

Once upon a time in the West

*Paleogenetic analyses on Mesolithic to Early Bronze Age individuals
from the Iberian Peninsula*

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Christina Roth

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“It is a capital mistake to theorise before one has data. Insensibly one begins to twist facts to suit theories, instead of theories to suit facts.”

Sir Arthur Conan Doyle, 1891, in “A Scandal in Bohemia”

Acknowledgement

Whenever someone asked me in the last three years how it is to do a PhD, I always answered “It is like sprinting a marathon”: You have a great distance to cover and you want to pace yourself, but there is never enough time.

There are many times when your feet are heavy, when you are short of breath, everything hurts and you just want to give up. But there are also these moments when everything seems to finally work, when you are running forward with your feet barely touching the ground and you think “I can make it”. Of course no one runs a marathon or writes a thesis all by himself; there are many people with you from the beginning. First of all you need a sponsor, someone who believes in you and gives you the financial support to start. Then there are people who train you and people who run with you; some you pass along the way, some run beside you and some let you run in their slipstream and help you to save some strength. And last but not least there is the ever cheering crowd, always ready to support you whenever you feel like giving up.

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Abbreviations

°C	degree in Celsius	HPLC	high performance liquid chromatography
A	adenine	i.e.	id est (that is)
and	ancient DNA	kb	kilobases
bp	base pairs	kya	thousand years ago
BP	before present	kyr	thousand years
BC	before Christ	LBK	Linear pottery culture
BSA	bovine serum albumin	MDS	multidimensional scaling
C	cytosine	mtDNA	mitochondrial DNA
Cal BC	calibrated	µl	microliter
rCRS	revised Cambridge reference sequence	n	number of
ddNTP	dideoxynucleotide-triphosphate	NaCl	sodium chloride
dNTP	deoxynucleotide-triphosphate	NE	northeast
DNA	deoxyribonucleic acid	NGS	Next Generation Sequencing
EDTA	ethylenediamine tetra-acetic acid	np	nucleotide position
e.g.	exempli gratia (for example)	p	page
et al.	et alii (and others)	PCA	principal component analyses
fig.	figure	PCR	polymerase chain reaction
ff	and the following (pages/chapters)	pp	pages
g	gramm	pers.	personal
G	guanine	RFLP	restriction fragment length polymorphism
HAK	non-template control with hydroxyapatite (milling-blank)	rpm	rotations per minute
hg	haplogroup	rRNA	ribosomal RNA
HVR I	hypervariable region I	SNP	single nucleotide polymorphism
HVR II	hypervariable region II	STR	short tandem repeats
		T	thymine
		TPC	test of population continuity
		tRNA	transfer RNA
		UV	ultraviolet

Abbreviations of ancient groups

Abbr.	Group	Region/Country
AVN	Late Neolithic of the Ambrona Valley	Iberian Peninsula
BAC	Baalberge culture	Central Europe
BAI	Bronze Age of the Iberian Peninsula	Iberian Peninsula
BBC	Bell Beaker of Central Europe	Central Europe
BEC	Bernburg culture	Central Europe
BLA	Blätterhöhle	Central Europe
CHI	Chalcolithic of the Iberian Peninsula	Iberian Peninsula
CPC	Chalcolithic of Central Portugal	Iberian Peninsula
CPE	Early Neolithic of Central Portugal	Iberian Peninsula
CPN	Late Neolithic of Central Portugal	Iberian Peninsula
CWC	Corded Ware culture	Central Europe
ENC	Early Neolithic of Central Europe (LBK, SCG, and RSC))	Central Europe
ENH	Early Neolithic of Hungary (Körös and Alföld Linear Pottery culture)	Hungary
ESBA	Bronze Age of East Spain (El Agar culture)	Iberian Peninsula
ESC	Chalcolithic of East Spain	Iberian Peninsula
EVN	Late Neolithic of the Ebro Valley	Iberian Peninsula
FBC	Funnel Beaker culture	Northern Europe
HGC	Hunter-gatherer Central	Central Europe
HGE	Hunter-gatherer East	East Europe
HGW	Hunter-gatherer West	Iberian Peninsula
LBK	Linear pottery culture	Central Europe
LRS	Early Iron Age (La Tène culture) from Switzerland	Switzerland
LTA	Early Iron Age (La Tène culture) from Austria	Austria
LTE	Early Iron Age (La Tène culture) from East Europe	East Europe
LTF	Early Iron Age (La Tène culture) from France	France
MNC	Middle Neolithic of Central Europe (BAC and SALZ))	Central Europe
NEB	Bronze Age of Northeast Spain	Iberian Peninsula
NEC	Chalcolithic of Northeast Spain	Iberian Peninsula
NEE	Early Neolithic of Northeast Spain	Iberian Peninsula
NEN	Late Neolithic of Northeast Spain	Iberian Peninsula
NEOI	Late Neolithic of the Iberian Peninsula	Iberian Peninsula
NMCB	Chalcolithic Bell Beaker of the Northern Meseta	Iberian Peninsula
NMN	Late Neolithic of the Northern Meseta	Iberian Peninsula
NSE	Early Neolithic of the Northern Spain	Iberian Peninsula
PWC	Pitted Ware culture	Northern Europe
RSC	Rössen culture	Central Europe
SALZ	Salzmünde culture	Central Europe
SCG	Schöningen group	Central Europe
SIC	Chalcolithic Southern of the Iberian Peninsula	Iberian Peninsula
SMC	Chalcolithic of the Southern Meseta	Iberian Peninsula
SMCB	Chalcolithic Bell Beaker of the Southern Meseta	Iberian Peninsula
TRE	Treilles	France
TROCE	Early Neolithic of Els Trocs	Iberian Peninsula
UC	Unetice culture	Central Europe

1 Introduction

The Neolithic transition started about 12,000 years ago in the Near East with a change in subsistence strategy, from foraging to farming, and thus from a very mobile way of life to sedentariness. It is widely agreed that this new lifestyle spread in the following millennia towards Europe via two main routes – the continental route, via the Balkans into Central Europe, and the Mediterranean route into Spain and Portugal. During the Neolithic and later periods more important changes occurred, the construction of larger residential areas culminating in fortified settlements, more elaborate burial customs, the production of first copper and later bronze and iron, and social stratification with the establishment of elite societies. All these innovations have significantly contributed to the forming of modern society as we know it. However, each newly introduced cultural or social element raises the question of its origin and dissemination, whether this was achieved via an exchange of ideas or directly via human migration. The latter may have taken place in the form of small pioneer groups, or a more conscious spread of larger communities. While archaeology can make assumptions and form models based on the material residues of these prehistoric societies, genetic methods, using actual archaeological human remains, can give information on the genetic composition of prehistoric communities and investigate possible connections and continuity between different groups in space and time.

Together, archaeology and bioarchaeology (also including biogeological methods like isotope analyses and of course classical osteoanthropology) can provide powerful insights into our past. Projects and publications on mostly Central European prehistory between the Mesolithic and Early Bronze Age have already proven the possibilities of these combined efforts (e.g. HAAK ET AL. 2005, 2008, 2010; BRAMANTI ET AL. 2009; BOLLONGINO ET AL. 2013; BRANDT ET AL. 2013, IN PRESS). However, there are still many white spots on the prehistoric European genetic landscape, only slowly filling in with new data.

While the dataset on ancient Iberian genetic data has increased over the last years, studies have almost exclusively focused on the Neolithic transition and only few conclusions have been made about Late Neolithic population dynamic processes. This thesis, conducted within the project "Rekonstruktion populationsdynamischer Prozesse auf der iberischen Halbinsel zwischen Neolithikum und Frühbronzezeit mittels aDNA-Analysen" funded by the German Research Foundation, was performed to fill the temporal and spatial gaps of Iberian ancient DNA data by analyzing mitochondrial DNA of more than 300 individuals from over 50 sites dating from the Late Mesolithic to the Early Bronze Age.

2 Archaeological basics

2.1 The origins of the Neolithic in the “Fertile Crescent”

The European Stone Age can be divided into three major periods: The Paleolithic, the Mesolithic, characterized as the era of the post-glacial hunter-gatherers, and the Neolithic (CUMMINGS 2014). The Neolithic is understood as the transition from foraging to farming, accompanied by sedentariness, and the so-called “Neolithic package”, often defined as the use of cultivated plants, domesticated animals, ground stone artifacts, and pottery (ÖZDOĞAN 2011). Nowadays, further elements are added to this package, for example the presence of prestige or cultic objects, architecture and arrangement of settlements as well as general lifestyle (ÖZDOĞAN 2011). It seems that there were various types of Neolithic communities and although almost all were accompanied by variations of the traditional Neolithic package, they had different social structures and ways of living (ÖZDOĞAN 2011). But how did this new way of living reach the European continent?

Before husbandry and agriculture were established, sedentariness and new technologies for food production and processing developed in some hunter-gatherer groups of the Levant during the Late Epipaleolithic (*Natufien*) around 13,000 years ago. It seems that sedentariness foremost arose around favorable ecological settings, for instance on lake shores, while in other regions foraging groups still had to practice seasonal nomadism or an even more mobile lifestyle to survive (GORING-MORRIS AND BELTER-COHEN 2011). For all groups, however, the hunting of wild animals – mostly gazelles – and gathering of fruits and indigenous wheat was most likely the dominant subsistence strategy during the Natufien. While there is clear evidence for intensified plant collection, like ground stone tools and sickles, no evidence for intentional plant cultivation is known that early (GORING-MORRIS AND BELFER-COHEN 2011). In Central Anatolia, the round-house phase, represented by the sites of Hallan Çemi, Demirköy, and Körtik Tepe, dates 12,000/11,000 years back, proving that sedentariness started very early in this region too, and was not limited to the Levant (HAUPTMANN AND ÖZDOĞAN 2007).

At the beginning of the Holocene, about 12,000 years ago, temperatures began to rise world-wide (BARKER 2006, 1). Over time, a variety of agricultural systems began to develop at different corners of the world. The Neolithic way of life that would later reach Europe, mainly originated in a region of the Near East that is often described as the “Fertile Crescent” (BREADSTEAD 1938) and extends over a territory, which encompasses parts of modern-day Iran, Iraq, Syria, and the Levant (HAUPTMANN AND ÖZDOĞAN 2007). The first domesticated plants like einkorn and emmer, barley, and rye, as well as leguminous plants like lentils, peas

and beans were indigenous to this area as were the first domestic animals like cattle, goat, sheep, and pig, marking this region very early as a “suspect” for the origin of the Neolithic (WATKINS 2007). In the Near East the phase at the beginning of the Holocene is called pre-pottery Neolithic A (PPNA) and evidence of plant cultivation was found in Gilgal (wild barley) and in Jerf el-Ahmar and Netiv Hagdud (lentil) (WEISS ET AL. 2006) as well as potentially cultivation of wild einkorn, wild emmer, wild barley, wild rye, and wild lentil at Jerf el Ahmar and Dja'de in northern Syria (WILLCOX ET AL. 2008). Several remarkable sites have been excavated in the Levant and Anatolia from that era. One well-known example is the site of Göbekli Tepe in southeast Turkey, where massive limestone pillars were built and decorated with faunal pictograms by what are believed to have been foraging, non-sedentary communities (SCHMIDT 2001).

Between 8,500 and 6,500 BC – in the so-called Pre-Pottery Neolithic B (PPNB) – many large settlements were built in Cyprus, southeastern Anatolia, the Levant, and possibly Iran. This phase is characterized by an increasing density of settlements (HAUPTMANN AND ÖZDOĞAN 2007). The greatest among them – with population sizes between 1,000 and 2,000 inhabitants – were Tell es-Sultan in Jericho, Beidha and 'Ain Gazhal in the southern Levant, Bouqras and Abu Hureira in the northern Levant, and Haçılar and Çatalhöyük in Turkey (BARKER 2006, 137). In the PPNB, the domestication of crops like winter wheat, barley, peas and lentils, chickpea, vetch, and horse bean was established (SIMMONS 2007, 139F). Emmer (*Triticum dicoccoides*) and Einkorn (*Triticum monococcum*) were probably domesticated in Southeast Turkey, although genetic diversity of the latter indicates multiple areas of domestication (HEUN ET AL. 1997; KILIAN ET AL. 2007; LUO ET AL. 2007; ÖZKAN ET AL. 2002). Furthermore, the first real evidence for domestication of livestock exists from that time. The oldest evidence for goat and sheep herding is known from the sites of Ganj Dareh and Ali Kosh in the Zagros and Taurus regions (BARKER 2006, 139). Domestication was not determined by a morphological basis however, but was proclaimed due to the practice of slaughtering of young male but not female goats (SIMMONS 2010, 142). It seems that the proportion of wild to domesticated animals as well as the composition of consumed animals differed in the various regions (WATKINS 2007).

Genetic analyses confirmed that sheep (*Ovis aries*) were likely first domesticated in the North of the Fertile Crescent at the Zagros Mountains from the mouflon (*O. orientalis*) and introduced to Europe via Anatolia and the Balkans (GEÖRG 2011). Likewise, ancient DNA-studies on pigs (*Sus scrofa*) showed that they were first domesticated in the Near East and imported into Europe during the Neolithic, although other domestication centers like Southeast Asia are known (LARSON ET AL. 2005, 2007). After the initial import, European

farmers seem to have relied strongly on local wild boar to supplement their breeding stock (LARSON ET AL. 2005, 2007). Like pigs, cattle were domesticated independently in both the Near East and East Asia. European cattle (*Bos taurus*) descend from the Near Eastern aurochs (*Bos primigenius*) and were imported to Europe during the initial Neolithic with no signs of further inbreeding (BOLLONGINO ET AL. 2006, 2008; EDWARDS ET AL. 2007).

From the 7th millennium BC onwards – in the so-called Pottery-Neolithic – ceramics were manufactured in the Fertile Crescent. At the same time the use of secondary animal products like milk began to spread, and great herds of sheep, goats, as well as cattle were found in many settlements (BARKER 2006, 160F; HAUPTMANN AND ÖZDOĞAN 2007). At this time, a lot of PPNB settlements were abandoned or suffered a decrease in population size. Reasons may have been changing climate conditions or social conflicts as a result of overpopulation (ÖZDOĞAN 2007). However, the development of new settlements like Fikirtepe or Pendik in the northern Aegean region testifies for an expansion of the Neolithic into Western Asia Minor at that time (ÖZDOĞAN 2007).

2.2 The Neolithic transition – Ways into Europe

The Neolithic spread further westwards between 7,000 and 6,200 BC in presumably three waves. It should be noted that the lands outside the Neolithic core region were not deserted and Mesolithic (“Epi-Gravettien”) communities are known from sites of western Turkey, the Marmara region, and Bulgaria (ÖZDOĞAN 2007). While the first wave of Neolithic expansion was presumably of a more unidirectional and sporadic way, the next – so-called monochrome phase – is linked to the Fikirtepe culture and its dark, globular ceramic that was distributed in western Anatolia, Thrace, and Bulgaria (ÖZDOĞAN 2007). Further material elements of this archaeological culture were stone- and bone tools (ÖZDOĞAN 2007, 2011). Interestingly, every type of artifact found in the western sites can be traced back to the core area of Neolithic transition, while other elements typical for Central Anatolian Neolithic like cultic buildings, artwork, jewelry, and status symbols were not adopted or only to a minor degree in western Anatolian settlements (ÖZDOĞAN 2007, 2011). Noteworthy, there is a striking difference in burial customs and house-forms between inland and coastal Fikirtepe culture settlements. Moreover, there is proof for hunting and fishing at the coastal sites but not at the inland ones, suggesting a more endemic origin for inland settlements while coastal sites show signs of acculturation of local hunter-gatherers (ÖZDOĞAN 2011).

A third wave of expansion of Neolithic lifestyle is connected to the distribution of red-slipped pottery, often polished and/or decorated, represented for example in the archaeological cultures of Sesklo in Greece, Karanovo in Bulgaria, and Starčevo and Körös/Criș in the northern Balkans (ÖZDOĞAN 2011). The Starčevo and Körös cultures diffused during the late 7th and early 6th millennium BC into the Hungarian Plain, where the Körös culture exclusively settled the Alföld region with settlements beside water habitats while the Starčevo culture populated both the valleys and the hills of Southern Transdanubia (BÁNFFY ET AL. 2010). The Linear pottery culture probably developed out of the Starčevo culture in Transdanubia and spread westwards around 5,500 BC over major parts of Europe from Southeast Poland to the Parisian Basin (VANDER LINDEN 2011, BÁNFFY 2006). Interestingly, in the eastern Marmara region, groups connected to red-slipped pottery did not settle areas previously occupied by the Fikirtepe culture. In this area a new archaeological culture, the Yarımburgaz culture, developed probably out of the preceding Fikirtepe culture (ÖZDOĞAN 2011). Yarımburgaz pottery was still produced in dark colors with various forms of decoration (ÖZDOĞAN 2011).

Besides the overland way of Neolithic expansion, findings in Crete and Cyprus argue for another important way of distribution of the Neolithic on seaway along the coastline (ÖZDOĞAN 2007). Cyprus had already been visited for fishing and hunting since the 10th millennium BC, but was not settled before 8,500 BC. Domesticated animals as well as spelt and barley were brought to the island at that time (GUILAINE 2007). From 7,500 BC onwards, the Cyprian Neolithic evolved independently from the mainland, developing its own archaeological culture, the Khirokitia culture (GUILAINE 2007). The Greek island Crete was settled at about 7,000 BC; both, colonization by settlers from the east and acculturation of indigenous hunter-gatherers are possible scenarios (GUILAINE 2007). The cultivation of einkorn, barley, peas, and lentils as well as the domestication of sheep, goat, and cattle, is proven (GUILAINE 2007).

Neolithic farming was established in mainland Greece at about 7,000 cal BC (PERLÈS 2001, 38). Geographically and cultural, it represents the “missing link” of Neolithic transition between Asia Minor and the Balkans on the one hand, and the western Mediterranean on the other hand (GEHLEN AND SCHÖN 2003). Between 6,000 BC and 5,400 BC farming and domestication spread throughout the whole western Mediterranean in association with groups characterized by an impressed pottery style (GUILAINE 2007). Connections between Central Greece and South Italy, particularly the Apulia region, can be drawn e.g. by similarities in ceramic styles and a particular form of red painted ceramic (MÜLLER 1994,

247). MÜLLER (1994, 260) states that the Apulian region had a prominent role in the Neolithisation of the Adriatic and south Italian regions.

The oldest evidences of agriculture in Italy are known from the sites of Coppa Nevigata and Rippa Tetta in Apulia, dating to about 5,900–5,600 BC (COSTANTINI AND STANCANELLI 1994 IN ZAPATA ET AL. 2004). The oldest Neolithic findings in Northwest Mediterranean Italy can be dated to 5,800 cal BC, whereas those from northern Adriatic Italy are younger, dating to about 5,500/5,400 cal BC (GEHLEN 2010; MÜLLER 1994, 257). However, the Neolithic seems to have expanded more steadily at the Adriatic site of Italy than alongside the Tyrrhenian Sea (MALONE 2003, 257). Around 5,000 cal BC, several distinct regional cultures developed in the north Italian plain (MÜLLER 1994, 259). Continuity between the preceding Mesolithic Castelnovian and the early farming communities can be observed in economic practices, location of settlements, in raw materials, and lithic techniques (MALONE 2003, 262).

In southern France, three sites have been found on the Mediterranean coast that are dated to around 5,800–5,600 cal BC and can directly be linked to Liguria or Tuscany in Italy by pottery: Pendimoun (Castellar), Pont de Roque-Haute and Peiro Signado (both Portiragnes) (GUILAINE AND MANEN 2007). The beginning of the Early Neolithic French Cardial culture can be dated to about 5,600 to 5,400/5,300 cal BC. Impressed Ware of northwestern Italy and the Cardial of southern France are linked by the appearance of symmetrical trapezes with dorsal facial retouch at the edges, decorative elements found on pottery, and the lack of microburin-technique (GEHLEN 2010). Although there are similarities in the style of ceramic decoration, form of ceramics as well as density of decoration on the pottery, the Italian Mediterranean-Adriatic Impressed and the Franco-Iberian Cardial ware should be regarded as different archaeological cultures (GUILAINE 1994). Cardial Sites exhibit the general types of cereals and pulses found throughout the Mediterranean but also the poppy (*Papaver somniferum*), which had probably been domesticated in the western Mediterranean region (VANDER LINDEN 2011). From the Provence and Languedoc in France the Cardial spread into the Iberian Peninsula (GUILAINE AND MANEN 2007). Several complex and regional models exist for the Neolithisation of the Iberian Peninsula (BERNABEU AUBÁN 1999; SCHUHMACHER AND SANZ GONZÁLEZ DE LEMA 2013) – an overview will be presented in chapter 2.3.1.

2.3 The Prehistory of the Iberian Peninsula

The following chapters will give a brief overview over the archaeological situation in the key research areas of this study – the Mediterranean coast of Spain and Portugal, Central Portugal, the Northern and Southern Meseta of Central Spain, and the pre-Pyrenean Ebro Valley – between the 6th and 2nd millennium BC.

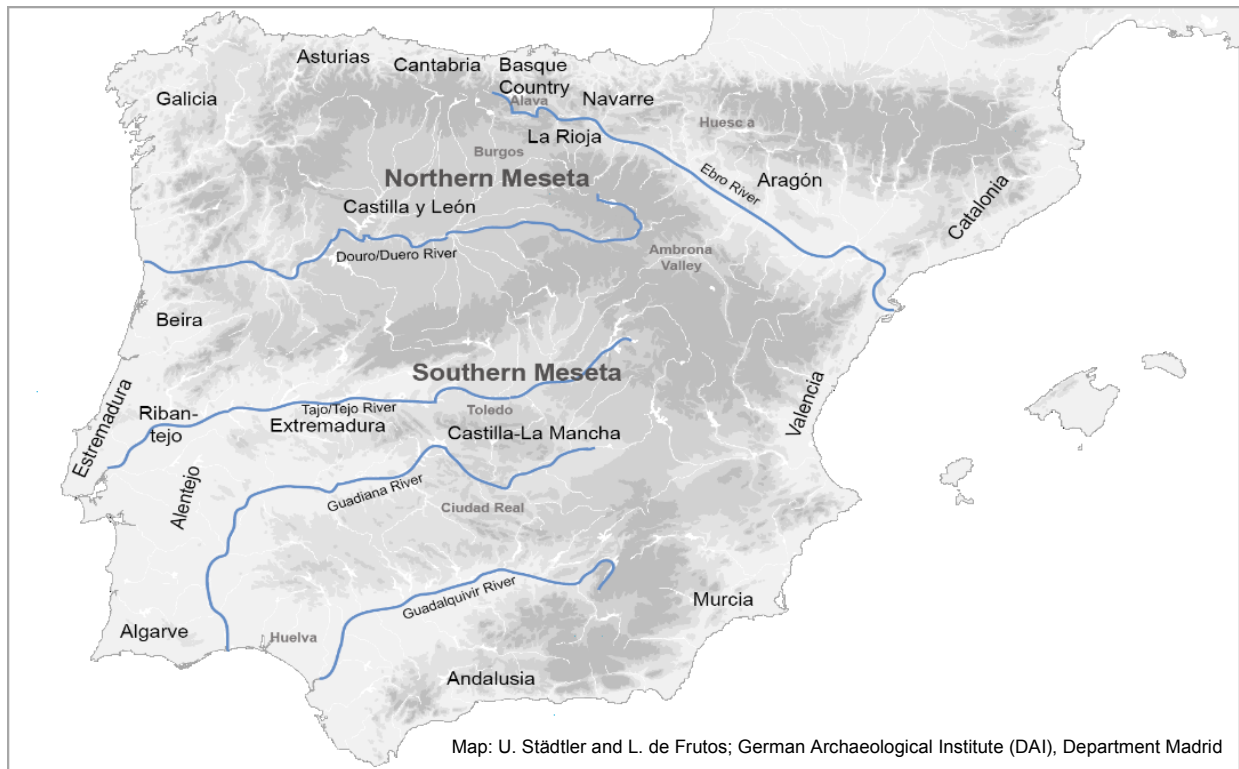


Figure 1 Regions, districts and major rivers of the Iberian Peninsula

2.3.1 The Late Mesolithic of the Iberian Peninsula

While Mesolithic groups of Europe are often believed to have been small in size and very mobile, some like the Ertebølle culture of southern Scandinavia and the Sado and Muge groups of Portugal seem to have had an almost sedentary lifestyle (PRICE 2000B; VAN DER SCHRIEK ET AL. 2007). In Portugal, Mesolithic human remains are mostly associated with shell middens. Early Mesolithic shell middens (11,000–6,200 cal BC) are smaller in size and mainly found along the present coastline, while later Mesolithic ones (6,200–4,800 cal BC) are located along Central-Southern river systems and considerably larger in size (VAN DER SCHRIEK ET AL. 2007; see also fig. 2). The best investigated shell middens are located at the Muge River, where the first excavations took place as early as 1860s (DIOGO MONTEIRO 2012). The best studied sites of the Muge complex are Moita do Sebastião, Cabeço da Arruda, and Cabeço do Amoreira. Together they comprise one of the largest burial

collections of the Mesolithic in Europe (MEIKLEJOHN ET AL. 2009). In the Muge shell middens complex two types of settlements were identified. Large shell middens such as Cabeço da Amoreira, Cabeço da Arruda and Moita do Sebastião are thought to be residential bases, while the smaller shell middens might rather have had logistical functions (DIOGO MONTEIRO 2012). The sites are thought to have been associated with long-term residential occupation (DIOGO MONTEIRO 2012). Another complex of eleven Mesolithic shell middens is located along the Sado River in the Alentejo province of Portugal. In only seven of these sites human remains were found of which three are securely dated: Cabeço das Amoreiras, Arapouco, and Cabeço do Pez (MEIKLEJOHN ET AL. 2009). Subsistence strategies seem to have been quite variable among the Sado river sites; in those situated closer to the mouth of the river, such as Arapouco, more fish remains and fewer mammal bones have been found, while further inland, like in Cabeço do Pez, many mammal bones of e.g. red deer and wild boar have been discovered (ZILHÃO 1993). The Sado shell middens probably had a similar pattern of long-term occupation as the Muge middens (FERREIRA BICHO 1994). The Mesolithic sites Fiais and Samouqueira are located 20 km inland from the Atlantic coast at the mouth of the Mira River (MEIKLEJOHN ET AL. 2009; ZILHÃO 1993). So far only Samouqueira I has yielded directly dated human material in a Mesolithic context. Some smaller Mesolithic sites are located further south, directly at the Atlantic coast, like Vale Marim, Medo Tojeiro, Monte de Azureque, and Castelejo (ZILHÃO 1993; CORTÉS SÁNCHEZ ET AL. 2012).

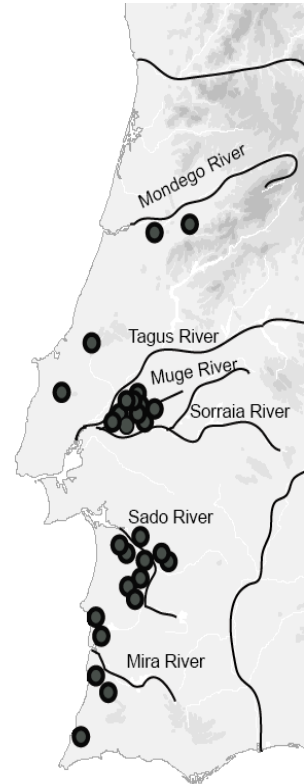


Figure 2 Late Mesolithic sites in Portugal
(based on VAN DER SCHRIEK ET AL. 2007)

In Spain, Mesolithic sites with human remains are mainly known from Cantabria and Basque country at the north coast of the country and from Valencia at the Mediterranean coast (ARIAS ET AL. 2005). Securely dated Mesolithic remains of northern Spain are for example a single individual of *Azipea* in Navarre, dated to 5,610–5,500 cal BC, a double inhumation in Cueva de Braña-Arintero in León, dated to 5,990–5,880 cal BC, five complete or partially complete skeletons in Los Canes in Asturias (6,740/6,230 cal BC to 5,720/5,630 cal BC), and one individual from El Truchiro in Cantabria (5,490–5,370 cal BC) (MEIKLEJOHN 2009). In contrast to many contemporary sites of the coastal Mesolithic in Asturias, the inhabitants of Cueva de los Canes, though situated near the Atlantic Ocean, appear to have had an

exclusively terrestrial diet (ARIAS ET AL. 2005). In 16 of the Alava and western Pyrenean sites, Mediterranean mollusk shells have been found. These findings argue for a certain density of Mesolithic groups between the western Pyrenees and the Mediterranean coast (ARIAS ET AL. 2005). In contrast to the Atlantic, in the Mediterranean regions of Spain there are very few Late Mesolithic funerary contexts and human samples (FERNÁNDEZ-LÓPEZ DE PABLO ET AL. 2013). Four additional sites with direct radiocarbon dating are known, two from eastern Spain, and two from Andalusia. In the Valencian region, securely dated Mesolithic sites are Cingle del Mas Nou in Castellón with six burials dated to 5,830–5,740 cal BC and fifteen burials from El Collado in Valencia dated to 8,450–8,070 cal BC (MEIKLEJOHN 2009). In Andalucía directly dated burials are only available from Cueva del Higueron in Málaga (MEIKLEJOHN 2009). Although in Spain there is a higher amount of archaeological sites which can most probably be assigned to the Mesolithic period, the sites are in general much smaller and contain fewer individuals than their Portuguese counterparts.

2.3.2 6th to 5th millennium BC – The first farmers and their descendants

A Neolithic way of life is documented on the Iberian Peninsula from ca. 5,700-5,600 cal BC onwards. By 5,400-5,300 cal BC, it was widespread in most of the territory except for the Cantabrian coast and the Northwest (ARIAS 2012). The earliest Neolithic of the Iberian Peninsula is mostly connected to the Cardial culture, which was established primarily on the Mediterranean coast in the first half of the 6th millennium cal BC. Some of the oldest sites with Cardial pottery along the Spanish Mediterranean coast are the cave Can Saturní in Catalonia, where the earliest dated cereals of Northeast Spain (5,470–5,300 BC) have been found (ZAPATA ET AL. 2004), and Cueva de los Tollos and Barranco de los Grajos in Murcia (BERNABEU AUBÁN AND MARTÍ OLIVER 2012). One of the oldest Cardial sites in Andalusia is La Cueva de la Carigüela, dated to about 5,600/5,500 cal BC (MOLINA GONZÁLEZ ET AL. 2012). The Early Neolithic Epicardial culture was established in the northwestern Mediterranean area from about 5,300 cal BC onwards, and characterized by hemispheric and globular ceramic wares (VAN WILLIGEN 2006, 260). In contrast to earlier beliefs from the 1960s, the Epicardial culture cannot be regarded as a late form of the Cardial culture; although influences in ceramic decoration by the Cardial culture are recognizable, both material cultures display differences in typology, occur often in different distribution areas, and are partly contemporary (VAN WILLIGEN 2006, 254FF).

Many of the burials in Early Neolithic Northeast Spain are associated with only a very small number of artifacts or no grave-goods at all (GIBAJA ET AL. 2012B). In Andalusia, the Early Neolithic sites of Los Murciélagos, Valdecuevas, El Cabezo, and Los Álamos also did not

contain pottery in Cardial tradition. (MOLINA GONZÁLEZ ET AL. 2012). Los Murciélagos is one of the sites with evidence of the earliest crop domestication in Andalusia; it was dated to 5,500 cal BC (ZAPATA ET AL. 2004). The earliest ceramic ware of Valencia (5,600/5,500 BC), found in the settlements of Barranquet and Mas d'Is, is decorated in a variety of impressed styles (Cardial, instrumento, boquique, and sillon) and decoration in Cardial valenciano style did not become prominent until 5,450 and 5,150 BC (BERNABEU AUBÁN AND MARTÍ OLIVER 2012). The oldest Neolithic sites situated on the Portuguese southwest coast date to the middle of the 6th millennium BC (Vale Pincel I, Samouqueira I, Vidigal, Medo-Tojeiro, and Padrão I) (JORGE 1999). On these sites decorated pottery (with Cardial ware in the minority) and microliths in the local Mesolithic tradition were found. They are slightly older than those of the Sado Valley and the Portuguese Estremadura, where the first settlements date to the last quarter of the 6th millennium BC (Cabeço do Pez, Gruta do Caldeirão, Correio-Mor, and Pena d'Água) (JORGE 1999). Cardial decoration has not been found at sites of the central and northern interior of the country so far (JORGE 1999).

The Early Neolithic did not only spread along the Mediterranean coast but distributed also along the Ebro River further inland, and signs of very early agriculture have been found in the Middle and Upper Ebro Valley, for example, barley, naked wheat, and pea have been identified in the cave of Balma Margineda (Andorra) and dated to 6,000–5,400 BC. Furthermore, domestic animals and indirect proof of agriculture such as lithic sickles and silos dating as early as 5,700/5,500 BC have been found in sites like Chaves, Forcas II, and Olvena (ZAPATA ET AL. 2004). About 5,400–5,200 cal BC, Neolithic farming spread into the interior of the Iberian Peninsula (ROJO GUERRA ET AL. 2006, 2008). Similar to the Mesolithic, Early Neolithic findings are very rare in inner Iberia. In the Northern Meseta, from Burgos, two Early Neolithic burials are known: El Alto de Rodilla and Fuente Celada. In both cases single individuals were buried in crouched position in pits (ROJO GUERRA AND GARRIDO-PENA 2012). Another site is Vaquera cave in Segovia that contained scattered remains in secondary position (ROJAS AND VILLA 1996; DELIBES ET AL. 1999). In the Southern Meseta, a single inhumation in a burial pit without grave goods was found in Ciudad Real (Villamayor de Calatrava) (ROJAS AND VILLA 1996). Two more sites were discovered in Madrid: A double inhumation inside a domestic pit at the site of El Congosto, and a burial in Arenero de Valdivia (JIMÉNEZ 2001; ROJO GUERRA AND GARRIDO PENA 2012). In general, no change in burial rites compared to the previous Mesolithic can be observed (BERNABEU AUBÁN 2010 IN ROJO GUERRA AND GARRIDO PENA 2012). In general, inhumations of early farmers in the interior of Iberia are scarce. They occurred mostly in the form of isolated graves of single or

double inhumations in crouched position in domestic context. Both, caves and open-air finds are known and grave goods are generally rare (ROJO GUERRA AND GARRIDO PENA 2012).

2.3.2.1 Archaeological models for the Neolithisation of the Iberian Peninsula

According to ZILHÃO (2001), the appearance of agriculture and animal husbandry on the Iberian Peninsula was induced by colonization by pioneers; archaeologically supported by the fact that most findings of Early Neolithic sites are located in areas with Mesolithic population gaps (GARCÍA PUCHOL ET AL. 2009). This is also known as the Cardial Model or Maritime pioneer colonization (MORAIS ARNAUD 1990; ZILHÃO 1993, 1997, 2000, 2001 IN MEDVED 2013, 30). SCHUMACHER AND SANZ GONZÁLEZ DE LEMA (2013) propose a Mosaic model especially for the Ebro Valley where some Mesolithic hunter-gatherer groups of the 7th millennium cal BC used ceramics while others had no pottery, explained as an encounter of Neolithic elements from France via the Pyrenees. From the 6th millennium onwards, however, settlements show a producing lifestyle, which seemed to have been a result of rather demic diffusion than of autochthonous development out of Mesolithic groups (SCHUMACHER AND SANZ GONZÁLEZ DE LEMA 2013). The evidence for pre-Cardial domestication of sheep and goat in Cova Fosca, Abri Dourgne, and Grotte Gazel respectively, previously used to support this theory, has been re-evaluated and excluded (SCHUMACHER AND SANZ GONZÁLEZ DE LEMA 2013; ZILHÃO 2001). For the southeast of Spain (Murcia, Almería, Granada, Málaga) ZILHÃO (2001) further pointed out that none of the evidence for pre-Cardial ceramics, stone axes, or houses have been found in an undisturbed and securely dated context. Other models, for example the dual model, assume that Neolithic settlers colonized the Spanish Levant and co-existed with indigenous hunter-gatherers. Subsequently, the latter would have adopted several Neolithic features and dispersed them (MARTÍ 1982; JUAN CABANILLES 1992; BERNABEU ET AL. 1993 IN SCHUMACHER AND SANZ GONZÁLEZ DE LEMA 2013). In the percolative or capillary model, hunter-gatherers were predominantly responsible for the Neolithisation of the Iberian Peninsula by exchanging ceramics and domesticated animal and plants between neighboring groups instead of long distance and directional movement of goods and information as has been stated in the axial/arterial model (RODRÍGUEZ ALCALDE ET AL. 1995; VICENT GARCÍA 1997 IN SCHUMACHER AND SANZ GONZÁLEZ DE LEMA 2013).

In their article from 2009, FÉRNANDEZ LÓPEZ DE PABLO AND GOMÉZ PUCHE revised these different models based on the archaeological state of research. They suggested that considering models based on acculturation as driving force of the Neolithisation only would make sense for regions with archaeological evidence for pre-Neolithic populations. They

reminded that all evidence for Mesolithic pottery production comes from unsecure and disturbed contexts. Recent research had revealed heterogeneity in material culture and settlement patterns which would argue against a simple model of pioneers as bearers of the Early Neolithic (FÉRNANDEZ LÓPEZ DE PABLO AND GOMÉZ PUCHE 2009). To summarize, different areas of the Iberian Peninsula present themselves with varying degrees and densities of the “Neolithic package” and Mesolithic background. Moreover, older, possibly biased radiocarbon dates and questionable contexts of many multiphasic archaeological sites complicate an interpretation of the data. It seems safe to say that the complexity of the shift from a foraging to a farming subsistence strategy cannot be covered by simplified models, and most likely has to be evaluated for different regions of the research area separately.

2.3.3 5th to 4th millennium BC – Emergence of megalithic monuments

From the second half of the 5th millennium BC onwards, burial monuments built in stone architecture arose on the Iberian Peninsula (GIBAJA ET AL. 2012A). Common forms of these megalithic monuments were passage graves (El Torrejón or El Teriñuelo in Salamanca, or Las Arnillas), dolmen (Fuente Pecina II in Burgos, El Guijo I in Salamanca), redondiles (Los Zumacales in Valladolid and La Velilla in Palencia), and limekiln tombs (BUENO RAMÍREZ ET AL. 2006; ROJO GUERRA AND GARRIDO PENA 2012). Passage graves were mostly built with a corridor oriented to the south-southeast, a circular or polygonal chamber at its end, and a stone mound on top. Redondiles are passage graves but with vertical instead of horizontal stone slabs and a basement-like structure with walls made of mud. In limekiln tombs, the burial structure made of limestone was presumably closed by burning down and melting the whole chamber, thus sealing the burials with a lime mantle (ROJO GUERRA AND GARRIDO PENA 2012).

The first megalithic structures of Northeast Spain were built near the Pyrenees at the sites of Rajols, Font de la Vena, and El Padró. They were rectangular or trapezoidal cists covered by large mounds and surrounded by an outer ring of standing stones (GIBAJA ET AL. 2012B). In Catalonia in the 4th millennium BC, many burials were associated with valuable objects sometimes originating from remote regions, like “honey flints”, which possibly came from southeast France, axes and adzes made out of serpentine or jadeite that in many cases can be traced back to the Alps, and obsidian objects from Italian islands (GIBAJA ET AL. 2012B). Burials with large numbers of these grave-goods were often found in isolation or as part of larger sites, like in Bòbila Madurell, Can Gambús, and the mines of Gavà. Prestige objects, however, were not equally available for men and women (GIBAJA ET AL. 2012B). In the

Valencian area, burial customs practiced since the Early Neolithic were continued and domestic areas and ditches of the previous phases were reused (GARCÍA PUCHOL ET AL. 2012). A principal change in funerary practices occurred during the middle of the 4th millennium cal BC, when collective burials in caves became the norm (GARCÍA PUCHOL ET AL. 2012). Here, in the central Mediterranean area of the Iberian Peninsula, megalithic monuments were absent and the funerary use of caves continued during the Chalcolithic until the Bronze Age (GARCÍA PUCHOL ET AL. 2012).

In southern Spain, there are no megalithic structures dating to the first half of the 5th millennium BC, (GARCÍA SANJUÁN ET AL. 2011) and the erection of megalith monuments started between 4,200 and 3,900 cal BC (DÍAZ-ZORITA ET AL. 2012). There are about 1,500 documented megalithic structures known from Andalusia alone (GARCÍA SANJUÁN 2009). In the south of Spain, smaller sites like Remedial, Cuesta de los Almendrillos, and El Palomar were common, while sites like Alberite or Menga with burial chambers constructed out of large upright standing stone cuboids represent a more uncommon class of megalithic monuments (GARCÍA SANJUÁN ET AL. 2011). In the interior of Central Portugal, besides some small burial mounds in the Serra da Aboboreira, no megalithic monuments dating to the 5th millennium have yet been found. In Estremadura, individual burials in caves continued (JORGE 1999). Finally in the first half of the 4th millennium BC, passage-graves of varying lengths with forecourts and dozens to hundreds of inhumations were built or reused in almost all of Portugal (JORGE 1999). In the interior of Iberia, mainly the western side of both Mesetas, monumental tombs had also not been erected before the 4th millennium cal BC (ROJO GUERRA AND GARRIDO PENA 2012). Limekiln tombs have been mainly documented in the Ambrona Valley (Soria), in the southeast of the Northern Meseta (ROJO GUERRA ET AL. 2005, 2010), but also at the center of the Duero basin (El Miradero, Valladolid) (DELIBES ET AL. 1986; ROJO GUERRA AND GARRIDO PENA 2012). In the Southern Meseta, most megalithic monuments were located in the western areas of the Toledo province. There is a strong diversity in the architecture of megalithic graves of the Southern Meseta, although in this area the passage grave was the most widely documented model (BUENO RAMÍREZ ET AL. 2010). Architectural features, particularly of the passage graves, reveal western Iberian connections to the Portuguese Beiras, Alentejo, and the Lisbon region (BUENO RAMÍREZ ET AL. 2006). These relationships are underlined by the presence of luxury grave goods like the variscite minerals from Zamora, shells from the Lisbon area, or jade from the North (BUENO RAMÍREZ ET AL. 2006).

2.3.4 3rd millennium BC – The Chalcolithic period

On the Iberian Peninsula, the 3rd millennium BC is generally referred to as the Copper Age or Chalcolithic period, due to the increased use and processing of copper. Of note, the processing of copper has been practiced on the Iberian Peninsula since the end of the 4th millennium (KUNST 2001). However, important changes in burial customs, settlement structures and possibly socio-economic changes took place at that time as well, especially in the Southeast and Southwest of the Iberian Peninsula as well as in Central Portugal. Changes in burial customs in this period were a lessened use of natural caves, and an increased deposition in artificial caves, so-called hypogea, as well as the emergence of a new type of burial monument – the Tholos tomb. (GARCÍA SANJUÁN 2006) Tholoi are a form of passage grave constructed with a passage and a main chamber covered by earthen tumuli. According to the radiocarbon chronology currently available, the earliest Tholoi currently known were built at the sites of Los Millares and of El Barranquete (GARCÍA SANJUÁN 2006). Another new and very important development in the Chalcolithic was the fortification of settlements in Central (Leceia, Zambujal, Vila Nova de São Pedro) and southern Portugal (Santa Justa, Monte da Tumba) and the Southeast of Spain (Los Millares) (GARCÍA SANJUÁN 2006). The site of Los Millares (Almería) extended over an area of about 6 hectares and had a complex defensive system of three lines of walls with bastions (LULL ET AL. 2010A). In front of the settlement was a cemetery with at least 80 known megalithic tombs, mostly Tholoi, with collective burials inside (LULL ET AL. 2010A). The Los Millares culture emerged at around 3,200 cal BC and developed over several phases until 2,200 cal BC (CASTRO ET AL. 1996; MOLINA GONZÁLEZ ET AL. 2004; LULL ET AL. 2010B). In many cases of Los Millares culture settlements, the size of the settlement corresponded to the size of the associated megalithic burials in their vicinity (LULL ET AL. 2010A). In general, the largest sites in Copper Age Iberia seem to be located in areas with favorable natural conditions (Valencina de la Concepción, La Pijotilla, Los Millares, Marroquíes Bajos) (DÍAZ-DEL RÍO 2010).

In Central Spain the transition from the Late Neolithic to the Late Copper Age seems not to have been accompanied by rapidly growing complexity or rise of egalitarian societies (GARRIDO PENA 2006). Socio-economic changes may have begun in the first half of the 4th millennium cal BC, but occurred over time rather than in an abrupt manner (GARRIDO PENA 2006). The pre-Beaker Copper Age in this area existed approximately between 3,000 and 2,500 cal BC (GARRIDO PENA 1997). There seems to be evidence of an increase in human settlements at the beginning of the Copper Age, indicating demographic growth and economic intensification at that time (GARRIDO PENA 1997). A change in burial customs was practiced from collective, monumental graves to more single graves with crouched

inhumations and rich grave goods in Bell Beaker associated burials (ROJO ET AL. 2005 IN GARRIDO PENA 2006). Altogether, archaeological records from the Copper Age are scarce in Central Iberian, and data regarding socioeconomic changes are lacking (GARRIDO PENA 2006).

From the first half of the 3rd millennium BC onwards, the first Bell Beaker artifacts appeared on the Iberian Peninsula. Chronologically, the oldest findings seem to be located in Portugal (SALANOVA 2005). Bell Beaker associated material was distributed from southern Scandinavia to northern Morocco and from Poland to Ireland and are dated to the second half of the 3rd millennium BC (VANDER LINDEN 2006). Different styles of beakers can be distinguished like the AOO (all over ornamented) and the AOC (all over corded) beaker,

beakers with “cord-impressed lines bordering the spatula zones”, or the Maritime type (CZM, Corded Zoned variety) (KUNST 2005). Further Bell Beaker styles mentioned are the Ciempozuelos and “geometric comb-decorated” style (ALDAY-RUIZ 2005). On the Iberian Peninsula corded ware beakers (AOC) are usually found in coastal or near coastal regions rather than in the interior (KUNST 2005; JORGE 2002). In Portugal, Bell Beaker artefacts are known from mainly four different regions: Northern Portugal, Central Portugal, the Alentejo, and the Algarve. From Northern Portugal 15 burial sites and 6 settlements are currently known (KUNST 2005). Similarly, the record of Bell Beaker settlements and burials in the Alentejo and Algarve regions is low, with only about nine settlements and two graves known in the Alentejo (KUNST 2005). On the other hand, the largest density of Bell Beaker pottery in the Iberian Peninsula was found in Central Portugal, in the Estremadura and Tagus region (KUNST 2005). Similarities in shape between pre-Bell Beaker pottery, the so-called “*copos canelados*”, and the Maritime Bell Beaker type as well as between Palmela bowls and pre-dating bowls of the Copper age of this region, have been pointed out (KUNST 2005).

From northeast Spain at least 160 sites with Beaker pottery, decorated in AOC and Maritime style amongst others, are known (CLOP GARCÍA 2005). However, Beaker elements in this region are almost always associated with Late Neolithic and Bronze Age horizons (CLOP GARCÍA 2005). CLOP GARCÍA (2005) associates the Bell Beaker phenomenon of Northeast



Figure 3: Bell Beaker distribution across Europe
(VAN DER LINDEN 2007)

Spain with small – possibly nomadic or seminomadic – groups that probably developed out of local communities. In the Upper and Middle Ebro Valley of Spain at least 108 sites with Bell Beaker findings have been described, with a wide variety of Beaker styles, burial rites, and chronology (ALAY RUIZ 2005). In Cantabria, Beaker findings are scarce; moreover, different types of Bell Beaker ware seem to have been bound to different contexts. AOC and incised types have been documented in hypogea, while the CZM beakers were exclusively found in megalithic structures (ONTAÑÓN PEREDO 2005). In the Southern Meseta, Bell Beakers occurred in the second half of the 3rd millennium cal BC. The variety in Beaker pottery forms was limited and highly standardized (GARRIDO PENA 1997). The typical Bell Beaker was found in every Bell Beaker grave of the Southern Meseta. Furthermore, Bell Beakers of the Ciempozuelos type were often accompanied by a hemispherical and a carinated bowl (GARRIDO PENA 1997).

2.3.4.1 Bell Beaker culture, Beaker people, Bell Beaker phenomenon or just pots?

As has already been mentioned, the Bell Beaker phenomenon was spread over vast areas of West and Central Europe, the British Isles, and parts of North Africa in the 3rd millennium BC, raising questions about cultural or ethnical relations among the different regional groups. The “Bell Beaker question” has had a long history in archaeological debates and many theories can be linked to science history and the predominant scholars of the particular time. Previously, the belief that a certain material assemblage defines a “culture”, in the sense of population, was widespread in archaeology. Changes in material culture and/or its distribution were often linked to migration processes like in the case of the Bell Beaker (GARRIDO PENA 2005). In the early approaches the search for the origin of the Bell Beaker was another major theme. Different researchers suspected the place of origin first in the Near East and later in the West, particularly on the Iberian Peninsula. In the 1960s and 1970s, the so-called “Dutch model” evolved that put the development of the Bell Beaker in the Lower Rhine area influenced by the Corded Ware culture (GARRIDO PENA 2005 AND CITATIONS THEREIN; SALANOVA 2005). However, it should be noted that available C₁₄ dates clearly link the earliest Bell Beaker to the Iberian Peninsula (SALANOVA 2005; MÜLLER AND VAN WILLINGEN 2001). In 1976, Clarke argued that the Bell Beaker material assemblages should be seen as elements that were exchanged between different groups rather than as an indicator for a certain group (GARRIDO PENA 2005). Another approach linked Beaker vessels to alcohol consumption and proposed that they, alongside weaponry often found in male Bell Beaker burials, would mark them as society leaders. Together with new technologies (“Secondary Product Revolution”), which developed at the same time as the rise of the

Beaker phenomenon, this would have led to the emergence of social stratigraphies at that time (GARRIDO PENA 2005). However, the fact that Bell Beaker pottery is linked to some kind of social elite is argued against by other scholars who rather regard it as common domestic pottery that was spread by exchange, marriage strategies or on a local scale (GARRIDO PENA 2005). In a very recent article, Christian Strahm summarized different models explaining the Bell Beaker phenomenon by reviewing Bell Beaker “standard pottery” and “*Komplementärkeramik*” (STRAHM 2014). He explained the Bell Beaker phenomenon as a new ideology of political, religious or economical origin that emerged in the 3rd millennium BC and spread rapidly over vast parts of Europe; archaeologically visible by the common “Bell Beaker-set”. The *Begleitkeramik* on the other hand shows very regional elements that can often be linked to preceding Neolithic groups (STRAHM 2014). In this model, the Bell Beaker phenomenon is explained by the assimilation of the “Bell Beaker ideology” by regional groups.

2.3.5 2nd millennium BC – Early Bronze Age societies

The beginning of the Iberian Bronze Age can be set to c. 2,200 cal BC and its end to about 900 cal BC (LULL ET AL. 2013A). Chronologically it can be divided into the Early Bronze Age (2,200–1,550 cal BC), sometimes further divided in Early and Middle Bronze Age, followed by the Late Bronze Age (1,550–1300 cal BC), and Final Bronze Age (1,300–900 cal BC) (LULL ET AL. 2013A). A continuation of the Bell Beaker phenomenon into the Early Bronze Age has been proven for some regions (LULL ET AL. 2013A).

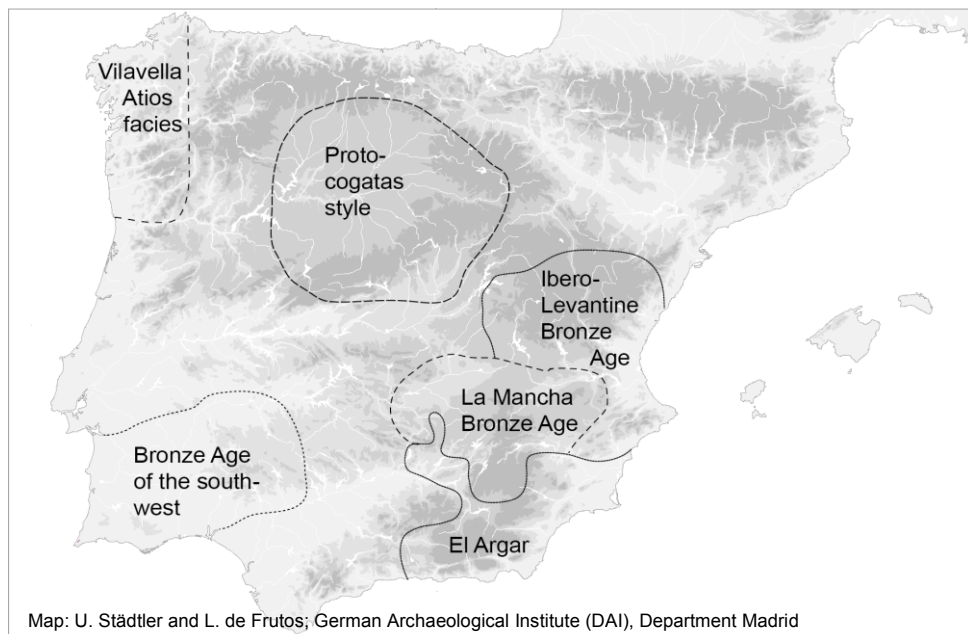


Figure 4 Distribution of Early Bronze Age material cultures
(based on LULL ET AL. 2013A, 597)

In Valencia, Bronze Age settlements were built in stone, often fortified and situated in upland regions, like Mola d'Agres and Mas de Menente in Alicante, Muntanya Assolada in Valencia, and Cerro de la Campana in Murcia. Settlements covered small areas of about 0.1 to 0.3 hectares and show patterns typical for farms or small villages (LULL ET AL. 2013A). Settlement density was high in this region but the average settlement size was small. Individual burials and entombments of small groups were mostly found in caves outside of settlements and common grave goods were bowls and vessels (LULL ET AL. 2013A).

Common forms of Bronze Age settlements in Northeast Spain but also in the Upper and Middle Ebro Valley, as well as in the West of the Iberian Peninsula alongside the rivers Duero, Tagus, Guadiana, and Guadalquivir are the so-called "*campos de hoyos*" (pit fields), which had already been built in Neolithic times (LULL ET AL. 2013A). They consisted of various structures used as storage silos, houses, and graves or for religious offerings and are thought to have been only temporarily occupied (LULL ET AL. 2013A). Examples of pit field settlements are Minferri in Lleida, Can Roqueta II in Barcelona, Loma del Lomo in Guadalajara, and Caserio de Perales in Madrid (LULL ET AL. 2013A). In the Northwest, however, they emerged no earlier than the Bronze Age and were mostly located near valley bottoms (PARCERO OUBIÑA AND CRIADO BOADO 2013). Beside the lowland pit field settlements, a significant number of hilltop settlements, like El Castillo de Cardenosa in Avila, El Parpantique in Soria, Moncin in Zaragoza, and Castillo de Alange in Badajoz are known as well (LULL ET AL. 2013A, 605). The pottery was marked by the predominance of plain vessels. Continuity in pottery styles up to the Late Bell Beaker is recognizable in some regions and certain Bell Beaker styles coexisted with the Early Bronze Age for some time (LULL ET AL. 2013A, 606). Funerary customs in the Northeast were for example burials in pits, caves, hypogea, mounds, and megalithic tombs (LULL ET AL. 2013A).

A very impressive development of the Iberian Bronze Age was without doubt the emergence of the El Argar culture in southeast Spain. It lasted from approximately 2,200 cal BC to 1,450 cal BC (ARANDA ET AL. 2010) and differed from the preceding Los Millares culture in its technological development, economic ties, settlement structures and territorial organization, as well as in funerary rituals (LULL ET AL. 2013B). El Argar settlements were constructed in the form of hilltop settlements situated on edges of mountain ranges like La Bastida near Totana in Murcia, or as smaller lowland settlements often located in river valleys (LULL ET AL. 2011 AND CITATIONS THEREIN). The two settlement forms of the El Argar culture showed contrasting patterns in terms of frequency of tools and grave goods (LULL ET AL. 2011). It was suggested that the lowland population had a dependency relationship to the "rulers" in the larger hilltop settlements (LULL ET AL. 2011). Instead of collective burials in megalithic or

caves tombs – common in the preceding Copper Age – inhumations were undertaken as single, or occasionally as double burials in stone cists¹, shafts or in rock chambers within the settlements (LULL ET AL. 2011; WEISS-KREJCI 2011). Argaric pottery shapes were highly standardized; there are only three different styles that can be traced back to eight simple shapes (LULL ET AL. 2013B). The Early Bronze Age of Galicia and northern Portugal can be characterized by the Montelavar-Atios horizon (see fig. 4). Inhumations were mostly performed as individual burials in pits or cists. Common grave goods were plain pottery vessels and metal objects in Bell Beaker tradition like tanged daggers, Palmela arrowheads, and gold ornaments, but also halberds, which are usually interpreted as a sign of connections to the Atlantic coast (LULL ET AL. 2013A). In the Spanish Extremadura, the majority of the Copper Age settlements and cemeteries had been abandoned and archaeological evidence of the Early Bronze Age is scarce (LULL ET AL. 2013A). The few cemeteries known from this region often consisted of several dozen cists with very few grave goods, e.g. El Castanuelo in Huelva (LULL ET AL. 2013A). In the Northern Meseta, the Protocogotas ceramic horizon (see fig. 4) emerged at about 1,700 cal BC. Its ceramic was characteristically decorated by impressed or incised motifs on the upper part of vessels. Its successor, the Cogotas I style, was widespread across the Iberian Peninsula from the middle of the 2nd millennium cal BC onwards (LULL ET AL. 2013A). From La Mancha (provinces of Albacete, Ciudad Real, Cuenca, and Toledo) a variety of Early Bronze Age settlement patterns is known: Fortified settlements on high ground (Morras and Castillejos), like Morra de Quintanar and Cerro del Cuchillo in Albacete, lowland settlements built in stone architecture (Motillas), like Santa Maria de Retamar in Ciudad Real and El Acequion in Albacete, but also small agricultural settlements (LULL ET AL. 2013A; ARANDA ET AL. 2008). Settlements of the Motillas type were situated every 4 to 5 km alongside waters with low salinity (ARANDA ET AL. 2008), while hilltop settlements were generally situated on naturally occurring defensive positions from where the lowland Motillas could be overseen (ARANDA ET AL. 2008). In general, the Bronze Age of La Mancha can be characterized by a high population density, demographic growth, and long-term occupation of sites (ARANDA ET AL. 2008). In all settlements plain, undecorated pottery was used. The most common objects made from copper were knives, awls, axes, and arrow- or spearheads (LULL ET AL. 2013A).

¹ An ancient coffin or burial chamber made from stone (Definition: Oxford Dictionary online).

² Author comment: It should be noted that this haplotype cannot clearly be classified as X1.

³ Author comment: Conclusions were drawn based on the assumption of a European Paleolithic origin

3 Genetic basics

3.1 Modern DNA

3.1.1 Mitochondrial DNA

Human mitochondria are cell organelles with their own circular, double-stranded genome of 16,569 bases in length (ANDERSON ET AL. 1981; ANDREWS ET AL. 1999). According to the endosymbiosis theory, mitochondria are remains of prokaryotic cells that were incorporated into pro-eukaryotic cells as symbionts about 1.5×10^9 years ago (MARGULIS 1975). They play an important role in the energy metabolism of cells as several steps of the cellular respiration take place inside them. During evolution a number of mitochondrial genes were transferred into the nuclear DNA; while some still encode for proteins of the energy metabolism, others – so-called pseudogenes – have long lost their function (ZISCHLER ET AL. 1995; ZHANG AND HEWITT 1996). Human cells contain – dependent on cell type – between 1,000 and 10,000 mitochondria, each of which possesses 2 to 10 copies of the mitochondrial genome (mt-genome) (JOBBLING ET AL. 2004, 39). Altogether, 37 genes are located on the mt-genome whereof 13 encode for proteins of the energy metabolism, 2 for ribosomal RNA (rRNA), and 22 for transfer RNA (tRNA) (ANDERSON ET AL. 1981; ALEXEJEV ET AL. 2013). The DNA-strands of mitochondrial genomes contain different proportions of guanine and cytosine and are therefore differentiated into a guanine-rich heavy (H)-strand and a cytosine-rich light (L)-strand.

Mitochondrial DNA (mtDNA) differs from nuclear DNA in several aspects: Like prokaryotic DNA, mtDNA is transcribed in a polycistronic manner (each strand is transcribed in total and cleaved into separate ORFs [open reading frames] afterwards) and the typical structure of exons and introns found in nuclear DNA is absent. In fact, only 7% of the mitochondrial genome is non-coding in contrast to 95% in the nuclear genome (STONEKING 2008). A large non-coding section of the mitochondrial genome, the so-called control region, is located between nucleotide position (np) 16024 and 576. It contains the promoters for transcription of both DNA strands along with one of the origins of replication (ALEXEJEV ET AL. 2013). Two parts of this control region are of special interest for population genetics; the hypervariable regions (HVR) I and II (np 16024–16365 and np 73–340) (JOBBLING ET AL. 2004, 40; see also fig. 5). Since the control region is non-coding, it is exposed to less selective pressure, therefore tending to accumulate mutations about 10 times faster than the coding region (BROWN ET AL. 1979; BALLARD AND WHITLOCK 2004; TATARENKOV AND AVISE 2007; SOARES ET AL. 2009).

The discovery that mitochondria are unable to repair UV-induced pyrimidine dimers and certain types of alkylation damage, had led to the theory that mtDNA had less effective DNA repair mechanisms than nuclear DNA (ALEXEJEV ET AL. 2013). However, recent research has found evidence for the presence of most known major repair systems in mitochondria, although there seem to be deficiencies in mismatch and nucleotide excision repair (ALEXEJEV ET AL. 2013). Due to the processes of energy metabolism, mtDNA is however exposed to a higher ratio of free radicals that can cause oxidative damage to the DNA. Therefore, mtDNA is prone to DNA damage and mutagenesis, especially in the non-coding control region that is not under selective pressure. The exact value of the mitochondrial mutation rate(s) has been under constant debate, mostly due to the use of different techniques, like modern pedigree analyses or estimation of accumulated variability since a certain point in time (FU ET AL. 2013). For the latter, the accumulation of mutations since the most recent common ancestor is estimated, for examples the split of humans and chimpanzees. However, no fossil has yet been identified that represents the most recent common ancestor between humans and chimpanzee (FU ET AL. 2013). Estimates of substitution rates of the mtDNA have ranged from 1.69×10^{-8} for the control region, using the peopling of Oceania 45kya ago as calibration point (FRIEDLAENDER ET AL. 2005) to 1.26×10^{-8} substitutions per site and year (MISHMAR ET AL. 2003) for the coding region, calibrated with a chimpanzee-human divergence time of 6.5 million years BP. In a recent study FU ET AL. (2013) used data from ten securely dated ancient modern humans as calibration points for the mitochondrial clock and estimated a mutation rate of 1.57×10^{-8} substitutions per site per year for the coding region and 2.67×10^{-8} substitutions per site per year for the whole molecule. Similarly, BROTHERTON ET AL. (2013) calculated based on 39 Neolithic to Bronze Age mt-genomes of haplogroup H a mutation rate of 2.4×10^{-8} for the entire mitochondrial genome.

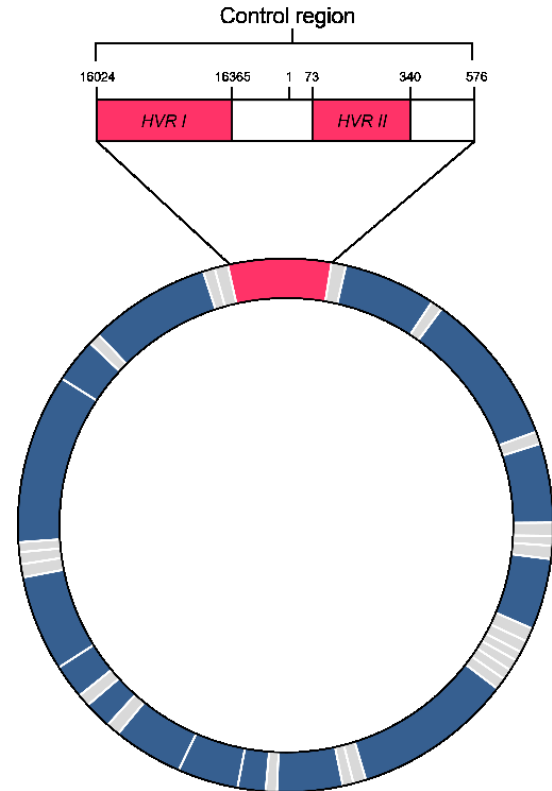


Figure 5 Schematic representation of the human mitochondrial genome

The control region is depicted in red. The small gray sections in the coding region indicate segments which code for tRNAs (based on JOBLING ET AL. 2004, 40)

Another fact, besides the high mutation rate, that renders mtDNA useful for population genetic objectives, is its uniparental inheritance. Mitochondrial DNA is only passed to the next generation by maternal lineage (JOBLING ET AL. 2004, 39; INGMANN ET AL. 2000; ALEXEJEV ET AL. 2013). Although a small number of sperm mitochondria enter the oocyte during fertilization, the number of maternal mitochondria in the oocyte is 10^3 times higher (ANKEL-SIMMONS ET AL. 1996). It is suspected that the remaining sperm mitochondria are destroyed in the following stages of the oogenesis (SCHWARTZ AND VISSING 2002). SUTOVSKY ET AL. (2004) suggest a labeling of the paternal mitochondria with ubiquitin and subsequent degradation by enzymes. Furthermore in egg cells the number of mitochondria is dramatically reduced in the early stage of the oogenesis resulting in a genetic bottleneck. Therefore egg cells are more or less homoplasmic in regard to their mitochondria (HAUSWIRTH AND LAIPIS 1982; THORBURN AND DAHL 2001).

Due to the high mutation rate in combination with maternal inheritance and absence of recombination, mitochondrial DNA – particularly the fast evolving HVR I and II – is an extremely useful marker for population genetic studies. Furthermore, because each cell contains up to 5,000 times more mitochondrial molecules than nuclear DNA and mtDNA degrades 2.0 to 2.5 times slower than nuclear DNA (ALLENTOFT ET AL. 2012), mitochondrial DNA is the ideal genetic marker for ancient DNA analysis, as it is often the only genetic material left.

3.1.2 Phylogeny of mitochondrial haplogroups

The haplotype of an individual is defined as the particular sequence of a haploid DNA molecule, for example the mitochondrial genome. The characterization of a single haplotype is carried out by listing all observed nucleotide variations in comparison to a reference sequence. The first reference sequence for the human mitochondrial genome was the Cambridge Reference Sequence (CRS) (ANDERSON ET AL. 1981). However, this sequence contained a number of mistakes and was re-sequenced in the 1990s and published as revised Cambridge Reference Sequence (rCRS) (ANDREWS ET AL. 1999). Recently a new reference sequence has been published, the so-called Reconstructed Sapiens Reference Sequence (RSRS) (BEHAR ET AL. 2012). The authors used mitochondrial genomes of *Homo neanderthalensis* to estimate the root sequence of all modern human mtDNA variation and suggested using this RSRS instead of the rCRS which is located in the middle of the mtDNA tree and belongs to haplogroup H2a2a1.

Mitochondrial haplotypes can be subsumed into monophyletic clades – haplogroups (hg) – that often show typical pan-regional distributions (see fig. 6). RFLP-Analyses (restriction fragment length polymorphism) led to the first nomenclature of mitochondrial haplogroups in the 1990s (TORRONI ET AL. 1994, 1996). By sequencing of the HVR I and later whole-mitochondrial genomes, a detailed phylogeny of the mitochondrial tree was generated (e.g. RICHARDS ET AL. 1996, 1998; INGMANN ET AL. 2000; FINNILÄ ET AL. 2001; HERRNSTADT ET AL. 2002). However, re-arrangement and -naming of sub-haplogroups as well as defining new sub-haplogroups is an ongoing process. About every six months a new version of the most recent mt-phylogeny is published at the database of phylotree (VAN OVEN AND KAYSER 2009).

Haplogroups are named starting with letters (e.g. hg J), followed by further subdivisions into sub-groups with numerals (e.g. J2). Further subdivisions are denoted by additional letter/numeral combinations (e.g. J21c).

African and non-African mitochondrial lineages can be separated at the very root of the mtDNA tree. All African lineages belong to hg L (L0 to L6) (WWW.MITOMAP.ORG). The variability of L-hgs is much greater than that of

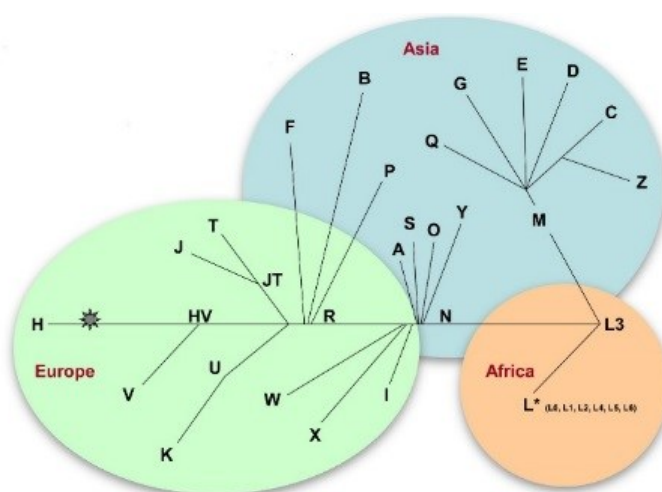


Figure 6 Simplified phylogenetic network of human mitochondrial haplogroups

The phylogenetic location of the rCRS haplotype is indicated by an asterisk (WWW.MITOMAP.ORG)

non-African hgs, pointing to an African origin for all AMHs (JOBILING ET AL. 2004, 290; INGMANN AND GYLLENSTEN 2001). All non-African haplogroups belong to the macro-haplogroups M and N which both developed out of the African hg L3 (MACA-MEYER ET AL. 2001). Driven by migration of the AMH these two macro-haplogroups dispersed into different geographical regions, where they differentiated over time into new hgs. M is mostly found in South- and East Asia as well as in America and is subdivided into several clusters that also contain hgs C, D, E, G, Q, and Z. Macro-hg N is widely distributed in western Asia, northern Africa, and Europe (JOBILING ET AL. 2004, 290). It is subdivided into several sub-clusters that contain hgs A, I, O, S, W, X, Y and the R-cluster. Hgs B, F, J, P, and T, as well as the hgs R0 and U are affiliated with the R-cluster. Hgs HV, H, and V belong to R0, while hg K is a sub-group of hg U8b (VAN OVEN AND KAYSER 2009).

3.1.3 Phylogeography of the major European mitochondrial haplogroups

Based on modern DNA analysis, the most ancient mtDNA lineages in Europe belong to haplogroups U4, U5, and U8. Of these, U5 and U8 are the oldest in Europe and are thought to have been introduced by the arrival of the first modern humans in Europe (MALYARCHUK ET AL. 2008; RICHARDS ET AL. 2000; SOARES ET AL. 2010). U5 is presently estimated to an age of about 37,000 years BP, although it might actually be older (SOARES ET AL. 2010). The sub-haplogroups U5a and U5b are estimated to be 16–20 and 20–24 ky old, respectively (MALYARCHUK ET AL. 2010). U8 has a coalescence age of about 50,000 years and its sub-clade K appeared in the Near East approximately around 30 kya (SOARES ET AL. 2010). Almost all other mitochondrial lineages are connected to expansions within Europe before or after the last glacial maximum. During the Late Glacial Maximum (LGM) between 25–19.5 kya, Europeans faced dramatic and rapid climatic changes and were forced to retreat to refuges in Southwest Europe, along the Mediterranean, in the Balkans and the Levant, and on the East European plain (MALYARCHUK ET AL. 2008; PALA ET AL. 2012; PEREIRA ET AL. 2005; TORRONI ET AL. 1998, 2001). Temperatures began to increase after the last glacial period about 15,000 years ago, and after some abrupt relapses to glacial climate conditions, the climate finally stabilized 11,500 years ago (ALLEY ET AL. 1993; PALA ET AL. 2009).

In the glacial refuges, genetic drift and founder effects affected human genetic variation. It is suspected that these effects were stronger for the uni-parental inherited mtDNA and Y-chromosome, due to their smaller effective population size (PALA ET AL. 2009). Thus, pre-LGM mtDNA and Y-chromosome haplotypes were most probably differently preserved (or lost) in the various refuges (PALA ET AL. 2009). The Iberian Peninsula, particularly Cantabria and Portugal, is often described as the principal southern refuge for human populations (GAMBLE ET AL. 2004; ZILHÃO 1997; STRAUS ET AL. 2000). However, Aquitaine in France has an important archaeological record dated to the last glacial period as does the lower Rhône region, while the Loire area, northern France, and Germany were probably only infrequently inhabited during that time (GAMBLE ET AL. 2004). While earlier views that these northern areas were completely abandoned at the LGM (WENIGER 1990) can no longer be supported (TERBERGER AND STREET 2002), there is a consensus that significant re-population of these areas happened from southern refuges (GAMBLE ET AL. 2004). Mitochondrial haplogroups that have been linked to a re-expansion into Europe from the Franco-Cantabrian refuge before the beginning of the Holocene are H1, H3, V, and U5b1b (TORRONI ET AL. 1998, 2001; ACHILLI ET AL. 2004, 2005; GAMBLE ET AL. 2004; LOOGVÄLLI ET AL. 2004; PEREIRA ET AL. 2005; ÁLVEREZ-IGLESIAS ET AL. 2009; PALA ET AL. 2012). On the contrary, based on phylogeographic distribution and age estimations, haplogroup U4(a1) and possibly some clusters of U5a may have re-expanded from refuges in the East European plains (PALA ET AL.

2012; SOARES ET AL. 2010; MALYARCHUK ET AL. 2008, 2010). However, especially coalescence estimations of haplogroup H, which constitutes about half of the European modern mitochondrial gene pool, should be considered under the light of the research state concerning its genealogical resolution. Publications based on phylogeographic questions concerning haplogroup H have interpreted results on the assumption of 11 (LOOGVÄLLI ET AL. 2004), 15 (ACHILLI ET AL. 2004), 21 (ROOSTALU ET AL. 2007) or 25 sub-haplogroups (ÁLVERZE-INGELSIAS ET AL. 2009) while the newest version of phylotree (VAN OVEN AND KAYSER 2009) recognizes more than 80.

Another paper focused specifically on the haplogroup U5b3 which was more recently defined on the basis of an uncommon haplotype found on the island of Sardinia and confirmed as an independent clade within the U5 phylogeny by whole genome sequencing (PALA ET AL. 2009). Its coalescence time of 10.1 to 8.1 kya is similar to that of H1 and H3 and was interpreted as sign of a population expansion at about the same time. By spatial comparison of frequencies of this hg in the areas of Sardinia, the Iberian Peninsula, Italy, Western Europe, and Eastern Europe, Italy was declared the most reasonable source region (PALA ET AL. 2009). On the basis of whole-mitochondrial-genome and HVR I datasets, a recent study has identified coalescence ages of haplogroups J and T, and their major sub-haplogroups respectively (PALA ET AL. 2012). The authors propose that haplogroups J and T have started to spread from the Near East into Europe immediately after the peak of the last glaciation some 19,000 years ago. For their sub-haplogroups they identified three predominant expansion events in Europe: During the last glaciation, about 16,000 to 12,000 years ago (J1c, J1b1a, J2a1, T1a1, T2a1b, and T2f1), one after the last glacial maximum at about 10,000 to 11,000 years ago (T2b and T2e) and one in the 8th millennium, possibly associated with the Neolithic expansion (T1a1a1) (PALA ET AL. 2012). Likewise haplogroups I and W probably originated in the Near East during the Last Glacial Maximum or shortly after, between 19,000 and 15,000 years ago. They may have been involved, particularly their sub-haplogroups I1, I2'3, I5, W3, W4, and W5, in Late Glacial expansions starting from the Near East into Europe between 18 and 12 ky ago (OLIVIERI ET AL. 2013).

3.2 Ancient DNA

The term ancient DNA (aDNA) describes DNA that is gained from prehistoric and historic remains. In the 1990s, the field of aDNA review grew considerably, especially with the possibilities of the newly developed polymerase chain reaction (PCR) (MULLIS AND FALOONA 1987). Within a few years, numerous publications were published, claiming successful

amplification of several million year old plant DNA (GOLENBERG ET AL. 1990; SOLTIS ET AL. 1992), Dinosaur DNA (WOODWARD ET AL. 1994) as well as DNA from amber fossil inclusions (CANO UND BORUCKI 1995; DESALLE ET AL. 1992). However, most of the results turned out to be modern human or bacterial contamination or were not reproducible (ZISCHLER ET AL. 1995; AUSTIN ET AL. 1997; GUTIERRÉZ AND MARÍN 1998). Nowadays the idea of amplifying several million years old DNA is seen to be more critically. Even under optimal conditions, DNA is probably only preserved for about 10,000 to maximal 1,000,000 years (WILLERSLEV UND COOPER 2005). New results from experiments with ancient Moa bones and Next Generation Sequencing (see also chapter 3.2.3) suggest that detectable amounts of DNA may be still present in more than 1,000,000 year old bones from deep frozen environments (ALLENTOFT ET AL. 2012). The oldest evidence of ancient DNA so far are a 43bp fragment of an 800,000 year old Pleistocene pygmy elephant sample (POULAKAKIS ET AL. 2006), between 550,000 to 800,000 year old floral DNA from Greenland ice cores (WILLERSLEV ET AL. 2007), and a complete horse genome dating to 560,000–780,000 years BP (ORLANDO ET AL. 2013).

When working with DNA one faces two main difficulties: After the death of an individual, DNA is exposed to a number of oxidative and hydrolytic processes resulting in extreme fragmentation and alteration of the DNA molecules (PÄÄBO ET AL. 2004). Additionally, the preservation of very few DNA molecules in (pre-) historic material results in a high risk of contamination with exogenous modern DNA (PÄÄBO ET AL. 1989; WILLERSLEV AND COOPER 2005; COOPER AND POINAR 2001). Especially when working with human DNA one has to be extremely careful, because both researcher and sample belong to the same species, complicating the detection of contaminations. Therefore the application of strict work protocols, reproduction of results by multiple experiments as well as contamination monitoring is extremely important to authenticate ancient DNA results (COOPER UND POINAR 2000; HOFREITER ET AL. 2001; PÄÄBO ET AL. 2004; GILBERT ET AL. 2005).

Despite the many difficulties when working with ancient DNA, improvements of methodology – especially in the last few years with the development of the so-called Next Generation Sequencing (see chapter 3.2.3) – have led to a vast explosion of publications. Fields of research in which ancient DNA techniques are used, are for example the phylogeny of early humans like *homo neanderthalensis*, *denisova*, and *homo sapiens* (KRAUSE ET AL. 2010A; GREEN ET AL. 2008, 2010; BRIGGS ET AL. 2007; MEYER ET AL. 2012, 2013) and extinct species in general (DRISCOLL ET AL. 2012; ROHLAND ET AL. 2010; DEBRUYNE ET AL. 2008; LISTER ET AL. 2005), domestication of plants and animals (LI ET AL. 2011; LÄGLER ET AL. 2006; PALMER ET AL. 2009; BOLLONGINO ET AL. 2012; NIEMI ET AL. 2013; LARSON ET AL. 2010, OTTONI ET AL. 2013), identification of personalities of historical value (VERNESI ET AL. 2001; HAWASS ET AL.

2010; BAUER ET AL. 2013A), investigation of putative kinship (HAAK ET AL. 2008; SIMÓN ET AL. 2011; BACA ET AL. 2012; LEE ET AL. 2012; MALMSTRÖM ET AL. 2012; BAUER ET AL. 2013B), paleoecology (WILLERSLEV ET AL. 2003), epidemiology and pathology (HAENSCH ET AL. 2010; TAUBENBERGER ET AL. 2007) as well as population genetic objectives (HAAK ET AL. 2010; GAMBA ET AL. 2011; DER SARKISSIAN ET AL. 2013; HERVELLA ET AL. 2012; BRANDT ET AL. 2013). Chapter 3.2.4 will give an overview over the state of research concerning the population genetics of prehistoric human populations between Paleolithic and Bronze Age.

3.2.1 Diagenesis and preservation of ancient DNA

DNA is exposed to a number of chemical and physical processes that can alter and damage it. The main damage is caused by hydrolysis, oxidation, uncontrolled methylation or alkylation as well as mutations induced by ultraviolet (UV) radiation (JANNING AND KNUST 2004, 205FF; MITCHELL ET AL. 2005). In general, reactive substances that can cause alteration of the DNA structure are called mutagenic. In a living cell, a set of different repair mechanisms make sure that the genetic code remains uncorrupted; special enzymes can for example recognize and correct false base incorporations during replication and reactions that release highly reactive molecules are only undertaken in compartmented areas of a cell (LINDAHL ET AL. 1993). After an individual's death, however, all repair mechanisms naturally become inactive and cell structures containing lysing reagents degrade, resulting in the so-called autolysis of the cells.

The degradation of DNA is further influenced by microorganisms and environmental factors like humidity, temperature, and pH-value. Best conditions for DNA preservation are aridity, because humid conditions abet hydrolytic processes, and low temperatures under which oxidative and hydrolytic reactions are decelerated (HÖSS 2001; POINAR ET AL. 2003). Furthermore, slightly positive to neutral pH-values favor DNA preservation, while negative pH-values lead to degradation of bone- and tooth tissue (NIELSEN-MARSH AND HEDGES 2000; MITCHELL ET AL. 2005). The results of all these factors are DNA strand breaks, loss and modification of DNA bases as well as cross links of different DNA molecules leading to extreme fragmentation and alteration of the DNA. The most frequent post-mortem damages will be discussed hereafter.

Possible damages than can accumulate post-mortem are cross-links between different DNA molecules or DNA molecules and proteins. The former is induced by alkylation of DNA bases that can lead to linkage between two DNA strands or between two different DNA molecules. Cross-links between DNA and proteins happen because of condense reactions between a

sugar molecule and the amino acid of a protein or a nucleic acid and can inhibit amplification during the PCR (PÄÄBO ET AL. 2004; WILLERSLEV AND COOPER 2005). Oxidative and hydrolytic reactions on the other hand can lead to the modification of the original bases that can block further amplifications or lead to an incorporation of incorrect DNA bases during PCR (PÄÄBO ET AL. 2004; GILBERT ET AL. 2003). Oxidative processes can lead to the transformation of pyrimidines to hydantoins, which block elongation of the DNA strand during amplification due to the loss of a carbon atom (LINDAHL ET AL. 1993). Oxidation of cytosine (C), thymine (T) and guanine (G) can lead to a number of base derivatives which in turn cause the incorporation of wrong nucleotides on the complementary DNA-strand during amplification (see fig. 7B): guanine can be transformed into 8-oxoguanine, which pairs with adenine instead of cytosine, leading to a transversion from guanine to thymine during amplification (STILLER ET AL. 2006).

Hydrolytic reactions can attack different spots of the DNA strand. They can destroy the phosphodiester bonds between nucleotides and lead to abasic sites because of depurination (WILLERSLEV UND COOPER 2005). This affects guanine more than adenine due to the high electronegativity of the ketone oxygen atom of guanine that leads to unfavorable resonance structures with the N-atom of the N-glycosyl bond between sugar and base. During hydrolytic attacks these are stabilized by electron dislocation, which in turn reduces the energy required to break the N-glycosyl bond (OVERBALLE-PETERSEN ET AL. 2012). Besides DNA fragmentation, hydrolytic reactions can also lead to DNA alterations, like deamination (see fig. 7C). Deamination processes can transform adenine into hypoxanthine that is complementary to cytosine instead of thymine, thus leading to an A → G substitution. The most commonly observed post-mortem damage is the deamination of cytosine to uracil, a substitute of thymine in the RNA that consequently pairs with adenine on the complementary DNA strand, leading to a transition of C to T on the original strand (HANSEN ET AL. 2001; HOFREITER ET AL. 2001). The same happens when 5-methyl-cytosine is transformed into thymine. Chemical alteration of guanine to xanthine on the other hand has no further effect on the DNA. During PCR each, the L- and the H-strand of the DNA can theoretically be amplified, therefore deamination effects like C to T transitions can be observed as C → T on the one strand or as G → A on the complementary strand. Likewise A to G transitions are visible as T to C transitions on the complementary strand (HANSEN ET AL. 2001; HOFREITER ET AL. 2001). Because only deaminations of cytosine and adenine lead to a change in pairing behavior, T to C and G to A transitions are always just reflections of deamination processes visible on the complementary DNA-strand. Hence, these “reflection transitions” and the actual transitions cannot be observed together on the same DNA-strand (GILBERT ET AL.

2003). However, in short DNA fragments one can observe so-called “jumping PCR events”, where the DNA-polymerase combines different PCR-fragments to one chimeric PCR product during the PCR (PÄÄBO ET AL. 1990). In this case, T to C and C to T transitions could theoretically be observed on the same DNA-strand. Studies using Next Generation Sequencing techniques have revealed an increased ratio of nucleotide misincorporation at the 5' and 3' ends of DNA sequences, possibly due to a single-stranded structure that potentiates the interaction of bases with water molecules (BRIGGS ET AL. 2007; ORLANDO ET AL. 2011; OVERBALLE-PETERSEN ET AL. 2012).

