	Levant_N	Lazaridis et al. (2016)
I1416	Levant_N	Lazaridis et al. (2016)
I1679	Levant_N	Lazaridis et al. (2016)
I1699	Levant_N	Lazaridis et al. (2016)
I1700	Levant_N	Lazaridis et al. (2016)
I1701	Levant_N	Lazaridis et al. (2016)
I1704	Levant_N	Lazaridis et al. (2016)
I1707	Levant_N	Lazaridis et al. (2016)
I1709	Levant_N	Lazaridis et al. (2016)
I1710	Levant_N	Lazaridis et al. (2016)
I1727	Levant_N	Lazaridis et al. (2016)
I0861	Natufian	Lazaridis et al. (2016)
I1069	Natufian	Lazaridis et al. (2016)
I1072	Natufian	Lazaridis et al. (2016)
I1685	Natufian	Lazaridis et al. (2016)
I1687	Natufian	Lazaridis et al. (2016)
I1690	Natufian	Lazaridis et al. (2016)
CabecoArruda117B	Portugal_LN-Chl	Martiniano et al. (2017)
CabecoArruda122A	Portugal_LN-Chl	Martiniano et al. (2017)
CovaMoura364	Portugal_LN-Chl	Martiniano et al. (2017)
CovaMoura9B	Portugal_LN-Chl	Martiniano et al. (2017)
DolmenAnsiao96B	Portugal_LN-Chl	Martiniano et al. (2017)
MonteCanelas337A	Portugal_LN-Chl	Martiniano et al. (2017)
MonteGato104	Portugal_MBA	Martiniano et al. (2017)
TV32032	Portugal_MBA	Martiniano et al. (2017)
TV3831	Portugal_MBA	Martiniano et al. (2017)
ValeOuro10207	Portugal_MBA	Martiniano et al. (2017)
LugarCanto41	Portugal_MN	Martiniano et al. (2017)
LugarCanto42	Portugal_MN	Martiniano et al. (2017)
LugarCanto44	Portugal_MN	Martiniano et al. (2017)
LugarCanto45	Portugal_MN	Martiniano et al. (2017)
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I0708	Anatolia_N	Mathieson et al. (2015)
I0709	Anatolia_N	Mathieson et al. (2015)
I0723	Anatolia_N	Mathieson et al. (2015)
I0724	Anatolia_N	Mathieson et al. (2015)
I0725	Anatolia_N	Mathieson et al. (2015)
I0726	Anatolia_N	Mathieson et al. (2015)
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I0744	Anatolia_N	Mathieson et al. (2015)
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I1099	Anatolia_N	Mathieson et al. (2015)
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I1103	Anatolia_N	Mathieson et al. (2015)
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I1583	Anatolia_N	Mathieson et al. (2015)
I1585	Anatolia_N	Mathieson et al. (2015)
I0061	EHG	Mathieson et al. (2015)
I0124	EHG	Mathieson et al. (2015)
I0231	Yamnaya	Mathieson et al. (2015)
I0357	Yamnaya	Mathieson et al. (2015)
I0370	Yamnaya	Mathieson et al. (2015)
I0429	Yamnaya	Mathieson et al. (2015)
I0438	Yamnaya	Mathieson et al. (2015)
I0439	Yamnaya	Mathieson et al. (2015)
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I7275	Central_Europe_BB	Olalde et al. (2018)
I7276	Central_Europe_BB	Olalde et al. (2018)

I7278	Central_Europe_BB	Olalde et al. (2018)
I7281	Central_Europe_BB	Olalde et al. (2018)
I7282	Central_Europe_BB	Olalde et al. (2018)
I7283	Central_Europe_BB	Olalde et al. (2018)
I7286	Central_Europe_BB	Olalde et al. (2018)
I7287	Central_Europe_BB	Olalde et al. (2018)
I7288	Central_Europe_BB	Olalde et al. (2018)
I7289	Central_Europe_BB	Olalde et al. (2018)
I7290	Central_Europe_BB	Olalde et al. (2018)
I7272	Central_Europe_CW	Olalde et al. (2018)
I7279	Central_Europe_CW	Olalde et al. (2018)
I7280	Central_Europe_CW	Olalde et al. (2018)
I4884	Central_Europe_EBA	Olalde et al. (2018)
I4892	Central_Europe_EBA	Olalde et al. (2018)
I5035	Central_Europe_EBA	Olalde et al. (2018)
I5037	Central_Europe_EBA	Olalde et al. (2018)
I5042	Central_Europe_EBA	Olalde et al. (2018)
I5043	Central_Europe_EBA	Olalde et al. (2018)
I5044	Central_Europe_EBA	Olalde et al. (2018)
I7195	Central_Europe_EBA	Olalde et al. (2018)
I7196	Central_Europe_EBA	Olalde et al. (2018)
I7197	Central_Europe_EBA	Olalde et al. (2018)
I7198	Central_Europe_EBA	Olalde et al. (2018)
I7199	Central_Europe_EBA	Olalde et al. (2018)
I7200	Central_Europe_EBA	Olalde et al. (2018)
I7201	Central_Europe_EBA	Olalde et al. (2018)
I7202	Central_Europe_EBA	Olalde et al. (2018)
I7203	Central_Europe_EBA	Olalde et al. (2018)
I5116	Central_Europe_LChl	Olalde et al. (2018)
I5117	Central_Europe_LChl	Olalde et al. (2018)
I5118	Central_Europe_LChl	Olalde et al. (2018)
I5119	Central_Europe_LChl	Olalde et al. (2018)
I4303	Central_Europe_MLN	Olalde et al. (2018)
I4304	Central_Europe_MLN	Olalde et al. (2018)
I4305	Central_Europe_MLN	Olalde et al. (2018)
I4308	Central_Europe_MLN	Olalde et al. (2018)
I4893	Central_Europe_MN	Olalde et al. (2018)
I4894	Central_Europe_MN	Olalde et al. (2018)
I1388	Mediterranean_BB	Olalde et al. (2018)
I2575	Mediterranean_BB	Olalde et al. (2018)
I3874	Mediterranean_BB	Olalde et al. (2018)
I3875	Mediterranean_BB	Olalde et al. (2018)
I4930	Mediterranean_BB	Olalde et al. (2018)
I4933	Mediterranean_BB	Olalde et al. (2018)
I4936	Mediterranean_BB	Olalde et al. (2018)
I0839	Portugal_BB	Olalde et al. (2018)
I0840	Portugal_BB	Olalde et al. (2018)
I1970	Portugal_BB	Olalde et al. (2018)
I4229	Portugal_BB	Olalde et al. (2018)
I6467	Portugal_BB	Olalde et al. (2018)
I6601	Portugal_N_EBA	Olalde et al. (2018)
I0257	Spain_BB	Olalde et al. (2018)
I0258	Spain_BB	Olalde et al. (2018)
I0260	Spain_BB	Olalde et al. (2018)
I0261	Spain_BB	Olalde et al. (2018)
I0262	Spain_BB	Olalde et al. (2018)
I0263	Spain_BB	Olalde et al. (2018)
I0453	Spain_BB	Olalde et al. (2018)
I0455	Spain_BB	Olalde et al. (2018)
I0459	Spain_BB	Olalde et al. (2018)
I0460	Spain_BB	Olalde et al. (2018)
I0461	Spain_BB	Olalde et al. (2018)
I0462	Spain_BB	Olalde et al. (2018)
I0823	Spain_BB	Olalde et al. (2018)
I0825	Spain_BB	Olalde et al. (2018)
I0826	Spain_BB	Olalde et al. (2018)
I1553	Spain_BB	Olalde et al. (2018)
I4245	Spain_BB	Olalde et al. (2018)
I4247	Spain_BB	Olalde et al. (2018)
I5665	Spain_BB	Olalde et al. (2018)
I6471	Spain_BB	Olalde et al. (2018)
I6472	Spain_BB	Olalde et al. (2018)
I6475	Spain_BB	Olalde et al. (2018)
I6539	Spain_BB	Olalde et al. (2018)
I6542	Spain_BB	Olalde et al. (2018)
I6584	Spain_BB	Olalde et al. (2018)
I6587	Spain_BB	Olalde et al. (2018)
I6588	Spain_BB	Olalde et al. (2018)
I6622	Spain_BB	Olalde et al. (2018)

I6623	Spain_BB	Olalde et al. (2018)
I0456	Spain_Chl	Olalde et al. (2018)
I0457	Spain_Chl	Olalde et al. (2018)
I6543	Spain_Chl	Olalde et al. (2018)
I6596	Spain_Chl	Olalde et al. (2018)
I6604	Spain_Chl	Olalde et al. (2018)
I6605	Spain_Chl	Olalde et al. (2018)
I6608	Spain_Chl	Olalde et al. (2018)
I6609	Spain_Chl	Olalde et al. (2018)
I6612	Spain_Chl	Olalde et al. (2018)
I6613	Spain_Chl	Olalde et al. (2018)
I6617	Spain_Chl	Olalde et al. (2018)
I6628	Spain_Chl	Olalde et al. (2018)
I6629	Spain_Chl	Olalde et al. (2018)
I6630	Spain_Chl	Olalde et al. (2018)
I10939	Gibraltar_BA	Olalde et al. (2019)
I10940	Gibraltar_BA	Olalde et al. (2019)
I10941	Gibraltar_BA	Olalde et al. (2019)
I10942	Gibraltar_EN	Olalde et al. (2019)
I7688	Portugal_BA	Olalde et al. (2019)
I7689	Portugal_BA	Olalde et al. (2019)
I7691	Portugal_BA	Olalde et al. (2019)
I7692	Portugal_BA	Olalde et al. (2019)
I8045	Portugal_BA	Olalde et al. (2019)
I5076	Portugal_Chl	Olalde et al. (2019)
I5428	Portugal_Chl	Olalde et al. (2019)
I5429	Portugal_Chl	Olalde et al. (2019)
I12208	Spain_BA	Olalde et al. (2019)
I12209	Spain_BA	Olalde et al. (2019)
I12809	Spain_BA	Olalde et al. (2019)
I1310	Spain_BA	Olalde et al. (2019)
I1836	Spain_BA	Olalde et al. (2019)
I1840	Spain_BA	Olalde et al. (2019)
I1977	Spain_BA	Olalde et al. (2019)
I1982	Spain_BA	Olalde et al. (2019)
I2469	Spain_BA	Olalde et al. (2019)
I2470	Spain_BA	Olalde et al. (2019)
I2471	Spain_BA	Olalde et al. (2019)
I2472	Spain_BA	Olalde et al. (2019)
I3486	Spain_BA	Olalde et al. (2019)
I3487	Spain_BA	Olalde et al. (2019)
I3488	Spain_BA	Olalde et al. (2019)
I3490	Spain_BA	Olalde et al. (2019)
I3491	Spain_BA	Olalde et al. (2019)
I3492	Spain_BA	Olalde et al. (2019)
I3493	Spain_BA	Olalde et al. (2019)
I3494	Spain_BA	Olalde et al. (2019)
I3576	Spain_BA	Olalde et al. (2019)
I3577	Spain_BA	Olalde et al. (2019)
I4559	Spain_BA	Olalde et al. (2019)
I4560	Spain_BA	Olalde et al. (2019)
I4561	Spain_BA	Olalde et al. (2019)
I4562	Spain_BA	Olalde et al. (2019)
I6470	Spain_BA	Olalde et al. (2019)
I6618	Spain_BA	Olalde et al. (2019)
I7162	Spain_BA	Olalde et al. (2019)
I8136	Spain_BA	Olalde et al. (2019)
I8144	Spain_BA	Olalde et al. (2019)
I8570	Spain_BA	Olalde et al. (2019)
I8571	Spain_BA	Olalde et al. (2019)
VAD001	Spain_BA	Olalde et al. (2019)
VAD002	Spain_BA	Olalde et al. (2019)
VAD003	Spain_BA	Olalde et al. (2019)
VAD004	Spain_BA	Olalde et al. (2019)
VAD005	Spain_BA	Olalde et al. (2019)
EHU001	Spain_Chl	Olalde et al. (2019)
EHU002	Spain_Chl	Olalde et al. (2019)
I1842	Spain_Chl	Olalde et al. (2019)
I1845	Spain_Chl	Olalde et al. (2019)
I1846	Spain_Chl	Olalde et al. (2019)
I1978	Spain_Chl	Olalde et al. (2019)
I3238	Spain_Chl	Olalde et al. (2019)
I3239	Spain_Chl	Olalde et al. (2019)
I3243	Spain_Chl	Olalde et al. (2019)
I3484	Spain_Chl	Olalde et al. (2019)
I3485	Spain_Chl	Olalde et al. (2019)
I4246	Spain_Chl	Olalde et al. (2019)
I4565	Spain_Chl	Olalde et al. (2019)
I7587	Spain_Chl	Olalde et al. (2019)

