Rats, cats and hares: exploring natural and humanly-mediated dispersal through a genetic approach

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Declaration

I, Alexandra Elizabeth Jamieson, declare that this thesis has never been submitted, either in the same or a different form, to this or any other university, for a degree or any other qualification. All the work presented in this thesis is the result of my own work unless otherwise stated in the author contributions. The work was carried out while I was registered as a graduate student at the Research Laboratory of Archaeology and the History of Art, under the supervision of Prof. Greger Larson.

Abstract

The natural world has been largely shaped by climate fluctuations throughout time. However, more recently in the earth's history this has changed. Humans have been manipulating the world around them for millennia, including moving a variety of species within and outside of their natural ranges. This can be deliberate: such as the raising of animals for subsistence, or accidental: such as stowaway animals on ships. In order to further our understanding of where and when people have moved animals in the past this thesis explores the movements of three understudied species. It begins with the study of a species whose range has been largely shaped by natural causes, the mountain hare. It's distribution across Europe and Russia has been shaped by the changing climate, however even with these changes, it maintained its population structure throughout its vast range through time. This thesis focuses on the western edge of the mountain hare range where it was cut off from the rest of the continuum on the edge of the ice sheet with the last advance of ice, surviving in refugia and recolonising when conditions became favourable similarly to other possible Celtic fringe species in Britain and Ireland. This demonstrates the resilience of this cold adapted species over millennia of climate fluctuation. The other two species studied were translocated by people, one intentionally and one accidently. The domestic cat was at least initially intentionally moved for pest control. The domestic cat arrived in Britain in the Iron Age and became widespread in the Roman period. It was also an early arrival in the Orkneys of Scotland in the Scottish Late Iron Age, contemporary with Roman Britain. Domestic cats then became widespread in the Viking and Norse periods of Orkney. In Ireland only two of the three domestic cat lineages were found which may demonstrate that they missed the first wave of introduction of domestic cats. The black rat was the final species investigated; they were unintentionally transferred as stowaways on boats. This research explores their initial movements into Europe in the Roman period followed by their decline, re-emergence and later decline. Studying all three species together gives us a greater breadth of understanding of the movements of animals in the past, both naturally and anthropogenically. In addition, the results of this thesis will provide information that will be useful in the conservation management of each of these species in the future.

Table of Contents

Table of Figures

Table of Tables

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Glossary of terms

The following terms are frequently used throughout this thesis. Due to their importance, the exact definition of each is described.

Anthropogenic — Change caused by humans or their activity

Commensalism —A long-term biological interaction of two species where one species gains benefits and the other neither benefits nor is harmed by the interaction

Haplogroup — A group which shares a similar set of haplotypes

Haplotype — Set of DNA variations that are inherited together

Human-mediated introduction — The intentional or accidental movement of a species by humans outside its native range

Native/Indigenous species — A species which arrived in an area by natural means (i.e. unaided by human action) in the distant past

Phylogeography — The study of the past process that may be responsible for the contemporary geographic distribution of a species

Refugia — A region that during an unfavourable climatic period for the species provides all the essential elements for survival of a subset of the population

Species — A group of interbreeding individuals that produce fertile offspring and is reproductively isolated from other groups

Translocation — The deliberate movement of an organism from one location to another by humans, either within or outside its natural range

1. Introduction and literature review

1.1 Motivations for thesis

Plant and animal species ranges are not geographically fixed, as throughout time their ranges have expanded and contracted naturally with the changing climate. There is, however, another factor — human activity. Humans have been changing the distribution of species for millennia, and since the transition from hunter-gatherer to agricultural societies around the start of the Holocene (11,700 years ago to today), humans have increased the rate at which species ranges have been changing (Bertolino 2020). While in the modern day the effects of humans are obvious, with anthropogenic climate change and habitat destruction being two of the leading factors of plant and animal population declines, there is also a third factor which is less-often discussed, although it has been occurring for the longest period of time and has always been one of the main drivers of extinctions — the translocation of species by people (Bellard, Genovesi, and Jeschke 2016; Bertolino 2020).

Anthropogenic climate change is only a recent factor in animal population changes, with human impact being measurable over the last few hundred years. Before this, the climate changed through gradual natural fluctuations (IPCC 2014; Abram et al. 2016; King et al. 2016; Meyer and Newman 2020). The other two human induced factors, destruction of habitat and movement of species, are not new occurrences, having been occurring on varying scales for thousands of years.

After the advent of agriculture, where people were no longer roaming the landscape looking for resources, the formation of settlements meant that land began to be used in ways convenient to the growing human population. This initially began on a small scale with the clearing of relatively small sections of land for farming and has accelerated with increases in global population and technological advances (Project 2019) . Of the habitable land on the planet, 43% is used for agriculture today, compared to an estimate of 0.5% in use 6,950 years ago (a few thousand years after the beginning of agricultural society) (Klein Goldewijk et al. 2017; Poore and Nemecek 2018; Project 2019). Of this 43%, 83% is used

for raising livestock, such as cows, sheep and pigs, with the remaining 17% used to grow food directly for human consumption (Poore and Nemecek 2018). This has led to significant damage to some of the richest environments on the planet including, most famously, the Amazon rainforest, which has seen a decline of over 19.7% of forest cover over the period 1970 to 2020 (Butler 2001). While only since the invention of agriculture has the land started to be shaped significantly by humans, animals and plants have been moved around by people for at least 20,000 years, shaping their current day distributions (Hofman and Rick 2018). This started off as small-scale movements in the late Pleistocene and early Holocene, which then accelerated with the invention of agriculture. This finally resulted in the domestication of both plants and animals which, due to their increased resilience/tameness, could be more easily moved around when compared to their wild counterparts (MacHugh, Larson, and Orlando 2016).

Understanding the movement of animals in the past, including the potential impacts on the species being moved in addition to species already present, will help with the conservation of animals in the future, including revealing potential future threats. To do this, an analysis of the various mechanisms of animal movement should be considered. This study looks at three separate species in Europe, and particularly Britain and Ireland, to understand how climate change and human intervention can lead to changes in animal population distributions. Selected species comprise the mountain hare (*Lepus timidus*), whose distribution around Europe was largely shaped by the natural fluctuation in climate since the Last Glacial Maximum, the domestic cat (*Felis catus*), which was first moved intentionally by people in the Neolithic period, and finally, the black rat (*Rattus rattus*), which was unintentionally introduced to Europe during the Roman period.

1.2 Changing species ranges

The geographical range of species has changed throughout time based on geological, climatic and other natural events. Some examples include tectonic activity breaking up landmasses, the expanding and contracting of ice sheets, and fluctuating temperatures (Berhane 2015; Avise 1999). These natural events demonstrate that species ranges are ever changing, and that this is not abnormal. What is, however, abnormal is the pace of this change we are seeing today; that humans can move species thousands of miles in the space of hours means that human-mediated dispersal of animals can vastly outpace the effects of natural events (Bertolino 2020). Humans can therefore homogenise the world's species in a way natural events never could (Vermeij 1991; Lodge 1993). Human influence on animal populations extends beyond the deliberate or accidental introduction of species to new areas. Construction of infrastructure can connect otherwise separate habitats, such as with the Panama Canal, as well as introducing new barriers which fragment habitats and therefore animal populations (Gollasch, Galil, and Cohen 2006). Adverse effects of the transposition of species can include the displacement of other species, disruption of food-webs, changing habitats, introduction of diseases, dilution of gene-pools through hybridisation, and can, in the worst cases, lead to species extinctions (Lodge 1993; Bellard, Genovesi, and Jeschke 2016; Browett, O'Meara, and McDevitt 2020; Spielman, Brook, and Frankham 2004; Braje and Erlandson 2013).

On the archaeological timescale, humans were unable to move species as fast as is possible today, albeit still faster than would occur naturally. As human population numbers have increased and the world has become more and more connected, the speed and distances of these biotic exchanges have accelerated. This does not, however, make the early movements of animals any less significant, as these allow us to understand the early consequences of species dispersal and landscape changes. While the effects would probably have been unknown to humans in the past, the actions of these people have greatly influenced the nature that we see around us today.

1.2.1 Climate change shaping species range

Before the influence of people, the main factor affecting species ranges was changing climate. Although the speed of these changes in the past was typically slower than we are

seeing today, studying the changes in species ranges due to natural climate fluctuations can help us to understand how the species may react to future climate change. Genetic studies using contemporary samples can be used to explore this, albeit with limitations. For example, modern samples would not reveal complete population replacement as there would be no trace of the replaced population in the modern samples. More information can be gained through the study of ancient samples from palaeontological and archaeological material as they provide direct information from the past (Hofman et al. 2015).

The current group of species most threatened by the increase in global temperatures are those with the most fragmented ranges, which are typically the Arctic species and those only found at high elevations (Crooks et al. 2017; Davidson et al. 2017). Both groups are adapted to a colder climate. As temperatures warm, they are pushed further north or to higher elevations, gradually reducing their species range. Once at the extremes of their range, further warming leads to significant population declines and the threat of extinction.

There have been relatively few studies looking at the change in species ranges of Arctic species over the Pleistocene or Holocene periods, and even fewer using ancient DNA. Arctic fox, lemming, mountain vole, northern pocket gopher, willow and rock ptarmigan and mountain hare have all been studied by ancient DNA methods to track their changes in range with climate fluctuation (Palkopoulou et al. 2016; Lagerholm et al. 2014, 2017; Hadly et al. 2004; Dalén et al. 2007; Prost et al. 2010; Smith et al. 2017). Most of these species were not able to adequately adapt their species ranges as conditions changed, instead becoming locally extinct in regions of unfavourable habitat (Lagerholm et al. 2017). Of the studied species, only the two ptarmigan species and the mountain hares have been shown to be capable of adjusting their habitat accordingly, thereby maintaining genetic continuity despite the changes in climate (Lagerholm et al. 2017; Smith et al. 2017). This is less surprising for the ptarmigans than the hares, as their ability to fly means they are less dependent on suitable habitats being connected. Smith et al. (2017) suggest that the resilience of the mountain hare compared to other cold-adapted species is due to its generalist nature making it less susceptible to environmental change. Their study concentrated on mountain hares in the late Pleistocene in central Europe, which has

provided an initial understanding of the demographic changes of hares. Given the results of the study, this genetic diversity is expected to have been seen in the late Pleistocene up to today across their range, however this has not been tested. Mountain hares are an important case study to understand species resilience to climate change, therefore this thesis expands on the work of Smith et al. (2017). Here, samples are taken from across the range, from Ireland to eastern Russia, tracking the changes both in time and space from the late Pleistocene to today, to see if genetic diversity was maintained throughout the range and throughout time. This thesis explores their entire range with a focus on their western expansion, an area of their range known for low genetic diversity which has never been investigated with ancient samples. Also included are ancient samples from islands off the west coast of Scotland, where it is unknown if mountain hares arrived naturally or with the aid of people.

1.2.2 The human-mediated dispersal of animals in the past

1.2.2.1 Earliest known animal translocations

People have been moving animals around for thousands of years (Searle 2008; Hulme 2009; Project 2019) for a number of different purposes including food, companionship, sport, ritual, social status, aesthetics and by mistake (Seddon, Strauss, and Innes 2012). Additionally, plants, algae, fungi, invertebrates and microorganisms have also been shown to have been moved by people from the early Holocene and possibly before (Zeder 2008; Sadler 1990; Panagiotakopulu and Buckland 2017; Gal and Bartosiewicz 2013). Discovering when these early translocations occurred can be difficult, and there are bound to be many unknown introductions as they can easily occur undetected (Lodge 1993).

The natural expansion of species ranges and the movement of animals by people can be difficult to differentiate, as both can result in the species appearing in the archaeological and palaeontological records outside of their presumed natural ranges. The only indisputable way to confirm whether a species has been moved by people is to look at geographically isolated locations, such as islands. Islands which have never been connected to the mainland by any form of land bridge since before the arrival of the species to the surrounding mainland provide ideal areas to detect human translocation of animals.

New Ireland in Papua New Guinea and Cyprus are two places which meet this criteria, and are also the locations of two of the earliest translocations of animals (Hofman and Rick 2018; Kealy 2018; Vigne et al. 2009). The earliest known human translocation is that of the flying possum (*phalanger breviceps*) to New Ireland, Papua New Guinea around 23,000-22,000 years ago (Hofman and Rick 2018; Kealy 2018; Leavesley 2005). The site, Buang Merabak, contained possum remains in deposits dated by the surrounding stratigraphy (Leavesley and Allen 1998). Given that marsupials are generally poor swimmers, most scholars agree that these possums were transported by humans to the islands (Heinsohn 2001; Heinsohn 2010; Spriggs 1997; O'Connor et al. 2010). The next earliest evidence for translocation is of wild boar (*Sus scrofa*) to Cyprus which occurred by 11,400 years ago (Vigne et al. 2009). Before this period there is no evidence of wild boar on the island, and the distance between Cyprus and the mainland was too great for them to have arrived independently. These two introductions are the most well-documented to date.

It was not until these human translocations became more widespread that they became more easily detected in the archaeological record. There are specific points in time where human civilisations underwent changes which resulted in larger scale trade and movement of people with their livestock: the advent of farming and settled society in the Neolithic, the rise of empires, the Medieval period, the industrial revolution and present-day globalisation (Kirch 2005; Hulme 2009; Boivin and Fuller 2009; Project 2019). Movements happened as a result of each of these societal changes, but most of the known movements have occurred in the last 200 years in the era of globalisation with fast, interconnected worldwide trade (Seebens et al. 2017; Hulme 2009). Before this point, movements were relatively slow, with it taking days to cross hundreds of miles instead of hours or even minutes today. It is these earlier, relatively slower movements which have only begun to be extensively studied in the last few decades with the use of ancient DNA techniques (Hofman and Rick 2018).

1.2.2.2 Intentional movement of animals

Many of the animals that have been intentionally moved were for subsistence purposes. As we know from section 1.2.2.1, this first known occurrence of intentional movement was around 23,000 years ago (Kealy 2018). Since then, the large-scale movements of animals

have been the result of domestication of animals and their movement with people or via trade (Boivin and Fuller 2009). There has been much research on the movement of domestic species for subsistence including, but not limited to, pigs, cows, horses, turkeys, sheep and goats (Frantz et al. 2020; Irving-Pease et al. 2018). Dogs have also been researched heavily in their role as working dogs and as companion animals (Botigué et al. 2017; Bergström et al. 2020; Larson et al. 2012). The world's second most popular companion animal, the domestic cat, has received far less attention. Current understanding is that domestic cats were most probably originally moved for pest control, although its movement as a pet or as a status symbol cannot be fully discounted (Cucchi et al. 2020). The earliest known translocation of a cat was to the island of Cyprus in the Neolithic period (~7,500 BCE) (Vigne et al. 2004). The cat was buried alongside a person which showed some form of connection between the two. In terms of studies of the early movement of cats, there has been one relatively comprehensive study of ancient cats in Europe, North Africa and the Near East along with studies of specific regions such as central Europe (Ottoni et al. 2017; Baca et al. 2018; Krajcarz et al. 2016). Given that there are relatively few studies on domestic cats and given their importance in society today, this thesis will explore the arrival of domestic cats in the islands of Britain and Ireland as an example of intentional movement of a species.

1.2.2.3 Unintentional movement of animals

It is known that many species have been moved unintentionally on human transportation including boats, trains and planes. In the past this would also have occurred, albeit on a smaller scale, first only by foot but later by animal-drawn transportation during the Neolithic period onwards. Naturally, the accidental movement of large species is very unlikely, so most of the documented unintentional movements are of invertebrates, algae, fungi, and microorganisms (Pyšek et al. 2020). However, small vertebrates are also known to be unintentionally moved by humans. Evidence for these include mice, rats, geckos, sparrows and great-tailed grackle (Searle et al. 2008; Aplin et al. 2011; Carranza and Arnold 2006; Haemig 2014; Heinsohn 2001; Shapiro and Domyan 2013). These species are relatively understudied compared to animals that have been intentionally moved, and particularly domesticated species.

This thesis focuses on the black rat as an example of unintentional movement of a species. It is well known that the black rats' present-day distribution is largely a result of human translocation in the medieval period, which later led to a global distribution (Aplin et al. 2011). As a possible vector for the spread of disease, it is thought they played a large role in the first documented plague pandemic, the Justinian Plague (started 541 CE) (Wagner et al. 2014; Meerburg, Singleton, and Kijlstra 2009). This highlights the devastating effect that introduced species can have on other populations. The natural range of black rats is South Asia, therefore this study will focus outside their natural range, on their introduction to Europe (Aplin et al. 2011; Baig et al. 2019).

1.2.3 Techniques to explore the movement of animals in the past

There are a number of lines of evidence which can be used to reconstruct past movements of animals. These include but are not limited to historic records, zooarchaeological analysis, absolute dating, stable isotope analysis and DNA analysis of both ancient and modern samples. Historical accounts, where available, are invaluable as they may record the arrival of a species or document where particular species are present at a given time. However, as secondary sources, these accounts must always be taken with caution. When faunal remains reveal a novel species to an area, absolute dating can provide a way to pinpoint when this species arrived. Zooarchaeological analysis can identify species. However, due to the nature of archaeological material preservation, fragmentary specimens can be hard to differentiate down to genus, and often even species level. When this is the case, other species identification techniques, such as zoological mass spectrometry or genetic analysis, alongside radiocarbon dating can be used to reconstruct a species' introduction.

Isotopic analysis can also be of use to identify the movement of species. Strontium and oxygen isotopes can be used to understand the movement of an individual species within its lifetime, but will not provide information of movements across multiple generations. Dietary stable isotopes, however, can be more useful, with nitrogen, carbon and sulphur isotopic analysis often used to reconstruct an animal's diet (Price and Burton 2010). If, for example, an animal demonstrated a similar trophic level signature to the contemporary human diet, this could be an indicator that the animal was living with people. If instead the diet was elevated in carbon-13, this could suggest a larger proportion of C4 cereals in the

diet, which may also be an indicator that the animal was eating an abnormal diet. Isotopic analysis can therefore be used to highlight incidences of commensalism and possible translocation, as it can identify individuals that are not eating a natural diet, but instead are eating a diet similar to people, or suggesting scavenging from a human settlement (Hofman and Rick 2018). For example, at the 5,050 to 3,050 BCE site of Quanhucun, China, researchers have discovered, through zooarchaeological and isotopic analysis, that the cats were living amongst people. It also revealed that one individual may have been cared for, as elevated levels of carbon-13 in the diet suggested that it was eating more millet than the other cats at the site (Hu et al. 2014). Stable isotope data can provide information on the possible relationships between animals and people, giving us insight into if the animal was wild or living in the human habitation site. However, one crucial disadvantage of this technique is that it is unable to determine where an individual originated from or identify relationships between individuals.

This is something which can be addressed through genetic analysis. In addition to confirming species identification, which is naturally critical to understanding when a species arrived in an area, by tracing genetic similarities between the individual of interest and the known ancient range of that species, the origin of that individual may be determined (Hofman and Rick 2018). This discipline is often referred to as phylogeography — the study of the past processes that may be responsible for the contemporary geographic distribution of a species. The historical distribution can be reconstructed using both modern and ancient DNA, but ancient DNA has the advantage of using material from throughout time, giving a direct window into the past (Searle 2008). Studies using only modern DNA may be unable to accurately reconstruct past distributions of lineages, as complete or partial replacement events can lead to the modern day populations being genetically dissimilar to the past populations in that area (de Bruyn et al. 2011; Frantz et al. 2019; Barnes et al. 2002). For the most accurate reconstruction of a species history both modern and ancient DNA data are required (Orlando and Cooper 2014).

Considering this review of techniques, this thesis uses modern and ancient DNA analysis, along with direct radiometric dating of specimens, to reconstruct the movements of animals in the past, with zooarchaeological analysis used to identify bones of interest to

the studies. It was not within the scope of the studies to conduct stable isotope analysis. For two of the species (cats and rats), stable isotope measurements have been collated and are being analysed by colleagues as part of wider projects.

1.3 Overview of thesis

This thesis consists of three papers exploring the movement of animals in the past using a predominantly ancient DNA approach. The first paper looks at the natural movement of mountain hares from the end of the Pleistocene to the modern day, with a focus on the western edge of Europe where their arrival is less well understood. It will also explore whether mountain hares arrived in the Western Isles of Scotland naturally or with the aid of people, as mountain hare remains have been found in the earliest human occupation layers on the islands.

The next two papers explore the human mediated dispersal of animals, looking at the intentional and unintentional movement of animals respectively. The paper on the intentional movement explores the arrival of domestic cats to Britain and Ireland. It uses genetic techniques alongside absolute radiometric dating to discover when cats reached Britain and Ireland and where they came from. The paper also explores the effects their arrival had on the native population of European wildcats. The final paper will explore the unintentional movement of black rats to Europe from the Roman to Medieval periods, including the cause(s) for their changing distribution. Currently it is unknown whether it was the collapse of the Roman empire, the plague pandemic, climatic change, a combination of all three or another factor entirely which caused their changing distribution.

In addition to furthering our understanding of the life histories of three understudied species and demonstrating the value of using a deep-time perspective, this thesis will also add to the growing number of sequenced full mitochondrial and nuclear genomes of archaeological and palaeontological species. Furthermore, the information gained through this thesis could also provide insights into population distribution mechanisms that will be useful to the conservation community, helping to protect species in the future.

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2. The continuity of mountain hares in the western fringe of Europe

2.1 Statement of Authorship

Research design: I designed the research, with input from Greger Larson.

Data generation: I performed all the laboratory analysis in Oxford for both the modern and ancient datasets generated as part of this project.

Analysis: I performed all the computational analysis under the guidance of Laurent Frantz. I interpreted the results with input from Laurent Frantz, José Melo-Ferreira, Fiona Beglane and Greger Larson.

Manuscript: I wrote the manuscript, with input from all other co-authors.

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2.3 Abstract

Mountain hares (*Lepus timidus*) were once a widespread species in Europe and Russia. Throughout the Holocene (around 11,700 years ago - today) their species range has been contracting, pushing them to northern latitudes and higher elevations. This study explores these changes from the Last Glacial Maximum (LGM, around 27,000 years ago) to today, with a focus on the western edge of their range in Ireland and the Western Isles of Scotland where they were cut off from the continuum on the edge of the ice sheet. We have used both ancient and modern DNA datasets from throughout the past range of mountain hares, with 50 ancient and 92 modern sequences generated. Although we focused on the western edge, mountain hares throughout the range have been analysed to contextualise the results. Mountain hares maintained their diversity through time from the Last Glacial Maximum to today and through most of their natural range. The highest diversity was found in central Europe where they most probably originated before expanding into Russia in the Pleistocene and Scandinavia in the Holocene when the ice retreated. On the western edge of Europe, hares were cut off from the rest of the range with the last advance of ice, surviving in refugia and recolonising when conditions became favourable similarly to other possible Celtic fringe species. This included the Western Isles of Scotland where we have shown hares arrived naturally and not with the aid of people.

2.4 Introduction

There is much uncertainty surrounding when and how terrestrial species colonised the western edge of the British Isles. Since at least the Last Glacial Maximum (LGM, around 27,000 years ago) neither the Western Isles of Scotland (often also referred to as the Outer Hebrides) or Ireland have been connected to mainland Britain (Edwards and Brooks 2008). This made recent natural crossings to Ireland and the Western Isles near impossible for all but a few terrestrial species capable of swimming great distances. The two most logical explanations for the arrival of terrestrial species after the Last Glacial Maximum, to both Ireland and the Western Isles, are therefore either human assistance in the Holocene (around 11,700 years ago - today) or natural arrival in the Pleistocene (around 2.6 million - 11,700 years ago). There are various mechanisms for natural arrival including survival in refugia (areas in which a population can survive through a period of unfavourable conditions) followed by over-land dispersal from those refugia when sea levels were still low or arrival by rafting either from these refugia or from the nearby western Scottish mainland or northern Ireland at any point prior to the Mesolithic. Focused genetic studies on modern Irish fauna have already been conducted on early arrivals to determine if they arrived with or without human intervention. For a number of these species such as pine marten stoats and badgers, unaided arrivals have been proposed, implying that arrival occurred prior to the Holocene (Martínková, McDonald, and Searle 2007; Searle et al. 2009; O'Meara et al. 2012; Ruiz-González et al. 2013). Refugia relevant to Ireland can be some considerable distance from the present mainland, for example in the Bay of Biscay. So far, none of these studies have focused on the Irish mountain hares (*Lepus timidus hibernicus*). Previous broader studies of mountain hares (*Lepus timidus*), showed that the modern-day population of Irish and Scottish hares (*Lepus timidus scoticus*) each form separate monophyletic groups (Melo-Ferreira et al. 2007). It is also known from previous work that mountain hares formed a continuous range in the late Pleistocene (Hamill, Doyle, and Duke 2006; Smith et al. 2017; Hamill, Doyle, and Duke 2007). The Irish hares' genetic distinctness, along with their climatic and fossil record puts them as a probable candidate for early arrival prior to the Holocene.

This study builds on these findings and adds a further deep-time dimension, by investigating palaeontological and archaeological mountain hare material from across the past mountain hare range, from the Pleistocene to the present day. This includes samples from an area of their range not studied before — the Western Isles of Scotland. This is the most comprehensive study of ancient mountain hares to date, being the first genetic study of any modern or ancient hares from the Western Isles and the first study of ancient Irish and British hares.

The aims of this study are to reconstruct the past movements of mountain hares from the late Pleistocene to today, throughout their range, with a focus on the western edge of Europe. The findings of this study will not only further our understanding of this cold-adapted species, but the results may help in its future conservation through furthering the understanding of its past adaptability and resilience.

2.4.1 The past and present distributions of mountain hares and other mammals

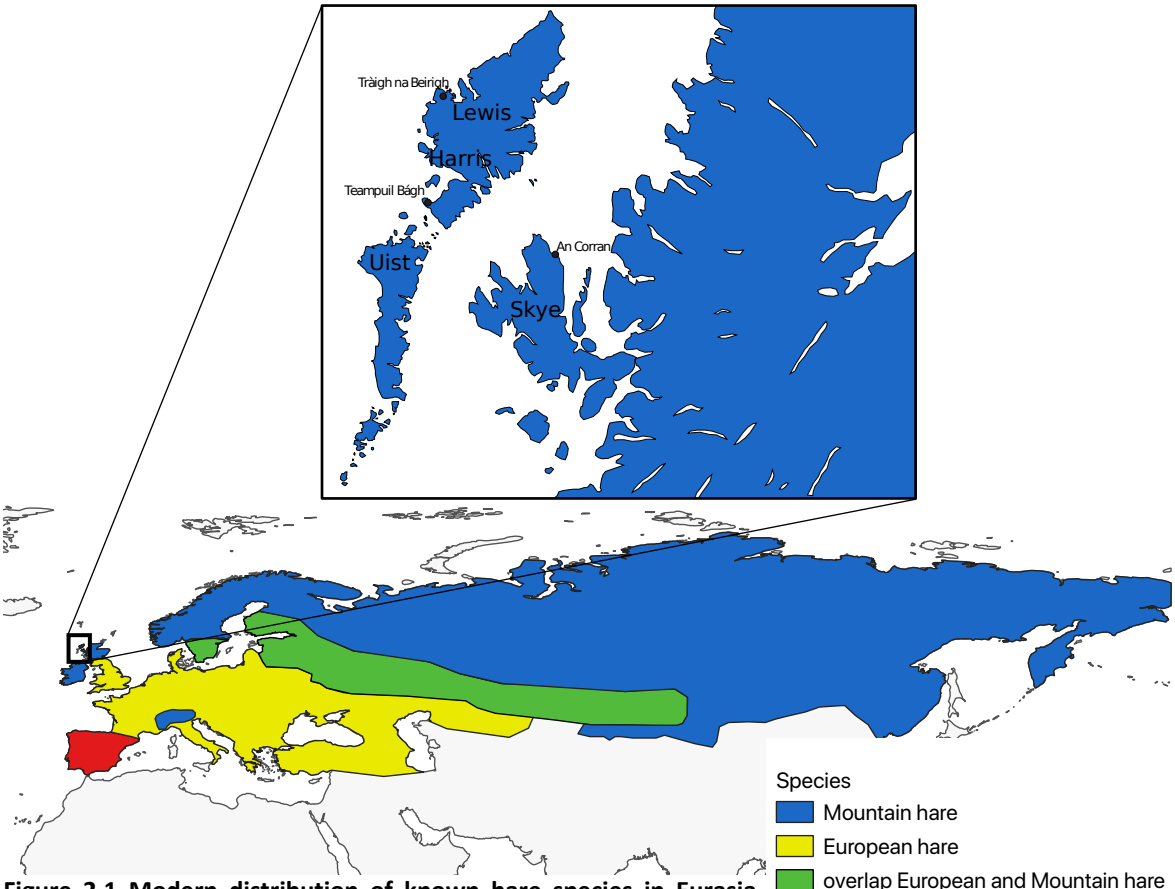

Figure 2.1 Modern distribution of known hare species in Eurasia. Areas in green are known areas with both mountain hares and European hares present. The zoom in pane is of the Hebrides of Scotland showing the islands and sites mentioned in the study.

Mountain hares are a nocturnal Arctic-alpine species adapted to mountainous habitats, found today throughout most of Eurasia and never below a latitude of 40° north (Figure 2.1) (Melo-Ferreira et al. 2007; Angerbjörn and Flux 1995; Chapman 1990). Hares, like almost all species, are affected by changes in climate. Over the last thousands of years Europe has seen several Ice Ages followed by warming periods which altered the distribution of various species. When climates change rapidly, most species retreat into southern refugia. This is not the case with mountain hares. Smith et al. (2017) found that mountain hares instead occupied the tundra of central Europe and were not isolated in southern refugia, maintaining their population structure throughout the Last Glacial Maximum. This is demonstrated by the lack of evidence for isolated populations within the sampled specimens, and by them all showing the same amount of genetic structure as modern mountain hares.

During the last glacial period, mountain hares were the most widely distributed hare species in Europe, according to the fossil evidence (Koby 1960; López Martínez 1980). This, however, changed with the end of the Last Glacial Maximum. The south of Europe became far more favourable to the European hare (*Lepus europaeus*, often also referred to as the brown hare), which is suited to temperate climates and open spaces at low elevations. Across the whole of southern and most of central Europe the temperate European hare and Iberian hare (*Lepus granatensis*) replaced the mountain hares in almost all areas except in the higher elevations of the Alps, where mountain hares still exist today (IUCN 2018). During these range replacements hybridisation occurred between the mountain hare and the north advancing southern hare species and as a result the mitochondrial lineage of the mountain hare is found in some of the other European hare species today. There is one other location along with the Alps which did not see the replacement of the mountain hares — Ireland. It is only since the 19th century, with the introduction of European hares to Ireland, that there is competition for the lowlands, with the mountain hares now being largely restricted to the highlands (Reid and Montgomery 2007). Mountain hares have therefore been seen to be pushed, by both climate and species competition, to the extreme northern and western edges of Europe (Figure 2.1), with only the small pocket of mountain hares left behind in the Alps. This has also been further accelerated in recent years due to climate change (Rehnus et al. 2018).

2.4.2 The origin of mountain hares on the western fringe

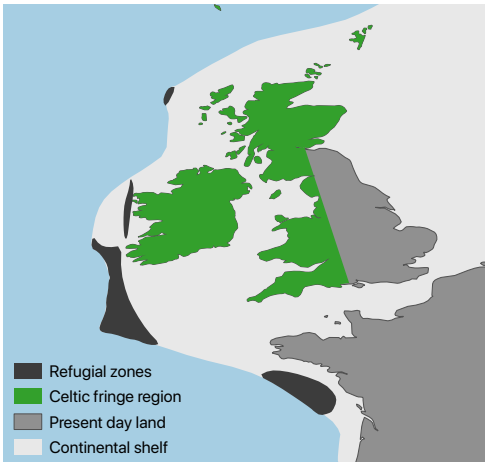

Figure 2.2 Map of the theoretical 'Celtic fringe' in green, and the possible refugia zones at 21,000 years ago proposed by Montgomery et al. (2014) in black, figures based on Montgomery et al. (2014), Beatty and Provan (2013) and Searle et al. (2009). The furthest south refugial zone is in the Bay of Biscay.

This study focuses on the distribution of mountain hares in the western edge of their range. In this section, the palaeontological, archaeological, modern genetic and climatic evidence is explored for each region separately, bringing together the current evidence for the arrival of mountain hares to each region. Britain is included, as the western and northern edges of the island are often considered part of the western fringe region (Figure 2.2).

