UNIVERSITY OF HUDDERSFIELD

DOCTORAL THESIS

GENETIC IMPACT OF THE BRONZE AGE AT THE FRINGES OF EUROPE

Author:
M. George B. FOODY

Supervisor: Dr. Ceiridwen J. EDWARDS

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in the

Archaeogenetics Research Group
School of Applied Sciences

University of HUDDERSFIELD

Declaration of Authorship

I, M. George B. FOODY, declare that this thesis titled, "GENETIC IMPACT OF THE BRONZE AGE AT THE FRINGES OF EUROPE" and the work presented in it are my own. I confirm that:

- This work was done wholly or mainly while in candidature for a research degree at this University.
- Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.
- Where I have consulted the published work of others, this is always clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
- I have acknowledged all main sources of help.
- Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself.

Signed: George Foody

Date: 13/04/2021

Acknowledgements

Firstly, I would like to express my sincerest thanks to my supervisor, Dr. Ceiridwen Edwards, for all the help, guidance and insight during my PhD. All that I have learned as a result of your teaching and the opportunities you helped provide will be extremely useful in my future career.

Similarly, I would also like to thank my co-supervisors, Prof. Martin Richards and Dr. Maria Pala, whose vast knowledge taught me a great deal and aided the progression of my thesis.

Also, I would like to convey my gratitude to the Leverhulme Trust for funding this PhD.

I am grateful to all the collaborators involved in the Cretan project. Dr. Peter Ditchfield (University of Oxford) for providing equipment, lab space and help regarding isotopic analysis. Bob Arnott and Holley Martlew for their aid in access to the samples and background information about the site.

Furthermore, I wish to express my appreciation to all those who helped during the PhD. Dr. Mike Buckley (University of Manchester) for providing lab space, interpretation and teaching how to conduct ZooMS. Drs. Umberto Albarella and Angelos Hadjikoumis for zooarchaeological assessment. Drs. Lara Cassidy (Trinity College Dublin) and Rui Martiniano (Liverpool John Moores University) for taking the time to discuss bioinformatic methodology and techniques. The Smurfit Institute of Genetics, Trinity College Dublin for sequencing the samples sent for screening. Dr Francesca Gandini for guidance regarding mitochondrial labwork. And Dr. Katharina Dulias for all her help with the background information for the samples in Chapters 8 and 9.

My immense gratitude goes to my family for all the encouragement and support to help me reach this stage. To my friends thank you for being there for me and providing me with needed distractions. To my girlfriend, Molly, for all the love and support, keeping me grounded and encouraging me away from the computer.

Finally, I would like to thank all my fellow PhD cohort; Ale, Marina, Katharina, Bobby, Gonzalo, Rita, Simao, Pierre, Rohan, Berni, Marissa, Dimi, Franci, Dulce, Joe and many more, for their friendship and camaraderie both inside and outside the office.

UNIVERSITY OF HUDDERSFIELD

Abstract

Biological and Geographical Sciences
School of Applied Sciences

Doctor of Philosophy

GENETIC IMPACT OF THE BRONZE AGE AT THE FRINGES OF EUROPE

by M. George B. FOODY

The Bronze Age had a major effect on societies across Europe, bringing new technologies, ideologies and languages. In recent years, archaeogenetic studies have demonstrated that this time period is also associated with a large-scale migration from the Eurasian steppe. This PhD thesis studies the genetic impact of the Bronze Age on two island fringes of Europe. The island of Crete lies in the Mediterranean, on the southeastern point of Europe. In contrast, the Orkney archipelago sits at the northwestern extreme of the coast of Britain. Although culturally different, they are both seen as being atypical compared to their mainland counterparts.

Crete hosted a flourishing civilisation, the Minoans, who developed their own language, writing and architectural styles. Hypotheses have associated this culture to a continuation of pre-existing Neolithic society. The necropolis of Armenoi presents a unique opportunity to understand this population as it dates to a transition period in Crete between the indigenous Minoan and the mainland Mycenaean culture. Analyses of the genetic composition of Armenoi provided insights into whether this cultural change occurred as the result of the movement of ideas or people. Genetic diversity, similarities to other ancient populations, and kin groups within the cemetery were investigated. Isotopic analysis will be used to demonstrate the dietary composition of the population.

The Bronze Age of Orkney is often seen as a cultural backwater, not undergoing the same cultural changes of the British mainland. Differences seen during the British Bronze Age are associated with a large population turnover. The Bronze Age in Orkney is different to other parts of Britain, and genomic analysis will determine whether Orkney was part of this migration or not. The impact of the Bronze Age will also be assessed in Britain by studying a time transect from across the island.

These studies will provide insights into the local populations and their place in comparison to the broader history of Europe.

Contents

List of Figures

List of Tables

List of Abbreviations

aDNA	Ancient DNA
ACN	acetonitrile
AD	Anno Domini
AIR	Ambient Inhalable Reservoir
AMH	Anatomically Modern Humans
ANF	Anatolian Neolithic Farmer
A-S	Anglo-Saxon
BA	Bronze Age
BAM	Binary Alignment Map
BC	Before Christ
bp	Base pair
BP	Before Present
Bst	*Bacillus stearothermophilus*
BWA	Burrows-Wheeler Aligner
C	Carbon
cal.	calibrated
CF-IRMS	Continuous Flow Isotope Ratio Mass Spectormeter
CHG	Caucasus Hunter-Gatherers
CI	confidence interval
CPC	Carsington Pasture Cave
CRS	Cambridge Reference Sequence
CV	cross-validation
D-loop	Displacement loop
ddH_2O	double distilled water
DNA	Deoxyribonucleic Acid
EAGER	Efficient Ancient Genome Reconstruction
EBA	Early Bronze Age
EBT	elution buffer + tween
EDTA	ethylenediaminetetraacetic acid
EHG	Eastern Hunter-Gatherers
EM	Early Minoan
EN	Early Neolithic
GATK	Genome Analysis Tool Kit
GRCh37	Genome Reference Consortium Human genome build 37
HCl	Hydrochloric acid
hg19	Human reference Genome build 19
HPC	High Pasture Cave
HTS	High Throughput Sequencing
HVR	Hypervariable Region
IBD	Identity by Descent

IBS	Identity by Segment
IGV	Integrative Genomic Viewer
Indel	Insertion or deletion of one or more nucleotides
IranN	Iranian Neolithic
ISEA	Island Southeast Asia
ISOGG	International Society of Genetic Genealogy
KoS	Knowe of Skea
kya	thousand years ago
LBA	Late Bronze Age
LBK	Linearbandkeramik
LD	Linkage Disequilibrium
LGM	Last Glacial Maximum
LM	Late Minoan
LN	Late Neolithic
LoN	Links of Noltland
LP	Lactase Persistance
LRM2	Lower Right Molar 2
MALDI-ToF	Matrix-Assisted Laser Desorption/Ionization -Time of Flight
MALDI-MS	Matrix-Assisted Laser Desorption/Ionization - Mass Spectrometer
MBA	Middle Bronze Age
MM	Middle Minoan
MN	Middle Neolithic
MNI	Minimum Number of Individuals
MS	Milla Skerra
MSY	Male Specific Y-chromosome
mtDNA	Mitochondrial DNA
N	Nitrogen
NGS	Next-generation sequencing
O	Oxygen
Oak	Oakridge
ORAU	Oxford Radiocarbon Accelerator Unit
PB	Phosphate-Buffered
PBS	Phosphate-Buffered Saline
PCA	Principal Components Analysis
PCR	Polymerase Chain Reaction
PE	Wash Buffer
PoBI	People of the British Isles
PPNB	Pre-Pottery Neolithic B
RC	Rosemarkie Cave
rCRS	revised Cambridge Reference Sequence
READ	Relationship Estimation from Ancient DNA
RLAHA	Research Laboratory for Archaeology and Art History
RoH	Runs of Homozygosity
rpm	revolutions per minute
SDS	Sodium Dodecyl Sulphate
SE	Standard Error
SNP	Single Nucleotide Position

Sr	Strontium
STR	Short Tandem Repeat
SUERC	Scottish Universities Environmental Research Centre
TFA	trifluoroacetic acid
TFAM	Transposed FAM (family) file
TPED	Transposed PED (pedigree) file
TRB	Trechterbekercultuur (Funnelbeaker culture)
Tris-HCl	Tris(hydroxymethyl)aminomethane hydrochloride
UDG	Uracil-D-Glycosylase
USER	Uracil-Specific Excision Reagent
USGS	United States Geological Survey reference material
UV	Ultraviolet
VCF	Variant Call File
VPDB	Vienna Pee Dee Belemnite
VSMOW	Vienna Standard Mean Ocean Water
WGS	Whole Genome Sequencing
WH	West Heslerton
WHG	Western Hunter-Gatherers
WM	Worth Matravers
YDNA	Y-chromosal DNA
ZooMS	Zooarchaeological Mass Spectrometry

Chapter 1

Introduction

Several significant cultural changes occurred across Europe during the Bronze Age, as can be seen in the archaeological record. Whether these were the result of the movement of people or the movement of ideas has been a topic of much archaeological debate (Section 3.3). However, recent ancient genomic studies have demonstrated that the changes were frequently associated with large-scale male-biased migration from the Eurasian steppe (explored in Chapter 3).

My thesis aims to study ancient genomes of two very different island populations on the peripheral fringes of Europe, Figure 1.1 (Armenoi in Crete, Figure 1.2, and the Links of Noltland in Orkney, Figure 1.3) to investigate if they too experienced the genetic change associated with the steppe expansion during the Bronze Age. In order to investigate these sites, similar methods were explored (the background and reasoning behind the methods used are outlined in Chapter 2 and the methods themselves are described in Chapter 4). To put the data in context, a brief background of European prehistory using archaeogenetic studies is given in Chapter 3, with a more in-depth review of Bronze Age European cultures through archaeogenetic studies detailed in Section 3.3. Understanding the background of European prehistoric archaeogenetic studies is essential in understanding the results generated in this thesis.

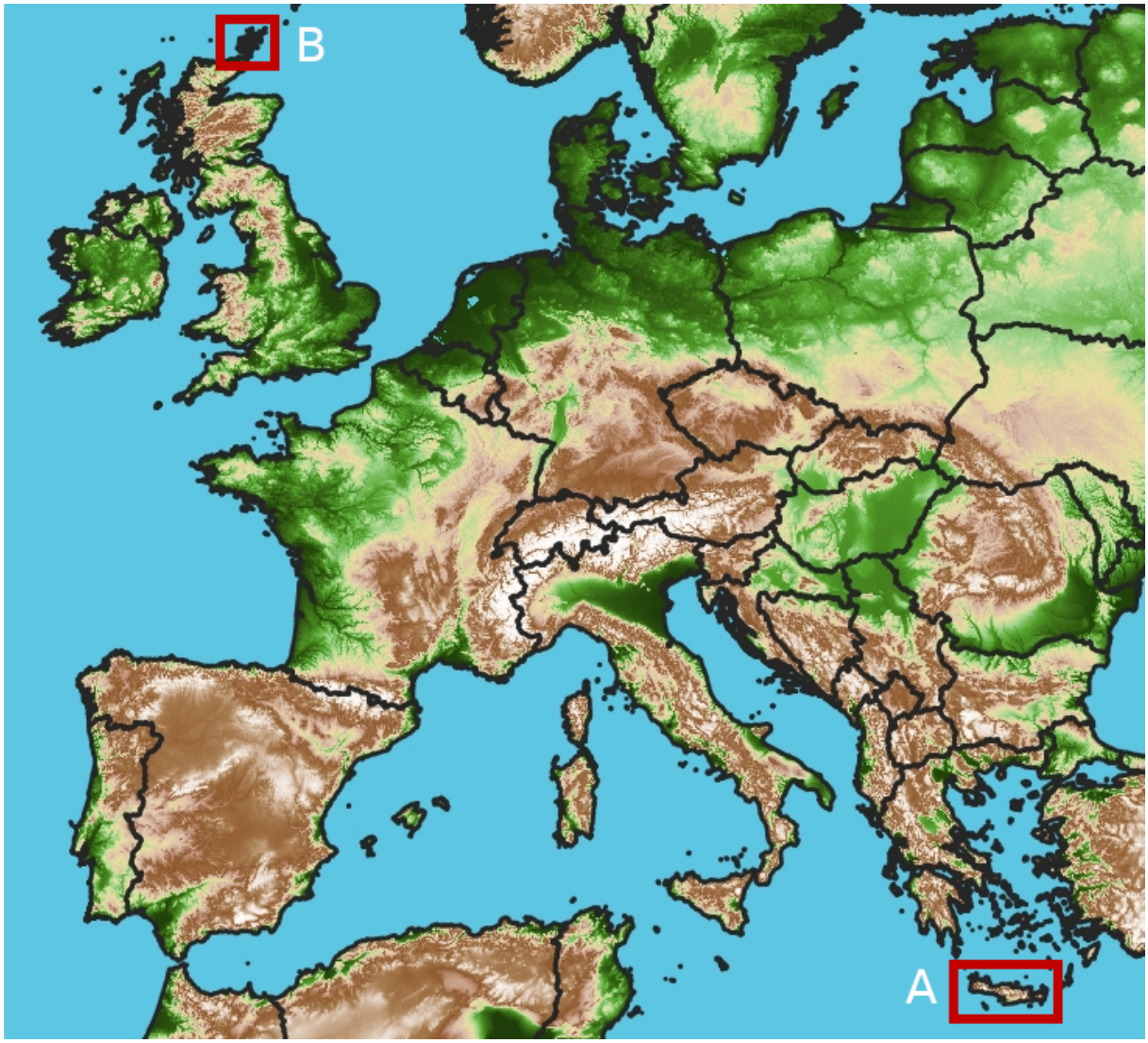


FIGURE 1.1: Map of Europe with the areas of interest highlighted by red boxes. A: Crete. B: Orkney.

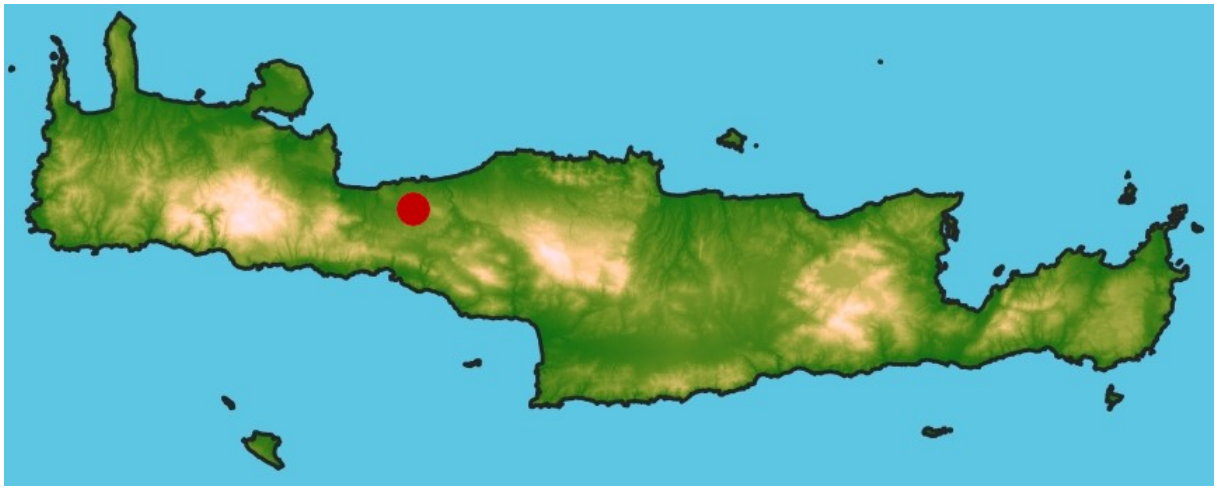


FIGURE 1.2: Map of Crete with Armenoi marked by a red circle.

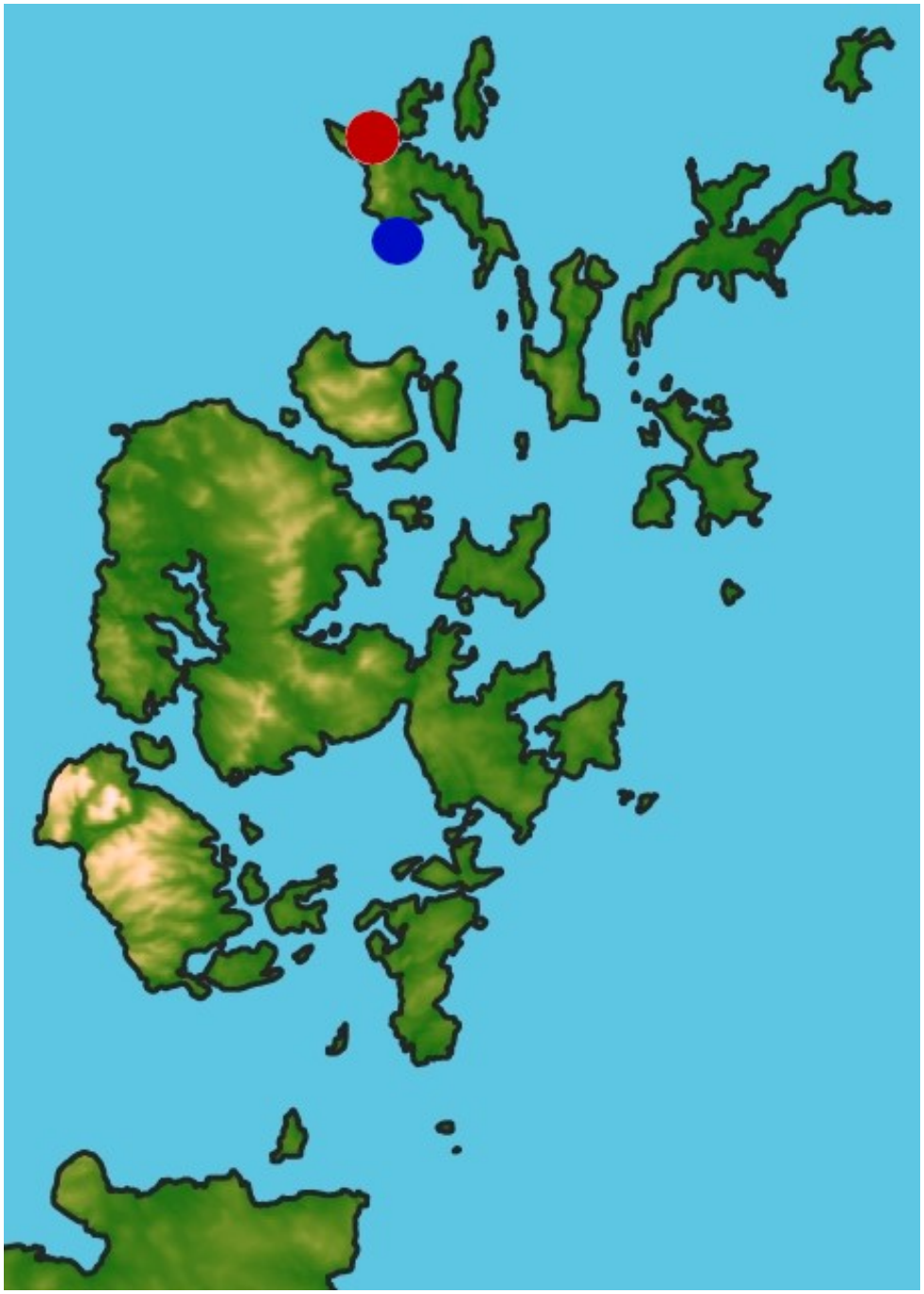


FIGURE 1.3: Map of Orkney with the Links of Noltland marked with a red circle and the Knowe of Skea with a blue circle.

Due to their differing locations and archaeological cultures, the two populations (Armenoi in Crete, and the Links of Noltland in Orkney) were analysed separately. More detailed backgrounds for Crete and Britain can be found in Chapter 5 and Chapter 7 respectively. I studied site-specific information, such as kinship and genetic homogeneity, as well as comparisons with other contemporaneous groups. Through this, I aimed to understand whether the steppe expansion made any genetic impact into either of the islands. Results are described in Chapters 6 (Crete) and 8 (Orkney).

As well as the study of Bronze Age Orkney, I undertook a time transect of Bronze Age to Early Medieval Britain to assess the lasting genetic impact of the Bronze Age. The results can be found in Chapter 9.

Islands have been described as having suitable 'laboratory' conditions for several fields of study, including phylogeography and anthropology, due to spatial isolation, definable island limits, and often small population size (Fitzhugh and Hunt, 1997; Shaw and Gillespie, 2016). This can make migration events more readily identifiable. In both cases, the sea acted as a cultural barrier, with Cretan and Orcadian societies developing differently from their mainland neighbours during the Neolithic. However, both saw cultural changes during the Bronze Age, which, in turn, made them more similar to the mainland. Using comparative analysis, my aim was to see whether the cultural changes in the Bronze Age were mirrored in the genomic record.

As well as focusing on how these sites fit into the 'big picture' interpretation of the Bronze Age, I used the genomic data to answer localised questions. Multiple individuals were available from both the Links of Noltland, Orkney, and Armenoi, Crete, and both sites have graves containing multiple individuals. This allowed me to answer several questions, including inter-site genomic diversity, as well as kinship. Kinship links can be used to identify the importance of family, and potentially suggest inherited wealth, which is thought of as a change associated with the Bronze Age (Chapter 3). Archaeological samples with sufficient ancient DNA are limited resources that require careful laboratory processes (Chapter 2) and each sample was fully investigated to generate as many results as possible.

In order to investigate these research questions, I analysed 81 ancient samples (23 samples I extracted and sequenced from Armenoi; and 58 samples from across Britain that were extracted and sequenced by Dr. Katharina Dulias).

A separate project concerning ancient Guam is presented in Appendix A.

1.1 Armenoi, Crete

My Late Bronze Age study of Crete focuses on the Minoan-Mycenaean transition. Minoan culture developed an advanced society on Crete but, during the Late Bronze Age, this culture declined and was replaced by Mycenaean culture from mainland Greece. Mycenaeans brought several cultural aspects associated with the Bronze Age, including a hierarchical society, male dominance and the earliest

written examples of Proto-Greek, an Indo-European language (see Chapter 5). I am privileged to have had access to a relatively intact, well-excavated necropolis site dating to the Minoan-Mycenaean transition. In addition, comparative samples were available from (Lazaridis et al., 2017), which identified significant differences between earlier, pre-decline Minoans and mainland Mycenaeans. Steppe ancestry has been identified in Mycenaeans but not Minoans. Using this published study, it should be possible to identify whether the changes on Crete were due to population replacement, Minoans adopting Mycenaean material culture, or admixture between the two groups. The site was compared to other relevant data to identify its genetic affinity to other populations, which aided interpretations of previous migration events.

Complementing the ancient DNA study of Armenoi, I also undertook a dietary isotopic analysis of the site. Diet is not just a reflection of the resources available but is influenced by culture (see Section 2.4), and dietary differences associated with social status have been seen in some Mycenaean sites (see Section 5.4). Isotopic analysis was used to identify whether the diet of the Armenoi population had similarities with Minoans or Mycenaeans. To ensure accurate baselines, local faunal isotopic values were also generated and calculated, and the faunal remains were identified using zooarchaeological assessment (Section 2.5) and Zooarchaeological Mass Spectrometry, ZooMS (Section 2.6)

To identify the legacy of the Late Bronze Age on the current population, mitochondrial haplotype diversity was also investigated (Appendix B). This was compared to the diversity of the mainland to investigate potential differences in ancestry. Currently, there are few published Cretan full mitochondrial genomes, so I created a dataset of newly collected modern day samples from Crete and also from Cyprus and mainland Greece, which, combined with published data, acted as comparative datasets for my ancient results. Modern and ancient samples were compared to determine potential genetic continuity.

1.2 Links of Noltland, Orkney

Orkney undergoes a less dramatic material culture change than seen in other areas of Britain during the Bronze Age (Chapters 7 and 8). Published ancient genome data from Britain demonstrated that a change of ancestry, associated with the steppe, was contemporaneous with this material culture change (Olalde et al., 2018). The Links of Noltland represents a well-preserved site with multiple individuals who were interred in multiple ways; cremation and inhumation in both single and multiple graves.

Previous unpublished work by Dr. Katharina Dulias from this site revealed that the males predominantly belonged to Y-chromosome haplogroup I. In areas with steppe ancestry, such as mainland Britain, the predominant Y-chromosome haplogroup is R1a or R1b. I built upon the work of Dr. Dulias and investigated whether the full genome data showed evidence of steppe ancestry, as in mainland Britain, or was more similar to the published data from Neolithic Orkney (Olalde et al., 2018). Furthermore, I investigated the genetic diversity of the site to determine whether multiple and single burials represented differing ancestries, and whether kinship could be determined in the cemetery. I also had access to data from a Scottish Neolithic sample and three Orcadian Iron Age samples, also generated by Dr. Dulias. The Neolithic individual is from the Isle of Skye, an understudied area for ancient DNA from Neolithic Scotland, and this sample provided additional information on the genetic ancestry of Britain prior to the Bronze Age. The Iron Age samples, also from Westray, but from the site of Knowe of Skea, were used to identify potential continuity through time from the Bronze Age Links of Noltland.

The impact of the Bronze Age in Britain was further examined by studying a time transect of samples from across mainland Britain dating from the Early Bronze Age to the Early Viking period. From some sites, multiple individuals are available and were investigated in terms of kinship and diversity. As well as understanding the long-term genetic impact of the Bronze Age, these samples were analysed to investigate later migrations and how they compared to more contemporaneous populations.

1.3 Notes on chronology

Archaeological periods can differ between regions (Chapter 3), which is especially true in Crete (Section 5.2.3.1). Therefore, where possible. I have included contextual dates in terms of BC/AD. In addition, absolute dates can be provided at the Links of Noltland and related sites due to radiocarbon dating (Section 2.4). Radiocarbon dates compliment many archaeological studies in Britain, greatly aiding the timescale of archaeological material culture. In contrast, the dates from Armenoi, and also Greece in general, have mainly been dated using typological sequences based on cultural material changes.

Chapter 2

Methodological concepts

2.1 Introduction

My thesis explores the archaeogenetics of two islands on either side of Europe: Crete and Britain. The section about Crete involves the Late Bronze Age transition from Minoan to Mycenaean cultures, which brought major changes to the society, culture and language of the island. The presence of a complex society using a pre-Indo-European language, and its replacement by the Mycenaean Indo-European speaking culture, represents an opportunity to explore the genetic component behind this language family. The analysis of Britain includes a much longer transect through time, representing several cultural transitions both prehistoric and within early historical records. A subsection of this assesses Late Bronze Age and Iron Age Orkney, an island archipelago off the northern coast of Britain. This thesis will analyse the people in these areas using archaeogenetic and isotopic analysis to understand their society and their relationships to other ancient cultures.

2.2 Archaeogenetics

Deoxyribonucleic acid (DNA) has an anti-parallel double-helix structure, comprising 4 different complementing nucleic bases: guanine (G), cytosine (C), adenine (A) and thymine (T). Guanine and cytosine, and thymine and adenine are complementary base pairs (bp). These nucleotides create the genetic code for life specifying the biological characteristics of an individual (Lemey et al., 2009; Rizzi et al., 2012; Jobling et al., 2014; Herrera and Garcia-Bertrand, 2018). By determining the sequences of these nucleotides along a chromosome, it is possible to determine several factors about an individual including the biological sex, indicators of phenotype, and ancestry information. In addition, kinship and genetic diversity can be determined in a population.

The term archaeogenetics is the application of molecular genetics to archaeological questions (Renfrew, 2000). Combined with archaeological, evolutionary and

linguistic information, it is possible to investigate, for example, structure within cemeteries, prehistoric migration associated with archaeological transitions, and the interaction between ancient hominids. Archaeogenetic analysis has been conducted using both modern human diversity and by analysing ancient DNA. Ancient DNA refers to the DNA that survives in ancient tissues, typically over 100 years old (Jobling, 2012; Kendall et al., 2018).

The first extraction of ancient DNA from an ancient sample, dates to 1984 with the recovery a 222bp sequence from a quagga, an extinct equine (Hofreiter et al., 2015; Linderholm, 2015; Jakobsson and Mattias, 2019). This was later followed by the extraction of DNA from a mummy (Hofreiter et al., 2015; Hagelberg et al., 2015), although this work has since been discredited(Gilbert et al., 2005; Lorenzen and Willerslev, 2010; Rizzi et al., 2012; Hofreiter et al., 2015). Interest in the field expanded with claims of extraction of DNA from dinosaurs and blood from stone tools (Woodward et al., 1994; Hardy et al., 1997). However early aDNA studies have been criticised for the large amount of ancient material that had to be destroyed, and many studies suffered from major contamination issues (Hofreiter et al., 2015; Linderholm, 2015; Hagelberg et al., 2015; Green and Speller, 2017).

Early genetic studies relied on data produced using the polymerase chain reaction (PCR) of small fragments, followed by chain-termination, or Sanger, sequencing (Linderholm, 2015). For ancient samples, where it is impossible to amplify long fragments, unlike modern tissues, overlapping sequences are targeted to reconstruct longer tracts of DNA (Hofreiter et al., 2015; Marciniak et al., 2015). One major drawback of Sanger sequencing was that longer DNA sequences were required for analysis, increasing the cost and workload involved. Concerning ancient DNA, this technique had a serious issue due to the bias of PCR towards longer sequences. These longer sequences are more likely to be modern contaminant DNA (Hofreiter et al., 2015; Marciniak et al., 2015; Linderholm, 2015; Vai et al., 2017; Jakobsson and Mattias, 2019).

The development of new sequencing technology, known as next-generation sequencing (NGS), revolutionised ancient genetic studies (Vai et al., 2017) as it allows millions of reads to be sequenced in parallel, whereas previous Sanger sequencing could only process one sequence at a time. This has radically reduced the cost, as well as increasing the amount of data produced, resulting in an increase of DNA studies (Heintzman et al., 2015; Marciniak et al., 2015; Vai et al., 2017). In addition, as more data can be generated from a single run, typically less biological material is required

compared to earlier Sanger studies. This has been particularly important concerning rare or limited samples (Marciniak et al., 2015).

In 2001, the first human genome reference sequence was published, which was the result of an international collaboration (Consortium, 2001). NGS has enabled a larger read depth and greater accuracy of sequenced data, and thus a greater ability to discover variants from both modern and ancient samples. Today several large-scale datasets investigating human genetic variation exist, including the 1000 Genomes Project, Human Origins Project, and the UK Biobank, and these are essential as comparisons for the ancient data generated.

There are two main NGS methodologies: whole genome shotgun and target-enriched capture (Heintzman et al., 2015; Hofreiter et al., 2015; Jobling and Tyler-Smith, 2017). Shotgun sequencing randomly sequences all the DNA present in a sample (Heintzman et al., 2015; Hofreiter et al., 2015; Charlton et al., 2019), so will amplify both exogenous (contaminant) and, if any is present, endogenous DNA. Whilst this provides information about the percentage of DNA present in a sample, it has been criticised as being prohibitively expensive (Heintzman et al., 2015). In contrast, capture arrays amplify selected loci by employing a series of baits (Linderholm, 2015). This method is less costly than shotgun per sample and significantly increases the proportion of targeted DNA compared to exogenous or non-target background endogenous DNA. However, sequences retrieved are limited to the design of the capture arrays, which can hinder future research; comparison of datasets constructed using different capture arrays can be limited and; novel SNPs often cannot be studied on captured sequences. Therefore, sequences captured on smaller, less commonly used capture arrays may not be relevant to later studies studying a larger number of SNPs (Marciniak et al., 2015; Hofreiter et al., 2015; Heintzman et al., 2015). There has also been discussion that, as many ancient samples are rare, we should be aiming to generate as much information from them as possible.

The invention of NGS dramatically increased the number of ancient DNA studies, with fewer than 10 published ancient genomes by 2010, to hundreds being published in a single paper in 2018, **Figure 2.1**. This more affordable sequencing has enabled better understanding of the post-mortem changes that DNA undergoes, and in turn, is helping the development of better strategies for laboratory and bioinformatic protocols.

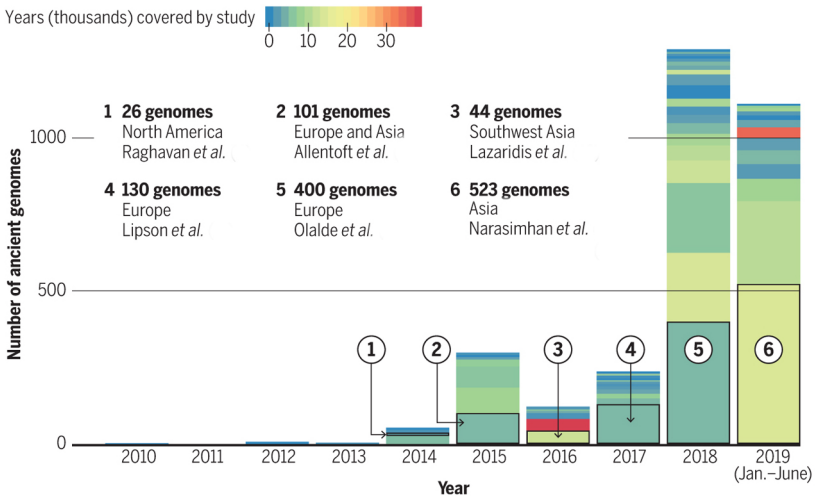


FIGURE 2.1: Bar chart displaying the number of ancient genomes published per year from 2010 until June 2019. Edited from Schaefer and Shapiro (2019).

2.2.1 aDNA

When an organism dies, its DNA undergoes post-mortem degradation due to taphonomic factors, such as temperature and pH, and processes such as hydrolysis, oxidation and microbial attack. These cause DNA fragmentation, deamination and a loss of endogenous DNA content. As ancient DNA is comprised of short fragments, PCR would often fail to amplify it; in contrast, NGS requires short fragments, which is ideal for aDNA studies (Heintzman et al., 2015; Marciniak and Perry, 2017).

Purines (A and G) are more likely to fragment from hydrolysis resulting in overhangs of pyrimidines at the 5′ end. Deamination occurs when the nitrous bases of the DNA are affected by hydrolytic loss. The deamination product of cytosine is uracil, which is misread by sequencers as thymine. This results in higher rates of C->T transition ~~occurs at higher rates at~~ the 5′ overhangs, which are complementary read as G->A transitions at the 3′ end (Jónsson et al., 2013; Dabney et al., 2013; Skoglund et al., 2014; Linderholm, 2015; Renaud et al., 2015; Vai et al., 2017; Jakobsson and Mattias, 2019). Deaminated DNA was often misread as sequencing errors when using Sanger technology (Linderholm, 2015; Vai et al., 2017; Jakobsson and Mattias, 2019). With the increased amount of reads per base produced by NGS, it is now possible to quantify the deamination patterns at the ends of reads and, in turn, use the deamination pattern to authenticate samples as containing ancient DNA (Jónsson et al., 2013; Dabney et al., 2013; Skoglund et al., 2014; Linderholm, 2015; Renaud et al., 2015; Vai et al., 2017; Jakobsson and Mattias, 2019). To reduce the number of sequencing errors due to cytosine deamination, some ancient laboratory protocols employ Uracil-DNA Glycosylase (UDG) treatment. This replaces the uracil with an abasic site, which is

then cleaved. Reads are, therefore, shorter, but have fewer errors. As deamination is important for authenticating ancient DNA, partial UDG treatment or non-UDG treatment on screening libraries (such as in this thesis) is often undertaken (Marciniak et al., 2015; Hofreiter et al., 2015; Rohland et al., 2015).

The fragmentation and loss of endogenous DNA leaves archaeological samples particularly vulnerable to contamination from exogenous modern DNA. The majority of the DNA extracted from a sample will be contaminant DNA from environmental microbes in the soil of the burial environment (Hagelberg et al., 2015; Charlton et al., 2019). When studying ancient humans and hominids, modern human contaminant DNA from archaeologists and other researchers is a particular problem, as DNA is present in sweat, skin flakes, and exhaled cells. Implementation of clean room conditions for laboratory processing of ancient samples analysis is essential, and having modern sequencing facilities that are physically separated from the ancient labs greatly reduces the potential for contamination. Other processes, including ultraviolet-irradiation and abrasion of the outer surface of the sample, reduces contaminant potential (Rizzi et al., 2012; Heintzman et al., 2015; Marciniak and Perry, 2017). In addition, bioinformatic programs have been developed to assess contamination in the resulting sequence data. Calculation of the heterozygosity of haploid regions of the genome (the mitochondrial and X-chromosome in males) has been commonly used to detect contaminant DNA. Comparison of samples to known datasets of modern human diversity also allows detection of potential contamination (Rasmussen et al., 2011; Jun et al., 2012; Renaud et al., 2015; Heintzman et al., 2015; Vai et al., 2017; Jakobsson and Mattias, 2019).

2.2.2 Sources of ancient DNA

Ancient DNA has been extracted from a number of sources including skeletal and dental material, coprolites (fossilised faeces), soil, preserved tissue, and dental calculus (calcified plaque) (Green and Speller, 2017). Taphonomic factors reduce the timespan and areas likely for DNA survival. Although time itself is not a factor in degradation, the more severe the taphonomic effects are, the less likely DNA is to survive. Areas with lower mean temperatures and less severe hydrolytic activities are more likely to preserve DNA; therefore, areas close to the equator are likely to have poorer DNA preservation. Deeper burials and burials in caves can protect samples from certain taphonomic effects (Hofreiter et al., 2015; Kistler et al., 2017; Kendall et al., 2018). The oldest DNA recovered is from a horse, dating to 700,000 years ago, found in Canada preserved in permafrost (Orlando et al., 2013). The oldest hominid was from a 90,000-year-old Denisovan from Russia (Slon et al., 2018), while the oldest modern

human was 45,000 years old from Ust Ishim, also in Russia (Fu et al., 2014). In contrast, the oldest human ancient genome from sub-Saharan Africa is only 8000 years old (Lipson et al., 2020).

Several studies have assessed which elements are most likely to preserve DNA (Gamba et al., 2014; Pinhasi et al., 2015; Hansen et al., 2017). In skeletal elements, the mineral component is thought to aid protection of DNA. Also, there is a link between collagen loss and DNA loss. Therefore, highly mineralised, denser bone (which protects the collagen from microbial attack) provides a greater opportunity for DNA survival (Gamba et al., 2014; Kendall et al., 2018). Gamba et al. (2014), Pinhasi et al. (2015), and Hansen et al. (2017) demonstrated that DNA survives better in denser bones, and that the petrous has significantly better endogenous DNA yield than other bones. The petrous forms part of the endocranial temporal bone, which protects the sensory organs of the inner ear. It is the hardest and densest bone in the human skeleton and, as a result, it tends to survive well archaeologically.

Teeth have also been shown to provide good DNA survival, particularly when found as part of the mandible or maxilla. Tooth structure is key to their preservation qualities. The crown is comprised of enamel, which is approximately 90% mineralised, making it the hardest, densest, most durable and least porous component of the human body. Covering the roots of the tooth is cementum, which also has a high mineral component. Hansen et al. (2017) showed that in cases with good tooth preservation, the tooth could have higher endogenous DNA concentrations than petrous bones. One thing to note here is that ancient DNA extraction is a destructive process, and both teeth and petrous bones are useful for a range of studies including morphological and isotopic analysis (Charlton et al., 2019). With this in mind, it is always important to ensure thorough sampling strategies.

2.3 The human genome

In humans, most DNA is found in the cell nucleus in the form of 23 chromatic pairs, with a very small proportion being located in the mitochondria. Nuclear DNA is inherited from both parents and, as a result, can provide information about them and their associated ancestry (Underhill and Kivisild, 2007; Jobling, 2012; Lindqvist and Rajora, 2019). The other mode of inheritance is via uniparental markers, which are DNA components only inherited from one parent, which include mitochondrial DNA and Y-chromosomal DNA. These markers were widely studied by early population geneticists as the mode of inheritance and their smaller size made them easier to

sequence and study (Jobling, 2012; Kivisild, 2015; Herrera and Garcia-Bertrand, 2018).

The majority of human DNA is identical across all populations. Genetic diversity is caused by mutations (nucleotide changes), insertions or deletions across the genome. These mutations can have positive, negative or neutral effects. Transition mutations - replacement of a purine (adenine, guanine) with a purine or a pyrimidine (cytosine, thymine) with a pyrimidine - are more common than transversions - replacement of a purine with a pyrimidine or vice versa (Nei and Kumar, 2000; Lemey et al., 2009; Herrera and Garcia-Bertrand, 2018)

2.3.1 Mitochondrial DNA

Mitochondrial DNA (mtDNA) is maternally inherited and found in cell organelles called mitochondria. The mtDNA genome is very small, at only 16,569 base pairs (bp) compared to three billion bp in the nuclear genome. Most of the mtDNA genome is relatively conserved, with the majority of mutations occurring in the non-coding control region, also known as the Hypervariable Segment (HVS) or D-loop. Tens to thousands of mitochondria are found in each human cell, whereas there are only two copies of the nuclear DNA (one from each parent). This abundance makes mtDNA easier to target and analyse, and made it the focus of early population genetic studies (Van De Graaf, 2009; Rizzi et al., 2012; Jobling et al., 2014; Kivisild, 2015; Van Oven, 2015).

The first mitochondrial reference, the Cambridge Reference Sequence (CRS), was released in 1981, followed by the revised Cambridge Reference Sequence, rCRS, in 1999 (Anderson et al., 1981; Andrews et al., 1999). As mtDNA is haploid, it does not undergo recombination, an exact copy of a mother's mtDNA will be passed on to her children (Rizzi et al., 2012; Jobling, 2012; Soares et al., 2013; Kivisild, 2015). As a result, any mutations that occur will also be passed onto her children. Individuals that share the same mitochondrial DNA sequence, including mutations, are said to share a haplotype. By comparing mutations in mtDNA sequences to the rCRS, it is possible to create phylogenetic trees. These are usually based on the principle of maximum parsimony, whereby the trees are built with the lowest number of mutations. These phylogenetic trees branch to contain groups of haplotypes, with similar mutation history, called haplogroups. When combined with human variation, geographic patterns can be seen, with different branches having different geographic frequencies. Calculation of the mutation rate of mtDNA has enabled branching times to be approximated (Van De Graaf, 2009; Brown and Brown, 2011; Jobling, 2012; Soares et al., 2013; Kivisild, 2015; Van Oven, 2015). Major branches of the human

mitochondrial tree are assigned by a capital letter, sub-branches are denoted by this letter followed by a number, then by a lowercase letter, then a number and so forth. Due to the nature of how the field began, the most diverse macro-haplogroups in Africa are denoted by the letter 'L', with the rest of the alphabet mainly denoting non-African branches (Van De Graaf, 2009; Jobling, 2012; Kivisild, 2015). Analysis of the mitochondrial tree has shown an African origin for all humans, with the most mitochondrial coalescence possibly occurring 200,000 years ago (Van De Graaf, 2009).

2.3.2 Y-chromosome

The Y-chromosome, found in the cell nucleus, is only present in males and is paternally inherited. The majority of the Y-chromosome, over 90% is non-recombining and is referred to as the Male-Specific Y-chromosome (MSY) (Jobling, 2012; Jobling et al., 2014). The Y-chromosome is much larger than mtDNA, at 60 Megabases (Mb), although it is still much smaller than the X-chromosome at 150Mb (Jobling et al., 2014; Jobling and Tyler-Smith, 2017).

To analyse the MSY, Short Tandem Repeat (STR) markers and Single Nucleotide Positions (SNPs) have been studied (Jobling, 2012; Jobling and Tyler-Smith, 2017). SNPs mutate at a slower rate than STRs, and are used to assign haplogroups and build phylogeographic trees using maximum parsimony. Conversely, the STRs have a very high mutation rate and vary across populations, making them useful for dating haplogroups (Karmin et al., 2015; Jobling and Tyler-Smith, 2017). The MSY tree is less well developed than its mtDNA counterpart due to several factors, but mainly due to the uncertainty concerning the mutation rates of STRs and SNPs and the size of the Y-chromosome. Another significant issue is that roughly half of the MSY comprises regions of continuous repetitive DNA sequence of around 23Mb in length, which, given that NGS reads are under 200bp, can hinder mapping, especially with low coverage samples. The description of the Y-chromosomal phylogenetic tree is laid out similarly to the mitochondrial phylogenetic tree, with major macrohaplogroups being denoted by capital letters, and sub-branches being followed by numbers then lowercase letters then numbers and so on, with A being the oldest branch located in Africa. Due to reconfiguration of the MSY tree, and the very long names, MSY haplogroups are sometimes referred to by their branch and terminal mutation; for example, R-S660 and R1b1a1a2a1a2c1a1a1a1a1a1a are the same haplogroup (Consortium, 2002; Karafet et al., 2008; Jobling, 2012; Wei et al., 2013; Jobling and Tyler-Smith, 2017; *Y-DNA project help*). Analysis of MSY phylogeny has revealed an expansion of non-African lineages approximately 60-50kya, corresponding with a similar mtDNA expansion, which has been interpreted as the expansion of humans out of Africa across the globe (Jobling

and Tyler-Smith, 2017).

Comparison of mtDNA and MSY phylogeographic diversity added with information concerning the timing of branch splits and haplogroup expansions, can reveal sex-biased migrations. Comparison of relative population sizes using Bayesian Skyline Plots (BSP) has been used to indicate the relative contribution of the sexes. However, it is important to note that conclusions based solely on modern data may be biased by recent demographic events.

2.3.3 Genome-wide analysis

Genome-wide analysis involves the study of variants across the whole genome, and can provide information about the overall ancestry of an individual. The nuclear genome is diploid, comprising 3.2Gb sorted into 23 pairs of chromosomes, 22 autosomal pairs and one pair of sex chromosomes, XX in females and XY in males. One chromosome of each pair is inherited from each parent, with the exception of males, whereby the Y-chromosome is only inherited from the father (Jobling et al., 2014). Autosomal chromosomes undergo recombination - this is the process whereby genetic material is exchanged between chromosomes or within a chromosome (Lemey et al., 2009). As autosomes are biparentally inherited and undergo recombination, analysis can reveal information about human evolution, as well as population diversity and ancestry (Herrera and Garcia-Bertrand, 2018).

Several factors affect population genetic variation, significantly genetic isolation and admixture. In order to study population genetic diversity, typically hundreds of thousands of SNP sites need to be analysed from across the genome as the majority of SNPs do not vary between individuals. SNPs can reveal kinship between individuals, diversity of particular populations and genetic affinity between populations (Jobling, 2012; Consortium, 2015; Herrera and Garcia-Bertrand, 2018; Bergström et al., 2020).

Taphonomic processes cause ancient DNA sequences to be degraded and have low coverage, preventing accurate calling of diploid genotypes (Günther and Nettelblad, 2019). To circumvent this issue, ancient samples are often called as pseudo-haploid (Cassidy et al., 2016). That is, at each known SNP site, one read is picked to represent a haploid genotype (Cassidy et al., 2016; Günther and Nettelblad, 2019).

2.4 Isotopes

Isotopes are atoms of the same element with a different number of neutrons. Lighter isotopes, those with fewer neutrons and a smaller mass number, are normally more frequent than heavier isotopes, and they can be stable or radioactive. Radioactive isotopes, such as ^{14}C, decay and reduce in frequency over time, whereas, by contrast, stable isotopes do not decay and can be measured across time (Brown and Brown, 2011; Sharp, 2017).

As carbon and nitrogen from food are incorporated into living tissue, their isotopic ratios can be used for dietary reconstruction (Richards, 2015; Dotsika et al., 2019). Dietary stable isotope analysis assesses the ratios of $^{13}C/^{12}C$ ($\delta^{13}C$) and the ratios of $^{15}C/^{14}N$ ($\delta^{15}N$) (Schulting, 1998; Brown and Brown, 2011; Richards, 2015).

Carbon isotopic analysis can differentiate diets based on C_3 (e.g. cereals) from C_4 plants (e.g. millet). The differing photosynthetic pathways of these plants results in C_4 plants having more positive $\delta^{13}C$ values ~~are a result of the differing photosynthetic pathways. C_4 plants tend to be from more arid environments as their photosynthetic pathway conserves more moisture~~ (Schulting, 1998; Lamb et al., 2014; Richards, 2015; Dotsika et al., 2019).

Carbon can also be used to differentiate terrestrial from marine based diets. Carbon in terrestrial food chains mainly derives from atmospheric carbon dioxide. In marine food chains, the main source of carbon is dissolved bicarbonate which is more enriched in $\delta^{13}C$ than atmospheric carbon. Diets reliant on marine sources are more positive than those reliant on terrestrial C_3 plants (Brown and Brown, 2011; Richards, 2015).

The nitrogen isotope ratio, $\delta^{15}N$, reflects the trophic level of the consumer. There is an increase of 3-5‰ between the plants and the herbivores that consume them. There is a similar increase between herbivores and their predators. Carnivores in long food chains can have very high $\delta^{15}N$ values. The longest food chains are typically found in marine ecosystems (Bogaard et al., 2007; Lamb et al., 2014; Richards, 2015; Dotsika et al., 2019). $\delta^{15}N$ can be affected by aridity, sea spray and manuring (Bogaard et al., 2007; Sluis et al., 2014).

Nitrogen and carbon values combined can more accurately differentiate diet (Brown and Brown, 2011; Dotsika et al., 2019). However, due to differences in the uptake of these isotopes at different locations by the species consumed, it is important to analyse

contemporary animal samples to create baselines for carbon and nitrogen when assessing human diets (Richards, 2015; Papathanasiou, 2015). Dietary isotope studies most commonly assess the carbon and nitrogen ratios of bone collagen. Collagen can survive quite well in the burial environment and is resistant to carbon or nitrogen diagenetic contamination from the local environment (Richards and Hedges, 2008; Richards, 2015). Different skeletal elements reflect differing periods in the life of an individual, due to remodelling and the rate of bone turnover. This rate differs with age and by element, but, for most bones, is generally thought to be a long process taking over a decade. However, the turnover rate and how it differs with age, health and by element is still poorly understood (Richards and Hedges, 2008; Schwarcz et al., 2010; Lamb et al., 2014; Richards, 2015). The petrous bone is not believed to remodel after infancy, and, therefore, should reflect foetal development until the age of two (Vanderpool and Turner, 2013; Snoeck et al., 2015). Teeth are formed incrementally, from the crown to the root, and do not undergo any remodelling. They, therefore, reflect the time at formation, with the tip reflecting a younger age than the root. The first molar (M1), the most commonly chosen tooth in this study, reflects the diet from utero until *c*. 8 years old (Schwarcz et al., 2010; Lamb et al., 2014).

Of note, though not conducted in this study, stable dietary analysis can also be conducted on bone apatite. Unlike collagen, apatite does not reflect predominantly the δ^{13}C of protein, but the δ^{13}C of protein, carbohydrates and lipids, thus providing clearer information on the main caloric contributors of diet, not just dietary protein. However, carbonate δ^{13}C values can be altered by the burial environment (Richards, 2015), so care needs to be taken with the interpretation of δ^{13}C apatite results.

Local animal carbon and nitrogen baselines are important due to geographical variance. A study of two British sites, 80km apart, showed increased nitrogen and carbon levels at one of the sites. However, an assessment of local animal baselines suggested that this difference was due to differences in the local isotope ratios instead of dietary differences (Bownes et al., 2018).

2.5 Zooarchaeology

Zooarchaeology is the study of archaeological animal remains, which includes bones, teeth and shells, as well as artefacts, literary sources and artistic representations (Tzedakis and Martlew, 2001; Albarella, 2017). Identifying the species present, as well as determining sex and age, can reveal much about the subsistence strategies of societies, including reliance on hunting versus pastoralism, and herd management (Reitz

and Wing, 2008; Gifford-Gonzalez, 2018). Palaeopathological analysis can elucidate animal health (Reitz and Wing, 2008; MacKinnon, 2010). Human-induced modifications, such as cut-marks and burning, can show butchery techniques, as well as cooking practices. Zooarchaeology can also be used to tackle further questions including reconstructing archaeological wildlife diversity and domestication; however, these are outside the scope of this thesis (Reitz and Wing, 2008; Albarella, 2017).

2.6 ZooMS

Animal bones are commonly found in archaeological sites and are important for human-animal interactions, including subsistence and diet. Faunal material is, however, often fragmentary due to human or taphonomic processes, making identification often difficult or impossible (Buckley et al., 2017). Zooarchaeological Mass Spectrometry (ZooMS) is a method of identifying taxa or even genus using the peptides in type 1 collagen. Collagen is insoluble, with a strong structure due to its coiled triple helix composition. The mineral component of bone can trap the collagen in a matrix, reducing its degradation (Buckley and Collins, 2011; Desmond et al., 2018; Brandt et al., 2018), and it survives well in many archaeological samples, and for much longer time periods than DNA. The Type 1 collagen targeted in ZooMS is the most abundant protein in vertebrates, particularly in bone (Buckley et al., 2010). Type 1 collagen has a triple helical structure, comprising of two identical alpha 1 (α1) chains and a genetically distinct alpha 2 (α2) chain (Buckley, 2018).

A typical analytical tool in ZooMS is Matrix-Assisted Laser Desorption/Ionization Time Of Flight (MALDI-TOF) Mass Spectrometry. This method irradiates the sample with a laser, and the time of flight of the peptide ions released is measured over a known distance, with larger peptide ions taking longer to traverse the distance than smaller ones. This produces spectra that displays the relative abundance of the ions detected, and creates a "peptide mass fingerprint", which can be compared to known spectra in order to identify the taxa or genus (Buckley et al., 2017; Brandt et al., 2018; McGrath et al., 2019). This method is of particular use when differentiating sheep from goats. Both species have long been major constituents of livestock populations, but are very difficult to differentiate through zooarchaeological assessment of bone (Buckley et al., 2010).

Chapter 3

A brief archaeogenetic history of Europe

To contextualise and understand the Bronze Age studies presented in this thesis, it is important to understand the genetic prehistory of Europe. This chapter provides a brief history of Europe, highlighted through relevant genomic studies. The archaeological background of the Bronze Age is further explained to describe cultural movements that may have impacted the samples analysed in my studies.

Ancient DNA survival (Section 2.2.1), accessibility of samples, research interests, and quality of accompanying archaeological information all impact any archaeogenetic interpretation (Booth, 2019). The summaries given here are broad, in order to provide background, and do not explore more localised histories. More in-depth backgrounds of Crete and Orkney are explored in Chapters 5 and 7 respectively.

3.1 Peopling of Europe

Fossil evidence suggests that anatomically modern humans (AMH) arose in sub-Saharan Africa approximately 200-400kya, before spreading out of Africa across the globe (Herrera and Garcia-Bertrand, 2018). Rather than multi-regional evolution, whereby AMH originated in several locations across the globe, population genetic evidence supports an out of Africa spread for humans, with the root of both mtDNA and MSY phylogeographic trees being in Africa. Genome-wide analysis also supports this, with a greater genomic diversity seen within Africa. This is consistent with the out of Africa model, as only a subset of original human diversity left Africa (Herrera and Garcia-Bertrand, 2018; Schlebusch and Jakobsson, 2018). Recent fossil evidence from Apidima cave in Greece has suggested that a migration of *Homo sapiens* out of Africa may have occurred as early as 210kya (Harvati et al., 2019), but there is some debate as to whether the skull in question belongs to a *H. sapiens* or to another species of *Homo* (Lumley et al., 2020). Despite this, and other potential migrations of

H. sapiens out of Africa, current genetic evidence, based on evidence from mtDNA, MSY and whole genome calculation of divergence of Sub-Saharan Africans from other populations, suggests that all extant AMH are the result of a migration 50-70kya (Skoglund and Mathieson, 2018; Haber et al., 2019; Vai et al., 2019; Bergström et al., 2020).

Fossil evidence suggests that AMH reached Europe around 45kya. Although earlier species of *Homo*, including Neanderthals, had already entered Europe before this time, when AMH arrived on the continent, only *Homo neanderthalis* was still extant (Fu et al., 2015; Herrera and Garcia-Bertrand, 2018). Whole genome analysis of modern humans demonstrates all non-African populations comprise 1.8-2.6% Neanderthal DNA. Oase 1, a 42-37kya individual from Romania, provided direct evidence of admixture with Neanderthals. Oase 1 had a Neanderthal ancestor 4 to 6 generations back (Fu et al., 2015; Herrera and Garcia-Bertrand, 2018; Yang and Fu, 2018; Villanea and Schraiber, 2019). By 40kya, Neanderthals had become extinct in Europe, although there is some evidence for the survival of small numbers in refugia for much longer (Fu et al., 2015; Devièse et al., 2017). Genetic divergence of West Eurasian (Europe, Anatolia, Near and Middle East) from East Asian lineages occurred between 55-45kya, as suggested by MSY and mtDNA phylogenies (Herrera and Garcia-Bertrand, 2018; Skoglund and Mathieson, 2018). This was further supported by analysis of Ust'-Ishim, a 45kya Russian individual who was equally related to both Upper Palaeolithic and East Asians. In comparison, Kostenki14 from western Russia, dating to 37kya, had ancestry that was part of a West Eurasian lineage (Fu et al., 2016).

Palaeolithic Europe witnessed a series of glacial expansions and contractions. During the glacial periods, humans were forced to retreat to lower latitude areas, referred to as glacial refugia. In West Eurasia, refugia are believed to have existed in the Iberian, Italian, and Balkan peninsulas, the Near East and Pontic-Caspian steppe. The use of these refugia created population bottlenecks (Pala et al., 2012; Gavashelishvili and Tarkhnishvili, 2016; Villalba-Mouco et al., 2019; Wren and Burke, 2019; Jones et al., 2020). Work by Fu et al. (2016) showed that during the Ice Age, Europe experienced little external migration. However, by the end of the Last Glacial Maximum, and after a period of warming around 14kya, most of Europe was largely homogeneous, having derived from a group that survived in the southern refugium of the Italian peninsula. This has been associated with expansion of the Gravettian culture. These Palaeolithic peoples are named by archaeogeneticists as the Villabruna Cluster, after a Gravettian site in Italy (Fu et al., 2016; Lipson et al., 2017; Skoglund and Mathieson, 2018; Herrera and Garcia-Bertrand, 2018; Villalba-Mouco et al., 2019).

The current geological epoch, the Holocene, began around 14kya, marking a period of relative climatic stability and the end of the Ice Ages. A corresponding human era, the Mesolithic, begins at this time. During the Mesolithic a largely genetically homogeneous group existed over much of Europe, commonly referred to as Western Hunter-Gatherers (WHG). These people have been interpreted as a genetic continuation of earlier Villabruna ancestry. A small amount of additional European Palaeolithic ancestry survived in southern Iberia (Fu et al., 2016; Lipson et al., 2017; Skoglund and Mathieson, 2018; Herrera and Garcia-Bertrand, 2018; Villalba-Mouco et al., 2019; Catalano et al., 2020). Another source of ancestry was present in western Russia, referred to as Eastern Hunter-Gatherers (EHG). Hunter-Gatherer populations in Scandinavia, eastern Europe and the Balkans fall on a cline between these two populations, and sit apart from the variation seen in modern-day people. Uniparental markers also suggest a high level of homogeneity, with the majority of WHG having mtDNA haplogroup U (mainly U5, but also U2 and U4 to a lesser extent) and MSY haplogroup of I (Jones et al., 2015; Fu et al., 2016; Lipson et al., 2017; Skoglund and Mathieson, 2018; Mathieson et al., 2018; Wang et al., 2019; Villalba-Mouco et al., 2019; Catalano et al., 2020). The Mesolithic population of Europe subsisted on hunting, gathering and fishing, and are largely considered to be partially or entirely nomadic (Richards and Schulting, 2006; Rowley-Conwy, 2011; Szécsényi-Nagy et al., 2015; Guilaine, 2017).

Outside of Europe, Palaeolithic and Mesolithic populations have been less extensively studied. However, the Mesolithic populations of Anatolia and the Caucasus appear genetically distinct from each other and those in Europe (Lipson et al., 2017).

3.2 Neolithic

Beginning around the mid-7th millennium BC, a series of major changes can be seen in the archaeological record in Europe. This is the start of the "Neolithic Revolution", a time period that saw the transition from hunter-gatherers to farming, the introduction of pottery, domesticated plants and animals, increased sedentism and land transformation (Rowley-Conwy, 2011; Szécsényi-Nagy et al., 2015; Guilaine, 2017; Mathieson et al., 2018). Archaeological evidence shows that the Neolithic began 10,000 years ago in the Fertile Crescent, before spreading through Anatolia and into southern Europe. From here it spread along two routes across Europe, along the Danube and along the Mediterranean (Zeder, 2006; Zeder, 2008; Szécsényi-Nagy et al., 2015; Hofmanová et al., 2016; Salavert, 2017; Mathieson et al., 2018). During this time, dietary isotopic analysis shows a move away from marine resources in several areas across Europe (Richards and Schulting, 2006; Bickle, 2018).

Whether the introduction of new technology and resources, and the accompanying societal changes were the result of the movement of people or ideas has been a major topic of debate in archaeology (Rowley-Conwy, 2011; Szécsényi-Nagy et al., 2015). Archaeogenetic analysis has revealed that across Europe the presence of Neolithic farmers was accompanied by a change in ancestry. These farmers were related to the peoples of northwest Anatolia, and were genetically distinct from the earlier Hunter-Gatherers of Europe (Jones et al., 2015; Szécsényi-Nagy et al., 2015; Skoglund and Mathieson, 2018; Wang et al., 2019). During this time new mitochondrial (including J, T, N1, X2, and H) and MSY haplogroups (G2) associated with the Anatolian Neolithic entered Europe (Fernández-Domínguez and Reynolds, 2017; Herrera and Garcia-Bertrand, 2018; Nikitin et al., 2019). Ancient DNA analysis indicates that Anatolian Neolithic farmers (ANF) migrated into the Balkans before spreading along the Danube and Mediterranean, suggesting a single source for both Danubian and Mediterranean migration (Mathieson et al., 2018; Wang et al., 2019; Nikitin et al., 2019; Sánchez-Quinto et al., 2019). Due to larger sample sizes, two groups are often used in archaeogenetic studies as proxies for the Danubian and Mediterranean routes: the Linearbandkeramik (LBK; so named after a particular pottery style) from Central Europe, and the Iberian Neolithic, respectively. In PCA and ADMIXTURE analysis, the ANF appear distinct from the WHG, with European farmers being admixed between ANF and WHG (Mathieson et al., 2018; Nikitin et al., 2019; Olalde et al., 2019). The contribution of WHG ancestry to Neolithic Europeans varies both with chronology and geography. Very little WHG is seen in Balkan and Central European groups, whereas there is increased WHG admixture in Iberia. During the Middle Neolithic, there is an increase in the WHG component in farming communities, which, in the Balkans, has been linked with a change in funerary customs (Haak et al., 2015; Mathieson et al., 2018; Nikitin et al., 2019; Olalde et al., 2019). Some exceptions to this pattern of admixture have been discovered in Latvia and the Ukraine, where farming people appear to be a continuation of Hunter-Gatherer populations. However, in the Late Neolithic, even these areas experience the introduction of steppe ancestry (Mathieson et al., 2018). In southeastern Europe, sporadic migration from the Caucasus also contributed to genetic variation (Mathieson et al., 2018).

3.3 Bronze Age

A number of major changes occurred during the Bronze Age, which began around 3000 BC. This included another large-scale change in the population genomics across

much of Europe. Y-chromosomal haplogroup diversity in Europe came to be dominated by haplogroups R1a and R1b, came during the Late Neolithic and Bronze Age, and today it is the most common MSY haplogroup in Europe (Allentoft et al., 2015; Haak et al., 2015; Olalde et al., 2018). Changes can be seen in the archaeological record such as the introduction of new technologies, bronze metal-working, domesticated horses, the wheel, and possibly the earliest forms of the Indo-European language (Kienlin, 2013; Herrera and Garcia-Bertrand, 2018; Wang et al., 2019). The migration of nomadic pastoralists from the Eurasian steppe, associated with the Yamnaya culture has been seen as the catalyst for these changes. Evidence of the Yamnaya (or pit-grave) culture is found from the Ural Mountains to the Ukraine. This steppe ancestry, of which the Yamnaya are the most frequently used representative, can be modelled as an admixture between Eastern (EHG) and Caucasus Hunter-Gatherers (CHG). CHG are another deeply divergent Eurasian population cluster, which was first identified in Mesolithic Georgia, and later in Mesolithic and Neolithic Iran (Lillie, 2004; Haak et al., 2015; Allentoft et al., 2015; Lazaridis et al., 2016; Skoglund and Mathieson, 2018; Herrera and Garcia-Bertrand, 2018; Mathieson et al., 2018; Wang et al., 2019). Ancient DNA analysis of Yamanya individuals demonstrate that whilst Groups in Russia comprise solely steppe ancestry, groups from the Caucasus and Europe also display the presence of Anatolian Neolithic and Western Hunter-Gatherer ancestry (Allentoft et al., 2015; Haak et al., 2015; Mathieson et al., 2018; Wang et al., 2019). The Russian steppe population had a high proportion of MSY haplogroup R1, which was rare outside this population before the Late Neolithic (Haak et al., 2015; Allentoft et al., 2015; Lazaridis et al., 2016; Skoglund and Mathieson, 2018; Herrera and Garcia-Bertrand, 2018; Mathieson et al., 2018; Wang et al., 2019).

During the early Bronze Age much of Europe is dominated by two cultural complexes named after their pottery styles: the Corded Ware Complex in northern and central Europe, and the Bell Beaker Complex in western Europe (**Figure 3.1**) (Olalde et al., 2018).

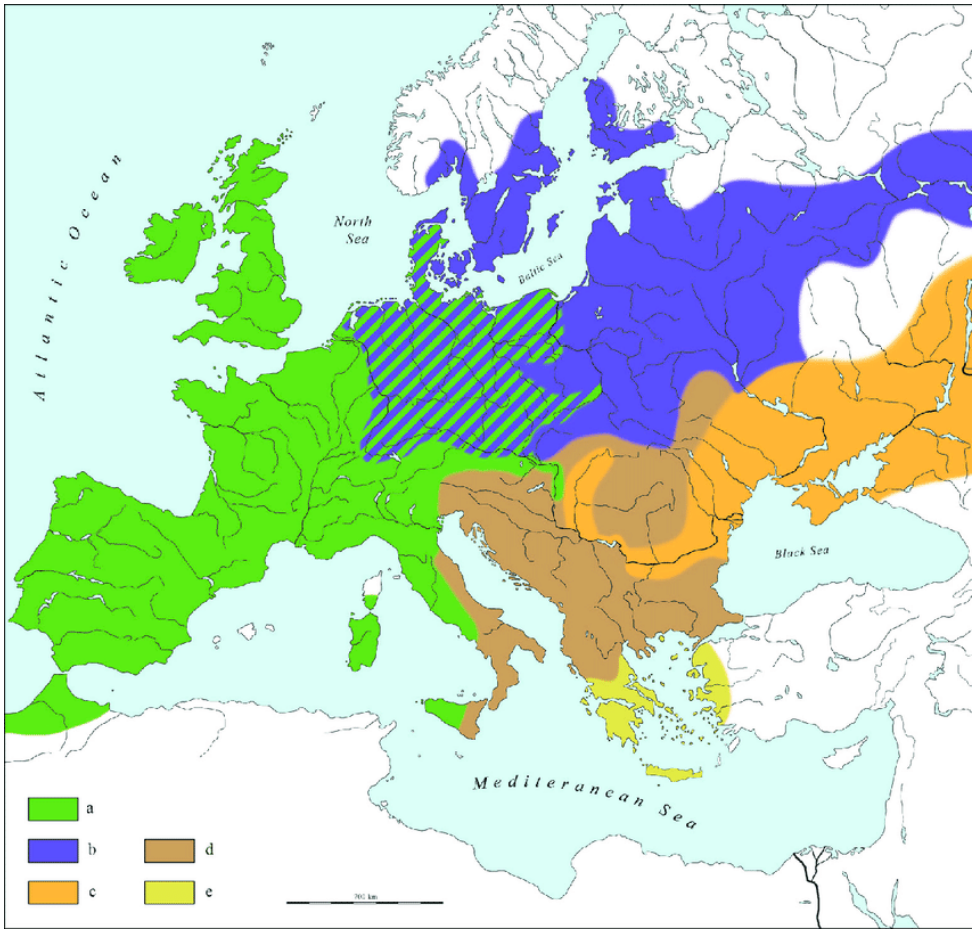


FIGURE 3.1: Early Bronze Age cultures from (Kadrow, 2016). A: Bell Beaker. B: Corded Ware. C: Yamnaya. D: Balkan cultures. E: Aegean cultures.

The 'Corded Ware culture' is named after the cord impressions found on the pottery. As well as this stylised pottery, this culture is associated with a number of other artefacts including amphorae, axe heads and flint flakes, usually found in single graves covered by a barrow. Lack of permanent settlement evidence has indicated that they employed a mobile herder economy, similar to that of the Yamnaya (Czebreszuk, 2004b; Sjögren et al., 2016). From around 3000 BC, the Corded Ware people exhibit a large steppe component in their genome and there is a near replacement of Y-chromosomal haplogroups associated with the Neolithic (Haak et al., 2015). Genome-wide analysis shows the presence of an admixture event between the earlier Neolithic population and incomers from the steppe similar to the Yamnaya (Allentoft et al., 2015). In some instances, the steppe component is greater in the autosomes than the X-chromosome, consistent with male-biased admixture; although this has not been identified in all Corded Ware sites (Mittnik et al., 2019). Strontium isotopes, which are influenced by local geology during childhood, are more variable in female skeletons in Corded Ware burials, suggesting that they were more likely to be buried

away from their place of birth than males. Evidence for the movement of women at higher frequencies than men indicates an exogamic system (Sjögren et al., 2016).

The other major Bronze Age culture defined by their pottery style is the 'Bell Beaker complex', found across central and western Europe, and from southern Scandinavia to Italy and central Europe to Iberia, Britain and Ireland. The Beaker people produced iconic thin-walled, handleless drinking vessels in the shape of inverted bells. Other grave goods commonly found in Bell Beaker assemblages include copper daggers, V-perforated buttons and items associated with archery, such as arrowheads and stone wrist guards (Czebreszuk, 2004a; Heyd et al., 2013; Olalde et al., 2018). There has been great debate over the possible origin or origins of this culture, and whether its spread was due to people or ideas. Ancient genomic analysis by Olalde et al. (2018) demonstrated the possibility of multiple origins for Bell Beaker culture, and they demonstrated that it could be modelled as the spread of both ideas and people. In central Europe, and Britain and Ireland, the Beaker culture is associated with an influx of steppe ancestry. In central Europe, there appears to be an admixture of this steppe component with the local Neolithic populations. The connection between Britain and central Europe can be seen in both the presence of steppe ancestry, but also the use of the 'All Over Corded' type of Beaker pottery in both areas. The steppe ancestry can be seen as contributing 50+% in central Europe and Britain (Olalde et al., 2018; Mathieson et al., 2018). A similar influx of steppe ancestry can be seen in France (Brunel et al., 2020), however, in contrast, the early Beaker period in Iberia (c.2500 BC) has similar genetic components to the earlier Neolithic period, with only a few sampled individuals having steppe ancestry. By 2000 BC, steppe ancestry comprised approximately 40% of the total ancestry in this area and, similar to other areas of Europe, there was a large scale replacement of the Y-chromosomal diversity, with R1b becoming the most prominent on the peninsula (Olalde et al., 2018; Olalde et al., 2019; Fernandes et al., 2020). In the Italian peninsula, R1b also becomes the dominant Y-chromosomal haplogroup, and approximately 30% of the genome comprises steppe ancestry (Antonio et al., 2019).

The Balkans cannot be described under an overarching cultural complex, as there were several burial customs and archaeological assemblages existing in the peninsula (Teržan and Karavanić, 2013). Settlements differ to most of the rest of Europe, with large tell sites (Brück and Fokkens, 2013). Archaeogenetic analysis indicates that the Balkan Bronze Age experienced a steppe contribution, however, like Italy, it only comprises 30% of the ancestry, lower than much of the rest of Europe. The presence of CHG ancestry (independent of accompanying EHG, which characterises the steppe

component), has been found in the Balkans in varying degrees since the Neolithic (Mathieson et al., 2018).

Most modern western Europeans can be modelled as mixtures of ancestries present in the Bronze Age: WHG, Anatolian Neolithic Farmers, and steppe pastoralists (Skoglund and Mathieson, 2018). The migrations of the Middle and Late Bronze Age resulted in relative homogeneity among European populations (Brunel et al., 2020); a consequence of which is that post-Bronze Age migrations may not be readily identifiable, particularly in low coverage samples (Martiniano et al., 2016; Brunel et al., 2020).

Chapter 4

Methodology

4.1 Ancient DNA laboratory methodology

4.1.1 Sample preparation

Samples were prepared in the dedicated Ancient DNA Facility at the University of Huddersfield under clean-room conditions. This facility is physically separated from all other molecular biology labs dealing with modern sources of DNA (Fulton and Shapiro, 2019), and has positive air pressure. Full body suits, face masks, two pairs of gloves and hairnets were worn throughout drilling, extraction and library creation. Equipment and surfaces were frequently wiped down using bleach and Look-Out®DNA Erase (Sigma-Aldrich) and exposed to UV light. Prior to processing, all samples were photographed, and sample surfaces were decontaminated by UV radiation for 30 minutes on each side. Samples were transported into the processing room in sterile plastic bags.

4.1.2 Sample processing

Under a fume hood, the external surface of the sample was removed using a 29μm aluminium-oxide powder air abrasive SWAM-Blaster system. This was to further remove potential contamination. A diamond-tipped circular saw attached to a hobby drill was used to sample relevant sections of the sample (tooth root or the densest part of the petrous bone Pinhasi et al. (2015)). The cut tooth/bone was reduced to powder using a Mixer Mill (Retsch MM400) for 30 seconds at a frequency of 30Hz/s. Powder was then transferred into O-ring tubes and weighed, and between 100 and 200mg taken for ancient DNA analysis, and between 250mg and 1g for isotope analysis.

4.1.3 DNA extraction

DNA extraction followed the protocol by Yang et al. (1998) with modifications by MacHugh et al. (2000). Extraction buffer was prepared as follows: 20μl of 1M Tris-HCl

(pH 8.0, to give 20mM final), 17μl of 20% SDS (0.5% final), and 940 μl of 0.5M EDTA (pH 8.0) were exposed to UV-light for 30 minutes before the addition of 13μl of proteinase K (200μg/ml final). 1ml of Extraction Buffer was added to each sample and the tubes were placed on a rotator and incubated at 37°C for 24 hours. This step ensured the solution was constantly mixed and prevented the formation of a hard pellet. The sample tubes were spun in a centrifuge at 13,000rpm for 10 minutes. The supernatant was removed and placed in a sterile 2ml O-ring tube and refrigerated. 1ml of new Extraction Buffer was added to the tube containing the precipitate, and samples were placed back on the rotator for a further 24 hours at 37°C. 30kDa filtration columns were prepared by adding 3ml of 10mM Tris-HCl. Samples were removed from the rotator and spun using the centrifuge at 13,000rpm for 15 minutes. The supernatant was transferred to the filtration columns and spun at 2,500rpm for 30 minutes. The flow-through was discarded, and a further 3ml of 10mM Tris-HCl was added to the columns and centrifuged again at 2,500rpm for 30 minutes. The liquid that remained above the filter (c.200μl) was collected and transferred to a sterile O-ring tube before being placed in the fridge for storage.

A QIAQuick MinElute Purification Kit was used to purify the extracted DNA. The standard (Qiagen) protocol was modified to include two 500μl PE wash steps (whereby the first flow-through was discarded) and the final elution step was undertaken with 100μl of EBT (supplied Elution Buffer and 0.05% Tween). In addition, the samples were placed on a 37°C heatblock for 15 minutes before the final centrifuge step. Purified DNA flow-through was stored in 2ml O-ring tubes in the fridge.

Blank controls from the sample processing and extraction stages were included to allow for detection and estimation of modern DNA contamination.

4.1.4 Library preparation and sequencing

Next-generation sequencing libraries were constructed using the methods outlined in Meyer and Kircher (2010), with modifications from Gamba et al. (2014) and Martiniano et al. (2014). Screened samples did not undergo USER®treatment, to allow assessment of DNA damage patterns for authentication purposes. Samples that were sent for in-depth shotgun high-throughput sequencing (HTS) did undergo USER®treatment in order to generate the most sequence data from the endogenous DNA as possible.

4.1.4.1 USER treatment

Uracil-Specific Excision Reagent (USER®) enzyme (NEBNext) is a UDG and Endonuclease VIII mix, which forms a single nucleotide gap at the location of a uracil. This is recommended for ancient DNA as uracil bases are the result of deamination (Section 2.2.1). 16.5μl of DNA extract was mixed with 5μl of USER enzyme, and incubated at 37°C for 3 hours.

4.1.4.2 Blunt-end repair

48.5μl blunt-end repair mix (NEBNext) was prepared for each sample (3.5μl End Prep Enzyme Mix, 7μl End Repair Reaction Buffer and 38μl ddH_2O). This mix was added to 21.5μl of DNA extract (USER treated for HTS) and incubated at 25°C for 15 minutes, then at 12°C for 5 minutes.

4.1.4.3 First sample clean-up

Sample purification was undertaken using QIAQuick MinElute Purification Kit (Qiagen). QiaQuick tubes were stored in the fridge prior to this stage. 350μl of binding buffer (PB) was added to each column before the sample was added, and then centrifuged at 13,000rpm for 1 minute. The flow-through was discarded, and 700μl of wash buffer (PE) added to each column. The column was again centrifuged at 13,000rpm for 1 minute, the flow-through discarded and the sample centrifuged at 13,000rpm for a further 1 minute to dry. The columns were placed in fresh sterile 1.5 ml tubes and 22μl of EBT (Qiagen 59.97μl EB plus 0.03μl of 0.05% Tween) added. After incubating at room temperature for a minute, the sample was centrifuged at 13,000rpm for 1 minute. The filtrate was transferred into 0.2ml PCR strip tubes.

4.1.4.4 Preparation of adapter mixes

Hybridization mix for adapters P5 and P7 (at 200μM each) were prepared on ice, as shown in **Table 4.1**. Each mix was incubated for 10 seconds at 95°C, then decreased from 95°C to 12°C at a rate of 0.1°C per second (which equates to a 1°C drop every 10 seconds over 84 cycles). Both mixes were combined (creating 100μM per adapter) and stored on ice.

Reagent	Volume x1 (μl)
IS1_adapter_P5.F (500μM) or IS2_adapter_P7.F (500μM)	0.2
IS3_adapter_P5+P7.R (500μM)	0.2
Oligo hybridization buffer (10x)	0.05
ddH_2O	0.05
Total	**0.5**

TABLE 4.1: Hydridization mix (200 μM). IS1_adapter_P5.F is used in P5 adapter mix, whereas IS2_adapter_P7.F is used in P7 adapter mix.

4.1.4.5 Adapter ligation

P5+P7 adapter mix prepared in Section 4.1.4.4 was used in this step. 20μl of T4 ligation mastermix was prepared per sample: 10μl ddH_2O, 4μl of 10x T4 DNA ligase buffer, 4 μl of 50% PEG-4000, 1μl Adapter mix (20μM each), 1μl T4 DNA ligase (5 U/ţl). 20μl of the sample was added to this and incubated for 30 minutes at 22°C.

4.1.4.6 Second sample clean-up

The second sample clean-up was undertaken following the same protocol as the first (Section 4.1.4.3), except that 200μl of PB was used.

4.1.4.7 Adapter fill-in

20μl of polymerisation mix (13.5 μl ddH_2O, 4μl of 10x Thermopol reaction buffer, 1μl of 10mM dNTPs, 1.5μl *Bst* polymerase large fragment (8U/μl)) was added to 20μl of sample. This was incubated for 30 minutes at 37°C, and then at 80°C for 20 minutes.

4.1.4.8 Amplification

42μl of amplification mix (41μl Accuprime Pfx Supermix, 1μl of 10μM primer IS4), plus 2μl of the appropriate indexing oligo, was added to 6μl of sample. These were then transferred to the modern lab in frozen PCR tubes, and amplification was run on an Applied BioSystems 2720 Thermal Cycler (**Table 4.2**).

Step	Temperature	Time	Cycles
Initial Denaturation	95 °C	5 minutes	1
Denaturation	95 °C	15 seconds	12
Annealing	60 °C	30 seconds	
Extension	68 °C	30 seconds	
Final Extension	68 °C	5 minutes	1
Hold	4 °C	Forever	1

TABLE 4.2: PCR protocol for whole ancient genome amplification.

4.1.4.9 Purification

The last stage of library preparation was a final purification step, which was performed using the QIAQuick MinElute Purification Kit (Qiagen). This was undertaken as previously, but with 125μl of PB and elution in 25μl of EBT buffer. The eluted purified library was stored in 2ml O-ring tubes in the fridge.

4.1.4.10 Library size measurement, pooling and sequencing

To quantify DNA concentration, 2μl of each library (including blanks) was measured using a Qubit 3 Flourometer (Invitrogen) using standard protocols.

A sub-sample of each library was then diluted five-fold with ddH_2O to allow assessment of fragment size distribution on a Bioanalyzer (Agilent), using the Agilent High Sensitivity DNA Kit. Successful libraries were pooled with approximately equimolar concentrations.

In total, my project involved screening of 55 samples, and HTS of 23 of these. Screening was undertaken on an Illumina MiSeq at Trinity College Dublin, Ireland. HTS samples were sequenced on an Illumina 4000 at Macrogen, Seoul, South Korea. The 14 samples with the highest endogenous content (**Table D.1**) were sent for HTS on seven lanes, two samples per lane, with three libraries each. Multiple libraries were sent to increase sequence complexity. A further nine samples were sent on two lanes with one library each, with either four or five samples per lane.

4.2 Bioinformatic methodology

4.2.1 Data processing and read mapping

Screened sequences were single-end. Adapters were trimmed using Cutadapt v.2.3 (Martin, 2011) with parameters (-m 34) to discard reads under 34bp length after trimming, and (-O 1) to allow a minimum overlap of 1bp between the read and the adapter.

Screened data were aligned to the human reference genome (hg19/GRCh37) with the mitochondrial genome replaced with the revised Cambridge Reference Sequence (rCRS, Accession number NC_012920.1). BWA 0.7.17 (Li and Durbin, 2009) was used for alignment, with the seed disabled (-l 16500) as recommended for ancient DNA (Schubert et al., 2012; Cassidy et al., 2016). The edit distance was set to 0.01 to allow for more substitutions (-n 0.01) and the amount of gaps allowed was raised (-o 2).

Samtools v1.9 (Li et al., 2009) was used to sort reads, and remove read duplicates and those with a mapping quality below 20 (-q 20).

Samples were assessed to calculate endogenous content. FastQC v0.11.7 and Qualimap v.2.2.1 were used to assess the quality of the sample. MapDamage 2.0.9 was used to check damage patterns characteristic of ancient DNA. The samples with the highest percentage of endogenous DNA were selected for further sequencing.

Samples sent for HTS sequencing were trimmed, and forward and reverse reads merged, using leeHom (Renaud et al., 2014). As recommended for ancient DNA sequences, the option –ancientdna was employed, which can merge paired-end reads that only share a partial overlap provided there is sufficient probabilistic support.

High-throughput sequences were aligned to the same reference using the same bwa parameters as the screening sequences.

BAM files were merged by sample using MergeSamFiles from Picard tools v2.9.2. PCR duplicates were removed and reads under 34bp in length, or mapping quality of less than 20, were removed using Samtools. MapDamage plots were used to identify the amount of damage at the ends of the reads. To reduce the effect of damage upon downstream analyses, soft-clipping of 2bp from both ends of each read was undertaken (Jakobsson and Mattias, 2019) using trimBam from bamUtil v1.0.14. The depth of coverage of the genome was estimated using Qualimap.

4.2.2 Molecular sex determination

Male and female skeletons differ due to sexual dimorphism, especially in the skull and pelvis, and can often be identified osteoarchaeologically. Experienced osteoarchaeologists working with complete pelvises and/or skulls have a 90-95% accuracy in determining sex. However, this number reduces with incomplete skeletons and is not generally possible for children (Mays, 2010). Sex determination is important for archaeological and bioinformatic reasons. Genetic sex can be determined from skeletal remains, following the methods outlined by Skoglund et al. (2013). For this thesis, the genetic sex of all individuals analysed was determined by calculation of the ratio of reads aligned to the Y-chromosome to reads aligning to both the X- and Y-chromosomes (R_y). Only reads with a mapping quality above 30 were considered. To be assigned as male, the R_y confidence interval (CI) lower bound had to be greater than 0.075. If the CI upper bound was lower than 0.016, the sample was assigned as female.

4.2.3 Contamination estimation

4.2.3.1 Mitochondrial contamination

Modern mitochondrial contamination was assessed using schmutzi (Renaud et al., 2015). The ContDeam command, of the schmutzi program, was used with the "–library double" option as the libraries analysed were paired-end. Samples were compared to all 197 modern haplotypes provided by schmutzi.