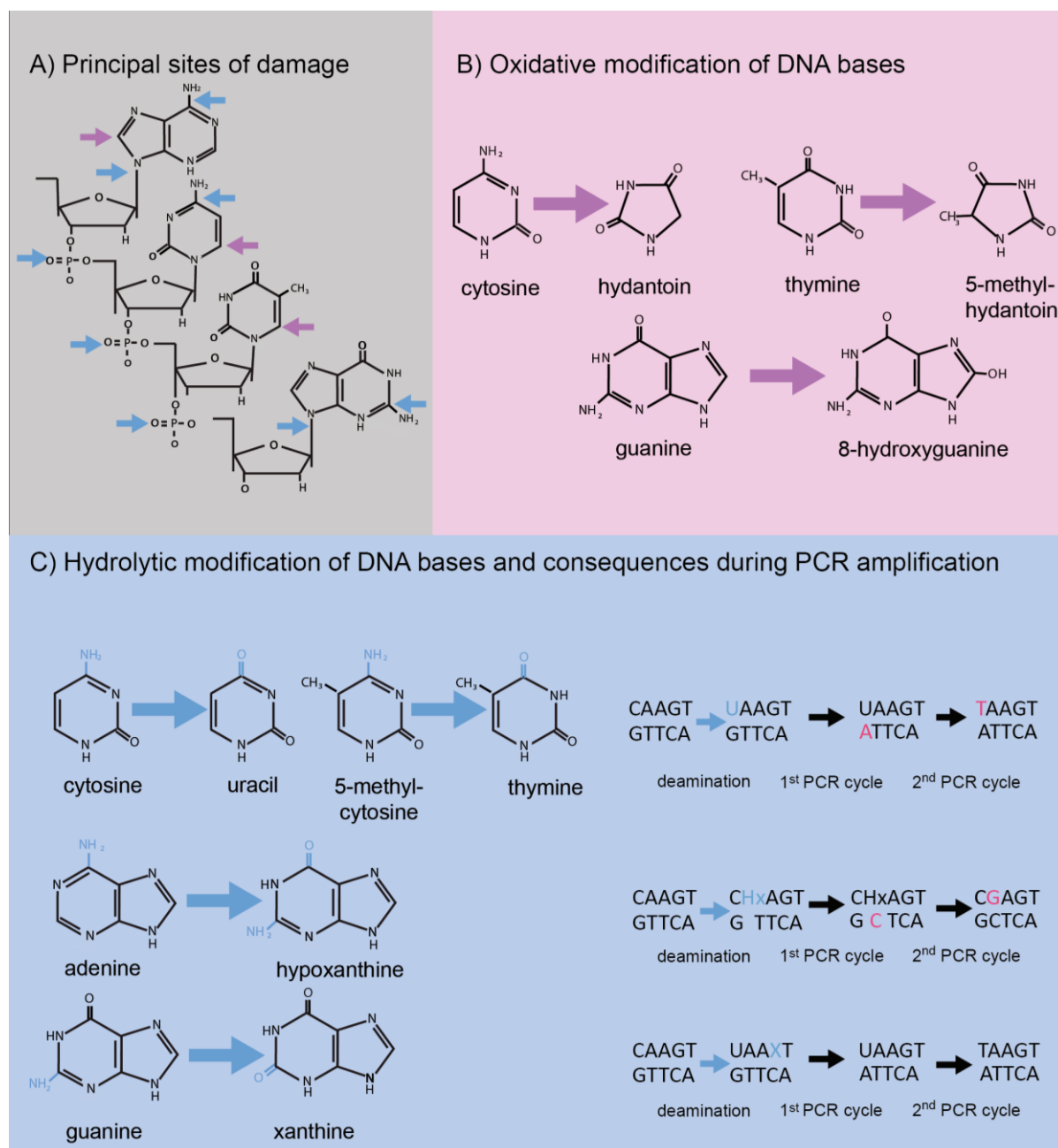


Figure 7 Comprehensive representation of post-mortem damages to DNA

A) Principal sites of DNA damage (red: oxidation; blue: hydrolytic damage). B) DNA bases and their derivatives after oxidative modification. C) DNA bases and their derivatives after hydrolytic modification and consequences of DNA modifications during PCR.

3.2.2 Authentication of ancient DNA

No matter which analytical approach is chosen, the danger of contamination is still ubiquitous when working with ancient (human) DNA. Ancient DNA samples can be contaminated by numerous sources: researchers, including archaeologists, anthropologists, museum personnel, and DNA researchers, by transmission of already amplified PCR products back into the pre-PCR area (carry-over contamination), they can contaminate each other when cleaning steps are insufficient (crossing-over contamination), and they can be contaminated by reagents and materials brought into and used in the lab. The working protocols to avoid contaminations and ensure authentication as applied in this study will be presented in chapter 6.1.

Because the risk of modern human DNA contamination in ancient human remains is very high in ancient DNA investigations, a number of criteria for securing aDNA result authenticity have been established (HANDT ET AL. 1994, 1996; POINAR ET AL. 1996; PÄÄBO ET AL. 1989, 2004; COOPER AND POINAR 2001; HOFREITER ET AL. 2001; HEBGAARD ET AL. 2005; WILLERSLEV AND COOPER 2005; GILBERT ET AL. 2005A). While some of the criteria apply to general work like the separation of pre- and post-PCR areas and contamination control via blank controls, other criteria target authentication of the results like reproduction via various PCRs, several samples, and cloning. Especially with the advent of new analyzing methods like library preparation and massively parallel sequencing on Next Generation Sequencing platforms, some of these criteria are not useful anymore and new ones have to be established. For instance, results of NGS experiments are rarely reproduced via several extracts, authentication is rather claimed by higher coverage, general short sequence length, monitoring of C → T and G → A transitions at the molecules 5' and 3' end respectively (GREEN ET AL. 2009; KRAUSE ET AL. 2010A), and an immoderation of purines directly before the sequencing start (BRIGGS ET AL. 2007; GINOLHAC ET AL. 2011).

3.2.3 Next Generation Sequencing in ancient DNA research

Advances in DNA sequencing have revolutionized the field of genetics over the last decade. New sequencing technologies have made it possible to rapidly generate large amounts of sequence data at substantially lower cost. These high-throughput sequencing technologies (e.g. Roche 454 FLX, Life Technology SOLiD, Illumina Genome Analyzer, and Ion Torrent) are generally summarized under the term “Next Generation Sequencing” (NGS). They have set new standards for applications like whole-genome sequencing, transcript sequencing, and quantification of gene expression, DNA-protein interactions, and DNA methylation (KIRCHER 2011, 3).

The first step of preparing ancient DNA extracts for sequencing is the preparation of so-called DNA libraries. Libraries are constructed by the ligation of adapters (short double-stranded DNA-molecules) to both ends of DNA molecules. The adapters contain priming sites for both, amplification and sequencing (KNAPP AND HOFREITER 2010). Amplification of molecules is still necessary because in spite of the high sensitivity and productivity of NGS platforms, their signal detection system is not sensitive enough to measure signals originating from a single molecule. They can only identify signals during sequencing that are generated by millions of DNA molecules (RIZZI ET AL. 2012). However, amplification of the library can lead to the usual problems in amplification of ancient products like mis-incorporations, and strand-breaks. Furthermore, only sequences that were correctly ligated to the adaptors, which are the starting point for the sequencing primers, can be amplified. However, even these new techniques seem to become outdated soon under the light of the development of the so-called “3rd Generation Sequencing”. These methods promise to work with the “single-molecule” principle, by sequencing individual molecules instead of molecule ensembles. Single molecule sequencing is not supposed to be affected by errors caused by library preparation or amplification steps, and may allow sequencing of the smallest amounts of DNA (KIRCHER AND KELSO 2010).

However, while cost and time for applying these new technologies are significantly lower than for traditional Sanger sequencing, the error profiles and limitations are increased. Furthermore, the types of errors observed as well as the number (about 20,000,000–60,000,000) and length (30–400bp) of sequences vary considerably between different platforms. Current high-throughput technologies have an average error rate of 1/25 to 1/1,000, which is considerably higher than the 1/10,000 to 1/100,000 observed for Sanger sequencing (KIRCHER AND KELSO 2010). One of the first ancient DNA studies using the new technique was able to generate 13 million bp from the nuclear genome of the extinct woolly mammoth, an enormous increase in information compared to earlier studies using traditional PCR techniques (POINAR ET AL. 2006). Soon others followed, sequencing mitochondrial (E.G. GILBERT ET AL. 2007, 2008; MILLER ET AL. 2009; KRAUSE ET AL. 2010A,B) or nuclear genome sequences (e.g. GREEN ET AL. 2006; MILLER ET AL. 2008; RAMÍREZ ET AL. 2009; RASMUSSEN ET AL. 2010) of mostly singular individuals of, for example, Neanderthals, Mammoths, or early modern humans. However, at the moment only few studies on anatomically modern humans of Paleolithic to Neolithic times have been published, mostly concerning very few individuals (RASMUSSEN ET AL. 2010; KRAUSE ET AL. 2010B; SÁNCHEZ-QUINTO ET AL. 2012; SKOGLUND ET AL. 2012; FU ET AL. 2012; BROTHERTON ET AL. 2013; BOLLONGINO ET AL. 2013; LAZARIDIS ET AL. 2013; OLALDE ET AL. 2014; RAGHAVAN ET AL. 2014). Despite decreasing sequencing costs,

time and effort of creating reliable ancient DNA libraries and sufficient sequence coverage are still high. Furthermore, despite the enormous advantages of these new techniques, the long-known problems of ancient DNA work – contamination and poor preservation – still remain a considerable factor. For example, one of the first studies using NGS to analyze Neanderthals was later shown to be massively influenced by modern human contamination, evoking memories of the first ancient DNA studies where the unreflected application of the new PCR technique led to many highly published wrong results (GREEN ET AL. 2006; WALL ET AL. 2007).

3.2.4 From the Paleolithic to the Early Bronze Age – state of ancient DNA research

The following sub-chapters will give an overview of published ancient DNA studies of pre-Neolithic, Neolithic, and Bronze Age human populations, differentiated by geographical regions. Please note that the interpretations of each study are those of the authors and do not necessarily coincide with the interpretation by the author of this study. A more detailed examination of results and interpretation of particular studies will be given in the discussion. Furthermore, studies with too questionable or insufficient ancient DNA results or methods were excluded (IZAGIRRE AND DE LA RÚA 1999; SIMÓN ET AL. 2011; FERNANDÉZ ET AL. 2008; GAMBA ET AL. 2008; BOUWMAN ET AL. 2008; GUBA ET AL. 2011; HUGHEY ET AL. 2013).

Eastern Europe

Ancient mtDNA from non-farming individuals are known from the sites of Chekhalino and Lebyazhinka from the Yelshanskaya Culture in the Samara region of Russia, dating to 8,000–7,000 cal BC (BRAMANTI ET AL. 2009) and from a very old specimen (30,000 BP) from the Kostenki site in Russia (KRAUSE ET AL. 2010B). The two individuals from the first two sites were assigned to hg U5a, while the Kostenki individual belongs to the mitochondrial hg U2. Furthermore, nine mtDNA results of foragers from the sites of Yuzhnyy Oleni Ostrov and Popovo from northwestern Russia dating to 7,500–7,000 BP are published (DER SARKISSIAN ET AL. 2013). Here, the mtDNA hgs U2, U4, and U5a as well as hgs H (one individual) and C1 (three individuals) were found. New whole-mitochondrial genome sequencing revealed that all three C1 individuals of Yuzhnyy Oleni Ostrov belong to a new hg C clade that was provisionally denoted as “C1f” (DER SARKISSIAN ET AL. 2014). The fact that this particular haplotype is absent in current data from ancient and present-day populations was explained by either an insufficient modern dataset or by demographic processes such as population extinction or replacement (DER SARKISSIAN ET AL. 2014). Neolithic results from Eastern

Europe are rare; a few Eneolithic results are known from the Verteba Cave in Ukraine (3,951–2,620 cal BC) belonging to hgs H, HV/V, T4, and J, but no HVR I results have been published (NIKITIN ET AL. 2010). In 2012, mitochondrial data from the two Neolithic sites of Nikolskoye and Yasinovatak (5,557 and 4,941 cal BC) from the Ukraine were published (NIKITIN ET AL. 2012). Mitochondrial hgs found in these two sites were C, C4, H, U3, and U5a. Additionally, DER SARKISSIAN ET AL. (2013) analyzed human remains from the Bronze Age site Bol'shoy Oleni from the Kola Peninsula in Northwestern Russia, dated to 3,500 BP, and found a mixture of Asian and European mitochondrial hgs such as C, C5, D, T, U4, U5a, and Z. Due to the presence of mitochondrial DNA haplogroups C, D, and Z in Early Metal Age individuals they suggested genetic discontinuity between Mesolithic hunter-gatherers and Bronze Age individuals in this region, probably caused by genetic influx from Central or Eastern Siberia (DER SARKISSIAN ET AL. 2013).

Northern Europe

In Scandinavia hunter-gatherer populations persisted until the appearance of the Neolithic Funnel Beaker Cultural complex (FBC) around 3,200 BC. The Pitted Ware culture (PWC), which bearers pursued a hunter-gatherer subsistence strategy, was distributed contemporarily to the FBC (FORNANDER 2005/2006, 5). In 2009, MALMSTRÖM ET AL. analyzed mitochondrial DNA of 16 individuals from the Pitted Ware culture and found high percentages (74%) of the haplogroups U4, U5b, and U5a. Three individuals of the Funnel Beaker Complex belonged to hg T2, H, and J (MALMSTRÖM ET AL. 2009). While the number of individuals from the Funnel Beaker individuals was too small for comparisons, the results of statistical analyses indicated that people of the PWC were not the direct ancestors of modern Scandinavians and supported the theory of Neolithic or post-Neolithic population admixture or replacement in Scandinavia (MALMSTRÖM ET AL. 2009). Further data from the Funnel Beaker culture were published in the same year by Bramanti and colleagues (BRAMANTI ET AL. 2009). In their dataset from the northern German site of Ostorf a mixed composition of hgs U5b (2 individuals), U5a (1 individual), T2 (2 individuals), J and K (1 individual each) was found (BRAMANTI ET AL. 2009). The first study analyzing nuclear genomes via NGS re-analyzed individuals that have already been part of the study of MALMSTRÖM ET AL. (2009). SKOGLUND ET AL. (2012) obtained genomic DNA from ~5,000 year old remains of three hunter-gatherers and one farmer from Scandinavia. Because of the incomplete coverage of the genomes, only small overlap between the SNPs gained from the different investigated individuals existed. To overcome this difficulty, SKOGLUND AND COLLEAGUES performed principal component analyses (PCA) separately for each individual and compared each to a dataset of 505 individuals of Europe and the Levant, using Procrustes transformation. The results suggested that the farmer of the Funnel Beaker culture was genetically similar to

extant Southern Europeans, in contrast to the hunter-gatherers of the Pitted Ware culture, whose distinct genetic signature was comparable to that of nowadays' Northern Europeans. Their conclusion was that farming practices were brought to Northern Europe by a group of people that were genetically distinct from indigenous hunter-gatherers. They found the Neolithic individual to be genetically most similar to populations from modern Mediterranean Europe, whereas the study of HAAK ET AL. (2010) who analyzed mitochondrial data from the Linear pottery culture suggested extant populations of Turkey and the Near East to be genetically most similar to Central European Neolithic farmers (see below). Finally, SKOGLUND AND COLLEAGUES (2012) concluded that long-term gene flow between farmer and hunter-gatherer populations shaped the present pattern of genetic variation in Europe. This view was also supported by the observation that most European populations appeared genetically intermediate to the two groups (SKOGLUND ET AL. 2012). A study on ancient populations from Denmark proved the presence of Hg U4 and U5a in two remains from the Bell Beaker site of Damsbo (2,200 cal BC) and in one individual from the Bronze Age site of Bredtoftgard (1,300–1,500 cal BC) arguing against a replacement of hunter-gatherer lineages in Scandinavia after the Pitted Ware culture as suggested by Malmström and colleagues (MELCHIOR ET AL. 2010).

Central Europe

The first published study on Neolithic individuals from Central Europe presented paleogenetic data of Neolithic groups from Germany, Hungary, and Austria. HAAK ET AL. (2005) focused on human remains originating from the Linear pottery culture (LBK) and one of its variants, the Altföld Linear pottery culture (AVK), which are associated with the beginning of farming in the temperate regions of Europe. Originating in Hungary, the LBK spread rapidly as far as the Parisian Basin and the Ukraine. A total of 24 individuals from 16 sites of the LBK/AVK yielded reliable HVR I sequences. Interpretations focused primarily on the explanation of the high frequency of the mitochondrial haplogroup N1a in the LBK area. Today, this lineage is rare but widespread in Europe. The genetic discontinuity between Neolithic farmers and modern Europeans was considered to be evidence for limited mitochondrial influence on modern Europeans by the first agriculturists. The authors proposed at that time a Paleolithic ancestry for modern Europeans (HAAK ET AL. 2005). In 2008, a study with six further individuals of the LBK of the Czech site Vedrovice was published (BRAMANTI 2008). All individuals belonged to the haplogroups H, J, K, and T2 and a Paleolithic origin for these lineages was assumed. However, the first paleogenetic study of European hunter-gatherers from Central and Northern Europe (22 individuals from Germany, Poland, Lithuania, and Russia), dating between 12,400 cal BC and 2,300 cal BC, revealed a surprisingly high frequency of mtDNA lineages U4, U5a, and U5b (82%), and none of the

lineages found in the LBK (BRAMANTI ET AL. 2009). Most of the hunter-gatherers were shown to have shared mtDNA types that are relatively rare in Central Europe today. The observed discontinuity between late hunter-gatherers, early farmers, and extant European populations from Central Europe strongly suggested that the first farmers were neither the descendants of local hunter-gatherers nor the direct ancestors of modern-day Europeans. Thus, post-Neolithic events would have remodeled the mitochondrial gene pool (BRAMANTI ET AL. 2009). In 2010, HAAK ET AL. re-evaluated the mitochondrial legacy of the LBK culture by publishing 21 new individuals from the Derenburg site in the Middle Elbe Saale region of Germany, dated to 5,500–4,900 cal BC. The new data were combined with LBK individuals from the previous study. Comprehensive phylogeographic and population genetic analyses revealed genetic affinities between LBK groups and modern-day Near Eastern and Anatolian populations, interpreted as a major genetic input from this area during the onset of farming in Europe. However, some regions of Central Europe were also shown to be closely affiliated to the LBK population, in accordance with an origin of the LBK in today's Hungary as proposed by archeologists (HAAK ET AL. 2010). Furthermore, the LBK population presented unique genetic features when compared to modern populations, confirming that major demographic events continued to take place in Europe after the Early Neolithic. The authors found support for a demic diffusion model with genetic input from the Near East into Central Europe. Additionally, they typed three individuals successfully for Y-chromosomal DNA, two of which belong to hg F* and one could be assigned to G2a3 (HAAK ET AL. 2010). In 2013, the hunter-gatherer dataset of Central/Eastern Europe was enlarged by five individuals of the sites Loschbour (Luxembourg), Bonn Oberkassel (Western Germany), and Dolní Věstonice (Czech Republic) (FU ET AL. 2013). The individuals belong to several (sub-) haplogroups of U. While U* and U5b have already been detected in previous studies, hg U8 was a “newcomer” to the known pre-Neolithic mtDNA pool. The bottom line of all these studies was discontinuity between autochthonous hunter-gatherers and first farmers of the LBK culture (BRAMANTI ET AL. 2009) as well as a discontinuity between the LBK and modern Europeans (HAAK ET AL. 2005; 2010, BRAMANTI ET AL. 2009; BRANDT ET AL. 2013).

Only few studies investigated the Late Neolithic periods. A kinship study on Corded Ware multiple burials produced mitochondrial results of six individuals (hgs H, I, K, U5b, and X), but they were not interpreted in a population genetic context (HAAK ET AL. 2008). Another small study presented results of six Bell Beaker individuals of the site Kromsdorf, Germany, dated to about 2,800 to 2,000 BC, and revealed mtDNA sequences of hgs I, K, T1, U2, U5, and W (LEE ET AL. 2012). Interestingly, hgs I and U2 were identified by BRANDT ET AL. (2013) as typical for the Corded Ware culture, a culture contemporary to the Bell Beaker in Central Europe. Additionally, two Y-chromosomal results of the Kromsdorf site were published; both

belonged to hg R1b. The authors did not interpret their data deeper in a population genetic context but noted differences in the phylogeny of haplogroup U5 between Mesolithic and Neolithic as well as to extant European populations (LEE ET AL. 2012). Recently a comprehensive ancient DNA study presented the first diachronic mitochondrial profile of Central European Neolithic, taking both early and Late Neolithic into account. BRANDT ET AL. (2013) successfully analyzed the mitochondrial DNA of 364 Early Neolithic to Bronze Age individuals and showed that after the initial Linear pottery colonization three successive population events occurred in Central Europe that brought new genetic input from the North (FBC), the East (Corded Ware culture) and the West of Europe (Bell Beaker culture) into Central Europe. Furthermore, they concluded that the latter three events majorly influenced the formation of modern Central European mtDNA diversity. Also in 2013, BROTHERTON ET AL. analyzed 39 complete mitochondrial genomes of hg H dating from the Early Neolithic to the Iron Age (5,450–500 BC) using individuals that are also part of the study from BRANDT ET AL. (2013). The data indicated minimal genetic continuity between the Early and Middle Neolithic in Central Europe suggesting that Early Neolithic lineages were largely superseded between 4,100 and 2,200 BC, which is more or less in line with the results from BRANDT ET AL. After comparison of the ancient data to the hg H diversity in present-day Central Europe, the authors proposed that much of the present-day diversity could be attributed to the incorporation of new lineages during the Middle Neolithic and Bronze Age. Furthermore they stated that the mtDNA H sub-hg diversity that was established during the Middle Neolithic is still present in Central Europe (BROTHERTON ET AL. 2013). Both studies displayed similar results claiming Western European affinities of the Bell Beaker culture (North/)Eastern affinities of the Corded Ware culture, one/several population shifts after the Early Neolithic, and continuity of (Middle/)Late Neolithic and Early Bronze Age cultures to the modern central European gene pool (BRANDT ET AL. 2013; BROTHERTON ET AL. 2013). Contemporary with the Brandt study, BOLLONGINO ET AL. (2013) published mitochondrial results from 25 Mesolithic and Neolithic individuals from the Blätterhöhle site in Hagen, Germany (dating between 9,210 and 8,340 cal BC for the Mesolithic samples and between 3,986 and 2,918 cal BC for the Neolithic). Mesolithic mitochondrial DNA sequences were typical of Central European foragers, displaying hg U5a, U5b, and U2, whereas the Neolithic sample included additional lineages like J and H. By carbon and nitrogen isotope analyses, the Neolithic sample set could be further divided into two groups: one with an agriculturalist diet and one with a forager diet. Individuals with an isotopic values typical for a foraging subsistence strategy carried only mitochondrial DNA sequences typical of Mesolithic hunter-gatherers. In contrast to BRANDT AND COLLEAGUES, they found a large proportion of hunter-gatherer U lineages in the Neolithic dataset. By combining the isotopic and genetic data, BOLLONGINO AND

COLLEAGUES concluded that some mitochondrial descendants of Mesolithic societies kept a hunter-gatherer subsistence strategy at least in this area for more than 2,000 years after the initial Neolithisation (BOLLONGINO ET AL. 2013).

Southern Europe

Very few ancient DNA results are known from Italy and Greece. Paleolithic/Mesolithic DNA evidence is known from two Paleolithic specimens of the Paglicci cave in Italy assigned to hgs N* and HV (CARAMELLI ET AL. 2003) and from one individual from the Grotta d'Oriente from the Favignana islands of Italy, determined as hg HV1 and dating to about 8,734–8,595 cal BC (MANNINO ET AL. 2012). Neolithic mtDNA data are only known from single individuals from the sites of Mezzocorona (6,326–6,444 BP) and Borgo Nuovo (5,930–6,240 BP) in South Tyrol, belonging to hgs T2b and H respectively (DI BENEDETTO ET AL. 2000). The result of the Mesolithic individual from this study was heavily contaminated and should not be regarded as authentic. When talking of Neolithic Italy, of course the famous Tyrolean Iceman has to be mentioned. Several studies on HVR I data, whole mitochondrial, and lately even the nuclear genome of the Late Neolithic specimen have been published assigning the mitochondrial haplotype to an nowadays unknown branch of hg K1 (HANDT ET AL. 1994; ROLLO ET AL. 2006; ERMINI ET AL. 2008; KELLER ET AL. 2012). At the moment, reliable Southern European Bronze Age data exist only from Sardinia. In a study from 2007, 22 mtDNA results of four Middle to Late Bronze Age and one Iron Age site were published (Alghero, Carbonia, Fluminimaggiore, Perdasdefogu, Seulo, and S.Teresa di Gallura) (CARAMELLI ET AL. 2007). The majority of haplogroups found was assigned to H and only two individuals belonged to hg J and V, respectively. The authors compared the results to datasets of Etruscan (VERNESI ET AL. 2004) and Iberian populations (SAMPIETRO ET AL. 2007) and found greater genetic similarities to the latter (CARAMELLI ET AL. 2007). Further Sardinian data were analyzed by CLEO DER SARKASSIAN. In her thesis she analyzed 16 Sardinian Bronze Age individuals from the cave sites of Su Bittoleris and Su Cannisoni dating to about 3,400–3,200 BP (DER SARKISSIAN 2011). Haplogroups found in these two sites were H, J, K, T2, V, and X. By comparison with modern data she concluded that her results argue for a genetical separation between Central Sardinia and the rest of the island and Europe as has been proposed by other researchers (DER SARKISSIAN 2011).

Western Europe

Especially recent ancient DNA studies of Western European have given insights into potential population dynamics at the beginning of the Neolithic on the Iberian Peninsula. For France, however, only Late Neolithic data are available. Taken together with the lack of Neolithic data of Italy, this has so far prevented a genetic investigation of the presumed

Mediterranean route. In 2011, LACAN ET AL. (2011A) published 29 Y-chromosomal/mtDNA data from the Cave I of Treilles, a collective burial from Saint-Jean-et-Saint-Paul, France, dating to about 3,000 BC. Concerning the maternal origin, the gene pool of Treilles consisted of a variety of lineages of hgs H1, H3, HV, J, K, T2, U5a, U5b, V, and X. For the mitochondrial data, they suggested a Mediterranean origin. Paternal lineages belonged to only two different haplogroups, I2a and G2a, with a proportion of shared lineages between the ancient and modern data of less than 2%. For Hg I2a they proposed a southern European origin, while they linked hg G(2a) to a demic diffusion from the Near East during the Neolithic. All in all, they suggested different geographic origins for the maternal and paternal lineages of the Treilles samples, but attested for both a contribution of the Neolithisation to the gene pool of the Treilles specimens. Furthermore, they claimed to be able to clearly support a Mediterranean route of Neolithisation due to their Y-chromosomal results. The only other study analyzing French Neolithic individual is from the megalithic site of Prissé-La-Charrière in Western France, dated to about 4,200 cal BC (DEGUILLLOUX ET AL. 2011). The three successfully analyzed individuals belong to hgs U5b, X2, and N1a. Especially, the finding of N1a, a rare mitochondrial hg in modern populations but very common in the Early Neolithic Linear pottery culture of Central Europe, in Western France was very interesting. The authors were very careful and offered a variety of explanations such as Mesolithic ancestry, demic diffusion during the Neolithic as well as long-distance matrimonial exchanges; however, they stated – in line with many other papers mentioned above – genetic discontinuity between modern and ancient Europeans.

From the Iberian Peninsula mainly hunter-gatherer and Early Neolithic data are available. Pre-Neolithic data of Iberian hunter-gatherers were published in three different studies (CHANDLER ET AL. 2005 AND CHANDLER 2003; SANCHÉZ-QUINTO ET AL. 2012; HERVELLA ET AL. 2012). Ancient DNA results of six hunter-gatherers from the north of Spain (from the sites La Chora, La Pasiega, Aizpea, and La Braña) are known so far, assignable to mitochondrial hgs H and U5b and dating between 12,310 and 6,600 BP, (HERVELLA ET AL. 2012; SANCHÉZ-QUINTO ET AL. 2012). For the two La Braña individuals even Next Generation Sequencing data of the whole mitochondrial and parts of the nuclear genome are available (SANCHÉZ-QUINTO ET AL. 2012; OLALDE ET AL. 2014). The seven Portuguese hunter-gatherer data from the sites of Toledo, Arapouco, Cabeço das Amoreiras, and Cabeço de Pez belong to the hg H, N*, U4, and U5b (CHANDLER ET AL. 2005 AND CHANDLER 2003) and were part of the first study on the Iberian prehistoric via ancient DNA. This study furthermore included data from Early to Late Neolithic/Chalcolithic individuals. Analyzed as part of the thesis of HELENA CHANDLER in 2003, the data were, however, not published in a peer-reviewed journal. The description of methods and results is extensive enough to evaluate the quality of the data

and use most of them for population genetic analyses. Samples from all Neolithic to Chalcolithic sites (Gruta do Caldeirão [Early Neolithic], Algar do Bom Santo [Middle Neolithic], and Perdigões [Chalcolithic]) can be assigned to hgs H, U5a, U5b, and V. Because of the absence of mtDNA haplogroup J in the Neolithic sample set, the author(s) concluded that these populations were not direct descendants from Near Eastern farmers. Furthermore, because of the few direct sequence matches between the hunter-gatherer and later groups they proposed some genetic distance between these two and therefore genetic discontinuity between the Mesolithic and Neolithic. They declared these findings to be consistent with the Maritime Pioneer Colonization model (ZILHÃO 1993, 2001) for the arrival of farming in Portugal. This model describes the Neolithisation as a process of formation of Neolithic enclaves by seafarers from the Mediterranean coast, who themselves had adopted farming through exchange or limited migration (CHANDLER 2003; CHANDLER ET AL. 2005). Another ancient DNA study was carried out on Neolithic samples (3,500–3,000 cal. BC) and gave results for 11 individuals from the site of Cami de Can Grau in northeastern Iberia (SAMPIETRO ET AL. 2007). Haplogroup frequencies were found to be similar to those of present-day populations and were interpreted as genetic continuity between Neolithic and modern-day Iberian populations. Because of the deviating results compared to the HAAK ET AL. (2005) study – the only more or less comparable data at that time – the authors assumed two different mechanisms for the spread of the Neolithic to Central and southwestern Europe: cultural diffusion in Central Europe and demic diffusion in the Mediterranean (SAMPIETRO ET AL. 2007). In the last three years, three main studies of Early (and Middle) Neolithic data from Navarre and Basque country in northern and from Catalonia in northeastern Spain have broadened the genetic picture of prehistoric Spain (GAMBA ET AL. 2011; HERVELLA ET AL. 2012; LACAN ET AL. 2011B). One of them presented results from 13 individuals of Catalunya and Aragón (GAMBA ET AL. 2011). They detected hgs H, K, N*, U5, and X in their dataset. By comparison with modern data, N* and X1² were assumed to have a Near Eastern origin, and when compared to the Middle Neolithic data of SAMPIETRO ET AL. (2007) genetic drift was assumed as explanation for the genetic differences observed between Early and Middle Catalonian Neolithic. By comparing calculated and simulated F_{st} values, the authors proposed a scenario with genetic drift at the beginning of the Neolithic as well as Near Eastern connections in this period, and therefore a succession of pioneer colonization events from the Near East. In the LACAN ET AL. (2011B) study, 7 successfully

² Author comment: It should be noted that this haplotype cannot clearly be classified as X1.

reproduced mtDNA data displayed hgs H, K, U5, and T2. Y-chromosome data of 5 of the individuals resulted in hg G2a and for one individual the hg E1b1b1a1b. They proclaimed their results to be concordant with those of the French Treilles site. The sex-specific diversity differences (more diversity in the mitochondrial results) were comparable to that of the Treilles cave as well. The mitochondrial lineages found were consistent with a genetic continuity in southern Europe, at least since Neolithic times³. The absence of the N1a haplogroup was taken as evidence for the existence of two routes of Neolithic dispersal in Europe. Due to these results they assumed a Paleolithic origin for most of the maternal lineages of both sites, but a more recent paternal ancestry. Furthermore, they suggested a common origin of the two Neolithic groups and a probable genetic continuity in the western Mediterranean area between 5,000 and 3,000 BC. The high frequency of the Y-chromosomal haplogroup G2a, rare nowadays, led them to suggest that men could have played a greater role in the Neolithic transition which is no longer visible today (LACAN ET AL. 2011B). Besides the hunter-gatherer samples mentioned above, the ancient DNA study of samples of Basque Country, Navarre, and Cantabria also analyzed Early and Late Neolithic as well as two Bronze Age samples (HERVELLA ET AL. 2012). The majority (about 80%) of the Neolithic samples belonged to hgs H, HV, U, and U5b, while only twenty percent of the samples had hgs I, J, K, T2, and X. The authors found similarities between Central and southwestern European hunter-gatherers, but differences between Central European Neolithic and French, Navarre, and Catalanian Neolithic. They explained these differences mainly by the absence of hg N1a, and to a lesser degree in different frequencies of H, J, and U in Western Europe. They concluded that the bearer of the Neolithisation in Central Europe were of a different genetic composition than the ones following the Mediterranean route. They proposed a potential gradient of Neolithisation for Central Europe and northern France respectively but support a random dispersion model for the Mediterranean possibly by maritime colonization (HERVELLA ET AL. 2012).

³ Author comment: Conclusions were drawn based on the assumption of a European Paleolithic origin for most of the mitochondrial haplogroups, supported by many modern DNA studies but not necessarily by ancient DNA publications (see also HAAK ET AL. 2010; BRANDT ET AL. 2013, IN PRESS)

4 Objectives and research goals

Paleogenetic studies of the last years have revealed a substantial amount of population dynamic processes in prehistoric Central Europe after the initial Neolithic transition and have emphasized the importance of the Iberian Peninsula in the genesis of the Bell Beaker phenomenon in this context (BROTHERTON ET AL. 2013; BRANDT ET AL. 2013, IN PRES). Ancient DNA studies from the Iberian Peninsula were mainly focussing on the Neolithic transition (SAMPIETRO ET AL. 2007; LACAN ET AL. 2011B; HERVELLA ET AL. 2012; GAMBA ET AL. 2011) and have revealed genetic differences between Atlantic and Mediterranean Spain, indicating varying forms of Neolithisation processes on the Iberian Peninsula (HERVELLA ET AL. 2012; BRANDT ET AL. 2013, IN PRESS). Archaeological research has likewise often emphasized the variety of cultural developments in different regions of the Iberian Peninsula (see also chapters 2.3.1–2.3.5). To sum up, on the one hand a strong regional component in population dynamic processes on the Iberian Peninsula has become apparent; on the other hand, the study of BRANDT ET AL. (2013) has emphasized the importance of post-Early Neolithic population dynamics and the potential of gapless diachronic datasets to confidently trace population shifts in the past.

The aim of this thesis was to draw conclusions about population dynamic processes on the Iberian Peninsula in the 4,000 years between the Neolithic transition and the Early Bronze Age by analyzing mitochondrial DNA of 344 prehistoric individuals. Samples were chosen to represent as many regions of the Iberian Peninsula as possible to confidently identify small-scale population dynamics. Research questions focused on a spatial comparison of contemporaneous groups on the one hand as well as tracing population shifts through time on the other hand. On a next level, the chronologically and spatially different Iberian groups were compared to published data from Central, North, and East Europe to reveal commonalities and/or differences in population dynamics in prehistoric Europe.

Specific research questions to be addressed were:

Level I Iberian Peninsula

1. How large is the amount of “new” mitochondrial lineages in Early Neolithic groups compared to previous hunter-gatherers?
2. Are differences in the Neolithic transition process recognizable across the Iberian Peninsula?
3. Is there genetic continuity between Early and Late Neolithic periods in all or some regions?
4. Do we see genetic continuity between the Late Neolithic and the Chalcolithic?

5. How uniform are Chalcolithic groups on a genetic level?
6. Can Bell Beaker associated groups be distinguished from Chalcolithic non-Bell Beaker groups?
7. Is an influx of new mitochondrial lineages recognizable at the onset of the Early Bronze Age?
8. Can individuals associated with the Early Bronze Age El Argar culture be genetically set apart from contemporaneous or preceding groups?

Level II Spanish and Portuguese groups in a European context

1. Are there genetic links of the Central European first farmers to the Early Neolithic of the Iberian Peninsula?
2. Are similarities to the Neolithic transition processes in North Europe recognizable?
3. Did a phase of genetic continuity in the first 3,000 years after the initial Neolithic transition exist on the Iberian Peninsula as was proposed for Central Europe (BRANDT ET AL. 2013, IN PRESS)?
4. Does a genetic connection exist between Iberian Bell Beaker groups and those of Central Europe as has been proposed by previous ancient DNA studies (BROTHERTON ET AL. 2013; BRANDT ET AL. 2013, IN PRESS)?
5. How does the Iberian Bronze Age present itself compared to the Unetice culture of Central Europe?
6. BROTHERTON ET AL. (2013) were able to distinguish Early and Middle/Late Neolithic Central European data by different frequencies of sub-haplogroups of H. Can the same trends be observed in the Iberian dataset?

5 Material

Altogether 344 individuals from 56 sites of Spain, Portugal, and Morocco have been analyzed. Whenever possible, chronological assignment was conducted according to C¹⁴ dates. However, for many sites no C¹⁴ dates are available and chronological assignment in the literature was often based on comprehensive archaeological information like grave goods, mortuary practices, and/or burial customs. Sites for which no information in the literature was available – mostly very old or very recent excavations – were classified into chronological periods after personal communication with the excavator or co-operating archaeologists of this project. C¹⁴ dates that are known to the author of this study but not published yet, are denoted as “C¹⁴ not published”. Radiocarbon datings that were conducted as part of the project at the Curt-Engelhorn-Zentrum für Archäometrie (Mannheim, Germany) and by the Beta Analytic Inc. (Miami, USA) are denoted as “this study” in table 1 (see also appendix VII).

Table 1 Archaeological sites investigated in this study

Site	Lab name	n	Region	Chronology	C ¹⁴	Reference
Alto de Rodilla	Rodi	1	Castilla y Leon	Early Neolithic	5297-4988 cal BC	JIMÉNEZ AND ALONSO (IN PRESS) AFTER ROJO GUERRA AND GARRIDO PENA 2012
Arroyal I	Roy	5	Castilla y Leon	Chalcolithic - Bell Beaker	C ¹⁴ not published	PERS. COMMUNICATION E. CARMONA
Balma de Sargantana	BAS	5	Catalonia	Chalcolithic		PERS. COMMUNICATION I. SORIANO LLOPIS
Barranc d'en Rifá	BAR	15	Catalonia	Chalcolithic	2900-2623 cal BC	THIS STUDY
Bolores	Bol	5	Extremadura	Chalcolithic Bell Beaker and non-Bell Beaker and Bronze Age	2800-1700 cal BC	LILLIOS ET AL. 2010
Cabezo Pardo	Cab	2	Valencia	Bronze Age – El Argar	1700-1500 cal BC	LOPEZ PADILLA AND XIMÉNEZ DE EMBÚN SÁNCHEZ 2011
Cadaval	CDV	3	Extremadura	Neolithic and Chalcolithic - Bell Beaker	4340-3520 cal BC	OOSTERBEEK 1994, 2003 IN TOMÉ AND SILVA 2013
Camino de Molino	CMOL	18	Murcia	Chalcolithic	2960-2420 cal BC	LOMBA MAURANDI ET AL. 2009
Camino de las Yeseras	Yese	14	Madrid	Chalcolithic Bell Beaker and non-Bell Beaker	4840-3740 cal BP	BLASCO ET AL. 2007
Can Gambús	GAM	8	Catalonia	Bronze Age		ROIG AND COLL 2007
Castillo de Lorca	Cast	1	Murcia	Bronze Age - El Argar		LULL ET AL. 2013A, 595
Cobre las Cruces	Cru	4	Andalusia	Bronze Age	1950-1690 cal BC	HUNT ORTIZ ET AL. 2008
Concheiro da Moita do Sebastião	Seba	3	Extremadura	Mesolithic	6219-5540 cal BC	LUBELL ET AL. 1986 IN VAN DER SCHRIEK ET AL. 2007
Concheiro do Cabeço da Arruda	Arru	2	Extremadura	Mesolithic	6090-5210 cal BC	LUBELL AND JACKES 1988 IN VAN DER SCHRIEK ET AL. 2007

5 Material

Site	Lab name	n	Region	Chronology	C ¹⁴	Reference
Cova d'en Pardo	Par	8	Valencia	Chalcolithic	3000-2500 cal BC	AZUAR RUÍZ ET AL. 2009, 51
Cova de la Ventosa	Vent	1	Andalusia	Chalcolithic - Bell Beaker		LLONGUERAS ET AL. 1981
Cova del Barranc del Migdia	Dia	7	Valencia	Chalcolithic	2852-2471 cal BC	HTTP://XABIA-MUSEUM-PROJECT.WIKIDOT.COM/
Cova del Cantal	Coca	5	Valencia	Chalcolithic		LÓPEZ SEGUÍ ET AL. 1990-1991
El Castillejo	Elca	2	Castilla la mancha	Chalcolithic and Neolithic	4535-3695 cal BC	BUENO RAMÍREZ ET AL. 1999
El Hundido	Hund	2	Castilla y Leon	Chalcolithic - Bell Beaker	2492-2334 cal BC	ALONSO FERNÁNDEZ 2013
El Juncal	Junc	14	Madrid	Chalcolithic - Bell Beaker		PERS. COMMUNICATION O. JIMINEZ
Els Trocs	Troc	10	Aragon	Early Neolithic - Neolithic	5315-5060 cal BC and 3940-3110 cal BC	ROJO GUERRA ET AL. SUBMITTED
Es Forat de ses Aritges	Fora	5	Menorca	Bronze Age	1400-1000 cal BC	LULL ET AL. 1999 IN CALCO TRIAS ET AL. 2013
Fuente Álamo	Fala	5	Andalusia	Bronze Ag- El Argar		LULL ET AL. 2013A, 595
Fuente Celada	Cel	3	Castilla y Leon	Early Neolithic and Chalcolithic	5083-4961 cal BC and 2702-2474 cal BC	ALAMEDA CUENCA-ROMERO ET AL. 2011
Fuente Pecina 1	Fupe	4	Castilla y Leon	Neolithic	4400-3700 cal BC	DELIBES AND ROJO GUERRA 1997
Fuente Pecina 2	Fupe	5	Castilla y Leon	Neolithic	4334-4055 cal BC	DELIBES AND ROJO GUERRA 1997
Fuente Pecina 4	Fupe	2	Castilla y Leon	Neolithic		MENTIONED IN NEOLITHIC CONTEXT IN JIMÉNEZ GUIJARRO 2010, 455
Gruta das Alcobertas	Alco	2	Estremadura	Neolithic		SANTOS ET AL. 1970
Gruta de Malgasta	Malga	2	Estremadura	no dating		
Gruta do Carvalho de Turquel	Turq	2	Estremadura	no dating		
Gruta do Poço Velho	Pove	2	Estremadura	no dating		
Gruta dos Ossos	Gro	5	Estremadura	Neolithic	3540-2130 cal BC	OOSTERBEEK 1993A, TOMÉ 2006
Humanejos	Hume	26	Madrid	Chalcolithic Bell Beaker and non-Bell Beaker, Bronze Age	C ¹⁴ not ublished	PERS. COMMUNICATION R. GARRIDO-PENA
Hypogeu de Monte Canelas I	Moca	8	Algarve	Endneolithic/Chalcolithic	3340-2880 cal BC	CUNHA ET AL. 2008
Hypogeu de Monte Canelas III	MCIII	2	Algarve	Endneolithic/Chalcolithic		NEVES AND SILVA 2010
Ifri N' ammar o Moussa	Iam	1	Morocco	no dating		
Illeta dels Banyets	Ban	7	Valencia	Bronze Age - El Argar	1960-1705 cal BC	SOLER DÍAZ ET AL. 2006, 107
La Bastida	Ba/Lab a	13	Murcia	Bronze Age - El Argar		LULL ET AL. 2013A, 595
La Huera	Hue	3	Andalusia	Chalcolithic		CRUZ AUÑÓN BRIONES AND MEJÍAS GARCÍA 2013

5 Material

Site	Lab name	n	Region	Chronology	C ¹⁴	Reference
La Mina	Mina	13	Castilla y Leon	Neolithic	3890-3600 cal BC	THIS STUDY
La Tarayuela	Tar	11	Castilla y Leon	Neolithic	3943-3636 cal BC	ROJO GUERRA ET AL. 2005
Los Tintores	Tint	2	Murcia	Bronze Age - El Argar		LULL ET AL. 2013A, 595
Madre Mercedarias Iglesias	MMI	3	Murcia	Bronze Age - El Argar		LULL ET AL. 2013A, 595
Miquel Vives	MIV	2	Catalonia	Bronze Age		MARÍN CASTRO 2010-2011
Molinos del Papel	MOP	3	Murcia	Late Chalcolithic to Bronze Age		MARÍN ET AL. (IN PRESS): AFTER SCHUHMACHER 2011
Nossa Senhora das Lapas	GSL	3	Estremadura	Early Neolithic - Neolithic	5220-3650 cal BC	OOSTERBEEK 1993,
Nuevo IES Valencina ROD 05-32	Cine	4	Andalusia	no dating		
Porroado de Alcalar	Alca	2	Algarve	Chalcolithic		MORÁN AND PARREIRA 2003
Reinoso	Rein	27	Castilla y Leon	Neolithic	3759-3643 cal BC	THIS STUDY
Rincón de Moncada	Rinc	2	Murcia	Chalcolithic		HABER URIARTE ET AL. 2008
Senorio de Guzman	Guz	4	Andalusia	Chalcolithic Bell Beaker		CRUZ AUÑÓN UND MEJÍAS 2012
Tabayá	Tab	4	Valencia	Bronze Age/El Argar		LULL ET AL. 2010A
Tholos de Pai Mogo I	Pai	16	Estremadura	Chalcolithic (Bell Beaker?)	3077-2475 cal BC	CUNHA ET AL. 2007
Valdescusa	Vald	5	La Rioja	Bronze Age Bell Beaker	C ¹⁴ not published	PERS. COMMUNICATION C. ALONSO FERNÁNDEZ
Valencina- calle Dinamarca 3-5	Din	8	Andalusia	no dating		
Valle de las Higueras	Hig	2	Castilla – La Mancha	Chalcolithic Bell Beaker	3830+40 BP	BUENO RAMÍREZ ET AL. 2005
Zapateria	Zapa	1	Murcia	Bronze Age/El Argar		LULL ET AL. 2013A, 595

6 Laboratory protocols

6.1 General procedures against contamination

The post- and pre-PCR labs are located in separate buildings with no other molecular biology work in the same building as the pre-PCR-lab. Sample decontamination and preparation, DNA extraction, and PCR set-up were carried out in the pre-PCR lab, while all cloning and sequencing work was conducted in the post-PCR lab. Working in the pre- and post-PCR laboratories as well as in the office is conducted in a strict “one way direction”, which means work flow can only proceed from pre- to post PCR. The

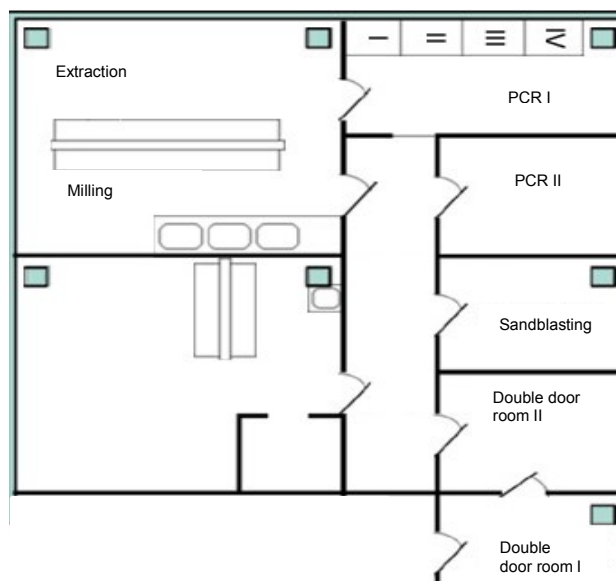


Figure 8 Layout of the pre-PCR lab

clean lab can only be entered freshly showered and with freshly washed clothing. In the clean lab all workers wear clean-room overalls with hood, laboratory designated shoes, surgical mask, face shield, and three layers of gloves to exclude sample contamination by investigators. Photography, sandblasting, DNA extraction, and PCR set-up are carried out in separate rooms (see fig. 8). All rooms, work benches, and instruments are routinely cleaned with bleach (Clorix) or DNA-Exitus and UV-irradiated overnight. All items entering the pre-PCR lab are cleaned with bleach and subsequently irradiated with UV for at least four hours. Analysis steps such as milling, DNA extraction, and PCR set-up are carried out in customized still-air boxes, which are cleaned with bleach in-between different work steps and after use, in addition to UV irradiation overnight.

6.2 Sampling

Almost all samples were taken by the principal aDNA researcher at the respective institutions or the ancient DNA facilities of the Institute of Anthropology in Mainz wearing gloves, surgical mask, and hair cover to avoid contamination. For all individuals two to three samples were taken, almost exclusively teeth. Where bones were taken, A and B sample were always from different bones except for samples from Cova del Cantal. Samples of La Mina, Arroyal, Els Trocs, and partly of La Bastida were taken directly at the excavations by other reserachers

with gloves and facemask, were cooled immediately and after excavation directly brought to the ancient DNA facility.

6.3 Sample preparation

First each sample was documented via digital photography from all sides. Each sample was then decontaminated by UV-irradiation of two sides for 30 minutes. From bone samples about 2 cm x 2 cm compacta was subsampled using a diamond drill. The surface of teeth and bone samples was removed by shot-blasting with aluminium-oxide-abrasive to get rid of superficial contaminations. Bone samples were subsequently cut into smaller pieces to facilitate the milling process. Before milling, the samples were UV-irradiated a second time from two sides for 30 minutes. Afterwards samples were ground to fine powder by using a mixer mill. Milling vessels were extensively washed with bleach as well as DNA-free water and cleaned with silicon-dioxide after every milling step to avoid cross contaminations. At the end of each milling day a sample consisting of synthetic hydroxyapatite was ground and treated exactly like the samples. It was used in subsequent extractions and PCRs to check the cleanliness of the milling process ("HAK": "Hydroxylapatite Kontrolle"). 0.2 – 0.7 g of each sample were aliquoted for extraction while remaining powder was set aside for putative re-extractions. All powder aliquots were stored at 4° C until further use.

6.4 Lysis and extraction

During this thesis two different methods of extraction were used: phenol-chloroform and silica extraction. The latter was slightly modified over the course of several extractions.

Phenol-Chloroform protocol (Extraction numbers TA-TD, RA-RU)

Digestion of teeth/bone powder was performed by incubating 0.2 – 0.5 g powder with 3.33 ml home-made lysis buffer consisting of 3 ml EDTA (0.5 M; pH 8.0), 300 µl 0.5% N-lauryl sarcosine and 30 µl proteinase K (20 mg/µl) on a rotary mixer over night at 37° C. In the subsequent extraction step, 3 ml phenol/chloroform/isoamylalcohol were pipetted to the samples, mixed, and centrifuged for 10 minutes at 4000 rpm. Then the aqueous phase containing the DNA was transferred into a new falcon. This step was repeated another time with phenol/chloroform/isoamylalcohol and in a final step with 3 ml chloroform to remove putative phenol residues. After the last step, the aqueous phase was transferred to Amicon Ultra-15 filter units with 50 kDa cut off and concentrated and washed several times with

DNA-free water until the extract was clear. DNA extracts were stored in volumes of between 90 µl and 150 µl at -20 °C until amplification. In each extraction at least one blank control was carried along.

Silica protocol (BROTHERTON ET AL. 2013) (Extraction numbers SA-SW)

A silica suspension was prepared by adding 6 g of silicon dioxide to 50 ml HPLC-water. The suspension was left to pellet for one hour. Subsequently, 40 ml of the supernatant containing the finest particles were transferred to a new tube and kept overnight for further settling. On the next day another 30 ml of the supernatant were discarded. On average, 0.25 g of tooth/bone powder were incubated overnight under constant rotation at 37 °C in 4.44 ml of lysis buffer consisting of 4 ml EDTA (0.5 M; pH 8.0), 400 µl N-lauroylsarcosine (0.5%) and 40 µl proteinase K (20 mg/µl). After lysis, samples were centrifuged at 4,600 rpm for one minute and the supernatant was transferred to a new tube. 125 µl silica suspension and 16 ml binding buffer (13.5 ml QG-buffer, 0.16 ml Triton X-100, 6.5 µl NaCl [5 M], and 1.6 ml acetic acid [2 M]) were added and DNA was left to bind to the silica at room temperature under slow and constant rotation for one hour. Afterwards, samples were centrifuged for one minute until the silica particles formed a solid pellet and the supernatant was poured off. The pellet was transferred to a new tube and washed and re-suspended in 1 ml 80% ethanol, centrifuged for one minute at 13,000 rpm, followed by removal of the supernatant. This step was repeated another two times. The pellets were left to dry for about 45 minutes with open lids in a closed box, subsequently re-suspended in 200 µl of pre-warmed (50°C) TE buffer and incubated for ten minutes. After centrifugation for one minute at 13,000 rpm, the supernatant was collected, aliquoted, and stored at -20 °C until further use. From extraction number SC onwards, the lysis buffer contained 4 ml EDTA (0.5 M) and 80 µl of proteinase K. Additionally, acetic acid was exchanged by sodium acetate in the binding buffer and binding buffer was set up in a final volume of 14 ml (12.73 ml QG-buffer, 0.18 ml Triton X-100, 70 µl NaCl [5 M], 1.02 ml sodium acetate [5 M]). From extraction number SK onwards, lysis was performed at room temperature over night with a subsequent incubation step at 50°C to 55°C for one hour. For extractions SO to SS samples were incubated with only EDTA over night at room temperature and proteinase K was added the next day followed by an incubation step of one hour at 55°C. For extractions ST to SW both EDTA and proteinase K were added at the same time again and incubation was performed over night at 55°C.

6.5 Amplification and sequencing of the control region

Amplification of the HVR I was performed by applying different primer pairs. By default, four overlapping primer pairs were used to amplify 413 bp of the HVR I (np 15997-16409). For samples with good preservation, the HVR I was amplified via two overlapping primer pairs that produce a sequence of 356 bp (np 16046-16401). For not so well preserved samples, a combination of six overlapping primer pairs was used (np 16019-16401). Anyway, in many cases samples were amplified using a combination of the 4-primer pair and 6-primer pair-system. The amplification of 364 bp (np 34–397) of the HVR II was performed by four overlapping primer pairs. HVR II amplification was only applied on some individuals of the sites of Reinoso and La Mina that had identical HVR I sequences to reveal a higher resolution on the sub-haplogroup level and to detect potential maternal kinship. At least two non-template controls were run in parallel in all PCRs.

The amplification was set up in a volume of 25 or 50 µl, containing 1–1.5 x PCR Gold Buffer, 3–2.5 mM MgCl₂ solution, 0.2 mM dNTP-Mix, 2.5 U AmpliTaq Gold® DNA polymerase, 0.2 µM of each primer, 1 µl 20 mg/ml BSA, and 3–8 µL DNA extract. The cycle conditions consisted of an initial denaturation at 94 °C for 6 minutes, 40–50 cycles of 35 seconds at 94°C, 35 seconds at 50–67°C and 40 seconds at 72°C, followed by a final extension at 60°C for 30 minutes. Later (from PCR 484 onwards) a slightly different and faster program was used for amplification: 94°C for 6 minutes, 40–50 cycles of 15 seconds at 94°C, 15 seconds at 50–67°C and 20 seconds at 72°C, followed by a final extension at 72°C for 10 minutes. The presence of PCR products of expected size was visually evaluated on a 2% agarose electrophoresis gel. Amplicons were purified either by using the Invisorb® Spin PCR Rapace Kit according to the manufacturer's instructions, or on MultiScreen₉₄ PCR Plates by eluting the PCR product in 180 µl of HPLC-water, transferring the mix to the MultiScreen₉₄ PCR Plates, applying vacuum for 10–15 minutes, washing with 50 µl of HPLC-water, applying vacuum for another 5 minutes, and re-suspending in 18 µl of water.

Table 2 HVR I and HVR II primers

HVR I and H30 primers are named after the last 5' base of the primer, HVR II primers are named after the first base or last base respectively of the amplified DNA fragment.

Primer	Sequence 5'→3'	Amplicon in bp with (without) primer	Temp. in °C	Reference
HVR I				
L16045	TGTTCTTTCATGGGGAAGCAGATT	240 (194)	56	BRANDT ET AL. (2013)
H16240	GGGTGGCTTTGGAGTTGCAGTT			BRANDT ET AL. (2013)
L16212	CCCCATGCTTACAAGCAAGTACA	236 (189)	56	ADLER ET AL. (2011)
H16402	GATATTGATTTACGGAGGATGGT			ADLER ET AL. (2011)
L15996	CTCCACCATTAGCACCCAAAGC	187 (145)	58	ENDICOTT ET AL. (2003)
H16142	ATGTACTACAGGTGGTCAAG			STONE AND STONEKING (1998)
L16117	TACATTACTGCCAGCCACCAT	162 (115)	58	HAAK ET AL. (2005)
H16233	GCTTTGGAGTTGCAGTTGATGTGT			HAAK ET AL. (2005)
L16209	CCCCATGCTTACAAGCAAGT	179 (138)	58	HANDT ET AL. (1996)
H16348	ATGGGGACGAGAAGGGATTTG			HAAK ET AL. (2005)
L16287	CACTAGGATACCAACAAACC	162 (122)	58	HANDT ET AL. (1996)
H16410	GCGGGATATTGATTTACGG			HANDT ET AL. (1996)
L16018	AGCACCCAAAGCTAAGATTCTAATTTAACTATT	139 (78)	57	KNIPPER ET AL. (2013)
H16097	ATATTCATGGTGGCTGGCAGTAATGTA			KNIPPER ET AL. (2013)
L16072	GGTACCACCCAAGTATTGACTCACC	123 (74)	57	KNIPPER ET AL. (2013)
H16144	TGGGTTTTTATGTACTACAGGTGGTCA			KNIPPER ET AL. (2013)
L16122	ATTTTCGTACATTACTGCCAGCCACCATGAATA	132 (76)	65	THIS STUDY
H16196	TAGTTGAGGGTTGATTGCTGTACTTGCTTGTAAGC			THIS STUDY
L16178	AGTACATAAAAACCCAATCCACAT	136 (91)	50	THIS STUDY
H16267	GTAGGTTTGTGGTATCCTAGTGG			THIS STUDY
L16231	GTACAGCAATCAACCCTCAACTAT	139 (94)	50	THIS STUDY
H16323	CTGTAATGTGCTATGTACGGTAAA			THIS STUDY
L16307	GGATACCAACAAACCTACCCACCCTTAACAGTACA	158 (94)	67	THIS STUDY
H16402.C	TGCGGGATATTGATTTACGGAGGATGGT			THIS STUDY
HVR II				
L00034	TCTATCACCTATTAACCACTCAC	192 (144)	58	HAAK ET AL. (2008)
H00177	TTAGTAAGTATGTTGCGCTGTAAT			HAAK ET AL. (2008)
L00144	CGCAGTATCTGTCTTTGATTCTTG	148 (100)	58	HAAK ET AL. (2008)
H00243	AAAGTGGCTGTGCAGACATTCAAT			HAAK ET AL. (2008)
L00172	ATCCTATTATTTATCGCACCTACG	204 (156)	58	HAAK ET AL. (2008)
H00327	TTGGCAGAGATGTGTTTAAAGTGCT			HAAK ET AL. (2008)
L00274	TGTCTGCACAGCCACTTTCCACAC	174 (124)	58	HAAK ET AL. (2008)
H00397	AGTGCATACCGCCAAAAGATAAAA			HAAK ET AL. (2008)
H30				
L08177	TATACTACGGTCAATGCTCTG	111 (63)	54	KEERL UNPUBLISHED
H08241	TACGGGCCCTATTTCAA			KEERL UNPUBLISHED

Sequencing was conducted in a final volume of 10 µl, consisting of 1 µl Big Dye® Terminator, 1.5 µl Big Dye® Terminator sequencing buffer, 1 µM primer (forward or reverse) and 1–2 µl PCR product. The cycling conditions were 25 cycles of 30 seconds at 92°C, 15 seconds at 58°C, and 2.5 minutes at 60°C. Sequencing products were purified using MultiScreen₃₈₄ SEQ Plates: Sequencing products were eluted in 10 µl HPLC-water, the mix was transferred to the MultiScreen₃₈₄ SEQ Plates, vacuum was applied for 5 minutes, the wells of the plates were washed with 50 µl HPLC-water, and again vacuum was applied for 15 minutes until the wells were dry. Afterwards, samples were re-suspended in 20 µl formamide and the solution was transferred into 96-well sequencing plates. This protocol was changed later to incubating each PCR product with 0.5 U shrimp alkaline phosphatase (SAP or FastAP) for 15 minutes at 37°C and subsequent inactivation of the enzyme at 75°C for 5 minutes. In the following step, the sequencing products were mixed with 50 µl of HPLC-water, transferred to the MultiScreen₃₈₄ SEQ Plates and vacuum was applied until the wells were dry. Afterwards, the products were re-suspended in 20 µl formamide and transferred into 96-well sequencing plates. The sequencing products were analyzed by capillary electrophoresis on an ABI PRISM™ 3130 Genetic Analyzer using the collection software. Sequence data analyses were performed using the programs SeqMan Pro™ and MegAlign™ which are part of the DNASTAR software package version 9.04.

6.6 Cloning of PCR products

PCR products were integrated into a pUC18 T-vector via TA-cloning. Ligation of 4 µl PCR product with the vector was set up in a volume of 10 µl, consisting of 4 U T4 DNA ligase, 1 x ligation buffer, 50 ng/µl T-vector, followed by a subsequent incubation at 16°C overnight, and agitation in a thermal mixer for one hour at 4,500 rpm at the next day. The enzyme was deactivated at 72°C for 15 minutes. 1 volume chloroform and HPLC-water were added and the mix was centrifuged. The chloroform phase was transferred into a new tube and DNA was precipitated with 1 µl sodium acetate (3 M, pH 4.6) and 50 µl ethanol (100%). The pellet was dried and re-suspended in 10 µl HPLC-water. In the following step the ligation mix was combined with 50 µl electro-competent cells (*Escherichia coli*, RRI) and transferred in an electroporation cuvette. The cuvettes were constantly kept on ice. Subsequently, the mix was electroporated with a currency of 2500 V. Afterwards, it was immediately transferred into 1 ml sterilized growing medium (LB-medium) consisting of 5 g trypton, 2.5 g yeast extract, 2.5 g NaCl, and 500 ml HPLC-water. The cells were then left to grow overnight at 37°C on LB-agar plates containing ampicillin, IPTG (isopropyl β-D-1-thiogalactopyranoside), and X-Gal (5-bromo-4-chloro-3-indolyl-beta-D-galactopyranoside) (5 g trypton, 2.5 g yeast, 2.5 g NaCl,

7.5 g agar agar, 500 ml HPLC-water, 50 mg ampicillin, 50 mg X-Gal, and 23.8 mg IPTG). Cells transformed with vectors containing PCR products produced white colonies while cells transformed with non-recombinant plasmids (i.e. only the vector) grew into blue colonies. Selected clones were picked directly into a PCR set-up (50 µl final volume), comprising 1 x PCR buffer, 2.5 mM MgCl₂ solution, 0.2 mM dNTP mix, 0.2 µM universal M13 forward and reverse primer and 1 U DNA polymerase. Cycle conditions consisted of an initial denaturation at 94°C for 15 minutes, followed by 30 cycles of 30 seconds at 94°C, 30 seconds at 58°C and 30 seconds at 72°C. PCR products carrying the expected insert length (screened on a 2% agarose gel) were purified enzymatically with 2 U exonuclease I (EXO I) and 0.5 U shrimp alkaline phosphatase (SAP). Incubation conditions were 37°C for 45 minutes with subsequent inactivation at 80°C for 15 minutes. The sequencing of clones was conducted according to the same protocol as described for PCR products.

6.7 Amplification and sequencing of coding region SNPs

For a better resolution of mitochondrial haplogroups especially for individuals with no results for the control region, several multiplex approaches were conducted. First, for every sample 22 haplogroup defining coding region SNPs were simultaneously analyzed using the GenoCoRe22 published by HAAK ET AL. (2010). For all individuals belonging to haplogroup H, a similar multiplex approach was conducted, targeting coding regions SNPs defining the 17 today most frequent H-sub-haplogroups in Europe (MARTÍNEZ-CRUZ ET AL. 2012). For all individuals that were assigned to haplogroup U, likewise six coding region SNPs were analyzed via a multiplex PCR (U-plex, KEERL UNPUBLISHED). For individuals that belonged to haplogroup T, a PCR targeting the defining SNPs for sub-haplogroups T1 and T2 was conducted (T-plex, KEERL UNPUBLISHED). These three Multiplex-PCR approaches together (H-Plex, T-Plex, and U-Plex) will be called ExtraCoRes in the following. According to new phylogenetic information the SNP for H1 is also defining haplogroup H30b. Therefore, for all individuals that were assigned to haplogroup H1 by the H-plex, the SNP that characterizes haplogroup H30 was sequenced to ensure correct haplogroup assignment (for H30 primer sequences see table 2).

GenoCoRe22

The set-up was mostly according to the description of HAAK AND COLLEAGUES (2010): PCR was set up in a volume of 25 µl containing 1 x PCR Gold buffer, 6 mM MgCl₂, 0.04 µg BSA, 600 µM dNTPs, ~0.02 µM of each primer, 1.25 U AmpliTaq Gold® DNA polymerase, and 2–3 µl DNA extract. Cycling conditions were 95°C for 10 minutes, followed by 35 cycles of 95°C

for 30 seconds, 60°C for 45 seconds, and 65°C for 30 seconds, followed by 65°C for 6 minutes. Amplification success was checked via gel electrophoresis (2–3% agarose gels). In the following 2.5 µl of PCR product were purified enzymatically with 0.4 U EXO I and 1 U SAP. Incubation conditions were 37°C for 45 minutes with subsequent inactivation at 80°C for 15 minutes.

The sequencing was conducted in a multiplex reaction as well. All sequencing primers hybridize to the DNA section directly upstream of the respective SNP nucleotide. In the following “mini-sequencing” step the primer were extended by adding only one base that is complementary to the SNP nucleotide (SBE, single base extension). This incorporated base is detected and determines the SNP allele. Adding ct-tails of different lengths to the primers results in different run times in the capillary electrophoreses, enabling to assign the detected SNPs to the different markers. SBE-primers were mixed with water and 10% ammonium sulfate (3 M) to a final concentration of 0.33–0.5 µM for each primer. The sequencing was set up in a volume of 7 µl containing 3 µl Ready Reaction Mix of the ABI PRISM® SNaPshot™ Multiplex Kit, 2 µl SBE-primer mix, 1 µl HPLC-water and 1 µl DNA. Cycling conditions were 35 cycles at 96°C for 10 seconds, 55°C for 5 seconds, and 60°C for 30 seconds. SBE products were purified with 1 U SAP at 37°C for 45 minutes, followed by inactivation of the enzyme at 80°C for 15 minutes. For the capillary electrophoreses 2 µl of each SBE product were mixed with 11.8 µl Hi-Di™ formamide and 0.2 µl GeneScan™ 120 LIZ™ size standard.

H- and U-Plex

PCRs were set up in a volume of 25 µl, containing 1 x PCR Gold buffer, 8 mM MgCl₂, 0.02 µg BSA (bovine serum albumin), 500 µM dNTPs, ~0.02 µM of each primer, 2 U AmpliTaq Gold® DNA polymerase, and 2–3 µl DNA extract. Cycling conditions were 95°C for 10 minutes, and 35 cycles of 95°C for 30 seconds, 56°C for 30 seconds, and 65°C for 30 seconds, followed of 65°C for 10 minutes for the U-Plex and only 32 cycles and an annealing temperature of 59°C for the H-Plex. Amplification success was checked via gel electrophoresis (2–3% agarose gels). Purification and SBE-reaction was set up according to the GenoCoRe22.

T-Plex

The T-Plex was set up according to the H- and U-Plex with an annealing temperature of 52°C. After purification of the PCR no SBE-reaction was performed, instead the two markers were sequenced directly with the particular primers for T1 and T2.

Table 3 Multiplex PCR primers

Detected SNP	hg	forward primer	Sequence 5'→3'	reverse primer	Sequence 5'→3'
GenoCoRe 22					
13928	R9	L13923	TTTCTCCAACATACTCGGATTCTAC	H13942	AGAAGGCCTAGATAGGGGATTGT
3594	L3'4	L03556	AGCTCTCACCATCGCTCTTC	H03597	AAATAGGAGGCCTAGGTTGAGG
10550	K	L10548	GAATACTAGTATATCGCTCACACCTCA	H10558	GCGATAGTATTATTCCTCTAGGCATAGTA
11467	U	L11454	ATCGCTGGGTCAATAGTACTTGC	H11479	TGAGTGTGAGGCGTATTATACCATAG
4248	A	L04237	TGATATGTCTCCATACCCATTACAA	H04253	CTTTTATCAGACATATTTCTTAGGTTTGAG
8994	W	L08970	CATACTAGTTATTATCGAAACCATCAGC	H09003	CTGCAGTAATGTTAGCGGTTAGG
13263	C	L13258	ATCGTAGCCTTCTCCACTTCAA	H13295	AGGAATGCTAGGTGTGGTTGGT
13368	T	L13350	CACGCCTTCTTCAAAGCCATA	H13372	GTTCAATTGTTAAGGTTGTGGATGAT
11719	R0 preHV	L11710	GGCGCAGTCATTCTCATAATC	H11735	AGTTTGAGTTTGCTAGGCAGAATAG
8280	B	L08268	AATAGGGCCCGTATTTACCTATA	H08295	AGGTTAATGCTAAGTTAGCTTTACAGTG
4580	V,M3	L04578	TTACCTGAGTAGGCCTAGAAATAAACA	H04618	GCAGCTTCTGTGGAACGAG
6371	X	L06363	ACCATCTTCTCCTTACACCTAGCAG	H06378	GATGAAATTGATGGCCCTAA
10238	N1	L10228	TCCCTTTCTCCATAAAATCTTCTT	H10249	AGGAGGGCAATTTCTAGATCAAATA
7028	H	L07003	GCAAACATCACTAGACATCGTACT	H07029	CCTATTGATAGGACATAGTGGAAGTG
10034	I	L10025	CTTTTAGTATAAATAGTACCGTTAACTTCCAA	H10037	AAGTTTATTACTCTTTTTGAATGTTGTCA
5178	D	L05171	ACCCTACTACTATCTCGCACCTGA	H05204	CTAGGGAGAGGAGGGTGGAT
14766	HV	L14759	AGAACACCAATGACCCCAATAC	H14799	GGTGGGGAGGTGCGATGA
12705	R	L12689	CAGACCCAAACATTAATCAGTTCTT	H12715	TGTTAGCGGTAACAAAGATTAGTATGGT
10873	N	L10870	CCACAGCCTAATTATTAGCATCATC	H10888	GCTAAATAGGTTGTTGTTGATTTGG
12612	J	L12611	CTACTTCTCCATAATATTATCCCTGT	H12621	AATTCTATGATGGACCATGTAACG
2758	L2'6	L02727	AACACAGCAAGACGAGAAGACC	H02760	GGACCTGTGGGTTTGTAGGT
10400	M	L10382	AAGTCTGGCCTATGAGTGACTACAA	H10421	TGAGTCGAAATCATTCGTTTTG
H-Plex					
3010	H1 /H30b	L03005	ACGACCTCGATGTTGGATCAGGACA	H03056	CCGGTCTGAACTCAGATCAGCTAGG
1438	H2	L01432	AGGGTCAAGGTGGATTTAGCAGT	H01477	AGGGTGACGGGCGGTGTGTA
6776	H3	L06744	GGCTTCCTAGGGTTTATCGTGTGAGC	H06802	GCGGAGGTGAAATATGCTCGTGTGT
3992	H4	L03965	GAATACGCCGACAGGCCCTT	H04010	AGGAAGATTGTAGTGGTGAGGGTGT
4793	H7	L04735	TCTCCGACAATGAACATAACCAATAC	H04795	TGGGACTCAGAAGTGAAGGGGG
13020	H9	L13013	AGCAGCAGGCAAATCAGCCCA	H13050	CTGAGACTGGGGTGGGCGCT
14470	H10	L14466	ACTCCTCAATAGCCATCGCTGTAGT	H14518	TCTGAATTTTGGGGGAGGTTATATGGGT
8448	H11	L08411	TGGCCCAACATAATTACCCCA	H08461	TTTGGTGAGGGAGGTAGGTGGTAG
3936	H12	L03911	ACCCCTTCGACCTTGCCGA	H03943	GGGCTGCGGCGTATTCGAT
7645	H14	L07608	GGCACATGCAGCGCAAGTAGG	H07647	TGAGGGCGTGATCATGAAAGGTGA
6253	H15	L06244	CCCTCTCTCTACTCCTGCTCGC	H06259	ACCTGTTCTGCTCCGCGCT
10394	H16	L10382	AAGTCTGGCCTATGAGTGACTACAA	H10421	TGAGTCGAAATCATTCGTTTTG
14364	H18	L14348	ACCACAACCACACCCCATCAT	H14371	TGGGGTTAGCGATGGAGGTAGGA
14869	H19/H13	L14865	GGCTCACTCCTTGCGCCTG	H14913	GGCGGTTGAGGCGTCTGGTG
10211	H23	L10202	ACCTATATCCCCCGCCGC	H10264	TGGTAGGGGTAAAGGAGGGCAA
9620	H25	L09590	AGTCCCACTCCTAAACACATCCGT	H09670	GCAGTGCTTGAATTATTTGTTTCGGT
U-Plex					
16051	U2	L16047	TCATGGGGAAGCAGATTTG	H16071	ATAGCGGTTGTTGATGGG
16343	U3	L16340	AAGCCATTTACCGTACATAGCACA	H16346	GGGGACGAGAAGGGATTTGAC

6 Laboratory protocols

Detected SNP	hg	forward primer	Sequence 5'→3'	reverse primer	Sequence 5'→3'
4646	U4	L04634	AAAAATAAACCCCTCGTTCACAGAAGCT	H04659	TATTAGAAGGATTATGGATGCGGTTGC
3197	U5	L03182	GCCTTCCCCGTAAATGATA	H03205	TGTTCTTGGGTGGGTGTGG
14793	U5a	L14766	CACCAATGACCCCAATACGCAAAAC	H14794	GGGGTGGGGAGGTGCGATGAATGAG
14182	U5b	L14179	CCCCGAGCAATCTCAATTACAATA	H14209	TGATTATGGGCGTTGATTAGTAGTAGTT
9698	U8	L09684	TAGAAAACAACCGAAACCAATAA	H09719	GAGGCTTGTAGGAGGGTAAAATAG
T-Plex					
12633	T1	L12623	CATCCCTGTAGCATTGTTCTGT	H12661	CTGATTAATGTTTGGGTCTGAGTT
11812	T2	L11793	TCACAGTCGCATCATAATCCTCTC	H11827	AGGCTTGCTAGAAGTCATCAAAAA

Table 4 Multiplex SBE primers

The primer name indicates, whether the SNP was detected in forward (snF) or reverse (snR) direction. ct-tails are marked in lower case.

SNP	SBE primer name	SBE primer 5'→3'	SBE primer size
GenoCoRe22			
R9	13928snR	tctctctctctGATTGTGCGGTGTGTGATG	32
L3'4	3594snR	ctctctctctctctctGAGGCCTAGGTTGAGGTT	36
K	10550snR	ctctctctctctctTCTAGGCATAGTAGGGAGGA	36
U	11467snF	ctctctctctctctctGTAAGTGGCCGAGTACTCTT	40
A	4248snF	tctctctctctctctATACCCATTACAATCTCCAGCAT	40
W	8994snF	ctctctctctctctctctTACTCATCAACCAATAGCCCT	44
C	13263snR	ctctctctctctctctCCGATTGTAATATTATGAGTCCTAG	44
T	13368snF	ctctctctctctctctctctCCATACTATTATGTGCTCCGG	48
R0/preHV	11719snR	tctctctctctctctctTAGGCAGAATAGTAATGAGGATGTAAG	48
B	8280delsnR	tctctctctctctctctctctCTTTACAGTGGGCTCTAGAGGGGGT	52
V,M3	4580snR	ctctctctctctctctctctTTTTGGTTAGAACTGGAATAAAAGCTAG	52
X	6371snR	tctctctctctctctctctctctctctctAAATTGATGGCCCTAAGATAGA	56
N1	10238snF	tctctctctctctctctctctCTTTCTCCATAAAATTCTTCTTAGTAGCTAT	56
H	7028snR	tctctctctctctctctctctctctctctCTATTGATAGACATAGTGGAAGTG	60
I	10034snF	ctctctctctctctctctctctGTATAAATAGTACCGTTAACTTCCAATTAAGTAG	60
D	5178snR	tctctctctctctctctctctctctctctctGGAATTAAGGGTGTAGTCATGTTA	64
HV	14766snR	ctctctctctctctctctctctctctctctGAGTGGTTAATTAATTTATTAGGGGGTTA	68
R	12705snR	ctctctctctctctctctctctctctctctctGGTAACTAAGATTAGTATGGTAATTAGGAA	72
N	10873snR	ctctctctctctctctctctctctctctctctGTTGTTGTTGATTGGTTAAAAATAGTAG	74
J	12612snF	ctctctctctctctctctctctctctctctctCTACTTCCATAAATTCATCCCTGT	77
L2'6	2758snF	ctctctctctctctctctctctctctctctctCTATGGAGCTTTAATTTATTAATGCAACA	80
M	10400snR	ctctctctctctctctctctctctctctctctAAATCATTCGTTTGTGTTAACTATATACCAATTC	83
H-Plex			
H10	14470AsnR	tctctctctctctctctctctctctctctctctGGGAATGATGGTTGTCTTTGG	68
H7	4793snR	tctctctctctCTCAGAAGTGAAAGGGGGC	32
H1/H30	3010snR	ctctctctctctTTAATAGCGGCTGCACCAT	36
H18	14364snR	ctctctctctctctCGATGGAGGTAGGATTGGTG	38
H4	3992snF	ctctctctctctctctCCCTATTCTTCATAGCCGAATACA	44
H11	8448snF	tctctctctctctctctctCTATTCTCATCACCCTAACTAAAAA	48

SNP	SBE primer name	SBE primer 5'→3'	SBE primer size
H2	1438snR	ctctctctctctctctctctctCCCTGTTCAACTAAGCACTCTACTCT	52
H16	10394snF	ctctctctctctctctctctctCCTATGAGTGACTACAAAAGGATTAGA	56
H15	6253snR	ctctctctctctctTGCTCCGGCCTCCACT	32
H9	13020snR	tctctctctctctctctGGGAGTCAGGGGTGGAG	36
H12	3936snR	tctctctctctctctCGGCGTATTCGATGTTGAA	36
H14	7645snR	ctctctctctctctctctctGCGTGATCATGAAAGGTGAT	44
H19	14869snF	tctctctctctctctctctctctctctCCTTGCGCGCTGCCT	50
H13	14872snR	tctctctctctctctctctctctAATAGTCCTGTGGTGATTTGGAG	52
H25	9620snR	tctctctctctctctctctctctctCAGGTGATTGATACTCCTGATGC	56
H23	10211snR	ctctctctctctctctctctctctGGTAATAGCTACTAAGAAGAATTTATGGA	60
H3	6776snR	tctctctctctctctctctctctctGTGTGTCTACGTCTATTCTACTGTAAATAT	64
U-Plex			
U2	16051snF	tctctctctctctTGGGGAAGCAGATTGGGT	34
U3	16343snR	GGACGAGAAGGGATTTGACTG	21
U4	4646snR	GGATGCGGTTGCTTGCCTGAGGAA	24
U5	3197snR	ctctctTTGGGTGGGTGTGGGTATAAT	28
U5a	14793snR	ctctcGGGGTGGGGAGGTCGATGAATGAG	29
U5b	14182snF	ctCGAGCAATCTCAATTACAATATA	25
U8	9698snR	ctctctctAGAGACCCAGTAAATTGTAAT	32

6.8 Reproduction strategy

Success of ancient DNA analyses of regions with warmer climate conditions like the Iberian Peninsula can be expected to be lower than for regions with a moderate climate like Central Europe. Another important factor for DNA preservation are the storage conditions of the skeletal remains after excavation which were not known for numerous sites analyzed in this study. Since ancient human specimens are precious material, they should not be used in destructive analyses lightly. Hence, from larger sites (>12 individuals) samples of the five to seven macroscopically best preserved individuals were chosen for a preliminary screening. In case of very low amplification success for a subset (<40–50%), no more samples from this particular site were analyzed. For sites where the macroscopic state of preservation was poor, only one sample per individual was analyzed and in case of unsuccessful amplification, no second sample was processed. However, for all other individuals a minimum of two independent samples (A and B) – almost exclusively teeth – were taken. Only in case of Cova del Cantal, A and B samples were taken out of different parts of the same bone. Though sample preparation (digital documentation, sandblasting, and milling) was often undertaken at the same day for both samples of an individual, they were treated as if being different individuals, thus regular cleaning steps to avoid cross-contamination were applied

(see chapter 6.3). Two samples of the same individual were never analyzed in the same extraction to ensure independent reproduction. After extraction, all samples were initially screened for DNA preservation with the GenoCoRe22 multiplex assay. This assay targets very small DNA fragments and will therefore most likely lead to successful amplification. Even samples that lacked results in the GenoCoRe22 were additionally tested in 2–3 PCRs with short HVR I primers before being excluded from further analyses. Initially screening for HVR I amplicons was usually conducted with the primer pair 16117–16233 of the 4-primer-system. In case of none-success, primers of the 6-primer-system were applied for amplification instead. The 2-primer-system was only used for individuals of the site Reinoso. In general, samples of the Iberian Peninsula were not preserved well enough for amplification of longer fragments and sequences that could be retrieved with the 2-primer-system often showed a great number of deaminations or contamination. Individuals with consistent HVR I profiles from both samples and only few ambiguous nucleotide positions were amplified over the whole HVR I at least three times from different extracts, producing 6–18 independent and overlapping amplicons (depending on the primer pairs used). Additionally, selected PCR products showing ambiguous nucleotide positions were cloned to monitor possible background contaminations and DNA damage. For less well-preserved individuals where sequencing revealed numerous ambiguous nucleotide positions, all PCR products (4–12) were cloned and, if necessary, additional amplifications were performed.

For some individuals of the sites Reinoso and La Mina that showed the same haplotype, the HVR II was additionally analyzed via four overlapping primer pairs. Finally, to magnify resolution of haplogroups especially where no HVR I data were available, three multiplex reactions, targeting sub-haplogroup defining coding region SNPs for haplogroups H, T, and U were performed on all samples that were assigned to one of these haplogroups.

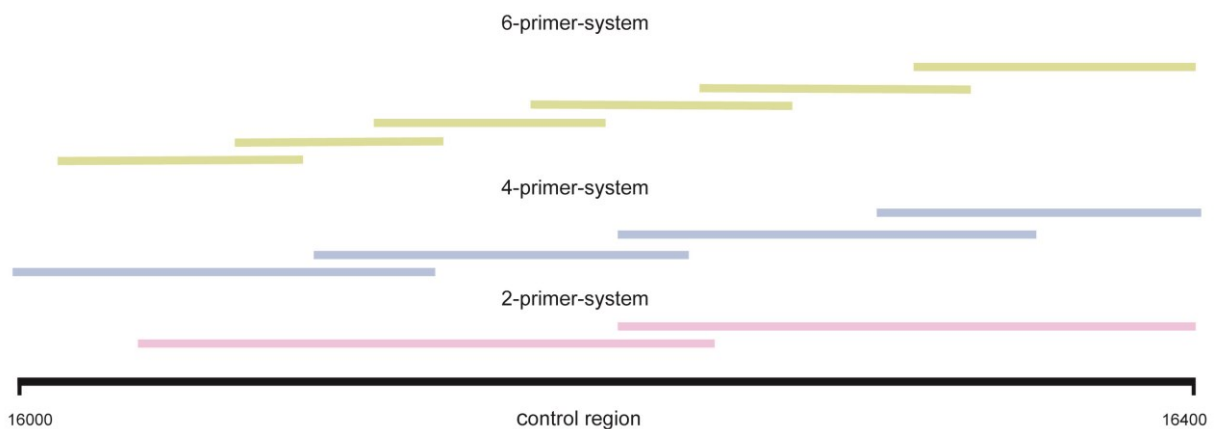


Figure 9 Amplicon sizes and overlap areas of the different HVR I primer-systems
Fragment lengths are illustrated to scale.

7 Statistical Methods

7.1 Datasets

To address the different research questions it was necessary to use different datasets; one comprising only individuals from the Iberian Peninsula and one using as much validated additional prehistoric data from outside the Iberian Peninsula as possible. For analyses of haplogroup H variability, the dataset had to be modified again for two main reasons: Due to the small number of individuals that belonged to haplogroup H, the Iberian dataset had to be pooled more roughly than in previous analyses. Furthermore, some Iberian data as well as many comparative data from outside the Iberian Peninsula could not be considered due to insufficient sub-haplogroup resolution of haplogroup H. However, it was possible to enlarge the dataset by adding unpublished data from the Early Iron Age and the Early Neolithic from Hungary for these analyses.

7.1.1 Iberian dataset

Groups were formed with both published data and data generated in this study. The denotation of the populations in statistical analyses and text is based on location, chronology and in few cases on cultural assignment of the samples. Please note that whenever groups were denoted as Early Neolithic or Late Neolithic, the terms referred to the classification of this study and not to any archaeological classification that may define very different chronologies dependent on region and/or researcher.