2.4.2.1 Ireland

Palaeontological evidence

Irish hares are a subspecies of mountain hare and are found across Ireland today. The earliest evidence of hares in Ireland comes from remains from two sites on the south coast. Both sites have direct dates on the hare bones, the remains from Foley Cave dated to >49,000 Before Present (BP) (OxA-24609) and Shandon dated to 33,071 ± 707 cal. BP (OxA-24611, 30,550 ± 370 BP) (Carden, Higham, and Woodman 2020; Monaghan 2017). This points to hares being present in Ireland from before the Last Glacial Maximum. The next dated specimen from Ireland is from 14,315 ± 524 cal. BP (OxA-5736, 12,190 ± 130 BP) from Plunkett Cave, Kesh Corran Cave complex, County Sligo in the west of Ireland (Woodman, McCarthy, and Monaghan 1997). As similarly aged specimens from Ireland and Britain have had their dates revised due to improved radiocarbon techniques, all dates from before 2006 need to be read with caution. Redating with up-to-date methods may shift the dates (Higham, Jacobi, and Ramsey 2006; Higham 2011). There are also hares present at the site

of Alice and Gwendoline Cave where contemporaneous bear remains have been dated to 12,803 ± 75 cal. BP (OxA-29358, 10,850 ± 50 BP) (Dowd and Carden 2016). These remains show the presence of mountain hares after the retraction of the ice sheet and prior to the Holocene in the Woodgrange Interstadial (13,000 - 11,000 BP). The earliest mountain hare remains found in the Holocene are from the Mesolithic (around 11,700 - 5,950 years ago) deposits of four sites: Mount Sandel, Ferriter's Cove, Sutton and Moynagh (Woodman 1985; Woodman 1999; Mitchell 1956; McCormick and Murray 2007). This puts hares present in Ireland up until the Last Glacial Maximum and then continuously present in Ireland from around 12,000 BP to today.

Climatic record

The lack of evidence for mountain hares and other fauna in Ireland in the Last Glacial Maximum is explained by Ireland being largely covered in ice and cut off from Britain. From the onset of the Last Glacial Maximum around 30,000 BP, Ireland started to be covered by an ice cap, with most of present-day Ireland covered by 29,000 - 28,000 BP and fully covered by around 27,000 BP. It remained covered until around 20,000 BP when parts of the south coast of Ireland become ice free (Patton et al. 2017; Clark et al. 2012; Hughes et al. 2016). Ireland was then recolonised by a number of land mammals from around 20,000 BP, as shown by the recent redating of specimens from the south coast of Ireland (Carden, Higham, and Woodman 2020). Although there is no directly dated evidence for hares at 20,000 BP, given that other cold-adapted species (e.g. giant deer, reindeer, Arctic fox) have been shown to recolonise Ireland at this point, it is probable that hares were also among them (Dowd and Carden 2016; Lister and Stuart 2019; García-Vázquez, Pinto Llona, and Grandal-d'Anglade 2019; Woodman, McCarthy, and Monaghan 1997; Carden, Higham, and Woodman 2020). It is unknown where these hares recolonised from, with possible candidates being from a northern refugium or directly from the continuum on the edge of the ice sheet (Figure 2.2). There was possibly a short-lived land connection until around 16,000 BP, when Ireland was still partially covered in ice, which would have allowed cold-tolerant taxa to arrive from Britain. However, this is debated (Edwards and Brooks 2008). Evidence of other taxa arriving in Ireland after the Last Glacial Maximum supports a possible northern European refugium in the Bay of Biscay (Figure 2.2) (Montgomery et al.

2014). Deglaciation of Ireland continued through the Woodgrange Interstadial (13 - 11,000 BP) (Monaghan 2017). There was then a brief cold stage, the Younger Dryas (around 12,900 – 11,700 years ago), followed by continued warming to present day (Wilson 2004; Patton et al. 2017). The lack of directly dated hare remains from 20,000 to 14,000 BP is probably due to lack of sampling and not an absence of hares. More studies of material from these periods are needed to conclude when hares arrived back in Ireland after the Last Glacial Maximum.

Genetic evidence

The modern Irish hares show greater affinity with the continent than to the modern Scottish population (Melo-Ferreira et al. 2007). Also, both populations form their own monophyletic clades (Hamill, Doyle, and Duke 2006, 2007). These observations suggest either the Irish and Scottish populations were not part of the same wave of colonisation from the mainland or both the Scottish and Irish populations passed through a bottleneck resulting in the fixation of different haplogroups. With the current modern data alone, these two processes are hard to distinguish. It is also difficult to ascertain where each population colonised from. Either population may have arrived from the continuum on the edge of the ice sheet or from refugia cut off from the continuum at some point in time.

Summary

The three lines of evidence together suggest that mountain hares arrived in Ireland naturally before the Last Glacial Maximum. They then retreated to currently unknown refugia during the Last Glacial Maximum or were part of the continuum with mainland Europe and Russia on the ice margin. As the ice melted, they recolonised and have been present ever since. It is unknown when in the Pleistocene the Irish population was cut off from the rest of the range. It is also unclear if Ireland was the only location where this population could be found, or whether it was far more widespread in the past.

2.4.2.2 Mainland Britain

Palaeontological evidence

Today, mountain hares are only present naturally in the Highlands of Scotland (Ritchie 2015). They have been (re-)introduced to various regions of Scotland, England and Wales in the recent past with varying success, with extant introduced populations present on various Scottish islands and in the Peak District of England (Barrett-Hamilton et al. 1910; O'Connor and Sykes 2010). They were not always confined to Scotland; they have been found in the fossil record of England from the Pleistocene. The earliest occurrence of mountain hares is from before the Last Glacial Maximum at Joint Mitnor Cave, Devon where the fauna have been dated to before 120,000 ± 6,000 BP (Gascoyne, Currant, and Lord 1981; Currant and Jacobi 2001). The next occurrence of mountain hares in Britain is after the Last Glacial Maximum, with the earliest directly dated hare dated to 14,645 ± 328 cal. BP from Creswell Crags, Derbyshire (OxA-17525, 12,465 ± 50 BP) (Ashton, Lewis, and Stringer 2011). Two other sites with dated mountain hare remains are Church Hole, Nottingham (OxA-18704, OxA-18706) and Gough's Cave, Cheddar gorge, Somerset (OxA-4107), all dating between 12,550–12,355 BP (Ashton, Lewis, and Stringer 2011; Tolan-Smith and Bonsall 1999). Undated specimens from other late Pleistocene sites range from the south coast up to Yorkshire (Ashton, Lewis, and Stringer 2011). There is one possible hare bone from the Mesolithic site of Star Carr, Yorkshire, however it is undated and is the only hare bone found at this site or at any other Mesolithic site in England to date (Fairnell 2011). From this one bone yet to be dated it is hard to conclude if mountain hares were present in the Mesolithic in England.

It is, however, known that mountain hares were present in Scotland in the Mesolithic period, with their remains having been found in Mesolithic shell middens. The only mainland site to have possible hare bones listed is the site of Land Mill Bay, near Oban (Bartosiewicz, Zapata, and Bonsall 2010; Saville et al. 2012). The only other hares listed in the Mesolithic of Scotland are from the islands of Harris, Lewis and Skye (Figure 2.1, see below section for further details on Scottish islands). These are the only Mesolithic sites with confirmed mountain hares. This is explained by Scotland being covered in an ice sheet until just prior to the Mesolithic, allowing hares to move to these areas once the ice had

receded. Additionally, the faunal remains in the early record of Scotland are scarce as many areas have acidic soil which is not conducive to bone preservation (Kitchener, Bonsall, and Bartosiewicz 2004). Furthermore, most of the sites are coastal shell midden sites where land mammals were less frequently hunted (Kitchener, Bonsall, and Bartosiewicz 2004). This makes the reconstruction of the distribution of mountain hares in the early Holocene difficult in Scotland. Based on their current natural range in the Highlands, in addition to them being found in the Mesolithic deposits on the western mainland and a few Hebridean Islands, their occurrence across the whole of Scotland in the past is expected. The decline in numbers of mountain hares in Scotland may be recent, and caused by the introduction of the European hare (Thulin 2003).

The exact timing of the disappearance of mountain hares from England and Wales is unknown, but it is possible that it occurred in the Bronze Age (around 4,450 - 2,750 years ago). At the site of Hartledale, both species are found in the Bronze Age layers, then in more recent layers only European hares were found (Turk 1964). O'Connor and Sykes (2010) theorise the mountain hares were pushed north as their range shrank with the increase in tree-cover in the Post-Glacial period, leaving them in the isolated region of the Highlands of Scotland where tree cover remains low at higher elevations. Another theory is that they were displaced by the arrival of the European hares, which is known to have occurred in other parts of the mountain hare range. However, it is uncertain when European hares arrived in Britain (Thulin 2003; O'Connor and Sykes 2010). The disappearance of the mountain hares from England and Wales, along with their decline in Scotland, is not within the scope of this study and warrants further investigation.

Climatic evidence

Britain in the Last Glacial Period (115,000 - 11,700 BP) has been through several cycles of expanding and contracting ice sheet margins. The last advance started around 32,000 BP and was at its most southerly extent around 23,000 BP (Hughes et al. 2016). The south of Britain was still ice-free when the ice was at its greatest extent. Mountain hares would have been able to survive on this ice-sheet margin in southern Britain. From this period onwards the ice retreated which would have allowed the mountain hares to expand their

range north in Britain. With Scotland beginning to become ice-free from around 15,000 BP. The hares would have still been able to be part of the continuous range with mainland Europe and Russia until sea-levels rose around 8,000 BP when Britain became an island (Weninger et al. 2008).

Genetic evidence

There is no extant population of mountain hares in England and so the only genetic evidence from Britain is from the Scottish population. The genetic evidence from the modern Scottish hare shows that it is less related to the continental populations than the Irish is with the continental population today (Melo-Ferreira et al. 2007). The Scottish population probably colonised from a sperate source than the Irish as there is little similarity between the two populations. Although a bottleneck event cannot be fully discounted. It is still unknown whether the now-extinct populations in England and Wales were of the same lineage as modern-day Scottish mountain hares, or whether they were distinct populations which have subsequently disappeared.

Summary

All the evidence from mainland Britain suggests that mountain hares arrived naturally before the Last Glacial Maximum, disappeared from most of Britain during it and then recolonised after it. Mountain hares now only remain naturally in Scotland and have disappeared from the rest of the British mainland. This disappearance possibly occurred in the Bronze Age, but this warrants further study as this is not well understood.

2.4.2.3 Inner and Outer Hebrides

Palaeontological evidence

Mountain hares are present today on islands in both the Inner and Outer Hebrides. All are introduced populations from the Scottish mainland and Ireland in the 19th century for sport (Hewson 1955). The islands that they are known to have been introduced to are the Orkneys, Harris and Lewis, Arran, Mull, Islay, Skye and Raasay (Hewson 1955; Barrett-Hamilton et al. 1910). All were brought from the Scottish mainland, apart from the population on Mull, which is recorded as having both Irish and Scottish hares present

(Harvie-Brown and Buckley 1892). Barrett-Hamilton et al. (1910) theorise that mountain hares may have been indigenous (occurred naturally without humans) to the Orkneys, Inner and Outer Hebrides. This may be the case with the Inner and Outer Hebrides, as mountain hare remains have been found in the earliest human occupation layers in the Mesolithic period of Harris, Lewis and Skye (Saville et al. 2012; Gregory et al. 2005). They were also found in the earliest occupation layers in the Neolithic period (around 5,950-4,450 years ago) at Cladh Hallan, Uist (Fairnell 2011). This demonstrates that mountain hares were at least early colonisers, if not natives. Land mammals could not have arrived unaided to the Orkneys or Outer Hebridean islands in the Holocene as the islands have not been connected to the mainland since the Last Glacial Maximum (Corbet 1961). At all these locations the hares may have been introduced by people or they occurred naturally on each of these islands and therefore were present before the arrival of people. This is explored in this present study.

Climatic record

The Hebrides and mainland Scotland were covered in ice from around 32,000 BP until 17,000 BP (Small et al. 2017; Stone and Ballantyne 2006). Following the warming at the end of this period, the temperatures decreased with the Younger Dryas around 12,900 - 11,700 BP (Ives, Denton, and Hughes 1981; Chandler and Lukas 2017). Deglaciation of the Outer Hebrides Ice Cap started in the period 16,400 - 14,400 BP and finished around 15,000 - 13,200 BP (Ives, Denton, and Hughes 1981). Through the Last Glacial Maximum and the Younger Dryas there have been suggestions of ice-free zones on the mountain summits (Bradwell et al. 2008). There have also been suggestions of refugia off the west coast (Figure 2.2) (Montgomery et al. 2014). If hares did exist in the Hebrides before the Last Glacial Maximum, they could have survived in these ice-free zones on the summits of Lewis or in a refugium off the west coast of the Western Isles. In this case, they then would have been able to recolonise the Western Isles when conditions improved. The Minch waterway would have provided an uncrossable barrier for further colonisation as it had been a deep cold open waterway between the Western Isles and Skye since 15,000 BP. Before this, in the Last Glacial Maximum, it was an ice stream (Bradwell 2007).

Genetic evidence

There have not been any extensive modern or ancient genetic studies of mountain hares from the islands of Scotland prior to this study. The only study to include samples from any of the Scottish islands is that of Melo-Ferreira et al. (2007) which included two modern samples from the Isle of Mull which clustered with the Irish not the Scottish populations. This was explained by the Irish hare being a recent introduction to Mull as it was introduced along with Scottish hares to the island in the 19th century (Harvie-Brown and Buckley 1892).

Summary

The arrival of mountain hares to the Western Isles and the other islands of Scotland is not well understood with the current evidence. From the archaeological record it is known that they were present in the Mesolithic period in the Inner and Outer Hebrides. With the Inner Hebrides it is possible that they arrived unaided from mainland Scotland, where we know mountain hares were present in this period. With the current evidence, it is hard to conclude if hares arrived in the Western Isles unaided or with the help of people.

2.4.2.4 Overview of origin of mountain hares to the western fringe

Current understanding based on the above evidence suggests that mountain hares naturally colonised mainland Britain and Ireland before the Last Glacial Maximum and then again after the Last Glacial Maximum, possibly from two separate refugia or from two distinct parts of the continuous range. It is unknown when they first colonised the Scottish islands, as the first conclusive evidence for them is after the Last Glacial Maximum in the Mesolithic period. Mountain hares are now only found naturally in the Scottish Highlands and Ireland.

2.4.3 Review of current understanding of the arrival of other land mammals to the western fringe

In order to understand the arrival of mountain hares, it is important to put this in the context of the arrival of other land mammals to the western fringe of Europe. The main areas of study: Ireland, the Western Isles of Scotland, are all islands today and have been cut off from the rest of the European continent for thousands of years (Edwards and Brooks 2008; Weninger et al. 2008). This has led to a reduced number of native terrestrial

mammals compared to the continent, Ireland 27 (13%) and Britain 43 (21%) compared to mainland Europe's 204 (Marnell, Kingston, and Looney 2009). There have been several studies to try and conclude the native status of species with unclear origins.

With these studies looking at the arrival of terrestrial mammals to Britain and Ireland, there is a pattern emerging, with the earliest arrivals colonising in two phases. This results in those in the Western fringes (Ireland, Scotland and sometimes Wales and Cornwall) looking genetically distinct from the eastern and central English populations. This area is often referred to as the 'Celtic fringe' as it correlates with the cultural Celtic regions of Ireland, Scotland, Wales, Cornwall and the Isle of Man (Figure 2.2) (Searle et al. 2009). A 'Celtic fringe' has been proposed already for the following species: pygmy shrew, stoat, badger, bank vole, field vole, red fox, pine marten, common shrew and water vole (Vega et al. 2020; Martínková, McDonald, and Searle 2007; O'Meara et al. 2012; Ruiz-González et al. 2013; Searle et al. 2009; Brace et al. 2016; McDevitt et al. 2020). In this study we will explore whether the mountain hares can be added to this growing list.

The two waves probably came from two separate regions; northern refugia and more central refugia (Vega et al. 2020; Searle et al. 2009). Speculations have been made for a few areas which could have been northern refugia. Montgomery et al. (2014) ran a hindcasting model for suitable habitat at 21,000 years ago for species which are known early colonisers. The model was created using a suite of climatic data to reconstruct the past sea levels and habitats. Projecting the refugial zones for each species was based on their current known suitable habitat and distribution. They found that there may have been land free of ice suitable as a habitat for stoat, red deer, mountain hare, Leisler's bat and pygmy shrew to the west and south of Ireland and in parts of the Bay of Biscay (Figure 2.2). The Bay of Biscay has also been proposed as a refugium for Lusitanian plant species, further supporting the idea that this was a probable northern refugial area for both plants and animals (Beatty and Provan 2013). These refugia may be where the first wave of colonisers after the Last Glacial Maximum originated from. Over the course of the Holocene, when Britain was still connected to the mainland, central European populations of each of these species (apart from the wood mouse) replaced the original populations in the central and eastern regions of England, leaving a peripheral population on the western

edges of Britain. Throughout the Holocene, Ireland and the Western Isles were cut off from Britain which explains why the populations were not replaced by the second wave of colonisation. The wood mouse is a unique case, as there are only a few examples of the central European lineage on the south-east coast with the rest of the mainland Britain population (Herman et al. 2016). It is possible that the wood mouse never fully underwent this second wave replacement, and that the observed species has persisted since the first recolonisation after the Last Glacial Maximum. The wood mouse was then later transported by people to Ireland, Iceland and the islands of Scotland, explaining why they have the same lineage as the mainland Britain population (Herman et al. 2016).

Of all these species which have been studied, archaeological/palaeontological material has only been used in one study, that of the water vole (*Arvicola amphibius*) (Brace et al. 2016). Samples used in the study were from the Pleistocene and Holocene from across mainland Britain. An analysis of both ancient and modern samples showed that there were two distinct waves of colonisation into Britain, with the first wave prior to the end of the Younger Dryas (around 12,900 – 11,700 years ago) and the second sometime between 12,081 and 2,900 BP (Brace et al. 2016). This was supported by the Pleistocene samples from England clustering with the modern Scottish samples and the Holocene samples from England clustering with the modern English. By studying the modern DNA, this north-south divide may have been inferred, but it is only with the use of ancient DNA that this has been confirmed. This study demonstrates the need for both modern and ancient samples to answer questions on the arrival of species in Britain and Ireland.

Another study used historic material from museum collections to investigate the origins of the European pine marten (*Martes martes*) (Jordan et al. 2012). The study includes modern samples from post-1981 and historic samples from 1865-1977. The historic population consists entirely of haplotype ‘i’ in Ireland, Wales, and England. Around 1915 ‘i’ was replaced by ‘p’. This is consistent with a known decline in the population, and the results show that the bottleneck favoured the survival of haplotype ‘p’ over ‘i’. The Scottish population before this study was thought to consist only of haplotype ‘a’. However, by using historic and more contemporary data, haplotype ‘i’ has also been found. This investigation also shows the advantage of using historic data.

2.5 Materials and Methods

2.5.1 Sample collection

A total of 161 ancient mountain hare bones from 76 sites were collected from across Europe and Russia (Figure 2.3). A muscle tissue sample from a roadkill modern mountain hare from the Isle of Lewis, Western Isles, Scotland, collected by the Natural History Museum of Scotland, was also collected at my request for inclusion in this study. The archaeological and palaeontological material ranged in age from 24,000 to 600 BP. The ancient samples were collected from museums and archaeological collections from throughout the modern and ancient mountain hare range (Figure 2.3 and Table S2.1). In additional to these samples, Dan Bradley, Trinity College Dublin, provided three ancient mountain hare mitochondrial sequences from the Neolithic site of Parknabinnia, County Clare, Ireland. Love Dalén, Swedish Museum of Natural History, provided 74 ancient extracts from Sweden, Lithuania, France, Switzerland, Russia, Austria, Greece, Poland and Belgium. All of Dalén's samples are from previous studies of short fragments of mitochondrial DNA and, for the most recent study, nuclear single nucleotide polymorphisms (SNPs) (Ahlgren et al. 2016; Smith et al. 2017; Lado et al. 2018). José Melo-Ferreira and Paulo Alves, CIBIO-InBIO, Portugal, provided 94 extracts from modern samples from Russia, Iberia, and Scotland, used in previous works. Melo-Ferreira and Alves also provided 63 modern mitochondrial DNA sequences extracted from whole genome sequencing data: 19 from Fennoscandia, 20 from Ireland, 4 from the Faroe Islands and 20 from the Alps (Table S2.4).

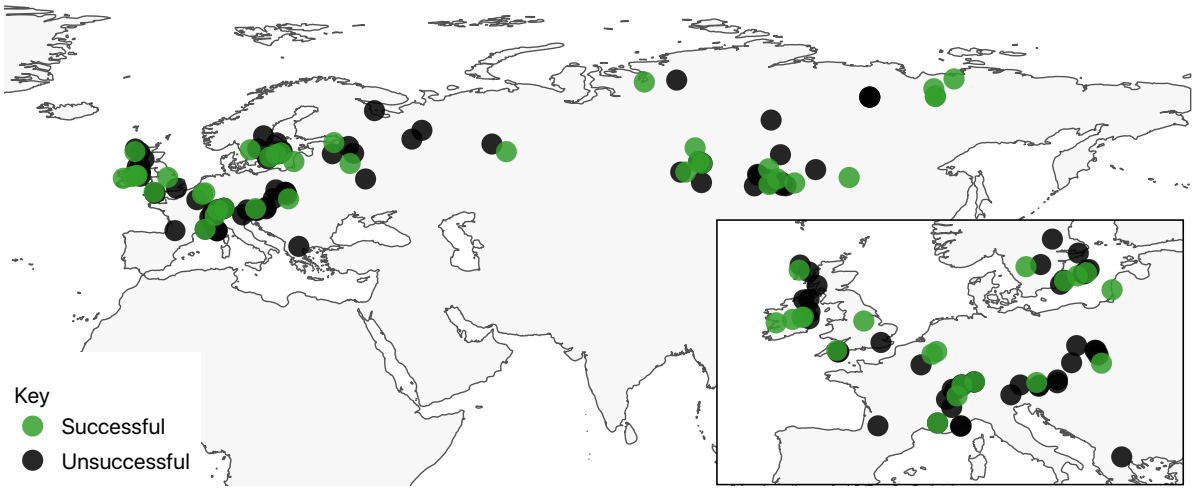

Figure 2.3 Locations of archaeological and palaeontological sites sampled for this study. Locations in green are samples which yielded over 2x or more mitochondrial depth of coverage and are used in the analysis.

Mountain hares and European hares interbreed and have fertile offspring, therefore all ancient material collected was only acquired from periods and/or regions where there is no known evidence of European hares living alongside the mountain hares. For example, in Britain and Ireland samples were from before the introduction of European hare and the majority of the continental samples were from either in the current range of only the mountain hare or from their probable range in the period of study. This ensures that no hybrid or introgressed individuals were in the study and only pure mountain hares. Of the modern hare samples, the individuals included from Iberia are not mountain hares. Instead they are European, Iberian and Broom hares (*Lepus castroviejoi*) with mountain hare mitochondrial DNA (Melo-Ferreira et al. 2005). These samples are included in this study because, while there are no modern populations of mountain hares in Iberia, it is known that they were present in this region in the past. These individuals can therefore act as a proxy for the ancient Iberian mountain hares (Melo-Ferreira et al. 2005). All other modern hare individuals are from mountain hare populations which have already been confirmed in published studies using nuclear analysis and/or shorter fragments of mitochondrial DNA (Giska et al. 2019; Melo-Ferreira et al. 2007, 2005, 2012). They are also from regions with no known evidence of persistence of introgressed mitochondrial DNA.

2.5.2 DNA Extraction and Sequencing

2.5.2.1 Ancient DNA

DNA was extracted from 50-250 mg of bone powder from all 161 ancient samples collected. All laboratory procedures were performed in the dedicated ancient DNA facility at the University of Oxford. All standard ancient DNA laboratory practices were adhered to minimise contamination. Blanks were included at every stage, from extraction to capture, as negative controls. The outer surface of the bone was removed prior to extraction using a Dremel drill. Any bones weighing under 50 mg had the entire bone used for extraction and all other bones had only a subset of the bone removed for analysis. The bones were cut using a Dremel drill with a clean cutting wheel per sample (Dremel no 409) and the samples were pulverised in a Micro-dismembrator (Sartorious-Stedim Biotech). Extractions were conducted using the Dabney protocol with a modification of the addition of a 30-minute pre-digestion stage (Dabney et al. 2013; Damgaard et al. 2015). All extracts

provided by Dalén were processed at the Centre for Palaeogenetics, Swedish Museum of Natural History, Sweden, and were from previously published studies (Smith et al. 2017; Ahlgren et al. 2016; Lado et al. 2018). All extracts had double-stranded Illumina libraries built at the University of Oxford following the Blunt-End Single-Tube Illumina library building (BEST) protocol, as described in Carøe et al. (2018). The libraries were double external indexed. There was an additional barcode ("external index") added to the IS1_adapter.P5 adapter. The libraries were then amplified on an Applied Biosystems StepOnePlus Real-Time PCR (polymerase chain reaction) system, to determine both the success of the library build and the number of optimum cycles to use for the indexing PCR reactions. Following amplification, the libraries were pooled at equimolar concentration in four batches for four separate sequencing runs for initial DNA screening to assess the percentage of endogenous DNA prior to deeper sequencing. The first batch of fourteen samples were pooled with other samples from the laboratory and sequenced at the Danish National High-Throughput Sequencing Centre, Copenhagen, on a HiSeq 2500. The second batch was pooled with other samples from the laboratory and sequenced at Queen Mary University, London on a NextSeq 500. The rest of the samples were sequenced on an Illumina HiSeq 4000 at the Danish National High-Throughput Sequencing Centre, Copenhagen or Novogene, Sacramento (Table S2.2).

In-solution targeted capture of the *Lepus* mitochondrial genome was performed on 84 samples following the myBaits v.4 (Arbor Biosciences) Hybridization Capture for Targeted NGS protocol, with the following conditions to optimise for ancient DNA: a hybridisation temperature of 60 °C and length of time for hybridizing of 48 hours. The *Lepus timidus* mitochondrial reference genome (NCBI: KJ397605.1) was used to synthesise the baits for capture.

Given the degraded nature of ancient DNA, the amount of endogenous DNA per sample is far less than would be expected from modern material. Due to this, we were able to add more samples per reaction for the mitochondrial capture. Between 19-23 ancient libraries were pooled equimolarly per reaction and the pools were determined based on the percentage endogenous DNA with mapping quality above 30. Two reactions were pooled per sequencing lane, with a total of 41 libraries across two reactions on the first lane and

43 libraries across two reactions on the second lane. The two lanes were sequenced on an Illumina HiSeq 4000 at Novogene, Sacramento.

2.5.2.2 Modern DNA

DNA was extracted from the muscle tissue of a modern mountain hare using the QIAGEN DNeasy Blood & Tissue Kit following the manufacturer's guidelines (Qiagen, Luxembourg). All modern laboratory procedures were carried out in a flow hood in the post-PCR laboratory of the PalaeoBARN at the University of Oxford, following modern laboratory standards. The tissue was stored in ethanol for transportation from the National Museum of Scotland to Oxford. Prior to extraction a small section of tissue was cut and washed three times with deionised (DI) water to remove any residual ethanol. A 2 mm cube (18 mg) of the washed tissue was used for the extraction. The DNA was fragmented to around 350 bp (base pairs) using a Covaris S220. The extract, along with extracts provided by Melo-Ferreira, had double stranded Illumina libraries built following Meyer and Kircher (2010). The libraries were double external indexed, the same way as the ancient samples, with some modification on the reagent ratios for the qPCR and PCR from the ancient protocol to account for there being a higher abundance of DNA. The amplified libraries were cleaned with AMPure SPRI (Solid Phase Reversible Immobilization) beads (Beckman Coulter) and sent for sequencing over two runs. The one sample processed entirely in Oxford was sequenced with seven other samples on a NovaSeq 6000 lane. The rest of the modern libraries were sequenced on one lane of an Illumina HiSeq 4000. This sequencing was performed at Novogene, Sacramento (Table S2.3).

2.5.3 Mitochondrial DNA initial processing

Libraries received back from sequencing were demultiplexed and processed by trimming the adapters and collapsing the reads using AdapterRemoval (v.2.3.0). All ancient and modern sequencing data was aligned to the full modern nuclear reference genome, GCA_009760805.1, and the mitochondrial reference genome, KJ397605.1 using BWA aln (Marques et al. 2020; Li 2013). Samtools rmdup (v.1.6) was used to remove potential PCR duplicates. The pair with the highest mapping quality was retained. Damage patterns for each library were checked using mapDamage (v.2.0.6) post removal of duplicates, but prior to mapping quality filtering (Jónsson et al. 2013). The mitochondrial DNA was extracted

and cut to the same length as the previously sequenced modern genomes provided by Melo-Ferreira, 16236 bp using Samtool view (v.1.6). They were reduced to this length to remove the repetitive region at the end of the D-loop, which is harder to assemble and map from short read data. The consensus mitochondrial sequences were then generated using HTSbox pileup with the following strict filters to ensure the exclusion of erroneous base calls and damage from terminal ends. Alignments shorter than 25bp were excluded along with those with mapping quality lower than 30 (accuracy of 99.9%) and bases within 5bp of the start and end of a read were also excluded. Additionally, bases with a quality score lower than 30 (accuracy of 99.9%) were coded as ns in the consensus sequence. All modern and ancient samples were then aligned with each other using MAFFT (Multiple Alignment using Fast Fourier Transform) (v. 6.240) for further downstream analysis along with the European rabbit (*Oryctolagus cuniculus*) as an outgroup and modern known Arctic and European hare species. The mitochondrial genome was split into the following regions; coding regions, control region, repetitive region, tRNA and rRNA using a custom script by Lin (2018).

2.5.4 Phylogenetic analysis

Phylogenetic trees were constructed from aligned modern and ancient sequences. Initially, a Bayesian tree was generated with all samples with 4x or more depth of coverage of the mitochondrial genome and less than 10% missing data, using the programme MrBayes v.3.2.7a. The European rabbit was used as an outgroup, along with other closely related hare species to ensure that all samples included in the analysis were mountain hares. Next, a dated phylogenetic tree was constructed using BEAST (Bayesian Evolutionary Analysis Sampling Trees) v. 2.5.2 including only sequences above 10x depth of coverage and less than 10% missing data. Ancient samples were only included if they had dates from either indirect or direct radiocarbon dating, or dated stratigraphy. Any samples with large uncertainties on their time ranges, such as Pleistocene or Marine isotope stage (MIS) III were excluded from the analysis. No age uncertainties were included as Molak et al. (2015) found that including uncertainties had negligible impact on the resulting estimates. The dates for the samples included in the analysis ranged from 40,000 to 850 BP. Partitions, for which fitted separate models of evolution, were defined based on the annotations from the KJ397605 accession obtained from the NCBI (National Center for Biotechnology

Information). They were the following regions: 1st,2nd and 3rd codon sites, D-loop, repetitive region, tRNA and rRNA. The mean of each of the dates for all the ancient samples were used as tip dates with a strict molecular clock of 1.0 x 10^{-8} and upper and lower bounds of 1.0 x10^{-6} and 1.0 x 10^{-10} respectively. This analysis was run multiple times with different starting seeds to ensure that the tree was robust. No outgroups were used to minimise the prior assumptions made on the probability distribution. Sampling was performed every 5,000 steps over a total of 5 million steps, with a burn-in of 20%. The clock and tree models were linked, and the site model was left unlinked. Two independent runs were performed, and their logs combined in LogCombiner to check for convergence using TRACER.

2.6 Results

2.6.1 Sequencing success

Of the 238 ancient samples sequenced, 50 yielded mitochondrial genomes with over 4x depth of coverage and less than 10% missing data (Figure 2.3, Table S2.2). These were from a total of 38 archaeological or palaeontological sites. Of these 50, 31 yielded mitochondrial genomes with over 10x depth of coverage and less than 10% missing data. These were from 26 sites. Of those samples successfully sequenced, samples ranged from eastern Russia to Ireland and the Western Isles, from 40,000 to 600 BP (Figure 2.4).

Out of the 101 modern sequences processed, 95 successfully amplified and were sequenced (the 6 excluded were found to have no DNA from the Qubit and TapeStation results post-amplification). All the modern samples sequenced yielded a depth of coverage between 4.1x and 107,772x with an average of 1,356x (Table S2.3). Three samples were excluded due to missing data, leaving 92 useable sequences along with the 63 previously generated sequences from Melo-Ferreira (one of these was excluded because of missing data), giving a total of 155 modern mountain hare genomes with 132 unique haplotypes from twelve countries (Figure 2.4).