4.2.3.2 X-chromosome contamination

Using the results of the sex determination, contamination of male individuals was estimated using ANGSD v0.925-21-g5de79b5. As males are haploid for the X-chromosome, heterozygous sites within the X-chromosome are either due to error (sequencing or mapping) or the result of contamination (Rasmussen et al., 2011). The estimation was undertaken using the program's recommended guidelines in two stages. The first step creates a binary count file of the X-chromosome using the command "angsd -i file.bam -r chrX:5000000-154900000 -doCounts 1 -iCounts 1 -minMapQ 30 -minQ 20 -out <prefix>". This only takes account of reads with a mapping quality $\geq$30 and bases with quality $\geq$20. The second step used the latest c++ script "contamination", which performs Fisher's exact test and jackknife to estimate contamination, deliminating analysis to known HapMap polymorphic sites "-h RES/HapMapChrX.gz" (`http://popgen.dk/angsd/index.php/Contamination`). Contamination is identifiable at polymorphic sites due to greater mismatch rates (Rasmussen et al., 2011).

4.2.3.3 Nuclear genome contamination

The level of nuclear contamination was estimated using verifyBamID v1.1.3 (Jun et al., 2012). This method estimates autosomal contamination by checking if the reads in a sample file match previously known genotypes for an individual or population. The 1000 Genome reference panel (`ftp://ftp.1000genomes.ebi.ac.uk/vol1/ftp/release/20130502/ALL.wgs.phase3_shapeit2_mvncall_integrated_v5b.20130502.sites.vcf.gz`) was used for contamination estimation. The parameters "–verbose" and "–ignoreRG" were used, following the method of Günther et al. (2017).

4.2.4 Uniparental haplotype analysis

4.2.4.1 Mitochondrial haplogroup determination

Samples were aligned, merged and filtered to the rCRS using the same methods used for alignment to the human reference genome (Section 4.2.1). Consensus sequences

were generated using samtools mpileup (with the parameters -B and -Q30) and vcfutils.pl (vcf2fq) as in Jones et al. (2015), Cassidy et al. (2016), Günther et al. (2017), and Sánchez-Quinto et al. (2019). Haplofind (Vianello et al., 2013) was used to identify defining mutations and assign haplogroups. Mutations were also checked manually using IGV v2.4.16 (Robinson et al., 2017). Haplogrep v2.1.19 (Weissensteiner et al., 2016) was used to confirm mtDNA haplogroups, and individual libraries from each individual were double-checked to ensure a correct assignment.

4.2.4.2 Y-chromosome analysis

Samples designated as male were assigned to a Y-chromosomal haplogroup using Yleafv1.0 (Ralf et al., 2018). Aligned samples were input using the parameter "-bam". The minimum number of reads above the quality threshold was set to 1 "-r 1", and the quality threshold was set to 20 "-q 20". A base was accepted if it was present in 90% of the reads "-b 90". Transition mutations were removed to assign haplogroup without potential deamination bias. The output of Yleaf, in conjunction with the Y-chromosomal trees from ISOGG 2019 and Yfull YTree v7.06.00, were used to assign the haplogroup. Y-chromosomal assignment was double-checked using pathPhynder `https://github.com/ruidlpm/pathPhynder`, a program designed for determining Y-chromosomal haplogroups. This software also provides a pdf output, displaying the number of markers present or not present for a particular haplogroup.

4.2.5 Genotype calling

Ancient samples were called as pseudo-haploid. GATK (Genome Analysis ToolKit v3.8 (McKenna et al., 2010)) pileup was used to call all the bases present at each site. This method was chosen after assessing other genotype calling techniques C. Only biallelic SNPs that had a minimum base quality of 30 were considered. A random base covering the position was called and the allele was presumed to be homozygous. This is a common practice in ancient genomic studies, as samples often have too low coverage for diploid calling (Günther and Nettelblad, 2019).

In order to conduct population genetics on the samples and compare them to previously published datasets, they were called with the following datasets:

Dataset 1: Affymetrix Human Origins (Patterson et al., 2012; Lazaridis et al., 2014; Lazaridis et al., 2016)
The Human Origins dataset consists of 2068 modern-day individuals from 166 populations covering 597,573 SNP positions. This dataset was used to perform PCA and

unsupervised ADMIXTURE analysis. For the PCA, only West Eurasian populations were selected.

Dataset 2: Autosomal SNPs from the 1240K SNP array.
All ancient individuals were screened for the 1,150,639 autosomal SNPs in this panel. Samples that overlapped with the panel were used for *D*-statistics and outgroup-f3 analysis. This dataset incorporates all the SNPs from Dataset 1; however, there is currently not enough modern data, which is required for ADMIXURE and PCA, publicly available for Dataset 2.

Dataset 3: 1000 Genomes Project (Consortium, 2015)
The 1000 Genomes Project was filtered biallelic transversion SNPs with a minor allele frequency of at least 10% in Europeans. This dataset was used for READ analysis. As much of the comparative data were generated using capture protocols from the 1240K SNP array, this dataset was not used in other statistical tests.

Ancient published samples: These were realigned following the same methods as outlined in Section 4.2.1, to be used as comparative reference for analysis.

4.2.6 Kinship analysis

Kinship analysis was primarily undertaken using the program READ (Relationship Estimation from Ancient DNA) (Kuhn et al., 2018). This program can be used on samples with low coverage, requiring only 1000 overlapping SNPs between the two comparative individuals. READ can identify four levels of relatedness: "Identical Twin/Same Individual", "First Degree", "Second Degree", and "Unrelated". Dataset 1 and 3 were used for READ analysis.

4.2.7 Principal Components Analysis

Principal Components Analysis (PCA) can reveal ancient population structure, such as long-term isolation-by-distance (Schiffels et al., 2016).

PCA plots were generated using modern genetic variation from the Human Origins Project (Patterson et al., 2012; Lazaridis et al., 2014; Lazaridis et al., 2016) using Smartpca v.16000 from EIGENSOFT (Patterson et al., 2006). Ancient samples were projected onto this background using the option "lsqproject: YES". This option is used for samples with missing data by solving least-squares equations. PCA plots of West Eurasian variation were created using 879 modern West Eurasian individuals from 61

populations from the Humans Origins Project (Patterson et al., 2012; Lazaridis et al., 2014; Lazaridis et al., 2016).

4.2.8 ADMIXTURE

ADMIXTURE v1.3.0 (Alexander et al., 2009) was used to estimate different ancestry components of the ancient samples in relation to modern populations and published ancient samples. The dataset was been pruned for Linkage Disequilibrium (LD) using plink v1.9, with the parameters (–indep-pairwise 200 25 0.4) leaving 351,826 SNPs.

Unsupervised ADMIXTURE analysis was performed using 2,149 present-day individuals from 167 worldwide populations, along with 1,171 ancient samples **(Appendix F)**. ADMIXTURE was run was with cross validation (–cv) for all ancestral population numbers from $K = 2$ to $K = 20$. The lowest CV error indicates which K has the best maximum log likelihood. ADMIXTURE analysis was replicated 20 times (using –seed time to ensure random seed) to ensure consistent results.

4.2.9 *f*-statistics

F-statistics measure shared drift or shared evolutionary history between samples or populations. This is undertaken by comparing allele frequencies (Patterson et al., 2012; Peter, 2016). The *f*-statistics tests used in my thesis compare the allele frequencies of two or more samples/populations in comparison to an outgroup, in order to measure the shared drift in comparison with two or more tested samples/populations.

4.2.9.1 outgroup-f3

Outgroup-f3 analysis was performed using qp3Pop v.412 from ADMIXTOOLS (Patterson et al., 2012). An outgroup-f3 test measures the shared drift between two test populations in comparison to an outgroup population. The higher the resulting $f3$ value, the more similar the shared drift. Modern-day Mbuti were used as an outgroup population in all analyses. As the Mbuti are a sub-Saharan population from the Congo, they have a long divergence from non-African populations and are commonly used in population analyses as an outgroup. Results with $|Z| > 2$ were taken to be significant.

4.2.9.2 *D*-statistics

D-statistics were performed using qpDstat from ADMIXTOOLS. The *D*-statistic can be used to identify which two of three samples share greater drift in comparison to an outgroup (Patterson et al., 2012). *D*-statistics are used to detect gene flow between

closely related groups (Zheng and Janke, 2018). Results with $|Z| > 3$ were taken to be significant, except in cases where, due to low coverage, this was reduced to $|Z| > 2$.

4.2.9.3 qpAdm

qpAdm determines whether the genetic ancestry of a target sample can be plausibly modelled from one or more source populations (Harney et al., 2021). The target sample and potential sources are referred to as "Left" populations. A set of "Right" populations is also required, and should be a set of outgroups or populations that are more distantly related to the target than those in the "Left" list. QpAdm calculates all possible statistics of the form f4(Left1, Left2; Right3, Right4). The test sample/population and potential source populations are classed as "Left", while outgroups and more distantly-related populations are classed as "Right". This method produces a p-value for the fit of the model, as well as admixture proportions (Fernandes et al., 2020; Harney et al., 2021). To model ancestry, and test relative admixture proportions of individuals, qpAdm from ADMIXTOOLS was used, with option allsnps: YES. "Right" populations were as follows, unless otherwise specified: Mota (Ethiopia 4500BP), Ust_Ishim (Russia), Kostenki14 (Russia), GoyetQ116_1 (Belgium), Vestonice16 (Czech Republic), MA1 (Russia), ElMiron (Spain), Villabruna (Italy), Natufians (Israel), Jordan_PPNB (Fu et al., 2014; Raghavan et al., 2014; Llorente et al., 2015; Fu et al., 2016; Lazaridis et al., 2016).

4.2.9.4 Sex-biased admixture

Following the methodology in Mathieson et al. (2018), evidence of sex bias was determined by comparing qpAdm from the autosomes and the X-chromosome. Differences in the proportions imply sex-biased admixture, as males only inherit a maternal X-chromosome. The option "chrom: 23" was added to the qpAdm parameter file to calculate the ancestry proportions on the X-chromosome. Z scores were calculated using the formula:

$$Z = (Pa - Px/\sqrt{\delta a^2 + \delta x^2})$$

Pa and Px are the autosomal and X-chromosomal qpAdm proportions for a population and δa and δx are the autosomal and X-chromosomal standard errors for the same population as the proportion values. Positive Z scores indicate that more males than females contributed to the admixture.

4.3 Dietary isotope analysis

Collagen extraction was undertaken in the University of Huddersfield (GF001-GF059) and RLAHA (Research Laboratory of Archaeology and History of Art), University

of Oxford (animal samples). Approximately 0.25-1g of bone powder was prepared (Section 4.1.1) at the University of Huddersfield. Standard procedures following (Richards and Hedges, 1999) were employed for collagen extraction. The bone was demineralised in approximately 10ml of 0.5M HCl at 4°C for 24 hours until it had finished reacting. The samples then underwent three rinses using Milli-Q deionised water to osmotically remove chloride ions. Weak HCl (pH3) was added to the samples, which were then sealed and placed on a heat block for 48 hours at 70°C, to allow gelatinisation. Samples were filtered using Ezee®-filters to remove any debris, and freeze-dried to remove any remaining water. Approximately 1mg of collagen was weighed into tin capsules.

Samples were analysed at RLAHA and compared with laboratory and international standards (alanine, USGS40 and USGS41) that were interspersed in the analytical run. Samples were combusted on a SerCon 'Callisto CF-IRMS' system, and results corrected using a three-point calibration relative to the in-house standards, whose values can be compared to the international standards of Vienna Pee-Dee Belemnite (VPDB) for carbon and Ambient Inhalable Reservoir (AIR) for nitrogen.

Samples with C:N ratios outside of 2.8-3.6, the expected range of C:N from diagentically unaltered mammalian collagen, were excluded from further analysis (DeNiro, 1985). In addition, sample GF035 was excluded due to having very low C and N yields.

4.4 Zooarchaeological analysis

4.4.1 Osteological identification of the animal remains

Zooarchaeological examination of the animal bones was undertaken at the University of Sheffield, with assessment by Dr. Umberto Albarella and Dr. Angelos Hadjikoumis. Identification and analysis of animal bones is important for dietary stable isotopic analysis of human remains, as they can be used to create dietary reference points, and provide insight into subsistence practices.

4.4.2 Zooarchaeological Mass Spectrometry

Zooarchaeological Mass Spectrometry (ZooMS) was undertaken at the Manchester Institute of Biotechnology, University of Manchester, under the supervision of Dr. Michael Buckley, following (Buckley et al., 2010). Collagen prepared in Section 4.3 underwent ultrafiltration into 50mM ammonium bicarbonate, and then underwent digestion

with sequencing-grade trypsin for 18 hours at 37°C. C18 ZipTip®pipette tips were prepared with one bed volume of 50%ACN/0.1%TFA (trifluoroacetic acid), followed by one bed volume of 0.1% TFA. This was to calibrate and zero the tip respectively. After the digestion, the samples were centrifuged at 13,000g for 10 minutes. The supernatant was acidified to 0.1% TFA and applied to the pipette tip. Two wash steps of 0.1% TFA were applied to the pipette tip to further purify the sample. In order to fractionate the sample, 100μL of first 10%, and then 50%, acetonitrile (ACN) in 0.1% aqueous TFA were applied to the pipette tip, and the eluting peptides were collected. The fractions were dried in a centrifugal evaporator and then re-suspended with 10μL of 0.1% TFA. 1μL of sample solution was then spotted, in triplicate, onto a Bruker ultraflex II target plate, and mixed together with 1μL of α-cyano-4-hydroxycinnamic acid matrix solution and allowed to dry. Each spot was analysed by MALDI-MS using a Bruker ultraflex III MALDI TOF/TOF mass spectrometer equipped with a Nd:YAG smart beam laser. The resulting spectra were compared to a known database of samples held at the Manchester Institute of Biotechnology.

Chapter 5

An introduction to Crete and Greece

The impact of the Bronze Age on the southeastern fringe of Europe was studied by using the Late Bronze Age necropolis of Armenoi, Crete, as a case study. To understand the genetic makeup of the Armenoi individuals, it is important to understand the demographic changes of Crete leading up to the Late Minoan Period and how the Minoan and Mycenaean cultures differed.

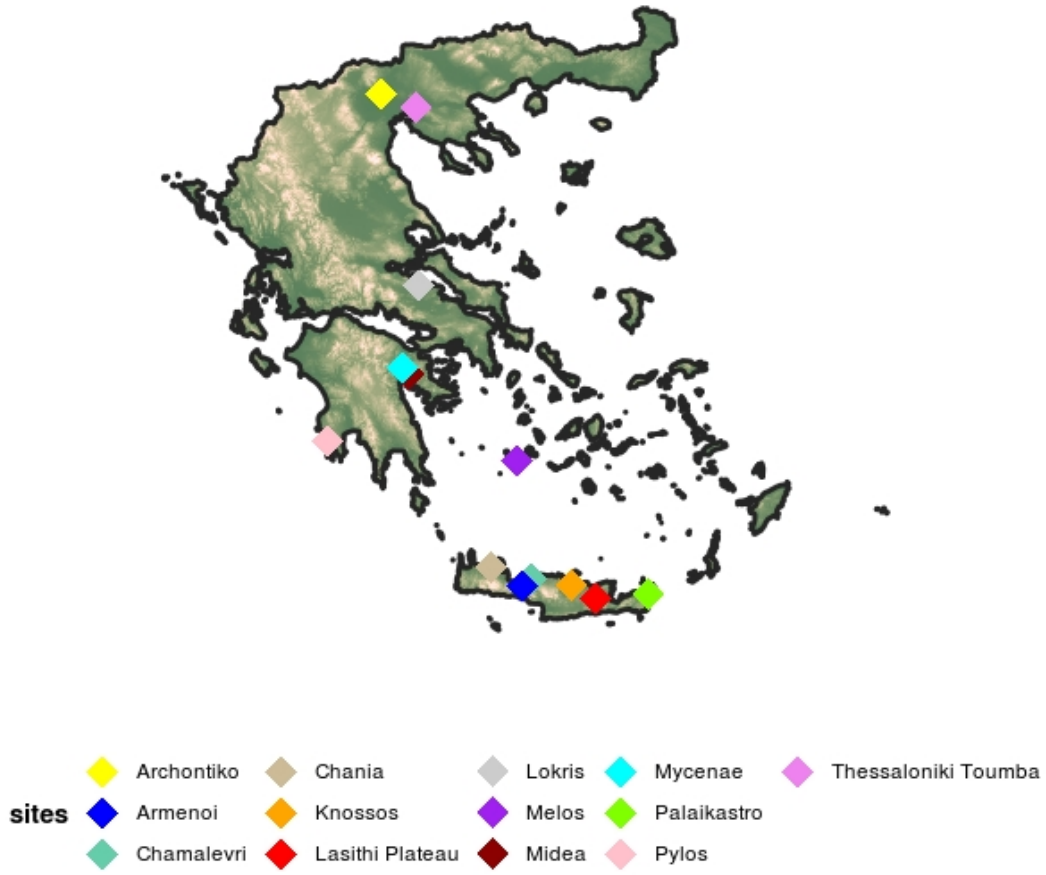


FIGURE 5.1: Map of archaeological sites mentioned in Chapters 5 and 6.

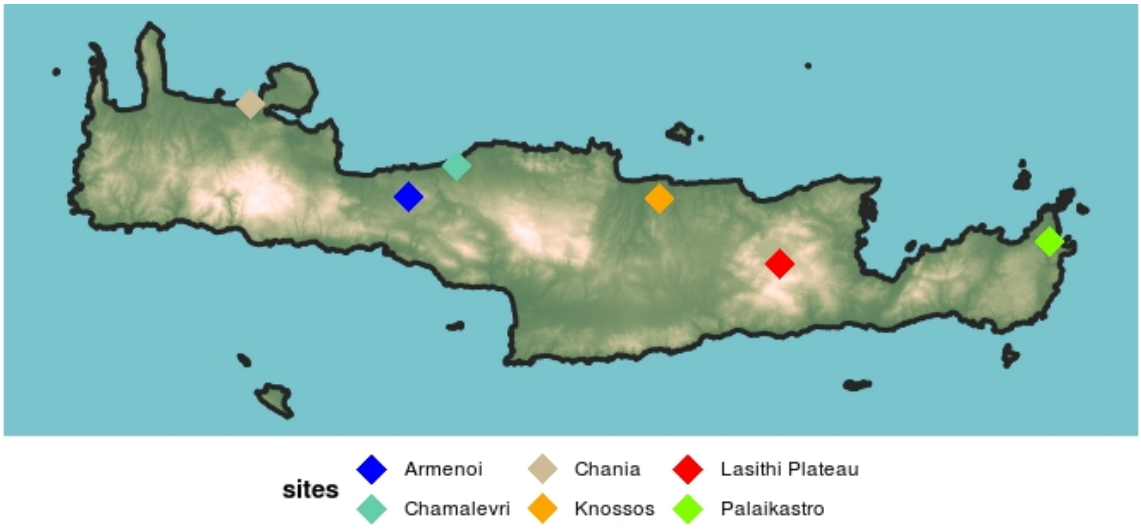


FIGURE 5.2: Map of archaeological sites of Crete mentioned in Chapters 5 and 6.

5.1 Geography of Crete

Crete is the fifth largest island in the Mediterranean. It is the most southerly Greek island, c.250km in length but ranging from only 12-56km north to south (Day, 2014). The centre of the island is characterised by large mountain ranges and deep gorges, which have largely restricted settlement to the coastlines and upland plateaus (McEnroe, 2010; Ripoll, 2013; Day, 2014). The island is located almost equidistant between mainland Greece, Anatolia, and Libya, and, like several other islands in the Aegean Sea, it acts as a "stepping stone" between Anatolia and Greece (Broodbank and Strasser, 1991; Nowicki, 2014; Herrera and Garcia-Bertrand, 2018; Berg, 2019).

5.2 Archaeology of Crete

5.2.1 Earliest settlement of Crete

The date of the earliest arrival of modern humans on Crete has been a topic of debate (Nowicki, 2014). Traditionally this has been dated to a Pre-Pottery Neolithic settlement layer at Knossos dating to 7000 BC (Nowicki, 2014; Herrera and Garcia-Bertrand, 2018). However, over the past decade, studies of lithic material and cave paintings have suggested an earlier occupation of Crete dating to the Mesolithic or even Palaeolithic (Strasser et al., 2018). but this early evidence is very scarce, suggesting that humans may have only used the island temporarily or seasonally (Horwitz, 2013; Efstratiou, 2013; Strasser et al., 2018). As Crete has been separated from the mainland since the Pleistocene, humans would have had to arrive via boats (Strasser et al., 2011), so it is possible that the changing coastlines could have destroyed any evidence of hunter-gatherer populations (Nowicki, 2014). If there were people in Crete in Mesolithic times,

it is unlikely that it would have been a large population, since the island would have been devoid of large and medium sized mammals (Ripoll, 2013; Horwitz, 2013; Efstratiou, 2013). there is also no evidence of Mesolithic material culture at the early Neolithic site of Knossos (Efstratiou, 2013).

5.2.2 Neolithic Crete

Crete is the second Mediterranean island, after Cyprus, to show evidence of Neolithic settlement (Horwitz, 2013). Knossos was the first large-scale permanent settlement of Crete and dates to the Pre-Pottery Neolithic c. 7000 BC (Day, 2014; Nowicki, 2014; Herrera and Garcia-Bertrand, 2018). The origins of the people at this settlement has been strongly debated, due to the location of Crete between Anatolia, Greece and North Africa (Horwitz, 2013; Efstratiou, 2013). The long, uninterrupted distance from North Africa, and the presence of predominant north/north-west winds throughout the year, make this an unlikely journey (Broodbank and Strasser, 1991; Agouridis, 1997; Nowicki, 2014; Berg, 2019). Some of the earliest radiocarbon dates of the Greek Neolithic are found on Crete (Carter et al., 2016; Douka et al., 2017), and similarities in material culture and farming techniques make Anatolia the most probable source of the Cretan Neolithic in Knossos (Papathanasiou, 2005; Martin, 2013; Horwitz, 2013; Day, 2014; Carter et al., 2016; Douka et al., 2017; Herrera and Garcia-Bertrand, 2018).

The Neolithic settlers introduced domesticated plants (emmer, wheat barley and legumes), domesticated animals (sheep, goats, cattle, pigs and dogs) and wild animals (martens, deer and badgers) to Crete (Papathanasiou, 2005; Ripoll, 2013; Horwitz, 2013). Pre-Pottery and Early Neolithic settlement on Crete appears to be small and only represented at Knossos. It is possible that in part this may be due to preferential excavation at Knossos, destruction of coastal sites or settlements that only enjoyed short lifespans. Despite its small settlement size, Crete was involved in trade networks with the mainland and other islands, as evidenced by the presence of obsidian from Melos in Crete (Efstratiou, 2013; Nowicki, 2014). In the Middle and Late Neolithic, there is an increased number of settlements in Crete, which increases in the Final Neolithic/Early Bronze Age, possibly as a result of further migration events from the east (Legarra Herrero, 2009; Nowicki, 2014).

5.2.3 Bronze Age Greece

The Greek Bronze Age lasted from 3000 BC until 1000 BC. This period gave rise to several societies, the most significant for this study are the Minoan and Mycenaean cultures.

5.2.3.1 Notes on chronology and terminology

During the historical, Classical Greek period, the Bronze Age was often depicted as an Age of Heroes, such as Homeric poems of the Iliad and the legend of King Minos. Early archaeologists named cultures, archaeological sites and features based on their understanding of these myths

(Higgins and Morgan, 1967). In the 2nd century AD, Pausanias stated "Most matters of Greek history have come to be disputed" (Jones, 1918; Martin, 2013); this is still true, particularly when referring to the Greek Bronze Age. Despite over a century of study, several debates exist over the chronology of Bronze Age Crete (Biers, 1996). Earliest chronologies were developed by assessing the changes in the makeup and style of material culture assemblages. As a result of several distinct regional variations, differing chronologies were developed for the Aegean islands, the Greek mainland, Anatolia and Crete (Manning and Cline, 2010). On Crete alone there exists two chronologies: Minoan and Palatial (Biers, 1996). Due to limited radiocarbon dating in Greece, Aegean chronologies rely on material culture chronologies and, therefore, relative, not absolute, dates (Wardle et al., 2014; Jones et al., 2017; Cosmopoulos et al., 2019; Katsianis et al., 2020).

The Minoan culture is named after the legendary King Minos (Biers, 1996; Legarra Herrero, 2009; Day, 2014). Minoan chronology was developed by Sir Arthur Evans in 1906, and is based on the changes in pottery style seen through stratigraphic layers excavated at Knossos. Knossos was the first excavated, and the largest, Minoan site (McNeal, 1973; Biers, 1996; Manning and Cline, 2010; Douka et al., 2017). The second chronological system is the Palatial chronology, based on the architectural changes of the 'palatial' structures (Manning and Cline, 2010).

Several criticisms have been levelled at both of these chronologies. The use of the term "Minoan" for both the society and chronology implies a continuous, relatively homogeneous society, without outside influences (Legarra Herrero, 2009). However, changes in material culture do not occur universally and concurrently. One such example is that Early Minoan (EM) III styles are continued in eastern Crete when much of the rest of the island has adopted Middle Minoan (MM) styles (Manning and Cline, 2010). The 'palatial' chronology as a term also has several issues, the most obvious being that it has connotations with modern palaces and monarchical societies (Schoep, 2006). These 'palatial' structures are thought to be multi-functional centres of power and distribution centres (Martin, 2013; Day, 2014), but what defines 'palatial' structures is unclear, as not all share the same features (Schoep, 2006). Both systems of relative dating have been accused of causing a Knossos-biased chronology (Legarra Herrero, 2009), which does not accurately reflect the island as a whole. For clarity, this dissertation will use, whenever possible, absolute dates or Minoan chronology.

Bronze Age	Minoan chronology	Years (BC)	Palatial chronology
Early Bronze Age	Early Minoan (EM)	3100-2100	Pre-Palatial
Middle Bronze Age	Middle Minoan (MM) IA	2100-1925	
	MM IB	1925-1875	Proto-palatial
	MM II	1875-1750	
	MM III	1750-1700	
Late Bronze Age	Late Minoan LM I	1700-1470	Neo-palatial
	LM II	1470-1430	Final palatial
	LM III A-B	1430-1200	
	LM III C	1200-1150/00	Post-palatial

TABLE 5.1: Minoan chronology, following Manning and Cline (2010).

5.2.3.2 Minoans

The Early Bronze Age in Crete is dated to 3000 BC, marking the start of the Early Minoan Period. Instead of a sudden shift from the Neolithic, the Early Minoan can be seen as a continuation of practices. Increased maritime trade can be seen, with imports from the Cyclades, mainland Greece, Syria and Egypt. This maritime network is iconic of the later Minoans (Tomkins and Schoep, 2010). In addition, colonisation of less productive land increases at this time.

During the Middle Minoan period, society moved from being egalitarian, with several small-scale rulers, to a more complex, state-like society, with central administrative centres (Schoep, 2006; Tomkins and Schoep, 2010; Schoep, 2010). The number of 'Palatial' structures increases at this time. Their function is not entirely clear, but they are believed to have been involved in administrative, economic and religious events (Schoep, 2010). Two alphabets, Cretan Hieroglyphic and Linear A, were developed during the Middle Minoan. Cretan Hieroglyphics were used mainly in the north-central and north-eastern areas of Crete, whereas Linear A was predominantly used in the south. Cretan Hieroglyphics were discontinued after MMIII, whereas Linear A could be found all over the island. The different scripts have been hypothesised to illustrate disunification in Crete (Tomas, 2010). Linear A and Cretan Hieroglyphic are both undeciphered, and are believed to represent an unknown Non-Indo-European language (Tomas, 2010; Martin, 2013; Day, 2014).

Crete undergoes several dramatic changes during the Late Minoan Period, c. 1700-1100 BC. During LMI, the Minoan civilisation appears to have flourished, with new buildings, manufacture of wealthy high status, and importation from across the Mediterranean. The Minoan trade network was thriving, with Minoan artefacts being found around the Mediterranean. However, by the end of this period, a number of palatial structures and towns show evidence of severe destruction (Hallager, 2010). This may be a result of Crete being earthquake prone, due to its position at the edge of the Eurasian and African plate boundaries. The eruption of

Thera, sometime around 1600-1525 BC, is also thought to have had a devastating effect (Giże, 2018a). An increased presence of Mycenaean pottery is found in Crete during LMII, with a decline of many Minoan towns, with the exception of Knossos. This period ends with a destruction event at Knossos, the reasons for which are unclear; but it might also be evidence of a Mycenaean invasion force (Preston, 2004; Hallager, 2010).

LMIIIA-B represents a major change in Crete. This has often been interpreted as a Mycenaean invasion (Legarra Herrero, 2009; Hallager, 2010). Linear B tablets have been argued to indicate the presence of a ruling Mycenaean elite. Despite the name, Linear B is unrelated to Linear A, but instead was the script of mainland Mycenaeans, representing an early form of Greek, an Indo-European language. During MM-LMII, settlements are commonly found, whereas tombs are not; however, the converse is true during LMIII. Architectural changes are seen during this time, from multi-storied wooden buildings to single-storey stone buildings (Hallager, 2010). Although the Minoan peak and cave sanctuaries fall out of use (Lupack, 2010), the appearance of high status tombs indicates an importance of symbolism, so that the elite can display their political power (Preston, 2004). These changes were not universal across Crete and have been used to argue for adoption of Mycenaean culture or an elite takeover of Crete, rather than a mass migration (Day, 2014; Preston, 2004).

5.2.3.3 Mycenaeans

The Mycenaean civilisation developed, expanded and collapsed during the Late Bronze Age, which roughly corresponds to the Late Minoan period in Crete (c. 1700-1100 BC). The Mycenaean culture is named after the palatial site at Mycenae (Manning and Cline, 2010; Shelton, 2010). Competition between mainland city states is thought to have led to the development of Mycenaean culture, and it was influenced by its contact with Minoans and other Aegean societies in the early periods (Shelton, 2010). The location of Mycenaean sites near water and quality agricultural land, in commanding positions provided them strategic control and protection of economic resources. This is further evidenced as some of these sites were fortified (Manning and Cline, 2010). Unlike Minoan 'palatial' structures, which were designed around a court with no throne room, Mycenaean palaces are based around a central throne room (Nakassis et al., 2010). Mycenaean states also differ as they appear to have valued elite individuals over the community. Wealthy tombs signalling elites can be found in Mycenaean settlements (Nakassis et al., 2010), and often highlight the individual's prowess in hunting and warfare (Manning and Cline, 2010). At its peak Mycenaean culture included the Peloponnese, Crete, the Dodecanese, as well as parts of Attica and Boeotia.

At the end of the Bronze Age, there is evidence of the destruction of many Mycenaean palaces and settlements across mainland and island Greece (Shelton, 2010). It is not clear why the Mycenaean civilisation collapsed, but other eastern Mediterranean civilisations also collapse at this time, including the Hittite empire. War, as evidenced by Homeric epics

and the Sea Peoples of Egyptian texts, climate change, natural disasters, famine, plague or a combination of these have all been suggested as possible reasons for this wide-scale civilisation collapse (Castleden, 2005).

5.3 Archaeogenetic background

5.3.1 Analysis of modern variation

Modern variation has been used to extrapolate Crete's past. Earlier studies focused on uniparental markers. A study of Cretan Y-haplogroups by Martinez et al. (2007), found differences between a modern 'refugia' of the Lasitihi Plateau, and other locations across the island, possibly indicating multiple migrations. The results were thought to highlight an affinity to the Balkans and North Italy. R1 represented the most frequent haplogroup on the island, which was interpreted as having a potential Palaeolithic origin. More recent studies have often associated the spread of R1 as being predominantly associated with the spread from the steppe following the early Bronze Age (Haak et al., 2015). King et al. (2008) also analysed Y-haplogroups from Crete, and also observed R1 lineages constituted the majority. The interpretation in this study focused on other lineages, and concluded that there was no genetic evidence of pre-Neolithic occupation of the island, and that the overall diversity had a closer affinity with Turkey and Lebanon than Greece. Similarities to mainland Greece were used to argue a potential Mycenaean impact on the island. Mitochondrial analysis by Martinez et al. (2008) identified a difference in haplogroup diversity between the Lasithi Plateau and other areas of Crete. This study suggested a Middle Eastern origin of the Cretans, with later European influences to the island. It is important to note that these two studies did not use the full uniparental markers, instead focusing on STR (Y) and the D-loop (mtDNA) respectively.

Modern whole genome studies have been used to infer past migrations to Greece and Crete. Sarno et al. (2017) identified fine-scale differences within the Greek population, particularly between the mainland (northern, central and Peloponnesian Greeks) and the islands (Crete, Cyprus and the Dodecanese). This study identified the island populations as clustering closer to southern Italians and Sicilians than mainland Greek populations, and the mainland populations clustering with Albanians and Kosovars. Studies by Paschou et al. (2014) and Stamatoyannopoulos et al. (2017) also identified differences between island and mainland Greece. Both studies concluded that Greece acted as a genetic link between southern Europe and the Near East, with Crete, Cyprus and the Dodecanese identified as being more similar to Near Eastern populations compared to Peloponnesian, northern and central Greek populations. The studies by Paschou et al. (2014) and Sarno et al. (2017) concluded that the Neolithic entered Europe through the southern Mediterranean, including Crete, and that a predominant Neolithic component is still present in this area today.

A study of 240 modern Peloponnesians was used to investigate a supposed near-total replacement by Avar and Slavic invaders in the 6th century AD (Stamatoyannopoulos et al., 2017). This study rejected the replacement hypothesis, noting the difference between modern Peloponnesian Greeks and modern Slavic groups. A fine-scale analysis of modern Cretans (Drineas et al., 2019) aimed to identify the effects of prehistorical and historical migrations to Crete. PCA and ADMIXTURE analysis placed Cretans with southeastern Europeans, yet Identity By Descent (IBD)-sharing demonstrated a link with modern Eastern Europeans. The PCA and ADMIXTURE results suggested a link to the Neolithic expansion, whereas the high IBD with eastern Europe was thought to potentially relate to the expansion of the Mycenaeans, although several other potential possibilities were also suggested.

Analysis of modern DNA variation has resulted in somewhat conflicting interpretations, as it has an inherent bias with the assumption of genetic continuity in these areas. Without ancient DNA, there is no way to identify how similar the ancient populations from these regions are to their modern counterparts.

5.3.2 Ancient DNA analysis

Ancient DNA analysis has been conducted on both Minoan and Mycenaean individuals, both in Crete and the mainland. Many of the early studies had high failure rates and low resolution (Bouwman et al., 2008; Chilvers et al., 2008; Hughey et al., 2013), with the most successful, conducted by Hughey et al. (2013), analysing the hypervariable region 1 (HVR1) of the mtDNA from 37 early Minoans from the Lasithi Plateau. The lack of L mitotypes was used to disprove a proposed African origin of the Minoans. Instead, haplogroups H, HV, K and T were identified, which are seen in other Neolithic populations. The paper concluded that the Minoan population are the descendants of the Neolithic settlers from Anatolia and the Near East, and that there is a similarity between Minoans and modern inhabitants of the Lasithi Plateau.

The earliest ancient mitogenomes in Greece date to two individuals from the Mesolithic (Hofmanová et al., 2016). Both individuals had mtDNA haplogroup K1c; K has been found in earlier Serbian Mesolithic individuals, but also Mesolithic Balkans. They cluster with other European Hunter-Gatherers, having a minor contribution from the Anatolian Neolithic (Hofmanová et al., 2016; Mathieson et al., 2018).

The Greek Neolithic samples were mainly related to other Balkan Neolithic groups, which were largely descended from Neolithic Anatolia, and were equally related to the European Neolithic that spread along the Mediterranean and Danubian routes. However, in the Peloponnese, an additional source of ancestry was discovered related to the Caucasus Hunter-Gatherers and the Iranian Neolithic. This has also been identified in a Neolithic

Bulgarian sample and in several Balkan Copper and Bronze Age samples (Hofmanová et al., 2016; Mathieson et al., 2018; Feldman et al., 2019; Skourtanioti et al., 2020).

Lazaridis et al. (2017) published several captured ancient genomes from Minoan and Mycenaean sites, including one sample from the cemetery of Armenoi. The Minoans and Mycenaeans clustered similarly on a PCA, between Anatolian Neolithic and Anatolian Bronze Age populations. ADMIXTURE analysis described these populations as comprising three components, which maximised in the Anatolian Neolithic, Iranian Neolithic and Western Hunter-Gatherers. *D*-statistics determined that the Minoans of eastern and central Crete formed a homogeneous population. Using qpAdm, ancestry was modelled in Minoan samples as an admixture of Anatolian Neolithic and Iranian Neolithic/CHG, without the additional ancestry of EHG, which is commonly associated with the steppe expansion. In contrast Mycenaeans did contain this EHG ancestry. This difference in ancestry has been used to associate the Mycenaeans with the introduction of Proto-Greek, as part of an Indo-European expansion alongside steppe-related ancestry. The Minoans in Lazaridis et al. (2017) all pre-date the Armenoi site and the possible Mycenanean conquest of Crete. The sample from Armenoi had too low coverage to undergo any detailed analyses.

5.4 Dietary isotope analysis

5.4.1 Greece

Dietary isotopic analysis of Neolithic and Early Bronze Age sites demonstrates a relatively homogenous diet with no status or sex differentiation. Carbon and nitrogen ratios are low, consistent with a terrestrial C_3-based diet (Kontopoulos and Sampson, 2015; Richards, 2015; Papathanasiou and Richards, 2015; Dotsika et al., 2019). As of yet there are no Neolithic dietary studies of Crete.

In the Late Bronze Age, many mainland Greek sites demonstrate a terrestrial based diet. There appears to be an overall increase in meat consumption in this time, and diets are no longer as homogenous as in the Neolithic and Early Bronze Age (Petroutsa and Manolis, 2010; Papathanasiou, 2015; Dotsika et al., 2019). The effects of differing foddering with C_4 and manuring techniques upon animal carbon and nitrogen values can be seen in several sites, such as Archontiko and Thessaloniki Toumba in northern Greece,which affects the carbon and nitrogen values of the humans who consume them. Without local baselines, it is possible to misinterpret these agropastoral practices for differing dietary habits (Nitsch et al., 2017). In sites without sufficient animal baselines, there are debates as to whether increased $\delta^{13}C$ values are the result of marine sources or C_4 plant, most likely millet (Petroutsa et al., 2007; Petroutsa and Manolis, 2010; Dotsika et al., 2019).

Sex and status differences can be seen in several Middle and Late Bronze Age sites (Triantaphyllou et al., 2008; Papathanasiou and Richards, 2015). Increased δ^{15}N can be seen in males and elites at several sites, indicating a larger input of animal protein (Triantaphyllou et al., 2008; Papathanasiou and Richards, 2015). This is seen at large palatial sites such as Pylos, but also even in smaller settlements such as Lokris (Papathanasiou and Richards, 2015; Iezzi, 2015). There is debate around possible consumption of marine resources at several Late Bronze Age sites (Petroutsa and Manolis, 2010; Papathanasiou and Richards, 2015; Dotsika et al., 2019). At Mycenae, in Grave Circle A, there is clear consumption of marine resources, as well as high animal protein consumption. Carbon and nitrogen ratios are noticeably higher than from Grave Circle B (Richards and Hedges, 2008; Petroutsa and Manolis, 2010; Papathanasiou and Richards, 2015).

5.4.2 Crete

Stable isotope analysis of two MMI-LMI cemeteries from close to Knossos was conducted by Nafplioti (2016). The study revealed two groups, the smaller of which had greater δ^{13}C, which was interpreted as being a result of marine input. However, this group does not display increased δ^{15}N, possibly suggesting that this population was eating C_4 plants, or animals foddered on them. No significant difference between males and females, nor by tomb group, was observed. The majority of the higher carbon ratio group dated to MMIII-LMI, which is often seen as the peak of Knossos' wealth.

Published literature shows a reliance of terrestrial C_3 plants on the Greek mainland with clear differences due to status and sex. Minoan Knossos, however, does not exhibit these divisions. A combination of diet and potential intra-population differences may aid interpretation of the Armenoi population as culturally more similar to Minoan or Mycenaean populations.

Chapter 6

Genomic analysis of the necropolis of Armenoi, Crete

6.1 Aims and objectives

The aim of this chapter is to explore the genetic impact of the Bronze Age on Crete, using the LMIII Necropolis of Armenoi as a case study. As well as this, I aimed to assess whether the cultural changes seen in Late Bronze Age were due to Minoans adopting Mycenaean culture, a total replacement by the Mycenaeans, an elite takeover or an admixture between the two groups.

It was hoped to complete these aims through the following objectives:

- Determine whether ancient DNA was recoverable at the site in sufficient quantity and quality for ancient genomic analyses.
- Determine the sex of the individuals.
- Identify the uniparental markers present.
- Assess whether kinship existed on site and, if so, build family trees.
- Assess the genetic diversity of the site.
- Undertake whole genome analysis to identify steppe migration in Crete, and how Armenoi related to other Bronze Age populations.
- Assess stable isotopic information to make inferences about diet.
- Combine results to determine whether there were any links between sex, status and genetic differences at the site.

6.2 Archaeological background of Armenoi

The Necropolis of Armenoi is unique in that it is the only completely intact Late Minoan (LM) III cemetery to date, and its tombs have survived relatively undamaged. Of the 232 tombs, only

four were plundered at the end of the Minoan period, a very rare occurrence. Apart from this, the only other significant damage was caused due to construction of a Nazi anti-aircraft gun near one tomb, and the effects of local badgers. In addition, as excavations did not begin until 1969, more modern excavations standards were employed than at other Greek archaeological sites (Tzedakis and Kolivaki, 2018).

6.2.1 Location

The Necropolis of Armenoi is located 8km south of the modern town of Rethymnon, on the north coast of the island. The site is on a ridge overlooking a valley that creates a north-south route through the island. Crete's mountainous geography and large valleys would have made this region, with its north-south route, valuable economic land (Chappell and Allender, 2018; Giże, 2018c; Tzedakis and Kolivaki, 2018). The Necropolis of Armenoi is located close to the Middle Minoan I-II peak sanctuary of Vrysinas. During excavations of this site, between 2004-2008, the peak sanctuary yielded LM III potsherds. As peak sanctuaries had fallen out of use by this time, current theory is that it was being used as a lookout post, from where it is possible to see both the Libyan and Aegean seas (Tzedakis and Kolivaki, 2018). Presence of fertile soil and fresh water also make this area prime agricultural land (Giże, 2018c), and so it is likely that geology played a role in its location. The necropolis was dug into unsilicifed limestone, which is hard enough to maintain its structure, whilst being soft enough to be excavated using bronze tools (Giże, 2018b; Giże, 2018a). Mineral deposits, such as copper and iron, are also located nearby. Although the copper mines are small, during a breakdown of wider trade links, the area would still be profitable (Tzedakis and Martlew, 2001). X-ray diffraction of metallic items from the necropolis suggest that they were made from local iron and copper deposits (Sherwood-Dickinson et al., 2018).

6.2.2 The necropolis

The site comprises of 232 rock-cut tombs laid out along two levels, with larger and richer tombs being located in the upper level (Tzedakis and Kolivaki, 2018). The majority of tombs consist of a stepped or sloped corridor (dromoi) and a chamber (tholoi). Tomb entrances were sealed with slabs or small stones (Tzedakis and Kolivaki, 2018). The whole site is located on the east side of the ridge, with all entrances facing the east, and with chambers towards the west. As a result, many face sun- and moonrise, possibly for religious purposes, and slight differences in entrance layout can be seen across the site due to where the shadow of Mount Vrysinias falls (Giże, 2018b). Tomb chambers vary in size and several have elaborate features, including pillars, benches and internal niches (Tzedakis and Kolivaki, 2018). Some tombs do not have a chamber and have been interpreted as cenotaphs (Tzedakis and Kolivaki, 2018). Evidence of funerary feasting has been found on the site, with pits containing domestic pottery

used for storage and consumption of food (Tzedakis and Kolivaki, 2018).

6.2.3 Graves and grave goods

Tombs vary from single burials to multiple interments, with the highest number of individuals, 12, interred in Tomb 19. When interred, the deceased appear to have been laid on the floor of the chamber. When later burials were added, the earlier remains were gathered into piles (Tzedakis and Kolivaki, 2018). These multiple interments may represent kin groups (McGeorge, 1983; Tzedakis and Kolivaki, 2018), and this has been hypothesised to reflect the increased importance of the family unit and hereditary elites at this time (McGeorge, 1983). Individuals were also placed in larnakes (terracotta coffins **Figure 6.1**) inside some tombs (Mee, 2010; Tzedakis and Kolivaki, 2018).

FIGURE 6.1: Larnake RM 1707, from Tomb 11, depicting a hunting scene by men in Mycenaean dress (Tzedakis and Kolivaki, 2018). Photo taken by the author.

To date, it has been estimated that the 232 tombs contain over 1000 individuals (Chappell and Allender, 2018). A partial osteoarchaeological study was undertaken by McGeorge (1983), analysing 250 adult and 106 child skeletons. The average life expectancy is estimated at between 30-35 years, with males living slightly longer than women. Evidence of disease and fractured bones was evident, but so was healing, indicating a society knowledgeable about medicine. The study revealed a predominance of males (with 143 males to 107 females), which is also seen in several Bronze Age cemeteries, including Grave Circle B in Mycenae, although several other sites show 1:1 ratios (Lagia et al., 2007).

Grave goods vary in type, quality and quantity across the site, with common items including pottery, bronze articles (such as weapons, jewellery and grooming items), and seal stones. Stylistic assessment of high-status pottery from the necropolis, indicates that they were imported from five different workshops, with the majority from Armenoi and Kydonia (Chania), although pottery from Knossos, Palaikastro, and Mycenae workshops are also

represented (Tzedakis and Kolivaki, 2018). The most archaeologically significant pottery item is a stirrup jar, RM 3363 (**Figure 6.2**). This is one of three similar stirrup jars from across Greece (the others being Knossos, Crete, and Midea, Peloponnese) with the same Linear B inscription that appears to be in the same hand. All these jars were used for the transport of wine (Tzedakis and Kolivaki, 2018).

FIGURE 6.2: Stirrup jar, RM 3363, from Tomb 146. Photo taken by the author.

The seal stones are often of high quality and made from precious stones, of which a number show importation from the Greek mainland (Tzedakis and Kolivaki, 2018), and suggest an administrative function (Tzedakis and Martlew, 2001; Godart, 2018).

The grave goods indicate a wealthy population with clear trade links; for example, one such significant find is a reed basket similar to the one found in Tutankhamun's tomb (Tzedakis and Kolivaki, 2018). Highly skilled workers would have been required to create

some of these items. Many pottery artefacts and larnakes are polychrome, with shades of yellow, orange, and red to black. This is a complex activity, achieved by increasing the number of layers of iron oxide-hydroxide applied to pottery before firing (Sherwood-Dickinson et al., 2018). It is unclear whether this society is a continuation of earlier Minoans or is Mycenaean or Mycenaean-dominated. Larnakes reveal both Minoan and Mycenaean stylistic elements (Tzedakis and Kolivaki, 2018). A steatite pendant with a Linear A inscription dating to LMIB suggests a continuation of earlier society but, in contrast, a boar's tusk helmet is typical of Mycenae (Tzedakis and Kolivaki, 2018).

6.2.4 Previous ancient DNA analysis

An adult female from Tomb 160 was previously sampled for anceint DNA analysis (Lazaridis et al., 2017). On the PCA, the sample plots midway between the Mycenaeans and Bronze Age populations from Western Europe. As the sample had a relatively low number of SNPs, it was not possible to conclude more about the difference between this sample and the Minoan and Mycenaeans. This current study will help identify whether the sample from Lazaridis et al. (2017) is a genetic outlier or whether additional demographic changes occurred in Crete.

6.2.5 Previous dietary isotopic analysis

A previous stable dietary isotope study of LM III individuals from Armenoi was undertaken by Richards and Hedges (2008), using faunal remains from the site of Chamalevri as a dietary baseline. One of the ovicaprid samples had increased carbon levels, indicating possible C_4 consumption. However, the human results indicate little variation, displaying a predominantly C_3 terrestrial derived diet. Males appear to have slightly increased nitrogen values compared to the females, but there were not enough samples to identify a clear difference. No status differences were observed.

6.3 Sampling and methodology

Sample selection was undertaken directly from the Armenoi storage collection in the Rethymnon Museum warehouse, Crete. Petrous bones and molar teeth were preferentially selected due to the increased possibility of DNA and collagen survival (see 2.2.1). Elements from broken and fragmented skulls were selected, so as to not damage intact skulls thus preventing future research, such as anthropological or palaeopathological studies. Hard, not flaky, petrous bones, and teeth without any obvious cracks, were selected. Although not a precise correlation, the better preserved the enamel/bone matrix is, the less likely the DNA/collagen inside is going to be subjected to post-mortem degradation, especially microbial attack (section 2.2.1). Boxes in the museum are arranged by tomb, meaning several individuals were placed in the same box. In boxes containing multiple fragmented skulls, the same element was chosen from each individual (for example, the left petrous), to avoid sampling the same individual twice. A

variety of tombs, with varying wealth (as designated by associated grave goods) were selected from across the site, to assess the possibility of status-related differences that may be viewed isotopically or genetically. Several people were selected from multiple burial tombs in order to assess the possibility of familial relationships at the site.

An axis vertebra and talus (ankle bone) were also chosen. These samples were from archaeologically significant tombs where no petrous bones or teeth were available. The axis vertebra came from Tomb 159, which is the largest tomb, with important archaeological features including niches and a column (Tzedakis and Kolivaki, 2018). The talus was found in Tomb 146, and an incisor from this tomb also was selected. This tomb contained the "most important find from Armenoi" (Martlew pers. comm.), the stirrup jar used for wine storage with the name, "Wi-na-jo" inscribed in Linear B (as discussed above) (Tzedakis and Kolivaki, 2018).

In total, 171 samples were selected from 48 tombs (which is (34% of the total tombs with skeletal material). The samples represented 118 individuals, of which:

- 54 individuals have petrous only
- 51 individuals have both petrous and tooth
- 11 individuals have tooth only
- 1 individual has vertebra and tooth
- 1 individual has talus and tooth

As well as the human remains, 13 animal bones were also chosen for analysis: 12 from Tomb 159 and one from Tomb 146. The animal remains were chosen to provide a local baseline for dietary isotopic studies. As discussed above, previous faunal isotope ratios used in analysis of Armenoi individuals came from Chamalevri, a site approximately 50km away (Richards and Hedges, 2008). The addition of these contemporaneously buried, and site-located animal samples should provide a more accurate comparison to the dietary isotope data generated from Armenoi.

Methodological techniques used in this chapter follow those outlined in Chapter 4.

Samples with the highest endogenous DNA content, and displaying mapDamage patterns consistent with ancient DNA, were sent for further in-depth sequencing at Macrogen, South Korea.

6.4 Results

6.4.1 Screening results and sample selection

Samples and blanks were screened at Trinity College Dublin using a MiSeq (**Table D.1**), with endogenous DNA content ranging from 0.01 to 26.93%. Endogenous content varied within tombs; for example, Tomb 198 contained two individuals with less than 1% endogenous DNA, two individuals with c.13%, and one individual with over 25%. This demonstrates that multiple factors in the burial environment are important for ancient DNA survival.

6.4.2 Coverage

In total, 23 samples from ten tombs were selected for sequencing. Lanes 1 to 7 had 14 samples on half a lane each, with three libraries per sample. Lanes 8 and 9 contained the remaining nine samples, with five samples on one lane, and four samples on the other, and only one library per sample (**Table 6.1**). The samples on the first seven lanes were sequenced to provide enough data for various whole genome analyses. The aim of the last two lanes was to mainly provide uniparental information and possible kinship information.

Of the ten tombs, five are described as rich in finds, of which three are particularly wealthy in terms of the number of grave goods and cost of materials buried. Of the 23 individuals chosen, 15 are from high status tombs, of which eight are from Tomb 203 (**Figure 6.3**).

Sample	Tomb no.	Sequencing lane	Whole genome coverage
GF008	Tomb 149	1	0.1121x
GF009	Tomb 149	1	0.1177x
GF010	Tomb 149	9	0.0278x
GF014	Tomb 167**	9	0.0188x
GF016	Tomb 167**	8	0.0416x
GF019	Tomb 198*	2	0.5809x
GF020	Tomb 198*	2	0.2058x
GF022	Tomb 198*	3	0.2288x
GF024	Tomb 203*	3	0.2790x
GF025	Tomb 203*	9	0.0300x
GF026	Tomb 203*	4	0.1491x
GF027	Tomb 203*	4	0.1377x
GF028	Tomb 203*	9	0.0188x
GF029	Tomb 203*	8	0.0608x
GF030	Tomb 203*	5	0.1478x
GF031	Tomb 203*	5	0.3224x
GF034	Tomb 206**	6	0.3352x
GF045	Tomb 208	8	0.0597x
GF047	Tomb 210	6	0.3606x
GF048	Tomb 210	9	0.0394x
GF051	Tomb 67*	7	0.5065x
GF053	Tomb 69	8	0.0674x
GF054	Tomb 78	7	0.2583x

TABLE 6.1: List of individuals analysed as part of this study, including sequence lanes, and whole genome and mitochondrial coverage. Asterisks refer to wealthy tombs as designated by the archaeologists; double asterisks refer to particularly wealthy tombs.

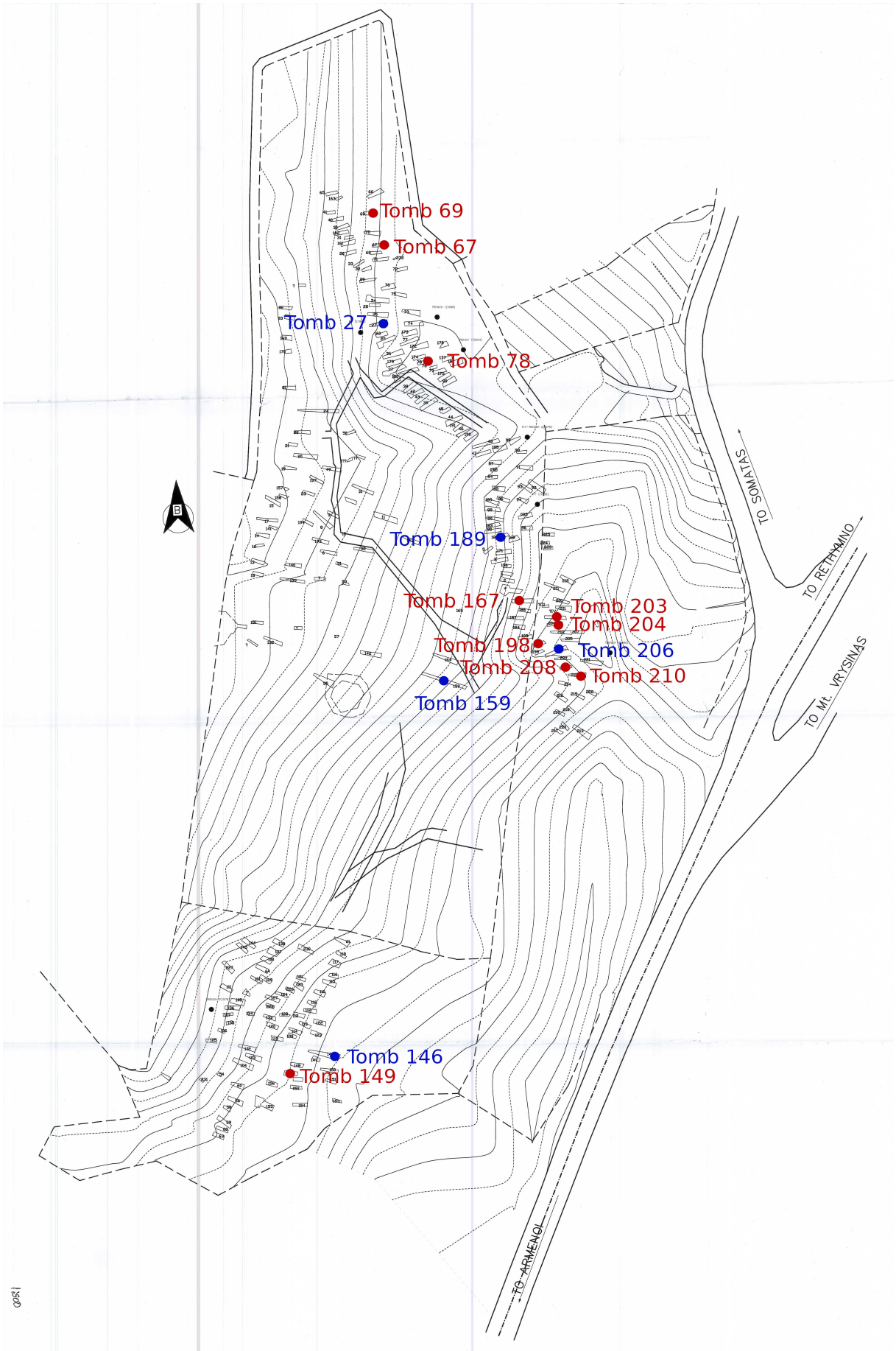


FIGURE 6.3: Plan of the Armenoi necropolis with sampled tombs labelled (stable isotopes only are blue; aDNA and stable isotopes are red).

6.4.3 Genetic sex determination

All samples could be confidently assigned to a genetic sex, including child GF047, who could not be sexed using osteological techniques. Sixteen samples are classed as female and seven as male.

6.4.4 Contamination estimation

In all three tests for contamination, only very low levels of contamination are observed (**Table 6.2**). Several of the samples produce no mitochondrial contamination estimates, producing the error "Unable to convert string="-nan"" in the contDeam stage of the schmutzi command. This can occur in samples that have undergone UDG treatment, as was the case for sequencing lanes 1 to 7. Not all samples sent in lanes 8 and 9 produce an output from schmutzi either, but this is more likely due to low coverage. Seven individuals are determined as male. Only male samples could be tested for X-chromosome contamination with ANGSD. One sample, GF010, could not produce an X-chromosome contamination result due to the low coverage of the sample. VerifyBamId produced low contamination results for all samples, although this program is not ideal for use on samples with coverage less than 0.1x. However, despite issues relating to coverage, all methods show little contamination evidence.

Sample	Sex	Schmutzi mtDNA contam [%]	ANGSD Xchr contam [%]	VerifyBamID Nuclear contam [%]
GF008	Female	0-2	n/a	2.0
GF009	Female	0-2	n/a	2.1
GF010	Male	NP	n/a*	1.5
GF014	Female	NP	n/a	2.4
GF016	Female	1-3	n/a	3.2
GF019	Female	0-2	n/a	0.7
GF020	Female	NP	n/a	1.2
GF022	Female	0-2	n/a	1.3
GF024	Female	0-2	n/a	1.2
GF025	Male	0-2	6.06	4.5
GF026	Female	NP	n/a	1.7
GF027	Male	0-2	1.47	2.4
GF028	Female	NP	n/a	5.7
GF029	Female	1-3	n/a	5.8
GF030	Female	NP	n/a	2.5
GF031	Male	0-2	2.21	1.6
GF034	Female	NP	n/a	1.4
GF045	Male	1-3	6.06	2.8
GF047	Female	NP	n/a	1.0
GF048	Female	0-2	0.60	3.5
GF051	Male	0-2	0.62	1.1
GF053	Female	0-2	n/a	2.7
GF054	Male	NP	1.03	0.9

TABLE 6.2: Sex determination and DNA contamination estimates. NP denotes that the Schmutzi test was not possible due to UDG treatment of the sample libraries; n/a denotes that the ANGSD X-chromosome test was not applicable due to the samples being female; for this test, the asterix denotes the male sample GF010 that has low coverage.

6.4.5 Uniparental markers

6.4.5.1 Mitochondrial haplogroup

Mitochondrial haplogroups were assigned to all individuals (**Tables 6.3 and D.2**). Of the 23 individuals, nine belong to haplogroup U, seven to haplogroup H, two to W, two to T, and one individual each to haplogroups HV, N1, and K respectively. Individuals sharing a first-degree maternal kinship (mother-child or siblings) also share mitochondrial haplotype. Whilst this can be difficult due to heteroplasmies and gaps caused by low coverage, it is possible to identify GF019 and GF022 as sharing the exact same haplotype. Closely assigned mitochondrial haplogroups may indicate a shared maternal heritage.

Sample	mtDNA coverage	Haplogroup
GF008	11.012X	H59
GF009	9.9074X	T2b
GF010	6.0161X	T1a1
GF014	1.7072X	U7
GF016	3.1221X	U7b
GF019	55.2623X	H
GF020	26.6944X	H4b
GF022	30.676X	H
GF024	28.7061X	U5b1b1
GF025	2.6052X	U5b1
GF026	10.4027X	K1
GF027	12.2182X	U5a1
GF028	0.8238X	H5a3
GF029	3.7232X	U5b1b1
GF030	10.9348X	U5b1b1
GF031	28.9515X	U5a1
GF034	27.1654X	N1a1a1a
GF045	6.0488X	H59
GF047	23.2111X	W
GF048	2.4604X	H
GF051	52.1299X	H1bz
GF053	3.0479X	H
GF054	20.7017X	HV1

TABLE 6.3: Mitochondrial haplogroup assignment and coverage.

6.4.5.2 Y-chromosome haplogroup

The Y-chromosome has much lower coverage than the mitochondrial genome, so it is not possible to give as precise a haplogroup as for the mtDNA. The results of both Yfull and pathPhynder provide approximately the same results for all seven males, with slight differences on the precision of haplogroup assignment (**Table 6.4** and **Appendix Section D.2.2**).

Of the four males who belong to Y-macrohaplogroup G2a, three can be further assigned to at least G2a2a (GF025, GF027 and GF031, all from Tomb 203). GF025 was originally assigned to a subhaplogroup different to the other G2a2a males; however, when reviewing the Yfull and pathphynder data, this is likely due to differences in coverage. The other male (GF054 from Tomb 78) is assigned to G2a2b, and is, therefore, not paternally related to any of the other three males.

For the other three males sampled from the site, both GF045 (Tomb 208) and GF051 (Tomb 61) are assigned as J, and GF010 is assigned to R1b, all using both methods. However, it should be noted that GF010 has a very low number of SNPs on the Y-chromosome.

Sample	Y-chromosomal coverage	Haplogroup
GF010	0.0048x	R1b1a
GF025	0.0054x	G2a2a
GF027	0.0252x	G2a2a1a2
GF031	0.0596x	G2a2a1a2
GF045	0.0105x	J2
GF051	0.0894x	J2
GF054	0.0469x	G2a2b

TABLE 6.4: Y-chromosomal results of pathPhynder and Y-leaf.

6.4.6 Kinship analysis

Kinship relationships were identified using READ and undertaken using samples called against the filtered 1000 Genomes Project and the Reichlab 1240k SNP lists (as described in Chapter 4, Section 4.2.5). Multiple datasets were used to ensure consistency of results (Section 4.2.6). Kinships were observed in Tomb 198 (females GF019 and GF022), Tomb 210 (females GF047 and GF048), and Tomb 203 (males GF025, GF027 and GF031, and females GF024, GF028, GF029 and GF030).

The females in Tomb 198 share a first-degree (parent-offspring or sibling) relationship. However, no further conclusions could be drawn. Similarly, the women in Tomb 210 share a first-degree relationship. As GF047 was recorded as a child, she is likely the child or sibling of GF048.

A family group can be reconstructed in Tomb 203 by using the results of READ, sex identification and uni-parental markers. Individuals GF024 (F), GF025 (M) and GF029 (F) share a first-degree relationship with each other, as well as the same mitochondrial haplotype. These individuals all share a first-degree kin relationship with GF027 (M) but no shared mitochondrial haplotype. As a result, they cannot have a sibling relationship, nor can either GF024 or GF029 be the mother of GF027. It is more likely that GF027 is the father of GF024, GF025 and GF029. As GF024, GF025 and GF029 also share a first-degree relationship with GF030 (F) and an mtDNA haplotype, but GF030 is not related to GF027, it can be concluded that GF030 is the mother of the group. GF031 (M) shares a first-degree relationship with GF027 and a second-degree relationship with GF024, GF025 and GF029 (grandparent-grandchild, uncle-niece, or half-sibling). As GF027 and GF031 share an mtDNA haplotype, and therefore potentially a maternal kinship, as well as a Y-chromosomal haplotype, the most probable scenario is that GF027 and GF031 are brothers, and that GF031 is the uncle of GF024, GF025 and GF029. Though not fully covered, GF025 and GF027 appear to share the same Y-chromosomal haplotype, further indicating a father-son relationship between these two.

Another relationship can be seen in this tomb, GF028 (F) shares second-degree relationship with the siblings GF024, GF025 and GF029, and their mother GF030, but no relationship to GF027. Genealogically, this is not a plausible result. Although READ produces an unrelated result for GF027 and GF028, the error margins overlap with the second-degree relatedness category. Furthermore, when using the Reich 1240k SNP list and the 1000 Genome Project filtered to remove SNPs found in less than 10% of African populations, GF027 and GF028 share a second-degree relationship. Also, of note GF025 and GF028 produce large error bars over the first- and second-degree assignments. When READ analysis was repeated using the 1240K SNP list, a first-degree relationship was noted between GF025 and GF028. Therefore, it is probable that GF028 is the granddaughter of GF027 and GF030, the daughter of GF025, and the niece of GF024 and GF029. As GF028 does not share a mitochondrial haplotype with GF024, GF029 or GF030, she must be paternally related to them (**Figure 6.4**).

An unrelated individual, GF026, is also present in Tomb 203. She does not share her mitochondrial haplotype with anyone else in the tomb. However, as the mean number of individuals interred in this tomb is 11, and eight were sampled for DNA, it is possible that she is related to someone not analysed in this study.

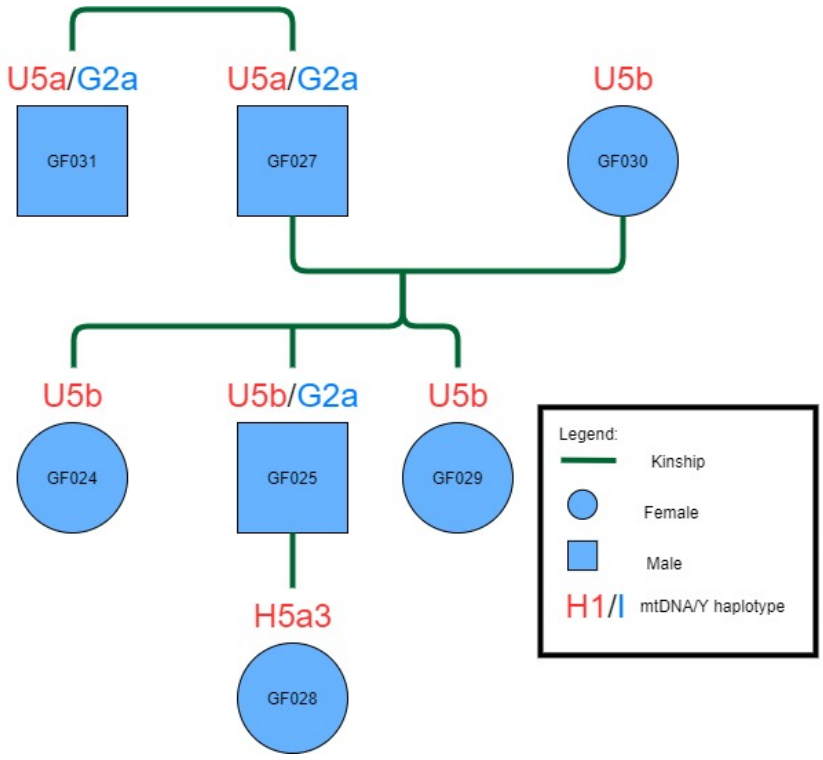


FIGURE 6.4: Possible kinship relationships in Tomb 203. This is one potential family tree, taking into consideration the results from READ, the genetic sex determination and the uniparental haplotype data.

6.4.7 PCA

As visible on the PCA, the majority of the Armenoi samples seem to form one population, except for individual GF010, who plots closer to Bronze Age individuals from western, northern and Central Europe, and will be discussed separately (**Figure 6.5**). The Armenoi samples excluding GF010 (which, from now on, will be referred to as 'the Armenoi population') overlap with Mycenaeans published in Lazaridis et al. (2017) from mainland Greece. However, the Armenoi population is also not clearly distinguished from the published Minoan populations.

The PCA displays the Armenoi, published Minoans and Mycenaeans forming a cline to the Greek Neolithic, clustering with the Anatolian Neolithic. In contrast, the Greek Bronze Age samples plot slightly closer to the CHG or Yamnaya than the Greek Neolithic. Unlike in several other areas of Europe, there appears to be no large-scale change associated with the Bronze Age.

The Armenoi population are placed differently to other Balkan Bronze Age genomes (from Croatia, Bulgaria and Montenegro), which all are situated closer to Hunter-Gatherer populations. They also do not cluster with Anatolian, Israeli/Palestinian and Jordanian Bronze Age, which all plot further away from the Hunter-Gatherers.

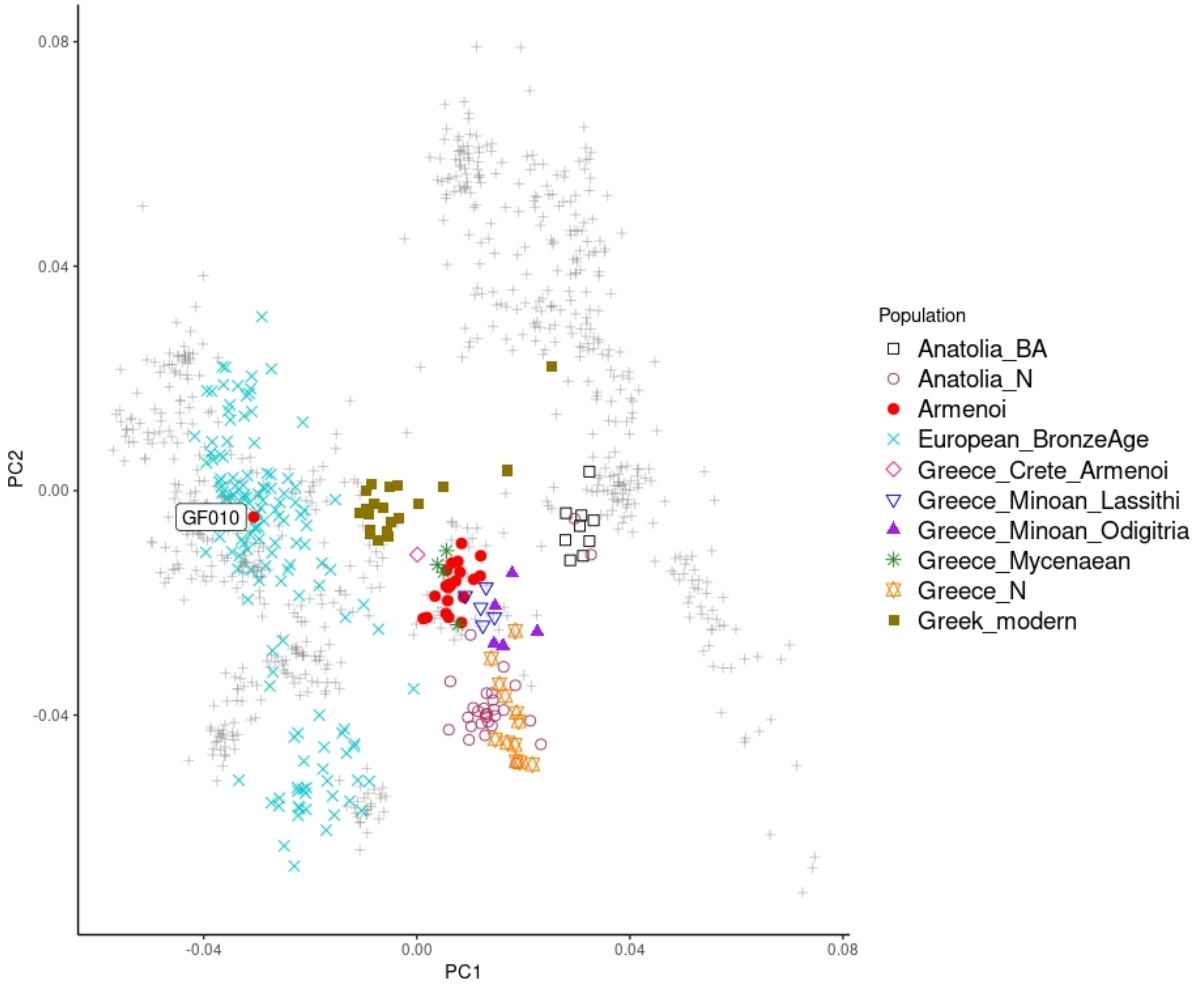


FIGURE 6.5: PCA of modern West Eurasian light grey with ancient samples projected. The outlier GF010 is labelled in the plot. As can be seen in the plot, the Armenoi population (red dots) plots between Minoans and Mycenaeans, and is distinct from earlier Neolithic and Anatolian Bronze Age populations. Also of note, modern Greeks can be seen as distinct from Bronze Age Greek populations.

6.4.8 ADMIXTURE analysis

The individuals in the Armenoi population comprise three main components, which maximise in the Anatolian Neolithic, Iranian Neolithic, and Western Hunter-Gatherers (c.60%, c.30% and c.10%, respectively) (**Figure 6.6**). There is a small fourth component in several individuals (GF016, GF025, GF028, GF029, GF045, GF048, GF053), which maximises in African populations. This component was also seen in the Anatolian Bronze Age, Natufians from modern Israel, and in ancient individuals from modern Jordan. However, this fourth component is present in certain Armenoi as only a very small percent (below 5%). The published sample from Armenoi (Lazaridis et al., 2017) has similar components to the Armenoi population here, but has a higher proportion of the WHG component. There is an identifiable difference between the Armenoi population and Greek Neolithic (including the Peloponnese), as these

populations have larger Anatolian Neolithic and smaller Iranian Neolithic components. As observed in Lazaridis et al. (2017), there is a slight difference in the ADMIXTURE proportions between Minoans and Mycenaeans, with Minoans having a higher Anatolian Neolithic component. In this regard, the Armenoi population in this study appear most similar to the published Mycenaeans.

There is a large difference between the ancient Armenoi population and modern Greeks. Although the WHG component has similar proportions, modern Greeks have a much higher Iranian Neolithic component than their ancient counterparts. Coupled with the PCA evidence, it is suggestive of further significant demographic movements in Greece after the Bronze Age. The Armenoi population has a slightly smaller Anatolian Neolithic and a slightly larger WHG component than Anatolian Bronze Age samples, and is also distinctive from Bronze Age populations from Bulgaria and Croatia.

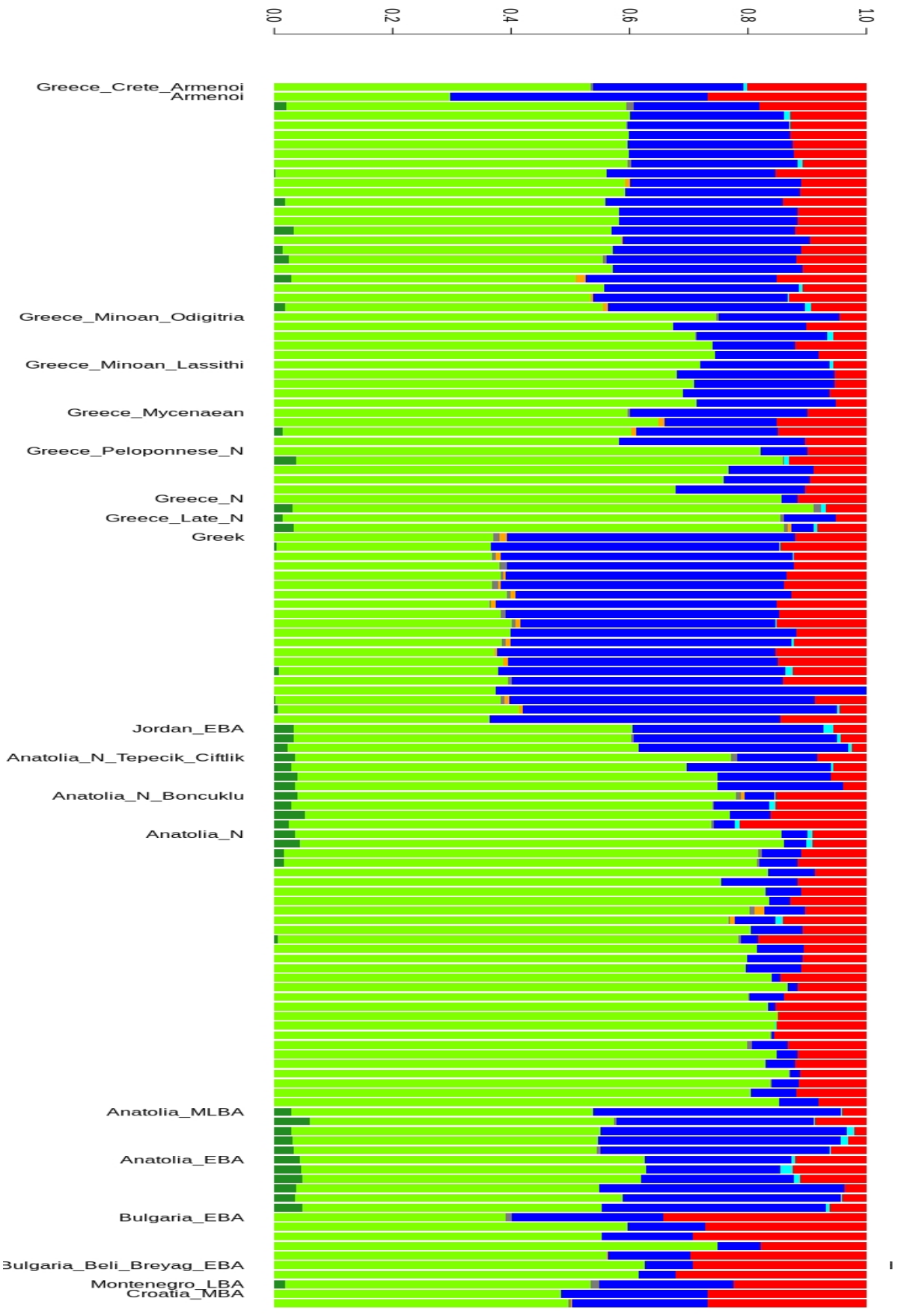


FIGURE 6.6: ADMIXTURE results from the Armenoi and other relevant populations. Green is maximised in Anatolian Neolithic Farmers; red in the WHG; blue in the CHG and Iranian Neolithic; and dark green in North African populations.

6.4.9 Assessing homogeneity of the Armenoi population

One of the key aspects of this study is to assess whether the Armenoi population represents genetic continuity from the Minoans, an incoming Mycenaean community, an admixture between both groups, or an elite takeover. In the elite takeover scenario, there may be individuals who appear to be Mycenaeans and others who appear more Minoan, which might be linked to tomb wealth. Assessment of the PCA and ADMIXTURE results suggest broadly similarities across the sampled Armenoi population. However, it is also noted that the differences between published Minoans and Mycenaneans are not striking in these analyses. Following analytical methods used by Mathieson et al. (2018), *D*-statistics were employed to determine whether the Armenoi samples form a homogenous group. They were compared to Anatolian Neolithic farmers and Yamnaya steppe pastoralists from Samara, using the test *D(Out, Sample, Anatolian Neolithic, Yamnaya)*; these populations were chosen as they appear to be very different from Armenoi in several types of analysis (**Figure 6.7**). Samples were plotted with 1.5 standard errors and were considered a homogenous population if they overlapped.

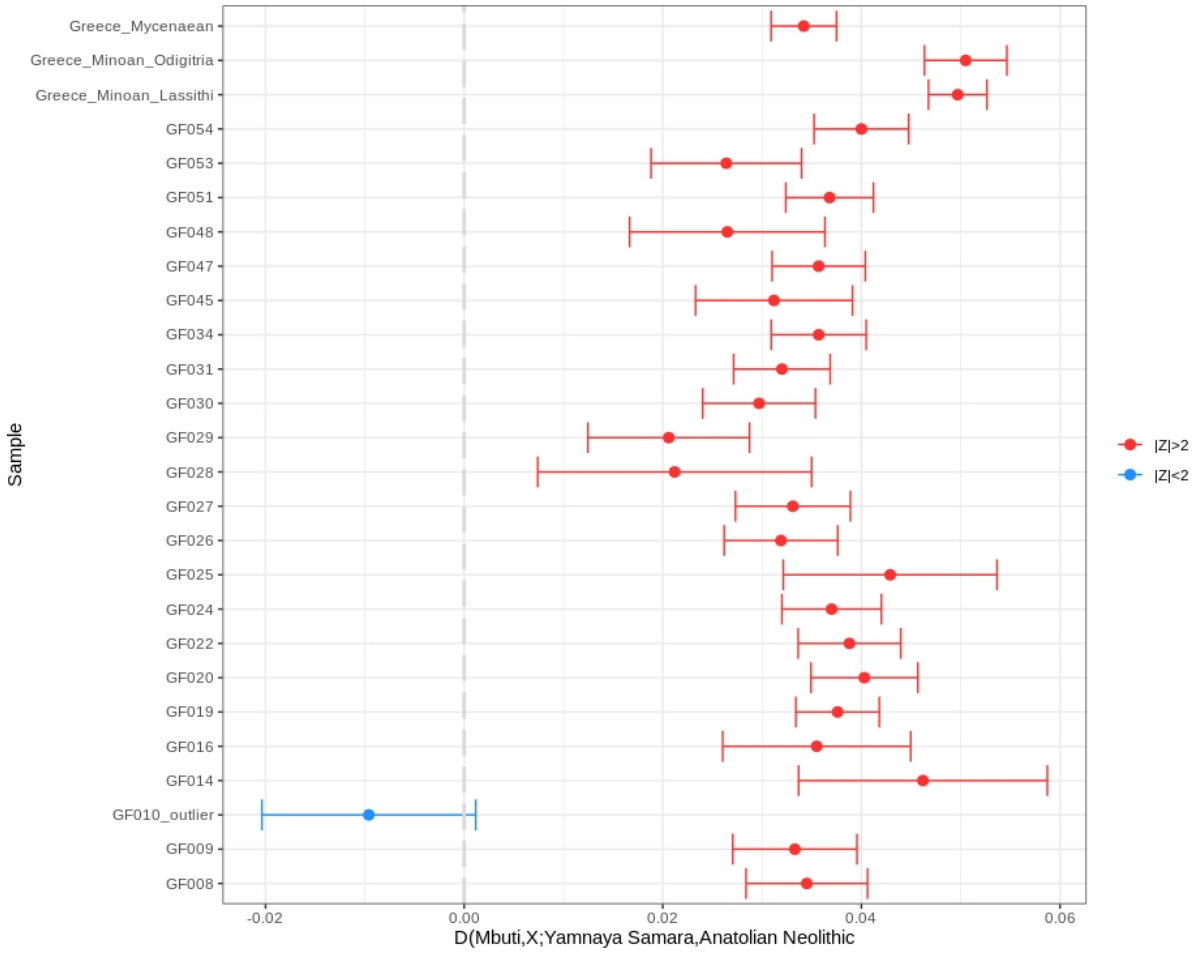


FIGURE 6.7: *D*(Out,X,Anatolia Neolithic, Yamnaya Samara), whereby X refers to an individual from Armenoi or a published Greek Bronze Age population. Samples are plotted with 1.5 standard error bars.

This analysis demonstrates that all the Armenoi samples, except GF010, significantly share more alleles with Anatolian Neolithic farmers than with the Yamnaya. All Armenoi samples overlap (again except GF010), potentially indicating that they form a homogenous population. Of note, published Minoans and Mycenaeans do not overlap with each other, and only two Armenoi samples (GF014 and GF025) overlap with the Minoans. However, not much weight can be given to this result as both samples have large error bars, most likely as a result of low coverage. All samples overlap with the Mycenaeans except GF029, which also has lower coverage, and the outlier GF010.

To further assess whether Armenoi individuals form a homogenous group, the most differentiated individuals in the PCA, ADMIXTURE, and Yamnaya versus Anatolian Neolithic *D*-statistics, were assessed using the formula *D(Outgroup,X; Potential outlier, Core group)*, whereby X is a series of Bronze Age European populations. A "Core group" was conservatively assigned to just seven individuals (GF008, GF009, GF027, GF031, GF034, GF047 and GF054). When the test produces $|Z|<3$, it is assumed that the potential outlier forms a clade with the core group. Only two individuals produced one or more significant results (GF010 and GF019). However, when conducting *D*(Out, GF019; X, Y), where X and Y are European Bronze Age populations, almost all tests show that GF019 has more gene flow with the Armenoi population than with Bronze Age populations. Therefore, GF019 can be considered to be a part of the Armenoi population. In contrast, GF010 does not produce similar results, and can be considered separately to the rest of the Armenoi population.

6.4.10 *f*-statistics

To assess which populations the Armenoi population shares the greatest drift with, outgroup-f3 was employed, where Mbuti were selected as the outgroup. The Armenoi population share higher drift with both European Chalcolithic and Minoan populations, than with Bronze Age populations, particularly those of Central Europe. Surprisingly, the Mycenaeans displayed little shared drift with the Armenoi population (**Figure 6.8**). Shared drift implies a shared evolutionary history. This is a surprising result, but is seen consistently across all outgroup-f3 tests by sample. The reasons for this result are unclear as they do not match the other forms of analysis.