To facilitate the interpretation of statistical results, Iberian groups were abbreviated in a consistent manner: The first two letters always indicate the geographic location: Northeast Spain (NE), Northern Spain (NS), Northern Meseta (NM), East Spain (ES), Southern Meseta (SM), Southern Iberian Peninsula (SI), Central Portugal (CP), Ebro Valley (EV), and Ambrona Valley (AV) (see fig. 10). The third letter gives the chronological information: Early Neolithic (E), Late Neolithic (N), Chalcolithic (C) or Bronze Age (B). If there is a fourth letter, it defines the cultural assignment: B for Bell Beaker and A for El Argar. The only inconsistency in denotation regards the cave site of Els Trocs where Early Neolithic samples were regarded as own group, TROCE. It should be noted that the group NSE (Early Neolithic of Northern Spain) comprises mainly samples that are located in the Upper Ebro Valley, close to the chronologically later samples that were pooled into the population EVN, but also two samples that are located in Burgos, where the samples of the NMN (Northern Meseta Neolithic) originate. Due to small sample size it was not possible to differentiate between

Ebro Valley and Northern Meseta samples in the Early Neolithic; thus, all of them were pooled into the same group.

All in all, 19 chronological and geographical different groups were defined:

- Western hunter-gatherers (HGW)
- Early Neolithic: Northeast Spain (NEE), Els Trocs (TROCE), Northern Spain (NSE), and Central Portugal (CPE)
- Late Neolithic: Northeast Spain (NEN), Ambrona Valley (AVN), Ebro Valley (EVN), Northern Meseta (NMN), and Central Portugal (CPN)
- Chalcolithic: Northeast Spain (NEC), Southern Meseta (SMC), East Spain (ESC), Southern Iberian Peninsula (SIC), and Central Portugal (CPC)
- Chalcolithic Bell Beaker: Northern Meseta (NMCB) and Southern Meseta (SMCB)
- Bronze Age: Northeast Spain (NEB) and East Spain El Agar culture (ESBA)

Due to insufficient authentication, the following published data were not used in any analyses: 1 individual of San Pau de Camp (26SP0102) and 2 individuals of Can Sadurní (CSA 0511, CSA 24) (GAMBA ET AL. 2011) as well as individual E10 from Montanissell Cave (SÍMON ET AL. 2011). HVR I data from the latter site were not sufficiently reproduced, therefore only haplogroup information provided and reproduced by RFLP analyses was used in statistical analyses.

Due to the high amplification success of the GenoCoRe22 and the ExtraCoRes (see also chapter 8.1) haplogroup information was available for 331 individuals (table 5). Because it was not possible to also reproduce HVR I sequences for all of these individuals, haplotype information was only available for 238 individuals (table 5). This led to different group sizes dependent on the type of statistical analyses used: haplogroup-based (PCA, cluster analysis, Fisher-test) or haplotype-based (F_{ST} values, MDS, SHA, AMOVA). Some groups could not be analyzed by haplotype-based analyses (SIC, NEB, ESBA) because haplotype information of no or too few individuals was available. The Chalcolithic group of Central Portugal (CPC) only contained 6 sequences – less than half of the dataset available for this group when computing on haplogroup level – of which 4 belonged to haplogroup K. Given that this dataset is clearly biased when only HVR I sequences are used, it was excluded from sequence based methods as well. All in all, 15 chronologically and geographically different groups were used in sequence-based statistical analyses.

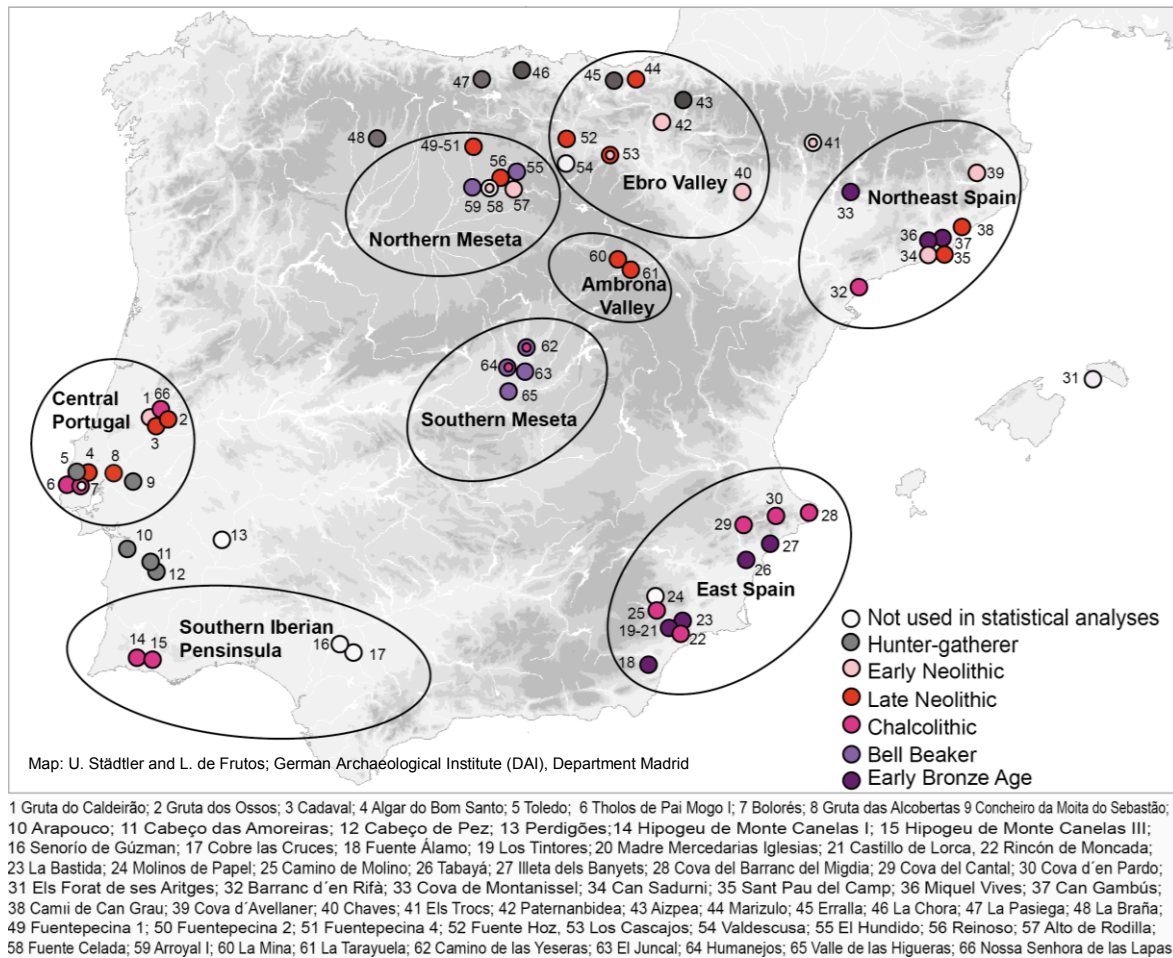


Figure 10 Archaeological sites and regional classifications used in population genetic analyses
 White circles represent sites that are mentioned in the discussion but not used in statistical analyses. Multiphasic sites are indicated by concentric circles. The map also includes sites published by other researchers; the respective publications are named in table 5.

Table 5 Groups used in statistical analyses

n_1 gives the number of individuals used in haplogroup-based statistical analyses and n_2 the number of individuals used in sequence-based statistical analyses. An asterisk in the column n_2 indicates that sequences of this particular site were available (see table 11), but overall sample-size for this group was too low to compute sequence-based statistical analyses.

	Groups and group size (haplogroup based/sequence based)	Site	Number of site in figure 10	n_1	n_2	Reference
Hunter-gatherer	HGW (14/13)	Toledo	5	1	1	CHANDLER 2003
		Concheiro da Moita do Sebasto	9	1	0	THIS STUDY
		Arapouco	10	2	2	CHANDLER 2003
		Cabeo das Amoreiras	11	1	1	CHANDLER 2003
		Cabeo de Pez	12	3	3	CHANDLER 2003

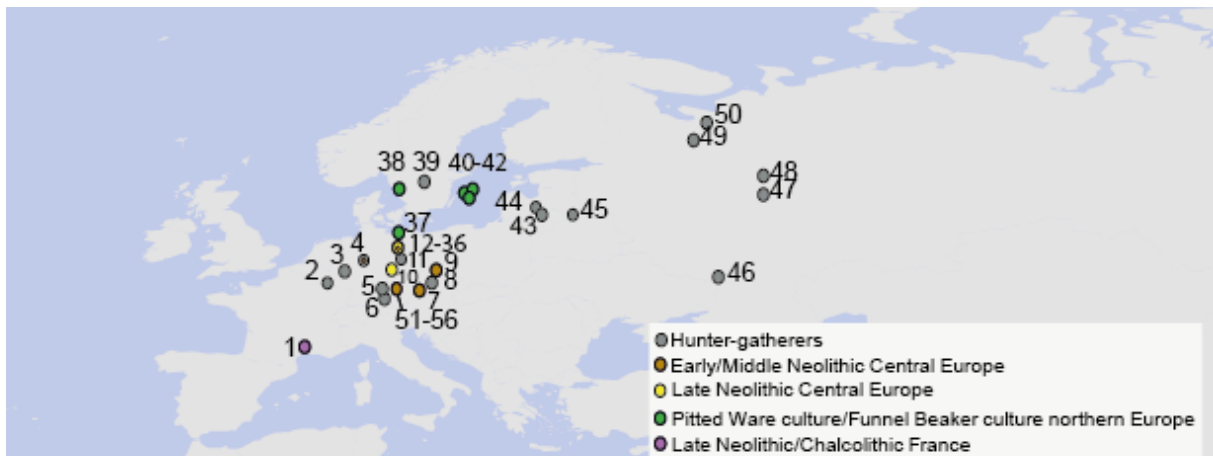
	Groups and group size (haplogroup based/sequence based)	Site	Number of site in figure 10	n ₁	n ₂	Reference
		Aizpea	43	1	1	HERVELLA ET AL. 2012
		Erralla	45	1	1	HERVELLA ET AL. 2012
		La Chora	46	1	1	HERVELLA ET AL. 2012
		La Pasiega	47	1	1	HERVELLA ET AL. 2012
		La Braña	48	2	2	SÁNCHEZ-QUÍNTO ET AL. 2012
Early Neolithic	Northeast Spain NEE (12/12)	Can Sadurni	34	5	5	GAMBA ET AL. 2011
		Cova d'Avellaner	39	7	7	LACAN ET AL. 2011B
	Els Trocs TROCE (7/7)	Els Trocs	41	7	7	THIS STUDY
	Northern Spain NSE (25/25)	Chaves	40	3	3	GAMBA ET AL. 2011
		Paternanbidea	42	9	9	HERVELLA ET AL. 2012
		Los Cascajos Phase I	53	11	11	HERVELLA ET AL. 2012
		Alto de Rodilla	57	1	1	THIS STUDY
		Fuente Celada	58	1	1	THIS STUDY
	Central Portugal CPE (9/9)	Gruta do Caldeirão	1	9	9	CHANDLER 2003
Late Neolithic	Northeast Spain NEN (13/13)	Sant Pau del Camp	35	2	2	GAMBA ET AL. 2011
		Camí de Can Grau	38	11	11	SAMPIETRO ET AL. 2007
	Ambrona Valley AVN (22/22)	La Mina	60	13	13	THIS STUDY
		La Taryuela	61	9	9	THIS STUDY
	Ebro Valley EVN (11/11)	Fuente Hoz	52	6	6	HERVELLA ET AL. 2012
		Los Cascajos Phase II	53	4	4	HERVELLA ET AL. 2012
		Marizulo	44	1	1	HERVELLA ET AL. 2012
	Northern Meseta NMN (37/36)	Fuentepecina 1	49	4	4	THIS STUDY
		Fuentepecina 2	50	4	4	THIS STUDY
		Fuentepecina 4	51	2	2	THIS STUDY
		Reinoso	56	27	26	THIS STUDY

	Groups and group size (haplogroup based/sequence based)	Site	Number of site in figure 10	n ₁	n ₂	Reference
	Central Portugal CPN (12/6)	Algar do Bom Santo	3	3	3	CHANDLER 2003
		Cadaval	3	3	2	THIS STUDY
		Gruta das Alcobertas	8	2	1	THIS STUDY
		Gruta dos Ossos	2	4	0	THIS STUDY
Chalcolithic	Northeast Spain NEC (15/15)	Barranc d'en Rifà	32	15	15	THIS STUDY
	Southern Meseta SMC (17/12)	Camino de las Yeseras	62	10	7	THIS STUDY
		Humanejos	64	7	5	THIS STUDY
	East Spain ESC (32/31)	Rincón de Moncada	22	2	2	THIS STUDY
		Camino de Molino	25	18	18	THIS STUDY
		Cova del Barranc del Migdia	28	1	0	THIS STUDY
		Cova del Cantal	29	5	5	THIS STUDY
		Cova d'en Pardo	30	6	6	THIS STUDY
	Southern Iberian Peninsula SIC (6/0)	Hipogeu de Monte Canelas I	14	5	0	THIS STUDY
		Hipogeu de Monte Canelas III	15	1	0	THIS STUDY
	Central Portugal CPC (15/0)	Tholos de Pai Mogo I	6	13	*	THIS STUDY
		Bolorés	7	1	0	THIS STUDY
		Nossa Senhora das Lapas	66	1	*	THIS STUDY
Bell Beaker	Southern Meseta SMCB (24/18)	Camino de las Yeseras	62	2	2	THIS STUDY
		El Juncal	63	14	14	THIS STUDY
		Humanejos	64	7	2	THIS STUDY
		Valle de las Higueras	65	1	0	THIS STUDY
	Northern Meseta NMCB (7/7)	El Hundido	55	2	2	THIS STUDY
		Arroyal	59	5	5	THIS STUDY
Early Bronze Age	Northeast Spain NEB (16/0)	Cova de Montanissell	33	7	0	SIMON ET AL. 2011
		Miquel Vives	36	1	*	THIS STUDY
		Can Gambús	37	8	*	THIS STUDY

	Groups and group size (haplogroup based/sequence based)	Site	Number of site in figure 10	n ₁	n ₂	Reference
	East Spain ESBA (10/0)	Fuente Álamo	18	3	*	THIS STUDY
		Los Tintores	19	1	*	THIS STUDY
		Madre Mercedarias Iglesias	20	1	0	THIS STUDY
		Castillo de Lorca	21	1	*	THIS STUDY
		La Bastida	23	2	*	THIS STUDY
		Tabayá	26	1	0	THIS STUDY
		Illeta dels Banyets	27	1	0	THIS STUDY

7.1.2 Additional prehistoric dataset from Central and northern Europe

To interpret the mitochondrial composition of the ancient Western European dataset in a European context, 472 additional individuals from ten different countries were added, dating from the Paleolithic to the Early Bronze Age (see table 6). Paleogenetic data of Central and Northern Europe were generally classified according to archaeological material cultures in line with previous publications (MALMSTRÖM ET AL. 2009; BRAMANTI ET AL. 2005, 2009; LEE ET AL. 2012; BRANDT ET AL. 2013, IN PRESS).



1 Treilles, 2 Loschbour, 3 Oberkassel, 4 Blätterhöhle, 5 Hohlenstein-Stadel, 6 Hohler Fels, 7 Aspam-Schletz, 8 Dolní Věstonice, 9 Vedrovice, 10 Kromsdorf, 11 Bad Duerrenberg, 12 Osterwieck, 13 Derenburg-Meerenstieg II, 14 Halberstadt-Sonntagsfeld, 15 Benzingenrode I, 16 Benzingenrode-Heimburg, 17 Quedlinburg VII, 18 Quedlinburg VIII, 19 Quedlinburg IX, 20 Quedlinburg XII, 21 Quedlinburg XIV, 22 Oberwiederstedt, 23 Oberwiederstedt 2, 24 Oberwiederstedt 3, 25 Oberwiederstedt 4, 26 Plötzkau 3, 27 Leau 2, 28 Salzmünde-Schiepzig, 29 Halle-Queis, 30 Rothenschimbach, 31 Alberstedt, 32 Esperstedt, 33 Karsdorf, 34 Eulau, 35 Röcken 2, 36 Naumburg, 37 Ostorf, 38 Frälsegården, 39 Motala, 40 Ajvide, 41 Fridtorp, 42 Ire, 43 Spiginas, 44 Donkalis, 45 Kretuonas, 46 Kostenki, 47 Lebyazhinka, 48 Chekalinol, 49 Yuzhnyy Oleni Ostrov, 50 Popovo, 51 Flomborn, 52 Eilsleben, 53 Schwetzingen, 54 Vaihingen, 55 Seehausen, 56 Stuttgart

Figure 11 Sites of the additional Eurasian dataset used in statistical analyses
Multiphasic sites are indicated by concentric circles.

Table 6 European comparative data

Group	Dating	Country	Site	n	Reference
Hunter-gatherer Eastern Eurasia HGE (14)	33,000 BP -7500 BP	Russia	Yuzhnyy Oleni Ostrov	9	DER SARKISSIAN ET AL. 2013
		Russia	Popovo	2	DER SARKISSIAN ET AL. 2013
		Russia	Chekalinol	1	BRAMANTI ET AL. 2009
		Russia	Lebyazhinka	1	BRAMANTI ET AL. 2009
		Russia	Kostenki	1	KRAUSE ET AL. 2010b
Hunter-gatherer Central Europe HGC (24)	26640±110 BP – 4000 cal BC	Germany	Bad Dürrenberg	1	BRAMANTI ET AL. 2009
		Germany	Hohlenstein-Stadel	2	BRAMANTI ET AL. 2009
		Germany	Hohler Fels	1	BRAMANTI ET AL. 2009
		Germany	Oberkassel	1	FU ET AL. 2013
		Germany	Blätterhöhle	4	BOLLONGINO ET AL.2013
		Luxembourg	Loschbour	1	FU ET AL. 2013
		Czech Republic	Dolní Věstonice	3	FU ET AL. 2013
		Lithuania	Donkalis	1	BRAMANTI ET AL. 2009
		Lithuania	Kretuonas	2	BRAMANTI ET AL. 2009
		Lithuania	Spiginas	1	BRAMANTI ET AL. 2009
		Sweden	Motala	7	LAZARIDIS ET AL. 2013
Linear pottery culture LBK (109)	5500-4775 cal BC	Austria	Asparn Schletz 2	1	HAAK ET AL. 2005
		Germany	Flomborn	6	HAAK ET AL. 2005
		Germany	Eilsleben	1	HAAK ET AL. 2005
		Germany	Derenburg, Meerenstieg II	22	HAAK ET AL. 2005
		Germany	Halberstadt, Sonntagsfeld	31	HAAK ET AL. 2005
		Germany	Karsdorf	23	BRANDT ET AL. 2013
		Germany	Naumburg	4	BRANDT ET AL. 2013
		Germany	Oberwiederstedt I, Untewiederstedt	8	HAAK ET AL. 2005
		Germany	Schwetzingen	4	HAAK ET AL. 2005
		Germany	Vaihingen	1	HAAK ET AL. 2005
		Germany	Seehausen	1	HAAK ET AL. 2005
		Germany	Stuttgart	1	LAZARIDIS ET AL. 2013
		Czech Republic	Vedrovice	6	BRAMANTI 2008
Rössen culture RSC (11)	4625-4250 cal BC	Germany	Esperstedt	1	BRANDT ET AL. 2013
		Germany	Halberstadt, Sonntagsfeld	1	BRANDT ET AL. 2013
		Germany	Oberwiederstedt III, Schrammhoehe	8	BRANDT ET AL. 2013
		Germany	Oberwiederstedt IV, Arschkerbe Ost	1	BRANDT ET AL. 2013
Schöningen group SCG (33)	4100-3950 cal BC	Germany	Salzmünde, Schiebig	33	BRANDT ET AL. 2013
Baalberge culture BAC (19)	3950-3400 cal BC	Germany	Halle-Queis	1	BRANDT ET AL. 2013
		Germany	Karsdorf	2	BRANDT ET AL. 2013
		Germany	Esperstedt	1	BRANDT ET AL. 2013
		Germany	Quedlinburg VII 2	8	BRANDT ET AL. 2013
		Germany	Quedlinburg IX	6	BRANDT ET AL. 2013
		Germany	Salzmünde, Schiebig	1	BRANDT ET AL. 2013

7 Statistical Methods

Group	Dating	Country	Site	n	Reference
Salzmünde culture SALZ (29)	3400-3100/3025 cal BC	Germany	Salzmünde, Schiebig	29	BRANDT ET AL. 2013
Bernburg culture BEC (17)	3100-2650 cal BC	Germany	Benzingerode I	17	BRANDT ET AL. 2013
Cord Ware culture CWC (44)	2800-2200/2050 cal BC	Germany	Benzingerode, Heimbürg	1	BRANDT ET AL. 2013
		Germany	Esperstedt	12	BRANDT ET AL. 2013
		Germany	Eulau	12	HAAK ET AL. 2008
		Germany	Karsdorf	13	BRANDT ET AL. 2013
		Germany	Oberwiederstedt II	4	BRANDT ET AL. 2013
		Germany	Quedlinburg VII 2	1	BRANDT ET AL. 2013
		Germany	Quedlinburg XII	1	BRANDT ET AL. 2013
Bell Beaker Central Europe BBC (35)	2500-2200/2050 cal BC	Germany	Alberstedt	2	BRANDT ET AL. 2013
		Germany	Benzingerode, Heimbürg	6	BRANDT ET AL. 2013
		Germany	Eulau	3	BRANDT ET AL. 2013
		Germany	Karsdorf	3	BRANDT ET AL. 2013
		Germany	Quedlinburg VII 2	7	BRANDT ET AL. 2013
		Germany	Quedlinburg XII	3	BRANDT ET AL. 2013
		Germany	Rothenschirnbach	5	BRANDT ET AL. 2013
Unetice culture UC (94)	2200-1550 cal BC	Germany	Kromsdorf	6	LEE ET AL. 2012
		Germany	Alberstedt	1	BRANDT ET AL. 2013
		Germany	Benzingerode, Heimbürg	9	BRANDT ET AL. 2013
		Germany	Esperstedt	11	BRANDT ET AL. 2013
		Germany	Eulau	19	BRANDT ET AL. 2013
		Germany	Karsdorf	12	BRANDT ET AL. 2013
		Germany	Leau 2	3	BRANDT ET AL. 2013
		Germany	Plötzkau 3	8	BRANDT ET AL. 2013
		Germany	Profen	1	BRANDT ET AL. 2013
		Germany	Quedlinburg VII 2	14	BRANDT ET AL. 2013
		Germany	Quedlinburg VIII	6	BRANDT ET AL. 2013
		Germany	Quedlinburg XIV	1	BRANDT ET AL. 2013
		Germany	Röcken 2	9	BRANDT ET AL. 2013
Funnel Beaker culture FBC (10)	3200-2950 cal BC	Germany	Ostorf	7	BRAMANTI ET AL. 2009
		Sweden	Frälsögården	3	MALMSTRÖM ET AL. 2009
Pitted Ware culture PWC (19)	3300-2150 cal BC	Sweden	Ajvide	11	MALMSTRÖM ET AL. 2009
		Sweden	Fridtorp	4	MALMSTRÖM ET AL. 2009
		Sweden	Ire	4	MALMSTRÖM ET AL. 2009
Blätterhöhle BLA (16)	3922-3020 cal BC	Germany	Blätterhöhle	16	BOLONGINO ET AL. 2013
Treilles TRE (29)	3000 BC	France	Treilles	29	LACAN ET AL. 2011A

7.1.3 Dataset for analyses focusing on haplogroup H

For analyses only including individuals of haplogroup H, it was necessary to re-arrange the dataset. The small sample size of individuals of hg H did not allow division of the Iberian data into geographical units or into separate Bell Beaker and non-Bell Beaker groups. Consequently, chronological resolution had to be limited to the periods of the Late Neolithic, Chalcolithic, and Bronze Age. On the other hand, data from sites that could not be used in other analyses due to small sample sizes such as the site of Perdigões (CHANDLER 2003) were included into the analyses.

Finding ancient DNA data in the literature, where individuals of haplogroup H have been similarly or better defined into sub-haplogroups than in this study, proved to be difficult. In most cases only H5, which can be recognized by HVR I sequencing alone, was defined. An exception is the study of BROTHERTON ET AL. (2013) who conducted whole-mitochondrial genome sequencing on 34 Early Neolithic to Bronze Age individuals of Central Europe belonging to haplogroup H. To avoid overrepresentation of H5 and of H1 and H3 for which additional markers have been analyzed in some studies (e.g. BOLLONGINO ET AL. 2013), further data were only taken from sites where haplogroup H sub-haplogroup information was available for all individuals.

Altogether, the dataset for hg H analyses was based on available data divided into the following groups.

- Late Neolithic of the Iberian Peninsula (NEOI)
- Chalcolithic of the Iberian Peninsula (CHI)
- Bronze Age of the Iberian Peninsula (BAI)
- Neolithic/Chalcolithic France (TRE)
- Early Neolithic Hungary (ENH): Körös and Alföld Linear pottery culture
- Early Neolithic Central Europe (ENC): Linear pottery culture, Schöningen group, and Rössen culture
- Middle Neolithic Central Europe (MNC): Baalberge and Salzmünde culture
- Bell Beaker Central Europe (BBC)
- Early Bronze Age Central Europe (UC): Unetice culture
- Early Iron Age (La Tène culture) from Austria (LTA)
- Early Iron Age (La Tène culture) East Europe (LTE)
- Early Iron Age (La Tène culture) from France (LTF)
- Early Iron Age (La Tène culture) from Switzerland (LTS)

Table 7 Dataset used in statistical analyses focusing on haplogroup H

Group	Country	Site	n	Reference
NEOI	Spain	La Mina	2	THIS STUDY
	Spain	Reinoso	1	THIS STUDY
	Spain	La Taryuela	4	THIS STUDY
	Spain	Els Trocs	1	THIS STUDY
CHI	Portugal	Bolores	1	THIS STUDY
	Spain	Cova del Barranc del Migdia	1	THIS STUDY
	Spain	Valle de las Higueras	1	THIS STUDY
	Portugal	Hipogeu de Monte Canelas I	3	THIS STUDY
	Portugal	Tholos de Pai Mogo I	2	THIS STUDY
	Portugal	Perdigões	4	CHANDLER 2003
	Spain	Barranc d'en Rifà	1	THIS STUDY
	Spain	Camino de Molino	5	THIS STUDY
	Spain	Cova del Cantal	3	THIS STUDY
	Spain	Humanejos	4	THIS STUDY
	Spain	Cova d'en Pardo	2	THIS STUDY
	Spain	Arroyal	1	THIS STUDY
	Spain	Camino de Yeseras	3	THIS STUDY
BAI	Spain	Castillo de Lorca	1	THIS STUDY
	Spain	Can Gambús	3	THIS STUDY
	Spain	La Bastida	1	THIS STUDY
	Spain	Humanejos	1	THIS STUDY
	Spain	Los Tintores	1	THIS STUDY
TRE	France	Treilles	6	LACAN ET AL.2011
ENH	Hungary	Berettyóújfalu-Nagy-Bócs dűlő	1	KEERL UNPUBLISHED
	Hungary	Hódmezővásárhely Kotacpart	1	KEERL UNPUBLISHED
	Hungary	Törökszentmiklós Tiszapüspöki Karanycs háromág 3. lh.	1	KEERL UNPUBLISHED
	Hungary	Füzesabony-Gubakút	2	KEERL UNPUBLISHED
	Hungary	Mezőkövesd-Mocsolyas	6	KEERL UNPUBLISHED
	Hungary	Pusztataksony Ledence 1	2	KEERL UNPUBLISHED
	Hungary	Abony 60.lh	1	KEERL UNPUBLISHED
	Hungary	Deszk -I. olajkút	1	KEERL UNPUBLISHED
	Hungary	Tiszaöldvár Téglagyár	1	KEERL UNPUBLISHED
	Hungary	Adács-Mancsos-rét	2	KEERL UNPUBLISHED
	Hungary	Cegléd 4/1	2	KEERL UNPUBLISHED
	Hungary	Tiszadob-Okenéz	3	KEERL UNPUBLISHED
	Hungary	Mezőzombor-Községi temető	1	KEERL UNPUBLISHED
	Hungary	Garadna- Elkerülő 2.lh	1	KEERL UNPUBLISHED
	Hungary	Debrecen Tócsópart Erdőalja	3	KEERL UNPUBLISHED
	Hungary	Berettyóújfalu-Nagy-Bócs dűlő	1	KEERL UNPUBLISHED
	Hungary	Mezőkeresztes-Cethalom	3	KEERL UNPUBLISHED
	Hungary	Tiszabura Bónishát	2	KEERL UNPUBLISHED
	Hungary	Tiszaszőlős-Domaháza	1	KEERL UNPUBLISHED
ENC	Germany	Derenburg	2	BROTHERTON ET AL.2013

Group	Country	Site	n	Reference
	Germany	Halberstadt	4	BROTHERTON ET AL.2013
	Germany	Karsdorf	3	BROTHERTON ET AL.2013
	Germany	Oberwiederstedt III, Schrammhoehe	4	BROTHERTON ET AL.2013
	Germany	Salzmünde	2	BROTHERTON ET AL.2013
	Czech Country	Vedrovice	1	BRAMANTI ET AL.2008
MNC	Germany	Esperstedt	1	BROTHERTON ET AL.2013
	Germany	Halle, Quais	1	BROTHERTON ET AL.2013
	Germany	Salzmünde, Schiebzig	7	BRANDT ET AL.2013
BBC	Germany	Alberstedt	1	BROTHERTON ET AL.2013
	Germany	Benzingerode, Heimbürg	1	BROTHERTON ET AL.2013
	Germany	Quedlinburg VII 2	2	BROTHERTON ET AL.2013
	Germany	Quedlinburg XII	3	BROTHERTON ET AL.2013
	Germany	Rothenschirnbach	3	BROTHERTON ET AL.2013
UC	Germany	Benzingerode, Heimbürg	3	BROTHERTON ET AL.2013
	Germany	Eulau	2	BROTHERTON ET AL.2013
	Germany	Quedlinburg VIII	1	BROTHERTON ET AL.2013
LTA	Austria	Oberndorf	2	WARNBERG UNPUBLISHED
	Austria	Ossarn	4	WARNBERG UNPUBLISHED
	Austria	Pottenbrunn	3	WARNBERG UNPUBLISHED
LTE	Romania	Aradu Nou	1	WARNBERG UNPUBLISHED
	Romania	Fantanele La Gata	2	WARNBERG UNPUBLISHED
	Hungary	Tiszavasvari	5	WARNBERG UNPUBLISHED
LTF	France	Bobigny	18	WARNBERG UNPUBLISHED
LTS	Switzerland	Basel Gasfabrik A	9	WARNBERG UNPUBLISHED
	Switzerland	Mont Mornont	10	WARNBERG UNPUBLISHED

7.2 Principal Component Analysis (PCA)

Categorical PCA was performed using the *prcomp* function of the package *stats* in R (VERSION 2.15.0, R DEVELOPMENT CORE TEAM 2012) and visualized by plotting the first and second principal component in a two-dimensional space. According to which haplogroups could be observed and distinguished in the particular datasets, the ancient Iberian dataset was subdivided into 18 haplogroups (H, HV, I, J, K, L1b, N*, N1a, T2, U, U2, U3, U4, U5a, U5b, V, W, X), while the dataset including all European data was classified into 24 haplogroups (C, H, H5, HV, I, J, K, L1b, N*, N1a, R, T1, T2, U, U2, U3, U4, U5, U5a, U5b, U8, V, W, X). Haplogroup frequencies for all groups are listed in appendix table V (p.229). For the analyses of haplogroup H variation, data were divided into 13 different hgs according to the resolution obtainable by the H-multiplex used in this study plus hg H5: H1, H2, H3, H4, H5, H7, H10, H11, H13, H14, H16, H23, and H (all individuals that do not belong into one of the previously mentioned sub-haplogroups). (Sub-) haplogroup frequencies for analyzes on haplogroup H are given in table 24 (p.111).

7.3 Cluster analysis

Cluster analyses were conducted according to Ward's hierarchical clustering method (WARD JR 1963) using Manhattan distances with the *hclust* function of the *stats* package in R (version 2.15.0, R DEVELOPMENT CORE TEAM 2012). The significance of each cluster was evaluated by 10,000 bootstrap replicates using the *pvclust* function of the package *pvclust* (SUZUKI AND SHIMODAIRA 2011).

7.4 Fisher Test

To test for significant differences in haplogroup composition among different groups, several Fisher-tests were conducted using the function *fisher.test* of the *stats* package in R (version 2.15.0, R DEVELOPMENT CORE TEAM 2012) and 10,000 bootstrap repeats.

7.5 Test of population continuity (TPC)

The test shows whether genetic differences between two groups of different chronology can be adequately explained by genetic drift alone or whether a discontinuity has to be assumed (BRANDT ET AL. 2013). A model of genetic drift is defined *a priori* based on the presumed number of generations separating the two populations and the effective population size. The fit of the model to the observed data is then evaluated with the Markov-Chain-Monte-Carlo method resulting in a p-value which depicts the probability of obtaining the observed data if the assumed model of drift was true. As in the Fisher-test, absolute haplogroup frequencies were used. The populations were tested against each other in pairs. The prior on the drift parameter was set for each population pair based on a presumed generation time of 20 years, an effective population size (N_e) of 10,000 individuals and the terminal dates of the groups (These dates are estimated dates based on archaeology and the chronological resolution used in this study).

The test was run in R using the packages *MCMCpack* for the MCMC simulation of the posterior distribution (MARTIN ET AL. 2011) and *mvtnorm* for the analysis of multivariate normal and t distributions (GENZ ET AL. 2014). The Markov Chain was run for 50 000 iterations with a burn-in of 2000 iterations (BRANDT ET AL 2013). The script for the TPC is available online at <https://github.com/joepickrell/tpc>.

Table 8 Terminal dates of the different epochs used for the TPC

Chronology	Terminal date
Western hunter-gatherers	5,500 BC
Early Neolithic	4,500 BC
Late Neolithic	3,000 BC
Chalcolithic	2,200 BC
Bronze Age	1,500 BC

7.6 F_{ST} values

Genetic distances were computed based on HVR I sequences (nucleotide positions 16051-16399) and were calculated in Arlequin (3.5.1, EXCOFFIER AND LISCHER 2010) using the Tamura & Nei substitution model (TAMURA AND NEI 1993) and a gamma value calculated for the particular dataset by jModelTest (version 0.1.1, GUINDON AND GASCUEL 2003; POSADA 2008). Because identical HVR I sequences can belong to different haplogroups the analyses were repeated with haplogroup specific SNPs. Therefore the results of the SNP profiles of the GenoCoRe22 multiplex assay were added to the HVR I sequences. In case of published data, for which these SNP profiles were not available, they were generated based on the haplogroup classification presented in the original publication. F_{ST} values were independently computed for both the original dataset and the dataset that included additional hg information

7.7 Multidimensional Scaling (MDS)

Genetic distances based on Slatkin's linearized F_{ST} values (SLATKIN 1995) that were calculated in Arlequin (EXCOFFIER AND LISCHER 2010) were reduced to two dimensions by nonmetric MDS using the *metaMDS* function of the package *vegan* (OKSANEN ET AL. 2013) in R (version 2.15.0, R DEVELOPMENT CORE TEAM 2012).

7.8 Shared haplotype analyses (SHA)

Shared haplotype analyses were used to track shared lineages between groups of interest. On the one hand, shared lineages between all groups of one period and all groups of the succeeding period were calculated (e.g. shared lineages of all Late Neolithic groups with all Early Neolithic groups). In this approach all individuals of one group were regarded, irrespective of different or identical HVR I haplotypes. This allowed revealing the number of individuals who had a putative mitochondrial predecessor in previous groups. For the second kind of SHAs that focused on shared lineages among contemporaneous groups, the dataset

of each group was reduced by identical lineages to just reveal the amount of lineages per se that are shared. For all comparisons focusing on hunter-gatherer to Late Neolithic datasets, rCRS lineages of haplogroup H were regarded as equal no matter the sub-haplogroup. For all individuals belonging to Late Neolithic groups of the Northern Meseta and the Ambrona Valley sub-haplogroup information of hg H was available, as well as for the Chalcolithic dataset that completely consisted of data generated in this study. Therefore, in SHAs with between these Late Neolithic groups and Chalcolithic groups as well as shared lineages among Chalcolithic groups (fig. 19a and b), only sequence hits that were also congruent on sub-haplogroup level (H1 or H3) were considered.

7.9 Analyses of Molecular Variance (AMOVA)

AMOVA (EXCOFFIER ET AL. 1992) were conducted in Arlequin (version 3.5.1.3, EXCOFFIER AND LISCHER 2010) to analyze the genetic composition of the Iberian dataset. After calculating a gamma value with jmodel Test (version 0.1.1, GUINDON AND GASCUEL 2003; POSADA 2008)), different models (repeated re-arrangements of groups into different clusters) were tested against each other. On the one hand, this was conducted using the western hunter-gatherer and all Spanish and Portuguese Early and Late Neolithic groups and on the other hand with all Chalcolithic Bell Beaker and non-Bell Beaker groups.

8 Results of molecular genetic analyses

8.1 Amplification success

All in all, reproduced HVR I results were obtained for 187 out of 344 analyzed individuals (54.4%). For five of these individuals (MIV2, MCIII2, Cast1, Gam1, Gam2) additional cloning would have been necessary⁴ (see table 10). Three of them (Cast1, Gam1, Gam2) could only potentially be assigned to a rCRS haplotype, because the amount of DNA damage displayed in the sequences was too severe for reliable haplotype assignment without cloning. Nonetheless their haplotypes were reproduced by two samples in several PCRs, thus they were considered as successfully amplified, although they were not used in population genetic analyses. Successful haplogroup determination by the GenoCoRe22 and/or one of the ExtraCoRes was possible for 72.4% out of all analyzed individuals (249 in total). For two of them (Dia1 and Tar2, both hg T), only GenoCoRe22 results but neither HVR I data nor data from the T-plex could be obtained. Because all other individuals were assignable to either sub-haplogroup T1 or T2, Dia1 and Tar2 were not considered for population genetic analyses.

For every major region of the Iberian Peninsula investigated in this study (Southern Meseta, Northern Meseta, Ebro Valley, Northeast Spain, East Spain, Southern Iberian Peninsula, and Central Portugal) the proportion of successfully typed individuals by the GenoCoRe22 and by HVR I amplification was calculated (see fig. 12). All regions were represented by at least two sites to overcome bias induced by other factors that may have influenced sample preservation. The best amplification success in both approaches was achieved in the northern regions of the Iberian Peninsula: Ambrona Valley, Northern Meseta, and Northeast Spain with values of 87–100% successful haplogroup assignment and 71–100% successful HVR sequencing. A considerably lower amplification success was obtained for samples from Central Portugal and the Southern Meseta: Between 71% and 76% samples gave reproducible haplogroup results but only 33–53% of them authentic HVR I profiles. The poorest results were achieved for samples from East Spain and particularly the southern part of the Iberian Peninsula with 29.5–58.5% GenoCoRe22 results and only 3.0–42.7% reproduced HVR I data.

⁴ Because from September 2013 onwards the ancient DNA facilities of the working group were closed by the University, it was not possible to finish the cloning of these individuals.

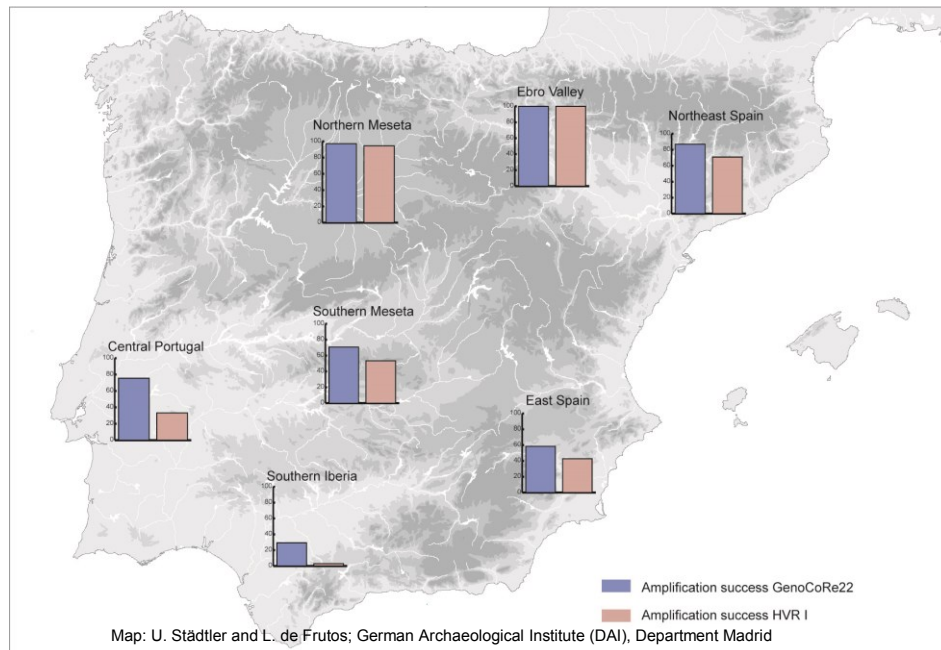


Figure 12 Amplification success in the different regions of the Iberian Peninsula

It has been discussed that due to the degradation of ancient DNA, amplification success depends on the length of the amplified fragment (PÄÄBO ET AL. 2004; COOPER AND POINAR 2001). Therefore, amplification success was estimated for all primer pairs (see fig. 13). In general, the amplification success of HVR I primer ranked between 61.8% and 72.6%, with only three primer pairs having a lower amplification success of 49.2% to 56.7% (16045–16240, 16209–16348, and 16307–16402.C). The GenoCoRe22 had a similar amplification success as the HVR I primer, while the ExtraCoRes each had an amplification success rate of more than 80% (88.2–92.1%). No relation between amplicon length of a particular primer pair and amplification success has been detected.

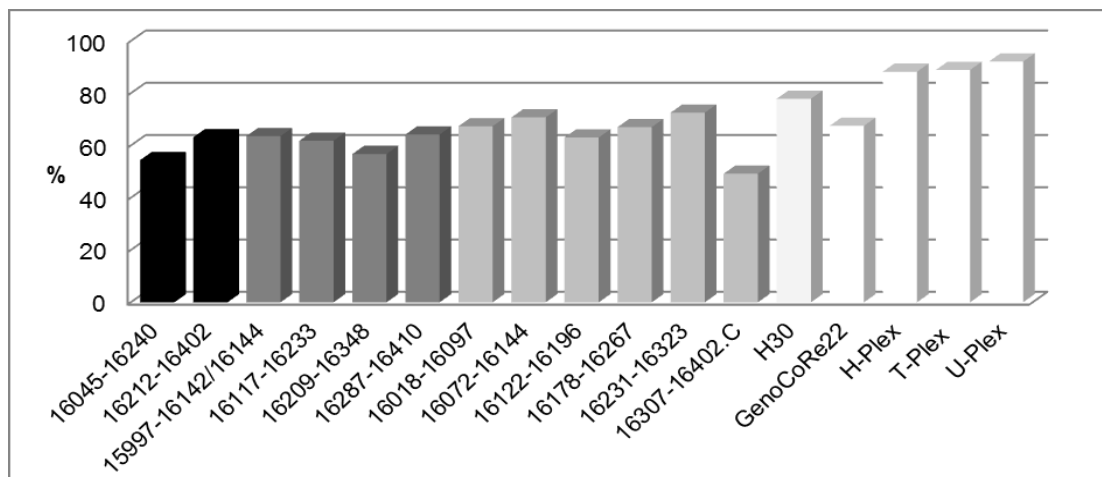


Figure 13 Amplification success of the different primer-systems

HVR I primer pairs of the 2-primer-system are depicted in black, of the 4-primer-system in dark gray, and of the 6-primer-system in light gray bars. Fragment-lengths: 16045-16240>16212-12402>15996-16142>16209-16348>16298-16410=16117-16233>16307-16402.C>16018-16097=16232-16323>16178-16267>16122-16196>16072-16144

8.2 Contamination

The HVR I haplotypes of all persons involved in sampling of individuals or involved in any work conducted in the pre-PCR laboratory were sequenced to track putative contaminating influence by researchers during one of the analyzing steps. The haplotype of the principal researcher (1) who participated in all analyses was found in none of the samples or blanks. Researchers 2 and 3 were mainly involved in sample preparation and participated in two extractions each and in a few PCRs. Their haplotypes coincided with a few samples (see table 9). Additionally, one extraction blank matched the haplotype of the researcher 3 in one HVR I fragment. Researcher 4 was involved in sample preparation and his haplotype was not detected in any sample or milling blank. Researchers 5 was not involved in any lab work, but in sampling during or after excavation.

Table 9 Haplotype matches of researchers to analyzed samples

	HVR I haplotype	HVR II haplotype	Samples handled during				
			Sampling	Photo	Sandblasting	Milling	Extraction
1	16223T 16257T 16292T	73G 143A 189G 194T 195C 204C 207A 263G 309.1C 315.1C	-	-	-	-	-
2	16069T 16126C	-	Troc1a Troc1b	Malga2a Malga2b	-	Malga2a, Malga2b Rinc2b, Troc1a Vald4a, Vald4b Mina10a, Mina10b	
3	rCRS	-		Rein28a Rein28b	Rein28a Rein28b	Rein28a, Rein28b	R141.5 Extraction blank RD.12
4	16311C	-	-	-	-	-	-
5	16051G 16162G 16259T	73G 263G 315.1C	-	-	-	-	-

Altogether, 51 of 2376 (2.15%) blank controls (non-template controls) were contaminated, whereas not a single contamination could be detected in any of the multiplex PCRs (GenoCoRe22, ExtraCoRes). Only blank controls that produced sequences were considered; if sequencing failed twice, controls were regarded as false-positive signals on the gel. Out of the 51 contaminated blanks, 0.96% (17 out of 1764) were PCR blanks (PCRLK), 6.4% (20 out of 311) hydroxyapatite blanks (HAK), and 4.7% (14 out of 301) extraction blanks (EXLK) (14 out of 301). However, in two PCRs (R368 and R416) the HAK showed the same contamination as one of the PCR blank controls – a transition at np 16298. This contamination occurred in several PCRs at that time and was only detected in one particular primer pair (16287–16410), and therefore probably can be explained by contamination during PCR. Four HAKs (RC.7, RN.17, RX.19, and SH.19) and two EXLK (RD.12, RO.14) were

contaminated in more than one PCR, in three of them the same haplotype was reproduced by two independent PCRs: 16126C-16223T in HAK RX.19, 16294T in EXLK RD.12, and (16239T)-16256T-16270T-16294T in RC.7. However, these particular haplotypes were not observed in any sample of the same extraction or PCR.

Furthermore, it was investigated if and to which degree contaminated non-template controls matched haplotypes of samples analyzed in the same PCR or, in case of extraction or HAK blanks, in the same PCR and the same extraction (see table 10). Sample haplotypes coincided with non-template controls in 23 PCRs, but exclusively in the common haplotypes rCRS, 16298C, and (16069T-) 16126C. Contaminating influence on parallel-amplified or extracted samples can be excluded for all other PCRs. A contaminating lineage detected in a sample only matched an identical contamination found in one or more blank controls of the same PCR or extraction in six PCRS. Three belonged to PCRs where the contamination 16298C was found in more than one blank. In two samples the contaminating lineage matched a lineage found in an associated extraction blank (marked in red in table 10).

Subsequently, the rate of contaminated PCRs was estimated for all individuals that were considered as reproduced: 52 out of 2670 (1.9%) successfully amplified PCR products had contaminations in several clones or in direct sequencing, a contamination similar to that of the blank controls. Fourteen individuals that were successfully amplified in two extractions had to be excluded due to multiple or reproducible contaminations (3.7%).

Table 10 Haplotype matches between blanks and parallel analyzed samples

Samples with PCR contamination that matched the haplotype of the associated blank are marked in red. In all other samples the haplotype of the blank matches the authenticated haplotype of the individual.

Date of PCR	PCR	Type of blank	Extraction	Primer pair	Haplotype	Date of Extraction	Putative PCR influence	Putative extraction influence
08.02.2010	R27.10	EXLK	RD.12	16117-16233	16126C	13.01.2010	Rein18a Rein19a	-
03.03.2010	R43.5	EXLK	RF.12	16209-16348	-	23.02.2010	-	Rein6b Rein9b Rein23b
16.02.2011	R128.10	PCRLK		16178-16267	-		Mop3a CRV1 Mop3b	-
04.04.2011	R141.5	EXLK	RD.12	16287-16410	-	13.01.2010	-	Ba16-1b
29.07.2011	R166.12	HAK	RJ.11	15997-16142	-	20.07.2011	Mina1a Mina4a Mina7a Mina9a Rein28a	Mina1a Mina4a Mina7a Mina9a
28.09.2011	R202.11	HAK	RM.11	16117-16233	-	29.09.2011	-	Rodi1a Bar2b Bar3b

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Date of PCR	PCR	Type of blank	Extraction	Primer pair	Haplotype	Date of Extraction	Putative PCR influence	Putative extraction influence
14.12.2011	R228.4	HAK	RN.17	16018-16097	16126C	07.11.2011	-	Bar2a(2)
04.01.2012	R240.10	HAK	RQ.10	16287-16410	-		-	Troc1a
18.01.2012	R248.13	HAK	RR.17	16117-16233	-	10.01.2012	Fupe1a	-
18.01.2012	R248.14	EXLK	RR.18	16117-16233	16126C	10.01.2012	Troc1a	-
24.01.2012	R251.9	HAK	RN.17	16018-16097	-	07.11.2011	Hume3a	Fupe1a Fupe4a Fupe5a
01.02.2012	R260.12	PCRLK		16117-16233	-		Vald3a	-
14.04.2012	R308.7	HAK	RX.19	16287-16409	-		-	Cmol123a Cmol139a Cmol140a Cmol154a Cmol165a
18.05.2012	R319.20	EXLK	RZ.20	16117-16233	-		-	GSL3a Junc4a
11.06.2012	R346.16	EXLK	SA.20	16287-16410	-	10.05.2012	-	CDV2b Pai11b
03.07.2012	R356.9	HAK	SF.19	16287-16410	-	05.06.2012	Yese4b	Yese3b Yese4b Pai18b
09.07.2012	R361.19	HAK	SH.19	16287-16410	-	15.06.2012	Malga2a	Cel 1a Cel3a Fala2b Malga2a
25.07.2012	R368.24	HAK	SJ.19	16287-16410	16298C	10.07.2012	Mina16a Cmol16a Yese1a	-
26.07.2012	R368.26	PCRLK		16287-16410	16298C		Mina16a Cmol16a Yese1a	-
27.08.2012	R388.21	PCRLK		16018-16097	-		Vald3b Turq2b CDV1a Junc5a Junc6a Yese7b Cel3a	-
27.08.2012	R391.20	PCRLK		16117-16233	-		Coca2b Junc 12a	-
16.10.2012	R416.21	HAK	SH.19	16287-16410	16298C	15.06.2012	Bar3a Bar3b Junc1a Coca2a Malga1b	Fala1b
16.10.2012	R416.35	PCRLK		16287-16410	16298C		Bar3a Bar3b Junc1a Coca2a Malga1b	-
23.10.2012	R426.17	HAK	SV.19	16209-16348	-		Troc6b2 Roy3b Roy3a	Troc6b2 Rinc2a Roy3b
25.02.2013	R452.35	HAK	SA.19	15996-16142	16069T 16126C		Hume5a Tar9c	-
09.04.2013	R470.5	PCRLK		16287-16410	16298C		Tar7b	-
09.04.2013	R470.51	PCRLK		16287-16410	16298C		Tar7b	-

Furthermore it was investigated if there was a correlation between amplicon length of a primer pair and the amount of contamination. The highest contamination rates were found in primer pairs 16212–16402 (6.6%) and 16287–16410 (6.2%), no contaminated blanks were detected when the primer pairs 16045–16240 and 16307–16402.C were used. Contamination rates were distributed randomly among the different primer-systems and no correlation to amplicon length could be detected.

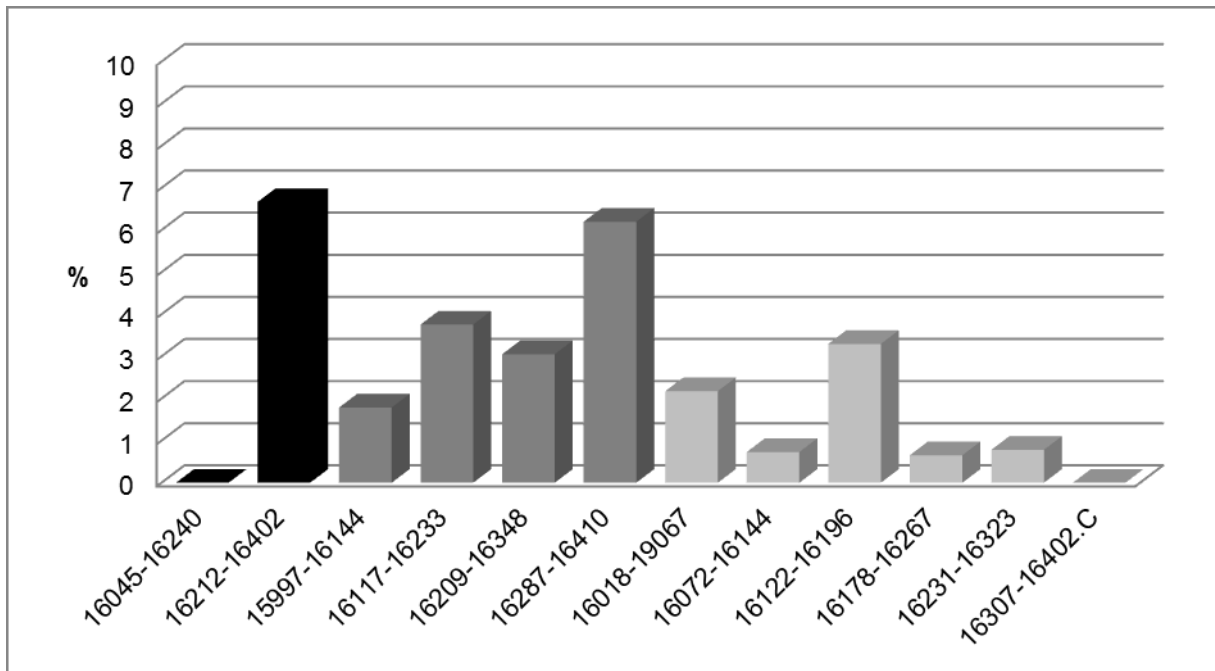


Figure 14 Contamination rates of the primer pairs

HVR I primer pairs of the 2-primer-system are depicted in black, of the 4-primer-system in dark gray, and of the 6-primer-system in light gray bars. Fragment lengths of the different primer pairs from large to small: 16045-16240>16212-12402>15996-16142>16209-16348>16298-16410=16117-16233>16307-16402.C>16018-16097=16232-16323>16178-16267>16122-16196>16072-16144

8.3 Authenticated individuals

Successfully analyzed samples belonged to the following 16 (sub-) haplogroups: H, H1, H3, HV, J, K, L1, N1a, T2, U2, U3, U4, U5a, U5b, V, and X. Haplogroup N1a was only present in one individual of the Early Neolithic dataset, U2 only in one individual dating to the Late Neolithic, and L1b in exclusively in one Bell Beaker individual, while U5a was detected in several individuals; however, exclusively in individuals with Bell Beaker chronology. The most frequent haplogroups in the dataset were K (27%), U5b (15%), J (13%), H1 (13%), and T2 (7%). All other haplogroups were present in less than 5% of the individuals (see fig. 15). No signs of haplogroups H8, I, N*, and W, reported in other studies of Mesolithic to Bronze

Age samples of the Iberian Peninsula, were found in the dataset. Moreover, haplogroups T1 and H5, reported from Early Neolithic samples from the Carpathian Basin (KEERL UNPUBLISHED) and Late Neolithic/Bronze Age samples from Central Germany (BRANDT ET AL. 2013, IN PRESS) appear to be absent so far in the Neolithic to Bronze Age of the Iberian Peninsula. The following table 12 shows all individuals with reproducible results either for HVR I and coding region multiplex assays or at least reproducible haplogroup determination by the latter. Authentication criteria are discussed in chapter 10.3.

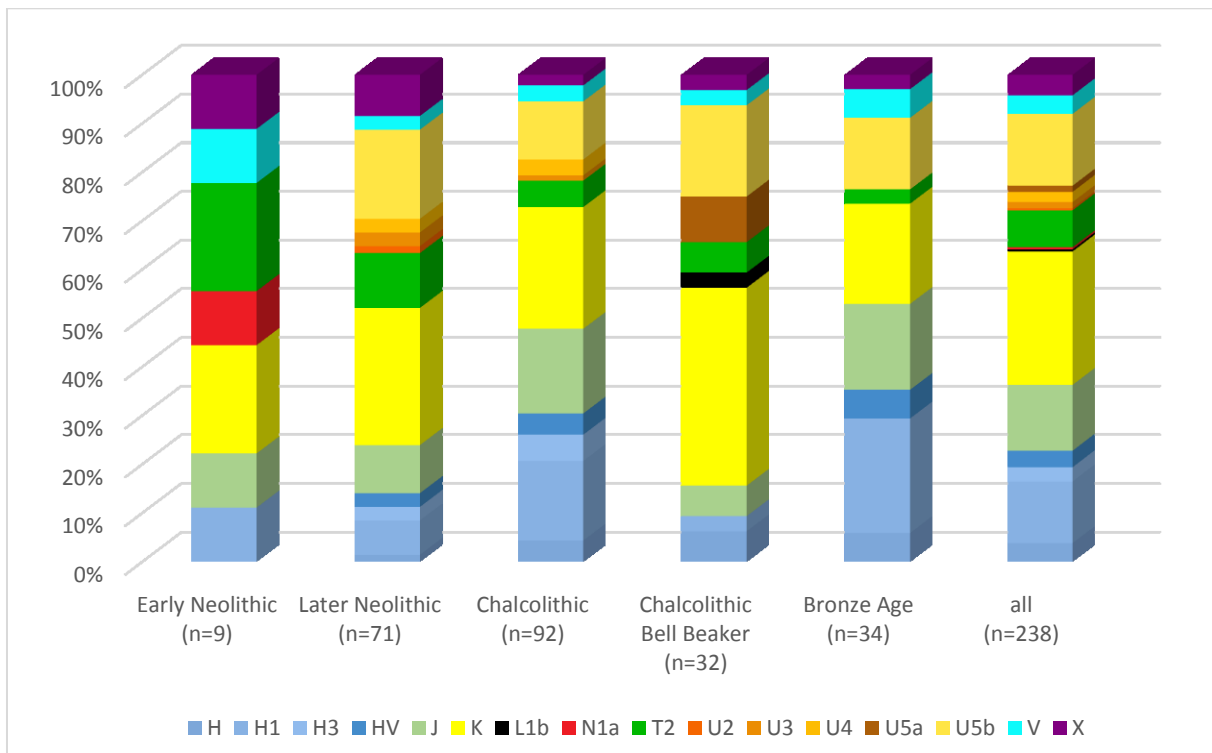


Figure 15 Chronological transect of haplogroup frequencies

Following sites/individuals (see tables 11 and 12) were not used in statistical analyses, either because they could not confidently be assigned to one of the groups, because chronological information was not available or because sample size was too small to form a group: Balma de Sargantana, Els Forat de ses Aritges, Gruta do Poço Velho, Molinos de Papel, Senhorío de Guzman, Gruta do Carvalho de Turquel, Valdescusa, Cobre las Cruces, Gruta de Malgasta, Cova de la Ventosa, Els Trocs (Trocs2, 6, 8), Fuente Celada (Cel1, 2), Nossa Senhora de las Lapas (GSL2, 3), Humanejos (Hume24).

Table 11 Successfully analyzed individuals per site

n_1 gives the number of analyzed individuals, n_2 the number of individuals with successfully reproduced GenoCoRe22 result, and n_3 the number of individuals with successfully amplified HVR I sequences.

Site	Lab name	n_1	n_2	n_3	Site	Lab name	n_1	n_2	n_3
Alto de Rodilla	Rodi	1	1	1	Gruta de Malgasta	Malga	2	2	1
Arroyal I	Roy	5	5	5	Gruta do Carvalho de Turquel	Turq	2	2	2
Balma de Sargantana	BAS	5	2	0	Gruta do Poço Velho	Pove	2	2	1
Barranc d'en Rifá	BAR	15	15	15	Gruta dos Ossos	Gro	5	4	0
Bolores	Bol	5	1	0	Humanejos	Hume	26	15	8
Cabezo Pardo	Cab	2	0	0	Hypogeu de Monte Canelas I	Moca	8	5	0
Cadaval	CDV	3	3	2	Hypogeu de Monte Canelas III	MCIII	2	1	1
Camino de Molino	CMOL	18	18	18	Ifri N' ammar o Moussa	Iam	1	0	0
Camino de las Yeseras	Yese	14	12	9	Illeta dels Banyets	Ban	7	1	0
Can Gambús	GAM	8	8	4	La Bastida	Ba/Laba	13	2	1
Castillo de Lorca	Cast	1	1	1	La Huera	Hue	3	0	0
Cobre las Cruces	Cru	4	2	0	La Mina	Mina	13	13	13
Concheiro da Moita do Sebastião	Seba	3	1	0	La Tarayuela	Tar	11	10	9
Concheiro do Cabeço da Arruda	Arru	2	0	0	Los Tintores	Tint	2	1	0
Cova d'en Pardo	Par	8	6	6	Madre Mercedarias Iglesias	MMI	3	1	0
Cova de la Ventosa	Vent	1	1	1	Miquel Vives	MIV	2	1	1
Cova del Barranc del Migdia	Dia	7	2	0	Molinos del Papel	MOP	3	3	1
Cova del Cantal	Coca	5	5	5	Nossa Senhora das Lapas	GSL	3	3	2
El Castillejo	Elca	2	0	0	Nuevo IES Valencina ROD 05-32	Cine	4	0	0
El Hundido	Hund	2	2	2	Poroad de Alcalar	Alca	2	0	0
El Juncal	Junc	14	14	14	Reinoso	Rein	27	27	26
Els Trocs	Troc	10	10	10	Rincón de Moncada	Rinc	2	2	2
Es Forat de ses Aritges	Fora	5	4	0	Senorio de Guzman	Guz	4	3	0
Fuente Álamo	Fala	5	3	1	Tabayá	Tab	4	1	0
Fuente Celada	Cel	3	3	3	Tholos de Pai Mogo I	Pai	16	13	6
Fuente Pecina 1	Fupe	4	4	4	Valdescusa	Vald	5	5	5
Fuente Pecina 2	Fupe	5	4	4	Valencina- calle Dinamarca 3-5	Din	8	0	0
Fuente Pecina 4	Fupe	2	2	2	Valle de las Higueras	Hig	2	1	0
Gruta das Alcobertas	Alco	2	2	1	Zapateria	Zapa	1	0	0

Table 12 Results of control and coding region SNPs for authenticated individuals

Individuals that could not be fully reproduced by cloning and were therefore not used in statistical analyses are denoted with a hash. Individuals for which sequences were only reproduced up to np 16322 are denoted with a “1” behind the haplotype. Individuals of haplogroup T which could not be resolved into sub-clades are indicated by bold letters. Samples for which the H-plex revealed no derived marker are denoted as “H-plex ancestral”. Unsuccessfully analyzed markers are denoted as “n.d.” (no data). For further information on how many PCRs were conducted on each individuals as well as on results for all markers of the multiplex PCRs see appendix tables III and IV (pp.197-229).

Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
Alto de Rodilla	Rodi1	rCRS			H	H1	H1
Arroyal I	Roy1	16093C 16224C 16311C			K		K
Arroyal I	Roy2	16270T			U	U5b	U5b
Arroyal I	Roy3	16188T			H	H-plex ancestral	H
Arroyal I	Roy4	16224C 16311C			K		K
Arroyal I	Roy5	16093C 16224C 16311C			K		K
Balma de Sargantana	Bas3	n.d.			K		K
Balma de Sargantana	Bas5	n.d.			K		K
Barranc d'en Rifa	Bar1	16126C 16294T 16304C			T	T2	T2b
Barranc d'en Rifa	Bar2	16343G 16390A			U	U3	U3a
Barranc d'en Rifa	Bar3	16298C			HV		HV0
Barranc d'en Rifa	Bar4	16093C 16224C 16311C			K		K
Barranc d'en Rifa	Bar5	16069T 16126C			J		J
Barranc d'en Rifa	Bar6	16298C			HV		HV0
Barranc d'en Rifa	Bar7	16224C 16311C			K		K
Barranc d'en Rifa	Bar8	16069T 16126C 16193T 16278T			J		J2b1a
Barranc d'en Rifa	Bar9	16189C 16270T			U	U5b	U5b
Barranc d'en Rifa	Bar10	16126C 16153A 16294T 16296T			T	T2	T2e
Barranc d'en Rifa	Bar11	16069T 16126C			J		J
Barranc d'en Rifa	Bar12	16093C 16224C 16311C			K		K
Barranc d'en Rifa	Bar13	rCRS			H	H-plex ancestral	H
Barranc d'en Rifa	Bar14	16069t 16126C 16193T 16278T			J		J2b1a

⁵ Given is only the common minimal authenticated sequence range for all individuals. Specific sequence ranges for each individual are given in appendix III.

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Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
Barranc d'en Rifa	Bar15	16093C 16224C 16311C			K		K
Bolores	Bol5	n.d.			H	H1	H1
Cadaval	CDV1	16224C 16311C			K		K
Cadaval	CDV2	16069C 16126T			J		J
Cadaval	CDV3	n.d.			K		K
Camino de Molino	Cmol6	16069T 16126C 16145A 16231C 16261T			J		J2a1a
Camino de Molino	Cmol16	16093C 16224C 16311C			K		K
Camino de Molino	Cmol12	rCRS			H	H3	H3
Camino de Molino	Cmol44	16222T			H	H1	H1
Camino de Molino	Cmol71	16069T 16126C			J		J
Camino de Molino	Cmol79	16298C			V		V
Camino de Molino	Cmol104	16298C			V		V
Camino de Molino	Cmol105	rCRS			H	H-plex ancestral	H
Camino de Molino	Cmol119	16093C 16224C 16311C			K		K
Camino de Molino	Cmol122	16189C 16223T 16278T			X		X
Camino de Molino	Cmol123	rCRS			H	H1	H1
Camino de Molino	Cmol138	16189T 16270T 16291T			U	U5b	U5b
Camino de Molino	Cmol139	rCRS			H	H1	H1
Camino de Molino	Cmol140	16192T			U	U5b	U5b2a1a
Camino de Molino	Cmol151	16356C			U	U4	U4
Camino de Molino	Cmol154	16069T 16126C 16193T 16278T			J		J2b1a
Camino de Molino	Cmol164	16224C 16291T 16311C			K		K
Camino de Molino	Cmol165	16069T 16126C			J		J
Camino de las Yeseras	Yese1	16126C 16187T 16189C 16223T 16264T 16270T 16278T 16293G 16311C			L		L1b
Camino de las Yeseras	Yese2	16086C 16189C 16270T 16311C			U	U5b	U5b
Camino de las Yeseras	Yese3	rCRS			H	H1	H1
Camino de las Yeseras	Yese4	16069T 16126C			J		J
Camino de las Yeseras	Yese5	ambiguous			J		J
Camino de las Yeseras	Yese6	ambiguous			U	U5b	U5b
Camino de las Yeseras	Yese7	16224C 16311C			K		K
Camino de las Yeseras	Yese8	rCRS			H	H1	H1
Camino de las Yeseras	Yese9	n.d.			J		J

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Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
Camino de las Yeseras	Yese10	16192T 16270T			U	U5b	U5b
Camino de las Yeseras	Yese12	16167T 16192T 16270T 16311C 16356C			U	U5b	U5b1i
Camino de las Yeseras	Yese13	rCRS			H	H1	H1
Can Gambús	Gam1	rCRS [#]			H	H1	H1
Can Gambús	Gam2	rCRS [#]			H	H1	H1
Can Gambús	Gam3	16093C 16224C 16311C			K		K
Can Gambús	Gam4	unfinished [#]			U	U5b	U5b
Can Gambús	Gam5	ambiguous			H	H-plex ancestral	H
Can Gambús	Gam6	ambiguous			X		X
Can Gambús	Gam7	ambiguous			U	U5b	U5b
Can Gambús	Gam8	16093C 16224C 16311C			K		K
Castillo de Lorca	Cast1	rCRS [#]			H	H1	H1
Cobre las Cruces	Cru1	n.d.			K		K
Cobre las Cruces	Cru4	n.d.			K		K
Concheiro da Moita do Sebastião	Seba1	n.d.			U	U5b	U5b
Cova d'en Pardo	Par1	16224C 16311C			K		K
Cova d'en Pardo	Par2	16093C			H	H-plex ancestral	H
Cova d'en Pardo	Par3	16192T 16270T			U	U5b	U5b
Cova d'en Pardo	Par4	16093C 16224C 16234T 16311C			K		K1a1a1a
Cova d'en Pardo	Par5	16093C 16224C 16311C			K		K
Cova d'en Pardo	Par7	16319A			H	H1	H1
Cova de la Ventosa	Vent1	16075C 16189C 16223T 16278T 16390A [#]			X		X
Cova del Barranc del Migdia	Dia1	n.d.			T		T
Cova del Barranc del Migdia	Dia3	n.d.			H	H1	H1
Cova del Cantal	Coca1	16356C			U	U4	U4
Cova del Cantal	Coca2	16266T 16298C			HV		HV0
Cova del Cantal	Coca3	rCRS			H	H3	H3
Cova del Cantal	Coca4	16311C			H	H-plex ancestral	H
Cova del Cantal	Coca5	rCRS			H	H1	H1
El Hundido	Hund1	16192T 16256T 16270T 16291T 16399G			U	U5a	U5a1b1
El Hundido	Hund2	16224C 16311C 16362C			K		K

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Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
El Juncal	Junc1	16093C 16224C 16311C			K		K
El Juncal	Junc2	16227G 16256T 16270T 16320T 16399G			U	U5a	U5a1
El Juncal	Junc3	16224C 16311C 16319A			K		K
El Juncal	Junc4	16093C 16224C 16311C 16319A			K		K
El Juncal	Junc5	16093C 16224C 16311C			K		K
El Juncal	Junc6	16126C 16153A 16294T 16296T			T	T2	T2e
El Juncal	Junc7	16069T 16126C			J		J
El Juncal	Junc8	16192T 16270T 16304C			U	U5b	U5b3
El Juncal	Junc9	16192T 16270T 16304C			U	U5b	U5b3
El Juncal	Junc10	16069T 16126C			J		J
El Juncal	Junc11	16093C 16224C 16311C			K		K
El Juncal	Junc12	16298C			V		V
El Juncal	Junc13	16192T 16256T 16270T 16320T 16399G			U	U5a	U5a1c
El Juncal	Junc14	16192T 16270T 16304C			U	n.d.	U5b3
Els Forat de ses Aritges	Fora1	n.d.			H	H1	H1
Els Forat de ses Aritges	Fora2	n.d.			J		J
Els Forat de ses Aritges	Fora3	n.d.			K		K
Els Forat de ses Aritges	Fora4	n.d.			H	H1	H1
Els Trocs	Troc1	16069T 16126C			J		J
Els Trocs	Troc2	16069T 16126C			J		K
Els Trocs	Troc3	16126C 16292t 16294T			T	T2	T2
Els Trocs	Troc4	16224C 16311C			K		K
Els Trocs	Troc5	16147a 16172C 16223T 16248T 16355T			N		N1a
Els Trocs	Troc6	16343G 16390A			U	U3	U3a
Els Trocs	Troc7	16298C			V		V
Els Trocs	Troc8	16185T 16189C			H	H1	H1
Els Trocs	Troc10	16224C 16311C			K		K
Els Trocs	Troc12	16126C 16292t 16294T			T	T2	T2
Fuente Álamo	Fala1	ambiguous			V		V
Fuente Álamo	Fala2	16069T 16126C			J		J
Fuente Álamo	Fala5	n.d.			U	U5b	U5b
Fuente Celada	Cel1	16189C 16223T 16278T			X		X

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Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
Fuente Celada	Cel2	16224C 16311C			K		K
Fuente Celada	Cel3	16189C 16223T 16278T 16287T			X		X
Fuentepecina 1	Fupe6	16192T 16270T 16304C			U	U5b	U5b3
Fuentepecina 1	Fupe7	16093C 16224C 16311C 16319A			K		K
Fuentepecina 1	Fupe8	16126C 16292T 16294T			T	T2	T2
Fuentepecina 1	Fupe9	16069T 16126C 16193T 16278T			J		J
Fuentepecina 2	Fupe1	16189C 16223T 16278T			X		X
Fuentepecina 2	Fupe3	16093C 16224C 16311C			K		K
Fuentepecina 2	Fupe4	16189C 16223T 16278T			X		X
Fuentepecina 2	Fupe5	16189C 16192T 16270T 16311C			U	U5b	U5b1
Fuentepecina 4	Fupe10	16126C 16292T 16294T			T	T2	T2
Fuentepecina 4	Fupe11	16298C			HV		HV0
Gruta das Alcobertas	Alco1	16093C 16224C 16311C			K		K
Gruta das Alcobertas	Alco2	n.d.			U	U4	U4
Gruta de Malgasta	Malga1	ambiguous			J		J
Gruta de Malgasta	Malga2	16069T 16126C			J		J
Gruta do Carvalho de Turquel	Turq1	16093C 16224C 16311C			K		K
Gruta do Carvalho de Turquel	Turq2	16224C 16311C			K		K
Gruta do Poço Velho	Pove1	ambiguous			T	T2	T2
Gruta do Poço Velho	Pove2	16126C 16292T 16294T 16304C ¹			T	T2	T2b
Gruta dos Ossos	Gro2	n.d.			K		K
Gruta dos Ossos	Gro3	n.d.			U	U5b	U5b
Gruta dos Ossos	Gro4	n.d.			K		K
Gruta dos Ossos	Gro5	n.d.			T	T2	T2
Hypogeu de Monte Canelas I	Moca1	n.d.			H	H1	H1
Hypogeu de Monte Canelas I	Moca2	n.d.			HV		HV
Hypogeu de Monte Canelas I	Moca3	n.d.			H	H1	H1
Hypogeu de Monte Canelas I	Moca4	n.d.			H	H1	H1
Hypogeu de Monte Canelas I	Moca7	n.d.			K		K
Hypogeu de Monte Canelas III	MCIII2	16069T 16126C ^{#1}			J		J
Humanejos	Hume1	16192T 16270T 16304C			U	U5b	U5b3

8 Results of molecular genetic analyses

Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
Humanejos	Hume2	rCRS			H	H1	H1
Humanejos	Hume3	16126C 16294T 16296T 16304C			T	T2	T2b
Humanejos	Hume4	n.d.			J		J
Humanejos	Hume5	16126C 16294T 16296T 16304C			T	T2	T2b
Humanejos	Hume8	16180G			H	H3	H3
Humanejos	Hume10	ambiguous			U	U5b	U5b
Humanejos	Hume11	n.d.			K		K
Humanejos	Hume14	n.d.			K		K
Humanejos	Hume15	ambiguous			K		K
Humanejos	Hume18	n.d.			K		K
Humanejos	Hume19	16189C			H	H1	H1
Humanejos	Hume21	rCRS			H	H-plex ancestral	H
Humanejos	Hume24	16222T			H	H1	H1
Humanejos	Hume25	n.d.			J		J
Illeta dels Banyets	Ban2	n.d.			H	n.d.	H
La Bastida	Ba12-1	ambiguous			K		K
La Bastida	Ba6-1	rCRS			n.a.	H1	H1
La Mina	Mina1	16343G 16390A			U	U3	U3a
La Mina	Mina2	16069T 16126C 16145A 16231C 16261T 16274A			J		J2a1a
La Mina	Mina3	16093C 16224C 16301T 16311C			K		K
La Mina	Mina4	rCRS	263G 315.1C	34- 397	H	H1	H1
La Mina	Mina5	16051G 16129C 16189C 16362C			U	U2	U2e
La Mina	Mina6	16093C 16224C 16311C 16319A			K		K
La Mina	Mina7	16189C 16223T 16278T			X		X
La Mina	Mina9	16189C 16270T 16311C			U	U5b	U5b2a5
La Mina	Mina10	16069T 16126C			J		J
La Mina	Mina14	16167T 16192T 16209C 16270T 16399G			U	U5b	U5b
La Mina	Mina16	16298C			HV		HV0
La Mina	Mina17	rCRS	251A 263G 315.1C	34- 397	H	H3	H3an
La Mina	Mina18	16167T 16192T 16209C 16270T 16399G			U	U5b	U5b
La Tarayuela	Tar2	n.d.			T	ambiguou s	T
La Tarayuela	Tar3	16093C 16224C 16311C			K		K

8 Results of molecular genetic analyses

Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
La Tarayuela	Tar4	16189C			H	H1	H1
La Tarayuela	Tar5	16295T			H	H1	H1
La Tarayuela	Tar6	rCRS			H	H-plex ancestral	H
La Tarayuela	Tar7	rCRS			H	H1	H1
La Tarayuela	Tar8	16093C 16224C 16311C			K		K
La Tarayuela	Tar9	16069T 16126C			J		J
La Tarayuela	Tar10	16126C 16291T 16294T 16296T 16304C 16311C			T	T2	T2
La Tarayuela	Tar11	16093C 16224C 16311C			K		K
Los Tintores	Tint1	n.d.			H	H1	H1
Madre Mercedarias Iglesias	MMI3	n.d.			T	T2	T2
Miquel Vives	Miv2	16167T 16192T 16270T 16311C 16356C [#]			U	U5b	U5b1i
Molinos de Papel	Mop1	n.d.			K		K
Molinos de Papel	Mop2	16298C			V		V
Molinos de Papel	Mop3	n.d.			HV		HV
Nossa Senhora das Lapas	GSL1	ambiguous			K		K
Nossa Senhora das Lapas	GSL2	16126C 16294T 16296T 16304C			T	T2	T2
Nossa Senhora das Lapas	GSL3	16069T 16126C			J		J
Reinoso	Rein1	16224C 16270T	73G 150T 263G 310C	49- 394	U	U5b	U5b3
Reinoso	Rein2	16224C 16270T	73G 150T 263G	49- 302	U	U5b	U5b3
Reinoso	Rein3	16192T 16270T 16304C			U	U5b	U5b3
Reinoso	Rein4	16224C 16270T	73G 150T 263G 309.1C 309.2C 315.1C	44- 321	U	U5b	U5b2b3
Reinoso	Rein5	16126C 16294T 16296T 16304C	73G 263G 309.1C 309.2C 315.1C	59- 324	T	T2	T2b
Reinoso	Rein6	rCRS			V		V
Reinoso	Rein8	16224C 16311C	73G 150T 263G 315.1C	45- 397	K		K
Reinoso	Rein9	rCRS			V		V
Reinoso	Rein10	ambiguous			K		K
Reinoso	Rein11	16093C 16224C 16311C	73G 114T 263G 315.1C	46- 397	K		K

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Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
Reinoso	Rein12	16224C 16311C	73G 195C 263G 315.1C	34- 327	K		K
Reinoso	Rein13	16183C 16189C 16223T 16278T			X		X
Reinoso	Rein14	16093C 16224C 16311C	73G 195C 263G 315.1C	44- 397	K		K1a1
Reinoso	Rein15	16224C 16270T	73G 150T 263G 310C	46- 397	U	U5b	U5b2b3
Reinoso	Rein16	16093C 16186T 16189C 16223T 16278T			X		X
Reinoso	Rein17	16093C 16224C 16311C	73G 114T 263G 315.1C	72- 397	K		K
Reinoso	Rein18	16126C 16294T 16296T 16304C			T	T2	T2b
Reinoso	Rein19	16126C 16294T 16296T 16304C			T	T2	T2b
Reinoso	Rein22	16270T			U	U5b	U5b
Reinoso	Rein23	16356C			U	U4	U4
Reinoso	Rein24	16093C 16224C 16311C	263G 315.1C	144- 397	K		K
Reinoso	Rein28	rCRS			H	H3	H3
Reinoso	Rein29	16069T 16126C 16176T 16311C			J		J1c
Reinoso	Rein30	16126C 16294T 16296T 16324C			T	T2	T2a1b
Reinoso	Rein31	16270T			U	U5b	U5b
Reinoso	Rein32	16224C 16311C	73G 195C 263G 315.1C	34- 397	K		K1a
Reinoso	Rein33	16189C 16223T 16278T			X		X
Rincón de Moncada	Rinc1	16093C 16224c 16311C 16319A			K		K
Rincón de Moncada	Rinc2	16069T 16126C			J		J
Senorio de Guzman	Guz1	n.d.			K		K
Senorio de Guzman	Guz2	n.d.			T	T2	T2
Senorio de Guzman	Guz4	n.d.			U	U4	U4
Tabayá	Tab2	n.d.			J		J
Tholos de Pai Mogo I	Pai1	16221T 16224C 16311C			K		K
Tholos de Pai Mogo I	Pai3	16093C 16224C 1311C			K		K
Tholos de Pai Mogo I	Pai6	n.d.			H	H3	H3
Tholos de Pai Mogo I	Pai7	n.d.			U	U5b	U5b
Tholos de Pai Mogo I	Pai11	16093C 16224C 16311C			K		K
Tholos de Pai Mogo I	Pai12	16093C 16224C 16311C			K		K
Tholos de Pai Mogo I	Pai13	n.d.			V		V

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Site	Labname	HVR I np 16048-16401 ⁵	HVR II	Seque nce range HVR II	Geno CoRe22	Extra- CoRes	Hg according to Phylotree (vs. 15, VAN OVEN AND KAYSER 2009)
Tholos de Pai Mogo I	Pai15	n.d.			H	H3	H3
Tholos de Pai Mogo I	Pai16	n.d.			U	U5b	U5b
Tholos de Pai Mogo I	Pai18	16189C 16192T 16270T			U	U5b	U5b
Tholos de Pai Mogo I	Pai19	16093C 16224C 16311C			K		K
Tholos de Pai Mogo I	Pai21	n.d.			T	T2	T2
Tholos de Pai Mogo I	Pai22	n.d.			J		J
Valdescusa	Vald1	16189C 16192T 16270T 16274A 16293G 16362C			U	U5b	U5b
Valdescusa	Vald2	16069T 16126C 16193T 16278T			J		J2b1a
Valdescusa	Vald3	16298C			HV		HV0
Valdescusa	Vald4	16069T 16126C			J		J
Valdescusa	Vald5	16069T 16126C 16193T 16278T 16290T			J		J2b1a
Valle de las Higueras	Hig2	n.d.			H	H1	H1

9 Results of population genetic analyses

9.1 Ancient Iberian groups

9.1.1 PCA

The first and second principal components (PCs) account for about 32% of the overall variability of the dataset (see fig. 16). The Late Neolithic of Northeast Spain (NEN) is separated from all other groups along the 2nd PC. The 1st PC mainly separates Els Trocs from the hunter-gatherers (HGW), Early Neolithic of Northern Spain (NSE) and Central Portugal (CPE), and Late Neolithic of the Ebro Valley (EVN). Late Neolithic groups of the Ambrona Valley (AVN), Northern Meseta (NMN), and Central Portugal (CPN) are located closer to Early Neolithic from Northeast Spain (NEE), while samples of the Ebro Valley (EVN) are close to the Early Neolithic of Northern Spain (NSE) and Central Portugal (CPE). The Chalcolithic samples are separated from each other as well; the groups from the Southern Meseta (SMC), Southern Iberian Peninsula (SIC), and East Spain (ESC) form a tight block in the right lower quadrant, while Chalcolithic groups of Central Portugal (CPC) and Northeast Spain (NEC) are located closer to Late Neolithic samples of Portugal and the Northern Meseta on the left side of the plot. The two Bronze Age groups of Northeast (NEB) and East Spain (ESBA) are situated in the middle of the plot close to some Chalcolithic samples.

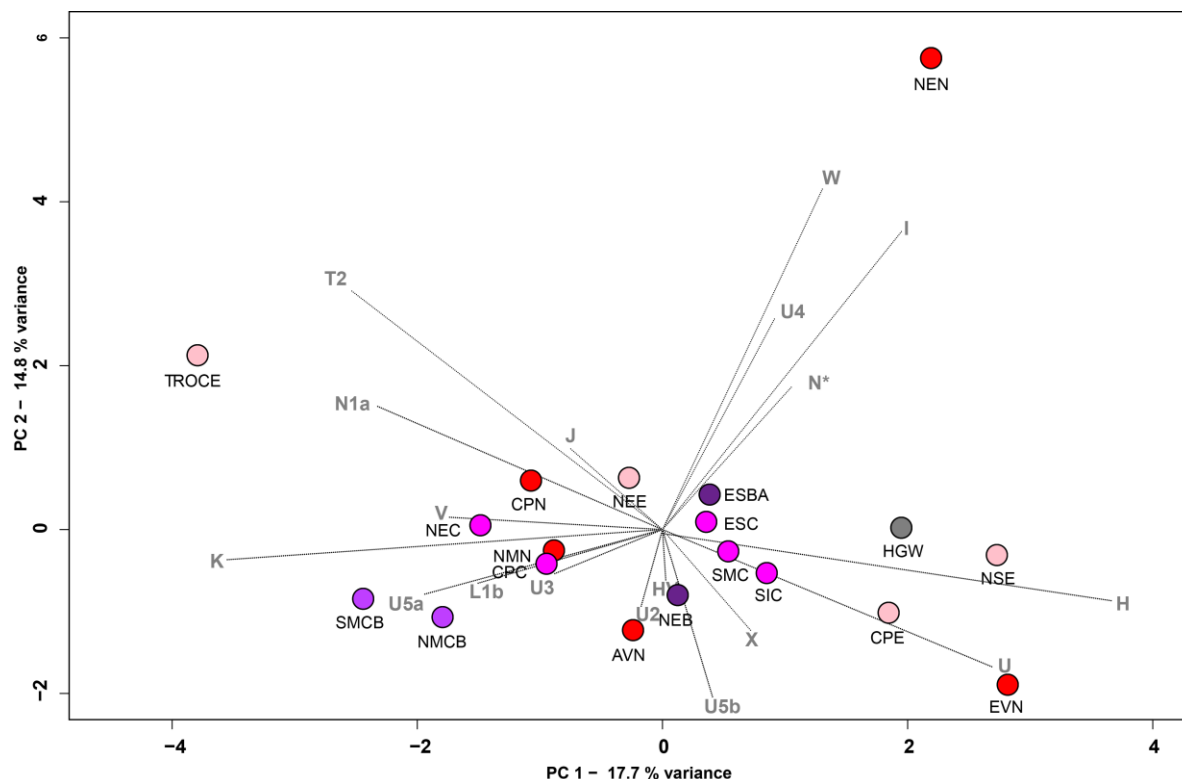


Figure 16 PCA of the Iberian dataset

Western European hunter-gatherers are symbolized by gray circles, Early Neolithic groups by pink circles, Late Neolithic groups by magenta colored circles, Bell Beaker groups are colored purple, and Bronze Age groups dark purple.