I8048	Spain_Chl	Olalde et al. (2019)
I8131	Spain_Chl	Olalde et al. (2019)
I8149	Spain_Chl	Olalde et al. (2019)
I8150	Spain_Chl	Olalde et al. (2019)
I8153	Spain_Chl	Olalde et al. (2019)
I8156	Spain_Chl	Olalde et al. (2019)
I8158	Spain_Chl	Olalde et al. (2019)
I8197	Spain_Chl	Olalde et al. (2019)
I8198	Spain_Chl	Olalde et al. (2019)
I8199	Spain_Chl	Olalde et al. (2019)
I8364	Spain_Chl	Olalde et al. (2019)
I8365	Spain_Chl	Olalde et al. (2019)
I8566	Spain_Chl	Olalde et al. (2019)
I8569	Spain_Chl	Olalde et al. (2019)
I0843	Spain_Meso	Olalde et al. (2019)
I3209	Spain_Meso	Olalde et al. (2019)
I8130	Spain_Meso	Olalde et al. (2019)
I10277	Spain_MLN	Olalde et al. (2019)
I10278	Spain_MLN	Olalde et al. (2019)
I10280	Spain_MLN	Olalde et al. (2019)
I10283	Spain_MLN	Olalde et al. (2019)
I10285	Spain_MLN	Olalde et al. (2019)
I10287	Spain_MLN	Olalde et al. (2019)
I11248	Spain_MLN	Olalde et al. (2019)
I11249	Spain_MLN	Olalde et al. (2019)
I11300	Spain_MLN	Olalde et al. (2019)
I11301	Spain_MLN	Olalde et al. (2019)
I11303	Spain_MLN	Olalde et al. (2019)
I11304	Spain_MLN	Olalde et al. (2019)
I11305	Spain_MLN	Olalde et al. (2019)
I11306	Spain_MLN	Olalde et al. (2019)
I3214	Spain_MLN	Olalde et al. (2019)
I7547	Spain_MLN	Olalde et al. (2019)
I7549	Spain_MLN	Olalde et al. (2019)
I7550	Spain_MLN	Olalde et al. (2019)
I7594	Spain_MLN	Olalde et al. (2019)
I7598	Spain_MLN	Olalde et al. (2019)
I7600	Spain_MLN	Olalde et al. (2019)
I7601	Spain_MLN	Olalde et al. (2019)
I7602	Spain_MLN	Olalde et al. (2019)
I7603	Spain_MLN	Olalde et al. (2019)
I7604	Spain_MLN	Olalde et al. (2019)
I7605	Spain_MLN	Olalde et al. (2019)
I7606	Spain_MLN	Olalde et al. (2019)
I7642	Spain_MLN	Olalde et al. (2019)
I7643	Spain_MLN	Olalde et al. (2019)
I7644	Spain_MLN	Olalde et al. (2019)
I7645	Spain_MLN	Olalde et al. (2019)
I7646	Spain_MLN	Olalde et al. (2019)
I7647	Spain_MLN	Olalde et al. (2019)
I8134	Spain_MLN	Olalde et al. (2019)
I8567	Spain_MLN	Olalde et al. (2019)
I8568	Spain_MLN	Olalde et al. (2019)
MS002	**Bolores**	**This study**
MS024	**Bolores**	**This study**
MS009	**CArrudaI**	**This study**
MS011	**CArrudaI**	**This study**
MS012	**CArrudaI**	**This study**
MS031	**CdAlmeida**	**This study**
MS033	**CdAlmeida**	**This study**
MS036	**CdAlmeida**	**This study**
MS037	**CdAlmeida**	**This study**
MS040	**CdAlmeida**	**This study**
MS041	**CdAlmeida**	**This study**
MS045	**CdAlmeida**	**This study**
MS046	**CdAlmeida**	**This study**
MS066	**CDiablets**	**This study**
MS068	**CLIguala**	**This study**
MS051	**MCarrascal2**	**This study**
MS014	**Paimogo**	**This study**
MS015	**Paimogo**	**This study**
MS065	**PlaRambla**	**This study**

Table S7. Outgroup-*f3* output table for the population of Bolores, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Outgroup-*f3* analysis on individual samples from Bolores in table Sx.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Britain_N	Bolores	Mbuti.DG	0.445244	0.00316	140.886	498899
Iberia_LN-Chl	Bolores	Mbuti.DG	0.442971	0.003148	140.718	492075
Iberia_MLN	Bolores	Mbuti.DG	0.440992	0.003128	140.96	480176
Central_Europe_BB	Bolores	Mbuti.DG	0.438991	0.00311	141.14	515579
Iberia_BA	Bolores	Mbuti.DG	0.438648	0.003123	140.475	490078
Anatolia_N	Bolores	Mbuti.DG	0.437604	0.003113	140.554	487246
Britain_BB	Bolores	Mbuti.DG	0.432063	0.003092	139.741	497730
Britain_MBA	Bolores	Mbuti.DG	0.431491	0.00312	138.303	491823
Central_Europe_BA	Bolores	Mbuti.DG	0.429587	0.003083	139.333	487732
Britain_Chl_EBA	Bolores	Mbuti.DG	0.428458	0.003083	138.96	486579
Iberia_BB	Bolores	Mbuti.DG	0.419473	0.003117	134.584	457691
Levant_Chl	Bolores	Mbuti.DG	0.413418	0.003073	134.548	460349
Central_Europe_MLN	Bolores	Mbuti.DG	0.393907	0.003224	122.189	412478
Britain_LBA	Bolores	Mbuti.DG	0.393574	0.003109	126.587	427058
Yamnaya	Bolores	Mbuti.DG	0.392138	0.00303	129.427	451203
Iberia_MN	Bolores	Mbuti.DG	0.387253	0.003063	126.448	425419
Central_Europe_CW	Bolores	Mbuti.DG	0.37915	0.00313	121.148	405655
Central_Europe_LChl	Bolores	Mbuti.DG	0.378288	0.003061	123.6	381137
Mediterranean_BB	Bolores	Mbuti.DG	0.377742	0.003158	119.626	391429
Central_Europe_MN	Bolores	Mbuti.DG	0.377289	0.003212	117.462	395764
Levant_BA	Bolores	Mbuti.DG	0.370385	0.00309	119.876	393092
Levant_N	Bolores	Mbuti.DG	0.362367	0.003153	114.912	365097
CdAlmeida	Bolores	Mbuti.DG	0.357205	0.003104	115.088	395791
CDiablets	Bolores	Mbuti.DG	0.354561	0.010165	34.882	8993
Iberia_Meso	Bolores	Mbuti.DG	0.347479	0.003165	109.804	371101
CArrudaI	Bolores	Mbuti.DG	0.342259	0.003284	104.224	239274
EHG	Bolores	Mbuti.DG	0.341434	0.003012	113.369	386328
Paimogo	Bolores	Mbuti.DG	0.341282	0.003561	95.826	239828
CHG	Bolores	Mbuti.DG	0.336309	0.003048	110.334	411232
Natufian	Bolores	Mbuti.DG	0.326809	0.003268	100.009	216702
CLIguala	Bolores	Mbuti.DG	0.325484	0.007621	42.707	15259
PlaRambla	Bolores	Mbuti.DG	0.324627	0.006453	50.304	21977
MCarrascal2	Bolores	Mbuti.DG	0.324074	0.003809	85.075	122787

Table S8. Outgroup-*f3* output table for the population of Paimogo I, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Outgroup-*f3* analysis on individual samples from Paimogo I in table Sx.

Source1	**Source2**	**Target**	**f_3**	**std.err.**	**Z**	**SNPs**
Britain_N	Paimogo	Mbuti.DG	0.422501	0.003441	122.782	349695
Iberia_LN-Chl	Paimogo	Mbuti.DG	0.421116	0.003437	122.514	344684
Iberia_MLN	Paimogo	Mbuti.DG	0.419062	0.003418	122.614	336528
Iberia_BA	Paimogo	Mbuti.DG	0.416475	0.003402	122.433	343209
Central_Europe_BB	Paimogo	Mbuti.DG	0.415211	0.003387	122.577	361707
Anatolia_N	Paimogo	Mbuti.DG	0.414963	0.003421	121.306	341130
Britain_MBA	Paimogo	Mbuti.DG	0.408682	0.003364	121.492	344876
Britain_BB	Paimogo	Mbuti.DG	0.408238	0.003359	121.547	348944
Central_Europe_BA	Paimogo	Mbuti.DG	0.407487	0.003375	120.74	341881
Britain_Chl_EBA	Paimogo	Mbuti.DG	0.406142	0.003395	119.616	341038
Iberia_BB	Paimogo	Mbuti.DG	0.401482	0.003409	117.756	320533
Levant_Chl	Paimogo	Mbuti.DG	0.391427	0.003371	116.122	322121
Central_Europe_MLN	Paimogo	Mbuti.DG	0.378996	0.003418	110.867	288190
Iberia_MN	Paimogo	Mbuti.DG	0.3764	0.003459	108.816	297087
Yamnaya	Paimogo	Mbuti.DG	0.375259	0.003276	114.536	315912
Britain_LBA	Paimogo	Mbuti.DG	0.37494	0.003353	111.837	298655
Mediterranean_BB	Paimogo	Mbuti.DG	0.364272	0.003396	107.269	274382
Central_Europe_CW	Paimogo	Mbuti.DG	0.364125	0.003411	106.761	283963
Central_Europe_LChl	Paimogo	Mbuti.DG	0.363946	0.003412	106.66	267551
Central_Europe_MN	Paimogo	Mbuti.DG	0.362469	0.003535	102.531	277368
Levant_BA	Paimogo	Mbuti.DG	0.354738	0.003349	105.917	274763
CDiablets	Paimogo	Mbuti.DG	0.349584	0.012254	28.527	6301
Levant_N	Paimogo	Mbuti.DG	0.346997	0.003324	104.405	254911
CdAlmeida	Paimogo	Mbuti.DG	0.346281	0.003335	103.822	276200
Bolores	Paimogo	Mbuti.DG	0.341282	0.003561	95.826	239828
Iberia_Meso	Paimogo	Mbuti.DG	0.339801	0.003418	99.408	260228
PlaRambla	Paimogo	Mbuti.DG	0.330088	0.008184	40.333	15317
EHG	Paimogo	Mbuti.DG	0.32913	0.003317	99.233	270904
CHG	Paimogo	Mbuti.DG	0.328046	0.003364	97.519	286757
CArrudaI	Paimogo	Mbuti.DG	0.327824	0.003778	86.762	168877
CLIguala	Paimogo	Mbuti.DG	0.322015	0.009628	33.445	10750
MCarrascal2	Paimogo	Mbuti.DG	0.316934	0.004359	72.705	85751
Natufian	Paimogo	Mbuti.DG	0.315706	0.00376	83.971	152445

Table S9. Outgroup-*f3* output table for the population of Cabeço da Arruda I, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Outgroup-*f3* analysis on individual samples from Cabeço da Arruda I in table Sx.

Source1	**Source2**	**Target**	**f_3**	**std.err.**	**Z**	**SNPs**
Britain_N	CArrudaI	Mbuti.DG	0.422523	0.003247	130.141	338649
Iberia_LN-Chl	CArrudaI	Mbuti.DG	0.420967	0.003214	130.968	333286
Iberia_MLN	CArrudaI	Mbuti.DG	0.418946	0.00324	129.314	326139
Iberia_BA	CArrudaI	Mbuti.DG	0.416884	0.003182	131.02	332094
Central_Europe_BB	CArrudaI	Mbuti.DG	0.415868	0.003213	129.438	349889
Anatolia_N	CArrudaI	Mbuti.DG	0.415603	0.00326	127.504	330122
Britain_BB	CArrudaI	Mbuti.DG	0.409269	0.003176	128.847	337972
Britain_MBA	CArrudaI	Mbuti.DG	0.408699	0.003184	128.348	334081
Central_Europe_BA	CArrudaI	Mbuti.DG	0.408336	0.003185	128.215	331680
Britain_Chl_EBA	CArrudaI	Mbuti.DG	0.407291	0.003213	126.777	330738
Iberia_BB	CArrudaI	Mbuti.DG	0.400387	0.003193	125.384	310874
Levant_Chl	CArrudaI	Mbuti.DG	0.393529	0.003127	125.832	313186
Central_Europe_MLN	CArrudaI	Mbuti.DG	0.377522	0.003151	119.813	282277
Britain_LBA	CArrudaI	Mbuti.DG	0.375292	0.003178	118.095	291900
Iberia_MN	CArrudaI	Mbuti.DG	0.374018	0.003213	116.39	287084
Yamnaya	CArrudaI	Mbuti.DG	0.373666	0.003115	119.946	305473
Central_Europe_CW	CArrudaI	Mbuti.DG	0.363334	0.0031	117.223	278780
Central_Europe_LChl	CArrudaI	Mbuti.DG	0.363279	0.003144	115.562	263427
Mediterranean_BB	CArrudaI	Mbuti.DG	0.362899	0.003182	114.031	270327
Central_Europe_MN	CArrudaI	Mbuti.DG	0.360144	0.003255	110.646	271680
Levant_BA	CArrudaI	Mbuti.DG	0.355167	0.003138	113.176	271624
Levant_N	CArrudaI	Mbuti.DG	0.348665	0.003233	107.856	253016
CdAlmeida	CArrudaI	Mbuti.DG	0.345655	0.003178	108.774	268321
Bolores	CArrudaI	Mbuti.DG	0.342259	0.003284	104.224	239274
Iberia_Meso	CArrudaI	Mbuti.DG	0.335682	0.003292	101.957	253463
EHG	CArrudaI	Mbuti.DG	0.331105	0.003107	106.562	263073
CDiablets	CArrudaI	Mbuti.DG	0.330346	0.012013	27.5	6274
Paimogo	CArrudaI	Mbuti.DG	0.327824	0.003778	86.762	168877
CHG	CArrudaI	Mbuti.DG	0.326652	0.003148	103.755	277350
PlaRambla	CArrudaI	Mbuti.DG	0.32189	0.007915	40.666	14815
Natufian	CArrudaI	Mbuti.DG	0.320784	0.003521	91.095	153061
MCarrascal2	CArrudaI	Mbuti.DG	0.314262	0.004069	77.231	83768
CLIguala	CArrudaI	Mbuti.DG	0.314057	0.009008	34.865	10379