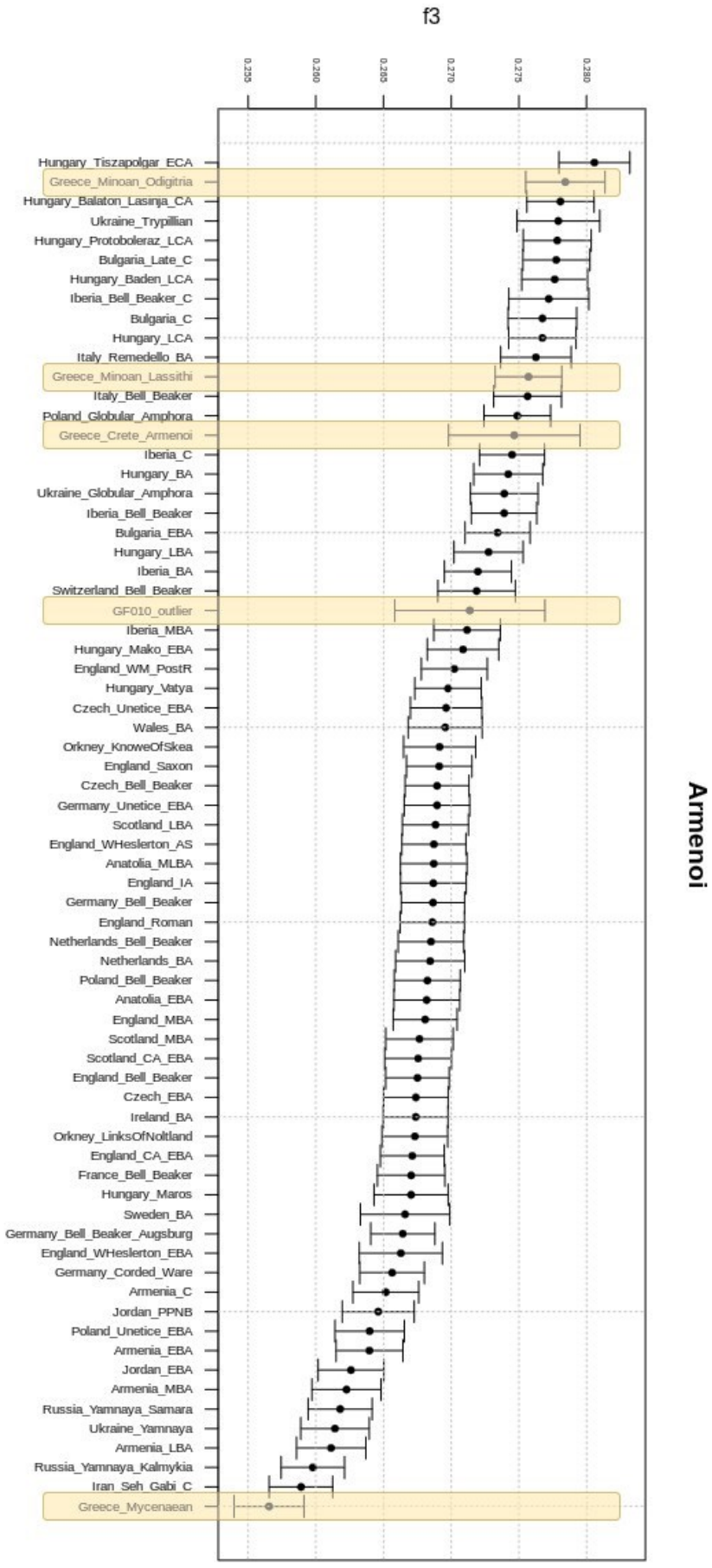


FIGURE 6.8: Outgroup-f3 for Armenoi, Greek Bronze Age groups are highlighted.

D-statistics were employed to assess the affinity of the Armenoi population to European Bronze Age populations. The Armenoi population has a greater similarity to populations from the Balkans and southern European Chalcolithic and Early Bronze Age populations, than to those from northern Europe or Anatolia. That is, the Armenoi population shows an affinity to populations with lower steppe ancestry, displaying greater shared drift with Ukrainian Trypillian and Globular Amphorae than northern European Bronze Age cultures. However, despite this, no affinity is seen to the Ukrainian Yamnaya. Mycenaeans have a greater affinity to the Armenoi population than northern and Western European Bronze Age groups but less than Minoans, Neolithic Greek and Serbian Early Neolithic groups, or the Italian Remedello Bronze Age. Minoans are significantly closer to the Armenoi population than almost all tested combinations, with both Minoan groups being equally related to the Armenoi population ($|Z|<3$). Similarly, no significant results are seen between the Minoans and populations belonging to Greek Neolithic, Anatolian Neolithic, Serbian Early Neolithic, Croatian Late Neolithic, Romanian Chalcolithic, Ukranian Trypillian, Bulgarian Chalcolithic and the published Cretan Armenoi individual. Of the few published Balkan populations that date to the Bronze Age, Bulgarian and Croatian samples have a greater affinity to the Armenoi population than northern and western groups, but less than Minoan, or Neolithic Balkan or Greek populations. No particular affinity can be seen with the Montenegrin Late Bronze Age, but this may be a result of low coverage. These patterns seem to indicate that the Armenoi population resembles groups with little or no steppe ancestry.

6.4.11 Admixture modelling

Admixture modelling was conducted using qpAdm on the Armenoi population as a whole, as well as on individuals. The "Left" (reference) and "Right" (outgroup) populations were decided using the results from the previous tests, particularly ADMIXTURE, and published papers of similar populations (Lazaridis et al., 2017; Mathieson et al., 2018; Fernandes et al., 2020). The Armenoi population (limited to non-related individuals with over 100,000 SNPs each) can be distally modelled as a two- or three-way admixture of Anatolian Neolithic Farmers (ANF) and either CHG, Iranian Neolithic (IranN), WHG and/or EHG. ANF was used in all combinations based on the results of ADMIXTURE and PCA. Significant results (>0.05) are displayed in **Table 6.5**.

Pop 1	Pop 2	Pop 3	Admixture Proportion			SE		
			Pop 1	Pop 2	Pop 3	Pop 1	Pop 2	Pop 3
ANF	CHG	n/a	0.770	0.230	n/a	0.4100	0.4100	n/a
ANF	IranN	n/a	0.777	0.223	n/a	0.37	0.37	n/a
ANF	CHG	EHG	0.739	0.185	0.076	0.041	0.4300	0.2500
ANF	CHG	WHG	0.733	0.233	0.034	0.044	0.040	0.016
ANF	IranN	EHG	0.748	0.178	0.073	0.037	0.038	0.026
ANF	IranN	WHG	0.725	0.233	0.042	0.040	0.035	0.1700
ANF	IranN	Yamnaya	0.755	0.149	0.096	0.036	0.045	0.037

TABLE 6.5: Admixture modelling of Armenoi using qpAdm.

The qpAdm results reveal only two significant distal two-way tests; that the Amenoi population is an admixture of Anatolian Neolithic and CHG, or ANF and Iranian Neolithic. Three-way admixture models all contained CHG or Iranian Neolithic, with EHG, WHG or Yamnaya. In both two- and three-way admixture models, Anatolian Neolithic comprises the majority (at over 75%), with a smaller proportion comprising CHG/Iranian Neolithic (c.15-23%). In three-way models, a smaller component can be modelled as WHG, EHG or Yamnaya (>10%). These results coupled show a similar pattern to those seen in the other f-statistic tests, that the Armenoi population does not comprise a major steppe component.

Sex-biased admixture was also investigated using the same populations by comparing autosomal and X-chromosomal admixture proportions (see 4.2.9.4). Only one combination provided feasible results, and then only using the X-chromosome: Anatolian Neolithic and CHG. The resulting Z score of the sex-biased admixture is -0.6695, which is insignificant, suggesting sex-biased admixture did not occur within the Armenoi population.

As well as distal modelling, where samples are modelled using distantly related groups, proximal modelling was employed. Proximal modelling uses samples that are closer in location and time to the test population. For proximal admixture modelling, the Armenoi population was modelled using Greek Neolithic, Balkan Chalcolithic (Bulgaria and Romania) and Bronze Age (Bulgaria and Croatia), as well as Minoan and Mycenaean populations. The Late Bronze Age individual from Montenegro (Allentoft et al., 2015) was not included due to low coverage, and also this population is represented by a single sample. In proximal testing, a revolving right list is employed, where populations not used as a left/reference population are included in the right/outgroup list. One exception is the Minoan populations, which one was excluded from the right list if the other was in the left list, due to the populations being too similar, and being classed essentially as largely homogenous (Lazaridis et al., 2017). Only one population gives a significant result using this test: the Minoans from Moni Odigitria, a site on the southern coast of Crete, 45km away from Armenoi. As this result is not in agreement with the other tests, two-way admixture modelling was explored.

Two-way admixtures were modelled as the first population being Minoan (from Odigitria or Lassithi) or Mycenaean, and the second population being Balkan Chalcolithic, Bronze Age, Minoan or Mycenaean. Several significant results (p>0.05) were observed, and filtered to only include feasible results (removing negative results and those with large standard errors (which may be the result of the right populations being equally close to left populations). Several significant results are produced (**Table 6.6**). As expected from the previous results, populations with steppe ancestry contribute less to the Armenoi. Of the possible admixture models, the combination of Minoan and either the Anatolian Bronze Age or the Mycenaeans is interesting. A greater contribution from the Minoans appears to match the *D*-statistic results, and the combination of both populations is broadly in line with the results from the PCA and ADMIXTURE.

Pop1	Pop2	p-value	Admix1	Admix2	SE
Minoan (Lassithi)	Anatolia EBA	0.320373	0.429	0.571	0.184
Minoan (Lassithi)	Anatolia MLBA	0.227309	0.526	0.484	0.244
Minoan (Lassithi)	Croatia MBA	0.402456	0.562	0.438	0.127
Minoan (Lassithi)	Iran N	0.224821	0.880	0.120	0.039
Minoan (Lassithi)	Yamnaya Samara	0.523077	0.900	0.100	0.330
Minoan (Odigitria)	Bulgaria Chalc	0.982653	0.685	0.315	0.261
Minoan (Odigitria)	Bulgaria EBA	0.985489	0.734	0.266	0.191
Minoan (Odigitria)	Croatia MBA	0.965760	0.862	0.138	0.196
Minoan (Odigitria)	Iran N	0.984742	0.947	0.053	0.090
Minoan (Odigitria)	Mycenaean	0.990066	0.823	0.177	0.184
Minoan (Odigitria)	Yamnaya Samara	0.950133	0.924	0.076	0.069
Mycenaean	Bulgaria EBA	0.215281	0.444	0.556	0.200
Mycenaean	Croatia MBA	0.117156	0.529	0.471	0.243
Mycenaean	Greece Peloponnese N	0.560929	0.220	0.780	0.236
Mycenaean	Romania C	0.566966	0.331	0.669	0.192

TABLE 6.6: QpAdm results of feasible two-way admixtures to model the Armenoi population.

6.4.12 GF010, the Armenoi outlier

One sample from the Armenoi necropolis is a noticeable outlier, GF010, on the PCA analysis. Unlike the rest of the Armenoi population, GF010 plots closer to Bronze Age populations from Western Europe (**Figure 6.9**). It is clear from the PCA that GF010 differs from the Greek and Balkan Bronze Age populations and plots with western populations including Germany, Britain and France.

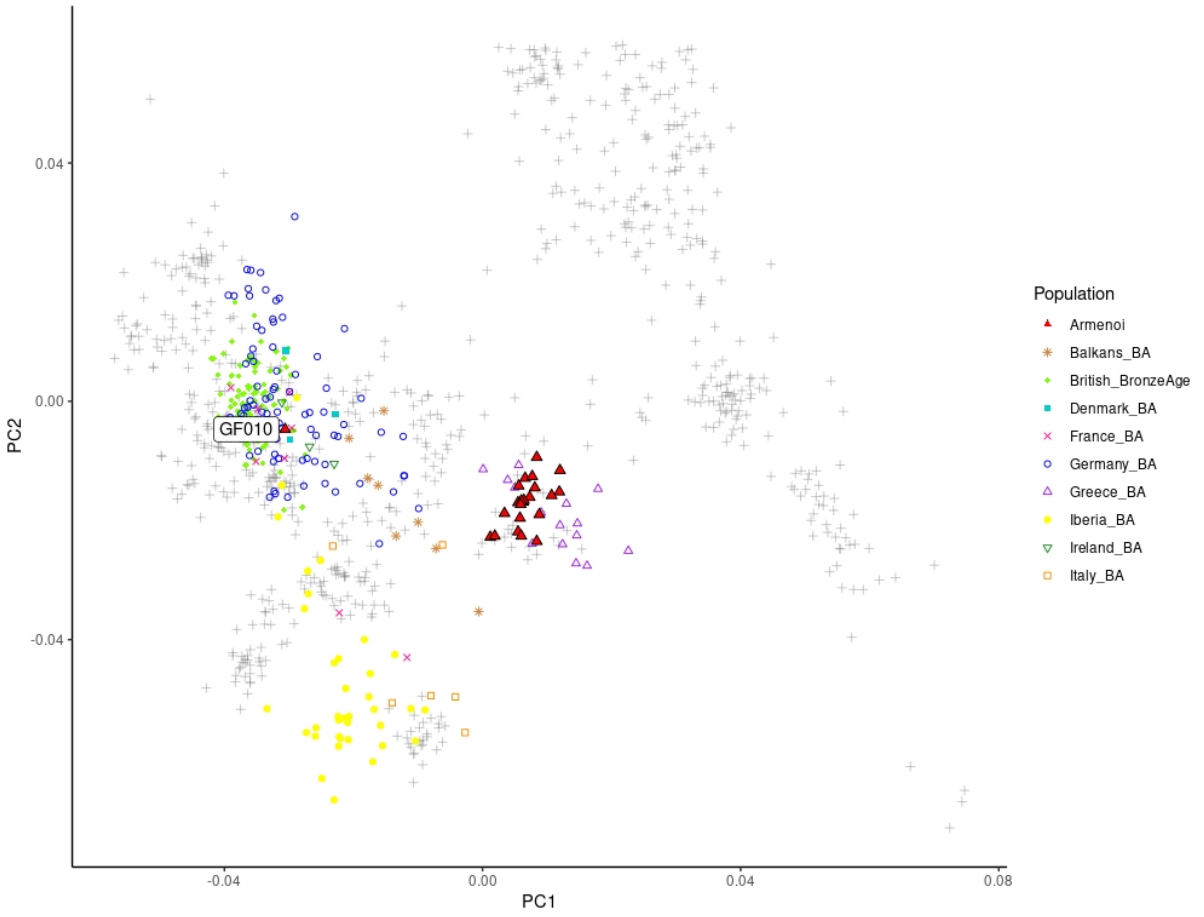


FIGURE 6.9: PCA of West Eurasians, light grey crosses, with ancient individuals projected on top. Armenoi samples are red triangles. Of note one individual, GF010, does not plot with the other Armenoi individuals.

ADMIXTURE analysis also shows GF010 to be more similar to Bronze Age populations of Western Europe than Armenoi (**Figure 6.10**). *D*-statistics in the form of D(Mbuti, Test; Yamnaya, Anatolia Neolithic), were employed to demonstrate GF010 was significantly different from the rest of the Armenoi population. GF010 was the only sample not to produce a significant different Z score (Z = -1.334) (**Figure 6.7**).

Outgroup-f3 was employed to determine a potential origin of the Armenoi outlier, unfortunately it was not possible to produce a significant result, possibly as a consequence of being an admixed individual and/or low coverage. Although several Bronze Age populations with steppe admixture appeared to have more shared drift with GF010, the error margins meant there was a great deal of potential overlap between all populations. Due to low coverage few significant *D*-statistics results were produced. The results produced show that GF010 shows a greater affinity to western Bronze Age populations than those from the Balkans or Greece. Scottish Bronze Age, French Bell Beaker and German Corded Ware populations all had greater shared drift than Armenoi. Several significant results were produced with qpAdm using a revolving set of left populations (Anatolian Neolithic, Iranian Neolithic, WHG, EHG,

Yamnaya Samara). Significant results were only produced when they included the Anatolian Neolithic and the Yamnaya, or when they included the Anatolian Neolithic, Iranian Neolithic and the EHG.

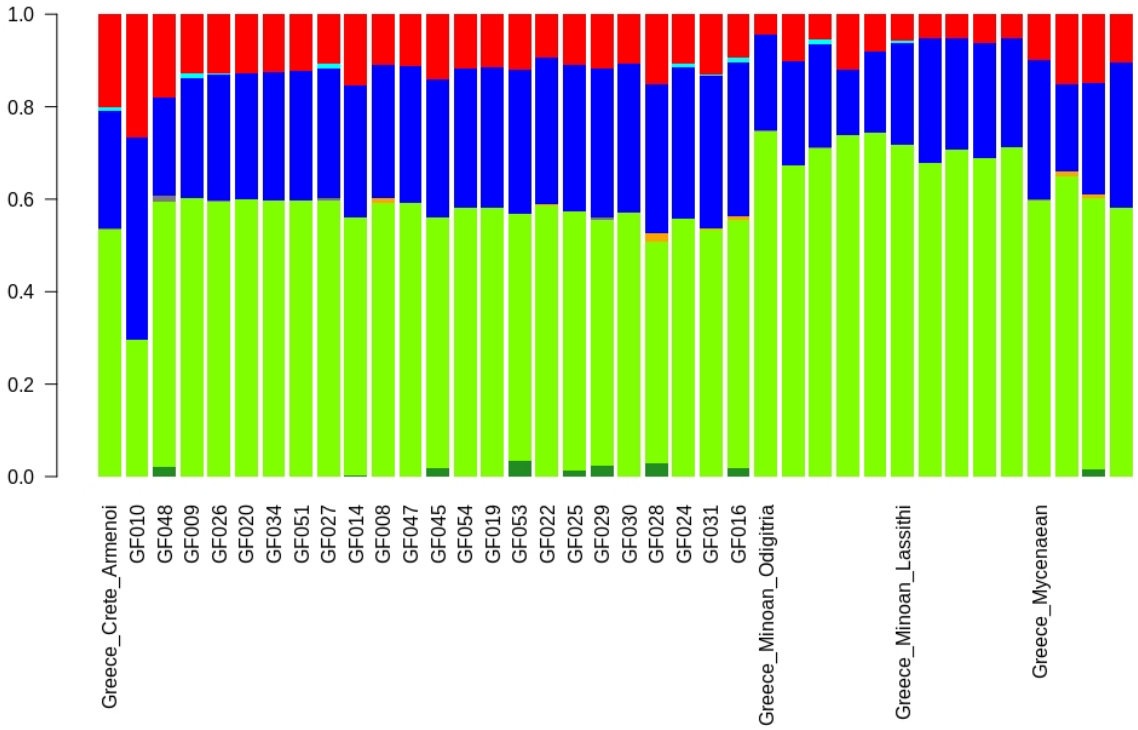


FIGURE 6.10: ADMIXTURE results of Armenoi population and published Bronze Age Greeks. Note the differing component proportions of GF010.

6.4.13 Zooarchaeological assessment

The long bone in Tomb 146 (GFa01) was identified as a fully fused sheep bone. Due to the fusion of both femoral epiphyses, this sheep was at least two and a half years old at death (Zeder, 2006; O'Connor, 2008).

The bones in Tomb 159 were identified as either lagomorphs or ovicaprids. The four lagomorph bones were a femur (GFa04) and three humeri (GFa09-11). Due to their large size, and historic rabbit-hare habitat ranges (Irving-Pease et al., 2018), the species was assessed as being hare. In addition, the bones were noted as being large for southern Europe. As there was no evidence of human alteration, such as butchery, cooking or gnawing, these hares may not have been consumed but may have been intrusive into the burial environment.

Ovicaprid is a term used for samples that are assigned as sheep or goat. Many skeletal elements, particularly those that are unfused, are difficult to distinguish between the two taxa (Buckley et al., 2010). Of the nine ovicaprids, six could not be assigned to sheep or goat. A

fused distal metatarsal (GFa03) was identified as a probable goat; however, this is questionable due to the amount of damage to the bone. The fused epiphysis would make this animal at least 18 months at death. A fusing distal humerus (GFa08) was identified as a sheep. As the bone was beginning to fuse, the animal died between 6 and 18 months. The mandible (GFa13) was identified as sheep due to the characteristics of the third deciduous premolar. The eruption pattern suggests that the animal was under two years old. From the twelve bones, the minimum number of individuals (MNI) for hares was two, and for sheep/goat was three. No cut marks were found on any of the bones. However, gnawing was found on the potential goat metatarsal (GFa03), and the puncture marks present suggested that these had been caused by a medium-sized carnivore, such as a dog or fox.

6.4.14 ZooMS results

The results of ZooMS analysis were able to identify four samples as lagomorphs, and nine as caprines. Of the lagomorphs, GF0a04 could be further identified as a probable *Lepus* (hare) through the presence of marker 2808. One of caprines, GF0a03, had the characteristic marker 3094, unique to *Capra* (goats). The other eight caprines were identified as *Ovis* (sheep). These results support the zoological assignment.

6.4.15 Dietary isotopic analysis

All animal samples produced collagen for analysis, however GFa01, a sheep, had a C:N ratio value of 4.6. This is higher than the range of values expected from diagenetically unaltered mammalian collagen of 2.9 to 3.6 (DeNiro, 1985; Van Klinken, 1999) and so it was, therefore, excluded from further analysis. Of the humans, 43 of the 59 produced enough well-preserved collagen to be analysed (see **Table D.10** and Figure 6.3). It had been hoped to compare the isotopic results of GF010 to the rest of the population, to see if it noticeably differed, as it may have provided further evidence that he was a foreign-born individual. However, despite producing DNA results and being run for SI analysis twice, the collagen from GF010 gave too high a C:N ratio (4.1 and 9.7 from each separate run respectively) to be included in the analysis. Two adolescents, GF005 and GF014, also produced collagen with high C:N ratios (3.9 and 4.1 respectively). As these values fall outside of the preservation criteria above, their results were interpreted with caution.

With the exclusion of the two juveniles (GF005: -21.64 δ^{13}C and 6.73 δ^{15}N; GF014: -21.49 δ^{13}C and 6.66 δ^{15}N), overall the Armenoi population produced δ^{13}C values between -19.02 and -20.69 and δ^{15}N values between 10.71 and 7.58. Whilst the δ^{13}C results produced in this study are broadly in line with those reported by Richards and Hedges (2008), the δ^{15}N values in this study are consistently higher (δ^{15}N values in Richards and Hedges (2008) are between 9.2 and 6.8). Dietary isotopic results from the animal baselines produced in this study also differed from those from Richards and Hedges (2008), with the Armenoi animals also having higher

δ^{15}N values than those from Chamalevri; this may be the result of local variation farming practices.

The human δ^{13}C and δ^{15}N results are approximately 1‰ and 3-4‰ higher than the animal baselines. This is line with consumption enrichment mentioned in Richards and Hedges (2008), and far below the expected δ^{13}C values for marine or C4 plant dietary protein. This suggests that the Armenoi population were mainly consuming local terrestrial animal and plant sources of protein in their diet. The δ^{13}C and δ^{15}N values suggest a terrestrial, C3-based diet was consumed. The Armenoi population appears relatively homogenous (**Figure 6.11**), and no differentiation between males and females, or between higher and lower status tombs, was identified. Only two individuals noticeably differ from the mean, GF005 and GF014, both of which are juveniles, and both have high C:N ratios as mentioned above, making them unreliable for dietary interpretation. The other two juveniles (GF021 and GF023) plotted with the Armenoi adults, with GF021 having the highest δ^{15}N value of the necropolis, which is likely to represent a pre-weaning/breast-feeding dietary signal in this individual.

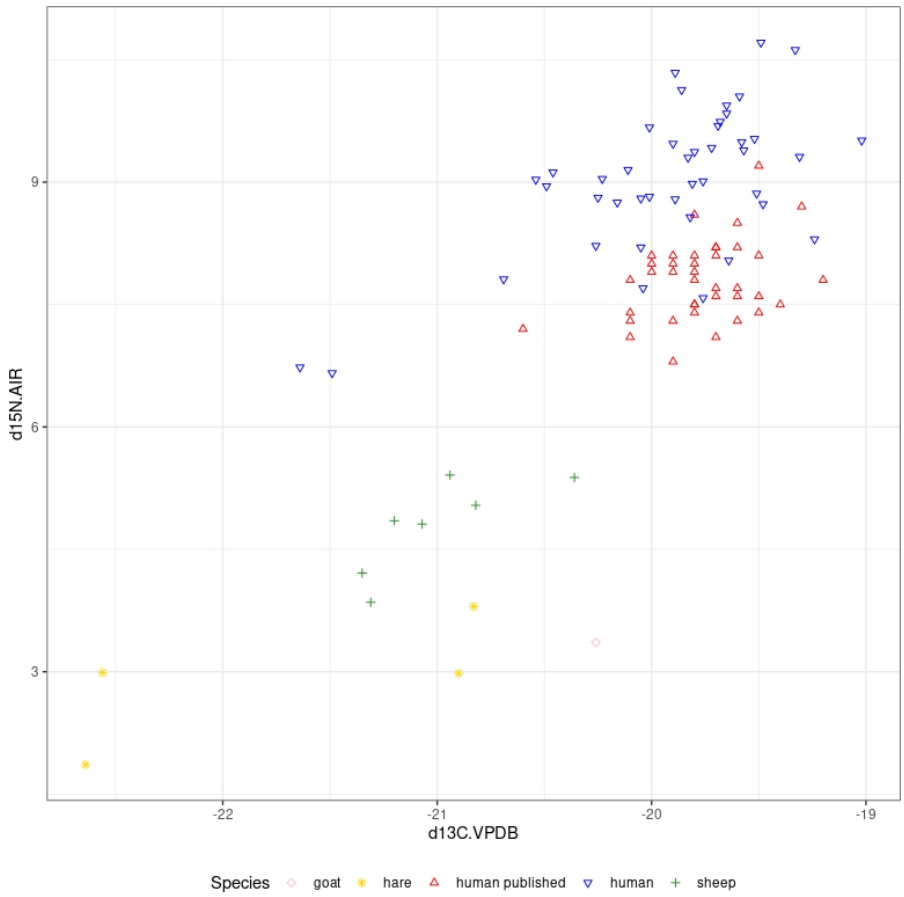


FIGURE 6.11: Dietary isotope results from Armenoi. Previously published human results from Richards and Hedges (2008) are represented by red triangles. Newly reported human results are represented by blue triangles. Animal results are those generated in this study.

6.5 Discussion

6.5.1 Sex ratio

The individuals selected for this study were revealed to be predominantly female (16 out of 23 individuals). As the sample selection was undertaken based purely upon preservation, these results are surprising. This is because previous osteoarchaeological work on Minoan cemeteries, including Armenoi, has suggested a 1:1 male to female ratio, or even a greater number of males (McGeorge, 1983). To the author's knowledge this is the first instance where a greater number of females has been noted. This may suggest that a re-evaluation of skeletal remains regarding demography is required.

6.5.2 Uniparental markers

The presence of Y-chromosomal haplogroups G2a and J has been associated with the Neolithic expansion (Lacan et al., 2011; Fernández-Domínguez and Reynolds, 2017). J and G2a are both found among published Minoan individuals, and J has also been noted in a Mycenaean individual (Lazaridis et al., 2017).

There is some overlap in the mitochondrial haplotypes found between published Minoan and Mycenaean populations and those found on Crete (Lazaridis et al., 2017). Whilst U has been associated with Mesolithic hunter-gatherers, the presence of mitochondrial haplogroups N1a, T2, K, J, HV, V, W, and X in western and central Europe has been associated with the arrival of the Neolithic (Haak et al., 2010; Brandt et al., 2013; Szécsényi-Nagy et al., 2015). However, it should be noted that K has been described in Mesolithic Greece (Hofmanová et al., 2016). Unlike the Y-chromosome, there are no new dominant mitochondrial haplogroups associated with the Bronze Age. Most of the mtDNA macrohaplogroups found in the Armenoi population have been previously described in Balkan Neolithic studies (Hofmanová et al., 2016; González-Fortes et al., 2017; Lazaridis et al., 2017; Mathieson et al., 2018). The exceptions are W, which to date has first been found in a Croatian Middle Bronze Age individual (Mathieson et al., 2018), and U7, which has not yet been found in the Balkans. Research has indicated that U7 entered Europe around the time of the Neolithic expansion from the Near East (Sahakyan et al., 2017).

In conclusion, the mitochondrial results are typical of post-Neolithic populations. In contrast, the Y-chromosomal results are similar to Neolithic data, but there is no evidence of the dominant R1 haplogroup, typical of populations that received an influx of steppe ancestry during the Bronze Age.

6.5.3 Kinship

With the current coverage of the Armenoi genomes, it is only possible to identify first- and second-degree relationships. However, despite this low level of resolution, several intra-tomb kinships could be identified. Most significantly is the multi-generational family group seen in Tomb 203, which agrees with the hypothesis that multiple interment represents kin groups.

6.5.4 Genetic ancestry

The majority of the Armenoi population appear to be relatively homogenous across ADMIXTURE, PCA and *D*-statistic tests, with no noticeable differences seen between the genomic composition of individuals and their tombs respective wealth, as expressed in grave goods. In all tests, GF010 appears as an outlier, and is likely an immigrant to Armenoi. The rest of the population appear similar to Greek Neolithic and Bronze Age populations, with little or no steppe ancestry seen in the ADMIXTURE or PCA analyses. Armenoi appears differently to earlier Minoan populations in ADMIXTURE and PCA, being more similar to Mycenaeans, with the opposite occurring in the *D*-statistics. Admixture modelling using qpAdm shows that the Armenoi population could be derived from Minoans (from Moni Odigitria) with a lesser contribution from Mycenaeans. As qpAdm can be used with proxy populations, this may be improved with more detailed sampling.

6.5.5 Outlier GF010

Despite low coverage of this individual, it was still possible to identify GF010 as an outlier. PCA, ADMIXTURE and *D*-statistic tests demonstrate this individual resembles Bronze Age populations from western Europe. The qpAdm results show that possible ancestry combinations always include the Yamnaya, and either the Iranian Neolithic or the EHG. This combination is more commonly seen in western European Bronze Age groups, further suggesting that this individual was an incoming migrant, likely from western Europe. His Y-chromosomal haplogroup also differs from the other males on the site with a R1b haplogroup, which is more commonly seen in areas that underwent steppe migration, such as western and northern Europe (Olalde et al., 2018).

6.5.6 Dietary isotopes

The Armenoi population had a C3, terrestrial-based diet. The lack of marine consumption is similar to several mainland Greek and Cretan Bronze Age sites, and contrasts with the Mycenaean elite graves of Grave Circle A (Richards and Hedges, 2008). The lack of differentiation associated with sex or status resembles the published dietary isotope study of Middle Minoan Knossos (Nafplioti, 2016), which differs from the Greek mainland (Petroutsa and Manolis, 2010; Papathanasiou, 2015). Despite the changes in material culture, dietary habits appear to have remained broadly similar to the earlier Minoan period.

6.6 Conclusion

The homogeneity, coupled with no noticeable differences associated with tomb status, suggests a Mycenaean elite takeover did not occur, or at least that this incoming elite only intermarried with other Mycenaeans. The majority of the population does not appear to be a simple continuation of earlier Minoan populations, nor is there evidence of complete replacement by mainland Mycenaeans. Instead, using the results of this project, the hypothesis that admixture occurred between Minoans and Mycenaeans is supported.

The presence of the genetic outlier shows that migrants were present in Late Minoan Crete. This individual was buried in a tomb with other, non-related individuals and does not appear to have been treated differently in death.

6.7 Ongoing and future work

Of the 118 individuals that were collected from Armenoi, only 55 were subjected to screening for endogenous DNA content, and 23 of these subjected to in-depth sequencing based on their endogenous content. It is hoped to secure a grant to screen the remaining 63 individuals and thus sequence more samples from the site. Any additional sequences, alongside those already produced that have high enough coverage, could undergo imputation analysis. Imputed sequences produce much greater coverage across the genome and, therefore, allow more in-depth analysis, allowing greater insight regarding kinship, phenotypic information and genetic diversity within the cemetery. This would allow me to further explore whether GF010 is the only outlier at the site, or whether he is part of a larger trend. In addition, programs with greater analytical power, such as ChromoPainter, could be employed to allow more detailed conclusions about genetic ancestry.

Ideally, I would also like to undertake dietary stable isotope analysis on all 118 individuals from the site. Based on the genomic analysis, and where tooth samples are available, a number of individuals could be targeted for oxygen and strontium isotopic values to assess locational data.

Chapter 7

Ancient DNA studies of Britain

Several ancient DNA studies have involved samples from the British Isles, ranging from the Mesolithic to Anglo-Saxon periods. The most in-depth studies are from the Neolithic and Bronze Age, but these have both chronological and geographical gaps as discussed below.

7.1 Mesolithic and Neolithic

The earliest British ancient DNA sample is from Aveline's Hole and dates to the Early Mesolithic (8750-8459 cal. BC). All six published Mesolithic samples (Brace et al., 2019) (**Figure 7.1**) cluster with Western Hunter-Gatherers (WHG) in a PCA. This close grouping has been further supported through allele-sharing analysis. Comparison of high coverage samples shows that the British Mesolithic plots closer to Mesolithic individuals from France and Luxembourg than those from Spain and Hungary (Brace et al., 2019). This is potentially the result of the isolation by distance occurring between Britain, Spain and Hungary, or introgression of other ancient groups (Chapter 5).

The Neolithic arrived in Britain around 4000 BC (Bradley, 2007). Similar to other areas of Europe (Haak et al., 2015; Mathieson et al., 2018), there appears to have been a large-scale population turnover in Britain associated with the Neolithic arrival across Europe, whereby ancestry from the Anatolian Neolithic replaced or was admixed with the indigenous Mesolithic hunter-gatherer groups (Brace et al., 2019; Sánchez-Quinto et al., 2019). All six Mesolithic individuals from Brace et al. (2019) belong to haplogroup U5 (although several are incorrectly reported in the paper), consistent with other European WHG mtDNA haplogroups (Brandt et al., 2015). In contrast, during the Neolithic, a diverse range of mtDNA haplogroups are introduced (JT, K, HV, X) (Brace et al., 2019; Sánchez-Quinto et al., 2019; Olalde et al., 2018). Admixture proportion modelling, using qpAdm, shows that a minority of WHG ancestry was admixed with Anatolian farmer ancestry Sánchez-Quinto et al. (2019), Brace et al. (2019), and Olalde et al. (2018), indicating a large-scale migration event during this time. This is consistent with the hypothesis that the presence of farming in the British Neolithic was not the result of indigenous adoption.

FIGURE 7.1: Location of published Mesolithic genomes from Brace et al. (2019).

Regional variation has been observed across Britain. The qpAdm results in Brace et al. (2019) suggest 20% WHG ancestry in Wales and southwestern England, increasing to over 30% in Scotland and southeastern England. However, the introgression from indigenous Mesolithic Britons appears to have been low, with the WHG component appearing to have arrived with Neolithic Europeans rather than being indigenous. The WHG component in British Neolithic groups differ slightly in Olalde et al. (2018), who also calculated Wales as having c. 20% WHG ancestry, but found England and Scotland to have c. 30% WHG. This may be a result of Olalde et al. (2018) having a smaller sample size or grouping regional differences within England together. Comparison of qpAdm of the X- and autosomal chromosomes by Sánchez-Quinto et al. (2019) shows relatively consistent proportions across Britain, indicating a lack of sex-bias. Middle Neolithic Scotland does not fit this pattern, and here male hunter-gatherers appear to have admixed more frequently with female Neolithic farmers.

The Neolithic spread across Europe following two major routes: the Danubian route across Central Europe, and the Mediterranean route (Sánchez-Quinto et al., 2019). Archaeologically there is debate as to which route entered Britain, or even if there was a mix of both routes arriving at different times and to different areas of the British Isles. f-statistics support a greater affinity between Britain and the Iberian Neolithic, over Central European populations (Olalde et al., 2018; Brace et al., 2019; Sánchez-Quinto et al., 2019; Scheib et al., 2019), but this affinity could be misleading as both Iberian and British samples contain a larger proportion of WHG than Central European Neolithic, which might lead to anomalous grouping (Brace et al., 2019; Sánchez-Quinto et al., 2019). To test this, (Sánchez-Quinto et al., 2019) used a paired f4-test, comparing f4(out, test; Germany EN, Iberia EN) to f4(out,

WHG; Anatolia EN, test), and the results supported the affinity between Britain and Iberia. Brace et al. (2019) produced similar results using chromosome-painting and inferred ancestry coefficient approaches. A potential second source of Neolithic ancestry, related to that in Central Europe, has been identified using qpGraph. This second Neolithic source is found to be more prevalent in England, to a lesser extent in Scotland, and not at all in Wales. The authors highlighted that these are preliminary tests due to the quality and availability of samples. Similarly, Olalde et al. (2018) demonstrated a slight presence of Central European ancestry with qpGraph. This ancestry was seen to be closer to Hungarian, rather than German, early Neolithic groups. However, the authors noted that the sparsity of Neolithic data, particularly from France, had likely led to an oversimplification of migration.

All YDNA haplogroups of British Mesolithic are haplogroup I (I2a2 and I2a1b in the samples with higher coverage), and I2 YDNA lineages are common amongst Mesolithic WHG groups across Europe (Olalde et al., 2018; Brace et al., 2019; Sánchez-Quinto et al., 2019). British Neolithic males also follow this pattern. As most areas of Britain do not show large amounts of admixture with the indigenous Mesolithic or evidence of sex-biased admixture, the presence of I YDNA haplogroups may be the result of early Neolithic migrants. Iberian Neolithic farmers, which are used as a proxy source for the Mediterranean route dispersal, have a higher percentage of I2 YDNA than Central European farmers (Olalde et al., 2018).

In concert, all of these results point toward the first Neolithic farmers in Britain being part of the Mediterranean expansion. The British Neolithic can be modelled as an admixture of mainly Iberian Neolithic (as a proxy for Mediterranean farmers), with a much lesser contribution from the indigenous British Mesolithic, and indicates that very little local admixture took place, suggesting a near complete population replacement (Brace et al., 2019).

To assess the possibility of inbreeding, Scheib et al. (2019) calculated lengths of Runs of Homozygosity (RoH) for Neolithic brothers from East Anglia. They were shown to have relatively high total lengths, but no very long tracts were observed. Rather than being due to inbreeding, this was interpreted as there being a low population size in the area. In contrast, a Neolithic individual from Derbyshire, and the Cheddar Man Mesolithic individual, were both determined to be from large or more admixed populations (Brace et al., 2019).

The availability of samples in Britain has led to geographical gaps, which has an impact on interpreting regional diversity (**Figure 7.2**). All British Mesolithic samples are restricted to southwest Britain, with the exception of one Scottish sample 7.1. Neolithic samples are more widely distributed across Britain, but still no samples have been tested from Eastern England, Cornwall, central Wales, or northwestern or southeastern Scotland, and only three samples exist from northern England.

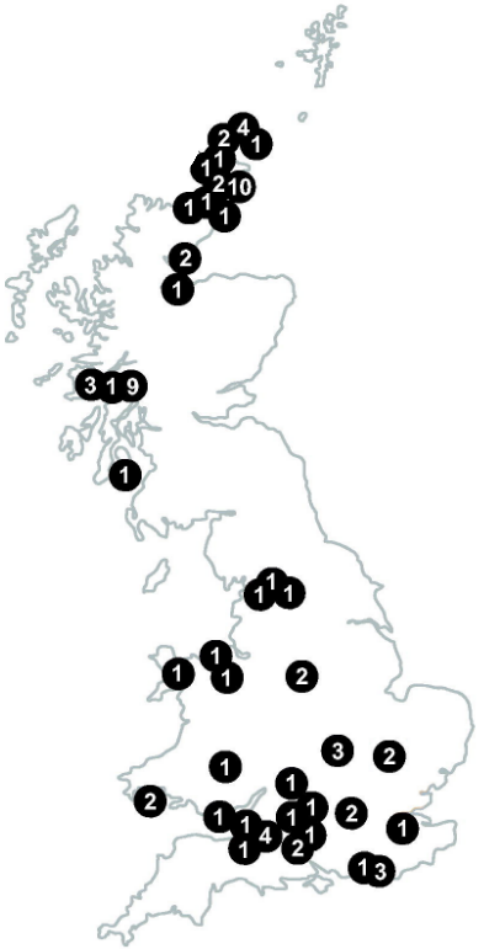


FIGURE 7.2: Location and number of sequenced Neolithic individuals from Great Britain. Adapted from Scheib et al. (2019). The number of Neolithic samples sequenced at each site is present on the figure.

7.2 Bronze Age

The Bronze Age began in Britain around c. 2500 BC. It should be noted that the terminology of this period has been debated, as no bronze is found in Britain until 2200 BC and, therefore, some archaeologists refer to the period from 2500 to 2200 BC as the Chalcolithic. The Bronze Age period is often linked to the Beaker culture (Parker Pearson, 1999), which is found across Continental Europe at this time, from Iberia to Central Europe. Debate has existed as to whether the extent of the Beaker 'package' (bell-shaped pots, flint or copper daggers, arrowheads, and archer's wrist-guards) seen in the archaeological record is the result of the spread of people or ideas (Pollard, 2008; Pearson, 2009; Fitzpatrick, 2013; Leslie et al., 2015; Pearson et al., 2016; Olalde et al., 2018). The origin of Beaker groups in Britain has been argued to be the Lower Rhine in Germany, Atlantic Iberia, or a mix of the two (Fitzpatrick, 2013; Leslie et al., 2015; Olalde et al., 2018).

The largest ancient genomic study of Bronze Age Britain was undertaken by Olalde et

al. (2018) with widespread sampling, particularly for the early Bronze Age, across the country (**Figure 7.3**. Large-scale replacement of YDNA has provided strong evidence of an extensive demographic movement at this time. R1b becomes dominant in the Bronze Age and later Britain, being present in up to 90% of the Bronze Age British males sampled. This haplogroup is commonly associated with Beaker groups outside Iberia, suggesting that Iberia was not the source of the British Beaker culture (Olalde et al., 2018). New mtDNA haplogroups are also introduced at this time, but evidence of replacement is less clear using mtDNA alone, as many haplogroups would have been present in both locations prior to the Bronze Age.

Further evidence of a Central European origin for the British Beakers comes from the presence of ancestry related to the Yamnaya culture of the Eurasian steppe. This 'steppe' ancestry is associated with Bronze Age cultures in Central and Eastern Europe, but is largely absent in the early Iberian Bronze Age. This connection has been further supported by f-statistics (Olalde et al., 2018).

Modelling of British Bronze Age samples using qpAdm, as an admixture of Central European Beakers and British Neoliths, suggests a near complete replacement of the British population by incoming Bronze Age peoples. These component ratios do not appear to change in the later Bronze Age, but Olalde et al. (2018) note that more Bronze Age samples are required to determine the rate and pattern of population change.

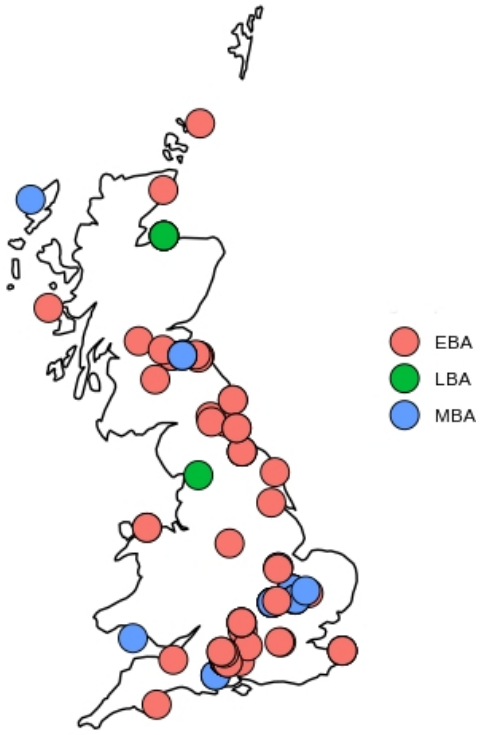


FIGURE 7.3: Map of the UK with the locations of the samples published in Olalde et al. (2018).

7.3 Iron Age and later

Bronze Age samples from western Europe appears similar to modern populations from the same areas in both PCA and ADMIXTURE studies (Olalde et al., 2018). Chapter 9 aims to determine whether subsequent population replacements occurred in Britain. As has been shown in a time transect study of Spain, major demographic change can occur within this time period. Despite Spanish modern samples appearing similar to those in Bronze Age Iberia, intervening periods showed significant North African admixture, which was subsequently replaced in the Medieval period (Olalde et al., 2019). Post-Bronze Age Europe has been far less studied than the preceding periods. To date, four Iron Age, seven Roman, and eight 'Anglo-Saxon' period samples have been published for Britain, in comparison to 64 Neolithic and 96 Bronze Age samples. These later studies are focused on only four locations: one Iron Age person from Melton, Yorkshire; three Iron Age and seven Anglo-Saxon individuals from Cambridgeshire, east England; one Anglo-Saxon from Norton-on-Tees, Durham, northeast England; and seven Romans from York (Martiniano et al., 2016; Schiffels et al., 2016). Of note, the Roman burials appear to be unusual, with a large number of skeletons at the site showing signs of decapitation.

The post-Bronze Age timeline is not as uniform across Britain as the Neolithic and Bronze Age. The Iron Age in Britain began around 800 BC and continued in England and Wales until the Roman conquest around 100 AD, whereas in Scotland, the Iron Age continues until 500 AD (Haselgrove, 2009). Settlement and material culture evidence varies throughout Britain during this period. Large hillforts are found in southern and eastern England, small fortified enclosures along the Atlantic coast, brochs (drystone towers) in northeastern Scotland, Orkney, Shetland and the Hebrides, and crannogs (artificial islands) across Scotland (Haselgrove, 2009; Leslie et al., 2015). To date, there are not enough ancient DNA data from this period to determine whether this regional variation is also reflected in genetic diversity. The mtDNA and YDNA present in the Iron Age are also found in the British Bronze Age, but, as these were common across northwestern Europe at this time, they are uninformative to determine migration (Schiffels et al., 2016). PCA and ADMIXTURE analyses group Iron Age individuals with Bronze Age populations, and so it is not possible to distinguish continuity against migration.

The Roman period in England and Wales lasted for approximately 400 years and had a profound effect on society and culture. Increased connections with the continent are evident from the presence of imported goods. Epigraphical, isotopic and archaeological evidence have all supported the presence of migrants during this time (Leach et al., 2009; Cleary, 2009; Leach et al., 2010). Roman migrants mainly appear to be those associated with trade, the army or high-status individuals, but their impact on the general population is unclear (Eckardt et al., 2014; Leslie et al., 2015). Of the six Roman ancient genomes, one male individual showed

evidence of being a migrant. He possesses the YDNA haplogroup J2-L228, which is now common among people from the Middle East, although also found in the Caucasus, Balkans and Italy. He plots with modern Middle Easterners in the PCA and, using strontium and oxygen isotope analysis, he was shown to be a first-generation migrant to Britain (Martiniano et al., 2016). The other Romans had YDNA and mtDNA similar to other periods. However, it must be noted that the Romans in this study were subjected to unusual burial practices, and have been hypothesised to have had foreign backgrounds, so they most likely are not representative of the general Romano-British population (Müldner et al., 2011).

The period following the Roman period has been dubbed the 'Dark Ages', or Early Medieval Period, and continues until the Norman invasion of 1066 AD (Hills, 2009). Migration and population turnover for this period has been greatly debated. Historical, linguistic and archaeological evidence has variously been used to indicate admixture, large-scale migrations or small elite groups controlling Britain (Härke, 2003).

Beginning in the mid-5th century AD, groups of Angles, Saxons and Jutes, originating in Jutland and northern Germany, started arriving in England, bringing major changes in linguistics, material culture and religion. Over the next 200 years they had conquered most of England, and Anglo-Saxon material culture was adopted almost exclusively in these areas. Parts of northwestern England, Cornwall and Devon were much less under Anglo-Saxon domination, and Romano-British culture continued in northeastern England and Wales. Scotland divided into several competing kingdoms, comprising divergent ethnic groups of Romano-Britons, Picts (descended from the Scottish Iron Age people) and Gaels/Scots from the north of Ireland (Haughton and Powlesland, 1999b; Hills, 2009; Driscoll, 2009; Leslie et al., 2015). An Anglo-Saxon individual from Norton-on-Tees had YDNA I1, which is common in modern Scandinavia (Martiniano et al., 2016), while other Anglo-Saxon males possess R1b (Schiffels et al., 2016). Although it is not possible to draw any conclusions from a single individual, the presence of I1 from Nordic areas corresponds with evidence of Anglo-Saxon migration. Although only small differences were visible in the PCA analysis, Schiffels et al. (2016) observed that their Cambridgeshire Iron Age samples appeared closer to modern English people, whilst the Anglo-Saxons appeared closer to modern Scots and Norwegians. This contrasts with the results from the Yorkshire samples in Martiniano et al. (2016), whose Iron Age and Roman samples plotted as being closer to modern Welsh and Scottish groups, whereas their Anglo-Saxons plotted closer to modern English populations. The difference in results between these papers is most likely due to regional diversity, small sample size, unrepresentative individuals, and/or problems comparing modern and ancient data.

Viking conquests of Britain occurred between 800-1000 AD, but, to date, no British Viking-era genomes have been analysed. Norwegian Vikings conquered Shetland, Orkney, the western Scottish islands and the northeastern Highlands, while Danish Vikings conquered much of England. Demographic changes in England may be difficult to determine as Danish Vikings

originated from the same area as several Anglo-Saxon tribes, 400 years earlier (Richards, 2005; Richards, 2009; Leslie et al., 2015; Martiniano et al., 2016).

7.4 Kinship

Determination of kinship in cemeteries has been used to understand the importance of family groups in society. Kinship can be identified using READ analysis. Megalithic tombs across the British Isles and northern Europe have been found to contain family groups (Sánchez-Quinto et al., 2019; Scheib et al., 2019), and the people in these tombs appear to have practiced patrilocality. Of note, neither of the two megalithic tombs studied from Orkney produced any kinship relationships. This might either suggest that the individuals deposited in these tombs were too distantly related to be identified (3rd-degree or more), or that they were not family-oriented monuments (Sánchez-Quinto et al., 2019).

7.5 Genotypes

Changes in demography, through migration and admixture, can introduce new genotypes into a population. Pigmentation has been predicted for British Mesolithic and Neolithic individuals using H-irisPlex (Brace et al., 2019; Scheib et al., 2019). Using this method, British Mesolithic peoples had blue/green eyes, with dark hair and dark to black skin. In contrast, Neolithic people had brown eyes with 'intermediate' skin colour. In the Bronze Age, although Olalde et al. (2018) did not use H-Irisplex, they recorded an increase in the derived allele of the *HERC2* and *SLC45A2* genes, which are associated with lighter skin. The Iron Age, Romans, and Anglo-Saxon individuals had predominantly brown eyes, and approximately half had black/brown hair, while the rest were blonde/brown (Martiniano et al., 2016).

While sample numbers are too low to make any conclusions, *LCT*, which is responsible for lactase persistence (LP), is absent in Mesolithic and Neolithic British individuals (Brace et al., 2019; Olalde et al., 2018; Scheib et al., 2019). Despite the larger dataset *LCT* was also absent in the Bronze Age (Olalde et al., 2018). Two of the four Romans had the allele for lactase persistence, however, as mentioned above, due to their unusual burial rites, they are most likely not representative of the Romano-British population as a whole (Martiniano et al., 2016). Whilst it is possible to digest lactose without LP, for example through certain gut flora and fermentation processes, the current LP of Britain and Ireland is 89-96%, suggesting it underwent a strong positive selection at some period in the past, or was introduced through extensive demographic changes (Gerbault et al., 2011).

7.6 Using modern genetics to infer past migrations

The first large fine-scale study of modern UK variation was the People of the British Isles (PoBI) (Leslie et al., 2015). Using fineSTRUCTURE, 17 genetic clusters were identified (**Figure 7.4**), which were then compared to modern European groups. It was possible to link some groups to putative historical events; for example, the distinctiveness of Orkney, and their contribution of Norwegian ancestry, is consistent with its long Viking history.

Relative homogeny was identified in southern and central England. This may be the result of large-scale migration, potentially linked to the Anglo-Saxons; however, this could also have occurred through relatively local migrations over many generations. The area does not have significant geographical barriers and, for much of the past two millennia, has not had any serious linguistic or political divisions. FineSTRUCTURE and GLOBETROTTER identified the presence of north German ancestry in Anglo-Saxon areas of Britain. However, this was identified at low levels, and is not consistent with a large-scale population replacement.

Cornwall appears much closer to southern and central England, rather than to Welsh populations to which Cornwall shared a greater cultural link through time. Scotland and Northern Ireland also show similarities, although it is not clear whether this is due to ancient movements of Scots/Gaels to Scotland, or rather to the more recent 'Ulster plantations', during which many native Ulster people were forcibly evicted by the British government and their lands given to Scottish settlers. These conclusions reached by Leslie et al. (2015) were largely mirrored by the later study by Byrne et al. (2018) that included data from across Ireland. The latter authors noted that the Northern Irish-Scottish similarities could be due to Gael moving into Scotland, the Ulster plantations or economic migrations to Scotland in the 19th and 20th centuries AD. A more detailed analysis of Scotland and its islands showed a northeast-southwest split, mirroring the difference of Pictish and Irish names (Gilbert et al., 2019). This study again highlighted the impact of Norse settlers in Orkney and Shetland, but also found that the Hebrides are much closer to mainland Scotland than Scandinavia.

Although these two studies generated and analysed huge amounts of data, using modern populations to determine past migrations has several drawbacks. Later migrations can completely replace earlier populations (as seen in the Mesolithic to Neolithic, and Neolithic to Bronze Age, transitions), making earlier populations difficult, or even impossible to locate in modern-day data. As noted in Leslie et al. (2015), homogeneous areas may be due to recent internal migrations, and can be seen in central and southern England, where the homogeneity is visible in areas of industrial growth. Migrating populations, with similar genetic makeup as the indigenous population, may also be hard to identify and quantify (Schiffels et al., 2016). This was noted by Byrne et al. (2018) regarding the similarity between Scotland and Northern Ireland.

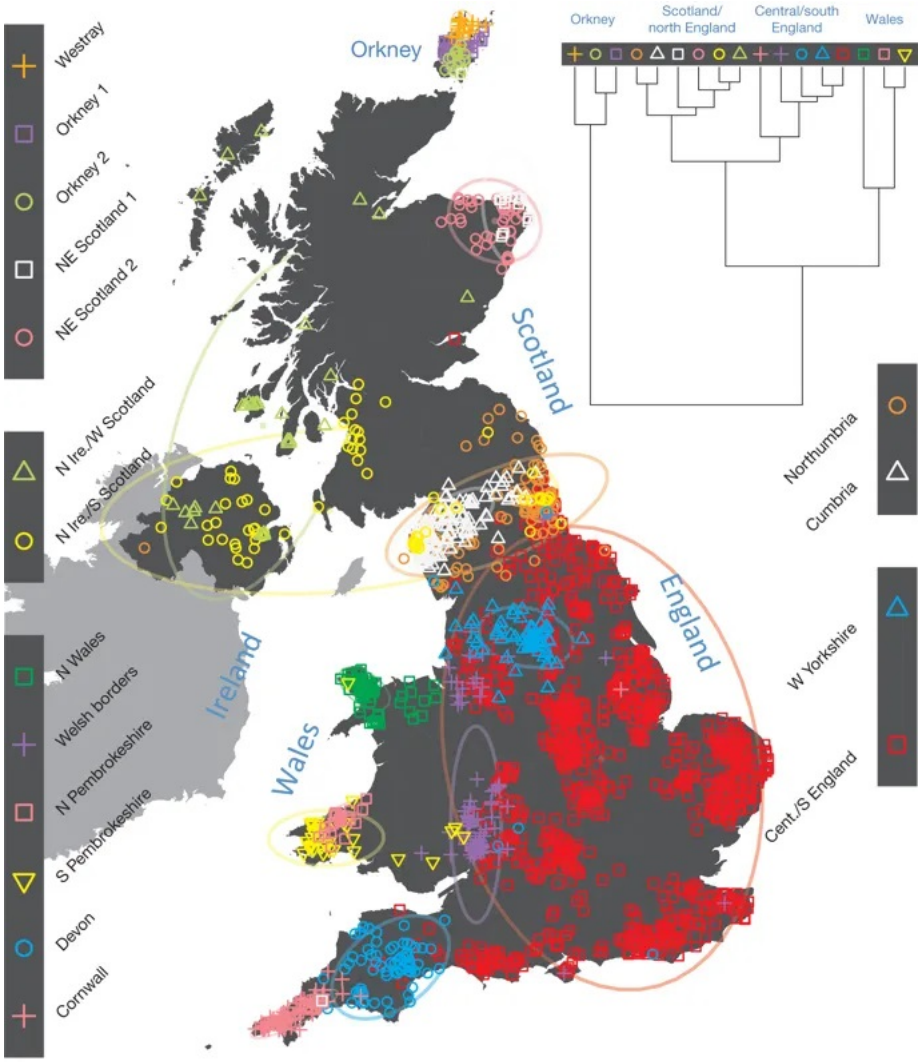


FIGURE 7.4: Clustering of UK individuals from PoBI project (Leslie et al., 2015).

7.7 Layout of chapters in this section

The analyses undertaken on samples from the British Isles as part of this thesis are divided into two separate projects, detailed in chapters 8 and 9. Chapter 8 concentrates on Bronze and Iron Age Orkney. Although Orkney is one of the areas with the highest numbers of published ancient genomes from Neolithic Britain, there is only one published Bronze Age genome. Due to the small geographic area, the Bronze Age samples from Orkney analysed here comprise an in-depth study. Chapter 9 is an analysis of post-Bronze Age Britain, with samples from across the island (**Figure 7.5**), including a multi-period site at West Heslerton.

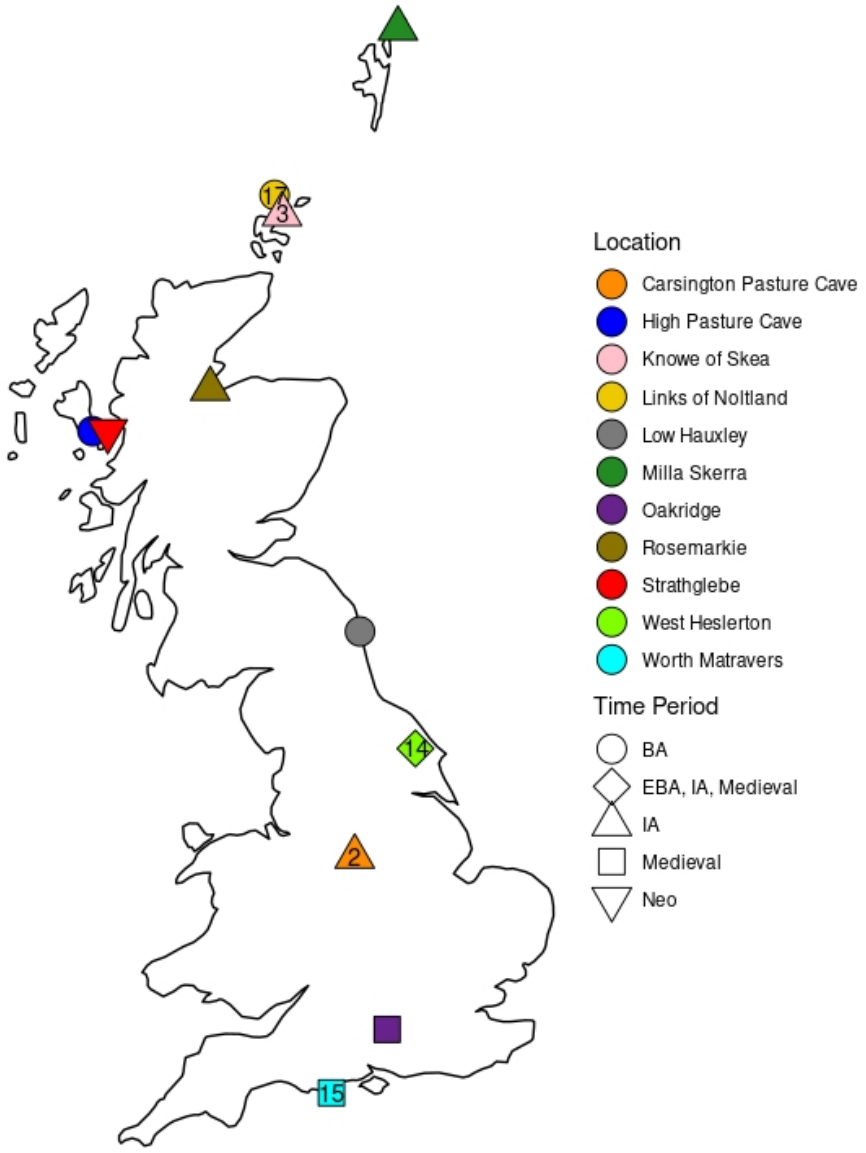


FIGURE 7.5: Map of Britain displaying the sites that will be investigated in the following chapters. Numbers represent sites with multiple ancient genomes.

Chapter 8

Genomic Analysis of the Scottish Isles

8.1 Introduction

Scotland represents one of the furthest northwestwardly points of the Neolithic and Bronze Age expansions. The large demographic migration that occurred during the Neolithic, beginning in 7,500 BC in Anatolia, reached Britain in 4,000 BC (Cummings, 2017), and has been reported as leading to a large population turnover (Olalde et al., 2018; Brace et al., 2019; Sánchez-Quinto et al., 2019). To date, Neolithic archaeogenetic studies have only sampled the eastern coast north of the Great Glen. However, Scotland's rugged landscape, divided by mountain ranges, and comprising of many peninsulas and islands, has influenced regionalisation within Scotland. For example, earthen long barrows and cursuses are found in eastern Scotland, whereas stone cairns dominate the west, and differences in pottery styles can be seen across the country (Noble, 2006). In order to investigate a possible east-west difference in Neolithic Scotland, a Neolithic individual from the west of Scotland, from Strathglebe on the Isle of Skye, was analysed.

The Orkney islands, situated off the northwestern coast of Scotland, have a rich Neolithic archaeological record (Mamwell, 2018) and are one of the best sampled areas of Neolithic Scotland (21 of the 43 published Scottish Neolithic genomes are from here(Olalde et al., 2018; Brace et al., 2019; Sánchez-Quinto et al., 2019)). In comparison, the Bronze Age in Orkney has been described as anti-climactic and dull (Ritchie, 1995; Mamwell, 2018), with only one published early Bronze Age ancient DNA sample (from Lop Ness, Sanday) (Olalde et al., 2018). A less dramatic change is seen in material culture during the Bronze Age than in other areas of Scotland, leading some archaeologists to question whether Orkney was more conservative and isolated during this time period (Wickham-Jones, 2013). However, some changes did occur, with a general abandonment of earlier Neolithic settlement. Bronze Age settlements are mainly identifiable by burnt mounds, the result of cooking. Burial practices changed from chambered tombs to mounds of earth (barrows) or stones (cairns), and cist burials. This change has been attributed to the rise of the individual over community or family groupings (Wickham-Jones, 2013). There is debate whether the changes in Orkney are the result of demographic change, internal cultural change, or a population reduction as a consequence of worsening climatic conditions (Wickham-Jones, 2013; Mamwell, 2018).

Whether Orkney underwent the same changes in genetic ancestry that occurred in the rest of Britain (Chapter 7) is unclear. This chapter will investigate whether the steppe expansion made a genetic impact on Orkney, similar to the rest of Britain.

Iron Age Orkney is characterised by a further change in the settlement record, with the appearance of stone roundhouses and brochs. Brochs are drystone hollow-walled structures found in Scotland, particularly Orkney, Shetland and the northwestern coast. Burial practices are less archaeologically visible at this time (Wickham-Jones, 2013). To date, there are no Iron Age ancient DNA samples from Scotland. Ancient DNA analysis presented in this thesis aimed to determine whether the genetic composition of Bronze Age Orkney continued until the Iron Age.

Influence of the Vikings can be seen in the Old Norse words found in everyday English, and Norn, an old Norse dialect, existed in the Northern Isles until the 18th century AD. In addition, Scandinavian place names are common in northern England and Scotland. The pre-Viking culture of Orkney appears to have been totally replaced, with even the meaning of Orkney being changed from 'the islands of young pigs' (Insi Orc in Old Irish) to 'the island of seal' (Orkneyjar in Old Norse) (Hjardar and Vike, 2016). It is unclear whether this cultural change was due to a large-scale migration, nor how this has contributed to modern variation (Richards, 2005; Richards, 2009; Leslie et al., 2015; Martiniano et al., 2016).

To study some of these questions, 23 Bronze Age individuals from the Links of Noltland, Westray, were analysed. The aims of this study were to determine whether Orkney underwent demographic changes associated with the Eurasian steppe, despite the archipelago's position on the northern fringe of Europe and differing Bronze Age culture to the British mainland. The relationship between Bronze Age and Iron Age Orkney was assessed by the inclusion of three Iron Age individuals from the Knowe of Skea, Westray, to determine genetic continuity or change. Kinship was also determined at these two sites.

FIGURE 8.1: Map of the Orkney archipelago displaying the Links of Noltland and Knowe of Skea sites.

8.2 Materials and methods

The Middle Neolithic individual from Strathglebe, Isle of Skye, was selected to study the genetic affinity of a Neolithic individual from northwestern Scotland. Although not directly dated, another individual from this site was radiocarbon dated to the mid- to late 4th millennium BC (4569 $\pm$ 39 uncal. bp; OxA-37513; 2σ 3494-3102 cal. BC).

The Links of Noltland (LoN), Westray, Orkney, covers an area of approximately four hectares and has revealed archaeological remains from the Neolithic to Iron Age. The Bronze Age cemetery is situated between two contemporaneous settlement structures (Historic Environment Scotland, 2018), with an enclosure at the centre of the cemetery. Both inhumations and cremations were interred at the cemetery, numbering over 50 burials, and over 100 people. The presence of different rites occurring in the same site may represent social and cultural diversity. Several multiple inhumation or cremation burials are present, and these have been interpreted as representing family groups. The samples selected for this study were all

inhumations due to the difficulty in retrieving ancient DNA from cremations. Several of the individuals were from a multiple burial in order to test the possibility of it being used as a family tomb (Moore et al., forthcoming). Radiocarbon dating was conducted on several of the samples (**Table 8.1**). All the dated samples in the multiple burial overlap (**Figure 8.2**, however, KD006 and KD047 only overlap by one year, even though KD047 is buried below KD006.

Sample	**Sex**	**Age (years)**	**Date (uncal. bp)**	**Calibrated date (cal. BC) to 2σ**	**Lab number**	**Element**
KD006*	-	>46	3285 ± 30	1621-1467	SUERC-35253	R petrous
KD044	-	36-45				LM3
KD045	F	18-25				upper incisor
KD046*	M	-				Molar
KD047*	M	>46	3155 ± 30	1500-1320	SUERC-36893	R petrous
KD048	-	non-adult	3195 ± 30	1508-1416	SUERC-35264	L petrous
KD049*	-	juvenile?				R petrous
KD050*	-	juvenile?				R petrous
KD051	-	1-12	3370 ± 30	1742-1543	SUERC-35255	R petrous
KD052	-	foetus				R petrous
KD053	-	neonate				R petrous
KD055	M	>46				URM3
KD057	M	>46				lower incisor
KD058*	F	26-35	3270 ± 30	1615-1456	SUERC-36895	R petrous
KD059	-	-	3280 ± 30	1619-1463	SUERC-27901	lower incisor
KD060	-	26-35				R petrous
KD061	-	neonate				L petrous
KD062*	-	-	3225 ± 30	1534-1426	SUERC-35261	R petrous
KD063	-	foetus				R petrous
KD064	-	neonate				L petrous
KD065*	-	foetus	3245 ± 30	1609-1438	SUERC-35498	L petrous
KD066*	-	adult				LLM1
KD067	-	neonate				L petrous

TABLE 8.1: LoN samples that underwent genetic analysis, with osteoarchaeological sex and age information, plus radiocarbon dates where applicable. Samples with an asterisk were from the multiple burial. Calibrated dates are to 95% confidence intervals.

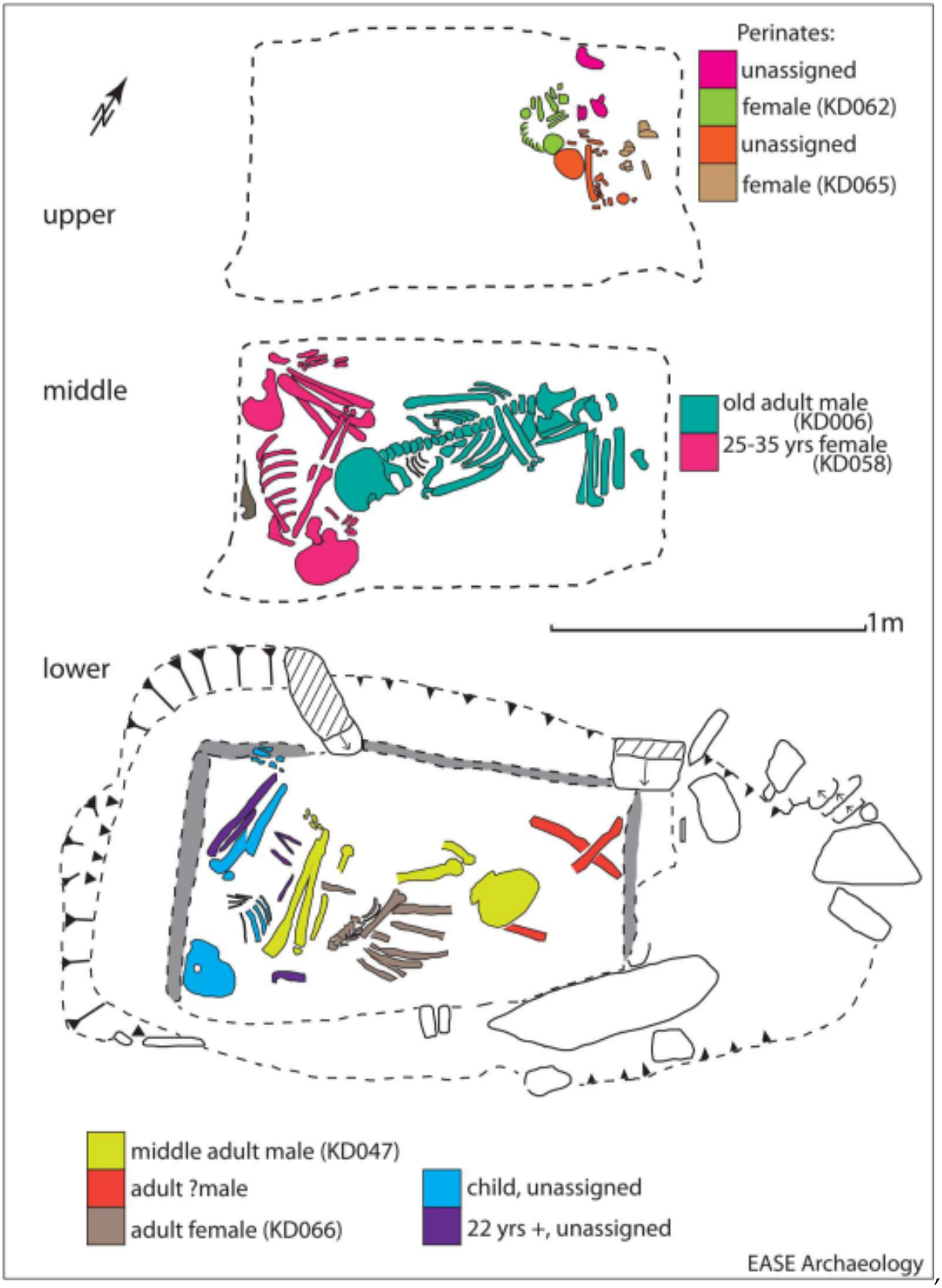


FIGURE 8.2: Position of skeletons from the multiple burial. Image courtesy of Hazel Moore and Graeme Wilson, EASE Archaeology.

Sample	Site	Sex	mtDNA	YDNA
KD026	Strathglebe	XY	U5b2c	I
KD006*	LoN	XY	T2a1b1a	I2a1b
KD044	LoN	XX	U5b2a3	n/a
KD045	LoN	XY	J1c2a	I2a1b
KD046*	LoN	XY	T2a1b1a	?
KD047*	LoN	XY	H39	I2a1a1a1
KD048	LoN	-	H39	?
KD049*	LoN	XY	H39	I
KD050*	LoN	XY	H39	n/a
KD051	LoN	-	-	-
KD052	LoN	XX	K1a29a	n/a
KD053	LoN	XY	-	?
KD055	LoN	XX	J1c2a	n/a
KD057	LoN	XY	H1n1	I
KD058*	LoN	XX	K1a3a	n/a
KD059	LoN	XY	T2b21	I2a1b
KD060	LoN	XY	H1n1	I
KD061	LoN	XY	K1c2	R1b1a1a2
KD062*	LoN	XX	U5b2a3	n/a
KD063	LoN	XX	H58a	n/a
KD064	LoN	XY	T2b21	I2a1b
KD065*	LoN	XX	H39	n/a
KD066*	LoN	XX	T2a1b1a	n/a
KD067	LoN	XX	H+195	n/a
KD004	KoS	XY	H1b	R1b1a1a2a1a2c1a2
KD042	KoS	XX	U5a1b1a	n/a
KD043	KoS	XY	H1b	R1ba1a2

TABLE 8.2: Genetic results from Dr. Dulias. Samples marked by an asterisk from the LoN refer to individuals excavated from the same multiple burial.

The Knowe of Skea, Westray, Orkney is an Iron Age burial site located on a tidal islet. The site consists of over 100 inhumations, with approximately 60% being neonate and child burials (Armit and Ginn, 2007). Several structures have been found at the site, including a long-lived central structure that appears to have been used solely for funerary purposes. The large number of burials makes it unusual for the Iron Age (Moore and Wilson, 2005; Armit and Ginn, 2007; Dulias et al., 2019). Three samples were selected, with osteoarchaeological age-at-death assessment determining two of the individuals (KD042 and KD043) to be adults

and KD004 to be c.15 years old. KD004 was dated to end of the 1st millennium BC (339 cal. BC - cal. AD 3; 2δ 2095 $\pm$ 35 uncal. bp SUERC-8410), whilst KD043 was dated to 25-214 cal. AD (2δ 1915$\pm$35 uncal. bp SUERC-8410).

The archaeological bone and teeth were processed and extracted by Dr. Katharina Dulias in the specialised ancient lab facilities at the University of Huddersfield. Dr. Dulias also aligned samples to the HG19 human reference genome and determined mitochondrial and Y-chromosomal haplogroups of the individuals (**Table 8.2**). These were undertaken using methodology similar that described in Chapter 4. The results presented here are new analyses undertaken for this thesis.

8.3 Results and discussion

8.3.1 Contamination estimates

VerifyBamId (Jun et al., 2012) was used to quantify autosomal contamination. All samples had low contamination estimates (from 3% to undetectable levels). MapDamage was conducted on all samples. As samples had undergone UDG treatment, little damage was observed, and reads were only clipped by 2bp. SNPs were called as described in Section 4.2.5. KD046, KD048, KD051, KD052 and KD053 were removed at this stage, due to having too low coverage for downstream analysis.

8.3.2 Genetic changes through time

A PCA plot reveals that the Bronze Age and Iron Age individuals cluster within the modern genetic variation of modern Europe (**Figure 8.3**). The Strathglebe individual sits just outside this modern variation, similar to Sardinians. The Links of Noltland samples are more diverse than modern British variation, represented by Scottish, English and Orcadian samples.

The Strathglebe individual plots with published British, Irish and western European Neolithic individuals (**Figure 8.4**), on a cline between the Anatolian Neolithic and Western Hunter-Gatherers (WHG), similar to other British Neolithic samples.

In contrast, the Bronze Age Links of Noltland individuals show a marked shift away from the British and European Neolithic populations towards the steppe Yamanya populations, and they plot closely with British and Central European Bronze Age people. Three of the LoN individuals plot closely with the Orkney Neolithic.

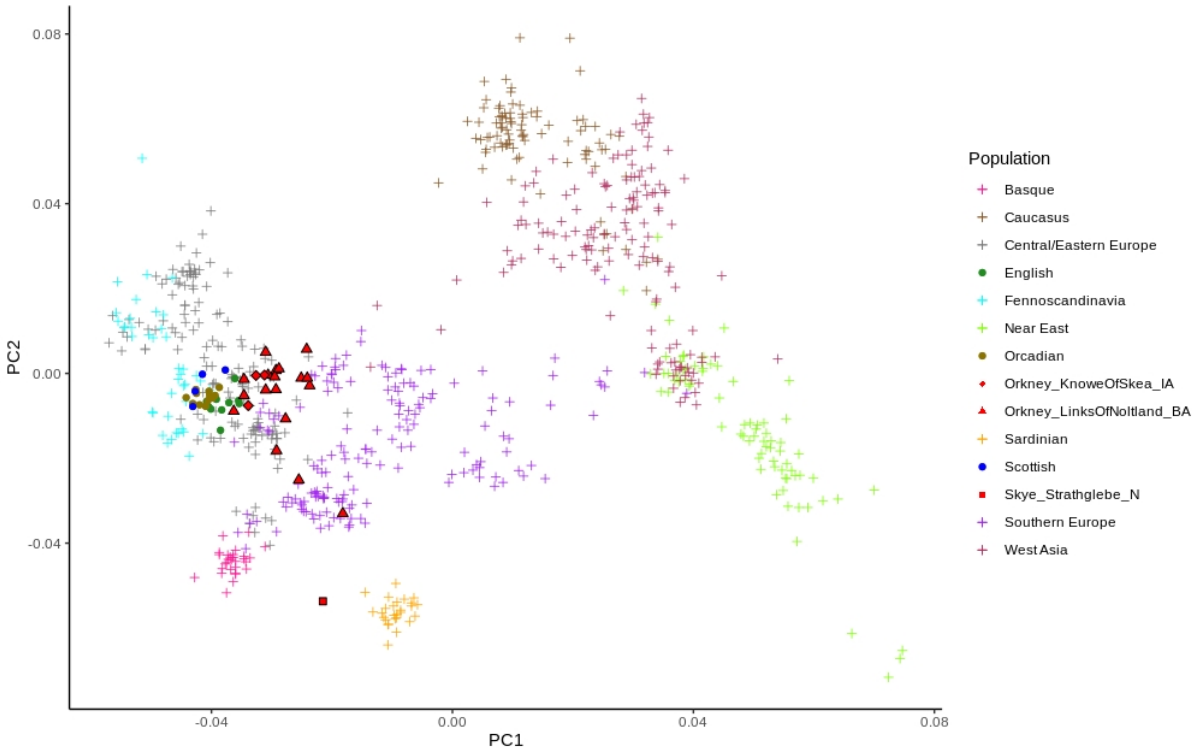


FIGURE 8.3: PCA of modern West Eurasian variation with ancient samples projected.

In contrast to the dramatic change seen between the Neolithic and Bronze Age, Iron Age samples from the Knowe of Skea plot within the diversity of the Bronze Age samples. This pattern is seen in other published Iron Age samples from the British Isles (Martiniano et al., 2016; Schiffels et al., 2016).

ADMIXTURE analysis was performed using $K = 7$; this was selected due to its low CV error values across 20 repetitions on differing seeds, and for best explaining modern and ancient variation. The ADMIXTURE results (**Figure 8.5**) display relevant West Eurasian populations (Gamba et al., 2014; Lazaridis et al., 2014; Olalde et al., 2014; Jones et al., 2015; Mathieson et al., 2015; Lazaridis et al., 2016; Narasimhan et al., 2019), published ancient Orkney and Scottish populations (Olalde et al., 2018; Brace et al., 2019; Sánchez-Quinto et al., 2019), and modern Orcadians (Lazaridis et al., 2016). ADMIXTURE analysis mirrors the PCA, with the Strathglebe individual having Anatolian Neolithic and Western Hunter-Gatherer components, similar to other Neolithic samples. The Links of Noltland and Knowe of Skea have another genetic component, seen in the Iranian Neolithic and Caucasus Hunter-Gatherers. The proportions of all three components in both LoN and KoS are similar to published Middle and Late Bronze Age samples.

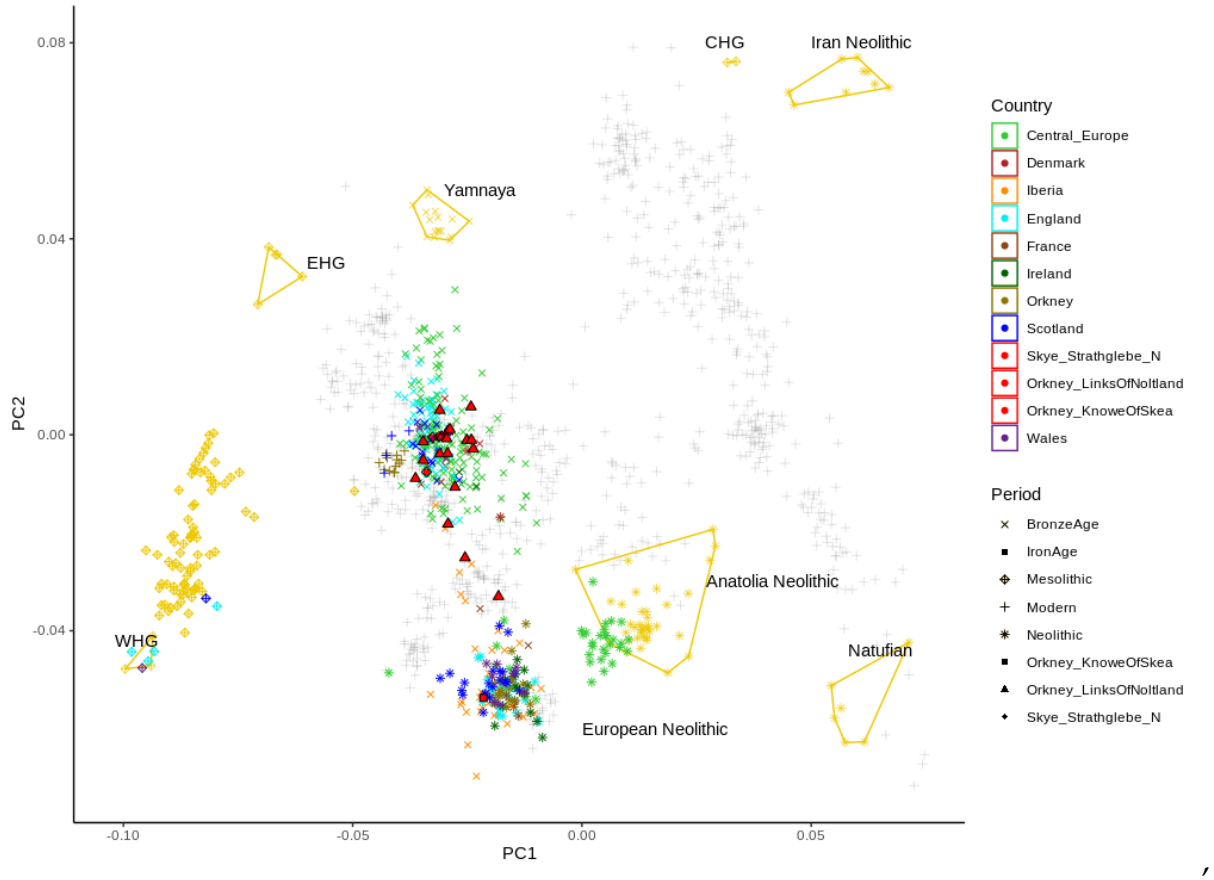


FIGURE 8.4: PCA of West Eurasia, with modern (grey crosses) and ancient (coloured) samples. Scottish samples discussed here are coloured red.