9.1.2 Cluster analysis

The cluster analysis (see fig. 17) reveals a separation of the dataset in two greater clusters: The first main cluster is further subdivided into two clusters: Bell Beaker associated groups (SMCB and NMCB) and the Portuguese Chalcolithic (CPC) and Late Neolithic (CPN) are clustered together on the one hand and the Early Neolithic groups of Northeast Spain (NEE) and Els Trocs (TROCE) together with the Late Neolithic of the Northern Meseta (NMN) and the Chalcolithic of Northeast Spain (NEC) on the other hand (see fig. 17). In the second major cluster, hunter-gatherers (HGW), the Early Neolithic of Northern Spain (NSE) and Late Neolithic of the Ebro Valley (EVN) as well as the early samples of Portugal (CPE) are separated from the rest. All other populations fall into several sub-clusters that show no pattern according to chronology or region. It should be mentioned that bootstrap values are significant (>95%) for only two clusters (CPE and NSE as well as AVN and ESC).

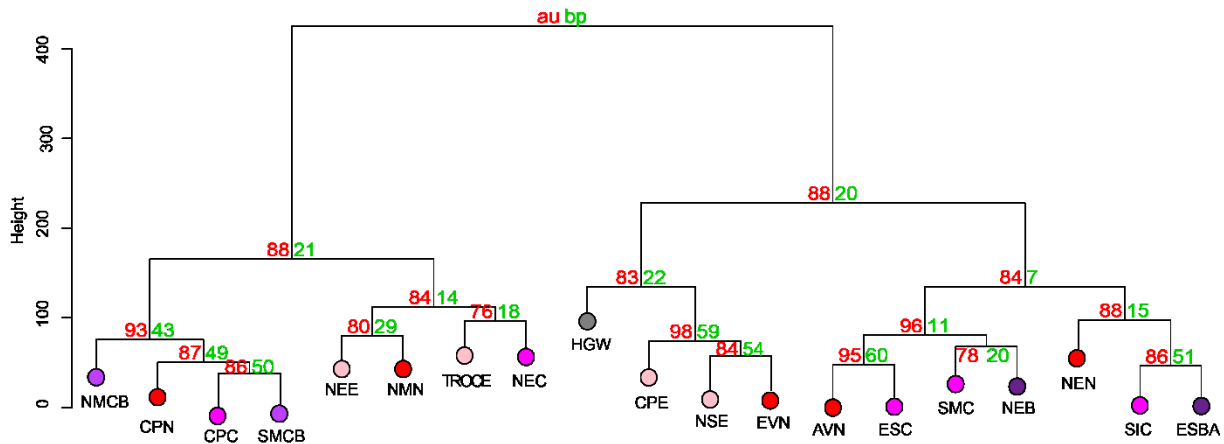


Figure 17 Cluster analysis of the Iberian dataset

Western European hunter-gatherers are symbolized by gray circles, Early Neolithic groups by pink circles, Late Neolithic groups by magenta colored circles, Bell Beaker groups are colored purple, and Bronze Age groups dark purple. “au” gives the approximately unbiased p-value and “bp” the bootstrap probability value.

9.1.3 Fisher-test

Table 13 gives the results of the Fisher-test. The hunter-gatherers show significant differences to all groups except for two Neolithic and two Chalcolithic groups: The Early Neolithic of Central Portugal (CPE) and the Late Neolithic of the Ebro Valley (EVN) as well as to the Chalcolithic of the Southern Iberian Peninsula (SIC) and the Southern Meseta (SMC). In the Early Neolithic, no significant differences exist between Northern Spain (NSE) and Central Portugal (CPE) on the one hand and Els Trocs and Northeast Spain (NEE) on the other hand. Among the Late Neolithic groups only few significant differences are observable, with the exception of the Northern Meseta (NMN) group that is significantly

different to the majority of the dataset. The Late Neolithic of the Ambrona Valley (AVN), Chalcolithic data from the Southern Iberian Peninsula (SIC), and the Bronze Age group from Northeast Spain (NEB) on the other hand have no significant differences to most investigated groups. Furthermore, no significant differences among the Chalcolithic non-Bell Beaker groups are recognizable. On a regional scale, no significant differences among the groups of Northeast Spain can be observed and none between the Early Neolithic of Northern Spain and the Late Neolithic of the Ebro Valley (EVN). In Portugal, however, significant differences of the Early Neolithic group to the Late Neolithic and Chalcolithic group of the same region are evident. Also significantly different to each other are Bell Beaker (SMCB) and non-Bell Beaker groups (SMC) of the Southern Meseta.

Table 13 Results of the Fisher-test with all Iberian data

Groups are displayed in chronological order. Significant differences ($p \leq 0.05$) are bold and underlined.

	HGW	NEE	TROCE	NSE	CPE	NEN	AVN	EVN	NMN	CPN	NEC	ESC	SIC	SMC	CPC	NMCB	SMCB	ESBA	NEB
HGW	*	<u>0.020</u>	<u>0.000</u>	<u>0.005</u>	0.106	<u>0.028</u>	<u>0.035</u>	0.091	<u>0.000</u>	<u>0.009</u>	<u>0.000</u>	<u>0.014</u>	0.063	0.061	<u>0.018</u>	<u>0.010</u>	<u>0.001</u>	<u>0.018</u>	<u>0.032</u>
NEE	<u>0.020</u>	*	0.457	<u>0.006</u>	<u>0.028</u>	0.413	0.501	<u>0.027</u>	0.256	0.842	0.223	0.062	0.379	<u>0.018</u>	0.613	0.732	0.254	0.261	0.203
TROCE	<u>0.000</u>	0.457	*	<u>0.002</u>	<u>0.005</u>	0.451	0.181	<u>0.002</u>	0.281	0.647	0.620	<u>0.032</u>	0.271	<u>0.008</u>	0.268	0.326	0.352	0.184	0.224
NSE	<u>0.005</u>	<u>0.006</u>	<u>0.002</u>	*	0.770	<u>0.049</u>	<u>0.054</u>	0.816	<u>0.000</u>	<u>0.009</u>	<u>0.001</u>	<u>0.032</u>	0.545	<u>0.021</u>	<u>0.006</u>	<u>0.025</u>	<u>0.000</u>	0.352	<u>0.043</u>
CPE	0.106	<u>0.028</u>	<u>0.005</u>	0.770	*	0.244	0.207	0.702	<u>0.000</u>	<u>0.031</u>	<u>0.003</u>	0.272	0.465	0.188	<u>0.050</u>	<u>0.013</u>	<u>0.002</u>	0.321	0.148
NEN	<u>0.028</u>	0.413	0.451	<u>0.049</u>	0.244	*	0.381	0.054	<u>0.002</u>	0.444	0.235	0.137	0.930	0.224	0.181	0.160	<u>0.007</u>	1.000	0.226
AVN	<u>0.035</u>	0.501	0.181	<u>0.054</u>	0.207	0.381	*	0.111	<u>0.048</u>	0.800	0.669	0.802	0.924	0.598	0.907	0.678	0.191	0.894	0.939
EVN	0.091	<u>0.027</u>	<u>0.002</u>	0.816	0.702	0.054	0.111	*	<u>0.000</u>	<u>0.017</u>	<u>0.002</u>	<u>0.034</u>	0.197	<u>0.053</u>	<u>0.022</u>	<u>0.025</u>	<u>0.000</u>	0.098	0.163
NMN	<u>0.000</u>	0.256	0.281	<u>0.000</u>	<u>0.000</u>	<u>0.002</u>	<u>0.048</u>	<u>0.000</u>	*	0.210	0.095	<u>0.001</u>	<u>0.011</u>	<u>0.002</u>	0.403	0.295	0.359	<u>0.008</u>	0.083
CPN	<u>0.009</u>	0.842	0.647	<u>0.009</u>	<u>0.031</u>	0.444	0.800	<u>0.017</u>	0.210	*	0.650	0.440	0.536	0.057	0.941	1.000	0.835	0.420	0.528
NEC	<u>0.000</u>	0.223	0.620	<u>0.001</u>	<u>0.003</u>	0.235	0.669	<u>0.002</u>	0.095	0.650	*	0.084	0.592	0.063	0.347	0.351	0.267	0.370	0.414
ESC	<u>0.014</u>	0.062	<u>0.032</u>	<u>0.032</u>	0.272	0.137	0.802	<u>0.034</u>	<u>0.001</u>	0.440	0.084	*	0.894	0.362	0.556	0.316	<u>0.015</u>	0.694	0.697
SIC	0.063	0.379	0.271	0.545	0.465	0.930	0.924	0.197	<u>0.011</u>	0.536	0.592	0.894	*	0.403	0.314	0.211	0.071	1.000	0.629
SMC	0.061	<u>0.018</u>	<u>0.008</u>	<u>0.021</u>	0.188	0.224	0.598	<u>0.053</u>	<u>0.002</u>	0.057	0.063	0.362	0.403	*	0.090	<u>0.014</u>	<u>0.009</u>	0.627	0.476
CPC	<u>0.018</u>	0.613	0.268	<u>0.006</u>	<u>0.050</u>	0.181	0.907	<u>0.022</u>	0.403	0.941	0.347	0.556	0.314	0.090	*	0.891	0.874	0.269	0.638
NMCB	<u>0.010</u>	0.732	0.326	<u>0.025</u>	<u>0.013</u>	0.160	0.678	<u>0.025</u>	0.295	1.000	0.351	0.316	0.211	<u>0.014</u>	0.891	*	0.982	0.080	0.453
SMCB	<u>0.001</u>	0.254	0.352	<u>0.000</u>	<u>0.002</u>	<u>0.007</u>	0.191	<u>0.000</u>	0.359	0.835	0.267	<u>0.015</u>	0.071	<u>0.009</u>	0.874	0.982	*	<u>0.040</u>	0.235
ESBA	<u>0.018</u>	0.261	0.184	0.352	0.321	1.000	0.894	0.098	<u>0.008</u>	0.420	0.370	0.694	1.000	0.627	0.269	0.080	<u>0.040</u>	*	0.572
NEB	<u>0.032</u>	0.203	0.224	<u>0.043</u>	0.148	0.226	0.939	0.163	0.083	0.528	0.414	0.697	0.629	0.476	0.638	0.453	0.235	0.572	*

A second Fisher-test was conducted to compare all different chronological periods to each other (see table 14). The group CPC was considered separately, because its chronology is ambiguous (Bell Beaker or non-Bell Beaker). All other samples were grouped according to chronology into superordinate groups of hunter-gatherers, Early Neolithic, Late Neolithic, Chalcolithic, Bell Beaker or Bronze Age.

All periods show significant (≤ 0.05) to highly significant (≤ 0.001) differences to the hunter-gatherers, except for the Late Neolithic. The latter in fact shows no significant differences to any of the other groups. The Early Neolithic is significantly different to all periods except the Late Neolithic and the Chalcolithic group of Portugal (CPC). The Chalcolithic non-Bell Beaker groups are significantly different to hunter-gatherers and Early Neolithic groups, and to the Bell Beaker. The Bell Beaker group has highly significant genetic differences to the hunter-gatherers, the Early Neolithic, and the Chalcolithic. The Bronze Age has significant differences only to the Bell Beaker group and to the hunter-gatherers.

Table 14 Results of the Fisher-test with superordinate groups

Significant values (≤ 0.05) are bold and underlined.

	Hunter-gatherer	Early Neolithic	Late Neolithic	Chalcolithic	Chalcolithic Central Portugal	Bell Beaker	Bronze Age
Hunter-gatherer	*	<u>0.021</u>	0.075	<u>0.005</u>	0.0189	<u>0.001</u>	<u>0.0184</u>
Early Neolithic	<u>0.021</u>	*	0.072	<u>0.002</u>	0.3221	<u>0.000</u>	0.377
Late Neolithic	0.075	0.072	*	0.095	0.9645	0.1581	0.8337
Chalcolithic	<u>0.005</u>	<u>0.002</u>	0.095	*	0.4877	<u>0.001</u>	0.8455
Chalcolithic Central Portugal	<u>0.019</u>	0.3221	0.9645	0.4877	*	0.8693	0.560
Bell Beaker	<u>0.001</u>	<u>0.0002</u>	0.1581	<u>0.0012</u>	0.8693	*	<u>0.0238</u>
Bronze Age	<u>0.018</u>	0.377	0.8337	0.8455	0.5602	<u>0.0238</u>	*

9.1.4 Test of population continuity

The test of population continuity was only applied to pairs of groups for which genetic discontinuity was assumed based on other analyses (see table 15). The test shows that the differences of hunter-gatherers to Northeast Spain and Els Trocs in the Early Neolithic cannot be explained by genetic drift alone. Likewise differences of the Late Neolithic of the Northern Meseta (NMN) to the Early Neolithic of Northern Spain (NSE) and between Early and Late Neolithic in Portugal (CPE and CPN) are not a cause of genetic drift alone. The haplogroup composition of the Late Neolithic of the Ambrona Valley on the other hand could be a result of genetic drift from a source population similar to that of Northern Spain (NSE) or Northeast Spain (NEE). Observed fluctuations and differences in haplogroup composition in

Northeast Spain between Early Neolithic and Bronze Age also may have been caused by genetic drift.

Table 15 Results of the test of population continuity

Significant values ($p \leq 0.05$) are bold and underlined.

Pop1	Pop2	Time difference	generation time	N_e	prior on C	p-value
HGW	NEE	1000	20	10,000	0.005	<u>0.00628717</u>
HGW	TROCE	1000	20	10,000	0.005	<u>1.95E-05</u>
CPE	CPN	1500	20	10,000	0.0075	<u>0.03833596</u>
NSE	NMN	1500	20	10,000	0.0075	<u>0.00352758</u>
NEE	NMN	1500	20	10,000	0.0075	0.3627558
NSE	AVN	1500	20	10,000	0.0075	0.150083
NEE	AVN	1500	20	10,000	0.0075	0.4651923
NEE	NEN	1500	20	10,000	0.0075	0.35875
NEN	NEC	800	20	10,000	0.004	0.468824
NEC	NEB	700	20	10,000	0.0035	0.4538806

9.1.5 F_{ST} values

Table 16 lists the F_{ST} values among the different regional and chronological groups. The table contains two F_{ST} values for every two compared groups, the one in the upper row contains the result of the genetic distance estimation with HVR I sequences alone (gamma value 0.197), while the lower row gives the results of sequences with additional haplogroup information attached (gamma value 0.291). One can see that some values are not very different from each other whether additional haplogroup information was considered or not, while others are doubled (TROCE and EVN) or divided in halves (e.g. HGW and ESC) when the sequences contain more phylogenetic information.

For the unaltered sequences, the most significant values to other groups can be observed in the Early Neolithic of Northern Spain (NSE) and hunter-gatherers (HGW). Genetic distances between Bell Beaker (SMCB and NMCB) and Chalcolithic non-Bell Beaker groups (SMC, ESC, NEC) are high but not significant in most cases. On the other hand, F_{ST} values computed for Early Neolithic groups are in most cases significant, for examples greater genetic distance can be recognized between Els Trocs and the groups of North Spain (NSE) and Portugal (CPE), between North Spain and Portugal as well as between North Spain and Northeast Spain (NEE) (F_{ST} values between 0.07 and 0.15).

When regarding F_{ST} values of HVR I profiles with additional phylogenetic information added, some of the highest F_{ST} values can be found between the hunter-gatherers and the groups of Els Trocs, Late Neolithic of the Northern Meseta (NMN), Northeast Spain Chalcolithic (NEC), and both Bell Beaker groups (SMCB and NMCB) ($F_{ST} > 0.08$). Similarly, the Early Neolithic of

Central Portugal (CPE) has significant great genetic distances to the almost all groups of Northeast Spain (NEE, NEN, NEC), to Els Trocs, and to both Bell Beaker groups (SMCB and NMCB). Both Bell Beaker groups show significant great genetic distance (F_{ST} values between 0.07 and 0.363) to hunter-gatherers, to Early Neolithic groups of Northern Spain (NSE) and Central Portugal, Late Neolithic groups of Northeast Spain and the Ebro Valley (EVN) and the Chalcolithic of the Southern Meseta (SMC). The non-Bell Beaker Chalcolithic groups exhibit low genetic distances to each other, however, not significantly. The same trend is observable among the Late Neolithic groups with the exception of the Northern Meseta (NMN) that shows a significantly high genetic distance to the Ebro Valley Neolithic (EVN) (0.09) and a significant moderate genetic distance to the contemporaneous group of Northeast Spain (NEN) (0.063).

Table 16 F_{ST} values among the Iberian groups

The upper row gives the F_{ST} values computed with unaltered sequences, the lower row contains the results of sequences with additional hg information attached. Significant F_{ST} values ($p \leq 0.05$) are bold and underlined. p-values are displayed in appendix tables VI.1 and VI.2.

	HGW	NEE	TROC E	NSE	CPE	NEN	AVN	EVN	NMN	CPN	NEC	ESC	SMC	SMCB	NMCB
HGW	0	<u>0.074</u>	<u>0.153</u>	<u>0.159</u>	0.080	<u>0.073</u>	<u>0.058</u>	0.056	<u>0.091</u>	0.088	<u>0.143</u>	<u>0.111</u>	0.036	<u>0.069</u>	<u>0.126</u>
	0	0.059	<u>0.145</u>	<u>0.072</u>	0.075	0.050	0.029	-0.012	<u>0.115</u>	0.021	<u>0.117</u>	<u>0.056</u>	0.000	<u>0.086</u>	<u>0.142</u>
NEE	<u>0.074</u>	0	-0.002	<u>0.072</u>	0.08	-0.033	-0.012	0.063	-0.018	-0.033	0.004	0.029	0.012	0.015	0.017
	0.059	0	-0.028	<u>0.105</u>	<u>0.177</u>	-0.018	-0.014	0.059	-0.018	-0.051	-0.012	0.026	0.043	0.002	0.021
TROC E	<u>0.153</u>	-0.002	0	<u>0.128</u>	<u>0.159</u>	-0.030	0.012	<u>0.132</u>	0.010	-0.024	-0.028	0.037	0.052	0.026	0.076
	<u>0.145</u>	-0.028	0	<u>0.177</u>	<u>0.263</u>	-0.023	0.025	<u>0.141</u>	0.004	-0.015	-0.033	0.056	0.100	0.014	0.095
NSE	<u>0.159</u>	<u>0.072</u>	<u>0.128</u>	0	<u>0.09</u>	<u>0.056</u>	0.011	-0.005	<u>0.063</u>	-0.012	<u>0.070</u>	0.009	0.038	<u>0.103</u>	<u>0.171</u>
	<u>0.072</u>	<u>0.105</u>	<u>0.177</u>	0	0.019	0.047	0.029	-0.030	<u>0.156</u>	-0.009	<u>0.119</u>	0.015	-0.012	<u>0.167</u>	<u>0.224</u>
CPE	0.084	0.079	<u>0.159</u>	<u>0.086</u>	0	0.064	0.045	0.066	<u>0.099</u>	<u>0.147</u>	<u>0.108</u>	0.050	<u>0.070</u>	<u>0.107</u>	<u>0.249</u>
	0.075	<u>0.177</u>	<u>0.263</u>	0.019	0	0.089	<u>0.098</u>	0.041	<u>0.241</u>	0.133	<u>0.211</u>	0.076	0.025	<u>0.230</u>	<u>0.363</u>
NEN	<u>0.073</u>	-0.033	-0.030	<u>0.056</u>	0.064	0	-0.009	0.044	0.015	-0.025	-0.013	0.031	0.004	0.023	0.080
	0.050	-0.018	-0.023	0.047	<u>0.089</u>	0	0.008	0.019	<u>0.063</u>	-0.036	0.001	0.030	0.004	<u>0.061</u>	<u>0.122</u>
AVN	<u>0.058</u>	-0.012	0.012	0.011	0.045	-0.009	0	-0.001	-0.003	-0.066	-0.011	-0.016	-0.025	0.008	<u>0.012</u>
	0.029	-0.014	0.025	0.029	0.098	0.008	0	-0.012	0.017	-0.088	-0.015	-0.023	-0.016	0.018	0.027
EVN	0.056	0.063	<u>0.132</u>	-0.005	0.066	0.044	-0.001	0	0.035	0.045	<u>0.069</u>	0.004	-0.025	0.053	0.191
	-0.011	0.059	<u>0.141</u>	-0.030	<u>0.041</u>	0.019	-0.012	0	<u>0.090</u>	-0.021	0.080	-0.011	-0.054	<u>0.090</u>	<u>0.196</u>
NMN	<u>0.091</u>	-0.019	0.010	<u>0.063</u>	<u>0.099</u>	0.015	-0.003	0.035	0	-0.040	-0.003	0.022	-0.006	0.000	0.020
	<u>0.115</u>	-0.018	0.004	<u>0.156</u>	0.241	<u>0.063</u>	0.017	<u>0.090</u>	0	-0.012	-0.003	<u>0.058</u>	<u>0.084</u>	-0.008	0.036
CPN	0.088	-0.033	-0.024	-0.012	<u>0.147</u>	-0.025	-0.066	0.045	-0.040	0	-0.044	-0.055	-0.024	-0.043	-0.062
	0.021	-0.051	-0.015	-0.009	0.133	-0.036	-0.088	-0.021	-0.012	0	-0.051	-0.076	-0.045	-0.031	-0.042
NEC	<u>0.143</u>	0.004	-0.028	<u>0.070</u>	0.108	-0.013	-0.011	<u>0.069</u>	-0.003	-0.044	0	-0.002	0.011	0.019	0.074
	<u>0.117</u>	-0.012	-0.033	<u>0.119</u>	<u>0.211</u>	0.001	-0.015	0.080	-0.003	-0.051	0	0.008	0.050	0.007	0.077
ESC	<u>0.111</u>	0.029	0.037	0.009	0.059	0.031	-0.022	0.004	0.022	-0.055	-0.001	0	0.005	<u>0.045</u>	0.054
	0.056	0.026	0.056	0.015	0.076	0.030	-0.023	-0.012	<u>0.058</u>	-0.076	0.008	0	-0.008	<u>0.065</u>	0.080
SMC	0.036	0.012	0.052	0.038	<u>0.070</u>	0.004	-0.025	-0.025	-0.006	-0.024	0.011	0.005	0	-0.014	0.092
	0.000	0.043	0.100	-0.013	0.025	0.004	-0.016	-0.054	<u>0.084</u>	-0.045	0.050	-0.008	0	<u>0.066</u>	<u>0.157</u>

	HGW	NEE	TROC E	NSE	CPE	NEN	AVN	EVN	NMN	CPN	NEC	ESC	SMC	SMCB	NMCB
SMCB	<u>0.069</u>	0.015	0.026	<u>0.103</u>	<u>0.107</u>	0.023	0.008	0.053	0.000	-0.042	0.019	<u>0.045</u>	-0.014	0	-0.004
	<u>0.086</u>	0.002	0.014	<u>0.167</u>	<u>0.230</u>	<u>0.061</u>	0.018	<u>0.090</u>	-0.008	-0.031	0.007	<u>0.065</u>	<u>0.066</u>	0	-0.007
NMCB	<u>0.126</u>	0.017	0.076	<u>0.171</u>	<u>0.249</u>	0.080	0.012	<u>0.191</u>	0.020	-0.062	0.074	0.054	0.092	-0.004	0
	<u>0.142</u>	0.021	0.095	<u>0.224</u>	<u>0.363</u>	<u>0.122</u>	0.027	<u>0.196</u>	0.036	-0.042	0.077	0.080	<u>0.157</u>	-0.007	0

9.1.6 MDS

Both MDS plots (fig. 18A and B) are deliberately displayed in the same scale.

The MDS with unaltered HVR I sequences (fig. 18A) shows that the overall genetic distances between the samples are low; the only exceptions are the hunter-gatherers and the groups of the Early Neolithic of Central Portugal (CPE) and Northern Spain (NSE) and the Late Neolithic of the Ebro Valley (EVN) at the left site of the plot. All Early Neolithic groups are positioned in greater distance to one another; with the greatest distance between those of Central Portugal (CPE) and Northern Spain (NSE) and the Early Neolithic group of Els Trocs. The Late Neolithic groups are all positioned in the middle of the plot except for the previously mentioned group of the Ebro Valley (EVN): The Chalcolithic groups are clearly separated from the Bell Beaker but do not form a tighter cluster on the plot. The two Bell Beaker groups (SMCB and NMCB) fall closely together. However, distances among all groups are too low for a detailed interpretation.

The MDS plot with additional haplogroup information (fig. 18B) does not alter the picture of the first MDS drastically, but allows to identify clusters. The Early Neolithic groups are not dispersed over the whole plot anymore and affinities between Northern Spain (NSE) and Central Portugal (CPE) on the one hand and Els Trocs and Northeast Spain (NEE) on the other hand become recognizable. The Late Neolithic of Northeast Spain (NEN) is located in some distance to all other groups while the contemporaneous groups of the Ambrona Valley (AVN) and Central Portugal (CPN) form a tight cluster. The two Bell Beaker groups (SMCB and NMCB) are still genetically closest to each other but this MDS places the Late Neolithic of the Northern Meseta (NMN) close to the SMCB. The Chalcolithic groups of the Southern Meseta (SMC) and East Spain (ESC) are also characterized by closer genetic affinities than in the first plot, while the group of Northeast Spain (NEC) is positioned closely to a chronologically preceding group of the same area (NEE) and Els Trocs.

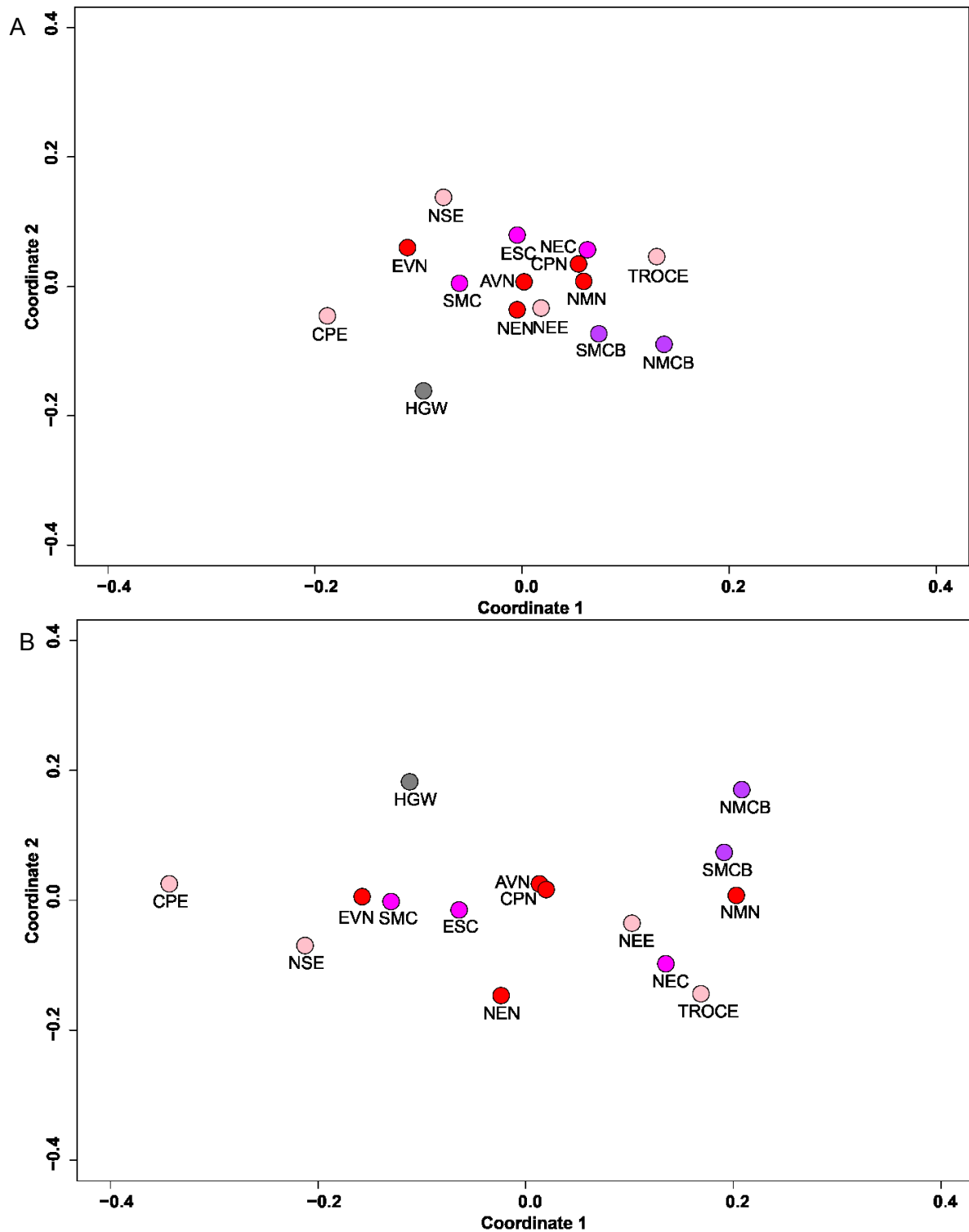


Figure 18 MDS with the Iberian dataset

A) MDS based on HVR I sequence. B) MDS based on HVR I sequences with phylogenetic information added. Western European hunter-gatherers are symbolized by gray circles, Early Neolithic groups by pink circles, Late Neolithic groups by magenta colored circles, and Bell Beaker groups are colored purple.

9.1.7 Shared haplotype analyses (SHA)

The first SHA (fig. 19A) focuses on the amount of hunter-gatherer haplogroups – H, U4, U5b, and N* – and lineages in the different Early Neolithic groups of the Iberian Peninsula. The bar chart reveals that in all groups the amount of hunter-gatherer haplogroups is higher than the amount of haplotype matches. It is evident, however, that the groups of Northern Spain and Central Portugal possess a much higher amount of hunter-gatherer mitochondrial lineages/haplogroups than the group of Northeast Spain. In the individuals of Els Trocs, a data set that only contains seven individuals, neither haplotypes nor haplogroups typical for Iberian hunter-gatherers have been detected.

The second analysis (fig. 19B) displays shared lineages among the different Early Neolithic groups. For all groups the amount of unique lineages is the highest (70–80%), while the amount of shared lineages with other Early Neolithic groups is low (~20%). The only exception is the group of Central Portugal (CPE), which has equal frequencies of shared lineages with Northeast Spain and Northern Spain to unique lineages only found in Central Portugal.

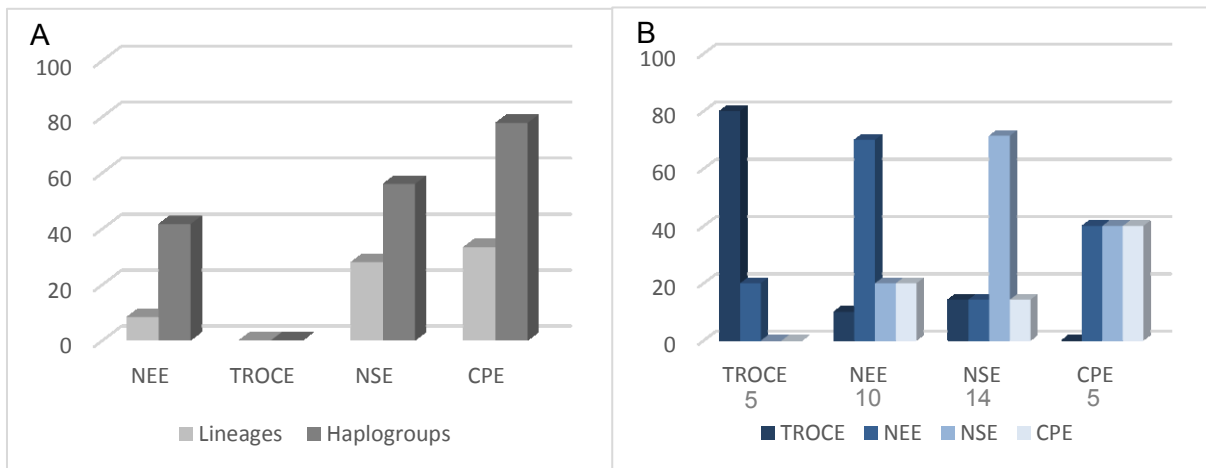


Figure 19 SHA of Early Neolithic groups

A) Hunter-gatherer lineages and haplogroups in Early Neolithic groups. B) Shared lineages among Early Neolithic groups. Because for the latter approach groups were reduced by identical lineages, the adjusted number of individuals is denoted below the group name.

In the Late Neolithic, all groups exhibit between 11% and 23% lineages typical for hunter-gatherers, with the exception of the Ebro Valley dataset, where even 45% of the individuals possess hunter-gatherer haplotypes (fig. 20A). The amount of lineages shared with the preceding Early Neolithic of Northeast Spain (NEE) lies between 9% and 13% for the Late Neolithic of the Ambrona Valley, Northeast Spain, and the Ebro Valley, but reaches values of 25% to 33% in the Northern Meseta and Central Portugal. Els Trocs, too, has the lowest

amount of matches to the Ebro Valley (0%) and the Ambrona Valley (9%) and more matches to Central Portugal (33%), but only few shared lineages with the Northern Meseta (13%) and elevated frequencies of shared lineages with Northeast Spain (23%). Nearly all Late Neolithic groups show high amounts of matches to the Early Neolithic of Northern Spain (NSE) (between 32% and 67%), except for the Northern Meseta (NMN) that has only 20% sequence matches. The Late Neolithic of the Ambrona Valley, especially the Northern Meseta, and interestingly Central Portugal only share a low to moderate percentage of their lineages with the Early Neolithic group of Central Portugal (18%, 3%, and 17%) while the remaining two Late Neolithic groups share between 23% (NEN) and 54% (EVN) of their lineages with it (fig. 20A).

When comparing the contemporaneous Late Neolithic groups to each other (fig. 20B), the majority of haplotypes of each group (66–70%) still has no match in any other group. An exception is, like in the Early Neolithic, the group of Central Portugal that has the highest amount of shared lineages with contemporaneous groups of Northeast Spain and the Northern Meseta. The two Late Neolithic groups that share the most lineages with each other are those of the Northern Meseta and the Ambrona Valley, while almost all other values for shared lineages between groups are lower than 20%.

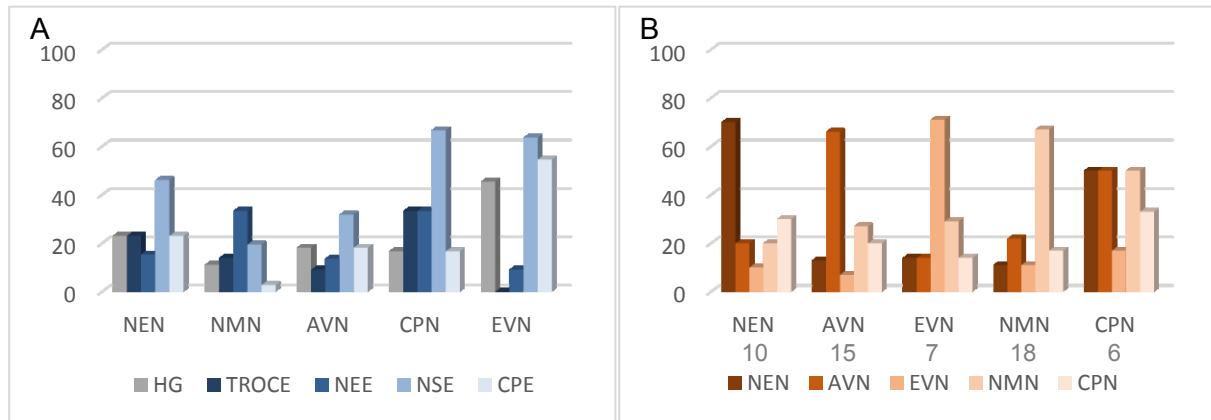


Figure 20 SHA of Late Neolithic groups

A) Hunter-gatherer and Early Neolithic lineages in the Late Neolithic. B) Shared lineages among Late Neolithic groups. Because for the latter approach groups were reduced by identical lineages, the adjusted number of individuals is denoted below the group name.

In a next step, the amount of Late Neolithic lineages in Chalcolithic groups was calculated (fig. 21A). Chalcolithic groups of East Spain (ESC) and the Southern Meseta (SMC) share a high amount of lineages with preceding Late Neolithic groups of Northeast Spain (NEN) (32–50%) and the Ambrona Valley (AVN) (48–50%). Haplotypes found in the Late Neolithic Ambrona Valley are also quite frequent in the Chalcolithic of Northeast Spain (60%), while

lineages shared with the Late Neolithic of the same region (NEN) are considerably lower (20%). Lineages found in these two Late Neolithic (AVN and NEN) groups are not very frequent in both Bell Beaker groups (14–17% and 26–9%). However, they show – together with the Chalcolithic of Northeast Spain (NEC) – the highest amounts of shared lineages with the Late Neolithic of the Northern Meseta (NMN) (44–60%). A contrasting trend can be seen for the amount of shared lineages with the Late Neolithic of the Ebro Valley, which is low in the Northeast and in the Bell Beaker (6–14%) but high in the other two Chalcolithic groups (29–42%).

When analysing shared haplotypes among Chalcolithic groups (fig. 21B), the greatest amounts of shared lineages exist between Northeast Spain and East Spain (50–60%). Samples from Northeast Spain furthermore have the greatest amount of shared lineages with Bell Beaker groups (SMCB and MNCB). In the Chalcolithic group of the Southern Meseta (SMC), a total of 33% lineages are shared with the Bell Beaker group of the same region. Shared lineages between the two Bell Beaker groups reach values of only 8% and 17% respectively.

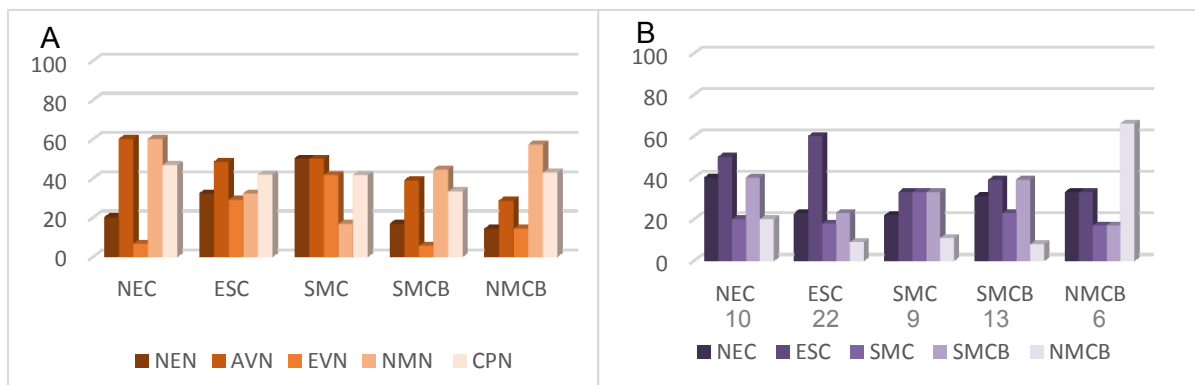


Figure 21 SHA of Chalcolithic groups

A) Late Neolithic lineages in Chalcolithic groups. B) Shared lineages among Chalcolithic groups. Because for the latter approach groups were reduced by identical lineages, the adjusted number of individuals is denoted below the group name.

In a next step, the percentage of new lineages in every period, i.e. lineages that had not been detected in previous periods, was estimated. Furthermore, the ratio of unique lineages, i.e. lineages not found in any other chronological period was calculated. Figure 22A shows a steady decrease of unique lineages from hunter-gatherers to Early Neolithic groups (23%), followed by a plateau of almost no changes until the Chalcolithic period (19%) and finally an increase in the Bell Beaker groups (32%). Figure 22B shows a constant decrease of new lineages from the hunter-gatherers to the Chalcolithic (19%) but again an increase of new

lineages in the Bell Beaker to 32%. While the values for lineages not detected in previous periods and those for unique lineages are identical for Bell Beaker and the Chalcolithic, the percentage of new lineages compared to that of unique lineages is very different in the Early (79% vs. 23%) and Late Neolithic (42% vs. 22%).

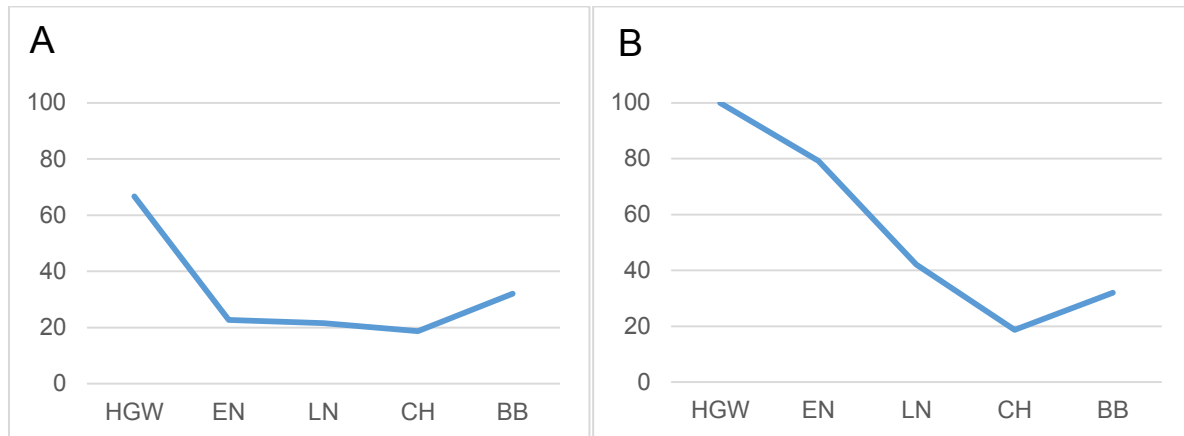


Figure 22 Chronological transect of new and unique lineages

A) Amount of unique lineages that were only present in the particular period. B) Amount of new lineages that have not been observed in previous periods. (HGW=hunter-gatherers (n=12); EN=Early Neolithic (n=53); LN=Late Neolithic (n=88); CH=Chalcolithic (n=64); BB=Bell Beaker (n=25))

9.1.8 AMOVA

To investigate genetic variation among the Iberian groups, AMOVAs were performed using HVR I sequences with additional haplogroup-specific profiles added. First, all Spanish and Portuguese pre-Neolithic to Late Neolithic groups were assigned into three different clusters and within-cluster⁶ and among-cluster molecular variance was calculated using a gamma value of 0.24. Due to the great number of possible combinations when estimating all possible three and four group arrangements, results of previous models were considered in subsequent AMOVAs, resulting in 56 different models tested. Table 17 visualizes the results when only the hunter-gatherer and Early Neolithic cultures are re-arranged between two different clusters and the Late Neolithic groups stay fixed in one cluster (table 17, models 1-10) and vice versa (table 17, models 11-20).

⁶ In AMOVAs this term is usually denoted as “within group” and “among group” molecular variance. Because in this work chronologically and/or geographically pooled samples were pooled into “groups”, the term “group” of the AMOVA was replaced by the term “cluster” to avoid confusion.

Table 17 Models 1–20 tested by AMOVA

The best models are highlighted by bold script. Groups that were pooled into one cluster are indicated by brackets. Different clusters are separated by “+”.

no.	arrangement	among clusters		within clusters	
		F _{st}	p	F _{st}	p
1	(HGW_NEE) + (TROCE_NSE_CPE) + (NEN_AVN_NMN_CPN_EVN)	0.01589	0.31378+- 0.01395	0.04715	0.00293+- 0.00164
2	(HGW_TROCE) + (NEE_NSE_CPE) + (NEN_AVN_NMN_CPN_EVN)	0.00636	0.45455+- 0.01559	0.05332	0.00000+- 0.00000
3	(HGW_NSE) + (NEE_TROCE_CPE) + (NEN_AVN_NMN_CPN_EVN)	0.01047	0.34995+- 0.01551	0.05060	0.00196+- 0.00136
4	(HGW_CPE) + (NEE_TROCE_NSE) + (NEN_AVN_NMN_CPN_EVN)	0.01764	0.31378+- 0.01684	0.04610	0.00391+- 0.00185
5	(HGW_NEE_TROCE) + (NSE_CPE) + (NEN_AVN_NMN_CPN_EVN)	0.03339	0.16911+- 0.00940	0.03541	0.02737+- 0.00585
6	(HGW_NEE_CPE) + (NSE_TROCE) + (NEN_AVN_NMN_CPN_EVN)	0.00132	0.48485+- 0.01209	0.05644	0.00196+- 0.00136
7	(HGW_NEE_NSE) + (CPE_TROCE) + (NEN_AVN_NMN_CPN_EVN)	-0.00018	0.54154+- 0.01492	0.05738	0.00000+- 0.00000
8	(HGW_TROCE_NSE) + (NEE_CPE) + (NEN_AVN_NMN_CPN_EVN)	-0.00639	0.59042+- 0.01749	0.06121	0.00000+- 0.00000
9	(HGW_TROCE_CPE) + (NEE_NSE) + (NEN_AVN_NMN_CPN_EVN)	-0.00346	0.54448+- 0.01536	0.05952	0.00098+- 0.00098
10	(HGW_NSE_CPE) + (NEE_TROCE) + (NEN_AVN_NMN_CPN_EVN)	0.05024	0.04497+- 0.00657	0.02474	0.04985+- 0.00605
11	(HGW_NEE_TROCE_NSE_CPE) + (NEN_AVN) + (NMN_CPN_EVN)	-0.00505	0.58553+- 0.01351	0.06080	0.00098+- 0.00098
12	(HGW_NEE_TROCE_NSE_CPE) + (NEN_NMN) + (AVN_CPN_EVN)	0.00842	0.37634+- 0.01557	0.05126	0.00489+- 0.00203
13	(HGW_NEE_TROCE_NSE_CPE) + (NEN_EVN) + (AVN_CPN_NMN)	0.01048	0.31672+- 0.01626	0.04765	0.00391+- 0.00185
14	(HGW_NEE_TROCE_NSE_CPE) + (NEN_CPN) + (AVN_NMN_EVN)	0.00391	0.42815+- 0.01836	0.05471	0.00196+- 0.00136
15	(HGW_NEE_TROCE_NSE_CPE) + (AVN_NMN) + (NEN_CPN_EVN)	0.01190	0.34409+- 0.01630	0.04893	0.00196+- 0.00136
16	(HGW_NEE_TROCE_NSE_CPE) + (AVN_EVN) + (NEN_NMN_CPN)	0.00339	0.46041+- 0.01671	0.05490	0.00293+- 0.00164
17	(HGW_NEE_TROCE_NSE_CPE) + (AVN_CPN) + (NEN_NMN_EVN)	-0.00714	0.61779+- 0.01181	0.06214	0.00000+- 0.00000
18	(HGW_NEE_TROCE_NSE_CPE) + (NMN_EVN) + (NEN_AVN_CPN)	-0.00235	0.55425+- 0.01646	0.05894	0.00000+- 0.00000
19	(HGW_NEE_TROCE_NSE_CPE) + (NMN_CPN) + (NEN_AVN_EVN)	0.01160	0.38416+- 0.01336	0.04894	0.00587+- 0.00219
20	(HGW_NEE_TROCE_NSE_CPE) + (EVN_CPN) + (NEN_AVN_NMN)	0.00654	0.42326+- 0.01898	0.05303	0.00000+- 0.00000

The best model of the first 10 tested separates the hunter-gatherers and the Early Neolithic of Northern Spain and Central Portugal from Els Trocs and Northeast Spain. When re-arranging the Late Neolithic groups against one fixed group of hunter-gatherers and all Early Neolithic samples (table 17, models 11–20), no suitable arrangement was found. Therefore in a next step, the analyses were repeated but this time using the best approach for separation of hunter-gatherers and Early Neolithic groups (table 17, model 10) instead of one fixed cluster of them. Thus, the following models (table 18, models 21–30) use arrangements

of 4 clusters (two fixed with Early Neolithic groups and two with different variations of Late Neolithic groups).

Table 18 Models 21–30 tested by AMOVA

The best models are highlighted by bold script. Groups that were pooled into one cluster are indicated by brackets. Different clusters are separated by “+”.

no	arrangement Based on models 1-20	among clusters		within clusters	
		F _{st}	p	F _{st}	p
21	(HGW_NSE_CPE) + (NEE_TROCE) + (NEN_AVN) + (NMN_CPN_EVN)	0.03533	0.15054+- 0.00750	0.02851	0.06940+- 0.00902
22	(HGW_NSE_CPE) + (NEE_TROCE) + (NEN_NMN) + (AVN_CPN_EVN)	0.04901	0.06940+- 0.00548	0.01653	0.14761+- 0.00908
23	(HGW_NSE_CPE) + (NEE_TROCE) + (NEN_EVN) + (AVN_CPN_NMN)	0.05344	0.05083+- 0.00904	0.01459	0.19159+- 0.01204
24	(HGW_NSE_CPE) + (NEE_TROCE) + (NEN_CPN) + (AVN_NMN_EVN)	0.04323	0.09482+- 0.00929	0.02404	0.08113+- 0.01017
25	(HGW_NSE_CPE) + (NEE_TROCE) + (AVN_NMN) + (NEN_CPN_EVN)	0.05091	0.04203+- 0.00623	0.01571	0.15445+- 0.00847
26	(HGW_NSE_CPE) + (NEE_TROCE) + (AVN_EVN) + (NEN_NMN_CPN)	0.04391	0.09677+- 0.00957	0.02173	0.10753+- 0.01105
27	(HGW_NSE_CPE) + (NEE_TROCE) + (AVN_CPN) + (NEN_NMN_EVN)	0.03349	0.18573+- 0.01086	0.03064	0.04790+- 0.00592
28	(HGW_NSE_CPE) + (NEE_TROCE) + (NMN_EVN) + (NEN_AVN_CPN)	0.03821	0.15640+- 0.01201	0.02582	0.07820+- 0.00841
29	(HGW_NSE_CPE) + (NEE_TROCE) + (NMN_CPN) + (NEN_AVN_EVN)	0.05339	0.04790+- 0.00625	0.01259	0.26002+- 0.01607
30	(HGW_NSE_CPE) + (NEE_TROCE) + (EVN_CPN) + (NEN_AVN_NMN)	0.04559	0.08602+- 0.00745	0.22600	0.07331+- 0.00741

It was not possible to find a model with both significant F_{ST} values for among-cluster and within-cluster variation. However, three models had the highest and significant F_{ST} values for among-clusters and the lowest for within-clusters. Each one of these models (table 18, models 23, 25, and 29) was taken to a next level, where every Late Neolithic group of the fourth cluster was assigned to each one of the first two hunter-gatherer/Early Neolithic clusters (table 19).

Table 19 Models 31–48 tested by AMOVA

The best models are highlighted by bold script. Groups that were pooled into one cluster are indicated by brackets. Different clusters are separated by “+”.

no.	arrangement Based on model 23	among clusters		within clusters	
		F _{st}	p	F _{st}	p
31	(HGW_NSE_CPE_NMN) + (NEE_TROCE) + (NEN_EVN) + (AVN_CPN)	-0.03351	0.87586+- 0.00824	0.07975	0.00000+- 0.00000
32	(HGW_NSE_CPE) + (NEE_TROCE_NMN) + (NEN_EVN) + (AVN_CPN)	0.06383	0.01466+- 0.00368	0.00369	0.36266+- 0.01867
33	(HGW_NSE_CPE_CPN) + (NEE_TROCE) + (NEN_EVN) + (AVN_NMN)	0.04802	0.07429+- 0.00920	0.01883	0.11828+- 0.00925
34	(HGW_NSE_CPE) + (NEE_TROCE_CPN) + (NEN_EVN) + (AVN_NMN)	0.04852	0.05865+- 0.00819	0.01762	0.12805+- 0.00828
35	(HGW_NSE_CPE_AVN) + (NEE_TROCE) + (NEN_EVN) + (CPN_NMN)	0.04181	0.11144+- 0.00998	0.02472	0.10068+- 0.00871
36	(HGW_NSE_CPE) + (NEE_TROCE_AVN) + (NEN_EVN) + (CPN_NMN)	0.04729	0.07234+- 0.00885	0.01744	0.15836+- 0.01011

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Based on model 25				
37	(HGW_NSE_CPE_EVN) + (NEE_TROCE) + (AVN_NMN) + (NEN_CPN)	0.06381	0.00782+- 0.00343	0.26588+- 0.00639 0.01525
38	(HGW_NSE_CPE) + (NEE_TROCE_EVN) + (AVN_NMN) + (NEN_CPN)	0.04323	0.10068+- 0.00800	0.08309+- 0.02404 0.00795
39	(HGW_NSE_CPE_CPN) + (NEE_TROCE) + (AVN_NMN) + (NEN_EVN)	0.04802	0.05767+- 0.00649	0.10753+- 0.01883 0.01157
40	(HGW_NSE_CPE) + (NEE_TROCE_CPN) + (AVN_NMN) + (NEN_EVN)	0.04852	0.07429+- 0.00641	0.12512+- 0.01762 0.00961
41	(HGW_NSE_CPE_NEN) + (NEE_TROCE) + (AVN_NMN) + (CPN_EVN)	0.04196	0.11046+- 0.00884	0.05572+- 0.02491 0.00675
42	(HGW_NSE_CPE) + (NEE_TROCE_NEN) + (AVN_NMN) + (CPN_EVN)	0.04852	0.06647+- 0.00836	0.13099+- 0.01762 0.01074
Based on model 29				
43	(HGW_NSE_CPE_EVN) + (NEE_TROCE) + (NMN_CPN) + (NEN_AVN)	0.06365	0.01466+- 0.00340	0.31574+- 0.00423 0.01499
44	(HGW_NSE_CPE) + (NEE_TROCE_EVN) + (NMN_CPN) + (NEN_AVN)	0.03487	0.15347+- 0.01200	0.06647+- 0.02806 0.00569
45	(HGW_NSE_CPE_AVN) + (NEE_TROCE) + (NMN_CPN) + (NEN_EVN)	0.0418	0.10068+- 0.00957	0.08798+- 0.02472 0.01026
46	(HGW_NSE_CPE) + (NEE_TROCE_AVN) + (NMN_CPN) + (NEN_EVN)	0.04729	0.08016+- 0.00814	0.16520+- 0.01744 0.01256
47	(HGW_NSE_CPE_NEN) + (NEE_TROCE) + (NMN_CPN) + (AVN_EVN)	0.04376	0.09677+- 0.00904	0.13001+- 0.02177 0.01072
48	(HGW_NSE_CPE) + (NEE_TROCE_NEN) + (NMN_CPN) + (AVN_EVN)	0.05979	0.02639+- 0.00482	0.39198+- 0.00583 0.01391

In this approach also no significant F_{ST} values for the within-cluster variation were obtained. However, it can be seen that models showed significant and higher F_{ST} values for among-cluster variation when EVN was grouped together with HGW/NSE/CPE/ (table 19, models 37 and 43) or when NMN was put together with NEE/TROCE (table 19, model 33). Based on all results, different two to four cluster combinations were tested to find the best model (see table 20).

Table 20 Models 49–56 tested by AMOVA

The best models are highlighted by bold script. Groups that were pooled into one cluster are indicated by brackets. Different clusters are separated by “+”.

no.	arrangement	among cluster		within cluster	
		F_{st}	p	F_{st}	p
49	(HGW_NSE_CPE_EVN) + (NEE_TROCE_NMN) + (NEN_AVN_CPN)	0.07721	0.00196+- 0.00136	-0.00281	0.50244+- 0.01661
50	(HGW_NSE_CPE_EVN) + (NEE_TROCE_NMN+ NEN_AVN_CPN)	0.08632	0.00196+- 0.00136	0.00899	0.23754+- 0.00975
51	(HGW_NSE_CPE_EVN) + (NEE_TROCE) + (NMN +NEN) + (AVN_CPN)	0.05862	0.02835+- 0.00543	0.00924	0.22483+- 0.01479
52	(HGW_NSE_CPE_EVN) + (NEE_TROCE) + (NMN +AVN) + (NEN_CPN)	0.06381	0.01662+- 0.00367	0.00639	0.26295+- 0.01321
53	(HGW_NSE_CPE_EVN) + (NEE_TROCE) + (NMN +CPN) + (NEN_AVN)	0.06365	0.00782+- 0.00280	0.00423	0.31281+- 0.01145
54	(HGW_NSE_CPE_) + (NEE_TROCE_NMN) + (EVN +NEN) + (AVN_CPN)	0.06383	0.00978+- 0.00294	0.00369	0.35484+- 0.01482
55	(HGW_NSE_CPE_) + (NEE_TROCE_NMN) + (EVN +AVN) + (NEN_CPN)	0.06247	0.01075+- 0.00300	0.00519	0.34409+- 0.01504
56	(HGW_NSE_CPE_) + (NEE_TROCE_NMN) + (EVN +CPN) + (NEN_AVN)	0.05881	0.02737+- 0.00474	0.00862	0.22678+- 0.01362

It was not possible to find a model that significantly showed the highest F_{ST} values for among-cluster variation and the lowest for within-cluster variation. However, it can be seen that preferred arrangements were always HGW/NSE/CPE/EVN and NEE/TROCE/NMN (see table 20).

In order to analyze genetic variation among the Iberian Chalcolithic Bell Beaker and non-Bell Beaker groups, AMOVAs were performed on HVR I data with additional haplogroup-specific profiles added (see also chapters 7.8 and 11.3) and a gamma value of 0.207. All possible arrangements were tested (see table 21). The F_{ST} value among the clusters exceeds the within-cluster variation only in one model: When the two Bell Beaker populations were tested against the remaining non-Bell Beaker groups. However, neither of both F_{ST} values is significant.

Table 21 Models 57–66 tested by AMOVA

The best models are highlighted by bold script. Groups that were pooled into one cluster are indicated by brackets. Different clusters are separated by “+”.

no.	arrangement	among clusters		within clusters	
		F_{st}	p	F_{st}	p
57	(SMCB_NMCB) + (SMC_ESC_NEC)	0.05613	0.09772+-0.00281	0.00459	0.37703+-0.00516
58	(SMCB_SMC) + (NMCB_ESC_NEC)	-0.01221	0.50010+-0.00486	0.04375	0.04446+-0.00214
59	(SMCB_ESC) + (NMCB_SMC_NEC)	-0.04839	1.00000+-0.00000	0.06519	0.00733+-0.00089
60	(SMCB_NEC) + (NMCB_SMC_ESC)	0.01579	0.30485+-0.00454	0.02679	0.10743+-0.00316
61	(NMCB_SMC) + (SMCB_ESC_NEC)	-0.02850	0.90515+-0.00320	0.04914	0.01772+-0.00141
62	(NMCB_ESC) + (SMCB_SMC_NEC)	-0.01936	0.60832+-0.00488	0.04869	0.03376+-0.00154
63	(NMCB_NEC) + (SMCB_SMC_ESC)	-0.02322	0.69950+-0.00437	0.04794	0.02327+-0.00148
64	(SMC_ESC) + (SMCB_NMCB_NEC)	0.03862	0.19465+-0.00394	0.01095	0.31178+-0.00515
65	(SMC_NEC) + (SMCB_NMCB_ESC)	-0.02590	0.79881+-0.00353	0.05081	0.02020+-0.00148
66	(ESC_NEC) + (SMCB_NMCB_SMC)	0.00084	0.40446+-0.00485	0.03609	0.08347+-0.00305

9.2 Ancient Iberian groups in the European context

9.2.1 PCA

The PCA with prehistoric groups from all over Europe (see fig. 23) displays 27.8% of the overall variability in its first two components. The 1st pPC separates most of the Early and Middle Neolithic groups of Central Europe from hunter-gatherers of East and Central Europe. The 2nd PC separates nearly all Central European groups from those of Western Europe. The distribution of Central European samples has been presented and discussed elsewhere (BRANDT ET AL. 2013, IN PRESS) and will not further be commented on in this chapter. Only few groups are excluded from this West-Central European arrangement: The Funnel Beaker culture (FBC) and the Neolithic samples of the Blätterhöhle (BLA) are the only non-Iberian groups that fall into the Western European cluster. Of all Iberian groups, only Els Trocs and the Chalcolithic group of Northeast Spain (NEC) show great affinities to the Early and Middle Neolithic samples of Central Europe. The Late Neolithic samples of Northeast Spain (NEN) are situated more closely to the Central European Late Neolithic. Western European hunter-gatherers, Early Neolithic groups of Central Portugal (CPE) and Northern Spain (NSE), Late Neolithic groups of the Ebro Valley (EVN) and Central Portugal (CPN) as well as Bell Beakers of the Northern Meseta (NMCB) are positioned in some distance to the tight block of the other Iberian data and closer to Central and East European hunter-gatherers.

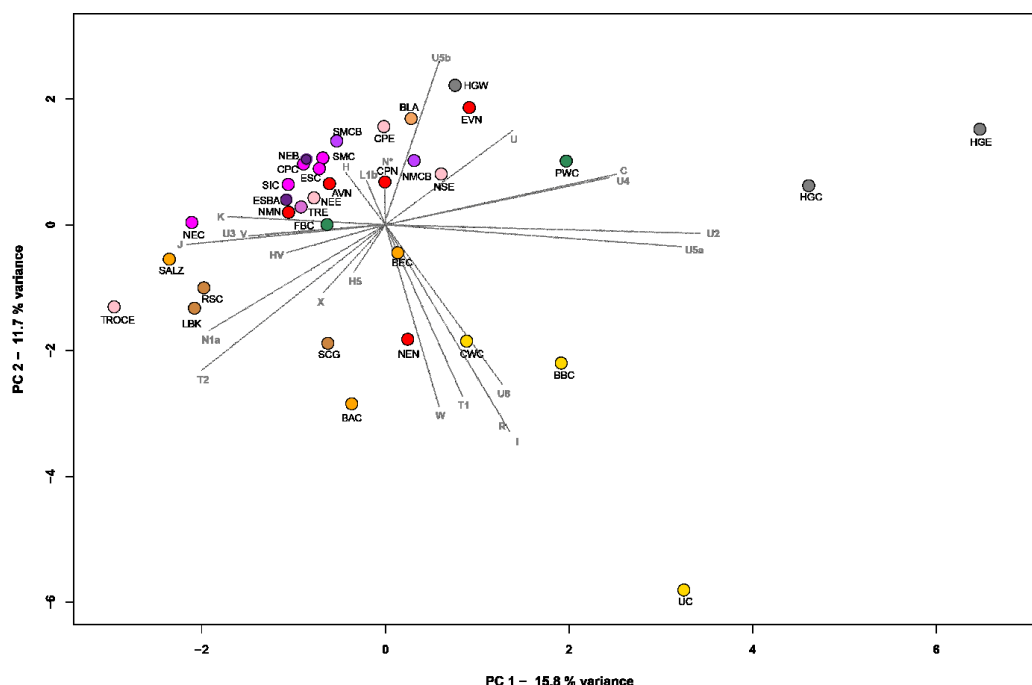


Figure 23 PCA with European dataset

Hunter-gatherer groups are symbolized by gray circles, Early Neolithic groups by pink circles, Late Neolithic groups by magenta colored circles, Bell Beaker groups are colored purple, and Bronze Age populations dark purple. Early Neolithic groups of Central Europe are depicted by brown circles, Middle Neolithic groups in orange and Late Neolithic and Bronze Age groups in yellow. The French samples of Treilles are colored purple and Northern European groups are colored green.

9.2.2 Cluster analysis

The results are displayed in fig. 24. Generally, all Iberian samples form the same clusters that already have been observed in the cluster analysis without the European comparative data (see fig. 17, p. 90). The particular Iberian sub-clusters are only in few cases extended by non-Iberian groups: Els Trocs and the Chalcolithic group of Northeast Spain (NEC) are separated from each other but still situated in the same main cluster and the former cluster of NEE and NMN is extended by the Bernburg culture (BEC). To describe the dendrogram from top to bottom: The main separation exists between hunter-gatherer groups, the Pitted Ware culture as well as few Early (CPE, NSE) and Late Neolithic (EVN, BLA) groups to the remaining Neolithic to Bronze Age groups. In the first cluster Iberian groups (NEE, CPE, EVN, HGW) and the samples of the Blätterhöhle are separated from the other two hunter-gatherer groups and the Pitted Ware culture. The other main cluster has a first split separating the Spanish Bell Beaker (SMCB and NMCB) and Portuguese groups (CPN and CPC) as well as the Bernburg culture of Central Europe (BEC), the Early Neolithic group of Northeast Spain (NEE) and the Late Neolithic group of the Northern Meseta (NMN) from all others. The other sub-cluster is subdivided several times; main splits are into one cluster of all Late Neolithic and Bronze Age cultures of Central Europe, another comprising most Early and Middle Neolithic Central European cultures together with the Funnel Beaker (FBC), Els Trocs, and Northeast Spain Chalcolithic (NEC), and one cluster including all remaining Iberian groups.

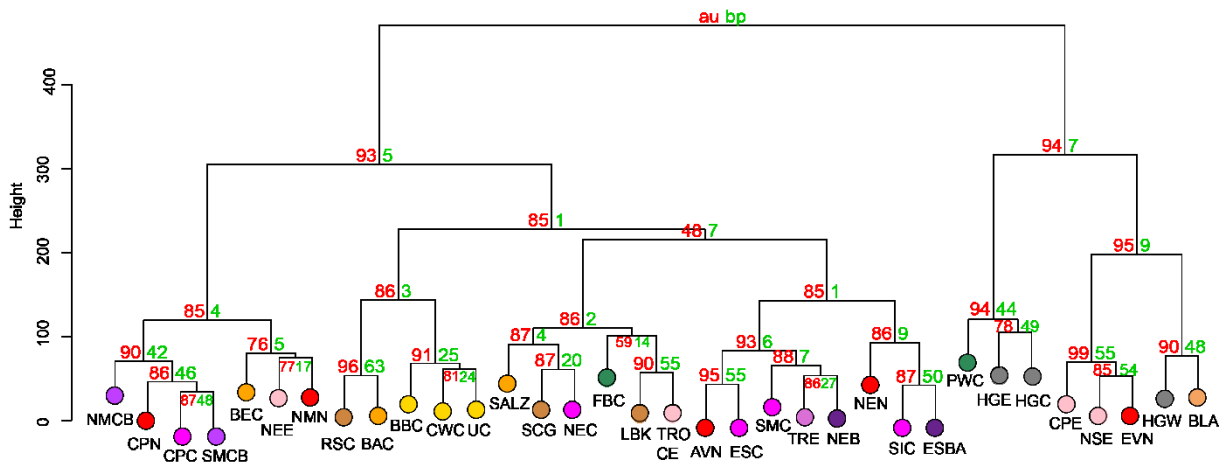


Figure 24 Cluster analysis of European dataset

Hunter-gatherer groups are symbolized by gray circles, Early Neolithic groups by pink circles, Late Neolithic groups by magenta colored circles, Bell Beaker groups are colored purple, and Bronze Age populations dark purple. Early Neolithic groups of Central Europe are depicted by brown circles, Middle Neolithic groups in orange and Late Neolithic and Bronze Age groups in yellow. The French samples of Treilles are colored purple and Northern European groups are colored green. “au” gives the approximately unbiased p-value and “bp” the bootstrap probability value.

9.2.3 Fisher-test

The results of the Fisher-test (see table 22) indicate that hunter-gatherers of East and Central Europe as well as the Pitted ware culture (PWC) from Northern Europe show significant differences in haplogroup composition to all Spanish and Portuguese groups, no matter the chronology. Most Central European groups that date between 5,500 and 3,000 cal BC (LBK, RSC, SCG, BAC, and SALZ) are significantly different to western hunter-gatherers (HGW), to Early Neolithic samples of Northern Spain (NSE) and Central Portugal (CPE), to Late Neolithic samples from the Northern Meseta (NMN) and Ebro Valley (EVN), to the Chalcolithic group of East Spain (ESC) as well as to the Bell Beaker group from the Southern Meseta (SMCB). The samples from the Blätterhöhle (BLA) are significantly different to all Iberian groups except for the HGW. Bernburg (BEC) and Funnel Beaker (FBC) samples on the other hand show almost no significant differences to any Iberian group, except to the Early Neolithic of Northern Spain (NSE) and Chalcolithic of East Spain (ESC). Central European Bell Beakers (BBC) are significantly different to those of the Southern Meseta (SMCB) but not to those of the Northern Meseta (NMCB). They furthermore differ from most Chalcolithic groups, except for those of East Spain (ESC) and the Southern Meseta (SMC). Spanish Bell Beakers of the Southern Meseta (SMCB) are different to most Central European cultures in general.

Table 22 Results of the Fisher-test between Iberian and non-Iberian groups

Significant values (≤ 0.05) are bold and underlined.

	HGW	NEE	TROCE	NSE	CPE	NEN	AVN	EVN	NMN	CPN	NEC	ESC	SMC	SIC	CPC	SMCB	NMCB	NEB	ESBA
HGE	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.01</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.01</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.01</u>	<u>0.00</u>	<u>0.00</u>	<u>0.01</u>	<u>0.00</u>	<u>0.00</u>
HGC	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>
LBK	<u>0.00</u>	<u>0.03</u>	0.90	<u>0.00</u>	<u>0.00</u>	<u>0.04</u>	<u>0.01</u>	<u>0.00</u>	<u>0.00</u>	0.14	0.24	<u>0.00</u>	<u>0.00</u>	0.46	0.07	<u>0.00</u>	0.11	<u>0.01</u>	0.64
RSC	<u>0.01</u>	0.57	0.78	<u>0.03</u>	0.46	0.81	0.28	0.13	<u>0.02</u>	0.31	0.19	<u>0.05</u>	<u>0.02</u>	0.94	0.15	<u>0.01</u>	0.24	0.13	0.81
SCG	<u>0.00</u>	0.47	0.51	<u>0.00</u>	<u>0.01</u>	0.36	0.65	<u>0.00</u>	<u>0.03</u>	0.79	0.76	0.10	0.09	0.62	0.71	0.18	0.57	0.36	0.74
BAC	<u>0.02</u>	0.70	0.54	<u>0.03</u>	0.28	0.81	0.56	0.16	<u>0.03</u>	0.44	0.28	<u>0.05</u>	0.12	0.90	0.27	<u>0.02</u>	0.29	0.23	0.90
SALZ	<u>0.00</u>	0.08	0.54	<u>0.00</u>	<u>0.04</u>	0.21	0.28	<u>0.01</u>	<u>0.00</u>	0.18	0.57	<u>0.02</u>	0.10	0.71	0.10	<u>0.01</u>	0.11	0.30	0.75
BLA	0.18	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.02</u>	<u>0.00</u>	<u>0.01</u>	<u>0.02</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.04</u>	<u>0.02</u>	<u>0.01</u>	<u>0.00</u>	<u>0.01</u>	<u>0.04</u>	<u>0.01</u>
BEC	0.07	0.76	0.50	<u>0.00</u>	0.24	0.35	0.47	0.15	0.17	0.88	0.15	<u>0.05</u>	0.06	0.47	0.77	0.49	0.92	0.36	0.41
CWC	<u>0.01</u>	0.51	0.29	<u>0.01</u>	0.14	0.80	0.62	<u>0.05</u>	<u>0.01</u>	0.95	0.32	0.16	0.24	0.90	0.41	0.06	0.73	0.31	0.96
BBC	<u>0.04</u>	<u>0.04</u>	<u>0.02</u>	<u>0.01</u>	0.38	0.49	<u>0.05</u>	0.08	<u>0.00</u>	0.28	<u>0.00</u>	<u>0.01</u>	0.06	0.51	<u>0.04</u>	<u>0.00</u>	0.26	<u>0.02</u>	0.59
UC	<u>0.00</u>	0.06	0.10	<u>0.01</u>	0.21	0.49	0.09	<u>0.03</u>	<u>0.00</u>	0.32	<u>0.02</u>	<u>0.00</u>	<u>0.03</u>	0.73	0.06	<u>0.00</u>	0.36	0.06	0.79
FBC	<u>0.02</u>	0.38	0.81	<u>0.00</u>	<u>0.02</u>	0.60	0.45	<u>0.02</u>	0.27	0.51	0.67	0.04	0.22	0.32	0.29	0.47	0.32	0.42	0.45
PWC	<u>0.00</u>	<u>0.00</u>	<u>0.01</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.02</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.02</u>	<u>0.00</u>	<u>0.00</u>

9.2.4 F_{ST} values

F_{ST} values are only displayed for the Iberian dataset in comparison to the Central European data. F_{ST} values were computed for HVR I sequences ([gamma value 0.234] upper row in table 23) and for HVR I sequences with additional haplogroup information added ([gamma value 0.332] lower row in table 23). For some F_{ST} values the addition of haplogroup profiles to the HVR I sequences had a great impact: One can see that while some values are not very different from each other whether haplogroup-specific SNPs were attached or not (e.g., HGE-NEE, RSC-EVN, PWC-NEE) some genetic distances are doubled (e.g., HGC-HGW, HGC-CPE, UC-NMN) or divided in half (e.g. UC-TROCE, SALZ-ESC) when the sequences contain more phylogenetic information.

The highest significant genetic distances of the unaltered sequences exist between Central European hunter-gatherers and all Iberian Neolithic to Bronze Age groups ($F_{ST} > 0.12$) and between western hunter-gatherers and most Central and North European Neolithic to Bronze Age groups, except for the Bernburg culture (BEC) and Neolithic samples of the Blätterhöhle (BLA). Central European Bell Beakers (BBC) furthermore show moderate (0.046) to high (0.108) significant genetic distances to Spanish Bell Beaker groups (SMCB and NMCB). Some of the highest genetic distances in general can be found between Central and North European groups and Spanish Bell Beakers, while Central Europeans show the lowest genetic distances mostly to the Early Neolithic samples of Els Trocs. The same trends can be seen when additional haplogroup information is added to the HVR I sequences.

Table 23 F_{ST} values between Iberian and non-Iberian groups

The upper row gives the F_{ST} values computed with unaltered sequences, the lower row contains the results of sequences with additional hg information attached. Significant F_{ST} values ($p \leq 0.05$) are bold and underlined. p-values are displayed in appendix tables VI.3 and VI.4.

	HGW	NEE	TROCE	NSE	CPE	NEN	AVN	EVN	NMN	CPN	NEC	ESC	SMC	SMCB	NMCB
HGE	-0.009	<u>0.084</u>	<u>0.111</u>	<u>0.132</u>	0.032	<u>0.106</u>	<u>0.067</u>	0.023	<u>0.097</u>	0.046	<u>0.123</u>	<u>0.097</u>	0.054	<u>0.084</u>	<u>0.120</u>
	0.051	0.083	<u>0.101</u>	<u>0.203</u>	<u>0.225</u>	<u>0.114</u>	<u>0.082</u>	<u>0.103</u>	<u>0.099</u>	0.068	<u>0.114</u>	<u>0.122</u>	<u>0.132</u>	<u>0.079</u>	<u>0.128</u>
HGC	<u>0.090</u>	<u>0.295</u>	<u>0.311</u>	<u>0.312</u>	<u>0.248</u>	<u>0.267</u>	<u>0.197</u>	<u>0.190</u>	<u>0.198</u>	<u>0.221</u>	<u>0.288</u>	<u>0.249</u>	<u>0.146</u>	<u>0.121</u>	<u>0.255</u>
	<u>0.200</u>	<u>0.283</u>	<u>0.341</u>	<u>0.389</u>	<u>0.492</u>	<u>0.290</u>	<u>0.215</u>	<u>0.312</u>	<u>0.192</u>	<u>0.275</u>	<u>0.292</u>	<u>0.273</u>	<u>0.298</u>	<u>0.123</u>	<u>0.267</u>
LBK	<u>0.135</u>	0.020	-0.040	<u>0.043</u>	0.045	0.012	<u>0.030</u>	0.026	<u>0.031</u>	-0.024	0.009	<u>0.038</u>	0.019	<u>0.048</u>	0.085
	<u>0.104</u>	0.019	-0.042	<u>0.082</u>	<u>0.118</u>	0.009	<u>0.029</u>	0.050	<u>0.040</u>	-0.015	0.006	<u>0.041</u>	0.040	<u>0.050</u>	<u>0.100</u>
RSC	<u>0.068</u>	0.016	-0.039	0.047	-0.004	0.008	0.010	-0.010	0.017	-0.008	0.013	0.031	-0.007	0.042	<u>0.102</u>
	0.040	0.047	0.009	0.022	0.007	0.002	0.019	-0.011	<u>0.087</u>	-0.009	0.044	0.022	-0.023	<u>0.094</u>	<u>0.162</u>
SCG	<u>0.108</u>	-0.016	-0.034	0.019	0.049	-0.007	-0.014	0.008	-0.009	-0.069	-0.016	0.000	0.001	0.019	0.031
	<u>0.086</u>	-0.016	-0.036	<u>0.086</u>	<u>0.150</u>	0.004	-0.009	0.045	0.000	-0.058	-0.022	0.014	0.038	0.012	0.036
BAC	<u>0.063</u>	-0.005	-0.043	0.032	0.016	-0.012	-0.001	-0.015	0.005	-0.038	-0.003	0.022	-0.014	0.027	0.070
	0.041	0.003	-0.027	<u>0.050</u>	<u>0.074</u>	-0.015	0.000	0.000	0.032	-0.032	0.002	0.019	-0.007	<u>0.047</u>	<u>0.105</u>
SALZ	<u>0.121</u>	0.032	-0.007	<u>0.038</u>	0.026	-0.008	0.021	0.013	<u>0.039</u>	-0.019	0.003	<u>0.032</u>	0.002	<u>0.049</u>	<u>0.119</u>
	<u>0.069</u>	0.044	0.013	<u>0.036</u>	0.061	-0.008	0.009	0.005	<u>0.069</u>	-0.032	0.007	0.013	-0.008	<u>0.068</u>	<u>0.137</u>

	HGW	NEE	TROCE	NSE	CPE	NEN	AVN	EVN	NMN	CPN	NEC	ESC	SMC	SMCB	NMCB
BLA	0.035	0.136	0.170	0.150	0.190	0.096	0.045	0.058	0.055	0.070	0.135	0.103	-0.009	0.005	0.128
	0.003	0.101	0.155	0.086	0.154	0.060	0.025	0.005	0.090	0.012	0.107	0.058	-0.014	0.049	0.137
BEC	0.030	0.016	0.016	0.035	0.009	0.021	-0.011	-0.036	-0.011	-0.055	0.025	0.015	-0.046	-0.022	0.014
	0.011	0.005	0.009	0.060	0.098	0.019	-0.020	-0.016	-0.001	-0.062	0.010	0.005	-0.018	-0.010	0.029
CWC	0.043	0.024	0.003	0.029	0.005	0.013	0.000	-0.020	0.010	-0.034	0.013	0.015	-0.024	0.023	0.073
	0.028	0.013	0.000	0.060	0.090	0.008	-0.006	0.001	0.020	-0.040	0.002	0.013	-0.002	0.027	0.080
BBC	0.054	0.062	0.036	0.031	0.007	0.034	0.027	-0.029	0.037	-0.018	0.060	0.041	-0.020	0.046	0.108
	0.015	0.053	0.058	0.022	0.035	0.010	0.017	-0.030	0.080	-0.034	0.060	0.026	-0.025	0.075	0.124
UC	0.038	0.033	0.027	0.011	0.008	0.023	0.017	-0.022	0.032	-0.033	0.050	0.034	-0.010	0.049	0.071
	0.023	0.020	0.014	0.045	0.077	0.001	0.014	-0.001	0.043	-0.031	0.035	0.031	0.008	0.050	0.084
FBC	0.134	0.045	-0.003	0.142	0.136	0.003	0.021	0.076	0.019	-0.012	-0.021	0.053	0.009	-0.009	0.124
	0.117	0.025	-0.025	0.172	0.251	0.003	0.017	0.104	0.012	-0.011	-0.031	0.056	0.060	-0.011	0.125
PWC	0.079	0.090	0.142	0.115	0.109	0.093	0.056	0.047	0.071	0.026	0.105	0.063	0.063	0.050	0.118
	0.116	0.091	0.152	0.214	0.320	0.122	0.064	0.135	0.072	0.040	0.107	0.104	0.157	0.036	0.102
TRE	0.083	0.035	0.016	0.038	0.040	-0.005	0.004	-0.007	0.011	-0.020	-0.002	0.014	-0.022	0.029	0.124
	0.082	0.040	0.053	0.087	0.133	0.015	0.013	0.033	0.064	-0.027	0.026	0.035	0.025	0.063	0.151

9.2.5 MDS

The first MDS (fig. 25A) mainly separates all hunter-gatherers, the samples of the Blätterhöhle (BLA) and the Pitted Ware culture (PWC) from all other groups. Most remaining groups cluster very closely together; only the Early Neolithic of Portugal (CPE) and Northern Spain (NSE) on the one hand and the Bell Beaker group of the Northern Meseta (NMCB) on the other hand is positioned slightly remote from them. A separation between Western and Central European groups cannot be seen. When including SNP profiles to the sequences the picture differentiates. Please note, that the second MDS plot (fig. 25B) is inverted compared to the first one. The lower right quadrant of the plot contains hunter-gatherers and few Neolithic groups like those of the Blätterhöhle (BLA) and in some distance the Pitted Ware culture (PWC). Likewise on the lower part of the plot but in the left quadrant are the Early Neolithic groups of Northern Spain (NSE) and Central Portugal (CPE). Above them one can find the Late Neolithic of the Ebro Valley (EVN), Chalcolithic groups of East Spain (ESC) and the Southern Meseta (SMC), and the Central European Bell Beaker (BBC). Another group is formed by the two Spanish Bell Beaker groups (SMCB and NMCB) and the Late Neolithic samples of the Northern Meseta (NMN). To their left, especially Els Trocs and the Funnel Beaker, but also the LBK and Schöningen group (SCG), and Early Neolithic and Chalcolithic of Northeast Spain (NEC and NEE) are located close to each other. The lowest distances seem to exist among the Corded Ware (CWC) and Bernburg (BEC) cultures and the Late Neolithic group of the Ambrona Valley (AVN) and Central Portugal (CPN). Again, Early

Neolithic samples of Northeast Spain and Els Trocs are genetically closer to each other than to those of Central Portugal (CPE) and Northern Spain (NSE).

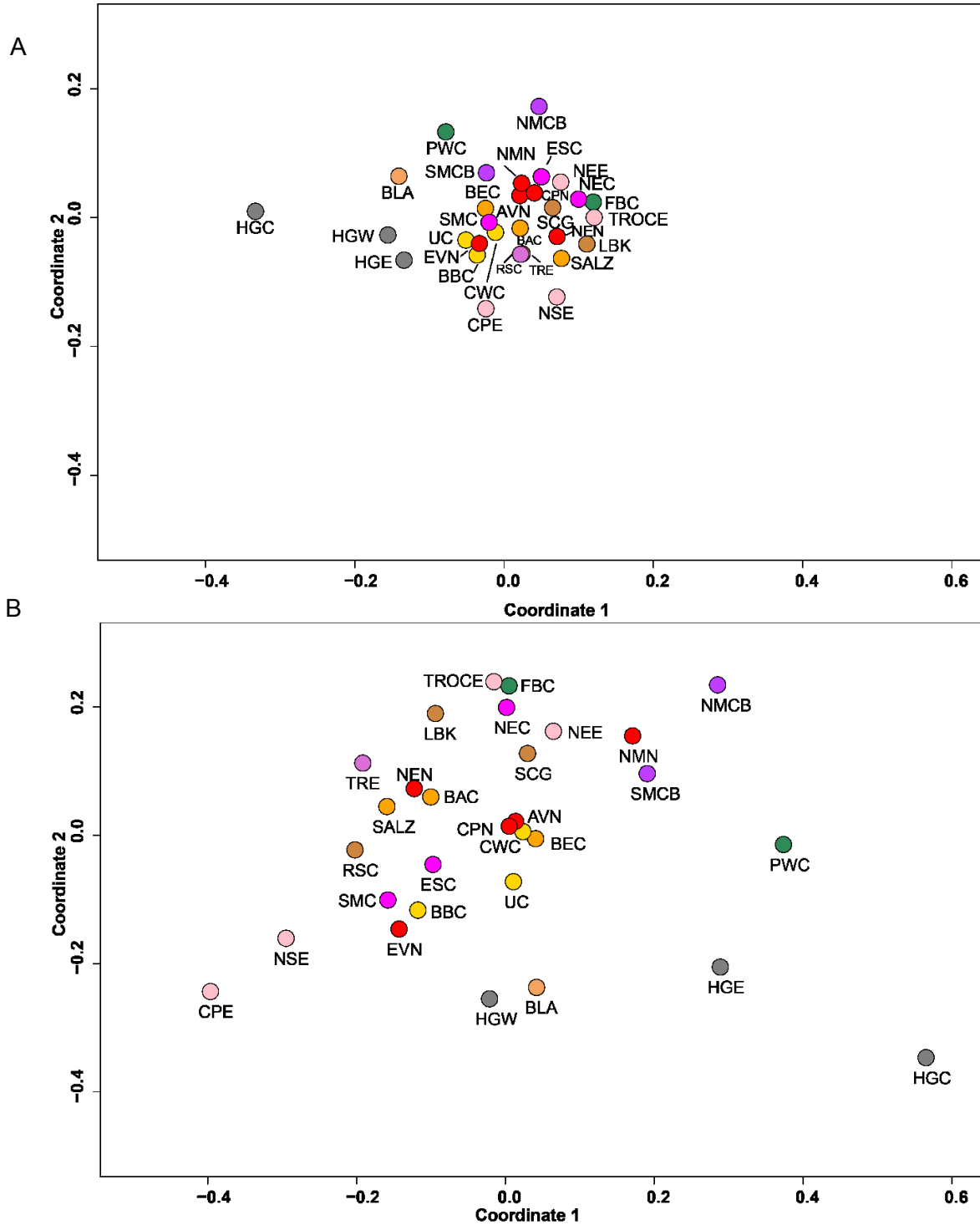


Figure 25 MDS with European dataset

A) MDS based on HVR I sequences. B) MDS based on HVR I sequences with additional phylogenetic information. Western European hunter-gatherers are symbolized by gray circles, Early Neolithic groups by pink circles, Late Neolithic groups by magenta colored circles, Bell Beakers are colored purple. Early Neolithic groups of Central Europe are depicted as brown circles, Middle Neolithic groups in orange and Late Neolithic and Bronze Age groups in yellow. The French samples of Treilles are colored light purple and Northern European groups are colored green.