Table S10. Outgroup-*f3* output table for the population of Covão d'Almeida, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Outgroup-*f3* analysis on individual samples from Covão d'Almeida in table Sx.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Iberia_LN-Chl	CdAlmeida	Mbuti.DG	0.466804	0.003141	148.631	698581
Britain_N	CdAlmeida	Mbuti.DG	0.466227	0.003156	147.736	687231
Central_Europe_BB	CdAlmeida	Mbuti.DG	0.463692	0.003139	147.705	723081
Anatolia_N	CdAlmeida	Mbuti.DG	0.459055	0.003122	147.02	683712
Iberia_BA	CdAlmeida	Mbuti.DG	0.458986	0.003089	148.604	691510
Iberia_MLN	CdAlmeida	Mbuti.DG	0.458304	0.003126	146.6	651275
Britain_BB	CdAlmeida	Mbuti.DG	0.451691	0.00309	146.16	687520
Britain_MBA	CdAlmeida	Mbuti.DG	0.449112	0.003099	144.917	667557
Central_Europe_BA	CdAlmeida	Mbuti.DG	0.445444	0.003109	143.255	657675
Britain_Chl_EBA	CdAlmeida	Mbuti.DG	0.443967	0.003075	144.385	656379
Iberia_BB	CdAlmeida	Mbuti.DG	0.433724	0.003059	141.785	621581
Levant_Chl	CdAlmeida	Mbuti.DG	0.424653	0.003035	139.904	606484
Yamnaya	CdAlmeida	Mbuti.DG	0.408833	0.002985	136.964	629071
Iberia_MN	CdAlmeida	Mbuti.DG	0.407479	0.003044	133.846	613104
Britain_LBA	CdAlmeida	Mbuti.DG	0.402817	0.003077	130.932	539075
Central_Europe_MLN	CdAlmeida	Mbuti.DG	0.402769	0.003098	129.989	519584
Central_Europe_CW	CdAlmeida	Mbuti.DG	0.387449	0.003062	126.546	499463
Mediterranean_BB	CdAlmeida	Mbuti.DG	0.38706	0.003062	126.39	471658
Central_Europe_LChl	CdAlmeida	Mbuti.DG	0.386759	0.003048	126.899	460645
Central_Europe_MN	CdAlmeida	Mbuti.DG	0.385587	0.003098	124.479	489914
Levant_BA	CdAlmeida	Mbuti.DG	0.379284	0.003038	124.85	471298
Levant_N	CdAlmeida	Mbuti.DG	0.370297	0.003037	121.932	440907
Iberia_Meso	CdAlmeida	Mbuti.DG	0.359236	0.003083	116.53	493820
Bolores	CdAlmeida	Mbuti.DG	0.357205	0.003104	115.088	395791
CHG	CdAlmeida	Mbuti.DG	0.352727	0.002994	117.827	592603
EHG	CdAlmeida	Mbuti.DG	0.352552	0.002932	120.257	521638
CDiablets	CdAlmeida	Mbuti.DG	0.34942	0.008812	39.655	12161
Paimogo	CdAlmeida	Mbuti.DG	0.346281	0.003335	103.822	276200
CArrudaI	CdAlmeida	Mbuti.DG	0.345655	0.003178	108.774	268321
Natufian	CdAlmeida	Mbuti.DG	0.33697	0.00327	103.05	256777
PlaRambla	CdAlmeida	Mbuti.DG	0.335674	0.005652	59.389	31635
CLIguala	CdAlmeida	Mbuti.DG	0.334307	0.006712	49.807	21094
MCarrascal2	CdAlmeida	Mbuti.DG	0.332873	0.003437	96.855	171834

Table S11. Outgroup-*f3* output table for Monte do Carrascal 2, using Mbuti as outgroup. Meso, (E/M/L)N, Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Comparisons with <10,000 SNPs in red.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Iberia_LN-Chl	*MCarrascal2*	Mbuti.DG	0.397629	0.003329	119.454	212328
Britain_N	*MCarrascal2*	Mbuti.DG	0.395718	0.003365	117.601	209588
Iberia_MLN	*MCarrascal2*	Mbuti.DG	0.392942	0.003387	116.031	198457
Anatolia_N	*MCarrascal2*	Mbuti.DG	0.391887	0.003367	116.38	208148
Iberia_BA	*MCarrascal2*	Mbuti.DG	0.39121	0.003286	119.061	210146
Central_Europe_BB	*MCarrascal2*	Mbuti.DG	0.38966	0.003325	117.193	220815
Britain_BB	*MCarrascal2*	Mbuti.DG	0.38157	0.003282	116.264	209670
Britain_MBA	*MCarrascal2*	Mbuti.DG	0.380424	0.003321	114.564	203540
Britain_Chl_EBA	*MCarrascal2*	Mbuti.DG	0.377741	0.00331	114.132	200427
Central_Europe_BA	*MCarrascal2*	Mbuti.DG	0.377109	0.003254	115.902	200877
Iberia_BB	*MCarrascal2*	Mbuti.DG	0.374186	0.00334	112.032	189402
Levant_Chl	*MCarrascal2*	Mbuti.DG	0.365753	0.003355	109.026	185285
Iberia_MN	*MCarrascal2*	Mbuti.DG	0.360739	0.003473	103.868	185980
Central_Europe_MLN	*MCarrascal2*	Mbuti.DG	0.355141	0.003625	97.975	159261
Yamnaya	*MCarrascal2*	Mbuti.DG	0.352713	0.00333	105.908	191158
Britain_LBA	*MCarrascal2*	Mbuti.DG	0.352684	0.003487	101.157	165102
Mediterranean_BB	*MCarrascal2*	Mbuti.DG	0.343882	0.003575	96.202	145043
Central_Europe_MN	*MCarrascal2*	Mbuti.DG	0.343513	0.003603	95.333	150122
Central_Europe_LChl	*MCarrascal2*	Mbuti.DG	0.342818	0.003462	99.033	141999
Central_Europe_CW	*MCarrascal2*	Mbuti.DG	0.342113	0.003373	101.421	153337
Levant_N	*MCarrascal2*	Mbuti.DG	0.335796	0.003631	92.485	136993
Levant_BA	*MCarrascal2*	Mbuti.DG	0.335295	0.003453	97.105	145310
CdAlmeida	*MCarrascal2*	Mbuti.DG	0.332873	0.003437	96.855	171834
CDiablets	*MCarrascal2*	Mbuti.DG	0.332736	0.014755	22.551	3821
Iberia_Meso	*MCarrascal2*	Mbuti.DG	0.329339	0.003706	88.864	151001
Bolores	*MCarrascal2*	Mbuti.DG	0.324074	0.003809	85.075	122787
CLIguala	*MCarrascal2*	Mbuti.DG	0.318496	0.011259	28.288	6518
EHG	*MCarrascal2*	Mbuti.DG	0.318449	0.003501	90.969	159255
Paimogo	*MCarrascal2*	Mbuti.DG	0.316934	0.004359	72.705	85751
CHG	*MCarrascal2*	Mbuti.DG	0.316722	0.003378	93.762	179615
CArrudaI	*MCarrascal2*	Mbuti.DG	0.314262	0.004069	77.231	83768
PlaRambla	*MCarrascal2*	Mbuti.DG	0.305851	0.009833	31.105	9849
Natufian	*MCarrascal2*	Mbuti.DG	0.304124	0.004248	71.586	81295

Table S12. Outgroup-*f3* output table for Pla Rambla, using Mbuti as outgroup. Meso, (E/M/L)N, Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Comparisons with <10,000 SNPs in red.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Iberia_LN-Chl	*PlaRambla*	Mbuti.DG	0.401071	0.005231	76.673	39226
Iberia_MLN	*PlaRambla*	Mbuti.DG	0.398256	0.005422	73.445	36391
Britain_N	*PlaRambla*	Mbuti.DG	0.39777	0.005412	73.495	38470
Iberia_BA	*PlaRambla*	Mbuti.DG	0.394807	0.005273	74.868	38770
Anatolia_N	*PlaRambla*	Mbuti.DG	0.394625	0.005325	74.109	38281
Central_Europe_BB	*PlaRambla*	Mbuti.DG	0.393642	0.005161	76.276	40665
CLIguala	*PlaRambla*	Mbuti.DG	0.386942	0.026312	14.706	1380
Britain_BB	*PlaRambla*	Mbuti.DG	0.386933	0.00519	74.559	38538
Central_Europe_BA	*PlaRambla*	Mbuti.DG	0.382302	0.005204	73.464	36747
Britain_MBA	*PlaRambla*	Mbuti.DG	0.381705	0.005223	73.087	37374
Iberia_BB	*PlaRambla*	Mbuti.DG	0.378534	0.005496	68.873	34810
Britain_Chl_EBA	*PlaRambla*	Mbuti.DG	0.377767	0.005306	71.199	36667
Levant_Chl	*PlaRambla*	Mbuti.DG	0.3686	0.005454	67.588	33898
Iberia_MN	*PlaRambla*	Mbuti.DG	0.367457	0.005544	66.281	34356
CDiablets	*PlaRambla*	Mbuti.DG	0.363811	0.032696	11.127	777
Central_Europe_MLN	*PlaRambla*	Mbuti.DG	0.361595	0.00608	59.471	28907
Yamnaya	*PlaRambla*	Mbuti.DG	0.357218	0.005374	66.477	35264
Britain_LBA	*PlaRambla*	Mbuti.DG	0.356424	0.00566	62.97	29945
Central_Europe_LChl	*PlaRambla*	Mbuti.DG	0.353503	0.006198	57.038	25647
Central_Europe_MN	*PlaRambla*	Mbuti.DG	0.347865	0.005952	58.442	27205
Central_Europe_CW	*PlaRambla*	Mbuti.DG	0.346513	0.005884	58.891	27721
Mediterranean_BB	*PlaRambla*	Mbuti.DG	0.344762	0.006277	54.926	26091
Levant_N	*PlaRambla*	Mbuti.DG	0.335836	0.006255	53.692	24562
CdAlmeida	*PlaRambla*	Mbuti.DG	0.335674	0.005652	59.389	31635
Levant_BA	*PlaRambla*	Mbuti.DG	0.335491	0.006137	54.67	26127
Paimogo	*PlaRambla*	Mbuti.DG	0.330088	0.008184	40.333	15317
Iberia_Meso	*PlaRambla*	Mbuti.DG	0.325669	0.006139	53.046	27703
Bolores	*PlaRambla*	Mbuti.DG	0.324627	0.006453	50.304	21977
CArrudaI	*PlaRambla*	Mbuti.DG	0.32189	0.007915	40.666	14815
CHG	*PlaRambla*	Mbuti.DG	0.319175	0.005313	60.07	33058
EHG	*PlaRambla*	Mbuti.DG	0.31802	0.006083	52.279	29135
Natufian	*PlaRambla*	Mbuti.DG	0.309033	0.007994	38.66	14649
MCarrascal2	*PlaRambla*	Mbuti.DG	0.305851	0.009833	31.105	9849

Table S13. Outgroup-*f3* output table for Cova del Diablets, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Comparisons with <10,000 SNPs in red.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Britain_N	*CDiablets*	Mbuti.DG	0.412132	0.008233	50.061	14840
Iberia_LN-Chl	*CDiablets*	Mbuti.DG	0.409808	0.008277	49.515	14937
CLIguala	*CDiablets*	Mbuti.DG	0.409391	0.041619	9.837	568
Iberia_MLN	*CDiablets*	Mbuti.DG	0.40736	0.00802	50.79	14079
Iberia_BA	*CDiablets*	Mbuti.DG	0.405654	0.008136	49.862	14833
Anatolia_N	*CDiablets*	Mbuti.DG	0.405028	0.008216	49.296	14714
Central_Europe_BB	*CDiablets*	Mbuti.DG	0.404862	0.00814	49.735	15617
Britain_BB	*CDiablets*	Mbuti.DG	0.398436	0.007972	49.977	14829
Britain_MBA	*CDiablets*	Mbuti.DG	0.396379	0.008306	47.72	14519
Britain_Chl_EBA	*CDiablets*	Mbuti.DG	0.394312	0.008125	48.53	14295
Central_Europe_BA	*CDiablets*	Mbuti.DG	0.394151	0.00809	48.722	14304
Central_Europe_MLN	*CDiablets*	Mbuti.DG	0.385206	0.009547	40.348	11417
Iberia_BB	*CDiablets*	Mbuti.DG	0.385017	0.008501	45.289	13445
Levant_Chl	*CDiablets*	Mbuti.DG	0.378623	0.00835	45.342	13282
Iberia_MN	*CDiablets*	Mbuti.DG	0.37063	0.008436	43.936	12997
Central_Europe_LChl	*CDiablets*	Mbuti.DG	0.367046	0.009372	39.163	10290
Britain_LBA	*CDiablets*	Mbuti.DG	0.366567	0.008779	41.753	11925
Mediterranean_BB	*CDiablets*	Mbuti.DG	0.365999	0.009256	39.541	10608
Yamnaya	*CDiablets*	Mbuti.DG	0.365935	0.007874	46.473	13579
Central_Europe_CW	*CDiablets*	Mbuti.DG	0.365634	0.009052	40.394	11075
PlaRambla	*CDiablets*	Mbuti.DG	0.363811	0.032696	11.127	777
Central_Europe_MN	*CDiablets*	Mbuti.DG	0.358332	0.009146	39.178	10847
Bolores	*CDiablets*	Mbuti.DG	0.354561	0.010165	34.882	8993
Levant_BA	*CDiablets*	Mbuti.DG	0.352091	0.009176	38.372	10570
Levant_N	*CDiablets*	Mbuti.DG	0.35157	0.009539	36.857	10000
Paimogo	*CDiablets*	Mbuti.DG	0.349584	0.012254	28.527	6301
CdAlmeida	*CDiablets*	Mbuti.DG	0.34942	0.008812	39.655	12161
Iberia_Meso	*CDiablets*	Mbuti.DG	0.344152	0.009962	34.546	10731
MCarrascal2	*CDiablets*	Mbuti.DG	0.332736	0.014755	22.551	3821
Natufian	*CDiablets*	Mbuti.DG	0.331596	0.012332	26.89	5894
CHG	*CDiablets*	Mbuti.DG	0.331031	0.008438	39.231	12579
CArrudaI	*CDiablets*	Mbuti.DG	0.330346	0.012013	27.5	6274
EHG	*CDiablets*	Mbuti.DG	0.32437	0.008928	36.33	11337