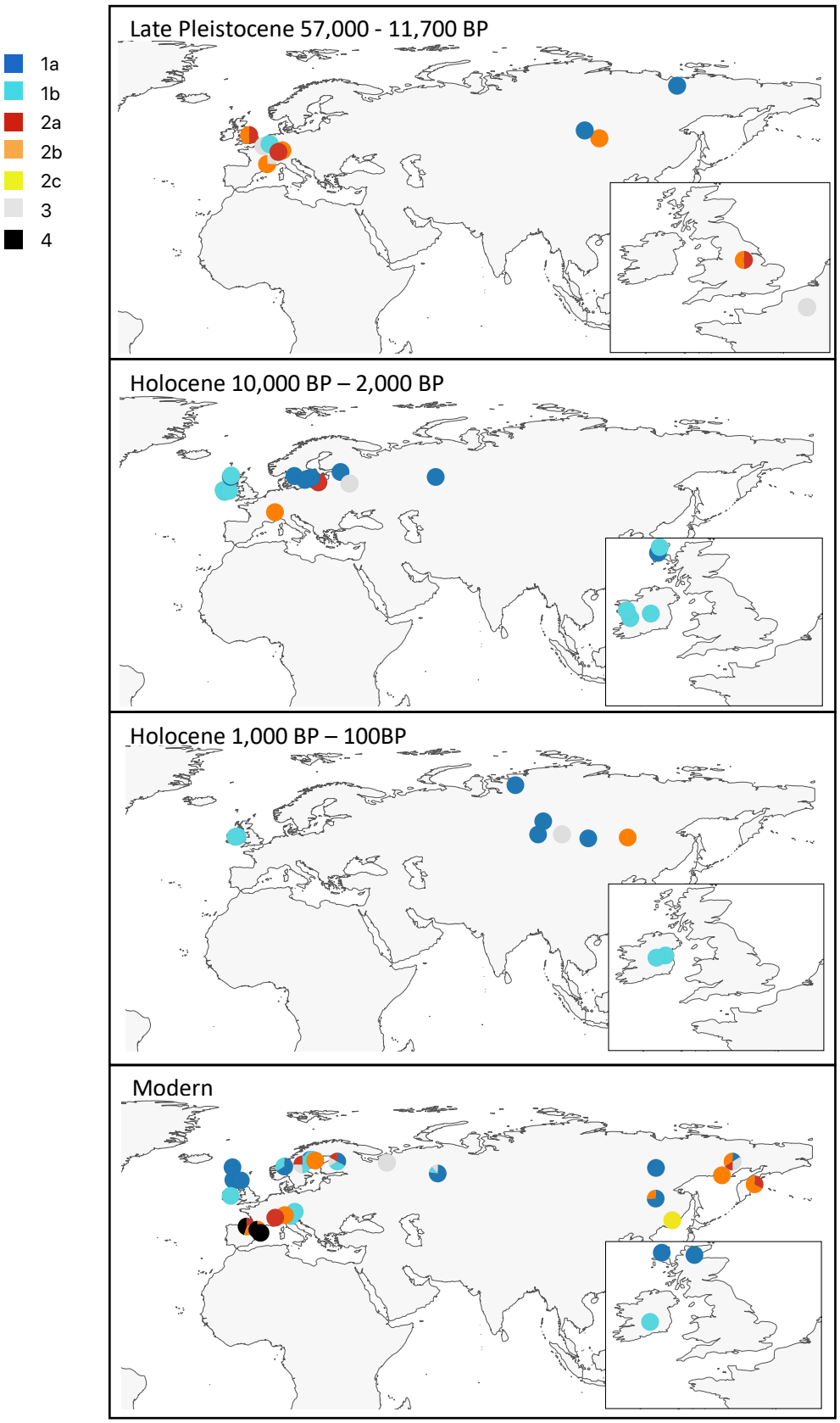

Figure 2.4 Summary of results visualised on a map including only samples with 4x or greater coverage and less than 10% missing data. The different coloured pie charts correspond to mitochondrial haplogroups and sub-haplogroups on the Bayesian trees. Each panel shows a different point in time from the Late Pleistocene to modern day. Where there are multiple haplogroups at a site the pie chart represents this. There is a zoom-in pane on the area of interest, the Western Edge of Europe.

2.6.2 Phylogenetic analysis of full mitochondrial DNA

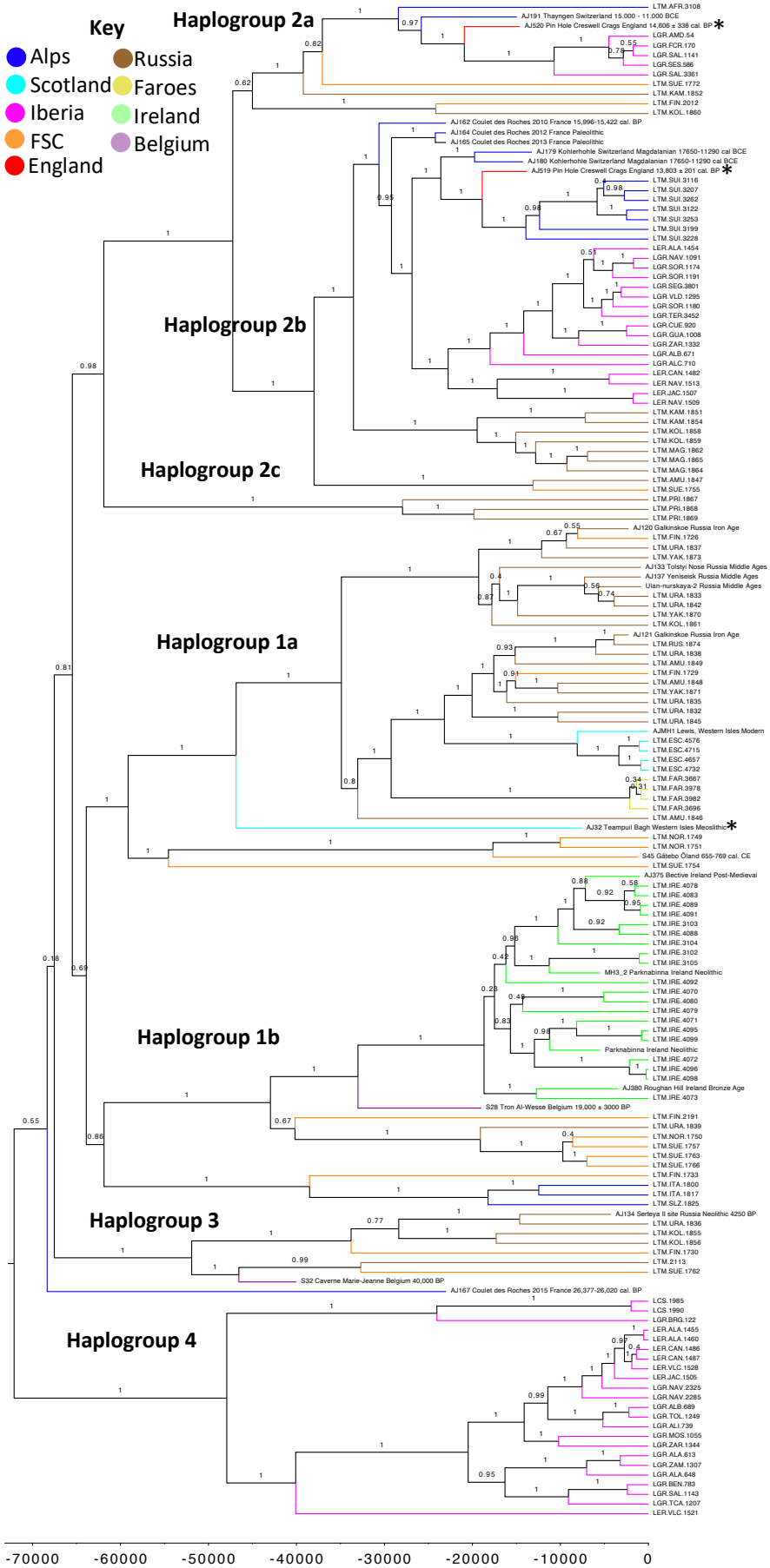

Figure 2.5 Bayesian phylogeny of the full mitochondrial DNA from modern and ancient mountain hares with coverage 10x or above and less than 10% missing data. The tree has been calibrated using tip dates from the ancient samples giving a mutation rate of 6.95% Myr^{-1}. The timescale along the bottom is in years before present. The branch colours correspond to regions (see key) and the numbers on the branches are the posterior probability scores (also see Figure S2.2 for further detail). * denotes samples mentioned directly in the text.

Most haplogroups are found throughout the range (Figure 2.4 and Figure 2.5, Figure S2.1 and S2.2). There are only a few regions which only have one haplogroup present: Ireland, the Faroe Islands, the Scottish mainland, and the Italian/Austrian Alps. Of these regions only Ireland has ancient and modern data.

In the dated Bayesian tree generated using BEAST (Figure 2.5, Figure S2.1), there are four major clades. The first to diverge was haplogroup 4 around 72,000 BP (95% confidence intervals (CIs): 83,000 - 62,000 BP). The second haplogroup 3 around 67,000 BP (95% CIs: 76,000 - 59,000 BP). The final two, haplogroup 1 and 2, diverged from each other around 66,000 BP (95% CIs: 76,000 - 59,000 BP). It is important to note the divergence times are not population split times, showing when that haplogroup diverged from the rest and not when a population itself split from the rest of the range. In some cases, these may coincide, however this cannot be assumed, and these times show only the earliest possible population divergence. Within each of these two final haplogroups there are subclades (1a,1b, 2a,2b,2c). These subclades do not show any regional partitioning apart from when a population has been isolated from the rest of the range. The undated Bayesians tree show similar well-resolved topologies (Figure S2.2).

The results from the dated Bayesian tree, along with the undated tree, are presented together in the following paragraphs. Haplogroup 4 is only seen in the modern Iberian samples with the dated tree (Figure 2.5). Those in haplogroup 3 are basal to haplogroups 1 and 2 in the dated tree, with very low support and are found grouped with haplogroup 4 in the undated tree (Figure S2.2, Figure 2.4). Due to the uncertainty of their placement, they are marked as a neutral colour on the map. This group only appears in the Pleistocene and the modern-day samples, but given the low support for the clade, it is not possible to make inferences about the results.

The main haplogroups seen throughout the range were haplogroups 1 and 2. They were both present in the Pleistocene (pre-11,700 BP) and the Holocene (11,700 BP – today). There is no clear regional separation between haplogroup 1 and 2 with either the ancient or modern samples throughout the range. Fennoscandia samples are found throughout the tree. Russian samples are predominantly haplogroup 1 in the Pleistocene and the Holocene. In the Pleistocene and Holocene of mainland Europe both haplogroups 1 and 2 are found. However, there is clear separation on the westernmost edge of their range. All ancient and modern Irish mountain hares studied (around 7,000 - 100 BP) cluster in the same internal sub-haplogroup, 1b, which was part of the larger range with the Italian/Austrian Alps, Norway, Finland, and Belgium until around 32,500 BP (95% CIs: 39,000 - 28,500 BP), at which point the Irish samples formed their own discrete group within the larger clade. Additionally, one of the two Mesolithic samples (AJ28) from the Western Isles is found within this group in the undated phylogeny and is basal to all but one Irish sample (Figure S2.2b). The other Mesolithic hare from the Western Isles (AJ32) is in haplogroup 1a in the dated phylogeny and is basal to the modern Scottish and ancient Russian samples (Figure 2.5). It is important to note, AJ32 appears grouped with haplogroup 1b in the undated phylogeny with a posterior support of 0.5. As there is 1.0 posterior support for AJ32's placement in the dated tree haplogroup 1a was assigned to this sample.

Haplogroup 2 was present in Britain in the Pleistocene. The two English samples included in this analysis are from Creswell Crags, Derbyshire. They are found on two different branches within haplogroup 2, with sample AJ519 clustering with the modern Swiss samples and AJ520 clustering with another Palaeolithic sample from Switzerland and the modern French Alps samples (Figure 2.5). They are both from the same cave at Creswell Crags (Pin Hole), and are from similar periods, with AJ520 dated to 14,606 ± 338 cal. BP (OxA-19163, 12430 ± 55 BP) and AJ519 dated to 13,803 ± 201 cal. BP (OxA-19526, 11900 ± 50 BP) (Ashton, Lewis, and Stringer 2011).

The modern Iberian hares with introgressed mountain hare mitochondrial DNA fall mostly into haplogroups 2 and 4. Those in 2 show most genetic affinity with the Swiss modern and ancient samples. Those in 4 form their own discrete basal clade to all the other lineages.

The modern Italian hares show more genetic similarity with the ancient and modern Irish then the modern or ancient samples from the Alps which are geographically closer. The hares from the Faroes are known to have arrived from Norway yet they show the greatest genetic affinity with the Scottish followed by the Russian samples.

2.6.3 Summary of results

Mountain hares are a monophyletic (one common ancestor) group with three distinct lineages (haplogroups 1, 2 and 4). They show no clear regional separation pattern as all haplogroups are found throughout the range, from Iberia to Siberia, either in the past or today. Within haplogroup 1, the Irish samples formed an internal, well-supported monophyletic lineage. Scottish modern samples similarly form a well-supported monophyletic lineage within the same larger group, as well as the modern samples from the Faroes. The Italian/Austrian group was more closely related to haplogroup 1 than the rest of the modern and ancient samples from the Alps. Both the main two lineages (haplogroups 1 and 2) are found together in all but the western edge of the range.

2.7 Discussion

2.7.1 Mountain hare phylogeography

The focus of this analysis is on the mountain hares found on the western edge of Europe. However, to put the western edge in context, mountain hares from across their past distribution were analysed. The samples in this study are from just prior to the Last Glacial Maximum to modern day. The last time in which mountain hares expanded their range was in the most recent glacial period (115,000 – 11,700 years ago). This ended with the warming at the start of the Holocene when their decline in population numbers started (Smith et al. 2017; Melo-Ferreira et al. 2007). Smith et al. (2017) demonstrated that the phylogenetic structure was already set before the decline began. This is supported by the results of our BEAST analysis as, similarly, all the structure of the tree is from before 11,700 BP. Any structure after this period is only within sites or local geographic regions. Our results further support the findings of Melo-Ferreira et al. (2007) and Smith et al. (2017) that there was a continuous population range of mountain hares in the past. Our results show this was the case both in the late-Pleistocene and Holocene.

2.7.1.1 Northern range of mountain hares and their origin

Today, Russia and Fennoscandia have the highest haplogroup diversities. This was not the case in the past. In the Pleistocene, central Europe, followed by Russia had the highest diversity from our dataset. This suggests central Europe as the origin of mountain hares as already proposed by Melo-Ferreira et al. (2007). Our results provide further support for this. Along with understanding the origins of mountain hares we are able to demonstrate Russia was the earliest expansion of mountain hares as they had the next highest haplogroup diversity in the Pleistocene.

Our results have also been able to provide us with further understanding of the spread of mountain hares as the ice retreated at the end of the Last Glacial Maximum. Every haplogroup and major sub-haplogroup apart from haplogroup 4 are found in Russia and Fennoscandia today. The diversity of haplogroups in Fennoscandia is most probably the result of a more recent expansion into the region. Fennoscandia would have been largely covered in ice up until around 10,000 BP, which is why there are no samples from this region until the Holocene. Once the ice began to retreat, it would have been possible for the hares living on the edges of the ice sheets to move north (Hughes et al. 2016). Their diversity reflects the early Holocene diversity in central Europe. This also explains the lack of haplogroup 4, as the haplogroup was not found in central Europe to the point at which hares began expanding into Fennoscandia. This further supports the theory of Melo-Ferreira et al. (2007) that there was a continuous mountain hare range on the edge of the ice sheet which then expanded northwards into the regions previously covered in ice (Fennoscandia and north-western Russia), resulting in a diverse population today in these regions. This modern diversity in these areas directly reflects the earlier diversity of the continuous range on the edge of the ice sheet. This also suggests people in the past were not moving mountain hares large distances or at all. This contrasts with domestic species, which we know were moved by people, as the modern population does not tend to be representative of the ancient population due to these human assisted movements.

2.7.1.2 Southern range of hares

The southern extent of the mountain hare range can be seen in the modern data from the Iberian Peninsula. The mountain hare lineages 2a, 2b and 4 made it as far south as Iberia as they are found introgressed into modern Iberian non-Arctic lineages. This further demonstrates how the range of hares was much larger in the Pleistocene, with the southern range extending as far as the north of Iberia. Haplogroup 4 is basal to all the other lineages, showing it to be the ancestral population, which is no longer found in any other modern or ancient populations. The lack of haplogroup 1 in Iberia suggests it was a lineage that stayed in the northern regions, with its most southerly extent being the modern Italian/Austrian Alps and Pleistocene Belgium. Haplogroup 2 is found throughout the range apart from the western fringe.

2.7.1.3 The Alps

As the climate warmed after the Last Glacial Maximum, the populations in the Alps were cut off, probably through disappearance of suitable habitats and possible competition with more temperate hare species, such as the European hare, which at lower elevations occupy a similar niche to mountain hares (Caravaggi et al. 2017) .With warming climates, European hares were able to push further north and to higher elevations throughout the Holocene (Stamatis et al. 2009). This isolation of the mountain hares in the Alps has been observed in the modern data by Melo-Ferreira et al. (2007). The modern-day population of mountain hares in the Italian/Austrian Alps are a different haplogroup from the modern western Alps populations. This is the same haplogroup which is found in Ireland today and in the past. This show haplogroup 1b was widespread in Europe, trapped on the peripheral edges in the Italian Alps as well as Ireland.

2.7.1.4 Eurasia summary

Mountain hares in continental Europe and Russia all formed a continuum on the ice sheet margin in the Late Pleistocene. They then expanded north in the Holocene as the ice-retreated, maintaining their population structure. Small subsets of the larger range were subsequently trapped as the climate warmed, leaving isolated populations which are partially differentiated due to drift and positive selection (Giska et al. 2019). These were

isolated in the Alps and another set of populations in the north-west corner of Europe in Ireland and Scotland.

2.7.1.5 Western edge of the mountain hare range

We have already established that during the Pleistocene, hares in Britain formed a continuum with the rest of the range. This was not, however, the case for Ireland. The Irish sub-group partially split from the rest of the haplogroup 1, forming their own monophyletic clade within this haplogroup. As there are no samples from outside Ireland within the monophyletic group this suggests that the split of the Irish hares was probably not far off the divergence time of 32,500 BP. This coincides with the beginning of the Last Glacial Maximum when at around 30,000 BP ice started to cover Ireland (Patton et al. 2017; Clark et al. 2012; Hughes et al. 2016). By 27,000 BP the ice sheet was at its full extent over Britain and Ireland. Mountain hares would have been pushed to the ice sheet margins, surviving on this edge until conditions allowed them to expand back onto the present-day mainland as the ice retreated north-east. The genetic isolation of the mountain hares in Ireland supports this theory, as only the one haplogroup (1b) is found in Ireland today and in the past. The climatic and genetic results together suggest that the mountain hares which recolonised Ireland were cut off from the continuous population on the ice sheet margins spanning from southern England to Russia at some point during the late Pleistocene. They may have then survived in a northern refugium such as in the Bay of Biscay and recolonised Ireland when conditions became favourable from around 20,000 BP to 16,000 BP (Figure 2.2).

2.7.1.5.1 Western Isles of Scotland

The Mesolithic samples from the Western Isles of Scotland further add to our understanding. Haplogroup 1a (AJ32) was present on Harris and 1b (AJ28) on Lewis in the Mesolithic period. Despite there only being two samples and the coverage of AJ28 being relatively low (5x), a lot can be learned from these two mountain hares. There are three possible explanations of how they arrived in the islands; human-mediated dispersal, the mountain hares being from relic populations left over from the Last Glacial Maximum, most probably from the same refugial origin as the Irish hares, or unaided arrival in or before

the Mesolithic period by rafting. The latter, with the current evidence, is hard to confirm due to the small number of samples. If they did arrive by rafting, an extreme founder effect would be observed ,however more data would be needed to test this possible scenario. There could also have been a combination of all three scenarios. To explain our genetic results with the former scenario, people would have had to have brought the mountain hares from two locations: mainland Scotland and Ireland.

There is no current evidence for contact between Scotland and Ireland until the Neolithic (Cummings 2017; Saville 2004). There is also no evidence of contact with the Western Isles specifically (Cummings 2011; Piper 2017) .This makes the movement of mountain hares from Ireland to the Western Isles by people improbable given the lack of clear contact between the two groups. Additionally, sample AJ28 (Isle of Lewis) is basal to most ancient and modern Irish hares, suggesting an earlier connection to Ireland, possibly before a human-mediated introduction in the Mesolithic would have been possible.

The connection of the Western Isles with the Inner Hebrides is more tangible, especially in the earlier Mesolithic, as there is extensive evidence of movement of raw materials to the Western Isles from the islands of Skye and Rum, in addition to the mainland. Trade links were therefore established by this time (Piper 2017). However, there is no known trade in livestock to the Western Isles in this period (Piper 2017). Trade in livestock is first seen in the Neolithic period where there is evidence for the movement of red deer around the Scottish islands, including the Western Isles (Stanton, Mulville, and Bruford 2016). Furthermore, if mountain hares were traded among the Hebridean islands, we would expect there to be evidence of their existence on other islands which were occupied during the Mesolithic period, such as on Rum and Oronsay (Wickham-Jones 1990; Mellars 1987). Mountain hares have been found in the Mesolithic on Skye, but due to the small distance between the island and mainland, which is 500 m today and possibly shorter in the past, unaided crossing of mountain hares to Skye could be an explanation for this (Selby et al. 2003). Given this understanding, there is a low probability that the mountain hares which appear in the earlier Mesolithic at Temple Bay (Teampuil Bagh), Harris, were imported. Furthermore, the mountain hare from Temple Bay, Harris (AJ32) is not only basal to the Scottish modern samples, but also to those from the rest of the range, which suggesting

that it was cut off from the continuum of mountain hares across Europe and Russia and not only from the Scottish mountain hares more recently.

Given the genetic results and the current understanding of links between people on the Western Isles and Ireland and mainland Scotland, the human-mediated introduction of mountain hares to Harris and Lewis is unlikely, pointing towards the presence of these mountain hare populations before the arrival of people in the Mesolithic. Montgomery et al. (2014) prediction of cryptic refugia in the Last Glacial Maximum off the western edge of Ireland and the Western Isles looks to be probable from the genetic results of this study. The mountain hares could have survived in these refugia and as the ice retreated followed the margins east to the Western Isles and Ireland. This would explain why the one Mesolithic mountain hare on Lewis is basal to all but one Irish hare, as it is from the relic population, along with the basal Irish hares. The other mountain hares found in the Mesolithic deposits of the Western Isles on Harris are basal to the modern Scottish and ancient Russian and Fennoscandian samples, which can be explained by them also being a relic population on the westernmost edge.

We observe that AJ32 (from Harris) is not as closely related to the modern Scottish samples as AJ28 (from Lewis) is with the Irish samples. This can be explained by considering the mountain hares on Harris as a relic population that became isolated from the rest of the continuum range, surviving on the westerly extreme of the range. Whereas AJ28 (from Lewis) was part of the Irish isolated population which survived in a western refugium and then subsequently expanded both to Lewis and Ireland. That both relic populations from the refugia only colonised as far east as the Western Isles and Ireland can be explained by the geographic barrier posed by the deep waterways separating both islands from mainland Britain, making further spread east impossible (Stewart 1997; Edwards and Brooks 2008).

The remainder of the mainland mountain hare population of Scotland would have survived on the southern extent of the ice sheet in a continuum with the rest of the range. They would have then moved north as the ice retreated, accounting for their presence in the late Pleistocene of England. The earliest remains of mountain hares in Scotland are from

the Mesolithic sites of Land Mill Bay near Oban, An Corran on the Isle of Skye in addition to the aforementioned Mesolithic sites on both Harris and Lewis (Bartosiewicz, Zapata, and Bonsall 2010; Saville et al. 2012; Gregory et al. 2005; Church et al. 2012; Blake et al. 2011). Although hare remains have only been found on the western side of Scotland starting in the Mesolithic period, it would be presumed that mountain hares were living throughout Scotland after the retreat of the ice sheets after the Younger Dryas around 11,700 BP, and possibly even before this in certain deglaciated pockets (Hughes et al. 2015). Unfortunately, the Inner Hebrides ancient Scottish mountain hares analysed from An Corran, Isle of Skye (AJ207-AJ211) did not yield enough DNA for further study, therefore we have no knowledge of the haplotypes found in the past on mainland Scotland. Modern Scottish samples that were analysed were of haplogroup 1a, but as only two populations have been sampled (one from the mainland and one from the recently reintroduced population on the Western Isles), the presence of the other unsampled haplogroups in Scotland cannot be discounted. Despite this, previous studies of modern Scottish mountain hares have also shown that Scottish mountain hares form their own discrete group within haplogroup 1 (Melo-Ferreira et al. 2007). Further study of the modern and historic mountain hare populations is required to prove or disprove the presence of other mitochondrial lineages in Scotland.

Based on current results, haplogroup 1 is the only haplogroup to have been found in Scotland and Ireland throughout time. Those in modern Scotland are genetically distinct from the late Pleistocene hares found in central England suggesting that the Scottish population arrived in an earlier wave. Our dated tree shows that the split between the Scottish hares and the continuum occurred around 24,000 BP (95% CIs: 28,000 - 18,500 BP) which was after the split of the Irish hares and the continuum. Our results also show that mountain hares most probably colonised Ireland and the Western Isles naturally and were present in the Western Isles before humans colonised in the Mesolithic period.

2.7.1.5.2 The Celtic Fringe

Given that the Irish and Western Isles mountain hares do not form their own basal clade to all other haplogroup 1 samples, this isolation on the Western fringe was relatively recent

— as shown by the dated tree (Figure 2.5), they split from the rest of the sub-haplogroup 1b around 32,500 BP. This is also true of the Scottish modern hares which split from the rest of the sampled range around 24,000 BP.

At the time of arrival for these mountain hares in the early-mid Pleistocene, the sea levels were probably much lower. Ireland and the Western Isles have not been connected to mainland Britain since the ice cover in the Last Glacial Maximum whereas mainland Britain remained connected to Europe until 8,000 BP (Weninger et al. 2008). This would have left any surviving mountain hares on the westernmost edge of Europe isolated from the rest of the range. As the ice sheet expanded during the Last Glacial Maximum they would have been pushed south and west possibly into the proposed refugia zone in the Bay of Biscay or off the coast of Ireland or the Western Isles (Figure 2.2). Then like the other Celtic fringe species they would have recolonised as the ice retreated and since then, or possibly even slightly earlier if they were separated in refugia, they would have been isolated in Ireland and the Western Isles, unable to move any further east. The mountain hares in present day Scotland were likely the first to recolonise from the continuum on the ice margins, with other populations moving in after. Those in England could move freely in and out of Britain up until it was separated from the continent (Weninger et al. 2008). This is supported by multiple haplogroups being found in Britain, haplogroup 2 was present after the Last Glacial Maximum in the Pleistocene and haplogroup 1 in modern day Scotland, demonstrating they were part of this continuum. Further support for this scenario is the Scottish, Irish and Western Isles hares are all haplogroup 1 and all split from the rest of the range before the arrival of the Pleistocene mountain hares in England. There looks to have been two waves of introduction with the first now only seen on the western margins and the latter only reaching as far as mid-England in the Pleistocene and then disappearing at some point in the Holocene as they were replaced by the humanly introduced European hares. More samples are needed from prehistoric British sites to confirm this possible conclusion but with the current evidence it looks like mountain hares can be added to the growing list of ‘Celtic fringe’ species.

2.7.2 Western Isles land mammals

Up until the results of this study, there was no conclusive evidence to suggest any land mammal colonised the Western Isles of Scotland naturally. The earliest possible arrivals are listed as occurring in prehistory with the aid of people, with all other species present arriving in the historic or very recent past. The results of this analysis provide evidence to demonstrate that there was at least one land mammal present in the Western Isles before the arrival of people — the mountain hare. It cannot be discounted that there were other mammals which also arrived from a western refugium before subsequently going extinct as the climate warmed in the Holocene. Further investigation of the paleontological record of the Western Isles is needed to understand which land mammals were present before the arrival of people in the Mesolithic and to help verify the results of our genetic analysis.

2.7.3 Clock rate

Through the BEAST analysis using dated tips we have been able to accurately predict the mutation rate for the mitochondrial DNA of mountain hares as 6.95% Myr^{-1} (Figure S2.3). This is slower than a rodent and faster than a hominin, which is expected given their size and generation time (Nabholz, Glémin, and Galtier 2008; Lin 2018). This is also close to the clock rate used for mountain hares up to this point for the control and Cytochrome B regions combined of 7.7% Myr^{-1},which was calibrated with fossil data (Cheng et al. 2014; Brown, George, and Wilson 1979; Smith et al. 2017). This demonstrates that, at least for hares, fossil dates are a relatively accurate calibration method when tip dating is not possible.

2.7.4 Implications for the conservation of mountain hares

Currently, mountain hares are not regarded as indigenous to the Western Isles by the Scottish government (Siar n.d.). From the archaeological evidence it is certain that mountain hares were at least present in the Mesolithic, making them an early coloniser. Given the results of this genetic study, the Mesolithic populations of hares can instead be considered indigenous to both islands. Further sampling of mountain hares remains from prehistoric deposits is needed to fully support their native status. Additionally, little is known about when they went extinct on the island, warranting further study.

2.8 Conclusions

Mountain hares once occupied a much larger region than they do today, from Iberia to the far east of Russia. They have survived through extreme changes in climate and maintained their population diversity throughout most of their range. They are a resilient species which even today occupy a wide range of habitats such as the lowlands of temperate Ireland to the highest latitudes of Siberia. Their disappearance from much of their southern range, except for the Alps, may be due to competition with other species that are better adapted for temperate climates, such as the European hares, rather than to the change in climate itself. Their survival through many interstadial and stadial events, in addition to their survival today in the lower and higher elevations of Ireland demonstrate their ability to adapt when not faced with competition.

Like other possible native species to Ireland, the mountain hare is genetically distinct in Ireland from most of its geographical range. Through this study we have shown that this was true throughout the Holocene. We have also expanded this range to include the Western Isles of Scotland, indicating the possible presence of relic populations that were isolated from the rest of the population near the edge of the ice sheet during the Last Glacial Maximum. These hares add to the growing evidence for a Western fringe of lineages in Ireland, the Western Isles and Scotland.

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2.10 Supplementary material

2.10.1 Supporting Information Figures

Figure S2.1 – More detailed version of Figure 2.5. Dated Bayesian tree with split time error bars. * indicate samples mentioned in the main text.

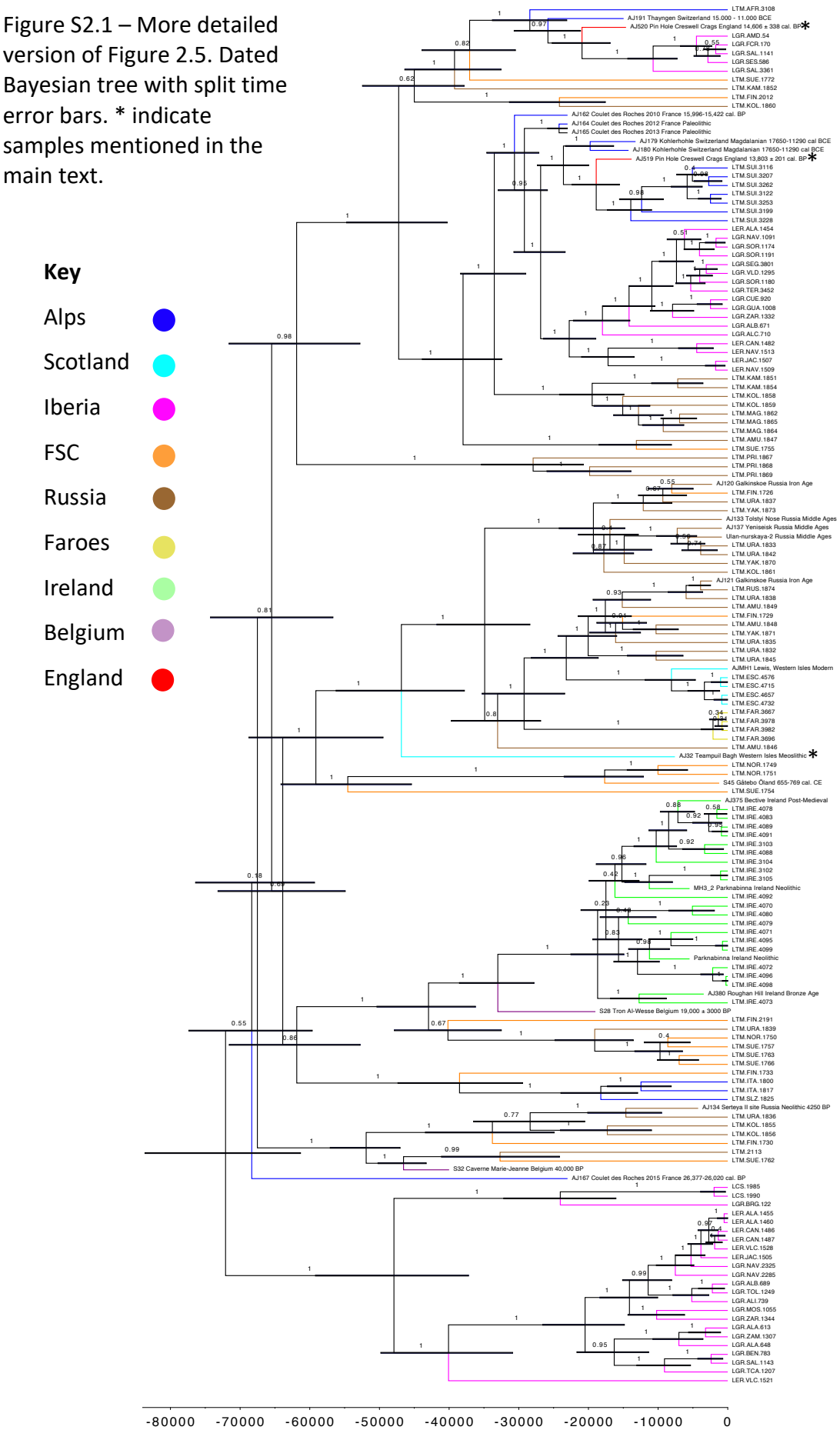


Figure S2.2a - Bayesian tree with all sequences above 4x coverage, colours of branches indicate posterior support for the branch, green is 75-100%, orange 25-75% and red is under 25%.