9.3 Distribution of mitochondrial sub-haplogroups of H in prehistoric Europe

All in all, 45 individuals of this study were successfully analyzed by the H-Plex. Nine individuals (20%) did not belong to any sub-haplogroup identifiable by the H-Plex, all other individuals belong to H1 (64.4%) and H3 (15.6%) (see table 24). Haplogroup H1 is present in all Neolithic groups with the highest values on the Iberian Peninsula and France (50–75%). In general, out of the 12 sub-hgs found in the overall dataset only hgs H1 and H3 were detected in French and Iberian samples. H3 is missing in the Iberian Bronze Age dataset, however. H3 is virtually absent in Early Neolithic samples of Central Europe and Hungary, only appearing in Central Europe from the Middle Neolithic onwards. High values of H1 can also be observed in the La Tène samples of France. In Eastern European Iron Age samples and the Unetice culture it is virtually absent, while they are – together with the Iron Age samples of Switzerland – the only populations in which hg H2 was detected. In general, the variability is low with only 2 to 5 different sub-hgs per population with the exception of the Iron Age samples of Switzerland, where seven different sub-hgs were detected (see table 24).

Table 24 Frequencies of sub-haplogroups of H in all analyzed groups

Abbr.	Epoch	frequencies of (sub-) haplogroups of H													n	Reference
		H	H1	H2	H3	H4	H5	H7	H10	H11	H13	H14	H16	H23		
NEOI	Late Neolithic Iberian Peninsula	12.5	63	0	25	0	0	0	0	0	0	0	0	0	8	THIS STUDY
CHI	Chalcolithic Iberian Peninsula	19.4	65	0	16	0	0	0	0	0	0	0	0	0	31	THIS STUDY; CHANDLER 2003
BAI	Bronze Age Iberian Peninsula	25	75	0	0	0	0	0	0	0	0	0	0	0	7	THIS STUDY
TRE	Treilles	0	50	0	50	0	0	0	0	0	0	0	0	0	6	LACAN ET AL. 2011A
ENH	Early Neolithic Hungary	51.4	5.7	0	0	0	23	20	0	0	0	0	0	0	35	KEERL UNPUBLISHED
ENC	Early Neolithic Central Europe	37.5	31	0	0	0	13	0	6.3	0	0	0	6.3	6.3	16	BROTHERTON ET AL. 2013; BRANDT ET AL. 2013; BRAMANTI ET AL. 2009
MNC	Middle Neolithic Central Europe	0	11	0	22	0	56	11	0	0	0	0	0	0	9	BROTHERTON ET AL. 2013; BRANDT ET AL. 2013
BBC	Bell Beaker Central Europe	10	30	0	20	20	20	0	0	0	0	0	0	0	10	BROTHERTON ET AL. 2013
UC	Unetice culture Central Europe	14.3	0	14	29	14	0	14	0	14	0	0	0	0	6	BROTHERTON ET AL. 2013
LTA	La Tène Austria	33.3	22	0	0	11	0	0	0	11	11	11	0	0	9	WARNBERG UNPUBLISHED
LTE	La Tène Hungary/Romania	25	0	13	0	0	38	0	0	0	0	0	25	0	8	WARNBERG UNPUBLISHED
LTF	La Tène France	5.56	50	0	22	0	11	11	0	0	0	0	0	0	18	WARNBERG UNPUBLISHED
LTS	La Tène Switzerland	21.1	11	16	21	5.3	11	11	0	0	0	5.3	0	0	19	WARNBERG UNPUBLISHED

9.3.1 PCA

The first two components of the PCA comprise 45.6% of the total variance (see fig. 26). The Iberian groups are grouped closely together with the French Treilles and La Tène culture, and the Middle Neolithic of Central Europe. The presence of H3 in the Unetice and Bell Beaker cultures and Middle Neolithic of Central Europe separates them from the Early Neolithic groups of Hungary and Central Europe alongside the second component. The presence of H4 in the BBC and UC of Central Europe, a haplogroup that is not present in any other Neolithic to Bronze Age group, results in their separation from the others alongside the first component: The strong H1 background in the Central European Bell Beaker, however, pulls them nearer to the Iberian cultures on this axis. The Early Neolithic samples from Hungary and Iron Age samples of Eastern Europe have the highest abundance of indefinable sub-hgs with only three diagnosable sub-haplogroups, resulting in their intermediate position on the plot. The same is true for the Bronze Age samples of Iberia, but their high values of sub-hg H1 place them close to the other Iberian groups.

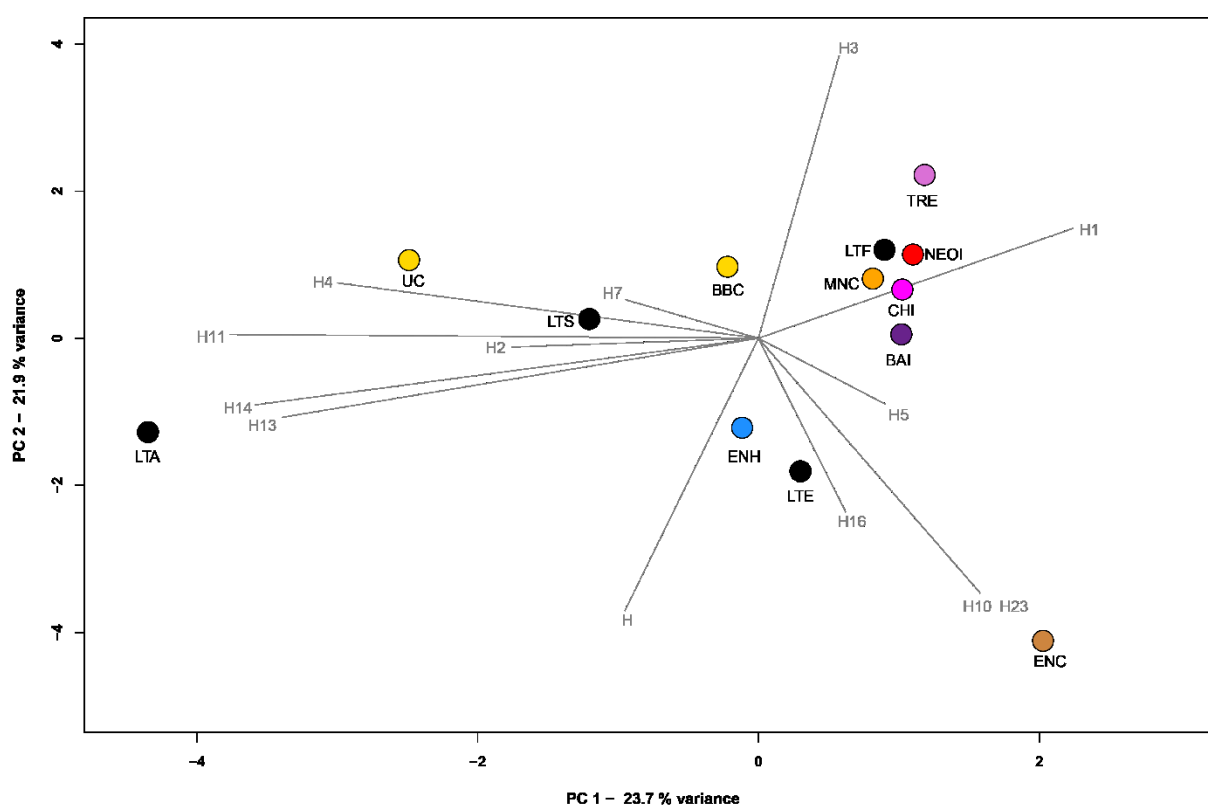


Figure 26 PCA with European haplogroup H dataset

The Late Neolithic of the Iberian Peninsula (NEOI) is colored red, Chalcolithic (CHI) magenta, and Bronze Age (BAI) purple. Treilles samples are colored light purple. The Early Neolithic of central Europe (ENC) is symbolized by a brown circle, the Middle Neolithic (MNC) by an orange circle, and Bell Beaker (BBC) and Unetice culture (UC) by yellow circles. The Early Neolithic of Hungary is represented by a blue circle and all Iron Age groups by black circles.

9.3.2 Cluster analysis

The cluster analysis first separates the two Iron Age populations of Hungary/Romania (LTE) and Austria (LTA) together with the Early Neolithic from Hungary (ENH) and Central Europe (ENC) from the remaining groups (see fig. 27). The other main cluster separates in its first split the three Iberian groups from the others with a significant bootstrap value for the cluster between the Iberian Neolithic and Chalcolithic. The other sub-cluster is subdivided into the Unetice culture (UC) and Iron Age Switzerland (LTS) samples on the one hand and in this order: Middle Neolithic Central Europe (MNC), Bell Beaker Central Europe (BBC), Treilles culture (TRE), and Iron Age France (LTF) on the other hand.

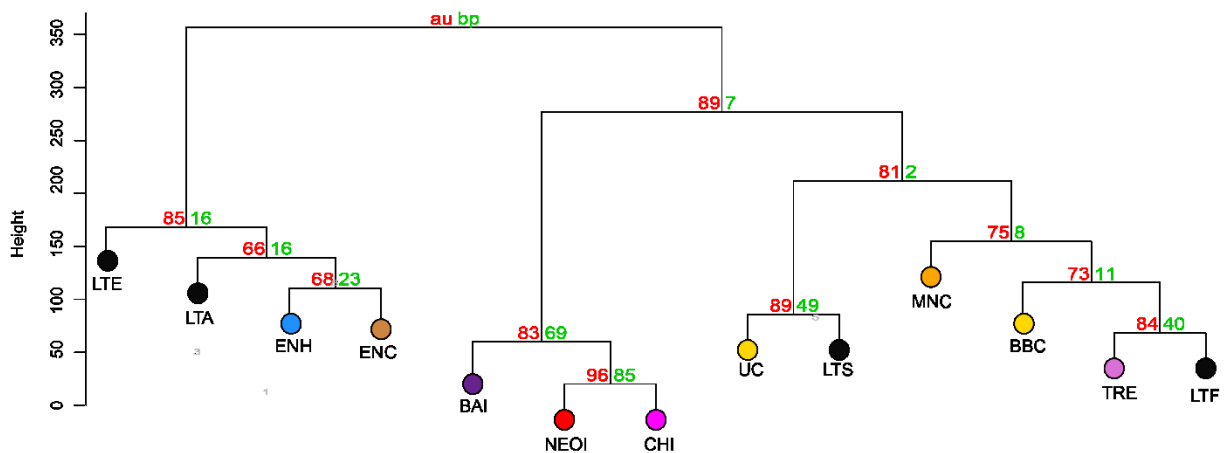


Figure 27 Cluster analysis of European haplogroup H dataset

The Late Neolithic of the Iberian Peninsula (NEOI) is colored red, Chalcolithic (CHI) magenta, and Bronze Age (BAI) purple. Treilles samples are colored light purple. The Early Neolithic of central Europe (ENC) is symbolized by a brown circle, the Middle Neolithic (MNC) by an orange circle, and Bell Beaker (BBC) and Unetice cultures (UC) by yellow circles. The Early Neolithic of Hungary is represented by a blue circle and all Iron Age groups by black circles. “au” gives the approximately unbiased p-value and “bp” the bootstrap probability value.

9.3.3 Fisher-test

To test whether the differences in haplogroup composition among the groups were significant, a Fisher-test was conducted (see table 25). The Iberian groups are not significantly different to each other, to the Treilles culture, and to the Iron Age samples from France (LTF), but to the Early Neolithic of Hungary (ENH), the Middle Neolithic of Central Europe (MNC), and the East European Iron Age (LTE). While the Chalcolithic dataset (CHI) shows significant differences to almost all non-Iberian groups, the Bronze Age (BAI) samples are only significantly different to two further groups, namely the Unetice culture (UC) and the Iron

Age from Switzerland (LTS). The Early Neolithic dataset of Hungary (ENH) is significantly different to all analyzed groups. Within the Central European Early Neolithic to Bronze Age groups, significant differences can only be observed between the Early Neolithic and Middle Neolithic and between the Early Neolithic and the Unetice culture. These two are furthermore the only Central European groups that show differences to any of the Iron Age groups, namely the La Tène samples from France (LTF) in both cases. Among the Iron Age samples significant differences can only be observed between the French dataset (LTF) and those from East Europe (LTE) and Austria (LTA) respectively.

Table 25 Results of the Fisher-test with the European haplogroup H dataset

Significant values (≤ 0.05) are bold and underlined.

	NEOI	CHI	BAI	TRE	ENH	ENC	MNC	BBC	UC	LTF	LTS	LTE	LTA
NEOI	*	0.8585	0.7183	0.7667	<u>0.0002</u>	0.1878	0.0248	0.5712	0.0830	1.0000	0.2929	<u>0.0042</u>	0.1885
CHI	0.8585	*	0.8212	0.1304	<u>0.0001</u>	<u>0.0045</u>	<u>0.0001</u>	<u>0.0062</u>	<u>0.0002</u>	0.0652	<u>0.0003</u>	<u>0.0001</u>	<u>0.0033</u>
BAI	0.7183	0.8212	*	0.1219	<u>0.0001</u>	0.3340	<u>0.0037</u>	0.1463	0.0047	0.3320	<u>0.0466</u>	<u>0.0026</u>	0.1867
TRE	0.7667	0.1304	0.1219	*	<u>0.0001</u>	<u>0.0429</u>	0.0760	0.5327	0.2004	0.7855	0.3555	<u>0.0029</u>	0.0892
ENH	<u>0.0002</u>	<u>0.0001</u>	<u>0.0001</u>	<u>0.0001</u>	*	<u>0.0052</u>	<u>0.0011</u>	<u>0.0003</u>	<u>0.0004</u>	<u>0.0001</u>	<u>0.0011</u>	<u>0.0114</u>	<u>0.0020</u>
ENC	0.1878	<u>0.0045</u>	0.3340	<u>0.0429</u>	<u>0.0052</u>	*	<u>0.0094</u>	0.1686	<u>0.0102</u>	<u>0.0265</u>	0.0570	0.1558	0.4161
MNC	<u>0.0248</u>	<u>0.0001</u>	<u>0.0037</u>	0.0760	<u>0.0011</u>	<u>0.0094</u>	*	0.2971	0.0811	0.0896	0.2463	0.1383	0.0078
BBC	0.5712	<u>0.0062</u>	0.1463	0.5327	<u>0.0003</u>	0.1686	0.2971	*	0.4569	0.4066	0.5691	0.1230	0.4099
UC	0.0830	<u>0.0002</u>	<u>0.0047</u>	0.2004	<u>0.0004</u>	<u>0.0102</u>	0.0811	0.4569	*	<u>0.0234</u>	0.8808	0.1870	0.5235
LTF	1.0000	0.0652	0.3320	0.7855	<u>0.0001</u>	<u>0.0265</u>	0.0896	0.4066	<u>0.0234</u>	*	0.0928	<u>0.0013</u>	<u>0.0144</u>
LTS	0.2929	<u>0.0003</u>	<u>0.0466</u>	0.3555	<u>0.0011</u>	0.0570	0.2463	0.5691	0.8808	0.0928	*	0.2524	0.2899
LTE	<u>0.0042</u>	<u>0.0001</u>	<u>0.0026</u>	<u>0.0029</u>	<u>0.0114</u>	0.1558	0.1383	0.1230	0.1870	<u>0.0013</u>	0.2524	*	0.0986
LTA	0.1885	<u>0.0033</u>	0.1867	0.0892	<u>0.0020</u>	0.4161	0.0078	0.4099	0.5235	<u>0.0144</u>	0.2899	0.0986	*

10 Discussion of molecular genetic methods

10.1 Amplification success

When comparing the amplification success for HVR I sequences and the GenoCoRe22, it is obvious that the latter is the more powerful approach (54% vs. 72% in this study), due to targeting substantially shorter amplicons – an important factor when working with degraded DNA. Similar results have been reported in other studies (HAAK ET AL. 2010; BRANDT ET AL. 2013). However, a differentiated view of the amplification success revealed strong differences among the different regions of the Iberian Peninsula: the highest amplification rates were observed in Northern Spain, the Ebro- and Ambrona Valley, and Northeast Spain (71-100%), while especially the southern part of the Iberian Peninsula had very low amplification success rates (3%). When compared to other publications about Iberian ancient DNA data, GAMBA ET AL. (2011) and SAMPIETRO ET AL.(2007) report considerably lower amplification success rates of 46-59% for samples of Northeast Spain and the Ebro Valley than the 71-100% achieved in this study. At the same time, HERVELLA ET AL. (2012) obtained similar amplification rates for samples out of the Ebro Valley and the Cantabrian region as were observed in this study (~91%). In her PhD thesis, Chandler reports an amplification success between 32% and 35% for Portuguese samples (CHANDLER 2003, 131FF). Obviously, besides different post-excavation histories that may result in various states of preservation, the region where samples have been taken seems to play an important role. Because all datasets for the particular regions consisted of at least two sites, the results cannot just be explained by poor preservation of one site.

Due to the amplification strategy in this study that included the application of different primer-systems according to appraisal of DNA preservation by preceding PCRs (see chapter 8.1) the amplification success per primer was not very meaningful. Since the GenoCoRe22 was initially applied to all samples, it naturally shows a comparably low amplification success. The shorter primers of the 6-primer-system were commonly used for less well preserved samples and therefore had similar amplification success rates to the ones from the 4-primer-system that was used for better preserved samples, despite amplifying shorter amplicons. However, the amplification success rate of the primer pair 16307–16402.C (45%) suggests that it was either not used under optimal conditions or it should be replaced

10.2 Contamination

In general, contamination of samples by genetic investigators and thus false-positive haplotype assignment is very unlikely. No sign of contamination by the principal genetic researcher, who was involved in most of the sampling and sample preparation as well as in all extractions and almost all PCRs, was found in the samples. Haplotypes of two of the other three genetic investigators (2 and 3) who were involved mainly in sample preparation coincided with haplotypes of some samples they worked with. No signs of contaminations were found in a number of other samples they handled at the same time. No milling control contamination matched the haplotype of any of the researchers that generated it. Above all, investigators 2 and 3 have very common haplotypes, both nowadays and in prehistory, arguing for a coincidental analogy of lineages with ancient samples. Of the two other researchers involved in sampling, one genetically matched the mtDNA lineage of one of the samples he handled. However, this lineage was not found in any other of the samples he handled – again arguing for a coincidental match.

The contamination rate of blank controls was very low for ancient DNA studies with 2.15%. When working with ancient human specimen it is impossible to avoid contamination completely. Anyway, sufficient reproduction of analyses and careful interpretation of results as presented in the next chapter still enable confident declaration of authenticity. Only few milling and extraction controls showed contaminations in more than one fragment of the HVR I and repetition of PCRs in the particular fragments led in most cases to uncontaminated results. In three extraction/milling blanks though, lineages could be reproduced in the same fragment. However, the particular lineages were neither found in any other overlapping fragments of the HVR I, nor in any sample associated in extraction, milling or PCR. When comparing sequencing results of blanks and associated samples, haplotype matches only occurred for very common lineages like rCRS, 16298C, and (16069T) 16126C. In all cases the haplotype of the samples in question was reproduced over several uncontaminated PCRs and independently extracted samples, arguing for authentic results despite matches to single blanks. In a few cases, haplotype contaminations of blanks matched contaminations in associated samples. In case of extraction blanks this occurred only in the PCRs R319 and R346 where a rCRS lineage in the second or fourth fragment of the 4-primer-system was found in blanks and (few clones of) an associated sample of the same extraction. In addition to the fact that rCRS lineages are very common, repetition of the blanks in the particular fragments led to uncontaminated results. Therefore, it is more likely that the contamination occurred during the particular PCRs rather than the extraction. Lineage matches of PCR blanks and contaminations in associated samples were almost

exclusively the case for three PCRs where two blanks and single samples show a mutation at position 16298C. This concerns only PCRs of the primer pair 16287–16410 and stopped after exchanging the primer stock solution. Therefore, contamination most likely happened during the initial dilution of this particular primer-pair. The only other cases of verifiable PCR contaminations are limited again to contaminations of blanks and samples (Fupe1a and Junc5a) with rCRS lineages. However, in the case of sample Fupe1a nearly all PCRs of the extract show a haplotype different from the haplotype of hg X confirmed by two other extractions, thus arguing for a contamination of the sample most likely during excavation or after. In case of sample Junc5a, repetition of the PCR confirmed the SNP at position 16093. A connection between amplicon length of the different primer pairs and contamination rate was not detected in this study.

Only 3.7% of the analyzed individuals had to be discarded due to multiple reproducible contaminations. In most cases, they belonged to sites that seemed to be poorly preserved in general (La Bastida, Fuente Álamo, Can Gambús, Humanejos) or very old excavations with unknown post-excavation history (Gruta de Malgasta, Gruta do Poço Velho). In case of sample Fupe2 from the site of Fuentepecina 2, HVR I and GenoCoRe22 results showed different haplogroups/haplotypes for both samples. It seems likely that two samples did not belong to the same individual. A contamination rate of about 2% in PCRs of authenticated individuals matched well that of the blanks, arguing for a successful monitoring of contaminations during analyses.

10.3 Authentication of results

Since the risk of modern human DNA contamination in prehistoric human remains is high in paleogenetic investigations, numerous criteria for endogenous aDNA authenticity have been established (see chapter 3.2.2). Even when considering all recommended criteria and applying strict scientific protocols, contamination of samples cannot be ruled out entirely. Therefore ancient human DNA analyses must be evaluated by conducting independent experiments in a logical framework thus ensuring the assessment of authenticity probability. Criteria for authentication of ancient DNA results that were applied in this work are discussed in the following:

1. All HVR I profiles were replicated and reconstructed from at least two independent extracts obtained from two anatomically distant regions. The HVR I was amplified by numerous overlapping amplicons. Ambiguous sequences from PCR products were cloned, and 4-8 clones per PCR were sequenced.

2. Due to the primer-systems applied, amplification of the HVR I enabled the identification of contiguous sequences with high SNP calling redundancy in the overlapping regions.
3. The authenticity of the individuals depended on several independent amplifications targeting different loci of the mitochondrial genome (HVR I and coding region SNPs). In all cases, the HVR I sequences supported the haplogroup assignment by the GenoCoRe22 SNP multiplex assay as did the results of the ExtraCoRe assays.
4. All haplotypes could be imbedded in the current mitochondrial phylogeny. In all cases of one step SNP differences of haplotypes to the current phylogeny – probable when working with ancient samples – the latter are safely confirmed by several PCRs and by sequencing in combination with other SNPs.
5. Characteristic post-mortem DNA damage-derived substitutions (mostly C→T and G→A transitions) were observed in PCR product sequences. Generally, these substitutions were neither reproducible nor consistent and can be distinguished from genuine SNP calls.
6. Blank controls (milling, extraction, PCR) allowed monitoring and controlling of contaminations within the laboratory or in the reagents. The contamination rate of blanks (2.15%) (see chapter 8.2) was very low for ancient DNA analyses as was the amount of contamination in individuals (1.9%). For the majority of detected contamination an influence on samples that were analyzed in parallel was excluded, the remaining can be assigned to very common haplotypes, mainly the rCRS. Due to independent reproduction of samples, loci, and PCRs, false-positive haplotype assignment of samples due to undetected contamination can be excluded.
7. Only few researchers were involved in the genetic analyses (CRO, JB, AP, and SL). The latter three were mainly engaged in sample preparation with only SL and AP being involved in few extractions and PCRs. HVR I and in some cases additional HVR II profiles of all genetic investigators and people involved in sampling and if possible in excavation were sequenced and compared to the aDNA results in order to monitor potential contamination.
8. Most sites show a variety of haplotypes and haplogroups arguing against contamination by researchers even if the haplotype of a researcher coincides with one individual.

11 Discussion of population genetic methods

11.1 Datasets

Defining populations or groups for population genetic analyses is naturally prone to criticism. This regards for example the definition of chronological entities, e.g. where to draw the line between Early and Late Neolithic, of geographical units, e.g. what should be regarded as Central Portugal, or to setting apart a group of individuals based on an archaeological cultural assignment like the Bell Beakers. The more specific a defined population can be assigned to a small time span or region, the better. However, ancient DNA analyses are often limited by available data and populations too small in size do not have much statistical value. Hence, pooling individuals and archaeological sites into separate groups is always a balancing act between the desire of archaeologists for very local and chronological close groups and the requirements of statistical analyses for greater datasets.

In this thesis, chronological classification was based on the one hand on archaeologically defined periods like Neolithic, Chalcolithic, and Bronze Age. On the other hand, especially detailed chronological classification of 6th to 4th millennium data was limited by the number of available samples. Therefore, it was only possible to differentiate between Early and Late Neolithic. However, this classification represents the finest resolution for Iberian data so far: In previous studies data between 5,400 and 4,000 cal BC (GAMBA ET AL. 2011) or even between 5,300 and 3,000 cal BC (HERVELLA ET AL. 2012; BRANDT ET AL. 2013, IN PRESS) were pooled into one Early Neolithic (!) group. As to geographical units, the classification used in this study is mostly in accordance with topography and archaeological research. However, in some cases this led to groups of very small sample sizes (< 10 individuals) and results for these groups should be considered with caution. Last but not least, investigating archaeological cultures separately by an independent discipline should not raise eyebrows but should rather be seen as an interesting chance to test archaeological hypotheses or assumptions. Of course any genetic interpretation should be undertaken with great care and by keeping in mind that a common material culture does not necessarily represent a population with a shared ethnic identity.

11.2 Haplogroup-based methods

In general, results of haplogroup-based methods are dependent on the degree of haplogroup resolution applied. In this study, the sub-haplogroup resolution was mostly limited by the amount of markers investigated by other researchers. Although resolution of haplogroup H at

least in H1 and H3 would have been feasible for all individuals of this study, it would not have been possible for most individuals that were taken from other publications. Hence, sub-hg resolution for only a fraction but not the total dataset would have caused biases in the analyses. The greater amount of haplogroups differentiated in analyses with the additional Central European dataset is due to the fact that outside the Iberian Peninsula additional haplogroups, like R and C, were detected.

11.3 Sequence-based methods

In this thesis, F_{ST} values and therefore the Slatkin Matrix used to conduct the MDS were computed for different datasets. On the hand in a classical approach, HVR I sequences of a defined sequence range were used. However, sequence-based genetic distances cannot differentiate identical HVR I sequence motifs of different haplogroup affiliation. As has already been mentioned (see chapter 7.5) this is especially a problem for the Iberian dataset where indeed a number of sequences are identical to the rCRS reference sequence but assigned via additional SNPs to hgs H, U, and V. Thus, genetic distances among different groups could easily be underestimated. Therefore, additional phylogenetic information was added in the form of the GenoCoRe22 results. In the GenoCoRe multiplex assay ancestral and derived SNPs for 22 coding region nucleotide positions of the mitochondrial genome were analyzed. While this might simply be an unusual approach for individuals for whom the GenoCoRe multiplex was indeed analyzed (all individuals of this study and the majority of the Central European comparative dataset derived from the study of BRANDT ET AL. [2013]), it causes problems with data from other working groups that did not use the multiplex assay. However, haplogroup assignment for the latter individuals was either determined by HVR I sequences or by analyzing particular SNPs on the coding region or HVR II. Most of the SNPs analyzed in the GenoCoRe are very specific for the particular haplogroup or else only occur in a derived form in few other sub-hgs of for example hgs B, L or F – haplogroups not detected in the Iberian dataset - and therefore individuals of a particular haplogroup always show the same pattern of ancestral and derived SNPs. All of the 249 successfully analyzed individuals of this study showed expected patterns for their haplogroup in the GenoCoRe22. Hence, when we trust the haplogroup information of the paper and the mitochondrial phylogeny in general, no biases should be caused by artificially creating GenoCoRe profiles for individuals of which they had not been on hand.

The direct comparison in the same scale of MDS plots with and without phylogenetic information added showed the power of the approach. In most cases, the same groups were clustered together due to low genetic distance but patterns became much more evident.

11.4 Shared haplotype analyses

Shared haplotype analyses are always just an indication of connections between groups and, because they are set in relation to the number of individuals, are highly dependent on the amount of data available. The likelihood of finding shared haplotypes increases with the amount of individuals present in one group. Therefore, estimated values should be considered with great caution as they just give an indication of genetic relations among different groups. Another problem is the ubiquitous amount of rCRS lineages of haplogroup H in almost all groups. Phylogenetic resolution of this work has shown that they often belong to different sub-haplogroups. However, information about sub-hgs was not available for the majority of individuals analyzed by other researchers. This concerns mostly the hunter-gatherer and Early Neolithic samples. Many Late Neolithic groups and all Chalcolithic groups on the other hand are made up of data from this study, where these information was available, and a more detailed estimation of shared haplotypes considering sub-hg information was possible for those. However, regarding all rCRS lineages of haplogroup H as identical led to an overestimation of shared lineages in many groups.

In this work the method of estimating shared haplotypes was adapted to the particular research question. When lineages were tracked between earlier and later populations, the question how many *individuals* had a genetic ancestor in preceding populations stood in the foreground. Therefore, all individuals of one group were considered whether they had different or identical HVR I sequences. When investigating the amount of shared lineages among contemporaneous groups, however, the ostensible question was how many *lineages* are actually shared between two groups. For this reason, the dataset was reduced by identical lineages. Likewise the amount of unique and new lineages was also estimated with a reduced dataset.

12 Discussion of population genetic results

12.1 Genetic structure and relations of Iberian groups from the Mesolithic to the Early Bronze Age

The following chapters will be summarizing and discussing the results of the population genetic analyses of chapter 9.1 in chronological order (Mesolithic to Early Bronze Age). In each chapter genetic relations to previous groups as well as among contemporaneous groups will be discussed. For an overview of groups and regions discussed in the following chapters, compare figure 11 (p. 63). Furthermore, this discussion will only focus on the mitochondrial DNA. Thus, every population dynamic event or detected population continuity discussed hereafter will only apply to the “female side” of prehistory.

12.1.1 Genetic make-up of the Iberian hunter-gatherers

Hunter-gatherer data available from the Iberian Peninsula range from Magdalenien sites (La Chora, La Pasiega, Erralla) to sites temporally overlapping with the arrival of the first farmers (Cabeço de Pez, Cabeço das Amoreiras) and include shell middens from the Sado Valley as well as sites with single or double inhumations like the individuals from La Braña in Asturias. In this study, five individuals of two sites of the Muge complex – Concheiro da Moita do Sebastião and Concheiro do Cabeço da Arruda – have been analyzed. While mitochondrial data of four individuals were too incomplete or no DNA could be amplified at all, one individual of the Concheiro da Moita do Sebastião was successfully assigned to haplogroup U5b, although no HVR I profiles were obtained. It represents therefore the first paleogenetic evidence from the well-known Muge shell middens in Central Portugal. Genetically it fits well within the western European hunter-gatherer haplogroup composition which consists of hgs H, U4, U5b, and N*. To date U4 and N*, represented by one and two individuals respectively, were only found in Portugal and not in the north of Spain. Please note that haplogroup N* was not exclusively found in Portuguese hunter-gatherers but in one Upper Paleolithic individual of the Pagglichi cave in Italy as well (CARAMELLI ET AL. 2003). However, haplotypes differ between the Italian and Portuguese individuals.

Genetically, the hunter-gatherers of Western Europe seem to be distinct from most of the succeeding groups, but genetic relations will be discussed in detail in the following chapters.

12.1.2 The Neolithic transition on the Iberian Peninsula

In this study, mitochondrial profiles of two Early Neolithic individuals from Burgos (Alto de Rodilla and Fuente Celada) in the Northern Meseta, and seven Early Neolithic individuals from the Pyrenean cave site of Els Trocs were generated. Together with published samples (LACAN ET AL. 2011; GAMBA ET AL. 2011; HERVELLA ET AL. 2012; CHANDLER 2003), 53 Early Neolithic data from different regions of the Iberian Peninsula were available for statistical analyses (see also table 5). The Early Neolithic data were subdivided according to their geographical location into four different groups: Northeast Spain, Northern Spain, Central Portugal, and Els Trocs. Els Trocs samples were treated as a separate group (TROCE) because of their geographic location between the groups of Northeast Spain and the Upper Ebro Valley. It should be noted, that the Early Neolithic group of Central Portugal only comprised data from one site (Gruta do Caldeirão), while the Northeast and Northern Spanish datasets were compiled out of two (Can Sadurní and Cova d'Avellaner) and five (Chaves, Paternanbidea, Los Cascajos, Alto de Rodilla, and Fuente Celada) sites respectively.

Haplogroups found in the Iberian Early Neolithic that were not detected in the preceding hunter-gatherer dataset were HV, I, J, K, N1a, T2, V, and X, but only hgs J, K, T2, and X were present in more than one group. Haplogroup N1a, very frequent in Early Neolithic Central European samples and often regarded as important genetic indicator for the Neolithisation of Central Europe (HAAK ET AL. 2005, 2010; BRANDT ET AL. 2013), was detected in Els Trocs for the first time in prehistoric Western Europe. Its haplotype directly matches haplotypes found each in one individual of the LBK sites Derenburg and Halberstadt in Central Europe (HAAK ET AL. 2005; BRANDT ET AL. 2013).

Almost all Early Neolithic groups have a high amount of typical hunter-gatherer haplogroups (H, U4, U5b, and N*), with frequencies of 42% in Northeast Spain, and high values of 56% in Northern Spain and 78% in Central Portugal, while none of these haplogroups was found in Els Trocs. On sequence level the same trends are observable; while the Els Trocs and the Northeast Spain groups only share 0–8% of their lineages with the hunter-gatherers of the Iberian Peninsula, groups of Northern Spain and Central Portugal have 28–33% sequence matches (see fig. 19, p.97). These values, however, are by no means absolute and should just be seen as indicators; the unsatisfying sub-haplogroup resolution of rCRS-lineages for example, might lead to an overestimation of haplogroup H heritage in the Early Neolithic and chronologically later groups. On the other hand, many basal lineages of the haplogroups U, U5b or N* found in Early Neolithic data have not yet been detected in the small hunter-

gatherer dataset, thus probably leading to an underestimation of hunter-gatherer mitochondrial lineages in the Neolithic data.

When compared to the hunter-gatherer mitochondrial gene pool, most Early Neolithic sample sets show high significant genetic differences on haplogroup and sequence level as revealed by Fisher-test and F_{ST} values (see tables 13 and 16, pp.91 and 94). Only the samples of Central Portugal are not significantly different to the hunter-gatherers on haplogroup level. Cluster and principal component analyses put both, the groups of Northern Spain and Central Portugal close to the hunter-gatherers due to their high percentage of haplogroups U, U5b, and H, while the Early Neolithic groups from Northeast Spain and especially Els Trocs were arranged more distant from the hunter-gatherers in both analyses (see figures 16 and 17, pp.89f). Genetic drift as possible factor for the differences between the hunter-gatherers and the Early Neolithic of Northeast Spain and Els Trocs respectively can be excluded by the TPC (see table 15, p.93). All Early Neolithic data pooled together are significantly different in their haplogroup composition to the hunter-gatherers (see table 14, p.92).

Besides their genetic relationship to the hunter-gatherers, the relations of the Early Neolithic groups to each other were of interest. Haplogroup-based statistical analyses (PCA, cluster analysis) reveal a clear separation of especially Els Trocs but also of the samples of Northeast Spain from those of Northern Spain and Portugal (see fig. 16 and 17 pp.89–90). The Fisher-test supports this with significant differences of Els Trocs and Northeast Spain to the Early Neolithic of Northern Spain and Central Portugal (see table 13, p.91). Sequence-based statistical analyses confirm these results: The separation among the four Early Neolithic groups is recognizable in the MDS plot (see fig. 18, p.96), and significantly supported by AMOVAs, where best models support a cluster of hunter-gatherers with Early Neolithic samples of Northern Spain and Portugal on the one hand and a separate cluster comprising Els Trocs and Northeast Spain on the other hand (see tables 17–20, pp.101–103). The number of shared lineages among the different Early Neolithic groups, however, is with 10–40% low and therefore impedes drawing direct genetic links between the different groups (see fig. 19, p.97).

Regarding research question I.1, it is obvious that in all analyzed regions a considerable amount of hunter-gatherer maternal heritage persisted during the Early Neolithic. Hence, the transition from foraging to farming seems to have been accompanied by acculturation of the indigenous hunter-gatherer populations. Regarding research question I.2, all analyses furthermore reveal genetic differences among the Early Neolithic groups, especially in the amount of hunter-gatherer haplogroups/lineages still present. This indicates different forms of Neolithic transitions on the Iberian Peninsula as has been stated by archaeological research

and some paleogenetic publications (HERVELLA ET AL. 2012; BRANDT ET AL. 2013, IN PRESS). It should be noted, however, that especially in Central Portugal, where only data from one Early Neolithic site are available at the moment, an early arrival of Early Neolithic lineages on other sites of the same region as discussed in the Pioneer Colonization model (ZILHÃO 2001) cannot be excluded. The genetic results, however, show that acculturation of hunter-gatherers must have been an important factor in the Neolithic transition of Central Portugal.

The greatest amount of “Neolithic” mitochondrial lineages was found in Northeast Spain, especially the Cova d’Avellaner, and in the Pyrenean cave site of Els Trocs in Aragón. The very early arrival of Neolithic lineages inland could either be explained by very fast dispersal of Neolithic farmers inwards or an alternative entrance of Neolithic lineages via the Pyrenees from France as has been suggested by some scholars (ZAPATA ET AL. 2004; STITKA 2005). Because Els Trocs is a site located in the mountains, it remains unclear at this point where the people who used it actually lived. Archaeological investigations will have to reveal connections via e.g. grave goods to Neolithic groups of Northeast Spain, western France or the Upper Ebro Valley to shed light on this question. However, all results point to Catalonia/Aragón as main entrance of Early Neolithic genetic input, followed by a gradual dispersion of mitochondrial lineages further inland (see fig. 28).

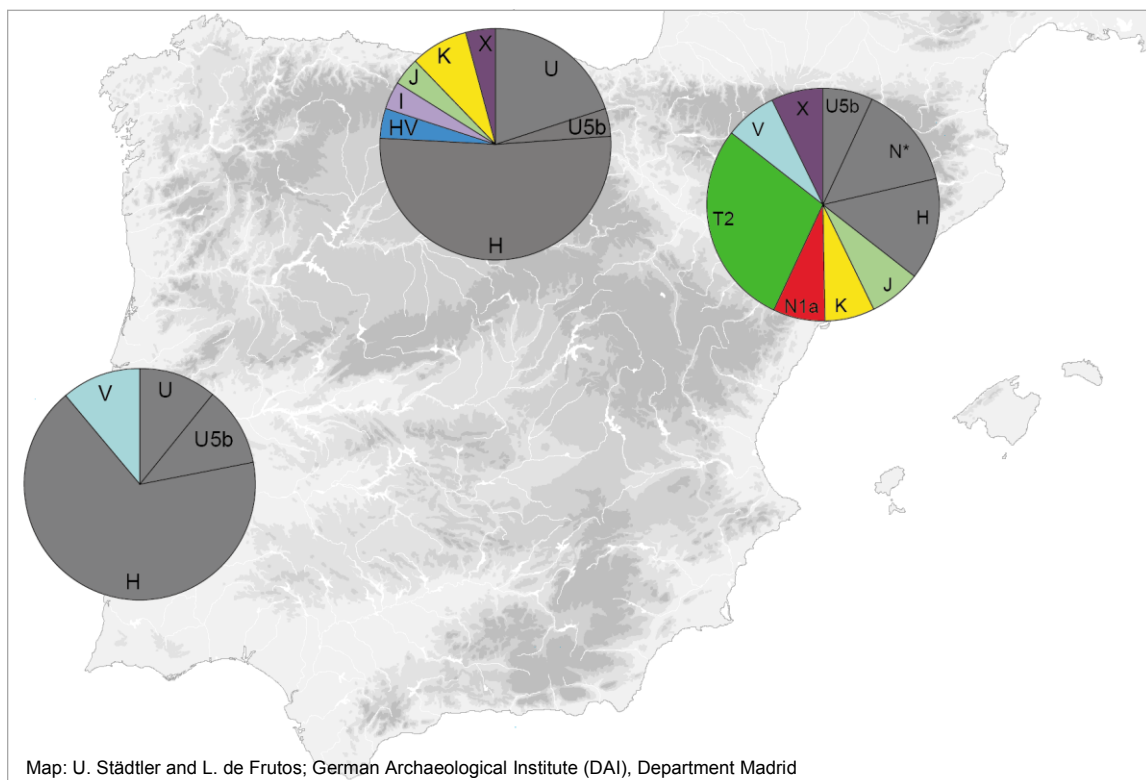


Figure 28 Haplogroup frequencies in the Early Neolithic

Hunter-gatherer haplogroups H, N*, and U5b are colored gray, all other hgs are depicted in different colors, corresponding to the particular haplogroup. The groups of Els Trocs and Northeast Spain were pooled in one pie chart.

12.1.3 Population dynamics during the Neolithic

With this study the amount of data that can be assigned to the Late Neolithic period has significantly increased. The data were pooled according to their geographical location into five different groups: Northeast Spain (NEN), Ambrona Valley (AVN), Ebro Valley (EVN), Northern Meseta (NMN), and Central Portugal (CPN). Advantageously, Late Neolithic data were available for all regions of which Early Neolithic data were discussed in the previous chapter. It should be mentioned that in some regions (Northeast Spain and Central Portugal) the groups comprised sites with deviating dates, ranging from about 4,200 cal BC to 3,000 cal BC. For Gruta dos Ossos in Portugal a single C¹⁴ date even dates into the 3rd millennium BC (OOSTERBEEK 1993B); all other dates of this cave put the burials into the 4th millennium, but none is actually associated with a particular individual (TOMÉ 2006; OOSTERBEEK 1993B). In general, there is a temporal gap of about 1,000 to 1,300 years between most of the Early Neolithic and most of the Late Neolithic groups.

New haplogroups that have not been detected in previous periods are U2 and U3 in the Ambrona Valley, haplogroup W in Northeast Spain, and haplogroup U5a – typical for Central and Eastern European hunter-gatherers – in Central Portugal. Each of these haplogroups was exclusively detected at only one site of each group except for U3, which is also present in one Late Neolithic sample of Els Trocs. Furthermore, haplogroups U2 and W were not found in any succeeding population and seem to have been rare in prehistoric Iberia. The proportion of lineages uniquely found in the Late Neolithic is 22% (see fig. 22, p.100). The difference of 20% between new and unique lineages represents the amount of continuing Late Neolithic lineages into succeeding epochs (see fig. 22, p.100). All Late Neolithic groups still have a considerable amount of haplogroup U5b (8.3% to 24%), while frequencies of haplogroup H are low in the Late Neolithic groups of Central Portugal (17%) and the Northern Meseta (2.7%), moderate in Northeast Spain (31%) and the Ambrona Valley (27%), and only elevated in the Ebro Valley (45%). However, only the Late Neolithic samples of the Ebro Valley (EVN) still clearly cluster with the hunter-gatherers in both cluster analysis and PCA and are not significantly different in the Fisher-test (see fig. 16-17, pp.89–90 and table 13, p.91). Thus, despite decreasing frequencies of hunter-gatherer haplogroups compared to some of the Early Neolithic groups, mitochondrial lineages and haplogroups that had been present on the Iberian Peninsula since pre-Neolithic times were persisting into the Late Neolithic to a considerable but varying degree. Besides the presence of hunter-gatherer haplogroups, the amount of “Neolithic” hgs I, J, K, T2, and X increases in many Late Neolithic groups compared to the Early Neolithic.

In the Northern Meseta genetic discontinuities exist to the preceding Early Neolithic of Northern Spain while on the other hand similarities to Early Neolithic groups of Els Trocs and Northeast Spain can be seen - visible in principal component, cluster and shared haplotype analyses, the MDS and significantly supported by the Fisher-test (see fig. 16–19, pp.89–97 and table 12, p.91). Genetic drift as an explanation for the observed differences to the Early Neolithic of the same and close areas (Northern Spain) can be excluded due to the results of the test of population continuity (TPC) (see table 15 p.93). The results argue for an influx of Neolithic lineages from Northeast Spain or Aragón into the Northern Meseta between the Early and Late Neolithic (see fig. 29). In the Ambrona Valley, no strong genetic links to any particular Early Neolithic group can be drawn, although the closest genetic relations seem to exist to the Early Neolithic of Northeast Spain in most analyses (see fig. 16–19, pp.89–97 and table 12, p.91). The interpretation of these results is complicated by the fact that no genetic data from the Early Neolithic in the Ambrona Valley are available. Early Neolithic groups of this region could either resemble those of Northern Spain or those of Northeastern Spain or a mixture of these two, therefore the amount of new genetic input between Early and Late Neolithic cannot confidently be evaluated (see fig. 29). The test of population continuity can neither exclude Northeast Spain nor Northern Spain as possible source regions (see table 15, p.93).

The Late Neolithic of Central Portugal is genetically distinct to the Early Neolithic of the same region and the Early Neolithic of Northern Spain, visible in principal component, cluster and shared haplotype analyses, the MDS and significantly supported by the Fisher-test (see fig. 16–19, pp.89–97 and table 12, p.91). The PCA arranges the Late Neolithic of Central Portugal in close proximity to the Early Neolithic samples of Northeast Spain as does the MDS (see fig. 16–19, pp.89–98). The changes in mitochondrial haplogroup/haplotype composition between Early and Late Neolithic in Central Portugal may be attributed to genetic influx from other parts of the Iberian Peninsula, for example Northeast Spain or regions with a similar haplogroup composition in the Early Neolithic, or by genetic influence from other Portuguese Early Neolithic sites that might have had a different, more “Neolithic” haplogroup composition compared to the Gruta do Caldeirão from where data are available (see fig. 29). However, because no further Early Neolithic ancient DNA data from Mediterranean Spain or Portugal are known yet, this question has to remain unanswered for now. Genetic drift as cause for the observed differences in Central Portugal can be excluded by the TPC (see table 15, p.93). In Northeast Spain, genetic differences between Early and Late Neolithic are not as evident as in Central Portugal, but strongly indicated by PCA, cluster analysis, and MDS. However, this group is genetically different from all other groups of Spain and Portugal. Situated at the northeastern Mediterranean coast of the Iberian

Peninsula it is naturally the best candidate to have been influenced by Central Europe or southwestern France respectively. However, its genetic dissimilarity to all preceding and succeeding groups of the same area and the Iberian Peninsula in general, raises questions about its representativeness, especially because the data set is mainly made up of one site that shows very rare hgs like I, W, and H8. Based on Bayesian simulations, GAMBA ET AL. (2011) argue in their study that high genetic differences between Early and Late Neolithic in Northeast Spain had to be rather a result of genetic drift than of new genetic influx. Although compositions of the Early and Late Neolithic groups in their study were different than in this study, the test of population continuity applied in this study can also not exclude genetic drift as cause for the observed genetic differences (see table 15, p.93).

Genetic continuity to previous populations of the same area can only be proposed for the Upper Ebro Valley. Cluster analysis and PCA both place the Late Neolithic samples of the Upper Ebro Valley close to the Early Neolithic samples of the same area (NSE) (see fig. 16–17, pp.89f, and fig. 29). This impression of genetic continuity from the Mesolithic onwards in the Upper Ebro Valley is supported by MDS and AMOVAs and mirrored in a high amount of shared lineages to hunter-gatherers and the Early Neolithic of Northern Spain (see fig. 18, p.96 and tables 17–21, pp.101–103).

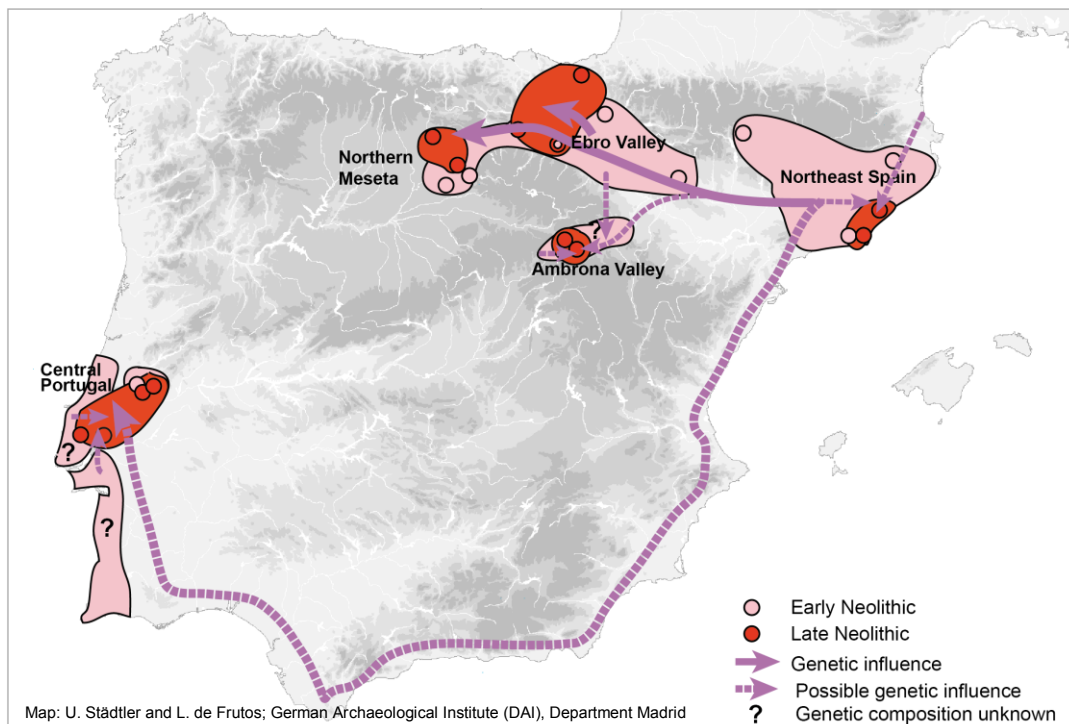


Figure 29 Possible scenarios to explain Late Neolithic genetic composition based on available data

Sites used in statistical analyses are depicted as pink (Early Neolithic) or red (Late Neolithic) circles. Pink areas cover regions with known Early Neolithic mitochondrial data, areas of which Late Neolithic data are available are depicted in red. Regions which potentially could have had an influence on Late Neolithic data, but from where no Early Neolithic data were available are indicated by question marks.

Most analyses (PCA, cluster analysis, F_{ST} values, and shared lineages) draw some connections in genetic composition between the Late Neolithic groups of the Northern Meseta and Central Portugal, while especially the MDS arranges those of the Ambrona Valley and Central Portugal in close proximity. The different genetic affinities of the Central Portuguese group in different statistical methods can most likely be explained by the fact that the dataset only comprised half as many individuals in the sequence-based statistical analyses compared to haplogroup-based statistical analyses. Direct lineage matches among the different Late Neolithic groups range between 7% and 22% (see fig. 20B, p.98). Only the Central Portuguese group shares 50% of their lineages with most of the contemporaneous groups, thus revealing similarities in population history to other parts of the Iberian Peninsula concordant to the observed discontinuity to the Early Neolithic in this area.

Most interestingly, Late Neolithic groups of the Upper Ebro Valley (EVN) and the Northern Meseta (NMN) – though situated in close geographical proximity – are very different to each other on the mitochondrial level. The most “natural” route from Northeast Spain to the Northern Meseta would have been along the Ebro Valley, directly passing at least the sites of Fuente Hoz and Los Cascajos (see fig. 29). How can the differences between the contemporaneous sites be explained? On the one hand, radiocarbon dates of Reinoso indicate a short occupation with no Early Neolithic chronology (see table 1), while Los Cascajos has been used since Early Neolithic times (HERVELLA ALFONSO 2012, p.68). Thus, continuation of mitochondrial lineages may at least in Los Cascajos just be a result of a continuous use of the site by a relatively unchanged population. Another possible explanation might be the difference in burial architecture: The sites of Reinoso (pers. communication M. ROJO GUERRA) and Fuentepecina in the Northern Meseta were built in megalithic architecture (ROJO GUERRA AND GARRIDO PENA 2012), while Los Cascajos and Fuente Hoz in the Upper Ebro Valley are an open-air site and a small cave respectively (HERVELLA ALFONSO 2012, pp.68; BALDEÓN ET AL. 1983). In this context, it would be interesting to analyze if megalithic burial sites in the Basque Country and Navarre rather resemble sites of the same region like Los Cascajos or sites like Reinoso in their haplogroup composition. By no means, however, shall be indicated that groups with megalithic burial tradition represent a population with a shared cultural or genetic identity. As can be seen from two other megalithic sites in the Ambrona Valley – La Mina and La Tarayuela – individuals from these sites do not share an identical genetic signature. Though genetically closer to each other than to the group of the Ebro Valley in most analyses, Northern Meseta and Ambrona Valley Late Neolithic groups were significantly different to each other in many analyses including the Fisher-test.

Summarized, the paleogenetic data from five geographically distinct regions of the Iberian Peninsula support the theory that the dispersal of Neolithic lineages after the initial Neolithic transition was not a uniform process but varying compositions of mitochondrial lineages of the Mesolithic and “Neolithic package” established or remained in the different areas. To answer research question I.3: In some areas genetic continuity to the Early Neolithic seems highly likely (Ebro Vally), while other regions show great genetic differences to the preceding period (Central Portugal, Northern Meseta). The example of the Upper Ebro Valley and the Northern Meseta shows that different population dynamic processes might have happened in close geographical proximity to each other. Genetic commonalties suggest a dispersal of Early Neolithic lineages from Northeast Spain and/or neighboring regions into the Northern Meseta and Central Portugal in the course of the 5th millennium BC. The interpretation of population dynamics in Northeast Spain is complicated by the disputable reliability of available data and the inconsistency of the results of the different statistical approaches used in this study. Likewise in the Ambrona Valley, results were not consistent enough to confidently assign an Early Neolithic source region for the observed genetic composition, furthermore complicated by the lack of Early Neolithic data from this region. Another important question that remains to be answered is the presence of haplogroup U5a in Portugal, a haplogroup that is very untypical for the prehistoric Iberian Peninsula. Either it has not been detected so far and has even already been present in pre-Neolithic hunter-gatherers or it represents a Central European influence. In this scenario, however, it remains to be answered why it has only been detected in the most western part of the Iberian Peninsula and not in areas that would have been part of the “natural” route of putative Central European immigrants.

12.1.4 The Chalcolithic

Chalcolithic data came from Northeast Spain, East Spain, Central Portugal, the Southern Iberian Peninsula (Mediterranean Portugal), and from the Southern Meseta.

Most of the Central Portuguese data (denoted as CPC in the analyses) cannot clearly be assigned to the Bell Beaker or non-Bell Beaker period: while the individual from Cadaval was buried with Bell Beaker pottery (TOMÉ AND SILVA 2013), stratigraphic information for the site Tholos de Paimogo I is scarce and the data may include Central Portuguese Bell Beaker and/or non-Bell Beaker individuals (pers. communication MICHAEL KUNST). Therefore, this group was considered separately in the Fisher-test. The site Hipogeu de Monte Canelas I was denoted as Southern Iberian Peninsula Chalcolithic, however, dating and archaeology put it at the transition from the Endneolithic to the Chalcolithic. Here, they were considered as Chalcolithic because its dating coincides rather with other Chalcolithic groups considered in this work than with the Late Neolithic groups. In general, many sites in Portugal of this time are denoted as “Endneolithic/Chalcolithic” in publications (e.g. SILVA 2003; SILVA AND FERREIRA 2008; WATERMAN ET AL. 2014). From both Portuguese groups, however, too few HVR I data were available and they were not part of any sequence-based statistical analyses.

Investigating local genetic continuity between the Chalcolithic and Late Neolithic was only possible for regions of which Late Neolithic data were available, thus excluding the Southern Meseta, East Spain as well as the southern Iberian Peninsula. Similarities in the genetic composition between the Late Neolithic and Chalcolithic can be observed in Central Portugal, where all analyses (PCA, cluster analysis, and Fisher-test) put the respective groups close together (see fig.17–18, pp.89f and table 13, p.91). In Northeast Spain, no significant genetic differences seem to exist between the Late Neolithic and the Chalcolithic group (see table 16, pp.94), but both groups are clearly separated from each other in PCA and cluster analysis. The Fisher-test, however, found the haplogroup differences to be not significant and the TPC cannot exclude genetic drift as possible driving force for the observed differences (see table 15, p.93). On the other hand genetic similarities between Early Neolithic and Chalcolithic are indicated by PCA, cluster analyses, MDS, and Fisher-test. A population shift between Early and Late Neolithic followed by another event in the Chalcolithic back to Early Neolithic genetic variation seems not too likely, thus further arguing for a closer look on the Late Neolithic of this region by analyzing additional sites.

For regions where no Neolithic data were available, comparisons of Chalcolithic groups to Late Neolithic groups of other regions were made. The Late Neolithic group of the Ambrona

Valley is the genetically closest Late Neolithic group to the Chalcolithic of East Spain and the Southern Meseta in both PCA and cluster analyses (see fig. 16–17, p.89f). The Chalcolithic of East Spain and the Southern Meseta share most lineages with the Late Neolithic groups of the Ambrona Valley (~50%) and Northeast Spain (38–50%), while especially the Chalcolithic group of the Southern Meseta has only few lineage matches to the Late Neolithic of the geographically closely located Northern Meseta (>20%) (see fig. 21, p.99). Interpretation of the genetic differences between the Late Neolithic of the Northern Meseta and the Chalcolithic of the Southern Meseta are complicated by the fact that neither Chalcolithic data from the Northern Meseta – if one does not count the Bell Beaker data – nor Neolithic data from the Southern Meseta are available. Thus, genetic differences might be due to regional or chronological reasons. Genetic similarities of East Spain to the Ambrona Valley do not necessarily argue for a genetic input from this region but may reflect genetic variation of Late Neolithic East Spain that was genetically influenced during the Neolithic by the same source region.

Besides drawing conclusions about genetic links to earlier epochs, the genetic relations of the Chalcolithic groups to each other were of interest: Although the Fisher-test estimates no significant differences among the non-Bell Beaker Chalcolithic groups, both PCA and cluster analysis separate the groups of Northeast Spain and Central Portugal from those of East Spain, the Southern Meseta, and the Southern Iberian Peninsula. The latter three have some of the highest frequencies of haplogroup H (34–50%) of all prehistoric Iberian groups, while Central Portugal and Northeast Spain have higher values of hg K (40% and 27%) and T2 (6.7% and 13%) but only a low amount of haplogroup H (20% and 6.7%). Thus, in Chalcolithic Portugal genetic differences between the southern and central parts of the country become evident. Both groups share only two haplogroups, J and K. While all individuals of haplogroup H of the South could be assigned to the sub-haplogroup H1, individuals of Central Portugal belonged almost exclusively to haplogroup H3, except for one individual from the site of Bolorés. Haplogroup HV, found in one individual of Monte Canelas I in the South, was not detected in Neolithic or Chalcolithic Central Portugal. The site of Perdigões that was not part of the statistical analyses is situated in the Alentejo region of Portugal, between southern and Central Portugal. Genetically it can be linked to the sites of the Estremadura in Central Portugal by the presence of haplogroup U5a and to the site Monte Canelas I in the southern part of the country by the presence of haplogroup H1. Due to the lack of Neolithic data from southern Portugal it is impossible to say if the different mitochondrial signatures had been established in Neolithic times or emerged within the Chalcolithic period.

While there were too few Portuguese samples for sequence-based statistical analyses, the Chalcolithic of Northeast Spain could be compared to other contemporaneous groups on sequence level as well. Only about 20% of the lineages found in the groups of East Spain and the Southern Meseta are shared with the Chalcolithic group of Northeast Spain (see fig. 21, p.99). The Northeast Chalcolithic group can be differentiated from those of East Spain and the Southern Meseta in the MDS as well, although F_{ST} values between Northeast Spain and both groups are not significant (see fig. 18, p.96 and table 16, p.94).

All in all, sequence-based statistical analyses confirm population differences between Northeast Spain and more southern and western located regions in the Chalcolithic. Why the Chalcolithic mitochondrial composition of Central Portugal and Northeast Spain show similarities to each other while the groups that are geographically located between them are different, cannot be answered without more Neolithic data. Conceivable scenarios would be on the one hand that East Spain and the southern Portugal were not as much affected by genetic influence of Neolithic farmers that passed these regions on their way to Central Portugal between the Early and Late Neolithic. Alternatively, Neolithic lineages could have reached Central Portugal via a different route, maybe from Central Spain. A third possible scenario would be that further population dynamic processes affected groups in the triangle between eastern Spain, southern Portugal, and the Southern Meseta after the Neolithic.

To sum up, especially in the Chalcolithic period proposing population dynamic scenarios is complicated by the lack of Early and Late Neolithic data in many regions, thus complicating the evaluation of research question I.4. However, in Central Portugal enough Neolithic data were available to suggest mitochondrial consistency in this region between the Late Neolithic and Chalcolithic while genetic differences existed between Chalcolithic Central and southern Portugal. The haplogroup composition of Chalcolithic Northeast Spain seems to have been similar to that of Central Portugal. Due to the disputable reliability of Late Neolithic data from Northeast Spain (see also chapter 12.1.3), conclusions about genetic continuity in this region are difficult to make, though genetic connections at least to the Early Neolithic are indicated by several analyses. Although it was not possible to draw genetic relations to previous epochs for data of East Spain, the Southern Meseta and the Southern Iberian Peninsula due to the lack of Neolithic data, all analyses confirm genetic similarities among these three regions in the Chalcolithic. Moreover, the genetic composition found in this triangle clearly differs from those found in Northeast Spain and Central Portugal.

12.1.5 Bell Beaker groups of the Iberian Peninsula

Bell Beaker data were available from the Southern and Northern Meseta. Additionally, three individuals from the site Senorío de Gúzman from Andalusia could be reproduced but were not used in population statistical analyses. The two Bell Beaker groups show significant differences on haplogroup level to Chalcolithic non-Bell Beaker from the Southern Meseta and all Early and Late Neolithic groups with strong genetic hunter-gatherer background (NSE, CPE, and EVN) (see table 13, p.91). They are clearly separated from all other Chalcolithic groups in PCA, cluster analysis, and MDS (see fig. 16–18, pp.89–96). Furthermore, AMOVA supports – though not significant – separation of Bell Beaker and non-Bell Beaker groups (see table 21, p.104). The Fisher-test with superordinate groups supports significant differences between Chalcolithic Bell Beaker and non-Bell Beaker groups as well (see table 14, p.92). Genetic differences between the two Bell Beaker groups are low but not significant while higher and mostly significant F_{ST} values to the Chalcolithic groups of the Southern Meseta and East Spain can be observed (see table 16, p.94).

The genetic distinctness of the Southern Meseta Bell Beaker and non-Bell Beaker groups can even be observed on the same sites: Camino de las Yeseras and Humanejos provided both, non-Bell Beaker and Bell Beaker individuals. The latter were pooled with the site of El Juncal and one individual of Valle de las Higueras to the Southern Meseta Bell Beaker group. However, even when only Bell Beaker associated individuals of the sites Humanejos and Camino de las Yeseras were pooled for statistical analyses, Bell-Beaker and non-Bell Beaker groups are separated from each other in both, PCA and cluster analysis (data not shown).

A common feature that is shared between the two Bell Beaker groups and that separates them from other Chalcolithic groups is the low amount of haplogroup H and the presence of haplogroup U5a, which was – apart from the Bell Beaker groups – only found in one Late Neolithic individual from Portugal and the Portuguese Chalcolithic site of Perdigões. The only available Bell-Beaker data from Southern Spain are those of three individuals of the site Senorío de Gúzman which belong to hgs K, T2, and U4 (see table 12, pp.80ff). While the absence of hg H, which is rare in Central Iberian Bell Beaker groups but frequent in Chalcolithic groups of neighboring regions, links these three Southern Iberian Bell Beaker individuals to the Bell Beaker groups of Inner Iberia, hgs T2 and K are rare in the latter. Another interesting fact is the increase of both unique and new lineages in the Bell Beaker groups as opposed to a general decreasing trend in all previous periods, possibly indicating genetic influx from other regions at that time.

Most interesting are the connections of Bell Beaker groups to Chalcolithic and Late Neolithic groups of Central Portugal that can be observed in cluster and PCA analyses: Portugal, especially Estremadura, where many of the sites of this study are localized, are often referred to as potential origins of certain Bell Beaker pottery styles (KUNST 2005; SALANOVA 2005). However, the Late Neolithic samples of the Northern Meseta also share affinities with the Northern and Southern Meseta Bell Beaker groups in many analyses and have even higher haplotype matches to the Bell Beaker populations than the Late Neolithic samples of Central Portugal, pointing to some continuity between Late Neolithic and Bell Beaker in the Northern Meseta.

The only new haplogroup found in the Bell Beaker dataset was the sub-Saharan lineage of haplogroup L1b in the Southern Meseta. All other haplogroups have already been detected in previous periods. To date, the evidence of a typical African lineage (L1b) on the Iberian Peninsula and not even on the coast but right in the heart of the research area is the first securely proven clue for African influence on Spain or Portugal in early prehistory. To find African influence in a Bell Beaker individual is of particular interest due to the fact that some models have emphasized the importance of North Africa on the genesis of the Bell Beaker phenomenon (TUREK 2012). In this model, the Bell Beaker phenomenon would have arisen out of cultural communications between Northwest Africa and the Portuguese Estremadura (TUREK 2012). Two sites in the coastal area of Northern Morocco exhibit pottery in Maritime Bell Beaker style, Kahf-Taht-el-Gar and Gar-Kahal, suggesting relations to the Tagus region in Portugal (TUREK 2012). However, insufficient radio carbon dating in Morocco (BOKBOT 2005; TUREK 2012) together with the lack of Bell Beaker findings in the southern Portuguese Algarve region that would form the natural bridge between Estremadura and Western Andalusia/Gibraltar make this theory hard to prove (TUREK 2012).

To sum up, research question I.6 can be answered with a “yes”: Chalcolithic Bell Beaker and most non-Bell Beaker groups analyzed in this thesis can be clearly separated from each other genetically. The most evident differences exist between both Bell Beaker groups and Chalcolithic groups of the Southern Meseta and – to a lesser degree – East Spain. Both Bell Beaker groups of Central Spain on the other hand, seem to be genetically closely related. These results and especially the genetic differences between Bell Beaker and non-Bell Beaker groups of the Southern Meseta argue against archaeological theories that see Bell Beaker material assemblages just as pottery elements or burial objects for society leaders (CLARKE 1976 IN GARRIDO PENA 2005). It remains to be seen, if genetic links to other Bell Beaker associated burial of the Iberian Peninsula can be drawn as well. A most interesting

fact that was revealed by the statistical analyses was the genetic relation of both Bell Beaker groups to the Central Portuguese Neolithic and Chalcolithic data as well as the African lineage detected in one Bell Beaker individual. Both Portuguese Estremadura and Northern Africa play an important role in the archaeological debate on the origin of the Bell Beaker phenomenon (BOKBOT 2005; KUNST 2005; TUREK 2012).

12.1.6 Bronze Age

From the majority of Bronze Age data in this study only haplogroup information was available. Therefore only results from PCA, cluster analysis, and Fisher-test can be interpreted. The dataset for this epoch was generally limited. Additionally to the 24 individuals used in statistical analyses, results from the sites of Molino de Papel, Cobre las Cruces, and Urtiaga (HERVELLA ET AL. 2012) as well as the result from a single individual from the site of Humanejos in the southern Meseta are available. Individuals of Molinos de Papel in Murcia belong to haplogroups K, V, and HV, individuals of Cobre las Cruces also to hg K and the individual Hume24 from the site of Humanejos can be assigned to haplogroup H1. The site of Valdescusa in La Rioja is the only example of a Bell Beaker associated site with Early Bronze Age chronology. Haplogroups found in this site are J, HV, and U5b. Two samples from the site of Urtiaga in Basque Country (3,475–3,430 BP) belong to hgs U5b and H (HERVELLA ET AL. 2012). Except for HV, all haplogroups were also represented in the sites used in statistical analyses. In general, all haplogroups found in Early Bronze Age individuals have already been present in preceding periods.

The PCA arranges the two Bronze Age groups (ESBA and NEB) close to the Chalcolithic groups of East Spain, the Southern Iberian Peninsula, and the Southern Meseta (see fig. 16, p. 89). Cluster analysis puts the two Early Bronze Age groups in the same sub-cluster but separates them on the next sub-cluster: Bronze Age data from East Spain cluster with Chalcolithic samples from the Southern Iberian Peninsula, while the Bronze Age of Northeast Spain is closest to the Chalcolithic group of the Southern Mesta (see fig. 17, p.90). The Fisher-test shows no significant differences in haplogroup composition between the two Bronze Age groups and only few differences to other groups of the Iberian Peninsula (see table 13, p.91).

When all groups of one period were pooled together, Bronze Age samples have significant genetic differences to the Bell Beaker individuals and the hunter-gatherers but not to the Early and Late Neolithic and to the Chalcolithic (see table 14, p.92). While significant differences to hunter-gatherers could be expected, genetic differences to Chalcolithic Bell Beakers but not to Chalcolithic non-Bell Beakers that can be recognized in PCA, cluster

analysis, and Fisher-test, are very interesting. Bell Beaker goods were still used in some groups of the Early Bronze Age (LULL ET AL. 2013A), represented for example by the site of Valdescua in this study. In Valdescua, three out of five individuals had (three different lineages of) haplogroup J. With each dataset consisting to 25% of hg J, the two other Bronze Age populations show some of the highest values for this haplogroup in the whole dataset. Naturally, datasets are too small at the moment to draw any conclusions. Anyhow, it would be interesting to see if connections between Chalcolithic and Bronze Age Bell Beaker sites could be drawn on a mitochondrial level, respectively if Bronze Age Bell Beaker and non-Bell Beaker associated groups can be differentiated genetically or not. The Fisher-test reveals no significant differences between the Bronze Age samples of East Spain and the preceding Chalcolithic group (ESC) of the same region. Principal component analysis puts them close together, while cluster analysis differentiates them on a lower sub-cluster level. Although, the dataset from the El Argar group of East Spain is very small, all signs point to a development out of local eastern Spanish communities. Regarding Northeast Spain, the Bronze Age is dissociated from all preceding groups in the PCA, and – except for the Late Neolithic – all preceding groups of this region are situated in a different main cluster in the cluster analysis, while the Fisher-test reveals no significant differences between the Bronze Age of Northeast Spain and any of these groups and the TPC accordingly cannot exclude genetic drift. PCA and cluster analysis so far rather suggest genetic similarities to eastern Spain and thus potential genetic influx by other Mediterranean Chalcolithic groups of East Spain and the southern part of the Iberian Peninsula as well as the contemporaneous Bronze Age group of East Spain than by Chalcolithic groups of the same region.

To sum up, the small amount of Early Bronze Age data in general, together with the fact that too few HVR I data could be amplified to apply sequence-based statistical analyses, does not allow to draw extensive conclusions about population dynamic processes and complicates answering research objectives. It can, however, be recognized that the El Argar culture of East Spain seems to have developed out of local or neighboring Chalcolithic communities. The same or genetically similar Chalcolithic groups might have influenced the Northeast Spanish Bronze Age groups as well but development out of Chalcolithic groups of Northeast Spain cannot be excluded.

12.2 Ancient Iberian groups in a prehistoric European context

The following chapter will be summarizing and discussing the results of chapter 9.2.

12.2.1 Setting the stage – hunter-gatherer populations in Europe

Hunter-gatherer genetic data available at present consist of 56 mtDNA sequences from 29 hunter-gatherer sites of Central, East, West, North, and South Europe (CARAMELLI ET AL. 2003; CHANDLER 2003; CHANDLER ET AL. 2005; BRAMANTI ET AL. 2009; MALMSTRÖM ET AL. 2009; KRAUSE ET AL. 2010B; HERVELLA ET AL. 2012; SANCHEZ-QUINTO ET AL. 2012; SKOGLUND ET AL. 2012; BOLLONGINO ET AL. 2013; DER SARKISSIAN ET AL. 2013; FU ET AL. 2013; LAZARIDIS ET AL. 2013; RAGHAVEN ET AL. 2014). However, sites with genetic data are distributed patchy over space and time, dating from the Upper Paleolithic to the late Mesolithic shortly before or temporally overlapping with the arrival of the first farmers in some regions. Their geographic distribution ranges from sides of the Portuguese Sado Valley to Russia and from southern Italy to Denmark. Following previous studies (BRANDT ET AL. 2013, IN PRESS), hunter-gatherer data were pooled into three groups: Western European hunter-gatherer, an admittedly widely dispersed group of Central European hunter-gatherer with data from Luxembourg, Germany, Sweden, and Lithuania, and an eastern hunter-gatherer group with data from Russia.

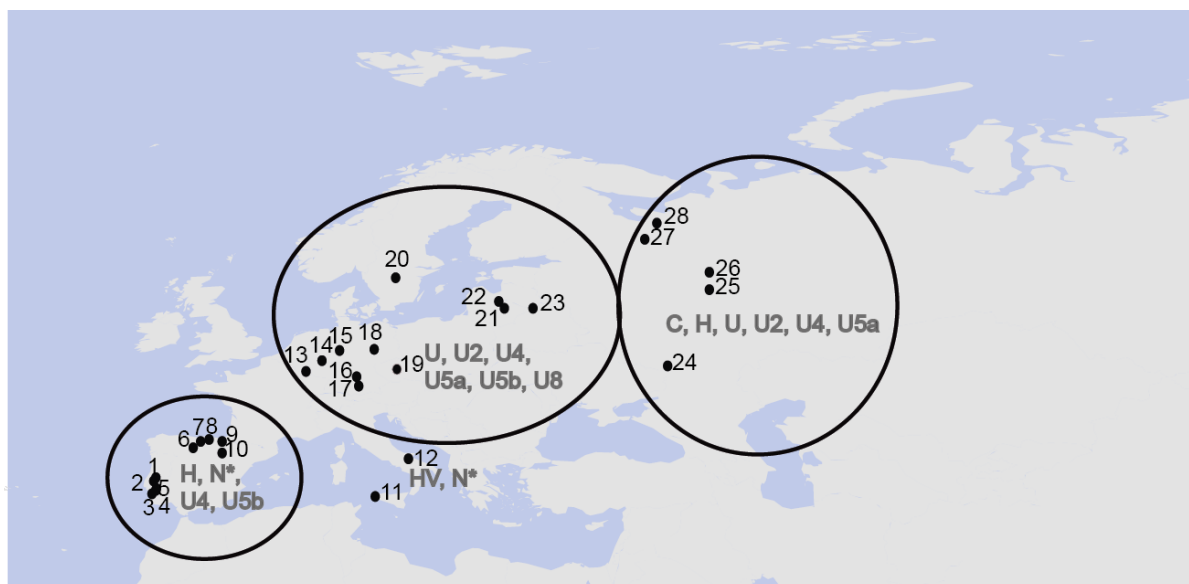
In general, the most striking commonality among the three different hunter-gatherer populations is the overall presence of hg U, e.g. U*, U2, U4, U5a, U5b, and U8 in pre-Neolithic individuals all over Europe (BRAMANTI ET AL. 2009; KRAUSE ET AL. 2010B; HERVELLA ET AL. 2012; SANCHEZ-QUINTO ET AL. 2012; DER SARKISSIAN ET AL. 2013; FU ET AL., 2013; BOLLONGINO ET AL. 2013; LAZARIDIS ET AL. 2013; RAGHAVEN ET AL. 2014). The predominance of hg U in pre-Neolithic Europeans interestingly coincides with a study of Richards and colleagues (RICHARDS ET AL. 2000) who, based on analyses of modern-day European population data, suggested that haplogroup U was one of the oldest Eurasian branches in the mitochondrial phylogeny and probably came to Europe with the initial peopling by anatomically modern humans some 42,000 years ago (see chapter 3.1.3).

However, despite the overall common hg U lineages, additional haplogroups have been present in the more peripheral regions of Europe. As has been discussed in previous publications (BRANDT ET AL. 2013, IN PRESS) further mitochondrial haplogroups have been found in hunter-gatherer individuals: H and N* in Western Europe (CHANDLER 2003; HERVELLA ET AL. 2012; SANCHEZ-QUINTO ET AL. 2012) (see also chapter 12.1.1), and haplogroups C and H in Russia (DER SARKISSIAN ET AL. 2012). To date, Central European foragers, however, only belong to haplogroup U. Based on the current state of research, the presence of haplogroups N*, H, U4, and U5b, but not U2 and U5a, make up the genetic

Mesolithic substratum of Western Europe. Additionally, in southern Italy hg HV has been found (CARAMELLI ET AL. 2003; MANNINO ET AL. 2012). In contrast, East Eurasian hunter-gatherers have a different haplogroup composition, which is compiled by hgs C, H, U2, U4, and U5a, but not U5b. As has been mentioned, the Central European maternal gene pool is made up of a mixed composition of sub-haplogroups of U: The presence of U2 and U5a links Central Europe to East European, the presence of U5b to West European hunter-gatherers. Additionally, sub-haplogroup U4 – present in both Western and Eastern hunter-gatherers – and U8 have been detected in pre-Neolithic individuals. The most western site, in which U5a has been found so far, is the site Blätterhöhle in northwestern Germany, while haplogroup U5b has been found as far east as Lithuania (BRAMANTI ET AL 2009; BOLLONGINO ET AL 2013). The contrasting regional patterns that can especially be observed for U5a and U5b fit well into models based on analyses of modern populations: Malyarchuk and colleagues (MALYARCHUK ET AL. 2010) analyzed sub-haplogroups of U5 and proposed different places of origins in the Upper Paleolithic for each of the sub-clades – U5b in the West and U5a in the East. This was supported by studies that linked sub-haplogroups of U5b, such as U5b1b1 and U5b3, with an expansion from southwestern refuges in Franco-Cantabria and Italy respectively after the last glacial maximum (ACHILLI ET AL. 2005; PALA ET AL. 2009). Sub-clade U4 seems nowadays to be most common around the Baltic region and South Scandinavia and has been proposed to have originated in a southeast European glacial refuge (MALYARCHUK ET AL. 2008). So far most conclusions on the distribution and origin of haplogroup U by modern DNA studies can be supported by ancient DNA data.

In the population genetic analyses especially hunter-gatherer meta-populations of East and Central Europe are always located remotely from all succeeding groups no matter in which geographic context, except for individuals associated with the Pitted Ware culture. The hunter-gatherers of the Iberian Peninsula on the other hand – though they were shown to be significantly different from most Iberian Neolithic to Bronze Age population – generally show greater genetic similarities to succeeding populations of the same region than to other pre-Neolithic groups. Though all hunter-gatherer groups share commonalities, especially the Iberian dataset differs from the other forager groups of Europe as shown in Fisher-test and by F_{ST} values (see tables 21–22, pp.107f). However, the hunter-gatherer datasets are small and at least in Central Europe and Eastern Europe distributed over a vast area and several thousand years.

At the moment at least, it seems that the mitochondrial haplogroup variability was greater at the peripheral regions of Eurasia and that the Central European groups were influenced from at least the West and East. In this context it is most interesting that no signs of haplogroups N* and H have been found in Central Europe.



1 Concheiro da Moita do Sebastião, 2 Toledo, 3 Arapouco, 4 Cabeço das Amoreiras, 5 Cabeço de Pez, 6 La Braña, 7 La Pasiaga, 8 La Chora, 9 Erralla, 10 Aizpea, 11 Grotta d'Oriente, 12 Paglicci cave, 13 Loschbour, 14 Oberkassel, 15 Blätterhöhle, 16 Hohlenstein-Stadel, 17 Hohler Fels, 18 Bad Duerrenberg, 19 Dolní Věstonice, 20 Motala, 21 Spiginas, 22 Donkalis, 23 Kretuonas, 24 Kostenki, 25 Lebyazhinka, 26 Chekalino, 28 Yuzhnyy Oleni Ostrov, 28 Popovo

Figure 30 Haplogroups found in the different hunter-gatherer groups

From left to right: Western hunter-gatherers, Central European hunter-gatherers, and East European hunter-gatherers. Italian (south European) hunter-gatherer sites are displayed as well although they were not used in any population genetic analyses.

12.2.2 Neolithic transition in the different regions of Europe

About 80% of the mitochondrial lineages found in the earliest Neolithic of Central Europe, represented by the Linear pottery culture (LBK), can be assigned to haplogroups HV, J, K, N1a, T2, V, W, and X, which thus have been defined as the “mitochondrial Neolithic package” of Central Europe in previous studies (BRANDT ET AL. 2013, IN PRESS). Mitochondrial lineages found in Central European hunter-gatherers so far are present to only 1.8% in the LBK (BRANDT ET AL. IN PRESS). Concordantly, discontinuity between hunter-gatherers and the first farmers of Central Europe has been supported by several studies (BRAMANTI ET AL. 2009; HAAK ET AL. 2010; BRANDT ET AL. 2013, IN PRESS). The overall mtDNA composition among different LBK communities, available from sites of eastern and southern Germany as well as Austria and the Czech Republic, appears very uniform without significant differences in haplotype or haplogroup composition (BRANDT ET AL. IN PRESS). Outside the LBK influence area, however, the picture might have been very different: Bollongino and

colleagues argued that at the Blätterhöhle in Central Germany some mitochondrial successors of Mesolithic societies kept a hunter-gatherer subsistence strategy at least in this area for more than 2,000 years after the initial Neolithic transition (BOLLONGINO ET AL. 2013). However, it is not certain to what extent the mitochondrial signature of the Blätterhöhle is genetically representative for that area and one should keep in mind that the Neolithic samples date between 3,922 and 3,020 cal BC. Thus, the predominance of hg U lineages in the foraging Neolithic individuals of this site could likewise be explained by a re-flux of people from for example western or northern Europe, a phenomenon that has at least genetically been observed in individuals from the Middle Neolithic site Bernburg in eastern Germany (BRANDT ET AL. 2013). Moreover, most individuals with non-U haplogroups date to the second half of the 4th millennium, thus questioning the interpretation of parallel societies.

Hunter-gatherer communities of northern Europe (North Germany, Denmark, and South Sweden) retained a foraging lifestyle for more than 1,500 years after the emergence of the LBK (PRICE 2000A). However, despite the time difference, the transition from hunter-gatherers to the Funnel Beaker complex as the first farmers of this area can be regarded as the Neolithic transition in this region and therefore be compared to the temporally preceding processes in other regions of Europe. Genetically, the people associated with the Funnel Beaker culture can be characterized by a mixture of typical hunter-gatherer haplogroups (U5a and U5b) and haplogroups from the “Central European Neolithic package”, such as T2, J, and K (BRAMANTI ET AL. 2009; MALMSTRÖM ET AL. 2009). Thus, it seems that the first farmers were not Central European immigrants, but an admixed population with maternal genetic influences of both indigenous hunter-gatherers and foreign Central Europeans (BRANDT ET AL. 2013, IN PRESS).

The analyses conducted in this thesis invariably support previous results of paleogenetic studies with a clear separation of not only the LBK but also succeeding populations of the Central European Neolithic from all hunter-gatherer groups. The Funnel Beaker individuals on the other hand were arranged between them but closer to the Central European Neolithic in PCA, cluster analysis, and MDS as could be expected due to their mixed composition of typical hunter-gatherer and Neolithic lineages (see fig. 23–25, pp.105–110).

When we turn westwards to the Iberian Peninsula, we see similarities and differences to both the first farmers of Central and northern Europe. On the one hand, hgs arriving on the Iberian Peninsula with the first Neolithic farmers seem to have been largely concordant to those described in Central Europe (HV, I, J, K, N1a, T2, V, and X). On a sequence level, 85% of

the Early Neolithic Iberian individuals with these haplogroups share direct sequence hits with individuals affiliated with the LBK. On the other hand, like 1,500 years later in the north of Europe, the amount of new mitochondrial input at the transition from foraging to farming has obviously been considerably lower on the Iberian Peninsula. Early Neolithic groups – except for the individuals of the cave site of Els Trocs in the Pyrenees – still possess 42–78% hunter-gatherer typical haplogroups and share 8–33% mitochondrial lineages directly with them (see fig. 19, p.97). Consequently, almost all Early Neolithic groups of the Iberian Peninsula are separated from their contemporaneous Central European neighbors in PCA and cluster analysis (see fig. 23–24, pp.105–106).