Table S14. Outgroup-*f3* output table for Cova L'Iguala, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual. Comparisons with <10,000 SNPs in red.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
CDiablets	*CLIguala*	Mbuti.DG	0.409391	0.041619	9.837	568
Iberia_MLN	*CLIguala*	Mbuti.DG	0.397667	0.006265	63.478	24493
Britain_N	*CLIguala*	Mbuti.DG	0.397662	0.006243	63.701	25757
Iberia_LN-Chl	*CLIguala*	Mbuti.DG	0.397491	0.006127	64.878	26059
Anatolia_N	*CLIguala*	Mbuti.DG	0.39629	0.006135	64.593	25532
Central_Europe_BB	*CLIguala*	Mbuti.DG	0.395826	0.006112	64.757	27094
Iberia_BA	*CLIguala*	Mbuti.DG	0.395443	0.006196	63.824	25699
Britain_BB	*CLIguala*	Mbuti.DG	0.391368	0.006123	63.916	25799
PlaRambla	*CLIguala*	Mbuti.DG	0.386942	0.026312	14.706	1380
Britain_MBA	*CLIguala*	Mbuti.DG	0.386625	0.006244	61.917	25052
Central_Europe_BA	*CLIguala*	Mbuti.DG	0.385511	0.006216	62.017	24759
Britain_Chl_EBA	*CLIguala*	Mbuti.DG	0.384394	0.006221	61.787	24712
Iberia_BB	*CLIguala*	Mbuti.DG	0.374362	0.006174	60.633	23236
Levant_Chl	*CLIguala*	Mbuti.DG	0.371228	0.006078	61.079	22861
Central_Europe_MLN	*CLIguala*	Mbuti.DG	0.365682	0.006808	53.71	19671
Yamnaya	*CLIguala*	Mbuti.DG	0.364522	0.006036	60.393	23510
Iberia_MN	*CLIguala*	Mbuti.DG	0.361389	0.006401	56.461	22747
Britain_LBA	*CLIguala*	Mbuti.DG	0.357423	0.006568	54.418	20554
Mediterranean_BB	*CLIguala*	Mbuti.DG	0.346498	0.007183	48.237	18090
Central_Europe_LChl	*CLIguala*	Mbuti.DG	0.343651	0.007113	48.316	17604
Central_Europe_MN	*CLIguala*	Mbuti.DG	0.342475	0.007218	47.444	18645
Central_Europe_CW	*CLIguala*	Mbuti.DG	0.342105	0.006729	50.844	19012
Levant_N	*CLIguala*	Mbuti.DG	0.340176	0.007446	45.683	16905
CdAlmeida	*CLIguala*	Mbuti.DG	0.334307	0.006712	49.807	21094
Levant_BA	*CLIguala*	Mbuti.DG	0.329238	0.00684	48.133	17930
Bolores	*CLIguala*	Mbuti.DG	0.325484	0.007621	42.707	15259
EHG	*CLIguala*	Mbuti.DG	0.324559	0.006895	47.069	19706
CHG	*CLIguala*	Mbuti.DG	0.322711	0.006272	51.452	22025
Iberia_Meso	*CLIguala*	Mbuti.DG	0.322339	0.007399	43.564	18553
Paimogo	*CLIguala*	Mbuti.DG	0.322015	0.009628	33.445	10750
MCarrascal2	*CLIguala*	Mbuti.DG	0.318496	0.011259	28.288	6518
CArrudaI	*CLIguala*	Mbuti.DG	0.314057	0.009008	34.865	10379
Natufian	*CLIguala*	Mbuti.DG	0.30798	0.009689	31.787	9731

Table S15. Outgroup-*f3* output table for individual samples from Bolores, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual.

Source1	**Source2**	**Target**	**f_3**	**std.err.**	**Z**	**SNPs**
Britain_N	MS002	Mbuti.DG	0.410807	0.003248	126.486	372803
Iberia_LN-Chl	MS002	Mbuti.DG	0.409329	0.003236	126.48	366819
Iberia_MLN	MS002	Mbuti.DG	0.408555	0.003206	127.445	359242
Iberia_BA	MS002	Mbuti.DG	0.405201	0.003207	126.335	365721
Anatolia_N	MS002	Mbuti.DG	0.403989	0.003198	126.31	363206
Central_Europe_BB	MS002	Mbuti.DG	0.403743	0.003186	126.706	385280
Britain_MBA	MS002	Mbuti.DG	0.398181	0.003206	124.184	368024
Britain_BB	MS002	Mbuti.DG	0.398165	0.003172	125.54	372088
Central_Europe_BA	MS002	Mbuti.DG	0.39693	0.003154	125.837	365247
Britain_Chl_EBA	MS002	Mbuti.DG	0.395442	0.00314	125.937	364350
Iberia_BB	MS002	Mbuti.DG	0.390512	0.003192	122.353	342067
Levant_Chl	MS002	Mbuti.DG	0.384038	0.003145	122.109	345062
Central_Europe_MLN	MS002	Mbuti.DG	0.372534	0.003362	110.819	311153
Britain_LBA	MS002	Mbuti.DG	0.369996	0.003238	114.258	322044
Iberia_MN	MS002	Mbuti.DG	0.366058	0.00327	111.947	315860
Yamnaya	MS002	Mbuti.DG	0.365928	0.003159	115.843	336137
Central_Europe_LChl	MS002	Mbuti.DG	0.358065	0.003286	108.951	291313
Central_Europe_MN	MS002	Mbuti.DG	0.357378	0.003372	105.969	299547
Central_Europe_CW	MS002	Mbuti.DG	0.356909	0.003199	111.573	307774
Mediterranean_BB	MS002	Mbuti.DG	0.356075	0.003245	109.73	298792
Levant_BA	MS002	Mbuti.DG	0.348322	0.003282	106.136	300203
Levant_N	MS002	Mbuti.DG	0.34346	0.003212	106.945	279284
Iberia_Meso	MS002	Mbuti.DG	0.333332	0.003389	98.357	278768
EHG	MS002	Mbuti.DG	0.326356	0.003203	101.892	288988
CHG	MS002	Mbuti.DG	0.319101	0.003186	100.147	304937
Natufian	MS002	Mbuti.DG	0.31012	0.003509	88.377	168311
Britain_N	MS024	Mbuti.DG	0.407836	0.003149	129.523	374919
Iberia_LN-Chl	MS024	Mbuti.DG	0.40661	0.00313	129.888	369430
Iberia_MLN	MS024	Mbuti.DG	0.405418	0.003142	129.023	360749
Anatolia_N	MS024	Mbuti.DG	0.402612	0.003124	128.889	365692
Iberia_BA	MS024	Mbuti.DG	0.402602	0.003119	129.095	368024
Central_Europe_BB	MS024	Mbuti.DG	0.400212	0.003098	129.172	387922
Britain_BB	MS024	Mbuti.DG	0.394484	0.00307	128.512	374114
Britain_MBA	MS024	Mbuti.DG	0.394403	0.003096	127.41	369649
Central_Europe_BA	MS024	Mbuti.DG	0.39323	0.00309	127.248	366832
Britain_Chl_EBA	MS024	Mbuti.DG	0.392625	0.003104	126.482	365990
Iberia_BB	MS024	Mbuti.DG	0.389302	0.003168	122.884	343891
Levant_Chl	MS024	Mbuti.DG	0.381818	0.003115	122.571	346284
Central_Europe_MLN	MS024	Mbuti.DG	0.369907	0.003304	111.947	311035
Iberia_MN	MS024	Mbuti.DG	0.366964	0.003104	118.206	318125
Britain_LBA	MS024	Mbuti.DG	0.366354	0.003139	116.695	321610
Yamnaya	MS024	Mbuti.DG	0.363461	0.003034	119.776	337880
Central_Europe_MN	MS024	Mbuti.DG	0.35631	0.003295	108.143	298975
Central_Europe_LChl	MS024	Mbuti.DG	0.356128	0.003093	115.145	289915
Mediterranean_BB	MS024	Mbuti.DG	0.355217	0.003243	109.526	297128
Central_Europe_CW	MS024	Mbuti.DG	0.354729	0.003227	109.911	306799
Levant_BA	MS024	Mbuti.DG	0.34863	0.003113	111.997	298639
Levant_N	MS024	Mbuti.DG	0.342651	0.003244	105.632	279299
Iberia_Meso	MS024	Mbuti.DG	0.332135	0.003233	102.73	279720
EHG	MS024	Mbuti.DG	0.323717	0.003074	105.319	290155
CHG	MS024	Mbuti.DG	0.320442	0.003136	102.168	307464
Natufian	MS024	Mbuti.DG	0.312833	0.003492	89.584	169276

Table S16. Outgroup-*f3* output table for individual samples from Cabeço da Arruda I, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual.

Source1	**Source2**	**Target**	**f_3**	**std.err.**	**Z**	**SNPs**
Britain_N	MS009	Mbuti.DG	0.407987	0.00332	122.904	280273
Iberia_LN-Chl	MS009	Mbuti.DG	0.406676	0.0033	123.229	275791
Iberia_MLN	MS009	Mbuti.DG	0.405182	0.00332	122.037	269864
Iberia_BA	MS009	Mbuti.DG	0.402467	0.003263	123.354	274818
Anatolia_N	MS009	Mbuti.DG	0.401255	0.003333	120.402	273132
Central_Europe_BB	MS009	Mbuti.DG	0.400544	0.003284	121.957	289709
Britain_BB	MS009	Mbuti.DG	0.394363	0.00326	120.974	279776
Britain_MBA	MS009	Mbuti.DG	0.39429	0.00327	120.589	276544
Central_Europe_BA	MS009	Mbuti.DG	0.393743	0.003272	120.352	274567
Britain_Chl_EBA	MS009	Mbuti.DG	0.393197	0.003292	119.431	273816
Iberia_BB	MS009	Mbuti.DG	0.387709	0.003292	117.775	257192
Levant_Chl	MS009	Mbuti.DG	0.380664	0.003245	117.316	259314
Central_Europe_MLN	MS009	Mbuti.DG	0.368214	0.0033	111.597	233684
Iberia_MN	MS009	Mbuti.DG	0.365327	0.003326	109.839	237180
Britain_LBA	MS009	Mbuti.DG	0.364491	0.003256	111.95	241796
Central_Europe_LChl	MS009	Mbuti.DG	0.354429	0.003317	106.856	218775
Mediterranean_BB	MS009	Mbuti.DG	0.354175	0.003357	105.517	224274
Central_Europe_CW	MS009	Mbuti.DG	0.35405	0.003251	108.908	231039
Central_Europe_MN	MS009	Mbuti.DG	0.351985	0.003332	105.639	225183
Levant_BA	MS009	Mbuti.DG	0.346179	0.00328	105.556	225354
Levant_N	MS009	Mbuti.DG	0.340686	0.003376	100.91	210006
Iberia_Meso	MS009	Mbuti.DG	0.329243	0.003492	94.297	209961
EHG	MS009	Mbuti.DG	0.324526	0.003347	96.947	217791
CHG	MS009	Mbuti.DG	0.318909	0.003241	98.389	228980
Natufian	MS009	Mbuti.DG	0.315393	0.003762	83.83	127460
Britain_N	MS011	Mbuti.DG	0.399661	0.004029	99.185	91238
Iberia_LN-Chl	MS011	Mbuti.DG	0.398352	0.004002	99.545	89637
Iberia_MLN	MS011	Mbuti.DG	0.397435	0.004045	98.254	87922
Iberia_BA	MS011	Mbuti.DG	0.395239	0.004027	98.143	89476
Anatolia_N	MS011	Mbuti.DG	0.394189	0.004034	97.72	88771
Central_Europe_BB	MS011	Mbuti.DG	0.392976	0.004009	98.035	94317
Central_Europe_BA	MS011	Mbuti.DG	0.388109	0.00395	98.249	89461
Britain_BB	MS011	Mbuti.DG	0.387293	0.003966	97.654	91045
Britain_MBA	MS011	Mbuti.DG	0.38683	0.004019	96.256	90041
Britain_Chl_EBA	MS011	Mbuti.DG	0.385934	0.003983	96.886	89229
Iberia_BB	MS011	Mbuti.DG	0.383576	0.003993	96.065	83858
Levant_Chl	MS011	Mbuti.DG	0.374905	0.003921	95.607	84533
Central_Europe_MLN	MS011	Mbuti.DG	0.362124	0.004029	89.869	76579
Iberia_MN	MS011	Mbuti.DG	0.359264	0.004124	87.126	77040
Britain_LBA	MS011	Mbuti.DG	0.358316	0.004077	87.894	78890
Yamnaya	MS011	Mbuti.DG	0.358246	0.00394	90.922	82026
Central_Europe_LChl	MS011	Mbuti.DG	0.349685	0.004209	83.083	71966
Mediterranean_BB	MS011	Mbuti.DG	0.348254	0.004106	84.822	73826
Central_Europe_CW	MS011	Mbuti.DG	0.348119	0.004011	86.781	75833
Central_Europe_MN	MS011	Mbuti.DG	0.344907	0.004366	78.999	73541
Levant_BA	MS011	Mbuti.DG	0.339832	0.004042	84.078	74166
Levant_N	MS011	Mbuti.DG	0.33385	0.004241	78.722	69747
Iberia_Meso	MS011	Mbuti.DG	0.329126	0.004478	73.492	68491
EHG	MS011	Mbuti.DG	0.319026	0.004236	75.308	70743
CHG	MS011	Mbuti.DG	0.315171	0.004241	74.323	74452
Natufian	MS011	Mbuti.DG	0.308182	0.004918	62.661	43354
Iberia_LN-Chl	MS012	Mbuti.DG	0.408017	0.005405	75.486	41848