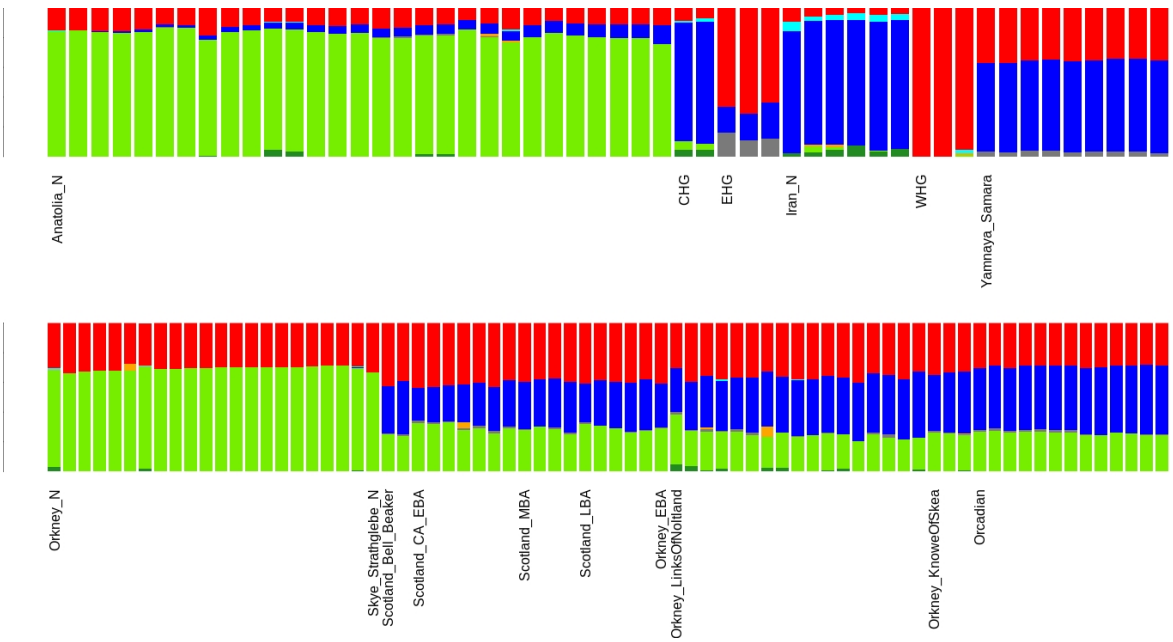


FIGURE 8.5: ADMIXTURE results of $K = 7$ of published populations alongside Strathglebe, LoN, and KoS.

8.3.3 Genetic ancestry of the Strathglebe Neolith

qpAdm was used to model admixture (section 4.2.9.3). The populations for this analysis, and other qpAdm tests, followed those in Olalde et al. (2018) (that is, a combination of modern populations: Mbuti, Papuan, Onge, Han and Karitiana (Patterson et al., 2012; Lazaridis et al., 2014; Lazaridis et al., 2016); and ancient individuals: Mota, Ust_Ishim, MA1 and Villabruna (Fu et al., 2014; Raghavan et al., 2014; Llorente et al., 2015; Fu et al., 2016)). This was undertaken to enable better comparisons to Olalde et al. (2018), as it is the largest study of ancient British genomes to date. Using qpAdm, the Strathglebe individual could be modelled as being composed of 72% Anatolian Neolithic farmer and 28% Western Hunter-Gatherer. By comparing the ancestry proportions on the autosomes and the X-chromosome, it was possible to determine sex-biased admixture (Section 4.2.9.4). This was undertaken following the technique in Mathieson et al. (2018), (section 4.2.9.4). Positive Z scores were attained when assessing the WHG contribution, indicating WHG males admixed with Anatolian Neolithic females.

Outgroup-f3 results (**Figure 8.6**) showed that Strathglebe has the greatest shared drift with other Scottish and British samples. Neolithic populations with higher amounts of WHG ancestry appear to have more shared drift; however, due to the large amount of overlap in error margins, caution must be taken not to over interpret these results.

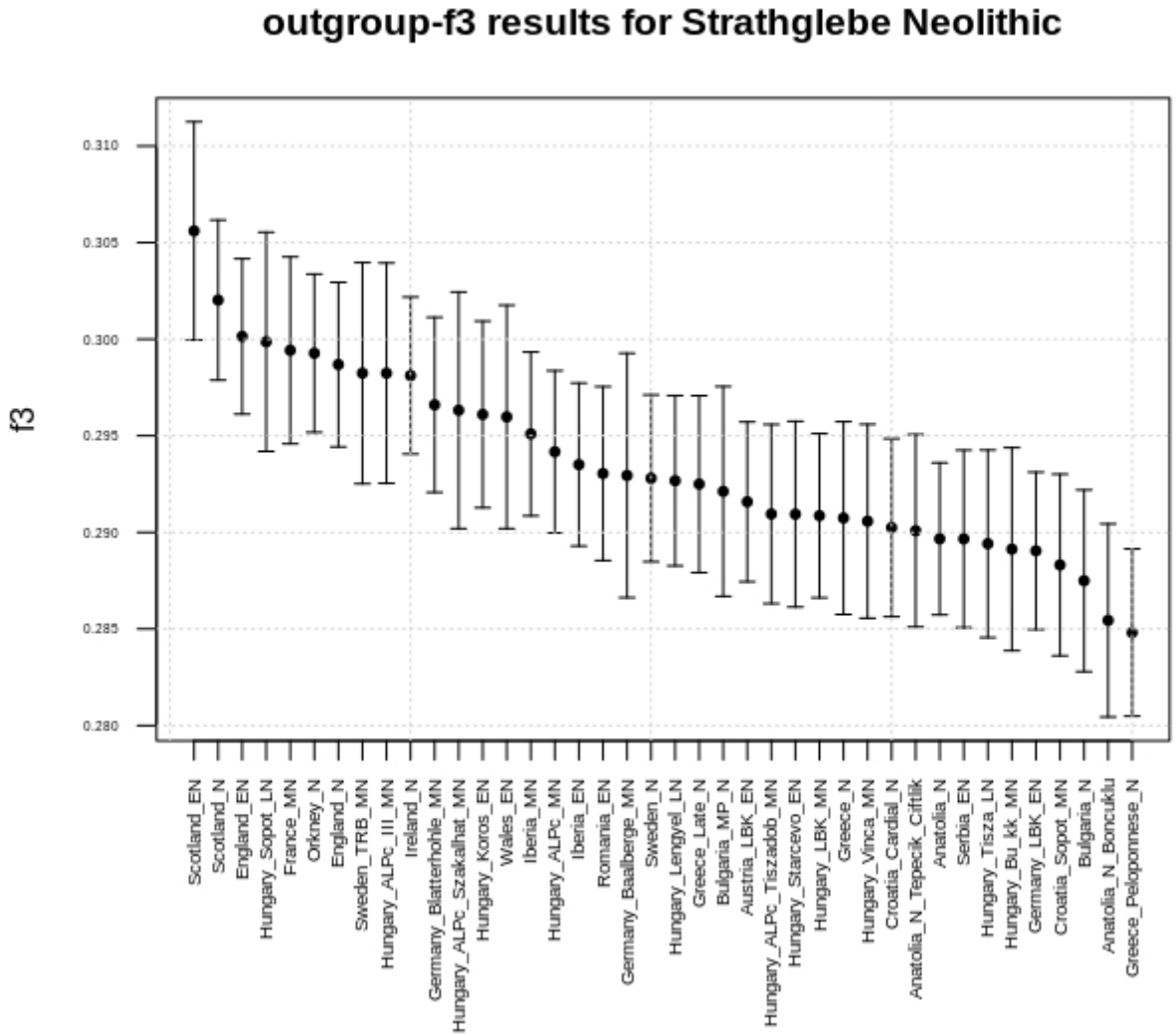


FIGURE 8.6: Outgroup-f3 results comparing the Strathglebe individual to European Bronze Age populations. The higher the f3 value, the more similar that group is to the Strathglebe individual.
Results were filtered for Z>3.

D-statistic analysis (in the form of *D(Mbuti, Strathglebe_N; Neolithic1, Neolithic2)* showed that the Strathglebe individual has the greatest affinity with samples from Neolithic Britain and Ireland. There was also an affinity to French, Iberian and Swedish Trechterbekercultuur (TRB) Neolithic populations compared to the Linearbandkeramik (LBK) culture in Germany, and other southeastern European Neolithic populations.

QpGraph analysis was attempted to determine if the Strathglebe individual was descended from Neolithic individuals travelling via the Mediterranean or Danubian Neolithic expansion routes. QpGraph from ADMIXTOOLS (Patterson et al., 2012) is an admixture graph that

calculates admixture proportions using *f*-statistics based on a supplied phylogenetic tree, as well as the feasibility of the supplied tree. Early Iberian Neolithic populations were used as a proxy for the Mediterranean Neolithic expansion, and LBK individuals were used to represent the Danubian route, similar to Olalde et al. (2018) and Brace et al. (2019). Unfortunately, it was not possible to reject either model, most likely due to low coverage from Strathglebe.

8.3.4 Population genetics of the Links of Noltland

Visual examination of the PCA and ADMIXTURE results suggests several LoN individuals may be genetic outliers, mainly due to their varying steppe-related ancestry. However, after conducting symmetry f4-statistics (in the form of *D(Mbuti, Test; Outlier, Links of Noltland)*), the apparent outliers were statistically indistinguishable from the LoN cluster. Two of the apparent outliers (KD059 and KD066), those which plotted closest to the Orkney Neolithic in the PCA, were excluded from further analysis due to their low number of SNPs.

As the LoN individuals in the PCA appear as an admixture between steppe populations and the Orkney Neolithic, a *D*-stat test was undertaken to test for introgression from the Orkney Neolithic when compared to other Bronze Age Europeans, modelled as (D(Mbuti, Orkney Neolithic; Links of Noltland, European Bronze Age)). No significant introgression with the Orkney Neolithic was found.

Outgroup-f3 and *D*-statistics comparing European Bronze Age populations (in the form of *D(Mbuti, Links of Noltland; European Bronze Age 1, European Bronze Age 2)*) revealed that the LoN individuals show the greatest affinity to other British, particularly Scottish Bronze Age, populations. Due to large overlapping error bars, the outgroup-f3 could not accurately determine a non-British source for the LoN population. *D*-statistics showed the Links of Noltland to have the greatest affinity to British, particularly Scottish populations. LoN showed greater affinity to Bronze Age populations of Central Europe over south-eastern, Iberian or Italian populations. Across all tests, LoN showed close affinity to the Orkney Early Bronze Age sample from Sanday (Olalde et al., 2018); however, as this was a single sample, there are large associated error margins.

qpAdm modelling using a mixture of steppe-ancestry (represented here by the Yamnaya Samara), Anatolia Neolithic and WHG showed that the highest proportion of the autosomal DNA of the LoN populaions (52%) was contributed by steppe populations. This is similar to other published British Bronze Age populations (Olalde et al., 2018). Sex-biased admixture was tested (Mathieson et al. (2018) and Section 4.2.9.4), and this produced a Z-score of -1.3, which is consistent with an unbiased sex admixture. Other published British Bronze Age populations produced similar results (Olalde et al., 2018).

In order to test the ancestry turnover of Orkney, qpAdm was conducted, and the LoN

were modelled as an admixture of the Orkney Neolithic with either a British or central European Bronze Age population. Anatolian Neolithic and Samara Yamnaya were added to the set of 'right' populations to increase the power to distinguish between the two sources of ancestry. British or Central European Bronze Age populations were selected as they showed higher affinity in the *D*-statistic tests. No feasible results were detected when running qpAdm as an admixture of Orkney Neolithic and British or Central European Bronze Age populations, with the exception of the Irish and Danish Bronze Ages (**Table 8.3**). As Orkney is an island population, it is hypothesised that the Neolithic population may have been completely replaced and, therefore, qpAdm was repeated as a 2-way admixture of British or Central European Bronze Age and a Neolithic population (either from Scotland or across Britain as a whole (similar to Olalde et al. (2018)). Again, the only feasible results were with Irish and Danish Bronze Age populations. In all scenarios (admixing with the Orkney Neolithic, Scottish Neolithic or British Neolithic), a near complete replacement of the pre-existing population was suggested.

Neo Pop	**Mixture proportion**	**BA Pop**	**Mixture proportion**	**SE**
British Neolithic	0.003	Denmark BA	0.997	0.025
British Neolithic	0.124	Ireland BA	0.876	0.115
Orkney Neolithic	0.003	Denmark BA	0.997	0.024
Orkney Neolithic	0.059	Ireland BA	0.941	0.028
Scottish Neolithic	0.062	Denmark BA	0.938	0.024
Scottish Neolithic	0.048	Ireland BA	0.952	0.028

TABLE 8.3: qpAdm results modelling the ancestry of the LoN samples. Only feasible and significant results are displayed.

In order to combat bias due to the limited number of SNPs present in some samples, qpAdm was repeated using only samples with over 100,000 SNPs (**Table 8.4**). This produced slightly different results to previously, such that German and Czech populations were modelled to be admixed with Neolithic populations to produce the Links of Noltland population. It was not possible to produce feasible results for any population using the X-chromosome. It might be that the Orkney Bronze Age possesses a more complex genomic history than a 2-way admixture, but it is not possible to determine it at this time.

Neo Pop	Mixture proportion	BA Pop	Mixture proportion	SE
British Neolithic	0.015	Denmark BA	0.985	0.025
British Neolithic	0.209	German Corded Ware	0.791	0.053
Orkney Neolithic	0.013	Czech Unetice EBA	0.987	0.082
Orkney Neolithic	0.001	German Unetice EBA	0.999	0.071
Orkney Neolithic	0.209	German Corded Ware	0.791	0.053
Scottish Neolithic	0.19	German Corded Ware	0.81	0.053

TABLE 8.4: qpAdm feasible and signficant results modelling the ancestry of the LoN samples with over 100,000 SNPs.

To test whether LoN has a different wave of ancestry to other Scottish Bronze Age samples, qpWave was employed, using the same 'right' list as for the qpAdm analyses. LoN could be modelled as being symmetrically related (f4rank=0) to Scottish Early Bronze Age (and to Scottish Beakers as denoted by Olalde et al. (2018)). However, LoN were differently related to Scottish Middle and Late Bronze Age populations (f4rank=1), suggesting that they had a different wave of ancestry. In contrast, Scottish Middle and Late Bronze Age populations could be modelled as symmetrically related to the 'right' populations (f4rank=0).

Previous work by Dr. Dulias clearly demonstrated that Y-chromosome I was predominant in Orkney (**Table 8.2**). This contrasts with the rest of Britain and much of western Europe (Olalde et al., 2018), where R1 haplogroups came to dominate. The PCA, ADMIXTURE and qpAdm results (**Figures 8.4 and 8.5**) clearly demonstrate a genomic change from Neolithic Orkney similar to those seen in Britain and western Europe.

8.3.5 Population genetics of the Knowe of Skea

No additional ancestry for the Knowe of Skea Iron Age samples is visible from the PCA or ADMIXTURE results. The qpAdm using Yamnaya Samara, Anatolian Neolithic, and Western Hunter-Gatherers as sources produced similar results as for LoN (KoS: 55.2% Yamnaya Samara, 35.2% Anatolian Neolithic, 9.6% WHG; LoN: 52.4%, 36%, 11.6% respectively).

To test for genetic continuity between the time periods, a *D*-statistic test (in the form of *D(Mbuti, Test, Knowe of Skea, Links of Noltland)*) was undertaken. No significant results ($|Z|>3$) imply that the Knowe of Skea and the Links of Noltland are symmetrically related to all tested populations. The results of qpWave further highlighted this point. The Knowe of Skea Iron Age samples could be modelled as being directly descended from the Links of Noltland using qpAdm.

8.3.6 Kinship at LoN and KoS

Kinship was analysed using READ (Kuhn et al., 2018). Due to low overlapping coverage between certain samples, READ was repeated using samples called against the 1000 Genomes Project (which had been filtered to keep only biallelic autosomal SNPs with a MAF of > 1%). As a precaution, this was repeated on the same list using transversion positions only; however, as samples had been UDG treated, there was little deamination present, as observed in the mapDamage plots (not shown). Using the results of READ, coupled with uni-parental markers and an age-at-death osteoarchaeological profile, it is possible to determine family groups. Two samples (KD050 and KD065) are either twins or from the same individual, sharing genetic sex and mtDNA haplotype. As the two samples were extracted from the right and left petrous respectively, and these were located from the same area of the same burial, they are most likely the same individual. They will, therefore, be referred to as KD050/65 from hereon-in.

Across all tests, it is clear that KD049 and KD050/65 share a first-degree relationship. As both died below reproductive age, and they share a mitochondrial haplotype, they were interpreted as full siblings. Therefore, all other samples must have the same relationship to both of these samples, which is especially important as KD049 has a lower resolution and thus greater error margins. Due to merging, KD050/65 had a larger number of SNPs, which allowed any relationships to be determined with more support.

Several kinships were identified within the LoN cemetery, particularly inside the mass burial (**Figure 8.7**). Of the seven individuals in the mass inhumation who passed the criteria for analysis, five have first- or second-degree relationships. It is possible that the other individuals in this grave were also related, but more distantly. In the rest of the cemetery, there were some potential kinships, but noticeably less than seen in the multiple burial.

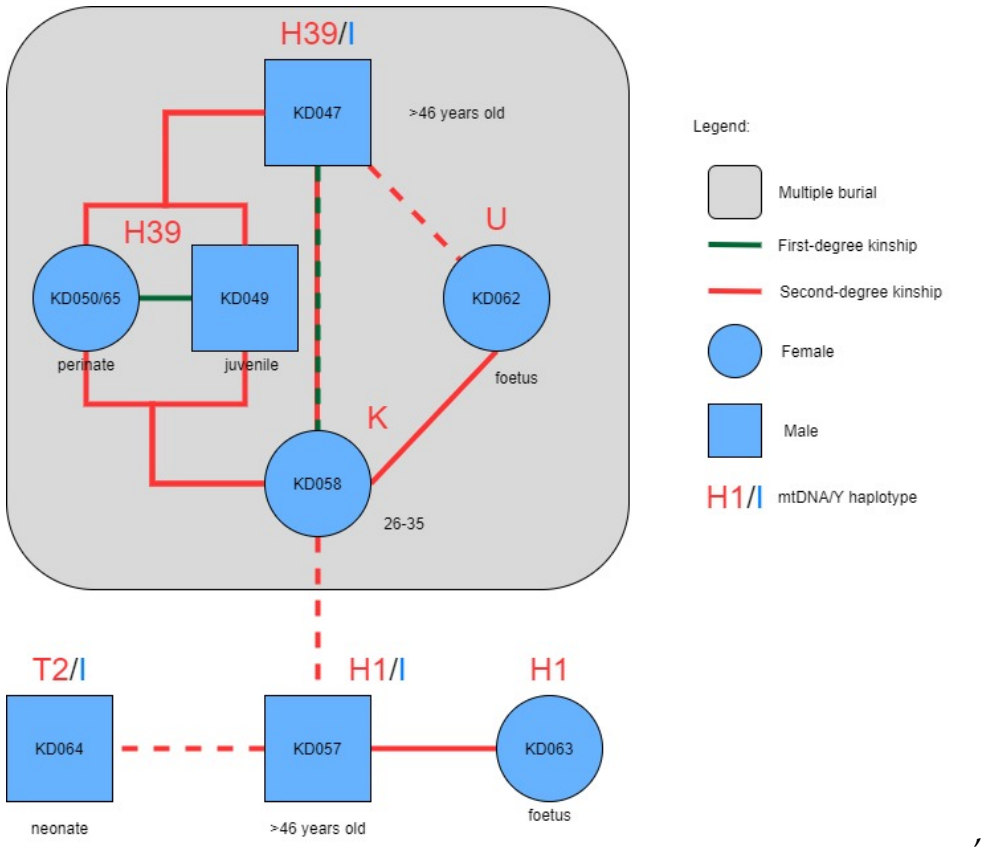
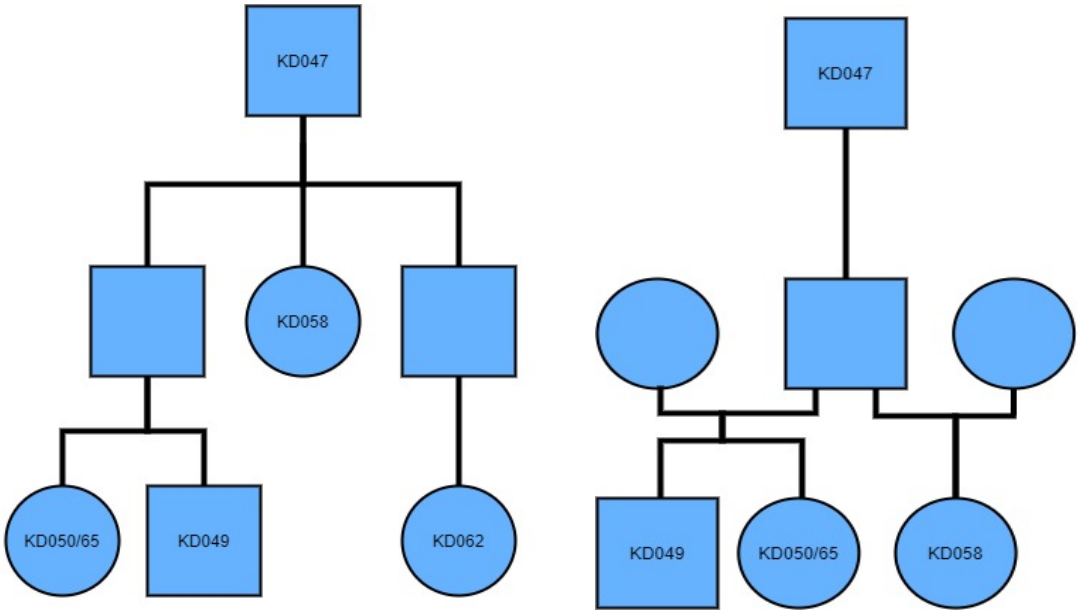


FIGURE 8.7: Kinship results from the Links of Noltland cemetery.

It was possible to reconstruct a family tree of some of the samples from the mass burial. Dotted lines shown in (**Figure 8.7** show the degree of uncertainty between KD047 and KD058, and KD047 and KD062, as the siblings (KD049 and KD050/65) have a second-degree relationship to both KD047 and KD058, and the siblings were not of reproductive age. If KD047 and KD058 were first-degree related, KD047 would have to have been the father of KD058, as they do not share the same mitochondrial haplotype. This would make KD047 the grandfather of the siblings, KD049 and KD050/65, as well as the grandfather of another child burial, KD062. As the siblings (KD049 and KD050/65), KD062 and KD058 do not share mitochondrial haplogroups, they have to be paternally related (Figure 8.8a).



(A) (B)

FIGURE 8.8: Two possible genealogical reconstructions of the relationships within the multiple burial from the LoN cemetery.

An alternative family tree is possible if KD058 was second-degree related to KD047. In this scenario, the siblings KD049 and KD050/65 could be half-siblings of KD058. All three of these individuals would then be the grandchildren of KD047. In this scenario, it would not be possible for KD047 and KD058 to share a second-degree relationship with KD062.

Another alternative could be that KD058 is the grandmother, and that KD049 and KD050/65 are paternal half-siblings of KD047. Although some of the date range produced by the radiocarbon results for KD058 are older than that of KD047, there is around an 80 year overlap, and so they may have died at the same time. Furthermore, as KD047 had a higher age-at-death than KD058, and was buried on a lower level, it is more probable that he was the elder of the two (Figure 8.8b).

At present it is unclear how long the multiple burial was in use, as all radiocarbon dates of the related individuals have some overlap. Using the age-at-death and family tree reconstruction, it is possible that this group were buried simultaneously or within a short time period. However, due the date range of the samples, it is possible that this multiple burial represents a family tomb.

Kinship analysis of the three Knowe of Skea individuals using READ revealed a second-degree kinship between female KD042 and male KD043. As the individuals did not share a mitochondrial haplotype, several potential kinships are possible. These include: KD042 is the paternal niece of KD043; KD043 is the paternal nephew of KD042; KD042 is the maternal grandmother of KD043; or KD043 is the grandfather of KD042. The two males, KD004 and

KD043, share a mitochondrial haplotype and potentially the same Y-chromosomal haplotype, but relationships could not be confirmed as KD043 had low coverage. Radiocarbon dates show that KD004 died earlier than KD043 (203-3 cal. BC versus 5-211 cal. AD). Despite not having a first- or second-degree kinship, it is possible that these individuals were more distantly related. However, as KD004 is an adolescent, under 15 years, it is unlikely that he is a direct ancestor of KD043.

8.4 Conclusions

The Strathglebe individual appears to be similar to published British, Irish and French samples in the PCA, qpAdm and admixture analyses (Olalde et al., 2018; Brace et al., 2019; Sánchez-Quinto et al., 2019), with a mixture of WHG and Anatolian Neolithic ancestry. If the Strathglebe individual is representative of the eastern Scottish Neolithic, then the large-scale population turnover that happened across Britain reached even the remote areas of Scotland. Male-dominated hunter-gatherer admixture was identified in this individual. A similar result has been observed in other Middle Neolithic populations from Orkney and northwestern Scotland (Sánchez-Quinto et al., 2019). This may suggest a common pattern across Scotland but, to date, there are not enough samples to fully identified a pattern. From the *D*-statistics, a greater affinity to Iberian than LBK Neolithic groups is indicated, although this does not prove that the Anatolian Neolithic ancestry was introduced into Britain via the Mediterranean route. It is possible that the affinity is solely the result of the higher proportions of Western Hunter-gatherer ancestry in the Iberian and British Neolithic groups. Higher WHG ancestry may also be why Strathglebe shares a greater affinity to the TRB, than LBK and southeast European Neolithic populations. As neither qpGraph model could be rejected, it is not clear which route the Neolithic entered Britain.

Bronze Age Orkney showed that instead of isolation, it experienced a demographic replacement. This change can be seen through the presence of a large steppe-ancestry component. *D*-statistics indicate a change of shared ancestry from Iberia in the Neolithic to Central Europe in the Bronze Age. Also, the published Orkney Neolithic did not show significant introgression to LoN, so it appears probable that a large demographic replacement occurred on Orkney. The high presence of steppe ancestry in ADMIXTURE and qpAdm analysis, and the position of the LoN towards the Yamnaya, and away from the Neolithic, on the PCA further demonstrate this conclusion.

However, Orkney clearly has a complex genetic history, as it does not fit any two-way model for either the autosome or X-chromosome, and cannot be modelled using the same populations as the rest of Scotland (as in Olalde et al. (2018)). This is perhaps less surprising, as the Early Bronze Age sample from Sanday also did not fit this 2-way modelling (Olalde et al., 2018). This, combined with the qpWave results, further indicates that different demographic

events were occurring on the Scottish mainland and the Orkney islands in the Middle Bronze Age. When incorporating YDNA haplogroup information, the Links of Noltland is unusual due to the high frequency of haplogroup I (8/9 males). This is in stark contrast to the rest of the British Isles, where the arrival of the Bronze Age is mirrored by a large-scale replacement of I with R1b (Olalde et al., 2018).

Three of the LoN samples plotted closer to the Orkney Neolithic in the PCA and had less steppe-ancestry compared to the other samples. This genetic diversity might be related to the variability in burial rites at the site, which may reflect admixture between different genetic groups. As two of these three individuals had too few SNPs to be further analysed, it was not possible to clarify this.

The presence of a family group in the multiple burial at the Links of Noltland may suggest the importance of kin groups in establishing importance in a local area. The results from Iron Age Knowe of Skea indicate a genetic continuity from the Bronze Age. Further Iron Age sampling is required to see if there is a Y-chromosomal change from I to R1b, as, although both Iron Age males have R1b, they are related, making this too small a sample size to draw any firm conclusions.

Despite being located at some of the furthest reaches of Europe, the Neolithic and the Bronze Age resulted in large scale demographic effects upon the Scottish Isles, and the effects are similar to those seen across Britain. The data presented here show that, instead of being isolated, Orkney experienced migration and probable large-scale replacement, and that differing complex admixture events were happening between mainland Scotland and Orkney. Modern Orcadians and Scots plot differently in the PCA (**Figure 8.3**) to the Bronze and Iron Age, reflecting the later admixture events that occurred, and which shaped the present-day population.

Bronze Age ancestry associated with the steppe migrations clearly did make an impact on Bronze Age Orkney. However, as shown in this study and the previous Y-chromosomal work by Dr. Dulias, this does not appear to have occurred in the same way as in Britain (Olalde et al., 2018). Analysis of Iron Age Orkney suggests that the continuation of Y-chromosomal haplogroup I had ended by this period. However, further research using more samples and with higher coverage may uncover more details about this arrival of steppe ancestry into Orkney.

8.5 Ongoing and future work

Several of the individuals analysed here, including the Strathglebe individual and several from LoN (KD045, KD047, KD049, KD057, KD059, KD060, KD061 and KD064), have been sent for

more in-depth sequencing to produce better coverage and, thus, improve analytical power. As well as this, two other individuals from Strathglebe are being resequenced. These additional data will provide clearer information as to the demographic changes occurring at these sites. With better coverage of the Strathglebe samples, it may be possible to determine by which Neolithic expansion route this population entered Britain. The new LoN results should make the kinship results clearer, as well as potentially aiding identification of the source of steppe ancestry in Orkney. Higher coverage samples may also allow chromosome painting methods in order to understand detailed ancestry, runs of homozygosity analysis to identify inbreeding and population diversity, and identification of phenotypes.

Chapter 9

Genomic analysis of post-Neolithic Britain

9.1 Introduction

The samples presented in this chapter are from across Britain, representing a transect from the Early Bronze Age to the late Anglo-Saxon period (**Table 9.1**). This chapter presents the largest dataset of British samples that post-date the Bronze Age, providing an opportunity to tackle the impact of long debated cultural changes, such as the introduction of the Iron Age, and the movements seen in the Roman and Anglo-Saxon periods. By comparing these samples to Bronze Age populations, it should be possible to identify the genetic legacy of the Bronze Age in Britain, and whether the population was replaced over later periods. The geographic spread of samples can be used to aid identification of regional, as well as chronological, demographic changes. It should be noted that a number of burial rites existed in the Early Bronze Age and Iron Age, including cremation (Haselgrove, 2009; Pearson, 2009). Therefore, as it is difficult to extract aDNA from cremated individuals, inhumation burials from these periods may represent unusual individuals, elites (particular in the case of Bronze Age barrows) or regional diversity like the West Heslerton Arras Iron Age burials.

9.2 Site backgrounds

9.2.1 Low Hauxley, Northumberland, England

The site of Low Hauxley is located along the coast of Northumberland. The site was discovered in 1983 due to coastal erosion in the area. Subsequent excavations over the next 30 years revealed several periods of human activity, from the Mesolithic to medieval periods. Of particular significance is the Early Bronze Age burial ground, which consists of two cairns (mounds of stones). Cairn 1 began as three cist (stone-lined) box graves, over which was built a cairn. Later burials were dug next to these cists, and the cairn extended to cover them. Radiocarbon dating demonstrates the cairn was in use for between 245 and 675 years, with at least nine burials (Waddington and Bonsall, 2016). As a result of coastal erosion, only a third of the original

cairn remained, and Burial 1, inside Cairn 1, was selected for aDNA analysis. This skeleton is one of the earliest dated Beaker burials from northern Britain, dating to 2466-2213 cal. BC. Accompanying the individual was a Short-Necked Beaker; a type of pot typologically similar to those found in the Rhineland. The individual is a juvenile, 12-16 years old, and had dental calculus and a dental abscess (Waddington and Bonsall, 2016).

9.2.2 Carsington Pasture Cave, Derbyshire, England

At least 20 individuals were discovered in Carsington Pasture Cave, approximately half of which were neonates and young children. There are several radiocarbon dates on humans and animals from this site, and it seems to have been widely used in the Neolithic period (Chamberlain, 1999). However, the individuals selected for aDNA analysis for this study were both radiocarbon dated (as part of a previous study) to the Iron Age, 760-205 cal. BC.

9.2.3 High Pasture Cave, Isle of Skye, Scotland

High Pasture Cave (HPC; Uamh an Ard Achadh) is located in Strath, on the Isle of Skye. Archaeological evidence dating from the Neolithic and Bronze Age has been discovered both in and around the cave; however, the majority of activity occurs in the Early-Middle Scottish Iron Age 800 cal. BC - 150 cal. AD. A large amount of deposited artefacts, and the construction of a low retaining wall and stairway in the cave during the Iron Age, all emphasise the importance of the site. High status artefacts, separation of butchery carcasses into left and right sides, burial of complete cattle skeletons, and other butchery signs have indicated that the cave was used for ritual purposes (McKenzie, 2018). The passage was back-filled and then sealed at some point towards the end of the 1st millennium BC, as evidenced from radiocarbon dating of charcoal from the top of the staircase (2115$\pm$40 bp; SUERC-14937), which calibrates to 350 cal. BC - cal. AD (Birch and Wildgoose, 2013). A 25-40 year-old woman was deposited amongst boulders used to block the passage. A foetus was placed near the woman's legs and a perinate near her pelvis. A foetal pig and perinatal dog were placed close to where the woman's feet would have been. Large boulders were then placed on top, causing severe trauma to the woman's skeleton. It is not possible to determine whether this trauma was the cause of her death or occurred afterwards (Shapland et al., 2019; Dulias et al., 2019). Work by Dulias et al. (2019) showed that the perinate (placed closest to the woman's pelvis) did not share an mtDNA haplotype and, therefore, could not be her child. In contrast, results from the foetus suggested a potential maternal kinship to the woman.

9.2.4 Milla Skerra, Sandwick, Unst, Shetland

Milla Skerra, is located on Unst, the most northernly island of the Shetland archipelago. Excavation revealed six main phases of settlement at Milla Skerra dating from the 6th century BC

to the 2nd century AD. The 50-60 years-old man, selected for aDNA analysis, was buried after the settlement at Milla Skerra had been abandoned (Lelong, 2019).

9.2.5 Rosemarkie Cave, Black Isle, Scotland

Excavations at Rosemarkie Cave uncovered several periods of use, with evidence including metal-working, post-holes and hearths. A Pictish (Late Iron Age/Early Medieval) skeleton of a young man was discovered in an alcove inside the cave, in an unusual cramped position. The skull was badly damaged, and osteological analysis discovered multiple trauma wounds from different types of weapons. There was no evidence of a grave cut, but several large stones had been placed on top of the body. The presence of animal bone over the body led to an interpretation of a ritual burial. Facial reconstruction of "Rosemarkie Man" has been undertaken by the University of Dundee (Birch and Peteranna, 2016).

9.2.6 West Heslerton, North Yorkshire, England

West Heslerton has a long history dating back to the Mesolithic (Haughton and Powlesland, 1999b). The samples for this study date to the Early Bronze Age, Iron Age and the Anglo-Saxon eras, a period stretching over 3000 years. Of those sampled, 14 individuals had high enough coverage for detailed analysis: three Early Bronze Age, two Iron Age, and nine individuals from the Anglo-Saxon cemetery.

Two of the EBA individuals (KD003 and KD041) were buried under a barrow in the centre of a Neolithic henge monument. Both graves were very deep (1m and 1.5m), with crouched inhumations, alongside flint blades, beaker food vessels, and secondary cremation burials. The third EBA individual (KD040) came from a flat grave close to the barrow. This burial also contained a flexed inhumation and beaker vessel (Haughton and Powlesland, 1999b). Osteoarchaeological examination revealed an unusually narrow auditory meatus, likely the result of a congenital defect that would have severely impeded his hearing. Parry and compression fractures were also discovered on the skeleton, both healed and unhealed, suggesting that he had been subjected to physical assault on at least two occasions, with the second occurring shortly before death (Haughton and Powlesland, 1999b).

Two Iron Age Arras burials were examined from West Heslerton (Tollefsen and Jones, 2017). The two skeletons were determined to be female by oseteoarchaeological analysis, and then later via genetic assessment undertaken by Dr. Dulias. The elder female, KD071, was buried with a pig. The Arras culture of Yorkshire has similarities in burial practice to northern France. Hypotheses of these similarities include migration or adoption of burial rites (Haselgrove, 2009).

The vast majority of the skeletons excavated at West Heslerton belong to the Anglo-Saxon period, with over 200 inhumations dating from c. 450-650 AD. The cemetery is located away from any settlement sites, as is typical of this time. The cemetery appears to have been created as a series of concentrations of graves, possibly as a result of kin groups. Several of the graves in this study are close to each other. Burials selected were a mixture of those with and without grave goods (Haughton and Powlesland, 1999b; Haughton and Powlesland, 1999a). Certain grave goods are common to those found in Scandinavia and northern Europe, including the Anglo-Saxon homelands. However, as noted in Haughton and Powlesland (1999b), Anglo-Saxon material culture was rapidly adopted across Britain, so this is not an accurate representation of migration.

9.2.7 Worth Matravers, Dorset, England

Worth Matravers (WM) is located in Dorset on the southern coast of England. The area has a long occupation history, demonstrated by a Neolithic enclosure, an Early Bronze Age stone alignment, and settlement evidence lasting from the Bronze Age until the end of the Iron Age. During the Roman period, the area continued as a small settlement based on agriculture. The post-Roman period (fourth to seventh centuries AD) is represented by a cemetery, which is located outside the settlement area, in keeping with Roman tradition. Excavation of the cemetery revealed 26 individuals from 21 graves, arranged east-west, with the heads of the individuals in the west. The graves included two double graves and a triple grave, where it appears that the individuals were interred at the same time. These have been interpreted as kin or marital relationships. No burials contained individuals below five years of age, similar to early Romano-British traditions. The organisation, layout and grave construction is similar to contemporaneous cemeteries in the west of Britain. The presence of multiple burials is rare at this time, with WM having a high frequency. The use of a limestone anchor as a headrest, found under one of the individuals in a double burial, is very rare (Ladle, 2018). These differences in burial culture from the rest of Britain may represent influence from outside Britain. 16 samples were selected for aDNA analysis (one of which, KD015, had too low coverage for further study). Genetic sex identification (by Dr. Dulias) found that the two double burials contained two males and a male and a female respectively, and the triple burial contained two males (KD017 and KD018) and a female (KD016). All individuals in the cemetery were adults, with the exception of KD018 who was aged osteologically as being around 15 years old.

9.2.8 Oakridge, Basingstoke, Hampshire, England

A skull was discovered in a spoil heap of a rescue excavation of a Romano-British burial and drainage ditch, but was radiocarbon dated to the late Anglo-Saxon period. She displayed clear evidence of peri-mortem trauma, with evidence of a linear cut to the frontal bone and also two cuts to the base of the nasal aperture, which would have removed the nose. The location of the

skull near to a boundary line, and the mutilation, may have been done as a punishment for a crime (Cole et al., 2020).

Sample	Site	Date (uncal. bp)	Calibrated date to 2σ	Lab number	Era
KD070	LH	3874±32	2464-2208 cal. BC	SUERC-49872	BA (Beaker)
CE003	CPC	2460±30	757-416 cal. BC	OxA-29233	Iron Age
CE004	CPC	2240±24	386-205 cal. BC	OxA-28865	Iron Age
KD005	HPC	1965±40/ 1890±40	46 cal. BC - cal. AD 202	SUERC-14946	Iron Age
KD073	MS	1755±35	236-402 cal. AD	SUERC-10745	Iron Age
KD001	RC	1508±30	441-641 cal. AD	SUERC-70721	Pictish
KD003	WH	n/a	n/a	n/a	EBA
KD040	WH	n/a	n/a	n/a	EBA
KD041	WH	n/a	n/a	n/a	EBA
KD071	WH	n/a	n/a	n/a	Iron Age
KD072	WH	n/a	n/a	n/a	Iron Age
KD002	WH	n/a	n/a	n/a	Anglo-Saxon
KD031	WH	n/a	n/a	n/a	Anglo-Saxon
KD032	WH	n/a	n/a	n/a	Anglo-Saxon
KD033	WH	n/a	n/a	n/a	Anglo-Saxon
KD034	WH	n/a	n/a	n/a	Anglo-Saxon
KD035	WH	n/a	n/a	n/a	Anglo-Saxon
KD036	WH	n/a	n/a	n/a	Anglo-Saxon
KD037	WH	n/a	n/a	n/a	Anglo-Saxon
KD038	WH	n/a	n/a	n/a	Anglo-Saxon
KD007	WM	1393±31	600-670 cal. AD	SUERC-61178	post-Roman
KD008	WM	1396±31	600-668 cal. AD	SUERC-61179	post-Roman
KD009	WM	n/a	n/a	n/a	post-Roman
KD010	WM	n/a	n/a	n/a	post-Roman
KD011	WM	n/a	n/a	n/a	post-Roman
KD012	WM	1340±31	645-773 cal. AD	SUERC-61177	post-Roman
KD013	WM	n/a	n/a	n/a	post-Roman
KD014	WM	1413±31	595-663 cal. AD	SUERC-61180	post-Roman
KD016	WM	1425±31	585-659 cal. AD	SUERC-61182	post-Roman
KD017	WM	n/a	n/a	n/a	post-Roman
KD018	WM	n/a	n/a	n/a	post-Roman
KD019	WM	1547±29	433-590 cal. AD	SUERC-61181	post-Roman
KD020	WM	n/a	n/a	n/a	post-Roman
KD021	WM	n/a	n/a	n/a	post-Roman
KD022	WM	n/a	n/a	n/a	post-Roman
CE005	O	1173±24	774-956 cal.	OxA-26646	Anglo-Saxon

TABLE 9.1: (previous page) Details of samples included in the analyses. Acronyms as follows: LH = Low Hauxley, MS = Milla Skerra, RC = Rosemarkie Cave, WH = West Heslerton, WM = Worth Matravers, O = Oakridge.

9.3 Materials and methods

The samples were processed and extracted by Dr. Katharina Dulias in specialised ancient lab facilities at the University of Huddersfield, with KD001, KD002 and KD003 being extracted twice - once in Huddersfield and once at Trinity College University, Dublin, Ireland. Dr. Dulias aligned samples to the HG19 human reference and determined their mitochondrial and Y-chromosomal haplogroups (**Table 9.2**). These were undertaken using methodology similar to that described in Chapter 4. The resulting data analyses presented here are my own work.

Methodology used in this section followed Section 4 unless otherwise stated. Another PCA was created to include North African variation, comprising of 958 modern West Eurasian and North African individuals from 72 populations from the Human Origins Project (Patterson et al., 2012; Lazaridis et al., 2014; Lazaridis et al., 2016). A set of 9 'right' populations were used for the qpAdm: Mbuti, Papuan, Onge, Han, Karitiana, Mota, Ust Ishim, MA1, Villabruna ((Patterson et al., 2012; Fu et al., 2014; Lazaridis et al., 2014; Raghavan et al., 2014; Llorente et al., 2015; Fu et al., 2016; Lazaridis et al., 2016) and Section 4.2.9.3). These populations followed the 'right' populations used by Olalde et al. (2018), who analysed similar populations, and the same populations were used as for Chapter 8 to aid comparison. The exception to this was the outlier sample from Worth Matravers (discussed below).

Sample	Site	Age (years)	Sex	mtDNA	YDNA	Era	Sequencing
KD070	LH	12-16	XY	T2e1a	R1b1a1a2	BA (Beaker)	Shotgun
CE003	CPC	17-25	XX	X2b4a1	n/a	Iron Age	Shotgun
CE004	CPC	35-45	XY	H10b	R1b1a1a2	Iron Age	Shotgun
KD005	HPC	25-40	XX	H7a1b	n/a	Iron Age	Shotgun
KD073	MS	50-60	XY	J1b1a1	?	Iron Age	Shotgun
KD001	RC	adult	XY	J1b1a1a	R1b1a1a2	Pictish	Shotgun
KD003	WH	adult	XX	T2e	n/a	EBA	Shotgun
KD040	WH	adult	XY	T2b4h	R1b1a1a2a	EBA	Shotgun
KD041	WH	25-35	XY	U5a1a2ah	R1b1a1a2	EBA	Shotgun
KD071	WH	24-75	XX	H1b1+16362	n/a	Iron Age	Shotgun
KD072	WH	25-35	XX	H1b1+16362	n/a	Iron Age	Shotgun

KD002	WH	25-35	XX	H6a1a	n/a	Anglo-Saxon	Shotgun
KD031	WH	adult	XY	H1c1	R1b1a1a2	Anglo-Saxon	Capture
KD032	WH	adult	XY	H1q	R1b1a1a2	Anglo-Saxon	Capture
KD033	WH	2-5	XX	H1b	n/a	Anglo-Saxon	Capture
KD034	WH	adult	XY	X2b4a	R1b1a1a2	Anglo-Saxon	Capture
KD035	WH	c.35	XX	U5a1a1e	n/a	Anglo-Saxon	Capture
KD036	WH	<16	XY	K1d1	I1a2	Anglo-Saxon	Capture
KD037	WH	25-35	XX	T2b2b	n/a	Anglo-Saxon	Capture
KD038	WH	adult	XY	K1a4a1a	I2a2b	Anglo-Saxon	Capture
KD007	WM	adult	XY	K1a2a	R1ba1a1a2	post-Roman	Capture
KD008	WM	17-25	XY	K1a2a	I1a2a1a2	post-Roman	Capture
KD009	WM	25-35	XX	T2a1a	n/a	post-Roman	Capture
KD010	WM	17-25	XY	U5b1	E1b1	post-Roman	Capture
KD011	WM	35-45	XX	H11a	n/a	post-Roman	Capture
KD012	WM	25-35	XX	HV6	n/a	post-Roman	Capture
KD013	WM	17-25	XY	HV6	R1ba1a1a2	post-Roman	Capture
KD014	WM	40-45	XY	HV6	R1ba1a1a2	post-Roman	Capture
KD016	WM	25-35	XX	H1bb	n/a	post-Roman	Capture
KD017	WM	45-49	XY	H1e1a	R1ba1a1a2	post-Roman	Capture
KD018	WM	15-16	XY	H1bb	R1ba1a1a2	post-Roman	Capture
KD019	WM	25-35	XX	U5b2bc1	n/a	post-Roman	Capture
KD020	WM	adult	XY	T2a1a	R1ba1a1a2	post-Roman	Capture
KD021	WM	17-25	XY	H5c	R1ba1a1a2	post-Roman	Capture
KD022	WM	16-17	XY	T2a1	I2a1b1	post-Roman	Capture
CE005	Oak	15-18	XX	H3g1a	n/a	Anglo-Saxon	Shotgun

TABLE 9.2: Results of work by Dr. Dulias concerning the samples assessed in this chapter. Only Y-chromosomal macrohaplogroups are displayed here.

9.4 Changes in ancestry from the Bronze Age onwards

As KD010 from Worth Matravers is an outlier, it was analysed separately to the other samples. The ancient British samples plot with modern Europeans, particularly those of central Europe (**Figure 9.1**). Although there is some overlap between the early Medieval samples and modern British individuals, which may be suggestive of demographic changes occurring in Britain, this similarity may be due to how representative the modern and ancient samples are of the general population, and errors due to low coverage of ancient genomes. In general, there is a lot of overlap between sites and time periods, indicating that post-Bronze Age migrations were

smaller in scale, and either did not make a significant genetic impact on the general population, or otherwise came from genetically similar locations.

FIGURE 9.1: PCA of modern West Eurasian populations with British samples from this study projected on top. A zoomed-in area containing the majority of the ancient samples can be seen in the inset in the top left corner.

9.4.1 Bronze Age

A PCA including published Bronze Age samples from Europe (**Figure 9.2**) shows the Bronze Age samples (from Low Hauxley and West Heslerton) of this study plotting similarly to other British and northern European Bronze Age individuals. The Bronze Age samples reported here plot between the European Neolithic (including the British Neolithic), and the Yamnaya steppe culture.

As can be seen in the ADMIXTURE plot (**Figure 9.3**), the composition of the samples appear relatively similar, as are the published post-Neolithic samples.

The British Early Bronze Age samples were compared to all British populations from all

periods using *D*-statistics. The West Heslerton Early Bronze Age population shared the greatest affinity with groups dating to the Bronze Age and later, rather than to Mesolithic or Neolithic groups, similar to the PCA and ADMIXTURE results (**Figure 9.3**). The West Heslerton group also appears genetically closer to several British Bronze Age groups, rather than to the published Anglo-Saxons (Schiffels et al., 2016) but this might be due to sample size and representation of the latter. There are fewer significant results (|Z|>=2) from *D*-statistic tests involving the Low Hauxley sample, possibly the result of low coverage. This sample shows more gene flow from the Scottish Late Bronze Age than from English or Scottish Bell Beaker groups.

Similar to published samples from Bronze Age Britain, the samples in this study show significant steppe influence.

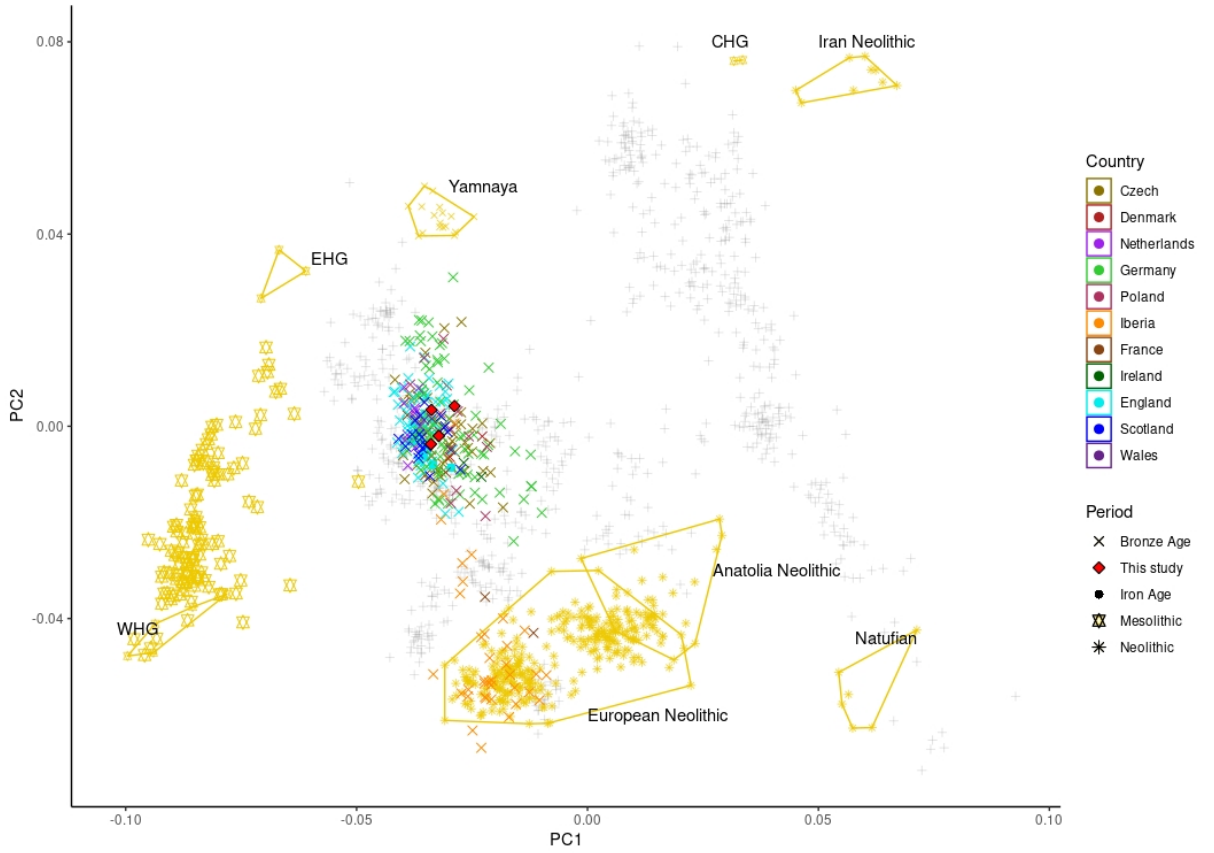


FIGURE 9.2: PCA of Bronze Age samples from this study (represented by red diamonds and marked with an asterisk in the legend) and published European Bronze Age samples (X's coloured by country) projected on modern West Eurasians. Other relevant reference populations are contained within polygons and labelled on the PCA.

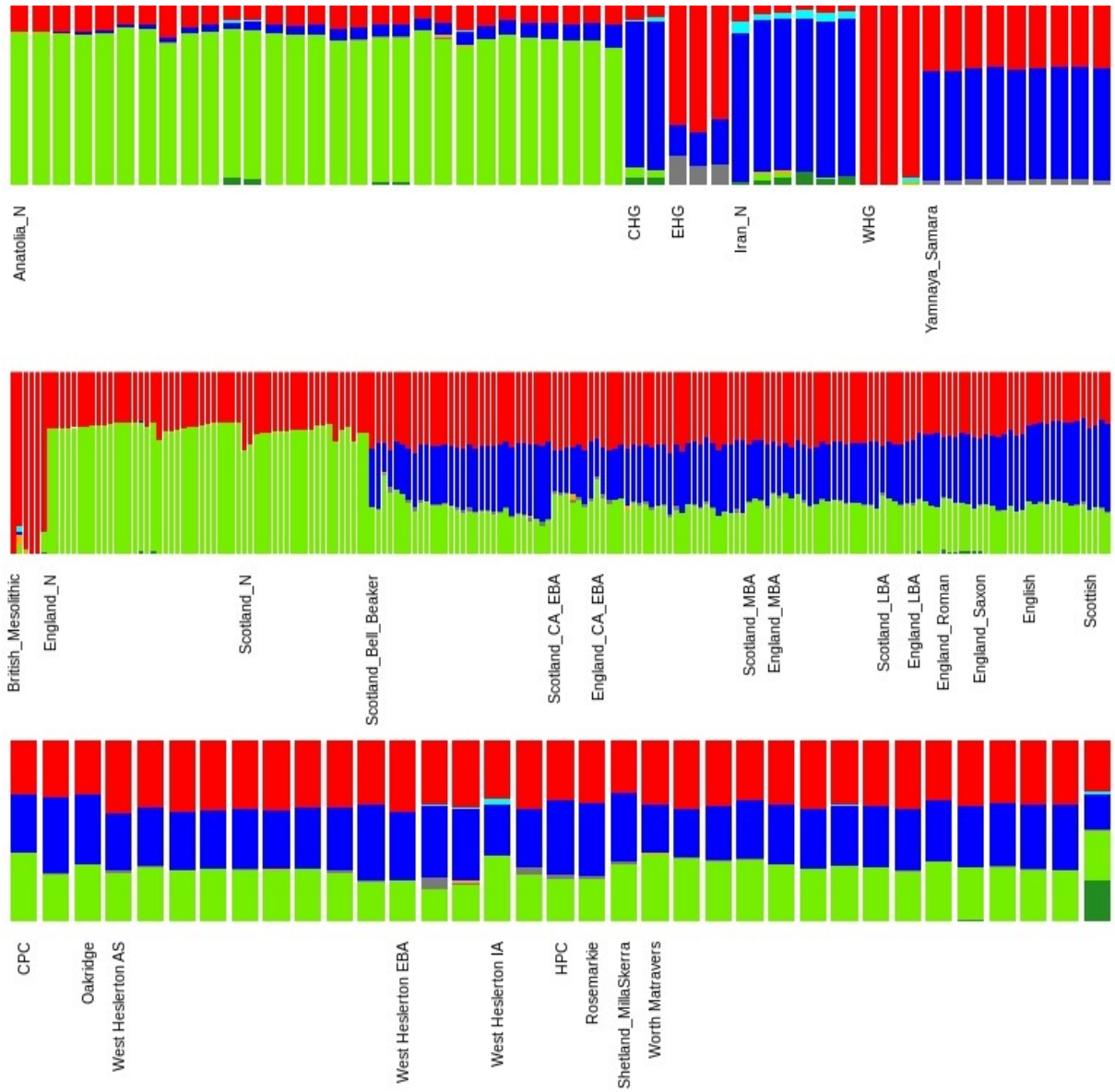


FIGURE 9.3: ADMIXTURE results. The first row displays relevant West Eurasian populations. The second row is published British samples. The third row displays the samples in this study. KD010 (the final sample) is noticeable as an outlier.

The *D*-statistic tests for the Early Bronze Age populations from Low Hauxley and West Heslerton were compared to contemporaneous populations from around Europe. These tests reveal both Bronze Age groups show greater gene flow with northern Bronze Age populations (Germany, Netherlands) than those from Iberia and southeastern Europe.

Admixture modelling (steppe ancestry as Samara Yamnaya, Anatolia Neolithic and WHG) using qpAdm shows a large contribution from the steppe to these samples (**Table 9.3**). Results across all samples are relatively consistent, showing that the majority of the ancestry is contributed from steppe populations. It should be noted that only one Bronze Age sample,

KD003, from West Heslerton, has over 100,000 SNPs, which is the minimum number of SNPs suggested for use with qpAdm by Olalde et al. (2018).

Sample	Site	p-value	steppe	SE	ANF	SE	WHG	SE
KD070	LH	0.540378	0.662	0.163	0.152	0.163	0.186	0.084
KD003*	WH	0.809818	0.667	0.082	0.291	0.080	0.042	0.038
KD040	WH	0.467414	0.504	0.264	0.169	0.280	0.327	0.109
KD041	WH	0.606536	0.631	0.160	0.356	0.164	0.013	0.067

TABLE 9.3: qpAdm results for the Early Bronze Age samples, showing admixture proportions and standard error (SE). The asterisk highlights the sample with above 100,000 SNPs. The steppe-ancestry proportion is represented by the Samara Yamnaya. Key: ANF = Anatolian Neolithic Farmers; WHG = Western Hunter-Gatherers;LH = Low Hauxley; WH = West Heslerton.

Two-way qpAdm tests were attempted using a Neolithic and a European Bronze Age population to determine ancestry proportions of the samples. English, Scottish, and combined British Neolithic populations were used as the Neolithic source. The Early Bronze Age populations from Europe with the highest affinity in the *D*-statistics were selected as the Bronze Age source (Denmark BA, France Bell Beaker, Germany Unetice, Netherlands BA and Netherlands Bell Beaker). No feasible 2-way model could be achieved for KD003 nor KD041, but feasible results were produced from the other two Bronze Age samples. From West Heslerton, KD040, produced feasible results from all combinations with c.80-95% ancestry derived from the European Bronze Age populations. The Low Hauxley individual produced feasible results with all combinations except the Netherlands BA, with c.92-99% ancestry deriving from European Bronze Age groups.

9.4.2 Iron Age

Admixture modelling of the Iron Age samples (CPC, HPC and West Heslerton), as a combination of Samara Yamnaya (steppe), Anatolia Neolithic and WHG, shows much greater diversity in the ancestry makeup than seen in the Bronze Age (**Table 9.4**). Whilst a large proportion of the ancestry of these individuals still appears to have been derived from the steppe, there appears to have been an increase in the proportion of Anatolian Neolithic derived ancestry at this time period.

Sample	Site	p-value	Steppe	SE	ANF	SE	WHG	SE
CE003*	CPC	0.289707	0.542	0.070	0.337	0.068	0.121	0.034
CE004	CPC	0.274662	0.385	0.113	0.407	0.122	0.208	0.054
KD005*	HPC	0.047189	0.602	0.068	0.287	0.065	0.111	0.032
KD073	MS	0.084393	0.423	0.336	0.412	0.362	0.165	0.111
KD071	WH	0.578036	0.231	0.211	0.543	0.211	0.226	0.105
KD072	WH	0.336367	0.602	0.253	0.242	0.257	0.157	0.117

TABLE 9.4: qpAdm results for the Iron Age samples, showing the admixture proportions and standard error (SE). The asterisk represents samples with above 100,000 SNPs. The steppe-ancestry proportion is represented by the Samara Yamnaya. Key: CPC = Carsington Pasture Cave; HPC = High Pasture Cave; MS = Milla Skerra; WH = West Heslerton.

Similar to the Bronze Age samples, the Iron Age *D*-statistic results demonstrated a greater affinity to northern European Bronze Age populations than to those from southern Europe. CPC and the West Heslerton Iron Age individuals were equally related to British Bronze Age and later groups. The West Heslerton Iron Age have much lower coverage than other samples, which may have resulted in fewer significant *D*-statistics results. *D*-statistic results show HPC to be closer to several groups over the English Early Bronze Age (including published English Iron Age and Saxon, Scottish Early and Late Bronze Age, Latvian Bronze Age and German Corded Ware groups, as well as post-Roman samples from Worth Matravers and the Rosemarkie Late Pictish man). Overall, the Iron Age *D*-statistics produced similar results between sites, and results were similar to the earlier Bronze Age analysis.

9.4.3 Early Medieval

The early Medieval samples in this study are geographically spread out across Britain, with Worth Matravers on the southern coast of England, West Heslerton in northern England, Oakridge in southeast England, and Rosemarkie Cave in Scotland. They also represent different cultures, from Romano-British (Worth Matravers), Anglo-Saxon (Oakridge and West Heslerton), and Pictish (Rosemarkie). Comparison of these sites aimed to determine whether geographical and cultural differences in Britain are reflected in the genome.

A PCA, of all ancient samples from this study and published post-Bronze Age cultures (**Figure 9.4**), demonstrates a lot of overlap between other sites dating from the Early Bronze Age to the Anglo-Saxon period. As mentioned above, one noticeable outlier can be seen from Worth Matravers. Post-Bronze Age Britain appears more homogenous than the published British Bronze Age samples and other large-scale studies from Europe (Early Medieval Germany, Swedish Vikings, Italian and Hungarian Langobards). Several of these studies have a large number of samples that overlap with the British samples, making it impossible to

determine if there was a migration to Britain using PCA alone. Furthermore, the published English post-Roman and Saxon individuals (Martiniano et al., 2016; Schiffels et al., 2016) sit outside the variation represented in this study. Modern Orcadian, Scottish and English populations from the Human Origins panel plot within the diversity, but so do several other countries from across Europe, suggesting demographic changes post-dating the time period of the current studies.

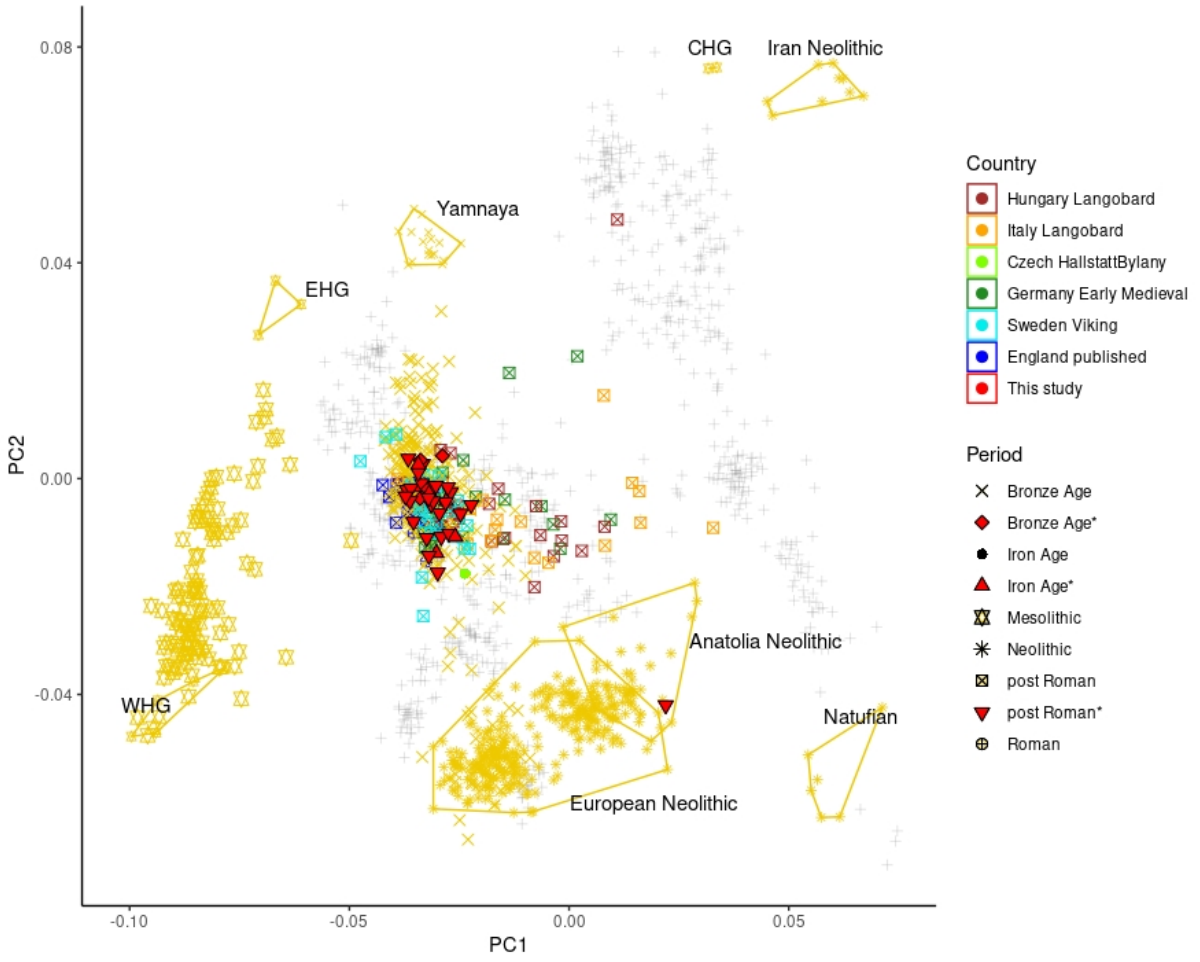


FIGURE 9.4: PCA of the samples in this study (in red and marked with an asterisk in the legend) and relevant populations projected on modern West Eurasians.

In the early Medieval period qpAdm analysis (**Table 9.5**), a slight reduction can be seen in the steppe-derived ancestry, with an increase in Anatolian Neolithic ancestry, when compared to the British Bronze Age samples.

Sample	Site	p-value	Steppe	SE	ANF	SE	WHG	SE
KD001*	RC	0.636225	0.659	0.057	0.236	0.056	0.105	0.025
KD002	WH	0.378227	0.358	0.200	0.513	0.205	0.129	0.081
KD031*	WH	0.810351	0.524	0.058	0.292	0.058	0.139	0.026
KD032*	WH	0.118049	0.569	0.063	0.292	0.062	0.139	0.028
KD033*	WH	0.790356	0.525	0.060	0.334	0.057	0.141	0.027
KD034*	WH	0.626644	0.569	0.060	0.325	0.058	0.105	0.024
KD035*	WH	0.786608	0.622	0.059	0.215	0.058	0.163	0.026
KD036*	WH	0.323659	0.602	0.072	0.231	0.074	0.168	0.031
KD037*	WH	0.411780	0.474	0.055	0.393	0.055	0.133	0.025
KD038*	WH	0.228273	0.461	0.056	0.356	0.055	0.184	0.026
KD007	WM	0.282717	0.412	0.099	0.410	0.099	0.177	0.043
KD008	WM	0.950812	0.616	0.159	0.161	0.163	0.224	0.066
KD009*	WM	0.738553	0.516	0.069	0.332	0.067	0.152	0.029
KD011*	WM	0.049220	0.533	0.075	0.333	0.071	0.134	0.033
KD012	WM	0.566076	0.510	0.119	0.404	0.118	0.086	0.052
KD013	WM	0.485727	0.410	0.138	0.497	0.133	0.093	0.052
KD014	WM	0.697868	0.622	0.105	0.324	0.107	0.055	0.048
KD016	WM	0.060490	0.742	0.104	0.149	0.100	0.109	0.044
KD017	WM	0.640799	0.391	0.090	0.421	0.087	0.189	0.045
KD018	WM	0.296553	0.456	0.127	0.456	0.127	0.088	0.054
KD019*	WM	0.588697	0.353	0.064	0.481	0.62	0.166	0.028
KD020	WM	0.972458	0.693	0.194	0.272	0.184	0.036	0.077
KD021*	WM	0.634850	0.487	0.072	0.362	0.074	0.151	0.031
KD022	WM	0.174501	0.347	0.185	0.552	0.164	0.101	0.070
CE005*	Oak	0.631975	0.411	0.069	0.491	0.068	0.098	0.031

TABLE 9.5: qpAdm results for the early Medieval Roman samples, showing the admixture proportions and standard error (SE). The asterisk represents samples with above 100,000 SNPs. The steppe-ancestry proportion is represented by the Samara Yamnaya. ANF = Anatolian Neolithic Farmers. WHG = Western Hunter-Gatherers. RC = Rosemarkie Cave. WH = West Heslerton. WM = Worth Matravers. Oak = Oakridge.

The number and coverage of the samples from this period enabled a greater number of conclusions to be derived from the *D*-statistic tests. Comparison of *D*-statistic tests assessing each site against published British populations (in the form of *D(Mbuti, Site; PopA, PopB)*, where PopA and PopB are published ancient British groups), revealed some consistent patterns across all samples (**Figure 9.5**). Rosemarkie Man has few significant results ($|Z| > 2$), which may be because this sample is equally related to both test populations; that is, the test populations form

a clade to the exclusion of Rosemarkie, which might be a result of low coverage and large error margins. The site of West Heslerton and Worth Matravers both clearly show similar trends in the results, despite being culturally different (Anglo-Saxon and Romano-British respectively). Both are more similar to the Scottish Late Bronze Age in several tests and are also less similar to more contemporary published Saxons (although it must be noted that there are very few published Anglo-Saxon samples). In contrast, several *D*-statistic results show the Oakridge individual as having greater gene flow with published Saxons than other British populations, which might be a factor of her not being a local (Cole et al. 2020).

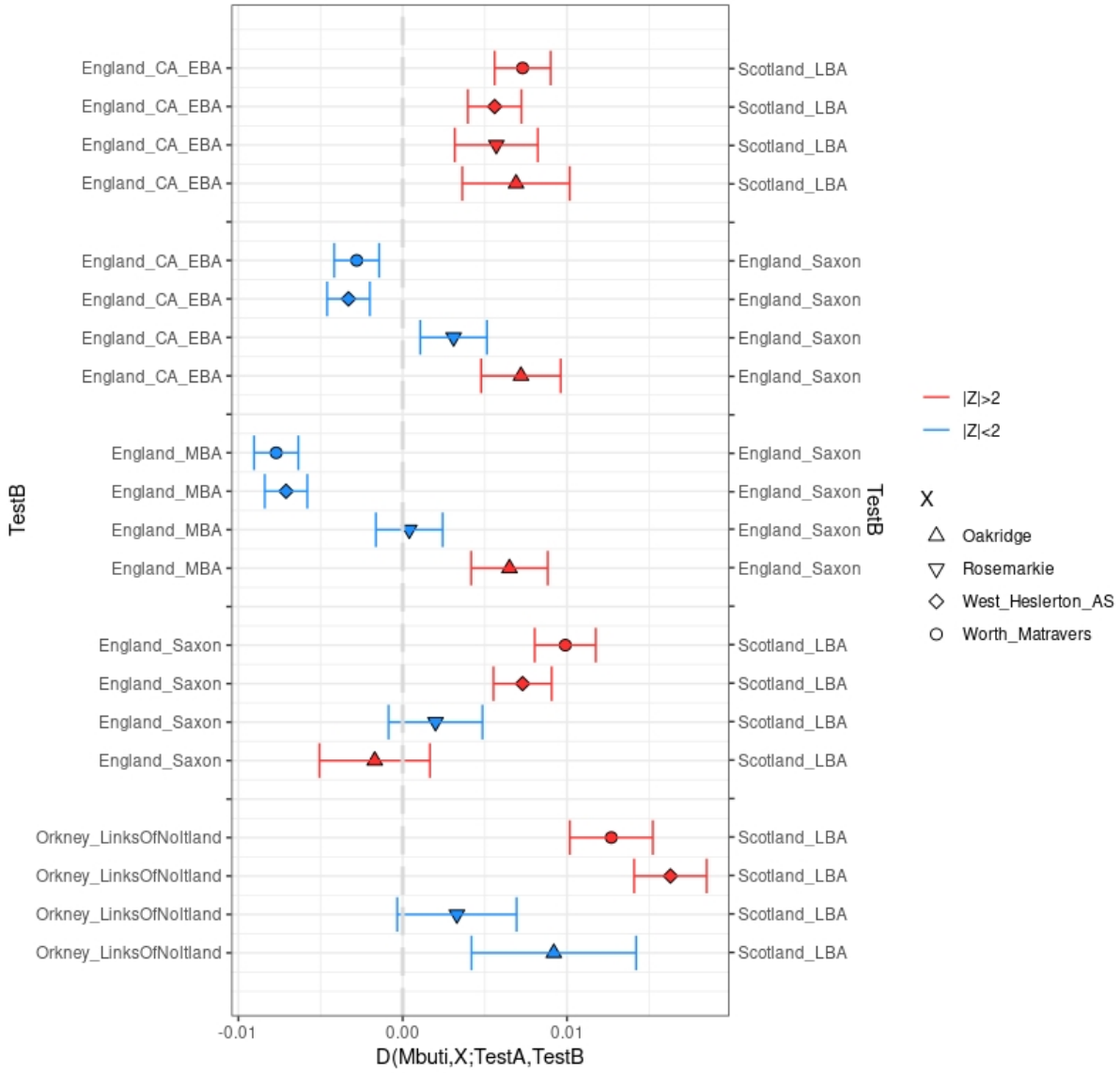


FIGURE 9.5: Selected *D*-statistics of early Medieval sites.

The early Medieval *D*-statistics show predominantly a greater affinity to British populations

than to other European populations, with the exceptions of the Orkney populations and published English Saxons and Romans **Figure 9.6**. The Bronze Age populations from the Netherlands have a greater affinity to West Heslerton and Worth Matravers than several British populations. No site showed a particular affinity to contemporaneous German Early Medieval or Swedish Vikings.

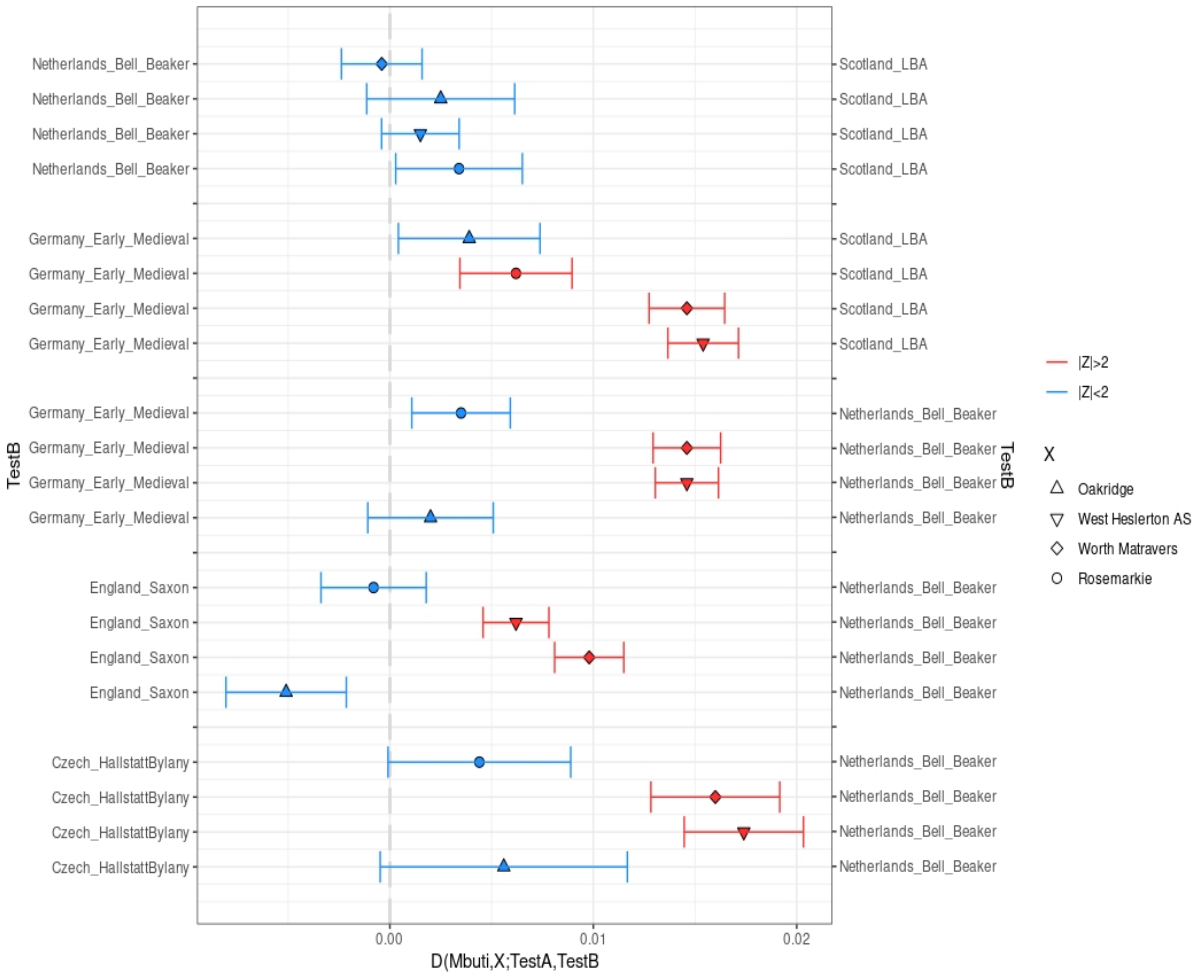


FIGURE 9.6: A subset of the results of *D*-statistic tests comparing early Medieval sites to ancient British and other European populations.

To assess whether the Worth Matravers and West Heslerton Anglo-Saxons could be modelled as a single population, *D*-statistics in the form of *D(Mbuti, Test; Worth Matravers, West Heslerton A-S)* were tested, where *Test* was ancient European population from the Bronze Age or later **Figure 9.7**. If no significant results could be produced, then it could be interpreted that they could be modelled as one population. Some significant results were detected with published English Saxons, English Early Bronze Age, Czech Early Bronze Age, Danish Late Neolithic, Swedish Bronze Age, Swedish Viking and German Early Medieval populations having a greater affinity to the West Heslerton Anglo-Saxons than Worth Matravers.

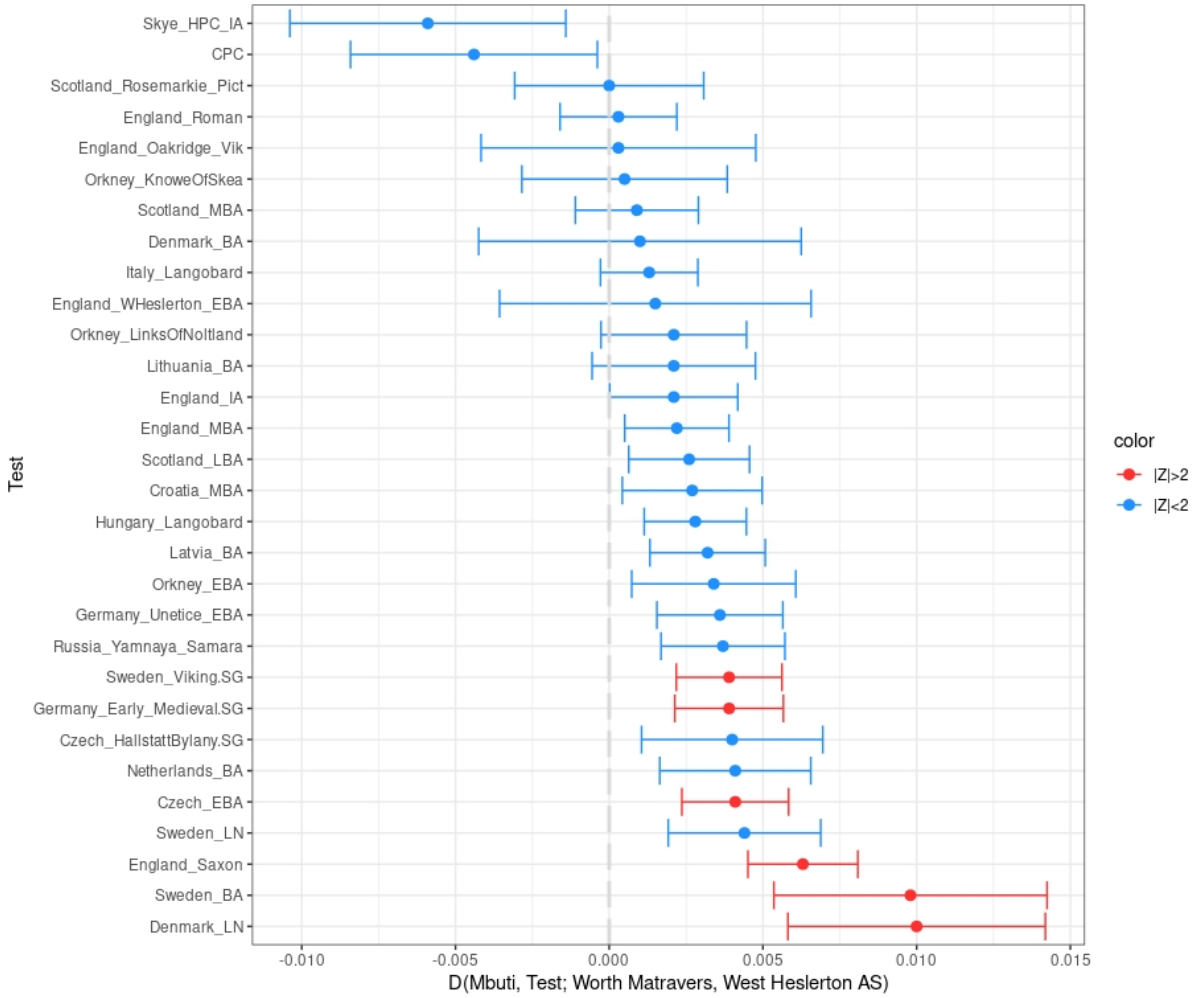


FIGURE 9.7: *D(Mbuti, Test; Worth Matravers, West Heslerton A-S)*, where *Test* was ancient European population from the Bronze Age or later.

9.4.3.1 Worth Matravers outlier

The PCA shown in **Figure 9.4** clearly shows the individual KD010 from Worth Matravers as an outlier to other British samples. This was also seen in the *D*-statistic tests. Admixture analysis demonstrates that KD010 has African ancestry. In order to better visualise the ancestry of this individual, another PCA was plotted using 72 West Eurasian and North African populations, and projecting ancient samples (**Figure 9.8**). This clearly shows KD010 plotting with modern North Africans, whereas all other samples in this study plot with modern European variation.

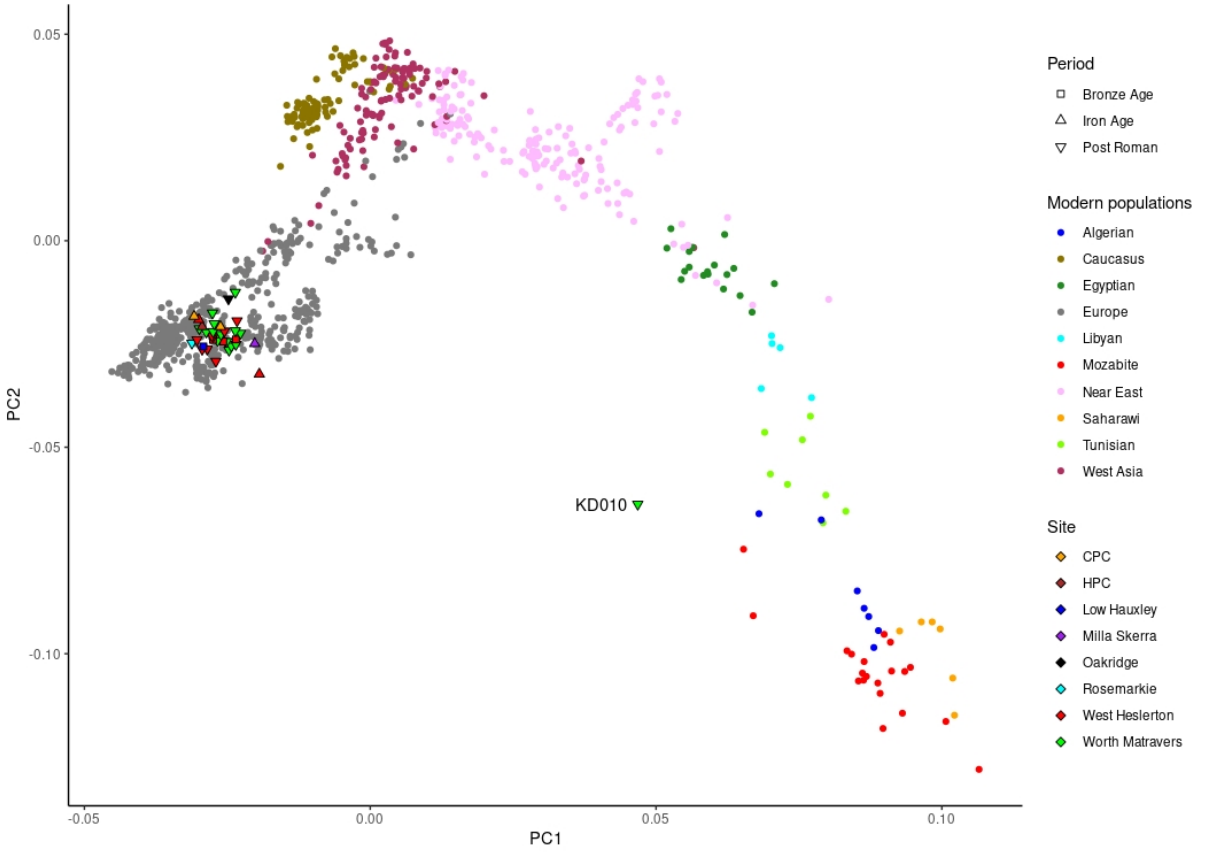


FIGURE 9.8: PCA of samples in this study projected onto West Eurasians and North Africans. KD010 from Worth Matravers plots with modern North Africans.