The Fisher-test reveals significant differences in haplogroup composition of Northern Spain to all Early and Middle Neolithic cultures from Central Europe, while Central Portugal is significantly different to the LBK and Schöningen culture but not to the Rössen culture. The Early Neolithic of Northeast Spain is only significantly different to the LBK (see table 22, p.107). F_{ST} values are generally lower between Northeast Spain and Early Neolithic Central European groups than between Northern Spain and Central Portugal and Central European groups (see table 23, p.108). Northern Spain and Central Portugal show the lowest genetic distances to the Rössen culture; however, F_{ST} values are not significant. In the MDS, Northeast Spain is located closer to the Schöningen group and the LBK, while the closest Central European Early Neolithic group to Central Portugal and Northern Spain is again Rössen (see fig.25, p.110). These indicated genetic similarities of Northern Spain and Central Portugal to the Rössen culture are supported by the Fisher-test but not visible in PCA or cluster analyses (see fig. 23, pp.105f). They are probably due to the high percentage of rCRS lineages of haplogroup H in all three datasets. Els Trocs is the only Iberian sample set which seems to have had a mitochondrial haplogroup composition comparable to the Early Neolithic of Central Europe, visible in cluster analyses, PCA, F_{ST} values, MDS, and significantly confirmed by the Fisher-test. It is therefore the only Early Neolithic group of Spain in which a comparable “Neolithic mitochondrial package” arrived. However, it is at the same time a very small dataset with only seven individuals.

Regarding research question II.2: When the northern European Funnel Beaker culture is compared to Early Neolithic Iberian groups, it is genetically closest to Northeast Spain in the PCA and to Els Trocs in the cluster analysis (see fig. 23–24, pp.105f). In the MDS, Els Trocs, Northeast Spain and Funnel Beaker are likewise closely grouped together (see fig. 25, p.110). F_{ST} values between Funnel Beaker individuals and Els Trocs and Northeast Spain are low but not significant (see table 23, p.108). On the other hand, Northern Spain and

Central Portugal are separated from the Funnel Beaker culture in cluster analysis, PCA, and MDS and significantly different in the Fisher-test and in F_{ST} values. Thus, the Neolithic mitochondrial influence in the Early Neolithic of northern Europe was greater than in Northern Spain and Central Portugal, but comparable to Northeast Spain and Els Trocs.

Summarized, the genetic heterogeneity among Early Neolithic Iberian groups is also reflected in their distinct relations to other Early Neolithic groups: The only Iberian Early Neolithic group that seems genetically very similar to all Central European Early Neolithic groups is Els Trocs. All other Early Neolithic groups of the Iberian Peninsula are at least different to the LBK, but show slight and varying affinities in the Fisher-test and F_{ST} values to some Early Neolithic cultures from Central Europe. While Els Trocs and Northeast Spain reveal similarities to the Northern European Funnel Beaker as well, the genetic signature in the regions of Northern Spain and Central Portugal has no congruence to Early Neolithic cultures of any other region. At best, some relations to the Rössen culture are recognizable. As has already been discussed in chapter 12.1.1 and been suggested by previous studies – although either investigated using a smaller dataset (GAMBA ET AL. 2011; HERVELLA ET AL. 2012) or very roughly pooled chronological groups (BRANDT ET AL. 2013, IN PRESS) – the hunter-gatherer legacy is more dominant in the Iberian Neolithic compared to Central Europe, indicating a Neolithic transition with a larger contribution of the indigenous population together with a reduced impact of early farmers. The amount of lasting mitochondrial hunter-gatherer influence increases with growing distance from Northeast Spain, both inland and alongside the coast. What becomes apparent is the great heterogeneity of Neolithic genetic input among the different areas of the Iberian Peninsula arguing for complex regional transition processes; very much in contrast to the mitochondrial and archaeological homogeneity of the LBK.

12.2.3 Further population dynamic processes in Neolithic Europe

The only region of which ancient DNA results dating between the end of the 5th and the late 4th millennium are available so far is Central Europe. A study of several groups with distinct archaeological features, in the following referred to as “cultures”, revealed great genetic continuity between the Linear pottery culture and succeeding cultures until the end of the 4th millennium in the Middle-Elbe Saale region of East Germany (BRANDT ET AL. 2013). Only in the chronologically latest group, the so-called Bernburg culture (3,100–2,650 cal BC), new genetic influences have been detected and were subscribed to a re-flux of mitochondrial lineages from northern Europe (BRANDT ET AL. 2013). Please note, that Central European cultures of this time are referred to as “Middle Neolithic” in line with previous studies, while

the contemporaneous Iberian data are summarized as “Late Neolithic”. The comparative Late Neolithic Central European data used in this study are contemporaneous to the Chalcolithic period on the Iberian Peninsula.

The Middle Neolithic Salzmünde and Baalberge cultures are distant from most contemporaneous groups of the Iberian Peninsula in PCA, cluster analysis, and MDS, but differences in haplogroup composition between Middle Neolithic cultures of Central Europe and Northeast Spain, the Ambrona Valley, and Central Portugal are not significant (see fig. 23–25, pp.105–110 and table 22, p.107). The Central European Bernburg culture on the other hand is located close to Iberian groups in the PCA, clusters with Early Neolithic samples of Northeast Spain and Late Neolithic samples of the Northern Meseta in the cluster analysis, and is situated close to Late Neolithic groups of the Ambrona Valley and Central Portugal in the MDS. This is probably mainly due to its elevated frequencies of hg U5b, as previously mentioned interpreted as North European influence (BRANDT ET AL. 2013, IN PRESS), and thus comparable to the Iberian Peninsula where the hunter-gatherer mitochondrial legacy retained into the Late Neolithic. The only Late Neolithic group of Spain that shows clear affinities to other populations of Central Europe in all analyses (PCA, cluster analysis, Fisher-test, and MDS) is that of Northeast Spain. However, as has been discussed in chapters 12.1.3 and 12.1.4 the results of this group seem questionable and therefore should not be over-interpreted.

To answer research question II.3: When we compare population dynamic processes between Early and Middle Neolithic in Central Europe and Late Neolithic on the Iberian Peninsula, we see about 2,500 years of genetic continuity in Central Europe on the one hand, and an increase in the amount of Neolithic lineages in most groups of the Iberian Peninsula on the other hand (see also chapter 12.1.3). On this account, the question arises if the “Neolithic mitochondrial package” of Central Europe that seems to have reached the Iberian Peninsula only in an extenuated form in the Early Neolithic, has finally been established in the Iberian Late Neolithic. In general, although the amount of “Neolithic” haplogroups/haplotypes is elevated in most Iberian Late Neolithic groups, resulting in affinities of some groups to Central Europe in the Fisher-test and MDS, they remain in most cases still genetically closest to previous populations of Western Europe and never reach haplogroup compositions found in the LBK and succeeding groups. Haplogroups of putative pre-Neolithic origin like U4, U5b, or H are still present in most groups arguing against a simply delayed arrival of the “mitochondrial Neolithic package” that has arrived in Central Europe so early and to such an extent. It rather seems that it spread from probably Catalonia/Aragón into other regions of the Iberian Peninsula after/during the Early Neolithic

and became manifested to a different extent in various regions. One should keep in mind though that the research area of the Iberian Peninsula is larger and topographically more heterogeneous than the Middle-Elbe-Saale region investigated in the BRANDT ET AL. (2013) study.

12.2.4 Genetic connections between the Iberian Peninsula and France

As natural connector between the Iberian Peninsula and Central Europe, paleogenetic data from France could provide the genetic missing link between these two regions. However, only few French data are available at the moment. Three mitochondrial lineages from a megalithic site from the Atlantic coast of France, dating to 4,345–4240 cal BC, belong to haplogroups N1a, U5b, and X2 (DEGUILLLOUX ET AL. 2011). Publications have mostly refrained from linking these data to either Central or Mediterranean Europe so far. While N1a and X2 have been detected in both Central European and the Iberian Peninsula, U5b can be rather linked to Western Europe in general. The only other study on French samples analyzed individuals from the site of Treilles at the western Mediterranean coast of France. Mitochondrial lineages belong to haplogroups H1, H3, HV, J, K1, T2b, U, U5a, U5b, and X2 (LACAN ET AL. 2011A). The site is dated to about 3,000 BC and thus contemporary with the late Middle Neolithic of Central Europe and the transition from the Late Neolithic to the Chalcolithic on the Iberian Peninsula.

In the statistical analyses, the Treilles site clusters with Iberian groups and the Funnel Beaker culture in the PCA, and with Chalcolithic Iberian groups in the cluster analysis (see fig. 23–24, pp.105f). In the MDS on the other hand, it is situated closer to the Central European Middle Neolithic Baalberge and Salzmünde culture and to the Late Neolithic of Northeast Spain (see fig. 25, p.110). Especially the connection between the Late Neolithic of Northeast Spain and Treilles would be very interesting, as they are chronologically and geographically very close; however, as has been already mentioned, the Late Neolithic dataset from Northeast Spain should rather be taken with a grain of salt and therefore it will be rescinded from further interpretations here. F_{ST} values between Treilles and Iberian Chalcolithic groups lie intermediate to those observed between the Corded Ware culture and Iberian Chalcolithic groups and the Bell Beaker of Central Europe and Iberian Chalcolithic groups. Particularly high F_{ST} values exist between Treilles and Iberian Bell Beaker groups (see table 23, p.108).

Summarized, at the moment it is difficult to state whether the few published French data show rather Iberian or Central European affinities. Haplogroup-based statistical analyses

indicate genetic links or a similar genetic population history to Iberian groups. This is also suggested by the relatively high amount of U5b (14%) in the dataset. One should keep in mind that if a similar mitochondrial haplogroup composition was present in France and Spain in Neolithic times, it will be difficult to detect genetic exchanges between the two countries in prehistory. Thus, putative population continuities in Spain could very likely have been a result of a hidden genetic influence from France.

12.2.5 Western and Central European Bell Beaker in comparison

The 3rd millennium BC marks a period of new genetic influx in Central Europe from different directions, mainly represented by the appearance of two contrasting pan-European phenomena: on the one hand the Corded Ware culture distributed over East Europe and the Bell Beaker complex on the other hand whose distribution area was more western and ranged from Portugal to Poland and from Italy to Britain. In Central Europe, pre-dominantly Saxony-Anhalt in eastern Germany, they were shown to have a quite contrasting mitochondrial signature; while the Corded Ware associated individuals had elevated frequencies of hgs I, U2, and U5a, the Bell Beaker mitochondrial signature was made up by a predominance of hg H. Based on comparisons with modern data, the high abundance of hg H in the Central European Bell Beakers has been interpreted as genetic influence from the Iberian Peninsula (BRANDT ET AL. 2013, IN PRESS; BROTHERTON ET AL. 2013). In this context it is of special interest to compare Iberian and Central European Bell Beaker groups without in anyway implementing a social or ethical connection among Bell Beaker associated sites in general. Interestingly, the Bell Beaker individuals of the site Kromsdorf in Thuringia, published by LEE ET AL. (2012) show “Corded Ware haplogroups”, such as I, T1, U2, and U5a, of which 50% directly match Corded Ware lineages of the Middle-Elbe-Saale region (BRANDT ET AL. IN PRESS). Likewise, one of the two Danish Bell Beaker samples (MELCHIOR ET AL. 2010) shares a U4 lineage identical with the Corded Ware dataset. BRANDT ET AL. (IN PRESS) interpreted this as a stronger and persisting impact of to the Corded Ware female lineages in these regions. Thuringia and Saxony-Anhalt are geographically very close, therefore, despite regional differences in Bell Beaker sites of Central (and North) Europe, all German Bell Beaker data were pooled into one group.

The results of all haplogroup-based methods reveal greater genetic similarities between the Central European Corded Ware and Bell Beaker groups than between Spanish and Central European Bell Beaker groups (see fig. 26–27 pp.112–113). The Fisher-test shows significant differences between Central European Bell Beaker and most Iberian groups including the Bell Beaker of the Southern Meseta (SMCB) (see table 22, p.107). No genetic differences on

the other hand exist between the Central European Bell Beakers and those of the Northern Meseta, possibly due to the small sample size of the latter. Like in previous epochs, Central European groups are genetically closer to each other than to contemporaneous Western European groups and vice versa.

When Spanish Bell Beaker groups are compared to each group of Central and Northern Europe, some of the highest genetic differences are found to the Central European Bell Beaker (see table 23, p.108). Furthermore, only 17% of the European Bell Beaker individuals share an identical lineage with one of the Bell Beaker individuals from the Iberian Peninsula. This is not surprising due to the fact that ancient DNA studies linked the Central European Bell Beaker individuals to the Iberian Peninsula or generally westwards based on a high abundance of haplogroup H (BRANDT ET AL. 2013, IN PRESS; BROTHERTON ET AL. 2013) – a haplogroup that has some of the lowest frequencies of all Spanish and Portuguese groups in the Bell Beaker data. On the other hand, genetic distances of Central European Bell Beaker to some Late Neolithic and non-Bell Beaker Chalcolithic groups of the Iberian Peninsula with high amounts of haplogroup H are lower, and a certain genetic proximity to Late Neolithic groups of the Ebro Valley and Chalcolithic groups of the Southern Meseta and East Spain can be observed in the MDS (see fig. 25, p.110). However, this is probably mainly due to the high abundance of rCRS lineages of haplogroup H in all four groups, as only one other lineage of hg H found in the Central European Bell Beaker has a direct sequence match to any of the Iberian groups.

Besides the Central European Bell Beaker group, the Corded Ware culture is partially contemporary to the Iberian Bell Beaker. Therefore it was of special interest to compare this group to the Iberian Bell Beaker as well. Although the Fisher-test does not find significant differences in haplogroup composition between the Corded Ware culture (CWC) of Central Europe and the Spanish Bell Beaker groups, they are located in great distance to each other in all other analyses (PCA, cluster analysis, MDS) and genetic distances between CWC and Iberian Bell Beaker are some of the greatest found between the Corded Ware culture and Iberian groups in general.

To answer research question II.4: While the Spanish Bell Beaker groups have no genetic affinities to any Central European group at all, Central European Bell Beaker show some similarities in the MDS to those Iberian groups who have a high abundance of haplogroup H. Chapter 12.3 will further discuss the analyses focusing on sub-haplogroups of H. Thus, while genetic influences from Portugal and Africa on the Iberian Bell Beaker hint at origins in or influences from those regions, concordant with certain archaeological models (see chapter 12.1.5), genetic links between Western and Central European Bell Beaker cannot be

detected. Genetic evidence available so far can therefore dismiss an Iberian origin of the Bell Beaker phenomenon with demic distribution into Central Europe – at least on mitochondrial level; one will have to await what Y-chromosomal or autosomal ancient DNA data will show. Anyway, one should not forget that one of these theories may very well be true for the distribution of the pottery itself, the incision style or any other archaeological assemblage via acculturation phenomena. However, as archaeological research of the last decades has tended to rather emphasize the differences in material culture between distinct Bell Beaker communities in Europe than to assume a more or less homogeneous Bell Beaker population across Europe, these findings are not too surprising (e.g. GARRIDO PENA 2005; STRAHM 2014).

It is however interesting to notice that in both Central Europe and the Mesetas of the Iberian Peninsula, Bell Beaker groups can be genetically distinguished from preceding groups of the same area, arguing against an assimilation of Bell Beaker ideology by local groups as has been for example proposed by CHRISTIAN STRAHM (2008, 2014). Although in this model the existence of missionaries that might have been send out to bring the Bell Beaker ideology to neighboring groups has been discussed, the genetic data rather point to a much larger influx of new genetic lineages in Bell Beaker groups compared to preceding populations. At least in the Middle-Elbe-Saale region, mitochondrial data furthermore suggest a link between the preceding and contemporary Corded Ware and later Early Bronze Age Unetice culture than between Bell Beaker and Unetice culture (BRANDT ET AL 2013), further highlighting the Bell Beaker as kind of “foreign element” in this region. On the Iberian Peninsula, Bell Beaker and Bronze Age data are only available for few regions at the moment, but here Bell Beaker groups are significant different to both pre-Bell Beaker Chalcolithic and Bronze Age groups as well. The individuals of the site of Kromsdorf in Germany on the other hand show many haplotypes typical for the Corded Ware culture (LEE ET AL. 2012; BRANDT ET AL. 2013) and might therefore indeed represent an example for assimilation of Bell Beaker “ideology” but not genetic lineages into an already existing population.

12.2.6 European Early Bronze Age groups

Because the two geographically distinct Spanish Bronze Age groups only yielded enough data for haplogroup-based methods and are small in sample size, conclusions about connections to the Central European Bronze Age can only be preliminary. Furthermore, only one sufficient Bronze Age dataset from outside the Iberian Peninsula was available, which can archaeologically be assigned to the Unetice culture. Mitochondrial results have linked the Unetice culture genetically close to the preceding Corded Ware group of Central Europe by

statistical analyses (BRANDT ET AL. 2013, IN PRESS). Both share elevated values of hgs I, T1, U2, U4, and U5a compared to preceding populations of this region (BRANDT ET AL. 2013, IN PRESS). These haplogroups are generally rare or virtually absent in the prehistoric Iberian dataset, consequently no genetic connections between Central European and Spanish Bronze Age groups are recognizable, significantly confirmed by the Fisher-test. Thus research question II.5 cannot be confidently answered with the available data.

12.3 Haplogroup H variability in prehistory

Haplogroup H dominates present-day European mitochondrial DNA variability. It is especially present in West European populations (>40%) but declines in frequency towards the Near East and the Caucasus down to 10%-30% (RICHARDS ET AL. 1996; LOOGVÄLI ET AL. 2004; ROOSTALU ET AL. 2007). Haplogroup H can be subdivided into more than 90 sub-hgs with varying frequencies in extant populations. The different sub-hgs were shown to display regional patterns (VAN OVEN AND KAISER 2009): H1 is the most common sub-haplogroup in Europe, with a frequency peak of about 46% among hg H on the Iberian Peninsula and gradually declining frequencies towards the northeast and south (northern Africa) (PEREIRA ET AL. 2004). Its sub-hg H1b on the other hand has higher frequencies in Eastern Europe and the Caucasus (LOOGVÄLI ET AL. 2004). H2a is likewise more common in eastern than western Europeans and even extends into Central Asia (LOOGVÄLI ET AL. 2004). Hg H3 shows a similar regional pattern as hg H1 and is exclusively found in Europe (PEREIRA ET AL. 2004, 2005; QUINTÁNS ET AL. 2004). Sub-hgs H6b and H8 are rare in extant Central Europe but found more frequently in modern Near Eastern and Central Asian populations (LOOGVÄLI ET AL. 2004). Most of the variability of haplogroup H can be found outside the mitochondrial control region and is therefore not well exploited especially in ancient DNA studies. One of the very few sub-haplogroups distinguishable by its HVR I motif alone is H5. As has been mentioned (see chapter 3.1.3) especially hgs H1 and H3 have been linked to a re-colonization from Franco-Cantabrian glacial refugees before the beginning of the Holocene (TORRONI ET AL. 1998, 2001; ACHILLI ET AL. 2004, 2005; GAMBLE ET AL. 2004; LOOGVÄLI ET AL. 2004; PEREIRA ET AL. 2005).

A study on whole mitochondrial genomes of exclusively haplogroup H of Central European Early to Late Neolithic individuals revealed discontinuities between these two periods in hg H composition (BROTHERTON ET AL. 2013). Furthermore, due to higher frequencies of hgs H1 and H3 in Central European Bell Beakers and their clustering with modern Iberian populations in several analyses, an Iberian origin for the Central European Bell Beaker was

proposed in the same study (BROTHERTON ET AL. 2013). Particularly because of the latter assumption but also because the study showed the potential of a greater resolution of mitochondrial hg H for population genetic studies, individuals of this thesis were screened for 17 different sub-hgs of H.

The only sub-hgs that were found on the Iberian Peninsula were H1 (64.4%) and H3 (15.6%). For the remaining individuals at least classification into the frequent modern sub-groups H4, H5, H7, H10, H11, H14, and H16 can be excluded. Both haplogroups H1 and H3 have already been present in the Early Neolithic on the sites Alto de Rodilla in Northern Spain (H1) and Cova d'Avellaner (H3) in Northeast Spain (LACAN ET AL. 2011B). Haplogroup H8 that was detected in one Late Neolithic individual of the site Camí de Can Grau was not found in any sample.

Regarding research question II.6: The three statistical methods applied on the dataset (PCA, cluster analysis, and Fisher-test) reveal Iberian Late Neolithic to Bronze Age samples to be genetically most similar to each other when compared to all other data pools (see fig. 26–27, pp.112f, and table 25, p.114) and no shift in sub-haplogroup H variability can be detected. Data from the French site Treilles, contemporary to the Iberian Chalcolithic, and the Early Iron Age of France are also located close to the Iberian groups in the PCA and no significant differences can be seen in the Fisher-test. The cluster analysis, however, puts them on a different sub-branch. Iberian groups are significantly different to most Early Neolithic to Bronze Age population pools of Central Europe and distanced from most of them – especially the Early Neolithic of Central Europe and Hungary – in the PCA. Some affinities to the Central European Middle Neolithic and Bell Beaker culture are recognizable in the PCA. The Middle Neolithic of Central Europe is chronologically also the first group of Central Europe in which hg H3 is present. It is virtually absent in the Early Neolithic of Hungary and Central Europe. Interesting is the separation of the main clusters in the cluster analysis: One branch contains only Eastern to Central European groups (La Tène of Hungary and Romania, La Tène Austria, and Early Neolithic of Hungary and Central Germany) while the other main branch is split into Spanish/Portuguese prehistoric groups on the one hand and Middle Neolithic to Bronze Age data from Central Europe together with the Treilles data and Iron Age samples of Switzerland and France on the other hand. Thus, it seems cluster analyses splits the groups based on geographical location or affinities into one eastern and one western main cluster. Though the Middle Neolithic dataset of Central Europe shows significant differences in its sub-hg H composition to all Western European groups, the cluster analysis and PCA hint some connections to the Iberian Peninsula probably based on the appearance of hg H3 in this dataset for the first time.

Regarding the Central European Bell Beaker, they show some affinities to the Iberian groups in the PCA, but are situated on a different sub-branch in the cluster analysis. Furthermore, when compared to Western European populations, the Central European Bell Beaker group is significantly different to just the Iberian Chalcolithic. Thus, affinities to some Chalcolithic Iberian groups indicated by the MDS with all European data (see fig. 25, p.110) are not confirmed. Generally, genetic links between the Central European Bell Beaker culture and Iberian groups based on haplogroup H are weak at best. Haplogroup H1 is present throughout all Central European prehistoric periods and haplogroup H3 has already been present in the Middle Neolithic.

The fact that H1 was detected in all Neolithic groups but with the highest frequencies in Spain, Portugal, and France (50–75%) and has already been present in the Mesolithic of the Iberian Peninsula (CHANDLER 2003) would theoretically be concordant with a dispersal of hg H1 from an Iberian glacial refuge before the Neolithic. However, the fact that hg H is absent from Central European pre-Neolithic individuals so far does not support this theory. A putative explanation would be that the individuals belong to different sub-branches of H1. Individuals of the Early Neolithic dataset of Central Europe for example have been assigned to H1b, H1j, and H1e (BROTHERTON ET AL. 2013) while for the Iberian samples resolution into sub-hgs of H1 is not available, yet. At least H1b has been linked to the Near East and the Caucasus rather than to Western Europe by modern geneticists (LOOGVÄLI ET AL. 2004). H5 seems to have been almost ubiquitous in prehistoric Central Europe and Hungary but virtually absent on the Iberian Peninsula. Thus, it potentially represents an Eastern European Neolithic component. Based on the analysis of this study, H3 on the other hand could be a potential marker of Western European influence on the Central European Neolithic. However, in general the variability is low in all analyzed populations with only 2 to 5 different sub-hgs per group with the exception of the Iron Age samples of Switzerland, where seven different sub-haplogroups were detected. This may both be due to the small sample sizes of some of the datasets and to the fact that for a varying amount of hg H individuals of each group it was not possible to determine a sub-hg with the applied methods.

13 Summary

Ancient DNA studies from the Iberian Peninsula or reviews of ancient DNA data in general have mainly focused on three topics: Neolithic transition on the Iberian Peninsula, continuity/discontinuity to the Later Iberian Neolithic and comparison to Central European prehistoric data. In this study, the Iberian dataset was enlarged by SNP-based haplogroup information for 249 new Mesolithic to Early Bronze Age individuals. For 187 of these individuals HVR I sequences could be reproducibly amplified as well. These new data allowed insights into post-Neolithisation population dynamic processes on the Iberian Peninsula. Furthermore, due to a high number of new data from Central Europe (BRANDT ET AL. 2013) comparisons of Western to contemporaneous Central European groups was possible. The results of this study revealed a strong genetic regionalization of Iberian groups throughout the Neolithic and partially in the Chalcolithic. Genetic continuity over the course of the Neolithic and Chalcolithic periods was only observed in few regions. Haplogroup-based statistical analyses clearly separated almost all Iberian and Central European groups from each other while sequence-based methods revealed some affinities between particular Iberian and Central European groups.

Main results were:

- 1.) Hunter-gatherer mitochondrial haplogroup variability was greater at the peripheral regions of Europe. Western European hunter-gatherers were significantly different from other hunter-gatherer groups from East and Central Europe in many analyses.
- 2.) A considerable amount of hunter-gatherer maternal heritage persisted during the Iberian Early Neolithic. Hence, the transition from foraging to farming seems to have been accompanied by acculturation of the indigenous hunter-gatherer populations. The greatest amount of “Neolithic” lineages of haplogroups J, K, N1a, T2, and X has been found in Northeast Spain and Aragón, suggesting these regions were the main entrance for Neolithic lineages into the Iberian Peninsula. The amount of lasting mitochondrial hunter-gatherer influence increases with growing distance from Northeast Spain, both inland and along the coast. This points to various forms of Neolithic transitions on the Iberian Peninsula as has been stated by archaeological research.
- 3.) Haplogroups arriving on the Iberian Peninsula with the first Neolithic farmers were largely concordant to those described in Central Europe (HV, I, J, K, N1a, T2, V, and X). On a sequence level, 85% of the Early Neolithic Iberian individuals with these “Neolithic haplogroups” shared direct sequence hits with individuals affiliated with the LBK.

- 4.) Data from five geographically distinct groups of the Late Neolithic period support the theory that the dispersal of Neolithic lineages after the initial Neolithic transition was not a uniform process. While in some areas genetic continuity to the Early Neolithic seems highly likely (Ebro Valley), other regions show great genetic differences to the preceding period (Central Portugal, Northern Meseta).
- 5.) In general, in comparison to the Early Neolithic, the amount of “Neolithic” haplogroups/haplotypes was elevated in most Iberian Late Neolithic groups resulting in slight genetic affinities of some Iberian groups to contemporaneous Central Europeans. However, they never reached haplogroup compositions found in the Linear pottery culture and succeeding groups.
- 6.) It seems that in the Iberian Chalcolithic some genetic uniformity existed in the “triangle” between the Southern Meseta, East Spain, and the southern part of Portugal, while Northeast Spain and Central Portugal were genetically different to them. In Central Portugal, genetic continuity to the previous Neolithic of the same region can be proposed.
- 7.) Central Iberian Bell Beaker groups were genetically distinct to most other Chalcolithic groups in all analyses. Both Bell Beaker groups showed genetic links to Chalcolithic and Late Neolithic groups of Central Portugal. No genetic connection between Iberian and Central European Bell Beaker or Iberian Bell Beaker and the Corded Ware culture was found.
- 8.) The only sub-haplogroups of haplogroup H that could be identified in the Iberian dataset were H1 (64.4%) and H3 (15.6%). Both haplogroups had already been present in the Early Neolithic, H1 even since the Mesolithic. While H1 was present in all Early and Later Neolithic groups from Central and Western Europe, H3 shows strong Western European affinities and is not detectable in Central Europe before the Middle Neolithic. Contrarily, H5 seems to have been ubiquitous in Central and East European groups, but absent in all western groups. Cluster analysis revealed a main split between two clusters of Western versus Eastern European affinities. Central European Early Neolithic clustered with groups of Eastern Europe while all chronologically later groups fell within a main cluster containing all Western European groups.

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Appendices

I Machines, chemicals, and software

Machines

- Compressor JUN-AIR Typ OF1202-40B, JUN-AIR GmbH, Ahrensburg Germany
- Digital gel-documentation-system INTAS Science Imaging Instruments GmbH, Göttingen, Germany
- Dispenser Dispensette® organic 0,5-5ml, Brand GmbH & Co. KG, Wertheim, Germany
- Electrophoresis chamber Midi, Carl Roth GmbH, Karlsruhe, Germany
- Electroporator EQUIBIO Easyject Prisma, peQLab Biotechnologie GmbH, Erlangen, Germany
- Extraction unit D-LE 280, Harnisch & Rieth GmbH, Winterbach, Germany
- Magnetic stirrer Variomag® Mobil Direct 600, Thermo Fisher Scientific, Waltham, USA
- Magnetic stirrer IKA-Combimag RCT, IKA-Werke GmbH & Co. KG, Staufen, Germany
- Milling cups zirconium oxide für MM200, Retsch GmbH, Haan, Germany
- Mini centrifuge Rotilabo®, Carl Roth GmbH, Karlsruhe, Germany
- Mirco centrifuge Eppendorf 5415R, Eppendorf GmbH, Hamburg, Germany
- Mixer mill MM200, Retsch GmbH, Haan, Germany
- pH-meter FiveEasy™ Starter-Kit FE20-Kit, Mettler-Toledo GmbH, Gießen, Germany
- Pipettes Discovery Comfort 10µl, 20µl, 100µl, 200µl, 1000µl, 5000µl, Abimed GmbH, Langenfeld, Germany
- Powersupply Consort EV243, Carl Roth GmbH, Karlsruhe, Germany
- Reverse osmosis machine Umwelt 3, IEM GmbH, Mainz, Germany
- Sand Blaster P-G 400/2 K, Harnisch & Rieth GmbH, Winterbach, Germany
- Saw KaVo EWL K11 Typ 4980, KaVo Dental GmbH; Leutkirch im Allgäu, Germany
- Scale PCB 1000-2, Kern & Sohn GmbH, Balingen, Germany
- Sequencer ABI PRISM™ 3130 Genetic Analyzer, Applied Biosystems GmbH, Darmstadt, Germany
- Table centrifuge Universal 320, A. Hettich GmbH & Co. KG, Tuttlingen, Germany
- Thermocycler Eppendorf Mastercycler 5333, Eppendorf GmbH, Hamburg, Germany
- Thermocycler Eppendorf Mastercycler Gradient 5331, Eppendorf GmbH, Hamburg, Germany
- Thermomixer Eppendorf Comfort 5355, Eppendorf GmbH, Hamburg, Germany
- UVC-immersion unit sterilAqua AQT2020, sterilAir GmbH, Kürten, Germany

- UV-lamp GPH303T5l/4, UV-Consulting Peschl e.k., Mainz, Germany
- Vacuum filtration system MultiScreen-HTS, Millipore GmbH, Schwalbach, Germany

Material

- Clean lab overall Tyvek® P2-TY Classic, DuPont, Wuppertal, Germany
- Corundum Kl. EW60/250my and Kl. 30B/50my, Harnisch & Rieth GmbH, Winterbach, Germany
- Cutting discs Horico H350 220, Hopf, Ringleb & Co. GmbH & CIE, Berlin, Germany
- Electroporation cuvettes 2mm, peQLab Biotechnologie GmbH, Erlangen, Germany
- Face shield Sekuroka®, Carl Roth GmbH, Karlsruhe, Germany
- Falcon tubes 15ml, 50ml, Sarstedt AG & Co., Nürnbrecht, Germany
- Filter units Amicon Ultra-15 50 kDa, Millipore GmbH, Schwalbach, Germany
- Filtration plates MultiScreen384 SEQ, Millipore GmbH, Schwalbach, Germany
- Filtration plates MultiScreen94 PCR, Millipore GmbH, Schwalbach, Germany
- Gloves Latex Medical 24, Hansa Trading, Hamburg, Germany
- Gloves Nitril Medical 24, Hansa Trading, Hamburg, Germany
- Hoods/hair cover, Hansa Trading, Hamburg, Germany
- OvershoesTyvek® UH-TY-50, DuPont, Wuppertal, Germany
- PCR strips (8) Rotilabo® PCR-Reaktionsstreifen, Carl Roth GmbH, Karlsruhe, Germany
- PCR TW 8-tube strips 0.1ml, Biozym Scientific GmbH, Hessisch Oldendorf, Germany (im Spurenlabor)
- PCR tubes 0.5ml Fisherbrand Premium PCR Tubes 0.5ml, Fisher Scientific GmbH, Schwerte, Germany
- Petri dish 92x16mm, Sarstedt AG & Co., Nürnbrecht, Germany
- Pipette tips Art® Barrier Tips 10µl, 20µl, 100µl, 200µl, 1000µl Fisher Scientific GmbH, Schwerte, Germany
- Pipette tips EcoLine 200µl, 1000µl, MS-L GmbH, Wiesloch, Germany
- Pipette tips epT.I.P.S.® Dualfilter 5000µl, Eppendorf GmbH, Hamburg, Germany
- Pipette tips OMNITIP 10µl, Abimed GmbH, Langenfeld, Germany
- Pipette tips UNITIPS 5000µl, Abimed GmbH, Langenfeld, Germany
- Polythene oversleeves DA01, HPC Healthline Ltd., Morden, UK • Safe-Lock PCR tubes 0.5ml, Eppendorf GmbH, Hamburg, Germany
- Safe-Lock PCR tubes 1.5ml, 2ml, Sarstedt AG & Co., Nürnbrecht, Germany
- cotton swabs for DNA sampling, Heinz Herenz Medizinbedarf GmbH, Hamburg, Germany

- Sealable plastic bags Rotilabo®, Carl Roth GmbH, Karlsruhe, Germany
- Sequencing plates MicroAmp™ Optical 96-Well Reaction Plate und 96-Well Plate Septa, Applied Biosystems GmbH, Darmstadt, Germany
- Surgical masks Medicom Safe + Mask Premier Tie-On, Medicom Inc., Quebec, Kanada
- weighing paper MN226 9 x 11,5cm, Macherey & Nagel via Carl Roth GmbH, Karlsruhe, Germany

Chemicals

Milling

- Hydroxyapatite, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- Silica sand Siliziumdioxid, Carl Roth GmbH, Karlsruhe, Germany

Lysis

- EDTA molecular biology grade 0.5M pH 8.0, Ambion GmbH, Darmstadt, Germany
- N-lauroyl sarcosine Natriumsalz, Merck KGaA, Darmstadt, Germany
- Proteinase K, Roche Diagnostics GmbH, Mannheim, Germany

Extraction phenol-chloroform

- HPLC-water, Fisher Scientific GmbH, Schwerte, Germany
- Roti®-phenol/chloroform/isoamylalcohol 25:24:1 pH 7,5-8,0, Carl Roth GmbH, Karlsruhe, Germany
- Trichloromethane/chloroform ROTISOLV®, Carl Roth GmbH, Karlsruhe, Germany

Extraction Silica

- Acetic acid 2M, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- Ethanol, 99%, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- QG-buffer, Qiagen GmbH, Hilden, Germany
- Silicon dioxide, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- Sodium acetate 5M, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- Sodium chlorid 5M, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- TE-buffer, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- Triton X-100, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany

PCR

- AmpliTaq Gold® DNA-Polymerase, PCR-Puffer und Magnesiumchlorid, Applied Biosystems GmbH, Darmstadt,
- Bovine serum albumin, Roche Diagnostics GmbH, Mannheim, Germany
- dNTP Mix PCR Grade 10mM, Qiagen, Hilden, Germany
- Primer, Biospring GmbH, Frankfurt am Main, Germany

Gelelektrophoresis

- Agarose UltraPure™, Invitrogen GmbH, Darmstadt,
- Boracic acid, Merck KGaA, Darmstadt, Germany
- Bromophenol blue, Carl Roth GmbH, Karlsruhe, Germany
- Ethidium bromide 1%, Carl Roth GmbH, Karlsruhe, Germany
- GeneRuler™ 50bp DNA Ladder, MBI Fermentas GmbH, St. Leon-Rot, Germany
- Sucrose, Sigmar-Alderich Chemie GmbH, Steinheim, Germany
- Tris-Puffer, Carl Roth GmbH, Karlsruhe, Germany

Cloning

- Agar Agar, Carl Roth GmbH, Karlsruhe, Germany
- Ampicillin sodium salt, Carl Roth GmbH, Karlsruhe, Germany
- IPTG, Carl Roth GmbH, Karlsruhe, Germany
- Sma I, MBI fermentas GmbH, St. Leon-Rot, Germany
- T4 DNA ligase und ligation buffer, MBI Fermentas GmbH, St. Leon-Rot, Germany
- Tryptone, Carl Roth GmbH, Karlsruhe, Germany
- TTP-Mix, peQLab Biotechnologie GmbH,, Germany
- Vector-DNA pUC18, in-house production
- X-β-GAL, Carl Roth GmbH, Karlsruhe, Germany
- Yeast extractt, Carl Roth GmbH, Karlsruhe, Germany

Kol-PCR

- dNTPs, MBI Fermentas GmbH, St. Leon-Rot, Germany
- Primer, Biospring GmbH, Frankfurt am Main, Germany
- Thermo-Start DNA-Polymerase, PCR-Puffer und magnesium chloride, Thermo Fisher Scientific, Waltham, USA

Enzymatic clean-up

- Exonuclease I, MBI Fermentas GmbH, St. Leon-Rot, Germany
- Shrimp alkaline phosphatase, MBI Fermentas GmbH, St. Leon-Rot, Germany
- FastAP Thermosensitive Alkaline Phosphatase, MBI Fermentas GmbH, St. Leon-Rot, Germany

Cycle-Sequencing

- Big Dye® Terminator v1.1 Cycle sequencing Kit, Applied Biosystems GmbH, Darmstadt, Germany
- Primer, Biospring GmbH, Frankfurt am Main, Germany

Snapshot reaction

- ABI PRISM® SNaPshot™ Multiplex-Kit, Applied Biosystems GmbH, Darmstadt, Germany

- GeneScan™ -120 Liz™ Size Standard, Applied Biosystems GmbH, Darmstadt, Germany

Capillary gel electrophoresis

- Hi-Di™ formamide, Applied Biosystems GmbH, Darmstadt, Germany
- POP-6™ polymer, Applied Biosystems GmbH, Darmstadt, Germany
- Running buffer EDTA 10x, Applied Biosystems GmbH, Darmstadt, Germany

Cleaning

- Alconox powdered precision cleaner, Sigmar-Aldrich Chemie GmbH, Steinheim, Germany
- DNA-ExitusPlus™ IF, AppliChem GmbH, Darmstadt, Germany
- Sodium hypochlorite DanKlorix, Palmolive-Colgate GmbH, Hamburg, Germany

Kits

- MSB® Spin PCR Rapace Kit, Invitex GmbH, Berlin, Germany
- Invisorb Spin Swab Kit, Invitex GmbH, Berlin, Germany

Software

- Arlequin Version 3.5.1, <http://cmpg.unibe.ch/software/arlequin35/> (EXCOFFIER AND LISCHER 2010)
- DNASTAR Version 9.04 DNASTAR Inc., Madison, USA
- HaploGrep, <http://haplogrep.uibk.ac.at/> (KLOSS-BRANDSTÄTTER ET AL. 2011)
- jModelTest Version 0.1.1, <http://darwin.uvigo.es/software/modeltest.html> (POSADA ET AL. 1998)
- R Version 2.13.1, The R Foundation for Statistical Computing 2011, <http://www.r-project.org/> (EFRON AND TIBSHIRANI 1994)

II Investigated individuals

The table gives information about the samples used for all analyzed individuals. “I” stands for incisivi, “m” for molars, and “pm” for praemolars. Apart from that, teeth are denoted according to the *Fédération Dentaire Internationale*. The subsequent columns give the extraction number, gramm bone/tooth powder used in the extraction and the volume of extract that was gained in the extraction. A, B, and C specify from which sample the extract derived. All or BII stand for repeated but independent extractions of bone/tooth powder residues of a sample.

Site	Archaeological Name	Lab name	A	B	C	EX A	g	μl	EX All	g	μl	EX B	g	μl	EX BII	g	μl	EX C	g	μl
Alto de Rodilla	E2*	Rodi1	36	46	85	RM.1	0.26	120				RO.12	0.26	160						
Arroyal I	Craneo suelto1	Roy1	26	27		ST.11	0.25	200				SV.6	0.24	200						
Arroyal I	Mandibula 1	Roy2	36	38		ST.12	0.28	200				SV.7	0.28	200						
Arroyal I	Craneo Suelto2	Roy3	27	28		ST.13	0.28	200				SV.8	0.99	200						
Arroyal I	Inhumacion 1	Roy4	..6	..8		ST.14	0.34	200				SV.9	0.25	200						
Arroyal I	Inhumacion 2	Roy5	26	27		ST.15	0.26	200				SV.10	0.33	200						
Balma de Sargantana	BS-C3-1154	BAS3	48	46		SC.14	0.25	200				SG.14	0.26	200						
Balma de Sargantana	BS-E4-240	BAS4	47	38		SC.15	0.29	200				SG.15	0.22	200						
Balma de Sargantana	BS-D3,2e 159	BAS5	46	47		SC.16	0.29	200				SG.16	0.22	200						
Balma de Sargantana	BS-D4-45	BAS6	46	48		SC.17	0.24	200				SG.17	0.25	200						
Balma de Sargantana	BS-D3-2c-128	BAS7	36	47		SC.18	0.22	200				SG.18	0.25	200						
Barranc d'en Rifá	BR14	BAR1	46	37		RL.8	0.29	120				RM.6	0.42	160						
Barranc d'en Rifá	BR17	BAR2	36	37		RL.9	0.29	120	RN.14	0.41	124	RM.7	0.45	140						
Barranc d'en Rifá	BRG	BAR3	37	47		RL.10	0.22	140				RM.8	0.41	165						
Barranc d'en Rifá	BRH	BAR4	37	38		RL.11	0.27	135	RN.15	0.46	118	RM.9	0.47	170						
Barranc d'en Rifá	BRI/L	BAR5	46	37		RL.12	0.23	160	RP.10	0.41	122	RM.10	0.4	120						
Barranc d'en Rifá	BRG	BAR6	35	34		ST.1	0.27	200				SU.1	0.26	200						
Barranc d'en Rifá	BRM	BAR7	47	45		ST.2	0.31	200				SU.2	0.28	200						
Barranc d'en Rifá	BR10	BAR8	36	47		ST.3	0.25	200				SU.3	0.24	200						
Barranc d'en Rifá	BR19	BAR9	43	36		ST.4	0.24	200				SU.4	0.27	200						
Barranc d'en Rifá	BR-CRO1	BAR10	36	37		ST.5	0.31	200				SU.10	0.26	200						
Barranc d'en Rifá	BR-CRO2	BAR11	36	37		ST.6	0.25	200				SU.6	0.24	200						
Barranc d'en Rifá	BR4	BAR12	37	48		ST.7	0.31	200				SU.7	0.27	200						
Barranc d'en Rifá	BR20	BAR13	36	46		ST.8	0.29	200				SU.8	0.26	200						
Barranc d'en Rifá	BRC	BAR14	36	38		ST.9	0.26	200				SU.9	0.26	200						
Barranc d'en Rifá	BRB	BAR15	38	37		ST.10	0.27	200				SU.5	0.26	200						
Bolores	Adolescent 1 11S 4 720	Bol1	15	26?		SP.14	0.3	200												
Bolores	Adult 1 11S 1 114	Bol2	37	38		SP.15	0.25	200												
Bolores	Adult 4 2 1 14	Bol3	48	46		SP.16	0.26	200												
Bolores	Adolescent 2 11S 5 676	Bol4	46	47		SP.17	0.35	200												
Bolores	Adult 2 11B 4 663	Bol5	46	47		SP.18	0.24	200				SU.18	0.31	200						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	μl	EX All	g	μl	EX B	g	μl	EX Bll	g	μl	EX C	g	μl
Cabezo Pardo	Tumba 1 (2007) Hueso 10 male	Cab1	bone	bone		SS.12	0.28	200				ST.17	0.24	200						
Cabezo Pardo	Tumba 1 (2007) Hueso 54 female	Cab2	36	47		SS.13	0.27	200				ST.18	0.89	200						
Cadaval	CDV SUP S-C39	CDV1	47	45		RX.8	0.24	200				SA.1	0.47	200						
Cadaval	CDV F30 S-C39	CDV2	85	84		RX.9	0.23	200				SA.2	0.5	200						
Cadaval	CDV H3 111	CDV3	46			RX.10	0.34	200				SA.3	0.26	200						
Camino de las Yeseras	Area 35 Ue 03 E 03-VIII Ind 1	Yese1	38	38	35	SE.5	0.25	200				SF.5	0.26	200						
Camino de las Yeseras	Area 10 Ue 03 E 01 Ind 2	Yese2	37	38	44	SE.6	0.25	200				SF.6	0.23	200						
Camino de las Yeseras	Area 10 Ue 05 E 07 Ind 1	Yese3	46	48	34	SE.7	0.24	200				SF.7	0.23	200						
Camino de las Yeseras	Area 10 E 01 Ind 1	Yese4	47	48	PM	SE.8	0.23	200				SF.8	0.24	200						
Camino de las Yeseras	Area 35 E 02 Ind 2	Yese5	36	37		SE.9	0.26	200				SF.9	0.24	200						
Camino de las Yeseras	Area 85 E02 Ind 2	Yese6	37	38	74	SE.10	0.27	200				SF.10	0.32	200				SW.4	0.35	200
Camino de las Yeseras	Area 10 Ue 05 E 07 Ind 8	Yese7	36	37	35	SE.11	0.24	200				SF.11	0.23	200						
Camino de las Yeseras	Area 10 E 07 Ind 7	Yese8	46	M	15	SO.3	0.23	200				SP.3	0.25	200						
Camino de las Yeseras	Area85 E02 Ind5	Yese9	37	34	84	SO.4	0.31	200				SP.4	0.25	200						
Camino de las Yeseras	Area10 UE05 E07 Ind3	Yese10	36	75	37	SO.5	0.27	200				SP.5	0.4	200						
Camino de las Yeseras	Area85 E02 Ind1	Yese11	37	27		SO.6	0.29	200				SP.6	0.25	200						
Camino de las Yeseras	Area31 UE09 Element1-I	Yese12	13	14		SO.7	0.29	200				SP.7	0.25	200						
Camino de las Yeseras	Area10 UE05 E7 Ind 4	Yese13	75	85		SO.8	0.25	200				SP.8	0.26	200						
Camino de las Yeseras	Area 85 E2 Ind3	Yese14	36	38		SO.9	0.31	200				SP.9	0.26	200						
Camino de Molino	CMOL 6	CMOL6	37	48	47	RQ.12	0.3	150				RR.1	0.22	125						
Camino de Molino	CMOL 12	CMOL12	46	38	47	RW.1	0.25	200				RY.1	0.21	200						
Camino de Molino	CMOL 16	CMOL16	46	37	36	RQ.13	0.24	160				RR.2	0.22	150						
Camino de Molino	CMOL 44	CMOL44	36	38	37	RQ.14	0.22	160				RR.3	0.24	130						
Camino de Molino	CMOL 71	CMOL71	46	37	36	RQ.15	0.26	130				RR.4	0.29	150						
Camino de Molino	CMOL 79	CMOL79	46	38	37	RW.2	0.33	200				RY.2	0.25	200						
Camino de Molino	CMOL 104	CMOL104	36	37	48	RW.3	0.31	200				RY.3	0.25	200						
Camino de Molino	CMOL 105	CMOL105	36	38	45	RW.4	0.32	200				RY.4	0.35	200						
Camino de Molino	CMOL 119	CMOL119	47	48	38	RW.5	0.26	200				RY.5	0.25	200						
Camino de Molino	CMOL 122	CMOL122	36	37		RW.6	0.31	200				RY.6	0.53	200						
Camino de Molino	CMOL 123	CMOL123	46	37	47	RX.1	0.41	200				RY.7	0.25	200						
Camino de Molino	CMOL 138	CMOL138	36	37	44	RX.2	0.31	200				RY.8	0.32	200						
Camino de Molino	CMOL 139	CMOL139	47	33		RX.3	0.3	200				RY.9	0.41	200						
Camino de Molino	CMOL 140	CMOL140	36	38	37	RX.4	0.36	200				RY.10	0.28	200						
Camino de Molino	CMOL 151	CMOL151	36	38	37	RQ.16	0.22	160				RR.5	0.23	135						
Camino de Molino	CMOI 154	CMOL154	37	37	46	RX.5	0.27	200				RY.11	0.29	200						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	µl	EX All	g	µl	EX B	g	µl	EX Bll	g	µl	EX C	g	µl
Camino de Molino	CMOI 164	CMOL164	47	28	38	RX.6	0.26	200				RY.12	0.56	200						
Camino de Molino	CMOI 165	CMOL165	36	37	35	RX.7	0.37	200				RY.13	0.32	200						
Can Gambús	1074	GAM1	17	28	27	RR.14	0.25	125				RS.9	0.25	110						
Can Gambús	1075	GAM2	36	37	34	RR.15	0.29	118				RS.10	0.29	120						
Can Gambús	1076	GAM3	37	38	33	RR.16	0.22	125				RS.11	0.22	130						
Can Gambús	E-172 UE-650 Ind 1	GAM4	47	46		SM.16	0.35	200				SQ.11	0.58	200						
Can Gambús	E-172 Ue-448	GAM5	36	47	46	SM.17	0.39	200				SQ.12	0.33	200						
Can Gambús	E-172 UE-655 Ind 6	GAM6	46	48	45	SM.18	0.33	200				SQ.13	0.37	200						
Can Gambús	E-172 UE-650	GAM7	17	28		SN.9	0.31	200				SQ.14	0.35	200						
Can Gambús	E-349 UE-1056 Coord. 76	GAM8	46	37	17	SN.10	0.31	200				SQ.15	0.4							
Cobre las Cruces (SE-K)	T17	Cru1	16	17	15	SJ.13	0.37	200				SL.8	0.4	200						
Cobre las Cruces (SE-K)	T12	Cru2	36	37		SJ.14	0.47	200				SL.9	0.43	200						
Cobre las Cruces (SE-K)	T23b	Cru3	M	M		SK.7	0.4	200				SN.14	0.35	200						
Cobre las Cruces (SE-K)	T23a	Cru4	46	44	45	SK.8	0.36	200				SN.15	0.45	200						
Concheiro da Moita do Sebastião	22	Seba1	37	35		RL.3	0.24	170				SJ.15	0.47	200						
Concheiro da Moita do Sebastião	54	Seba2	37	47		RL.4	0.25	115				RM.2	0.42	155						
Concheiro da Moita do Sebastião	XI.X	Seba3	38	48		RL.5	0.24	140				RM.3	0.42	140						
Concheiro do Cabeço da Arruda	XIII (113)	Arru1	36	37		RL.6	0.25	110				RM.4	0.42	125						
Concheiro do Cabeço da Arruda	42	Arru2	46	47		RL.7	0.26	120				RM.5	0.44	125						
Cova d'en Pardo	ENP'98 6.6 D III (48)	Par1	36	37		SB.5	0.34	200				SC.1	0.26	200						
Cova d'en Pardo	ENP'97 5.6 A IIb(79)	Par2	37	36	46	SB.6	0.34	200				SC.2	0.34	200						
Cova d'en Pardo	ENP '98 6.6 D IIb(15) /5.6A IIb	Par3	37	36		SB.7	0.36	200				SC.3	0.31	200						
Cova d'en Pardo	ENP' 99 5.4 DIII (17)	Par4	47	48	47	SB.8	0.34	200				SC.4	0.3	200						
Cova d'en Pardo	Enp'94 4.5 BII (49)/ ENP'94 5.4 BIII	Par5	46	36		SB.9	0.28	200				SC.5	0.29	200						
Cova d'en Pardo	ENP'03 7.5A III	Par6	femur	femur		SB.10	0.29	200				SC.6	0.31	200						
Cova d'en Pardo	ENP '95 7.5 AIII (25)	Par7	bone	bone		SB.11	0.39	200				SC.7	0.35	200						
Cova d'en Pardo	ENP '97 5.5 CIII (19)	Par8	humerus	humerus		SB.12	0.26	200				SC.8	0.27	200						
Cova de la Ventose		Vent1	36			SS.18	0.27	200				SU.15	0.25	200						
Cova del Barranc del Migdia	CBMX10 Ue46- mujer	Dia 1	26	27		SR.1	0.26	200				SS.1	0.29	200						
Cova del Barranc del Migdia	CBMX10 Ue46- hueso 29 infantil	Dia 2	bone	bone		SR.2	0.46	200				SS.2	0.35	200						
Cova del Barranc del Migdia	CBMX10 UE26	Dia 3	M	M		SR.3	0.28	200				SS.3	0.28	200						
Cova del Barranc del Migdia	CBMX10 Ue34 hueso 49 infantil	Dia 4	bone	bone		SR.4	0.3	200				SS.4	0.5	200						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	µl	EX All	g	µl	EX B	g	µl	EX BII	g	µl	EX C	g	µl
Cova del Barranc del Migdia	CBMX10 Ue34 hueso 75 man	Dia 5	bone	bone		SR.5	0.27	200				SS.5	0.52	200						
Cova del Barranc del Migdia	CBMX10 Ue50 hueso 13 mujer	Dia 6	femur	femur		SR.6	0.27	200												
Cova del Barranc del Migdia	CBMX10 Ue50 hueso18 hombre	Dia 7	fibula?	fibula?		SR.7	0.34	200												
Cova del Cantal	CC '90 Caja 3 No 2	Coca1	bone	bone		SC.9	0.32	200				SD.1	0.24	200						
Cova del Cantal	CC '90 Caja 3 No 20c	Coca2	bone	bone		SC.10	0.35	200				SD.2	0.3	200						
Cova del Cantal	Cc'90 Caja 4 No2	Coca3	bone	bone		SC.11	0.34	200				SD.3	0.33	200						
Cova del Cantal	Cc'90 Caja 4 No55	Coca4	bone	bone		SC.12	0.34	200				SD.4	0.32	200						
Cova del Cantal	CC'90 Caja 3 No16	Coca5	bone	bone		SC.13	0.34	200				SD.5	0.35	200						
El Castillejo	Corte Este Nivel III Muerto 2	Elca1	tooth	tooth	tooth	SP.1	0.33	200				SQ.1	0.25	200				SX.2	0.5	200
El Castillejo	1b2 nivel I Muerto 13	Elca2	tooth	tooth	tooth	SP.2	0.26	200				SQ.2	0.31	200						
El Hundido	UE 750	Hund1	38	43	35	RX.16	0.25	200				SB.3	0.26	200						
El Hundido	UE 450*	Hund2	48	38	47	RX.17	0.26	200				SB.4	0.25	200						
El Juncal	UE 03 Est 93 Ind 6	Junc1	16	18	17	RZ.13	0.23	200				SA.13	0.27	200						
El Juncal	UE 03 Est 93 Ind 5	Junc2	18	13	15	RZ.14	0.26	200				SA.14	0.22	200						
El Juncal	UE 01 Est 199 Ind 2	Junc3	36	38	37	RZ.15	0.24	200				SA.15	0.27	200						
El Juncal	UE 03 Est 93 Ind 9	Junc4	37	36	33	RZ.16	0.23	200				SA.16	0.34	200						
El Juncal	UE 03 Est 93 Ind 4	Junc5	36	38	37	RZ.17	0.25	200				SA.17	0.34	200						
El Juncal	UE 01 Est 93 Ind 1	Junc6	36	38	37	RZ.18	0.25	200				SA.18	0.35	200						
El Juncal	UE 03 Est 93 Ind 8	Junc7	36	46		SM.8	0.39	200				SN.1	0.47	200						
El Juncal	UE 01 Est 199 Ind 4	Junc8	46	47	45	SM.9	0.45	200				SN.2	0.35	200						
El Juncal	UE 01 Est 199 Ind 1	Junc9	36	38	33	SM.10	0.37	200				SN.3	0.27	200						
El Juncal	UE 03 Est 93 Ind 3	Junc10	33	34	32	SM.11	0.34	200				SN.4	0.27	200						
El Juncal	UE 03 Est 93 Ind 11	Junc11	16	18	17	SM.12	0.49	200				SN.5	0.27	200						
El Juncal	UE 01 Est 199 Ind 5	Junc12	36?	37?		SM.13	0.31	200				SN.6	0.25	200						
El Juncal	UE 03 Est 93 Ind 7	Junc13	16	26	65	SM.14	0.35	200				SN.7	0.27	200						
El Juncal	UE 01 Est 199 Ind 3	Junc14	36	37	32	SM.15	0.33	200				SN.8	0.25	200						
Els Trocs	UE:63 C:558 S:6 No Inv: 1623	Troc1	65	64		RQ.11	0.27	140				RT.12	0.4	135						
Els Trocs	UE 14 C: 589 S:7 No Inv: 14227	Troc2	46	47		SO.10	0.31	200				SP.10	0.27	200						
Els Trocs	UE 16 C: 560 S: 7 No Inv: 14296	Troc3	47	48		SO.11	0.24	200				SP.11	0.28	200						
Els Trocs	UE 85 C: 557 S: 9 No Inv: 14402	Troc4	64	65		SO.12	0.28	200				SP.12	0.31	200						
Els Trocs	UE:99 C: 558 S:5 No Inv:22743	Troc5	36	37		SS.8	0.28	200				SU.11	0.3	200						
Els Trocs	UE:01 C: 650 S:1 No Inv: 22404	Troc6	36	37		SS.9	0.25	200				SU.12	0.28	0	SV.1	0.2	200			

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	μl	EX All	g	μl	EX B	g	μl	EX Bll	g	μl	EX C	g	μl
Els Trocs	UE:98 C:617 S3 No Inv: 22658	Troc7	65	64		SS.10	0.33	200				SU.13	0.3	200						
Els Trocs	2009:13:00	Troc8	16	13		SS.11	0.31	200				SU.14	0.48	200						
Els Trocs		Troc10	24	25		SX.4	0.36	200				OW.1	0.44	200						
Els Trocs		Troc12	17	13		SX.5	0.3	200				OW.2	0.35	200						
Els Trocs		Troc13	85	84		SX.6	0.45	200				OW.3	0.14	200						
Es Forat de ses Aritges	FA 32-3592	Fora1	36	38	37	SD.14	0.29	200				SG.1	0.29	200						
Es Forat de ses Aritges	FA 47-8890	Fora2	36	38	37	SD.15	0.38	200				SG.2	0.27	200						
Es Forat de ses Aritges	FA 47- 12159	Fora3	36	38	37	SD.16	0.32	200				SG.3	0.21	200						
Es Forat de ses Aritges	FA 49-9819	Fora4	36	47	46	SD.17	0.26	200				SG.4	0.32	200						
Es Forat de ses Aritges	FA 42-6094	Fora5	46	47	36	SD.18	0.36	200				SG.5	0.22	200						
Fuente Álamo	75	Fala1	46	48	47	RY.14	0.24	200	SJ.18	0.62	200	SH.4	0.5	200						
Fuente Álamo	75a	Fala2	46	47	33	RY.15	0.24	200				SH.5	0.45	200						
Fuente Álamo	93	Fala3	13	23	43	RY.16	0.22	200				SI.4	0.46	200						
Fuente Álamo	111	Fala4	47	46	45	RY.17	0.21	200				SI.5	0.36	200						
Fuente Álamo	112	Fala5	28	26	24	RY.18	0.21	200				SI.6	0.48	200						
Fuente Celada	UE 53 hoyo 5 Ind 3	Cel1	M	M	M	SH.1	0.25	200				SI.1	1.19/0. 25	200						
Fuente Celada	UE 193 hoyo1? Ind 4	Cel2	46	47	43	SH.2	0.22	200				SI.2	1.12/0. 22	200						
Fuente Celada	UE 622 Hoyo 62 Ind 5	Cel3	45	tooth	tooth	SH.3	0.28	200				SI.3	0.86/0. 22	200			SW.3	0.4	200 0	
Fuente Pecina 1	Quadr NE	Fupe6	36	35		RO.6	0.26	160				RP.11	0.39	185						
Fuente Pecina 1	Quadr Central 50x50	Fupe7	45	33	44	RO.7	0.33	125				RP.12	0.37	150						
Fuente Pecina 1	Quadr. SE 2x2	Fupe8	36	37	35	RO.8	0.25	140				RP.13	0.26	125						
Fuente Pecina 1	Quadr S 1x1	Fupe9	37	35		RO.9	0.26	140				RP.14	0.24	150						
Fuente Pecina 2	FP2-M2	Fupe1	46	33	34	RN.9	0.23	120				RO.1	0.24	140			SW.2	0.45	200	
Fuente Pecina 2	FP2-M5	Fupe2	46	45		RN.10	0.24	135				RO.2	0.23	118						
Fuente Pecina 2	FP2-M1	Fupe3	46	47	85	RN.11	0.26	140				RO.3	0.23	145						
Fuente Pecina 2	FP2-M5	Fupe4	M	PM	PM	RN.12	0.25	150				RO.4	0.22	119						
Fuente Pecina 2	FP2-M7	Fupe5	36	37		RN.13	0.24	158				RO.5	0.23	150						
Fuente Pecina 4	no name	Fupe10	26	28	27	RO.10	0.25	160				RP.15	0.24	125						
Fuente Pecina 4	no name	Fupe11	26	27		RO.11	0.24	160				RP.16	0.24	140						
Gruta das Alcobertas	221,127	Alco1	36	35	38	SE.1	0.24	200				SF.1	0.23	200						
Gruta das Alcobertas	221,132	Alco2	46	45	35	SE.2	0.24	200				SF.2	0.22	200						
Gruta de Malgasta	1	Malga1	37	38		SH.8	0.23	200				SI.7	0.23	200						
Gruta de Malgasta	2	Malga2	36	38		SH.9	0.25	200				SI.8	0.23	200						
Gruta do Carvalho de Turquel		Turq1	46	47		RW.7	0.24	200				SB.1	0.25	200						
Gruta do Carvalho de Turquel		Turq2	46	47		RW.8	0.24	200				SB.2	0.25	200						
Gruta do Poço Velho	223.1912	Pove1	37	38	47	SE.3	0.25	200				SF.3	0.23	200						
Gruta do Poço Velho	223.1921	Pove2	47	48	45	SE.4	0.23	200				SF.4	0.24	200						
Gruta dos Ossos	GRO 8 VI 46	Gro1	46	37	48	RX.11	0.32	200				SG.9	0.29	200						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	µl	EX All	g	µl	EX B	g	µl	EX Bll	g	µl	EX C	g	µl
Gruta dos Ossos	GRO 9 VII 107	Gro2	38	48	35	RX.12	0.28	200				SG.10	0.28	200						
Gruta dos Ossos	GRO 9 VI 44 + 195	Gro3	36	33	44	RX.13	0.35	200				SG.11	0.45	200						
Gruta dos Ossos	GRO 9VI 10	Gro4	36	32	45	RX.14	0.31	200				SG.12	0.43	200						
Gruta dos Ossos	GRO LGG S-C 27	Gro5	47	48	46	RX.15	0.29	200	SW.18	0.45	200	SG.13	0.36	200						
Humanejos	443	Hume1	46	47	45	RR.6	0.26	135				RS.1	0.24	140						
Humanejos	146187	Hume2	26	27	25	RR.7	0.25	140				RS.2	0.24	105						
Humanejos	146154	Hume3	26	25	24	RR.8	0.26	130				RS.3	0.44	150						
Humanejos	146143	Hume4	26	28	25	RR.9	0.25	150				RS.4	0.25	150						
Humanejos	4552	Hume5	36	38	46	RR.10	0.24	125				RS.5	0.25	150						
Humanejos	1762	Hume6	36	75	I	RR.11	0.24	150				RS.6	0.23	130						
Humanejos	19413	Hume7	46	48	36	RR.12	0.25	118				RS.7	0.23	140						
Humanejos	146176	Hume8	26	27	16	RR.13	0.26	130				RS.8	0.25	130						
Humanejos	4557	Hume9	27?	28?	PM	SH.13	0.24	200				SI.9	0.41	200						
Humanejos	4552	Hume10	46	45	43	SH.14	0.33	200				SI.10	0.26	200	SW.10	0.6	200			
Humanejos	4559	Hume11	26	27		SH.15	0.36	200				SI.11	0.24	200	SW.11	0.6	200			
Humanejos	18354	Hume12	36	38	37	SH.16	0.24	200				SI.12	0.4	200						
Humanejos	395	Hume13	36	85	46	SH.17	0.22	200				SI.13	0.35	200						
Humanejos	18536	Hume14	46	48	47	SH.18	0.29	200				SI.14	0.34	200						
Humanejos	20141/201431?	Hume15	23	21	25	SJ.1	0.33	200	SW.12	0.77	200	SK.1	0.41	200						
Humanejos	392	Hume16	16	17	27	SJ.2	0.62	200												
Humanejos	187	Hume17	26	34	M	SJ.3	0.31	200												
Humanejos	201442	Hume18	46	43	44	SJ.4	0.26	200	SW.13	0.66	200	SK.2	0.42	200						
Humanejos	14612 Ind 1	Hume19	36	37	46	SJ.5	0.33	200				SK.3	0.25	200						
Humanejos	1938	Hume20	46	15	15	SJ.6	0.57	200												
Humanejos	1964	Hume21	46	45	45	SJ.7	0.37	200				SK.4	0.22	200						
Humanejos	184302	Hume22	46?	47?	Pm	SJ.8	0.67	200												
Humanejos	18162	Hume23	46	44	43	SJ.9	0.32	200												
Humanejos	17502	Hume24	46	45	44	SJ.10	0.27	200				SK.5	0.37	200						
Humanejos	2784	Hume25	46	47	26	SJ.11	0.4	200				SK.6	0.5	200						
Humanejos	17225	Hume26	6er	7er	8er	SJ.12	0;36	200												
Ifri N' ammar o Moussa	Ind 6	Iam1	M			SO.13	0.29	200				SP.13	0.28	200						
Illeta dels Banyets	Tumba I - 439 (Caja 38)	Ban1	bone	bone		SL.1	0.51	200				SM.1	0.44	200						
Illeta dels Banyets	Tumba I - 449 (Caja 39)	Ban2	27	25		SL.2	0.38	200				SM.2	0.4	200						
Illeta dels Banyets	Tumba II-40 (Caja 45)	Ban3	bone	bone		SL.3	0.43	200				SM.3	0.4	200						
Illeta dels Banyets	Tumba II-48 (Caja 46)	Ban4	femur	tibia		SL.4	0.32	200				SM.4	0.42	200						
Illeta dels Banyets	Tumba IV - 1978 (Caja 209)	Ban5	bone	bone		SL.5	0.35	200				SM.5	0.36	200						
Illeta dels Banyets	Tumba IV - 1977 (Caja 213)	Ban6	femur	bone		SL.6	0.58	200				SM.6	0.35	200						
Illeta dels Banyets	Tumba V - 1966 (Caja 214)	Ban7	femur	femur		SL.7	0.33	200				SM.7	0.47	200						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	μl	EX All	g	μl	EX B	g	μl	EX BII	g	μl	EX C	g	μl
La Bastida	Ba 6-1	Ba6-1	48	22	46	RC.4	0.37	130				RD.1	0.37	115						
La Bastida	Ba12-1	Ba12-1	44	32		RC.5	0.41	95				RD.2	0.41	110						
La Bastida	Ba12-2	Ba12-2	36	31	16	RC.6	0.3	105	TF.13	0.56	140	RE.1	0.3	130				RG.1	0.34	138
La Bastida	ba 16-1	Ba16-1	M2	P1	M2	RG.2	0.29	120				SH.6	0.13	200						
La Bastida	Ba 16-2	Ba16-2	37	31		RG.4	0.33	140	RH.7	0.34	122	SH.7	0.3	200						
La Bastida	Ba 18-1	Ba18-1	47	35	15	RG.3	0.34	120												
La Bastida	Ba 18-2	Ba18-2	46	47	M2	RG.5	0.22	140				RH.8	0.53	140						
La Bastida	Ba 33	Ba33	46	47	24	Tf.14	0.4	150												
La Bastida	Ba 14085	LaBa1	37	38	35	RJ.10	0.23	115				RK.10	0.45	140						
La Bastida	Bamam 6	Bq62	?	?	46	Sl.15	0.3	200												
La Bastida	Bamam 10	LaBa3	46	36		Sl.16	0.28	200												
La Bastida	Bamam 9	LaBa4	16	27	25	Sl.17	0.25	200												
La Bastida	Bamam 8	LaBa5	26	28	27	Sl.18	0.23	200												
La Huera	UE 2229,188	Hue1	46	47	45	SK.17	0.43	200				SN.16	0.39	200						
La Huera	UE 2229, 48	Hue2	36	37	35	SK.18	0.29	200				SN.17	0.3	200						
La Huera	UE 2229,160	Hue3	36	38		SL.18	0.42	200				SN.18	0.31	200						
La Mina	Probe 1 skull 3	Mina1	26	28	27	RJ.1	0.23	140				RK.1	0.26	150						
La Mina	Probe 2 skull 1	Mina2	16	18	17	RJ.2	0.29	130				RK.2	0.26	180						
La Mina	Probe 3 skull 7	Mina3	36	38	37	RJ.3	0.22	130				RK.3	0.24	123						
La Mina	Probe 4 skull 8	Mina4	16	18	17	RJ.4	0.23	118				RK.4	0.24	140						
La Mina	Probe 5 skull 9	Mina5	16	18	17	RJ.5	0.23	145				RK.5	0.24	150						
La Mina	Probe 6 skull 10	Mina6	16	17		RJ.6	0.23	130				RK.6	0.25	120						
La Mina	Probe7 skull 11	Mina7	16	17		RJ.7	0.24	170				RK.7	0.25	140	RL.1	0.4	160			
La Mina	Probe 9 skull 13	Mina9	36	38	37	RJ.9	0.28	150				RK.9	0.24	170				RL.2		160
La Mina	UE 8 2404-2407 Craneo 15	Mina10	?	?		RP.1	0.32	120				RQ.1	0.26	150						
La Mina	UE 8 3437-3439	Mina14	48	47	46	RP.5	0.32	125				RQ.5	0.35	150						
La Mina	UE 8 2480-2482	Mina16	47	47	47	RP.7	0.32	130				RQ.7	0.25	150						
La Mina	UE 8 2408-2410	Mina17	?	?		RP.8	0.32	185				RQ.8	0.26	140						
La Mina	UE 8 2871-2872	Mina18	47/48?	46		RP.9	0.32	110				RQ.9	0.24	150						
La Tarayuela	UE 13 H-22	Tar1	47?	48?	46?	RT.1	0.33	140	ST.16	0.43	200	RU.1	140	0.4						
La Tarayuela	UE 13 H82	Tar2	16	15	M	RT.2	0.33	125				RU.2	120	0.3				SX.3	0.48	200
La Tarayuela	UE 15 F2-H1	Tar3	16	26		RT.3	0.33	160				RU.3	160	0.2						
La Tarayuela	UE 7	Tar4	47	48	tooth	RT.4	0.32	145				RU.4	140	0.3						
La Tarayuela	UE 14 RH-H56	Tar5	46	47	43	RT.5	0.32	160				RU.5	130	0.3						
La Tarayuela	UE 13 HUEso 99	Tar6	46	48	38	RT.6	0.38	150				RU.6	130	0.4				Sw.5	0.4	
La Tarayuela	UE13 H66	Tar7	36	38	37	RT.7	0.24	150				RU.7	130	0.2						
La Tarayuela	UE 14 RH-H62	Tar8	46	48	47	RT.8	0.26	160				RU.8	130	0.2						
La Tarayuela	UE 14 HUEso 84	Tar9	M	46	85	RT.9	0.32	160				RU.9	140	0.3				SW.6	0.7	
La Tarayuela	UE 13 H 108	Tar10	36	37	35	RT.10	0.33	150	SW.16	0.56	200	RU.10	130	0.4						
La Tarayuela	UE 14 Inventario 521	Tar11	85	75	74	RT.11	0.47	140				RU.11	140	0.4						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	μl	EX All	g	μl	EX B	g	μl	EX BII	g	μl	EX C	g	μl
Lorca	Madre Mercedarias Iglesias Tomb 2	MMI1a	37	14	47	SB.13	0.28	200												
Lorca	Madre Mercedarias Iglesias Tomb 11-1	MMI2a	46	48		SB.14	0.23	200												
Lorca	Madre Mercedarias Iglesia Tomb 4-1	MMI3a	46	47	33	SB.15	0.21	200				SH.10		200						
Lorca	Los Tintores 2-1	Tint1	37	38		SB.16	0.22	200				SH.11		200						
Lorca	Los Tintores 2-2	Tint2	46	47		SU.17	0.25	200				SV.3	0.25	200						
Lorca	Castillo de Lorca Loc 4	Cast1a	36	38		SB.17	0.27	200				SH.12		200						
Lorca	Zapateria Uma 3 Tumba 3	Zapa1a	36	37		SB.18	0.26	200												
Miquel Vives	Miquel Vives 39	MIV1	36	37		SN.11	0.21	200				SO.1	0.23	200						
Miquel Vives	Miquel Vives 259	MIV2	16	55		SN.12	0.29	200				SO.2	0.22	200						
Molinos del Papel	MP1039	MOP1	26	28	25	RH.10	0.36	14									SW.7	0.39	200	
Molinos del Papel	MP1059	MOP2	37	36	12?	RH.11	0.27	160				RI.13	0.23	140						
Molinos del Papel	MP1065	MOP3	36	38	36	RH.12	0.29	120				RI.14	0.42	140						
Monte Canelas I	MCI 145.48	Moca1	36	47	46	RN.1	0.43	170				SD.6	0.32	200						
Monte Canelas I	MCI 225.42	Moca2	46	47	37	RN.2	0.35	130	SV.18	0.63	200	SD.7	0.33	200						
Monte Canelas I	MCI 145.88	Moca3	46	47	38	RN.3	0.29	150				SD.8	0.31	200						
Monte Canelas I	MCI 225.1	Moca4	36	37	46	RN.4	0.33	127				SD.9	0.22	200	Sw.19	0.4	200			
Monte Canelas I	MCI 218.19 + 335.11	Moca5	36	37	46	RN.5	0.21	150				SD.10	0.35	200						
Monte Canelas I	MCI 419.126	Moca6	36	37		RN.6	0.21	162				SD.11	0.22	200						
Monte Canelas I	MCI 384.45	Moca7	36	38	37	RN.7	0.4	140				SD.12	0.36	200						
Monte Canelas I	MCI 218.21	Moca8	36	37	46	RN.8	0.32	125				SD.13	0.35	200						
Monte Canelas III	172.25	MCIII1	36	35		SQ.18	0.26	200				SR.10	0.33	200						
Monte Canelas III	172.54	MCIII2	26	27		SR.11	0.32	200				SS.6	0.29	200						
Nossa Senhora das Lapas	GSL Q-Ind	GSL1	16	18		RZ.1	0.23	200				SG.6	0.26	200						
Nossa Senhora das Lapas	GSL P25 S-C47	GSL2	15	14		RZ.2	0.65	200				SG.7	0.25	200						
Nossa Senhora das Lapas	GSL LSS-C15	GSL3	16	17		RZ.3	0.23	200				SG.8	0.28	200	SW.17	0.3	200			
Nuevo IES Valencia ROD 05-32	ROH 64 Cranéo 4 26.08.05 12	Cine1	26	27	25	SK.9	0.42	200				SL.10	0.36	200				SX.1	0.4	
Nuevo IES Valencia ROD 05-32	ROH 64 Cranéo 10 26.08.05 20	Cine2	46	44	43	SK.10	0.35	200				SL.11	0.33	200						
Nuevo IES Valencia ROD 05-32	ROH 281 Cranéo 26.08.05 2	Cine3	28	27		SK.11	0.26	200				SL.12	0.38	200						
Nuevo IES Valencia ROD 05-32	ROH 283 Cranéo 4 26.08.05 1	Cine4	25	24	tooth	SK.12	0.49	200				SL.13	0.57	200						
Poroad de Alcalar	494.13	Alca1	26	24		SQ.16	0.28	200				SR.8	0.31	200						
Poroad de Alcalar	530.33.494	Alca2	24	26		SQ.17	0.26	200				SR.9	0.25	200						
Reinoso	Individual 1	Rein1	36	37	27	RA.1	0.45	115				RB.1	0.41	120						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	μl	EX All	g	μl	EX B	g	μl	EX Bll	g	μl	EX C	g	μl
Reinoso	Individual 2	Rein2	26	28	27	RA.2	0.64	90				RB.2	0.51	115				0.29		
Reinoso	Individual 3	Rein3	46	48	47	RA.3	0.71	110				RB.3	0.77	125						
Reinoso	Individual 4	Rein4	26	28	27	RA.4	0.55	95				RB.4	0.77	140						
Reinoso	Individual 5	Rein5	26	27	25	RA.5	0.73	135				RB.5	0.49	160						
Reinoso	Individual 6 (3203-3206)	Rein6	femur	femur	femur	RC.1	0.33	110				RF.3	0.53	145				RI.1	0.29	120
Reinoso	Individual 8	Rein8	M1	M2	p2?	RA.6	0.58	85				RB.6	0.52	105						
Reinoso	Individual 9	Rein9	femur	femur		RC.3	0.3	120				RF.5	0.3	130						
Reinoso	Individual 10	Rein10	26?	M3?	27	RA.7	0.59	140				RB.7	0.43	140	RF.10	0.2	130	RI.3	0.32	140
Reinoso	Individual 11? (2835-2838)	Rein11	36			RA.8	0.6	110				RB.8	0.54	130						
Reinoso	Individual 12	Rein12	M	tooth 2		TD.14	0.3	160				RG.6	0.33	150						
Reinoso	Assamblege 6, 1173-1174	Rein13	mand left	mand right	mand left	RD.3	0.61	160				RE.2	0.2	158						
Reinoso	Assamblege 6, 1171-1172	Rein14	26	27	M	RD.4	0.33	110				RE.3	0.22	105						
Reinoso	Assamblege 9 (1149-1150)	Rein15	46	48 47?		RD.5	33	125				RE.4	0.23	123						
Reinoso	Assamblege 9 (1158-1160)	Rein16	46	47		RD.6	0.35	120				RE.5	0.23	115						
Reinoso	1022-1023	Rein17	16	28		RD.7	0.29	120				RE.6	0.23	150						
Reinoso	3102-3105	Rein18	26	28		RD.8	0.48	170				RE.7	0.24	127						
Reinoso	Assemblege 6 (3029)	Rein19	36	47		RD.9	0.42	155				RE.8	0.32	135						
Reinoso	1295-1998	Rein21	46	36		RD.10	0.34	160				RE.9	0.22	150						
Reinoso	ass6 2948-2951	Rein22	M	33	43	RE.10	0.33	130				RF.7	0.29	120				RI.4	0.24	120
Reinoso	ass3	Rein23	16	18	17	RE.11	0.39	130				RF.8	0.21	140				0.21		
Reinoso	ass6 2799-2801A	Rein24	46	37/38?	47	RE.12	0.37	140				RF.9	0.23	130						
Reinoso	ass 7 kiste 7 (1014-1015)	Rein28	M1	M2		RG.7	0.39	160				NA.2	0.26	160						
Reinoso	ass 1 (Kiste 7)	Rein29	26	28		RG.8	0.39	130				NA.3	0.26	130						
Reinoso	poss Ind 689 A	Rein30	36	37		Tf.8	0.37	140				TG.7	0.36	160						
Reinoso	1000-1002 (Kiste 11)	Rein31	26	28	27	RH.1	0.24	145				RI.6	0.21	120						
Reinoso	1265-1266 (Kiste 11)	Rein32	46	48	47	RH.2	0.23	145				RI.7	0.29	120						
Reinoso	2362-2365(Kiste15)	Rein33	27?	28		RH.3	0.27	160				RI.8	0.27	130						
Rincón de Moncada	1	Rinc1	36	38	37	SV.4	0.25	200				SW.8	0.25	200						
Rincón de Moncada	2	Rinc2	36	37	16	SV.5	0.27	200				SW.9	0.25	200						
Senorio de Guzman	UE 1286	Guz1	46	47		SK.13	0.45	200				SL.14	0.35	200						
Senorio de Guzman	UE1288	Guz2	46	47	45	SK.14	0.3	200				SL.15	0.27	200						
Senorio de Guzman	UE1289	Guz3	36	38		SK.15	0.51	200				SL.16	0.29	200						
Senorio de Guzman	UE 1290	Guz4	46	48		SK.16	0.38	200				SL.17	0.38	200						
Tabayá	Tumba 1 (1988) - Corte 11	Tab1	bone	bone		SS.14	0.36	200				SV.11	0.52	200						
Tabayá	Tumba 3 (1988) - Corte 10	Tab2	tibia	humerus		SS.15	0.28	200				SV.12	0.47	200						
Tabayá	Tumba 4 (1991) - Corte 7	Tab3	femur	femur		SS.16	0.35	200				SV.13	0.6	200						

II Investigated individuals

Site	Archaeological Name	Lab name	A	B	C	EX A	g	μl	EX All	g	μl	EX B	g	μl	EX BII	g	μl	EX C	g	μl
Tabayá	Tumba 5 (1991) - Corte 16	Tab4	femur	fibula?		SS.17	0.26	200				SV.14	0.43	200						
Tholos de Pai Mogo I	12951	Pai1	46	48	?	Rz.4	0.32	200				SA.4	0.33	200						
Tholos de Pai Mogo I	12267	Pai3	36	48	46	RZ.5	0.26	200				SA.5	0.23	200						
Tholos de Pai Mogo I	12338	Pai6	46	47	48	RZ.6	0.31	200				SA.6	0.35	200						
Tholos de Pai Mogo I	12600	Pai7	47	48	46	RZ.7	0.39	200				SA.7	0.26	200	SJ.17	0.4	200			
Tholos de Pai Mogo I	12327	Pai11	46	47		RZ.8	0.39	200				SA.8	0.32	200						
Tholos de Pai Mogo I	3250	Pai12	47	48		RZ.9	0.36	200				SA.9	0.35	200						
Tholos de Pai Mogo I	12377	Pai13	47	48		RZ.10	0.32	200	SJ.16	0.53	200	SA.10	0.33	200						
Tholos de Pai Mogo I	12396	Pai14	46/47	47/48		RZ.11	0.22	200				SA.11	0.33	200						
Tholos de Pai Mogo I	12425	Pai15	46	48	47	RZ.12	0.32	200	SV.15	0.47	200	SA.12	0.38	200						
Tholos de Pai Mogo I	12357	Pai16	47	48		SE.12	0.31	200				SF.12	0.34	200						
Tholos de Pai Mogo I	12251	Pai17	47	48		SE.13	0.27	200				SF.13	0.32	200	SW.14	0.6	200			
Tholos de Pai Mogo I	12556	Pai18	46	47		SE.14	0.32	200				SF.14	0.35	200						
Tholos de Pai Mogo I	12916	Pai19	46	47	45	SE.15	0.33	200				SF.15	0.35	200						
Tholos de Pai Mogo I	12562	Pai20	46	45	44	SE.16	0.24	200	SV.16	0.42	200	SF.16	0.23	200						
Tholos de Pai Mogo I	12395	Pai21	46	47	44	SE.17	0.33	200				SF.17	0.33	200						
Tholos de Pai Mogo I	12726	Pai22	46	47		SE.18	0.33	200	SV.17	0.67	200	SF.18	0.34	200	SW.15	0.5	200			
Valdescusa	E 45	Vald1	46	47	45	RS.12	0.26	118				RU.12	0.35	130						
Valdescusa	E 47	Vald2	75	55/56?	84	RS.13	0.23	125				RU.13	0.24	145						
Valdescusa	E 69	Vald3	36	85	75	RS.14	0.25	130				RU.14	0.23	150						
Valdescusa	E 74	Vald4	46	37	46	RS.15	0.26	130				RU.15	0.27	140						
Valdescusa	E 77	Vald5	46	36	37	RS.16	0.26	120				RU.16	0.35	140						
Valencina-calle Dinamarca 3-5	Ue 60 Cranéo 4	Din1	27?	23		SO.14	0.29	200				SQ.3	0.29	200						
Valencina-calle Dinamarca 3-5	UE 31 Mand 51	Din2	38	36	37	SO.15	0.25	200				SQ.4	0.24	200						
Valencina-calle Dinamarca 3-5	UE 6 Cranéo 6	Din3	35	33	34	SO.16	0.27	200				SQ.5	0.27	200						
Valencina-calle Dinamarca 3-5	UE 52 Ind 1 Mand	Din4	46	45	47	SO.17	0.27	200				SQ.6	0.34	200						
Valencina-calle Dinamarca 3-5	UE 60 Cranéo 9	Din5	26	27	27	SO.18	0.29	200				SQ.7	0.31	200						
Valencina-calle Dinamarca 3-5	UE 32 Cranéo y mandíbula 11 y 12	Din6	26	23	24	SQ.8	0.33	200												
Valencina-calle Dinamarca 3-5	UE 60 Cranéo 14	Din7	24	23	12	SQ.9	0.25	200												
Valencina-calle Dinamarca 3-5	UE 60 Cranéo 12	Din8	16	18	17	SQ.10	0.29	200												
Valle de las Higueras	Cueva 3c Muerto 8	Hig1	36?	37?		SR.12		200				SS.7	0.25	200						
Valle de las Higueras	Cueva 3c Muerto 3	Hig2	26	28		SU.16	0.23	200				SV.2	0.26	200						

III PCRs of authenticated individuals

All PCRs used for reproduction of the individuals are denoted. PCRs marked in bold were cloned, PCRs colored red were contaminated at least in few clones. The sequence range given is the summarized sequence range of the HVR I covered by at least two samples.