Britain_N	MS012	Mbuti.DG	0.407687	0.00542	75.215	42534
Iberia_MLN	MS012	Mbuti.DG	0.407092	0.005475	74.358	41051
Anatolia_N	MS012	Mbuti.DG	0.403967	0.005396	74.869	41440
Iberia_BA	MS012	Mbuti.DG	0.403892	0.005424	74.467	41649
Central_Europe_BB	MS012	Mbuti.DG	0.4023	0.005331	75.471	43944
Britain_BB	MS012	Mbuti.DG	0.396873	0.005286	75.073	42573
Britain_MBA	MS012	Mbuti.DG	0.396194	0.005396	73.424	42051
Central_Europe_BA	MS012	Mbuti.DG	0.39538	0.005309	74.472	41797
Britain_Chl_EBA	MS012	Mbuti.DG	0.394319	0.005341	73.827	41656
Iberia_BB	MS012	Mbuti.DG	0.390086	0.00523	74.59	39065
Levant_Chl	MS012	Mbuti.DG	0.385264	0.005294	72.774	39547
Central_Europe_MLN	MS012	Mbuti.DG	0.370375	0.005449	67.968	35771
Iberia_MN	MS012	Mbuti.DG	0.369396	0.005503	67.13	35843
Britain_LBA	MS012	Mbuti.DG	0.368001	0.005424	67.845	36937
Yamnaya	MS012	Mbuti.DG	0.366323	0.005323	68.816	38344
Central_Europe_CW	MS012	Mbuti.DG	0.358753	0.005274	68.023	35498
Central_Europe_LChl	MS012	Mbuti.DG	0.356795	0.005673	62.893	33876
Mediterranean_BB	MS012	Mbuti.DG	0.35662	0.005507	64.758	34518
Central_Europe_MN	MS012	Mbuti.DG	0.355476	0.005699	62.371	34544
Levant_BA	MS012	Mbuti.DG	0.352803	0.005354	65.901	34774
Levant_N	MS012	Mbuti.DG	0.347308	0.005696	60.971	32722
EHG	MS012	Mbuti.DG	0.329411	0.00547	60.222	33113
Iberia_Meso	MS012	Mbuti.DG	0.328562	0.00605	54.311	32068
CHG	MS012	Mbuti.DG	0.327672	0.005545	59.092	34678
Natufian	MS012	Mbuti.DG	0.313462	0.006803	46.08	20794

Table S17. Outgroup-*f3* output table for individual samples from Paimogo I, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Iberia_LN-Chl	MS014	Mbuti.DG	0.410759	0.005797	70.86	38309
Britain_N	MS014	Mbuti.DG	0.410719	0.005753	71.394	38849
Iberia_MLN	MS014	Mbuti.DG	0.410047	0.005754	71.258	37530
Anatolia_N	MS014	Mbuti.DG	0.405563	0.00576	70.405	37956
Iberia_BA	MS014	Mbuti.DG	0.404415	0.005811	69.597	38151
Central_Europe_BB	MS014	Mbuti.DG	0.402259	0.005695	70.633	40252
Central_Europe_BA	MS014	Mbuti.DG	0.397043	0.005757	68.973	38072
Britain_BB	MS014	Mbuti.DG	0.396844	0.005655	70.179	38918
Britain_MBA	MS014	Mbuti.DG	0.395857	0.005709	69.341	38427
Britain_Chl_EBA	MS014	Mbuti.DG	0.395208	0.005761	68.597	38104
Iberia_BB	MS014	Mbuti.DG	0.393978	0.005797	67.962	35762
Levant_Chl	MS014	Mbuti.DG	0.382363	0.005725	66.785	35973
Central_Europe_MLN	MS014	Mbuti.DG	0.372282	0.00585	63.639	32464
Iberia_MN	MS014	Mbuti.DG	0.371944	0.006025	61.734	32888
Britain_LBA	MS014	Mbuti.DG	0.369733	0.005675	65.148	33542
Yamnaya	MS014	Mbuti.DG	0.36836	0.005576	66.06	35135
Central_Europe_CW	MS014	Mbuti.DG	0.361279	0.005883	61.407	32022
Central_Europe_MN	MS014	Mbuti.DG	0.356916	0.005903	60.459	31292
Central_Europe_LChl	MS014	Mbuti.DG	0.353429	0.005859	60.318	30401
Mediterranean_BB	MS014	Mbuti.DG	0.352691	0.005876	60.02	31152
Levant_N	MS014	Mbuti.DG	0.343334	0.0058	59.193	29232
Levant_BA	MS014	Mbuti.DG	0.342385	0.005826	58.765	31235
Iberia_Meso	MS014	Mbuti.DG	0.331106	0.006464	51.227	29220
EHG	MS014	Mbuti.DG	0.324354	0.00588	55.163	30137
CHG	MS014	Mbuti.DG	0.319045	0.005889	54.176	31724
Natufian	MS014	Mbuti.DG	0.304804	0.007097	42.949	18092
Britain_N	MS015	Mbuti.DG	0.417899	0.003414	122.413	333625
Iberia_LN-Chl	MS015	Mbuti.DG	0.416551	0.003404	122.358	328770
Iberia_MLN	MS015	Mbuti.DG	0.414485	0.003397	122.017	321015
Iberia_BA	MS015	Mbuti.DG	0.412074	0.00337	122.262	327419
Central_Europe_BB	MS015	Mbuti.DG	0.410551	0.003358	122.261	345109
Anatolia_N	MS015	Mbuti.DG	0.410433	0.003392	120.984	325360
Britain_MBA	MS015	Mbuti.DG	0.40426	0.003337	121.135	329038
Britain_BB	MS015	Mbuti.DG	0.403708	0.003332	121.178	332875
Central_Europe_BA	MS015	Mbuti.DG	0.402943	0.003344	120.482	326215
Britain_Chl_EBA	MS015	Mbuti.DG	0.401685	0.003359	119.597	325325
Iberia_BB	MS015	Mbuti.DG	0.397445	0.003393	117.122	305733
Levant_Chl	MS015	Mbuti.DG	0.387449	0.003347	115.744	307332
Central_Europe_MLN	MS015	Mbuti.DG	0.376046	0.003424	109.815	274919
Iberia_MN	MS015	Mbuti.DG	0.373305	0.003445	108.347	283310
Yamnaya	MS015	Mbuti.DG	0.37149	0.00327	113.597	301279
Britain_LBA	MS015	Mbuti.DG	0.371398	0.003349	110.909	284891
Central_Europe_LChl	MS015	Mbuti.DG	0.361591	0.003425	105.56	255401
Mediterranean_BB	MS015	Mbuti.DG	0.361534	0.003398	106.386	261900
Central_Europe_CW	MS015	Mbuti.DG	0.360528	0.003402	105.99	270954
Central_Europe_MN	MS015	Mbuti.DG	0.35981	0.003542	101.583	264684
Levant_BA	MS015	Mbuti.DG	0.352222	0.003353	105.06	262272
Levant_N	MS015	Mbuti.DG	0.344445	0.00335	102.834	243336
Iberia_Meso	MS015	Mbuti.DG	0.337904	0.003436	98.335	248270
EHG	MS015	Mbuti.DG	0.32651	0.003334	97.946	258482
CHG	MS015	Mbuti.DG	0.326118	0.003377	96.564	273435
Natufian	MS015	Mbuti.DG	0.314091	0.003794	82.778	145538

Table S18. Outgroup-*f3* output table for individual samples from Covão d'Almeida, using Mbuti as outgroup. Meso, (E/M/L)N , Chl, BA and BB stand for Mesolithic, (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively. Populations in italics are represented by one single individual.

Source1	Source2	Target	f_3	std.err.	Z	SNPs
Iberia_LN-Chl	MS031	Mbuti.DG	0.405277	0.007004	57.861	18388
Britain_N	MS031	Mbuti.DG	0.402811	0.006994	57.591	18018
Anatolia_N	MS031	Mbuti.DG	0.400922	0.007091	56.54	17986
Iberia_MLN	MS031	Mbuti.DG	0.399719	0.007158	55.843	17051
Central_Europe_BB	MS031	Mbuti.DG	0.396123	0.007005	56.546	19086
Iberia_BA	MS031	Mbuti.DG	0.394346	0.006945	56.783	18186
Britain_BB	MS031	Mbuti.DG	0.389572	0.007073	55.079	18036
Britain_MBA	MS031	Mbuti.DG	0.388735	0.007113	54.655	17465
Central_Europe_BA	MS031	Mbuti.DG	0.386096	0.007244	53.301	17182
Iberia_BB	MS031	Mbuti.DG	0.382828	0.007348	52.1	16245
Britain_Chl_EBA	MS031	Mbuti.DG	0.378229	0.007086	53.379	17172
Levant_Chl	MS031	Mbuti.DG	0.375391	0.007272	51.622	15928
Iberia_MN	MS031	Mbuti.DG	0.374838	0.007349	51.008	16150
Central_Europe_MLN	MS031	Mbuti.DG	0.364954	0.007723	47.253	13498
Yamnaya	MS031	Mbuti.DG	0.36249	0.007057	51.364	16508
Britain_LBA	MS031	Mbuti.DG	0.362066	0.007856	46.089	14013
Central_Europe_MN	MS031	Mbuti.DG	0.358537	0.008172	43.876	12782
Central_Europe_LChl	MS031	Mbuti.DG	0.355366	0.008589	41.377	11917
Central_Europe_CW	MS031	Mbuti.DG	0.350922	0.008168	42.965	12934
Mediterranean_BB	MS031	Mbuti.DG	0.344854	0.008295	41.574	12146
Levant_N	MS031	Mbuti.DG	0.344577	0.008594	40.093	11432
Levant_BA	MS031	Mbuti.DG	0.340018	0.008242	41.256	12244
Iberia_Meso	MS031	Mbuti.DG	0.332122	0.008339	39.829	13019
EHG	MS031	Mbuti.DG	0.32342	0.008279	39.067	13736
Natufian	MS031	Mbuti.DG	0.318831	0.011497	27.732	6789
CHG	MS031	Mbuti.DG	0.317863	0.006902	46.055	15622
Iberia_LN-Chl	MS033	Mbuti.DG	0.40766	0.003092	131.863	500088
Britain_N	MS033	Mbuti.DG	0.406652	0.003103	131.06	496415
Iberia_MLN	MS033	Mbuti.DG	0.403509	0.003107	129.869	471094
Iberia_BA	MS033	Mbuti.DG	0.401518	0.003042	132.003	495387
Anatolia_N	MS033	Mbuti.DG	0.401202	0.003098	129.521	490981
Central_Europe_BB	MS033	Mbuti.DG	0.400914	0.003062	130.94	520838
Britain_BB	MS033	Mbuti.DG	0.392715	0.003043	129.052	495972
Britain_MBA	MS033	Mbuti.DG	0.391311	0.003081	127.004	483343
Britain_Chl_EBA	MS033	Mbuti.DG	0.388961	0.003053	127.401	475817
Central_Europe_BA	MS033	Mbuti.DG	0.388809	0.003102	125.324	476703
Iberia_BB	MS033	Mbuti.DG	0.385745	0.003076	125.409	448905
Levant_Chl	MS033	Mbuti.DG	0.375369	0.003053	122.949	441095
Iberia_MN	MS033	Mbuti.DG	0.368726	0.003117	118.305	436486
Central_Europe_MLN	MS033	Mbuti.DG	0.366774	0.003208	114.313	380478
Britain_LBA	MS033	Mbuti.DG	0.362708	0.003117	116.38	395284
Yamnaya	MS033	Mbuti.DG	0.362411	0.003032	119.513	451264
Central_Europe_MN	MS033	Mbuti.DG	0.354304	0.003279	108.066	359728
Central_Europe_LChl	MS033	Mbuti.DG	0.353444	0.003162	111.773	340557
Mediterranean_BB	MS033	Mbuti.DG	0.352971	0.003205	110.127	348639
Central_Europe_CW	MS033	Mbuti.DG	0.351532	0.003152	111.515	368187
Levant_BA	MS033	Mbuti.DG	0.343958	0.003147	109.301	348869
Levant_N	MS033	Mbuti.DG	0.340204	0.003205	106.163	326580
Iberia_Meso	MS033	Mbuti.DG	0.337978	0.003222	104.888	357236
EHG	MS033	Mbuti.DG	0.325108	0.003121	104.176	377310
CHG	MS033	Mbuti.DG	0.323309	0.003112	103.889	421372
Natufian	MS033	Mbuti.DG	0.312816	0.003454	90.574	191252
Iberia_LN-Chl	MS036	Mbuti.DG	0.405904	0.003341	121.51	262592