When other ancient samples were added to the PCA (**Figure 9.9**), KD010 plotted approximately between the Worth Matravers population and the Iberomaurusians and Moroccan hunter-gatherer populations, dating between 15,100 and 13,900 cal. BP. KD010 plotted closest to broadly contemporary Guanches from the Canary Islands (Rodríguez-Varela et al., 2017). There are much fewer published ancient North African samples.

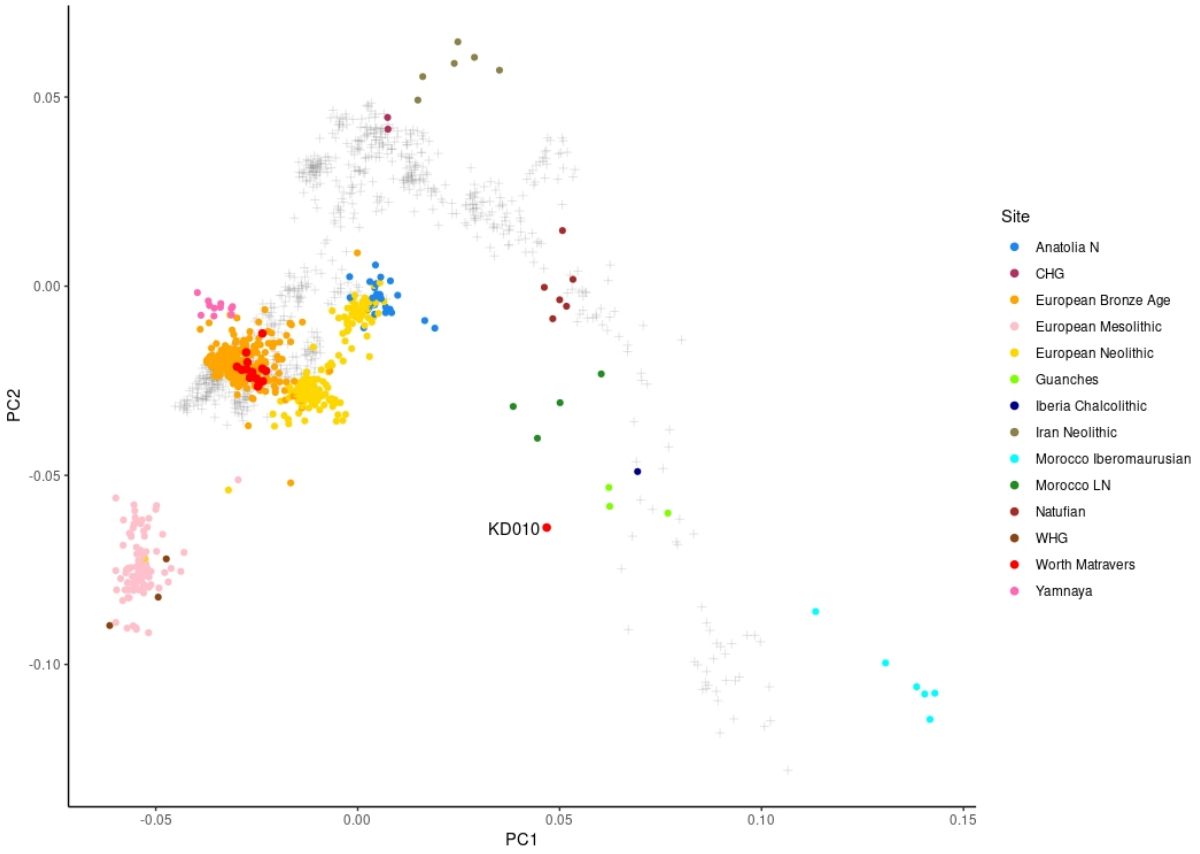


FIGURE 9.9: PCA of modern West Eurasians and North Africans (grey), published ancient samples and the Worth Matravers samples (red).

ADMIXTURE results (**Figure 9.10**) also clearly demonstrate KD010 as an outlier compared to the Worth Matravers and other English samples. KD010 comprises four components that are maximised in sub-Saharan African populations, WHG, Anatolian Neolithic, and the CHG/Iranian Neolithic. KD010 appears most similar to Guanches, but differs from these by having a higher WHG component and less Anatolian Neolithic component.

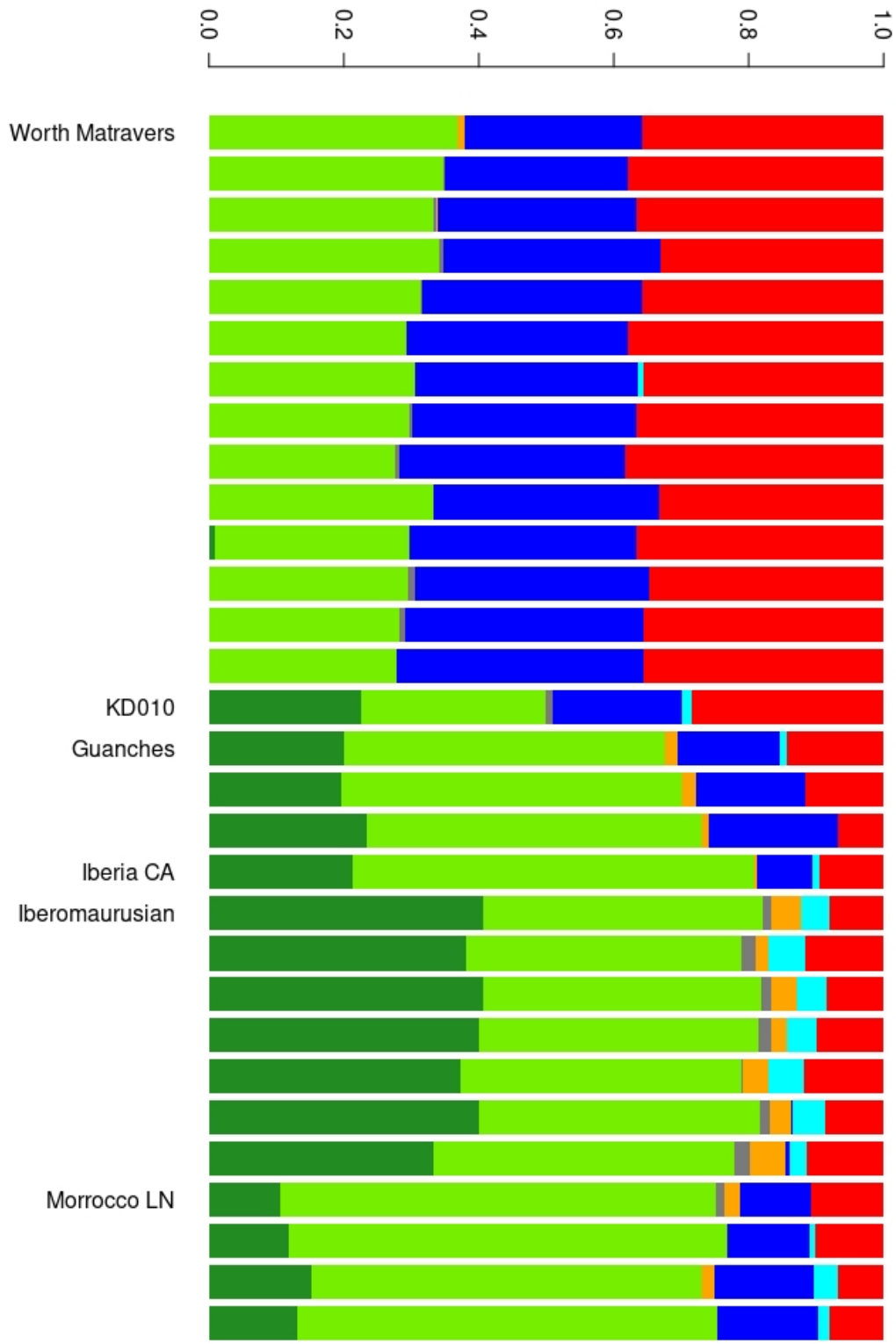


FIGURE 9.10: ADMIXTURE results (K = 7) of the Worth Matravers and published ancient samples with North African ancestry. KD010 is the last sample of the Worth Matravers group.

A large proportion of this individual's ancestry can be associated with the Moroccan Late Neolithic (Fregel et al., 2018). This does not mean that KD010 descended directly from this population, but rather that he descended from a group that was similar at some point in the past. Further analysis of ancient Africans and other admixed populations would certainly improve this result. Large errors are attributed to both the Anatolian Neolithic farmer and Moroccan Late Neolithic derived proportions, which may be due to the limited number of SNPs from KD010, or may reflect that Late Neolithic Morocco is not an ideal source population. Even with this error, a large proportion of this individual's ancestry can be seen to have derived from ancient North Africa.

As this individual had African ancestry, *D*-statistics were repeated with several outgroups, including Mbuti, Ust Ishim, and a chimp reference sequence but, as the source of African ancestry is not known, the Mbuti may not represent a suitable outgroup. Across all *D*-statistic tests KD010 shares a greater affinity with ancient European, rather than to either North African (as represented by the Moroccan Late Neolithic, Iberomaurasians and Guanches) populations, or to an Iberian Chalcolithic individual with North African ancestry (Olalde et al., 2019) 9.11. Within the African populations, the Guanches and Moroccan Late Neolithic are closer to KD010 than Iberomaurusians. There is a greater affinity to northern than southern European populations, with a slight affinity to English samples compared to other northern and central Europeans. However, it must be noted that few significant results were produced, potentially because KD010 is equally related to most ancient Europeans, but also as analysis is limited with this sample due to the low number of SNPs recovered.

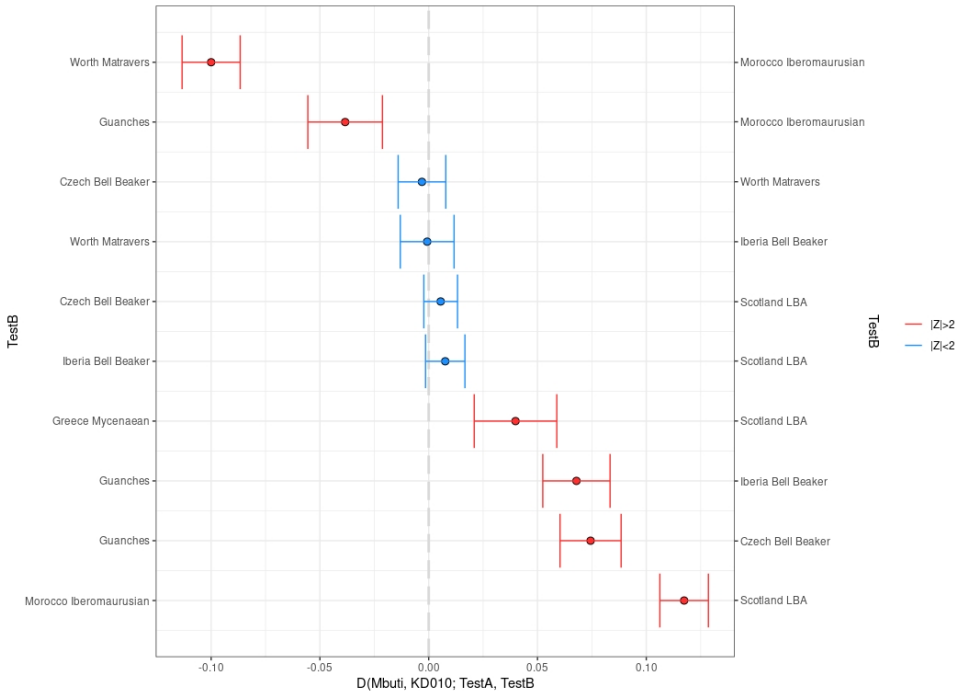


FIGURE 9.11: Results of *D(Chimp, KD010; TestA, TestB* comparing European and North African ancient populations.

The similarity of the *D*-statistics showing an affinity to northern Europe, coupled with KD010 having a European mtDNA and an African Y-chromosomal haplogroup, suggests that this individual is admixed. To test this, the other Worth Matravers individuals and published Guanches (Rodríguez-Varela et al., 2017) were used as populations to model KD010 using qpAdm (**Table 9.6**). Guanches were chosen as the source of African ancestry due to their similarity on the PCA, and the fact that they are broadly contemporary with the WM individual. A set of 'right' populations was selected following Olalde et al. (2019), whose analysis included samples with North African admixture (Mota, Ust Ishim, Kosteniki14, Goyet Q116, Vestonice16, MA1, El Miron, Villabruna, EHG, Iran Ganj Neolithic, Jordan PPNB, Israel Natufian, Iberomaurusian, Han, WHG, Anatolian Neolithic, Yamnaya Samara and the Moroccan Late Neolithic). KD010 could be modelled as deriving half his DNA from the Worth Matravers population, and half from the Guanches (**Table 9.6**). This result suggests that this individual is the child of local and African admixture, most likely a British mother and African father. However, it is not possible to investigate this further due to the low coverage of the sample.

Sample	p-value	Guanches	SE	Worth Matravers	SE
KD010	0.282048	0.467	0.073	0.533	0.073

TABLE 9.6: qpAdm results of KD010 from Worth Matravers as an admixture of steppe (represented by Yamnaya Samara), Anatolian Neolithic farmer, Western Hunter Gatherer, and Moroccan Late Neolithic.

9.4.3.2 Kinship

Of the 15 individuals at the Worth Matravers cemetery, six kinships were identified using READ (**Figure 9.12**). There are no female to female relationships, but both male to male, and female to male, kinships were identified. All male to female relationships shared mtDNA haplotypes, demonstrating that none of the males were the fathers of the related females. Of the 15 samples, the majority of those with shared mtDNA were related (exceptions to this are KD020 and KD022, which both have very low number of overlapping SNPs, and so large errors in the READ results).

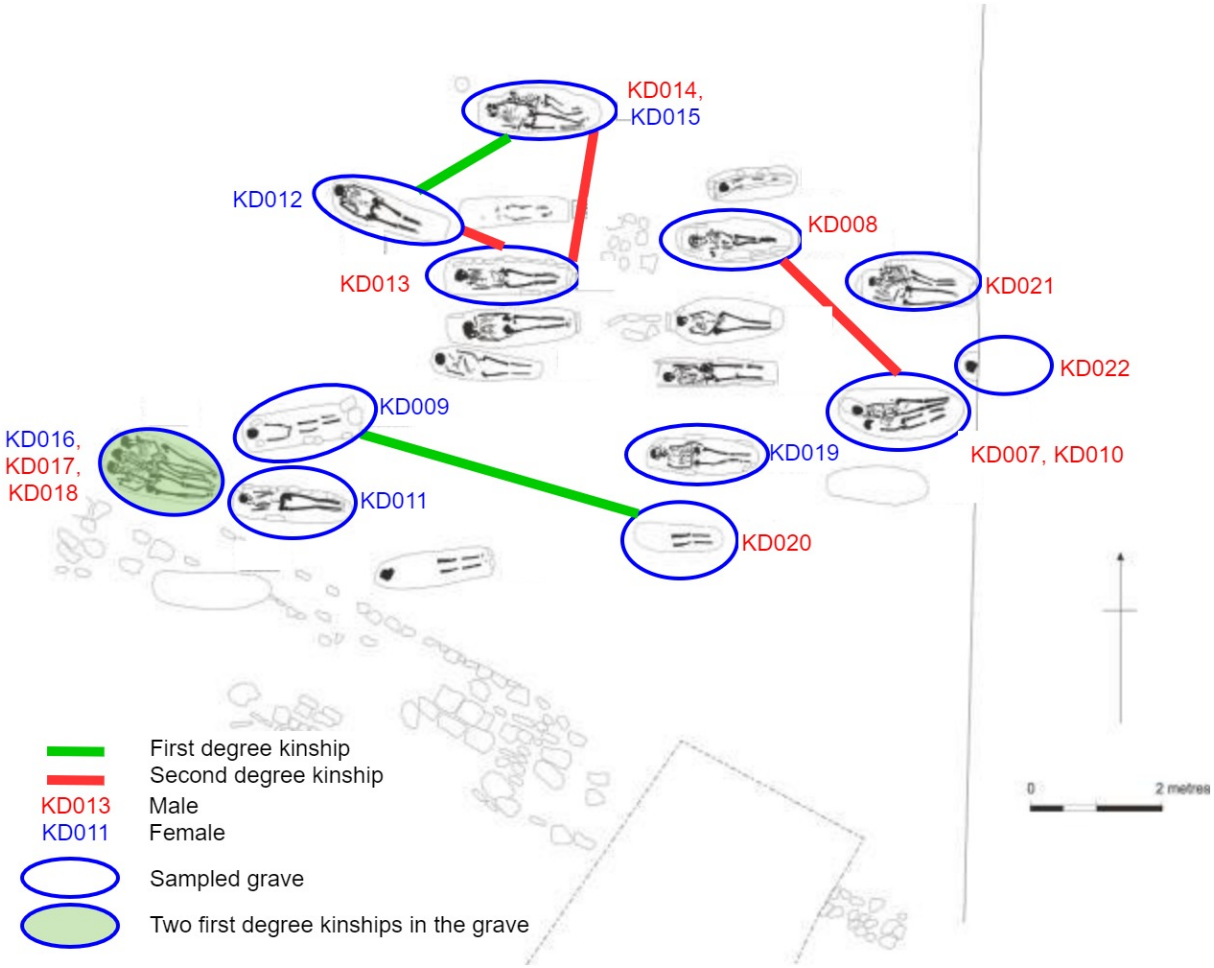


FIGURE 9.12: READ kinship results shown on a plan of the Worth Matravers cemetery. Edited from Ladle and Morgan (2012).

KD016 (25-35 year old female) and KD018 (15-16 year old male), who share a first-degree relationship and mtDNA, are buried in the same grave, alongside KD017 (45-49 year old male) with whom neither shared a close kinship (despite sharing a Y haplogroup with KD018). As the bodies are thought to have been interred at the same time, it is most likely that KD016 is the mother or sister of KD018.

The two males in a double burial (adult KD007 and 17-25 year old KD010) also do not share any close kinship. However, KD007 does have a second-degree relationship with KD008 (17-25 year old male), who shares the same mtDNA but not Y-chromosomal haplotype. This suggests they had a potential maternal relationship, either as half-siblings, grandfather-grandson or uncle-nephew.

A first-degree relationship can be seen between KD009 (25-35 year old female) and KD020 (adult male), who were both individually interred. Both share a mtDNA haplotype, making them likely siblings or mother and son.

It was not possible to identify kinship in tomb 1678 between KD014 (40-45 year old male) and KD015 (15-16 year old female) as individual KD015 had too low coverage, but they did share an mtDNA haplotype.

With three other samples, it was also possible to identify kinship. KD012 (25-35 year old female) and KD014 shared a first-degree kinship and mtDNA haplotype. Both also shared a second-degree kinship with KD013 (17-25 year old male). All three shared the same mtDNA haplotype, and KD013 and KD014 shared the same YDNA haplogroup. It is interesting to note that six of the nine males at the cemetery shared the same YDNA haplogroup, but, due to coverage, it is not possible to accurately identify the exact haplotype in each individual. As there is greater diversity of mtDNA haplogroups compared to YDNA, greater weight can be given to mtDNA in building family trees. There are several possible genealogical trees. One kin group could be that KD013 is the half-brother of KD012 and KD014. Another possibility is that KD013 is the maternal uncle or maternal nephew of KD012 and KD014, who would be siblings. KD012 could potentially be the mother of KD014 and the maternal grandmother of KD013.

Although kinship was only discovered at Worth Matravers, this does not mean that individuals at other sites were not related, but only that they did not possess first- or second-degree relationships.

9.5 Conclusion

The Bronze Age migration had a large and lasting impact upon Britain. However, after this time, there are little noticeable differences in the PCA, ADMIXTURE and qpAdm results between the Bronze Age and early Medieval populations, despite a difference of several millennia. No large demographic changes can be seen during this intervening period, in contrast to the Mesolithic-Neolithic and Neolithic-Bronze Age transitions. The populations all comprise of three components related to WHG, Anatolian Neolithic and steppe pastoralists.

The *D*-statistic results show a great deal of homogeny across all sites. Continued similarity can be seen to Bronze Age populations of northern Europe, however, some chronological and regional differences can be observed. As expected, no particular affinity is seen between these populations and those from Orkney (presented in Chapter 8), nor to the small number of published Romans and Saxons.

The majority of the samples come from the early Medieval period, a time when there exists historical evidence of migrations and the arrival of new cultures (see Section 7.3). Despite this, the post-Roman population of Worth Matravers and the Anglo-Saxon population of West Heslerton are very similar, as shown by the *D*-statistic results, despite their geographic and cultural differences. Both sites show a greater affinity to the British Bronze Age than to published Saxons or other Medieval individuals. In contrast, Oakridge is closer to published Saxons than any other British group. The Oakridge woman does not follow the pattern shown in other Medieval samples of being closer to Dutch and Czech Bronze Age groups over other populations. This hints at a genomic difference in southeastern Britain compared to the rest of the island, possibly as the result of a migration to the area, the timing and location of which might hint at Anglo-Saxon migrations. However, she is a single sample, and it is possible, due to the manner of her death, that she is a genetic outlier, especially given that, from stable isotopic analysis, she was not raised locally. More sampling and in-depth sequencing is required before drawing any further conclusions.

Although only Worth Matravers shows evidence of kinship, this does not mean that more distantly related individuals are not present at the sites, and people who are not genetically related may still have been viewed as part of extended family groups, through adoption, marital groups, and in-laws. No female to female kinships were directly identified at Worth Matravers, even though there was indirect evidence for females present in the family groupings. All relationships found at this site shared mitochondrial haplotypes and, therefore, could be interpreted as maternal. Kinship analysis also revealed that multiple burials, including the shared burial of the genetic outlier (KD010), may not have been reserved for closely related kinsmen, as seen in the Early Bronze Age barrow burial from West Heslerton.

9.6 Ongoing and Future work

The following samples were sent for further sequencing:

Sample	Site	Era
KD070	Low Hauxley	EBA
KD040	West Heslerton	EBA
KD041	West Heslerton	EBA
KD039	West Heslerton	Anglo-Saxon
KD073	Milla Skerra	Iron Age

TABLE 9.7: Samples sent for further sequencing.

KD070 represents the earliest Beaker burial in northern Britain, so more sequence coverage could allow a better understanding of the Beaker migration, while more data from Early Bronze Age West Heslerton would complement this. The Milla Skerra individual is the first ancient DNA data from Shetland so, due to its low endogenous DNA content, further sequencing is necessary to allow any type of analysis of the historical occupation of Shetland. More data from this sample would allow further comparison with the IA samples from Orkney, and allow a more thorough typing of the Y-chromosomal haplogroup of this sample. This is of interest as haplogroup I is at high proportion in BA Orkney, whereas IA Orkney samples studied here had R1b.

The West Heslerton project has been expanded and, as well as KD039, a further 41 samples have been sent for capture sequencing at Harvard. It is hoped this will create detailed information concerning genetic diversity of the site. A further two individuals from Worth Matravers have also been sent for capture analysis: the other individual from burial 1722, and an individual from burial 1660. These additional sequences should increase kinship knowledge across the site and genomic information from post-Roman Britain.

The outlier individual from Worth Matravers, KD010, has been sent for radiocarbon dating. This will provide another date for the site, improving our knowledge of its period of use. It is also hoped to undertake further sequencing of this sample to understand his African ancestry.

Margaryan and co-authors published a paper on September 14th 2020, which reports analysis of Viking Age samples from across northern Europe, including Britain. The data within this paper (Margaryan et al., 2020) largely post-date the samples in Chapters 8 and 9, as their earliest English samples date to 880-1000 AD, while their Orkney samples date to 970-1025 AD. It was too late to include these data into the British analyses presented in this thesis, but doing so might improve assessment of the early Medieval groups.

Chapter 10

Conclusions

10.1 Conclusions and Discussions

The aim of this thesis was to identify whether, and, if so, to what degree, the steppe ancestry linked to changes seen in the Bronze Age made an impact on the island fringes of Europe, focussing on the LMIII Necropolis of Armenoi on Crete, and the Links of Noltland on Orkney. Assessment of whole genome and uniparental markers was undertaken to identify migrations and dis/similarities with both earlier and more contemporaneous populations. In addition, identification of kinship was used to identify potential evidence for inherited status versus community setting of burial grounds.

10.2 Uniparental markers

Steppe ancestry is often linked to the presence of Y-chromosomal haplogroups R1a and R1b (Allentoft et al., 2015; Haak et al., 2015; Olalde et al., 2018). However, both Aremnoi and the Links of Noltland displayed Y-chromosomal haplogroups consistent with the Neolithic, with only one male from each site having R1b. The R1b male at Armenoi appears to be a genetic outlier across his whole genome. In contrast, the post-Bronze Age data from Britain and Orkney demonstrated a predominance of R1b.

The Bronze Age is less associated with an introduction of any particular mitochondrial haplogroups. The haplogroups found at Armenoi and the Links of Noltland were already present by the Neolithic.

10.3 Presence of steppe ancestry in the whole genome

ADMIXTURE and PCA results clearly demonstrated a change in ancestry from the Neolithic to Bronze Age period on both islands. In Orkney, the Links of Noltland population appeared similar to other Bronze Age populations of Britain and western Europe. This was further supported by the f-statistics, where the LoN appeared more similar to other Bronze Age groups that had steppe ancestry. In addition, LoN was modelled as comprising over 50%

steppe ancestry similar to other British Bronze Age populations (Olalde et al., 2018).

The presence of steppe ancestry is less clear amongst the Armenoi population. Continued gene-flow from areas with Caucasus Hunter-Gatherer or Iranian Neolithic ancestry to the Balkans and Greece begins in the Neolithic (Mathieson et al., 2018). Therefore, although they, along with other Greek Bronze Age groups, appeared different to the Greek Neolithic in the PCA and ADMIXTURE results, this was not necessarily the result of steppe ancestry, but could instead be associated with migration from areas with CHG ancestry. Analysis of f-statistics showed an affinity of Armenoi to populations with low amounts of steppe ancestry. QpAdm modelled Armenoi as having a low amount of steppe ancestry.

These results demonstrated that the steppe migration had a genetic impact on both corners of Europe, although apparently to a greater extent on Orkney than on Crete. Both sites were relatively homogenous, demonstrating that the cultural changes associated with Bronze culture were unlikely the result of an elite takeover, despite the differing burial styles seen at the Links of Noltland. Whilst there was one genetic outlier at Armenoi with higher steppe component, this did not appear to correlate to status via greater tomb wealth.

10.4 Evidence of Bronze Age cultural practices

Kinship was clearly important to the Armenoi population. Three of the five tombs with multiple individuals showed evidence of kinship. In one instance, Tomb 203, it was possible to recreate a family tree over three generations (Figure 6.4), suggesting that the idea of family and inherited wealth was important to the Armenoi population. It was not possible to identify evidence of a patriarchal society from the genetic analyses. Of interest, more females than males were present in my dataset (16 females: 7 males). This may be indicative that Late Minoan III Crete was not a patriarchal society, however, more samples, alongside increased inter-disciplinary research, are required to explore this issue further.

Kinship was also identified at the Links of Noltland. The presence of a large grave containing multiple related individuals suggests that this had a family rather than community importance. The continuation of Y-chromosome haplogroup I, despite the introduction of steppe ancestry, suggested a patriarchal system, but one that may have predated the Bronze Age in the area.

10.5 Lasting genetic impact

The differences between the modern and ancient mitochondrial diversity of Crete demonstrated that subsequent migrations clearly changed the mitochondrial diversity of the island, Chapter B. This is further evidenced in the PCA, Figure 6.5 and ADMIXTURE, Figure 6.6.

In contrast, the same tests on the Orkney data showed little genetic difference between modern and ancient populations, Figures 8.3 and 8.5. The male Iron Age samples from the Knowe of Skea, Orkney, all had the R1b Y-chromosomal haplotype, which is also seen in other areas that have high steppe ancestry. Later British samples also appeared similar to LoN, modern British samples, and populations from western Europe.

The genetic impact of the Bronze Age made a lasting impact on western Europe, and this carried through into subsequent periods.

10.6 Final conclusions

The Bronze Age expansion from the steppe into Europe brought technological and demographic changes across the continent. This distinctive genetic component can be clearly seen in Orkney, but much less so in Crete. However, neither appear to follow the patterns of their local mainlands. In Orkney, this can be seen in the dominance of Y-haplogroup I, despite having whole genome ancestry similar to the rest of Britain. In Crete, the genetic contribution from the steppe was much smaller, suggesting, in this instance, that the cultural changes were linked with the migration of ideas rather than people. Both studies have shown that the Bronze Age resulted in genetic changes, even at the fringes of Europe.

References

Agouridis, C. (1997). "Sea routes and navigation in the third millennium Aegean". *Oxford Journal of Archaeology* 16 (1):1–24.

Albarella, U (2017). "Zooarchaeology in the twenty-first century: where we come from, where we are now, and where we are going".

Alexander, D., Novembre, J., and Lange, K. (2009). "Fast model-based estimation of ancestry in unrelated individuals". *Genome Research*.

Allentoft, M., Sikora, M., Sjögren, K.-G., Rasmussen, S., Rasmussen, M., Stenderup, J., Damgaard, P., Schroeder, H., Ahlström, T., Vinner, L., Malaspinas, A.-S., Margaryan, A., Higham T. Chivall, D., Lynnerup, N., Harvig, L., Baron, J., Della Casa, P., Dąbrowski, P., Duffy, P., Ebel, A., Epimakhov, A., Frei, K., Furmanek, M., Gralak, T., Gromov, A., Gronkiewicz, S., Grupe, G., Hajdu, T., Jarysz, R., Khartanovich, V., Khokhlov, A., Kiss, V., Kolář, J., Kriiska, A., Lasak, I., Longhi, C., McGlynn, G., Merkevicius, A., Merkyte, I., Metspalu, M., Mkrtchyan, R., Moiseyev, V., Paja, L., Pálfi, G., Pokutta D. Pospieszny, L., Price, T., Saag, L., Sablin, M., Shishlina, N., SmrČka, V., Soenov, V., Szeverényi, V., Tóth, G., Trifanova, S., Varul, L., Vicze, M., Yepiskoposyan, L., Zhitenev, V., Orlando, L., Sicheritz-Pontén, T., Brunak, S., Nielsen, R., Kristiansen, K., and Willerslev, E. (2015). "Population genomics of Bronze Age Eurasia". *Nature* 522 (7555):167–172.

Ambrose, S. H., Butler, B. M., Hanson, D. B., Hunter-Anderson, R. L., and Krueger, H. W. (1997). "Stable isotopic analysis of human diet in the Marianas Archipelago, Western Pacific". *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 104 (3):343–361.

Anderson, S., Bankier, A., Barrell, B., de Bruijn, M., Coulson, A., Drouin, J., Eperon, I., Nierlich, D., Roe, B., Sanger, F., Schreier, P., Smith, A., Staden, R., and Young, I. (1981). "Sequence and organization of the human mitochondrial genome". *Nature* 290 (5806):457.

Andrews, R. M., Kubacka, I., Chinnery, P. F., Lightowlers, R. N., Turnbull, D. M., and Howell, N. (1999). "Reanalysis and revision of the Cambridge reference sequence for human mitochondrial DNA". *Nature genetics* 23 (2):147–147.

Antonio, M. L., Gao, Z., Moots, H. M., Lucci, M., Candilio, F., Sawyer, S., Oberreiter, V., Calderon, D., Devitofranceschi, K., Aikens, R. C., Aneli, S., Bartoli, F., Bedini, A., Cheronet, O., Cotter, D. J., Fernandes, D. M., Gasperetti, G., Grifoni, R., Guidi, A.,

La Pastina, F., Loreti, E., Manacorda, D., Matullo, G., Morretta, S., Nava, A., Fiocchi Nicolai, V., Nomi, F., Pavolini, C., Pentiricci, M., Pergola, P., Piranomonte, M., Schmidt, R., Spinola, G., Sperduti, A., Rubini, M., Bondioli, L., Coppa, A., Pinhasi, R., and Pritchard, J. K. (2019). "Ancient Rome: A genetic crossroads of Europe and the Mediterranean". *Science* 366 (6466):708–714.

Armit, I. and Ginn, V. (2007). "Beyond the grave: human remains from domestic contexts in Iron Age Atlantic Scotland". In: *Proceedings of the Prehistoric Society*. Vol. 73. Cambridge University Press, p. 113–134.

Batini, C., Hallast, P., Vågene, Å. J., Zadik, D., Eriksen, H. A., Pamjav, H., Sajantila, A., Wetton, J., and Jobling, M. (2017). "Population resequencing of European mitochondrial genomes highlights sex-bias in Bronze Age demographic expansions". *Scientific Reports* 7 (1):12086.

Behar, D., Van Oven, M., Rosset, S., Metspalu, M., Loogväli, E.-L., Silva, N., Kivisild, T., Torroni, A., and Villems, R. (2012). "A Copernican reassessment of the human mitochondrial DNA tree from its root". *The American Journal of Human Genetics* 90 (4):675–684.

Berg, I. (2019). *The Cycladic and Aegean Islands in Prehistory*. Routledge.

Bergström, A., McCarthy, S. A., Hui, R., Almarri, M. A., Ayub, Q., Danecek, P., Chen, Y., Felkel, S., Hallast, P., Kamm, J., Blanché, H., Deleuze, J.-F., Cann, H., Mallick, S., Reich, D., Sandhu, M. S., Skoglund, P., Scally, A., Xue, Y., Durbin, R., and Tyler-Smith, C. (2020). "Insights into human genetic variation and population history from 929 diverse genomes". *Science* 367 (6484).

Bickle, P. (2018). "Stable isotopes and dynamic diets: The Mesolithic-Neolithic dietary transition in terrestrial central Europe". *Journal of Archaeological Science: Reports* 22:444–451.

Biers, W. R. (1996). *The archaeology of Greece : an introduction*. Cornell University Press.

Birch, S. and Peteranna, M. (2016). *Rosemarkie Caves Project:Data Structure Report: Archaeological Excavation in Learnie 2B Near Rosemarkie, Ross-Shire. 2016.*

Birch, S. and Wildgoose, M. (2013). *Uamh an Ard Achadh (High Pasture Cave). Strath, Isle of Skye 2010/11 (NGR NG 5943 1971). The Preliminary Assessment and Analysis of Late Prehistoric Cultural Deposits from a Limestone Cave and Associated Surface Features. Data Structure Report – HPC007*. National Museums Scotland, University of Durham: West Coast Archaeological Services.

Bogaard, A., Heaton, T. H., Poulton, P., and Merbach, I. (2007). "The impact of manuring on nitrogen isotope ratios in cereals: archaeological implications for reconstruction of diet and crop management practices". *Journal of Archaeological Science* 34 (3):335–343.

Booth, T. J. (2019). "A stranger in a strange land: a perspective on archaeological responses to the palaeogenetic revolution from an archaeologist working amongst palaeogeneticists". *World Archaeology* 51 (4):586–601.

Bouwman, A. S., Brown, K. A., Prag, A. J. N., and Brown, T. A. (2008). "Kinship between burials from Grave Circle B at Mycenae revealed by ancient DNA typing". *Journal of Archaeological Science* 35 (9):2580–2584.

Bownes, J., Clarke, L., and Buckberry, J. (2018). "The importance of animal baselines: Using isotope analysis to compare diet in a British medieval hospital and lay population". *Journal of Archaeological Science: Reports* 17:103–110.

Brace, S., Diekmann, Y., Booth, T. J., Dorp, L. van, Faltyskova, Z., Rohland, N., Mallick, S., Olalde, I., Ferry, M., Michel, M., Oppenheimer, J., Broomandkhoshbacht, N., Stewardson, K., Martiniano, R., Walsh, S., Kayser, M., Charlton, S., Hellenthal, G., Armit, I., Schulting, R., Craig, O. E., Sheridan, A., Parker Pearson, M., Stringer, C., Reich, D., Thomas, M. G., and Barnes, I. (2019). "Ancient genomes indicate population replacement in Early Neolithic Britain". *Nature ecology & evolution* 3 (5):765.

Bradley, R. (2007). *The Prehistory of Britain and Ireland*. Cambridge University Press.

Brandt, G., Haak, W., Adler, C., Roth, C., Szécsényi-Nagy, A., Karimnia, S., Möller-Rieker, S., Meller, H., Ganslmeier, R., Friederich, S., Dresely, V., Nicklisch, N., Pickrell, J., Sirocko, F., Reich, D., Cooper, A., Alt, K., and The Genographic Consortium (2013). "Ancient DNA reveals key stages in the formation of central European mitochondrial genetic diversity". *Science* 342 (6155):257–261.

Brandt, G., Szécsényi-Nagy, A., Roth, C., Alt, K. W., and Haak, W. (2015). "Human paleogenetics of Europe–The known knowns and the known unknowns". *Journal of human evolution* 79:73–92.

Brandt, L. Ø., Haase, K., and Collins, M. J. (2018). "Species identification using ZooMS, with reference to the exploitation of animal resources in the medieval town of Odense". *Danish Journal of Archaeology* 7 (2):139–153.

Broodbank, C. and Strasser, T. F. (1991). "Migrant farmers and the Neolithic colonization of Crete". *Antiquity* 65 (247):233–245.

Brotherton, P., Haak, W., Templeton, J., Brandt, G., Soubrier, J., Adler, C., Richards, S., Der Sarkissian, C., Ganslmeier, R., Friederich, S., Dresely, V., van Oven, M., Kenyon, R., Van der Hoek, M., Korlach, J., Luong, K., Ho, S., Quintana-Murci, L., Behar, D., Meller, H., Alt, K., Cooper, A., and The Genographic Consortium (2013). "Neolithic mitochondrial haplogroup H genomes and the genetic origins of Europeans". *Nature Communications* 4:1764.

Brown, T. A. and Brown, K. (2011). *Biomolecular archaeology: an introduction*. John Wiley & Sons.

Brunel, S., Bennett, E. A., Cardin, L., Garraud, D., Barrand Emam, H., Beylier, A., Boulestin, B., Chenal, F., Ciesielski, E., Convertini, F., Dedet, B., Desbrosse-Degobertiere, S., Desenne, S., Dubouloz, J., Duday, H., Escalon, G., Fabre, V., Gailledrat, E., Gandelin, M., Gleize, Y., Goepfert, S., Guilaine, J., Hachem, L., Ilett, M., Lambach, F., Maziere, F., Perrin, B., Plouin, S., Pinard, E., Praud, I., Richard, I., Riquier, V., Roure, R., Sendra, B., Thevenet, C., Thiol, S., Vauquelin, E., Vergnaud, L., Grange, T., Geigl, E.-M., and Pruvost, M. (2020). "Ancient genomes from present-day France unveil 7,000 years of its demographic history". *Proceedings of the National Academy of Sciences*.

Brück, J. and Fokkens, H. (2013). "Bronze Age Settlements". In: *The Oxford Handbook of the European Bronze Age*. Ed. by H. Fokkens and A. Harding. Oxford University Press.

Buckley, M. (2018). "Zooarchaeology by mass spectrometry (ZooMS) collagen fingerprinting for the species identification of archaeological bone fragments". In: *Zooarchaeology in Practice*. Springer, p. 227–247.

Buckley, M., Harvey, V. L., and Chamberlain, A. T. (2017). "Species identification and decay assessment of Late Pleistocene fragmentary vertebrate remains from Pin Hole Cave (Creswell Crags, UK) using collagen fingerprinting". *Boreas* 46 (3):402–411.

Buckley, M. and Collins, M. J. (2011). "Collagen survival and its use for species identification in Holocene-lower Pleistocene bone fragments from British archaeological and paleontological sites". *Antiqua* 1 (1):e1–e1.

Buckley, M., Kansa, S. W., Howard, S., Campbell, S., Thomas-Oates, J., and Collins, M. (2010). "Distinguishing between archaeological sheep and goat bones using a single collagen peptide". *Journal of Archaeological Science* 37 (1):13–20.

Byrne, R., Martiniano, R., Cassidy, L., Carrigan, M., Hellenthal, G., Hardiman, O., Bradley, D., and McLaughlin, R. (2018). "Insular celtic population structure and genomic footprints of migration". *PLoS Genetics* 14 (1):e1007152.

Carter, T., Contreras, D. A., Doyle, S., Mihailović, D., and Skarpelis, N. (2016). "Early Holocene interaction in the Aegean Islands: mesolithic chert exploitation at Stélida (Naxos, Greece) in context". *Géoarchéologie des Îles de Méditerranée. CNRS éditions, Paris*:275–286.

Cassidy, L., Martiniano, R., Murphy, E., Teasdale, M., Mallory, J., Hartwell, B., and Bradley, D. (2016). "Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome". *Proceedings of the National Academy of Sciences of the United States of America* 113 (2):368–373.

Castleden, R. (2005). *The Mycenaeans*. Routledge.

Catalano, G., Vetro, D. L., Fabbri, P. F., Mallick, S., Reich, D., Rohland, N., Sineo, L., Mathieson, I., and Martini, F. (2020). "Late Upper Palaeolithic hunter-gatherers in the Central Mediterranean: new archaeological and genetic data from the Late Epigravettian burial Oriente C (Favignana, Sicily)". *Quaternary International* 537:24–32.

Chamberlain, A. (1999). "Carsington Pasture Cave, Brassington, Derbyshire: a prehistoric burial site." *Capra* 1.

Chappell, E. and Allender, S. (2018). "Site Investigations of the necropolis and Its Environs: The Search for the Town":111.

Charlton, S., Booth, T., and Barnes, I. (2019). "The problem with petrous? A consideration of the potential biases in the utilization of pars petrosa for ancient DNA analysis". *World Archaeology*:1–12.

Chilvers, E. R., Bouwman, A. S., Brown, K. A., Arnott, R. G., Prag, A. J. N., and Brown, T. A. (2008). "Ancient DNA in human bones from Neolithic and Bronze Age sites in Greece and Crete". *Journal of Archaeological Science* 35 (10):2707–2714.

Cleary, S. E. (2009). "Roman Britain: civil and rural society". In: *The Archaeology of Britain: An Introduction from Earliest Times to the Twenty-First Century*. Routledge, p. 216–236.

Cole, G., Ditchfield, P., Dulias, K., Edwards, C., Reynolds, A., and Waldron, T. (2020). "Summary justice or the Kings will?: The first case of formal facial mutilation from Anglo-Saxon England". *Antiquity* 94:1263–1277.

Consortium, G. P. (2015). "A global reference for human genetic variation". *Nature* 526 (7571):68–74.

Consortium, I. H. G. S. (2001). "Initial sequencing and analysis of the human genome". *Nature* 409:860–921.

Consortium, Y. C. (2002). "A nomenclature system for the tree of human Y-chromosomal binary haplogroups". *Genome research* 12 (2):339–348.

Cosmopoulos, M., Allen, S. E., Riebe, D. J., Ruscillo, D., and Liston, M. (2019). "New accelerator mass spectrometry 14C dates from the Mycenaean site of Iklaina". *Journal of Archaeological Science: Reports* 24:888–899.

Costa, M. D., Pereira, J. B., Pala, M., Fernandes, V., Olivieri, A., Achilli, A., Perego, U. A., Rychkov, S., Naumova, O., Hatina, J., Woodward, S. R., Khong Eng, K., Macaulay, V., Carr, M., Soares, P., Pereira, L., and Richards, M. B. (2013). "A substantial prehistoric European ancestry amongst Ashkenazi maternal lineages". *Nature communications* 4 (1):1–10.

Cummings, V. (2017). *The Neolithic of Britain and Ireland*. Taylor & Francis.

Czebreszuk, J. (2004a). "Bell Beakers from west to east". In: *Ancient Europe, 8000 BC to AD 1000: An Encyclopedia of the Barbarian World*. Ed. by P. Bogucki and P. Crabtree. Thomson Gale, p. 476–485.

Czebreszuk, J. (2004b). "Corded Ware from east to west". In: *Ancient Europe, 8000 BC to AD 1000: An Encyclopedia of the Barbarian World*. Ed. by P. Bogucki and P. Crabtree. Thomson Gale, p. 467–475.

Dabney, J., Meyer, M., and Pääbo, S. (2013). "Ancient DNA damage". *Cold Spring Harbor Perspectives in Biology* 5 (7):a012567.

Day, J. (2014). "Crete, Archaeology of". *Encyclopedia of Global Archaeology*:1738–1753.

De Fanti, S., Barbieri, C., Sarno, S., Sevini, F., Vianello, D., Tamm, E., Metspalu, E., Van Oven, M., Hübner, A., Sazzini, M., Franceschi, C., Pettener, D., and Luiselli, D. (2015). "Fine dissection of human mitochondrial DNA haplogroup HV lineages reveals Paleolithic signatures from European glacial refugia". *PloS one* 10 (12):e0144391.

DeNiro, M. J. (1985). "Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction". *Nature* 317 (6040):806–809.

Desmond, A., Barton, N., Bouzouggar, A., Douka, K., Fernandez, P., Humphrey, L., Morales, J., Turner, E., and Buckley, M. (2018). "ZooMS identification of bone tools from the North African Later Stone Age". *Journal of Archaeological Science* 98:149–157.

Devièse, T., Karavanić, I., Comeskey, D., Kubiak, C., Korlević, P., Hajdinjak, M., Radović, S., Procopio, N., Buckley, M., Pääbo, S., and Higham, T. (2017). "Direct dating of Neanderthal remains from the site of Vindija Cave and implications for the Middle to Upper Paleolithic transition". *Proceedings of the National Academy of Sciences* 114 (40):10606–10611.

Dotsika, E., Diamantopoulos, G., Lykoudis, S., Gougoura, S., Kranioti, E., Karalis, P., Michael, D., Samartzidou, E., and Palaigeorgiou, E. (2019). "Establishment of a Greek Food Database for Palaeodiet Reconstruction: Case Study of Human and Fauna Remains from Neolithic to Late Bronze Age from Greece". *Geosciences* 9 (4):165.

Douka, K., Efstratiou, N., Hald, M. M., Henriksen, P. S., and Karetsou, A. (2017). "Dating Knossos and the arrival of the earliest Neolithic in the southern Aegean". *antiquity* 91 (356):304–321.

Drineas, P., Tsetsos, F., Plantinga, A., Lazaridis, I., Yannaki, E., Razou, A., Kanaki, K., Michalodimitrakis, M., Perez-Jimenez, F., De Silvestro, G., Renda, M. C., Stamatoyannopoulos, J. A., Kidd, K. K., Browning, B. L., Paschou, P., and Stamatoyannopoulos, G. (2019). "Genetic history of the population of Crete". *Annals of human genetics*.

Driscoll, S. T. (2009). "Celtic Britain in The early Historic Period". In: *The Archaeology of Britain: An Introduction from Earliest Times to the Twenty-First Century*. Routledge, p. 219–241.

Duggan, A. T., Evans, B., Friedlaender, F. R., Friedlaender, J. S., Koki, G., Merriwether, D. A., Kayser, M., and Stoneking, M. (2014). "Maternal history of Oceania from complete mtDNA genomes: contrasting ancient diversity with recent homogenization due to the Austronesian expansion". *The American Journal of Human Genetics* 94 (5):721–733.

Dulias, K., Birch, S., Wilson, J. F., Justeau, P., Gandini, F., Flaquer, A., Soares, P., Richards, M. B., Pala, M., and Edwards, C. J. (2019). "Maternal relationships within an Iron Age burial at the High Pasture Cave, Isle of Skye, Scotland". *Journal of Archaeological Science* 110:104978.

Eckardt, H., Müldner, G., and Lewis, M. (2014). "People on the move in Roman Britain". *World Archaeology* 46 (4):534–550.

Efstratiou, N. (2013). "Knossos and the beginning of the Neolithic in Greece and the Aegean islands". *The Neolithic settlement of Knossos in Crete New Evidence for the Early Occupation of Crete and the Aegean Islands/N. Efstratiou, A. Karetsou, and M. Ntinou eds*:201–214.

Feldman, M., Fernández-Domínguez, E., Reynolds, L., Baird, D., Pearson, J., Hershkovitz, I., May, H., Goring-Morris, N., Benz, M., Gresky, J., Bianco, R. A., Fairbairn, A., Mustafaolu, G., Stockhammer, P. W., Posth, C., Haak, W., Jeong, C., and Krause, J. (2019). "Late Pleistocene human genome suggests a local origin for the first farmers of central Anatolia". *Nature communications* 10 (1):1–10.

Fernandes, D. M., Mittnik, A., Olalde, I., Lazaridis, I., Cheronet, O., Rohland, N., Mallick, S., Bernardos, R., Broomandkhoshbacht, N., Carlsson, J., Culleton, B. J., Ferry, M., Gamarra, B., Lari, M., Mah, M., Michel, M., Modi Alessandra Novak, M., Oppenheimer, J., Sirak, K. A., Stewardson, K., Mandl, K., Schattke, C., Özdoan, K. T., Lucci, M., Gasperetti, G., Candilio, F., Salis, G., Vai, S., Camarós, E., Calò, C., Catalano, G., Cueto, M., Forgia, V., Lozano, M., Marini, E., Micheletti, M., Miccichè, R. M., Palombo, M. R., Ramis, D., Schimmenti, V., Sureda, P., Teira, L., Teschler-Nicola, M., Kennett, D. J., Lalueza-Fox, C., Patterson, N., Sineo, L., Coppa, A., Caramelli, D., Pinhasi, R., and Reich, D. (2020). "The spread of steppe and Iranian-related ancestry in the islands of the western Mediterranean". *Nature ecology & evolution* 4 (3):334–345.

Fernandes, V., Alshamali, F., Alves, M., Costa, M. D., Pereira, J. B., Silva, N. M., Cherni, L., Harich, N., Cerny, V., Soares, P., Richards, M. B., and Pereira, L (2012). "The Arabian cradle: mitochondrial relicts of the first steps along the southern route out of Africa". *The American Journal of Human Genetics* 90 (2):347–355.

Fernandes, V., Triska, P., Pereira, J. B., Alshamali, F., Rito, T., Machado, A., Fajkošová, Z., Cavadas, B., Černỳ, V., Soares, P., Richards, M. B., and Pereira, L (2015). "Genetic stratigraphy of key demographic events in Arabia". *PloS one* 10 (3):e0118625.

Fernández-Domínguez, E. and Reynolds, L. (2017). "The Mesolithic-Neolithic transition in Europe: a perspective from ancient human DNA". In: *Times of Neolithic transition along the Western Mediterranean*. Springer, p. 311–338.

Fitzhugh, B. and Hunt, T. L. (1997). "Introduction: Islands as laboratories: Archaeological research in comparative perspective". *Human Ecology* 25 (3):379–383.

Fitzpatrick, A. (2013). "The arrival of the Bell Beaker set in Britain and Ireland":ed. by J. Koch and B. Cunliffe, 41–70.

Fitzpatrick, S. M. and Callaghan, R. T. (2013). "Estimating trajectories of colonisation to the Mariana Islands, western Pacific". *Antiquity* 87 (337):840–853.

Fregel, R., Méndez, F. L., Bokbot, Y., Martín-Socas, D., Camalich-Massieu, M. D., Santana, J., Morales, J., Ávila-Arcos, M. C., Underhill, P. A., Shapiro, B., Wojcik, G., Rasmussen, M., Soares, A. E. R., Kapp, J., Sockell, A., Rodríguez-Santos, F. J., Mikdad, A., Trujillo-Mederos, A., and D., B. C. (2018). "Ancient genomes from North Africa evidence prehistoric migrations to the Maghreb from both the Levant and Europe". *Proceedings of the National Academy of Sciences* 115 (26):6774–6779.

Friedlaender, J. S., Friedlaender, F. R., Hodgson, J. A., Stoltz, M., Koki, G., Horvat, G., Zhadanov, S., Schurr, T. G., and Merriwether, D. A. (2007). "Melanesian mtDNA complexity". *PloS one* 2 (2):e248.

Fu, Q., Posth, C., Hajdinjak, M., Petr, M., Mallick, S., Fernandes, D., Furtwängler, A., Haak, W., Meyer, M., Mittnik, A., Nickel, B., Peltzer, A., Rohland, N., Slon, V., Talamo, S., Lazaridis, I., Lipson, M., Mathieson, I., Schiffels, S., Skoglund, P., Derevianko, A., Drozdov, N., Slavinksy, V., Tsybankov, A., Cremonesi, R., Mallegni, F., Gély, B., Vacca, E., González Morales, M., Straus, L., Neugebauer-Maresch, C., Teschler-Nicola, M., Constantin, S., Moldovan, O., Benazzi, S., Peresani, M., Coppola, D., Lari, M., Ricci, S., Ronchitelli, A., Valentin, F., Thevenet, C., Wehrberger, K., Grigorescu, D., Rougier, H., Crevecoeur, I., Flas, D., Semal, P., Mannino, M., Cupillard, C., Bocherens, H., Conrad, N., Harvati, K., Moiseyev, V., Drucker, D., Svoboda, J., Richards, M., Caramelli, D., Pinhasi, R., Kelso, J., Patterson, N., Krause, J., Pääbo, S., and Reich, D. (2016). "The genetic history of Ice Age Europe". *Nature* 534 (7606):200–205.

Fu, Q., Hajdinjak, M., Moldovan, O. T., Constantin, S., Mallick, S., Skoglund, P., Patterson, N., Rohland, N., Lazaridis, I., Nickel, B., Viola, B., Prüfer, K., Meyer, M., Kelso, J., Reich, D., and Pääbo, S. (2015). "An early modern human from Romania with a recent Neanderthal ancestor". *Nature* 524 (7564):216–219.

Fu, Q., Li, H., Moorjani, P., Jay, F., Slepchenko, S. M., Bondarev, A. A., Johnson, P. L., Aximu-Petri, A., Prüfer, K., Filippo, C. de, Meyer, M., Zwyns, N., Salazar-García, D. C., Kuzmin, Y. V., Keates, S. G., Kosintsev, P. A., Razhev, D. I., Richards, M. P., Peristov, N. V., Lachmann, M., Douka, K., Higham, T. F. G., Slatkin, M., Hublin,

J.-J., Reich, D., Kelso, J., Viola, T. B., and Pääbo, S. (2014). "Genome sequence of a 45,000-year-old modern human from western Siberia". *Nature* 514 (7523):445–449.

Fulton, T. L. and Shapiro, B. (2019). "Setting up an ancient DNA laboratory". In: *Ancient DNA*. Springer, p. 1–13.

GADM (2020). URL: `https://gadm.org/data.html`. "(accessed 02-09-20)".

Gamba, C., Jones, E., Teasdale, M., McLaughlin, R., Gonzalez-Fortes, G., Mattiangeli, V., Domboróczki, L., Kővári, I., Pap, I., Anders, A., Whittle, A., Dani, J., Raczky, P., Higham, T., Hofreiter, M., Bradley, D., and Pinhasi, R. (2014). "Genome flux and stasis in a five millennium transect of European prehistory". *Nature Communications* 5:5257.

Gandini, F., Achilli, A., Pala, M., Bodner, M., Brandini, S., Huber, G., Egyed, B., Ferretti, L., Gómez-Carballa, A., Salas, A., Scozzari, R., Cruciani, F., Coppa, A., Parson, W., Semino, O., Soares, P., Torroni, A., Richards, M., and Olivieri, A. (2016). "Mapping human dispersals into the Horn of Africa from Arabian Ice Age refugia using mitogenomes". *Scientific Reports* 6:25472.

Gavashelishvili, A. and Tarkhnishvili, D. (2016). "Biomes and human distribution during the last ice age". *Global Ecology and Biogeography* 25 (5):563–574.

Gerbault, P., Liebert, A., Itan, Y., Powell, A., Currat, M., Burger, J., Swallow, D. M., and Thomas, M. G. (2011). "Evolution of lactase persistence: an example of human niche construction". *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (1566):863–877.

Gifford-Gonzalez, D. (2018). "Zooarchaeology and Ecology: Mortality Profiles, Species Abundance, Diversity". In: *An Introduction to Zooarchaeology*. Springer, p. 475–501.

Gilbert, E., OReilly, S., Merrigan, M., McGettigan, D., Vitart, V., Joshi, P. K., Clark, D. W., Campbell, H., Hayward, C., Ring, S. M., Golding, J., Goodfellow, S., Navarro, P., Kerr, S. M., Amador, C., Campbell, A., Haley, C. S., Porteous, D. J., Cavalleri, G. L., and Wilson, J. F. (2019). "The genetic landscape of Scotland and the Isles". *Proceedings of the National Academy of Sciences* 116 (38):19064–19070.

Gilbert, M. T. P., Barnes, I., Collins, M. J., Smith, C., Eklund, J., Goudsmit, J., Poinar, H., and Cooper, A. (2005). "Long-term survival of ancient DNA in Egypt: Response to Zink and Nerlich (2003)". *American journal of physical anthropology* 128 (1):110–114.

Giże, A. P. (2018a). "Geological Setting". In: *The Late Minoan III Necropolis of Armenoi: Volume 1: Introduction and Background*. Ed. by Tzedakis, Martlew, and Arnott. INSTAP Academic Press (Institute for Aegean Prehistory), p. 213–230.

— (2018b). "Proposed Method of Tomb Construction". In: *The Late Minoan III Necropolis of Armenoi: Volume 1: Introduction and Background*. Ed. by Tzedakis, Martlew, and Arnott. INSTAP Academic Press (Institute for Aegean Prehistory), p. 231–240.

Giże, A. P. (2018c). "Topographical Setting". In: *The Late Minoan III Necropolis of Armenoi: Volume 1: Introduction and Background*. Ed. by Tzedakis, Martlew, and Arnott. INSTAP Academic Press (Institute for Aegean Prehistory), p. 19–22.

Godart, L. (2018). "Armenoi, Western Crete, and the Linear B Tablets from Knossos". *The Late Minoan III Necropolis of Armenoi: Volume 1: Introduction and Background* 60:249.

González-Fortes, G., Jones, E. R., Lightfoot, E., Bonsall, C., Lazar, C., GrandaldAnglade, A., Garralda, M. D., Drak, L., Siska, V., Simalcsik, A., Boronean, A., Vidal Romaní, J. R., Vaqueiro Rodríguez, M., Arias, P., Pinhasi, R., Manica, A., and Hofreiter, M. (2017). "Paleogenomic evidence for multi-generational mixing between Neolithic farmers and Mesolithic hunter-gatherers in the Lower Danube Basin". *Current Biology* 27 (12):1801–1810.

Green, E. J. and Speller, C. F. (2017). "Novel substrates as sources of ancient DNA: prospects and hurdles". *Genes* 8 (7):180.

Guilaine, J. (2017). "The Neolithic transition: from the Eastern to the Western Mediterranean". In: *Times of Neolithic Transition along the Western Mediterranean*. Springer, p. 15–31.

Günther, T., Malmström, H., Svensson, E., Omrak, A., Sánchez-Quinto, F., Kılınç, G. M., Krzewińska, M., Eriksson, G., Fraser, M., Edlund, H., Munters, A. R., Coutinho, A., Simões, L. G., Vicente, M., Sjölander, A., Jansen Sellevold, B., Jørgensen, R., Claes, P., Shriver, M. D., Valdiosera, C., Netea, M. G., Apel, J., Lidén, K., Skar, B., Storå, J., Götherström, A., and Jakobsson, M. (2017). "Genomics of Mesolithic Scandinavia reveal colonization routes and high-latitude adaptation". *bioRxiv*:164400.

Günther, T. and Nettelblad, C. (2019). "The presence and impact of reference bias on population genomic studies of prehistoric human populations". *PLoS genetics* 15 (7):e1008302.

Haak, W., Balanovsky, O., Sanchez, J., Koshel, S., Zaporozhchenko, V., Adler, C., Der Sarkissian, C., Brandt, G., Schwarz, C., Nicklisch, N., Dresely, V., Fritsch, B., Balanovska, E., Villems, R., Meller, H., Alt, K., Cooper, A., and the Genographic Consortium (2010). "Ancient DNA from European Early Neolithic farmers reveals their Near Eastern affinities". *PLoS Biology* 8 (11):e1000536.

Haak, W., Lazaridis, I., Patterson, N., Rohland, N., Mallick, S., Llamas, B., Brandt, G., Nordenfelt, S., Harney, E., Stewardson, K., Fu, Q., Mittnik, A., Bánffy, E., Economou, C., Francken, M., Friederich, S., Pena, R., Hallgren, F., Khartanovich, V., Khokhlov, A., Kunst, M., Kuznetsov, P., Meller, H., Mochalov, O., Moiseyev, V., Nicklisch, N., Pichler, S., Risch, R., Rojo Guerra, M., Roth, C., Szécsényi-Nagy, A., Wahl, J., Meyer, M., Krause, J., Brown, D., Anthony, D., Cooper, A., Alt, K., and Reich, D. (2015).

"Massive migration from the steppe was a source for Indo-European languages in Europe". *Nature* 522 (7555):207–211.

Haber, M., Jones, A. L., Connell, B. A., Arciero, E., Yang, H., Thomas, M. G., Xue, Y., and Tyler-Smith, C. (2019). "A Rare Deep-Rooting D0 African Y-Chromosomal Haplogroup and Its Implications for the Expansion of Modern Humans Out of Africa". *Genetics* 212 (4):1421–1428.

Hagelberg, E., Hofreiter, M., and Keyser, C. (2015). *Ancient DNA: the first three decades*.

Hallager, E. (2010). "Crete". In: *The Oxford Handbook of the Bronze Age Aegean*.

Hansen, H., de Barros Damgaard, P., Margaryan, A., Stenderup, J., Lynnerup, N., Willerslev, E., and Allentoft, M. (2017). "Comparing ancient DNA preservation in petrous bone and tooth cementum". *PloS One* 12 (1):e0170940.

Hanson, D. B. (1989). *The skeletal biology of prehistoric human mortuary remains from the Duty Free Site, Garapan Village, Saipan*. Micronesian Archaeological Survey, Division of Historic Preservation

Hardy, B. L., Raff, R. A., and Raman, V. (1997). "Recovery of mammalian DNA from Middle Paleolithic stone tools". *Journal of Archaeological Science* 24 (7):601–611.

Härke, H (2003). "Population replacement or acculturation? An archaeological perspective on population and migration in post-Roman Britain". In: *The Celtic Englishes III*. Ed. by H. Tristram. Winter.

Harney, É., Patterson, N., Reich, D., and Wakeley, J. (2021). "Assessing the Performance of qpAdm: A Statistical Tool for Studying Population Admixture". *Genetics*.

Harrison, T., Krigbaum, J., and Manser, J. (2006). "Primate biogeography and ecology on the Sunda Shelf Islands: a paleontological and zooarchaeological perspective". In: *Primate biogeography*. Springer, p. 331–372.

Harvati, K., Röding, C., Bosman, A. M., Karakostis, F. A., Grün, R., Stringer, C., Karkanas, P., Thompson, N. C., Koutoulidis, V., Moulopoulos, L. A., Gorgoulis, V. G., and Kouloukoussa, M. (2019). "Apidima Cave fossils provide earliest evidence of Homo sapiens in Eurasia". *Nature* 571 (7766):500–504.

Haselgrove, C. (2009). "The iron age". In: *The Archaeology of Britain: An Introduction from Earliest Times to the Twenty-First Century*. Routledge, p. 167–192.

Haughton, C. and Powlesland, D. (1999a). "West Heslerton The Anglian Cemetery. Catalogue of the Anglian Graves and Associated Assemblages". In: vol. 2. English Heritage.

— (1999b). "West Heslerton The Anglian Cemetery. The Excavation and Discussion of the Evidence". In: vol. 1. English Heritage.

Heintzman, P. D., Soares, A. E., Chang, D., and Shapiro, B. (2015). "Paleogenomics". *Reviews in Cell Biology and Molecular Medicine* 1 (3):243–267.

Herrera, R. J. and Garcia-Bertrand, R. (2018). *Ancestral DNA, human origins, and migrations*. Academic Press.

Herzfeld, M. (2003). "Localism and the logic of nationalistic folklore: Cretan reflections". *Comparative Studies in Society and History* 45 (2):281–310.

Heyd, V., Harding, A, and Fokkens, H (2013). "Europe 2500 to 2200 BC: Between Expiring Ideologies and Emerging Complexity". *The Oxford Handbook of the European Bronze Age*:47–67.

Higgins, R. A. and Morgan, L. (1967). *Minoan and Mycenaean art*. Thames and Hudson London.

Hill, C., Soares, P., Mormina, M., Macaulay, V., Clarke, D., Blumbach, P. B., Vizuete-Forster, M., Forster, P., Bulbeck, D., Oppenheimer, S., and B, R. M. (2007). "A mitochondrial stratigraphy for island southeast Asia". *The American Journal of Human Genetics* 80 (1):29–43.

Hills, C. (2009). "Anglo-Saxon DNA". In: *Mortuary Practices and Social Identities in the Middle Ages: Essays in Burial Archaeology in Honour of Heinrich Härke*. Ed. by Sayer and Williams. University of Exeter Press, p. 123–40.

Historic Environment Scotland (2018). *Links of Noltland, Statement of Significance*. Tech. rep.

Hjardar, K. and Vike, V. (2016). *Vikings at War*. Casemate.

Hofmanová, Z., Kreutzer, S., Hellenthal, G., Sell, C., Diekmann, Y., Díez-del-Molino, D., van Dorp, L., López, S., Kousathanas, A., Link, V., Kirsanow, K., Cassidy, L., Martiniano, R., Strobel, M., Scheu, A., Kotsakis, K., Halstead, P., Triantaphyllou, S., Kyparissi-Apostolika, N., Urem-Kotsou, D., Ziota, C., Adaktylou, F., Gopalan, S., Bobo, D., Winkelbach, L., Blöcher, J., Unterländer, M., Leuenberger, C., Çilingiroğlu, Ç., Horejs, B., Gerritsen, F., Shennan, S., Bradley, D., Currat, M., Veeramah, K., Wegmann, D., Thomas, M., Papageorgopoulou, C., and Burger, J. (2016). "Early farmers from across Europe directly descended from Neolithic Aegeans". *Proceedings of the National Academy of Sciences of the United States of America* 113 (25):6886–6891.

Hofreiter, M., Paijmans, J. L., Goodchild, H., Speller, C. F., Barlow, A., Fortes, G. G., Thomas, J. A., Ludwig, A., and Collins, M. J. (2015). "The future of ancient DNA: Technical advances and conceptual shifts". *BioEssays* 37 (3):284–293.

Homer, O. (1996). "trans. Robert Fagles". *New York: Penguin* 4:432–35.

Horwitz, L. K. (2013). "The earliest settlement on Crete: an archaeozoological perspective". *The Neolithic settlement of Knossos in Crete. New evidence for the early occupation of Crete and the Aegean Islands*:171–92.

Hughey, J. R., Paschou, P., Drineas, P., Mastropaolo, D., Lotakis, D. M., Navas, P. A., Michalodimitrakis, M., Stamatoyannopoulos, J. A., and Stamatoyannopoulos, G.

(2013). "A European population in Minoan Bronze Age Crete". *Nature Communications* 4:1861.

Hung, H.-c., Carson, M. T., Bellwood, P., Campos, F. Z., Piper, P. J., Dizon, E., Bolunia, M. J. L. A., Oxenham, M., and Chi, Z. (2011). "The first settlement of Remote Oceania: the Philippines to the Marianas". *Antiquity* 85 (329):909–926.

Iezzi, C. A. (2015). "Existence and subsistence in Mycenaean-era East Lokris: The isotopic evidence". *Hesperia Supplements* 49:89–104.

Irving-Pease, E. K., Frantz, L. A., Sykes, N., Callou, C., and Larson, G. (2018). "Rabbits and the specious origins of domestication". *Trends in ecology & evolution* 33 (3):149–152.

Irwin, J., Saunier, J., Strouss, K., Paintner, C., Diegoli, T., Sturk, K., Kovatsi, L., Brandstätter, A., Cariolou, M. A., Parson, W., and Parsons, T. J. (2008). "Mitochondrial control region sequences from northern Greece and Greek Cypriots". *International journal of legal medicine* 122 (1):87–89.

ISOGG. *Y-DNA project help*. URL: `https://isogg.org/wiki/Y-DNA_project_help#Nomenclature_System_.28YCC.29`. (accessed: 11.04.2020).

Jakobsson, T. G. and Mattias (2019). "Population Genomic Analyses of DNA from Ancient Remains". *Handbook of Statistical Genomics 4e 2V SET*:295–40.

Jobling, M., Hollox, E, Hurles, M, Kivisild, T, and Tyler-Smith, C (2014). "Human Evolutionary Genetics. 2nd". *Garland Science*.

Jobling, M. A. (2012). "The impact of recent events on human genetic diversity". *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1590):793–799.

Jobling, M. A. and Tyler-Smith, C. (2017). "Human Y-chromosome variation in the genome-sequencing era". *Nature Reviews Genetics* 18 (8):485.

Jones, E., Gonzalez-Fortes, G., Connell, S., Siska, V., Eriksson, A., Martiniano, R., McLaughlin, R., Llorente, M., Cassidy, L., Gamba, C., Meshveliani, T., Bar-Yosef, O., Müller, W., Belfer-Cohen, A., Matskevich, Z., Jakeli, N., Higham, T., Currat, M., Lordkipanidze, D., Hofreiter, M., Manica, A., Pinhasi, R., and Bradley, D. (2015). "Upper Palaeolithic genomes reveal deep roots of modern Eurasians". *Nature Communications* 6:8912.

Jones, J. R., Marín-Arroyo, A. B., Straus, L. G., and Richards, M. P. (2020). "Adaptability, resilience and environmental buffering in European Refugia during the Late Pleistocene: Insights from La Riera cave (Asturias, cantabria, Spain)". *Scientific Reports* 10 (1):1–17.

Jones, O. A., Plicht, J. van der, Papazoglou-Manioudaki, L., and Petropoulos, M. (2017). "Timing is everything: radiocarbon dating multiple levels in the Mycenaean tholos tomb of Petroto, Achaia, Greece". *STAR: Science & Technology of Archaeological Research* 3 (2):456–465.

Jones, W (1918). *Pausanias. Pausanias Description of Greece with an English translation in 4 Volumes*.

Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P., and Orlando, L. (2013). "mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters". *Bioinformatics* 29 (13):1682–1684.

Jun, G., Flickinger, M., Hetrick, K. N., Romm, J. M., Doheny, K. F., Abecasis, G. R., Boehnke, M., and Kang, H. M. (2012). "Detecting and estimating contamination of human DNA samples in sequencing and array-based genotype data". *The American Journal of Human Genetics* 91 (5):839–848.

Kadrow, S. (2016). "Exchange of People, Ideas and ings between Cucuteni Trypillian Complex and Areas of South-Eastern Poland". In: *Cucuteni Culture within the European Neo-Eneolithic Context. Proceedings of the International Colloquium Cucuteni 130. 1517 October 2014, Piatra-Neam, Romania. In Memoriam Dan Monah. In Memoriam Gheorghe Dumitroaia*. Bibliotheca Memoriae Antiquitatis, p. 649–677.

Karafet, T. M., Mendez, F. L., Meilerman, M. B., Underhill, P. A., Zegura, S. L., and Hammer, M. F. (2008). "New binary polymorphisms reshape and increase resolution of the human Y chromosomal haplogroup tree". *Genome research* 18 (5):830–838.

Karmin, M., Saag, L., Vicente, M., Sayres, M. A. W., Järve, M., Talas, U. G., Rootsi, S., Ilumäe, A.-M., Mägi, R., Mitt, M., Pagani, L., Puurand, T., Faltyskova, Z., Clemente, F., Cardona, A., Metspalu, E., Sahakyan, H., Yunusbayev, B., Hudjashov, G., DeGiorgio, M., Loogväli, E., Eichstaedt, C., Eelmets, M., Chaubey, G., Tambets, K., Litvinov, S., Mormina, M., Xue, Y., Ayub, Q., Zoraqi, G., Korneliussen, T., Akhatova, F., Lachance, J., Tishkoff, S., Momynaliev, K., Ricaut, F., Kusuma, P., Razafindrazaka, H., Pierron, D., Cox, M., Sultana, G., Willerslev, R., Muller, C., Westaway, M., Lambert, D., Skaro, V., Kovaevi, L., Turdikulova, S., Dalimova, D., Khusainova, R., Trofimova, N., Akhmetova, V., Khidiyatova, I., Lichman, D., Isakova, J., Pocheshkhova, E., Sabitov, Z., Barashkov, N., Nymadawa, P., Mihailov, E., Seng, J., Evseeva, I., A., M., Abdullah, S., Andriadze, G., D., P., Atramentova, L., Utevska, O., Yepiskoposyan, L., Marjanovi, D., Kushniarevich, A., and Behar, D. (2015). "A recent bottleneck of Y chromosome diversity coincides with a global change in culture". *Genome research* 25 (4):459–466.

Katsianis, M., Bevan, A., Styliaras, G., and Maniatis, Y. (2020). "An Aegean History and Archaeology Written through Radiocarbon Dates". *Journal of Open Archaeology Data* 8 (1).

Kendall, C., Eriksen, A. M. H., Kontopoulos, I., Collins, M. J., and Turner-Walker, G. (2018). "Diagenesis of archaeological bone and tooth". *Palaeogeography, Palaeoclimatology, Palaeoecology* 491:21–37.

Kienlin, T. L. (2013). "Copper and bronze: Bronze Age metalworking in context". In: *The Oxford Handbook of the European Bronze Age*.

King, R., Özcan, S., Carter, T, Kalfoğlu, E, Atasoy, S, Triantaphyllidis, C, Kouvatsi, A, Lin, A., Chow, C.-E., Zhivotovsky, L., Michalodimitrakis, M, and Underhill, P. A. (2008). "Differential Y-chromosome Anatolian influences on the Greek and Cretan Neolithic". *Annals of human genetics* 72 (2):205–214.

Kistler, L., Ware, R., Smith, O., Collins, M., and Allaby, R. G. (2017). "A new model for ancient DNA decay based on paleogenomic meta-analysis". *Nucleic Acids Research* 45 (11):6310–6320.

Kivisild, T. (2015). "Maternal ancestry and population history from whole mitochondrial genomes". *Investigative genetics* 6 (1):3.

Ko, A. M.-S., Chen, C.-Y., Fu, Q., Delfin, F., Li, M., Chiu, H.-L., Stoneking, M., and Ko, Y.-C. (2014). "Early Austronesians: into and out of Taiwan". *The American Journal of Human Genetics* 94 (3):426–436.

Kontopoulos, I. and Sampson, A. (2015). "Prehistoric diet on the island of Euboea, Greece: An isotopic investigation". *Mediterranean Archaeology and Archaeometry* 15 (3):97–111.

Kuhn, J. M. M., Jakobsson, M., and Günther, T. (2018). "Estimating genetic kin relationships in prehistoric populations". *PLoS One* 13 (4):e0195491.

Kushniarevich, A., Sivitskaya, L., Danilenko, N., Novogrodskii, T., Tsybovsky, I., Kiseleva, A., Kotova, S., Chaubey, G., Metspalu, E., Sahakyan, H., Bahmanimehr, A., Reidla, M., Rootsi, S., Parik, J., Reisberg, T., Achilli, A., Kashani, B. H., Gandini, F., Olivieri, A., Behar, D. M., Torroni, A., Davydenko, O., and Villems, R. (2013). "Uniparental genetic heritage of Belarusians: encounter of rare Middle Eastern matrilineages with a Central European mitochondrial DNA pool". *PloS one* 8 (6):e66499.

Lacan, M., Keyser, C., Ricaut, F.-X., Brucato, N., Duranthon, F., Guilaine, J., Crubézy, E., and Ludes, B. (2011). "Ancient DNA reveals male diffusion through the Neolithic Mediterranean route". *Proceedings of the National Academy of Sciences of the United States of America* 108 (24):9788–9791.

Ladle, L. (2018). "Interpretation and discussion". In: *Multi-Period Occupation at Football Field, Worth Matravers, Dorset 2006-2011, Bar Monograph (British Series)*. Ed. by L. Ladle. Chap. 16.

Ladle, L. and Morgan, A. (2012). *Worth Matravers Archaeology Project*.

Lagia, A., Petroutsa, E, and Manolis, S (2007). "Health and Diet During the MBA in the Peloponnese: the site of Kouphovouno". *Cooking Up the Past: Food and Culinary Practices in the Neolithic and Bronze Age Aegean*:313–328.

Lamb, A. L., Evans, J. E., Buckley, R., and Appleby, J. (2014). "Multi-isotope analysis demonstrates significant lifestyle changes in King Richard III". *Journal of Archaeological Science* 50:559–565.

Lazaridis, I., Mittnik, A., Patterson, N., Mallick, S., Rohland, N., Pfrengle, S., Furtwängler, A., Peltzer, A., Posth, C., Vasilakis, A., McGeorge, P., Konsolaki-Yannopoulou, E., Korres, G., Martlew, H., Michaldimitrakis, M., Özsait, M., Özsait, N., Papathanasiou, A., Richards, M., Roodenberg, S., Tzedakis, Y., Arnott, R., Fernandes, D., Hughey, J., Lotakis, D., Navas, P., Maniatis, Y., Stamatoyannopoulos, J., Stewardson, K., Stockhammer, P., Pinhasi, R., Reich, D., Krause, J., and Stamatoyannopoulos, G. (2017). "Genetic origins of the Minoans and Mycenaeans". *Nature* 548 (7666):214.

Lazaridis, I., Nadel, D., Rollefson, G., Merrett, D., Rohland, N., Mallick, S., Fernandes, D., Novak, M., Gamarra, B., Sirak, K., Connell, S., Stewardson, K., Harney, E., Fu, Q., Gonzalez-Fortes, G., Jones, E., Roodenberg, S., Lengyel, G., Bocquentin, B., Monge, J., Gregg, M., Eshed, V., Mizrahi, A.-S., Meiklejohn, C., Gerritsen, F., Bejenaru, L., Blüher, M., Campbell, A., Cavalleri, G., Comas, D., Froguel, P., Gilbert, E., Kerr, S., Kovacs, P., Krause, J., McGettigan, D., Merrigan, M., Merriwether, D., O'Reilly, S., Richards, M., Semino, O., Shamoon-Pour, M., Stefanescu, G., Stumvoll, M., Tönjes, A., Torroni, A., Wilson, J., Yengo, L., Hovhannisyan, N., Patterson, N., Pinhasi, R., and Reich, D. (2016). "Genomic insights into the origin of farming in the ancient Near East". *Nature* 536 (7617):419–424.

Lazaridis, I., Patterson, N., Mittnik, A., Renaud, G., Mallick, S., Kirsanow, K., Sudmant, P., Schraiber, J., Castellano, S., Lipson, M., Berger, B., Economou, C., Bollongino, R., Fu, Q., Bos, K., Nordenfelt, S., Li, H., de Filippo, C., Prüfer, K., Sawyer, S., Posth, C., Haak, W., Hallgren, F., Fornander, E., Rohland, N., Delsate, D., Francken, M., Guinet, J.-M., Wahl, J., Ayodo, G., Babiker, H., Bailliet, G., Balanovska, E., Balanovsky, O., Barrantes, R., Bedoya, G., Ben-Ami, H., Bene, J., Berrada, F., Bravi, C., Brisighelli, F., Busby, G., Cali, F., Churnosov, M., Cole, D., Corach, D., Damba, L., van Driem, G., Dryomov, S., Dugoujon, J.-M., Fedorova, S., Gallego Romero, I., Gubina, M., Hammer, M., Henn, B., Hervig, T., Hodoglugil, U., Jha, A., Karachanak-Yankova, S., Khusainova, R., Khusnutdinova, E., Kittles, R., Kivisild, T., Klitz, W., Kučinskas, V., Kushniarevich, A., Laredj, L., Litvinov, S., Loukidis, T., Mahley, R., Melegh, B., Metspalu, E., Molina, J., Mountain, J., Näkkäläjärvi, K., Nesheva, D., Nyambo, T., Osipova, L., Parik, J., Platonov, F., Posukh, O., Romano, V., Rothhammer, F., Rudan, I., Ruizbakiev, R., Sahakyan, H., Sajantila, A., Salas, A., Starikovskaya, E., Tarekegn, A., Toncheva, D., Turdikulova, S., Uktveryte, I., Utevska, O., Vasquez, R., Villena, M., Voevoda, M., Winkler, C., Yepiskoposyan, L., Zalloua, P., Zemunik, T., Cooper, A., Capelli, C., Thomas, M., Ruiz-Linares, A., Tishkoff, S., Singh, L., Thangaraj, K., Villems, R., Comas, D., Sukernik, R., Metspalu,

M., Meyer, M., Eichler, E., Burger, J., Slatkin, M., Pääbo, S., Kelso, J., Reich, D., and Krause, J. (2014). "Ancient human genomes suggest three ancestral populations for present-day Europeans". *Nature* 513 (7518):409.

Leach, S., Eckardt, H., Chenery, C., Müldner, G., and Lewis, M. (2010). "A Lady of York: migration, ethnicity and identity in Roman Britain". *Antiquity* 84 (323):131–145.

Leach, S., Lewis, M., Chenery, C., Müldner, G., and Eckardt, H. (2009). "Migration and diversity in Roman Britain: a multidisciplinary approach to the identification of immigrants in Roman York, England". *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 140 (3):546–561.

Legarra Herrero, B. (2009). "The Minoan fallacy: cultural diversity and mortuary behaviour on Crete at the beginning of the Bronze Age". *Oxford Journal of Archaeology* 28 (1):29–57.

Lelong, O. (2019). *Excavations at Milla Skerra Sandwick, Unst: Rythmns of Life in Iron Age Shetland*. Oxbow Books.

Lemey, P., Salemi, M., and Vandamme, A.-M. (2009). *The phylogenetic handbook: a practical approach to phylogenetic analysis and hypothesis testing*. Cambridge University Press.

Leslie, S., Winney, B., Hellenthal, G., Davison, D., Boumertit, A., Day, T., Hutnik, K., Royrvik, E., Cunliffe, B., Wellcome Trust Case Control Consortium, International Multiple Sclerosis Genetics Consortium, Lawson, D., Falush, D., Freeman, C., Pirinen, M., Myers, S., Robinson, M., and Donnelly P. Bodmer, W. (2015). "The fine-scale genetic structure of the British population". *Nature* 519 (7543):309–314.

Li, H. and Durbin, R. (2009). "Fast and accurate short read alignment with Burrows–Wheeler transform". *Bioinformatics* 25 (14):1754–1760.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R., and 1000 Genome Project Data Processing Subgroup (2009). "The sequence alignment/map format and SAMtools". *Bioinformatics* 25 (16):2078–2079.

Lillie, M. (2004). "Late Neolithic/Copper Age Eastern Europe". In: *Ancient Europe, 8000 BC to AD 1000: An Encyclopedia of the Barbarian World*. Ed. by P. Bogucki and P. Crabtree. Thomson Gale, p. 354–363.

Linderholm, A. (2015). "Ancient DNA: the next generation–chapter and verse". *Biological journal of the Linnean society* 117 (1):150–160.

Lindqvist, C. and Rajora, O. P. (2019). *Paleogenomics: Genome-Scale Analysis of Ancient DNA*. Springer.

Lipson, M., Szécsényi-Nagy, A., Mallick, S., Pósa, A., Stégmár, B., Keerl, V., Rohland, N., Stewardson, K., Ferry, M., Michel, M., Oppenheimer, J., Broomandkhoshbacht, N., Harney, E., Nordenfelt, S., Llamas, B., Mende, B., Köhler, K., Oross, K., Bondár,

M., Marton, T., Osztás, A., Jakucs, J., Paluch, T., Horváth, F., Csengeri, P., Koós, J., Sebök, K., Anders, A., Raczky, P., Regenye, J., Barna, J., Fábián, S., Serlegi, G., Toldi, Z., Nagy, E., Dani, J., Molnár, E., Pálfi, G., Márk, L., Melegh, B., Bánfai, Z., Domboróczki, L., Fernández-Eraso, J., Mujika-Alustiza, J., Fernández, C., Echevarría, J., Bollongino, R., Orschiedt, J., Schierhold, K., Meller, H., Cooper, A., Burger, J., Bánffy, E., Alt, K., Lalueza-Fox, C., Haak, W., and Reich, D. (2017). "Parallel palaeogenomic transects reveal complex genetic history of early European farmers". *Nature* 551 (7680):368–372.

Lipson, M., Ribot, I., Mallick, S., Rohland, N., Olalde, I., Adamski, N., Broomandkhoshbacht, N., Lawson, A. M., López, S., Oppenheimer, J., Stewardson, K., Asombang, R. N., Bocherens, H., Bradman, N., Culleton, B. J., Cornelissen, E., Crevecoeur, I., Maret, P. de, Fomine, F. L. M., Lavachery, P., Mindzie, C. M., Orban, R., Sawchuk, E., Semal, P., Thomas, M. G., Van Neer, W., Veeramah Krishna R.and Kennett, D. J., Patterson, N., Hellenthal, G., Lalueza-Fox, C., MacEachern, S., Prendergast, M. E., and Reich, D. (2020). "Ancient West African foragers in the context of African population history". *Nature* 577 (7792):665–670.

Llorente, M. G., Jones, E. R., Eriksson, A, Siska, V, Arthur, K., Arthur, J., Curtis, M., Stock, J. T., Coltorti, M, Pieruccini, P, Stretton, S., Brock, F., Higham, T., Park, Y., Hofreiter, M., Bradley, D. G., Bhak, J., Pinhasi, R., and Manica, A. (2015). "Ancient Ethiopian genome reveals extensive Eurasian admixture in Eastern Africa". *Science* 350 (6262):820–822.