Lab code	sequence range	16045-16240	16018-16097	16097-16144	15996-16142	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348	16231-16323	16287-16410	16307-16402.C
Rodi1a	15997-16401				R209.1		R205.1			R208.1			R206.1
Rodi1b					R225.12		R223.12	R493.3		R226.12	R488.1	R234.19 R390.1	
Roy1a	15997-16409				R427.21 R442.28 R427.38		R425.19 R428.1			R426.19 R429.29		R455.1	
Roy1b							R428.38			R426.6		R430.29 R430.44 R455.21	
Roy2a	15997-16409				R427.22		R428.22 R425.20			R429.30		R440.40 R430.45 R455.22	
Roy2b					R427.39 R444.29 R478.21		R428.39 R475.19			R426.7 R429.45 R476.10			
Roy3a	15997-16401				R436.32		R464.32			R469.38		R470.38	R473.63
Roy3b					R478.23		R468.42			R469.40		R470.40	R473.64
Roy4a	15997-16401				R427.23 R440.30 R427.40		R428.23 R425.21			R429.46		R430.31 R430.46	
Roy4b							R428.40			R429.46		R445.23	
Roy5a	15997-16409				R427.24 R427.41 R444.31		R425.22 R428.24			R429.32 R426.22		R430.32 R430.47 R445.25	
Roy5b							R428.41			R426.9		R271.4	
Bar1a	15997-16409		R210.4	R211.4	R268.12 R209.6	R198.9	R269.15 R205.6	R199.9		R270.4	R207.4	R214.1	
Bar1b					R231.19 R288.7			R422.1 R340.3		R280.6		R234.21	
Bar2a2	15997-16401		R502.4	R503.4			R217.12 R205.7 R415.2			R265.6	R350.2	R289.10	R227.16
Bar2b					R209.7					R208.7		R206.7	
Bar3a	16019-16409		R210.5 R433.1	R252.9 R434.1		R198.10	R232.19 R205.8	R431.49 R459.2		R239.7 R208.8	R207.5	R214.2 R416.1 R416.2	
Bar3b					R209.8								
Bar4a2	16019-16401		R438.1	R457.2	R225.16		R217.13 R205.9 R415.3			R220.10 R208.9 R265.7			R227.17
Bar4b					R209.9							R266.7	R206.9
Bar5a2	16019-16409		R210.6	R457.6	R231.10		R232.10			R233.10		R214.3 R254.15	
Bar5b					R209.10 R427.12		R205.10 R415.1 R435.27			R208.10		R430.8 R338.11	
Bar6a	16019-16401				R452.28		R428.12	R431.35 R431.28 R449.12			R432.35 R432.28 R450.12	R430.20 R455.29 R440.41	R447.28
Bar6b			R433.28	R434.28			R428.27						R447.31
Bar7a	15997-16409				R427.13 R449.19 R427.28		R428.13 R428.28, R425.2			R429.21		R430.21 R430.36	
Bar7b								R449.13 R431.36 R449.11		R429.36	R450.13	R445.9	
Bar8a	16019-16401		R433.26 R456.25	R519.15 R480.40			R428.14 R425.3	R459.42			R450.11 R460.36		R437.37 R437.41 R447.32
Bar8b			R433.31 R433.27	R439.42			R428.29	R449.14			R460.39		
Bar9a	16019-16401						R428.15 R425.4 R428.30			R429.23		R445.11 R437.18 R455.38 R430.24	R437.38
Bar9b					R427.30 R44.21			R449.15		R429.38	R450.15		
Bar10a	15997-16409				R427.16 R427.35 R444.26		R428.16 R428.25 R425.10			R429.24			
Bar10b								R449.20		R429.34	R460.41	R430.43	R437.42
Bar11a	15997-16409				R427.17 R444.23 R427.32		R428.17 R428.32 R425.6			R429.25	R460.37	R430.25 R430.40 R455.13	
Bar11b								R449.17 R483.21		R429.40			
Bar12a	16019-16401				R427.18		R428.18 R425.7 R428.33	R459.43 R431.41 R449.18			R432.23 R432.41 R450.18 R472.46	R430.41 R445.14	R437.39
Bar12b			R433.32	R434.32	R444.24			R483.12 R471.46 R471.47			R488.23 R472.47	R470.37 R470.39	R473.61
Bar13a	16019-16401		R479.38	R480.38	R463.31	R482.12	R464.31 R468.41						
Bar13b			R479.39	R480.39									
Bar14a	15998-16409				R427.19 R444.35 r427.34		R428.19 R428.34 R425.9			R429.27		R430.27 R430.42 R445.15 R430.28	
Bar14b								R449.19		R429.42	R460.40	R455.50 R445.12	
Bar15a	15999-16409				R427.20 R452.29		R428.20 R428.31	R449.16		R429.28			
Bar15b					R427.31		R425.5	R431.40			R450.16 R432.40	R455.40	

III PCRs of authenticated individuals

Lab code	sequence range	16045-16240	16018-16097	16097-16144	15996-16142	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348	16231-16323	16287-16410	16307-16402.C
CDV1a	16019-16409		R388.3 R302.14	R389.4 R303.14 R332.2			R391.2	R422.3		R367.6	R318.8	R352.5	
CDV1b			R377.4	R378.3			R415.13 R319.1			R326.1		R416.10 R352.17	
CDV2a	16019-16401		R302.15 R388.4	R303.15 R480.41			R391.3 r415.7	R422.4		R367.7	R318.9	R416.6 R327.2 R424.13	
CDV2b					R328.2		R319.2			R326.2			
Cmol6a	16019-16401		R456.5 R251.2	R252.2 R457.7		R255.2	R415.4	R459.5 R277.3			R257.2 VK510.1 9 R460.4	R455.2 R281.2	R258.3
Cmol6b			R262.1	R261.3			R248.1 R294.1	R256.2			R278.3	R338.10	R447.1 R296.1
Cmol12a	15997-16401				R293.1 R463.10		R248.1 R294.1 R464.10 R468.10			R295.1 R469.6 R469.9		R470.6 R470.9	R473.14 R473.20
Cmol12b					R478.6								
Cmol16a	16019-16409		R456.6		R279.11	R255.3		R256.3			R257.3	R368.2	
Cmol16b			R263.2 R252.3 R261.2	R261.2			R248.2 R415.5			R419.2 R249.2		R261.3 R352.3	
Cmol44a	16019-16401		R465.1 R479.1 R479.5 R484.2	R466.1 R491.2		R482.1 R514.2		R471.1 R483.1			R472.1 R488.2		R496.1 R473.2 R496.2
Cmol44b				R480.5		R498.2		R471.2			R472.2		
Cmol71a	16019-16401		R251.4	R252.4		R255.4		R256.4			R257.4		R258.5
Cmol71b				R274.3 R393.1 R293.2			R264.8 R394.1 R294.2 R394.2 R306.9			R294.3 R395.1 R395.2 R295.2 R307.9		R396.1 R261.4 R396.2 R338.13 R308.9	R296.2
Cmol79a	15997-16409			R305.9									
Cmol79b													
Cmol104a	15997-16401				R293.3		R294.3			R327.11 R376.8 R395.3 R429.1		R390.7 R308.10	R384.1 R324.8
Cmol104b					R305.10 R393.3		R394.3 R306.10 R294.4 R464.11 R475.5						
Cmol105a	16019-16401		R465.10	R466.10	R293.4					R469.7	R472.17		R296.4 R473.15
Cmol105b												R472.20	
Cmol119a	15997-16409			R478.8 R293.5 R393.4			R475.8 R394.4, R294.5	R471.20		R469.10 R307.21 R395.4	R470.20	R470.10 R396.4 R308.21	R473.21
Cmol119b													
Cmol122a	15997-16409			R305.11 R443.3 R293.6			R306.11 R453.11 R306.6			R307.11	R494.9 R423.1 R423.2 R450.1	R308.11 R416.4 R440.15 R362.8 R440.18	
Cmol122b				R305.12 R463.12 R478.7			R311.2 R464.12 R475.7	R459.17 R449.1					
Cmol123a	15997-16401									R469.8 R476.3		R470.8	R473.18
Cmol123b													
Cmol138a	15997-16409			R478.9 R444.4 R305.1		R458.7	R468.12			R469.11 R372.13 R312.8		R470.11	R473.22
Cmol138b					R355.16		R391.4	R487.9			R436.5 VK506.1 1	R477.3 R314.8	R473.6
Cmol139a	16019-16401		R465.12 R479.16	R466.12 R480.16 R480.18		R482.8	R492.9	R483.8 R471.19			R472.19	R495.5	
Cmol139b			R479.18	R485.17 R439.15			R492.11	R471.21					
Cmol140a	16019-16409			R359.3 R359.4 R438.13	R360.3	R458.8	R311.1	R340.13 R487.10 R493.15 R256.5 R459.6			R472.21 R318.1 R460.11	R473.23 R352.9 R352.7 R430.9	R497.6 R437.7
Cmol140b				R360.4			R337.7			R460.12 R257.5 R350.8		R356.14 R455.3 R261.5	
Cmol151a	16019-16409		R251.5	R252.5	R444.2	R255.5							
Cmol151b					R247.4		R453.7 R248.5 R453.12 R406.3			R320.20			
Cmol154a	16019-16401		R438.14	r439.16	R305.3					R312.9 R307.15 R372.10 R395.5 R372.12	R436.7	R308.3 R308.15 R416.7 R352.4 R396.5	R384.2 R525.2
Cmol154b					R310.3 R305.4 R393.5		R415.8 r394.5 R306.4						
Cmol164a	15998-16409									R307.16		R352.6 R308.5 R396.6	
Cmol164b					R305.16		R306.16 R306.5 R394.6	R317.2		R395.6	R318.2		
Cmol165a	15997-16401				R310.1 R305.17 R413.7		R306.17			R312.12		R430.48	R501.5
Cmol165b													
Yese1a	16019-16401		R377.11	R434.39			R342.2 R344.5 R415.17	R379.6		R367.17	R436.16	R368.10	R384.7 R447.9 R409.5
Yese1b					R355.3 R413.12			R379.9			R423.9		
Yese2a	15997-16409				R345.3 R355.4 R444.12		R342.6 R344.6 R464.42			r367.18 R343.6 R454.30		R346.3 R455.2	
Yese2b				R466.16 R485.8								R455.25	
Yese3a	16019-16401		R502.10 R484.7	R480.27			R464.23	R471.28 R487.18		R472.28 R429.1			R497.10 R489.17 VK528.4
Yese3b			R479.28	R480.28		R482.10	R492.24	R471.29		R511.9			

III PCRs of authenticated individuals

Lab code	sequence range	16045-16240	16018-16097	16097-16144	15996-16142	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348	16231-16323	16287-16410	16307-16402.C
Yese4a	16019-16409		R465.23	R466.23	R354.4		R342.8 R444.8 R415.18			R429.9 R343.8 R429.12		R346.4 R256.3 R361.10	
Yese4b					R355.5								
Yese7a	16019-16401		R377.13 R465.24	R389.14 R457.14		R458.14		R379.7 R422.6 R459.24			R423.8 R460.18 R406.20	R356.13	R462.12
Yese7b			R388.13	R408.4			R344.11 R371.2					R368.13	
Yese8a	16019-16401		R490.22	R491.18	R463.28		R464.28 R468.29 R492.35			R469.31		R470.31	R497.25
Yese8b			R490.24 R407.9	R491.20				R493.37		R469.33	R494.32		R497.26
Yese10a	16019-16401		R438.35	R408.9 R408.18			R400.2 R449.8	R422.12 R449.8			R406.2 R406.11 R450.8	R440.36	R409.9 R409.15 VK528.5
Yese10b			R456.28	R457.23		R403.11 R458.26		R410.14			R423.15 R460.29	R455.32	R409.11 R425.13 R510.16
Yese12a	16019-16401		R407.11	R408.11	R444.16		R464.45 R400.4	R459.35 R410.9					
Yese12b			R433.16	R434.16		R403.13		R410.15			R432.50		
Yese13a	16019-16401		R490.23	R491.19	R463.29		R492.34 R464.29 R468.30	R493.26		R469.32 R469.34	R494.31	R470.32 R470.34	R473.54
Yese13b			R490.25	R491.21									
Gam3a	16019-16401		R251.8 R456.7	R252.8 R263.3	R452.13	R458.3 R290.1	R248.10	R256.11 R499.1 R277.5			R350.7 R460.5 R436.2 R278.5	R271.3 R455.6 R368.3	R525.1
Gam3b				R509.4				R499.13 R510.8			VK510.1 3		R437.28 R427.28
Gam8a	16019-16401		R433.14	R434.14		R435.20 R435.35 R458.27		R531.24 R499.18			R432.23 R460.32	R455.7	R437.35
Gam8b			R438.37	R439.37	R444.17								
Par1a	15997-16409				R345.15 R427.1		R325.5 R428.1			R320.5 R326.13 R429.7		R330.5 R390.9 R430.10	
Par1b					R328.13 R463.16 R444.10		R321.1 R325.6 R464.16 R468.13						
Par2a	16019-16401							R471.23		R320.7	R472.23	R470.12	R473.27
Par2b			R479.22	R480.22			R321.2	R487.15					
Par3a	15997-16409				R345.17 R344.9		R325.7 R442.22			R320.8 R454.26		R330.7 R455.21	
Par3b					R328.15 R345.18		R321.3 R325.8			R326.15 R320.9		R390.11	
Par4a	15997-16409				R444.10 R328.16		R442.23 R321.4			R454.27 R326.16		R330.8	
Par4b					R345.19 R441.24		R325.9 R442.24			R320.10 R454.28		R330.9 R440.21	
Par5a	15997-16409				R328.17 R463.17		R321.5			R326.17 R320.12		R390.12	
Par5b					R478.10 R328.18					R469.13 R469.19	R472.24	R470.13 R470.19	R473.28
Par7a	15997-16401					R486.15	R464.17 R468.14	R471.24					
Par7b													
Coca1a	16019-16409		R377.7 R490.11	R460.18			R337.14 R375.1 R415.15	R340.7 R349.8 R431.28			R436.13 R350.5	R361.14 R416.16 R346.13	
Coca1b				R457.13	R374.1		R415.14 R321.10	R349.9 R340.8		R335.5		R416.15 R390.10 R346.14	
Coca2a	16019-16409		R388.8 R456.14	R360.19 R378.6			R391.6 R464.20				R423.7 R350.6		
Coca2b					R413.11 R463.20		R475.11 R468.15			R335.6 R469.17			
Coca3a	15997-16401				R478.13 R478.15		R476.6 R475.12			R476.6 R469.21		R470.17 R470.21	R471.31 R473.34
Coca3b					R463.21 R478.14		R464.21 R468.16			R476.7 R469.18 R469.22		R470.18 R470.22	R473.32 R473.25
Coca4a	16019-16401		R479.23	R480.23		R498.9 R482.9	R492.15	R483.9 R471.26		R469.20	R472.26		R473.33
Coca4b													
Coca5a	16019-16401		R479.21 R484.5	R480.21 R480.24						R469.23	R472.27	R470.23	R469.9 R462.2 R324.20
Coca5b			R479.24	R485.5		R498.10		R471.27					
Hund1a	16019-16401		R495.6	R303.22			R300.13			R312.10 R454.25 R320.3		R330.3 R416.13	
Hund1b					R420.12 R452.18	R458.12	R325.3 R453.13 R300.14 R453.13	R493.18					
Hund2a	16019-16409		R456.10	R303.23						R312.11 R320.4 R419.6		R455.12 R330.4 R416.4	
Hund2b			R456.13	R457.12	R420.13 R370.5		R325.4 r311.21 R371.3					R352.10 R416.8	
Junc1a	15997-16409				R452.18 R328.7					R367.10 R429.5 R326.7			
Junc1b							R319.3 R391.5					R327.7	
Junc2a	16019-16409		R377.2	R360.12	R444.5		R311.22	R340.5		R429.3	R436.10 R460.16 R423.5	R352.11 R327.8 R455.19	
Junc2b					R328.8		R319.4	R319.14					
Junc3a	16019-16401		R438.16	R460.13	R444.6		R371.4 R319.15			R367.11 R372.17 R326.9 R454.24		R352.12 R327.9 R455.20	
Jund3b					R328.9 R370.7 R420.10 R328.10		R453.21 R371.5 R315.8 R319.16			R454.21 R367.12 R326.10		R352.13 R424.8 R327.10	
Junc4a	15997-16409					R458.11 VK507.1 2							
Junc4b													
Junc5a	16019-16401		R388.5 R518.13 R438.19	R439.18 R360.14			R371.6	R459.22		R372.18			R462.10
Junc5b			R377.6	R360.17			R319.17	R340.4			R423.6 R460.17	R368.9	R473.26

III PCRs of authenticated individuals

Lab code	sequence range	16045-16240	16018-16097	16097-16144	15996-16142	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348	16231-16323	16287-16410	16307-16402.C
Junc6a	16019-16409		R388.6	r389.6	R444.8	R383.1	R453.17 R371.7	R379.3		R367.14	R460.15	R390.8 R424.12 R455.16	
Junc6b					R328.12		R319.18			R326.12			
Junc7a	15997-16409				R393.7 R427.4 R413.13	R458.22		R459.31		R387.3 R395.7 R429.13		R470.47 R396.7 R430.13	R462.18
Junc7b							R394.7 R428.4						
Junc8a	15997-16401				R393.8 R413.14 r427.5		R391.18 R428.5 R394.8			R387.4 R395.8 r429.14		R390.18 R396.8 R420.14	
Junc8b													
Junc9a	15997-16401				R393.8 R413.15 R427.6		R391.19 R394.9 R428.6			R387.5 R429.15 R395.9		R416.31 R396.9 R430.15	
Junc9b													
Junc10a	15997-16409				R427.49 R352.26 R413.16	R403.19		R431.50 R449.4 R431.15		R429.4		R390.20 R430.16 R396.10	
Junc10b							R394.10			R387.6	R432.15		
Junc11a	15997-16409				R393.11 R427.8 R413.17		R391.21 R394.11 R428.8	R431.14		R387.7	R432.14	R390.21 R396.11 R430.17	
Junc11b										R429.17			
Junc12a	16019-16409				R393.12		R391.22 R428.9			R387.8		R396.12 R430.18 R455.29	
Junc12b		R433.12	R434.12		R427.9 R393.13 R452.25 R413.19		R394.12 R453.34 R391.23 R394.13	R449.5		R429.18	R450.5	R390.23 R455.26 R396.13	
Junc13a	15997-16409									R387.9 R395.13	R450.6		
Junc13b													
Junc14a	15997-16409				R393.14 R413.20 R427.11		R391.24 R428.11 r394.14			R387.10 R395.14 R429.19		R390.24 R396.14 R430.19 R390.2	
Junc14b													
Troc1a	16019-16401	R251.1 R433.2 R302.4	R389.1 R434.2 R303.4			R435.1 R290.5	R248.11	R431.14 R291.6		R238.13	R432.1 R292.8	R261.6	R437.1 R324.5
Troc1b													
Troc2a	16019-16401	R407.12	R408.12				R400.6 R400.18 R428.42	R410.10 R410.16 R431.18			R406.5 R432.18 R406.14		R409.12
Troc2b		R407.21	R408.21	r427.42								R430.1	R412.16
Troc3a	16019-16401	R456.24	R408.13				R400.7	R410.11 R410.17 R431.19			r406.6 R406.15 r432.19		R409.13
Troc3b		R407.22	R408.22	r427.43	R403.15	r428.43						R320.2	R409.22
Troc4a	16019-16401	R407.14	r408.14				r400.8	R410.12 R410.18			R406.7 R406.16		R409.14
Troc4b		r407.23	R408.23	R427.44	r403.16	R428.44	R431.20				R432.20 R460.35 R431.29	R430.3	R409.23
Troc5a	16019-16409	R438.39		R420.1			R415.25 R425.11 R428.45	R459.41 r431.29			R459.41	R424.1 R424.16 R430.4 r445.17	
Troc5b			R434.23	R444.27				r422.17			R422.17		
Troc6a	15997-16409				R420.2		R415.26	R431.30			R432.30	R424.2 R430.5	
Troc6b2					R427.46 R452.30		R428.46 R453.38			R426.1 R454.38		R445.18 R455.42	
Troc7a	16019-16409				R420.3		R415.27 R453.36	R422.13 r431.31		r434.35	R432.31	r424.3 R424.17 R430.6 R445.19	
Troc7b		R433.29	R434.29	R427.47			R428.47	R422.18 R431.42			R432.42		
Troc8a	16019-16409				R420.4		R415.28	R431.32		R454.36	R432.32	R424.4 R424.18 R430.7 R445.20	
Troc8b		R433.30	R434.30 R491.27 R485.12 R503.21	R427.48			R428.48 R425.13	R422.19			R423.21		
Troc10a	16019-16401		R502.32 R502.1 R508.1	R485.13 R503.22		R482.16 R504.25 R498.22 r505.1		R483.16 R510.1 R505.1			R506.24 R511.1 R506.1	R507.1	R489.24 R501.23
Troc10b													
Troc12a	16019-16401		R502.25 R484.13	R485.13 R503.22		R482.17 R498.23 R504.2		R510.11 R510.2 R505.2			R488.26 R511.2 R506.2	R507.2	R489.25 R501.24
Troc12b			R502.2 R465.22 R479.17 R438.15	R503.2 R503.7 R480.31									
Fala2a	16019-16401					R504.9	R492.10	R349.3 R471.22 R483.11 R487.11 R471.32			R436.8 R488.16		R462.7
Fala2b		R484.10	R503.10			R482.11	R357.5				R472.32		R437.17 R473.42 R462.14 R462.15
Cel1a	15997-16401		R457.18		R452.22 R370.12 R370.23 R370.13 R452.23 R370.24	R458.19	R357.1 R375.12 R357.2 R453.28 R375.13	R493.27		R372.19 R454.31 R376.13 R372.20 R454.32 R376.14		R470.43 R390.13	
Cel1b													
Cel2a	15997-16401											R361.3 R390.14	
Cel2b													
Cel3a	15997-16401	R388.18											
Cel3b					R370.25 R452.31	R483.14	R375.14 R442.3	R449.23		R376.15 R454.40	R460.25 R460.45	R445.28	R447.14 R051.20

III PCRs of authenticated individuals

Lab code	sequence range	16045-16240	16018-16097	16097-16144	15996-16142 R441.3	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348	16231-16323 R450.23	16287-16410	16307-16402.C
Fupe6a	15997-16409				R288.8 R231.11 R452.9		R223.6 R337.6	R340.1		R226.6	R341.1	R224.6 R289.11	
Fupe6b							R232.11 R223.7			R233.11		R234.11	
Fupe7a	15997-16401				R225.7 R231.12 R452.10		R311.7	R340.2		R226.7	R341.2	R289.12	R227.3
Fupe7b							R232.12			R233.12 R454.4 R226.8		R234.12	
Fupe8a	15997-16401				R225.8 R231.13 R310.7		R223.8 R232.13 R311.10 R223.9					R455.33	R227.4
Fupe8b							R232.13 R311.10 R223.9			R233.13 R226.9 R454.4 R233.14 R253.1 R220.4		R234.13	
Fupe9a	16019-16401		R490.3	r457.4	R225.9 R231.14		R453.5 R232.14					R289.13 R234.14	R227.5
Fupe9b													
Fupe1a	15997-16401				R247.12 R225.1 R452.3 R441.2 R452.34 R241.3 R225.3		R248.12 R453.2 R306.22 R453.40			R233.20 R469.42 R454.39		R455.27	R501.1 R501.19
Fupe1b			R502.6									R455.30 R224.4	
Fupe1c													
Fupe3a	15997-16401						R306.23 R337.4			R220.6 R226.3		R224.3	
Fupe3b													
Fupe4a	15997-16401				R241.4 R268.11 R225.4		R217.10			R220.7		R266.1 R224.4 r282.11	R227.14
Fupe4b							R223.4			R226.4			
Fupe5a	16019-16401				R241.5		R271.11 R453.4 R223.5 R306.18 R223.10 R453.6 R232.15	VK509.1 5		R220.8	R460.2		R227.15
Fupe5b			R456.2	R467.3	R225.5 R225.10 R452.7 R231.15					R454.3 R226.5 R454.6 R226.10		R2224.5 R470.44	
Fupe10a	15997-16401											R455.34 R234.15	R227.6
Fupe10b													
Fupe11a	16019-16401		R490.2	R491.1 R457.5	R225.11 R231.16	R458.2	R223.11 R232.16	R487.3		R226.11 R233.16	R460.3	R289.14 R234.16	R227.7
Fupe11b													
Alco1a	16019-16409		R377.10	R378.9			R344.1			R538.3		R346.1 R361.13 R470.42 R455.24 R361.5 R470.48 R462.17	
Alco1b					R452.21 R355.1	r458.15	R464.43	R487.17		R454.29 R376.1			
Malga2a	15997-16409				R370.17 R444.14 R374.11 R463.35 R293.7 R345.13	r458.17		R459.27		R372.5	R460.22		
Malga2b													
Turq1a	15997-16401						R475.6 R325.1			r295.7 R469.43		R390.16	
Turq1b								R487.12 R493.13 R410.3 R471.18 R487.8		R488.9	R330.1	R473.16 R489.9	
Turq2a	16019-16401		R302.13 R479.15	R303.13 R480.15 R332.5 R480.20		R486.11	R468.9	R487.8		R469.44	R472.18 R494.10		R473.17 R489.10
Turq2b													
Pove2a	16019-16322			R480.26 R485.7 R509.3 R508.4		R486.14 R498.10 R504.11 R514.5		R499.6 R493.25 R499.9 R493.39 R487.24			R472.18 R494.10 VK510.1 5 VK510.1 4 R460.33 R494.34		
Pove2b													
MCLIII2a	16019-16322		R438.38	R509.9		R435.29	R492.37						VK528.6 R498.22 VK511.2 6
MCLIII2b			R465.31 R456.27	VK522.5		R458.24	R492.40 R248.5 R453.8 R260.1	R493.40			R494.35 R436.37		
Hume1a	15997-16409				R247.5 R452.11 R268.10					R249.5 R454.8 R235.5		R261.1 R455.4 R338.8	
Hume1b													
Hume2a	16019-16401		R465.5 R479.6	R480.6 R466.5		VK507.1 3 R482.4 R486.6		R471.3 R483.4 R471.7			R494.3 R472.7 R488.5		R473.3 R496.3
Hume2b													
Hume3a	16019-16409		R251.6	R252.6 R466.6 R332.6 R360.1			R248.6 R464.33	R256.9		R257.9		R271.1	
Hume3b													
Hume5a	16019-16409				R247.8 R452.12		r260.2 R464.24 R248.8 R453.9 R306.23	R277.4 VK526.9			R278.4 R460.6	R455.7 R254.6 R271.2 R455.5 R254.8	
Hume5b										R454.9 R253.8	R257.10		
Hume8a	16019-16401		R359.2 R465.2 R479.2	R360.2 R466.2 R480.2		R498.4	R492.3	R471.4		R472.4		R513.4 R489.5 R501.4 R497.5	
Hume8b								R471.8 R483.5		R488.6 R472.8			
Hume19a	16019-16401		R479.9 R479.33 R518.16 R479.34	R480.9 R466.17 R480.33 R480.34		R482.5	R504.17	R492.26	R471.36 R471.39 R487.20		R472.36 R494.25 R472.39 R494.23 R506.14		R473.43 R497.16
Hume19b													
Hume21a	16020-16401		R502.13 R490.17 R502.14	R503.11 R491.13 R503.12		R498.15 r498.14 R514.10		R493.28 R510.6 R493.30					R489.19 R501.11 R525.9
Hume21b													
Hume24	16020-		R508.5	R491.12			R492.25	VK509.1			R494.26 R472.37		R501.13 R497.17

III PCRs of authenticated individuals

Lab code	sequence range	16045-16240	16018-16097	16097-16144	15996-16142	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348	16231-16323	16287-16410	16307-16402.C
Hume24b	16019-16401		R479.35 R508.6	R480.35 R503.13		VK507.1 4	R492.28	R510.5 R487.21 R493.31			R488.19 r494.27		R501.14 R497.20 R473.46
Ba6-1a	16019-16401		R490.1		R23.5	R514.1	R24.5	R29.1	R10.5		R28.1 R494.1		R497.17
Ba6-1b	15997-16401			R30.1	R23.4 R268.1	R63.1	R161.1 R264.1 R181.1			R15.1 R162.1 R265.1 R170.1			R116.1 R172.1 R180.1 R171.1
Mina1a	15997-16401				R166.1 R175.1 R268.2 R166.2								
Mina1b	15997-16401						R161.2 R167.2 R185.1			R162.2 R176.1		R177.2	R172.2
Mina2a	15997-16401									R208.14			R171.2
Mina2b	15997-16409				R175.2								
Mina3a	15997-16409				R166.3 R184.3		R161.3 R181.2			R162.3 R182.3		R163.3 R214.6	
Mina3b	15997-16401				R268.3 R166.4 R175.3 R268.4 R166.5 R174.1 R268.5		R264.2 R161.4 R167.4 R161.5 R264.3 R167.5			R162.4 R265.2 R170.3 R162.5 R265.3 R170.4		R163.4 R266.2 R163.5 R266.3	
Mina4a	15997-16401												R171.4
Mina4b	15997-16401												
Mina5a	15997-16401												
Mina5b	16019-16409												R171.5
Mina6a	16019-16409		R210.1	R211.1	R166.6		R161.6 R167.6 R264.4 R161.7 R264.5			R162.6 R186.3 R265.4 R162.7 R265.5		R163.6 R214.7 R266.4 R163.7 R266.5	
Mina6b	15997-16401				R209.15 R268.6 R166.7 R209.13	R198.1			R199.1		R207.1		R193.1
Mina7a	15997-16401												
Mina7b	15997-16409												
Mina9a	15997-16409				R166.9		R300.4			R162.9 R176.3 R182.1 R170.8 R208.13			R172.3 R171.9 R180.2 R193.2
Mina9b	15997-16401				R173.4 R209.14 R268.7 R231.1	R255.6							
Mina9c	15997-16401												
Mina10a	16019-16401						R237.1 R264.6	R256.6		R233.1		R240.1 R266.6	R258.2
Mina10b	16019-16401				R236.1			R301.1* (16178-16323) R277.1 R277.2		R242.3	R350.9		
Mina14a	15999-16409				R268.8 R231.5 R236.5		R269.16 R232.5 R237.5			R239.4 R270.5 R238.5	R257.8 R278.1 R278.2	R361.1 R234.5 R240.5 R268.1 R234.7 R261.7	
Mina14b	15997-16409												
Mina16a	15997-16409				R231.7		R232.7 R237.7 R329.31 R232.8 R357.17			R233.7			
Mina16b	15998-16409				R236.7 R365.13 R231.8			R349.10		R238.7		R240.7 R352.2 R234.8	
Mina17a	15998-16409									R233.8 R367.1 R238.8	R360.10		
Mina17b	15999-16401				R236.8 R268.9 R231.9 R236.9		R237.8 R269.17 R232.9 R237.9 R492.7 R269.3	R340.12		R233.9 R249.11	R318.12	R240.8 R234.9 R271.6 R254.4 R282.1 R440.8	
Mina18a	16019-16409												
Mina18b	16019-16409												
Tar3a	16019-16409				R279.1					R281.1			
Tar3b	16019-16401		R302.7 R438.9	R303.7 R439.11 R466.7			R280.3	R459.12		R312.4	R460.10	R455.9	
Tar4a	16019-16401		R479.11	R480.11	R479.2	R498.5	R269.4			R281.2	R472.11	R382.2	R477.4
Tar4b	15997-16409		R479.14	R480.14			R280.4 R269.5 R464.7 R280.5 R475.4	R493.7 R471.14			R472.14	R489.6	
Tar5a	15997-16409				R463.7 R279.3					R281.3		R282.3 R470.3	
Tar5b	16019-16409		R508.3	R503.6	R298.7			R471.15		R476.1	R472.15	R477.5	R473.13
Tar6a	16019-16409		R490.5					R471.12			R472.12	R477.6	
Tar6b	16019-16401		R490.7 R484.4	R480.12 R466.8 R485.4			R280.6 R464.48 R442.5 R464.8 R269.7	R449.24 R459.47		R454.16 R454.42	R460.46 R450.25	R455.30 R455.44	
Tar6c	16019-16401			R480.13 R491.4	R441.5 R279.5					R281.5		R282.5	R489.7
Tar7a	16019-16401		R490.6					R487.6 R471.16 R493.8			R472.16 R488.7	R470.4 R495.4	R489.8
Tar7b	16019-16409		R490.8	R491.5			R280.7			R261.6 R454.14			
Tar8a	16019-16409				R279.6		R269.8					R282.6 R269.4 R440.14 R314.5	
Tar8b	15997-16401		R302.8 R438.10	R303.8 R439.12			R492.8 R280.8			R312.5			
Tar9a	15997-16401				R279.7 R452.14		R269.9 R464.41 R442.6 R468.44 R453.41	R493.9		R281.7	R494.8	R282.7 R455.11	
Tar9b	16019-16401				R441.6 R463.28			R449.26 R459.48		R454.43	R450.26	R445.32 R455.45	
Tar9c	16019-16401		R438.7 R302.3	R439. R303.3									
Tar10a	16019-16401						R453.42 R442.16 R280.10	R449.36			R318.6	R455.48 R445.37 R289.6	
Tar10a2	16019-16401				R441.16								
Tar10b	16019-16401		R302.10	R303.10						R312.6			

III PCRs of authenticated individuals

Lab code	sequence range	16045-16240	16018-16097 R438.11	16097-16144 R439.13	15996-16142	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348	16231-16323	16287-16410	16307-16402.C
Tar11a	16019-16401				R288.6	R290.4	R269.11	R459.10 R291.3			R292.3 R460.8	R282.8 R440.10	
Tar11b			R302.11 R438.12	R303.11 R439.14			R280.11 R468.28	R493.11			R318.5 VK510.6	R289.7	
Miv2a	16019-16401		R479.37 R502.15	R480.37 R519.19			R492.31	R487.23 R499.15			R488.21 R494.30		R516.6 R525.11
Miv2b			R490.21 R502.16	R503.17 R519.14		R498.19	R492.33	R493.35			R529.4		R497.24
Mop2a	16001-16401				R492.2 R113.7		R115.7 R119.10		R104.13	R122.1		R214.4	
Mop2b					R118.13	R117.11	R121.1	R126.5 R459.20			R127.4 R460.14		R116.10
Gsl2a	16019-16401		R456.12 R359.6	R332.3 R457.10 R360.6			R492.12 R391.10	R410.6 R493.16			R318.7 R494.12 R436.21	R495.6	
Gsl2b			R438.26 R359.7	R457.16 R360.7	R355.15 R374.9		R375.9	R459.26			R460.20	R361.7	R497.14
Gsl3a	16019-16401		R490.9 R456.34	R457.11		R458.10		R499.4			R506.7 R423.4 R450.37	r445.38	R384.4
Gsl3b				R357.34			R442.17 R453.43	R449.37					R462.39
Rein1a	16046-16401	R1.1 R4.1							R5.1 R10.1	R15.1		R20.1	
Rein1b	15997-16401				Te11.11		Te9.11 R139.1 R152.1			Te10.14		R7.2	
Rein2a			R4.2		R151.1					R153.1		R154.1	
Rein2b	16046-16409	R1.3 R110.3								R8.2		R7.3 R7.9	
Rein3a	16046-16401		R14.2	R30.4		R18.1		R29.4			R16.1		
Rein3b													
Rein4a	16046-16401	R83.1			Te11.12		Te9.12			Te10.15		R7.4	
Rein4b		R4.4							G48.5 R84.1				
Rein5a	16046-16401	R1.5 R4.5								R8.3		r7.5	
Rein5b									R84.2				
Rein6a	16046-16401	R9.1					Te12.15		R13.1				
Rein6b		R36.13						R56.3				R50.1 R62.1	
Rein6c			R124.13		R151.4		R115.10			R120.1	R292.7		R123.1 R116.2
Rein8a	16046-16401	R1.6 R4.6								R8.4		R7.6	
Rein8b									R84.4 R13.2 R59.1 R38.2				
Rein9a	16046-16401	R9.3 R36.15										R137.2	
Rein9b													
Rein11a	16046-16401	R1.8 R4.8								R8.5		R7.8	
Rein11b									G48.8				
Rein12a	16019-16409		R73.4	R71.6		R255.1		R72.6		Te34.7		R80.3 R80.5	
Rein12b					R147.1		Te39.7		R84.5		R75.4		
Rein13a	16046-16401				R26.2		R27.3		R13.6 R25.2				
Rein13b		R36.1											
Rein14a	16046-16401				R26.3		R27.4		R13.7 R25.3	R140.1		R137.1	
Rein14b		R36.2											
Rein15a	16046-16401				R26.4		R27.5 R40.2		R13.8 R25.4				
Rein15b		R39.1											
Rein16a	16046-16401	R22.5					Te39.13 R40.3		R13.9 R59.3	Te43.17			
Rein16b					R39.2								
Rein17a	16046-16401	R22.6 R36.5							R13.10 R25.6			R141.2	
Rein17b													
Rein18a	15997-16401				R26.5 R39.3		R27.6 R40.4		R13.11 R25.7	Te14.13 Te14.14			
Rein18b													
Rein19a	16046-16401				R26.6		R27.7		R13.12 R25.8				
Rein19b		R36.7											
Rein22a	16046-16401	R36.9 R36.17					R139.2		R25.10 R36.4	Te43.18 Te43.19			R87.2 R116.4
Rein22b			R124.5	R149.2			R119.4 R139.3 Te39.11 Te39.12 R152.2		R84.7 R38.5				R154.2
Rein23a	15997-16401	R36.10 R36.18			R138.3 R151.2					R153.2			
Rein23b													
Rein23c													
Rein24a	16046-16401	R26.11							R25.12 R84.8				
Rein24d			Te44.7		R138.4 R147.4 R166.10		Te42.7 Te39.8 R119.1		R93.5	Te34.16 R186.1 R99.1			R172.4 R112.1
Rein28a	16046-16401												
Rein28b		R94.2										R352.1	
Rein29a	16019-16401		R73.5	R252.11	R147.5 R113.2		Te39.9 R119.2 R115.3	R349.1	R93.6		R75.5		R180.5 R172.5
Rein29b										R99.2			
Rein30a	15997-1641				R328.24		Te42.8		R93.2	Te43.8		R282.12	

III PCRs of authenticated individuals

Lab code	sequence range	16045-16240	16018-16097	16097-16144	15996-16142	16122-16196	16117-16233	16178-16267	16212-16402	16209-16348 Te47.7 R182.2	16231-16323	16287-16410	16307-16402.C R180.4 R112.3
Rein30b	15997-16401	R94.1			R184.1	R255.7	R264.7						
Rein31a					R113.3		R115.2 R300.1 R119.6		R104.3	R186.2			
Rein31b				R118.7					R213.3		R137.3		
Rein32a	16046-16401		R110.3						R104.4				
Rein32b					R118.8		R329.22 R121.3	R128.4		R270.1		R116.6	
Rein33a	15997-16401	R110.4				R184.2 R147.6		R185.2 R212.1		R104.5			
Rein33b							R128.5		R233.21	R129.4		R116.7	
			R465.32 R433.35 R456.29 R502.19	R434.35 R457.28		R458.28 R425.34		R431.43 R459.45 R449.28			R460.34 VK510.18		
Rinc1a	16019-16401							R459.50 R431.44 R459.46					R447.33 VK516.25
Rinc1b			R490.27 R456.30	R491.25 R457.29			R442.8					R455.33	
Rinc2a	16019-16401		R433.36 R490.28 R502.21	R434.36		R458.29 R435.35					R432.44 R529.5		R447.34 VK511.24
Rinc2b				R491.26		R504.22		R449.29			R450.29	R445.34 R455.13 R352.18	
Pai1a	16019-16409			R407.1	R360.8	R370.8 R328.3		R315.3 R415.10 R391.4		R454.19 R367.28 R326.3		R416.11	
Pai1b													
Pai3a	16019-16409			R407.2	R408.2								
Pai3b						R452.17 R328.4		R415.11 R453.18 R319.5		R367.9 R326.4 R454.22		R455.14 R416.12 R455.17	
Pai11a	16019-16409		R407.3 R359.10	R408.3 R360.10	R370.11		R415.12 R319.8 R453.19 R311.19	VK505.13		R335.9 R454.23 R335.1 R464.20	VK506.10	R361.18 R368.8 R455.18 R352.15	
Pai11b						R328.5 R452.15 R310.16 R328.6 R345.8 R427.2 R355.9 R345.9 R427.3 R355.10							
Pai12a	15997-16401												R384.5
Pai12b													
Pai18a	15997-16409												
Pai18b													
Pai19a	15997-16409												R346.9 R430.12 R361.12
Pai19b													
Vald1a	16019-16401		R438.2	R439.2	R305.20 R288.1		R306.15 r464.35 R280.12			R253.10 R454.10 R281.12		R390.3 R455.8	R324.1
Vald1b													
Vald2a	15997-16409			R438.3	R439.4	R305.21 R288.2 R463.9						R257.12	R254.11 R282.15 R396.18 R254.12 R440.3 R282.16 R254.13 R440.4 R289.8 R254.14 R440.5 R390.4 R289.9
Vald2b										R281.13 R454.17 R253.12 R454.11 R281.14 R253.13 R454.12			
Vald3a	16019-16409			R438.4 R388.1	R439.5 R389.3	R259.8	R482.6	R260.6 R280.14 R260.7 R475.2 R280.15	R483.6				
Vald3b													
Vald4a	16019-16409			R438.5	R439.6	R305.22 R288.4							
Vald4b									R291.4			R292.4	
Vald5a	16019-16409			R438.6	R439.7	R305.23 R288.5		R260.8 R464.28 R280.16		R253.14 R454.13			
Vald5b								R280.16	R291.5		R292.5		

IV Snapshot results

IV.1 GenoCoRe22

Underlined SNPs in the headline were detected in reverse direction. Derived SNPs are colored dark gray, derived SNPs with a peak height lower than 50 light gray. Ancestral SNPs that had a peak height lower than 50 are marked in bold.

PCR	Ex	Sample	HG	deri- ved	<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>
					g/t	g	c	c	g	a	c	a	c	t	g	a	c	c	g	t	g	g	a	g	g	a
					ancestral	a	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	a	g	a	a	g
R363.7	SE.1	Alco1a	K		c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g/a	g	-
R339.1	SF.1	Alco1b	K		-	-	c	-	g	g	t	g	t	c	g	g	-	-	a	-	a	g	a	-	g	g
R333.2	SE.2	Alco2a	U		c	-	t	-	g	g	t	g	t	-	c	g	-	t	a	-	a	g	a	-	g	g
R339.2	SF.2	Alco2b	U		c	-	t	t	g	g	t	g	t	c	-	g	t	t	a	g	a	g	a	a	g	g
R222.19	RL.4	Arru1a	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	g/a	g	-	g	a	a	g	g
R204.4	RM.4	Arru1b	U/J		c	-	t	t	g	-	t	g	t	c	a	g	t	t	a	g	a	g	a	g/a	g	g
R215.18	RM.4	Arru1b	U/J		c	-	t	t	g	g	t	g	t	c	-	g	t	t	a	-	a	g	a	a	g	g
R143.32	RC.5	Ba12-1a	K		c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g
R215.21	RD.2	Ba12-1b	K		c	g	c	g	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g
R143.33	RC.6	Ba12-2a	R0/H		c	-	t	t	a	g	t	g	-	c	a	g	t	t	a	g	-	g	-	a	g	g
R373.2	SL.2	Ban2a	V?		c	-	t	-	a	g	t	g	c	c	a	g	t	t	g	-	g	g	a	a	g	g
R381.2	SM.2	Ban2b	H		c	g	-	-	a	g	t	g	c	c	a	g	-	t	g	-	g	g	a	a	g	g
R373.7	SL.7	Ban7a	H		c	g	-	-	a	g	t	g	c	c	a	g	-	t	g	-	g	g	a	a	g	g
R191.11	RL.6	Bar1a	R/J		c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	-	g	a	-	g	g
R191.11	RL.6	Bar1a	T		c	-	t	-	-	g	t	a	t	-	-	g	-	t	a	-	-	g	a	a	-	-
R204.6	RM.6	Bar1b	T		c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	t	a	g	a	a	g	g
R215.14	RN	Bar2a(2)	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R204.7	RM.7	Bar2b	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R215.16	RL.8	Bar3a	HV		c	g	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g
R204.8	RM.8	Bar3b	HV		c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g
R215.15	RL.9	Bar4a2	K		c	-	c	-	g	g	t	g	t	-	-	g	-	t	a	g	-	g	a	a	-	-
R204.9	RM.9	Bar4b	K		c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R191.15	RL.10	Bar5a	J?		g	g	t	-	-	g	-	g	-	-	-	g	-	-	-	g	-	-	a	g	-	-
R215.17	RL.10	Bar5a	J		c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g
R230.20	RP.10	Bar5a(2)	J		c	-	t	t	-	g	t	g	t	c	a	g	t	t	g/a	g	-	g	g	-	g	g
R204.10	RM.10	Bar5b	J?		c	g	t	t	a	g	t	g	t	c	a	g	-	t	-	g	g	-	a	g	g	g
R283.19	RM.10	Bar5b	J		c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g
R414.19	ST.1	Bar6a	HV		c	-	t	t	a	g	t	g	-	c	a	g	t	t	a	g	g	g/a	a	a	g	g
R417.1	SU.1	Bar6b	HV/H		c	g	t	t	a	g	t	g	c	c	a	g	t	t	g/a	g	g	g	a	a	g	g

IV Snapshot results

					<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>
R433.32	SU.1	Bar6b	HV	K	c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g
R414.20	ST.2	Bar7a	K	K	c	g	c	t	g	g	t	g	t		a	g	t	t	a	g		g	a	a	g	g
R417.2	SU.2	Bar7b	J	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g
R418.14	ST.3	Bar8a	J	J	c	g	t	t	a	g	t	g	t		a	g		t	g/a		g/	g	a	g	g	g
R417.3	SU.3	Bar8b	U	U	c	g	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g
R418.15	ST.4	Bar9a	U	U	c		t	t	g	g	t	g	t			g		t	a			g	a	a	g	g
R417.4	SU.4	Bar9b	T	U	c	g		t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g
R418.16	ST.5	Bar10a	T	T	c		t	t	a	g	t	a	t	c	a	g	t	t	a	g		g	a	a	g	g
R417.5	SU.10	Bar10b	J	T	c		t	t	a	g	t	a	t	c	a	g	t	t	a	g		g	a	a	g	g
R414.24	ST.6	Bar11a	J	J	c		t	t	a	g		g	t	c	a	g	t	t	g/a	g	a	g/	a	a	g	g
R418.15	ST.6	Bar11a	J	J	c	g	t	t	a	g	t	g	t		a	g		t	g/a	g		g	a	g	g	g
R417.6	SU.6	Bar11b	K	J	c	g	t	t	a	g	t	g	t	c	a	g		t	a	g		g	a	g	g	g
R414.25	ST.7	Bar12a	K	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g		g	a	a	g	g
R417.7	SU.7	Bar12b	H	K	c		c	t	g	g	t	g	t	c	a	g		t	a			g	a	a	g	g
R467.33	ST.8	Bar13a	H	H	c		t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
R417.8	SU.8	Bar13b	J	H	c		t	t	a	g	t	g	c	c	a	g		t	g		g	g	a	a	g	g
R414.27	ST.9	Bar14a	J	J	c		t	t	a	g	t	g	t		a	g	t	t	a	g		g	a	g	g	g
R443.31	ST.9	Bar14a	J	J	c		t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g
R417.9	SU.9	Bar14b	K	J	c	g	t	t	a	g	t	g	t	c	a	g		t	g/a	g		g	a	g	g	g
R414.28	ST.10	Bar15a	K	K	c	g	c	t	g	g	t	g	t			g		t	a	g		a	a	a	g	g
R417.10	SU.5	Bar15b	K	K	c		c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R322.14	SC.14	Bas3a	K	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R347.14	SG.14	Bas3b	K	K	c	-	c	t	g	a	t	g	t	c	-	g	t	t	a	g	a	g	a	a	g	g
R322.16	SC.16	Bas5a	K	K	c	-	c	t	g	g	t	g	t	c	-	g	t	t	a	g	a	g	a	a	g	g
R347.16	SG.16	Bas5b	K	K	c	-	c	t	g	-	t	g	t	-	-	g	-	t	a	g	a	g	a	-	-	g
R481.6	SC.17	Bas6a	K/U	K/U	-	-	-	-	g	g	t	g	t	-	-	g	-	-	-	-	a	-	a	-	-	g
R347.17	SG.17	Bas6b	K	K	c	-	c	t	g	a	t	g	t	c	-	g	t	t	a	g	a	g	a	-	g	g
R398.18	SP.18	Bol5a	H	H	c	g	t	t	a	g	t	g	c	-	a	g	t	t	g	g	-	g	a	a	g	g
R414.13	SS.13	Cab2a	K	K	c	g	c	-	g	g	t	g	t	c	a	g	-	-	g	g	a	g	a	a	g	g
R481.24		Cab2b	K/T	K/T	c	g	t	t	a	g	t	a	t	-	a	g	t	t	a	g	-	g	a	a	g	g
R322.27	SB.17	Cast1a	H	H	c	-	t	t	a	g	t	g	c	c	-	g	t	t	g	g	g	g	a	a	g	g
R348.12	SH.12	Cast1b	H	H	c	g	t	t	a	g	t	g	c	c	-	g	t	t	g	g	g	g	a	a	g	g
R297.18	RX.9	CDV1a	K	K	c	-	c	t	g	g	t	g	t	c	-	g	t	t	a	g	a	g	a	a	g	g
R313.1	SA.1	CDV1b	K	K	c	-	c	-	g	g	t	g	t	c	a	-	g	-	a	-	a	g	a	-	g	g
R297.19	RX.10	CDV2a	J	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g
R313.2	SA.2	CDV2b	J	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	g	g	g
R297.20	RX.11	CDV3a	K	K	c	-	c	t	g	g	t	g	t	c	-	g	t	t	a	-	a	g	a	a	g	g
R348.1	SH.1	Cel1a	X	X	c	-	t	t	a	g	t	g	t	c	a	a	t	t	a	a	a	a	a	a	g	g
R404.14	SI.1	Cel1b	?	?	c	-	t	t	a	g	t	g	t	-	a	g	t	t	a	-	-	-	a	a	-	-

IV Snapshot results

				<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V/M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>	
R467.12	SI.2	Cel1b	X	c	-	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g	
R348.2	SH.2	Cel2a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g	
R443.22	SI.2	Cel2b	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R348.3	SH.3	Cel3a	X	c	-	t	t	a	g	t	g	t	c	g/	g/	t	t	g/a	g	a	a	a	a	g	g	
R351.3	SI.3	Cel3b	X	c	-	t	-	a	g	t	g	t	c	a	a	t	t	a	-	-	-	a	-	g	g	
R392.2	SI.3	Cel3b	X	c	-	-	-	g/	a	g	t	g	t	c	a	a	-	a	-	a	a	a	a	g/	g	
R382.9	SI.3	Cel3b	X/U	c	-	t	t	g/	a	g	t	g	t	c	a	a	t	t	a	g	a	-	a	g	g	
R443.3	SW.3	Cel3c	X	c	-	t	-	g/	a	g	t	g	t	c	a	a	-	a	-	a	a	a	a	g	g	
R369.9	SK.9	Cine1a	U	c	g	t	t	g	g	t	g	t	c	g	g	t	t	g/a	g	-	g	a	-	-	g	
R373.10	SL.10	Cine1b	?	c	g	t	t	-	g	t	g	t	-	-	g	t	t	a	-	-	-	a	-	-	-	
R382.2	SL.10	Cine1b	?	c	g	-	-	-	-	t	g	t	c	a	g	-	t	g	-	a	g	a	-	-	-	
VK503.3	SL.10	Cine1b	J	-	-	t	-	-	g	-	g	t	-	-	g	-	-	-	-	-	-	-	g	-	-	
R369.10	SK.10	Cine2a	K	c	g	c	t	g	g	-	g	t	-	-	g	-	t	-	-	-	g	a	a	-	g	
R297.3	RW.3	Cmol104a	V	c	-	t	t	a	g	t	g	c	t	g/	a	g	t	t	a	g	g	g	a	a	g	g
R334.14	RY.3	Cmol104b	V	c	-	t	t	a	g	t	g	c	t	-	g	t	t	a	g	g	g	a	a	a	g	g
R297.4	RW.4	Cmol105a	H	c	-	t	-	a	g	t	g	c	c	g/	a	g	-	t	g	g	g	g	a	-	g	g
R299.4	RY.4	Cmol105b	H?	-	-	t	-	g	g	t	g	c	c	a	g	-	-	g	-	g	g	a	-	a	g	
R363.11	RY.4	Cmol105b	H	c	g/	a	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	g/	a	g
R297.5	RW.5	Cmol119a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	a	g	g
R299.5	RY.5	Cmol119b	K	c	-	c	-	g	g	t	g	t	c	-	g	-	-	a	-	a	g	a	-	-	g	
R297.6	RW.6	Cmol122a	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	a	g	g
R334.11	RY.6	Cmol122b	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	a	g	g
R297.7	RX.1	Cmol123a	H	c	-	t	t	a	g	t	g	c	c	g/	a	g	t	t	g	g	g	g	a	a	g	g
R299.7	RY.7	Cmol123b	H	c	-	t	t	g	g	t	g	c	c	a	g	-	t	g	-	-	g	a	-	g	g	
R297.1	RW.1	Cmol12a	H	c	-	t	-	a	g	t	g	c	c	g/	a	g	-	-	g--	-	g	g	a	-	g	g
R334.12	RY.1	Cmol12b	H	c	-	t	t	a	g	t	g	c	c	g/	a	g	t	t	g	g	g	g	a	g/	a	g
R297.8	RX.2	Cmol138a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	a	g	g
R299.8	RY.8	Cmol138b	U	c	-	t	t	g	g	-	g	t	c	a	g	-	-	a	g	-	g	a	a	g/	a	g
R363.12	RY.8	Cmol138b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	a	g	g
R297.9	RX.3	Cmol139a	H	c	g	t	t	a	g	t	g	c	c	g/	a	g	t	t	g	g	g	g	a	a	g	g
R299.9	RY.9	Cmol139b	H	c	-	t	t	a	g	t	g	c	c	-	g	-	t	g	g	g	g	a	a	a	g	g
R297.10	RX.4	Cmol140a	U	c	-	t	t	g	g	t	g	t	c	-	g	t	t	a	g	a	g	a	a	a	g	g
R299.10	RY.10	Cmol140b	U	c	-	t	t	g	g	t	g	t	c	-	g	-	t	a	-	-	g	a	-	-	g	
R235.15	RQ.16	Cmol151a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	a	g	g
R244.5	RR.5	Cmol151b	U	g/	c	g	t	t	g	g	t	g	t	c	g/	a	g	t	t	a	g	a	-	g	g	
R297.15	RX.5	Cmol154a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R334.10	RY.11	Cmol154b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R297.16	RX.6	Cmol164a	K	c	-	c	t	g	g	t	g	t	c	-	g	t	t	a	-	a	g	a	a	a	g	g
R299.12	RY.12	Cmol164b	K	c	-	c	t	g	g	t	g	t	c	-	g	-	t	a	g	a	g	a	a	a	a	g

IV Snapshot results

					R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V_M3_4580	B_8280	X_6371	N1_10238	L_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
R297.17	RX.7	Cmol165a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R299.13	RY.13	Cmol165b	J	c	-	t	t	a	g	t	g	t	c	-	g	-	t	a	-	-	g	a	g	g	g	g
R245.12	RQ.13	Cmol16a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R244.2	RR.2	Cmol16b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R245.13	RQ.14	Cmol44a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R244.3	RR.3	Cmol44b	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R245.11	RQ.12	Cmol6a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	g
R244.1	RR.1	Cmol6b	J	c	-	t	-	a	g	t	g	t	c	a	g	t	t	a	-	a	g	a	g	g	g	g
R245.14	RQ.15	Cmol71a	U/J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R283.20	RQ.15	Cmol71a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R244.4	RR.4	Cmol71b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R297.2	RW.2	Cmol79a	V	c	-	t	-	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	-	g	g	g
R334.13	RY.2	Cmol79b	V	c	-	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g	g
R322.10	SC.9	Coca1a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R323.1	SD.1	Coca1b	HV	g	g	t	-	g	g	t	g	t	c	a	g	-	-	g/a	g	a	g	a	-	g	g	g
R322.10	SC.10	Coca2a	HV	c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g	g
R334.15	SD.2	Coca2b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g	g
R322.11	SC.11	Coca3a	H	c	-	t	t	a	g	-	-	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R334.16	SD.3	Coca3b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R322.12	SC.12	Coca4a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R334.17	SD.4	Coca4b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R322.13	SC.13	Coca5a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R323.5	SD.5	Coca5b	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	g
R369.19	SJ.13	Cru1a	K	-	g	c	t	-	g	t	g	t	-	a	g	-	t	-	-	-	-	a	a	-	g	g
R373.8	SL.8	Cru1b	?	c	-	-	t	-	g	-	g	t	-	a	g	t	t	a	-	-	g	a	a	-	-	g
R392.7	SJ.8	Cru1b	K	c	g	c	t	-	-	-	g	t	-	-	g	t	t	g/a	-	-	g/a	a	a	-	g	g
R369.8	SK.8	Cru4a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	g
R467.21	SN.15	Cru4b	K	c	-	c	t	g	g	-	g	t	-	-	g	-	t	-	-	-	-	a	a	-	-	g
R143.43	RH.9	CRV1a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R145.42	RI.15	CRV1b	K	c	-	c	t	a	g	-	g	t	-	-	g	t	t	a	g	-	g	a	a	-	-	g
R467.29	SR.1	Dia1a	T	c	-	t	-	-	g	t	a	-	-	-	g	-	t	a	-	-	g	a	a	-	g	g
R481.17	SS.1	Dia1b	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	g/a	g	-	g	a	a	g	g	g
R404.3	SR.3	Dia3a	H	c	-	-	-	-	g	t	g	c	c	a	g	-	-	g	-	g	g	-	g	-	g	g
R481.16	SS.3	Dia3b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	-	a	g	g	g
R467.13	SJ.18	Fala1a2	V	c	-	t	t	a	g	t	g	c	t	-	g	t	t	a	-	-	g	a	a	g	g	g
R348.4	SH.4	Fala1b	V	c	-	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g	g
R481.9	RY.15	Fala2a	J	c	-	t	t	a	g	-	-	t	c	a	g	t	t	g/a	g	-	g	a	g	g	g	g
R467.4	RY.15	Fala2a	J	c	-	t	-	-	g	t	g	t	c	a	g	-	-	-	-	-	g	a	g	g	g	g
R348.5	SH.5	Fala2b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g

				R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V_M3_4580	B_8280	X_6371	N1_10238	L_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
R481.3	RY.8	Fala5a	U	-	-	t	-	g	g	-	-	t	c	a	g	-	-	-	-	-	g	a	a	-	g
R351.6	SI.6	Fala5b	U	c	-	t	t	g	g	t	g	t	-	-	y	-	t	a	-	-	g	a	a	-	-
R334.3	SD.14	Fora1a	H	c	g	t	t	a	g	t	g	c	c	-	g	t	t	g	g	-	g	a	a	g	g
R347.1	SG.1	Fora1b	H	c	-	t	t	a	g	t	g	-	c	-	g	t	t	g	g	g	g	a	a	g	g
R334.5	SD.15	Fora2a	J	c	-	t	t	a	g	t	g	t	c	g	g	t	t	g/a	g	a	g	a	g	g	g
R347.2	SG.2	Fora2b	J	c	-	t	t	a	g	t	g	t	c	-	g	t	t	a	g	a	g	a	g	g	g
R334.6	SD.16	Fora3a	K	-	-	c	t	g	g	t	g	t	c	-	g	t	t	g/a	g	a	g	a	a	g	g
R347.3	SG.3	Fora3b	K	-	-	c	t	g	g	t	g	t	c	-	g	t	t	g/a	g	-	g	a	a	g	g
R334.7	SD.17	Fora4a	H	c	-	t	t	a	g	t	g	c	c	-	g	t	t	g	-	g	g	a	a	g	g
R347.4	SG.4	Fora4b	H	c	-	t	-	a	g	t	g	c	c	-	g	-	t	g	g	g	g	a	-	g	g
R215.9	RM.9	Fupe1a	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g
R222.1	RO.1	Fupe1b	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g
R467.39	SW.2	Fupe1c	X	c	-	t	t	a	g	t	g	t	-	a	a	t	t	a	g	-	-	a	a	-	g
R215.10	RM.10	Fupe2a	HV	c	g	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g
R222.20	RO.2	Fupe2b	K	c	g/a	a	c	-	g	g	t	g	t	c	a	g	t	-	a	g	a	g/a	-	g	g
R215.11	RM.11	Fupe3a	K/X	c	a	g/a	c	t	g	g	t	g	t	c	a	a	-	-	g	-	-	a	a	g	g
R230.2	RM.11	Fupe3a	K	c	g	c	g	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R245.10	RO.3	Fupe3b	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R215.12	RM.12	Fupe4a	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g
R230.1	RO.4	Fupe4b	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g
R215.13	RM.13	Fupe5a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R222.5	RO.5	Fupe5b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/a	a	a	g	g
R222.6	RO.6	Fupe6a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R230.21	RP.11	Fupe6b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R245.15	RO.7	Fupe7a	K	c	-	c	t	g	g	t	g	t	-	a	g	t	t	a	g	-					

IV Snapshot results

					<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>
R283.21	RS.10	Gam2b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R244.16	RR.16	Gam3a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R246.11	RS.11	Gam3b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R418.3	SM.16	Gam4a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	-	g	g	
R399.11	SQ.11	Gam4b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	-	g	g	
R392.10	SM.17	Gam5a	H	c	g	t	t	-	g	t	g	c	-	a	g	-	t	g	-	-	g	a	a	-	-	
R399.12	SQ.12	Gam5b	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R392.11	SM.18	Gam6a	X	c	g	t	t	-	g	-	g	t	-	-	a	t	t	-	-	-	a	a	a	-	-	
R399.13	SQ.13	Gam6b	?	c	g	t	t	a	g	t	g	t	-	-	g	-	t	a	-	-	-	a	a	-	g	
R418.8	SQ.13	Gam6b	X	c	g	t	t	a	g	t	g	t	-	a	a	-	t	a	-	-	a	a	a	g	g	
R385.9	SN.9	Gam7a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R399.14	SQ.14	Gam7b	U	c	-	t	t	g	g	t	g	t	-	a	g	t	t	a	-	-	g	a	-	g	-	
R385.10	SN.10	Gam8a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R399.14	SQ.15	Gam8b	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R297.22	RX.12	Gro2a	K	c	-	c	t	g	g	t	g	t	c	-	g	-	t	a	-	a	g	a	-	-	g	
R347.10	SG.10	Gro2b	K	-	-	c	t	g	a	t	g	t	-	-	g	-	t	-	-	a	g	-	a	-	g	
R297.23	RX.13	Gro3a	U	c	-	t	t	g	g	t	g	t	c	-	g	-	t	a	-	a	g	a	-	-	g	
R347.11	SG.11	Gro3b	U	c	-	t	t	g	g	t	g	t	-	-	g	-	t	a	-	a	g	a	-	-	g	
R297.24	RX.14	Gro4a	K	-	-	c	t	g	g	t	g	t	c	-	g	-	t	a	-	-	g	a	-	-	g	
R467.10	SG.12	Gro4b	K	c	-	c	-	-	g	t	g	t	-	-	g	-	-	-	-	-	g	a	-	-	g	
R297.25	RX.15	Gro5a	T	c	-	t	t	a	g	t	a	t	c	-	g	t	t	a	-	a	g	a	a	g	g	
R443.18	SW.18	Gro5a2	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	g/a	-	a	g	a	a	g	g	
R347.13	SG.12	Gro5b	T	c	-	t	t	a	g	t	a	t	-	-	g	t	t	-	-	a	-	a	a	-	-	
R304.1	RZ.1	Gsl1a	K	c	-	c	t	g	g	t	g	t	c	a	g	-	t	a	g	a	g	a	-	g	g	
R347.6	SG.6	Gsl1b	K	c	-	c	t	g	g	t	g	t	c	-	g	-	t	a	g	a	g	-	a	g	g	
R304.2	RZ.2	Gsl2a	T	c	g	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R347.6	SG.7	Gsl2b	T	c	-	t	t	a	g	t	a	t	-	-	g	-	t	a	-	-	g	a	a	g	g	
R304.3	RZ.3	Gsl3a	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	
R347.7	SG.8	Gsl3b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	-	a	g	a	g	g	g	
R369.13	SK.13	Guz1a	K	c	-	c	t	g	g	t	g	t	-	-	g	t	t	a	-	-	g	a	a	-	g	
R373.14	SL.14	Guz1b	K	c	g	c	t	g	g	t	g	t	-	-	g	-	t	-	-	-	-	a	a	-	-	
R382.4	SL.14	Guz1b	K	c	g	c	-	-	-	t	g	t	c	-	g	-	-	-	-	-	-	a	a	-	g	
R369.14	SK.14	Guz2a	T	-	g	t	t	-	-	-	a	t	-	-	g	t	t	-	-	-	-	a	a	g	-	
R373.15	SL.15	Guz2b	T	c	g	-	-	a	g	-	a	t	-	-	g	-	-	-	-	-	-	a	a	-	-	
R369.15	SK.15	Guz3a	HV/H/ V	c	g	t	t	-	g	-	g	t	c	a	g	t	t	-	-	g	-	a	a	g	g	
R481.13		Guz3a	HV/H/ V	c	-	t	-	-	g	-	g	c	-	-	g	-	-	-	-	g	-	a	a	-	-	
R373.16	SL.16	Guz3b	HV/H/ V	c	g	t	t	-	g	-	-	c	-	a	g	-	t	-	-	-	-	-	a	-	-	
R382.5	SL.16	Guz3b	HV/H/ V	c	g	t	t	-	g	-	g	c	-	-	g	t	t	-	-	-	g	-	a	g	g	
R467.14	SK.16	Guz4a	T/K/U	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	

IV Snapshot results

				<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>G_N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>	
R373.17	SL.17	Guz4b	U	c	-	t	t	g	g	t	g	t	-	a	g	t	t	-	g	-	g	a	a	-	a	
R417.15	SU.16	Hig2a	H	c	-	t	t	-	g	-	g	c	-	a	g	t	t	g	-	-	g	a	a	-	-	
R421.2	SV.2	Hig2b	H	c	g	t	-	g/	a	g	t	g	c	c	a	g	-	-	g	g	g	a	-	g	g	
R244.6	RR.6	Hume1a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g	
R246.1	RS.1	Hume1b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R244.7	RR.7	Hume2a	H	c	-	t	t	a	g	t	g	c	c	g/	a	g	t	t	g	g	g	g	a	a	g	g
R246.2	RS.2	Hume2b	H	c	g	t	t	a	g	t	g	c	c	g/	a	g	t	t	g	g	g/	g	a	a	g	g
R244.8	RR.8	Hume3a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	g/a	g	a	g/	g	a	a	g	g
R246.3	RS.3	Hume3b	T	c	-	t	-	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R244.9	RR.9	Hume4a	J	c	g	t	-	a	-	t	g	t	c	-	g	t	t	g/a	g	-	g	a	g	-	g	
R246.4	RS.4	Hume4b	J	c	-	t	-	-	g	t	g	t	c	-	g	t	t	-	g	-	g	a	g	g	g	
R244.10	RR.10	Hume5a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R246.5	RS.5	Hume5b	T	c	g	t	t	a	g	t	a	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R244.13	RR.13	Hume8a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R246.8	RS.8	Hume8b	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R348.14	SH.14	Hume10a	U	c	-	t	t	g	g	t	g	t	c	-	g	t	t	a	g	-	g	a	a	-	g	
R351.10	SI.10	Hume10b	U	c	g	t	t	g	-	-	g	t	-	-	g	-	t	-	-	-	-	a	a	-	-	
R443.10	SW.10	Hume10b2	U	c	-	t	-	g	g	t	g	t	c	a	g	-	-	a	-	-	g	a	-	g	g	
R467.11	SH.15	Hume11a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R351.11	SI.11	Hume11b	K	c	g	c	t	g	g	t	g	t	-	-	g	t	t	a	-	-	g	a	a	g	g	
r443.11	SW.11	Hume11b2		c	-	-	-	g	g	t	g	t	c	a	g	-	-	a	-	a	g	a	a	g	g	
R363.5	SH.18	Hume14a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	-	a	g	a	a	g	g	
R373.20	SI.14	Hume14b	K	c	g	c	t	g	g	-	g	t	-	-	g	-	t	-	-	-	-	a	a	-	-	
R481.10	SI.14	Hume14b	K	c	-	c	-	g	g	t	g	t	c	a	g	-	-	-	a	g	a	-	g	g	g	
R362.1	SJ.1	Hume15a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g	
R443.12	SW.12	Hume15a2	K	c	-	c	t	g	g	t	g	t	-	a	g	-	t	a	-	-	g	a	a	g	g	
R369.1	SK.1	Hume15b	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	-	a	g	a	-	g	g	
R362.4	SK.2	Hume18a	K	c	-	c	t	g	g	t	g	t	-	-	g	t	t	a	-	-	g	a	a	-	-	
R443.13	SW.13	Hume18a2	U/K	c	-	-	-	g	g	t	g	t	c	a	g	-	-	-	-	-	-	a	a	g	g	
R369.2	SI.18	Hume18b	U/K	c	-	-	-	g	g	t	g	t	c	a	g	-	-	a	-	a	g	a	-	g	g	
R362.5	SJ.5	Hume19a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R369.3	SK.3	Hume19b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R362.7	SJ.7	Hume21a	H	c	g	t	t	a	g	t	g	c	c	-	g	t	t	g	-	-	g	a	a	g	g	
R382.16	SK.4	Hume21b	H	c	g	t	t	-	g	-	g	-	-	a	g	-	t	g	-	-	g	a	a	-	a	
R467.15	SK.5	Hume21b	H	c	-	t	t	a	g	t	g	c	c	a	g	-	t	g	g	g	g	a	a	g	g	
R362.10	SJ.10	Hume24a	H	c	-	t	t	a	g	t	g	c	-	-	g	t	t	g	-	-	g	a	a	g	g	
R369.5	SK.5	Hume24b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	-	-	g	a	a	g	g	
VK503.2																										
8	SJ.11	Hume25a	J	c	-	t	t	-	g	t	g	T	-	-	g	-	t	-	-	-	-	a	g	g	g	
R481.12	SJ.11	Hume25a	J	c	-	t	t	a	g	-	g	t	c	a	g	t	t	g/a	g	-	g	a	g	g	g	g

IV Snapshot results

					<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>
R369.6	SK.6	Hume25b	R/J/U	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	-	a	g	a	-	g	g	
R467.16	SK.7	Hume25b	J	c	-	t	t	a	g	t	g	t	-	a	g	t	t	g/a	g	-	g	g/a	g	-	g	g
R362.12	SJ.12	Hume26a	U	c	-	t	t	g	g	-	g	t	-	-	g	-	t	-	-	-	-	-	a	a	-	-
R297.26	RX.16	Hund1a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R322.21	SB.3	Hund1b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	g
R297.27	RX.17	Hund2a	K	c	g/	a	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R322.22	SB.4	Hund2b	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	g
R304.13	RZ.13	Junc1a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R313.13	SA.13	Junc1b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g	g
R304.14	RZ.14	Junc2a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R313.14	SA.14	Junc2b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g	g
R304.15	RZ.15	Junc3a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R313.15	SA.15	Junc3b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g	g
R304.16	RZ.16	Junc4a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g	g
R313.16	SA.16	Junc4b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R304.17	RZ.17	Junc5a	K	c	-	c	t	g	g	t	g	t	-	-	g	-	t	a	-	-	g	a	a	-	g	g
R313.17	SA.17	Junc5b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g	g
R304.18	RZ.18	Junc6a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R313.18	SA.18	Junc6b	T	c	g	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R381.8	SM.8	Junc7a	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g/	a	g	g	g	g
R467.20	SM.9	Junc7a	J	c	-	t	-	-	g	t	g	t	-	-	-	-	-	-	-	-	-	a	g	-	g	g
R418.4	SN.10	Junc7b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	g
R443.25	SN.10	Junc7b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	g
R381.9	SM.9	Junc8a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R385.2	SN.2	Junc8b	U	c	-	t	t	g	g	t	g	t	c	a	g	-	-	g/a	-	a	g	a	a	g	g	g
R381.10	SM.10	Junc9a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	g
R385.3	SN.3	Junc9b	U	c	-	t	t	g	g	t	g	t	c	a	g	-	t	a	-	-	g	a	a	-	g	g
R392.8	SM.11	Junc10a	J	c	-	t	t	a	g	t	g	t	c	a	g	-	t	g/a	-	-	g	a	g	-	g	g
R443.23	SM.11	Junc10a	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	g
R385.4	SN.4	Junc10b	U/J	c	-	t	t	a	g	t	g	t	-	a	g	-	t	g/a	-	-	g	a	-	-	g	g
R418.6	SN.4	Junc10b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	g
R392.9	SM.12	Junc11a	K/U	c	g	-	-	g	g	t	g	t	-	-	g	-	-	a	-	-	g	a	a	-	-	-
R443.24	SM.12	Junc11a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R385.5	SN.5	Junc11b	K	c	-	c	t	g	g	t	g	t	c	a	g	-	t	a	-	a	g	a	a	g	g	g
R381.13	SM.13	Junc12a	preH V/HV/ H/V V	c	g	t	t	a	g	t	g	c	-	a	g	-	t	a	-	-	g	a	a	-	g	g
R418.2	SM.13	Junc12a	preH V/HV/ H/V V	c	g	t	t	a	g	t	g	c	t	a	g	t	t	g/a	g	g	g	a	a	g	g	g
R392.17	SN.6	Junc12b	preH V/HV/ H/V V	c	g	t	t	a	g	t	g	c	-	a	g	t	t	a	-	-	g	a	a	-	-	-
R443.26	SN.6	Junc12b	preH V/HV/ H/V V	c	-	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g	g

IV Snapshot results

					<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>
R381.14	SM.14	Junc13a	U	c	g	t	t	g	g	t	g	t	-	a	g	-	t	a	-	-	g	a	a	-	-	
R385.7	SN.7	Junc13b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R381.15	SM.15	Junc14a	U	c	-	t	t	g	g	t	g	t	-	a	g	-	t	a	-	-	g	a	a	-	g	
R385.8	SN.8	Junc14b	U	c	-	t	t	g	g	-	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R348.8	SH.8	Malga1a	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	
R351.7	SI.7	Malga1b	J	c	-	t	t	a	g	t	g	t	c	-	g	-	t	a	-	a	g	a	g	g	g	
R348.9	SH.9	Malga2a	J	g/ c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	
R351.8	SI.8	Malga2b	J	g/ c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	-	a	g	a	g	g	g	
R404.11	SR.11	MCIII2a	J	c	-	t	t	-	g	-	g	t	-	-	g	-	t	a	-	-	g	a	g	-	-	
R443.30	SR.11	MCIII2a	J	c	-	t	t	a	g	t	g	t	c	g/ a	g	t	t	g/a	g	a	g	a	g	g	g	
R467.30	SS.6	MCIII2b	J	-	-	t	t	a	g	t	g	t	-	-	g	-	t	-	-	-	g	a	g	-	g	
R204.11	RJ.1	Mina1a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R164.1	RJ.2	Mina1b	U	c	g	t	-	g	g	t	g	t	c	a	g	-	-	a	-	-	g	a	-	g	g	
R222.20	RK.2	Mina2a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	-	g	a	g	g	g	
R215.20	RJ.3	Mina2b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	
R160.3	RK.3	Mina3a	K	c	-	c	-	g	g	t	g	t	c	a	g	-	-	a	g	a	g	a	a	g	g	
R164.3		Mina3b	K	c	-	c	-	g	g	t	g	t	c	a	g	-	-	a	g	a	g	a	a	g	g	
R160.4	RJ.4	Mina4a	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R164.4	RK.4	Mina4b	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R160.5	RJ.5	Mina5a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R164.5	RK.5	Mina5b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R160.6	RJ.6	Mina6a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R164.6	RK.6	Mina6b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R160.7	RJ.7	Mina7a	X	c	g	t	t	a	g	t	g	t	g	a	g/ a	-	t	a	g	a	a	a	a	g	g	
R191.4	RL.1	Mina7b(2)	X	c	g	t	t	a	g	t	g	t	c	a	g/ a	a	t	t	a	g	a	a	a	a	g	g
R160.8	RJ.8	Mina8a	X	c	-	t	t	a	g	t	g	t	c	a	a	-	t	a	g	-	a	a	a	g	g	
R164.8	RK.8	Mina8b	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g	
R160.9	RJ.9	Mina9a	U	c	-	t	t	g	g	t	g	t	c	a	g	-	-	a	g	-	g	a	a	g	g	
R164.9	RK.9	Mina9b	U	c	-	t	t	g	g	t	g	t	-	a	g	t	t	a	g	-	g	a	a	g	g	
R191.5	RL.2	Mina9c	U	-	-	t	-	g	g	t	g	t	c	a	g	-	t	a	-	-	g	a	a	-	-	
R230.11	RP.1	Mina10a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	
R235.1	RQ.1	Mina10b	J	c	g	t	-	a	g	t	g	t	c	a	g	-	t	a	-	-	g	a	g	g	g	
R230.12	RP.2	Mina11a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R245.1	RQ.2	Mina11b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R244.17	RP.3	Mina12a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R235.3	RQ.3	Mina12b	U	c	g	t	-	g	g	t	g	t	c	a	g	-	-	g/a	g	-	g	a	-	-	g	
R245.2	RQ.3	Mina12b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g	
R230.14	RP.4	Mina13a	K	c	a	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R245.3	RQ.4	Mina13b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R230.15	RP.5	Mina14a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	

IV Snapshot results

					R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V_M3_4580	B_8280	X_6371	N1_10238	L_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
R235.5	RQ.5	Mina14b	K/U?		c	-	t	-	-	g	t	g	t	-	-	g	t	-	-	g	-	-	a	a	-	-
R245.4	RQ.5	Mina14b	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R230.16	RP.6	Mina15a	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	-	a	g	g
R234.5	RQ.6	Mina15b	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R283.17	RQ.6	Mina15b	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	-	a	g	g
R283.18	RP.7	Mina16a	HV		c	g	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g
R245.6	RQ.7	Mina16b	HV/V		c	g	t	t	a	g	t	g	c	-	-	g	t	t	a	g	g	g	a	a	-	g
R245.6	RQ.7	Mina16b	preH		c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	a	g	a	a	g	g
R316.13	RQ.7	Mina16b	V/HV		c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g
R230.18	RP.8	Mina17a	HV		c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
R245.7	RQ.8	Mina17b	H		c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
R230.19	RP.9	Mina18a	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R245.8	RQ.9	Mina18b	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R385.11	SN.11	MIV1a	J/U		c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	g	g	a	g	g	g
R481.16	SN.11	Miv1a	J		c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	-	a	g	a	g	-	g
R467.23	SO.2	MIV1b	J		-	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	-	g	a	g	-	g
R385.12	SN.12	MIV2a	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g
R397.2	SO.2	MIV2b	U/K		c	-	-	-	g	g	t	g	t	c	a	g	-	-	g	-	a	a	a	-	-	a
R322.25	SB.15	MMI3a	T		c	-	t	t	a	g	t	a	t	c	-	g	t	t	a	g	-	g	a	a	g	g
R348.10	SH.10	MMI3b	T		c	g	t	t	a	g	t	a	t	c	-	g	t	t	g/a	g	-	g	a	a	g	g
R215.1	RM.1	Moca1a	H		-	-	-	-	a	g	t	g	c	c	-	g	-	-	g	-	g	g	a	-	-	g
R222.13	RM.1	Moca1a	H		c	t	-	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
R323.6	SD.6	Moca1b	H		c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
R443.35	SV.18	Moca2a2	preH		c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	-	g	a	a	g	g
R467.38	SV.19	Moca2a2	V/HV		c	-	t	t	a	g	-	g	c	-	-	g	t	t	a	g	g	g	a	a	g	g
R323.7	SD.7	Moca2b	HV		c	-	t	t	a	g	t	g	c	c	-	g	t	t	a	g	g	g	a	a	g	g
R215.3	RM.3	Moca3a	H		c	g	t	-	a	g	t	g	c	c	-	g	t	-	g	g	g	g	a	-	g	g
R323.8	SD.8	Moca3b	H		-	-	t	t	a	g	t	g	c	c	-	g	t	t	g	g	-	g	a	-	-	g
R215.4	RM.4	Moca4a	H		c	-	t	-	a	g	t	g	c	c	-	g	-	-	g	-	g	g	a	-	-	g
R323.9	SD.9	Moca4b	?		c	-	t	-	a	g	t	g	t	c	-	g	-	t	g/a	-	-	g	a	-	-	g
R363.16	SD.9	Moca4b	H/J		c	-	t	t	a	g	t	g	c/	t	c	a	g	t	t	g/a	g	g/	a	a	g/	g
R443.19	SW.19	Moca4b2	H		c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g/	g	a	a	g	g
R215.7	RM.7	Moca7a	K		c	-	c	-	g	g	t	g	t	c	-	g	t	t	-	g	a	g	a	a	g	g
R334.1	SD.13	Moca7b	K		c	-	c	t	g	g	t	g	t	-	-	g	-	t	a	-	a	g	a	-	-	g
R215.8	RM.8	Moca8a	K		c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R143.39	RH.10	Mop1a	K		c	-	c	t	g	g	t	g	t	-	-	g	t	t	a	-	-	g	a	a	g	g
R150.3	CA.11	Mop1b	K		c	-	c	t	g	g	t	g	-	-	-	g	t	t	-	-	-	g	a	a	g	g
R443.7	SW.7	Mop1c	K		c	-	c	t	g	g	t	g	t	c	a	g	t	t	g/a	a	g	a	a	g	g	g
R204.17	RH.1	Mop2a	V		c	-	t	t	a	g	t	g	c	t	a	g	t	t	a	g	-	g	a	a	g	g
R145.40	RI.13	Mop2b	V		c	-	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g

IV Snapshot results

					<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>
R143.41	RH.12	Mop3a	HV		c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g
R145.41	RI.14	Mop3b	HV		c	-	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	-
R304.8	RZ.8	Pai11a	K		c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R313.8	SA.8	Pai11b	K		c	g	c	t	g	g	t	g	t	c	a	t	g	t	a	g	a	g	a	a	g	g
R304.9	RZ.9	Pai12a	K		c	g/	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R313.9	SA.9	Pai12b	K		c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R304.10	RZ.10	Pai13a	V		c	-	t	t	a	g	t	g	c	t	-	g	t	t	a	-	g	g/	a	a	g	g
R313.10	SA.10	Pai13b	V		c	-	t	t	a	g	t	g	t	t	-	g	t	t	-	g	g	-	a	a	g	g
R421.15	SV.15	Pai15a2	H		c	-	t	t	-	g	t	g	c	-	-	g	-	-	g	-	-	g	a	a	g	g
R313.12	SA.12	Pai15b	H		c	-	t	t	-	g	-	g	-	c	-	g	t	t	g	g	g	a	a	-	-	g
R363.8	SE.12	Pai16a	U		c	-	t	t	g	g	t	g	t	c	-	g	t	t	g/a	g	a	g	a	a	g	g
R339.12	SF.12	Pai16b	U		c	-	t	t	g	g	t	g	t	c	-	g	t	t	a	-	-	g	a	a	g	g
R333.13	SE.13	Pai17a	U		c	-	t	t	g	g	t	g	t	-	-	g	t	t	a	g	-	g	a	a	-	g
R382.13	SF.13	Pai17b	U		c	g	t	t	g	g	t	g	t	-	-	g	-	t	a	-	-	g	a	a	-	-
R443.14	SW.14	Pai17b2	U		c	-	t	t	g	g	t	g	t	c	a	g	-	t	a	-	a	g	a	a	g	g
R333.14	SE.14	Pai18a	U		c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R339.14	SF.14	Pai18b	U		c	-	t	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g
R333.16	SE.15	Pai19a	K		c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R334.17	SF.15	Pai19b	K		c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R304.4	RZ.4	Pai1a	K		c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g
R313.4	SA.4	Pai1b	K		c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R382.14	SE.17	Pai21a	T		c	g	t	t	-	g	-	a	-	-	-	g	-	t	a	-	-	-	a	a	-	-
R418.1	SE.17	Pai21a	T		c	-	t	t	a	g	t	a	t	c	a	g	t	t	g	-	a	g	a	a	g	g
R339.15	SF.17	Pai21b	T		c	-	t	t	a	g	t	a	t	-	-	g	t	t	a	-	-	g	a	a	g	g
R421.17	SV.17	Pai22a2	J?		-	g	t	t	-	g	-	g	t	-	-	g	-	t	g/a	-	-	-	a	g		
R467.37	SV.18	Pai22a2	J		c	-	t	t	a	g	-	g	t	-	-	g	t	t	g	-	-	-	a	g		
R443.15	SW.14	Pai22b2	J		c	-	t	t	a	g	t	g	t	-	a	g	-	t	-	-	-	-	a	g		
R304.5	RZ.5	Pai3a	K		c	g	c	t	g	g	t	g	t	c	a	g	-	-	-	-	a	g	a	a	g	g
R313.5	SA.5	Pai3b	K		c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R304.6	RZ.6	Pai6a	H		c	-	t	t	a	g	t	g	c	t	-	g	t	t	g	g	g	g	a	a	g	g
R334.8	SA.6	Pai6b	H		c	-	t	t	a	g	t	g	c	c	-	g	t	t	g	g	g	g	a	a	g	g
R304.7	RZ.7	Pai7a	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R313.7	SA.7	Pai7b	U		c	g	t	t	g	g	t	g	t	t	-	g	t	t	a	g	g	a	a	a	g	g
R316.1	SB.5	Par1a	K		c	g	c	t	g	g	t	g	t	c	a	g	-	-	-	g	a	g	a	a	g	g
R322.1	SC.1	Par1b	K		c	g	c	-	g	g	t	-	t	c	a	g	-	t	a	g	-	g	a	-	g	g
R316.2	SB.6	Par2a	H		c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
R322.2	SC.2	Par2b	H		c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g
R316.3	SB.7	Par3a	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g
R322.3	SC.3	Par3b	U		c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g