Britain_N	MS036	Mbuti.DG	0.404188	0.003359	120.331	260473
Iberia_MLN	MS036	Mbuti.DG	0.401053	0.003344	119.924	246965
Central_Europe_BB	MS036	Mbuti.DG	0.399105	0.003294	121.174	273605
Iberia_BA	MS036	Mbuti.DG	0.398921	0.003315	120.344	260300
Anatolia_N	MS036	Mbuti.DG	0.398893	0.003358	118.794	257683
Britain_BB	MS036	Mbuti.DG	0.390618	0.003253	120.065	260449
Britain_MBA	MS036	Mbuti.DG	0.388941	0.0033	117.849	253469
Central_Europe_BA	MS036	Mbuti.DG	0.387164	0.003297	117.421	250075
Britain_Chl_EBA	MS036	Mbuti.DG	0.386097	0.003286	117.513	249532
Iberia_BB	MS036	Mbuti.DG	0.382997	0.003318	115.432	235492
Levant_Chl	MS036	Mbuti.DG	0.376931	0.003333	113.081	231223
Iberia_MN	MS036	Mbuti.DG	0.370239	0.00336	110.195	229360
Central_Europe_MLN	MS036	Mbuti.DG	0.36585	0.003544	103.241	199395
Yamnaya	MS036	Mbuti.DG	0.361203	0.003227	111.938	236984
Britain_LBA	MS036	Mbuti.DG	0.360521	0.003342	107.885	207156
Central_Europe_MN	MS036	Mbuti.DG	0.353442	0.003442	102.696	188663
Mediterranean_BB	MS036	Mbuti.DG	0.351506	0.003496	100.536	182809
Central_Europe_LChl	MS036	Mbuti.DG	0.351283	0.003463	101.44	178239
Central_Europe_CW	MS036	Mbuti.DG	0.349881	0.003388	103.264	192440
Levant_BA	MS036	Mbuti.DG	0.342932	0.003409	100.588	183134
Levant_N	MS036	Mbuti.DG	0.339415	0.00349	97.249	171159
Iberia_Meso	MS036	Mbuti.DG	0.331803	0.003607	91.987	187808
EHG	MS036	Mbuti.DG	0.323476	0.003339	96.891	197820
CHG	MS036	Mbuti.DG	0.320894	0.003243	98.942	221715
Natufian	MS036	Mbuti.DG	0.313291	0.004062	77.124	100837
Iberia_LN-Chl	MS037	Mbuti.DG	0.401307	0.003427	117.099	195606
Britain_N	MS037	Mbuti.DG	0.398541	0.003394	117.44	193353
Iberia_MLN	MS037	Mbuti.DG	0.395537	0.003427	115.427	183112
Anatolia_N	MS037	Mbuti.DG	0.394171	0.003358	117.379	191728
Iberia_BA	MS037	Mbuti.DG	0.39344	0.003414	115.253	193685
Central_Europe_BB	MS037	Mbuti.DG	0.393043	0.003377	116.391	203511
Britain_BB	MS037	Mbuti.DG	0.385997	0.003356	115.01	193546
Britain_MBA	MS037	Mbuti.DG	0.383967	0.003354	114.479	188074
Central_Europe_BA	MS037	Mbuti.DG	0.381966	0.003382	112.929	185487
Britain_Chl_EBA	MS037	Mbuti.DG	0.38054	0.003373	112.816	185080
Iberia_BB	MS037	Mbuti.DG	0.377837	0.003441	109.807	174930
Levant_Chl	MS037	Mbuti.DG	0.368218	0.003393	108.526	171358
Iberia_MN	MS037	Mbuti.DG	0.364199	0.003526	103.283	170820
Central_Europe_MLN	MS037	Mbuti.DG	0.357977	0.003666	97.651	147287
Yamnaya	MS037	Mbuti.DG	0.357373	0.003351	106.633	176338
Britain_LBA	MS037	Mbuti.DG	0.35376	0.00354	99.918	152980
Central_Europe_LChl	MS037	Mbuti.DG	0.349429	0.003588	97.401	131249
Mediterranean_BB	MS037	Mbuti.DG	0.347868	0.003654	95.195	134776
Central_Europe_MN	MS037	Mbuti.DG	0.346117	0.003633	95.265	139252
Central_Europe_CW	MS037	Mbuti.DG	0.344787	0.003568	96.64	142041
Levant_BA	MS037	Mbuti.DG	0.336096	0.003593	93.55	134460
Levant_N	MS037	Mbuti.DG	0.335008	0.003755	89.225	126109
Iberia_Meso	MS037	Mbuti.DG	0.326737	0.003766	86.77	139115
EHG	MS037	Mbuti.DG	0.320655	0.003537	90.652	147170
CHG	MS037	Mbuti.DG	0.319487	0.0035	91.283	165028
Natufian	MS037	Mbuti.DG	0.302819	0.004225	71.667	74218
Britain_N	MS040	Mbuti.DG	0.401398	0.005557	72.237	38929
Iberia_MLN	MS040	Mbuti.DG	0.399218	0.005528	72.218	36868
Anatolia_N	MS040	Mbuti.DG	0.398192	0.005453	73.022	38790
Central_Europe_BB	MS040	Mbuti.DG	0.397961	0.005423	73.39	41110
Iberia_BA	MS040	Mbuti.DG	0.397432	0.005422	73.297	39252
Britain_MBA	MS040	Mbuti.DG	0.387346	0.005455	71.004	37774
Britain_BB	MS040	Mbuti.DG	0.386438	0.005386	71.752	39025
Central_Europe_BA	MS040	Mbuti.DG	0.385721	0.005439	70.911	37093
Britain_Chl_EBA	MS040	Mbuti.DG	0.385618	0.005547	69.52	37104
Iberia_BB	MS040	Mbuti.DG	0.378908	0.005461	69.385	35112

Levant_Chl	MS040	Mbuti.DG	0.370802	0.005686	65.211	34128
Iberia_MN	MS040	Mbuti.DG	0.36695	0.005705	64.315	34823
Yamnaya	MS040	Mbuti.DG	0.360636	0.005363	67.245	35620
Central_Europe_MLN	MS040	Mbuti.DG	0.359852	0.006123	58.769	29016
Britain_LBA	MS040	Mbuti.DG	0.356193	0.005853	60.86	30203
Central_Europe_MN	MS040	Mbuti.DG	0.35184	0.006228	56.489	27380
Central_Europe_CW	MS040	Mbuti.DG	0.349827	0.006031	58.005	27923
Central_Europe_LChl	MS040	Mbuti.DG	0.349272	0.006407	54.516	25619
Mediterranean_BB	MS040	Mbuti.DG	0.347796	0.00631	55.115	26171
Levant_BA	MS040	Mbuti.DG	0.341066	0.006126	55.677	26124
Levant_N	MS040	Mbuti.DG	0.333783	0.006289	53.077	24571
Iberia_Meso	MS040	Mbuti.DG	0.331421	0.006111	54.235	27860
EHG	MS040	Mbuti.DG	0.326087	0.005946	54.843	29412
CHG	MS040	Mbuti.DG	0.323924	0.005492	58.978	33681
Natufian	MS040	Mbuti.DG	0.313072	0.008079	38.753	14515
Iberia_LN-Chl	MS041	Mbuti.DG	0.409052	0.004097	99.844	84211
Britain_N	MS041	Mbuti.DG	0.408408	0.004211	96.982	81850
Iberia_BA	MS041	Mbuti.DG	0.404347	0.004042	100.035	83219
Central_Europe_BB	MS041	Mbuti.DG	0.402511	0.00406	99.128	86998
Anatolia_N	MS041	Mbuti.DG	0.402242	0.004151	96.895	82002
Iberia_MLN	MS041	Mbuti.DG	0.401751	0.00427	94.078	77144
Britain_BB	MS041	Mbuti.DG	0.393956	0.004085	96.433	81945
Britain_MBA	MS041	Mbuti.DG	0.392811	0.004101	95.783	79111
Central_Europe_BA	MS041	Mbuti.DG	0.388672	0.004065	95.607	77790
Iberia_BB	MS041	Mbuti.DG	0.388363	0.004215	92.135	73646
Britain_Chl_EBA	MS041	Mbuti.DG	0.385417	0.004149	92.901	77465
Levant_Chl	MS041	Mbuti.DG	0.376246	0.004192	89.748	71064
Iberia_MN	MS041	Mbuti.DG	0.371652	0.0043	86.426	74276
Yamnaya	MS041	Mbuti.DG	0.365005	0.004123	88.529	75052
Central_Europe_MLN	MS041	Mbuti.DG	0.362386	0.004553	79.587	60205
Britain_LBA	MS041	Mbuti.DG	0.361904	0.0044	82.254	62238
Mediterranean_BB	MS041	Mbuti.DG	0.353431	0.004675	75.597	53729
Central_Europe_MN	MS041	Mbuti.DG	0.352879	0.004774	73.922	56382
Central_Europe_CW	MS041	Mbuti.DG	0.351973	0.004632	75.989	57200
Central_Europe_LChl	MS041	Mbuti.DG	0.351329	0.004915	71.478	52409
Levant_BA	MS041	Mbuti.DG	0.343785	0.004716	72.904	53744
Levant_N	MS041	Mbuti.DG	0.341089	0.004746	71.87	50863
Iberia_Meso	MS041	Mbuti.DG	0.337265	0.004876	69.172	58525
CHG	MS041	Mbuti.DG	0.324917	0.004429	73.357	71640
EHG	MS041	Mbuti.DG	0.324395	0.00448	72.411	61782
Natufian	MS041	Mbuti.DG	0.304033	0.005954	51.067	29962
Iberia_LN-Chl	MS045	Mbuti.DG	0.40491	0.003146	128.7	295508
Britain_N	MS045	Mbuti.DG	0.403988	0.003187	126.762	290289
Iberia_MLN	MS045	Mbuti.DG	0.400295	0.003166	126.452	274434
Anatolia_N	MS045	Mbuti.DG	0.39981	0.003105	128.765	288841
Iberia_BA	MS045	Mbuti.DG	0.39952	0.003121	128.02	292397
Central_Europe_BB	MS045	Mbuti.DG	0.398467	0.003139	126.942	306445
Britain_BB	MS045	Mbuti.DG	0.390768	0.003139	124.496	290482
Britain_MBA	MS045	Mbuti.DG	0.389401	0.003138	124.093	281405
Central_Europe_BA	MS045	Mbuti.DG	0.387363	0.003129	123.807	277202
Britain_Chl_EBA	MS045	Mbuti.DG	0.386457	0.003134	123.299	276588
Iberia_BB	MS045	Mbuti.DG	0.383031	0.003152	121.529	261494
Levant_Chl	MS045	Mbuti.DG	0.374739	0.003122	120.032	254995
Iberia_MN	MS045	Mbuti.DG	0.369932	0.003221	114.834	259061
Central_Europe_MLN	MS045	Mbuti.DG	0.364571	0.00334	109.161	217357
Yamnaya	MS045	Mbuti.DG	0.362811	0.003092	117.323	264935
Britain_LBA	MS045	Mbuti.DG	0.360331	0.003252	110.801	224723
Central_Europe_LChl	MS045	Mbuti.DG	0.353524	0.003316	106.625	191658
Mediterranean_BB	MS045	Mbuti.DG	0.352318	0.003319	106.164	196463
Central_Europe_CW	MS045	Mbuti.DG	0.3503	0.003207	109.214	208410
Central_Europe_MN	MS045	Mbuti.DG	0.350093	0.003346	104.62	203967

Levant_BA	MS045	Mbuti.DG	0.343142	0.003279	104.637	196482
Levant_N	MS045	Mbuti.DG	0.341659	0.003233	105.683	185772
Iberia_Meso	MS045	Mbuti.DG	0.335947	0.003399	98.826	208135
EHG	MS045	Mbuti.DG	0.325874	0.003244	100.45	219404
CHG	MS045	Mbuti.DG	0.322839	0.003167	101.939	249896
Natufian	MS045	Mbuti.DG	0.316085	0.003791	83.37	109991
Britain_N	MS046	Mbuti.DG	0.397635	0.005112	77.784	41032
Iberia_LN-Chl	MS046	Mbuti.DG	0.397428	0.005124	77.57	41594
Anatolia_N	MS046	Mbuti.DG	0.3938	0.00518	76.016	40811
Iberia_MLN	MS046	Mbuti.DG	0.391358	0.005244	74.624	38897
Iberia_BA	MS046	Mbuti.DG	0.390278	0.005056	77.191	41169
Central_Europe_BB	MS046	Mbuti.DG	0.388379	0.005062	76.72	43205
Britain_MBA	MS046	Mbuti.DG	0.382561	0.005069	75.469	39790
Britain_BB	MS046	Mbuti.DG	0.381867	0.005046	75.679	41044
Central_Europe_BA	MS046	Mbuti.DG	0.379849	0.005066	74.98	39224
Iberia_BB	MS046	Mbuti.DG	0.378216	0.005213	72.554	37019
Britain_Chl_EBA	MS046	Mbuti.DG	0.377818	0.005206	72.577	39235
Levant_Chl	MS046	Mbuti.DG	0.364901	0.005094	71.633	36235
Central_Europe_MLN	MS046	Mbuti.DG	0.356531	0.005491	64.929	31121
Iberia_MN	MS046	Mbuti.DG	0.356013	0.005051	70.482	36358
Yamnaya	MS046	Mbuti.DG	0.355683	0.00514	69.198	37376
Britain_LBA	MS046	Mbuti.DG	0.351802	0.005691	61.815	32248
Central_Europe_LChl	MS046	Mbuti.DG	0.349287	0.005779	60.444	27522
Central_Europe_CW	MS046	Mbuti.DG	0.346763	0.005624	61.655	29873
Mediterranean_BB	MS046	Mbuti.DG	0.343369	0.006101	56.282	28275
Central_Europe_MN	MS046	Mbuti.DG	0.342172	0.005567	61.467	29431
Levant_N	MS046	Mbuti.DG	0.335101	0.005806	57.717	26361
Levant_BA	MS046	Mbuti.DG	0.333602	0.005675	58.783	28148
EHG	MS046	Mbuti.DG	0.319892	0.005722	55.904	31090
Iberia_Meso	MS046	Mbuti.DG	0.318561	0.006125	52.011	29467
CHG	MS046	Mbuti.DG	0.313538	0.005169	60.653	35105
Natufian	MS046	Mbuti.DG	0.311179	0.007692	40.455	15541

Table S19. *D*-statistics output table: *D*(Mbuti, Cova L'Iguala (MS068), Pop X, Pop. Y). Rows in bold showing results with a |Z|-score >3, which are considered significant. Positive *D*-stats values show higher affinity with Pop. Y (in blue) than with Pop. X. (E/M/L)N, Chl, BA and BB stand for (Early/Middle/Late) Neolithic, Chalcolithic, Bronze Age and Bell Beaker, respectively.