Figure S2.2b - Bayesian tree with all sequences above 4x coverage, Branch lengths are ignored to make the tree easier to read. Haplogroups are labelled according to the dated Bayesian tree (Figure 2.5). * indicate samples mentioned in the main text.

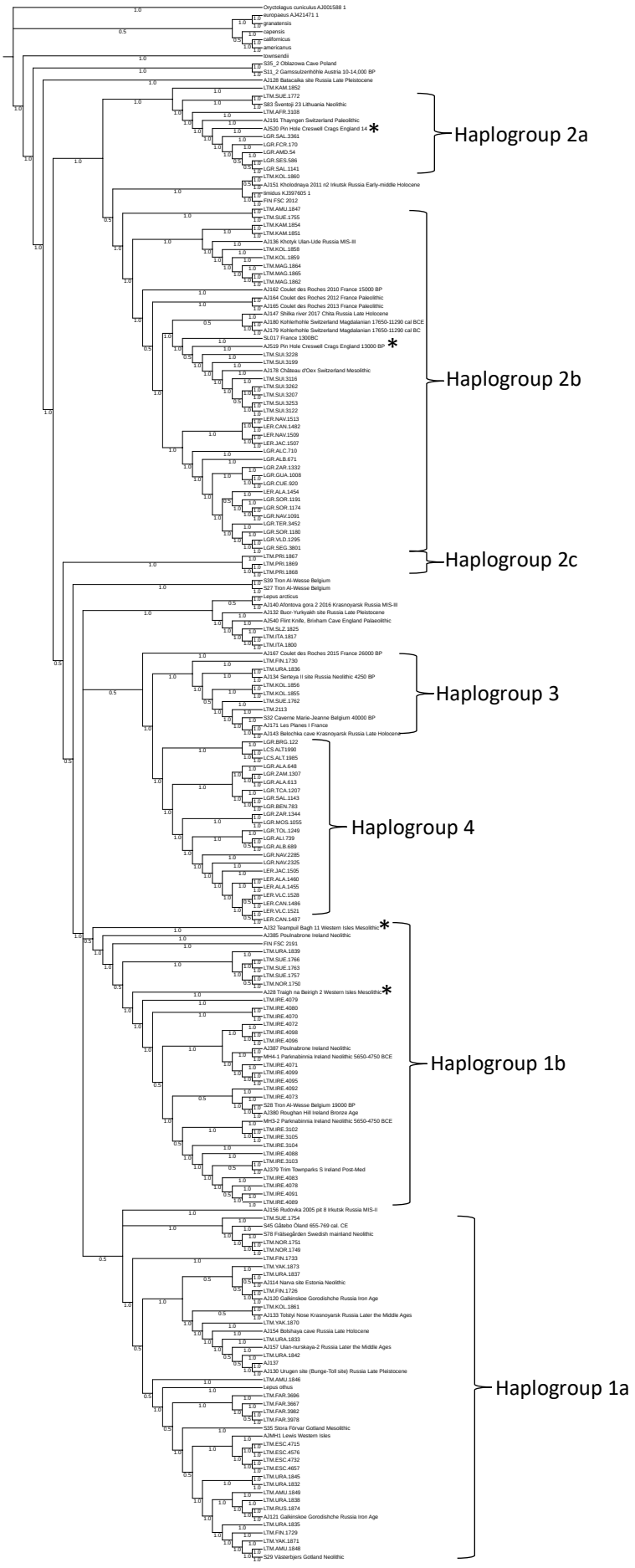
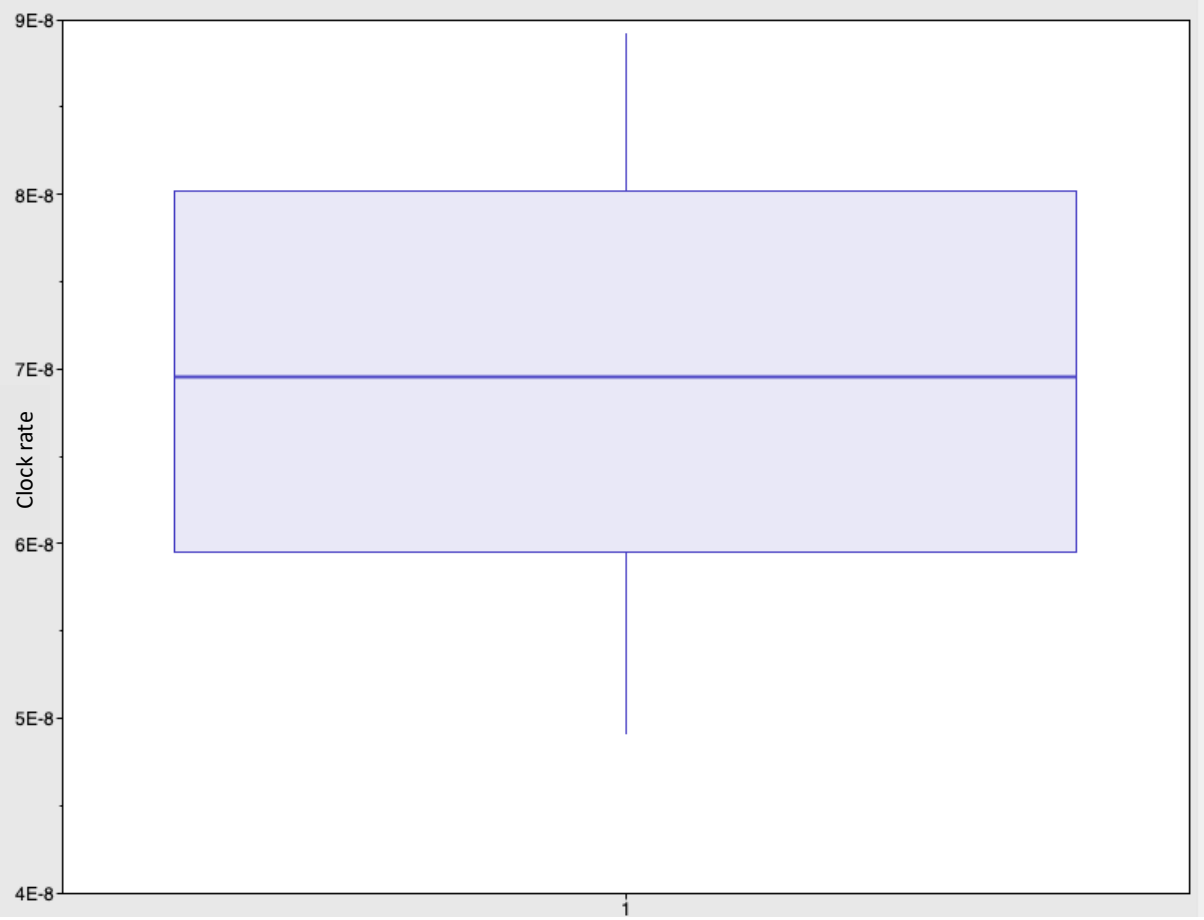


Figure S2.3 – Clock rate Box and Whisker plot



2.10.2 Supporting Information Tables

Table S2.1 – Archaeological and Paleontological sites analysed in the study

Site	Country	Site Age/Period	Sample provider	Number of samples
Cunturines Cave It.	Austria	Early Holocene	Florian Fladerer	1
Gamssulzenhöhle	Austria	12,000 ± 3000 BP	Florian Fladerer	1
Knochenhöle	Austria	~14,100 BP	Florian Fladerer	1
Lindabrunn	Austria	Late Glacial	Florian Fladerer	1
Luegloch Styria	Austria	Full to Late Glacial	Florian Fladerer	2
Mehlwurmhöhle NÖ	Austria	Full to Late Glacial	Florian Fladerer	1
Nixloch NÖ	Austria	10,000 ± 3000 BP	Florian Fladerer	1
Predmosti Moravia	Austria	28-25,000 BP	Florian Fladerer	1
Tron Al-Wesse	Belgium	19,000 ± 3000 BP	John Stewart	3
Caverne Marie-Jeanne	Belgium	40,000 BP	Mietje Germonpre	7
Creswell Crags	England	Palaeolithic (43,000-10,000 BP)	Angharad Jones/Lindsey Loughtman	4
Flint-Kinfe Gallery, Brixham Cave, Torquay, Devon	England	Palaeolithic	Pip Brewer	3

Ightham, Kent	England	Palaeolithic	Pip Brewer	1
Kent's Cavern, Torquay, Devon	England	Palaeolithic	Pip Brewer	3
Pin Hole Cave, Creswell, Derbyshire	England	Palaeolithic	Pip Brewer	5
Terminal Chamber, Neale's Cave, Paignton, Devon	England	Palaeolithic	Pip Brewer	1
Narva site	Estonia	5000-4000 cal. BCE	Mikhail Sablin	1
Aven des Planes	France	Palaeolithic	Evelyne Crégut	7
Coulet des Roches 2010	France	Palaeolithic	Evelyne Crégut	8
Grotte Capi	France	Palaeolithic	Jean-Christophe Castel	2
Chenet des Pierres, Bozel	France	4000-3000 cal. BCE	Patricia Anne Chique	2
Les Vautes	France	3500 BCE	Vianney Forest	7
Péras 1	France	5000 BCE	Vianney Forest	4
Puech-Haut	France	3500 BCE	Vianney Forest	5
Loutra Aridea Cave	Greece	~11,230 BP	Florian Fladerer	5
Poulnabrone	Ireland	3696 – 3535 cal. BCE	Edward Bourke	3
Bective	Ireland	High medieval/Post-medieval	Fiona Beglane	5
Drumadoon	Ireland	early medieval	Fiona Beglane	1
Greencastle	Ireland	14th century	Fiona Beglane	1
Mountgorry	Ireland	11-12 century	Fiona Beglane	1
Roughan Hill	Ireland	Bronze Age	Fiona Beglane	1
Trim Townparks South	Ireland	Post-Medieval	Fiona Beglane	2
Mount Sandel	Ireland	Mesolithic	Greer Ramsey	1
Mentone	Italy	unknown	Andre Rehazek	2
Šventoji 23	Lithuania	Neolithic	Love Dalén	1
Borsuka Cave	Poland	unknown	Piotr Wojtal	1
Deszczowa Cave	Poland	22000 ± 3000 BP	Piotr Wojtal	1
Kruczaskata	Poland	unknown	Piotr Wojtal	1
Mamutowa Cave	Poland	unknown	Piotr Wojtal	1
Oblazowa Cave	Poland	20000 ± 3000 BP	Piotr Wojtal	1
Kocтемku 1-I	Russia	unknown	Mikhail Sablin	4
Podgay Gorodishche	Russia	200 BC-200 CE	Mikhail Sablin	2
Бетово	Russia	unknown	Mikhail Sablin	2
Afontova Gora, Krasnoyarsk	Russia	Palaeolithic	Sergey Federov	1
Badiarikha River Indigirka river basin	Russia	unknown	Sergey Federov	1
Batacaika site	Russia	unknown	Sergey Federov	1
Belochka cave, Krasnoyarsk	Russia	Late Holocene	Sergey Federov	1
Belyi Gozod 2016, Irkutsk	Russia	Late Pleistocene	Sergey Federov	1
Bolshaya cave, Bronnaya 2016, Krasnoyarsk	Russia	Late Holocene	Sergey Federov	1

Buor-Yurkyakh site	Russia	Late Pleistocene	Sergey Federov	1
Calcitovovaya cave 1990, Irkutsk	Russia	Modern	Sergey Federov	1
Dolganskaya Yama 1990 Picket D-4, Bagdarin	Russia	Late Holocene	Sergey Federov	1
Igeteisky, Irkutsk	Russia	MIS-II	Sergey Federov	1
Kamenka, 1993, Ulan-Ude	Russia	MIS-III	Sergey Federov	1
Kholodnaya, Irkutsk	Russia	Early-middle Holocene	Sergey Federov	1
Khotyk, Ulan-Ude	Russia	MIS-III	Sergey Federov	1
Kurtun-1, Irkutsk	Russia	Late Pleistocene and Holocene	Sergey Federov	1
Mankay, Irkutsk	Russia	Middle Ages	Sergey Federov	1
Mendol'syaka cave, Irkutsk	Russia	Late Holocene	Sergey Federov	1
Moustakch Ynyakh River Basin of Kolyma River	Russia	Late Holocene	Sergey Federov	1
Nikolaevka 1, Krasnoyarsk	Russia	Later the middle ages	Sergey Federov	1
Pervomaisky 2017, Irkutsk	Russia	Late Pleistocene	Sergey Federov	1
Pymia Shor	Russia	24,276-23,930 cal. BP	Sergey Federov	3
Radost 2016 cave	Russia	Late Holocene	Sergey Federov	1
Rudovka, Irkutsk	Russia	MIS-II	Sergey Federov	1
Shilka river, Chita	Russia	Late Holocene	Sergey Federov	1
Sumarlakh River Indigirka river basin	Russia	unknown	Sergey Federov	1
Tolstyi Nose, Krasnoyarsk	Russia	later the Middle Ages	Sergey Federov	1
Tuyana, Irkutsk	Russia	MIS 3	Sergey Federov	1
Udinsky ostrog, Ulan-Ude	Russia	Late middle ages	Sergey Federov	1
Ul'kan, Irkutsk	Russia	Late Pleistocene	Sergey Federov	1
Ulan-nurskaya, Airdie, Alberta	Russia	Later the Middle Ages	Sergey Federov	1
Unugen site Bunge roll site yana river basin	Russia	Late Pleistocene	Sergey Federov	2
Yeniseisk, Lenin's manor, Krasnoyarsk	Russia	Later the Middle Ages	Sergey Federov	2
Yukhta, Krasnoyarsk	Russia	unknown	Sergey Federov	1
Zaostravnaya, Irkutsk	Russia	Modern	Sergey Federov	1
Zimoveinaya cave, Irkutsk	Russia	Late Holocene	Sergey Federov	1
Galkinskoe Gorodishche	Russia	2250 BP	Mikhail Sablin	2
Chernousovo 4 site	Russia	3950 - 1750 BP	Sergey Federov	1
Rodanovo Gorodishche	Russia	1100 CE	Mikhail Sablin	1
Yuzhniy Oleniy Ostrov cemetry	Russia	Mesolithic	Mikhail Sablin	1
Anashkino site	Russia	600 BCE	Mikhail Sablin	1

Serteya II site	Russia	2300 cal. BCE	Mikhail Sablin	2
Usviaty IV site	Russia	4000-3000 cal. BCE	Mikhail Sablin	1
MacKay cave	Scotland	Mesolithic	Andrew Kitchener	1
An Corran	Scotland, Isle of Skye	Mesolithic	Alison Sheridan	5
Teampuil Bagh (Temple Bay)	Scotland, Western Isles, Harris	5715 to 5555 cal. BCE	Mike Church	5
Pabbaigh Mor South	Scotland, Western Isles, Lewis	~4,300 cal. BCE	Mike Church	4
Traigh na Beirigh	Scotland, Western Isles, Lewis	4350-4050 cal. BCE	Mike Church	10
Gisslause	Sweden, Gotland	Mesolithic	Love Dalén	1
Lilla Hultungs	Sweden, Gotland	Medieval	Love Dalén	1
Lilla Sojvide	Sweden, Gotland	1472-1641 cal. CE	Love Dalén	1
Stora Förvar	Sweden, Gotland	972-1150 cal. CE, 7066-6713 cal. BCE	Love Dalén	2
Strå	Sweden, Gotland	Mesolithic	Love Dalén	1
Västerbjers	Sweden, Gotland	Neolithic	Love Dalén	1
Alvastra	Sweden, mainland	Neolithic	Love Dalén	1
Frälsegården	Sweden, mainland	3354-2581 cal. BCE	Love Dalén	1
Korsnäs	Sweden, mainland	Neolithic	Love Dalén	1
Scheelegatan	Sweden, mainland	2624-2296 cal. BCE	Love Dalén	1
Gåtebo	Sweden, Öland	655-769 cal. CE	Love Dalén	1
Klinta	Sweden, Öland	3081-2890 cal. BCE	Love Dalén	1
Mysinge	Sweden, Öland	Neolithic	Love Dalén	2
Kaltbrunnental	Switzerland	unknown	Andre Rehazek	2
Schweizersbild	Switzerland	~12000 BCE	Andre Rehazek	3
Thayngen	Switzerland	15000 - 11000 BCE	Andre Rehazek	6
Kesslerloch	Switzerland	Palaeolithic	Hannes Napierla	7
Les Douattes	Switzerland	Palaeolithic	Jean-Christophe Castel	1
Les Plaints	Switzerland	Palaeolithic	Jean-Christophe Castel	3

Veyrier	Switzerland	Magdalenian, Palaeolithic	Jean-Christophe Castel	1
Abri Buttenloch	Switzerland	Upper Palaeolithic	Loïc Costeur	7
Château d'Oex	Switzerland	Mesolithic	Pierre Crotti	2
Kohlerhohle	Switzerland	17650-11290 cal. BCE	Silvia Kalabis	3
Monruz	Switzerland	15000 BP	Vern Mueller	5
Parknabinnia	Ireland	Neolithic	Dan Bradley	3

Table S2.2 – Ancient samples analysed in this study

Extraction ID	Sample ID/ information (if known)	Site	Country/ Region	Date type	Date	C14 ID	Lab performed extraction	Lab performed rest of analysis	Sample provider	Depth of Mitochondrial coverage	Included in analysis	Notes
S45_2		Cunturines Cave It.	Austria	contextual	Early Holocene		Sweden	Oxford	Florian Fladerer	0		
S11_2		Gamssulzenhöhle	Austria	contextual	12,000 ± 3000 BP		Sweden	Oxford	Florian Fladerer	29.2	YES	
S9		Knochenhöle	Austria	contextual	~14,100 BP		Sweden	Oxford	Florian Fladerer	0		
S14		Lindabrunn	Austria	contextual	Late Glacial		Sweden	Oxford	Florian Fladerer	0		
S38		Luegloch Styria	Austria	contextual	Full to Late Glacial		Sweden	Oxford	Florian Fladerer	0		
S43		Luegloch Styria	Austria	contextual	Full to Late Glacial		Sweden	Oxford	Florian Fladerer	0		
S44		Mehlwurmhöhle NÖ	Austria	contextual	Full to late glacial		Sweden	Oxford	Florian Fladerer	0.3		
S10		Nixloch NÖ	Austria	contextual	10,000 ± 3000 BP		Sweden	Oxford	Florian Fladerer	0		
S13		Predmosti Moravia	Austria	contextual	25-28 000 BP		Sweden	Oxford	Florian Fladerer	0		
S29		Caverne Marie-Jeanne	Belgium	contextual	40,000 BP		Sweden	Oxford	Mietje Germonpre	4	YES	
S30		Caverne Marie-Jeanne	Belgium	contextual	40,000 BP		Sweden	Oxford	Mietje Germonpre	0		
S31		Caverne Marie-Jeanne	Belgium	contextual	40,000 BP		Sweden	Oxford	Mietje Germonpre	0		
S32		Caverne Marie-Jeanne	Belgium	contextual	40,000 BP		Sweden	Oxford	Mietje Germonpre	12.5	YES	
S40		Caverne Marie-Jeanne	Belgium	contextual	40,000 BP		Sweden	Oxford	Mietje Germonpre	2.1		
S41		Caverne Marie-Jeanne	Belgium	contextual	40,000 BP		Sweden	Oxford	Mietje Germonpre	0		
S42		Caverne Marie-Jeanne	Belgium	contextual	40,000 BP		Sweden	Oxford	Mietje Germonpre	0		
S27		Tron Al-Wesse	Belgium	contextual	19,000 ± 3000 BP		Sweden	Oxford	John Stewart	4.7	YES	
S28		Tron Al-Wesse	Belgium	contextual	19,000 ± 3000 BP		Sweden	Oxford	John Stewart	21	YES	

S39		Tron Al-Wesse	Belgium	contextual	19,000 ± 3000 BP		Sweden	Oxford	John Stewart	7.4	YES	
AJ114		Narva site	Estonia	C14 indirect	5000-4000 cal. BCE		Oxford	Oxford	Mikhail Sablin	7.3	YES	
AJ172	Reindeer fissure est	Aven des Planes	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ173	Reindeer fissure est	Aven des Planes	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ174	Reindeer fissure south level 2	Aven des Planes	France	C14 indirect	26,377-26,020 cal. BP	BA 422567	Oxford	Oxford	Evelyne Crégut	1.1		
AJ175	Reindeer fissure south level 2	Aven des Planes	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ176	MR.4.01.903.24	Aven des Planes	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ170	Reindeer fissure est	Aven des Planes I	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ171	Reindeer fissure est	Aven des Planes I	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	6.5	YES	
AJ212	area 3 square E12b context 592	Chenet des Pierres, Bozel	France	C14 indirect	4000-3000 cal. BCE		Oxford	Oxford	Patricia Anne Chique	0		
AJ213	area 3 square F13a context 631	Chenet des Pierres, Bozel	France	C14 indirect	4000-3000 cal. BCE		Oxford	Oxford	Patricia Anne Chique	0		
AJ162	93	Coulet des Roches 2010	France	C14 indirect	15,996-15,422 cal. BP	BA 267380	Oxford	Oxford	Evelyne Crégut	32.4	YES	
AJ163	264	Coulet des Roches 2011	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ164	530	Coulet des Roches 2012	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	32.4	YES	
AJ165	565	Coulet des Roches 2013	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	83.8	YES	
AJ166	24	Coulet des Roches 2014	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ167	40	Coulet des Roches 2015	France	C14 indirect	26,377-26,020 cal. BP	BA 422567	Oxford	Oxford	Evelyne Crégut	29.9	YES	
AJ168	112.6	Coulet des Roches 2016	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		
AJ169	1.10	Coulet des Roches 2017	France	contextual	Palaeolithic		Oxford	Oxford	Evelyne Crégut	0		

AJ353	97	Grotte Capi	France	contextual	Palaeolithic		Oxford	Oxford	Jean-Christophe Castel	1.7		
AJ358	98	Grotte Capi	France	contextual	Palaeolithic		Oxford	Oxford	Jean-Christophe Castel	0		
SL005		Les Vautes	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0.7		
SL006		Les Vautes	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL007		Les Vautes	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL008		Les Vautes	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL009		Les Vautes	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL010		Les Vautes	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL012		Les Vautes	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL001		Péras 1	France	contextual	5000 BCE		Sweden	Oxford	Vianney Forest	0		
SL002		Péras 1	France	contextual	5000 BCE		Sweden	Oxford	Vianney Forest	0		
SL003		Péras 1	France	contextual	5000 BCE		Sweden	Oxford	Vianney Forest	0		
SL004		Péras 1	France	contextual	5000 BCE		Sweden	Oxford	Vianney Forest	0		
SL013		Puech-Haut	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL014		Puech-Haut	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL015		Puech-Haut	France	contextual	3500 BCE		Sweden	Oxford	Vianney Forest	0		
SL016		Puech-Haut	France	contextual	2000 BCE		Sweden	Oxford	Vianney Forest	0		
SL017		Puech-Haut	France	contextual	1300 BCE		Sweden	Oxford	Vianney Forest	8.4	YES	
S15		Loutra Aridea Cave	Greece	contextual	~11,230 BP		Sweden	Oxford	Florian Fladerer	0		
S16		Loutra Aridea Cave	Greece	contextual	~11,230 BP		Sweden	Oxford	Florian Fladerer	0		

S23		Loutra Aridea Cave	Greece	contextual	~11,230 BP		Sweden	Oxford	Florian Fladerer	0		
S25		Loutra Aridea Cave	Greece	contextual	~11,230 BP		Sweden	Oxford	Florian Fladerer	0		
S26		Loutra Aridea Cave	Greece	contextual	~11,230 BP		Sweden	Oxford	Florian Fladerer	0		
AJ372	6607	Bective	Ireland	contextual	High Medieval		Oxford	Oxford	Fiona Beglane	3.2		ID: 6607
AJ373	7387	Bective	Ireland	contextual	High Medieval		Oxford	Oxford	Fiona Beglane	1.4		ID:7387
AJ374	10335	Bective	Ireland	contextual	Late Medieval		Oxford	Oxford	Fiona Beglane	0		ID: 10335
AJ375	8780	Bective	Ireland	contextual	Post-Medieval		Oxford	Oxford	Fiona Beglane	12.5	YES	ID:8780
AJ376	8636	Bective	Ireland	contextual	Post-Medieval		Oxford	Oxford	Fiona Beglane	0		ID:8636
AJ381	6126	Drumadoon	Ireland	contextual	Early Medieval		Oxford	Oxford	Fiona Beglane	1.1		ID:6126
AJ384	6319	Greencastle	Ireland	contextual	14th century CE		Oxford	Oxford	Fiona Beglane	0		ID:6319
AJ550	BELUM.AX44(F16)	Mount Sandel	Ireland	contextual	Mesolithic		Oxford	Oxford	Greer Ramsey	0		ID: BELUM.AX44(F16)
AJ377	6359	Mountgorry	Ireland	contextual	11-12 century CE		Oxford	Oxford	Fiona Beglane	0		ID:6359
MH2-4		Parknabinnia	Ireland	contextual	5650-4750 BCE		Dublin	Dublin	Dan Bradley	627		same haplotype as MH4-1
MH3-2		Parknabinnia	Ireland	contextual	5650-4750 BCE		Dublin	Dublin	Dan Bradley	456.2	YES	
MH4-1		Parknabinnia	Ireland	contextual	5650-4750 BCE		Dublin	Dublin	Dan Bradley	2650	YES	
AJ385	Context F28C	Poulnabrone	Ireland	C14 indirect	3696 – 3535 cal. BCE	OxA-25949	Oxford	Oxford	Edward Bourke	6.6	YES	
AJ386	Context F28B	Poulnabrone	Ireland	C14 indirect	3786-3524 cal. BCE	OxA-26052, OxA-26717	Oxford	Oxford	Edward Bourke	1.7		
AJ387	Context F24	Poulnabrone	Ireland	C14 indirect	3947 – 3536 cal. BCE	OxA-1905	Oxford	Oxford	Edward Bourke	8.5	YES	
AJ380	5861	Roughan Hill	Ireland	contextual	Bronze Age		Oxford	Oxford	Fiona Beglane	515.8	YES	ID:5861
AJ378	6714	Trim Townparks S	Ireland	contextual	Later Medieval		Oxford	Oxford	Fiona Beglane	0		ID:6714

AJ379	5690	Trim Townparks S	Ireland	contextual	Post-Medieval		Oxford	Oxford	Fiona Beglane	3.1	YES	ID:5690
AJ198		Mentone	Italy	No information			Oxford	Oxford	Andre Rehazek	0		
AJ199		Mentone	Italy	No information			Oxford	Oxford	Andre Rehazek	0		
S83		Šventoji 23	Lithuania	contextual	Neolithic		Sweden	Oxford	Love Dalén	6.4	YES	
S33		Borsuka Cave	Poland	No information			Sweden	Oxford	Piotr Wojtal	0		
S37		Deszczowa Cave	Poland	contextual	22000 ± 3000 BP		Sweden	Oxford	Piotr Wojtal	0		
S36		Kruczaskata	Poland	No information			Sweden	Oxford	Piotr Wojtal	0		
S34		Mamutowa Cave	Poland	No information			Sweden	Oxford	Piotr Wojtal	0		
S35_2		Oblazowa Cave	Poland	contextual	20000 ± 3000 BP		Sweden	Oxford	Piotr Wojtal	17.8	YES	
AJ140	exc.4.1 layer 3a no.109	Afontova gora 2 2016, Krasnoyarsk	Russia	contextual	Palaeolithic		Oxford	Oxford	Sergey Federov	34.1	YES	
AJ160	2 - 2015 AB-B-01	Badiarikha River Indigirka river basin	Russia	No information			Oxford	Oxford	Sergey Federov	0		
AJ128		Batacaika site	Russia	contextual			Oxford	Oxford	Sergey Federov	102.8	YES	
AJ143		Belochka cave, Krasnoyarsk	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	258.8	YES	
AJ155		Belyi Gozod 2016, Irkutsk	Russia	contextual	Late Pleistocene		Oxford	Oxford	Sergey Federov	0		
AJ154		Bolshaya cave, Bronnaya 2016, Krasnoyarsk	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	162	YES	
AJ132		Buor-Yurkyakh site	Russia	contextual	Late Pleistocene		Oxford	Oxford	Sergey Federov	209.8	YES	
AJ138		Calcitovovaya cave 1990, Irkutsk	Russia	contextual	Modern		Oxford	Oxford	Sergey Federov	0		
AJ145	Picket D-4	Dolganskaya Yama 1990 Picket D-4, Bagdarin	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	0		
AJ121		Galkinskoe Gorodishche, Chusovaya River, Ekaterinburg district	Russia	contextual	2250 BP		Oxford	Oxford	Mikhail Sablin	164.3	YES	
AJ150	sq vi-31	Igeteisky log 1 1977 sq vi-31, Irkutsk	Russia	contextual	MIS-II		Oxford	Oxford	Sergey Federov	0		

AJ152	sq.A-10, 1993	Kamenka-A sq.A-10, 1993, Ulan-Ude	Russia	contextual	MIS-III		Oxford	Oxford	Sergey Federov	0		
AJ151		Kholodnaya 2011, n2, Irkutsk	Russia	contextual	Early-Middle Holocene		Oxford	Oxford	Sergey Federov	110.1	YES	
AJ136	ex. 2 layer 3	Khotyk, Ulan-Ude	Russia	contextual	MIS-III		Oxford	Oxford	Sergey Federov	8.9	YES	
S17		Koctemku 1-I	Russia	No information			Sweden	Oxford	Mikhail Sablin	0		
S18		Koctemku 1-I	Russia	No information			Sweden	Oxford	Mikhail Sablin	0		
S19		Koctemku 1-I	Russia	No information			Sweden	Oxford	Mikhail Sablin	0		
S20		Koctemku 1-I	Russia	No information			Sweden	Oxford	Mikhail Sablin	0		
AJ146		Kurtun-1, Irkutsk	Russia	contextual	Late Pleistocene and Holocene		Oxford	Oxford	Sergey Federov	0		
AJ153	exc. 1 household pit	Mankay 2010 exc. 1 household pit, Irkutsk	Russia	contextual	Middle Ages		Oxford	Oxford	Sergey Federov	0		
AJ126		Mendol'syaka cave, Irkutsk	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	0		
AJ161	2017SK-MK-01	Moustakch Ynyakh River Basin of Kolyma River	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	0		
AJ141	exc.36 cellar, no.972b	Nikolaevka 1, Krasnoyarsk	Russia	contextual	Later the Middle Ages		Oxford	Oxford	Sergey Federov	0		
AJ148		Pervomaisky 2017, Irkutsk	Russia	contextual	Late Pleistocene		Oxford	Oxford	Sergey Federov	0		
AJ124		Podgay Gorodishche	Russia	contextual	200 BCE-200 CE		Oxford	Oxford	Mikhail Sablin	0		
AJ125		Podgay Gorodishche	Russia	contextual	200 BCE-200 CE		Oxford	Oxford	Mikhail Sablin	0		
AJ547	109/95	Pymia Shor	Russia	No information			Oxford	Oxford		0		
AJ546	81/95	Pymia Shor I	Russia	No information			Oxford	Oxford		0		
AJ548	82/95	Pymia Shor I	Russia	C14 indirect	24,276-23,930 cal. BP		Oxford	Oxford		0.9		
AJ158		Radost 2016 cave	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	0		