Lorenzen, E. D. and Willerslev, E. (2010). "King Tutankhamuns family and demise". *Jama* 303 (24):2471–2475.

Lumley, M.-A. de, Guipert, G., Lumley, H. de, Protopapa, N., and Pitsios, T. (2020). "Apidima 1 and Apidima 2: Two anteneandertal skulls in the Peloponnese, Greece". *L'Anthropologie*:102743.

Lupack, S. (2010). "Minoan religion". *The Oxford Handbook of the Bronze Age Aegean (ca. 3000–1000 BC)*:251–62.

MacHugh, D., Edwards, C., Bailey, J., Bancroft, D., and Bradley, D. (2000). "The extraction and analysis of ancient DNA from bone and teeth: a survey of current methodologies". *Ancient Biomolecules* 3:81–102.

MacKinnon, M. (2010). "Sick as a dog: zooarchaeological evidence for pet dog health and welfare in the Roman world". *World Archaeology* 42 (2):290–309.

Mallick, S., Li, H., Lipson, M., Mathieson, I., Gymrek, M., Racimo, F., Zhao, M., Chennagiri, N., Nordenfelt, S., Tandon, A., Skoglund, P., Lazaridis, I., Sankararaman, S., Fu, Q., Rohland, N., Renaud, G., Erlich, Y., Willems, T., Gallo, C., Spence, J. P., Song, Y. S., Poletti, G., Balloux, F., Driem, G. van, Knijff, P. de, Gallego Romero, I., Jha,

A. R., Behar, D. M., Bravi, C. M., Capelli, C., Hervig, T., Moreno-Estrada, A., Posukh, O. L., Balanovska, E., Balanovsky, O., Karachanak-Yankova, S., Sahakyan, H., Toncheva, D., Yepiskoposyan, L., Tyler-Smith, C., Xue, Y., Abdullah, M. S., Ruiz-Linares, A., Beall, C. M., Di Rienzo, A., Jeong, C., Starikovskaya, E. B., Metspalu, E., Parik, J., Villems, R., Henn, B. M., Hodoglugil, U., Mahley, R., Sajantila, A., Stamatoyannopoulos, G., Wee, J. T. S., Khusainova, R., Khusnutdinova, E., Litvinov, S., Ayodo, G., Comas, D., Hammer, M. F., Kivisild, T., Klitz, W., Winkler, C. A., Labuda, D., Bamshad, M., Jorde, L. B., Tishkoff, S. A., Watkins, W. S., Metspalu, M., Dryomov, S., Sukernik, R., Singh, L., Thangaraj, K., Pääbo, S., Kelso, J., Patterson, N., and Reich, D. (2016). "The Simons genome diversity project: 300 genomes from 142 diverse populations". *Nature* 538 (7624):201–206.

Mamwell, C. J. (2018). "It rained a lot and nothing much happened: Settlement and society in Bronze Age Orkney".

Manning, S. W. and Cline, E. (2010). *Chronology and terminology*. Oxford University Press, New York.

Marciniak, S., Klunk, J., Devault, A., Enk, J., and Poinar, H. N. (2015). "Ancient human genomics: the methodology behind reconstructing evolutionary pathways". *Journal of human evolution* 79:21–34.

Marciniak, S. and Perry, G. H. (2017). "Harnessing ancient genomes to study the history of human adaptation". *Nature Reviews Genetics* 18 (11):659.

Margaryan, A., Lawson, D. J., Sikora, M., Racimo, F., Rasmussen, S., Moltke, I., Cassidy, L. M., Jørsboe, E., Ingason, A., Pedersen, M. W., Korneliussen, T., Wilhelmson, H., Bu, M. M., Barros Damgaard, P., Martiniano, R., Renaud, G., Bhérer, C., Moreno-Mayar, J. V., Fotakis, A. K., Allen, M., Allmäe, R., Molak, M., Cappellini, E., Scorrano, G., McColl, H., Buzhilova, A., Fox, A., Albrechtsen, A., Schütz, B., Skar, B., Arcini, C., Falys, C., Jonson, C. H., Baszczyk, D., Pezhemsky, D., Turner-Walker, G., Gestsdóttir, H., Lundstrøm, I., Gustin, I., Mainland, I., Potekhina, I., Muntoni, I. M., Cheng, J., Stenderup, J., Ma, J., Gibson, J., Peets, J., Gustafsson, J., Iversen, K. H., Simpson, L., Strand, L., Loe, L., Sikora, M., Florek, M., Vretemark, M., Redknap, M., Bajka, M., Pushkina, T., Søvsø, M., Grigoreva, N., Christensen, T., Kastholm, O., Uldum, O., Favia, P., Holck, P., Sten, S., Arge, S. V., Ellingvåg, S., Moiseyev, V., Bogdanowicz, W., Magnusson, Y., Orlando, L., Pentz, P., Jessen, M. D., Pedersen, A., Collard, M., Bradley, D. G., Jørkov, M. L., Arneborg, J., Lynnerup, N., Price, N., Gilbert, M. T. P., Allentoft, M. E., Bill, J., Sindbæk, S. M., Hedeager, L., Kristiansen, K., Nielsen, R., Werge, T., and Willerslev, E. (2020). "Population genomics of the Viking world". *Nature* 585 (7825):390–396.

Martin, M. (2011). "Cutadapt removes adapter sequences from high-throughput sequencing reads". *EMBnet. Journal Bioinformatics in Action* 17 (1):pp–10.

Martin, T. R. (2013). *Ancient Greece: from prehistoric to Hellenistic times*. Yale University Press.

Martinez, L., Mirabal, S., Luis, J. R., and Herrera, R. J. (2008). "Middle Eastern and European mtDNA lineages characterize populations from eastern Crete". *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 137 (2):213–223.

Martinez, L., Underhill, P. A., Zhivotovsky, L. A., Gayden, T., Moschonas, N. K., Chow, C.-E. T., Conti, S., Mamolini, E., Cavalli-Sforza, L. L., and Herrera, R. J. (2007). "Paleolithic Y-haplogroup heritage predominates in a Cretan highland plateau". *European Journal of Human Genetics* 15 (4):485.

Martiniano, R., Caffell, A., Holst, M., Hunter-Mann, K., Montgomery, J., Müldner, G., McLaughlin, R., Teasdale, M., Van Rheenen, W., Veldink, J., van den Berg, L., Hardiman, O., Carroll, M., Roskams, S., Oxley, J., Morgan, C., Thomas, M., Barnes, I., McDonnell, C., Collins, M., and Bradley, D. (2016). "Genomic signals of migration and continuity in Britain before the Anglo-Saxons". *Nature Communications* 7:10326.

Martiniano, R., Coelho, C., Ferreira, M., Neves, M., Pinhasi, R., and Bradley, D. (2014). "Genetic evidence of African slavery at the beginning of the trans-Atlantic slave trade". *Scientific Reports* 4:5994.

Mathieson, I., Alpaslan-Roodenberg, S., Posth, C., Szécsényi-Nagy, A., Rohland, N., Mallick, S., Olalde, I., Broomandkhoshbacht, N., Candilio, F., Cheronet, O., Fernandes, D., Ferry, M., Gamarra, B., Fortes, G., Haak, W., Harney, E., Jones, E., Keating, D., Krause-Kyora, B., Kucukkalipci, I., Michel, M., Mittnik, A., Nägele, K., Novak, M., Oppenheimer, J., Patterson, N., Pfrengele, S., Sirak, K., Stewardson, K., Vai, S., Alexandrov, S., Alt, K., Andreescu, R., Antonović, D., Ash, A., Atanassova, N., Bacvarov, K., Gusztáv, M., Bocherens, H., Bolus, M., Boroneanţ, A., Boyadzhiev, Y., Budnik, A., Burmaz, J., Chohadzhiev, S., Conrad, N., Cottiaux, R., Čuka, M., Cupillard, C., Drucker, D., Elenski, N., Francken, M., Galabova, B., Ganetsovski, G., Gély, B., Hajdu, T., Handzhyiska, V., Harvati, K., Higham, T., Iliev, S., Janković, I., Karavanić I. Kennett, D., Komšo, D., Kozak, A., Labuda, D., Lari, M., Lazar, C., Leppek, M., Leshtakov, K., Lo Vetro, D., Los, D., Lozanov, I., Malina, M., Martini, F., McSweeney, K., Meller, H., Men

ušić, M., Mirea, P., Moiseyev, V., Petrova, V., Price, T., Simalcsik, A., Sineo, L., Šlaus, M., Slavchev, V., Stanev, P., Starović, A., Szeniczey, T., Talamo, S., Teschler-Nicola, M., Thevenet, C., Valchev, I., Valentin, F., Vasilyev, S., Veljanovska, F., Venelinova, S., Veselovskaya, E., Viola, B., Virag, C., Zaninović, J., Zäuner, S., Stockhammer, P., Catalano, G., Krauß, R., Caramelli, D., Zariņa, G., Gaydarska, B., Lillie, M., Niktin, A., Potekhina, I., Papathanasiou, A., Borić, D., Bonsall, C., Krause, J., Pinhasi, R.,

and Reich, D. (2018). "The genomic history of southeastern Europe". *Nature* 555 (7695):197–203.

Mathieson, I., Lazaridis, I., Rohland, N., Mallick, S., Patterson, N., Roodenberg, S., Harney, E., Stewardson, K., Fernandes, D., Novak, M., Sirak, K., Gamba, C., Jones, E., Llamas, B., Dryomov, S., Pickrell, J., Arsuaga, J., Bermúdez de Castro, J., Carbonell, E., Gerritsen, F., Khokhlov, A., Kuznetsov, P., Lozano, M., Meller, H., Mochalov, O., Moiseyev, V., Rojo Guerra, M., Roodenberg, J., Vergès, J., Krause, J., Cooper, A., Alt, K., Brown, D., Anthony, D., Lalueza-Fox, C., Haak, W., Pinhasi, R., and Reich, D. (2015). "Genome-wide patterns of selection in 230 ancient Eurasians". *Nature* 528 (7583):499.

Matisoo-Smith, E. (2015). "Ancient DNA and the human settlement of the Pacific: A review". *Journal of Human Evolution* 79:93–104.

Mays, S. (2010). *The archaeology of human bones*. Routledge.

McEnroe, J. C. (2010). *Architecture of Minoan Crete: constructing identity in the Aegean Bronze age*. University of Texas Press.

McGeorge, P. J. (1983). "The Minoans: demography, physical variations and affinities". PhD thesis. University of London.

McGovern-Wilson, R. and Quinn, C. (1996). "Stable isotope analysis of ten individuals from Afetna, Saipan, Northern Mariana Islands". *Journal of Archaeological Science* 23 (1):59–65.

McGrath, K., Rowsell, K., St-Pierre, C. G., Tedder, A., Foody, M. G. B., Roberts, C., Speller, C., and Collins, M. (2019). "identifying Archaeological Bone via non-Destructive ZooMS and the Materiality of Symbolic expression: examples from iroquoian Bone points". *Scientific reports* 9 (1):11027.

McKenna, A., Hanna, M., Banks, E., Sivachenko, A., Cibulskis, K., Kernytsky, A., Garimella, K., Altshuler, D., Gabriel, S., Daly, M., and DePristo, M (2010). "The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data". *Genome research* 20 (9):1297–1303.

McKenzie, J. (2018). "Sacred to the Soil: Micromorphology, Geoarchaeology, and the Bioarchaeology of Ritual and Religion, with Reference to the Iron Age Site of High Pasture Cave, Scotland". In: *The Bioarchaeology of Ritual and Religion*. Ed. by A. Livarda, R. Madgwick, and S. Riera Mora. Oxbow Books Oxford.

McNeal, R. (1973). "The Legacy of Arthur Evans". *California Studies in Classical Antiquity* 6:205–220.

Mee, C. (2010). "Death and burial". *The Oxford Handbook of the Bronze Age Aegean*:277–90.

Meyer, M. and Kircher, M. (2010). "Illumina sequencing library preparation for highly multiplexed target capture and sequencing". *Cold Spring Harbor Protocols* 2010 (6).

Mittnik, A., Massy, K., Knipper, C., Wittenborn, F., Friedrich, R., Pfrengle, S., Burri, M., Carlichi-Witjes, N., Deeg, H., Furtwängler, A., Harbeck, M., Heyking, K. von, Kociumaka, C., Kucukkalipci, I., Lindauer, S., Metz, S., Staskiewicz, A., Thiel, A., Wahl, J., Haak, W., Pernicka, E., Schiffels, S., Stockhammer, P. W., and Krause, J. (2019). "Kinship-based social inequality in Bronze Age Europe". *Science* 366 (6466):731–734.

Modi, A., Tassi, F., Susca, R. R., Vai, S., Rizzi, E., De Bellis, G., Lugliè, C., Fortes, G. G., Lari, M., Barbujani, G., Caramelli, D., and Ghirotto, S. (2017). "Complete mitochondrial sequences from Mesolithic Sardinia". *Scientific reports* 7:42869.

Moore, D. R. (2012). "Whats new and whats cooking in the latte period pots". *Micronesica* 42 (1/2):121–147.

Moore, D. R. (2015). "Pre-contact foodways in the Mariana Islands". *Journal of Indo-Pacific Archaeology* 37:49–58.

Moore, H. and Wilson, G. (2005). "Iron Age buildings, burials and metal-working at Knowe of Skea Ness, Orkney". *the Archaeologist* 56:24–25.

Moore, H., Wilson, G., and Ni Challanain, M. (forthcoming). "Preliminary Findings from The Bronze Age Cemetery at Links of Noltland".

Müldner, G., Chenery, C., and Eckardt, H. (2011). "The Headless Romans: multi-isotope investigations of an unusual burial ground from Roman Britain". *Journal of Archaeological Science* 38 (2):280–290.

Nafplioti, A. (2016). "Eating in prosperity: First stable isotope evidence of diet from Palatial Knossos". *Journal of Archaeological Science: Reports* 6:42–52.

Nakassis, D., Galaty, M. L., and Parkinson, W. A. (2010). "State and society". In: *The Oxford Handbook of the Bronze Age Aegean*.

Narasimhan, V. M., Patterson, N., Moorjani, P., Rohland, N., Bernardos, R., Mallick, S., Lazaridis, I., Nakatsuka, N., Olalde, I., Lipson, M., Kim, A. M., Olivieri, L. M., Coppa, A., Vidale, M., Mallory, J., Moiseyev, V., Kitov, E., Monge, J., Adamski, N., Alex, N., Broomandkhoshbacht, N., Candilio, F., Callan, K., Cheronet, O., Culleton, B. J., Ferry, M., Fernandes, D., Freilich, S., Gamarra, B., Gaudio, D., Hajdinjak, M., Harney,., Harper, T. K., Keating, D., Lawson, A. M., Mah, M., Mandl, K., Michel, M., Novak, M., Oppenheimer, J., Rai, N., Sirak, K., Slon, V., Stewardson, K., Zalzala, F., Zhang, Z., Akhatov, G., Bagashev, A. N., Bagnera, A., Baitanayev, B., Bendezu-Sarmiento, J., Bissembaev, A. A., Bonora, G. L., Chargynov, T. T., Chikisheva, T., Dashkovskiy, P. K., Derevianko, A., Dobe, M., Douka, K., Dubova, N., Duisengali, M. N., Enshin, D., Epimakhov, A., Fribus, A. V., Fuller, D., Goryachev, A., Gromov, A., Grushin, S. P., Hanks, B., Judd, M., Kazizov, E., Khokhlov, A., Krygin, A. P., Kupriyanova, E., Kuznetsov, P., Luiselli, D., Maksudov, F., Mamedov, A. M., Mamirov, T. B., Meiklejohn, C., Merrett, D. C., Micheli,

R., Mochalov, O., Mustafokulov, S., Nayak, A., Pettener, D., Potts, R., Razhev, D., Rykun, M., Sarno, S., Savenkova, T. M., Sikhymbaeva, K., Slepchenko, S. M., Soltobaev, O. A., Stepanova, N., Svyatko, S., Tabaldiev, K., Teschler-Nicola, M., Tishkin, A. A., Tkachev, V. V., Vasilyev, S., Velemínský, P., Voyakin, D., Yermolayeva, A., Zahir, M., Zubkov, V. S., Zubova, A., Shinde, V. S., Lalueza-Fox, C., Meyer, M., Anthony, D., Boivin, N., Thangaraj, K., Kennett, D. J., Frachetti, M., Pinhasi, R., and Reich, D. (2019). "The formation of human populations in South and Central Asia". *Science* 365 (6457):eaat7487.

Nei, M. and Kumar, S. (2000). *Molecular evolution and phylogenetics*. Oxford university press.

Nikitin, A. G., Stadler, P., Kotova, N., Teschler-Nicola, M., Price, T. D., Hoover, J., Kennett, D. J., Lazaridis, I., Rohland, N., Lipson, M., and Reich, D. (2019). "Interactions between earliest Linearbandkeramik farmers and central European hunter gatherers at the dawn of European Neolithization". *Scientific Reports* 9 (1):1–10.

Nitsch, E., Andreou, S., Creuzieux, A., Gardeisen, A., Halstead, P., Isaakidou, V., Karathanou, A., Kotsachristou, D., Nikolaidou, D., Papanthimou, A., Petridou, C., Triantaphyllou, S., Valamoti, S. M., Vasileiadou, A., and Bogaard, A. (2017). "A bottom-up view of food surplus: using stable carbon and nitrogen isotope analysis to investigate agricultural strategies and diet at Bronze Age Archontiko and Thessaloniki Toumba, northern Greece". *World Archaeology* 49 (1):105–137.

Noble, G. (2006). *Neolithic Scotland: Timber, Stone, Earth and Fire: Timber, Stone, Earth and Fire*. Edinburgh University Press.

Nowicki, K. (2014). *Final Neolithic Crete and the Southeast Aegean*. Walter de Gruyter GmbH & Co KG.

O'Connor, T. (2008). *The archaeology of animal bones*. 4. Texas A&M University Press.

Olalde, I., Brace, S., Allentoft, M., Armit, I., Kristiansen, K., Booth, T., Rohland, N., Mallick, S., Szécsényi-Nagy, A., Mittnik, A., Altena, E., Lipson, M., Lazaridis, I., Harper, T., Patterson, N., Broomandkhoshbacht, N., Diekmann, Y., Faltyskova, Z., Fernandes, D., Ferry, M., Harney, E., de Knijff, P., Michel, M., Oppenheimer, J., Stewardson, K., Barclay, A., Alt, K., Liesau, C., Ríos, P., Blasco, C., Miguel, J., García, R., Fernández, A., Bánffy, E., Bernabó-Brea, M., Billoin, D., Bonsall, C., Bonsall, L., Allen, T., Büster, L., Carver, S., Navarro, L., Craig, O., Cook, G., Cunliffe, B., Denaire, A., Egging Dinwiddy, K., Dodwell, N., Ernée, M., Evans, C., Kuchařík, M., Farré, J., Fowler, C., Gazenbeek, M., Peno, R., Haber-Uriarte, M., Haduch, E., Hey, G., Jowett, N., Knowles, T., Massy, K., Pfrengle, S., Lefranc, P., Lemercier, O., Lefebvre, A., Martínez, C., Olmo, V., Ramírez, A., Maurandi, J., Majó, T., McKinley, J., McSweeney, K., Mende, B., Modi, A., Kulcsár, G., Kiss, V., Czene, A., Patay, R., Endrödi, A., Köhler, K., Hajdu, T., Szeniczey, T., Dani, J., Bernet, Z., Hoole, M.,

Cheronet, O., Keating, D., Velemínský, P., Dobeš, M., Candilio, F., Brown, F., Fernández, R., Herrero-Corral, A.-M., Tusa, S., Carnieri, E., Lentini, L., Valenti, A., Zanini, A., Waddington, C., Delibes, G., Guerra-Doce, E., Neil, B., Brittain, M., Luke, M., Mortimer, R., Desideri, J., Besse, M., Brücken, G., Furmanek, M., Hałuszko, A., Mackiewicz, M., Rapiński, A., Leach, S., Soriano, I., Lillios, K., Cardoso, J., Parker Pearson, M., Włodarczak, P., Price, T., Prieto, P., Rey, P.-J., Risch, R., Rojo Guerra, M., Schmitt, A., Serralongue, J., Silva, A., Smrčka, V., Vergnaud, L., Zilhão, J., Caramelli, D., Higham, T., Thomas, M., Kennett, D., Fokkens, H., Heyd, V., Sheridan, A., Sjögren, K.-G., Stockhammer, P., Krause, J., Pinhasi, R., Haak, W., Barnes, I., Lalueza-Fox, C., and Reich, D. (2018). "The Beaker phenomenon and the genomic transformation of northwest Europe". *Nature* 555 (7695):190–196.

Olalde, I., Allentoft, M. E., Sánchez-Quinto, F., Santpere, G., Chiang, C. W., DeGiorgio, M., Prado-Martinez, J., Rodríguez, J. A., Rasmussen, S., Quilez, J., Ramírez, O., Marigorta, U. M., Fernández-Callejo, M., Encina Prada, M., Vidal Encinas, J. M., Nielsen, R., Netea, M. G., Novembre, J., Sturm, R. A., Sabeti, P., Marquès-Bonet, T., Navarro, A., Willerslev, E., and Lalueza-Fox, C. (2014). "Derived immune and ancestral pigmentation alleles in a 7,000-year-old Mesolithic European". *Nature* 507 (7491):225–228.

Olalde, I., Mallick, S., Patterson, N., Rohland, N., Villalba-Mouco, V., Silva, M., Dulias, K., Edwards, C. J., Gandini, F., Pala, M., Soares, P., Ferrando-Bernal, M., Adamski, N., Broomandkhoshbacht, N., Cheronet, O., Culleton, B. J., Fernandes, D., Lawson, A. M., Mah, M., Oppenheimer, J., Stewardson, K., Zhang, Z., Jiménez Arenas, J. M., Toro Moyano, I. J., Salazar-García, D. C., Castanyer, P., Santos, M., Tremoleda, J., Lozano, M., García Borja, P., Fernández-Eraso, J., Mujika-Alustiza, J. A., Barroso, C., Bermúdez, F. J., Viguera Mínguez, E., Burch, J., Coromina, N., Vivó, D., Cebrià, A., Fullola, J. M., García-Puchol, O., Morales, J. I., Oms, F. X., Majó, T., Maria Vergès, J., Díaz-Carvajal, A., Ollich-Castanyer, I., López-Cachero, F. J., Silva, A. M., Alonso-Fernández, C., Castro, G. Delibes de, Jiménez Echevarría, J., Moreno-Márquez, A., Berlanga, G., Ramos-García, P., Ramos-Muñoz, J., Vijande Vila, E., Aguilella Arzo, G., Esparza Arroyo,., Lillios, K., Mack, J., Velasco-Vázquez, J., Waterman, A., Lugo Enrich, L. Benítez de, Benito Sánchez, M., Agustí, B., Codina, F., Prado, G. de, Estalrrich, A., Fernández Flores,., Finlayson, C., Finlayson, G., Finlayson, S., Giles-Guzmán, F., Rosas, A., Barciela González, V., García Atiénzar, G., Hernández Pérez, M., Llanos, A., Carrión Marco, Y., Collado Beneyto, I., López-Serrano, D., Sanz Tormo, M., Valera, A., Blasco, C., Liesau, C., Ríos, P., Daura, J., Pedro Michó, M. de, Diez-Castillo, A., Flores Fernández, R., Francès Farré, J., Garrido-Pena, R., Gonçalves, V., Guerra-Doce, E., Mercedes Herrero-Corral, A., Juan-Cabanilles, J., López-Reyes, D., McClure, S., Merino Pérez, M., Foix, A., Sanz Borràs, M., Catarina

Sousa, A., Vidal Encinas, J., Kennett, D., Richards, M. B., Alt, K., Haak, W., Pinhasi, R., Lalueza-Fox, C., and Reich, D. (2019). "The genomic history of the Iberian Peninsula over the past 8000 years". *Science* 363 (6432):1230–1234.

Olivieri, A., Achilli, A., Pala, M., Battaglia, V., Fornarino, S., Al-Zahery, N., Scozzari, R., Cruciani, F., Behar, D. M., Dugoujon, J.-M., Coudray, C., Santachiara-Benerecetti, A. S., Semino, O., Bandelt, H.-J., and Torroni, A. (2006). "The mtDNA legacy of the Levantine early Upper Palaeolithic in Africa". *Science* 314 (5806):1767–1770.

Omrak, A., Günther, T., Valdiosera, C., Svensson, E. M., Malmström, H., Kiesewetter, H., Aylward, W., Storå, J., Jakobsson, M., and Götherström, A. (2016). "Genomic evidence establishes Anatolia as the source of the European Neolithic gene pool". *Current Biology* 26 (2):270–275.

Orlando, L., Ginolhac, A., Zhang, G., Froese, D., Albrechtsen, A., Stiller, M., Schubert, M., Cappellini, E., Petersen, B., Moltke, I., Johnson, P., Fumagalli, M., Vilstrup, J., Raghavan, M., Korneliussen, T., Malaspinas, A.-S., Vogt, J., Szklarczyk, D., Kelstrup, C., Vinther, J., Dolocan, A., Stenderup, J., Velazquez, A., Cahill, J., Rasmussen, M., Wang, X., Min, J., Zazula, G., Seguin-Orlando, A., Mortensen, C., Magnussen, K., Thompson, J., Weinstock, J., Gregersen, K., Røed, K., Eisenmann, V., Rubin, C., Miller, D., Antczak, D., Bertelsen, M., Brunak, S., Al-Rasheid, K., Ryder, O., Andersson, L., Mundy, J., Krogh, A., Gilbert, M., Kjær, K., Sicheritz-Ponten, T., Juhl Jensen, L., Olsen, J., Hofreite, M., Nielsen, R., Shapiro, B., Wang, J., and Willerslev, E. (2013). "Recalibrating *Equus* evolution using the genome sequence of an early Middle Pleistocene horse". *Nature* 499 (7456):74–78.

Pala, M., Olivieri, A., Achilli, A., Accetturo, M., Metspalu, E., Reidla, M., Tamm, E., Karmin, M., Reisberg, T., Kashani, B., Perego, U. A., Carossa, V., Gandini, F., Pereira, J., Soares, P., Angerhofer, N., Rychkov, S., Al-Zahery, N., Carelli, V., Sanati, M., Houshmand, M., Hatina, J., Macaulay, V., Pereira, L., Woodward, S., Davies, W., Gamble, C., Baird, D., Semino, O., Villems, R., Torroni, A., and Richards, M. (2012). "Mitochondrial DNA signals of Late Glacial recolonization of Europe from Near Eastern refugia". *The American Journal of Human Genetics* 90 (5):915–924.

Pala, M., Achilli, A., Olivieri, A., Kashani, B. H., Perego, U. A., Sanna, D., Metspalu, E., Tambets, K., Tamm, E., Accetturo, M., Carossa, V., Lancioni, H., Panara, F., Zimmermann, B., Huber, G., Al-Zahery, N., Brisighelli, F., Woodward, S. R., Francalacci, P., Parson, W., Salas, A., Behar, D. M., Villems, R., Semino, O., Bandelt, H.-J., and Torroni, A. (2009). "Mitochondrial haplogroup U5b3: a distant echo of the epipaleolithic in Italy and the legacy of the early Sardinians". *The American Journal of Human Genetics* 84 (6):814–821.

Papathanasiou, A. (2005). "Health status of the Neolithic population of Alepotrypa Cave, Greece". *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 126 (4):377–390.

— (2015). "Stable isotope analyses in neolithic and Bronze age greece: an overview". *Hesperia Supplements* 49:25–55.

Papathanasiou, A. and Richards, M. P. (2015). "Summary: patterns in the carbon and nitrogen isotope data through time". *Hesperia Supplements* 49:195–203.

Parker Pearson, M. (1999). "The Earlier Bronze Age". In: *The Archaeology of Britain: An Introduction from the Upper Palaeolithic to the Industrial Revolution*. Ed. by J. Hunter and I. Ralston. Psychology Press. Chap. 5, p. 77–94.

Paschou, P., Drineas, P., Yannaki, E., Razou, A., Kanaki, K., Tsetsos, F., Padmanabhuni, S. S., Michalodimitrakis, M., Renda, M. C., Pavlovic, S., Anagnostopoulos, A., Stamatoyannopoulos, J. A., Kidd, K. K., and Stamatoyannopoulos, G. (2014). "Maritime route of colonization of Europe". *Proceedings of the National Academy of Sciences* 111 (25):9211–9216.

Pate, F. D., Craib, J. L., and Heathcot, G. M. (2001). "Stable isotopic analysis of prehistoric human diet in the Mariana Islands, western Pacific". *Australian Archaeology* 52 (1):1–4.

Patterson, N., Price, A., and Reich, D. (2006). "Population structure and eigenanalysis". *PLoS Genetics* 2 (12):e190.

Patterson, N., Moorjani, P., Luo, Y., Mallick, S., Rohland, N., Zhan, Y., Genschoreck, T., Webster, T., and Reich, D. (2012). "Ancient admixture in human history". *Genetics* 192 (3):1065–1093.

Pawley, A. (2006). "Nayacakalou medal address: Explaining the aberrant Austronesian languages of Southeast Melanesia: 150 years of debate". *The Journal of the Polynesian Society* 115 (3):215–258.

Pearson, M. P. (2009). "The Earlier Bronze Age". In: *The archaeology of Britain*. Routledge, p. 121–143.

Pearson, M., Chamberlain, A., Jay, M., Richards, M., Sheridan, A., Curtis, N., Evans, J., Gibson, A., Hutchison, M., Mahoney, P., Marshall, P., Montgomery, J., Needham, S., O'Mahoney, S., Pellegrini, M., and Wilkin, N. (2016). "Beaker people in Britain: migration, mobility and diet". *Antiquity* 90 (351):620–637.

Peltzer, A., Jäger, G., Herbig, A., Seitz, A., Kniep, C., Krause, J., and Nieselt, K. (2016). "EAGER: efficient ancient genome reconstruction". *Genome biology* 17 (1):60.

Pereira, J. B., Costa, M. D., Vieira, D., Pala, M., Bamford, L., Harich, N., Cherni, L., Alshamali, F., Hatina, J., Rychkov, S., Stefanescu, G., King, T., Torroni, A., Soares, P., Pereira, L., and Richards, M. B. (2017). "Reconciling evidence from ancient and contemporary genomes: a major source for the European Neolithic within

Mediterranean Europe". *Proceedings of the Royal Society B: Biological Sciences* 284 (1851):20161976.

Peter, B. M. (2016). "Admixture, population structure, and F-statistics". *Genetics* 202 (4):1485–1501.

Petroutsa, E. I. and Manolis, S. K. (2010). "Reconstructing Late Bronze Age diet in mainland Greece using stable isotope analysis". *Journal of Archaeological Science* 37 (3):614–620.

Petroutsa, E. I., Richards, M. P., and Manolis, S. K. (2007). "Stable isotope analysis of human remains from the Early Helladic site of Perachora, Korinth, Greece". *Cooking up the past: Food and culinary practices in the Neolithic and Bronze Age Aegean*:290–296.

Pietrusewsky, M., Douglas, M. T., Swift, M. K., Harper, R. A., and Fleming, M. A. (2014). "Health in ancient Mariana Islanders: A bioarchaeological perspective". *The Journal of Island and Coastal Archaeology* 9 (3):319–340.

Pinhasi, R., Fernandes, D., Sirak, K., Novak, M., Connell, S., Alpaslan-Roodenberg, S., Gerritsen, F., Moiseyev, V., Gromov, A., Raczky, P., Anders, A., Pietrusewsky, M., Rollefson, G., Jovanovic, M., Trinhhoang, H., Bar-Oz, G., Oxenham, M., Matsumura, H., and Hofreiter, M. (2015). "Optimal ancient DNA yields from the inner ear part of the human petrous bone". *PloS one* 10 (6):e0129102.

Pollard, J. (2008). "The construction of prehistoric Britain". *Blackwell studies in Global Archaeology* 11:1.

Preston, L. (2004). "A mortuary perspective on political changes in Late Minoan II-IIIB Crete". *American Journal of Archaeology*:321–348.

Pugach, I., Hubner, A., Hung, H.-C., Meyer, M., Carson, M. T., and Stoneking, M. (2020). "Ancient DNA from Guam and the Peopling of the Pacific". *bioRxiv*.

Quinn, C. J. (1990). "Stable isotopes and diet: indications of the marine and terrestrial component in the diets of prehistoric populations from New Zealand and the Pacific". PhD thesis. University of Otago.

Raghavan, M., Skoglund, P., Graf, K. E., Metspalu, M., Albrechtsen, A., Moltke, I., Rasmussen, S., Stafford Jr, T. W., Orlando, L., Metspalu, E., Karmin, M., Tambets, K., Rootsi, S., Mägi, R., Campos, P. F., Balanovska, E., Balanovsky, O., Khusnutdinova, E., Litvinov, S., Osipova, L. P., Fedorova, S. A., Voevoda, M. I., DeGiorgio, M., Sicheritz-Ponten, T., Brunak, S., Demeshchenko, S., Kivisild, T., Villems, R., Nielsen, R., Jakobsson, M., and Willerslev, E. (2014). "Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans". *Nature* 505 (7481):87–91.

Ralf, A., Montiel González, D., Zhong, K., and Kayser, M. (2018). "Yleaf: software for human Y-chromosomal haplogroup inference from next-generation sequencing data". *Molecular Biology and Evolution* 35 (5):1291–1294.

Rasmussen, M., Guo, X., Wang, Y., Lohmueller, K. E., Rasmussen, S., Albrechtsen, A., Skotte, L., Lindgreen, S., Metspalu, M., Jombart, T., Kivisild, T., Zhai, W., Eriksson, A., Manica, A., Orlando, L., De La Vega, F. M., Tridico, S., Metspalu, E., Nielsen, K., Avila-Arcos, M. C., Moreno-Mayar, J. V., Muller, C., Dortch, J., Gilbert, M. T., Lund, O., Wesolowska, A., Karmin, M., Weinert, L. A., Wang, B., Li, J., Tai, S., Xiao, F., Hanihara, T., Driem, G. van, Jha, A. R., Ricaut, F. X., Knijff, P. de, Migliano, A. B., Gallego Romero, I., Kristiansen, K., Lambert, D. M., Brunak, S., Forster, P., Brinkmann, B., Nehlich, O., Bunce, M., Richards, M., Gupta, R., Bustamante, C. D., Krogh, A., Foley, R. A., Lahr, M. M., Balloux, F., Sicheritz-Ponten, T., Villems, R., Nielsen, R., Wang, J., and Willerslev, E. (2011). "An Aboriginal Australian genome reveals separate human dispersals into Asia". *Science* 334 (6052):94–98.

Raule, N., Sevini, F., Li, S., Barbieri, A., Tallaro, F., Lomartire, L., Vianello, D., Montesanto, A., Moilanen, J., Bezrukov, V., Blanché, H., Hervonen, A., Christensen, K., Deiana, L., Gonos, E., Kirkwood, T., Kristensen, P., Leon, A., Pelicci, P., Poulain, M., Rea, I., Remacle, J., Robine, J., Schreiber, S., Sikora, E., Slagboom, P., Spazzafumo, L., Stazi, M., Toussaint, O., Vaupel, J., Rose, G., Majamaa, K., Perola, M., Johnson, T., Bolund, L., Yang, H., Passarino, G., and Franceschi, C. (2014). "The co-occurrence of mtDNA mutations on different oxidative phosphorylation subunits, not detected by haplogroup analysis, affects human longevity and is population specific". *Aging Cell* 13 (3):401–407.

Reitz, E. J. and Wing, E. S. (2008). *Zooarchaeology (2nd Edition)*. Cambridge University Press.

Renaud, G., Slon, V., Duggan, A., and Kelso, J. (2015). "Schmutzi: estimation of contamination and endogenous mitochondrial consensus calling for ancient DNA". *Genome Biology* 16 (1):224.

Renaud, G., Stenzel, U., and Kelso, J. (2014). "leeHom: adaptor trimming and merging for Illumina sequencing reads". *Nucleic acids research* 42 (18):e141–e141.

Renfrew, C. (2000). "Archaeogenetics: towards a population prehistory of Europe". *Archaeogenetics: DNA and the population prehistory of Europe*:3–11.

Richards, J. D. (2005). *The Vikings: A very short introduction*. OUP Oxford.

— (2009). "The Scandinavian Presence". In: *The Archaeology of Britain: An Introduction from Earliest Times to the Twenty-First Century*. Routledge, p. 265–284.

Richards, M. P. (2015). "Stable isotope analysis of bone and teeth as a means for reconstructing past human diets in Greece". *Hesperia Supplements* 49:15–23.

Richards, M. P. and Hedges, R. E. (1999). "Stable isotope evidence for similarities in the types of marine foods used by Late Mesolithic humans at sites along the Atlantic coast of Europe". *Journal of Archaeological Science* 26 (6):717–722.

Richards, M. P. and Schulting, R. J. (2006). "Touch not the fish: the Mesolithic-Neolithic change of diet and its significance". *Antiquity* 80 (308):444–456.

Richards, M. and Hedges, R. (2008). "Stable isotope results from the sites of Gerani, Armenoi and Mycenae". *Archaeology meets science: biomolecular and site investigations in Bronze Age Greece. Oxford: Oxbow Books. p*:220–230.

Ripoll, M. P. (2013). "The Knossos fauna and the beginning of the Neolithic in the Mediterranean islands". *The Neolithic Settlement of Knossos in Crete: New Evidence for the Early Occupation of Crete and the Aegean Islands*:133.

Ritchie, A. (1995). *Prehistoric Orkney*. Sterling Publishing Company, Inc.

Rizzi, E., Lari, M., Gigli, E., De Bellis, G., and Caramelli, D. (2012). "Ancient DNA studies: new perspectives on old samples". *Genetics Selection Evolution* 44 (1):21.

Robinson, J. T., Thorvaldsdóttir, H., Wenger, A. M., Zehir, A., and Mesirov, J. P. (2017). "Variant review with the integrative genomics viewer". *Cancer research* 77 (21):e31–e34.

Rodríguez-Varela, R., Günther, T., Krzewińska, M., Storå, J., Gillingwater, T. H., MacCallum, M., Arsuaga, J. L., Dobney, K., Valdiosera, C., Jakobsson, M., Götherström, A., and Girdland-Flink, L. (2017). "Genomic analyses of Pre-European conquest human remains from the Canary Islands reveal close affinity to modern North Africans". *Current Biology* 27 (21):3396–3402.

Rohland, N., Harney, E., Mallick, S., Nordenfelt, S., and Reich, D. (2015). "Partial uracil–DNA–glycosylase treatment for screening of ancient DNA". *Philosophical Transactions of the Royal Society B: Biological Sciences* 370 (1660):20130624.

Rowley-Conwy, P. (2011). "Westward Ho! The spread of agriculture from Central Europe to the Atlantic". *Current anthropology* 52 (S4):S431–S451.

Sahakyan, H., Kashani, B. H., Tamang, R., Kushniarevich, A., Francis, A., Costa, M. D., Pathak, A. K., Khachatryan, Z., Sharma, I., Van Oven, M., Parik, J., Hovhannisyan, H., Metspalu, E., Pennarun, E., Karmin, M., Tamm, E., Tambets, K., Bahmanimehr, A., Reisberg, T., Reidla, M., Achilli, A., Olivieri, A., Gandini, F., Perego, U. A., Al-Zahery, N., Houshmand, M., Sanati, M. H., Soares, P., Rai, E., arac, J., ari, T., Sharma, V., Pereira, L., Fernandes, V., erný, V., Farjadian, S., Singh, D. P., Azakli, H., Üstek, D., Ekomasova, N., Kutuev, I., Litvinov, S., Bermisheva, M., Khusnutdinova, E. K., Rai, N., Singh, M., Singh, V. K., Reddy, A. G., Tolk, H.-V., Cvjetan, S., Lauc, L. B., Rudan, P., Michalodimitrakis, E. N., Anagnou, N. P., Pappa, K. I., Golubenko, M. V., Orekhov, V., Borinskaya, S. A., Kaldma, K., Schauer, M. A., Simionescu, M., Gusar, V., Grechanina, E., Govindaraj, P., Voevoda, M., Damba, L., Sharma, S., Singh, L., Semino, O., Behar, D. M., Yepiskoposyan, L., Richards, M. B., Metspalu, M., Kivisild, T., Thangaraj, K., Endicott, P., Chaubey, G., Torroni, A., and

Villems, R. (2017). "Origin and spread of human mitochondrial DNA haplogroup U7". *Scientific reports* 7 (1):1–9.

Salavert, A. (2017). "Agricultural dispersals in Mediterranean and temperate Europe". In: *Oxford Research Encyclopedia of Environmental Science*.

Sánchez-Quinto, F., Malmström, H., Fraser, M., Girdland-Flink, L., Svensson, E. M., Simões, L. G., George, R., Hollfelder, N., Burenhult, G., Noble, G., Britton, K., Talamo, S., Curtis, N., Brzobohata, H., Sumberova, R., Götherström, A., Storå, J., and Jakobsson, M. (2019). "Megalithic tombs in western and northern Neolithic Europe were linked to a kindred society". *Proceedings of the National Academy of Sciences* 116 (19):9469–9474.

Sarno, S., Boattini, A., Pagani, L., Sazzini, M., De Fanti, S., Quagliariello, A., Ruscone, G. A. G., Guichard, E., Ciani, G., Bortolini, E., Barbieri, C., Cilli, E., Petrilli, R., Mikerezi, I., Sineo, L., Vilar, M., Wells, S., Luiselli, D., and Pettener, D. (2017). "Ancient and recent admixture layers in Sicily and Southern Italy trace multiple migration routes along the Mediterranean". *Scientific reports* 7 (1):1984.

Schaefer, N. K. and Shapiro, B. (2019). "New middle chapter in the story of human evolution". *Science* 365 (6457):981–982.

Scheib, C. L., Hui, R., DAtanasio, E., Wohns, A. W., Inskip, S. A., Rose, A., Cessford, C., OConnell, T. C., Robb, J. E., Evans, C., Patten, R., and Kivisild, T. (2019). "East Anglian early Neolithic monument burial linked to contemporary Megaliths". *Annals of human biology* 46 (2):145–149.

Schiffels, S., Haak, W., Paajanen, P., Llamas, B., Popescu, E., Loe, L., Clarke, R., Lyons, A., Mortimer, R., Sayer, D., Tyler-Smith, C., Cooper, A., and Durbin, R. (2016). "Iron Age and Anglo-Saxon genomes from east England reveal British migration history". *Nature communications* 7:10408.

Schlebusch, C. M. and Jakobsson, M. (2018). "Tales of human migration, admixture, and selection in Africa". *Annual review of genomics and human genetics* 19:405–428.

Schoep, I. (2006). "Looking beyond the first palaces: elites and the agency of power in EM III-MM II Crete". *American Journal of Archaeology*:37–64.

— (2010). "Crete". In: *The Oxford Handbook of the Bronze Age Aegean*.

Schubert, M., Ginolhac, A., Lindgreen, S., Thompson, J., Al-Rasheid, K., Willerslev, E., Krogh, A., and Orlando, L. (2012). "Improving ancient DNA read mapping against modern reference genomes". *BMC Genomics* 13 (1):178.

Schulting, R. J. (1998). "Slighting the sea: stable isotope evidence for the transition to farming in northwestern Europe". *Documenta Praehistorica* 25 (203):18.

Schwarcz, H. P., White, C. D., and Longstaffe, F. J. (2010). "Stable and radiogenic isotopes in biological archaeology: some applications". In: *Isoscapes*. Springer, p. 335–356.

Shapland, F., Sinfield, L., and McSweeney, K. (2019). "High Pasture cave human remains". In: *High Pasture Cave: Ritual, Memory and Identity in the Iron Age of Skye*. Ed. by S. Birch, G. Cruickshanks, and J. Mckenzie. Oxbow Books Oxford.

Sharp, Z. (2017). "Principles of stable isotope geochemistry".

Shaw, K. L. and Gillespie, R. G. (2016). "Comparative phylogeography of oceanic archipelagos: Hotspots for inferences of evolutionary process". *Proceedings of the National Academy of Sciences* 113 (29):7986–7993.

Shelton, K. (2010). "Mainland Greece". *The Bronze Age Aegean (ca. 3000-1000 BC)*:139–148.

Sherwood-Dickinson, C., Droop, G., and Giże, A. P. (2018). "Ano Valsamonero Iron Deposit: A Potential Metal Resource for the Late Minoan III Community". *The Late Minoan III Necropolis of Armenoi: Volume 1: Introduction and Background* 60:241.

Sjögren, K.-G., Price, T. D., and Kristiansen, K. (2016). "Diet and mobility in the Corded Ware of Central Europe". *PloS one* 11 (5).

Skoglund, P., Malmström, H., Omrak, A., Raghavan, M., Valdiosera, C., Günther, T., Hall, P., Tambets, K., Parik, J., Sjögren, K.-G., Apel, J., Willerslev, E., Storøa, J., Götherström, A., and Jakobsson, M. (2014). "Genomic diversity and admixture differs for Stone-Age Scandinavian foragers and farmers". *Science* 344 (6185):747–750.

Skoglund, P., Storå, J., Götherström, A., and Jakobsson, M. (2013). "Accurate sex identification of ancient human remains using DNA shotgun sequencing". *Journal of Archaeological Science* 40 (12):4477–4482.

Skoglund, P. and Mathieson, I. (2018). "Ancient genomics of modern humans: the first decade". *Annual review of genomics and human genetics* 19:381–404.

Skourtanioti, E., Erdal, Y. S., Frangipane, M., Restelli, F. B., Yener, K. A., Pinnock, F., Matthiae, P., Özbal, R., Schoop, U.-D., Guliyev, F., Akhundov, T., Lyonnet, B., Hammer, E. L., Nugent, S. E., Burri, M., Neumann, G. U., Penske, S., Ingman, T., Akar, M., Shafiq, R., Palumbi, G., Eisenmann, S., DAndrea, M., Rohrlach, A. B., Warinner, C., Jeong, C., Stockhammer, P. W., Haak, W., and Krause, J. (2020). "Genomic History of Neolithic to Bronze Age Anatolia, Northern Levant, and Southern Caucasus". *Cell* 181 (5):1158–1175.

Slon, V., Mafessoni, F., Vernot, B., Filippo, C. de, Grote, S., Viola, B., Hajdinjak, M., Peyrégne, S., Nagel, S., Brown, S., Douka, K., Higham, T., Kozlikin, M. B., Shunkov, M. V., Derevianko, A. P., Kelso, J., Meyer, M., Prüfer, K., and Paabo, S. (2018). "The genome of the offspring of a Neanderthal mother and a Denisovan father". *Nature* 561 (7721):113–116.

Sluis, L. G. van der, Hollund, H. I., Buckley, M., De Louw, P. G., Rijsdijk, K. F., and Kars, H. (2014). "Combining histology, stable isotope analysis and ZooMS collagen fingerprinting to investigate the taphonomic history and dietary behaviour of extinct

giant tortoises from the Mare aux Songes deposit on Mauritius". *Palaeogeography, Palaeoclimatology, Palaeoecology* 416:80–91.

Snoeck, C., Lee-Thorp, J., Schulting, R., De Jong, J., Debouge, W., and Mattielli, N. (2015). "Calcined bone provides a reliable substrate for strontium isotope ratios as shown by an enrichment experiment". *Rapid communications in mass spectrometry* 29 (1):107–114.

Soares, P., Ermini, L., Thomson, N., Mormina, M., Rito, T., Röhl, A., Salas, A., Oppenheimer, S., Macaulay, V., and Richards, M. (2009). "Correcting for purifying selection: an improved human mitochondrial molecular clock". *The American Journal of Human Genetics* 84 (6):740–759.

Soares, P., Abrantes, D., Rito, T., Thomson, N., Radivojac, P., Li, B., Macaulay, V., Samuels, D. C., and Pereira, L. (2013). "Evaluating purifying selection in the mitochondrial DNA of various mammalian species". *PloS one* 8 (3).

Stamatoyannopoulos, G., Bose, A., Teodosiadis, A., Tsetsos, F., Plantinga, A., Psatha, N., Zogas, N., Yannaki, E., Zalloua, P., Kidd, K. K., Browning, B. L., Stamatoyannopoulos, J., Paschou, P., and Drineas, P. (2017). "Genetics of the Peloponnesean populations and the theory of extinction of the medieval Peloponnesean Greeks". *European Journal of Human Genetics* 25 (5):637.

Strasser, T. F., Murray, S. C., Geer, A. van der, Kolb, C., and Ruprecht Jr, L. A. (2018). "Palaeolithic cave art from Crete, Greece". *Journal of Archaeological Science: Reports* 18:100–108.

Strasser, T. F., Runnels, C., Wegmann, K., Panagopoulou, E., Mccoy, F., Digregorio, C., Karkanas, P., and Thompson, N. (2011). "Dating Palaeolithic sites in southwestern Crete, Greece". *Journal of Quaternary Science* 26 (5):553–560.

Szécsényi-Nagy, A., Brandt, G., Haak, W., Keerl, V., Jakucs, J., Möller-Rieker, S., Köhler, K., Mende, B. G., Oross, K., Marton, T., Osztás, A., Kiss, V., Fecher, M., Pálfi, G., Molnár, E., Sebk, K., Czene, A., Paluch, T., laus, M., Novak, M., Peina-laus, N., sz, B., Voicsek, V., Somogyi, K., Tóth, G., Kromer, B., Bánffy, E., and Alt, K. W. (2015). "Tracing the genetic origin of Europe's first farmers reveals insights into their social organization". *Proceedings of the Royal Society B: Biological Sciences* 282 (1805):20150339.

Teržan, B. and Karavanić, S. (2013). "The Western Balkans in the Bronze Age". In: *The Oxford Handbook of the European Bronze Age*. Ed. by H. Fokkens and A. Harding. Oxford University Press.

Tollefsen, E. and Jones, C. (2017). *Osetoarchaeological Analysis West Heslerton North Yorkshire. Site Code: 82 CA*.

Tomas, H. (2010). "Cretan Hieroglyphic and Linear A". In: *The Oxford Handbook of the Bronze Age Aegean*.

Tomkins, P. and Schoep, I. (2010). "Crete". In: *The Oxford Handbook of the Bronze Age Aegean*.

Triantaphyllou, S., Richards, M. P., Zerner, C., and Voutsaki, S. (2008). "Isotopic dietary reconstruction of humans from Middle Bronze age Lerna, Argolid, Greece". *Journal of Archaeological Science* 35 (11):3028–3034.

Tzedakis, Y. and Kolivaki, V. (2018). "Background and History of the Excavation". In: *The Late Minoan III Necropolis of Armenoi: Volume 1: Introduction and Background*. Ed. by Tzedakis, Martlew, and Arnott. INSTAP Academic Press (Institute for Aegean Prehistory), p. 1–19.

Tzedakis, Y. and Martlew, H. (2001). *Archaeology meets science: Minoans and Mycenaeans flavors of their time*. Kapon Editions.

Underhill, P. A. and Kivisild, T. (2007). "Use of Y chromosome and mitochondrial DNA population structure in tracing human migrations". *Annu. Rev. Genet.* 41:539–564.

Vai, S., Lari, M., and Caramelli, D. (2017). "DNA sequencing in cultural heritage". In: *Analytical Chemistry for Cultural Heritage*. Springer, p. 329–346.

Vai, S., Sarno, S., Lari, M., Luiselli, D., Manzi, G., Gallinaro, M., Mataich, S., Hübner, A., Modi, A., Pilli, E., Tafuri, M. A., Caramelli, D., and Lernia, S. di (2019). "Ancestral mitochondrial N lineage from the Neolithic greenSahara". *Scientific reports* 9 (1):1–9.

Van De Graaf, R. (2009). "Some remarks on the revival of rhinoplasty in Europe in the early nineteenth century". *Acta Otorhinolaryngologica Italica* 29:226–227.

Van Klinken, G. J. (1999). "Bone collagen quality indicators for palaeodietary and radiocarbon measurements". *Journal of Archaeological Science* 26 (6):687–695.

Van Oven, M. (2015). "PhyloTree Build 17: Growing the human mitochondrial DNA tree". *Forensic Science International: Genetics Supplement Series* 5:e392–e394.

Vanderpool, E. M. and Turner, B. L. (2013). "Stable isotopic reconstruction of diet and residential mobility in a postbellum African American community in rural Georgia". *Southeastern Archaeology* 32 (1):97–110.

Vianello, D., Sevini, F., Castellani, G., Lomartire, L., Capri, M., and Franceschi, C. (2013). "HAPLOFIND: a new method for high-throughput mtDNA haplogroup assignment". *Human Mutation* 34 (9):1189–1194.

Vilar, M. G., Chan, C. W., Santos, D. R., Lynch, D., Spathis, R., Garruto, R. M., and Lum, J. K. (2013). "The origins and genetic distinctiveness of the Chamorros of the Marianas Islands: an mtDNA perspective". *American Journal of Human Biology* 25 (1):116–122.

Villalba-Mouco, V., Loosdrecht, M. S. van de, Posth, C., Mora, R., Martínez-Moreno, J., Rojo-Guerra, M., Salazar-García, D. C., Royo-Guillén, J. I., Kunst, M., Rougier, H., Crevecoeur, I., Arcusa-Magallón, H., Tejedor-Rodríguez, C., Lagrán, I. García-Martínez de, Garrido-Pena, R., Alt, K. W., Jeong, C., Schiffels, S., Utrilla, P., Krause,

J., and Haak, W. (2019). "Survival of Late Pleistocene hunter-gatherer ancestry in the Iberian Peninsula". *Current Biology* 29 (7):1169–1177.

Villanea, F. A. and Schraiber, J. G. (2019). "Multiple episodes of interbreeding between Neanderthal and modern humans". *Nature ecology & evolution* 3 (1):39–44.

Waddington, C. and Bonsall, C. (2016). "Archaeology and Environment on the North Sea Littoral. A Case Study from Low Hauxley". In: Archaeological Research Services.

Walth, C. K. (2014). "Archaeological Investigations at the Naton Beach Site, Tumon Bay, Guam". *Bioarchaeology in Southeast Asia and the Pacific* 10.

Wang, C.-C., Reinhold, S., Kalmykov, A., Wissgott, A., Brandt, G., Jeong, C., Cheronet, O., Ferry, M., Harney, E., Keating, D., Mallick, S., Rohland, N., Stewardson, K., Kantorovich, A. R., Maslov, V. E., Petrenko, V. G., Erlikh, V. R., Atabiev, B. C., Magomedov, R. G., Kohl, P. L., Alt, K. W., Pichler, S. L., Gerling, C., Meller, H., Vardanyan, B., Yeganyan, L., Rezepkin, A. D., Mariaschk, D., Berezina, N., Gresky, J., Fuchs, K., Knipper, C., Schiffels, S., Balanovska, E., Balanovsky, O., Mathieson, I., Higham, T., Berezin, Y. B., Buzhilova, A., Trifonov, V., Pinhasi, R., Belinskij, A. B., Reich, D., Hansen, S., Johannes, K., and Haak, W. (2019). "Ancient human genome-wide data from a 3000-year interval in the Caucasus corresponds with eco-geographic regions". *Nature communications* 10 (1):590.

Wardle, K., Higham, T., and Kromer, B. (2014). "Dating the end of the Greek Bronze Age: a robust radiocarbon-based chronology from Assiros Toumba". *PloS one* 9 (9):e106672.

Wei, W., Ayub, Q., Chen, Y., McCarthy, S., Hou, Y., Carbone, I., Xue, Y., and Tyler-Smith, C. (2013). "A calibrated human Y-chromosomal phylogeny based on resequencing". *Genome research* 23 (2):388–395.

Weissensteiner, H., Pacher, D., Kloss-Brandstätter, A., Forer, L., Specht, G., Bandelt, H.-J., Kronenberg, F., Salas, A., and Schönherr, S. (2016). "HaploGrep 2: mitochondrial haplogroup classification in the era of high-throughput sequencing". *Nucleic Acids Research* 44 (W1):W58–W63.

Wickham-Jones, C. (2013). *Orkney: a historical guide*. Birlinn.

Woodward, S. R., Weyand, N. J., and Bunnell, M. (1994). "DNA sequence from Cretaceous period bone fragments". *Science* 266 (5188):1229–1232.

Wren, C. D. and Burke, A. (2019). "Habitat suitability and the genetic structure of human populations during the Last Glacial Maximum (LGM) in Western Europe". *PloS one* 14 (6).

Yacobi, D. and Bedford, F. L. (2016). "Evidence of early gene flow between Ashkenazi Jews and non-Jewish Europeans in mitochondrial DNA haplogroup H7". *J Genet Geneal* 8:21–34.

Yang, D., Eng, B., Waye, J., Dudar, J., and Saunders, S. (1998). "Technical note: improved DNA extraction from ancient bones using silica-based spin columns". *American Journal of Physical Anthropology* 105 (4):539–543.

Yang, M. A. and Fu, Q. (2018). "Insights into modern human prehistory using ancient genomes". *Trends in Genetics* 34 (3):184–196.

Zeder, M. A. (2006). "Reconciling rates of long bone fusion and tooth eruption and wear in sheep (Ovis) and goat (Capra)". *Recent advances in ageing and sexing animal bones*:87–118.

— (2008). "Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact". *Proceedings of the National Academy of Sciences* 105 (33):11597–11604.

Zheng, Y. and Janke, A. (2018). "Gene flow analysis method, the D-statistic, is robust in a wide parameter space". *BMC bioinformatics* 19 (1):10.

Appendix A

Biomolecular analysis of Pre-Latte individuals from Guam

A.1 Introduction

The settlement of Guam, located in the Marianas archipelago in the north-western Pacific, represents one of the longest single migration events in the populating of the world. The origin of the first settlers is still unclear. Guams prehistory is often divided into two main periods: the Pre-Latte (1500BC-1000AD) and Latte (1000-1521AD). The Latte Period reveals a marked change in material culture, settlements and burial practices, but it is unclear whether this change was the result of immigration.

Samples were analysed from the Naton Beach Site, which contains the majority of Pre-Latte burials found on Guam. Assessment of ancient DNA aimed to identify the origins of the earliest settlers of Guam, through comparison to ancient south-east Asian and Oceanic populations. Stable carbon and nitrogen isotopic analysis was undertaken to provide a direct insight into the Pre-Latte diet and, by comparison to published data, identify whether the change in material culture reflects a shift in diet.

A.2 Aims

Analyses will be conducted on two individuals from the Naton beach cemetery to provide insight into the Pre-Latte culture, and see whether the changes introduced in the Latte period were caused by immigration, and the dietary impact of this change.

A.2.1 Dating and stable isotopic analysis

- Firstly, radiocarbon dating will be conducted to confirm that the burials are from the Pre-Latte period.

- Carbon and nitrogen isotopic ratios will be used to identify the main protein sources of the Naton individuals - this will be the first Pre-Latte Guamanian analysis.
- Data will be compared to published studies to identify whether there is a dietary change in the Latte Period, and how the Naton Beach Pre-Latte diet compares to the diets on other Mariana islands.

A.2.2 Genetic analysis

- Samples will be assessed to determine the mitochondrial haplogroups and sex of each individual - this will be the first ancient DNA from Guams oldest burial site.
- Data will be compared to modern and ancient published whole genome and mitochondrial data to determine potential genetic continuity, as well as sources of migration.

A.3 Literature review

A.3.1 Background of Guam and the Marianas

The Mariana Islands are an archipelago consisting of approximately 15 volcanic and coralline islands located in Micronesia, in the north-western Pacific (Figure A.1). Four of the largest islands, Guam, Tinian, Rota and Saipan, have been preferably settled in prehistory, and will be referred to as the Marianas in this project. Guam is the largest island, both in the Marianas and in Micronesia as a whole. The islands have a marine tropical climate with a pronounced summer monsoon. Only Guam has permanent surface water (Ambrose et al., 1997; Pate et al., 2001; Hung et al., 2011; Fitzpatrick and Callaghan, 2013; Pietrusewsky et al., 2014; Moore, 2015).

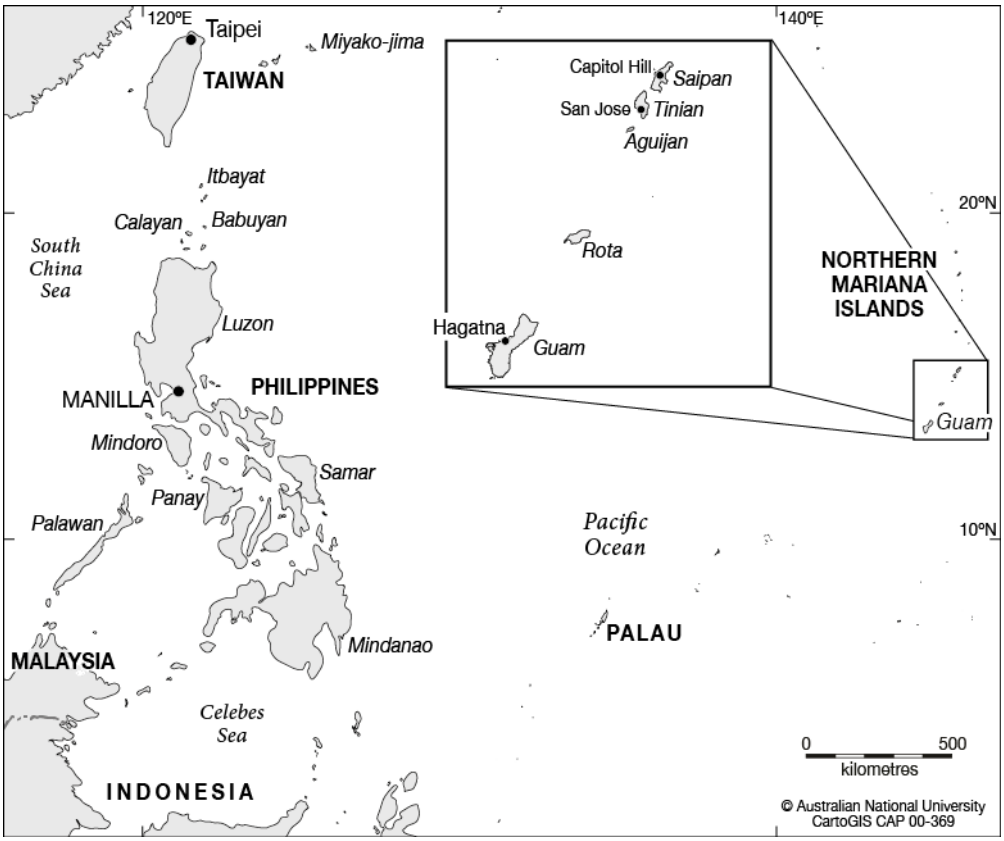


FIGURE A.1: Map showing the location of Guam (taken from http://asiapacific.anu.edu.au/mapsonline/base-maps/guamand-nearby-islands).

The Marianas prehistory is typically divided into two periods: the Pre-Latte Period 1500BC-1000AD, and Latte Period 1000-1521AD (Ambrose et al., 1997; Moore, 2012; Vilar et al., 2013). The Pre-Latte period population was small, consisting of coastal villages relying on fishing and subsistence agriculture of cultivated root and tree crops, such as banana and yam (Hung et al., 2011; Pietrusewsky et al., 2014). Very few burials have been found during this period (Ambrose et al., 1997). The end of the Pre-Latte period is characterised by several centuries of a transitional period involving adaptive change, increase in population, and expansion in to the island interiors (Hung et al., 2011; Pietrusewsky et al., 2014).

A series of noticeable changes occurred during the Latte period, most noticeably the presence of *latte* stones, rice cultivation, larger villages, pottery changes, and more inland settlements (Ambrose et al., 1997; Pate et al., 2001; Hung et al., 2011; Pietrusewsky et al., 2014; Moore, 2015). *Latte* are 5m tall stone columns topped with hemispheres, which may have functioned as house supports. Although similar wooden supports exist in Wallacea, stone *latte* are unique to the Marianas. Rice is commonly cultivated in Island South-east Asia (ISEA), yet the Marianas are the only Polynesian island to cultivate rice (Ambrose et al., 1997; Vilar et al., 2013; Moore, 2015).

In 1521AD, Spanish galleons arrived on Guam as part of Magellan's circumnaviagation of the globe, marking the first recorded contacted with Europeans. The Spanish later colonised Guam and decimated the Chamorro (indigenous) population by disease and war. The Chamorro population declined from 50,000-100,000 in the early 17th century AD to fewer than 1,000 by 1820AD (Vilar et al., 2013; Pietrusewsky et al., 2014). This would have caused a drastic genetic bottleneck that likely reduced the genomic variation. In an effort to maintain control, the Spanish forcibly emptied the island of Saipan of Chamorros, resettling them in Guam and repopulating Saipan with Carolinians. Today many Saipan islanders trace their ancestry to the Caroline Islands, or as a mix of Carolinians and Chamorros who later resettled on the island. It is believed that these populations would have been largely genetically isolated (Vilar et al., 2013). The terrible exploitation of the Chamorros has drastically changed the island and the population, and it is likely that the genetic diversity of the Latte period does not survive today.

A.3.2 Archaeological and linguistic evidence for the settlement of the Marianas

When modern humans first reached Southeast Asia c.60,000BP, mainland south-east Asia and ISEA were part of a super-continent called Sundra. These settlers spread quickly throughout Sundra, crossing the 70km to Sahul (Figure A.2). However, they did not venture further to Remote Oceania (Hill et al., 2007; Vilar et al., 2013; Duggan et al., 2014; Pietrusewsky et al., 2014; Matisoo-Smith, 2015).

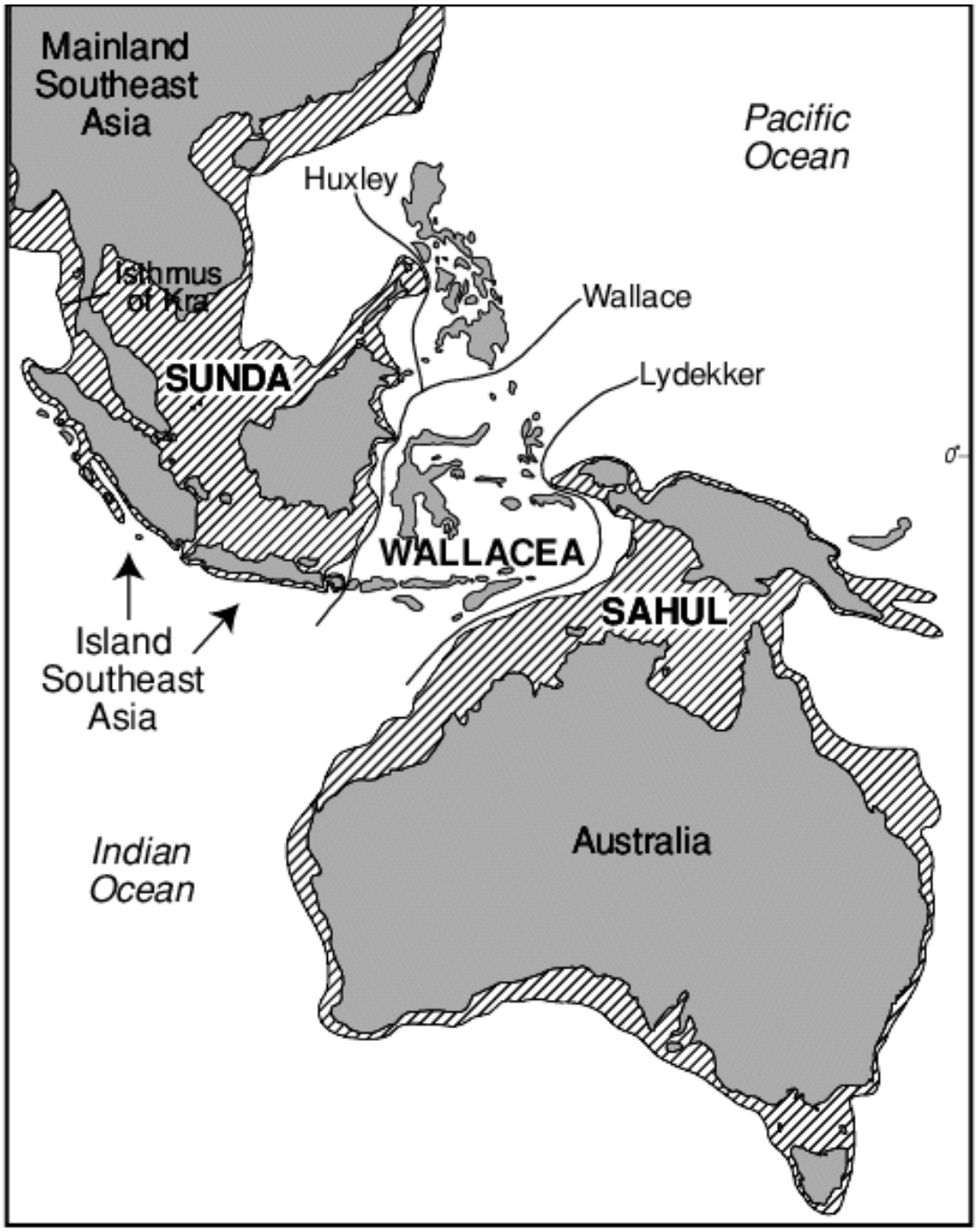


FIGURE A.2: Map of Sahul and Sundra. Ancient coastlines are represented by cross-hatching, while modern coastlines are represented by solid grey outlines (Harrison et al., 2006).

ISEA became separated from the mainland as sea levels rose at the end of the Pleistocene. Sea levels again increased during the mid-Holocene, forcing the people of ISEA to either move inland or expand out of ISEA (Hill et al., 2007; Vilar et al., 2013; Duggan et al., 2014; Pietrusewsky et al., 2014). This Out of Taiwan expansion, beginning in 5-6000BP, reached the Marianas and Near Oceania (New Guinea, Bismarck, Solomon Islands and Makira) around 3500 to 3300 years ago, and Remote Oceania by 3100BP (Duggan et al., 2014). This expansion is believed to have spread Austronesian languages (Hung et al., 2011; Duggan et al., 2014; Ko et al., 2014).

Two major branches of the Austronesian language exist outside of Taiwan: Western Malayo-Polynesian, including Chamorro, and Oceanic (Figure A.3) (Hill et al., 2007; Hung et al., 2011; Vilar et al., 2013; Pietrusewsky et al., 2014). Chamorro is believed to have developed in isolation and is only distantly related to languages in the Philippines and Sulawesi (Vilar et al., 2013; Pietrusewsky et al., 2014). The neighbouring Caroline Islands to the south and east speak Oceanic (Vilar et al., 2013). The current linguistic evidence indicates that the settlement of the Marianas is associated with the Austronesian expansion, but not with the Lapita culture that spread Oceanic throughout much of remote Oceania. The Out of Taiwan expansion is associated the spread of the Neolithic in ISEA, but there is a great degree of local diversity, and mapping the spread of a Neolithic package, or parts of it, has yet to be achieved (Hill et al., 2007).

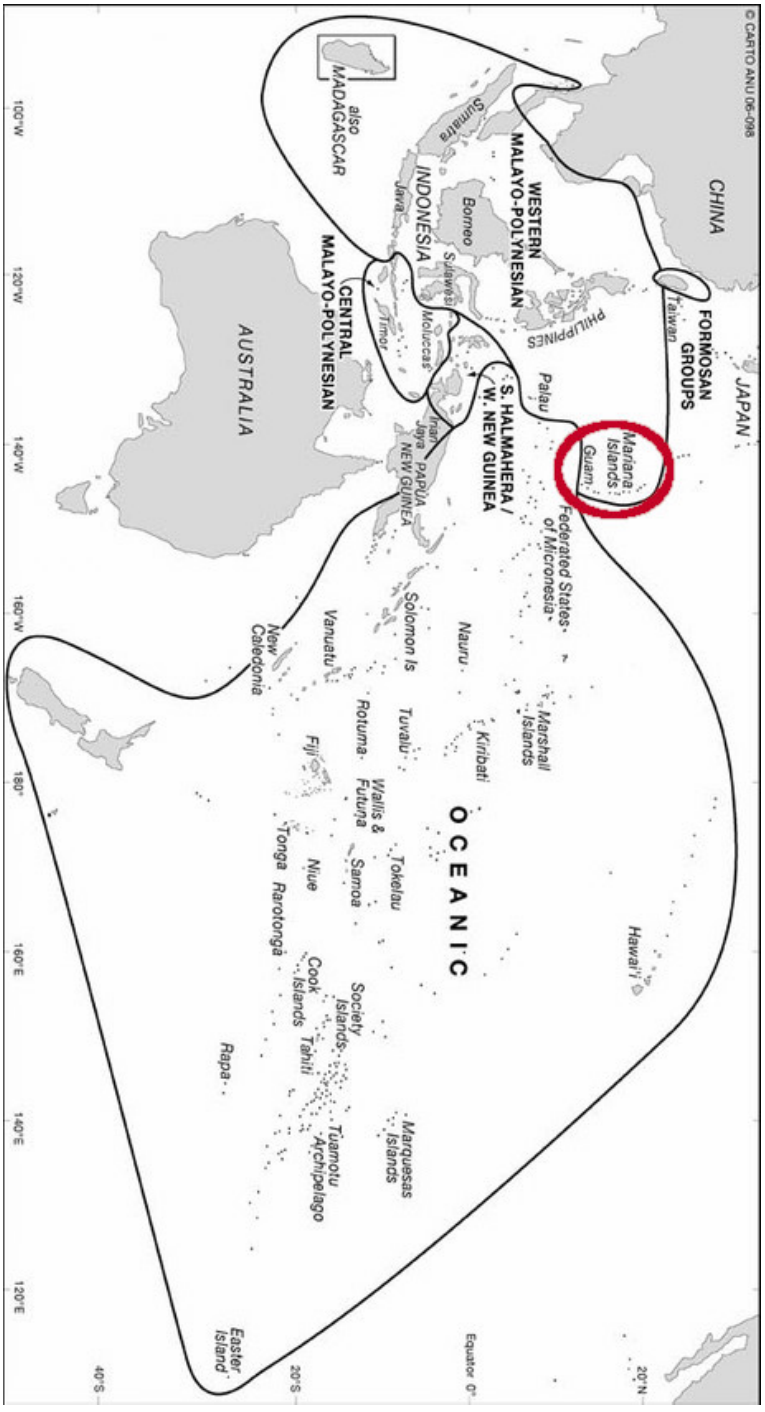


FIGURE A.3: Map of Austronesian languages, with the Marianas circled Pawley (2006).

The Marianas Red pottery, unique to the Marianas, is the first evidence of human occupation (Fitzpatrick and Callaghan, 2013; Vilar et al., 2013). The most similar pottery in style and decoration to Mariana Red can be found on Luzon in the Philippines (Hung et al., 2011). Despite linguistics and archaeology indicating the Philippines as a most likely source population, there is much debate. Sea travel simulations by Fitzpatrick and Callaghan (2013) indicated that New Guinea or the Bismarcks were a more likely origin.

A.3.3 Dietary analysis of the Marianas

The Marianas have relatively small and comparatively simple ecosystem in which terrestrial dietary resources have low carbon and nitrogen ratios, whilst the marine resources have high carbon and nitrogen ratios. The only terrestrial animals are crabs, fruit bats, monitor lizards and bird species. The majority of plants in the Marianas are C3, and the most significant C4 plants are sugar cane and seaweed (Ambrose et al., 1997).

Archaeological evidence indicates that fish and terrestrial tree and root crops are important across all of Chamorro prehistory (Pate et al., 2001). Faunal remains are dominated by fish and shellfish, of both near-shore and deep-water species (Ambrose et al., 1997). During the Latte Period, ceramic forms change indicating an emphasis on boiling and storage. Pestles and mortars, often associated with rice production, also appear at this time. These material culture changes, coupled with the increase in inland settlements, indicate increased production and reliance on plants during this time (Ambrose et al., 1997; Moore, 2015).

McGovern-Wilson and Quinn (1996) analysed 10 individuals from the late Pre-Latte Period of Saipan, all of whom showed a high reliance on marine resources. Comparison to previous research by Hanson (1989) and Quinn (1990) of six Latte and a number of historic individuals shows a decline in nitrogen levels through time, but consistent carbon levels. This has been interpreted as a move from marine to terrestrial C4 resources. Ambrose et al. (1997) analysed carbon and nitrogen values from several Latte Period individuals from Rota (n = 10), Saipan (n = 9) and Guam (n = 5). The results indicated a reliance on marine resources, and they concluded that the Chamorro diet of Guam and Rota relied mainly on C3 plants with some deep-water fish. In contrast, the individuals from Saipan consumed less marine resources, but had a greater reliance on C4 plants. The known C4 plants in this area are sugar cane or seaweed. Pate et al. (2001) analysed 12 individuals from Rota dating to the Latte period, and similar carbon and nitrogen means and ranges were obtained as from the Rota samples. On average, marine foods contributed 20% of the diet, but the range was between 10 and 40%, and it appears that there was intra-population differences between those who relied largely on a terrestrial diet and those who consumed deep-water fish. The Latte period diets in Saipan (McGovern-Wilson and Quinn, 1996) showed a much lower nitrogen level, but a high carbon level, indicating less marine consumption and a greater reliance on C4 plants. In contrast, the pre-Latte individuals had much higher marine reliance.

A.3.4 Genetic analysis of the Marianas

Vilar et al. (2013) analysed the HVS1 of 105 Chamorros (85 of which were from Guam), 17 Saipan islanders of Carolinian ancestry, and 210 from Palau, Yap and the Caroline Islands. Further whole mitogenome analysis revealed some Chamorro specific lineages. Around 92% of Chamorros belonged to mitochondrial haplogroup E, E1 (c.27%) and E2 (c.65%). The other 8% of Chamorros belonged to haplogroup B4: B4 accounted for 100% of the Carolinian Saipan population. A unique Chamorro B4 haplotype, B4a1a1a+C16114T, was found in Guam and Rota.

Haplogroup E, which includes E1 and E2, has been dated, using a molecular clock, to have arisen around 30,000 years ago. Although the oldest sample with this haplogroup which dates to 8,0608,320 cal. BP, was from southern China, it is presently very uncommon in this area. The modern distribution of E is among Austronesian-speaking groups in Taiwan, the Philippines, Malay Peninsula, Micronesia and ISEA (Friedlaender et al., 2007; Duggan et al., 2014; Ko et al., 2014). The presence of E1 and E2 in both the Philippines and the Marianas, and its high frequency among the Chamorros, led Vilar et al. (2013) to conclude that these lineages arrived with the earliest settlers from ISEA c.4000BP.

The ancestral B4a1a1a is known as *the Polynesian motif*". It has been found in high frequencies throughout Micronesia, Melanesia and Polynesia, but in low frequencies in ISEA (Hill et al., 2007). The genetic homogeneity of the unique B4a1a1a+C16114T suggests a more recent arrival, and has been hypothesised as being linked to the transition to the Latte period. However, as B4a1a1a+C16114T is a branch of the Polynesian motif, associated with Remote Oceania, which has neither rice cultivation nor *latte* stones, it is more likely that it is not associated with the Latte period transition (Vilar et al., 2013).

A.3.5 Naton Beach Site

Naton Beach Site is located in northern Tumon Bay, Guam. Excavations from 2006-2008 uncovered 370 burials containing 430 individuals, 170 Pre-Latte and 260 Latte. This is the largest Pre-Latte burial site found to date. Radiocarbon dating and artefact analysis indicated use of the site from the middle of the Pre-Latte period in 800BC until the early historical period, a period of approximately 2000 years. Preservation at the site is poor due to leaching, as well as more recent animal and human interaction at the site (Walth, 2014).

Several of the burials contained grave goods, which can be used to provide information on the lives of these individuals. A small number of fish bones were found, belonging to both in-shore reef species and those that are found in both reef and open sea environments; however, due to the small bone size of this latter group, it is thought they were most likely caught close to the shore. Some burials contained large shell fishhooks, which indicate

open-ocean fishing. Two bird bones were found, and sling stones and ground stones suggest that some terrestrial hunting and plant preparation occurred. Associated pottery was most likely used for cooking, not storage, but it is not indicative of terrestrial or marine resource use (Walth, 2014).

A change in grave goods can be seen during the Latte period, with presence of adzes, changes to ceramic styles, greater fish variety and greater evidence of hunting and terrestrial plant processing. Dental and skeletal morphological differences were observed between Pre-Latte and Latte individuals, potentially due to different genetic origins of these groups, but possibly as a result of adaptation to the different lifestyle. Betel nut chewing and dental incising were found in Latte individuals but not in the earlier Pre-Latte people. Yaws was present in some of the Latte skeletons, and the arrival of this disease may be resultant of human migration (Walth, 2014).

A.4 Methodology

A.4.1 Samples

The two individuals used in this study are from burials 161 and 272. Burial 161 contained a young adult, probable male, buried with a shell bead. The second lower right molar (LRM2) was taken for analysis, and this individual underwent radiocarbon, stable isotopic (carbon and nitrogen) and aDNA analysis. A probable female aged 18-25 was uncovered in burial 272. This grave contained a shell bracelet and 422 shell beads, making this one of the wealthiest burials. Of note, this is one of only 12 individuals, all Pre-Latte, to have staining due to yellow ochre, further suggesting this was an important individual in life. A petrous bone was taken for ancient DNA analysis.

A.4.2 Radiocarbon dating

Radioactive carbon, ^{14}C, is reflective of atmospheric radiocarbon, being ingested directly or indirectly from plants. When an organism dies, this radiocarbon is not replaced and decays at a steady rate. By measuring the remaining radiocarbon, it is possible to date when the organism died. Radiocarbon dating was undertaken on burial 161 at ORAU at the University of Oxford by Dr. Peter Ditchfield. Raw BP dates were calibrated using Oxcal 4.3.

A.4.3 Isotopic analysis

Dietary stable isotopes were analysed at RLAHA as in 4.3. Oxygen and strontium was analysed from both samples, as well as four other Pre-Latte Guamanian samples, at the University of Oxford. These were compared to published data.

A.4.4 Ancient DNA

Ancient DNA analysis was conducted following the methodology outlined in 4.1. Both individuals were sequenced on a single lane alongside 10 other individuals from other projects. Burial 161 was further sequences with three additional libraries on a lane with one other sample.

A.5 Results

The uncalibrated BP radiocarbon date from burial 161 was 2483±27. Using Oxcal, a calibrated date of 774-509BC was assigned with a 95% probability.

Only burial 161 passed the Carbon:Nitrogen ratio test for dietary isotope analysis, with a resulting δ^{13}C value of 18.07, and a δ^{15}N value of 9.42. The two individuals (161 and 272) had δ^{18}O VSMOW (drift corrected) values of 23.500 and 23.954 respectively, and burial 272 had a $^{87}Sr/^{86}Sr$ of 0.709156. When compared to the other four Pre-Latte Guamanian, these values were similar, with oxygen values being between 23.746 and 24.764, and strontium values between 0.709112 and 0.709166.

Both samples had low DNA coverage, due to the DNA being extremely damaged. This was the case even after undertaking more sequencing reads for burial 161. Due to this low coverage and damage, it was not possible to determine the mitochondrial haplogroup to any level from either individual.

A.6 Discussion

The radiocarbon result confirmed that burial 161 was Pre-Latte, which acts as a confirmation of the artefact topological dating of the site. The δ^{18}O and $^{87}Sr/^{86}Sr$ results were all local to the Marianas. This shows that both burial 161 and 272, and the other four individuals analysed at Oxford, were born locally. This does not disprove a large-scale migration to the archipelago initiated by the transition to the Latte period, as more sampling and results are required.