Outgroup	Target	Pop. X	Pop. Y	D-stat	std.err.	|Z|	BABA	ABBA	SNPs
Mbuti.DG	**CLIguala**	**Central_Europe_BB**	**Central_Europe_MLN**	**0.0365**	**0.009035**	**4.036**	**1229**	**1143**	**30458**
Mbuti.DG	**CLIguala**	**Central_Europe_BB**	**Iberia_BA**	**0.0157**	**0.004264**	**3.68**	**1378**	**1336**	**26651**
Mbuti.DG	**CLIguala**	**Central_Europe_BB**	**Iberia_LN-Chl**	**0.0155**	**0.004319**	**3.593**	**1385**	**1343**	**30426**
Mbuti.DG	**CLIguala**	**Central_Europe_BA**	**Iberia_LN-Chl**	**0.0165**	**0.005449**	**3.037**	**1349**	**1305**	**29471**
Mbuti.DG	**CLIguala**	**Central_Europe_BA**	**Central_Europe_MLN**	**0.0298**	**0.009916**	**3.007**	**1213**	**1143**	**31551**
Mbuti.DG	CLIguala	Central_Europe_BA	Iberia_BA	0.0154	0.005553	2.767	1341	1301	26420
Mbuti.DG	CLIguala	Iberia_BB	Central_Europe_MLN	0.0272	0.010809	2.514	1189	1126	31527
Mbuti.DG	CLIguala	Central_Europe_LChl	Central_Europe_MLN	0.0271	0.013161	2.06	1025	971	30112
Mbuti.DG	CLIguala	Central_Europe_LChl	Iberia_LN-Chl	0.0106	0.010483	1.015	1069	1046	31551
Mbuti.DG	CLIguala	Central_Europe_BB	Iberia_BB	0.0053	0.006425	0.83	1319	1305	26420
Mbuti.DG	CLIguala	Central_Europe_LChl	Iberia_BA	0.0081	0.010562	0.772	1073	1056	24277
Mbuti.DG	CLIguala	Central_Europe_BA	Iberia_BB	0.0017	0.007422	0.229	1295	1290	22873
Mbuti.DG	CLIguala	Central_Europe_LChl	Iberia_BB	-0.0024	0.011999	0.197	1048	1053	24267
Mbuti.DG	CLIguala	Iberia_BA	Iberia_LN-Chl	-0.0007	0.004645	0.158	1345	1347	24008

Table S20. *D*-statistics output table: *D*(Mbuti, published population; Cova L'Iguala, other newly reported Iberian population). All tests have a |Z|-score <3, and are therefore considered non-significant.

Outgroup	**Target**	**Pop. X**	**Pop. Y**	**D-stat**	**std.err.**	**|Z|**	**BABA**	**ABBA**	**SNPs**
Mbuti.DG	Yamnaya	CLIguala	CdAlmeida	-0.0228	0.010723	2.127	1216	1272	28184
Mbuti.DG	Yamnaya	CLIguala	MCarrascal2	-0.038	0.021641	1.758	383	413	9173
Mbuti.DG	Central_Europe_MLN	CLIguala	Bolores	-0.0222	0.013938	1.592	915	956	20472
Mbuti.DG	Central_Europe_MLN	CLIguala	CdAlmeida	-0.0198	0.012539	1.579	1101	1145	24988
Mbuti.DG	Iberia_BB	CLIguala	CDiablets	-0.1078	0.071651	1.504	24	30	801
Mbuti.DG	Central_Europe_MLN	CLIguala	MCarrascal2	-0.0388	0.026401	1.471	351	380	8188
Mbuti.DG	Yamnaya	CLIguala	Bolores	-0.0184	0.013105	1.404	921	956	21222
Mbuti.DG	Britain_Chl_EBA	CLIguala	CDiablets	-0.0893	0.066007	1.353	26	31	805
Mbuti.DG	CHG	CLIguala	Bolores	-0.0213	0.016194	1.312	904	943	21004
Mbuti.DG	Central_Europe_BA	CLIguala	CdAlmeida	-0.0126	0.010164	1.237	1223	1255	27954
Mbuti.DG	Britain_BB	CLIguala	CdAlmeida	-0.0117	0.009606	1.218	1248	1278	28484
Mbuti.DG	Central_Europe_LChl	CLIguala	CDiablets	-0.1162	0.099276	1.171	23	29	689
Mbuti.DG	Britain_Chl_EBA	CLIguala	MCarrascal2	-0.0229	0.0197	1.162	388	406	9101
Mbuti.DG	Britain_Chl_EBA	CLIguala	CdAlmeida	-0.0112	0.009907	1.131	1218	1245	27946
Mbuti.DG	Central_Europe_BA	CLIguala	Bolores	-0.0121	0.011299	1.071	942	965	21339
Mbuti.DG	Central_Europe_BB	CLIguala	CdAlmeida	-0.0095	0.009213	1.036	1263	1288	28814
Mbuti.DG	Yamnaya	CLIguala	CDiablets	-0.0728	0.075395	0.966	27	31	812
Mbuti.DG	Britain_BB	CLIguala	Bolores	-0.0102	0.010861	0.942	949	968	21401
Mbuti.DG	Iberia_BA	CLIguala	CdAlmeida	-0.009	0.009572	0.936	1264	1286	28866
Mbuti.DG	Central_Europe_LChl	CLIguala	Bolores	-0.0149	0.01622	0.92	853	879	19331
Mbuti.DG	Yamnaya	CLIguala	CArrudaI	-0.0154	0.017263	0.894	646	667	14662
Mbuti.DG	Anatolia_N	CLIguala	Bolores	-0.0096	0.011196	0.859	951	970	21401
Mbuti.DG	Central_Europe_BB	CLIguala	Bolores	-0.0091	0.010605	0.854	950	968	21420
Mbuti.DG	Central_Europe_BB	CLIguala	MCarrascal2	-0.0148	0.018564	0.797	404	417	9316
Mbuti.DG	Iberia_BA	CLIguala	MCarrascal2	-0.0153	0.019357	0.792	408	421	9347
Mbuti.DG	CHG	CLIguala	MCarrascal2	-0.018	0.0269	0.668	396	410	9247
Mbuti.DG	Iberia_BA	CLIguala	CDiablets	-0.0423	0.066115	0.64	28	30	826
Mbuti.DG	Central_Europe_BA	CLIguala	MCarrascal2	-0.0129	0.020201	0.639	395	405	9081
Mbuti.DG	CHG	CLIguala	Paimogo	-0.012	0.019851	0.603	663	679	15075
Mbuti.DG	Central_Europe_BB	CLIguala	CDiablets	-0.0362	0.062207	0.582	28	30	826

Mbuti.DG	Iberia_BA	CLIguala	Bolores	-0.006	0.011129	0.537	953	964	21414
Mbuti.DG	Anatolia_N	CLIguala	MCarrascal2	-0.0101	0.019494	0.517	406	414	9309
Mbuti.DG	Central_Europe_MLN	CLIguala	Paimogo	-0.0091	0.018494	0.49	684	696	14712
Mbuti.DG	Britain_BB	CLIguala	MCarrascal2	-0.0095	0.019414	0.489	406	413	9252
Mbuti.DG	Iberia_LN-Chl	CLIguala	Bolores	-0.005	0.010936	0.457	949	958	21414
Mbuti.DG	Iberia_LN-Chl	CLIguala	CDiablets	-0.0275	0.063285	0.434	28	30	828
Mbuti.DG	Iberia_BB	CLIguala	MCarrascal2	-0.0095	0.021898	0.432	398	405	9035
Mbuti.DG	Britain_Chl_EBA	CLIguala	Bolores	-0.0047	0.011329	0.418	947	956	21349
Mbuti.DG	Central_Europe_BA	CLIguala	CArrudaI	-0.0058	0.015523	0.375	666	674	14742
Mbuti.DG	Natufian	CLIguala	CDiablets	-0.051	0.147986	0.345	15	17	394
Mbuti.DG	Central_Europe_BA	CLIguala	CDiablets	-0.0224	0.067734	0.33	28	29	807
Mbuti.DG	Britain_BB	CLIguala	CArrudaI	-0.0048	0.015267	0.316	666	672	14760
Mbuti.DG	Anatolia_N	CLIguala	CArrudaI	-0.0041	0.015794	0.262	669	674	14762
Mbuti.DG	Central_Europe_BB	CLIguala	PlaRambla	-0.0102	0.043104	0.236	72	74	1985
Mbuti.DG	CHG	CLIguala	CdAlmeida	-0.0029	0.012813	0.23	1249	1257	28257
Mbuti.DG	Britain_N	CLIguala	Bolores	-0.002	0.010892	0.183	961	965	21400
Mbuti.DG	CHG	CLIguala	CArrudaI	-0.0037	0.020542	0.181	648	652	14513
Mbuti.DG	Central_Europe_BB	CLIguala	CArrudaI	-0.0023	0.014911	0.154	668	671	14772
Mbuti.DG	Iberia_LN-Chl	CLIguala	PlaRambla	-0.0068	0.045668	0.15	74	75	1991
Mbuti.DG	Iberia_LN-Chl	CLIguala	CdAlmeida	-0.0007	0.009563	0.075	1276	1278	28927
Mbuti.DG	Britain_Chl_EBA	CLIguala	CArrudaI	-0.0011	0.015828	0.067	667	668	14739
Mbuti.DG	Yamnaya	CLIguala	Paimogo	-0.001	0.015666	0.063	700	701	15196
Mbuti.DG	CHG	CLIguala	CDiablets	-0.0048	0.095083	0.051	29	29	808
Mbuti.DG	Iberia_LN-Chl	CLIguala	CArrudaI	-0.0002	0.015137	0.012	669	669	14770
Mbuti.DG	Iberia_BA	CLIguala	CArrudaI	0.0002	0.015364	0.011	667	667	14768
Mbuti.DG	Central_Europe_LChl	CLIguala	MCarrascal2	0.0004	0.029144	0.015	326	325	7461
Mbuti.DG	Anatolia_N	CLIguala	CdAlmeida	0.0004	0.009982	0.039	1278	1277	28725
Mbuti.DG	Britain_Chl_EBA	CLIguala	Paimogo	0.0006	0.014334	0.041	691	691	15283
Mbuti.DG	Britain_Chl_EBA	CLIguala	PlaRambla	0.0023	0.045443	0.05	71	70	1920
Mbuti.DG	Iberia_BB	CLIguala	CdAlmeida	0.0006	0.0113	0.055	1231	1229	27748
Mbuti.DG	Central_Europe_LChl	CLIguala	CArrudaI	0.0019	0.020356	0.093	612	610	13585
Mbuti.DG	Iberia_LN-Chl	CLIguala	MCarrascal2	0.0022	0.018804	0.117	413	412	9359
Mbuti.DG	Britain_BB	CLIguala	PlaRambla	0.0055	0.046008	0.12	74	73	1963
Mbuti.DG	Britain_N	CLIguala	MCarrascal2	0.0032	0.020023	0.16	417	415	9223
Mbuti.DG	Iberia_BA	CLIguala	PlaRambla	0.0076	0.044312	0.17	74	73	1984
Mbuti.DG	Yamnaya	CLIguala	PlaRambla	0.0103	0.04873	0.211	72	71	1958

Mbuti.DG	CHG	CLIguala	PlaRambla	0.0135	0.063356	0.214	73	71	1959
Mbuti.DG	Central_Europe_MLN	CLIguala	CArrudaI	0.0043	0.019156	0.222	658	653	14298
Mbuti.DG	Britain_N	CLIguala	CdAlmeida	0.0027	0.009714	0.275	1273	1266	28463
Mbuti.DG	Anatolia_N	CLIguala	CDiablets	0.0189	0.067515	0.279	30	29	825
Mbuti.DG	Britain_N	CLIguala	PlaRambla	0.0135	0.046758	0.288	74	72	1965
Mbuti.DG	Britain_BB	CLIguala	Paimogo	0.0044	0.01408	0.314	699	693	15324
Mbuti.DG	Central_Europe_BA	CLIguala	PlaRambla	0.0151	0.046502	0.324	71	69	1917
Mbuti.DG	Britain_N	CLIguala	CArrudaI	0.0057	0.01561	0.366	679	671	14763
Mbuti.DG	Natufian	CLIguala	PlaRambla	0.0403	0.10779	0.374	34	31	900
Mbuti.DG	Central_Europe_MLN	CLIguala	PlaRambla	0.0233	0.061836	0.376	71	68	1710
Mbuti.DG	Iberia_BB	CLIguala	Paimogo	0.0063	0.015937	0.395	700	692	15227
Mbuti.DG	Iberia_BB	CLIguala	Bolores	0.0049	0.012125	0.408	952	942	21221
Mbuti.DG	Anatolia_N	CLIguala	Paimogo	0.0067	0.015102	0.446	705	695	15321
Mbuti.DG	Iberia_BB	CLIguala	CArrudaI	0.0076	0.016712	0.454	667	657	14681
Mbuti.DG	Natufian	CLIguala	Paimogo	0.0155	0.031328	0.496	374	362	8421
Mbuti.DG	Iberia_BB	CLIguala	PlaRambla	0.0261	0.05246	0.498	70	66	1909
Mbuti.DG	Central_Europe_BB	CLIguala	Paimogo	0.0071	0.013964	0.507	703	693	15338
Mbuti.DG	Anatolia_N	CLIguala	PlaRambla	0.0237	0.044873	0.527	75	72	1976
Mbuti.DG	Central_Europe_BA	CLIguala	Paimogo	0.0077	0.014399	0.534	708	698	15293
Mbuti.DG	Central_Europe_LChl	CLIguala	Paimogo	0.011	0.02017	0.545	644	630	13906
Mbuti.DG	Britain_BB	CLIguala	CDiablets	0.0367	0.066886	0.548	31	29	819
Mbuti.DG	Britain_N	CLIguala	CDiablets	0.0354	0.06401	0.553	31	29	819
Mbuti.DG	Natufian	CLIguala	Bolores	0.0127	0.022416	0.568	501	489	11570
Mbuti.DG	Central_Europe_LChl	CLIguala	CdAlmeida	0.0088	0.014529	0.604	1026	1008	22660
Mbuti.DG	Central_Europe_MLN	CLIguala	CDiablets	0.0549	0.087833	0.625	29	26	741
Mbuti.DG	Natufian	CLIguala	MCarrascal2	0.0342	0.041001	0.834	193	181	4537
Mbuti.DG	Iberia_BA	CLIguala	Paimogo	0.0127	0.014532	0.871	706	688	15331
Mbuti.DG	Iberia_LN-Chl	CLIguala	Paimogo	0.0146	0.01447	1.011	707	686	15337
Mbuti.DG	Britain_N	CLIguala	Paimogo	0.0158	0.014587	1.086	714	692	15319
Mbuti.DG	Natufian	CLIguala	CArrudaI	0.0313	0.028675	1.091	389	365	8359
Mbuti.DG	Central_Europe_LChl	CLIguala	PlaRambla	0.0879	0.069198	1.271	62	52	1551
Mbuti.DG	Natufian	CLIguala	CdAlmeida	0.0289	0.020516	1.411	590	557	13211