AJ156	Pit 8	Rudovka 2005 pit 8, Irkutsk	Russia	contextual	MIS-II		Oxford	Oxford	Sergey Federov	9.9	YES	
AJ134		Serteya II site, Pskov district	Russia	contextual	4250 BP		Oxford	Oxford	Mikhail Sablin	473.1	YES	
AJ147		Shilka river 2017, Chita	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	4.3	YES	
AJ159	1-2015-AD-S-05	Sumarlakh River Indigirka river basin	Russia	No information			Oxford	Oxford	Sergey Federov	0		
AJ133	pit 2 horizon 2 2016	Tolstyi Nose, Krasnoyarsk	Russia	contextual	Later the Middle Ages		Oxford	Oxford	Sergey Federov	82	YES	
AJ129		Tuyana 2011, Irkutsk	Russia	contextual	MIS 3		Oxford	Oxford	Sergey Federov	0		
AJ131	sq J-20	Udinsky ostrog 2016, Ulan-Ude	Russia	contextual	Late Middle Ages		Oxford	Oxford	Sergey Federov	0		
AJ144	exc.1 no.7	Ul'kan exc.1 no.7, Irkutsk	Russia	contextual	Late Pleistocene		Oxford	Oxford	Sergey Federov	0		
AJ157		Ulan-nurskaya-2 2011, Airdie, Alberta	Russia	contextual	Later the Middle Ages		Oxford	Oxford	Sergey Federov	378.8	YES	
AJ139		Unugen site Bunge roll site yana river basin	Russia	contextual	Late Pleistocene		Oxford	Oxford	Sergey Federov	0		
AJ130		Urugen site (Bunge-Toll site)	Russia	contextual	Late Pleistocene		Oxford	Oxford	Sergey Federov	122	YES	
AJ137	106, 2014, Exc.1 layer 6 no.4068	Yeniseisk, Lenin's manor, Krasnoyarsk	Russia	contextual	Later the Middle Ages		Oxford	Oxford	Sergey Federov	24.5	YES	
AJ142	106,2014,exc1 structure 13 cellar no.5026	Yeniseisk, Lenin's manor, Krasnoyarsk	Russia	contextual	Later the Middle Ages		Oxford	Oxford	Sergey Federov	0.2		
AJ127	Exc 31 square f-12	Yukhta, Krasnoyarsk	Russia	No information			Oxford	Oxford	Sergey Federov	0		
AJ135		Zaostravnaya, Irkutsk	Russia	contextual	Modern		Oxford	Oxford	Sergey Federov	0		
AJ149		Zimoveinaya cave, Irkutsk	Russia	contextual	Late Holocene		Oxford	Oxford	Sergey Federov	0		
S21		Бетово	Russia	No information			Sweden	Oxford	Mikhail Sablin	0		
S22		Бетово	Russia	No information			Sweden	Oxford	Mikhail Sablin	0		
AJ120		Galkinskoe Gorodishche	Russia	contextual	2250 BP		Oxford	Oxford	Mikhail Sablin	245.5	YES	
AJ123		Chernousovo 4 site	Russia	contextual	3950 - 1750 BP		Oxford	Oxford	Mikhail Sablin	1		

AJ122		Rodanovo Gorodishche	Russia	contextual	1100 CE		Oxford	Oxford	Mikhail Sablin	0.8		
AJ119		Yuzhniy Oleniy Ostrov cemetry	Russia	contextual	Mesolithic		Oxford	Oxford	Mikhail Sablin	1.3		
AJ118		Anashkino site	Russia	contextual	600 BCE		Oxford	Oxford	Mikhail Sablin	1.7		
AJ117		Serteya II site	Russia	C14 indirect	2300 cal. BCE		Oxford	Oxford	Mikhail Sablin	0		
AJ115		Usviaty IV site	Russia	C14 indirect	4000-3000 cal. BCE		Oxford	Oxford	Mikhail Sablin	0.6		
AJ436		MacKay cave	Scotland	contextual	Mesolithic		Oxford	Oxford	Andrew Kitchener	0		
AJ207	AC0619	An Corran	Scotland, Isle of Skye	contextual	Mesolithic		Oxford	Oxford	Alison Sheridan	0		
AJ208	AC0395	An Corran	Scotland, Isle of Skye	contextual	Mesolithic		Oxford	Oxford	Alison Sheridan	0		
AJ209	AC0386	An Corran	Scotland, Isle of Skye	contextual	Mesolithic		Oxford	Oxford	Alison Sheridan	0		
AJ210	AC0388	An Corran	Scotland, Isle of Skye	contextual	Mesolithic		Oxford	Oxford	Alison Sheridan	0		
AJ211	AC0398	An Corran	Scotland, Isle of Skye	contextual	Mesolithic		Oxford	Oxford	Alison Sheridan	0		
AJ3.2		Teampuil Bagh 1, Temple Bay	Scotland, Western Isles, Harris	C14 indirect	5715 to 5555 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ31		Teampuil Bagh 11, Temple Bay	Scotland, Western Isles, Harris	C14 indirect	5715 to 5555 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ32		Teampuil Bagh 11, Temple Bay	Scotland, Western Isles, Harris	C14 indirect	5715 to 5555 cal. BCE		Oxford	Oxford	Mike Church	26.8	YES	
AJ2.2		Teampuil Bagh 2, Temple Bay	Scotland, Western Isles, Harris	C14 indirect	5715 to 5555 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ30		Teampuil Bagh 2, Temple Bay	Scotland, Western Isles, Harris	C14 indirect	5715 to 5555 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ33		Pabbaigh Mor South	Scotland, Western Isles, Lewis	C14 indirect	~4,300 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ34		Pabbaigh Mor South	Scotland, Western Isles, Lewis	C14 indirect	~4,300 cal. BCE		Oxford	Oxford	Mike Church	0		

AJ35		Pabbaigh Mor South	Scotland, Western Isles, Lewis	C14 indirect	~4,300 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ36		Pabbaigh Mor South	Scotland, Western Isles, Lewis	C14 indirect	~4,300 cal. BCE		Oxford	Oxford	Mike Church	1.5		
AJ20		Traigh na Beirigh 1	Scotland, Western Isles, Lewis	C14 indirect	4350-4050 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ21		Traigh na Beirigh 1	Scotland, Western Isles, Lewis	C14 indirect	4350-4050 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ22		Traigh na Beirigh 1	Scotland, Western Isles, Lewis	C14 indirect	4350-4050 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ23		Traigh na Beirigh 1	Scotland, Western Isles, Lewis	C14 indirect	4350-4050 cal. BCE		Oxford	Oxford	Mike Church	1		
AJ24		Traigh na Beirigh 1	Scotland, Western Isles, Lewis	C14 indirect	4350-4050 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ25		Traigh na Beirigh 2	Scotland, Western Isles, Lewis	C14 indirect	4400-4300 cal. BCE		Oxford	Oxford	Mike Church	1.3		
AJ26		Traigh na Beirigh 2	Scotland, Western Isles, Lewis	C14 indirect	4400-4300 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ27		Traigh na Beirigh 2	Scotland, Western Isles, Lewis	C14 indirect	4400-4300 cal. BCE		Oxford	Oxford	Mike Church	0		
AJ28		Traigh na Beirigh 2	Scotland, Western Isles, Lewis	C14 indirect	4400-4300 cal. BCE		Oxford	Oxford	Mike Church	5.4	YES	
AJ29		Traigh na Beirigh 2	Scotland, Western Isles, Lewis	C14 indirect	4400-4300 cal. BCE		Oxford	Oxford	Mike Church	0		
S11		Gisslause	Sweden, Gotland	contextual	Mesolithic		Sweden	Oxford	Love Dalén	2.4		
S5		Lilla Hultungs	Sweden, Gotland	contextual	Medieval		Sweden	Oxford	Love Dalén	0		
S19		Lilla Sojvide	Sweden, Gotland	C14 direct	1472-1641 cal. CE		Sweden	Oxford	Love Dalén	0		

S33_2		Stora Förvar	Sweden, Gotland	C14 direct	972-1150 cal. CE		Sweden	Oxford	Love Dalén	4.6		
S35		Stora Förvar	Sweden, Gotland	C14 direct	7066-6713 cal. BCE		Sweden	Oxford	Love Dalén	16.6	YES	
S73		Strå	Sweden, Gotland	contextual	Mesolithic		Sweden	Oxford	Love Dalén	0		
S29		Västerbjers	Sweden, Gotland	contextual	Neolithic		Sweden	Oxford	Love Dalén	4		
S52		Alvastra	Sweden, mainland	contextual	Neolithic		Sweden	Oxford	Love Dalén	0		
S78		Frälsegården	Sweden, mainland	C14 direct	3354-2581 cal. BCE		Sweden	Oxford	Love Dalén	7.3	YES	
S58		Korsnäs	Sweden, mainland	contextual	Neolithic		Sweden	Oxford	Love Dalén	0		
S47		Scheelegatan	Sweden, mainland	C14 direct	2624-2296 cal. BCE		Sweden	Oxford	Love Dalén	0.8		
S45		Gåtebo	Sweden, Öland	C14 direct	655-769 cal. CE		Sweden	Oxford	Love Dalén	31.3	YES	
S63		Klinta	Sweden, Öland	C14 direct	3081-2890 cal. BCE		Sweden	Oxford	Love Dalén	0		
S55		Mysinge	Sweden, Öland	contextual	Neolithic		Sweden	Oxford	Love Dalén	0		
S71		Mysinge	Sweden, Öland	contextual	Neolithic		Sweden	Oxford	Love Dalén	0		
AJ200	B.4321	Abri Buttenloch Ettingen 1924	Switzerland	contextual	Upper Palaeolithic		Oxford	Oxford	Loïc Costeur	1.4		
AJ201	B4226	Abri Buttenloch Ettingen 1924	Switzerland	contextual	Upper Palaeolithic		Oxford	Oxford	Loïc Costeur	0		
AJ202	B4248	Abri Buttenloch Ettingen 1924	Switzerland	contextual	Upper Palaeolithic		Oxford	Oxford	Loïc Costeur	0		
AJ203	A	Abri Buttenloch Ettingen 1924	Switzerland	contextual	Upper Palaeolithic		Oxford	Oxford	Loïc Costeur	0		
AJ204	B.4244	Abri Buttenloch Ettingen 1924	Switzerland	contextual	Upper Palaeolithic		Oxford	Oxford	Loïc Costeur	0		
AJ205	B.4238	Abri Buttenloch Ettingen 1924	Switzerland	contextual	Upper Palaeolithic		Oxford	Oxford	Loïc Costeur	0		
AJ206	B.4228	Abri Buttenloch Ettingen 1924	Switzerland	contextual	Upper Palaeolithic		Oxford	Oxford	Loïc Costeur	0		
AJ177	CP/J3.719 + CP/297.60	Château d'Oex	Switzerland	contextual	Mesolithic		Oxford	Oxford	Pierre Crotti	1.1		
AJ178	CP/J3.134	Château d'Oex	Switzerland	contextual	Mesolithic		Oxford	Oxford	Pierre Crotti	7.5	YES	

AJ196	Th8 Scap sin	Kaltbrunnental	Switzerland	No information			Oxford	Oxford	Andre Rehazek	0		
AJ197	TH7 Scap sin	Kaltbrunnental	Switzerland	No information			Oxford	Oxford	Andre Rehazek	0		
S1		Kesslerloch	Switzerland	contextual	11,000 ± 3000 BP		Sweden	Oxford	Hannes Napierla	0		
S2		Kesslerloch	Switzerland	contextual	11,000 ± 3000 BP		Sweden	Oxford	Hannes Napierla	0		
S3		Kesslerloch	Switzerland	contextual	11,000 ± 3000 BP		Sweden	Oxford	Hannes Napierla	12.3		
S4		Kesslerloch	Switzerland	contextual	11,000 ± 3000 BP		Sweden	Oxford	Hannes Napierla	0		
S5		Kesslerloch	Switzerland	contextual	11,000 ± 3000 BP		Sweden	Oxford	Hannes Napierla	0		
S7		Kesslerloch	Switzerland	contextual	11,000 ± 3000 BP		Sweden	Oxford	Hannes Napierla	0		
S8		Kesslerloch	Switzerland	contextual	11,000 ± 3000 BP		Sweden	Oxford	Hannes Napierla	0		
AJ179		Kohlerhohle	Switzerland	C14 indirect	17650-11290 cal BCE		Oxford	Oxford	Silvia Kalabis	36	YES	
AJ180		Kohlerhohle	Switzerland	C14 indirect	17650-11290 cal BCE		Oxford	Oxford	Silvia Kalabis	22.4	YES	
AJ181		Kohlerhohle	Switzerland	C14 indirect	17650-11290 cal BCE		Oxford	Oxford	Silvia Kalabis	0		
AJ357	D7	Les Douattes	Switzerland	contextual	Palaeolithic		Oxford	Oxford	Jean-Christophe Castel	0		
AJ354	S.P.58 2748	Les Plaints	Switzerland	contextual	Palaeolithic		Oxford	Oxford	Jean-Christophe Castel	0		
AJ355	S.P.58 2748	Les Plaints	Switzerland	contextual	Palaeolithic		Oxford	Oxford	Jean-Christophe Castel	0		
AJ356	S.P.58 2752	Les Plaints	Switzerland	contextual	Palaeolithic		Oxford	Oxford	Jean-Christophe Castel	0		
AJ182	NE-N2 91 L51 36	Monruz	Switzerland	contextual	15,000 BP		Oxford	Oxford	Vern Mueller	0		
AJ183	NE-N2 91 N52 52	Monruz	Switzerland	contextual	15,000 BP		Oxford	Oxford	Vern Mueller	0		
AJ184	NE MZ 92 M 47 os 97	Monruz	Switzerland	contextual	15,000 BP		Oxford	Oxford	Vern Mueller	0		

AJ185	NE N2 92 N50 252	Monruz	Switzerland	contextual	15,000 BP		Oxford	Oxford	Vern Mueller	0.1		
AJ186	NE N2 92 N53 183	Monruz	Switzerland	contextual	15,000 BP		Oxford	Oxford	Vern Mueller	0.1		
AJ193	Context: 20806	Schweizersbild	Switzerland	contextual	~12,000 BC		Oxford	Oxford	Andre Rehazek	1.6		
AJ194		Schweizersbild	Switzerland	contextual	~12,000 BC		Oxford	Oxford	Andre Rehazek	0		
AJ195		Schweizersbild	Switzerland	contextual	~12,000 BC		Oxford	Oxford	Andre Rehazek	0		
AJ187		Thayngen	Switzerland	contextual	15,000 - 11,000 BCE		Oxford	Oxford	Andre Rehazek	0		
AJ188		Thayngen	Switzerland	contextual	15,000 - 11,000 BCE		Oxford	Oxford	Andre Rehazek	2.4		
AJ189		Thayngen	Switzerland	contextual	15,000 - 11,000 BCE		Oxford	Oxford	Andre Rehazek	0		
AJ190		Thayngen	Switzerland	contextual	15,000 - 11,000 BCE		Oxford	Oxford	Andre Rehazek	0		
AJ191		Thayngen	Switzerland	contextual	15,000 - 11,000 BCE		Oxford	Oxford	Andre Rehazek	34.3	YES	
AJ192		Thayngen	Switzerland	contextual	15.000 - 11.000 BCE		Oxford	Oxford	Andre Rehazek	0		
AJ352	652/80	Veyrier	Switzerland	contextual	Magdalenian, Palaeolithic		Oxford	Oxford	Jean-Christophe Castel	0		
AJ543	M656	Cave Earth 1st Level, Kent's Cavern, Torquay, Devon	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0		
AJ544	M649	Cave Earth 1st Level, Kent's Cavern, Torquay, Devon	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0.7		
AJ522	LL.7431	Church Hole, Creswell Crags	England	C14 direct	14,534 ± 317 cal. BP	OxA-18704	Oxford	Oxford	Lindsey Loughtman	3.6		
AJ551	RH 578-587 OXA-1670 Prox. right hum.	Creswell Crags	England	C14 direct	14,645 ± 328 cal. BP	OXA-17525	Oxford	Oxford	Angharad Jones	1.1		
AJ552	RH 600-609 cut dital left femur OXA-17546	Creswell Crags	England	C14 direct	14,541 ± 318 cal. BP	OXA-17546	Oxford	Oxford	Angharad Jones	0		

AJ553	RH 222-237 OXA 1619 distal right scapula	Creswell Crags	England	C14 direct	14,624 ± 314 cal. BP	OXA-17542	Oxford	Oxford	Angharad Jones	0.7		
AJ540	M102273	Flint-Kinfe Gallery, Brixham Cave, Torquay, Devon	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	4.5	YES	
AJ541	M102277	Flint-Kinfe Gallery, Brixham Cave, Torquay, Devon	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0		
AJ542	M102276	Flint-Kinfe Gallery, Brixham Cave, Torquay, Devon	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0		
AJ538	M104806	Ightham, Kent	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0		
AJ545	M1063	Kent's Cavern, Torquay, Devon	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0		
AJ539	M102289	Pin Hole Cave, Creswell, Derbyshire	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0		
AJ518	LL.1138	Pin Hole, Creswell Crags	England	C14 direct	14,507 ± 341 cal. BP	OxA-19162	Oxford	Oxford	Lindsey Loughtman	2		
AJ519	LL.7989	Pin Hole, Creswell Crags	England	C14 direct	13,803 ± 201 cal. BP	OxA-19526	Oxford	Oxford	Lindsey Loughtman	477.2	YES	Still included although just over 10% missing data
AJ520	LL.7990	Pin Hole, Creswell Crags	England	C14 direct	14,606 ± 338 cal. BP	OxA-19163	Oxford	Oxford	Lindsey Loughtman	17.5	YES	
AJ521	LL.7991	Pin Hole, Creswell Crags	England	C14 direct	14,087 ± 222 cal. BP	OxA-18348	Oxford	Oxford	Lindsey Loughtman	2.3		
AJ536	M104804	Terminal Chamber, Neale's Cave, Paignton, Devon	England	contextual	Palaeolithic		Oxford	Oxford	Pip Brewer	0		

Table S2.3 – Modern samples processed for this study, all provided by Jose Melo-Ferreira and Paulo Alves apart from AJMH1 and the Scottish samples provided by Andrew Kitchener and LTM.2113 provided by University of Alaska Museum.

Sample	Region	Country	MT depth of coverage	Included in analysis
AJMH1	Isle of Lewis	Scotland	107771.0	YES
LTM.ESC.4576	Bonar Bridge	Scotland	269.7	YES
LTM.ESC.4657	Bonar Bridge	Scotland	707.6	YES
LTM.ESC.4715	Bonar Bridge	Scotland	277.0	YES
LTM.ESC.4732	Bonar Bridge	Scotland	376.6	YES
LTM.ESC.4771	Bonar Bridge	Scotland	552.9	same as LTM.ESC.4715
LCS.ALT.1985	Alto Sil	Spain	52.6	YES
LCS.ALT.1986	Alto Sil	Spain	44.2	same as LCS.1985
LCS.ALT.1987	Alto Sil	Spain	36.2	same as LCS.1985
LCS.ALT.1989	Alto Sil	Spain	43.1	same as LCS.1985
LCS.ALT.1990	Alto Sil	Spain	60.6	YES
LER.ALA.1454	Subivana de Alava, Vitoria-Gasteiz	Spain	37.2	YES
LER.ALA.1455	Okariz	Spain	38.9	YES
LER.ALA.1460	Lubiano, Vitoria-Gasteiz	Spain	56.3	YES
LER.CAN.1482	Costa de Cantabria	Spain	99.3	YES
LER.CAN.1486	Costa de Cantabria	Spain	66.9	YES
LER.CAN.1487	Costa de Cantabria	Spain	219.6	YES
LER.JAC.1499	Jaca	Spain	6.2	Did not meet criteria
LER.JAC.1505	Villareal del Canal	Spain	74.9	YES
LER.JAC.1507	Artieda	Spain	81.1	YES
LER.NAV.1509	Zazaga	Spain	76.2	YES
LER.NAV.1510	Aoiz	Spain	304.5	same as LER.NAV.1509
LER.NAV.1513	Verdiáin	Spain	41.2	YES
LER.VLC.1521	Villarcayo	Spain	10.9	YES
LER.VLC.1528	Villarcayo	Spain	44.7	YES
LER.VLC.1529	Villarcayo	Spain	21.5	same as LER.CAN.1486
LGR.ALA.613	Álava	Spain	102.3	YES
LGR.ALA.648	Leza	Spain	53.3	YES
LGR.ALB.671	Povedilla	Spain	39.8	YES
LGR.ALB.689	Madrigueras	Spain	13.1	YES
LGR.ALC.710	Alcañiz	Spain	77.7	YES
LGR.ALI.739	Alicante (province)	Spain	21.4	YES
LGR.AMD.54	Almeida	Portugal	12.2	YES
LGR.BEN.783	Benavente y Los Valles	Spain	39.0	YES
LGR.BRG.122	Bragança	Portugal	85.1	YES
LGR.CUE.920	La Almarcha	Spain	38.1	YES
LGR.FCR.170	Almofala	Portugal	140.9	YES

LGR.GUA.1008	Guadalajara	Spain	214.7	YES
LGR.HUE.1015	Sangarrén	Spain	9.1	Did not meet criteria
LGR.MOS.1055	Mosqueruela	Spain	174.0	YES
LGR.NAV.1091	Sesma	Spain	245.2	YES
LGR.NAV.2285	Funes	Spain	877.8	YES
LGR.NAV.2325	Tauste	Spain	705.6	YES
LGR.SAL.1141	Serradilla del Arroyo	Spain	114.8	YES
LGR.SAL.1143	Cantalapiedra	Spain	160.3	YES
LGR.SAL.3361	Narros de Matalayegua	Spain	22.3	YES
LGR.SEG.3801	Valseca	Spain	42.5	YES
LGR.SEN.566	Sendim	Portugal	4.1	Did not meet criteria
LGR.SES.586	Sabugal, Guarda	Portugal	25.8	YES
LGR.SOR.1174	La Muela, Golmayo	Spain	115.0	YES
LGR.SOR.1180	Beltejar, Medinaceli	Spain	52.7	YES
LGR.SOR.1191	Fuentelfresno	Spain	41.5	YES
LGR.TCA.1207	Tierra de Campos (Valladolid and Palencia)	Spain	33.6	YES
LGR.TER.3452	Singra	Spain	84.9	YES
LGR.TOL.1249	Toledo	Spain	192.3	YES
LGR.VLD.1295	Renedo de Esgueva	Spain	12.8	YES
LGR.ZAM.1307	Zamora	Spain	190.6	YES
LGR.ZAR.1332	Longares	Spain	148.4	YES
LGR.ZAR.1344	Pina de Ebro	Spain	23.9	YES
LTM.2113	Arkhangelsk Oblast	Russia	594.1	YES
LTM.AMU.1846	Amurskaya territory (Selemdzha river)	Russia	64.7	YES
LTM.AMU.1847	Amurskaya territory (Norsky reserve)	Russia	15.1	YES
LTM.AMU.1848	Amurskaya territory (Norsky reserve)	Russia	97.4	YES
LTM.AMU.1849	Amurskaya territory (Norsky reserve)	Russia	73.6	YES
LTM.KAM.1851	Kamchatka peninsula (central part	Russia	273.7	YES
LTM.KAM.1852	Kamchatka peninsula (central part	Russia	485.3	YES
LTM.KAM.1853	Kamchatka peninsula (central part	Russia	90.6	same as LTM.KAM.1851
LTM.KAM.1854	Kamchatka peninsula (central part	Russia	289.4	YES
LTM.KOL.1855	Kolyma river basin (lower Balygchan river)	Russia	34.7	YES
LTM.KOL.1856	Kolyma river basin (mouth of Balygchan river)	Russia	37.5	YES
LTM.KOL.1858	Kolyma river basin (mouth of Balygchan river)	Russia	32.9	YES

LTM.KOL.1859	Kolyma river basin (mouth of Balygchan river–Seimchan settl)	Russia	48.4	YES
LTM.KOL.1860	Kolyma river basin (mouth of Balygchan river–Seimchan settl)	Russia	36.4	YES
LTM.KOL.1861	Kolyma river basin (mouth of Balygchan river–Seimchan settl)	Russia	38.7	YES
LTM.MAG.1862	Magdan city	Russia	63.4	YES
LTM.MAG.1864	Magdan city	Russia	45.7	YES
LTM.MAG.1865	Magdan city	Russia	80.9	YES
LTM.PRI.1867	Primorsky territory (river Malinovka)	Russia	15.3	YES
LTM.PRI.1868	Primorsky territory (river Gornaya)	Russia	64.1	YES
LTM.PRI.1869	Primorsky territory (river Orekhovka)	Russia	34.1	YES
LTM.RUS.1874	West	Russia	66.1	YES
LTM.URA.1832	Urals	Russia	319.4	YES
LTM.URA.1833	Urals	Russia	4063.1	YES
LTM.URA.1835	Urals	Russia	718.6	YES
LTM.URA.1836	Urals	Russia	395.7	YES
LTM.URA.1837	Urals	Russia	1013.6	YES
LTM.URA.1838	Urals	Russia	557.2	YES
LTM.URA.1839	Urals	Russia	1974.7	YES
LTM.URA.1840	Urals	Russia	706.7	same as LTM.URA.1832
LTM.URA.1841	Urals	Russia	1530.4	same as LTM.URA.1835
LTM.URA.1842	Urals	Russia	265.5	YES
LTM.URA.1845	Urals	Russia	364.7	YES
LTM.YAK.1870	Siberia near Yakutsk	Russia	186.5	YES
LTM.YAK.1871	Siberia near Yakutsk	Russia	25.1	YES
LTM.YAK.1873	Siberia near Yakutsk	Russia	31.6	YES
LTM.URA.1834	Urals	Russia	was not sequenced	
LTM.URA.1843	Urals	Russia	was not sequenced	
LTM.KOL.1857	Kolyma river basin (mouth of Balygchan river)	Russia	was not sequenced	
LTM.MAG.1863	Magdan city	Russia	was not sequenced	
LTM.MAG.1866	Magdan city	Russia	was not sequenced	
LTM.YAK.1872	Siberia near Yakutsk	Russia	was not sequenced	

Table S2.4 – Sequenced provided by Jose Melo-Ferreira and Paulo Alves for this study

Sample	Region	Country	Sample provider / SRA Data accession / GenBank Data accession	Data Reference	Included in analysis	Notes
LTM.ITA.1798	Cercivento	Italy	SAMN12710295	Giska et al. 2019	NO	same as ALP.LTM.1800
LTM.ITA.1800	Ris. Comelico Sup. Loc. Casoni	Italy	SAMN12710296	Giska et al. 2019	YES	
LTM.ITA.1817	Castello Molina	Italy	SAMN12710297	Giska et al. 2019	YES	
LTM.SLZ.1825	Salzburg	Austria	SAMN12710298	Giska et al. 2019	YES	
LTM.SLZ.1827	Salzburg	Austria	SAMN12710299	Giska et al. 2019	NO	10% or more missing data
LTM.SLZ.1828	Salzburg	Austria	SAMN12710300	Giska et al. 2019	NO	same as ALP.LTM.1825
LTM.AFR.2772	St-Gervais-les-Bains	France	SAMN12710301	Giska et al. 2019	NO	10% or more missing data
LTM.AFR.2773	Les Contamines-Montjoie	France	SAMN12710302	Giska et al. 2019	NO	10% or more missing data
LTM.AFR.2775	Samoens	France	SAMN12710303	Giska et al. 2019	NO	10% or more missing data
LTM.AFR.2776	Les Carroz, Arâches-la-Frasse	France	SAMN12710304	Giska et al. 2019	NO	same as ALP.LTM.3108
LTM.AFR.3108	Arbaron, Arâches-la-Frasse	France	SAMN12710305	Giska et al. 2019	YES	
LTM.AFR.3109	Nancy-sur-Cluses	France	SAMN12710306	Giska et al. 2019	NO	10% or more missing data
LTM.AFR.3110	Les Grolays, Montriond	France	SAMN12710307	Giska et al. 2019	NO	10% or more missing data
LTM.SUI.3116	Maienfeld, Guscha	Switzerland	SAMN12710308	Giska et al. 2019	YES	
LTM.SUI.3122	Kip Laus, Sumvitg	Switzerland	SAMN12710309	Giska et al. 2019	YES	
LTM.SUI.3199	La Motta, Brienz/Brinzauls	Switzerland	SAMN12710310	Giska et al. 2019	YES	
LTM.SUI.3207	Höbord, Conters im Prättigau	Switzerland	SAMN12710311	Giska et al. 2019	YES	
LTM.SUI.3228	Zur, Brusio	Switzerland	SAMN12710312	Giska et al. 2019	YES	
LTM.SUI.3253	Plan da Gisep, Tschlin	Switzerland	SAMN12710313	Giska et al. 2019	YES	
LTM.SUI.3262	Padella, Samendan	Switzerland	SAMN12710314	Giska et al. 2019	YES	
LTM.FIN.1726		Finland	SAMN12710277	Giska et al. 2019	YES	
LTM.FIN.1729		Finland	SAMN12710278	Giska et al. 2019	YES	
LTM.FIN.1730		Finland	SAMN12710279	Giska et al. 2019	YES	

LTM.FIN.1731		Finland	SAMN12710280	Giska et al. 2019	NO	10% or more missing data
LTM.FIN.1733		Finland	SAMN12710286	Giska et al. 2019	YES	
LTM.NOR.1749		Norway	SAMN12710283	Giska et al. 2019	YES	
LTM.NOR.1750		Norway	SAMN12710284	Giska et al. 2019	YES	
LTM.NOR.1751		Norway	SAMN12710285	Giska et al. 2019	YES	
LTM.SUE.1754	Kroksjö	Sweden	SAMN12710287	Giska et al. 2019	YES	
LTM.SUE.1755	Hällnäs	Sweden	SAMN12710288	Giska et al. 2019	YES	
LTM.SUE.1756	Hällnäs	Sweden	SAMN12710289	Giska et al. 2019	NO	10% or more missing data
LTM.SUE.1757	Lycksele	Sweden	SAMN12710290	Giska et al. 2019	YES	
LTM.SUE.1762		Sweden	SAMN12710291	Giska et al. 2019	YES	
LTM.SUE.1763		Sweden	SAMN12710292	Giska et al. 2019	YES	
LTM.SUE.1766		Sweden	SAMN12710293	Giska et al. 2019	YES	
LTM.SUE.1772		Sweden	SAMN12710294	Giska et al. 2019	YES	
LTM.CAT.2012		Finland (captive)	SAMN12710276	Giska et al. 2019	YES	
LTM.FIN.2191	Jyväskylä, Keski Suomi	Finland	SAMN12710281	Giska et al. 2019	YES	
LTM.FIN.2192	Jyväskylä, Keski Suomi	Finland	SAMN12710282	Giska et al. 2019	NO	same as FSC.LTM.1730
LTM.IRE.3102	Borris-in-Ossory	Ireland	Paulo Célio Alves, José Melo-Ferreira, Neil Reid	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.3103	Borris-in-Ossory	Ireland	Paulo Célio Alves, José Melo-Ferreira, Neil Reid	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.3104	Borris-in-Ossory	Ireland	Paulo Célio Alves, José Melo-Ferreira, Neil Reid	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.3105	Borris-in-Ossory	Ireland	Paulo Célio Alves, José Melo-Ferreira, Neil Reid	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4070	Cavan	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4080	Limerick	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4079	Limerick	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4096	Westport	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4098	Westport	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4072	Cavan	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	

LTM.IRE.4095	Westport	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4099	Westport	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4071	Cavan	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4091	Waterford	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4089	Waterford	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4078	Limerick	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4083	Limerick	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4088	Waterford	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4073	Cavan	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.IRE.4092	Waterford	Ireland	Paulo Prodhol	Melo-Ferreira et al. unpublished	YES	
LTM.FAR.3978	Kollafjørður - Signabøshagi	Faroe Islands	SAMN12710256	Giska et al. 2019	YES	
LTM.FAR.3982	Kvívík - Fjallið	Faroe Islands	SAMN12710275	Giska et al. 2019	YES	
LTM.FAR.3667	Kaldbak - Býggjarhagi, Yngstugimbrar	Faroe Islands	SAMN12710261	Giska et al. 2019	YES	
LTM.FAR.3696	Vestmanna - Dalar, Eystanfyri	Faroe Islands	SAMN12710271	Giska et al. 2019	YES	
Oryctolagus cuniculus			NC_001913	Gissi et al. 1998	YES	AJ001588.1
Lepus europaeus	Skane	Sweden	NC_004028	Arnason et al. 2002	YES	AJ421471.1
Lepus granatensis	Huelva	Spain	KJ397611	Melo-Ferreira et al. 2014	YES	
Lepus capensis	Mauritania		KJ397612	Melo-Ferreira et al. 2014	YES	
Lepus americanus	Montana	USA	KJ397613	Melo-Ferreira et al. 2014	YES	
Lepus californicus	Texas	USA	KJ397614	Melo-Ferreira et al. 2014	YES	
Lepus townsendii	Wyoming	USA	KJ397609	Melo-Ferreira et al. 2014	YES	
Lepus timidus		Finland	KJ397605	Melo-Ferreira et al. 2014	YES	KJ397605.1
Lepus arcticus	Northwest Territories	Canada	KJ397607	Melo-Ferreira et al. 2014	YES	
Lepus othus	Alaska	USA	KJ397608	Melo-Ferreira et al. 2014	YES	

2.11 Acknowledgments

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2.12 Permission from co-authors

I hereby give permission to Alexandra Jamieson to use our joint work as contribution towards her D. Phil thesis to be submitted for examination at Oxford University.