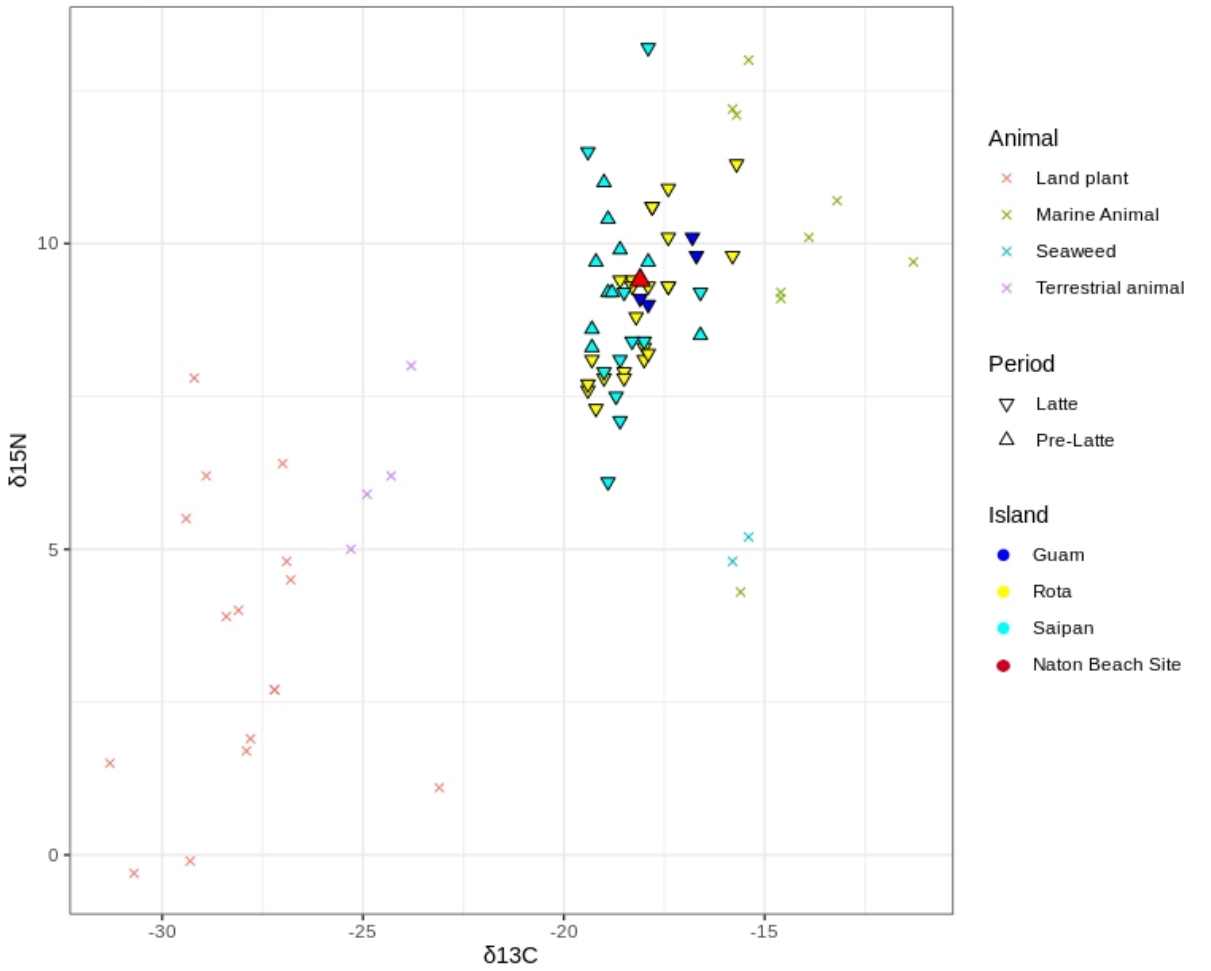


FIGURE A.4: Dietary isotopes of ancient published human and modern reference material and the Naton beach individual, burial 161, from this study. The human samples are represented in the legend by their island location.

As can be seen in the scatter plot (**Figure A.4**), the Naton Beach individual 161 has a similar isotopic ratio to other prehistoric individuals from the Marianas. However, although its δ^{15}N value is comparable to those from Latte Guam (Ambrose et al., 1997), the δ^{13}C value is amongst the lowest of these. This is possibly a result of burial 161 either consuming more reef fish than pelagic fish, or more C3 plants, than the later Latte individuals. A similar difference can be seen between Pre-Latte and Latte populations on Rota, which was concluded to be due to increased exploitation of C4 plants, such as seaweed and sugar cane (Ambrose et al., 1997; Pate et al., 2001). It is possible that the percentage of marine input could be biased by the number or species of reference plants/animals included in the analysis. The dietary isotopic values from burial 161 are similar to the average Pre-Latte individuals from Saipan. The Pre-Latte Guamanian sample sequenced as part of this project has a similar isotopic value to the published Latte Guamanians. However, in all published populations, there is a wide range of values seen across the samples and, due to being a single individual, burial 161 from Naton Beach may not be representative of the Pre-Latte period on Guam.

DNA recovered from the two individuals was too badly preserved to undergo ancient DNA analysis. The samples were since sent to Harvard University to undergo whole genome and mitochondrial capture. Even obtaining the mitochondrial haplogroup alone could reveal important details about genetic continuity and the Pre-Latte population. However, although it is possible that burial 161 is female and burial 272 appears to have some Y-chromosome reads, both samples have failed the preliminary tests at Harvard, further supporting the fact that the DNA is too badly damaged to recover any useful information from these samples.

A.7 Comments

A paper analysing two pre-Latte individuals from Guam was deposited into bioRXiv on October 14th 2020 (Pugach et al., 2020). However, it was too late to include the results into the discussion of Appendix Chapter A due to time constraints.

Appendix B

Mitochondrial analysis of modern Cretan DNA

B.1 Aims and objectives

To identify potential genetic continuity on Crete, a database of local mitogenomes was generated. Mitogenomes were targeted, as opposed to autosomal or Y-chromosomal DNA, for several reasons. Firstly, published autosomal DNA from Crete was already freely available, which was not the case for mtDNA. Secondly, it was more cost effective to create a sizeable database of mitogenomes than the other DNA markers. Furthermore, as knowledge of the mtDNA mutation rate and phyolgenetic tree is well understood, it should be possible to identify Cretan-specific haplogroups. The modern mitogenomic data was compared to the ancient Armenoi population, as well as data from Cyprus and the Greek mainland, to identify differences in diversity.

B.2 Published data

The use of modern DNA to explain past migrations to Crete has already been presented in Section 5.3.1. To summarise, the only published mitochondrial DNA study of Crete is by Martinez et al. (2008), who only produced D-loop sequences. Full mitogenomes were generated in studies by Olivieri et al. (2006), Pala et al. (2012) and Sahakyan et al. (2017), but these were haplogroup-specific studies and, as such, do not represent the mtDNA diversity of Crete.

B.3 History of Crete after the Bronze Age

To better understand differences between modern and ancient populations, it is necessary to summarise the migration events in Crete after the end of the Bronze Age. Archaeological and archaeogenetic studies of Crete are explored in Chapters 5 and 6. To date, no ancient DNA analysis has been conducted on post-Bronze Age samples from the island, so this section will deal with historical texts.

The Iron Age (1050-700 BC) in Crete is characterised by a withdrawal from settlements on coastal regions. This changed in the Archaic period with the rise of multiple competing and trading city-states. From the Archaic until the Hellenistic era, Crete was a major port connecting Egypt, Phoenicia and Greece (Day, 2014). The Odyssey (19.4), supposedly written in the Archaic Period, describes Crete as being a "confusion of tongues" with many different populations of Greeks present (Homer, 1996; McEnroe, 2010).

In 67 BC, Crete was conquered by the Romans and later became part of the Byzantine (Eastern Roman) Empire (Day, 2014). During the 9th century AD, the island was briefly conquered by Arabs originating in Andalusia (Iberia), who established a pirate state on the island. Very little evidence survives from Arabic Crete and linguistic evidence suggests a limited impact on the populace. This is likely due to the reconquest by the Byzantines 140 years later, as they slaughtered or expelled many Arabs. This may have created a population void, as it is recorded that Byzantine authorities brought in settlers of "Romans (Byzantines) and Armenians" (Martinez et al., 2007; Paschou et al., 2014; Day, 2014; Drineas et al., 2019). The LM III necropolis of Armenoi is named after the local town, which dervies its name from the Armenian troops who settled here in *c.* 960 AD (Chappell and Allender, 2018). In 1210 AD, Venetians conquered the island. In response to armed rebellions, they brought in a large military force and 2000 settlers, many of whom were from the Peloponnese. There are significant cultural impacts as a result of this Venetian occupation, but it has been suggested that the presence of the Venetian immigrants was confined to the major urban centres (Day, 2014; Drineas et al., 2019). The Ottomans conquered the island in 1699 AD and controlled it until 1898 AD when Crete received its independence. At this time, many Jews, Armenians, Turks and other minorities left. Crete was united with Greece in 1913, and in 1923, a Greek-Turkish population exchange was undertaken in which a large number of Muslims and Turks left, while Anatolian Greeks and Christian Turks entered Crete (Herzfeld, 2003; McEnroe, 2010; Paschou et al., 2014; Day, 2014).

Historical sources of migrations and invasions can be over- or under-exaggerated depending on the outlook of the author and the society at the time of composition of the text. Terminology can also often be confusing, as the Andalusian Arabs would have also included Iberian converts and admixed groups. Similarly, Byzantines during the reconquest of Crete would have considered many peoples from the Balkans to Syria as "Romans", and Ottoman Turk and Venetian forces are unlikely to have been composed solely of those specific ethnicities (Drineas et al., 2019).

B.4 Methodology

B.4.1 Sampling

Modern DNA was collected from native Cretans, mainland Greeks, and Cypriots (Figures B.1, B.2 and B.3). Maps of collected samples were created using information from GADM (2020). The birthplace, year of birth, and ethnicity/language of an individual's grandparents was recorded, in particular the maternal grandmother. Donors had to complete a consent form outlining the purpose of the project, what the samples would be used for, their right to withdraw from the study at any time, and their guaranteed anonymity. Cheek cells were collected for modern DNA analysis. Donors rubbed forensic buccal swabs against the inside of their cheeks for 30 seconds, whilst avoiding the tongue and teeth, before leaving the swab inside a sealed tube.

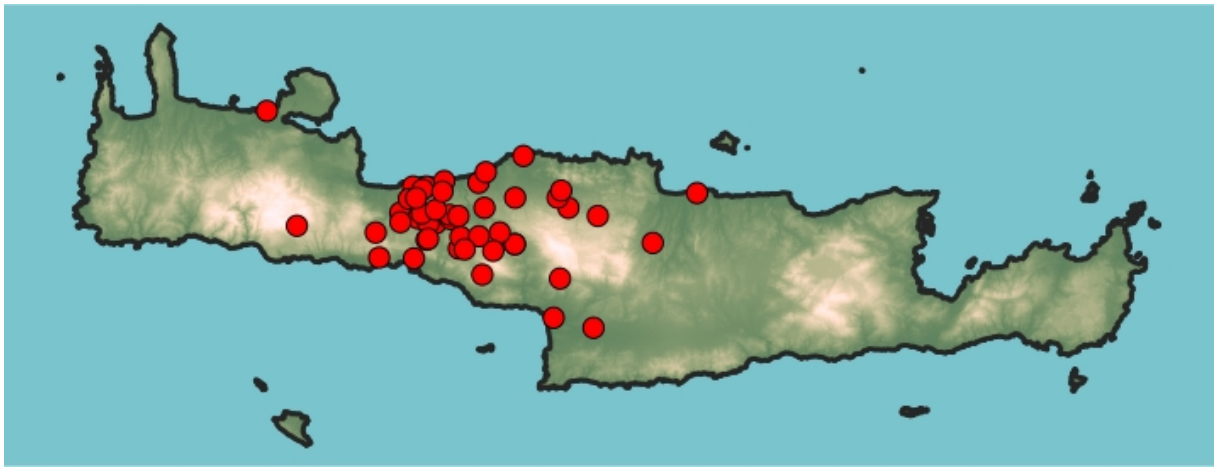


FIGURE B.1: Map of the sites in Crete where samples were attained. A list of all the locations and co-ordinates is located in the appendix (Table B.3).

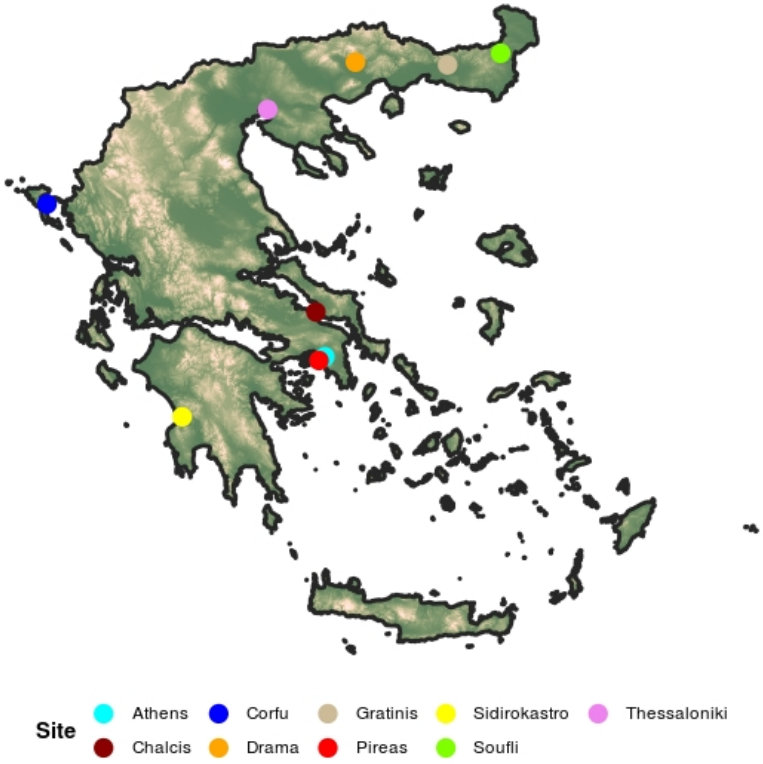


FIGURE B.2: Map of the sites in mainland Greece where samples were attained.

FIGURE B.3: Map of the sites in Cyprus where samples were attained.

Samples where the control region sequences had previously been analysed (Irwin et al. (2008))

were re-amplified and sequenced. A further 53 unpublished Athenian sequences from Dr. Anna Olivieri (University of Pavia) were also included in the phylogeographic analysis.

B.4.2 DNA extraction

A Pure Link Genomic DNA Kit (ThermoFisher Scientific) was used for DNA extraction. The cotton of the buccal swab was separated from the stick and placed in a sterile 2ml microcentrifuge tube using sterilised tweezers. 400μl of PBS and 20μl of proteinase K were then added to the sample, and mixed well through pipetting. 420μl of PureLink Genomic Lysis/Binding Buffer was added to the lysate, which was then briefly vortexed. From the incubation stage onwards, the manufacturers protocol was followed. DNA was eluted in 100μl of elution buffer. Extracted DNA samples were stored in 1.5ml centrifuge tubes at -20°C.

B.4.3 Amplification

Polymerase Chain Reaction (PCR) was used to increase the targeted (mitochondrial) DNA. The entire mitogenome was amplified in two overlapping fragments using two separate primer sets (**Table B.1**).

Fragment 1	5871F	GCTTCACTCAGCCATTTTACCT
	13829R	AGTCCTAGGAAAGTGACAGCGA
Fragment 2	13477F	GCAGGAATACCTTTCCTCACAG
	6345R	AGATGGTTAGGTCTACGGAGGC

TABLE B.1: Primers used for each fragment of the mitogenome.

The master mix for each fragment was prepared separately (**Table B.2**). 2μl of DNA extract was added to 24.5μl of the master mix. PCR was conducted in an Applied BioSystems 2720 Thermal Cycler. The PCR program was as follows; 94°C for 2 minutes, with 30 cycles of 30 seconds at 94°C, 30 seconds at 55°C, 9 minutes at 65°C, and then 72°C for 10 minutes. Gel electrophoresis was conducted to visually test whether the PCR was successful.

Master mix	**Volume (μl)**	**Concentration**
Nuclease-free water	11	
GoTaq®Long PCR Master Mix (PROMEGA) 2x	12.5	MgCl2 [2.5mM]
Forward Primer (10pmol/μl)	0.5	0.4μM
Reverse Primer (10pmol/μl)	0.5	0.4μM

TABLE B.2: Master mix ingredients.

B.4.4 Purification, quantification and dilution

Purification was undertaken to remove excess nucleotides and primers. The Promega Wizard®SV Gel and PCR Clean-Up System was used for purification following the manufacturers protocol, with the exception that elution buffer, not nuclease-free water, was used at the elution stage.

Quantification of each sample was necessary in order to create the correct dilution of each sample before equimolar mixing. A Thermo Fisher Qubit®Fluorometer kit was used on a Qubit®3.0 following the manufacturers protocol. Samples were diluted to achieve a final volume of 1ng/μl. When diluted, 20μl of each fragment of the same sample was then placed into a well on a 96-well plate and sent for next-generation sequencing on a MiSeq250 (PE-Nano x1) at the Earlham Institute, Norwich.

B.4.5 Bioinformatic analysis

Sequences were received as paired-end FASTQ files. EAGER (Efficient Ancient Genome Reconstruction) (Peltzer et al., 2016) was used to align sequences to the rCRS. The options BWA-MEM and HaplotypeCaller were selected to create BAMs (Binary Alignment Map) and VCFs (Variant Call Files). Within HaplotypeCaller, minimum coverage was set to 2 and the ploidy was set to 100; although the ploidy of the mitogenome is 1, setting it to 100 provides the percentage represented by each allele and, therefore, heteroplasmies can be more easily identified. All other settings were left as default.

EAGER produces a report displaying coverage. Samples under 99% 1x coverage were assessed individually using IGV v2.4.16 (Robinson et al., 2017) to determine whether they could be used to identify the haplotype. For samples with over 99% coverage, their VCFs were filtered by allele frequency to determine mutations. Allele frequencies ≥ 0.7 were considered as true mutations. Frequencies between 0.69 and 0.3 were assigned to be heteroplasmies and visually checked using IGV to determine if they were a result of poor alignment. Below 0.3, differences to the reference were deemed likely to be sequencing errors. Unstable 'hot spot' mutations, as denoted in PhyloTree Build 17 (Van Oven, 2015), were not considered for phylogenetic construction as their disproportionately fast mutation rate hinders phylogenetic analysis (Soares et al., 2009). Haplotypes were assigned using Haplogrep2 (Weissensteiner et al., 2016).

The 'cleaned' mutation lists were converted into FASTA files, and the sequences analysed alongside publicly available data. A phylogeographic tree was created using mtPhyl v4.015 (https://sites.google.com/site/mtphyl/home) with PhyloTree Build 17, and compared to haplogroup-specific trees to identify the possibility of location-specific haplotypes. Heteroplasmies that were not unique to the individual were set as mutations, and the FASTA files

were edited accordingly.

B.5 Results and discussion

In total, 247 individuals were successfully sequenced as part of this thesis: 113 Cretans, 90 other Greeks, and 44 Greek Cypriots (including the 61 reprocessed Greek individuals from Irwin et al. (2008)). Published data included 2 Cretans, 79 other Greeks and 2 Cypriots (from (Olivieri et al., 2006; Irwin et al., 2008; Pala et al., 2009; Pala et al., 2012; Behar et al., 2012; Fernandes et al., 2012; Costa et al., 2013; Kushniarevich et al., 2013; Raule et al., 2014; De Fanti et al., 2015; Mallick et al., 2016; Yacobi and Bedford, 2016; Pereira et al., 2017; Batini et al., 2017) and 53 sequences from Dr. Olivieri) **Table B.4**.

Of the 115 Cretans analysed in this study, 66 (57%) belonged to the same haplotype, a lineage of H8b, with no sub-branches observed. The consent forms were reassessed, but no familial links could be established. Based on the mitochondrial molecular clock (Soares et al., 2009; Fernandes et al., 2015; Gandini et al., 2016), at least one mutation would be expected to have happened within the last c.2500-3600 years, which suggests that this lineage is recent. The samples were added to a phylogenetic tree of H8. Mitochondrial haplogroup H8 is composed primarily of three sub-branches: H8a, H8b and H8c. While H8c is comprised mainly of pan-European individuals, H8a is found only in Armenia and the eastern Mediterranean. In contrast, the majority of published samples from H8b belong to a sub-branch called H8b1, of which the majority are eastern Russian and Chinese. European samples have also been observed splitting from basal H8b, however these are represented by three single sample from Wales, France and Italy respectively. Rho age calculation indicated that this branch was under 200 years old. The young age of the branch, that no differing mutations were observed, and that all the individuals were found in a small geographic area, suggest that this is a local occurrence and does not reflect the whole of Crete. As these samples caused significant bias in the dataset, they were removed when making overall conclusions based on the mitochondrial make-up of Crete.

The remaining 49 Cretans were compared to haplogroup-specific trees composed of published and unpublished data. This was undertaken to try to identify if geographic-specific haplogroups were present in Crete, Greece, and/or Cyprus. Two potential geographic-specific haplogroups were found, including a Cretan sub-haplogroup of N1b1a2 and a Cypriot sub-haplogroup of H13a2b3. N1b1a2 is largely found in the South Caucasus and Near East, whereas H13a2 is found quite widely, from Iran to Scotland. More in-depth surveys of these haplogroups would be required to make any commentary about the arrival and timing of these haplogroups to these areas.

Haplotypic diversity differed between Crete (**Figure B.4**), the rest of Greece (**Figure B.5**),

and Cyprus (**Figure B.6**). Crete has a lower proportion of H haplotypes than the rest of Greece or Cyprus, and a larger proportion of JT and UK haplotypes. Haplogroup X appears absent from Crete, yet is present in both Cyprus and the rest of Greece. The majority of the Cretan samples originate from the area around the Armenoi necropolis, therefore, these samples are more representative of that area than the island as a whole. Differences also exist between Cyprus and Greece, with Cyprus having a larger percentage of sequences belonging to haplogroup N1 and less to JT. The most common haplogroups across all three locations are H, JT, UK and N1. Haplogroup H is the most common haplogroup in Europe comprising 40-60% of total diversity and around 10-30% in the Near East, but its origins and spread are unclear (Brotherton et al., 2013; Omrak et al., 2016). Most of Mesolithic Europe is represented by haplogroup U, with K1c present in Mesolithic Greece, and J in Mesolithic Sardinia. The presence of most of the JT and other K1 branches (including K1a), and N1 haplogroups are associated with the arrival of the Neolithic (Brandt et al., 2013; Hofmanová et al., 2016; Pereira et al., 2017; Modi et al., 2017).

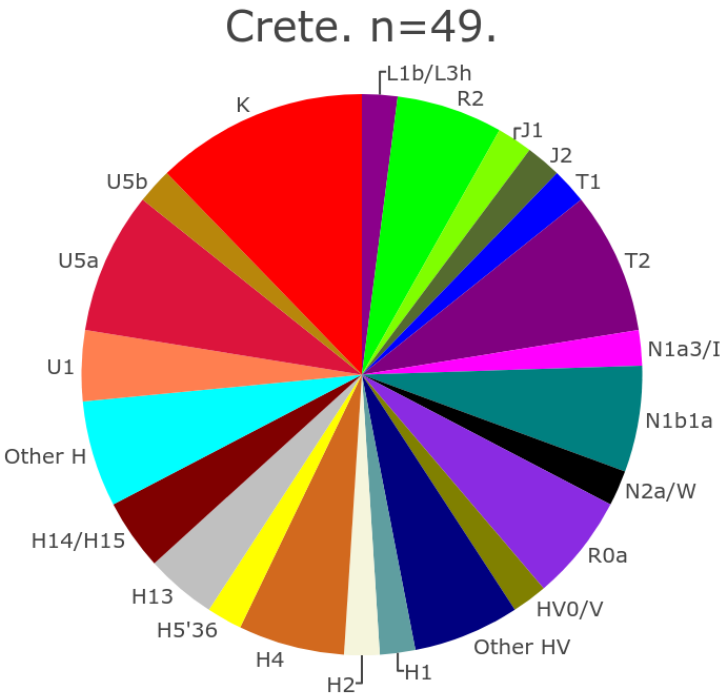


FIGURE B.4: Mitochondrial haplogroups of Crete, excluding H8.

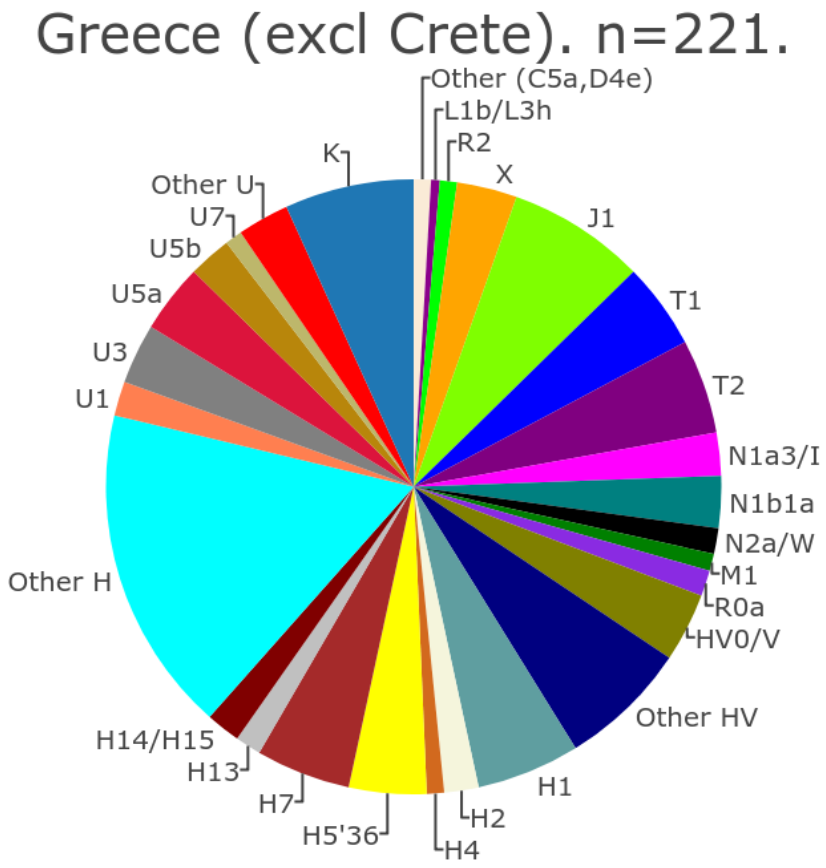


FIGURE B.5: Mitochondrial haplogroups of Greece, excluding Crete.

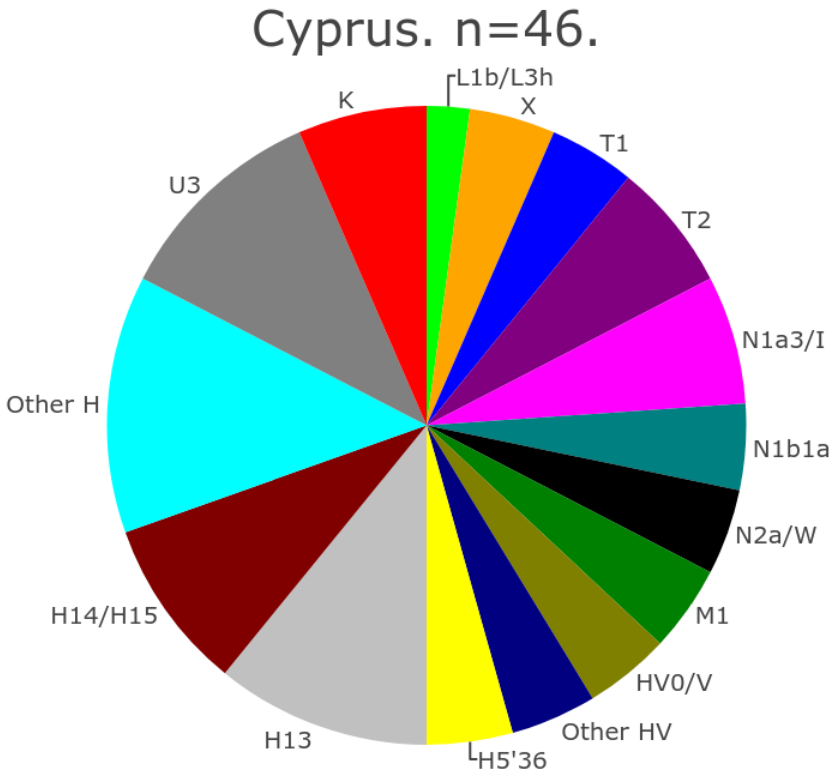


FIGURE B.6: Mitochondrial haplogroups of Cyprus.

The modern haplotypic diversity of the Armenoi area differs from the Late Bronze Age cemetery. After removing maternal or potentially maternally related ancient individuals, only 17 (of 23) remained. The majority of the ancient population belong to haplogroup H. Several of the lineages represented in the ancient population were not present in modern day Crete (**Tables 6.3 and D.2**).

It is clear from the haplotypic diversity that these locations have undergone differing migration and population expansion and contraction events. To further understand the migrations in these areas, large-scale sampling is required. The mitochondrial diversity of the ancient Armenoi population differs from that of modern Cretans, including the absence of certain lineages present in the ancient population. These differences argue against any type of mitochondrial genetic continuity, and instead reflect the severe demographic changes that Crete has undergone since the Bronze Age.

B.6 Data used for mitochondrial analysis of modern Crete.

Site	longitude	latitude
Agros	33.0169873	34.9204806
Agios Andronikos	34.1643200999999	35.5031406
Ammochostou	33.3695018	35.1751369
Avgorou	33.8522923	35.0385384
Pyla	33.6958809	35.009574
Deryneia	33.9582783000001	35.0586943
Famagusta	33.919245	35.1149116
Frenaros	33.8969328000001	35.043964
Fterikoudi	33.0690537	34.9426694
Gastria	33.9805756000001	35.3338704
Limassol	33.0226173999999	34.7071301
Güzelyurt	32.9775675	35.2123165
Nicosia	33.3822764	35.1855659
Paphos	32.4297369	34.7720133
Paralimni	33.986149	35.0352421
Rizokarpasou	33.0331931000001	34.7038396
Vasili	34.1587575999999	35.4516433

TABLE B.3: Table of sites where mitochondrial samples were collected (Figure B.1).

NCBI or lab ID	**Macro-Haplo-group**	**Haplo-group**	**Country**	**Region**	**Reference**
1.A12	R0	H2a5b	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.A7	R0	H12a	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.B7	U-K	U5a2b	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.D3	R0	H1b	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.E10	U-K	U5a1g	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.E12	R0	H1at1a	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.F1	R0	H7b1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.F3	R0	H1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.F4	C	C5a1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.F6	R0	H55 +153	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.F7	R0	H	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.F9	R0	H	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.G1	U-K	K1a2	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.G7	R0	H5	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.H3	JT	J1b2	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.H6	X	X2i1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
1.H7	R0	H	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.E10	U-K	U3b2a1	GRC	Northern Greece	D-loop published in Irwin et al. 2008

2.E4	R0	H33	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.E5	U-K	U4a	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.E7	U-K	U1a1b	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.E9	R0	HV +16311	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.F1	R0	H +195 +146	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.F3	N2	W5	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.G6	U-K	K1a28	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.G7	R0	HV12a	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.G9	X	X2o	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.H1	R0	H14a2a	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.H2	U-K	K1a4f	GRC	Northern Greece	D-loop published in Irwin et al. 2008
2.H5	R0	H1c	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.A10	R0	H5	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.A12	U-K	U5a1a1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.A5	JT	J1c5b	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.A9	R0	HV4a2a	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.B12	R0	H11a1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.B3	R0	H +16129	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.B4	R0	H66	GRC	Northern Greece	D-loop published in Irwin et al. 2008

3.C10	U-K	K1b1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.C2	R0	H34	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.D3	N1a	I5a2	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.E2	R0	HV4a2B	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.E5	U-K	U5a1a1	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.E9	U-K	U7a	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.F11	JT	J1c +16261	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.H10	R0	H	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.H6	R0	H	GRC	Northern Greece	D-loop published in Irwin et al. 2008
3.H7	R0	H55b	GRC	Northern Greece	D-loop published in Irwin et al. 2008
AK02A	D	D4e1	GRC		This study
AK02B	R0	HV1b	GRC		This study
AK03	R0	H5a	GRC	Corfu	This study
AK04	JT	T1a1	GRC	Corfu	This study
AK05	R0	HV +16311	GRC	Athens	This study
AK06	R0	H	GRC	Central Greece	This study
AK07	R2	R2	GRC	Crete	This study
AK08	R0	HV4a2a	GRC	Crete	This study
AK09	U-K	U3b2a1	GRC	Central Macedonia	This study
AK10	R2	R2	GRC	Crete	This study
AK11	R0	H14a	GRC	Crete	This study
AK12	JT	T2e	GRC	Athens	This study
AK13	JT	J1c2e	GRC	Peloponnese	This study
AK14	R0	HV0	GRC	Crete	This study

AK15	U-K	U5b1 +16189 +@16192	GRC	Western Macedonia	This study
AK16	R0	H7g	GRC	Crete	This study
AK17	R0	R0a3a	GRC	Athens	This study
AK18	R0	R0a3a	GRC	Athens	This study
AK19	R0	H7	GRC		This study
AK20	U-K	U5b2a1a	GRC		This study
AK21	R0	H2	GRC		This study
AK22	R0	H4a1	GRC		This study
AK23	R0	HV +16311	GRC		This study
AK24	JT	J1c	GRC		This study
AK25	R0	V1a	GRC	Crete	This study
AK26	JT	J1c	GRC	Crete	This study
C.A4	R0	H	GRC	Northern Greece	This study
C.A6	R0	V1a1	GRC	Northern Greece	This study
C.A8	R0	HV +16311	GRC	Northern Greece	This study
C.A9	R0	H14b	GRC	Northern Greece	This study
C.B4	R0	HV4a2a	GRC	Northern Greece	This study
C.B5	R0	H20a2	GRC	Northern Greece	This study
C.D6	JT	J1c2e	GRC	Northern Greece	This study
C.E4	U-K	U3b2a	GRC	Northern Greece	This study
C.E6	R0	H	GRC	Northern Greece	This study
C.E9	R0	R0a1 +152	GRC	Northern Greece	This study
C.G4	R0	H12a	GRC	Northern Greece	This study
C.G6	R0	H55 +153	GRC	Northern Greece	This study

C.H3	R0	HV9	GRC	Northern Greece	This study
C.H4	N1b	N1b1a	GRC	Northern Greece	This study
Crete05	JT	T2b37	GRC	Crete	This study
Crete08	JT	T1a1	GRC	Crete	This study
Crete14	N1a	I5c1	GRC	Crete	This study
Crete15	R0	H1e1b1	GRC	Crete	This study
Crete16	JT	J2a1a1	GRC	Crete	This study
EF060329	M	M1a1	GRC	Crete	Olivieri et al. 2006
EF060330	M	M1a1	GRC	Lemnos	Olivieri et al. 2006
GFM001	R2	R2	GRC	Crete	This study
GFM002	R0	H4a1c	GRC	Crete	This study
GFM003	U-K	K1b2a	GRC	Crete	This study
GFM004	JT	T2f1a1	GRC	Crete	This study
GFM005	N2	N2a	GRC	Crete	This study
GFM006	R0	H	GRC	Crete	This study
GFM007	U-K	K1c1	GRC	Crete	This study
GFM008	R2	R2	GRC	Crete	This study
GFM009	R2	R2	GRC	Crete	This study
GFM010	N1b	N1b1a2	GRC	Crete	This study
GFM011	N1b	N1b1a2	GRC	Crete	This study
GFM012	R0	H8b	GRC	Crete	This study
GFM013	R0	H8b	GRC	Crete	This study
GFM014	U-K	K1a3	GRC	Crete	This study
GFM015	U-K	K1a	GRC	Crete	This study
GFM016	R0	R0a5	GRC	Crete	This study
GFM017	R0	R0a5	GRC	Crete	This study
GFM018	R0	R0a5	GRC	Crete	This study
GFM019	R0	H8b	GRC	Crete	This study
GFM020	R0	H2b	GRC	Crete	This study
GFM022	U-K	U1b2	GRC	Crete	This study
GFM023	R0	H14a	GRC	Crete	This study
GFM024	JT	J1c10	GRC	Crete	This study
GFM026	R0	H55b	GRC	Crete	This study
GFM027	JT	T2b37	GRC	Crete	This study
GFM028	R0	H5a1a	GRC	Crete	This study
GFM029	R0	HV7	GRC	Crete	This study
GFM030	R0	H8b	GRC	Crete	This study

GFM031	R0	H15b1	GRC	Crete	This study
GFM032	R0	H4	GRC	Crete	This study
GFM033	R0	H4	GRC	Crete	This study
GFM034	R0	H13a1a	GRC	Crete	This study
GFM035	R0	H13a1a	GRC	Crete	This study
GFM036	JT	T2e	GRC	Crete	This study
GFM037	L1	L1b1a5	GRC	Crete	This study
GFM038	U-K	U5a1b1	GRC	Crete	This study
GFM039	U-K	K1a19	GRC	Crete	This study
GFM040	U-K	U5a2b	GRC	Crete	This study
GFM041	U-K	U5a2b	GRC	Crete	This study
GFM042	U-K	U5b2a1a1d	GRC	Crete	This study
GFM043	U-K	U5a2b	GRC	Crete	This study
GFM044	R0	H8b	GRC	Crete	This study
GFM045	R0	H8b	GRC	Crete	This study
GFM046	R0	H8b	GRC	Crete	This study
GFM047	R0	H8b	GRC	Crete	This study
GFM048	R0	H8b	GRC	Crete	This study
GFM049	R0	H8b	GRC	Athens	This study
GFM050	R0	H8b	GRC	Crete	This study
GFM051	R0	H8b	GRC	Crete	This study
GFM052	R0	H8b	GRC	Crete	This study
GFM053	R0	H8b	GRC	Crete	This study
GFM054	R0	H8b	GRC	Crete	This study
GFM055	R0	H8b	GRC	Crete	This study
GFM056	R0	H8b	GRC	Crete	This study
GFM057	R0	H8b	GRC	Crete	This study
GFM058	R0	H8b	GRC	Crete	This study
GFM059	R0	H8b	GRC	Crete	This study
GFM060	R0	H8b	GRC	Crete	This study
GFM061	R0	H8b	GRC	Crete	This study
GFM062	R0	H8b	GRC	Crete	This study
GFM063	R0	H8b	GRC	Crete	This study
GFM064	R0	H8b	GRC	Crete	This study
GFM065	R0	H8b	GRC	Crete	This study
GFM066	R0	H8b	GRC	Crete	This study
GFM067	R0	H8b	GRC	Crete	This study
GFM068	R0	H8b	GRC	Crete	This study
GFM069	R0	H8b	GRC	Crete	This study

GFM070	U-K	U1a1a2	GRC	Crete	This study
GFM071	R0	H8b	GRC	Crete	This study
GFM072	R0	H8b	GRC	Crete	This study
GFM073	R0	H8b	GRC	Crete	This study
GFM074	R0	H8b	GRC	Crete	This study
GFM075	R0	H8b	GRC	Crete	This study
GFM076	R0	H8b	GRC	Crete	This study
GFM077	R0	H8b	GRC	Crete	This study
GFM078	R0	H8b	GRC	Crete	This study
GFM079	R0	H8b	GRC	Crete	This study
GFM080	R0	H8b	GRC	Crete	This study
GFM081	R0	H8b	GRC	Crete	This study
GFM082	R0	H8b	GRC	Crete	This study
GFM083	R0	H8b	GRC	Crete	This study
GFM084	R0	H8b	GRC	Crete	This study
GFM085	R0	H8b	GRC	Crete	This study
GFM086	R0	H8b	GRC	Crete	This study
GFM087	R0	H8b	GRC	Crete	This study
GFM088	R0	H8b	GRC	Crete	This study
GFM089	U-K	K1a	GRC	Crete	This study
GFM090	R0	H8b	GRC	Crete	This study
GFM091	N1b	N1b1a2	GRC	Crete	This study
GFM092	R0	H8b	GRC	Crete	This study
GFM093	R0	H8b	GRC	Crete	This study
GFM094	R0	H8b	GRC	Crete	This study
GFM095	R0	H8b	GRC	Crete	This study
GFM096	R0	H8b	GRC	Crete	This study
GFM097	R0	H8b	GRC	Crete	This study
GFM098	R0	H8b	GRC	Crete	This study
GFM099	R0	H8b	GRC	Crete	This study
GFM100A	R0	H8b	GRC	Crete	This study
GFM100B	R0	H8b	GRC	Crete	This study
GFM101	R0	H8b	GRC	Crete	This study
GFM102	R0	H8b	GRC	Crete	This study
GFM103	R0	H8b	GRC	Crete	This study
GFM104	R0	H8b	GRC	Crete	This study
GFM105	R0	H8b	GRC	Crete	This study
GFM106	R0	H8b	GRC	Crete	This study
GFM107	R0	H8b	GRC	Crete	This study

GFM108	R0	H8b	GRC	Crete	This study
GFM109	R0	H	GRC	Crete	This study
GFM110	U-K	U3c	CYP	Karpass (Iskele)	This study
GFM111	R0	HV4b	CYP	Larnaca	This study
GFM112	U-K	U3b2a1	GRC	Central Macedonia	This study
GFM113	R0	H7g	GRC		This study
GFM114	JT	T2b4h	CYP	Vasili (Gelincik)	This study
GQ129165	U-K	U5b3b	GRC		Pala et al. 2009
GR1	R0	H80	GRC	Athens	Olivieri unpub.
GR10	JT	T1a1l	GRC	Athens	Olivieri unpub.
GR11	N1b	N1b1a	GRC	Athens	Olivieri unpub.
GR12	JT	J1c8a	GRC	Athens	Olivieri unpub.
GR13	R0	H33a	GRC	Athens	Olivieri unpub.
GR14	R0	H	GRC	Athens	Olivieri unpub.
GR15	JT	T1a10	GRC	Athens	Olivieri unpub.
GR17	JT	T2	GRC	Athens	Olivieri unpub.
GR18	R0	H	GRC	Athens	Olivieri unpub.
GR20	U-K	U3b1a	GRC	Athens	Olivieri unpub.
GR21	JT	T2e	GRC	Athens	Olivieri unpub.
GR22	R0	HV0	GRC	Athens	Olivieri unpub.
GR23	JT	J1c3f	GRC	Athens	Olivieri unpub.
GR24	N2	W6	GRC	Athens	Olivieri unpub.
GR25	R0	H80	GRC	Athens	Olivieri unpub.
GR26	JT	T2b	GRC	Athens	Olivieri unpub.
GR28	R0	H55	GRC	Athens	Olivieri unpub.
GR29	R0	H11a2	GRC	Athens	Olivieri unpub.
GR30	JT	T1a10	GRC	Athens	Olivieri unpub.
GR31	N1b	N1b1a	GRC	Athens	Olivieri unpub.
GR34	R0	H7g	GRC	Athens	Olivieri unpub.
GR35	R0	H7	GRC	Athens	Olivieri unpub.
GR36	R0	H5a3a +152	GRC	Athens	Olivieri unpub.
GR38	U-K	K1a3a3	GRC	Athens	Olivieri unpub.
GR4	X	X2d1	GRC	Athens	Olivieri unpub.
GR40	R0	H14a	GRC	Athens	Olivieri unpub.
GR42	R0	H7c1	GRC	Athens	Olivieri unpub.

GR43	R0	HV0c	GRC	Athens	Olivieri unpub.
GR44	N1b	N1b1a2	GRC	Athens	Olivieri unpub.
GR45	N1a	I5	GRC	Athens	Olivieri unpub.
GR47	U-K	U5a1g1	GRC	Athens	Olivieri unpub.
GR48	M	M1a1	GRC	Athens	Olivieri unpub.
GR49	R0	H	GRC	Athens	Olivieri unpub.
GR50	JT	J1c +16261	GRC	Athens	Olivieri unpub.
GR51	U-K	U5b2b	GRC	Athens	Olivieri unpub.
GR52	R0	H80	GRC	Athens	Olivieri unpub.
GR53	JT	T2b3 +151	GRC	Athens	Olivieri unpub.
GR54	U-K	U9	GRC	Athens	Olivieri unpub.
GR57	R0	H105	GRC	Athens	Olivieri unpub.
GR62	R0	H5b3	GRC	Athens	Olivieri unpub.
GR64	R0	H55	GRC	Athens	Olivieri unpub.
GR66	U-K	K1a4a1	GRC	Athens	Olivieri unpub.
GR67	R0	H1b1e	GRC	Athens	Olivieri unpub.
GR68	U-K	U5a1b	GRC	Athens	Olivieri unpub.
GR70	U-K	U3b1a	GRC	Athens	Olivieri unpub.
GR71	JT	J1c17	GRC	Athens	Olivieri unpub.
GR73	R0	H1 +16189	GRC	Athens	Olivieri unpub.
GR74	R0	H1c +152	GRC	Athens	Olivieri unpub.
GR75	U-K	K2b1a1	GRC	Athens	Olivieri unpub.
GR78	R0	H	GRC	Athens	Olivieri unpub.
GR79	R0	H5a	GRC	Athens	Olivieri unpub.
GR80	N1b	N1b1a	GRC	Athens	Olivieri unpub.
GR9	R0	H13a2	GRC	Athens	Olivieri unpub.
gre-1	JT	T1a1l	GRC		Batini et al. 2012
gre-10	R0	H7c4	GRC		Batini et al. 2012
gre-11	U-K	K1a12a1a	GRC		Batini et al. 2012
gre-12	JT	J1c	GRC		Batini et al. 2012
gre-15	M	M1a1	GRC		Batini et al. 2012
gre-17	X	X1	GRC		Batini et al. 2012
gre-2	R0	H9a	GRC		Batini et al. 2012
gre-3	R0	H8a	GRC		Batini et al. 2012
gre-4	U-K	K1a	GRC		Batini et al. 2012
gre-5	JT	T1a1l	GRC		Batini et al. 2012

gre-77	N1b	N1b1a4	GRC		Batini et al. 2012
gre-78	U-K	U6a1a1	GRC		Batini et al. 2012
gre-79	R0	H1	GRC		Batini et al. 2012
gre-80	R0	HV1b	GRC		Batini et al. 2012
gre-82	R0	V	GRC		Batini et al. 2012
gre-83m	R0	V6	GRC		Batini et al. 2012
gre-84m	JT	J1c7a	GRC		Batini et al. 2012
gre-85m	JT	T1b3	GRC		Batini et al. 2012
gre-86	JT	T2	GRC		Batini et al. 2012
gre-87	U-K	U5a1a1	GRC		Batini et al. 2012
GreekAth01	R0	H1e1b1	GRC	Athens	This study
GU218692	U-K	U1a1	GRC	Crete	FamilyTreeDNA
JF828090	R0	H13a2	GRC	Crete	FamilyTreeDNA
JN207845	N2	N2a2	GRC	Aromanian Greek	FamilyTreeDNA
JQ074232	U-K	U5b3a2	GRC	Epirus	FamilyTreeDNA
JQ245750	X	X2d1	GRC		Fernandes et al. 2012
JQ245751	N1a	I3a	GRC		Fernandes et al. 2012
JQ668027	U-K	K1a1b1	GRC		FamilyTreeDNA
JQ702344	JT	T2a1b	GRC		Behar et al. 2012
JQ702571	R0	H5a5	GRC		Behar et al. 2012
JQ702757	R0	H1	GRC	Rhodes	Behar et al. 2012
JQ702833	R0	H1	GRC		Behar et al. 2012
JQ702925	JT	T1a1a1j	GRC	Rhodes	Behar et al. 2012
JQ702943	R0	H2	GRC	Rhodes	Behar et al. 2012
JQ703087	U-K	U5a2b1	GRC		Behar et al. 2012
JQ703793	U-K	U1a1	GRC		Behar et al. 2012
JQ703870	JT	J1c2a	GRC		Behar et al. 2012
JQ704460	R0	H55b	GRC		Behar et al. 2012
JQ704706	R0	H5e1a	GRC		Behar et al. 2012
JQ704816	JT	J1c5c	GRC		Behar et al. 2012
JQ705721	R0	H7b1	GRC		Behar et al. 2012
JQ797762	JT	J1b1a2a	GRC		Pala et al. 2012
JQ797775	JT	J1b3b	GRC		Pala et al. 2012
JQ797776	JT	J1b4	GRC	Crete	Pala et al. 2012
JQ797785	JT	J1b	CYP		Pala et al. 2012
JQ797804	JT	J1c2a	GRC	Crete	Pala et al. 2012

JQ797805	JT	J1c2a	GRC	Crete	Pala et al. 2012
JQ797806	JT	J1c2a	GRC		Pala et al. 2012
JQ797811	JT	J1c2a5	GRC		Pala et al. 2012
JQ797812	JT	J1c2a5	GRC		Pala et al. 2012
JQ797813	JT	J1c2a5	GRC		Pala et al. 2012
JQ797814	JT	J1c2a5	GRC		Pala et al. 2012
JQ797823	JT	J1c3	GRC		Pala et al. 2012
JQ797824	JT	J1c3a1	GRC	Crete	Pala et al. 2012
JQ797825	JT	J1c3a1	GRC		Pala et al. 2012
JQ797847	JT	J1c7	GRC		Pala et al. 2012
JQ797848	JT	J1c7	GRC		Pala et al. 2012
JQ797851	JT	J1c7	GRC		Pala et al. 2012
JQ797854	JT	J1c7	GRC		Pala et al. 2012
JQ797863	JT	J1c8	GRC	Crete	Pala et al. 2012
JQ797868	JT	J1c8	GRC	Crete	Pala et al. 2012
JQ797875	JT	J1c	GRC		Pala et al. 2012
JQ797884	JT	J1c	GRC	Crete	Pala et al. 2012
JQ797892	JT	J1d1b1	CYP		Pala et al. 2012
JQ797910	JT	J2a1a2	GRC	Crete	Pala et al. 2012
JQ797914	JT	J2a1b	GRC		Pala et al. 2012
JQ797927	JT	J2a2b	GRC		Pala et al. 2012
JQ797941	JT	J2b1a3	GRC		Pala et al. 2012
JQ797950	JT	J2b1c	GRC	Crete	Pala et al. 2012
JQ797951	JT	J2b1c	GRC	Crete	Pala et al. 2012
JQ797952	JT	J2b1c	GRC		Pala et al. 2012
JQ797983	JT	T1a1a1	GRC		Pala et al. 2012
JQ797992	JT	T1a1a1b	GRC	Crete	Pala et al. 2012
JQ798003	JT	T1a1a1	GRC		Pala et al. 2012
JQ798004	JT	T1a1a1	GRC		Pala et al. 2012
JQ798011	JT	T1a1c1	GRC	Crete	Pala et al. 2012
JQ798020	JT	T1a1e	GRC	Crete	Pala et al. 2012
JQ798029	JT	T1a	GRC	Crete	Pala et al. 2012
JQ798032	JT	T1a3	GRC		Pala et al. 2012
JQ798050	JT	T1b4	GRC		Pala et al. 2012
JQ798071	JT	T2b4	GRC		Pala et al. 2012
JQ798089	JT	T2b	GRC	Crete	Pala et al. 2012
JQ798102	JT	T2c1c	GRC	Crete	Pala et al. 2012
JQ798111	JT	T2e	GRC		Pala et al. 2012
JQ798112	JT	T2e	GRC		Pala et al. 2012

JQ798125	JT	T2f2	GRC		Pala et al. 2012
JQ798135	JT	T2	GRC	Crete	Pala et al. 2012
JQ798136	JT	T2	GRC		Pala et al. 2012
JX152961	R0	V1a1b	GRC		Raule et al. 2014
JX152962	R0	H2a1	GRC		Raule et al. 2014
JX152963	U-K	U4b1a1a1	GRC		Raule et al. 2014
JX152964	R0	H1as2	GRC		Raule et al. 2014
JX153047	U-K	U8b1a2	GRC		Raule et al. 2014
JX153048	JT	T2f	GRC		Raule et al. 2014
JX153049	JT	T1a1l	GRC		Raule et al. 2014
JX153050	JT	J1c2e	GRC		Raule et al. 2014
JX153051	R0	HV1a2	GRC		Raule et al. 2014
JX153052	R0	H36	GRC		Raule et al. 2014
JX153053	JT	T2b	GRC		Raule et al. 2014
JX153054	R0	H7b1	GRC		Raule et al. 2014
JX153055	U-K	U3b2a1	GRC		Raule et al. 2014
JX153056	U-K	K1a1	GRC		Raule et al. 2014
JX153057	R0	HV	GRC		Raule et al. 2014
JX153058	U-K	U8b1b	GRC		Raule et al. 2014
JX153059	R0	H20a	GRC		Raule et al. 2014
JX153060	X	X2i	GRC		Raule et al. 2014
JX153061	R0	H94	GRC		Raule et al. 2014
JX153116	U-K	U1a1c	GRC		Raule et al. 2014
JX153117	R0	H13a2a	GRC		Raule et al. 2014
JX153118	R0	H4	GRC		Raule et al. 2014
JX273262	U-K	K1a29	GRC		Costa et al. 2013
KC847159	U-K	K1b1	GRC	Crete	FamilyTreeDNA
KC867106	N1a	N1a3a	GRC		Kushniarevich et al. 2013
KC867109	N1a	N1a3a	CYP		Kushniarevich et al. 2013
KC900995	U-K	K1a4f	GRC	Athens	FamilyTreeDNA
KM062184	JT	T1a2	CYP	Nicosia	FamilyTreeDNA
KM259909	U-K	K1a3	GRC		FamilyTreeDNA
KP340180	R0	HV4b	GRC		De Fanti et al. 2015
KR902534	X	X2e2a	GRC	Crete	FamilyTreeDNA
KT748522	N1a	I5a4	GRC		FamilyTreeDNA
KX440312	JT	T1b3	GRC		Pereira et al. 2017
KX440318	JT	T2a1b	GRC		Pereira et al. 2017

KY818807	JT	T2	GRC	Central Greece	FamilyTreeDNA
KY824877	U-K	U7a17a	GRC	Rhodes	Sahakyan et al. 2017
KY824878	U-K	U7a19	GRC	Rhodes	Sahakyan et al. 2017
KY824886	U-K	U7b1b*	GRC	Crete	Sahakyan et al. 2017
KY824887	U-K	U7b5a*	GRC	Crete	Sahakyan et al. 2017
KY824888	U-K	U7b5*	GRC	Crete	Sahakyan et al. 2017
KY824889	U-K	U7b5*	GRC	Crete	Sahakyan et al. 2017
KY824890	U-K	U7a3a1e	GRC	Crete	Sahakyan et al. 2017
KY824891	U-K	U7b5a1	GRC		Sahakyan et al. 2017
LK01	JT	T2g1a1	CYP	Famagusta	This study
LK02	R0	H13a2b3	CYP	Dheryneia	This study
LK03	X	X2b10	CYP	Assos	This study
LK04	U-K	K1a4	CYP	Limassol	This study
LK05	N2	W6c1a	CYP	Limassol	This study
LK06	N1b	N1b1a3	CYP	Nicosia	This study
LK07	U-K	U3b2a1	CYP	Limassol	This study
LK08	R0	HV9 +152	CYP	Nicosia	This study
LK09	R0	H5u	CYP	Ammochostou	This study
LK10	M	M1a	CYP	Nicosia	This study
LK11	X	X2	CYP	Paphos	This study
LK12	R0	V	CYP	Morfou	This study
LK13	L3	L3h1b2	CYP	Limassol	This study
LK14	R0	H5n	CYP		This study
LK15	N1a	I5c1	CYP	Famagusta	This study
LK16	R0	H80	CYP		This study
LK17	R0	H107	CYP		This study
LK18	JT	T2b	CYP	Famagusta	This study
LK19	R0	H13a2b3	CYP	Dheryneia	This study
LK20	R0	H13a2b3	CYP	Dheryneia	This study
LK21	N2	W +194	CYP		This study
LK22	R0	H14b	CYP		This study
LK23	R0	H3	CYP		This study
LK24	U-K	K1a4	CYP		This study
LK25	R0	H13a2b3	CYP	Dheryneia	This study
LK26	U-K	U3b2a1a	CYP	Keryneia	This study
LK27	R0	H9a	CYP	Paralimni	This study
LK28	M	M1a1i	CYP	Agros	This study

LK29	U-K	U3c	CYP		This study
LK30	R0	H14a2c	CYP	Famagusta	This study
LK31	N1b	N1b1a6	CYP	Dheryneia	This study
LK32	U-K	K1a4c	CYP	Frenaros	This study
LK33	R0	H13a2b3	CYP	Paralimni	This study
LK34	R0	H +73	CYP	Paralimni	This study
LK35	JT	T1a1b	CYP	Paralimni	This study
LK36	R0	H15a1	CYP	Limassol	This study
LK37	U-K	U3a	CYP	Gastria	This study
LK38	R0	H20	CYP	Avgorou	This study
LK39	R0	H15a1	CYP	Gialousa	This study
LK40	N1a	I5c1	CYP	Fterikoudi	This study
LK41	R0	V6	CYP	Deryneia	This study
LP6005442-DNA_G07	R0	H11a	GRC		Mallick et al. 2016
LP6005443-DNA_A01	L3	L3e2b +152	GRC		Mallick et al. 2016
LP6007068-DNA_A01	R0	HV +16311	GRC	Crete	Mallick et al. 2016
LP6007069-DNA_A01	R0	HV1a	GRC	Crete	Mallick et al. 2016

TABLE B.4: Samples used in modern mitochondrial analysis. GRC refers to Greece and CYP refers to Cyprus.

Appendix C

Issues with SNP calling

SNPs were called as psuedo-haploid with random call. Firstly the alleles present at each of the desired SNPs were called, and then a random allele present was picked as homozygous for that position. The widely-available software, pileupCaller, was employed for this. This software uses a pileup file created with samtools mpileup, with parameters -Q30 -q30 (which filter base and read quality 30), -B (which disables base alignment quality recalibration), and -R (ignore readgroups). The file was then used as an input for pileupCaller.

The samples were then merged with publicly available databases from David Reich's Lab (https://reich.hms.harvard.edu/downloadable-genotypes-present-day- and-ancient-dna-data-compiled-published-papers). When conducting *D*- and *f3*-statistics 4, it was noticed that there was a large bias between samples called with pileupCaller. This was investigated by calling samples with the in-house GATKscript, and with pileupcaller, and comparing the results with those publicly available. A *D*-statistic test was conducted by comparing populations called with the in-house GATK, to those called with pileupcaller and the Reich lab dataset; i.e. *D(outgroup, test; sample_pileupCaller, sample_public)*. If there was no bias in SNP calling methods, the *D*-stat value should be approximately zero. However, when testing this, it was observed that samples called with pileupcaller were consistently closer to each other (**Figure C.1**).

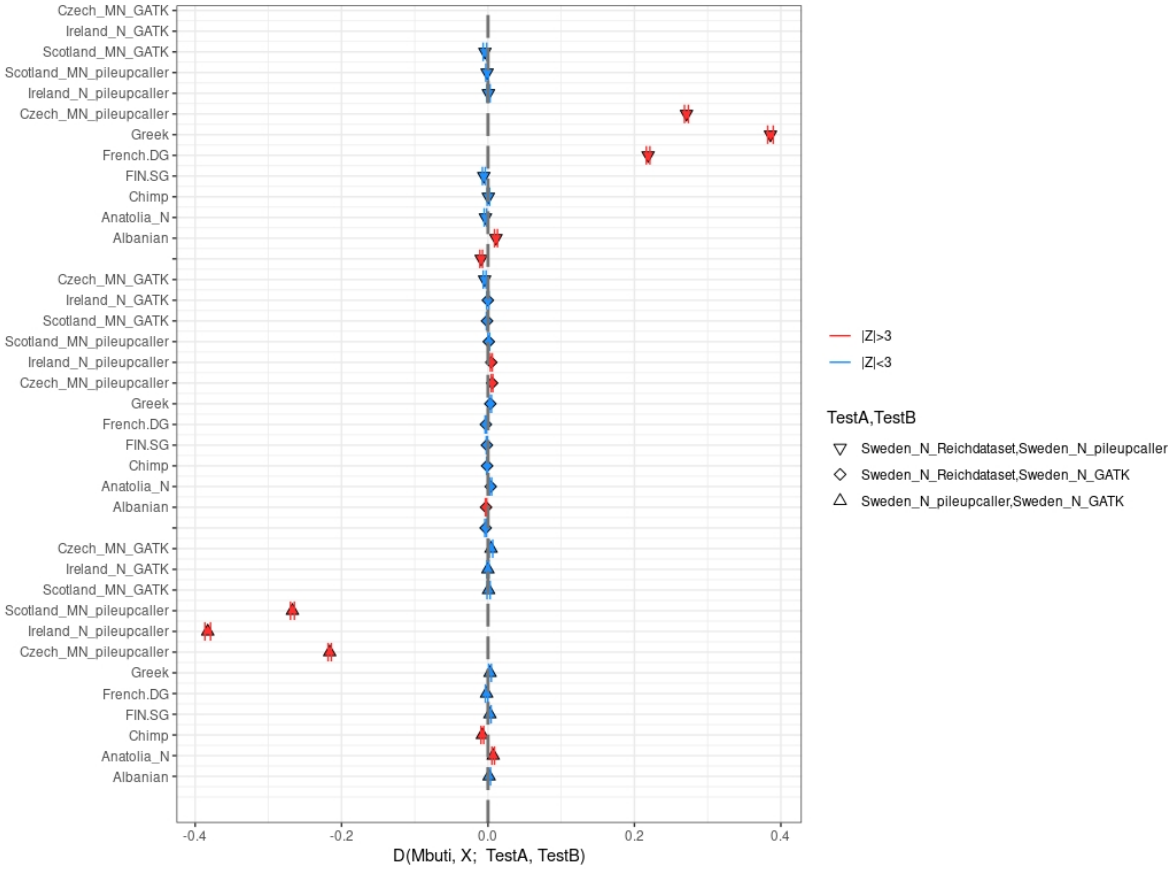


FIGURE C.1: A *D*-statistic test comparing ancient and modern populations to Swedish Neolithic samples (Sánchez-Quinto et al., 2019) called with pileupCaller, the in-house GATK script, and publicly available from Reich lab.

After identifying, and thoroughly testing, this issue was brought to the attention of Dr. Stephan Schiffels, the creator of pileupCaller. In response a new modified version was released.

In order to minimise biases associated with bioinformatic processing, ancient reference samples were realigned, filtered and called using the same the same methodology outlined in Chapter 4.

Appendix D

Supplementary tables for the Necropolis at Armenoi, Crete

D.1 Screening coverage

Sample	Tomb	Endogenous Content	Element
GF001	146	0.84	talus
GF002	159	0.23	petrous
GF003	159	0.3	axis
GF004	159	0.28	petrous
GF005	27	0.04	petrous
GF006	27	0.05	petrous
GF007	149	0.3	petrous
GF008*	149	9.93	petrous
GF009*	149	7.01	petrous
GF010*	149	3.7	petrous
GF011	149	0.29	petrous
GF012	167	1.33	petrous
GF013	167	0.27	molar
GF014*	167	2.91	petrous
GF015	167	0.41	molar
GF016*	167	4.12	petrous
GF017	189	0.07	petrous
GF018	189	0.05	petrous
GF019*	198	25.43	petrous
GF020*	198	13.02	molar
GF021	198	0.11	petrous
GF022*	198	12.96	petrous
GF023	198	0.13	molar
GF024*	203	14.79	petrous

GF025*	203	3.99	petrous
GF026*	203	6.93	petrous
GF027*	203	7.11	petrous
GF028*	203	2.68	petrous
GF029*	203	5.55	petrous
GF030*	203	9.12	petrous
GF031*	203	16.47	petrous
GF032	204	0.28	petrous
GF033	204	0.14	petrous
GF034*	204	17.18	petrous
GF035	206	0.07	petrous
GF036	206	0.04	molar
GF037	206	0.04	petrous
GF038	206	0.01	petrous
GF039	206	0.28	petrous
GF040	206	0.02	petrous
GF041	206	0.01	petrous
GF042	206	0.07	petrous
GF043	206	0.02	petrous
GF044	208	0.02	petrous
GF045*	208	5.17	petrous
GF046	210	0.04	petrous
GF047*	210	11.45	petrous
GF048*	210	2.57	petrous
GF049	210	0.42	petrous
GF050	210	0.7	petrous
GF051*	67	26.93	petrous
GF052	67	0.46	petrous
GF053*	69	4.48	petrous
GF054*	78	13.48	petrous
GF055	108	1.73	petrous

TABLE D.1: Screening results. Samples with an asterisk were sent for further sequencing.

D.2 Uniparental markers

D.2.1 Mitochondrial haplogroup

TABLE D.2: Mitochondrial haplogroup assignment.

Sample	mtDNA coverage	Haplogroup	Mutations
GF008	11.012X	H59	263G 750G 1438G 4769G 7958T 8860G 12674G 14153C 15326G
GF009	9.9074X	T2b	73G 168C 263G 709A 930A 1438G 1888A 2706G 4769G 4917G 5147A 7028T 8697A 8860G 10463C 11251G 11719A 11812G 13368A 14233G 14766T 14905A 15326G 15607G 15928A 16126C 16294T 16304C
GF010	6.0161X	T1a1	73G 152C 195C 263G 709A 750G 1438G 1888A 2706G 4216C 4769G 4917G 7028T 8697A 8860G 9899C 10463C 11251A 11719G 12308G 12633A 13368A 13810A 14569A 14766T 14905A 15326G 15452A 15607G 15928A 16126C 16163G 16186T 16189C 16294T
GF014	1.7072X	U7	73G 152C 231T 263G 750G 980C 1379T 1438G 1811G 2400T 2706G 3394C 3741T 4769G 5360T 7028T 8137T 8684T 8860G 10142T 11467G 12308G 13500C 14569A 14766T 15326G 16318T
GF016	3.1221X	U7b	73G 164G 263G 750G 1438G 1811G 2706G 3312T 3394C 3741T 5360T 7028T 8137T 8684T 8860G 10084C 10142T 11467G 11719G 12308G 12372A 13500C 14569A 14766T 15326G 16318T
GF019	55.2623X	H	263G 750G 1438G 4769G 8860G 15326G 15817G
GF020	26.6944X	H4b	263G 750G 951A 1438G 3992T 4769G 5004C 8860G 9123A 10166C 15326G 16261T

Continued on next page

Table D.2 – *Continued from previous page*

Sample	**mtDNA coverage**	**Haplogroup**	**Mutations**
GF022	30.676X	H	263G 750G 1438G 4769G 8860G 15326G 15817G
GF024	28.7061X	U5b1b1	73G 150T 263G 750G 1438G 2706G 3197C 4769G 5656G 7028T 7385G 7768G 8860G 9477A 10927C 11467G 11719A 12308G 12372A 12618A 13617C 14182C 14207A 14766T 15326G 16189C 16192T 16270T
GF025	2.6052X	U5b1	150T 263G 750G 1438G 2706G 3197C 3597T 4769G 5656G 7028T 8860G 9477A 10927C 11467G 11719G 12308G 12372A 13617T 14182C 14766T 15326G 16189C
GF026	10.4027X	K1	73G 263G 461T 469T 750G 1189C 1438G 1811G 2706G 3480G 4769G 7028T 8860G 9055A 9698C 10398G 10550G 11025C 11299C 11467G 11719A 12308G 12372A 14167T 14766T 14798C 15326G 16224C 16311C
GF027	12.2182X	U5a1	73G 263G 750G 1438G 2706G 3197C 3591A 4769G 7028T 8610C 8860G 9477A 11467G 11719A 12308G 12372A 12811C 13617C 14766T 14793G 15218G 15326G 15453A 16192T 16256T 16270T 16355T 16399G
GF028	0.8238X	H5a3	513A 1438G 4769G 7028T 8860G 9477A 11719A 12308G 14766T 16270T
GF029	3.7232X	U5b1b1	73G 150T 263G 457T 750G 1438G 2706G 4769G 5656G 7028T 7768G 8860G 9477A 10927C 11467G 11719A 12308G 12372A 12618A 13617C 14182C 14766T 15326G 16189C 16192T 16270T

Continued on next page

Table D.2 – *Continued from previous page*

Sample	**mtDNA coverage**	**Haplogroup**	**Mutations**
GF030	10.9348X	U5b1b1	73G 150T 263G 750G 1438G 2706G 3197C 4769G 5656G 7028T 7385G 7768G 8860G 9477A 10927C 11467G 11719A 12308G 12372A 12618A 13617C 14182C 14207A 14766T 15326G 16189C 16192T 16270T
GF031	28.9515X	U5a1	73G 263G 750G 1438G 2706G 3197C 3591A 4769G 7028T 8610C 8860G 9477A 11467G 11719A 12308G 12372A 12811C 13617C 14766T 14793G 15218G 15326G 15453A 16192T 16256T 16270T 16355T 16399G
GF034	27.1654X	N1a1a1a	73G 152C 199C 204C 263G 462T 669C 750G 1438G 1597T 1719A 2702A 2706G 3336C 4769G 5315G 7028T 8860G 8901G 10238C 10398G 11719A 12501A 12705T 13780G 14766T 15043A 15326G 16147A 16172C 16209C 16223T 16248T 16320T 16355T
GF045	6.0488X	H59	263G 368T 750G 1438G 4769G 7958T 8860G 12674G 15326G
GF047	23.2111X	W	73G 119C 152C 189G 194T 195C 204C 207A 263G 709A 750G 1243C 1438G 2706G 3505G 4769G 5046A 5460A 7028T 8251A 8860G 8994A 11674T 11719A 11947G 12414C 12705T 13135A 14766T 15326G 15884C 16223T 16270T 16292T
GF048	2.4604X	H	73G 189G 263G 709A 750G 1438G 3505G 4769G 7028T 8251A 8860G 8994A 9123A 11674 11719A 14766T 15326G 15884C 16223T 16270T
GF051	52.1299X	H1bz	263G 750G 1438G 1531T 3010A 4769G 4924A 8860G 15326G

Continued on next page

Table D.2 – *Continued from previous page*

Sample	**mtDNA coverage**	**Haplogroup**	**Mutations**
GF053	3.0479X	H	263G 750G 951A 1438G 4769G 5004C 8860G 9489A 15326G 16261T
GF054	20.7017X	HV1	263G 750G 1438G 2706G 4769G 7028T 8014T 8296G 8347G 8860G 9064A 11476T 12279G 15326G 15788G 16067T 16218T 16354T 16362C

D.2.2 Y-chromosomal analysis

D.2.2.1 Y-leaf

Position	Marker name	Haplogroup	Mutation
6753296	L1095	A0-T	A->G
2710154	P305	A1	A->G
10008803	L418	BT	C->G
10068588	Z40376	BT	A->G
13821858	Z40381	BT	C->G
15542606	M9141	BT	A->T
17270785	M9204	BT	C->A
17571812	M9220	BT	T->A
2906950	M8956	BT	C->T
7032507	Z17366	BT	C->T
14943290	CTS3460	CT	C->T
7416169	M5600	CT	T->C
19303108	CTS10168	P	A->C
10008791	L150.1	R1b1a1a2	C->T
16971648	CTS6532	R1b1a1a2	T->G
23379254	CTS11948	R1b1a1a2	G->A

TABLE D.3: Y-leaf output of GF010. Transitions are displayed for this sample due to the low number of SNPs.

Position	Marker name	Haplogroup	Mutation
22191266	L1155	A0-T	G->C
13841677	Y8316	BT	A->G
14069414	M9079	BT	C->T
17372321	M9213	BT	G->A
17620657	M9221	BT	C->T
19445252	M9295	BT	A->C
21541028	Z40396	BT	C->T
28725413	M9425	BT	T->C
28772048	Y10888	BT	C->T
23555082	M5821	CT	T->A
28790215	PF1337	CT	G->C
14469411	L382	G	C->A
17210745	CTS6957	G	C->T
21162869	M3580	G	C->G

8602816	M3487	G	G->C
22109159	M3408	G2a	G->C
17572142	PF3168	G2a2a	T->C
16345569	Z19485	Q1a2a1a1a8a	G->A

TABLE D.4: Y-leaf output of GF025. Transitions are displayed for this sample due to the low number of SNPs.

Position	**Marker name**	**Haplogroup**	**Mutation**
15323457	FGC8027	A1b	T->A
14344506	M9094	BT	C->G
18016799	Y9422	BT	T->A
28746408	Z17390	BT	G->C
7037901	M8976	BT	G->C
7171532	M8977	BT	G->T
7735760	M8997	BT	C->G
14149520	M5652	CT	T->A
16465771	CTS5746	CT	T->G
17174326	CTS6890	CT	G->C
18607673	M5749	CT	T->A
23898115	S25934	E1b1a1a1a1c1a1a3a1d1b1b1a3	C->A
15955432	F2048	F	A->T
16364286	F2142	F	C->A
18051289	F2688	F	C->G
8131538	F3692	F	G->T
17747521	CTS7929	G	C->G
19030998	CTS9707	G	C->A
21334507	M3582	G	G->T
22714204	CTS10706	G	G->T
22997377	CTS11185	G	C->G
23793740	M3628	G	C->A
8318375	M3264	G	G->T
21637589	F3220	G2	G->C
23739606	PF3119	G2	G->T
14815695	PF3159	G2a2a	C->G
15702713	PF3161	G2a2a	A->C
21645555	L91	G2a2a1a2	G->C
13142723	Z12542	H1a1a4b3a1	A->C

TABLE D.5: Y-leaf output of GF027.

Position	Marker name	Haplogroup	Mutation
14289022	L1235	A0-T	A->T
4898665	V171	A1	C->G
7374927	L985	A1	A->C
14394777	Z11918	A1b	C->A
14467641	Z11906	A1b	C->G
23125773	Z11892	A1b	C->A
23440815	Z11899	A1b	C->A
8349696	Z11903	A1b	G->C
13592206	Z40378	BT	C->A
14541174	M9103	BT	T->G
15219209	PF713	BT	T->A
15450357	M9138	BT	C->A
15558761	M9142	BT	G->T
18067088	M9245	BT	T->A
19416000	M9293	BT	C->G
21665439	M9338	BT	C->A
21968581	M9343	BT	G->T
22817840	M9365	BT	G->C
23005081	M9372	BT	G->T
23190598	Y8325	BT	A->T
23757465	M9397	BT	G->C
2868656	M8953	BT	A->T
7661695	M8994	BT	A->C
14149520	M5652	CT	T->A
16262390	M5691	CT	T->A
17975155	FGC33852	CT	G->T
18616467	CTS9014	CT	T->A
19407727	M5769	CT	C->G
23555082	M5821	CT	T->A
24470911	M5826	CT	C->A
2744386	CTS125	CT	G->T
28789895	Y1580	CT	A->T
7707484	M5607	CT	C->A
16839641	P316	F	A->T
18051289	F2688	F	C->G
22673903	F3335	F	T->G
2756471	M3637	F	A->T
28650343	CTS12632	F	C->G

22163252	M3603	G	G->T
2785630	CTS175	G	A->T
7132348	CTS995	G	G->C
7309873	CTS1283	G	T->G
7397510	CTS1437	G	C->G
7823146	M3469	G2	G->T
14028148	L31	G2a	C->A
18819146	CTS9318	G2a	T->A
18179271	Z6491	G2a2a1	G->C
18029229	Z6787	G2a2a1a2a2a	T->G
13824095	Y23139	I1a2a1a4a1a1a2a	A->T
22474589	BY191.1	R1b1a1a2a1a2c1a1a1a1a1	G->T

TABLE D.6: Y-leaf output of GF031.

Position	**Marker name**	**Haplogroup**	**Mutation**
14231291	L1118	A0-T	T->C
18914286	L1136	A0-T	A->G
21903971	L1150	A0-T	A->G
3544962	L1090	A0-T	G->C
8466995	L1112	A1	G->A
15995289	M9157	BT	C->T
21518721	M9328	BT	A->T
21541028	Z40396	BT	C->T
21674225	L969	BT	T->C
22180636	M9352	BT	C->A
10049308	Z17708	CT	A->G
13852599	PF629	CT	A->G
15932327	Y1528	CT	A->G
21267676	M5777	CT	C->T
23081753	CTS11358	CT	A->G
8635526	M5636	CT	C->A
22882865	M6525	D1b1c1b	G->A
22548424	Y6770	E1b1b1a1a1c1b1a2	G->A
14996960	CTS3536	F	A->G
15526751	M213	F	T->C
17152659	F2402	F	T->C
7726849	M3647	F	A->G
8572150	F1320	F	G->A

23073303	Z12961	H3a2b	A->G
18238499	FGC3500	I1a2b4	C->T
16674560	CTS6101	IJ	A->G
17040447	F2366	IJ	C->A
21040853	F3102	IJ	A->C
21220741	FGC1560	IJ	T->C
8222299	FGC1573	IJ	T->C
14084606	PF4535	J	G->T
15476324	CTS4204	J	G->A
21495992	PF4594	J	C->A

TABLE D.7: Y-leaf output of GF045. Transitions are displayed for this sample due to the low number of SNPs.

Position	**Marker name**	**Haplogroup**	**Mutation**
22191266	L1155	A0-T	G->C
6847637	L1098	A0-T	C->A
14467641	Z11906	A1b	C->G
18759708	L1053	A1b	C->A
23440815	Z11899	A1b	C->A
23551003	L989	A1b	T->A
4501479	Z11901	A1b	A->T
8349696	Z11903	A1b	G->C
10008803	L418	BT	C->G
13821858	Z40381	BT	C->G
14096790	M9081	BT	C->A
14108214	M9083	BT	T->A
14344506	M9094	BT	C->G
14541174	M9103	BT	T->G
14713690	M9109	BT	T->A
14726334	M9112	BT	A->C
14762104	M9114	BT	G->C
14786996	M9116	BT	A->T
15068525	M9125	BT	A->T
15219209	PF713	BT	T->A
15382324	M9136	BT	C->G
15905094	M9152	BT	G->T
16682167	Y8489	BT	G->C
17571812	M9220	BT	T->A

19445252	M9295	BT	A->C
21046360	Y8323	BT	G->T
21268114	M9312	BT	C->G
21289152	M9315	BT	T->G
21518721	M9328	BT	A->T
21567686	M9331	BT	C->G
21866840	M42	BT	A->T
21968581	M9343	BT	G->T
21975362	M9344	BT	C->A
22079278	M9348	BT	A->T
22180636	M9352	BT	C->A
22521712	Z40408	BT	C->A
22817840	M9365	BT	G->C
23005081	M9372	BT	G->T
23117154	L604	BT	C->A
23201899	Z40411	BT	A->C
6719048	M8961	BT	T->G
6936412	M8971	BT	G->C
7021041	Z17365	BT	G->T
7171532	M8977	BT	G->T
7735760	M8997	BT	C->G
8165769	M9016	BT	G->T
8226191	M9017	BT	C->A
8446082	M9025	BT	A->T
8520679	M9027	BT	C->A
8729512	M9038	BT	G->C
13867088	Z12163	C2	A->T
14149520	M5652	CT	T->A
14172842	CTS2077	CT	T->G
16325663	M5692	CT	A->C
16887784	M5709	CT	G->C
17104433	M5712	CT	A->C
17517587	CTS7517	CT	T->A
17751557	CTS7936	CT	A->T
18961511	CTS9555	CT	G->C
18961874	CTS9556	CT	C->A
19039750	M5762	CT	G->C
19059200	CTS9760	CT	C->A
21413635	M5782	CT	A->C

2744386	CTS125	CT	G->T
28789895	Y1580	CT	A->T
7707484	M5607	CT	C->A
7887815	M5615	CT	A->T
8635526	M5636	CT	C->A
17331463	CTS7165	D1b	G->T
14294504	F1753	F	T->G
14334396	F1767	F	G->T
16178042	F2075	F	A->T
16839641	P316	F	A->T
22673903	F3335	F	T->G
13822326	Y23135	I1a2a1a4a1a1a2a	A->T
13822330	Y23136	I1a2a1a4a1a1a2a	A->C
13822356	S14669	I1a2a1a4a1a1a2a	A->T
10002861	FGC1569	IJ	G->T
17040447	F2366	IJ	C->A
18633084	F2794	IJ	C->A
19038302	P124	IJ	A->C
21321273	FGC1571	IJ	A->T
13943183	PF4533	J	G->C
15607864	CTS4356	J	T->A
15913787	CTS4937	J	A->C
17367321	CTS7229	J	C->A
17605948	PF4567	J	A->C
18567169	CTS8938	J	T->G
19460042	CTS10446	J	G->C
21858778	PF4595	J	C->A
21923739	FGC1599	J	A->T
23163701	CTS11571	J	C->A
23251880	PF4619	J	A->C
7126936	PF4506	J	G->T
7296343	CTS1250	J	G->T
7367950	M10434	J	C->A
7517252	PF4511	J	G->T
8418927	F1181	J	G->C
14969634	M172	J2	T->G
21855964	Z16313	R1b1a1a2a1a2c1a5c1a	G->T

TABLE D.8: Y-leaf result for GF051.

Position	Marker name	Haplogroup	Mutation
4898665	V171	A1	C->G
14467641	Z11906	A1b	C->G
23596262	Z11896	A1b	C->G
13596520	Z40400	BT	T->A
14096790	M9081	BT	C->A
14344506	M9094	BT	C->G
14726334	M9112	BT	A->C
15132194	M9129	BT	T->G
15219209	PF713	BT	T->A
15656524	M9146	BT	G->C
18005126	Y8319	BT	T->A
19416000	M9293	BT	C->G
19555949	Z17372	BT	T->G
21470547	M9322	BT	T->G
21492793	M9327	BT	T->A
22180636	M9352	BT	C->A
22881961	M9368	BT	G->C
23005081	M9372	BT	G->T
23117154	L604	BT	C->A
23240528	Z40412	BT	C->G
23244049	M9379	BT	G->C
23609441	M9396	BT	G->C
7021041	Z17365	BT	G->T
8446082	M9025	BT	A->T
9869354	M11760	BT	C->A
16465771	CTS5746	CT	T->G
16887784	M5709	CT	G->C
17975155	FGC33852	CT	G->T
18054506	M5742	CT	T->A
18607673	M5749	CT	T->A
18961874	CTS9556	CT	C->A
21413635	M5782	CT	A->C
22067044	M5794	CT	A->T
28590906	Y1578	CT	A->T
28789895	Y1580	CT	A->T
7256433	CTS1181	CT	A->T
8849835	M5639	CT	C->A
15955432	F2048	F	A->T

19205814	L470	F	A->T
22156498	M3752	F	C->A
8131538	F3692	F	G->T
13658486	Z3258	G	C->G
14469411	L382	G	C->A
17533325	L522	G	A->C
18979775	CTS9593	G	T->A
2863466	L770	G	A->T
7397510	CTS1437	G	C->G
8318375	M3264	G	G->T
14116322	CTS1900	G2	T->A
7571775	M3465	G2	G->T
21493984	M3393	G2a	G->T
22109159	M3408	G2a	G->C
23973594	PF3141	G2a	T->G
16291728	F2121	G2a2b2	C->A
14648305	Z6363	G2a2b2a3b	C->A
16626505	Z6371	G2a2b2a3b	A->C
6651173	Z6148	G2a2b2a3b	G->T
21270634	Z13155	H3a1	G->T
13822326	Y23135	I1a2a1a4a1a1a2a	A->T
13822330	Y23136	I1a2a1a4a1a1a2a	A->C

TABLE D.9: Y-leaf output of GF054.

D.2.2.2 pathPhynder

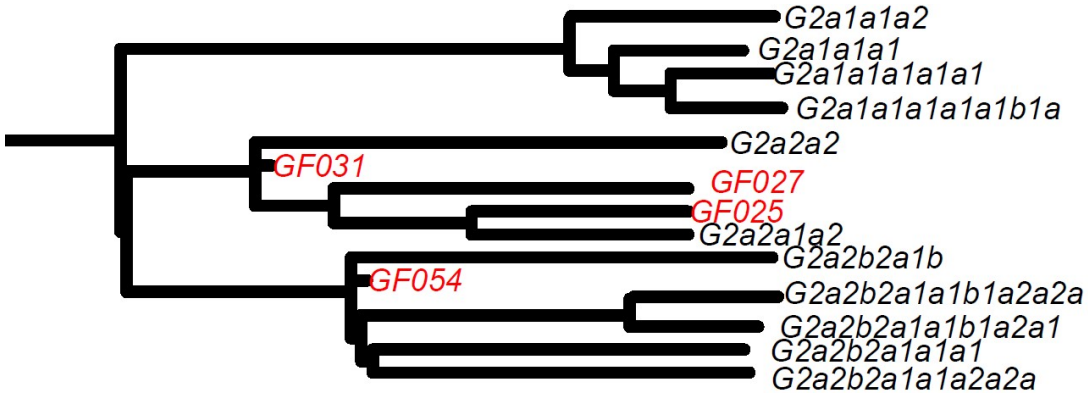


FIGURE D.1: An edited output image from pathPhynder of all samples determined to be Y-chromosomal haplogroup G.

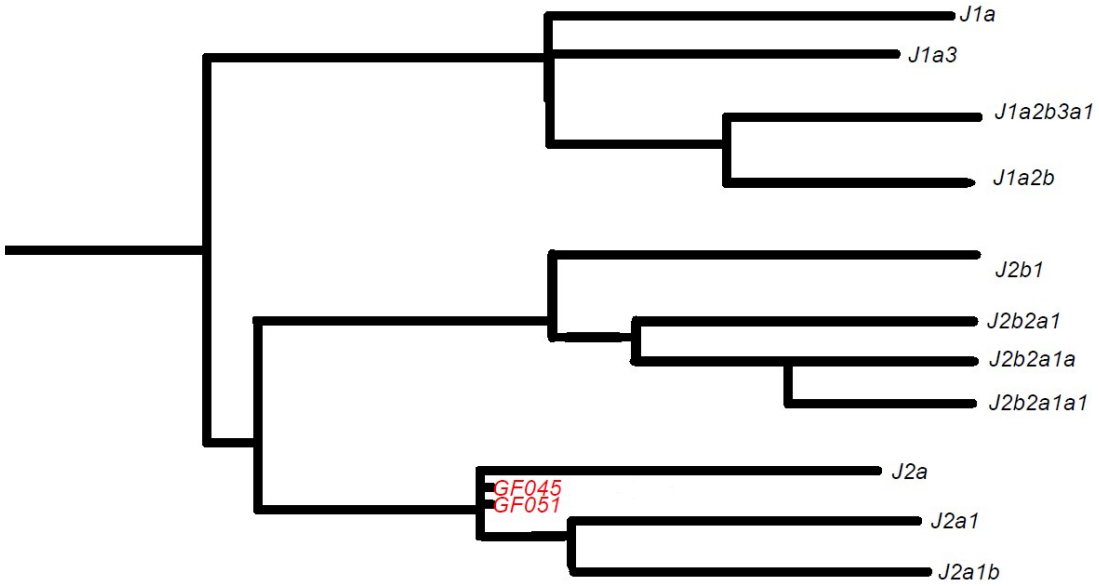


FIGURE D.2: An edited output image from pathPhynder of all samples determined to be Y-chromosomal haplogroup J.