IV Snapshot results

				<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>	
R316.4	SB.8	Par4a	K	c	-	c	t	g	g	t	g	t	-	-	g	t	t	a	g	-	g	a	a	g	g	
R322.4	SC.5	Par4b	K	c	g/	a	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R316.5	SB.9	Par5a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R322.5	SC.5	Par5b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R316.7	SB.11	Par7a	H	c	g	t	t	a	g	t	g	c	c	-	g	t	t	g	g	g	g	a	a	g	g	
R322.7	SC.7	Par7b	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R333.3	SE.3	Pove1a	T	c	-	t	t	a	g	t	a	t	c	-	g	t	t	a	g	-	g	a	a	g	g	
R339.3	SF.3	Pove1b	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R333.4	SE.4	Pove2a	T	c	-	t	t	a	g	t	a	t	c	-	g	t	t	a	g	a	g	a	a	g	g	
R467.8	SF.4	Pove2b	T	c	-	t	-	a	g	t	a	t	c	a	g	-	-	a	-	a	g	a	a	g	g	
R144.15	RA.1	Rein1a	U	c	-	t	t	g	g	t	g	t	-	a	g	-	t	-	g	-	g	-	a	-	-	
R146.15	RB.2	Rein1b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.16	RA.2	Rein2a	U	c	-	t	t	g	g	t	-	t	c	a	g	t	t	-	g	-	g	-	a	-	g	
R146.16	RB.2	Rein2b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	a	g	g
R204.12	RA.3	Rein3a	U	c	g	t	t	g	g	t	g	t	-	a	g	t	t	a	-	-	g	a	a	g	g	
R146.17	RB.3	Rein3b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.18	RA.4	Rein4a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	-	g	
R146.18	RB.4	Rein4b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.19	RA.5	Rein5a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.19	RB.5	Rein5b	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R144.20	RC.1	Rein6a	V	c	-	t	t	a	g	t	g	-	t	a	g	t	t	a	g	g	g	a	a	g	g	
R146.20	RI.1	Rein6c	V	c	g	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g	
R144.21	RC.2	Rein7a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R146.21	RI.2	Rein7c	H	c	-	t	t	a	g	t	g	c	c	a	g	-	t	g	g	g	g	a	a	g	g	
R144.22	RA.6	Rein8a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.22	RB.6	Rein8b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.23	RC.3	Rein9a	V	c	-	t	t	a	g	t	g	-	t	a	g	t	t	a	g	g	g	-	a	g	g	
R146.23	RF.5	Rein9b	V	c	g	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g	
R144.24	RA.7	Rein10a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.24	RB.7	Rein10b	K	c	g/	a	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R144.25	RA.8	Rein11a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.25	RB.8	Rein11b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.26	TD.14	Rein12a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.26	RG.6	Rein12b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.27	RD.3	Rein13a	X	c	-	t	t	a	g	t	g	t	c	a	a	t	t	a	g	-	-	a	a	g	g	
R146.27	RE.2	Rein13b	X	c	-	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g	
R144.28	RD.4	Rein14a	K	c	-	c	t	g	g	t	?	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R146.28	RE.3	Rein14b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.29	RD.5	Rein15a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	-	g	-	g	a	a	-	g	
R146.29	RE.4	Rein15b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	

IV Snapshot results

				<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V/M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>	
R144.30	RD.6	Rein16a	X	c	-	t	t	a	g	t	g	t	c	a	a	t	t	a	g	-	a	a	a	g	g	
R146.30	RE.5	Rein16b	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g	
R144.31	RD.7	Rein17a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R146.31	RE.6	Rein17b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g	
R144.32	RD.8	Rein18a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
R146.32	RE.7	Rein18b	T	c	g	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.33	RD.9	Rein19a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.33	RE.8	Rein19b	T	c	g/	a	a	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R144.34	RF.6	Rein20a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.34	TD.13	Rein20b	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.36	RE.10	Rein22a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g/	a	a	g	g	
R146.36	RF.7	Rein22b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.37	RE.11	Rein23a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.37	RF.8	Rein23b	U	c	g/	a	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R144.38	RE.12	Rein24a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.38	TF.7	Rein24d	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.39	RG.7	Rein28a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R146.39	NA.2	Rein28b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g/	a	a	g	g	
R144.40	RG.8	Rein29a	J	c	-	g	t	a	g	t	g	t	c	a	g	t	t	a?	g	-	g	a	g	g	g	
R146.40	NA.3	Rein29b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	a/	g	a	g	g	
R144.41	TF.8	Rein30a	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R146.41	TG.7	Rein30b	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.42	RH.1	Rein31a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	-	a	a	a	g	g	
R146.42	RI.6	Rein31b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.43	RH.2	Rein32a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	-	-	-	g	-	a	g	g	
R146.43	RI.7	Rein32b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R144.44	RH.3	Rein33a	X	c	-	t	t	a	g	t	g	t	c	a	g/	a	t	t	a	g	a	a	a	g	g	
R146.44	RI.8	Rein33b	X	c	g	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g	
R421.4	SV.4	Rinc1a	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g	
R443.8	SW.8	Rinc1b	K	c	-	c	t	g	g	t	g	t	c	a	g	-	t	a	-	a	g	a	a	g	g	
R421.5	SV.5	Rinc2a	J	c	g	t	-	a	g	t	g	t	c	a	g	-	-	a	-	a	g	a	g	g	g	
R443.9	Sw.9	Rinc2b	J	c	-	t	-	a	g	t	g	t	c	a	g	-	-	a	-	a	g	a	g	-	g	
R204.1	RM.1	Rodi1a	H	c	g	t	t	a	g	t	g	c	c	a	g	t	t	g	t	g	g	g	a	g	g	
R222.12	RO.12	Rodi1b	H	c	g/	a	t	t	a	g	t	g	c	c	a	t	g	t	g	g	g	g	a	a	g	g
R414.29	ST.11	Roy1a	K	c	g	c	t	g	g	t	g	t	-	a	g	-	t	a	g	-	g	a	a	-	-	
R421.6	SV.6	Roy1b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R414.30	ST.12	Roy2a	U	c	g	t	t	g	g	t	g	t	-	-	g	-	t	a	g	-	g	a	a	-	-	
R421.7	SV.7	Roy2b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R414.31	ST.13	Roy3a	H	c	g	t	t	a	g	t	g	c	-	a	g	-	t	g	g	-	g	a	a	g	g	
R421.8	SV.8	Roy3b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	

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IV Snapshot results

					<u>R9_13928</u>	<u>L3/4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2/6_2758</u>	<u>M_10400</u>
R283.11	RU.11	Tar11b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R322.26	SB.16	Tint1a	H	c	-	t	t	a	g	t	g	c	c	-	g	t	t	g	g	g	g	a	a	g	g	
R348.11	SH.11	Tint1b	H	c	-	t	t	-	g	t	g	c	-	-	g	t	t	g	-	-	g	a	a	-	-	
R421.3	SV.3	Tint2b	J	g	g	-	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	
R481.26 VK503.4 1	SX.4	Troc10a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	-	g	a	a	g	g	
	OWG. 1	Troc10b	T	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R481.27 VK503.4 2	SX.5	Troc12a	T	c	-	t	t	a	g	t	a	t	-	a	g	t	t	a	g	-	g	a	a	g	g	
	OWG. 2	Troc12b	HV/V	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R482.28 VK515.1 4	SX.6	Troc13a	V	c	-	t	t	a	g	t	g	c	-	a	g	-	t	a	g	g	g	a	a	g	g	
	SX.6 VK503.4 3	Troc13a	V	c	-	t	-	a	g	t	g	c	t	a	g	-	-	a	g	g	g	a	a	g	g	
R482.28 VK515.1 3	OWG. 3	Troc13b	J	g	-	t	t	-	g	t	g	c	t	a	g	-	t	a	g	g	g	a	a	g	g	
			J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	
R245.9	RQ.11	Troc1a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	
R267.12	RT.12	Troc1b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	
R397.10	SO.10	Troc2a	U/J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	
R398.10	SP.10	Troc2b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g	
R443.29	SP.10	Troc2b	T	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R397.11	SO.11	Troc3a	t	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R398.11	SP.11	Troc3b	K	c	-	t	t	a	g	t	a	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R397.12	SO.12	Troc4a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R398.12	SP.12	Troc4b	N1	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R414.8	SS.8	Troc5a	N1	c	-	t	-	a	g	t	g	t	c	a	g	c	-	a	-	a	a	a	a	a	a	
R418.10	SS.8	Troc5a	N/N1	c	g	t	t	a	g	t	g	t	c	a	g	c	t	a	g	a	a	a	a	a	g	
R417.11	SU.11	Troc5b	N1	c	g	t	t	a	g	t	g	t	c	a	g	-	t	a	g	-	a	a	a	g	g	
R467.25	SU.12	Troc5b	U	c	-	t	t	a	g	t	g	t	c	a	g	c	t	a	g	a	a	a	a	g	g	
R414.9	SS.9	Troc6a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	a	a	a	g	g	
R421.1	SV.1	Troc6b2	HV/V	c	g	t	-	g	g	t	g	t	c	a	g	-	-	a	g	a	g	a	a	g	g	
R414.10	SS.10	Troc7a	V	c	g	-	t	-	a	g	t	g	c	-	a	g	-	-	a	g	-	g	a	a	-	
R418.11	SS.10	Troc7a	HV/V	c	a	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g	
R417.12	SU.13	Troc7b	V	c	-	t	t	a	g	t	g	c	-	a	g	-	-	a	-	-	g	a	a	g	g	
R443.33	SU.13	Troc7b	H	c	g	t	t	a	g	t	g	c	t	a	g	t	t	a	g	g	g	a	a	g	g	
R414.11	SS.11	Troc8a	H	c	-	t	-	a	g	t	g	-	-	a	g	-	-	g	g	a	g	g	-	-	g	
R418.12	SS.11	Troc8a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g	
R417.13	SU.14	Troc8b		c	g	t	t	a	g	t	g	c	c	a	g	-	t	g	g	g	g	a	a	g	g	
R297.7	RW.7	Turq1a	K	c	g	c	-	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R322.19	SB.1	Turq1b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R297.8	RW.8	Turq2a	K	c	-	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R322.20	SB.2	Turq2b	K	c	g	c	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R246.12	RS.12	Vald1a	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	
R283.12	RU.12	Vald1b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	

IV Snapshot results

					R9_13928	L3'4_3594	K_10550	A_4248	U_11467	W_8994	C_13263	T_13368	R0/preHV_11719	V_M3_4580	B_8280	X_6371	N1_10238	L_10034	H_7028	D_5178	HV_14766	R_12705	N_10873	J_12612	L2'6_2758	M_10400
R246.13	RS.13	Vald2a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	g
R283.13	RU.13	Vald2b	J	c	g	t	g	t	a	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R246.14	RS.14	Vald3a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R297.28	RS.14	Vald3a	HV	c	g	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g	g
R283.14	RU.14	Vald3b	HV	c	g	t	t	a	g	t	g	c	c	a	g	t	t	a	g	g	g	a	a	g	g	g
R246.15	RS.15	Vald4a	J	g	g	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	g	g	g	g
R297.22	RS.15	Vald4a	J	c	-	t	g	t	a	g	t	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R283.15	RU.15	Vald4b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R246.16	RS.16	Vald5a	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R283.16	RU.16	Vald5b	J	c	g	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R414.18	SS.18	Vent1a	X	c	-	t	t	a	g	t	g	t	c	a	a	t	t	a	g	a	a	a	a	g	g	g
R417.14	SU.15	Vent1b	X	-	g	t	t	a	g	t	g	t	c	a	a	-	t	a	-	-	a	a	a	g	g	g
R333.5	SE.5	Yese1a	L/M/R 9	c	-	t	t	a	g	t	g	t	c	-	g	t	t	a	g	-	a	g	a	-	-	-
R481.7	SE.5	Yese1a	L/R9 L/N/R	c	-	t	-	a	g	t	g	t	c	a	g	-	-	a	-	-	-	-	-	-	g	g
R363.6	SF.5	Yese1b	9	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	-	a	-	a	-	g	g
R467.9	SF.6	Yese1b	L/N/R 9	c	-	t	-	a	g	t	g	t	c	a	g	-	t	a	g	-	a	-	a	-	g	g
R333.6	SE.6	Yese2a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R339.6	SF.6	Yese2b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R333.7	SE.7	Yese3a	H	c	-	t	t	a	g	t	g	c	c	-	g	t	t	g	g	g	g	a	a	g	g	g
R339.7	SF.7	Yese3b	H	c	-	t	t	a	g	t	g	c	c	-	g	t	t	g	-	g	g	a	-	g	g	g
R333.8	SE.8	Yese4a	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	g/a	g	-	g	a	g	g	g	g
R339.8	SF.8	Yese4b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	a	g	a	g	g	g	g
R333.9	SE.9	Yese5a	J	c	-	t	t	a	g	t	g	t	-	-	g	t	t	g/a	g	a	g	a	g	g	g	g
R339.9	SF.9	Yese5b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	a	g	-	g	a	g	g	-	g
R333.10	SE.10	Yese6a	U	c	-	t	t	g	g	t	g	t	c	-	g	t	t	a	g	-	g	a	a	g	g	g
R382.10	SF.10	Yese6b	U	c	g	t	t	g	g	t	g	t	-	a	g	-	t	a	-	-	g	a	a	-	g	g
R443.4	SW.4	Yese6c	U	c	-	t	t	g	g	t	g	t	c	a	g	-	t	a	-	a	g	a	a	g	g	g
R333.11	SE.11	Yese7a	K	c	-	c	t	g	g	t	g	t	c	-	g	t	t	a	g	a	g	a	a	g	g	g
R339.11	SF.11	Yese7b	K	c	-	c	t	g	g	t	g	t	c	-	g	t	t	a	g	-	g	a	a	g	g	g
R397.3	SO.3	Yese8a	H	-	g	-	-	-	g	t	g	-	c	a	g	-	-	g	-	g	-	-	-	-	g	g
R467.24	SO.4	Yese8a	H	c	-	t	t	-	-	-	g	-	-	-	g	-	-	g	g	g	-	-	-	-	-	g
R398.3	SP.3	Yese8b	H	c	g	t	t	-	-	-	g	c	-	a	g	-	-	g	-	g	-	a	-	g	-	g
R397.4	SO.4	Yese9a	?	c	-	-	-	-	-	t	g	t	c	a	g	-	-	a	-	-	g	a	-	-	g	g
VK503.3	SO.4	Yese9a	J	-	-	t	-	a	g	t	g	t	c	a	g	-	t	a	-	g	-	a	g	-	g	g
R398.4	SP.4	Yese9b	?	g/ c	a	t	t	a	g	t	g	t	c	a	g	t	t	g/a	-	a	g	a	-	g	g	g
VK503.3	SP.4	Yese9b	J	c	-	t	t	a	g	t	g	t	c	a	g	t	t	g	g	a	g	a	g	g	g	g
R397.5	SO.5	Yese10a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R398.5	SP.5	Yese10b	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g	g
R398.6	SP.6	Yese11b	H?	-	g	-	t	-	g	-	-	-	-	a	-	-	-	g	g	-	-	-	a	-	-	g

IV Snapshot results

				<u>R9_13928</u>	<u>L3'4_3594</u>	<u>K_10550</u>	<u>A_4248</u>	<u>U_11467</u>	<u>W_8994</u>	<u>C_13263</u>	<u>T_13368</u>	<u>R0/preHV_11719</u>	<u>V_M3_4580</u>	<u>B_8280</u>	<u>X_6371</u>	<u>N1_10238</u>	<u>L_10034</u>	<u>H_7028</u>	<u>D_5178</u>	<u>HV_14766</u>	<u>R_12705</u>	<u>N_10873</u>	<u>J_12612</u>	<u>L2'6_2758</u>	<u>M_10400</u>
R397.7	SO.7	Yese12a	U	c	-	t	t	g	g	t	g	t	c	a	g	t	t	a	g	a	g	a	a	g	g
R398.7	SP.7	Yese12b	U	c	g	t	t	g	g	t	g	t	c	a	g	t	t	g/a	g	a	g	a	a	g	g
R397.8	SO.8	Yese13a	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g/a	a	a	g	g
R398.8	SP.8	Yese13b	H	c	-	t	t	a	g	t	g	c	c	a	g	t	t	g	g	g	g	a	a	g	g

IV.2 H-Plex

Derived SNPs are colored dark gray, derived SNPs with a peak height under 50 light gray. Ancestral SNPs that had a peak height lower than 50 are marked in bold.

				H12_3636																	H10
				H2_1438	H3_6776	H23_10211	H25_9620	H13_14872	H19_14869	H14_7645	H9_13020/H12	H15_6253	H16_10394	H11_8448	H4_3992	H18_14364	H1_3010	H7_4793			
				derived	a	t	g	a	a	a	a	g	g/a	g/a	t	c	t	t	t	c/t	t
				ancestral	g	c	a	g	g	g	g	a	a	a	c	t	c	c	c	t	a
PCR	Ex	Sample	HG																		
R523.1	RC.4	Ba6-1a	H1	g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	t	a/t	
R527.1	RC.4	Ba6-1a	H1	g	c	a	g	g	g	g	a	g/a	a	c	t	c	c	t	t	a	
R526.2	RD.1	Ba6-1b	H1	g	c	a	g	g	g	g	a	a	a	c/t	t	c	c	t	t	a	
R526.37	SM.2	Ban2b	-	g	c	g	g	-	g	g	a	-	a	c	-	c	c	-	-	-	
R523.47	ST.8	Bar13a	-	g	c	a	g	g	g	g	a	-	a	c	t	c	c	c	t	a	
R526.44	SU.8	Bar13b	-	g	c	a	g	g	g	g	-	-	a	c	t	c	c	c	t	a	
R523.43	SP.18	Bol5a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R526.43	SU.18	Bol5b	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R523.26	SB.17	Cast1a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R526.32	SH.12	Cast1b	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R523.19	RW.3	Cmol105a	-	g	c	a	g	g	g	g	a	-	a	c	t	c	c	c	t	a	
R527.8	Ry.4	Cmol105b	-	g	c	g	g	g	g	g	a	a	a	c	t	c	c	c	t	a	
R523.20	RX.1	Cmol123a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R526.16	RY.7	Cmol123b	H1	g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a	
R523.18	RW.1	Cmol12a	H3	g	c	g	g	g	g	g	a	-	a	c	c	t	c	c	t	a	
R526.14	RY.1	Cmol12b	H3	g	c	g	g	g	g	g	a	-	a	c	t	c	c	c	t	a	
R523.21	RX.3	Cmol139a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R526.17	RY.9	Cmol139b	H1	g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	t	a/t	
R523.9	RQ.14	Cmol44a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R526.6	RR.3	Cmol44b	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R523.28	SC.11	Coca3a	H3	g	c	g	g	g	g	g	a	-	a	c/t	c	t	c	c	t	a	
R526.22	SD.3	Coca3b	H3	g	c	g	g	g	g	g	a	-	a	c	t	c	c	c	t	a	
R523.29	SC.12	Coca4a	-	g	c	a	g	g	g	g	a	-	a	c	t	-	-	c	t	a	
R527.10	SC.12	Coca4a	-	g	c	a	g	g	g	g	a	g/a	a	c	t	c	-	c	t	a	
R526.23	SD.4	Coca4b	-	g	c	a	g	g	g	g	a	a	a	c	t	-	-	c	t	a	
VK518.17	SD.4	Coca4b	-	g	c	a	g	g	g	g	a	a	a	c	t	-	-	c	t	a	
R523.30	SC.13	Coca5a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R526.24	SD.5	Coca5b	H1	g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	t	a	
R526.41	SS.3	Dia3b	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a	
R527.12	SR.3	Dia3a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	-	a	
R523.31	SD.14	Fora1a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	-	a	
R526.29	SG.1	Fora1b	H1	g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a	
R523.32	SD.17	Fora4a	H1	g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	-	
R526.30	SG.4	Fora4b	H1	g	c	a	-	g	g	g	a	-	a	c	t	c	c	t	t	a	

IV Snapshot results

				H9_13020/H12																
				H12_3636	H2_1438	H3_6776	H23_10211	H25_9620	H13_14872	H19_14869	H14_7645	H15_6253	H16_10394	H11_8448	H4_3992	H18_14364	H1_3010	H7_4793	H10	
R523.11	RR.14	Gam1a	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R526.10	RS.9	Gam1b	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R523.12	RR.15	Gam2a	H1	g	c	a	-	g	g/a	g	a	-	a	c/t	-	c	c	t	-	
R527.5	RR.15	Gam2a	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R527.5	RR.15	Gam2a	H1	g	c	a	g	g/a	g	g/a	a	a	a	c	-	c	-	t	a	
R526.7	RS.10	Gam2b	H1	g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	a/t	
VK518.17	RS.10	Gam2b	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R523.39	SM.17	Gam5a	-	g	c	a	g	g	g	a	a	a	c	t	c	c	c	t	a	
R526.40	SQ.12	Gam5b	-	g	c	a	g	g/a	g	g	a	a	a	c	t	c	c	-	a	
VK518.19	SQ.12	Gam5b	-	g	c	a	g	g	g	a	a	a	c	t	c	c	c	t	a	
R523.48	SU.16	Hig2a	H1	g	c	a	g	g	g	a	-	a	c	t	c	c	-	-		
VK518.20	SU.16	Hig2a	H1	-	-	a	-	g	g	g	-	-	a	c	-	-	c	-	a	
R526.46	SV.2	Hig2b	H1	g	c	a	g	g	g	g	-	-	a	c	t	c	c	t	a	
R523.35	SJ.5	Hume19a	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R526.33	SK.3	Hume19b	H1	g	c	a	g	g	g	a	-	a	c	t	c	c	t	t	a	
R523.36	SJ.7	Hume21a	-	g	c	a	g	g	g	a	-	a	c	t	-	-	c	t	a	
R526.34	SK.4	Hume21b	-	g	c	a	g	g	g	g	-	-	a	c	t	t	-	-	a	
R523.34	SJ.10	Hume24a	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R526.35	SK.5	Hume24b	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R523.13	RR.7	Hume2a	H1	g	c	a	g	g	g	a	a	a	c/t	t	c	c	t	t	a/t	
R526.8	RS.2	Hume2b	H1	g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	a/t	
R527.6	RS.2	Hume2b	H1	g	c	a	g	g	g	a	-	a	c	t	c	c	t	t	a	
R523.10	RR.13	Hume8a	H3	g	c	g	g	g	g/a	a	g/a	a	c	t	c	c	-	t	a	
R527.4	RR.13	Hume8a	H3	g	c	g	g	g	g	a	a	a	c	t	c	c	c	t	a	
R526.9	RS.8	Hume8b	H3	g	c	g	g	g	g/a	g	a	a	a	c/t	t	c	c	t	a/t	
R523.8	RP.8	Mina17a	H3	g	c	g	g	g	g	a	a	a	c	t	c	c	c	t	a	
R526.5	RQ.8	Mina17b	H3	g	c	g	g	g	g	a	a	a	c	t	c	c	c	t	a	
R523.3	RJ.4	Mina4a	H1	g	c	a	g	g	g	a	g/a	a	c	t	c	c	t	t	a	
R526.3	RK.4	Mina4b	H1	g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	a	
R523.5	RN.1	Moca1a	H1	g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	a	
R526.25	SD.6	Moca1b	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	t	a	
R523.6	RN.3	Moca3a	H1	g	c	a	g	g	g	a	a	a	c/t	t	c	c	t	-		
R526.26	SD.8	Moca3b	H1	g	c	a	g	g	g	a	-	a	c	-	c/t	c	-	-		
VK518.21	SD.8	Moca3b	-	g	-	a	g	g	g	a	-	a	c	-	c	c	t	-		
R523.7	RN.4	Moca4a	H1	g	-	a	g	-	g	g	-	-	a	c	-	c	c	-	a	
R527.3	RN.4	Moca4a	H1	g	c	a	g	g	g	a	a	a	c	t	c	c	t	-	a	
R526.27	SD.9	Moca4b	H1	g	c	a	g	g	g	a	-	a	c	t	c	c	t	t	a	
R523.22	SV.18	Pai15a2	H3	g	c	g	g	g	g	a	-	a	c	c	t	c	c	t	a	
R526.18	SA.12	Pai15b	H3	g	c	g	g/a	g/a	g	a	-	a	c/t	t	c	c	c	t	a/t	
R527.9	SA.12	Pai15b	H3	g	c	g	g	g	g	a	a	a	c	t	c	c	c	c/t	-	
R523.23	RZ.6	Pai6a	H3	g	c	g	g	-	g	a	-	a	c	-	c	c	c	-	-	

IV Snapshot results

					H12_3636	H2_1438	H3_6776	H23_10211	H25_9620	H13_14872	H19_14869	H14_7645	H9_13020/H12	H15_6253	H16_10394	H11_8448	H4_3992	H18_14364	H1_3010	H7_4793	H10
R526.19	SA.6	Pai6b	-		g	c	-	g	-	g	g	-	a	a	c	-	c	c	-	t	-
R527.16	SA.6	Pai6b	H3		-	-	g	-	g	-	g	-	-	a	-	t	c/t	c	c	t	-
R523.27	SB.6	Par2a	-		g	c	a	g	g	g	g	a	a	a	c	t	c	c	c	t	a
R526.20	SC.2	Par2b	-		g	c	a	g	g	g	g	a	a	a	c	t	c	c	c	t	a
R523.24	SB.11	Par7a	H1		g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a
R526.21	SC.7	Par7b	H1		g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a
R523.2	RG.7	Rein28a	H3		g	c	g	g	g	g/a	g	a	a	a	c/t	c	c	c	c	t	a/t
R527.2	RG.7	Rein28a	H3		g	c	g	g	g	g	g	a	a	a	c	t	c	c	c	c/t	a
R526.1	NA.2	Rein28b	H3		g	c	g	g	g	g/a	g	a	a	a	c/t	t	c	c	c	t	a/t
VK518.22	NA.2	Rein28b	H3		g	c	g	g	g	g	g	a	a	a	c	t	c	c	c	t	-
R523.4	RM.1	Rodi1a	H1		g	c	a	g	g	g/a	g	a	a	a	c/t	t	c	c	t	t	a
R526.4	RO.12	Rodi1b	H1		g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a
R523.46	ST.13	Roy3a	-		g	c	a	g	g	g	g	a	g/a	a	c	t	c	c	c	t	a
R526.47	SV.8	Roy3b	-		g	c	a	g	g	g	g	-	-	a	c	t	c	c	c	t	a
VK518.23	SV.8	Roy3b	-		g	c	a	g	g	g	g	g	a	a	c	t	c	c	c	t	a
R523.14	RT.4	Tar4a	H1		g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a
R526.11	RU.4	Tar4b	H1		g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a
R523.15	RT.5	Tar5a	H1		g	c	a	g	g	g	g	a	g/a	a	c	t	c	c	t	t	a
R526.12	RU.5	Tar5b	H1		g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a
R523.16	RT.6	Tar6a	-		g	c	a	g	g	g	g	a	-	a	c	t	c	c	c	t	-
-	RZ.6	Tar6b	-		g	-	a	g	g	g	g	a	-	a	c/t	-	c	c/t	c	t	a
R526.48	SW.5	Tar6c	-		g	c	a	g	g	g	g	-	-	g/a	c	t	c	c	c	t	-
R523.17	RT.7	Tar7a	H1		g	c	a	g	g	g	g	a	-	a	c/t	t	c	c	t	t	a/t
R526.13	RU.7	Tar7b	H1		g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a
R523.25	SB.16	Tint1a	H1		g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a
R526.31	SH.11	Tint1b	-		g	c	a	g	g	g	g	a	-	a	c	t	c	c	-	t	a
VK521.11	SH.11	Tint1b	H1		g	c	a	g	g	g	g	a	-	a	c	-	c	c	t	t	a
R523.44	SS.11	Troc8a	H1		g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a
R526.42	SU.14	Troc8b	H1		g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a
R523.42	SO.8	Yese13a	H1		g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	t	a
R526.39	SP.8	Yese13b	H1		g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a
VK518.24	SF.7	Yese3b	H1		g	c	a	g	g	g	g	a	a	a	c	t	c	c	t	-	a
R523.33	SE.7	Yese3a	H1		g	c	a	g	g	g	g	a	-	a	c	t	c	c	t	t	a
R523.41	SO.3	Yese8a	H1		g	c	a	g	-	g	g	-	-	-	c	-	c	c	t	t	a

IV.3 T-Plex

Derived SNPs are indicated by a “d” and colored gray and ancestral SNPs by an “a”.

Sample	Extract	T1	T2	Sample	Extract	T1	T2
Bar10a	ST.5	a	d	Bar10b	SU.5	-	d
Bar1a	RL.8	a	d	Bar1b	RM.6	a	d
Fupe10a	RO.10	a	d	Fupe10b	RP.15	a	d
Fupe8a	RO.8	a	d	Fupe8b	RP.13	a	d
Gro5a2a	SW.18	a	d	Gro5b	SG.13	a	d
GSL2a	RZ.2	-	d	GSL2b	SG.7	a	d
Guz2a	SK.14	a	d	Guz2b	SL.15	-	d
Hume3a	RR.8	-	d	Hume3b	RS.3	a	-
Hume5a	RR.10	a	d	Hume5b	RS.5	-	d
Junc6a	RZ.18	a	d	Junc6b	SA.18	a	d
MMI3a	SB.15	a	d	MMI3b	SH.10	a	d
Pai21a	SE.17	a	d	Pai21b	SF.17	-	d
Pove1a	SE.3	a	d	Pove1b	SF.3	a	d
Pove2a	SE.4	a	d	Pove2b	SF.4	a	d
Rein18a	RD.8	a	d	Rein18b	RE.7	a	d
Rein19a	RD.9	a	d	Rein19b	RE.8	a	d
Rein30a	TF.8	-	d	Rein30b	TG.7	-	d
Rein5a	RA.5	a	d	Rein5b	RB.5	a	d
Tar10a	RT.10	a	-	Tar10b	RU.10	a	d
Tar2a	RT.2	a	d	Tar2c	SX.3	a	a
Troc12a	SX.5	-	d	Troc12b	OWG.2	a	d
Troc3a	SO.11	a	d	Troc3b	SP.11	a	a

IV.4 U-Plex

Underlined SNPs in the headline were detected in reverse direction. Derived SNPs are colored dark gray, derived SNPs with a peak height lower than 50 light gray. Ancestral SNPs that had a peak height lower than 50 are marked in bold.

				<u>U3_16343</u>	<u>U4_4646</u>	<u>U5_3197</u>	<u>U5b_14182</u>	<u>U8_9698</u>	<u>U5a_14793</u>	<u>U2_16051</u>
				<u>c</u> t	<u>g</u> a	<u>g</u> a	c t	<u>g</u> a	<u>c</u> t	g a
PCR	Ex	Sample	HG	derived ancestral						
R517.29	SF.2	Alco2a	U4	t	g	a	t	a	t	a
R520.25	SF.2	Alco2b	U4	t	g	a	c	a	t	a
R517.10	RL.4	Arru1a	U5?	t	g/a	g	c	a	c	a
VK428.18	RL.9	Bar2a	U3	c	a	a	t	-	t	-
VK440.25	RM7	Bar2b	U3	c	a	a	t	a	t	a
R517.45	ST.4	Bar9a	U5b	t	a	g	c	-	t	a
R524.7	ST.4	Bar9a	U5b	t	a	g	c	a	c/t	a
R520.42	SU.4	Bar9b	U5b	t	a	g	c	a	t	a
R517.19	RX.2	Cmol138a	U5b	t	a	g	c	a	t	a
R520.16	RY.8	Cmol138b	U5b	t	a	g	c	a	t	a
R517.20	RX.4	Cmol140a	U5b	t	a	g	c		t	a
R520.15	RY.10	Cmol140b	U5b	t	a	g	c	a	t	a
VK428.19	RQ.16	Cmol151a	U4?	t	g/a	-	t	a	t	-
VK440.26	RR5	Cmol151b	U4	t	g	a	t	a	t	a
R517.21	RY.8	Fala5a	U5b	t	a	g	c	-	t	a
R520.29	SI.6	Fala5b	U5b	t	a	g	c	a	c/t	a
R517.11	RN.13	Fupe5a	U5b	t	a	g	c	a	t	a
R520.10	RO.5	Fupe5b	U5b	t	a	g	c	a	t	a
R517.12	RO.6	Fupe6a	U5b	t	a	g	c	a	t	a
R520.11	RP.11	Fupe6b	U5b	t	a	g	c	a	t	a
R517.37	SM.16	Gam4a	U5b	t	a	g	c	a	-	a
R520.40	SQ.11	Gam4b	U5b	t	a	g	c	a	t	a
R517.40	SN.9	Gam7a	U5b	t	a	g	c	a	t	a
R520.41	SQ.14	Gam7b	U5b	t	a	g	c	a	t	a
R517.17	RX.13	Gro3a	U5b	t	a	g	c	a	t	a
R520.27	SG.11	Gro3a	U5b	t	a	g	c	a	t	a
R517.33	SK.16	Guz4a	U4	t	a	a	t	a	c	a
R524.4	SL.17	Guz4b	U4	c/t	a	a	t	-	t	a
R517.30	SH.14	Hume10a	U5b	t	a	g	c	a	t	a
R520.28	SI.10	Hume10b	U5b	t	a	g	c	a	c/t	a
R517.14	RR.6	Hume1a	U5b	t	a	g	c	a	t	a
R520.13	RS.1	Hume1b	U5b	t	a	g	c	a	t	a

IV Snapshot results

				<u>U3_16343</u>	<u>U4_4646</u>	<u>U5_3197</u>	<u>U5b_14182</u>	<u>U8_9698</u>	<u>U5a_14793</u>	<u>U2_16051</u>
R517.31	SJ.11	Hume25a	U*	t	a	a	t	a	t	a
R520.31	SK.6	Hume25b	U*	t	a	a	t	a	t	a
R517.32	SJ.12	Hume26a	U5b	t	a	g	c	-	-	a
R517.18	RX.16	Hund1a	U5a	t	g/a	g	t	a	c	a
R520.19	SB.3	Hund1b	U5a	t	g/a	g	t	a	c	a
R517.35	SM.13	Junc13a	U/U4	t	g/a	a	t	a	t	a
R524.5	SM.13	Junc13a	U5a	t	a	g	t	-	c	a
R520.35	SN.7	Junc13b	U5a	t	g/a	g	t	a	c	a
R517.22	RZ.14	Junc2a	U5a	t	a	g	t	a	c	a
R520.17	SA.14	Junc2b	U5a	t	a	g	t	a	c	a
R517.38	SM.9	Junc8a	U5b	t	a	g	c	-	-	a
R520.33	SN.2	Junc8b	U5b	t	a	g	c	a	c/t	a
R517.34	SM.10	Junc9a	U5b	t	a	g	c	a	t	a
R520.34	SN.3	Junc9b	U5b	t	a	g	c	a	t	a
VK428.23	RP.5	Mina14a	U5b	t	a	g	c	a	t	-
VK440.30	RQ5	Mina14b	U5b	t	a	g	c	a	t	a
R524.3	RP.9	Mina18a	U5b	t	a	g	c	a	t	a
R520.12	RQ.9	Mina18b	U5b	t	a	g	c	a	t	a
VK428.21	RJ.1	Mina1a	U3	c	a	a	t	a	t	-
VK440.28	RK1	Mina1b	U3	c	a	a	t	a	t	a
VK428.22	RJ.5	Mina5a	U2	t	-	a	t	a	t	g
VK440.29	RK5	Mina5b	U2	t	a	a	t	a	t	g
R517.8	RJ.9	Mina9a	U5b	t	a	g	c	a	t	a
R520.8	RK.9	Mina9b	U5b	t	a	g	c	a	t	a
R517.39	SN.12	MIV2a	U5b	t	a	g	c	a	t	a
R524.8	SO.2	MIV2b	U5b	t	a	g	c	a	t	a
R517.26	SE.12	Pai16a	U5b	t	a	g	c	a	t	a
R520.22	SF.12	Pai16b	U5b	t	a	g	c	a	t	a
R517.27	SE.13	Pai17a	U5a/U5b	t	a	g	c	a	t/c	a
R520.23	SF.13	Pai17b	U5a/U5b	t	a	g	c	a	c/t	a
R517.28	SE.14	Pai18a	U5b	t	a	g	c	a	t	a
R520.24	SF.14	Pai18b	U5b	t	a	g	c	a	t	a
VK455.7	RZ.7	Pai7a	U5b	t	a	g	c	a	c/t	a
R517.23	RZ.7	Pai7a	U5b/U5a	t	a	g	c	a	c/t	a
R520.18	SA.7	Pai7b	U5b	t	a	g	c	a	t	a
R517.24	SB.7	Par3a	U5b	t	a	g	c	a	t	a
R520.20	SC.3	Par3b	U5b	t	a	g	c	a	t	a
R517.5	RD.5	Rein15a	U5b	t	a	g	c	a	t	a
R520.5	RE.4	Rein15b	U5a/U5b	t	a	g	c	a	c/t	a
R524.1	RE.4	Rein15b	U5b	t	a	g	c	a	t	a
R517.1	RA.1	Rein1a	U5b	t	a	g	c	-	t	a
R520.1	RB.1	Rein1b	U5b	t	a	g	c	a	t	a

IV Snapshot results

				<u>U3_16343</u>	<u>U4_4646</u>	<u>U5_3197</u>	<u>U5b_14182</u>	<u>U8_9698</u>	<u>U5a_14793</u>	<u>U2_16051</u>
R517.6	RE.10	Rein22a	U5b	t	a	g	c	a	t	a
R520.6	RF.7	Rein22b	U5b	t	a	g	c	a	t	a
R517.7	RE.11	Rein23a	U4	t	g	a	t	a	t	a
R520.7	RF.8	Rein23b	U4	t	g	a	t	a	t	a
R517.2	RA.2	Rein2a	U5b	t	a	g	c	-	c/t	a
R520.2	RB.2	Rein2b	U5b	t	a	g	c	a	t	a
VK428.24	RH.1	Rein31a	U5b	t	a	g	c	a	t	-
VK440.31	RI6	Rein31b	U5b	t	a	g	c	a	t	a
R517.3	RA.3	Rein3a	U5b	t	a	g	c	a	t	a
R520.3	RB.3	Rein3b	U5b	t	a	g	c	a	t	a
R517.4	RA.4	Rein4a	U5b	t	a	g	c	-	t	a
R520.4	RB.4	Rein4b	U5b	t	a	g	c	a	t	a
R517.44	ST.12	Roy2a	U5b	t	a	g	c	a	t	a
R520.44	SV.7	Roy2b	U5b	t	a	g	c	a	t	a
R517.9	RL.3	Seba1a	U5/U5b	t	a	g	c/t	-	t	a
R520.30	SJ.15	Seba1b	U5b	t	a	g	c	a	t	a
VK428.20	SS.9	Troc6a	U3	c	a	a	t	a	t	
R517.43	SS.9	Troc6a	U3?	c/t	a	a	t	a	t	a
VK440.27	SV1	Troc6b	U3	c	a	a	t	a	t	a
R520.43	SV.1	Troc6b2	U3	c	a	a	t	a	t	a
R517.15	RS.12	Vald1a	U5b	t	a	g	c	a	t	a
R520.14	RU.12	Vald1b	U5b	t	a	g	c	a	t	a
R517.41	SO.5	Yese10a	U5b	t	a	g	c	a	t	a
R520.38	SP.5	Yese10b	U5b	t	a	g	c	a	t	a
R517.42	SO.7	Yese12a	U5b	t	a	g	c	a	t	a
R520.39	SP.7	Yese12b	U5a/U5b	t	a	g	c	a	c/t	a
R524.6	SP.7	Yese12b	U5b	t	a	g	c	a	t	a
R517.16	SE.6	Yese2a	U5b	t	a	g	c	a	t	a
R520.26	SF.6	Yese2b	U5b	t	a	g	c	a	t	a
R517.25	SE.10	Yese6a	U5b	t	a	g	c	a	t	a
R520.21	SF.10	Yese6b	U5b	t	a	g	c	a	t	a

V Haplogroup frequencies of groups used for statistical analyses

	C	F	I ⁵	I ⁷	L	M	N	O ^{1b}	O ²	O ^{3a}	R	T ¹	T ²	U	U ²	U ³	U ⁴	U ^{5a}	U ^{5b}	U ⁸	V	W	X	Y
HGE	20	7	0	0	0	0	0	0	0	0	0	0	0	7	20	0	27	20	0	0	0	0	0	14
HGC	0	0	0	0	0	0	0	0	0	0	0	0	0	12	12	0	8	32	32	4	0	0	0	24
HGW	0	36	0	0	0	0	0	0	14	0	0	0	0	0	0	0	7	0	43	0	0	0	0	14
LBK	0	15	2	5	0	12	20	0	0	12	0	0	23	0	0	1	0	2	1	0	5	3	1	109
RSC	0	27	9	9	0	0	9	0	0	9	0	0	18	0	0	0	0	0	0	0	9	0	9	11
SCG	0	15	0	3	0	15	30	0	0	3	0	0	12	0	0	0	0	0	6	3	0	9	3	33
BAC	0	26	0	5	0	5	11	0	0	5	0	5	21	0	0	0	0	0	5	5	0	0	11	19
SALZ	0	14	17	3	0	21	10	0	0	7	0	0	7	0	0	10	0	0	3	0	3	0	3	29
BEC	0	18	6	0	0	0	18	0	0	0	0	0	12	0	0	0	0	12	18	0	6	6	6	17
BLA	0	19	19	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	56	0	0	0	0	16
CWC	0	20	2	2	2	9	14	0	0	0	0	7	11	0	2	0	7	9	5	0	0	2	7	44
BBC	0	31	9	0	3	3	6	0	0	0	0	6	6	0	3	0	6	14	6	0	0	9	0	35
UC	0	18	4	2	13	6	7	0	0	0	1	2	6	1	6	0	1	13	2	3	3	4	5	94
FBC	0	10	0	0	0	20	10	0	0	0	0	0	30	0	0	0	0	10	20	0	0	0	0	10
PWC	0	0	0	11	0	0	5	0	0	0	0	0	5	0	0	0	42	16	16	0	5	0	0	19
TRE	0	21	0	7	0	21	7	0	0	0	0	0	7	3	0	0	0	3	14	0	3	0	14	29
NEE	0	17	0	0	0	0	33	0	17	0	0	0	17	0	0	0	0	0	8	0	0	0	8	12
TROCE	0	0	0	0	0	14	29	0	0	14	0	0	29	0	0	0	0	0	0	0	14	0	0	7
NSE	0	52	0	4	4	4	8	0	0	0	0	0	0	20	0	0	0	0	4	0	0	0	4	25
CPE	0	67	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	11	0	11	0	0	9
NEN	0	31	0	0	8	15	8	0	8	0	0	0	15	0	0	0	8	0	0	0	0	8	0	13
AVN	0	27	0	5	0	14	23	0	0	0	0	0	5	0	5	5	0	0	14	0	0	0	5	22
EVN	0	45	0	0	0	0	0	0	0	0	0	0	0	27	0	0	0	0	18	0	0	0	9	11
NMN	0	3	0	3	0	5	27	0	0	0	0	0	16	0	0	0	3	0	24	0	5	0	14	37
CPN	0	17	0	0	0	8	42	0	0	0	0	0	8	0	0	0	8	8	8	0	0	0	0	12
NEC	0	7	0	13	0	27	27	0	0	0	0	0	13	0	0	7	0	0	7	0	0	0	0	15
SMC	0	35	0	0	0	28	6	0	0	0	0	0	6	0	0	0	0	0	22	0	0	0	0	17
SIC	0	50	0	17	0	17	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
CPC	0	20	0	0	0	7	40	0	0	0	0	0	7	0	0	0	0	0	20	0	7	0	0	15
ESC	0	34	0	3	0	16	22	0	0	0	0	0	0	0	0	0	6	0	9	0	6	0	3	32
NMCB	0	14	0	0	0	0	57	0	0	0	0	0	0	0	0	0	0	14	14	0	0	0	0	7
SMCB	0	8	0	0	0	9	39	4	0	0	0	0	9	0	0	0	0	9	22	0	4	0	0	24
NEB	0	19	0	0	0	25	19	0	0	0	0	0	0	6	0	0	0	0	19	0	6	0	6	16
ESBA	0	50	0	0	0	25	13	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	10

VI p-values of F_{st} calculations

VI.1 p-values Iberian dataset without additional haplogroup information

	HGW	NEE	TROCE	NSE	CPE	NEN	AVN	EVN	NSN	CPN	NEC	ESC	SMC	SMCB	NMCB
HGW	*	0.04297 +- 0.0020	0.00366 +- 0.0006	0.00000 +- 0.0000	0.06613 +- 0.0027	0.02257 +- 0.0015	0.02287 +- 0.0014	0.10791 +- 0.0027	0.00396 +- 0.0006	0.07504 +- 0.0022	0.00030 +- 0.0002	0.00129 +- 0.0004	0.15147 +- 0.0035	0.01980 +- 0.0012	0.03237 +- 0.0016
NEE	0.04297 +- 0.0020	*	0.41709 +- 0.0045	0.02911 +- 0.0019	0.07781 +- 0.0030	0.81764 +- 0.0042	0.59717 +- 0.0043	0.08306 +- 0.0028	0.69953 +- 0.0044	0.66231 +- 0.0047	0.36323 +- 0.0050	0.12731 +- 0.0030	0.36066 +- 0.0052	0.25968 +- 0.0045	0.30789 +- 0.0049
TROCE	0.00366 +- 0.0006	0.41709 +- 0.0045	*	0.01010 +- 0.0010	0.00267 +- 0.0005	0.70874 +- 0.0045	0.29829 +- 0.0043	0.00535 +- 0.0008	0.32373 +- 0.0050	0.59558 +- 0.0052	0.65192 +- 0.0047	0.16107 +- 0.0038	0.13870 +- 0.0036	0.22800 +- 0.0046	0.14365 +- 0.0039
NSE	0.00000 +- 0.0000	0.02911 +- 0.0019	0.01010 +- 0.0010	*	0.01752 +- 0.0013	0.02693 +- 0.0016	0.21542 +- 0.0045	0.45837 +- 0.0048	0.00475 +- 0.0007	0.50282 +- 0.0049	0.01485 +- 0.0012	0.21087 +- 0.0040	0.07316 +- 0.0028	0.00040 +- 0.0002	0.00743 +- 0.0009
CPE	0.06613 +- 0.0027	0.07781 +- 0.0030	0.00267 +- 0.0005	0.01752 +- 0.0013	*	0.06663 +- 0.0024	0.08851 +- 0.0028	0.07791 +- 0.0027	0.01544 +- 0.0011	0.01634 +- 0.0012	0.02069 +- 0.0013	0.07524 +- 0.0024	0.04000 +- 0.0019	0.01089 +- 0.0009	0.00416 +- 0.0006
NEN	0.02257 +- 0.0015	0.81764 +- 0.0042	0.70874 +- 0.0045	0.02693 +- 0.0016	0.06663 +- 0.0024	*	0.59776 +- 0.0050	0.10128 +- 0.0029	0.21612 +- 0.0047	0.61934 +- 0.0050	0.61707 +- 0.0054	0.07544 +- 0.0024	0.38957 +- 0.0057	0.18533 +- 0.0033	0.06148 +- 0.0023
AVN	0.02287 +- 0.0014	0.59717 +- 0.0043	0.29829 +- 0.0045	0.01752 +- 0.0045	0.08851 +- 0.0028	0.59776 +- 0.0050	*	0.44887 +- 0.0048	0.48629 +- 0.0048	0.97802 +- 0.0016	0.61855 +- 0.0049	0.87071 +- 0.0035	0.83823 +- 0.0035	0.28839 +- 0.0048	0.30641 +- 0.0047
EVN	0.10791 +- 0.0027	0.08306 +- 0.0028	0.00535 +- 0.0008	0.45837 +- 0.0048	0.07791 +- 0.0027	0.10128 +- 0.0029	0.44887 +- 0.0048	*	0.12870 +- 0.0030	0.16018 +- 0.0038	0.04722 +- 0.0023	0.34007 +- 0.0051	0.71825 +- 0.0039	0.06732 +- 0.0023	0.01198 +- 0.0011
NSN	0.00396 +- 0.0006	0.69953 +- 0.0044	0.32373 +- 0.0050	0.00475 +- 0.0007	0.01544 +- 0.0011	0.21612 +- 0.0047	0.48629 +- 0.0048	0.12870 +- 0.0030	*	0.78260 +- 0.0043	0.45461 +- 0.0052	0.07732 +- 0.0024	0.50351 +- 0.0050	0.43075 +- 0.0048	0.25255 +- 0.0043
CPN	0.07504 +- 0.0022	0.66231 +- 0.0047	0.59558 +- 0.0052	0.50282 +- 0.0049	0.01634 +- 0.0012	0.61934 +- 0.0050	0.97802 +- 0.0016	0.16018 +- 0.0038	0.78260 +- 0.0043	*	0.73755 +- 0.0043	0.89922 +- 0.0028	0.64202 +- 0.0056	0.78081 +- 0.0043	0.69973 +- 0.0046
NEC	0.00030 +- 0.0002	0.36323 +- 0.0050	0.65192 +- 0.0047	0.01485 +- 0.0012	0.02069 +- 0.0013	0.61707 +- 0.0054	0.61855 +- 0.0049	0.04722 +- 0.0023	0.45461 +- 0.0052	0.73755 +- 0.0043	*	0.40699 +- 0.0050	0.31561 +- 0.0041	0.21384 +- 0.0040	0.08425 +- 0.0024
ESC	0.00129 +- 0.0004	0.12731 +- 0.0030	0.16107 +- 0.0038	0.21087 +- 0.0040	0.07524 +- 0.0024	0.07544 +- 0.0024	0.87071 +- 0.0035	0.34007 +- 0.0051	0.07732 +- 0.0024	0.89922 +- 0.0028	0.40699 +- 0.0050	*	0.33343 +- 0.0044	0.03000 +- 0.0017	0.10514 +- 0.0030
SMC	0.15147 +- 0.0035	0.36066 +- 0.0052	0.13870 +- 0.0036	0.07316 +- 0.0028	0.04000 +- 0.0019	0.38957 +- 0.0057	0.83823 +- 0.0035	0.71825 +- 0.0039	0.50351 +- 0.0050	0.64202 +- 0.0056	0.31561 +- 0.0041	0.33343 +- 0.0044	*	0.60529 +- 0.0050	0.07385 +- 0.0027
SMCB	0.01980 +- 0.0012	0.25968 +- 0.0045	0.22800 +- 0.0046	0.00040 +- 0.0002	0.01089 +- 0.0009	0.18533 +- 0.0033	0.28839 +- 0.0048	0.06732 +- 0.0023	0.43075 +- 0.0048	0.78081 +- 0.0043	0.21384 +- 0.0040	0.03000 +- 0.0017	0.60529 +- 0.0050	*	0.43966 +- 0.0053
NMCB	0.03237 +- 0.0016	0.30789 +- 0.0049	0.14365 +- 0.0039	0.00743 +- 0.0009	0.00416 +- 0.0006	0.06148 +- 0.0023	0.30641 +- 0.0047	0.01198 +- 0.0011	0.25255 +- 0.0043	0.69973 +- 0.0046	0.08425 +- 0.0024	0.10514 +- 0.0030	0.07385 +- 0.0027	0.43966 +- 0.0053	*

VI.2 p-values Iberian dataset with additional haplogroup information

	HGW	NEE	TROCE	NSE	CPE	NEN	AVN	EVN	NSN	CPN	NEC	ESC	SMC	SMCB	NMCB
HGW	*	0.0877 1+ 0.0023	0.0109 9+ 0.0010	0.0524 7+ 0.0021	0.1110 8+ 0.0035	0.0988 0+ 0.0031	0.1446 4+ 0.0033	0.4753 0+ 0.0050	0.0017 8+ 0.0004	0.3052 2+ 0.0042	0.0072 3+ 0.0008	0.0495 0+ 0.0020	0.3697 7+ 0.0036	0.0143 6+ 0.0012	0.0312 8+ 0.0018
NEE	0.0877 1+ 0.0023	*	0.5848 9+ 0.0050	0.0203 0+ 0.0013	0.0133 7+ 0.0011	0.5897 4+ 0.0056	0.6012 3+ 0.0049	0.1182 1+ 0.0034	0.8601 3+ 0.0047	0.7223 0+ 0.0043	0.5240 1+ 0.0051	0.1696 9+ 0.0035	0.1734 5+ 0.0039	0.3848 1+ 0.0047	0.2961 1+ 0.0043
TROCE	0.0109 9+ 0.0010	0.5848 9+ 0.0050	*	0.0072 3+ 0.0009	0.0019 8+ 0.0004	0.6240 0+ 0.0050	0.2426 5+ 0.0040	0.0175 2+ 0.0013	0.3704 6+ 0.0043	0.5103 5+ 0.0046	0.6751 8+ 0.0048	0.1145 4+ 0.0033	0.0570 2+ 0.0021	0.3120 5+ 0.0047	0.1156 3+ 0.0030
NSE	0.0524 7+ 0.0021	0.0203 0+ 0.0013	0.0072 3+ 0.0009	*	0.2254 2+ 0.0041	0.0810 8+ 0.0025	0.1094 9+ 0.0031	0.7184 4+ 0.0051	0.0000 0+ 0.0000	0.4028 3+ 0.0007	0.0072 3+ 0.0007	0.1802 8+ 0.0039	0.5170 8+ 0.0051	0.0001 0+ 0.0001	0.0080 2+ 0.0009
CPE	0.1110 8+ 0.0035	0.0133 7+ 0.0011	0.0019 8+ 0.0004	0.02254 2+ 0.0041	*	0.0550 4+ 0.0022	0.0361 4+ 0.0019	0.2037 4+ 0.0043	0.0000 0+ 0.0000	0.0954 4+ 0.0031	0.0030 7+ 0.0005	0.0587 1+ 0.0023	0.2193 8+ 0.0042	0.0001 0+ 0.0001	0.0058 4+ 0.0008
NEN	0.0988 0+ 0.0031	0.5897 4+ 0.0056	0.6240 0+ 0.0050	0.0019 8+ 0.0025	0.0810 4+ 0.0022	*	0.3101 7+ 0.0051	0.2540 3+ 0.0037	0.0210 2+ 0.0014	0.6906 2+ 0.0049	0.4038 2+ 0.0050	0.1332 5+ 0.0035	0.3696 7+ 0.0048	0.0310 9+ 0.0015	0.0237 6+ 0.0015
AVN	0.1446 4+ 0.0033	0.6012 3+ 0.0049	0.2426 5+ 0.0040	0.1094 9+ 0.0031	0.0361 4+ 0.0019	0.3101 7+ 0.0051	*	0.5418 4+ 0.0049	0.1541 8+ 0.0033	0.9919 4+ 0.0009	0.6393 4+ 0.0049	0.9282 2+ 0.0026	0.6022 2+ 0.0047	0.1803 8+ 0.0041	0.2208 7+ 0.0037
EVN	0.4753 0+ 0.0050	0.1182 1+ 0.0034	0.0175 2+ 0.0013	0.07184 4+ 0.0051	0.2037 3+ 0.0043	0.2540 3+ 0.0037	0.5418 4+ 0.0049	*	0.0149 5+ 0.0011	0.4327 3+ 0.0060	0.0561 3+ 0.0024	0.5241 1+ 0.0044	0.9047 6+ 0.0025	0.0172 3+ 0.0014	0.0337 6+ 0.0019
NSN	0.0017 8+ 0.0004	0.6601 3+ 0.0047	0.3704 6+ 0.0043	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0210 9+ 0.0014	0.1541 4+ 0.0033	0.0149 5+ 0.0011	*	0.5205 4+ 0.0046	0.4523 3+ 0.0049	0.0061 4+ 0.0007	0.0161 4+ 0.0012	0.5553 9+ 0.0051	0.1729 5+ 0.0038
CPN	0.3052 2+ 0.0042	0.7223 0+ 0.0043	0.5103 5+ 0.0046	0.4028 3+ 0.0047	0.0954 4+ 0.0031	0.6906 2+ 0.0049	0.9919 8+ 0.0009	0.4327 3+ 0.0060	0.5205 4+ 0.0046	*	0.7248 8+ 0.0044	0.9734 7+ 0.0018	0.6508 3+ 0.0044	0.6630 4+ 0.0046	0.5401 0+ 0.0049
NEC	0.0072 3+ 0.0008	0.5240 1+ 0.0051	0.6751 8+ 0.0048	0.0072 3+ 0.0007	0.0030 7+ 0.0005	0.0438 2+ 0.0050	0.6393 4+ 0.0049	0.0561 3+ 0.0024	0.4523 8+ 0.0049	0.7248 8+ 0.0044	*	0.2826 5+ 0.0043	0.1152 4+ 0.0033	0.3146 2+ 0.0040	0.0946 4+ 0.0030

VI p-values of Fst calculations

ESC	0.0495 0+ 0.0020	0.1696 9+ 0.0035	0.1145 4+ 0.0033	0.1802 8+ 0.0039	0.0587 1+ 0.0023	0.1332 5+ 0.0035	0.9282 2+ 0.0026	0.5241 1+ 0.0044	0.0061 4+ 0.0007	0.9734 7+ 0.0018	0.2826 5+ 0.0043	*	0.4817 3+ 0.0049	0.0162 4+ 0.0013	0.0793 0+ 0.0025
SMC	0.3697 7+ 0.0036	0.1734 5+ 0.0039	0.0570 2+ 0.0021	0.5170 8+ 0.0051	0.2193 8+ 0.0042	0.3696 7+ 0.0048	0.6022 2+ 0.0047	0.9047 6+ 0.0025	0.0161 4+ 0.0012	0.6508 3+ 0.0044	0.1152 4+ 0.0033	0.4817 3+ 0.0049	*	0.0516 8+ 0.0022	0.0403 9+ 0.0018
SMC B	0.0143 6+ 0.0012	0.3848 1+ 0.0047	0.3120 5+ 0.0047	0.0001 0+ 0.0001	0.0001 0+ 0.0001	0.0310 9+ 0.0015	0.1803 8+ 0.0041	0.0172 3+ 0.0014	0.5553 9+ 0.0051	0.6630 0+ 0.0046	0.3146 2+ 0.0040	0.0162 4+ 0.0013	0.0516 8+ 0.0022	*	0.4746 1+ 0.0055
NMC B	0.0312 8+ 0.0018	0.2961 1+ 0.0043	0.1156 3+ 0.0030	0.0080 2+ 0.0009	0.0058 4+ 0.0008	0.0237 6+ 0.0015	0.2208 7+ 0.0037	0.0337 6+ 0.0019	0.1729 5+ 0.0038	0.5401 4+ 0.0049	0.0946 4+ 0.0030	0.0793 0+ 0.0025	0.0403 9+ 0.0018	0.4746 1+ 0.0055	*

VI.3 p-values Eurasian dataset without additional haplogroup information

	HGW	NEE	TRO CE	NSE	CPE	NEN	AVN	EVN	NMN	CPN	TRE	NEC	ESC	SMC	SMC B	NMC B
HGW	*	0.0209 9+ 0.0014	0.0034 7+ 0.0006	0.0001 0+ 0.0001	0.1227 6+ 0.0029	0.0111 9+ 0.0010	0.0330 7+ 0.0018	0.1967 1+ 0.0043	0.0067 3+ 0.0008	0.0761 3+ 0.0025	0.0088 1+ 0.0009	0.0000 0+ 0.0000	0.0016 8+ 0.0004	0.1636 5+ 0.0037	0.0320 8+ 0.0019	0.0378 2+ 0.0018
HGE	0.5057 9+ 0.0052	0.0352 4+ 0.0018	0.0351 5+ 0.0018	0.0004 0+ 0.0002	0.2289 9+ 0.0044	0.0020 8+ 0.0005	0.0162 4+ 0.0012	0.2644 3+ 0.0041	0.0018 8+ 0.0004	0.1991 9+ 0.0042	0.0088 1+ 0.0010	0.0088 9+ 0.0003	0.0019 8+ 0.0005	0.0982 1+ 0.0030	0.0111 9+ 0.0009	0.0479 2+ 0.0020
HGC	0.0311 9+ 0.0019	0.0000 0+ 0.0000	0.0001 0+ 0.0001	0.0000 0+ 0.0000	0.0028 7+ 0.0005	0.0000 0+ 0.0000	0.0000 5+ 0.0000	0.0000 0+ 0.0000	0.0049 5+ 0.0009	0.0000 3+ 0.0000	0.0074 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0061 9+ 0.0004	0.0009 6+ 0.0006
LBK	0.0009 9+ 0.0003	0.1793 9+ 0.0039	0.8403 1+ 0.0032	0.0153 5+ 0.0012	0.0986 0+ 0.0031	0.2318 6+ 0.0046	0.0462 3+ 0.0022	0.1533 5+ 0.0034	0.0150 2+ 0.0012	0.6016 5+ 0.0052	0.0277 2+ 0.0016	0.2527 5+ 0.0046	0.0124 7+ 0.0011	0.1866 2+ 0.0032	0.0245 5+ 0.0014	0.0502 9+ 0.0022
RSC	0.0299 0+ 0.0016	0.2817 5+ 0.0037	0.7281 5+ 0.0047	0.0580 1+ 0.0024	0.5340 1+ 0.0052	0.3155 1+ 0.0046	0.3019 5+ 0.0046	0.6143 0+ 0.0052	0.2262 2+ 0.0046	0.4962 9+ 0.0049	0.5539 1+ 0.0046	0.2854 2+ 0.0045	0.1209 8+ 0.0029	0.5218 3+ 0.0054	0.0955 4+ 0.0028	0.0292 1+ 0.0016
SCG	0.0006 9+ 0.0003	0.6650 8+ 0.0046	0.7522 0+ 0.0046	0.1050 4+ 0.0033	0.0794 0+ 0.0029	0.5347 0+ 0.0052	0.7911 1+ 0.0043	0.3201 7+ 0.0049	0.7054 7+ 0.0047	0.9497 1+ 0.0025	0.2259 2+ 0.0039	0.7156 7+ 0.0042	0.3855 1+ 0.0047	0.3973 9+ 0.0044	0.1470 2+ 0.0036	0.2040 4+ 0.0037
BAC	0.0201 0+ 0.0015	0.4471 8+ 0.0048	0.8623 9+ 0.0034	0.0583 1+ 0.0024	0.2560 1+ 0.0045	0.6275 6+ 0.0040	0.4346 1+ 0.0049	0.6531 0+ 0.0046	0.3198 7+ 0.0045	0.7638 8+ 0.0044	0.3922 4+ 0.0047	0.4608 5+ 0.0055	0.1074 2+ 0.0032	0.6682 5+ 0.0044	0.1121 7+ 0.0027	0.0629 6+ 0.0026
SALZ	0.0000 0+ 0.0000	0.1366 2+ 0.0034	0.4597 6+ 0.0051	0.0272 3+ 0.0015	0.1688 0+ 0.0035	0.5381 6+ 0.0053	0.1195 9+ 0.0032	0.2545 3+ 0.0049	0.0220 8+ 0.0016	0.5790 5+ 0.0051	0.2553 2+ 0.0042	0.3710 5+ 0.0048	0.0375 2+ 0.0017	0.3736 3+ 0.0046	0.0212 9+ 0.0014	0.0309 9+ 0.0019
BEC	0.1490 0+ 0.0037	0.2744 3+ 0.0040	0.2994 8+ 0.0043	0.0640 5+ 0.0027	0.3342 2+ 0.0046	0.2118 6+ 0.0042	0.6246 9+ 0.0046	0.8679 3+ 0.0034	0.6242 0+ 0.0048	0.8826 8+ 0.0034	0.3983 8+ 0.0051	0.1739 4+ 0.0035	0.1827 5+ 0.0036	0.9688 1+ 0.0016	0.7775 5+ 0.0043	0.2980 9+ 0.0046
CWC	0.0409 9+ 0.0018	0.1432 5+ 0.0034	0.3781 8+ 0.0050	0.0346 5+ 0.0018	0.3561 0+ 0.0049	0.2387 9+ 0.0047	0.4050 1+ 0.0049	0.1753 3+ 0.0038	0.7791 3+ 0.0041	0.1753 7+ 0.0038	0.6683 5+ 0.0044	0.2162 2+ 0.0040	0.1021 7+ 0.0032	0.8794 2+ 0.0034	0.1025 8+ 0.0030	0.0412 8+ 0.0020
BBC	0.0185 1+ 0.0012	0.0187 1+ 0.0014	0.1341 5+ 0.0033	0.0237 6+ 0.0014	0.3277 9+ 0.0048	0.0789 0+ 0.0026	0.0486 1+ 0.0021	0.9258 5+ 0.0023	0.0132 7+ 0.0011	0.5892 5+ 0.0044	0.2125 5+ 0.0042	0.0074 3+ 0.0009	0.0065 3+ 0.0008	0.8159 6+ 0.0040	0.0166 3+ 0.0013	0.0187 1+ 0.0014
UC	0.0335 6+ 0.0017	0.0567 3+ 0.0025	0.1647 4+ 0.0037	0.1346 4+ 0.0032	0.2982 9+ 0.0046	0.0927 6+ 0.0027	0.0774 2+ 0.0024	0.8843 7+ 0.0029	0.0027 7+ 0.0005	0.8199 2+ 0.0038	0.1673 1+ 0.0033	0.0092 1+ 0.0009	0.0024 8+ 0.0005	0.6559 7+ 0.0044	0.0041 6+ 0.0006	0.0301 0+ 0.0014
FBC	0.0065 3+ 0.0009	0.1518 7+ 0.0034	0.4297 6+ 0.0049	0.0011 9+ 0.0003	0.0164 3+ 0.0014	0.4030 0+ 0.0046	0.2175 0+ 0.0035	0.0599 0+ 0.0023	0.2283 9+ 0.0042	0.4749 0+ 0.0050	0.2588 9+ 0.0038	0.6140 0+ 0.0047	0.0638 6+ 0.0025	0.3395 7+ 0.0050	0.4974 8+ 0.0050	0.0575 2+ 0.0022
PWC	0.0217 8+ 0.0013	0.0206 9+ 0.0016	0.0067 3+ 0.0007	0.0001 0+ 0.0001	0.0179 2+ 0.0012	0.0037 6+ 0.0006	0.0215 8+ 0.0015	0.0092 2+ 0.0032	0.0063 4+ 0.0008	0.2780 9+ 0.0043	0.0007 9+ 0.0003	0.0053 5+ 0.0007	0.0099 0+ 0.0009	0.0412 8+ 0.0020	0.0430 7+ 0.0018	0.0323 7+ 0.0017
BLA	0.1431 5+ 0.0033	0.0050 5+ 0.0007	0.0094 1+ 0.0010	0.0003 0+ 0.0002	0.0079 2+ 0.0008	0.0156 4+ 0.0013	0.0566 3+ 0.0021	0.1084 1+ 0.0033	0.0301 0+ 0.0018	0.1138 5+ 0.0033	0.0196 0+ 0.0012	0.0035 6+ 0.0005	0.0018 8+ 0.0004	0.4779 7+ 0.0047	0.3413 5+ 0.0043	0.0284 1+ 0.0016
NEE	0.0209 9+ 0.0014	*	0.2572 0+ 0.0042	0.0615 8+ 0.0024	0.1553 3+ 0.0033	0.0521 8+ 0.0049	0.0076 7+ 0.0048	0.2341 4+ 0.0037	0.4535 2+ 0.0043	0.7734 9+ 0.0040	0.1320 7+ 0.0035	0.4057 0+ 0.0051	0.2627 5+ 0.0048	0.2301 8+ 0.0038	0.1567 2+ 0.0039	0.3252 2+ 0.0045
TRO CE	0.0034 7+ 0.0006	0.2572 0+ 0.0042	*	0.0239 6+ 0.0017	0.0137 6+ 0.0013	0.7022 1+ 0.0043	0.3252 2+ 0.0046	0.0301 0+ 0.0015	0.3218 5+ 0.0050	0.6579 5+ 0.0045	0.2793 8+ 0.0041	0.6106 3+ 0.0050	0.2062 2+ 0.0044	0.1912 7+ 0.0044	0.2200 8+ 0.0044	0.0998 9+ 0.0027

VI.4 p-values Eurasian dataset with additional haplogroup information

	HGW	NEE	TRO CE	NSE	CPE	NEN	AVN	EVN	NMN	CPN	TRE	NEC	ESC	SMC	SMC B	NMC B
HGE	0.1176 1+ 0.0029	0.0348 5+ 0.0018	0.0345 5+ 0.0018	0.0001 0+ 0.0001	0.0019 8+ 0.0005	0.0016 8+ 0.0004	0.0100 0+ 0.0010	0.0437 6+ 0.0021	0.0022 8+ 0.0005	0.1019 7+ 0.0029	0.0001 0+ 0.0001	0.0020 8+ 0.0005	0.0004 0+ 0.0002	0.0056 4+ 0.0007	0.0127 7+ 0.0011	0.0296 0+ 0.0015
HGC	0.0006 9+ 0.0003	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0005 9+ 0.0002	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0000 0+ 0.0000	0.0005 0+ 0.0002	0.0004 0+ 0.0002
LBK	0.0013 9+ 0.0004	0.1858 2+ 0.0035	0.8773 4+ 0.0034	0.0002 0+ 0.0001	0.0068 3+ 0.0008	0.2715 6+ 0.0046	0.0470 3+ 0.0023	0.0510 8+ 0.0021	0.0038 6+ 0.0006	0.5534 1+ 0.0046	0.0022 8+ 0.0005	0.3073 0+ 0.0005	0.0022 3+ 0.0008	0.0069 1+ 0.0008	0.0687 5+ 0.0022	0.0144 7+ 0.0012
RSC	0.1331 6+ 0.0037	0.1478 1+ 0.0039	0.3729 3+ 0.0050	0.1952 3+ 0.0037	0.3487 8+ 0.0047	0.3885 8+ 0.0051	0.2198 4+ 0.0044	0.5404 6+ 0.0046	0.4723 6+ 0.0011	0.1427 3+ 0.0052	0.1139 5+ 0.0038	0.1892 9+ 0.0027	0.0638 8+ 0.0045	0.6848 1+ 0.0045	0.0086 7+ 0.0010	0.0131 1+ 0.0011
SCG	0.0048 5+ 0.0007	0.6609 2+ 0.0046	0.8022 0+ 0.0043	0.0025 7+ 0.0005	0.0016 8+ 0.0044	0.3612 5+ 0.0044	0.0265 7+ 0.0048	0.0791 0+ 0.0028	0.4168 9+ 0.0049	0.9033 2+ 0.0030	0.0276 8+ 0.0038	0.8340 2+ 0.0038	0.1663 8+ 0.0038	0.0964 3+ 0.0029	0.2210 7+ 0.0042	0.1721 6+ 0.0036
BAC	0.0738 5+ 0.0027	0.3688 7+ 0.0049	0.6739 9+ 0.0050	0.0353 4+ 0.0019	0.0433 6+ 0.0019	0.6652 8+ 0.0049	0.4060 0+ 0.0050	0.4219 4+ 0.0051	0.0663 3+ 0.0025	0.7030 0+ 0.0044	0.1799 8+ 0.0039	0.3766 0+ 0.0043	0.1528 6+ 0.0039	0.5053 0+ 0.0054	0.0370 3+ 0.0019	0.0229 7+ 0.0016
SALZ	0.0166 3+ 0.0013	0.0859 3+ 0.0025	0.3022 5+ 0.0042	0.0469 3+ 0.0022	0.0761 3+ 0.0028	0.5468 8+ 0.0047	0.2486 9+ 0.0042	0.3387 8+ 0.0047	0.0012 9+ 0.0003	0.6894 4+ 0.0052	0.0807 8+ 0.0025	0.3219 5+ 0.0049	0.1882 0+ 0.0036	0.5182 7+ 0.0049	0.0048 5+ 0.0007	0.0097 0+ 0.0011

VI p-values of Fst calculations

BEC	0.2857 1+-	0.3796 7+-	0.3664 0+-	0.0353 4+-	0.0335 6+-	0.2282 0+-	0.7740 8+-	0.5859 8+-	0.4190 7+-	0.9179 3+-	0.1179 1+-	0.3062 1+-	0.3201 7+-	0.6120 2+-	0.5714 3+-	0.2395 8+-
	0.0046	0.0052	0.0044	0.0019	0.0017	0.0040	0.0041	0.0052	0.0052	0.0028	0.0029	0.0048	0.0045	0.0051	0.0055	0.0046
CWC	0.1060 3+-	0.2490 8+-	0.4185 7+-	0.0049 5+-	0.0134 6+-	0.2935 0+-	0.5842 7+-	0.3994 8+-	0.0711 6+-	0.8351 5+-	0.2030 1+-	0.3756 2+-	0.1463 3+-	0.4429 3+-	0.0706 9+-	0.0305 9+-
	0.0029	0.0042	0.0051	0.0008	0.0011	0.0045	0.0041	0.0048	0.0022	0.0036	0.0037	0.0049	0.0034	0.0046	0.0024	0.0015
BBC	0.2260 2+-	0.0469 3+-	0.0862 3+-	0.0996 9+-	0.1390 0+-	0.2776 0+-	0.1490 9+-	0.8816 0+-	0.0005 0+-	0.7174 5+-	0.1339 5+-	0.0204 9+-	0.0580 1+-	0.8392 2+-	0.0039 6+-	0.0144 5+-
	0.0044	0.0024	0.0031	0.0031	0.0033	0.0050	0.0038	0.0032	0.0002	0.0046	0.0028	0.0014	0.0024	0.0034	0.0006	0.0012
UC	0.1092 0+-	0.1411 7+-	0.2617 6+-	0.0049 5+-	0.0142 6+-	0.4116 4+-	0.1263 2+-	0.4431 2+-	0.0007 9+-	0.7921 0+-	0.1565 2+-	0.0364 3+-	0.0095 0+-	0.2749 2+-	0.0053 5+-	0.0203 9+-
	0.0032	0.0037	0.0040	0.0007	0.0012	0.0049	0.0034	0.0049	0.0003	0.0039	0.0037	0.0018	0.0009	0.0047	0.0007	0.0016
FBC	0.0177 2+-	0.2443 3+-	0.6087 5+-	0.0022 8+-	0.0021 8+-	0.3960 0+-	0.2631 4+-	0.0427 7+-	0.2823 5+-	0.4845 1+-	0.1455 3+-	0.7092 4+-	0.0647 5+-	0.1235 5+-	0.5370 8+-	0.0488 1+-
	0.0012	0.0045	0.0048	0.0005	0.0005	0.0047	0.0045	0.0021	0.0046	0.0048	0.0035	0.0048	0.0023	0.0028	0.0055	0.0018
PWC	0.0057 4+-	0.0134 6+-	0.0054 5+-	0.0000 0+-	0.0002 0+-	0.0006 9+-	0.0181 2+-	0.0068 3+-	0.0045 5+-	0.1880 0+-	0.0001 0+-	0.0045 5+-	0.0016 8+-	0.0024 8+-	0.0773 2+-	0.0395 0+-
	0.0008	0.0012	0.0008	0.0000	0.0001	0.0003	0.0013	0.0008	0.0007	0.0041	0.0001	0.0008	0.0004	0.0005	0.0026	0.0022
BLA	0.3503 6+-	0.0267 3+-	0.0136 6+-	0.0288 1+-	0.0398 0+-	0.0657 4+-	0.1599 8+-	0.3179 9+-	0.0025 7+-	0.3218 5+-	0.0588 1+-	0.0152 5+-	0.0372 2+-	0.4813 4+-	0.0600 9+-	0.0415 8+-
	0.0048	0.0015	0.0012	0.0017	0.0018	0.0027	0.0035	0.0047	0.0005	0.0045	0.0024	0.0012	0.0021	0.0048	0.0027	0.0018

VII C¹⁴ dates

VI.1 Reinoso

Radion carbon dating was conducted at the Curt-Engelhorn-Zentrum für Archäometrie in Mannheim.

Labor No.	Sample name	sample	C ¹⁴	±	13C	Cal 1 sigma	Cal 2 sigma	C:N	%C	%coll
MAMS14325	Rein 1	Os occipital	4911	25	-20,9	cal BC 3698-3657	calBC3759-3643	3,3	19,6	7,8
MAMS14326	Rein 17	Os parietale	4854	26	-23,4	cal BC 3691-3636	calBC3697-3540	3,3	22,8	4,7
MAMS14327	Rein 29	Os parietale	4933	27	-26,1	cal BC 3756-3658	calBC3769-3654	3,3	40,7	13,4

VI.2 La Mina

Radion carbon dating was conducted by the Beta Analytic Inc. in Miami, Florida.

Labor No.	Sample name	sample	C ¹⁴	±	13C	Cal 1 sigma	Cal 2 sigma
Beta - 31613 2	Mina3633	Human bone	4870	30	-19.1	cal BC 370-3700	cal BC 3890-3660

VI.3 Barranc d'en Rifà

Radion carbon dating was conducted at the Curt-Engelhorn-Zentrum für Archäometrie in Mannheim.

Labor No.	Sample name	sample	C ¹⁴	±	13C	Cal 1 sigma	Cal 2 sigma	C:N	%C	%coll
MAMS14854	Bar 1	dentin	4138	26	-21,6	cal BC 2861-2635	calBC2872-2623	3,3	24,3	6.0
MAMS14855	Bar 2	dentin	4217	25	-15.5	cal BC 2891-2764	calBC2900-2700	3,3	14.7	9.3

VIII Curriculum Vitae

Persönliche Daten

Name	Christina Roth
Geburtsdatum	28.01.1984
Geburtsort	Bückeburg, Niedersachsen
Nationalität	Deutsch

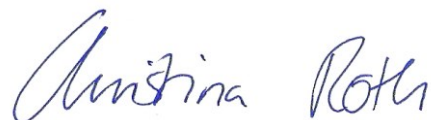
Berufliche Tätigkeiten

01/2011 - 12/2013	Wissenschaftliche Mitarbeiterin im Bereich Paläogenetik im DFG-Projekt AI 287/14-1 Institut für Anthropologie, Johannes Gutenberg-Universität Mainz
05/2013 - 08/2013	Projektleiterin im Bereich gentechnische Sicherheit Institut für Anthropologie, Johannes Gutenberg-Universität Mainz
11/2012 - 12/2012 (6-wöchig)	Forschungsaufenthalt am <i>Australian Centre for Ancient DNA</i> The University of Adelaide, Australien
12/2008 - 12/2010	Wissenschaftliche Mitarbeiterin im Bereich Paläogenetik in verschiedenen Projekten Institut für Anthropologie, Johannes Gutenberg-Universität Mainz
07/2010 (2-wöchig)	Mitglied des internationalen Grabungsteams in Körtik Tepe (Diyarbakır, Südosttürkei) Kooperation der Universitäten Freiburg, Mainz und Diyarbakır

Ausbildung

01/2011 - heute	Promotion im Fachbereich Biologie im Institut für Anthropologie, Johannes Gutenberg-Universität Mainz. Promotionsthema: "Once upon a time in the west – Paleogenetic analyses on human Neolithic to Bronze Age populations of the Iberian Peninsula."
10/2003 - 11/2008	Studium der Biologie mit den Prüfungsfächern Anthropologie, Zoologie und Vor- und Frühgeschichte an der Johannes Gutenberg-Universität Mainz Förderungsstipendium im Rahmen der Diplomarbeit durch die Johannes Gutenberg-Universität Mainz. Abschluss: Diplom 1,2 Diplomarbeitsthema: „Paläogenetische Analysen an Skeletmaterial aus dem Mittelbe-Saale Gebiet. Haplotypisierung von Individuen der Gaterslebener and Schnurkeramischen Kultur aus Eulau (Sachsen-Anhalt).“
08/1996 - 06/2003	Besuch des Gymnasiums Adolfinum in Bückeburg, Niedersachsen Abschluss: Abitur 1,6

Mainz, 23.09.2014



IX Publikationsverzeichnis

Veröffentlichungen

- 2014 Brandt G, Szécsényi-Nagy A, **Roth C**, Alt KW, Haak W: Human paleogenetics of Europe - the known knowns and the known unknowns. *Journal of Human Evolution*. In press
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- 2013 Brandt G, Haak W, Adler CJ, **Roth C**, Szécsényi-Nagy A, Karimnia S, Möller-Rieker S, Meller H, Ganslmeier R, Friederich S, Dresely V, Nicklisch N, Pickrell JK, Sirocko F, Reich D, Cooper A, Alt KW, The Genographic Consortium Ancient DNA reveals key stages in the formation of Central European mitochondrial genetic diversity. *Science* 342 (6155), 2013: 257-261.
- Meyer C, Hansen L, Jacobi F, Knipper C, Fecher M, **Roth C**, Alt KW: Irreguläre Bestattungen in der Eisenzeit? Bioarchäologische Ansätze zur Deutung am Beispiel der menschlichen Skelettfunde vom Glauberg. In: Müller-Scheeßel N (Hrsg.) "Irreguläre" Bestattungen in der Urgeschichte: Norm, Ritual, Strafe...?. *Kolloquien zur Vor- und Frühgeschichte* 19, 2013: 425-438.
- 2012 Alt KW, Knipper C, Held P, Niklisch N, Fecher M, **Roth C**, Enzman F, Tuckermann J, Seitz H, Polzin C, Klopsch V, Brauns M, Horton M, Pike AWG: Königin Editha – Ein Indizienbeweis zur Identifikation einer historischen Persönlichkeit aus dem Magdeburger Dom. In: Meller H, Schenkluhn W, Schmuhl BEH (Hrsg.) *Königin Editha und ihre Grablegen in Magdeburg*. *Archäologie in Sachsen-Anhalt* 18. Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt, 2012: 105-157.
- 2010 **Roth C**, Alt KW: Molekulargenetisches Profil mittels alter DNA. In: Hotz G, von Greyerz K, Burkart L (Hrsg.) *Theo der Pfeifenraucher - Leben in Kleinbasel um 1800*. Christoph Merian Verlag, 2010: 63-65.
- Brandt G, Knipper C, **Roth C**, Siebert A, Alt KW: Beprobungsstrategien für aDNA und Isotopenanalysen an Skelettmaterial. In: Meller H, Alt KW (Hrsg.) *Anthropologie, Isotope und DNA*. Tagungsband 2. Mitteldeutscher Archäologentag in Halle. Oktober 2009. Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt, 2010: 17-32.
- 2008-2009 Meyer C, Jacobi F, Knipper C, **Roth C**, Fecher M, Alt KW: Anthropologische Analyse der eisenzeitlichen Bestattungen vom Glauberg. Ein Beispiel für das Potential einer integrativen Bioarchäologie. *Berichte der Kommission für archäologische Landesforschung in Hessen* 10, 2008/2009: 237-244

- 09/2014 **Roth C**, Brandt G, Knipper C, Alt, KW: Samples and sampling - methodological outlines for ancient DNA and stable isotope research in archaeology. XVII World congress of the International Union of Prehistoric and Protohistoric Sciences, Burgos. (Präsentation)
- Roth C**, Garrido Pena R, Haak W, Kunst M, Risch R, Rojo Guerra M, Alt KW: Once upon a time in the West – New ancient DNA data from the Iberian Peninsula. XVII World congress of the International Union of Prehistoric and Protohistoric Sciences, Burgos. (Präsentation)
- Roth C**, Garrido Pena R, Haak W, Kunst M, Risch R, Rojo Guerra M, Alt KW: aDNA data from the Iberian Peninsula in an European context. XVII World congress of the International Union of Prehistoric and Protohistoric Sciences, Burgos. (Präsentation)
- 09/2013 **Roth C**, Rojo Guerra MA, Garrido Pena R, García-Martínez de Lagrán I, Tejedor Rodriguez C, Alt KW: Neolithic Iberia - what ancient DNA can tell us. 18th Annual Meeting of the European Association of Archaeologists, Pilsen. (Präsentation)
- 09/2010 **Roth C**, Meyer C, Jacobi F, Knipper C, Tölpel I, Fecher M, Hansen L, Alt KW: The Celtic princely seat of Glauberg (Hesse, Germany) – a bioarchaeological interdisciplinary approach. 4th International Symposium on Biomolecular Archaeology, Copenhagen. (Poster)
- 09/2010 **Roth C**, Meyer C, Jacobi F, Knipper C, Tölpel I, Fecher M, Hansen L, Alt KW: Entombed in burial mounds, thrown into pits – Interdisciplinary bioarchaeological analyses on the burials of Glauberg (Hesse, Germany). 16th Annual Meeting of the European Association of Archaeologists, Den Haag. (Präsentation)
- 09/2009 **Roth C**, Brandt G, Dresely V, Alt KW: Palaeogenetic analyses on skeletal remains of the Gatersleben, Corded Ware and Unetice Culture from Eulau (Saxony-Anhalt). 8. Internationaler Kongress der Gesellschaft für Anthropologie, München. (Poster)
- 05/2009 **Roth C**, Brandt G, Dresely V, Alt KW: Paläogenetische Analysen an Individuen der Gaterslebener und Schnurkeramischen Kultur aus Eulau (Sachsen Anhalt). 1. Österreichischer Archäometrie Kongress, Salzburg. (Präsentation)