I confirm that to the best of my knowledge, the author contribution statement below is accurate and Alexandra Jamieson's contribution towards the work is greater or equal than that of any other co-author.

Chapter author contribution statement:
A.J and G.L. designed the project; A.J. generated data; A.J. analysed data; G.L., J.M.-F, F.B, and L.F provided support in interpreting results; A.J. wrote the paper with contributions from all other authors.

Date: January 26, 2021

Name: Greger Larson

Signature: 

Date: 28/1/21

Name: FIONA BEGLANE

Signature: 

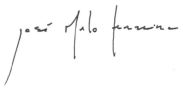
Date: 27/01/2021

Name: Laurent Frantz

Signature: 

Date: 26 January 2021

Name: José Melo-Ferreira

Signature: 

3. The movement of domestic cats to Britain and Ireland

3.1 Statement of Authorship

Research design: I designed the research, with input from Greger Larson and Naomi Sykes.

Data generation: I performed all the genetic laboratory analysis in Oxford for both the historic and ancient datasets generated as part of this project.

Analysis: I performed the majority of the computational analysis under the guidance of Laurent Frantz. Laurent Frantz called the nuclear SNPs and generated the PCA plot. I interpreted the results with input from Laurent Frantz, Greger Larson, Mark Beaumont, Helen Senn, Naomi Sykes, Ingrid Mainland and Fiona Beglane.

Manuscript: I wrote the manuscript, with input from all co-authors.

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3.3 Abstract

Cats are one of the most popular pets around the world today yet, despite their popularity, very little is known about their worldwide distribution. This study adds to the already growing research on the movement of domestic cats around the world, focusing on their arrival to Britain and Ireland. Specifically, this research studies their introduction to three areas: England, the Northern Isles of Scotland, and Ireland, all of which could only have been reached by maritime transport for most of the Holocene. Using an ancient DNA approach in conjunction with radiocarbon dating, we confirm that domestic cats first arrived in England in the Iron Age (800 BCE-100 CE), the Northern Isles by the Scottish Middle Iron Age (200 BCE – 400 CE), at the latest and to Ireland by the 7th century CE. Additionally, we discovered that the Vikings introduced their own lineage of domestic cats during their settlement of the Northern Isles. This study also begins to suggest that hybridisation between European wildcats and domestic cats was unlikely to have been a common occurrence in the Medieval period or earlier in Britain or Ireland, which could support the hypothesis that high levels of hybridisation is only a recent phenomenon in modern European wildcat populations.

3.4 Introduction

Cats and humans have been coexisting in close proximity to each other for thousands of years. They are one of the world's most popular pets, demonstrated by their worldwide distribution and Internet fame. Despite their popularity, studies are only just beginning to untangle our understanding of the anthropogenic dispersal of cats. The first decade (2007-2017) of research on the origins of cats focused on establishing the genetic relationships between each of the wildcat subspecies and locating where they started their close association with people (Driscoll et al. 2007). It was not until 2017 that ancient DNA was used to provide temporal depth (Ottoni et al. 2017). Ottoni et al. (2017) included a number of sites and periods, mainly in southern Europe, which was comprehensive for demonstrating the spread of domestic cats (*Felis catus*) across mainland Europe.

Although the distribution of sites investigated was varied, it was lacking many samples from northern and western Europe. Our study fills in this gap, adding samples from Ireland,

mainland Britain, the Northern Isles (Orkneys and Shetland) and Denmark. The samples from Denmark were included to provide a northern European comparison to test the hypothesis that the Norse may have translocated cats (Prehal 2011; Ottoni and Van Neer 2020). Ireland, mainland Britain and the Northern Isles provide useful regions for study as they are all geographic areas which can only be reached by maritime transport in the periods of interest. We look at 259 cats from 62 sites, ranging from the Mesolithic (9,000 - 4,300 BCE) to the Medieval/Post-Medieval period (410 - 1900 CE) thus providing both spatial and temporal breadth. The study of Irish cats focuses on a shorter timespan than Britain as the earliest current evidence for domestic cats in Ireland is from the early Medieval period (400 - 1169 CE) onwards. And the study of the Northern Isles was from their first appearance which was in the Scottish Iron Age (700 BCE - 900 CE). The aim of the study is to confirm when domestic cats first arrived in mainland Britain and the Northern Isles and to investigate their arrival in Ireland in the early Medieval period. Both mitochondrial and nuclear DNA analysis are used to answer the above questions and to identify the presence of domestic cat/European wildcat hybrid individuals in the past. This will help us to understand how recently hybridisation began between these two species.

Questions posed by this study:

1) When were domestic cats first introduced to mainland Britain?
2) From where do domestic cats in the Northern Isles originate?
3) Where was the origin of the domestic cats in Medieval Ireland?
4) Is there any evidence for hybridisation between domestic cats and European wildcats in ancient British or Irish cats?

3.4.1 Overview of current research into the arrival of domestic cats to mainland Europe

To understand the arrival of cats to Britain, it is important to first understand their origins and initial human-aided dispersal. There are currently six recognised species of Old World small cats. The following are the main species and sub-species found in European and African: the European wildcat (*Felis silvestris silvestris*), African wildcat (*Felis lybica lybica*), Asiatic wildcat (*Felis lybica ornata*), Southern African wildcat (*Felis lybica cafra*), Black-footed cat (*Felis nigripes*), Sand cat (*Felis margarita*) and Jungle cat (*Felis chaus*) (Kitchener et al. 2017). The Chinese mountain cat (*Felis bieti*) has recently been recognised as its own

species and is no longer considered a subspecies of wildcat (Kitchener et al. 2017). Of these wildcat species and subspecies, only one of is known to have been domesticated — the African wildcat (*F. l. lybica*), which started its commensal relationship (where the human-animal relationship benefits the animals without negatively impacting humans) with people in the Neolithic period in the Near East (around 9,800-3,300 BCE) (Driscoll et al. 2007; Ottoni et al. 2017; Ottoni and Van Neer 2020). Our current understanding of the dispersal of cats is that all modern domestic cats trace their origins back to at least five founder populations of North African wildcat located around the coast of the Levantine Sea from Egypt to Turkey (Ottoni et al. 2017).

The cats found in human homes all around the world today are domestic cats (*Felis catus*). The North African wildcat became the domestic cat through commensalism, followed by domestication, resulting in the formation of this separate subspecies. This transformation from the African wildcat to the tame housecat is not the typical route of most domestic animals. Cats lack most of the typical hypothesised characteristics of domestication, for example, neoteny (retention of juvenile features in the adult animal) (Bradshaw, Casey, and Brown 2012). However, they do demonstrate some behavioural differences from their wild ancestors. For example, domestic cats show increased tameness in comparison to their wild relatives which tend to avoid both people and human habitation (Macdonald 1987; Berteselli et al. 2017). With the cats acting as natural pest control, there was little need for humans to alter the behaviour of their cats (Driscoll et al. 2007; Berteselli et al. 2017; Serpell 1988). Domestic cats have been shown to have an attachment to the habitation site and not the humans themselves, unlike other domestic species, such as dogs (Davis 1987). This is as potentially as true today as it was in the Neolithic of the Near East.

Given that their behaviour, morphology and physiology did not significantly change upon domestication, it is not surprising that domestic cats are genetically hard to differentiate from the North African wildcat. This is further complicated by the close proximity in which domestic cats and North African wildcats lived. They dwelt alongside each other for much of their early existence, allowing for regular genetic exchange and therefore low levels of differentiation (Montague et al. 2014). The genetic similarity between the domestic cat and North African wildcat makes it difficult to establish when exactly the North African wildcat

became the domestic cat (Montague et al. 2014). Montague et al. (2014) have, however, identified certain nuclear genetic regions which differentiate domestic cats from their wild relatives. Their analysis was conducted using high coverage full nuclear genomes (~7-58x), which is outside the aims of this study and would involve the difficulty of acquiring high coverage full genomes from ancient DNA. Due to this genetic similarity, from here on we will refer to the North African wildcat as the domestic cat when it is found associated with people.

Bearing the above in mind, how did the North African wildcat go from living in the wild to living in our homes today as a domestic cat? Wildcats have been found on human settlements in the Near East since around 10,000 years ago and must have arrived by one of two ways. Either the cats wandered into the settlement of their own accord or people transferred them from the wild to their domestic settings (Ottoni et al. 2017; Ottoni and Van Neer 2020). Either is possible the former given the ability of the wildcat to adapt to new environments and the later as there are historic as well as recent accounts of wildcat kittens being found and adopted by people (Serpell 1988).

The Neolithic was the start of farming and settled societies, opening up the opportunity for the domestication of a number of plants and animals including sheep, goats, cows, pigs, wheat, barley and rye (Salamini et al. 2002; Zeder 2012, 2011). This, in turn, led to storage areas for grains and other goods as well as large amounts of refuse. These would have attracted small mammals like voles, rats and mice (Cucchi et al. 2020). The presence of live prey species and also the refuse would have attracted cats and, given their small size, they could be largely unnoticed while scavenging in human settlements, as opposed to other carnivores in the area, such as leopards (Peters and Schmidt 2004; Macdonald 1987). Cats are small enough to appear unthreatening to humans, which may be a reason why they were not pushed away from human settlements. This would have allowed for their gradual adoption as a commensal species, followed by their domestication and, later, their adoption as pets. As the North African wildcat was the only wildcat species present in the Near East during the Neolithic period, it became the ancestor to all modern-day domestic cats.

The current understanding is that only one cat species or subspecies has been domesticated. However, there is now another cat among the larger *felid* sub-family which, from recent research, is thought to have followed this commensal pathway and may be regarded as domesticated. Through geomorphometric analysis, the leopard cat (*Prionailurus bengalensis*) has been identified at Neolithic sites in the Shaanxi and Henan Provinces of modern day China (Vigne et al. 2016). Their arrival through hunting cannot be completely ruled out. However, the authors argue for commensalism based on the extensive wear on many of the specimens' teeth (suggesting a human-manipulated diet), the smaller size of all the mandibles compared to wild leopard cats and the intentionality in the burial of the articulated cat skeleton at Wuzhuangguoliang (Vigne et al. 2016). Further excavation and analysis of cats from Chinese Neolithic sites will help to improve our understanding. Even though the leopard cat was potentially interacting with people in the past, it did not survive as a domesticate to the modern-day. All modern-day domestic cats derive from the Near Eastern cat subspecies, the North African wildcat, including all domestic cats found in China (Driscoll et al. 2007). This demonstrates that the domestic relationship formed in the Near East was not the only instance of cat-human interaction, but it was the only one to survive to the present day.

Given that we now have two examples of cat species in separate parts of the world which formed commensal relationships with people, could there be another? So far there is no evidence for any other cat species or subspecies found to have lived on human habitation sites in the past, apart from when hunted and brought back as kill. There is, however, still a possibility that commensal relationships with wildcats could have occurred in places other than the Near East and China. All species of cats within the *felid* sub-family existed alongside people in various locations throughout their natural range. The Neolithic period, with its permanent settlements, opened up an opportunity for the North African wildcat in the Near East and, similarly, the leopard cat in China. There are other parts of the world where cat species and humans coexisted with potential niches for cats to exploit before the worldwide domination of the North African wildcat as the domestic cat. In addition to studying the earliest domestic cats in Britain and Ireland, this study could also reveal evidence for the wildcat native to Britain, the European wildcat, living among humans in the past.

3.4.2 Human movement of the domestic cat

The earliest agreed-upon evidence for the North African wildcat outside of its natural range is from the Neolithic site (around 7,500 BCE) of Shillourokambos on the island of Cyprus, which was previously uninhabited by any cat species (Vigne et al. 2004). At the site, an eight-month-old kitten with no visible cut marks was found buried in a small pit beside a high-status human burial. The intentionality of burial and the absence of cut marks suggests that this cat was not a source of food, but had some other use to the people of Shillourokambos (Vigne et al. 2004). This is seen as the earliest evidence for cats as a domesticate as it is the first evidence for people manipulating the distribution of cats. It demonstrates that people had attributed some form of value to cats for them to be moved to the island. A probable reason is to guard food stores against pests. From around 7,500 BCE onwards, we have both archaeological evidence for the North African wildcat being moved by people and genetic evidence confirming this (Ottoni et al. 2017). Domestic cats became widespread in Europe with the Romans, and the only evidence prior to the Romans of cats being found north of the Alps is from a handful of Iron Age sites in Britain. The cat bones on these sites were classified as domestic due to the presence of a litter of kittens as well as adult and juvenile bones found on the site (Harcourt 1979).

Using domestic cats for pest control is a practice that is still often used today in farming communities around the world. However, there has been some debate as to whether domestic cats are actually capable of keeping pest numbers down, as it is known that they do not actively hunt mice, rats and other small mammals in large numbers. There is some truth to these arguments, as demonstrated by a survey of Lowland English farmers conducted in 1978 (Macdonald 1987). Domestic cats are not able to stop an existing infestation, but are able to reduce the likelihood of future infestations by preventing large increases in pest numbers (Elton 1953). It is also worth noting that the reason given by most farmers for keeping cats was to keep pest numbers down (81.7% of English farmers had cats, 86.7% of whom claimed to have cats to keep pest numbers down) (Macdonald 1987; Corbet and Harris 1996). There has also been some research which shows domestic cat urine odour can deter commensal rodents (Mulungu et al. 2017). Exploiting cats thinking it will help maintain food supplies seems worthwhile to farming communities who often store

food for several months and rely on these supplies in leaner parts of the year. This is as true today as it would have been in the past. Whether or not cats keep pests under control it is important that people believe they do for at least their initial global spread.

The use of cats for pest control is the most plausible reason for cats interacting with people, but there are other possible routes which cannot be discounted. The anthropologist, Serpell, observed that hunters in the Amazon brought back young cats and gave them to the women of the community who would hand-rear them and keep them rather like pets (Serpell 1988). He also observed that these wildcats were mourned when they died, which could explain the burial of the cat on the island of Cyprus in the Neolithic period. It is well known that wildcats in Africa are relatively easy to tame. Georg Schweinfurth observed in South Sudan in the 1860s that wildcats lived and foraged near to human settlements. He reported that people often brought back wild kittens, tied them up for a few days so as to calm them, which led to them acting like house cats preying upon rats (Schweinfurth 1879). Schweinfurth even tied a cat to his bag to help keep the rats away from him and his belongings. These anthropological accounts demonstrate the ease with which cats are adopted into communities. This, alongside the archaeological evidence, has made possible the reconstruction of the conceivable routes cats took to form their close relationships with people in the past.

3.4.3 Background to cats in Britain and Ireland

3.4.3.1 The native European wildcat arrival in Britain and Ireland

Domestic cats were not the first wildcat species to arrive in Britain as the European wildcat was present long before humans introduced domestic cats. The earliest evidence in Britain for the European wildcat is from two Hoxnian Interglacial sites: Joint Mitnor Cave, Devon (Marine Isotope Stage (MIS) 5e, 124,000-119,000 years ago) and Barnfield Pit, Swanscombe, Kent (MIS 11, 424,000-374,000 years ago) (Sutcliffe 1960; Schreve 1996). Adult European wildcat bones were found at both of these sites, presumably as a result of hunting. A recent genetic study has been conducted examining the early European wildcats of Britain (15,000 – 1,618 BP) (Marr 2016). Marr (2016) found that all of the wildcats grouped into the west-central European clade and that their origins were France or

Belgium. This is not surprising given that Britain would have been connected to the continent at the time of the earliest cats.

European wildcats were widespread in Britain in the past. There is evidence for wildcats on British archaeological sites, such as the Neolithic (4,000-2,500 BCE) to Bronze Age (2,500-800 BCE) site of Windmill Hill, the Iron Age site of Glastonbury Lake village and the Medieval site (14-15th century) of Kilton Castle where wildcats were found among domestic cats (Yalden 1999; O'Connor 2007; Smith 1965; Zeuner 1951). Wildcats were found throughout Britain until relatively recently, however they are now confined to the highlands of Scotland. Their presence on archaeological sites has been hard to determine using morphometrics due to the morphological similarities between European wildcat and domestic cat bones. Cat bones found from the Roman period onwards on human settlements have largely been classified as domestic cats, partially due to this difficulty. However, a zooarchaeological linear metric study conducted by O'Connor has shown that wildcats were present as late as the Medieval period at Kilton Castle, Lincoln and York (O'Connor 2007).

While European wildcats arrived naturally to the mainland of Britain, their arrival to Ireland and the Northern Isles may not have been this way. Wildcats first possibly appear in the Mesolithic period in Ireland around 7,500 BCE (van Wijngaarden-Bakker 1989). The earliest site with evidence for the presence of European wildcats is the Mesolithic site of Lough Boora however the bones themselves were not directly dated only the charcoal (Montgomery et al. 2014; van Wijngaarden-Bakker 1974; Ryan 1984). They have also been found at the site of Newgrange in the Beaker period, however these also have not been directly dated and horse remains from the same deposits have been dated as Iron Age (Bendrey et al. 2013). It is believed that these cats arrived with the aid of people as no substantial evidence has been found of wildcats in the early Holocene of Ireland (McCormick 1999). It is possible that wildcats may have been present in Ireland before the Last Glacial Maximum (around 27,000 years ago), disappearing when the ice advanced. There is evidence for them in early cave deposits alongside other temperate fauna, such as those found at Kilgreany Cave, however none of these remains have been directly dated and so it is not possible to draw conclusions from these (Jackson 1929). As European

wildcats are a temperate species, and given that Ireland was covered by an ice sheet until the end of the Pleistocene, it is unlikely that cats arrived by their own means prior to the Holocene. Furthermore, Ireland has been cut off from Britain since the Last Glacial Maximum, making a natural land-crossing impossible, and their survival through the Last Glacial Maximum very unlikely (Hughes et al. 2016; Edwards and Brooks 2008). Therefore, arrival with people is the most probable explanation for the presence of European wildcats in Ireland.

The exact date of their disappearance from Ireland and most of Britain is unknown. Wildcats disappeared from large swathes of Britain by the beginning of the 20th century at the latest, a similar time to the polecat and pine martin, two other larger predators (Sainsbury et al. 2019). The main reason for the population decline for all three species was the increase in game hunting for sport and the start of the gamekeeper profession around the 18th and 19th centuries (Langley and Yalden 1977; Stuart 1982). This was especially true for the wildcats, which were blamed for stealing chickens and young lambs, and therefore persecuted, as well as hunted for their furs (Corbet 1974). Wildcats were listed as vermin in the 'Act for the Preservation of Grayne' (*An Act for Preservation of Grain* 1566), and there are several accounts of churchwardens placing a bounty on them. Nelson (1881) recounts the Churchwardens books from Corbridge-on-Tyne which show accounts of wildcats being exchanged for money. One wildcat was worth 4d (£1.94 in today's money). There are entries for both 1677 and 1723 of wildcats being caught and the total recorded by the churchwarden between 1677 and 1724 was 141 (Nelson 1881). This persecution by people from the 16th century onwards plus the gradual decline of their natural habitat, the forest, is the likely reason for their eventual disappearance from most of Britain (O'Connor and Sykes 2010).

Their disappearance from Ireland looks to be much earlier. It is thought that wildcats disappeared sometime in the Bronze Age as no remains have been found after this point. However, this is not a certainty (Benecke 1999). The latest site where the remains of a European wildcat have been found is at the Bronze Age site of Chancellorland (Kelly 1997). It is known that there was an increase in intensive farming in the Late Bronze Age which resulted in deforestation, destroying parts of the natural habitat of the wildcat (Spencer et

al. 2020). If the wildcats were present only in small numbers, such habitat destruction could have led to their extinction. Overhunting is also a possible explanation. Exploring the disappearance of European wildcats from Ireland is not within the scope of this study, but warrants further investigation as very little is known about the arrival or disappearance of the European wildcat in Ireland.

3.4.3.2 The arrival of domestic cats to mainland Britain

There has been much speculation as to when people first brought domestic cats to Britain. Up until the late 1970s, scholars agreed that cats arrived in the Roman period as a method to keep rodent numbers down, as was done in other parts of the Roman world (Lazenby 1949). There was clear evidence for them at the Roman site of Silchester, Hampshire. In the 1891 excavation a full cat skull was uncovered and cat footprints were found on two tiles (Jones 1892; Lever 1979). The skull was compared to known European wildcats and domestic cats and was classified as domestic, putting the Roman period as the first occurrence of domestic cats in Britain. This was pushed back further with the analysis of the cat remains from the Iron Age (300-100 BCE) site of Gussage All Saints, on the south coast of Britain (Harcourt 1979). The cats on the site were classified as domestic based on the five new-born kittens being found together in a feature as an associated bone group (Wainwright 1979). The rationale behind this classification was that kittens were unlikely to have been killed for meat or fur; additionally, it was also unlikely that a wildcat would intentionally enter a human settlement to give birth. The Iron Age is therefore the current agreed-upon period for the arrival of domestic cats in Britain, based on this one site and five kitten skeletons (Harcourt 1979; Wainwright 1979; Faure and Kitchener 2009; Buhrs 2012; Davis 1987; Kitchener and O'Connor 2010; Beaumont et al. 2001). These kitten bones are included in this study and our analysis has been able to shed more light on Iron Age Britain's cats.

The earliest textual evidence for domestic cats in Britain comes from the laws of the 10th century Welsh prince, Hywel. One law refers to the punishment for killing a cat which guards the king's barns (Wade-Evans 2016). By the Medieval period, cats were well established in Britain and their role in aiding with pest control is clear.

3.4.3.3 The arrival of domestic cats to the Northern Isles

In addition to the British mainland, there is early evidence for cats on the islands of Orkney and Shetland, also known as the Northern Isles of Scotland. The Orkneys and Shetland have never been connected to the mainland, or only connected for a very short period of time between the retreat of the ice sheet and the rising sea levels, making crossing unlikely for European wildcats (Phillips 2004, Ballin 2017). It is therefore believed that European wildcats have never been present naturally on either island. Current understanding is that domestic cats arrived in the Iron Age (Kitchener and O'Connor 2010). In the Shetland Islands, the earliest cats have been found at Old Scatness in the Iron Age phase 6 of the site (1st-4th century CE) and the Late Iron Age phases of Jarlshof (Cussans et al. 2010; Hamilton 1956). In the Orkneys, the earliest cat remains are from the site of Howe where cats have been found in the site's phase 4/5 (5th-3rd century BCE) (Smith 1994). It is important to note that the Scottish Iron Age lasts up to the 10th century CE (much later than the Iron Age in England) and ended with the arrival of the Vikings in the 10th century CE to both the Orkneys and Shetland Islands (Pearson, Sharples, and Mulville 1996; Hunter 2007; Bond and Dockrill 2016; Griffiths 2019).

The earliest cats found in these Iron Age deposits were initially thought to be wildcats due to their context date being before the expected arrival of domestic cats in Britain (Smith 1994). However, Kitchener and O'Connor (2010) have suggested that the earliest cats should not be assumed to be European wildcats, and that further study of these remains is needed. O'Connor (2007) studied the cats from Howe and found the cats from phase 8 (5-8th century CE) to be predominantly domestic cats with one possible wildcat. He also found a possible wildcat among the domestic cats at Earl's Bu which was a high-status Viking to Late Norse site (10-12th century CE). While the majority of the cats studied were domestic cats, the finding of a few potential wildcats in these later deposits may indicate the presence of native wildcats in the earlier periods. O'Connor points out that the Orkneys were well outside the range of Roman influence and he therefore suggests that the domestic cats in Orkney were not introduced from the Roman world (O'Connor 2007). As the individuals from Howe were from before the arrival of the Vikings, a Viking-mediated introduction can also be discounted. The only known contact during this time was with mainland Scotland (Ritchie and Renfrew 1985). From this information, the most probable

source of domestic cats in the Northern Isles in the pre-Viking era was mainland Scotland. However, the Iron Age people on the mainland may not have been the only source of trade. Contact with the Roman world cannot be fully discounted, as was done by O'Connor. There is evidence of Roman trade, such as the finding of a Haltern 70 Roman amphora at the Iron Age site of the Broch of Gurness, Orkneys (Fitzpatrick 1989). Whether this Roman artefact arrived in the Orkneys through direct trade with the Romans or through trade with the Middle Iron Age communities of Mainland Scotland, who in turn had traded with the Romans, cannot be determined. However, there is further evidence of the direct contact between the Orkneys and the Roman world. There is written evidence in the 4th century CE where the historian Eutropius declared the Orkney Islands submitted to Claudius (Erickson 1990). This shows that the Orkneys were at least known to the Romans at this time. Given the presence of Roman artefacts in the Orkneys in the Iron Age, and the Roman knowledge of their existence, it is therefore possible that the domestic cats found on the Iron Age sites may have come from the Roman world prior to the arrival of the Vikings, either directly or through trade networks. Through this genetic study, it will be possible to further add to this understanding.

By the Viking/Norse period (late 8th-13th century CE), cat remains are found in much higher numbers compared to the Iron Age (Cooke 2017; Mainland, Ewens, and Webster 2019). Additionally, this period is the first time that cat associated bone groups (ABGs) are found in the Orkneys, with the earliest two individuals at Snusgar (9th-10th century CE) (Cooke 2017). They were found in the foundation deposit of the doorway between the byre and the hall. There is also evidence of a paired cat burial in the Viking/Norse period at the site of Pool, the Orkneys (Bond 2007). It is hard to interpret the significance of finding associated bone groups; they may indicate that cats were living and dying at the sites as pets, or merely that cats were present on the site, butchered and the carcasses left intact, or they formed part of a ritual or superstition. Nonetheless, evidence of cat burials in the Northern Isles suggests that cats were thought of as important, and possibly kept as pets. There is also cultural evidence, which may explain the increase in cat numbers with the arrival of the Norse people. It is thought that cats arrived in Scandinavia as Norse traded in the Mediterranean and Black Sea regions (Engels 2018). However, there is evidence of their presence in Denmark even before this in the Bronze Age and Roman Iron Age (Bitz-Thorsen

and Gotfredsen 2018). This does not mean the Norse did not bring cats back to Scandinavia from further south, however it shows these were not the first. Cats were seen to have magical and symbolic properties, as they associated them with Freyja (Prehal 2011), the goddess of home, fertility and female magic. This would provide a strong motivation for Norse to bring traded cats back home to Scandinavia. It is known that cats were used in rituals for special occasions and were buried with important chieftains, such as at the Gokstad ship burial (Prehal 2011; Toplak 2019). Their value can be further seen by their cost, as cat skin was worth three fox skins in 12th century Iceland (Hårding 1990). Cats were highly valued either for their magic properties or for their rarity by the Norse people and therefore it seems plausible that they brought their cats with them when they came to the Orkneys and Shetland. It is through this genetic study that we will be able to determine if Norse cats were brought to the Northern Isles.

3.4.3.4 The arrival of domestic cats in Ireland

From current understanding, domestic cats arrived relatively late in Ireland compared to the rest of Europe. They are only unequivocally found in the early Medieval period of Ireland (McCormick and Murray 2007). There is possible earlier zooarchaeological evidence from the 2nd century CE, but only from one site at Scariff Bridge, Country Meath (Mitchell 1987; Maccoitir 2015). Van Wijngaarden-Baker proposed that domestic cats most probably arrived in Ireland from the 1st century CE as they were present in England at that time. However, the lack of evidence makes this difficult to confirm (van Wijngaarden-Bakker 1974). Knowth is the first site where it is clear that domestic cats were present, first being seen in the 7th-8th century contexts of the site (McCormick and Murray 2007). There is also historical evidence for cats in Ireland in this period. The famous poem written by an Irish monk about his white cat, Pangur Bán, is from the 9th century (Thurneysen 1975; Murphy 1956). Cats are also illustrated in the Book of Kells, another 9th century manuscript produced partly in Ireland (Unattributed 800). Although their arrival in the 1st-2nd century CE cannot be completely discounted, it is clear that domestic cats were widespread in Ireland in the early Medieval period and have been present ever since.

3.4.4 Hybridisation between wildcat and domestic cat

It is well known that European wildcats and domestic cats interbreed and produce fertile offspring (Senn and Ogden 2015; Beaumont et al. 2001). This has been observed throughout their range, with high levels of hybridisation in Hungary and Scotland today and lower levels throughout the rest of their modern range (Mattucci et al. 2016; Steyer et al. 2018; Tiesmeyer et al. 2020; Quilodrán et al. 2019). What is unknown is how far back in time this hybridisation has been occurring and at what frequency. Hybridisation has probably occurred wherever the species overlapped, but given the low hybridisation levels in most of the range today, even in areas where the European wildcats' habitat is under threat, it looks not to be this simple. Ottoni et al. (2017) demonstrated that the North African wildcat naturally expanded its range into Europe and that admixture was expected between the two species in this overlapping range. Although hybridisation is low between domestic cats and European wildcats in most of Europe, there is one place where it is a large-scale issue. From studies of modern and historic cats (1895-1985), Senn et al. (2018) found there has been a recent acceleration in hybridisation in Scotland from the historic period to today, with most of this being in the last decade.

The current understanding is that a high level of hybridisation in wildcat populations is a recent occurrence, accelerating in the second half of the 20th century (Senn et al. 2018). However, since domestic and wildcats are interfertile and have been in contact for many thousands of years we cannot assume that there was no hybridisation in the past and indeed even if hybridisation was a rare event we would expect to see some genetic legacy. Therefore, for this study, full genomes have been generated for a small subset of the data with enough endogenous DNA content to assess the level of past hybridisation. Additionally, all ancient cats in the study with enough coverage have had their nuclear DNA screened using a new species identification method (HAYSTAC) to ensure that species assignment is not based solely on the mitochondrial DNA which only shows the maternal lineage of the cat. From modern studies of cats in Germany, a mating event between a female wildcat and a male domestic cat is the most common, resulting in European wildcat mitochondrial DNA being passed on (Steyer et al. 2018). In order to detect hybridisation nuclear DNA needs to be analysed as mitochondrial DNA only reflects the maternal lineage.

3.5 Material and Methods

Differentiating between domestic cats and European wildcats is not always easy morphologically but it was crucial for this study to distinguish unquestionably between the two subspecies. This was especially true for the juvenile and kitten remains, for which it is very difficult to identify the subspecies morphologically as the bones are not fully grown. With their presence providing us with the most convincing evidence for commensal cats, accurate determination of their subspecies is highly significant to this study. We used genetic analysis to determine subspecies identifications for the cat samples in this study, allowing us to identify when domestic cats arrived and who brought them to each area of interest.

3.5.1 Sample collection

193 cat bones were collected from 34 sites across Britain, Ireland and Denmark (Table S3.1). For each site, where possible, the MNI (Minimum Number of Individuals) was taken from each stratigraphic layer to maximise the likelihood of successfully extracting DNA from at least one specimen from the site, and ideally a few from each time period when a site was multi-period. All of the samples were collected either directly from the excavator or from the zooarchaeologist or museum where the bones were housed. The sites range from the Mesolithic through to the Post-Medieval period.

For the ancient DNA analysis, 30 extracts were provided by Anne Birgitte Gotfredsen from 11 Danish sites. Another 36 individuals were provided by Claudio Ottoni from 17 locations across mainland Europe, the Middle East and Tanzania (Table S3.1). All samples from Ottoni have had short fragments of their mitochondrial DNA and Single Nucleotide Polymorphisms (SNPs) in the Transmembrane aminopeptidase Q (Taqpep) gene (gene responsible for tabby pattern variation) sequenced previously (Ottoni et al. 2017).