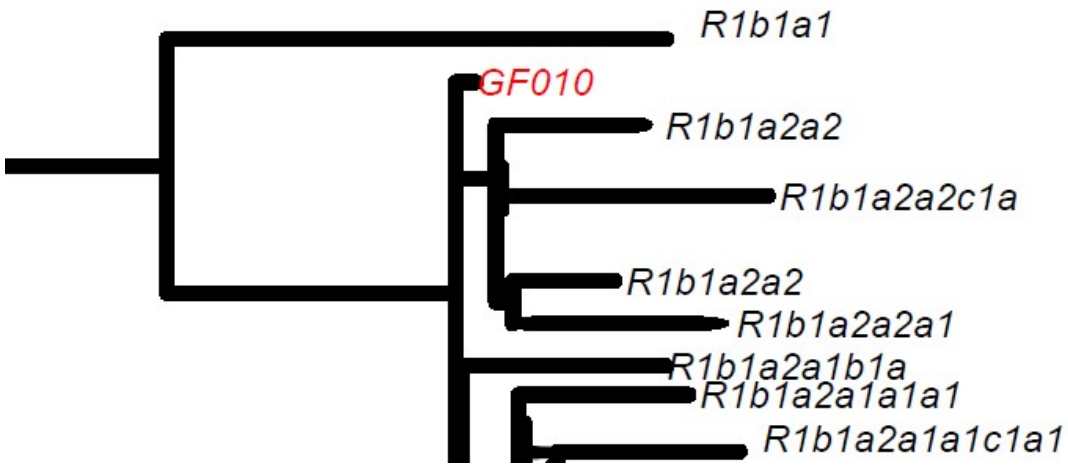


FIGURE D.3: An edited output image from pathPhynder of GF010, within a sub-branch of Y-chromosomal haplogroup R1b

D.3 Dietary stable isotope data

Species	Code	Element	Tomb	Skeleton	d13C VPDB	d15N AIR	C:N	Tomb Wealth
human	GF001	talus	146	A	-19.31	9.31	3.3	
human	GF002	petrous	159	A	-20.04	7.70	3.3	**
human	GF004	LLM3	159	G	-19.33	10.62	3.2	**
human	GF005	petrous	27	JUV	-21.64	6.73	4.1	
human	GF006	petrous	27	ADULT	-20.01	9.67	3.3	
human	GF007	petrous	149	H	-20.46	9.12	3.4	

human	GF008	petrous	149	D	-19.72	9.42	3.3	
human	GF009	petrous	149	ST	-19.52	9.53	3.2	
human	GF012	petrous	167	ST	-19.57	9.39	3.2	**
human	GF013	ULM3	167	B	-19.02	9.51	3.2	**
human	GF014	petrous	167	Z	-21.49	6.66	3.9	**
human	GF015	ULM2	167	D	-19.76	7.58	3.3	**
human	GF016	petrous	167	E	-19.51	8.86	3.2	**
human	GF017	petrous	189	2	-19.80	9.37	3.3	
human	GF019	petrous	198	G	-20.54	9.03	3.5	*
human	GF020	ULM2	198	D	-19.48	8.73	3.2	*
human	GF021	petrous	198	ST	-19.49	10.71	3.3	*
human	GF022	petrous	198	B	-19.90	9.47	3.3	*
human	GF023	LRM2	198		-19.81	8.98	3.3	*
human	GF024	petrous	203	T	-19.86	10.13	3.4	*
human	GF025	petrous	203	E	-19.69	9.69	3.2	*
human	GF026	petrous	203	ET	-20.05	8.80	3.3	*
human	GF027	petrous	203	I	-19.83	9.30	3.3	*
human	GF028	petrous	203	A	-19.65	9.84	3.3	*
human	GF029	petrous	203	H	-20.49	8.95	3.3	*
human	GF030	petrous	203	Z	-19.65	9.94	3.3	*
human	GF031	petrous	203	K	-19.58	9.49	3.4	*
human	GF032	petrous	204	A	-19.82	8.57	3.5	
human	GF033	petrous	204	E	-19.89	10.34	3.4	
human	GF034	petrous	204	Z	-20.01	8.82	3.4	
human	GF036	URM2	206	D	-19.24	8.30	3.2	**
human	GF039	petrous	206	I	-19.68	9.74	3.3	**
human	GF042	petrous	206	O	-19.89	8.79	3.3	**
human	GF045	petrous	208	E	-20.25	8.81	3.3	
human	GF046	petrous	210	3	-19.64	8.04	3.2	
human	GF047	petrous	210	4	-20.11	9.15	3.3	
human	GF048	petrous	210	E	-20.69	7.81	3.2	
human	GF049	petrous	210	2	-20.05	8.20	3.2	
human	GF050	petrous	210	1	-20.16	8.75	3.2	
human	GF051	petrous	67	E	-19.59	10.05	3.2	**
human	GF052	petrous	67	H	-20.23	9.04	3.5	**
human	GF053	petrous	69	G	-20.26	8.22	3.5	
human	GF054	petrous	78	Z	-19.76	9.01	3.3	
sheep	GFa02	metatarsal	159		-20.36	5.38	3.3	
goat	GFa03	metatarsal	159		-20.26	3.36	3.3	

hare	GFa04	femur	159		-22.64	1.86	3.4	
sheep	GFa05	humerus	159		-21.20	4.85	3.4	
sheep	GFa06	femur	159		-21.31	3.85	3.4	
sheep	GFa07	femur	159		-21.07	4.81	3.4	
sheep	GFa08	humerus	159		-21.35	4.21	3.4	
hare	GFa09	humerus	159		-20.90	2.98	3.4	
hare	GFa10	humerus	159		-22.56	2.99	3.4	
hare	GFa11	humerus	159		-20.83	3.80	3.3	
sheep	GFa12	tibia	159		-20.94	5.41	3.3	
sheep	GFa13	mandible	159		-20.82	5.04	3.4	

TABLE D.10: Dietary stable isotope results produced during this study. The asterisks refer to wealthy tombs and double asterisks refer to very wealthy tombs (Martlew pers comm).

Appendix E

Supplementary tables for Genomic Analsis of Post-Bronze Age Britain

Sample	Skeleton No.	Grave No.
KD002	2BA100	78
KD031	2BA790	134
KD032	2BA22	83
KD033	2BA148	100
KD034	2BA766	131
KD035	2BA775	133
KD036	2BA802	138
KD037	2BA805	139
KD038	2BA890	145

TABLE E.1: Grave information for the analysed West Heslerton Anglo-Saxon individuals.

Sample	Site	Age (years)	Sex	mtDNA	YDNA
KD070	LH	12-16	XY	T2e1a	R1b1a1a2
CE003	CPC	17-25	XX	X2b4a1	n/a
CE004	CPC	35-45	XY	H10b	R1b1a1a2a1a
KD005	HPC	25-40	XX	H7a1b	n/a
KD073	MS	50-60	XY	J1b1a1	?
KD001	RC	adult	XY	J1b1a1a	R1b1a1a2a1a
KD003	WH	adult	XX	T2e	n/a
KD040	WH	adult	XY	T2b4h	R1b1a1a2a
KD041	WH	25-35	XY	U5a1a2ah	R1b1a1a2
KD071	WH	24-75	XX	H1b1+16362	n/a
KD072	WH	25-35	XX	H1b1+16362	n/a
KD002	WH	25-35	XX	H6a1a	n/a
KD031	WH	adult	XY	H1c1	R1b1a1a2a1a1
KD032	WH	adult	XY	H1q	R1b1a1a2a1a1
KD033	WH	2-5	XX	H1b	n/a
KD034	WH	adult	XY	X2b4a	R1b1a1a2a1a2c1a4b2c
KD035	WH	c.35	XX	U5a1a1e	n/a
KD036	WH	<16	XY	K1d1	I1a2
KD037	WH	25-35	XX	T2b2b	n/a
KD038	WH	adult	XY	K1a4a1a	I2a2b
KD007	WM	adult	XY	K1a2a	R1ba1a1a2a1a2c1a2a2a1a1a
KD008	WM	17-25	XY	K1a2a	I1a2a1a2
KD009	WM	25-35	XX	T2a1a	n/a
KD010	WM	17-25	XY	U5b1	E1b1
KD011	WM	35-45	XX	H11a	n/a
KD012	WM	25-35	XX	HV6	n/a
KD013	WM	17-25	XY	HV6	R1ba1a1a2a1a
KD014	WM	40-45	XY	HV6	R1ba1a1a2a1a
KD016	WM	25-35	XX	H1bb	n/a
KD017	WM	45-49	XY	H1e1a	R1ba1a1a2a1a
KD018	WM	15-16	XY	H1bb	R1ba1a1a2a1a
KD019	WM	25-35	XX	U5b2bc1	n/a
KD020	WM	adult	XY	T2a1a	R1ba1a1a2a1a2c1a
KD021	WM	17-25	XY	H5c	R1ba1a1a2a1a1c2b2b1a
KD022	WM	16-17	XY	T2a1	I2a1b1
CE005	O	15-18	XX	H3g1a	n/a

TABLE E.2: Results of Dr. Dulias, concerning the samples assessed in this chapter. Acronyms as follows: LH = Low Hauxley, CPC = Carsington Pasture Cave, HPC = High Pature Cave, MS = Milla Skerra, RC = Rosemarkie Cave, WH = West Heslerton, WM = Worth Matravers, O = Oakridge.

Appendix F

Published ancient samples used throughout the thesis

ID	Group_ID	Reference	Country
Bon001	Boncuklu_N	Kilinc et al. 2016	Anatolia
Bon002	Boncuklu_N	Kilinc et al. 2016	Anatolia
Bon004	Boncuklu_N	Kilinc et al. 2016	Anatolia
Bon005	Boncuklu_N	Kilinc et al. 2016	Anatolia
I1584	C	Lazaridis et al. 2016	Anatolia
I2683	EBA	Lazaridis et al. 2017	Anatolia
I2495	EBA	Lazaridis et al. 2017	Anatolia
I2499	EBA	Lazaridis et al. 2017	Anatolia
MA2210	EBA	Damgaard et al. 2018	Anatolia
MA2212	EBA	Damgaard et al. 2018	Anatolia
MA2213	EBA	Damgaard et al. 2018	Anatolia
MA2197	IA	Damgaard et al. 2018	Anatolia
MA2198	IA	Damgaard et al. 2018	Anatolia
MA2200	MLBA	Damgaard et al. 2018	Anatolia
MA2203	MLBA	Damgaard et al. 2018	Anatolia
MA2205	MLBA	Damgaard et al. 2018	Anatolia
MA2206	MLBA	Damgaard et al. 2018	Anatolia
MA2208	MLBA	Damgaard et al. 2018	Anatolia
I1100	Neolithic	Mathieson et al. 2015	Anatolia
I1102	Neolithic	Mathieson et al. 2015	Anatolia
I1099	Neolithic	Mathieson et al. 2015	Anatolia
I1103	Neolithic	Mathieson et al. 2015	Anatolia
I1101	Neolithic	Mathieson et al. 2015	Anatolia
I1097	Neolithic	Mathieson et al. 2015	Anatolia
I0744	Neolithic	Mathieson et al. 2015	Anatolia
I1096	Neolithic	Mathieson et al. 2015	Anatolia

I1098	Neolithic	Mathieson et al. 2015	Anatolia
I0708	Neolithic	Mathieson et al. 2015	Anatolia
I0745	Neolithic	Mathieson et al. 2015	Anatolia
I0746	Neolithic	Mathieson et al. 2015	Anatolia
I0707	Neolithic	Mathieson et al. 2015	Anatolia
I0709	Neolithic	Mathieson et al. 2015	Anatolia
I0725	Neolithic	Mathieson et al. 2015	Anatolia
I0736	Neolithic	Mathieson et al. 2015	Anatolia
I0726	Neolithic	Mathieson et al. 2015	Anatolia
Bar31	Neolithic	Hofmanova et al. 2016	Anatolia
Bar8	Neolithic	Hofmanova et al. 2016	Anatolia
I1579	Neolithic	Mathieson et al. 2015	Anatolia
I1581	Neolithic	Mathieson et al. 2015	Anatolia
I1580	Neolithic	Mathieson et al. 2015	Anatolia
I1585	Neolithic	Mathieson et al. 2015	Anatolia
I1583	Neolithic	Mathieson et al. 2015	Anatolia
I0727	Neolithic	Mathieson et al. 2015	Anatolia
I0724	Neolithic	Mathieson et al. 2015	Anatolia
I0723	Neolithic	Mathieson et al. 2015	Anatolia
MA2195	Ottoman_1	Damgaard et al. 2018	Anatolia
MA2196	Ottoman_2	Damgaard et al. 2018	Anatolia
Tep002	TepecikCiftlik_N	Kilinc et al. 2016	Anatolia
Tep003	TepecikCiftlik_N	Kilinc et al. 2016	Anatolia
Tep004	TepecikCiftlik_N	Kilinc et al. 2016	Anatolia
Tep006	TepecikCiftlik_N	Kilinc et al. 2016	Anatolia
I1634	Chalcolithic	Lazaridis et al. 2016	Armenia
I1632	Chalcolithic	Lazaridis et al. 2016	Armenia
I1631	Chalcolithic	Lazaridis et al. 2016	Armenia
I1409	Chalcolithic	Lazaridis et al. 2016	Armenia
I1407	Chalcolithic	Lazaridis et al. 2016	Armenia
I1635	EBA	Lazaridis et al. 2016	Armenia
I1633	EBA	Lazaridis et al. 2016	Armenia
I1658	EBA	Lazaridis et al. 2016	Armenia
RISE396	LBA	Allentoft et al. 2015	Armenia
RISE397	LBA	Allentoft et al. 2015	Armenia
RISE407	LBA	Allentoft et al. 2015	Armenia
RISE408	LBA	Allentoft et al. 2015	Armenia
RISE412	LBA	Allentoft et al. 2015	Armenia
I1656	MBA	Lazaridis et al. 2016	Armenia

RISE413	MBA	Allentoft et al. 2015	Armenia
RISE416	MBA	Allentoft et al. 2015	Armenia
RISE423	MBA	Allentoft et al. 2015	Armenia
I5068	EN_LBK	Mathieson et al. 2018	Austria
I5069	EN_LBK	Mathieson et al. 2018	Austria
I5070	EN_LBK	Mathieson et al. 2018	Austria
I5204	EN_LBK	Mathieson et al. 2018	Austria
I5205	EN_LBK	Mathieson et al. 2018	Austria
I5206	EN_LBK	Mathieson et al. 2018	Austria
I5207	EN_LBK	Mathieson et al. 2018	Austria
I5208	EN_LBK	Mathieson et al. 2018	Austria
I1577	KremsWA3	Fu et al. 2016	Austria
GoyetQ116-1	GoyetQ116_1	Fu et al. 2016	Belgium
I2416	England_BellBeaker	Olalde et al. 2018	Britain
I2418	England_BellBeaker	Olalde et al. 2018	Britain
I2459	England_BellBeaker	Olalde et al. 2018	Britain
I2445	England_BellBeaker	Olalde et al. 2018	Britain
I2452	England_BellBeaker	Olalde et al. 2018	Britain
I2453	England_BellBeaker	Olalde et al. 2018	Britain
I2454	England_BellBeaker	Olalde et al. 2018	Britain
I2455	England_BellBeaker	Olalde et al. 2018	Britain
I3255	England_BellBeaker	Olalde et al. 2018	Britain
I3256	England_BellBeaker	Olalde et al. 2018	Britain
I1767	England_BellBeaker	Olalde et al. 2018	Britain
I1770	England_BellBeaker	Olalde et al. 2018	Britain
I4950	England_BellBeaker	Olalde et al. 2018	Britain
I4951	England_BellBeaker	Olalde et al. 2018	Britain
I5512	England_BellBeaker	Olalde et al. 2018	Britain
I5513	England_BellBeaker	Olalde et al. 2018	Britain
I2417	England_BellBeaker	Olalde et al. 2018	Britain
I2443	England_BellBeaker	Olalde et al. 2018	Britain
I2447	England_BellBeaker	Olalde et al. 2018	Britain
I2450	England_BellBeaker	Olalde et al. 2018	Britain
I5376	England_BellBeaker	Olalde et al. 2018	Britain
I5379	England_BellBeaker	Olalde et al. 2018	Britain
I5382	England_BellBeaker	Olalde et al. 2018	Britain
I6774	England_BellBeaker	Olalde et al. 2018	Britain
I6775	England_BellBeaker	Olalde et al. 2018	Britain
I6777	England_BellBeaker	Olalde et al. 2018	Britain

I6778	England_BellBeaker	Olalde et al. 2018	Britain
I6679	England_BellBeaker	Olalde et al. 2018	Britain
I2446	England_BellBeaker	Olalde et al. 2018	Britain
I7630	England_EBA	Olalde et al. 2018	Britain
I7635	England_EBA	Olalde et al. 2018	Britain
I7638	England_EBA	Olalde et al. 2018	Britain
I7639	England_EBA	Olalde et al. 2018	Britain
I2421	England_EBA	Olalde et al. 2018	Britain
I2457	England_EBA	Olalde et al. 2018	Britain
I2460	England_EBA	Olalde et al. 2018	Britain
I2463	England_EBA	Olalde et al. 2018	Britain
I2464	England_EBA	Olalde et al. 2018	Britain
I2566	England_EBA	Olalde et al. 2018	Britain
I2601	England_EBA	Olalde et al. 2018	Britain
I2602	England_EBA	Olalde et al. 2018	Britain
I2609	England_EBA	Olalde et al. 2018	Britain
I2610	England_EBA	Olalde et al. 2018	Britain
I2612	England_EBA	Olalde et al. 2018	Britain
I2618	England_EBA	Olalde et al. 2018	Britain
I2461	England_EBA	Olalde et al. 2018	Britain
I2462	England_EBA	Olalde et al. 2018	Britain
I5373	England_EBA	Olalde et al. 2018	Britain
I5441	England_EBA	Olalde et al. 2018	Britain
I2597	England_EBA	Olalde et al. 2018	Britain
I2604	England_EBA	Olalde et al. 2018	Britain
I5377	England_EBA	Olalde et al. 2018	Britain
I6680	England_EBA	Olalde et al. 2018	Britain
I2598	England_EBA	Olalde et al. 2018	Britain
I0789	England_IA	Schiffels et al. 2016	Britain
I5383	England_LBA	Olalde et al. 2018	Britain
I0160	England_IA	Schiffels et al. 2016	Britain
M1489	England_IA	Martiniano et al. 2016	Britain
I0156	England_IA	Schiffels et al. 2016	Britain
I7580	England_MBA	Olalde et al. 2018	Britain
I7568	England_MBA	Olalde et al. 2018	Britain
I7569	England_MBA	Olalde et al. 2018	Britain
I7570	England_MBA	Olalde et al. 2018	Britain
I7571	England_MBA	Olalde et al. 2018	Britain
I7572	England_MBA	Olalde et al. 2018	Britain

I7573	England_MBA	Olalde et al. 2018	Britain
I7574	England_MBA	Olalde et al. 2018	Britain
I7575	England_MBA	Olalde et al. 2018	Britain
I7576	England_MBA	Olalde et al. 2018	Britain
I7577	England_MBA	Olalde et al. 2018	Britain
I7578	England_MBA	Olalde et al. 2018	Britain
I7626	England_MBA	Olalde et al. 2018	Britain
I7627	England_MBA	Olalde et al. 2018	Britain
I7628	England_MBA	Olalde et al. 2018	Britain
I7640	England_MBA	Olalde et al. 2018	Britain
I2639	England_MBA	Olalde et al. 2018	Britain
I2458	England_MBA	Olalde et al. 2018	Britain
I3082	England_MBA	Olalde et al. 2018	Britain
I2605	England_N	Olalde et al. 2018	Britain
I6761	England_N	Olalde et al. 2018	Britain
I2606	England_N	Olalde et al. 2018	Britain
I0519	England_N	Olalde et al. 2018	Britain
I0520	England_N	Olalde et al. 2018	Britain
I0518	England_N	Olalde et al. 2018	Britain
I3068	England_N	Brace et al. 2019	Britain
I5374	England_N	Brace et al. 2019	Britain
I5366	England_N	Brace et al. 2019	Britain
I6759	England_N	Olalde et al. 2018	Britain
I6762	England_N	Brace et al. 2019	Britain
I6750	England_N	Olalde et al. 2018	Britain
I6751	England_N	Olalde et al. 2018	Britain
I4949	England_N	Olalde et al. 2018	Britain
3DT16	England_Roman	Martiniano et al. 2016	Britain
6DT18	England_Roman	Martiniano et al. 2016	Britain
6DT21	England_Roman	Martiniano et al. 2016	Britain
6DT22	England_Roman	Martiniano et al. 2016	Britain
6DT23	England_Roman	Martiniano et al. 2016	Britain
6DT3	England_Roman	Martiniano et al. 2016	Britain
3DT26	England_Roman_o	Martiniano et al. 2016	Britain
I0157	England_Saxon	Schiffels et al. 2016	Britain
I0159	England_Saxon	Schiffels et al. 2016	Britain
I0161	England_Saxon	Schiffels et al. 2016	Britain
I0769	England_Saxon	Schiffels et al. 2016	Britain
I0773	England_Saxon	Schiffels et al. 2016	Britain

I0774	England_Saxon	Schiffels et al. 2016	Britain
I0777	England_Saxon	Schiffels et al. 2016	Britain
I17268	England_Saxon	Martiniano et al. 2016	Britain
I5367	Scotland_BellBeaker	Olalde et al. 2018	Britain
I5385	Scotland_BellBeaker	Olalde et al. 2018	Britain
I2981	Scotland_EBA	Olalde et al. 2018	Britain
I3132	Scotland_EBA	Olalde et al. 2018	Britain
I2567	Scotland_EBA	Olalde et al. 2018	Britain
I2568	Scotland_EBA	Olalde et al. 2018	Britain
I5515	Scotland_EBA	Olalde et al. 2018	Britain
I5516	Scotland_EBA	Olalde et al. 2018	Britain
I2569	Scotland_EBA	Olalde et al. 2018	Britain
I5471	Scotland_EBA	Olalde et al. 2018	Britain
I2859	Scotland_LBA	Olalde et al. 2018	Britain
I2860	Scotland_LBA	Olalde et al. 2018	Britain
I2861	Scotland_LBA	Olalde et al. 2018	Britain
I3130	Scotland_LBA	Olalde et al. 2018	Britain
I2573	Scotland_MBA	Olalde et al. 2018	Britain
I2653	Scotland_MBA	Olalde et al. 2018	Britain
I2654	Scotland_MBA	Olalde et al. 2018	Britain
I2655	Scotland_MBA	Olalde et al. 2018	Britain
mid001	Scotland_N	Sanchez-Quinto et al. 2019	Britain
mid002	Scotland_N	Sanchez-Quinto et al. 2019	Britain
I7554	Scotland_N	Olalde et al. 2018	Britain
I2634	Scotland_N	Olalde et al. 2018	Britain
I2636	Scotland_N	Olalde et al. 2018	Britain
I2980	Scotland_N	Olalde et al. 2018	Britain
I2988	Scotland_N	Olalde et al. 2018	Britain
I3136	Scotland_N	Olalde et al. 2018	Britain
I3138	Scotland_N	Olalde et al. 2018	Britain
I2977	Scotland_N	Olalde et al. 2018	Britain
I2978	Scotland_N	Olalde et al. 2018	Britain
I3133	Scotland_N	Olalde et al. 2018	Britain
I2979	Scotland_N	Olalde et al. 2018	Britain
I3134	Scotland_N	Olalde et al. 2018	Britain
I3135	Scotland_N	Olalde et al. 2018	Britain
I2630	Scotland_N	Olalde et al. 2018	Britain
I2631	Scotland_N	Olalde et al. 2018	Britain
I2633	Scotland_N	Olalde et al. 2018	Britain

I2635	Scotland_N	Olalde et al. 2018	Britain
I2637	Scotland_N	Olalde et al. 2018	Britain
I2650	Scotland_N	Olalde et al. 2018	Britain
I2651	Scotland_N	Olalde et al. 2018	Britain
I2659	Scotland_N	Olalde et al. 2018	Britain
I2660	Scotland_N	Olalde et al. 2018	Britain
I2691	Scotland_N	Olalde et al. 2018	Britain
I2932	Scotland_N	Olalde et al. 2018	Britain
I2933	Scotland_N	Olalde et al. 2018	Britain
I2934	Scotland_N	Olalde et al. 2018	Britain
I2935	Scotland_N	Olalde et al. 2018	Britain
I3041	Scotland_N	Olalde et al. 2018	Britain
I3085	Scotland_N	Olalde et al. 2018	Britain
I5370	Scotland_N	Olalde et al. 2018	Britain
I5371	Scotland_N	Olalde et al. 2018	Britain
I2657	Scotland_N_o	Olalde et al. 2018	Britain
I3137	Scotland_N	Olalde et al. 2018	Britain
I2629	Scotland_N	Olalde et al. 2018	Britain
I2796	Scotland_N	Olalde et al. 2018	Britain
I5359	Wales_C	Olalde et al. 2018	Britain
I5359	Wales_C	Brace et al. 2019	Britain
I1775	Wales_EBA	Olalde et al. 2018	Britain
I2574	Wales_EBA	Olalde et al. 2018	Britain
I5358	Wales_LN	Olalde et al. 2018	Britain
I5358	Wales_LN	Brace et al. 2019	Britain
I5364	Wales_MBA	Olalde et al. 2018	Britain
Bul6	BeliBreyag_EBA	Mathieson et al. 2018	Bulgaria
Bul8	BeliBreyag_EBA	Mathieson et al. 2018	Bulgaria
ANI153	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2427	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2431	Chalcolithic	Mathieson et al. 2018	Bulgaria
I0785	Chalcolithic	Mathieson et al. 2018	Bulgaria
I0781	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2509	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2519	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2423	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2424	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2425	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2430	Chalcolithic	Mathieson et al. 2018	Bulgaria

I2526	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2181	Chalcolithic	Mathieson et al. 2018	Bulgaria
I2426	Chalcolithic	Mathieson et al. 2018	Bulgaria
I0706	Dzhulyunitsa_N	Mathieson et al. 2018	Bulgaria
I2165	EBA	Mathieson et al. 2018	Bulgaria
I2510	EBA	Mathieson et al. 2018	Bulgaria
I2520	EBA	Mathieson et al. 2018	Bulgaria
I2175	EBA	Mathieson et al. 2018	Bulgaria
I2176	EBA	Mathieson et al. 2018	Bulgaria
Bul4	Yamnaya_o	Mathieson et al. 2018	Bulgaria
I5769	IA	Mathieson et al. 2018	Bulgaria
I0679	Krepost_N	Mathieson et al. 2018	Bulgaria
I3879	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I1108	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I1109	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I1113	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I1295	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I1297	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I1296	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I2215	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I2216	MalakPreslavets_N	Mathieson et al. 2018	Bulgaria
I2163	MLBA	Mathieson et al. 2018	Bulgaria
I2521	Neolithic	Mathieson et al. 2018	Bulgaria
I0704	Neolithic	Mathieson et al. 2018	Bulgaria
I2529	Neolithic	Mathieson et al. 2018	Bulgaria
I0698	Neolithic	Mathieson et al. 2018	Bulgaria
I1298	Neolithic	Mathieson et al. 2018	Bulgaria
ANI152	Varna_C	Mathieson et al. 2018	Bulgaria
ANI160	Varna_C	Mathieson et al. 2018	Bulgaria
ANI159-ANI181	Varna_C	Mathieson et al. 2018	Bulgaria
gun005	Guanche	Rodríguez-Varela et al. 2017	Canaries
gun008	Guanche	Rodríguez-Varela et al. 2017	Canaries
gun012	Guanche	Rodríguez-Varela et al. 2017	Canaries
I3313	EIA	Mathieson et al. 2018	Croatia
I5071	EN_Impressa	Mathieson et al. 2018	Croatia
I5072	EN_Impressa	Mathieson et al. 2018	Croatia
I4167	EN_Starcevo	Mathieson et al. 2018	Croatia
I3499	LateC_EBA_Vucedol	Mathieson et al. 2018	Croatia
I4175	LateC_EBA_Vucedol	Mathieson et al. 2018	Croatia

I5079	LN_Starcevo	Mathieson et al. 2018	Croatia
I4331	MBA	Mathieson et al. 2018	Croatia
I4332	MBA	Mathieson et al. 2018	Croatia
I1875	Mesolithic_HG	Mathieson et al. 2018	Croatia
I3498	MN_Sopot	Mathieson et al. 2018	Croatia
I4168	MN_Sopot	Mathieson et al. 2018	Croatia
I5077	MN_Sopot	Mathieson et al. 2018	Croatia
I5078	MN_Sopot	Mathieson et al. 2018	Croatia
I3433	N_Cardial	Mathieson et al. 2018	Croatia
I3947	N_Cardial	Mathieson et al. 2018	Croatia
I3948	N_Cardial	Mathieson et al. 2018	Croatia
I2792	Vucedol	Mathieson et al. 2018	Croatia
I7278	BellBeaker	Olalde et al. 2018	Czechia
I7282	BellBeaker	Olalde et al. 2018	Czechia
I7212	BellBeaker	Olalde et al. 2018	Czechia
I7214	BellBeaker	Olalde et al. 2018	Czechia
I7205	BellBeaker	Olalde et al. 2018	Czechia
I7211	BellBeaker	Olalde et al. 2018	Czechia
I7213	BellBeaker	Olalde et al. 2018	Czechia
I7249	BellBeaker	Olalde et al. 2018	Czechia
I7251	BellBeaker	Olalde et al. 2018	Czechia
I7250	BellBeaker	Olalde et al. 2018	Czechia
I7269	BellBeaker	Olalde et al. 2018	Czechia
I7270	BellBeaker	Olalde et al. 2018	Czechia
I7275	BellBeaker	Olalde et al. 2018	Czechia
I7276	BellBeaker	Olalde et al. 2018	Czechia
I7281	BellBeaker	Olalde et al. 2018	Czechia
I7286	BellBeaker	Olalde et al. 2018	Czechia
I7287	BellBeaker	Olalde et al. 2018	Czechia
I7288	BellBeaker	Olalde et al. 2018	Czechia
I7290	BellBeaker	Olalde et al. 2018	Czechia
I4145	BellBeaker	Olalde et al. 2018	Czechia
I4136	BellBeaker	Olalde et al. 2018	Czechia
I4945	BellBeaker	Olalde et al. 2018	Czechia
I4946	BellBeaker	Olalde et al. 2018	Czechia
I4885	BellBeaker	Olalde et al. 2018	Czechia
I4886	BellBeaker	Olalde et al. 2018	Czechia
I4888	BellBeaker	Olalde et al. 2018	Czechia
I4889	BellBeaker	Olalde et al. 2018	Czechia

I4890	BellBeaker	Olalde et al. 2018	Czechia
I4891	BellBeaker	Olalde et al. 2018	Czechia
I4895	BellBeaker	Olalde et al. 2018	Czechia
I4896	BellBeaker	Olalde et al. 2018	Czechia
I5514	BellBeaker	Olalde et al. 2018	Czechia
I5666	BellBeaker	Olalde et al. 2018	Czechia
I6468	BellBeaker	Olalde et al. 2018	Czechia
I6476	BellBeaker	Olalde et al. 2018	Czechia
I6480	BellBeaker	Olalde et al. 2018	Czechia
I7279	CordedWare	Olalde et al. 2018	Czechia
I7280	CordedWare	Olalde et al. 2018	Czechia
I5026	EarlySlav	Allentoft et al. 2015	Czechia
I7195	EBA	Olalde et al. 2018	Czechia
I7196	EBA	Olalde et al. 2018	Czechia
I7198	EBA	Olalde et al. 2018	Czechia
I7199	EBA	Olalde et al. 2018	Czechia
I7200	EBA	Olalde et al. 2018	Czechia
I7201	EBA	Olalde et al. 2018	Czechia
I7202	EBA	Olalde et al. 2018	Czechia
I7203	EBA	Olalde et al. 2018	Czechia
I4884	EBA	Olalde et al. 2018	Czechia
I4892	EBA	Olalde et al. 2018	Czechia
I5037	EBA_Protounetice	Olalde et al. 2018	Czechia
I5042	EBA_Protounetice	Olalde et al. 2018	Czechia
I4141	EBA_Unetice	Olalde et al. 2018	Czechia
I4130	EBA_Unetice	Olalde et al. 2018	Czechia
I7272	Eneolithic	Olalde et al. 2018	Czechia
kol002	Neolithic	Sanchez-Quinto et al. 2019	Czechia
kol006	Neolithic	Sanchez-Quinto et al. 2019	Czechia
I7197	MN	Olalde et al. 2018	Czechia
I4893	Neolithic	Olalde et al. 2018	Czechia
I4894	Neolithic	Olalde et al. 2018	Czechia
Vestonice16	Vestonice16	Fu et al. 2016	Czechia
Pavlov1	Pavlov1	Fu et al. 2016	Czechia
Vestonice13	Vestonice13	Fu et al. 2016	Czechia
Vestonice15	Vestonice15	Fu et al. 2016	Czechia
Vestonice43	Vestonice43	Fu et al 2016	Czechia
RISE21	BA	Allentoft et al. 2015	Denmark
RISE47	BA	Allentoft et al. 2015	Denmark

RISE276	LBA	Allentoft et al. 2015	Denmark
RISE42	LN	Allentoft et al. 2015	Denmark
RISE71	LN	Allentoft et al. 2015	Denmark
RISE61	MN_B	Allentoft et al. 2015	Denmark
Sope	CordedWare	Saag et al. 2017	Estonia
I5950 (Mota)	Mota_4500BP	Llorente et al. 2015	Ethiopia
BerryAuBac	BerryAuBac	Fu et al. 2016	France
Rochedane	Rochedane	Fu et al. 2016	France
Iboussieres25-1	Iboussieres25_1	Mathieson et al. 2018	France
Iboussieres31-2	Iboussieres31_2	Mathieson et al. 2018	France
Rochedane	Rochedane	Mathieson et al. 2018	France
BerryAuBac	BerryAuBac	Mathieson et al. 2018	France
I1382	BellBeaker	Olalde et al. 2018	France
I1381	BellBeaker	Olalde et al. 2018	France
I1390	BellBeaker	Olalde et al. 2018	France
I3874	BellBeaker	Olalde et al. 2018	France
I3875	BellBeaker	Olalde et al. 2018	France
I1388	BellBeaker_lowSteppe	Olalde et al. 2018	France
I1392	BellBeaker_lowSteppe	Olalde et al. 2018	France
I1391	BellBeaker	Olalde et al. 2018	France
I2575	BellBeaker	Olalde et al. 2018	France
I4303	MN	Olalde et al. 2018	France
I4304	MN	Olalde et al. 2018	France
I4305	MN	Olalde et al. 2018	France
I4308	MN	Olalde et al. 2018	France
KK1	CHG	Jones et al. 2015	Georgia
SATP	CHG	Jones et al. 2015	Georgia
RISE471	BA	Allentoft et al. 2015	Germany
I1546	BellBeaker	Mathieson et al. 2015	Germany
I0806	BellBeaker	Mathieson et al. 2015	Germany
I0805	BellBeaker	Mathieson et al. 2015	Germany
I0113	BellBeaker	Mathieson et al. 2015	Germany
I0112	BellBeaker	Mathieson et al. 2015	Germany
I0111	BellBeaker	Mathieson et al. 2015	Germany
I0108	BellBeaker	Mathieson et al. 2015	Germany
I1549	BellBeaker	Mathieson et al. 2015	Germany
I3600	BellBeaker	Olalde et al. 2018	Germany
I3601	BellBeaker	Olalde et al. 2018	Germany
I3588	BellBeaker	Olalde et al. 2018	Germany

I3589	BellBeaker	Olalde et al. 2018	Germany
I3590	BellBeaker	Olalde et al. 2018	Germany
I3594	BellBeaker	Olalde et al. 2018	Germany
I3592	BellBeaker	Olalde et al. 2018	Germany
I5014	BellBeaker	Olalde et al. 2018	Germany
I4124	BellBeaker	Olalde et al. 2018	Germany
I4143	BellBeaker	Olalde et al. 2018	Germany
I4144	BellBeaker	Olalde et al. 2018	Germany
I4134	BellBeaker	Olalde et al. 2018	Germany
I5023	BellBeaker	Olalde et al. 2018	Germany
I5519	BellBeaker	Olalde et al. 2018	Germany
I5520	BellBeaker	Olalde et al. 2018	Germany
I5521	BellBeaker	Olalde et al. 2018	Germany
I5523	BellBeaker	Olalde et al. 2018	Germany
I5524	BellBeaker	Olalde et al. 2018	Germany
I5525	BellBeaker	Olalde et al. 2018	Germany
I5527	BellBeaker	Olalde et al. 2018	Germany
I5529	BellBeaker	Olalde et al. 2018	Germany
I5531	BellBeaker	Olalde et al. 2018	Germany
I5833	BellBeaker	Olalde et al. 2018	Germany
I5834	BellBeaker	Olalde et al. 2018	Germany
I5836	BellBeaker	Olalde et al. 2018	Germany
I5658	BellBeaker	Olalde et al. 2018	Germany
I5659	BellBeaker	Olalde et al. 2018	Germany
I6482	BellBeaker	Olalde et al. 2018	Germany
I6590	BellBeaker	Olalde et al. 2018	Germany
I6591	BellBeaker	Olalde et al. 2018	Germany
I6624	BellBeaker	Olalde et al. 2018	Germany
I3602	BellBeaker	Olalde et al. 2018	Germany
I3604	BellBeaker	Olalde et al. 2018	Germany
I4249	BellBeaker	Olalde et al. 2018	Germany
I4250	BellBeaker	Olalde et al. 2018	Germany
I5655	BellBeaker	Olalde et al. 2018	Germany
I5661	BellBeaker	Olalde et al. 2018	Germany
I5663	BellBeaker	Olalde et al. 2018	Germany
I0060	BellBeaker	Mathieson et al. 2015	Germany
I1542	CordedWare	Mathieson et al. 2015	Germany
I1536	CordedWare	Mathieson et al. 2015	Germany
I1544	CordedWare	Mathieson et al. 2015	Germany

I1538	CordedWare	Mathieson et al. 2015	Germany
I1539	CordedWare	Mathieson et al. 2015	Germany
I1534	CordedWare	Mathieson et al. 2015	Germany
I0106	CordedWare	Mathieson et al. 2015	Germany
I1532	CordedWare	Mathieson et al. 2015	Germany
I0049	CordedWare	Mathieson et al. 2015	Germany
I0103	CordedWare	Mathieson et al. 2015	Germany
I0104	CordedWare	Mathieson et al. 2015	Germany
RISE434	CordedWare	Allentoft et al. 2015	Germany
RISE435	CordedWare	Allentoft et al. 2015	Germany
RISE436	CordedWare	Allentoft et al. 2015	Germany
RISE446	CordedWare	Allentoft et al. 2015	Germany
I0115	EBA_Unetice	Mathieson et al. 2015	Germany
I0117	EBA_Unetice	Mathieson et al. 2015	Germany
I0804	EBA_Unetice	Mathieson et al. 2015	Germany
I0803	EBA_Unetice	Mathieson et al. 2015	Germany
I0164	EBA_Unetice	Mathieson et al. 2015	Germany
I0116	EBA_Unetice	Mathieson et al. 2015	Germany
I0047	EBA_Unetice	Mathieson et al. 2015	Germany
I0797	EN_LBK	Mathieson et al. 2015	Germany
I0795	EN_LBK	Mathieson et al. 2015	Germany
I0022	EN_LBK	Mathieson et al. 2015	Germany
I0026	EN_LBK	Mathieson et al. 2015	Germany
I0025	EN_LBK	Mathieson et al. 2015	Germany
I0054	EN_LBK	Mathieson et al. 2015	Germany
I0056	EN_LBK	Lipson et al. 2017	Germany
I0100	EN_LBK	Lipson et al. 2017	Germany
I2014	EN_LBK	Lipson et al. 2017	Germany
I2022	EN_LBK	Lipson et al. 2017	Germany
I0018	EN_LBK	Lipson et al. 2017	Germany
I0046	EN_LBK	Lipson et al. 2017	Germany
I0659	EN_LBK	Lipson et al. 2017	Germany
I0048	EN_LBK	Lipson et al. 2017	Germany
I1550	EN_LBK	Lipson et al. 2017	Germany
I0821	EN_LBK	Lipson et al. 2017	Germany
I0057	EN_LBK	Lipson et al. 2017	Germany
I2008	EN_LBK	Lipson et al. 2017	Germany
I2026	EN_LBK	Lipson et al. 2017	Germany
I2029	EN_LBK	Lipson et al. 2017	Germany

I2030	EN_LBK	Lipson et al. 2017	Germany
I2032	EN_LBK	Lipson et al. 2017	Germany
I2036	EN_LBK	Lipson et al. 2017	Germany
I2037	EN_LBK	Lipson et al. 2017	Germany
I2038	EN_LBK	Lipson et al. 2017	Germany
I0018	EN_LBK_Stuttgart	Lazaridis et al. 2014	Germany
Falkenstein	Falkenstein	Fu et al. 2016	Germany
I0099	LBA	Mathieson et al. 2015	Germany
HUGO_168	BellBeaker	Mittnik et al. 2019	Germany
UNTA58_68Sk1	BellBeaker	Mittnik et al. 2019	Germany
UNTA58_68Sk2	BellBeaker	Mittnik et al. 2019	Germany
UNTA85_1343	BellBeaker	Mittnik et al. 2019	Germany
I0118	LN	Mathieson et al. 2015	Germany
I0171	LN	Mathieson et al. 2015	Germany
I0059	LN	Mathieson et al. 2015	Germany
I0550	LN	Mathieson et al. 2015	Germany
I0807	MN_Baalberge	Mathieson et al. 2015	Germany
I0559	MN_Baalberge	Mathieson et al. 2015	Germany
I0560	MN_Baalberge	Mathieson et al. 2015	Germany
I1593	MN_Blatterhohle	Lipson et al. 2017	Germany
I1563	MN_Blatterhohle	Lipson et al. 2017	Germany
I1565	MN_Blatterhohle	Lipson et al. 2017	Germany
I1594	MN_Blatterhohle	Lipson et al. 2017	Germany
I0172	MN_Esperstedt	Mathieson et al. 2015	Germany
I1560	MN_lc	Lipson et al. 2017	Germany
I0802	MN_Salzmuende	Lipson et al. 2017	Germany
I0800	MN_Salzmuende	Lipson et al. 2017	Germany
I0551	MN_Salzmuende	Mathieson et al. 2015	Germany
I0166	Neolithic	Lipson et al. 2017	Germany
I9010	Mycenaean	Lazaridis et al. 2017	Greece
I9006	Mycenaean	Lazaridis et al. 2017	Greece
I9041	Mycenaean	Lazaridis et al. 2017	Greece
I9033	Mycenaean_Pylos	Lazaridis et al. 2017	Greece
I9123	Crete_Armenoi	Lazaridis et al. 2017	Greece
Klei10	LN	Hofmanova et al. 2016	Greece
Pal7	LN	Hofmanova et al. 2016	Greece
I0070	Minoan_Lassithi	Lazaridis et al. 2017	Greece
I0071	Minoan_Lassithi	Lazaridis et al. 2017	Greece
I0073	Minoan_Lassithi	Lazaridis et al. 2017	Greece

I0074	Minoan_Lassithi	Lazaridis et al. 2017	Greece
I9005	Minoan_Lassithi	Lazaridis et al. 2017	Greece
I9127	Minoan_Odigitria	Lazaridis et al. 2017	Greece
I9128	Minoan_Odigitria	Lazaridis et al. 2017	Greece
I9129	Minoan_Odigitria	Lazaridis et al. 2017	Greece
I9130	Minoan_Odigitria	Lazaridis et al. 2017	Greece
I9131	Minoan_Odigitria	Lazaridis et al. 2017	Greece
I5427	Neolithic	Mathieson et al. 2018	Greece
Rev5	Neolithic	Hofmanova et al. 2016	Greece
I3708	Peloponnese_N	Mathieson et al. 2018	Greece
I3709	Peloponnese_N	Mathieson et al. 2018	Greece
I2318	Peloponnese_N	Mathieson et al. 2018	Greece
I2937	Peloponnese_N	Lazaridis et al. 2017	Greece
I3920	Peloponnese_N	Mathieson et al. 2018	Greece
I2937	Peloponnese_N	Lazaridis et al. 2017	Greece
I1499	ALPc_Bukk_MN	Gamba et al. 2014	Hungary
I1505	ALPc_MN	Gamba et al. 2014	Hungary
I1500	ALPc_MN	Gamba et al. 2014	Hungary
I1498	ALPc_MN	Gamba et al. 2014	Hungary
I1497	Baden_LCA	Gamba et al. 2014	Hungary
I2351	Chalcolithic	Lipson et al. 2017	Hungary
I2394	Chalcolithic	Lipson et al. 2017	Hungary
I4189	Chalcolithic	Lipson et al. 2017	Hungary
I1908	Chalcolithic	Lipson et al. 2017	Hungary
I1909	Chalcolithic	Lipson et al. 2017	Hungary
I1907	Chalcolithic	Lipson et al. 2017	Hungary
I2353	EarlyC	Lipson et al. 2017	Hungary
I2354	EarlyC	Lipson et al. 2017	Hungary
I2356	EarlyC	Lipson et al. 2017	Hungary
I2395	EarlyC	Lipson et al. 2017	Hungary
I2793	EarlyC	Lipson et al. 2017	Hungary
I7044	BellBeaker	Olalde et al. 2018	Hungary
I7045	BellBeaker	Olalde et al. 2018	Hungary
I2364	BellBeaker	Olalde et al. 2018	Hungary
I3528	BellBeaker	Olalde et al. 2018	Hungary
I3529	BellBeaker	Olalde et al. 2018	Hungary
I2365	BellBeaker	Olalde et al. 2018	Hungary
I4178	BellBeaker	Olalde et al. 2018	Hungary
I2787	BellBeaker	Olalde et al. 2018	Hungary

I4131	BellBeaker	Olalde et al. 2018	Hungary
I2786	BellBeaker	Olalde et al. 2018	Hungary
I1502	EBA	Mathieson et al. 2015	Hungary
I7043	EBA	Olalde et al. 2018	Hungary
I7040	EBA	Olalde et al. 2018	Hungary
I1507	EN_HG_Koros	Mathieson et al. 2015	Hungary
I4971	EN_HG_Koros	Lipson et al. 2017	Hungary
I1507	EN_HG_Koros	Gamba et al. 2014	Hungary
I1508	EN_Koros	Mathieson et al. 2015	Hungary
I2374	EN_Koros	Lipson et al. 2017	Hungary
I2794	EN_Koros	Lipson et al. 2017	Hungary
I2373	EN_Koros	Lipson et al. 2017	Hungary
I0174	EN_Starcevo	Mathieson et al. 2015	Hungary
I1876	EN_Starcevo	Lipson et al. 2017	Hungary
I1880	EN_Starcevo	Lipson et al. 2017	Hungary
I1877	EN_Starcevo	Lipson et al. 2017	Hungary
I2783	MCHA	Lipson et al. 2017	Hungary
I1508	Koros_EN	Gamba et al. 2014	Hungary
I1497	LateC	Mathieson et al. 2015	Hungary
I2368	LateC	Lipson et al. 2017	Hungary
I2369	LateC	Lipson et al. 2017	Hungary
I2370	LateC	Lipson et al. 2017	Hungary
I2371	LateC	Lipson et al. 2017	Hungary
I2752	LateC	Lipson et al. 2017	Hungary
I2753	LateC	Lipson et al. 2017	Hungary
I2754	LateC	Lipson et al. 2017	Hungary
I2755	LateC	Lipson et al. 2017	Hungary
I2763	LateC	Lipson et al. 2017	Hungary
I2785	LateC	Lipson et al. 2017	Hungary
I2366	LateC	Lipson et al. 2017	Hungary
I2367	LateC	Lipson et al. 2017	Hungary
I2788	LateC	Lipson et al. 2017	Hungary
I2789	LateC	Lipson et al. 2017	Hungary
I2790	LateC	Lipson et al. 2017	Hungary
I2791	LateC	Lipson et al. 2017	Hungary
I1504	LBA	Gamba et al. 2014	Hungary
I1504	LBA	Mathieson et al. 2015	Hungary
I1506	LBK_MN	Gamba et al. 2014	Hungary
I5116	Baden_Yamnaya	Olalde et al. 2018	Hungary

I5117	Baden_Yamnaya	Olalde et al. 2018	Hungary
I5118	Baden_Yamnaya	Olalde et al. 2018	Hungary
I5119	Baden_Yamnaya	Olalde et al. 2018	Hungary
I1495	LN_Lengyel	Mathieson et al. 2015	Hungary
I2352	LN_Lengyel	Lipson et al. 2017	Hungary
I1899	LN_Lengyel	Lipson et al. 2017	Hungary
I1900	LN_Lengyel	Lipson et al. 2017	Hungary
I1901	LN_Lengyel	Lipson et al. 2017	Hungary
I1906	LN_Lengyel	Lipson et al. 2017	Hungary
I1902	LN_Lengyel	Lipson et al. 2017	Hungary
I1905	LN_Lengyel	Lipson et al. 2017	Hungary
I1893	LN_Sopot	Lipson et al. 2017	Hungary
I4184	LN_Sopot	Lipson et al. 2017	Hungary
I4185	LN_Sopot	Lipson et al. 2017	Hungary
I1890	LN_Sopot	Lipson et al. 2017	Hungary
I1891	LN_Sopot	Lipson et al. 2017	Hungary
I0449	LN_Tisza	Lipson et al. 2017	Hungary
I2358	LN_Tisza	Lipson et al. 2017	Hungary
I2359	LN_Tisza	Lipson et al. 2017	Hungary
I2387	LN_Tisza	Lipson et al. 2017	Hungary
I2746	LN_Tisza	Lipson et al. 2017	Hungary
I0447	LN_Tisza	Lipson et al. 2017	Hungary
I1502	Mako_EBA	Gamba et al. 2014	Hungary
RISE349	Maros_EBA	Allentoft et al. 2015	Hungary
RISE371	Maros_EBA	Allentoft et al. 2015	Hungary
RISE373	Maros_EBA	Allentoft et al. 2015	Hungary
RISE374	Maros_EBA	Allentoft et al. 2015	Hungary
RISE247	MBA_Vatya	Allentoft et al. 2015	Hungary
RISE254	MBA_Vatya	Allentoft et al. 2015	Hungary
RISE479	MBA_Vatya	Allentoft et al. 2015	Hungary
RISE480	MBA_Vatya	Allentoft et al. 2015	Hungary
RISE483	MBA_Vatya	Allentoft et al. 2015	Hungary
RISE484	MBA_Vatya	Allentoft et al. 2015	Hungary
I7042	MN	Olalde et al. 2018	Hungary
I2355	MN_ALBK	Lipson et al. 2017	Hungary
I2357	MN_ALBK	Lipson et al. 2017	Hungary
I2357	MN_ALBK	Lipson et al. 2017	Hungary
I1500	MN_ALPc	Mathieson et al. 2015	Hungary
I1498	MN_ALPc	Mathieson et al. 2015	Hungary

I1506	MN_ALPc	Mathieson et al. 2015	Hungary
I1505	MN_ALPc	Mathieson et al. 2015	Hungary
I1499	MN_ALPc_Bukk	Mathieson et al. 2015	Hungary
I4186	MN_ALPc_Esztar	Lipson et al. 2017	Hungary
I4187	MN_ALPc_Esztar	Lipson et al. 2017	Hungary
I4188	MN_ALPc_I	Lipson et al. 2017	Hungary
I2383	MN_ALPc_III	Lipson et al. 2017	Hungary
I3535	MN_ALPc_III	Lipson et al. 2017	Hungary
I2384	MN_ALPc_III	Lipson et al. 2017	Hungary
I2743	MN_ALPc	Lipson et al. 2017	Hungary
I2744	MN_ALPc	Lipson et al. 2017	Hungary
I2745	MN_ALPc	Lipson et al. 2017	Hungary
I2380	MN_ALPc	Lipson et al. 2017	Hungary
I2382	MN_ALPc	Lipson et al. 2017	Hungary
I3537	MN_ALPc	Lipson et al. 2017	Hungary
I2375	MN_ALPc	Lipson et al. 2017	Hungary
I2376	MN_ALPc	Lipson et al. 2017	Hungary
I2377	MN_ALPc	Lipson et al. 2017	Hungary
I2378	MN_ALPc	Lipson et al. 2017	Hungary
I2379	MN_ALPc	Lipson et al. 2017	Hungary
I4199	MN_ALPc	Lipson et al. 2017	Hungary
I0176	MN_LBK	Mathieson et al. 2015	Hungary
I1496	MN_LBK	Mathieson et al. 2015	Hungary
I1904	MN_LBK	Lipson et al. 2017	Hungary
I1882	MN_LBK	Lipson et al. 2017	Hungary
I1883	MN_LBK	Lipson et al. 2017	Hungary
I3536	MN_LBK	Lipson et al. 2017	Hungary
I4196	MN_LBK	Lipson et al. 2017	Hungary
I2739	MN_LBK	Lipson et al. 2017	Hungary
I1496	MN_LBK	Gamba et al. 2014	Hungary
I1885	MN_Vinca	Lipson et al. 2017	Hungary
I1887	MN_Vinca	Lipson et al. 2017	Hungary
I1889	MN_Vinca	Lipson et al. 2017	Hungary
I1894	MN_Vinca	Lipson et al. 2017	Hungary
I1896	MN_Vinca	Lipson et al. 2017	Hungary
I1895	MN_Vinca	Lipson et al. 2017	Hungary
I1503	Prescythian_IA	Gamba et al. 2014	Hungary
I1661	C_SehGabi	Lazaridis et al. 2016	Iran
I1670	C_SehGabi	Lazaridis et al. 2016	Iran

I1662	C_SehGabi	Lazaridis et al. 2016	Iran
I1674	C_SehGabi	Lazaridis et al. 2016	Iran
I1665	C_SehGabi	Lazaridis et al. 2016	Iran
I2925	C_TepeHissar	Narasimhan et al. 2019	Iran
I1290	GanjDareh_N	Lazaridis et al. 2016	Iran
I1944	GanjDareh_N	Narasimhan et al. 2019	Iran
I1945	GanjDareh_N	Narasimhan et al. 2019	Iran
I1949	GanjDareh_N	Narasimhan et al. 2019	Iran
I1955	Historic_GanjDareh	Lazaridis et al. 2016	Iran
F38	IA_Hasanlu	Broushaki et al. 2016	Iran
I1671	LN_SehGabi	Lazaridis et al. 2016	Iran
I1293	Mesolithic_HotuIIIb	Lazaridis et al. 2016	Iran
AH1	TepeAbdulHosein_N	Broushaki et al. 2016	Iran
AH2	TepeAbdulHosein_N	Broushaki et al. 2016	Iran
AH4	TepeAbdulHosein_N	Broushaki et al. 2016	Iran
WC1	Wezmeh_N	Broushaki et al. 2016	Iran
car004	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs002	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs003/015	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs006/011	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs008/009	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs010	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs012	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs013/014	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs016	Neolithic	Sanchez-Quinto et al. 2019	Ireland
prs018	Neolithic	Sanchez-Quinto et al. 2019	Ireland
I0861	Natufian	Lazaridis et al. 2016	Israel
I1072	Natufian	Lazaridis et al. 2016	Israel
I1069	Natufian	Lazaridis et al. 2016	Israel
I1685	Natufian	Lazaridis et al. 2016	Israel
I1687	Natufian	Lazaridis et al. 2016	Israel
I1690	Natufian	Lazaridis et al. 2016	Israel
I0867	PPNB	Lazaridis et al. 2016	Israel
Paglicci133	HG_Paglicci133	Fu et al. 2016	Italy
Villabruna	Villabruna_HG	Fu et al. 2016	Italy
Ostuni2	HG_Ostuni2	Fu et al. 2016	Italy
Ostuni1	HG_Ostuni1	Fu et al. 2016	Italy
I2478	BellBeaker	Olalde et al. 2018	Italy
I2477	BellBeaker	Olalde et al. 2018	Italy

I1979	BellBeaker	Olalde et al. 2018	Italy
RISE487	Remedello_C	Allentoft et al. 2015	Italy
RISE489	Remedello_C	Allentoft et al. 2015	Italy
RISE486	Remedello_EBA	Allentoft et al. 2015	Italy
I4933	Sicily_BellBeaker	Olalde et al. 2018	Italy
I4936	Sicily_BellBeaker	Olalde et al. 2018	Italy
I4930	Sicily_C_o	Olalde et al. 2018	Italy
I2158	Sicily_HG_OrienteC	Mathieson et al. 2018	Italy
I1705	EBA	Lazaridis et al. 2016	Jordan
I1706	EBA	Lazaridis et al. 2016	Jordan
I1730	EBA	Lazaridis et al. 2016	Jordan
I1727	PPNB	Lazaridis et al. 2016	Jordan
I1710	PPNB	Lazaridis et al. 2016	Jordan
I1707	PPNB	Lazaridis et al. 2016	Jordan
I1704	PPNB	Lazaridis et al. 2016	Jordan
I1701	PPNB	Lazaridis et al. 2016	Jordan
I1414	PPNB	Lazaridis et al. 2016	Jordan
I1415	PPNB	Lazaridis et al. 2016	Jordan
I1700	PPNB	Lazaridis et al. 2016	Jordan
I1699	PPNC	Lazaridis et al. 2016	Jordan
I1679	PPNC	Lazaridis et al. 2016	Jordan
I4432	HG	Mathieson et al. 2018	Latvia
I4434	HG	Mathieson et al. 2018	Latvia
I4438	HG	Mathieson et al. 2018	Latvia
I4439	HG	Mathieson et al. 2018	Latvia
I4440	HG	Mathieson et al. 2018	Latvia
I4441	HG	Mathieson et al. 2018	Latvia
I4550	HG	Mathieson et al. 2018	Latvia
I4551	HG	Mathieson et al. 2018	Latvia
I4552	HG	Mathieson et al. 2018	Latvia
I4553	HG	Mathieson et al. 2018	Latvia
I4626	HG	Mathieson et al. 2018	Latvia
I4628	HG	Mathieson et al. 2018	Latvia
I4595	HG	Mathieson et al. 2018	Latvia
I4596	HG	Mathieson et al. 2018	Latvia
I4630	HG	Mathieson et al. 2018	Latvia
I4632	HG	Mathieson et al. 2018	Latvia
I4626	HG	Jones et al. 2017	Latvia
I4629	LN_CordedWare	Mathieson et al. 2018	Latvia

I4629	LN_CordedWare	Jones et al. 2017	Latvia
I4435	MN	Mathieson et al. 2018	Latvia
I4436	MN	Mathieson et al. 2018	Latvia
I4437	MN	Mathieson et al. 2018	Latvia
I4554	MN	Mathieson et al. 2018	Latvia
I4627	MN	Mathieson et al. 2018	Latvia
I4627	MN	Jones et al. 2017	Latvia
MN2	MN_Comb_Ware	Jones et al. 2017	Latvia
RISE598	LBA	Allentoft et al. 2015	Lithuania
I0001	Loschbour	Pruefer et al. 2017	Luxembourg
I0676	Neolithic	Mathieson et al. 2018	Macedonia
RISE595	LBA	Allentoft et al. 2015	Montenegro
TAF009	Iberomaurusian	Van de Loosdrecht et al. 2018	Morocco
TAF010	Iberomaurusian	Van de Loosdrecht et al. 2018	Morocco
TAF011	Iberomaurusian	Van de Loosdrecht et al. 2018	Morocco
TAF013	Iberomaurusian	Van de Loosdrecht et al. 2018	Morocco
TAF014	Iberomaurusian	Van de Loosdrecht et al. 2018	Morocco
TAF015	Iberomaurusian	Van de Loosdrecht et al. 2018	Morocco
KEB.4	LN	Fregel et al. 2018	Morocco
KEB.6	LN	Fregel et al. 2018	Morocco
KEB.1_KEB.8	LN	Fregel et al. 2018	Morocco
I4070	BA	Olalde et al. 2018	Netherlands
I4071	BA	Olalde et al. 2018	Netherlands
I4068	BellBeaker	Olalde et al. 2018	Netherlands
I4069	BellBeaker	Olalde et al. 2018	Netherlands
I4073	BellBeaker	Olalde et al. 2018	Netherlands
I4075	BellBeaker	Olalde et al. 2018	Netherlands
I4076	BellBeaker	Olalde et al. 2018	Netherlands
I4074	BellBeaker	Olalde et al. 2018	Netherlands
I5748	BellBeaker	Olalde et al. 2018	Netherlands
I5750	BellBeaker	Olalde et al. 2018	Netherlands
I4067	BellBeaker	Olalde et al. 2018	Netherlands
Hum1	Mesolithic	Gunther et al. 2018	Norway
Hum2	Mesolithic	Gunther et al. 2018	Norway
Steigen	N_HG	Gunther et al. 2018	Norway
I12968	IA_Butkara	Narasimhan et al. 2019	Pakistan
I10974	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I12980	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I12988	IA_Loebanr	Narasimhan et al. 2019	Pakistan

I12982	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I12981	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I12987	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I12984	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I12979	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I12983	IA_Loebanr	Narasimhan et al. 2019	Pakistan
I4253	BellBeaker	Olalde et al. 2018	Poland
I6534	BellBeaker	Olalde et al. 2018	Poland
I6538	BellBeaker	Olalde et al. 2018	Poland
I6580	BellBeaker	Olalde et al. 2018	Poland
I6582	BellBeaker	Olalde et al. 2018	Poland
I6583	BellBeaker	Olalde et al. 2018	Poland
I4251	BellBeaker	Olalde et al. 2018	Poland
I4252	BellBeaker	Olalde et al. 2018	Poland
I6531	ChopiceVesele	Olalde et al. 2018	Poland
I6537	ChopiceVesele	Olalde et al. 2018	Poland
RISE1	CordedWare	Allentoft et al. 2015	Poland
RISE431	CordedWare	Allentoft et al. 2015	Poland
I6579	EBA	Olalde et al. 2018	Poland
I2433	Globular_Amphora	Mathieson et al. 2018	Poland
I2434	Globular_Amphora	Mathieson et al. 2018	Poland
I2440	Globular_Amphora	Mathieson et al. 2018	Poland
I2441	Globular_Amphora	Mathieson et al. 2018	Poland
I2403	Globular_Amphora	Mathieson et al. 2018	Poland
I2405	Globular_Amphora	Mathieson et al. 2018	Poland
RISE109	Unetice_EBA	Allentoft et al. 2015	Poland
RISE139	Unetice_EBA	Allentoft et al. 2015	Poland
RISE145	Unetice_EBA	Allentoft et al. 2015	Poland
RISE150	Unetice_EBA	Allentoft et al. 2015	Poland
RISE154	Unetice_EBA	Allentoft et al. 2015	Poland
I0840	Iberia_BellBeaker	Olalde et al. 2018	Portugal
I1970	Iberia_BellBeaker	Olalde et al. 2018	Portugal
I0839	Iberia_BellBeaker	Olalde et al. 2019	Portugal
I4229	Iberia_BellBeaker	Olalde et al. 2018	Portugal
CabecoArruda117B	Iberia_LN_C	Martiniano et al. 2017	Portugal
CovaMoura364	Iberia_LN	Martiniano et al. 2017	Portugal
CovaMoura9B	Iberia_LN	Martiniano et al. 2017	Portugal
DolmenAnsiao96B	Iberia_LN	Martiniano et al. 2017	Portugal
MonteCanelas337A	Iberia_LN	Martiniano et al. 2017	Portugal

MonteGato104	Iberia_MBA	Martiniano et al. 2017	Portugal
TV32032extra	Iberia_MBA	Martiniano et al. 2017	Portugal
TV3831	Iberia_MBA	Martiniano et al. 2017	Portugal
ValeOuro10207	Iberia_MBA	Martiniano et al. 2017	Portugal
LugarCanto41	Iberia_MN	Martiniano et al. 2017	Portugal
LugarCanto42	Iberia_MN	Martiniano et al. 2017	Portugal
LugarCanto44	Iberia_MN	Martiniano et al. 2017	Portugal
LugarCanto45	Iberia_MN	Martiniano et al. 2017	Portugal
I6601	Iberia_N_EBA	Olalde et al. 2018	Portugal
Muierii2	Muierii2	Fu et al. 2016	Romania
I4088	Chalcolithic	Mathieson et al. 2018	Romania
I4089	Chalcolithic	Mathieson et al. 2018	Romania
GB	Chalcolithic	Gonzales-Fortes et al. 2017	Romania
I2532	EN	Mathieson et al. 2018	Romania
I2533	EN	Mathieson et al. 2018	Romania
I2534	Mesolithic	Mathieson et al. 2018	Romania
I5408	Meso_IronGates	Mathieson et al. 2018	Romania
I5411	Meso_IronGates	Mathieson et al. 2018	Romania
I4582	Meso_IronGates	Mathieson et al. 2018	Romania
I5436	Meso_IronGates	Mathieson et al. 2018	Romania
I5408	Meso_IronGates	Gonzales-Fortes et al. 2017	Romania
I4081	Meso_IronGates	Mathieson et al. 2018	Romania
I4655	Meso_IronGates	Mathieson et al. 2018	Romania
I4607	Meso_IronGates	Mathieson et al. 2018	Romania
RISE510	Afanasievo	Allentoft et al. 2015	Russia
AfontovaGora3	AfontovaGora3	Fu et al. 2016	Russia
RISE500	Andronovo	Allentoft et al. 2015	Russia
RISE503	Andronovo	Allentoft et al. 2015	Russia
RISE505	Andronovo	Allentoft et al. 2015	Russia
RISE512	Andronovo	Allentoft et al. 2015	Russia
RISE515	BA_Okunevo	Damgaard et al. 2018	Russia
RISE555	EBA	Allentoft et al. 2015	Russia
RISE240	Yamnaya_Kalmykia	Allentoft et al. 2015	Russia
RISE546	Yamnaya_Kalmykia	Allentoft et al. 2015	Russia
RISE547	Yamnaya_Kalmykia	Allentoft et al. 2015	Russia
RISE548	Yamnaya_Kalmykia	Allentoft et al. 2015	Russia
RISE552	Yamnaya_Kalmykia	Allentoft et al. 2015	Russia
I0370	Yamnaya_Samara	Mathieson et al. 2015	Russia
I0441	Yamnaya_Samara	Mathieson et al. 2015	Russia

I0444	Yamnaya_Samara	Mathieson et al. 2015	Russia
I0439	Yamnaya_Samara	Mathieson et al. 2015	Russia
I0357	Yamnaya_Samara	Mathieson et al. 2015	Russia
I0429	Yamnaya_Samara	Mathieson et al. 2015	Russia
I0438	Yamnaya_Samara	Mathieson et al. 2015	Russia
I0443	Yamnaya_Samara	Mathieson et al. 2015	Russia
I0231	Yamnaya_Samara	Narasimhan et al. 2019	Russia
I0211	HG_Karelia	Mathieson et al. 2015	Russia
I0061	HG_Karelia	Mathieson et al. 2015	Russia
I0061	HG_Karelia	Fu et al. 2016	Russia
I0124	HG_Samara	Mathieson et al. 2015	Russia
RISE492	IA	Allentoft et al. 2015	Russia
RISE504	IA	Allentoft et al. 2015	Russia
RISE600	IA	Allentoft et al. 2015	Russia
RISE601	IA	Allentoft et al. 2015	Russia
RISE602	IA	Allentoft et al. 2015	Russia
RISE550	Yamnaya_Kalmykia	Allentoft et al. 2015	Russia
RISE493	Karasuk	Allentoft et al. 2015	Russia
RISE495	Karasuk	Allentoft et al. 2015	Russia
RISE496	Karasuk	Allentoft et al. 2015	Russia
RISE499	Karasuk	Allentoft et al. 2015	Russia
RISE502	Karasuk	Allentoft et al. 2015	Russia
I0434	Eneolithic	Mathieson et al. 2015	Russia
I0433	Eneolithic	Mathieson et al. 2015	Russia
I0122	Eneolithic	Mathieson et al. 2015	Russia
I11133	LateMaikop	Wang et al. 2019	Russia
RISE553	LBA	Allentoft et al. 2015	Russia
RISE554	LBA	Allentoft et al. 2015	Russia
RISE523	Mezhovskaya	Allentoft et al. 2015	Russia
RISE524	Mezhovskaya	Allentoft et al. 2015	Russia
RISE525	Mezhovskaya	Allentoft et al. 2015	Russia
I0126	Poltavka	Mathieson et al. 2015	Russia
I0440	Poltavka	Mathieson et al. 2015	Russia
I0374	Poltavka	Mathieson et al. 2015	Russia
I0371	Poltavka	Mathieson et al. 2015	Russia
I0418	Potapovka	Mathieson et al. 2015	Russia
I0419	Potapovka	Narasimhan et al. 2019	Russia
RISE386	Sintashta_MLBA	Allentoft et al. 2015	Russia
RISE392	Sintashta_MLBA	Allentoft et al. 2015	Russia

RISE394	Sintashta_MLBA	Allentoft et al. 2015	Russia
RISE395	Sintashta_MLBA	Allentoft et al. 2015	Russia
I0234	Srubnaya	Mathieson et al. 2015	Russia
I0423	Srubnaya	Mathieson et al. 2015	Russia
I0232	Srubnaya	Narasimhan et al. 2019	Russia
I0358	Srubnaya	Narasimhan et al. 2019	Russia
I0359	Srubnaya	Narasimhan et al. 2019	Russia
I0361	Srubnaya	Narasimhan et al. 2019	Russia
I0422	Srubnaya	Narasimhan et al. 2019	Russia
I0424	Srubnaya	Narasimhan et al. 2019	Russia
I0430	Srubnaya	Narasimhan et al. 2019	Russia
I0431	Srubnaya	Narasimhan et al. 2019	Russia
I0235	Srubnaya	Mathieson et al. 2015	Russia
I0431	Srubnaya	Mathieson et al. 2015	Russia
MA1	MA1_HG	Raghavan et al. 2014	Russia
Kostenki12	Kostenki12	Fu et al. 2016	Russia
Kostenki14	Kostenki14	Fu et al. 2016	Russia
Ust_Ishim	Ust_Ishim_HG	Fu et al. 2014	Russia
I0633	EN	Mathieson et al. 2018	Serbia
I0634	EN	Mathieson et al. 2018	Serbia
I1131	EN	Mathieson et al. 2018	Serbia
I4665	EN	Mathieson et al. 2018	Serbia
I4666	EN	Mathieson et al. 2018	Serbia
I4918	EN_Starcevo	Mathieson et al. 2018	Serbia
I4871	Meso_IronGates	Mathieson et al. 2018	Serbia
I4872	Meso_IronGates	Mathieson et al. 2018	Serbia
I4873	Meso_IronGates	Mathieson et al. 2018	Serbia
I4874	Meso_IronGates	Mathieson et al. 2018	Serbia
I4875	Meso_IronGates	Mathieson et al. 2018	Serbia
I4876	Meso_IronGates	Mathieson et al. 2018	Serbia
I4877	Meso_IronGates	Mathieson et al. 2018	Serbia
I4878	Meso_IronGates	Mathieson et al. 2018	Serbia
I4880	Meso_IronGates	Mathieson et al. 2018	Serbia
I4915	Meso_IronGates	Mathieson et al. 2018	Serbia
I4916	Meso_IronGates	Mathieson et al. 2018	Serbia
I4917	Meso_IronGates	Mathieson et al. 2018	Serbia
I5233	Meso_IronGates	Mathieson et al. 2018	Serbia
I5234	Meso_IronGates	Mathieson et al. 2018	Serbia
I5235	Meso_IronGates	Mathieson et al. 2018	Serbia

I5236	Meso_IronGates	Mathieson et al. 2018	Serbia
I5237	Meso_IronGates	Mathieson et al. 2018	Serbia
I5238	Meso_IronGates	Mathieson et al. 2018	Serbia
I5239	Meso_IronGates	Mathieson et al. 2018	Serbia
I5240	Meso_IronGates	Mathieson et al. 2018	Serbia
I5242	Meso_IronGates	Mathieson et al. 2018	Serbia
I5244	Meso_IronGates	Mathieson et al. 2018	Serbia
I5771	Meso_IronGates	Mathieson et al. 2018	Serbia
I5772	Meso_IronGates	Mathieson et al. 2018	Serbia
I5401	Meso_IronGates	Mathieson et al. 2018	Serbia
I5402	Meso_IronGates	Mathieson et al. 2018	Serbia
I5407	Meso_IronGates	Mathieson et al. 2018	Serbia
I4660	Meso_IronGates	Mathieson et al. 2018	Serbia
I4870	Meso_IronGates	Mathieson et al. 2018	Serbia
I4657	Meso_IronGates	Mathieson et al. 2018	Serbia
I4881	Meso_IronGates	Mathieson et al. 2018	Serbia
I4914	Meso_IronGates	Mathieson et al. 2018	Serbia
I5773	Meso_IronGates	Mathieson et al. 2018	Serbia
I5409	Meso_IronGates	Mathieson et al. 2018	Serbia
I5405	Neolithic	Mathieson et al. 2018	Serbia
ATP9	Iberia_BA	Gunther et al. 2015	Spain
esp005	Iberia_BA	Valdiosera et al. 2018	Spain
pir001	Iberia_BA	Valdiosera et al. 2018	Spain
I0460	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0459	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0457	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0456	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0453	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0455	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0263	Iberia_BellBeaker	Olalde et al. 2018	Spain
I1553	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0825	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0260	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0261	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0823	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0258	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0262	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0257	Iberia_BellBeaker	Olalde et al. 2018	Spain
I0826	Iberia_BellBeaker	Olalde et al. 2018	Spain

I0461	Iberia_BellBeaker	Olalde et al. 2018	Spain
I4247	Iberia_BellBeaker	Olalde et al. 2018	Spain
I5665	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6475	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6539	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6584	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6587	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6588	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6623	Iberia_BellBeaker	Olalde et al. 2018	Spain
I4245	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6472	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6622	Iberia_BellBeaker	Olalde et al. 2019	Spain
I6471	Iberia_BellBeaker	Olalde et al. 2018	Spain
I6542	Iberia_BellBeaker	Olalde et al. 2018	Spain
I2467	Iberia_C	Lipson et al. 2017	Spain
I1282	Iberia_C	Mathieson et al. 2015	Spain
I1276	Iberia_C	Mathieson et al. 2015	Spain
I1284	Iberia_C	Mathieson et al. 2015	Spain
I1280	Iberia_C	Mathieson et al. 2015	Spain
I1314	Iberia_C	Mathieson et al. 2015	Spain
I1277	Iberia_C	Mathieson et al. 2015	Spain
I1272	Iberia_C	Mathieson et al. 2015	Spain
I1281	Iberia_C	Mathieson et al. 2015	Spain
I1300	Iberia_C	Mathieson et al. 2015	Spain
I1271	Iberia_C	Mathieson et al. 2015	Spain
I1303	Iberia_C	Mathieson et al. 2015	Spain
I1981	Iberia_C	Lipson et al. 2017	Spain
I3270	Iberia_C	Lipson et al. 2017	Spain
I3271	Iberia_C	Lipson et al. 2017	Spain
I3272	Iberia_C	Lipson et al. 2017	Spain
I3269	Iberia_C	Lipson et al. 2017	Spain
I1838	Iberia_C	Lipson et al. 2017	Spain
I1843	Iberia_C	Lipson et al. 2017	Spain
I1975	Iberia_C	Lipson et al. 2017	Spain
I5838	Iberia_C	Lipson et al. 2017	Spain
I6543	Iberia_C	Olalde et al. 2018	Spain
I6604	Iberia_C	Olalde et al. 2018	Spain
I6612	Iberia_C	Olalde et al. 2018	Spain
I6617	Iberia_C	Olalde et al. 2018	Spain

I6628	Iberia_C	Olalde et al. 2018	Spain
I6629	Iberia_C	Olalde et al. 2018	Spain
I6630	Iberia_C	Olalde et al. 2018	Spain
I6609	Iberia_C	Olalde et al. 2018	Spain
I1976	Iberia_C	Olalde et al. 2019	Spain
I2473	Iberia_C	Olalde et al. 2019	Spain
I3277	Iberia_C	Olalde et al. 2019	Spain
atp002	Iberia_C	Valdiosera et al. 2018	Spain
atp016	Iberia_C	Valdiosera et al. 2018	Spain
atp12-1420	Iberia_C	Valdiosera et al. 2018	Spain
por002	Iberia_C	Valdiosera et al. 2018	Spain
por004	Iberia_C	Valdiosera et al. 2018	Spain
I6596	Iberia_C	Olalde et al. 2018	Spain
I6608	Iberia_C	Olalde et al. 2018	Spain
I0581	Iberia_C	Mathieson et al. 2015	Spain
I3273	Iberia_C	Lipson et al. 2017	Spain
I3276	Iberia_C	Lipson et al. 2017	Spain
I12809	Iberia_EBA	Olalde et al. 2019	Spain
I2199	Iberia_EN	Lipson et al. 2017	Spain
I0409	Iberia_EN	Mathieson et al. 2015	Spain
I0412	Iberia_EN	Mathieson et al. 2015	Spain
I0410	Iberia_EN	Mathieson et al. 2015	Spain
I0413	Iberia_EN	Mathieson et al. 2015	Spain
I1972	Iberia_EN	Lipson et al. 2017	Spain
CB13	Iberia_EN	Olalde et al. 2015	Spain
mur	Iberia_EN	Valdiosera et al. 2018	Spain
I0585	Iberia_HG	Mathieson et al. 2015	Spain
Canes	Iberia_HG	Gonzales-Fortes et al. 2017	Spain
Chan	Iberia_HG	Gonzales-Fortes et al. 2017	Spain
I0585	Iberia_HG	Olalde et al. 2014	Spain
c40331	Iberia_LN	Valdiosera et al. 2018	Spain
san216	Iberia_LN	Valdiosera et al. 2018	Spain
I0405	Iberia_MN	Mathieson et al. 2015	Spain
I0407	Iberia_MN	Mathieson et al. 2015	Spain
I0408	Iberia_MN	Mathieson et al. 2015	Spain
I0406	Iberia_MN	Mathieson et al. 2015	Spain
ElMiron	Iberia_ElMiron	Fu et al. 2016	Spain
RISE175	BA	Allentoft et al. 2015	Sweden
RISE207	BA	Allentoft et al. 2015	Sweden

RISE210	BA	Allentoft et al. 2015	Sweden
RISE94	BattleAxe	Allentoft et al. 2015	Sweden
I0013	HG_Motala	Mathieson et al. 2015	Sweden
I0011	HG_Motala	Mathieson et al. 2015	Sweden
I0015	HG_Motala	Mathieson et al. 2015	Sweden
I0012	HG_Motala	Mathieson et al. 2015	Sweden
I0014	HG_Motala	Mathieson et al. 2015	Sweden
I0017	HG_Motala	Mathieson et al. 2015	Sweden
I0017	HG_Motala	Lazaridis et al. 2014	Sweden
RISE174	IA	Allentoft et al. 2015	Sweden
RISE97	LN	Allentoft et al. 2015	Sweden
RISE98	LN	Allentoft et al. 2015	Sweden
RISE179	LN	Allentoft et al. 2015	Sweden
ans003	Neolithic	Sanchez-Quinto et al. 2019	Sweden
ans005	Neolithic	Sanchez-Quinto et al. 2019	Sweden
ans008	Neolithic	Sanchez-Quinto et al. 2019	Sweden
ans014	Neolithic	Sanchez-Quinto et al. 2019	Sweden
ans016	Neolithic	Sanchez-Quinto et al. 2019	Sweden
ans017	Neolithic	Sanchez-Quinto et al. 2019	Sweden
bal004	Neolithic	Sanchez-Quinto et al. 2019	Sweden
lai001	Neolithic	Sanchez-Quinto et al. 2019	Sweden
SBj	Mesolithic	Gunther et al. 2018	Sweden
SF12	Mesolithic	Gunther et al. 2018	Sweden
Ajvide52	PWC_NHG	Skoglund et al. 2014	Sweden
Ajvide58	PWC_NHG	Skoglund et al. 2014	Sweden
Ajvide70	PWC_NHG	Skoglund et al. 2014	Sweden
Gokhem2	TRB_MN	Skoglund et al. 2014	Sweden
Gokhem4	TRB_MN	Skoglund et al. 2014	Sweden
Gokhem5	TRB_MN	Skoglund et al. 2014	Sweden
I5755	BellBeaker	Olalde et al. 2018	Switzerland
I5757	BellBeaker	Olalde et al. 2018	Switzerland
I5759	BellBeaker	Olalde et al. 2018	Switzerland
Bichon	Bichon	Jones et al. 2015	Switzerland
I11039	BA	Narasimhan et al. 2019	Turkmenistan
ILK002	GlobularAmphora	Mathieson et al. 2018	Ukraine
I5884	EBA	Mathieson et al. 2018	Ukraine
I2105	Yamnaya	Mathieson et al. 2018	Ukraine
I3141	Yamnaya	Mathieson et al. 2018	Ukraine
I5882	Eneolithic	Mathieson et al. 2018	Ukraine

I4110	Eneolithic	Mathieson et al. 2018	Ukraine
I2110	Eneolithic_Trypillia	Mathieson et al. 2018	Ukraine
I1926	Eneolithic_Trypillia	Mathieson et al. 2018	Ukraine
I3151	Eneolithic_Trypillia	Mathieson et al. 2018	Ukraine
I2111	Eneolithic_Trypillia	Mathieson et al. 2018	Ukraine
ILK001	Globular_Amphora	Mathieson et al. 2018	Ukraine
ILK003	Globular_Amphora	Mathieson et al. 2018	Ukraine
I1763	Mesolithic	Mathieson et al. 2018	Ukraine
I1819	Mesolithic	Mathieson et al. 2018	Ukraine
I1733	Mesolithic	Mathieson et al. 2018	Ukraine
I5876	Mesolithic	Mathieson et al. 2018	Ukraine
I5885	Mesolithic	Mathieson et al. 2018	Ukraine
I1737	Mesolithic	Mathieson et al. 2018	Ukraine
I1736	Neolithic	Mathieson et al. 2018	Ukraine
I1734	Neolithic	Mathieson et al. 2018	Ukraine
I1738	Neolithic	Mathieson et al. 2018	Ukraine
I3714	Neolithic	Mathieson et al. 2018	Ukraine
I3715	Neolithic	Mathieson et al. 2018	Ukraine
I3717	Neolithic	Mathieson et al. 2018	Ukraine
I4111	Neolithic	Mathieson et al. 2018	Ukraine
I4114	Neolithic	Mathieson et al. 2018	Ukraine
I5870	Neolithic	Mathieson et al. 2018	Ukraine
I5875	Neolithic	Mathieson et al. 2018	Ukraine
I5883	Neolithic	Mathieson et al. 2018	Ukraine
I5890	Neolithic	Mathieson et al. 2018	Ukraine
I5892	Neolithic	Mathieson et al. 2018	Ukraine
I3718	Neolithic	Mathieson et al. 2018	Ukraine
I4112	Neolithic	Mathieson et al. 2018	Ukraine
I3712	Neolithic	Mathieson et al. 2018	Ukraine
I3713	Neolithic	Mathieson et al. 2018	Ukraine
I3716	Neolithic	Mathieson et al. 2018	Ukraine
I5868	Neolithic	Mathieson et al. 2018	Ukraine
I5872	Neolithic	Mathieson et al. 2018	Ukraine
I5873	Neolithic	Mathieson et al. 2018	Ukraine
I5881	Neolithic	Mathieson et al. 2018	Ukraine
I5886	Neolithic	Mathieson et al. 2018	Ukraine
I5889	Neolithic	Mathieson et al. 2018	Ukraine
I5957	Neolithic	Mathieson et al. 2018	Ukraine
I6133	Neolithic	Mathieson et al. 2018	Ukraine

I1917	Ozera_Yamnaya	Mathieson et al. 2018	Ukraine
I11026	BA_Bustan	Narasimhan et al. 2019	Uzbekistan
I11027	BA_Bustan	Narasimhan et al. 2019	Uzbekistan
I11025	BA_Bustan	Narasimhan et al. 2019	Uzbekistan
I11028	Eneolithic	Narasimhan et al. 2019	Uzbekistan

TABLE F.1: Published ancient samples used in this thesis. For analysis samples were analysed as Country_GroupID, except for British samples that were separated by country and Spanish and Portuguese that were analysed together as Iberian.