Table S21. *D*-statistics output table: *D*(Mbuti, published population; individual with Steppe component in supervised ADMIXTURE, other individual from the same site without Steppe component). All tests have a |Z|-score <3, and are therefore considered non-significant.

Outgroup	Target	Pop. X	Pop. Y	D-stat	std.err.	|Z|	BABA	ABBA	SNPs
Mbuti.DG	Yamnaya	MS002	MS024	-0.0007	0.004277	0.154	13364	13382	292872
Mbuti.DG	Central_Europe_BA	MS002	MS024	0.0016	0.003568	0.451	13541	13498	294413
Mbuti.DG	Central_Europe_BB	MS002	MS024	0.0017	0.003513	0.498	13555	13508	294547
Mbuti.DG	Iberia_BA	MS002	MS024	0.001	0.003621	0.267	13496	13470	294480
Mbuti.DG	Iberia_BB	MS002	MS024	0.0031	0.003938	0.798	13609	13524	293669
Mbuti.DG	Iberia_LN-Chl	MS002	MS024	0.0016	0.003643	0.43	13588	13545	294508
Mbuti.DG	Central_Europe_MLN	MS002	MS024	-0.0027	0.004561	0.584	13534	13606	289802
Mbuti.DG	Central_Europe_LChl	MS002	MS024	0.0008	0.004755	0.174	13103	13082	281228
Mbuti.DG	Britain_N	MS002	MS024	0.002	0.003593	0.545	13694	13641	294518
Mbuti.DG	Britain_Chl_EBA	MS002	MS024	0.0021	0.003642	0.565	13524	13468	294383
Mbuti.DG	Britain_BB	MS002	MS024	0.0008	0.00361	0.214	13529	13508	294494
Mbuti.DG	CHG	MS002	MS024	-0.0006	0.005219	0.116	13200	13216	289651
Mbuti.DG	Natufian	MS002	MS024	0.0039	0.006626	0.581	7977	7916	179880
Mbuti.DG	Anatolia_N	MS002	MS024	0.0031	0.003763	0.811	13607	13525	294455
Mbuti.DG	Yamnaya	MS009	MS011	0.0227	0.008689	2.613	2621	2504	57885
Mbuti.DG	Central_Europe_BA	MS009	MS011	0.0123	0.007496	1.64	2630	2567	58149
Mbuti.DG	Central_Europe_BB	MS009	MS011	0.0093	0.007332	1.271	2623	2574	58165
Mbuti.DG	Iberia_BA	MS009	MS011	0.0116	0.007657	1.515	2612	2552	58154
Mbuti.DG	Iberia_BB	MS009	MS011	0.0067	0.007999	0.842	2607	2572	58035
Mbuti.DG	Iberia_LN-Chl	MS009	MS011	0.009	0.007482	1.209	2627	2580	58160
Mbuti.DG	Central_Europe_MLN	MS009	MS011	0.0073	0.009902	0.741	2627	2588	57460
Mbuti.DG	Central_Europe_LChl	MS009	MS011	0.0047	0.009846	0.477	2550	2526	56154
Mbuti.DG	Britain_N	MS009	MS011	0.0059	0.007685	0.765	2637	2607	58160
Mbuti.DG	Britain_Chl_EBA	MS009	MS011	0.0076	0.007512	1.014	2615	2575	58146
Mbuti.DG	Britain_BB	MS009	MS011	0.011	0.007492	1.467	2623	2566	58159
Mbuti.DG	CHG	MS009	MS011	0.0159	0.011176	1.425	2548	2468	57281
Mbuti.DG	Natufian	MS009	MS011	0.0031	0.014689	0.211	1598	1589	37179
Mbuti.DG	Anatolia_N	MS009	MS011	0.0061	0.007612	0.8	2616	2584	58147
Mbuti.DG	Yamnaya	MS012	MS011	0.0128	0.021127	0.605	428	417	9459
Mbuti.DG	Central_Europe_BA	MS012	MS011	-0.0064	0.017467	0.368	420	425	9497
Mbuti.DG	Central_Europe_BB	MS012	MS011	-0.0069	0.017106	0.401	421	427	9499

Mbuti.DG	Iberia_BA	MS012	MS011	0.0012	0.01792	0.064	419	418	9497
Mbuti.DG	Iberia_BB	MS012	MS011	-0.0047	0.0196	0.239	421	425	9479
Mbuti.DG	Iberia_LN-Chl	MS012	MS011	-0.0079	0.017988	0.442	416	423	9496
Mbuti.DG	Central_Europe_MLN	MS012	MS011	-0.0062	0.023118	0.268	414	419	9417
Mbuti.DG	Central_Europe_LChl	MS012	MS011	0.0112	0.023907	0.47	410	401	9268
Mbuti.DG	Britain_N	MS012	MS011	0.0007	0.017629	0.037	428	427	9499
Mbuti.DG	Britain_Chl_EBA	MS012	MS011	-0.007	0.017766	0.396	418	424	9499
Mbuti.DG	Britain_BB	MS012	MS011	-0.0018	0.017544	0.101	421	423	9498
Mbuti.DG	CHG	MS012	MS011	-0.0122	0.026611	0.459	410	420	9373
Mbuti.DG	Natufian	MS012	MS011	0.0361	0.033362	1.083	283	263	6367
Mbuti.DG	Anatolia_N	MS012	MS011	-0.0057	0.017858	0.319	422	427	9499

Table S22. Genotypes and depth of position (DP) of SNPs found in HIrisPlex-S panel. Alleles according to genomic reference sequence (in forward strand).

SNP	**gene**	**SNP-capture**								**Multiple-library WGS**				
		MS002	**MS009**	**MS011**	**MS012**	**MS014**	**MS015**	**MS017**	**MS024**	**MS033**	**MS036**	**MS037**	**MS045**	**MS051**
rs16891982	*SLC45A2*	C/C (3)	-	-	-	-	C/C (2)	-	C/C (3)	G/- (1)	G/- (1)	-	-	C/- (1)
rs28777	*SLC45A2*	-	-	-	-	-	-	C/- (1)	-	-	-	-	-	-
rs12203592	*IRF4*	-	-	-	-	-	C/- (1)	T/T (2)	-	C/C (3)	C/C (2)	C/- (1)	-	C/C (2)
rs4959270	*LOC105374875*	-	C/- (1)	-	-	-	-	C/- (1)	-	C/- (1)	-	-	-	-
rs683	*TYRP1*	-	-	-	-	-	-	-	-	-	-	-	A/- (1)	-
rs10756819	*BNC2*	-	-	-	-	-	-	-	-	A/- (1)	G/- (1)	-	-	-
rs1042602	*TYR*	C/C (3)	C/- (1)	C/C (2)	-	-	C/- (1)	-	C/A (3)	C/C (2)	C/- (1)	-	-	C/C (3)
rs1393350	*TYR*	G/G (5)	G/G (2)	-	-	-	G/- (1)	G/G (2)	G/- (1)	A/A (3)	G/- (1)	-	-	-
rs1126809	*TYR*	G/- (1)	-	-	-	-	G/- (1)	-	G/- (1)	-	-	-	-	-
rs12821256	*KITLG*	T/- (1)	-	-	-	-	-	-	-	-	-	-	-	-
rs12896399	*LOC105370627*	-	G/- (1)	-	-	-	-	-	-	T/T (2)	G/- (1)	-	G/G (2)	-
rs2402130	*SLC24A4*	G/- (1)	-	-	-	-	-	G/- (1)	-	-	-	-	G/- (1)	-
rs17128291	*SLC24A4*	A/- (1)	-	-	-	-	-	A/A (4)	A/G (4)	G/G (3)	A/- (1)	A/- (1)	A/- (1)	-
rs1545397	*OCA2*	-	-	-	-	-	-	-	-	A/- (1)	-	-	-	-
rs1800414	*OCA2*	-	-	T/- (1)	-	T/- (1)	T/T (2)	T/T (2)	T/- (1)	T/T (6)	-	T/- (1)	-	-
rs1800407	*OCA2*	C/C (3)	C/C (2)	-	-	-	C/- (1)	C/- (1)	C/C (4)	C/- (1)	-	-	-	-
rs12441727	*OCA2*	G/- (1)	-	-	-	-	-	-	G/- (1)	-	-	-	-	-
rs1470608	*OCA2*	-	-	-	-	-	-	-	-	-	-	-	-	-
rs1129038	*HERC2*	-	C/C (3)	-	-	-	C/- (1)	-	C/- (1)	C/- (1)	T/- (1)	-	-	-
rs12913832	*HERC2*	A/A (4)	A/- (1)	-	-	-	A/- (1)	A/- (1)	A/A (4)	A/A (3)	-	-	-	-
rs2238289	*HERC2*	-	-	-	-	-	-	A/A (3)	A/- (1)	-	-	A/- (1)	A/- (1)	-
rs6497292	*HERC2*	-	-	-	-	-	-	-	-	A/A (2)	-	-	-	-
rs1667394	*HERC2*	-	-	-	-	-	-	-	-	C/C (3)	C/- (1)	-	-	-
rs1426654	*SLC24A5*	-	-	-	-	-	A/- (1)	-	-	A/G (3)	-	A/- (1)	A/A (2)	A/A (2)
rs3114908	*ANKRD11*	-	-	-	-	-	-	-	-	C/C (3)	-	C/- (1)	-	-

rs3212355	*MC1R*	-	-	-	-	-	-	-	-	C/C (2)	C/- (1)	-	-	-
rs312262906	*MC1R*	-	-	-	-	-	-	-	-	-	-	-	-	-
rs1805005	*MC1R*	G/G (2)	G/- (1)	-	-	-	-	-	G/- (1)	G/G (3)	G/- (1)	-	G/- (1)	G/- (1)
rs1805006	*MC1R*	C/C (4)	C/C (2)	-	-	-	C/C (3)	C/C (3)	C/C (2)	C/C (3)	-	-	-	C/C (2)
rs2228479	*MC1R*	G/G (3)	-	-	-	-	G/G (3)	G/G (3)	G/- (1)	G/G (2)	-	-	G/- (1)	G/- (1)
rs11547464	*MC1R*	G/G (6)	G/G (2)	-	-	-	G/- (1)	G/G (2)	G/G (2)	-	G/- (1)	-	-	G/- (1)
rs1805007	*MC1R*	C/C (4)	C/- (1)	-	-	-	C/C (2)	C/C (3)	C/C (2)	-	C/- (1)	-	-	-
rs201326893	*MC1R*	C/C (3)	C/- (1)	-	-	C/- (1)	C/- (1)	C/C (2)	C/C (2)	-	C/- (1)	-	-	-
rs1110400	*MC1R*	T/T (3)	T/- (1)	-	-	T/- (1)	T/T (2)	T/T (2)	T/T (3)	-	T/- (1)	-	-	-
rs1805008	*MC1R*	C/C (2)	C/- (1)	-	-	C/- (1)	C/- (1)	-	C/C (3)	-	C/- (1)	-	-	-
rs885479	*MC1R*	G/G (2)	-	-	G/- (1)	G/- (1)	G/- (1)	-	G/G (3)	-	-	-	-	-
rs1805009	*TUBB3*	G/G (4)	-	G/- (1)	-	-	-	G/- (1)	G/G (4)	G/G (5)	-	-	-	-
rs8051733	*DEF8*	A/- (1)	-	A/- (1)	-	-	A/- (1)	-	A/- (1)	A/- (1)	-	-	-	-
rs6059655	*RALY*	-	-	-	-	-	-	-	-	G/G (3)	G/- (1)	-	-	-
rs6119471	*ASIP*	C/C (2)	C/C (3)	-	-	-	C/- (1)	C/- (1)	C/C (2)	-	-	-	-	C/- (1)
rs2378249	*PIGU*	G/- (1)	-	-	-	-	-	-	A/A (2)	-	-	-	-	-

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