Historic cats were also included for comparison. Helen Senn, Andrew Kitchener and Louise Tomsett provided extracts for 39 historic cats and one modern cat from across Scotland (Table S3.2). They were all acquired from the collections of the Natural History Museum of Scotland, Natural History Museum, London and the New Walk Museum, Leicester. These

were part of a wider study looking at 35 SNP loci of Scottish cats, so none have had their full mitochondrial genome previously sequenced (Senn et al. 2018).

Modern full genome sequences were provided to us by Carlos Driscoll for comparison to our ancient dataset, along with one modern Scottish wildcat provided by Mark Beaumont and Helen Senn for use in the HAYSTAC (High-AccuracY and Scalable Taxonomic Assignment of metagenomiC data) custom database (Table S3.3, S3.4). Bill Murphy provided a further two sequences from modern cats for use in the analysis. These are all from currently unpublished forthcoming papers. We were also provided with a full genome sequence of an ancient cat from the early Medieval city of Dhzankent, Kazakhstan by Ashleigh Haruda (Haruda et al. 2020). For HAYSTAC we used two sequences from a preprint of a soon to be published paper (Yu et al. 2020).

3.5.2 Ancient DNA laboratory methods

3.5.2.1 Extraction, library building and sequencing

All samples were prepared in a dedicated ancient DNA facility at the University of Oxford. Bone samples were cut using a Dremel multi-tool drill to between 50-200 mg. The surface of the bone was removed using a circular cutting disk to eliminate any surface contamination of modern DNA. The benchtop was cleaned with 70% ethanol and 10% bleach between each sample and gloves were changed to reduce the risk of cross-contamination. Protective clothing was used to reduce the risk of contamination from the researcher. Blanks were used as negative controls at every stage of the laboratory procedures from extraction to capture.

The bones were powdered using a micro dismembrator. Equipment and surfaces which had been in contact with the sample were thoroughly washed between samples with ethanol and bleach. The DNA was extracted using a protocol based on Dabney et al. (2013) with modifications from Damgaard et al. (2015). The powder was pre-digested in 1 ml of extraction buffer (water, 10 mg/ml Proteinase K, TWEEN 20 and 0.5 M EDTA, pH 8.0) for 30 minutes to remove contaminant DNA. They were then incubated overnight in a fresh batch of 1 ml of extraction buffer at 37 °C to completely dissolve the powder. The samples were spun on a benchtop centrifuge to pellet the bone powder, and the supernatant was

removed and mixed with binding buffer (guanidine hydrochloride, isopropanol, TWEEN 20 and water) and sodium acetate. The samples mixed with the binding buffer and sodium acetate were then run through a MinElute spin column to collect the DNA. This was then washed in PE buffer (QIAGEN) and finally eluted with 84 µl of TET (0.5 M EDTA, pH 8.0, Tris-HCl, pH 8.0, TWEEN 20 and water) into a fresh collection tube.

Next-generation sequencing libraries were built on 32 µl of DNA extract using Carøe et al.'s method (Carøe et al. 2018). SPRI (Solid Phase Reversible Immobilization) beads (Beckman Coulter) were used for purification of the libraries as instructed in the protocol. The prepared libraries were then assessed for the optimal number of cycles for PCR (polymerase chain reaction). The number of PCR cycles was determined by performing qPCR (Quantitative PCR) using the StepOne Real-Time PCR System (Applied Biosystems) according to the manufacturer's instructions, using the same length of forward and reverse primers as for PCR. This gave the optimal number of PCR cycles for each library. DNA libraries were then double external indexed using standard Illumina P5 and P7 primers and amplified in a 50 µl PCR reaction (15 µl of library, 25µl AccuPrime SuperMix I, 4 µl BSA (10 mg/ml), 3 µl of P5 primer and 3 µl of P7 primer). Thermocycling conditions comprised an initial denaturation step of 2 minutes at 95 °C, followed by cycles of 15 seconds denaturation step at 95 °C, 30 seconds annealing step at 60 °C and 30 seconds extension step at 68 °C for the number of cycles specified for each sample, followed by a final extension step of 7 minutes at 68 °C. The amplified libraries were then pooled together in three batches and purified using the QIAGEN MinElute columns following the manufacturer's instructions. This was followed by size selection using SPRI beads (Beckman Coulter), and quality control conducted on a TapeStation 2200 (Agilent Technologies) prior to being sent for sequencing. The first batch was sequenced on a single lane of a HiSeq 4000 instrument at the Crick Institute, London. The second and third batches were sequenced on a single lane each of a HiSeq4000 instrument at Novogene, Sacramento.

3.5.2.2 Ancient mitochondrial DNA capture

In-solution targeted capture of the *Felis* mitochondrial genome was performed on 78 samples following the myBaits v.4 (Arbor Biosciences) Hybridization Capture for Targeted Next-Generation Sequencing (NGS) protocol with the following conditions: a hybridisation

temperature of 60 °C and a hybridisation time of 48 hours. The *Felis catus* mitochondrial reference genome (NCBI: NC_001700.1) was used to synthesise the baits for capture.

Given the degraded nature of ancient DNA, the amount of endogenous DNA per sample is far less than would be expected of modern samples. Due to this, we were able to add more samples per reaction. First, between 8-19 ancient libraries were pooled equimolarly per reaction and the pools were decided based on the percentage of endogenous DNA with mapping quality above 30. Then, three reactions were pooled for the first sequencing lane which consisted of a total of 40 libraries and then two reactions were pooled for the second lane which consisted of a total of 38 libraries. The two lanes were sequenced on an Illumina HiSeq 4000 at Novogene, Sacramento.

3.5.2.3 Ancient full genome DNA deeper sequencing

Libraries with mapping scores above 15% were selected for deeper sequencing. In total, this included eleven individuals. These libraries were sequenced in two batches, the first consisted of five libraries sequenced alongside another five libraries from another project, the second batch consisted of six libraries sequenced alongside another ten libraries from another project. Both were sequenced on one lane each of a NovaSeq 6000 at Novogene, Sacramento.

3.5.2.4 Historic mitochondrial DNA

Extracts of historic Scottish cats were processed in the same way as the ancient as they all came from museum specimens. They were sequenced in the second screening run of ancient samples on a HiSeq 4000 at Novogene, Sacramento.

3.5.3 Bioinformatic analysis

3.5.3.1 Mitochondrial analysis of sequencing data

Both ancient and historic sequences were processed by trimming the adapters and collapsing the reads using AdapterRemoval (v.2.3.0). The sequences were then aligned against the indexed *Felis catus* reference genome (NCBI: GCF_000181335.3) using BWA aln (Text S1) (Li 2013). The mitochondrial genomes were then extracted from the complete sequence files using Samtool view (v.1.6). The ancient, historic and modern mitochondrial

sequences were aligned against each other using MAFFT (Multiple Alignment using Fast Fourier Transform) (v. 6.240). To ensure that the tree was constructed with only the most informative reads, only samples with over 2x depth of coverage and less than 40% missing data were used for downstream analysis. This cut off of 40% was chosen due to the issue of regions of the mitochondrial genome mapping to the nuclear genome due to nuclear mitochondrial DNA (NUMT) (Text S3.1). This left 66 ancient samples from 36 sites for analysis. An initial maximum likelihood tree was created from these aligned sequences using RAxML (Randomized Accelerated Maximum Likelihood) (v. 8.2.9). Further analysis of the topography of the tree was explored using two Bayesian trees, first a Bayesian tree constructed with MrBayes using the same aligned sequences as was used with RAxML and, secondly, a stricter Bayesian tree using only samples with 10x depth of coverage and the stricter criteria of less than 10% of missing data. These mitochondrial genomes were further cut to the ND5 and ND6 region for comparison to the already published modern wildcat datasets from Driscoll et al. (2007). This was visualised using RAxML. The dataset from Ottoni et al. (2017) was not included as it did not fit our missing data criteria for inclusion. In our dataset we have some samples which were first used in the Ottoni et al. study. We have included their lineage assignment from the 2017 study in their label names on the trees.

3.5.3.2 Nuclear subspecies identification

As it was beyond the scope of this study to perform extensive nuclear analysis, we used a species identification method on the nuclear genomes to verify if the nuclear DNA was the same subspecies as the mitochondrial DNA for each ancient sample. We passed the sequences through the newly-developed programme, HAYSTAC, to identify the nuclear DNA using a custom RefSeq-like (Reference Sequence) database of nuclear cats for comparison (Table S3.4, Text S3.2) (Dimopoulos et al. 2020). Simulations were also run for this analysis to ensure authenticity of results (Text S3.3). The use of HAYSTAC has allowed us to identify down to subspecies level for the nuclear DNA.

3.5.3.3 Ancestry analysis

We used publicly available data from 357 domestic cats, thirteen European wildcats and two North African wildcats, which were genotyped on the 62,897 SNPs Illumina Infinium iSelect DNA array (Gandolfi et al. 2018). To minimize issues arising from ancient DNA damage, we excluded all transitions from this analysis, resulting in 10,380 nuclear SNPs. We then pseudo haploidised the data by first selecting an allele at random for all cats available in the 62,897 SNPs using a custom Perl script. We then merged this data with pseudo haploid data from ancient samples obtained using HTSbox pileup and PLINK (v1.90b3.38). A PCA (Principal Component Analysis) was then performed using smartpca by projecting ancient data onto axes defined by modern high-coverage data from Gandolfi et al. (2018) (option LsqProject=YES) (Patterson, Price, and Reich 2006; Price et al. 2006).

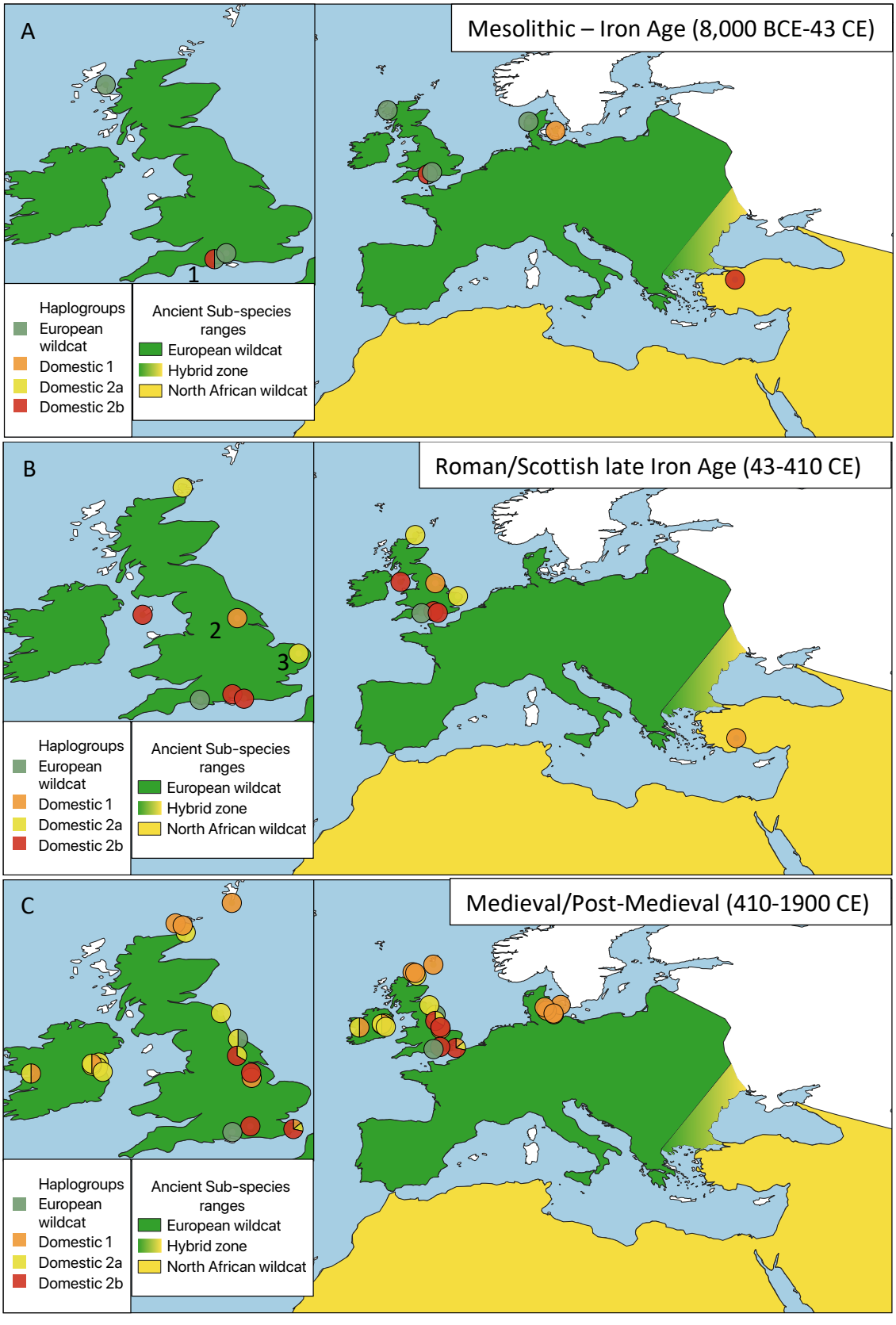
ADMIXTURE 1.3.0 was used to assess the ancestry of the twelve cats using the same 10,380 SNPs as was used for the PCA analysis (Alexander and Lange 2011). The cross-validation results suggested K=10 (K is the number of subpopulations) would show the most informative differences between all the samples (Figure S3.4c). Therefore, K was plotted from K=2 to K=10.

3.5.4 Radiocarbon dating

Fifteen samples were radiocarbon dated by either the Oxford Radiocarbon Accelerator Unit or Beta Analytic. This included the oldest cat in the analysis, from the Mesolithic site of An Corran, Scotland and twelve individuals covering the earliest possible arrival of domestic cats to the south coast of Britain and to the Northern Isles. Two individuals from Ireland with uncertain dates were also dated. In addition, a radiocarbon date had already been obtained, as part of another project, for a sample from the Anglo-Saxon period site of Lyminge (OxA-31749). All radiocarbon dates reported are calibrated using OxCal 4.4 and the INTCAL20 calibration curve (Reimer et al. 2020). One sample (AJ517) had a high delta 13C value (-14.7) so has been calculated using the mixed curve approach using the Marine as well as the INTCAL20 calibration curve.

3.6 Results

3.6.1 Summary of mitochondrial results



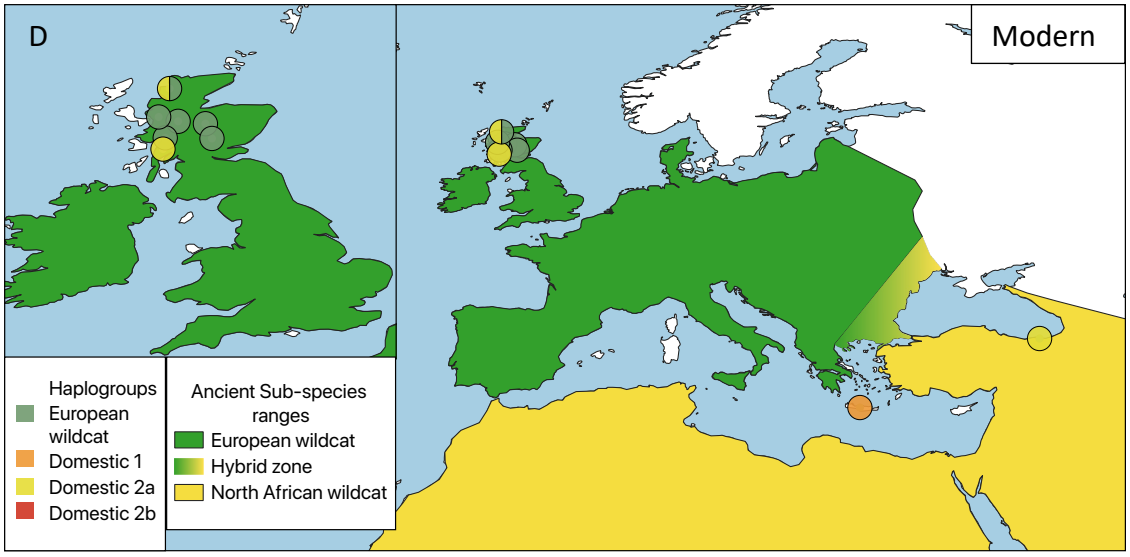


Figure 3.1 Map illustrating the results of the mitocondrial analysis including all samples with 4x or more depth of coverage. Each panel is a different period of time (A-D). The map background shows the theoretical ancient range of the European wildcat and the North African wildcat. There was a known hybrid zone in eastern Europe which is also represented. The results are shown as pie charts for each site, the colours represent the different mitcondrial haplogroups and sub-haplogroups as seen on the phylogenetic trees (see Figure 3.2). Numbers on panel A and B refer to the following sites with the earliest representation of each of the three haplogroup/sub-haplogroups in Britain: 1 = Gussage All Saints (339-54 cal. BCE), 2 = York (1st-4th century CE), 3 = Caistor Roman Town (2-4th century CE).

Once the analysis was completed, mitochondrial subspecies identifications were assigned to 65 ancient samples from 36 sites (Figure 3.1, Table S3.5). For samples with both nuclear and mitochondrial DNA analysed the results matched in all but four cases (P138, P161, AJ75, AJ341) which will be discussed further in section 3.6.3.2.1. Figure 3.1 both shows the locations of each of the sites as well as the subspecies and lineage assignment for those above 4x depth of coverage. This is all based on the results of Table S3.5. The dataset also included historic cats from Scotland, 21 of which were identified down to subspecies, 9 of which were above 4x depth of coverage (Table S3.6).

3.6.2 Radiocarbon dating

Sample	Genetic species ID	Site	Country	Date lab reference	Uncalibrated date (BP)	Standard Deviation	d13C	d15N	Date cal. BCE/CE (95.4%, overall range IntCal 20)
AJ342	Felis silvestris	Danebury	England	OxA-38897	2257	21	-20.08	9.3	392-208 cal. BCE
AJ343	Felis silvestris	Gussage All Saints	England	BETA-568254	2180	30	-20.2	7.6	361-168 cal. BCE
AJ100	Felis catus/Felis lybica	Gussage All Saints	England	OxA-38874	2125	17	-20.71	9.2	339-54 cal. BCE
AJ85	Felis silvestris?	Fishbourne	England	OxA-38875	2038	16	-19.97	11.5	94 cal. BCE - 21 cal. CE
AJ86	Felis catus/Felis lybica	Fishbourne	England	OxA-38877	1950	17	-19.67	9.4	24-123 cal. CE
AJ341	Felis catus/Felis lybica	Owslebury	England	OxA-38873	1847	16	-20.36	6.97	130-239 cal. CE
AJ340	Felis silvestris	Owslebury	England	OxA-38872	1274	16	-19.76	7.3	674-774 cal. CE
AJ93	Felis silvestris	Dorchester	England	OxA-39001	1825	19	-20.55	9.1	132-317 cal. CE
AJ448	Felis catus/Felis lybica	Lyminge	England	OxA-31749	1313	26	-19.1	9.4	656-775 cal. CE
AJ419	Felis silvestris	An Corran	Scotland	OxA-40487	7540	27	-21.09	4.9	6459-6272 cal. BCE
AJ514	Felis catus/Felis lybica	Howe, Orkney	Scotland	OxA-40486	1741	18	-19.83	10.8	247-380 cal. CE
AJ516	Felis catus/Felis lybica	Howe, Orkney	Scotland	BETA-570176	1280	30	-20	10.9	661-774 cal. CE
AJ517	Felis catus/Felis lybica	Howe, Orkney	Scotland	OxA-40465	1130	24	-14.73	14.4	1053 - 1317 cal. CE*
AJ431	Felis catus/Felis lybica	Jarlshof, Shetland	Scotland	OxA-40488	1044	18	-19.3	9.9	989-1029 cal. CE
AJ249	Felis catus/Felis lybica	Ratoath	Ireland	OxA-40489	1424	19	-21.59	10.7	602-653 cal. CE
AJ248	Felis catus/Felis lybica	Ballyhanna	Ireland	OxA-40490	200	18	-18.53	9.5	1656-1804 cal. CE

Table 3.1 Radiocarbon dates for samples dated as part of this study. Species assignment of AJ100 is based on the genetic results of two kitten bones (AJ98, AJ99) from the same context and feature as AJ100 * marine offset

Of the 16 samples submitted for radiocarbon dating all were successfully dated. The earliest dated domestic cat from England is the kitten bone from Gussage All Saints (AJ100) dated to 339-54 cal. BCE (Table 3.1). The earliest domestic cat from the Orkneys is from Howe and is dated to 247-380 cal. CE and the earliest from Ireland is from 602-653 cal. CE. We were able to confirm the European wildcat from An Corran, Scotland was Mesolithic in age dating to 6459-6272 cal. BCE.

3.6.3 Genetic analysis

3.6.3.1 Mitochondrial phylogenetic analysis

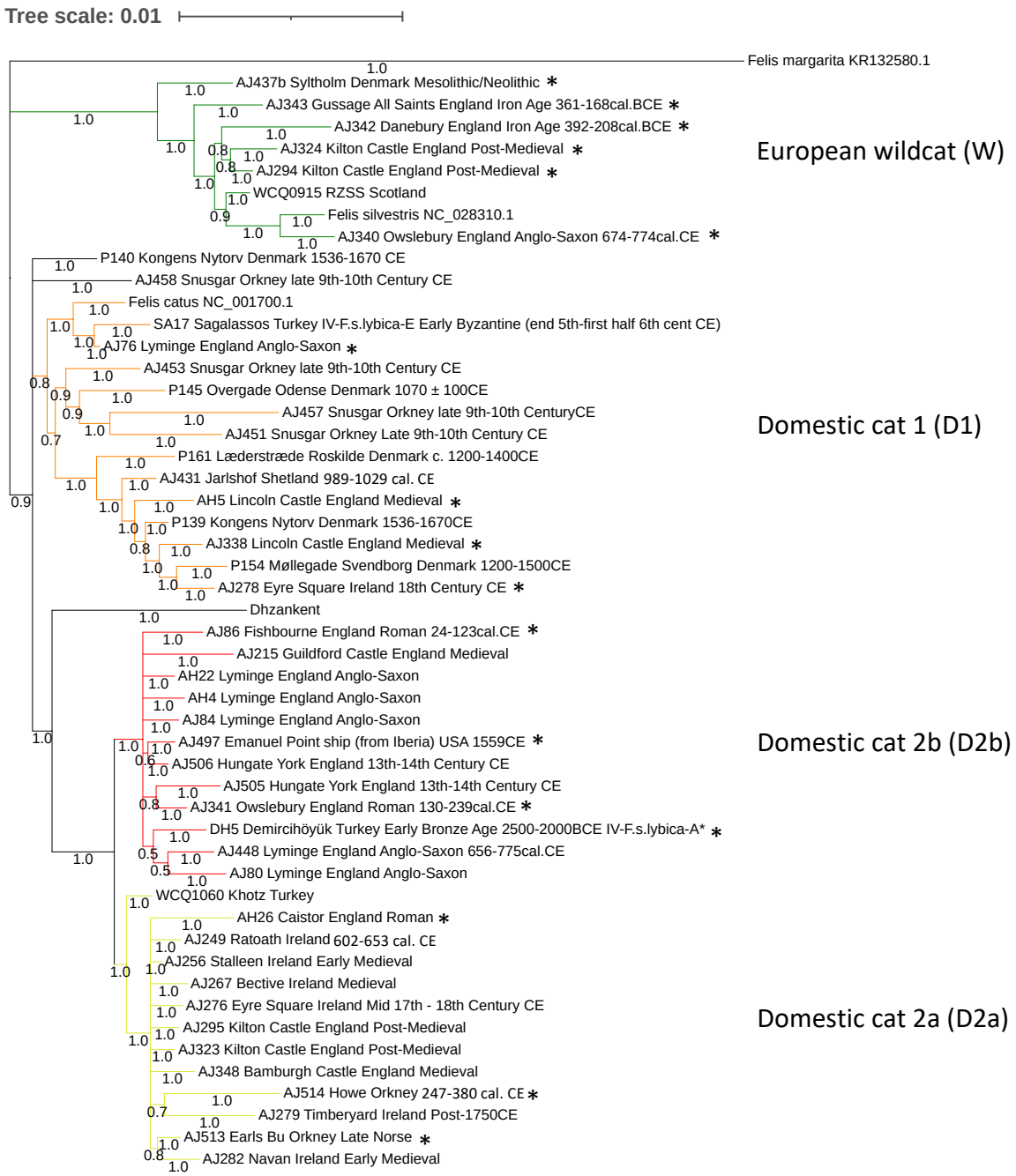


Figure 3.2 Bayesian mitochondrial phylogenetic tree of ancient samples with 10x or more depth of coverage and less than 10% of missing data. Posterior support values are displayed on the branch lengths. The colours of the branches represent the haplogroups and sub-haplogroups and correspond to the colours in Figure 3.1. * Indicate samples mentioned directly in the text.

The maximum likelihood tree of the ND5/ND6 mitochondrial region as well as the other Bayesian and maximum likelihood trees of the full mitochondrial genome all showed the same topology as Figure 3.2, with samples from this study falling into two mitochondrial

clades: domestic cat and European wildcat (Figure S3.1, S3.2, S3.3). No samples from this study fell into any other lineage of cat (Figure S3.1). The domestic cat clade split into two further clades “domestic cat 1” and “domestic cat 2”, the latter further splitting into clades 2a and 2b. This resulted in three clear separate domestic cat clades (D1, D2a and D2b) and one European wildcat clade (W), all with posterior supports above 0.9 (Figure 3.2, S3.2 and S3.3).

3.6.3.1.1 European wildcat clade

The earliest samples in this study were European wildcats. They were from the Mesolithic site of An Corran, Scotland (AJ419) and the Mesolithic/Neolithic site of Syltholm, Denmark (AJ437b). The samples analysed from the two Iron Age sites of Gussage All Saints (AJ343) and Danebury (AJ342) demonstrated that both had European wildcat individuals on site. There was also a wildcat identified at the Roman site of Dorchester (AJ93), the Anglo-Saxon site of Owslebury (AJ340) and the Medieval site of Kilton Castle (AJ324, AJ294). None of the samples analysed from the Orkneys or Ireland were identified as European wildcats. The modern and historic Scottish European wildcats all formed their own sub-clade within the wider European wildcat clade (Figure S3.2).

3.6.3.1.2 Domestic cat clade

The earliest appearance of domestic cats known in Britain was in the Iron Age, with the kitten remains from Gussage All Saints (AJ98). The depth of coverage of this sample was low, therefore the results need to be taken with caution. The kitten that was analysed clustered into the domestic cat clade. Domestic cats were also seen in the Roman period with samples from the Roman contexts of Caistor (AH26), York (AJ499), Owslebury (AJ341) and Fishbourne (AJ86). All Anglo-Saxon and Medieval sites analysed in this study contained only domestic cats, apart from those from the Anglo-Saxon site of Owslebury and the Medieval site of Kilton Castle.

Domestic cat subclade D1

Subclade D1 is first seen in Almosen (P141), Denmark, 1100-500 BCE, and is seen in Denmark from this period onwards. All Danish samples analysed, apart from one, were

assigned as D1. The one sample with a different lineage has been disregarded due to low coverage depth (P138 2.3x) D1 first appeared in mainland Britain at the Roman site of Hungate, York (AJ499) in the 1st to 4th century CE. It is then also present in later periods in England at Anglo-Saxon Lyminge (AJ76) and Medieval Lincoln Castle (AH5, AJ338). In the Orkneys it appears in the Norse period (1053-1317 cal. CE, OxA-40465, 1130 ± 24 BP) at the site of Howe (AJ517) and is seen at the Norse sites of Snusgar (AJ451, AJ453, AJ454, AJ457, AJ458) Orkney and Jarlshof (AJ426, AJ431), Shetland (989-1029 cal. CE, OxA-40488, 1044 ± 18 BP). This subclade is also seen in Ireland at the early Medieval site of Navan (AJ257) and the 18th century site of Eyre Square (AJ278), Galway. This lineage is not seen in modern day Scottish samples in this study, however this is not unsurprising as we did not analyse many Scottish domestic cats.

Domestic cat subclade D2a

This lineage arrives in Britain at a similar time to D1. The first appearance is at the Roman site of Caistor (2nd-4th century CE, AH26) on the east coast of Britain. It is also found in the Anglo-Saxon and Medieval periods at Lyminge (AJ75) on the south coast as well as York (AJ507), Bamburgh Castle (AJ348) and Kilton Castle (AJ295, AJ323) in the North-East of England. In the Orkney Islands it is seen at one Middle Iron Age site, Howe (AJ514) and one Norse site Earls Bu (AJ513). Subclade D2a is the predominant lineage seen in Ireland and is found from the early Medieval period onwards. It is seen in historic Scottish samples analysed in this study.

Domestic cat subclade D2b

This lineage is the first domestic cat lineage seen in Britain with the kittens at Gussage All Saints (AJ98). It is then seen in the Roman period at Fishbourne (AJ86) and Owslebury (AJ341). It is the predominant lineage at Lyminge and is found at various Medieval sites. There are no samples in the Northern Isles or Ireland with this lineage. It is also the lineage seen for the one successful sample from the 1559 Emanuel Point shipwreck (AJ497) off the coast of Florida. It is the sub-haplogroup of the earliest cats from Turkey (DH5) in this dataset, from the Early Bronze Age.

3.6.3.2 Nuclear analysis

3.6.3.2.1 Subspecies identification method

ID	Location	Country	Period	Haystack ID
P138	Kongens Nytorv	Denmark	1536-1670 CE	F. beiti
P161	Læderstræd 4, Roskilde	Denmark	c. 1200-1400 CE	F. beiti
P154	Møllegade 6, Svendborg	Denmark	1200-1500 CE	F. l. lybica
P145	Overgade, Odense	Denmark	1070 ± 100 CE	F. l. lybica
AJ437b	Syltholm	Denmark	Mesolithic/Neolithic	F. s. silvestris
AJ348	Bambrugh Castle	England	Medieval	F. l. lybica
AH26	Caistor Roman Town	England	Roman	F. l. lybica
AJ342	Danebury	England	Iron Age	F. s. silvestris
AJ93	Dorchester	England	Roman	F. s. silvestris
AH34	Flaxengate	England	Medieval	F. l. catus
AJ270	Guildford castle	England	Medieval	F. l. catus
AJ215	Guildford castle	England	Medieval	F. l. catus
AJ269	Guildford castle	England	Medieval	F. l. catus?
AJ98	Gussage All Saints	England	Iron Age	F. l. catus?
AJ99	Gussage All Saints	England	Iron Age	F. l. lybica
AJ343	Gussage All Saints	England	Iron Age	F. s. silvestris
AJ508	Hungate, York	England	13th-14th century	F. s. catus
AJ505	Hungate, York	England	13th-14th century	F. s. catus
AJ506	Hungate, York	England	13th-14th century	F. s. catus
AJ295	Kilton Castle	England	14th-15th century	F. s. lybica
AJ323	Kilton Castle	England	14th-15th century	F. s. lybica
AJ294	Kilton Castle	England	14th-15th century	F. s. silvestris
AJ75	Lyminge	England	Anglo-Saxon	F. chaus
AJ84	Lyminge	England	Anglo-Saxon	F. s. catus
AJ448	Lyminge	England	Anglo-Saxon	F. s. catus
AH22	Lyminge	England	Anglo-Saxon	F. s. catus
AJ80	Lyminge	England	Anglo-Saxon	F. s. catus?
AH4	Lyminge	England	Anglo-Saxon	F. s. catus
AJ340	Owslebury	England	Anglo-Saxon	F. s. silvestris
AJ446	Whitehall farm	England	Roman	F. s. catus
AJ282	Navan 2 & 3	Ireland	Early Medieval	F. s. lybica
AJ256	Stalleen	Ireland	Early Medieval	F. s. lybica
AJ419	An Corran	Scotland	Mesolithic	F. s. silvestris
AJ513	Earls Bu	Scotland, Orkney	Late Norse	F. s. lybica
AJ516	Howe	Scotland, Orkney	661-774 cal. CE	F. s. catus
AJ454	Snusgar	Scotland, Orkney	late 9th-10th century	F. s. catus
DH5	Daemircihöyük	Turkey	2500-2000 BCE	F. s. catus
SA06	Sagalassos	Turkey	Early Byzantine (end 5th-first half 6th cent CE)	F. s. catus
AJ497	Emanuel Point ship	USA	1559	F. s. catus

Table 3.2 HAYSTAC nuclear abundance results for all successful species identifications. ? refers to samples with unsure identification. See Text S3.2 for more details.

HAYSTAC (High-AccuracY and Scalable Taxonomic Assignment of metagenomiC data) was able to distinguish between the different subspecies with the ancient data when only one subspecies was confidently assigned. 'Confidently' is defined here as when the first call has more than twice the abundance of the next call. Under this criterion, the identification

matched that of the mitochondrial DNA in all but four cases (Table 3.2, S3.5), where the nuclear species assignment was either Chinese mountain cat (*F. beiti*) (P138, P161, AJ341) or jungle cat (*F. chaus*) (AJ75). Given that Chinese mountain cat is only found in Western China today this assignment seems unlikely. The assignment as jungle cat is also implausible but not impossible as the species range reaches the Near East today and so it could theoretically have been imported to Britain. Further investigation on these four samples is needed to conclude their identification. Where there were two species assigned (AJ98, AJ269, AJ80) (the first call is less than two times the abundance of the second call), we have marked these as uncertain species identifications. For the majority of the samples analysed and marked as uncertain, neither the first nor second call have the same subspecies assignments as the mitochondrial DNA. This is biologically unlikely, and all samples which were assigned as uncertain require further investigation, as the nuclear subspecies identification is inconclusive from this study.

3.6.3.2.2 Ancestorial analysis

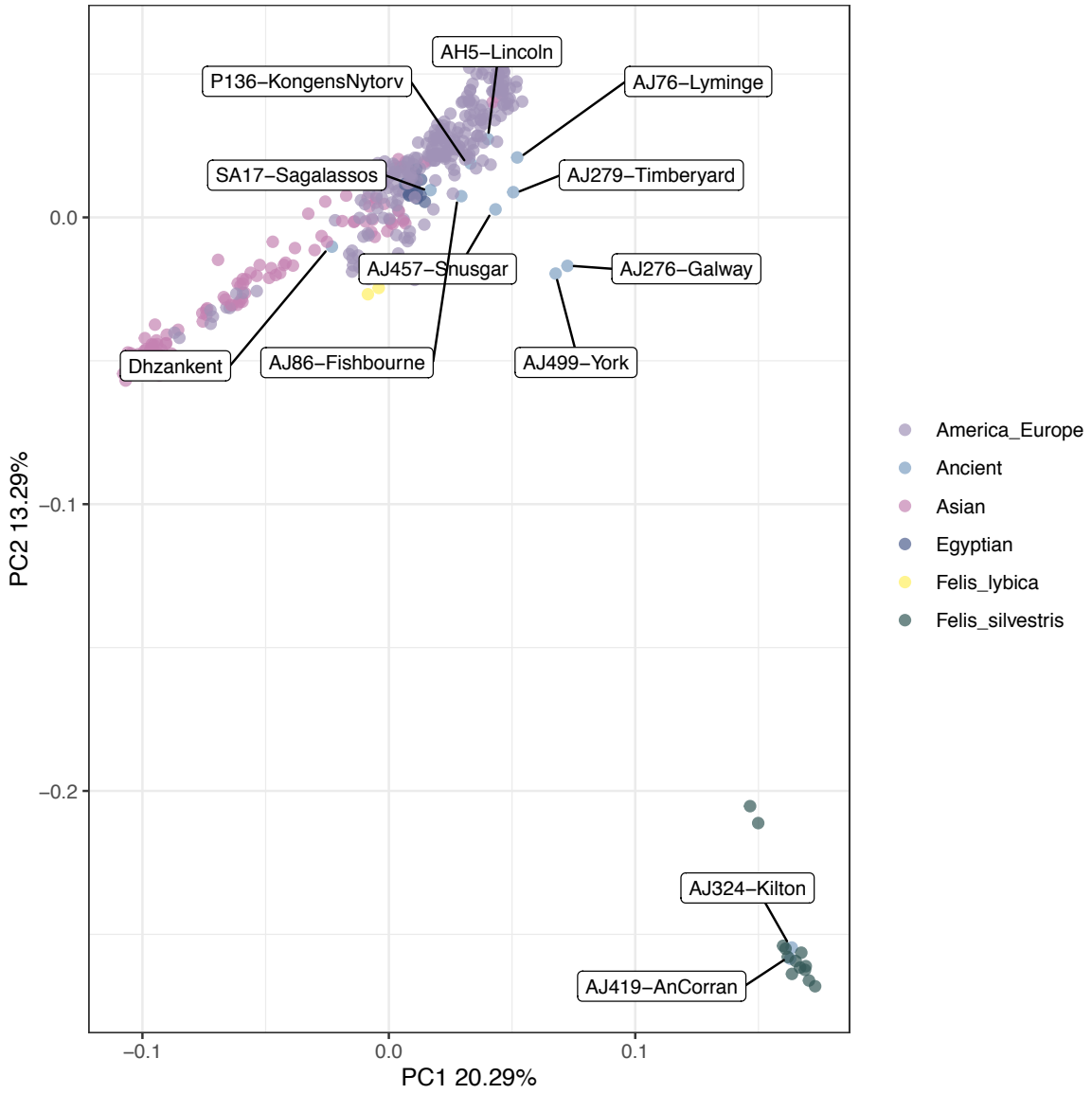


Figure 3.3 Principal component analysis (PCA) showing PC1 and PC2 of the 10,380 SNPs. The ancient samples have been labelled with their sample numbers and are shown in light blue.

The two ancient European wildcats included in the study grouped in with the modern European wildcats included in the PCA analysis (Figure 3.3). Two of the modern wildcats, both from Scotland, fall slightly outside the tight cluster of *F. s. silvestris*, this may be due to recent hybridisation with domestic cats or missing data. The majority of the domestic cats were found inside the variations of modern-day domestic cats and North African wildcats. The cat from the 1st-4th century CE of York (AJ499) and Eyre Square, Ireland (AJ276) fell slightly outside this range.

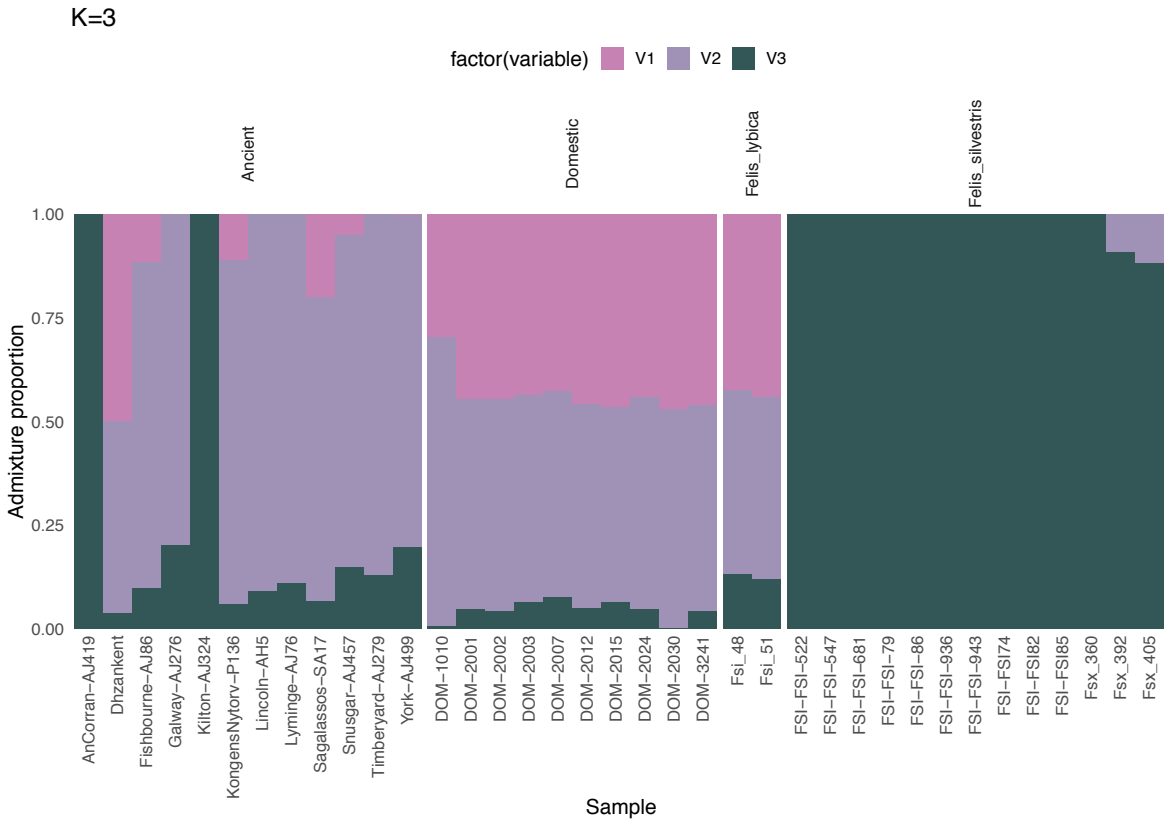


Figure 3.4 Subset of the larger ADMIXTURE plot, modelling each ancient population as a mixture of three populations, European wildcat (green), Asian domestic cat (pink) and European domestic cat (purple). The full figure with confidence intervals is found in Figure S3.4.

The programme ADMIXTURE was used to inform on species-level differentiation (Figure 3.4, S3.4). With K=3 (number of subpopulations as 3), it was possible to see differences between wildcats, Asian domestic and European domestic cats. The admixture plot further backs up the results of the PCA. The ancient European wildcat individuals from Kilton Castle (AJ324) and An Corran (AJ419) are 100% wildcat (V3) and the domestic cats from Britain and Ireland are predominantly of European domestic cat descent (V2). The individuals from Snusgar (AJ457) and Fishbourne (AJ86) are the only British cats to show any Asian ancestry (V1). Both the Danish (P136) and Turkish (SA17) domestic cats that were analysed had a small percentage of Asian ancestry. The cat from Dhzankent, Kazakhstan had both Asian and European ancestry.

3.7. Discussion

3.7.1 The arrival of domestic cats to the south coast of Britain

Our genetic analysis of the samples from Gussage All Saints shows that the cat remains found at the site is the earliest domestic cat found in Britain. The kitten remains (AJ98) have

been shown to be domestic cat, which has been verified through the use of two independent genetic species identification methods using the mitochondrial and nuclear DNA. This matches with the hypothesis of the site excavators, who originally listed the kittens as domestic cats in the site report. Given what is currently known about the movement of domestic cats in the rest of Europe, these findings are significant. From the work of Ottoni et al. (2017), cats do not appear north of the Alps until the Roman period, suggesting that it was the Romans who were responsible for the spread of domestic cats throughout the Roman world. The Gussage All Saints domestic cat kitten were dated to 339-52 cal. BCE, before the arrival of the Romans in Britain, showing that this suggestion was incorrect, and that domestic cats had in fact been brought to Britain prior to the Romans, although most probably from the Roman world. That this kitten is the only English Iron Age domestic cat found so far, may suggest that domestic cats were rare in Britain in the period, and that only during the Roman period did they become more widespread. Deeper sequencing and further nuclear analysis of the kitten is required to verify this result.

The Roman sites of Fishbourne, Caistor, Owselbury and York all showed the presence of domestic cats (Allen and Sykes 2011; Maltby 1987; Davies 1992; Sykes, n.d.). The cats are from all three domestic cat mitochondrial haplogroups/sub-haplogroups (D1, D2a, D2b). That these cats were all dated to within 600 years, shows that the three haplogroups arrived in Britain at relatively similar times (in the late Iron Age/Roman periods). Fishbourne (AJ86) is the earliest of these Roman sites (1st-2nd century CE) and the cat found there is from the same lineage as the kitten from Gussage All Saints (sub-haplogroup D2b). As Fishbourne is a palace site known for its unusual early-introduced species such as fallow deer, European hare and fancy breed fowl, this finding is unsurprising (Sykes et al. 2011; Sykes 2014). The other Roman site to share the same sub-haplogroup (D2b) as the Gussage All Saints kitten is the farming village of Owslebury, a 4th century CE late-Roman site. The other two sites Caistor (2nd-4th century CE) and Hungate, York (1st-4th century CE) are larger settlements and have only sub-haplogroup D2a and haplogroup D1 present. This could indicate a rural-urban divide, with the rural, wealthy villa sites and farms having one type of domestic cat and the urban sites another.

There are other Roman sites with evidence of domestic cats, further demonstrating how widespread they were in the period. Cat remains have been found on villa and settlement sites such as Silchester, Dursley, Hambledon, Dalton-on-Tees and Lullingstone (Zeuner 1951; Buglass and West 2014). Evidence found at two of these sites provides further clues for the cats on the sites being domesticated. At Silchester alongside the cat remains found at the site, a tile was found with cat footprints, which suggests at least one cat was living on the site (Wainwright 1979). At the site of Dalton-on-Tees (2nd-4th century CE) a cat bone was found with what would ordinarily be fatal injuries. The animal, however, survived, suggesting that people cared for it (Buglass and West 2014). Both examples show that cats were living close to the human population. The samples from both sites need further analysis to confirm whether they are domestic cats, but given the evidence previously mentioned this is highly probable. The genetic results generated from our study combined with zooarchaeological evidence strongly supports the arrival of domestic cats in the Iron Age. They most probably arrived from the Roman world, but it was during the Roman period that they then became widespread throughout Britain. There were three lineages introduced, one of which is associated with the Roman elite in their villas, and the others with urban centres.

We are also able to speculate on where the first domestic cats arrived from. By sequencing some of Ottoni's samples (SA17, DH5), we have shown that lineage 2b is the same as Ottoni's mitochondrial ND5/ND6 lineage IV-A* (Figure S3.1). This was one of the earliest mitochondrial types seen in Europe, first appearing around 4,400 BCE in Bulgaria (Ottoni et al. 2017). Haplogroup IV-A* has also been found in Greece and Romania before its arrival on the south coast of Britain. It was also the most common lineage seen in Turkey and the Arab peninsula. The most probable route for the arrival of the domestic cat to Britain was from northern Gaul (present day France, Belgium and parts of Germany) as there was known contact between the Iron Age people of the south coast of Britain and France (Cunliffe 2010). Gussage All Saints also shows evidence of this contact, as Gallo-Belgic type wares have been found at the site (Wainwright 1979). From Ottoni's work, lineage IV-A* was not found in Gaul at this time, but this is based on a small sample size, as domestic cat remains were only analysed from one French site. Given that domestic cats were found in other parts of the mainland Europe, there is a strong likelihood that this lineage of domestic

cat would have been present in Gaul. And assuming this is true, direct trade of cats between tribes of the south coast of England such as the Durotriges and those in Gaul would have been possible. This is even more probable when considering many tribes of the south coast of Britain were descendants from tribes in Gaul (Williams 2001). Further evidence from a site close to Gussage All Saints supports contact with the people in Gaul and the import of goods from the Roman world. The nearby Iron Age ballast quarry site of Hengistbury Head in Dorset (20 miles away) had large quantities of wine amphora found, which are believed to have arrived from the Roman world, possibly via Gaul (de Jersey 1993). Hengistbury was a known trading post and is a possible point of arrival for the first domestic cats in Britain. The close proximity of Gussage All Saints to this port points to this being the route that might have been taken by domestic cats to Gussage All Saints from mainland Europe. This same lineage is then seen a few centuries later at the Roman sites of Fishbourne and Owslebury, on the south coast further supporting the origin of the Gussage All Saints domestic kittens being the Roman world.

3.7.1.1 Wildcats in the Iron Age

We have not found any clear evidence for European wildcats living in human habitation sites. At Iron Age Danbury, Gussage All Saints and Fishbourne, European wildcat remains have been identified, but there is no evidence to show that these cats were living amongst the people. Instead, they most probably arrived on the site having been hunted for fur, as they are known to have been hunted for this reason well into the early 20th century. Our results reflect this, as wildcat remains were also found at the Anglo-Saxon site of Owslebury (AJ340) and the Medieval site of Kilton Castle (AJ294, AJ324). This arrival as a result of hunting could be disputed due to the lack of recorded cut marks on the bones suggesting they were not butchered. However skilled meat butchery need not leave cut marks and similarly skinning a cat because the fur is wanted may leave no obvious signs. If cut marks are present, as a result of skinning, they are usually seen on the mandible/skull and on the feet, only two of the European wildcat bones analysed were mandibles the rest with elements assigned were long bones or teeth which may explain the lack of cut marks if they were skinned (Richter 2005; Fairnell 2008). As there is a lack of any other evidence of the European wildcats living on the sites such as kitten remains or intentionality in burial, their

arrival as a result of hunting is still the most probable explanation. The North African wildcat and leopard cat remain the only wildcats with clear evidence for domestication.

3.7.1.2 Summary

Our evidence suggests domestic cats first arrived in the Iron Age to the south coast of England, they became widespread in the Roman period and have remained ever since. Lineage D2b was the first to arrive in the late Iron Age, followed in the Roman period by D1 and D2a. D2b is found at high-status sites in the Roman period and became more widespread in the Medieval period. Haplogroups D1 and D2a are found in city and castle sites from the Roman period onwards.

3.7.2 Later movement of domestic cats to the Northern Isles, a case study

In order to understand the origin of cats in the Northern Isles, their arrival in the possible source populations needs to be fully understood first. Above we have already established how and when domestic cats arrived in mainland Britain, and we will now briefly explore their arrival in Denmark, one of the three Norse kingdoms in the Viking era and the location of another likely source population. From our study, and from that of Bitz-Thorsen and Gotfredsen (2018), it is known the very first domestic cat was present in Denmark in the Late Bronze Age at the site of Almosen (P141), but it was not until the Roman Iron Age of Denmark that they are found more routinely. This one Danish Bronze Age cat may be unique and a result of early trading with the south of Europe, where cats were widespread in this period. The cats found in the Roman Iron Age of Denmark would have arrived during the northward expansion of the Roman Empire. This brought further cats with the D1 haplogroup. Haplogroup D1, which was present in Denmark since the Bronze Age, continued to be the predominant haplogroup in all Danish periods in this study.

All cats analysed from the Northern Isles in this study were domestic cats that arrived from the Scottish Middle Iron Age (3rd century CE) onwards, contemporary with the Roman period of southern Britain. The samples' radiocarbon dates were all either later or earlier than the contextual date, which confirms the importance of directly dating samples for accurate interpretations of results. Two lineages of domestic cat are found in the Orkneys and one is found in the Shetland Islands.

The earliest cat remains so far dated from the Orkneys were from lineage D2a from the site of Howe (AJ514). The bone was dated to 247-380 cal. CE (OxA-40486, 1741 ± 18 BP) in the Scottish Middle Iron Age. This lineage was also seen at the contemporary Roman site of Caistor in the east of England. The route of this domestic cat lineage to the Orkneys may have been either through direct or indirect trade with the Romans in southern Britain or from somewhere else in the Roman world. The low numbers of this lineage in the Orkneys may be due to a subsequent large-scale replacement of cats by the arrival of the Viking/Norse people. Cats from the Viking/Norse period in the Northern Isles predominantly have the D1 lineage (8 out of 10 cats), which is the only lineage of cats in Denmark from our dataset, suggesting this was the cat's origin. D1 was also present throughout the Roman world but given the known association with Denmark and the predominance of this one haplogroup there, Denmark seems the most logical origin of these cats. Given the importance of cats to the Vikings, due to their association with the goddess Freyja who is said to have ridden a chariot pulled by two cats, it is not unexpected that they brought their cats with them when arriving in the Orkneys (Prehal 2011). The first lineage seen in the Orkneys, D2a, is then seen again at the sites of Earl's Bu (AJ513). Earl's Bu is a significant site as it was the house of the Earls of Orkney, as referenced in the Orkneyinga Saga (Palsson 1981; Barrett 1997; Omand 2003; Mainland and Batey 2018). Earl's Bu was also the site where the first lap dog was found on the Orkneys, suggesting that Earls of Orkney had connections that enabled them to acquire unusual animals (Mainland 1995). This lineage of cat may therefore have been acquired using the Earl's contacts with the rest of the Norse world or it may have persisted in small numbers since the Middle Iron Age. This D2a lineage is also found at York (AJ323, AJ507), another site occupied by the Norse, further demonstrating that this D2a lineage of cat most probably arrived through trade routes through the Viking territories, such as the Kingdom of Northumbria where it is also found.

Of the samples analysed in this study from the Orkneys and Shetland, none were identified as European wildcats. Further dating and genetic analysis is needed of early cats in the Northern Isles to conclude whether wildcats were ever present on the islands. It is clear from this analysis that domestic cats arrived in the Northern Isles by the 3rd century CE, at

the latest. There was then a replacement of cats with the arrival of the Norse. This introduced a new lineage to the islands from Denmark, haplogroup D1. There was also a slightly later arrival of a lineage which had previously disappeared from the islands (D2a), possibly from the surrounding Norse territories. The cat remains on the Northern Isles demonstrate that the people on the islands were well connected within the Norse world, importing cats from at least Denmark and possibly further afield. This is just the start of research on the cats of the Northern Isles and more samples and additional nuclear analysis are needed to shed further light on our understanding.

3.7.3 Movement of domestic cats to Ireland, a case study

From studying domestic cats in Ireland from the early Medieval period, we show that the early domestic cats in Ireland were only from two of the three haplogroups/sub-haplogroups, as there is no sub-haplogroup D2b found in Ireland from the studied specimens. As D2b is first seen in England in the British Iron Age it may be that Ireland missed the first wave of domestic cat introduction or we have not sampled early enough periods and it subsequently disappeared. The absence of D2b specimens does not preclude their existence in Ireland in an unsampled population but, given that D2b has not been found in the nine Irish cats analysed for this study, if it was present, it was presumably in small numbers.

The other two lineages, D1 and D2a, were present on mainland Britain, the Northern Isles and on continental Europe before their introduction to Ireland. It is therefore difficult to distinguish where they arrived from. It can be inferred that cats with lineage D1 all came originally from the Roman world and then later from the Norse Kingdom. Parts of Ireland were occupied by the Vikings from the 9th century CE, with extended influence over a larger area than the urban coastal centres they occupied (Valante 2008). Navan (AJ257), County Meath, is one of the sites with haplogroup D1 present, and it was within this area of Viking influence as shown by the discovery of a Viking burial in Navan (O'Keeffe 2000). Galway was not within the known area of influence, but had some link to the Viking people, as a Viking burial was found nearby (Raftery 1960). However, the first evidence we have of a domestic cat with lineage D1 in Galway (AJ278) was in the Post-Medieval period, by which point the town was a major trading post, with links to England, France, Spain, Portugal and

Flanders (Duffy 2005). The domestic cats in Galway could therefore have arrived from any of these locations, in addition to other settlements in Ireland. Further analysis of earlier cat remains from Galway are needed to conclude when and where domestic cats arrived from.

The D1 lineage may have arrived in Galway with the Vikings however this is impossible to conclude with the current evidence. It is well known domestic cats were traveling on ships in the Medieval period as there are documentary sources referring to ships having cats (Kert 2015; Mason 1984). Additionally, we have direct evidence for cats on a ship from this study, with the cat (AJ497) found on the 1599 Emanuel Point shipwreck off the coast of Florida. This adds to our understanding of the movement of cats in the Medieval period and provides another possible source of domestic cats to Medieval Ireland as well as worldwide.

The first lineage to be found in Ireland and the predominant lineage through time was D2a, which was found on both the east and west coasts of Ireland. It was first seen at the site of Ratoath (AJ249), on the east coast near Dublin, in the 7th century CE. All Irish domestic cats studied were of this lineage, aside from the two potentially Norse cats mentioned previously of D1 lineage. D2a was found in urban contexts as well as at the Abbey of Bective. Unlike in Britain, where there is a potential rural-urban divide between lineages, there was no urban-rural differentiation seen. In order to establish where each lineage arrived from, further study is needed.

3.7.4 Hybridisation between European wildcats and domestic cats in the past and their implications for conservation

Given that domestic cats and European wildcats are able to interbreed, hybridisation could have started to occur in Britain from when domestic cats first arrived in the Iron Age on the south coast. However, the results of this study begin to suggest that this was not a widespread occurrence. The PCA and admixture analysis suggest that there are no clear hybrids in the dataset, with all cats either grouped with the modern domestic and North African wildcat or with the European wildcat. The results need to be taken with caution as the modern dataset predominately consisted of domestic breed cats and very few European wildcats with SNPs selected based on differentiating the domestic cat breeds.

Exploratory analysis with HAYSTAC was unable to conclusively identify hybrids, but further investigation of the samples with inconclusive species identifications may change our understanding in the future. It is not possible to confidently identify any individuals as hybrids from the HAYSTAC results or PCA and admixture plots at present.

PCA analysis has identified two ancient domestic cats which fall slightly outside the variation of modern domestic cats (AJ276, AJ499). However, whether these specimens are hybrids with other cat species, or whether this variation is within the natural expected variation of domestic cats and North African wildcats, remains to be determined. In future studies, the addition of further known hybrid individuals and more North African wildcats would be of benefit. The two ancient European wildcat individuals (AJ419, AJ324) were shown to be genetically similar to the pure wildcats in the modern-day population.

One of these ancient wildcats was found at the Mesolithic site of An Corran (AJ419), Scotland. During this period, only European wildcats were present in Britain and the population would have been cut off from mainland Europe well before the domestic cat was present in central or western continental Europe (Weninger et al. 2008). This individual from An Corran could therefore be used as a baseline for 'pure' wildcat as it would be impossible that it could have any recent North African wildcat heritage. Further nuclear analysis is needed in order to confirm this assignment.

The other individual that was identified as 'pure' wildcat is from the Medieval site of Kilton Castle (AJ324). From our mitochondrial DNA findings, we know that there were contemporary wildcats and domestic cats present on the site. If these two species were living on the site and breeding, hybridisation between the two species could be considered a possibility, but high levels of hybridisation were not seen in this wildcat individual. As discussed in section 3.4.3.1, the most probable explanation for this is that the wildcat was hunted before being brought to the site. Other Medieval sites in Lincoln and York in the $10^{th}/11^{th}$ century show further evidence for wildcats being found among the domestic cat assemblages (Kitchener and O'Connor 2010), with the wildcats most probably arriving at the site as a result of being hunted. Further analysis of cats from Kilton Castle is needed to

verify if this one individual is representative, but it is clear that there were 'pure' wildcats still in existence in Britain in the Medieval period. That we have so far seen no evidence of high levels of hybridisation in ancient wildcats further supports Senn's findings that there has been an acceleration of hybridisation over the last few decades, with hybridisation levels in the past being much lower than are seen today in Britain (Senn et al. 2018). Given the small dataset, further analysis and more samples would aid in clarifying this result. This European wildcat from Kilton Castle could also be used as the baseline for 'pure' wildcats from the Medieval period of Britain. Data form both these "pure" wildcat individuals is of high relevance to conservation practitioners working on wildcats as this will help with the benchmarking of hybridisation in contemporary wild-living cats, eliminating doubts about circularity and shifting baselines (Senn and Ogden 2015; Senn et al. 2018).

The rest of the ancient cats studied were within the ranges of the modern domestic cats and North African wildcats. The domestic cats closer to -0.1 on PC1 (principal component 1) of the PCA plot (Figure 3.3) had more Asian ancestry than those closer to 0.1. This is also seen in the admixture plot (Figure S3.4a). The cat from Dhzankent, Kazakhstan has the most Asian ancestry, which was expected given its geographic location. All domestic cats have relatively low levels of European wildcat ancestry, with modern-day Asian domestic cats having similar levels as modern domestic cats in Europe. For all of the domestic cats sampled in England, Ireland and the Northern Isles, the predominant ancestry was domestic cats from Europe, as would be expected. All show low levels of introgression from European wildcat, which is slightly higher than the natural variation seen in modern-day domestic cats (Figure 3.4, Figure S3.4). Given that these levels are relatively low, and that all samples fall within the variation of modern domestic/North African wildcats on the PCA plot, this introgression is expected to be from the ancestral populations of the domestic cats in mainland Europe. Domestic cats and wildcats had been living alongside each other for much longer than they would have been in Britain and Ireland (Ottoni et al. 2017; Ottoni and Van Neer 2020). Another indicator this introgression is not in recent generations is that the levels in Ireland are the same as Britain and, as no European wildcats are believed to have existed in Ireland in the Medieval period, recent introgression would not be possible. The levels of introgression looking slightly higher than the modern domestic cats can be further explained by the modern cats used in this study being predominantly from breed

populations. It is well known that breed populations are often highly inbred in order to select for certain characteristic traits. Additionally, all the modern domestic cats in the PCA are from a SNP array, therefore ascertainment bias may account for the greater variation seen in the domestic cats compared to the variation between the domestic and European wildcats. Given these limitations, further analysis of the nuclear data is needed to establish levels of hybridisation and so these results need to be interpreted with care. These ancient samples may show the more natural levels of European wildcat ancestry in domestic cats. These results are a first step towards establishing a baseline for past levels of hybridisation in Britain and Ireland, further supporting that levels of interbreeding between the two wildcat species were probably low in the past.

To summarise, based on this analysis, we are unable to fully show with certainty whether hybridisation occurred in the past. So far, we have found no evidence of European wildcats and domestic cats interbreeding in the past, despite them living alongside each other from at least the late Iron Age, although further analysis is required to confirm this. High levels of admixture with domestic cats may be only a recent occurrence of the last few decades, with large-scale efforts currently being implemented to try and save the Scottish wildcat population ("Saving Wildcats" 2020; Senn et al. 2018). We have found no mitochondrial evidence for wildcats existing in the Northern Isles or Ireland when domestic cats were introduced and, given that the full genome results show low levels of European wildcat ancestry, our results suggest that there was unlikely to have been interbreeding in these regions. Additional nuclear analysis would strengthen the certainty of these conclusions.

In addition to our initial inconclusive findings on hybridisation, we have seen in the mitochondrial results that the diversity of Scottish European wildcats has decreased since before the historic period (1895-1985). The Scottish modern and historic samples form their own discrete clade within the larger European wildcat clade. This may have implications for the conservation of the Scottish wildcat. These results show the importance of looking further back into the past to reconstruct a species history.

The study of more recent domestic cats from Britain during the period of the decline of the European wildcat would be valuable, in particular to investigate shifts in ancestry resulting

from the disappearance of the European wildcat from England and Wales in the 18th -20th century (Langley and Yalden 1977). Wildcats were routinely hunted throughout Britain, and so wildcats would be expected to avoid human settlements, therefore reducing the chance of interacting with domestic cats. In earlier periods, when persecution was less aggressive, it is unclear whether domestic and wildcat interactions were more common. Understanding the frequency of domestic cat and wildcat interactions, and the subsequent effects on hybridisation, over the period of their persecution could lead to useful insights that could inform modern day wildcat conservation.

3.8 Conclusions

Through the use of genetic analysis, it has been possible to discover more about the arrival of domestic cats in Britain and Ireland, and what happened to the native European wildcat. We have confirmed that the known first occurrence of domestic cats in Britain was in the Iron Age and that they became more widespread in the Roman period. We have investigated levels of hybridisation in the past, with our current results suggesting there is no evidence for high levels of hybridisation between domestic and European wildcats in the Medieval period or before, suggesting that this may be a recent occurrence in Scotland, although to add to the certainty of these conclusions higher depth of nuclear analysis and further sampling would be required. Our study of the Northern Isles domestic cats has revealed that the Norse people brought their own cats with them when they arrived from Scandinavia, in the process replacing the domestic cats already living in the Northern Isles. The results of our study of the Irish cats were less conclusive. We have confirmed that domestic cats were present in the Medieval period from at least the 7th century CE, with no evidence of European wildcats, but where these Irish domestic cats were introduced from is unclear.

This analysis has allowed us to understand more about the movement of domestic cats in and around Britain and Ireland, as well as gaining further understanding of their relationship with the European wildcats in the past. We have shown that the introduction of cats to Britain and Ireland is complicated, with introductions from different civilisations at different periods. The powerful analytic techniques used have shed a light on domestic

cat and European wildcat interactions, in a way that could aid conservation management professionals today, as they act to preserve the populations of wildcats in Scotland that are at risk due to high levels of interbreeding with domestic cats. Further work on domestic cat and wildcat populations during more recent time periods would allow us to understand in even more detail why the British wildcat populations have declined so rapidly, and why interbreeding with domestic cats has become such an issue today.

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3.10 Supplementary material

3.10.1 Supplementary information Figures

Figure S3.1 Maximum likelihood tree of the ND5/ND6 region (2540 bp) from our samples and Driscoll et al. 2007. Branches were collapsed when no samples from this study were in them. Branch lengths were ignored to make the tree easier to read. The assigned lineages I-V from Driscoll have been noted in the tree using their taxonomy.

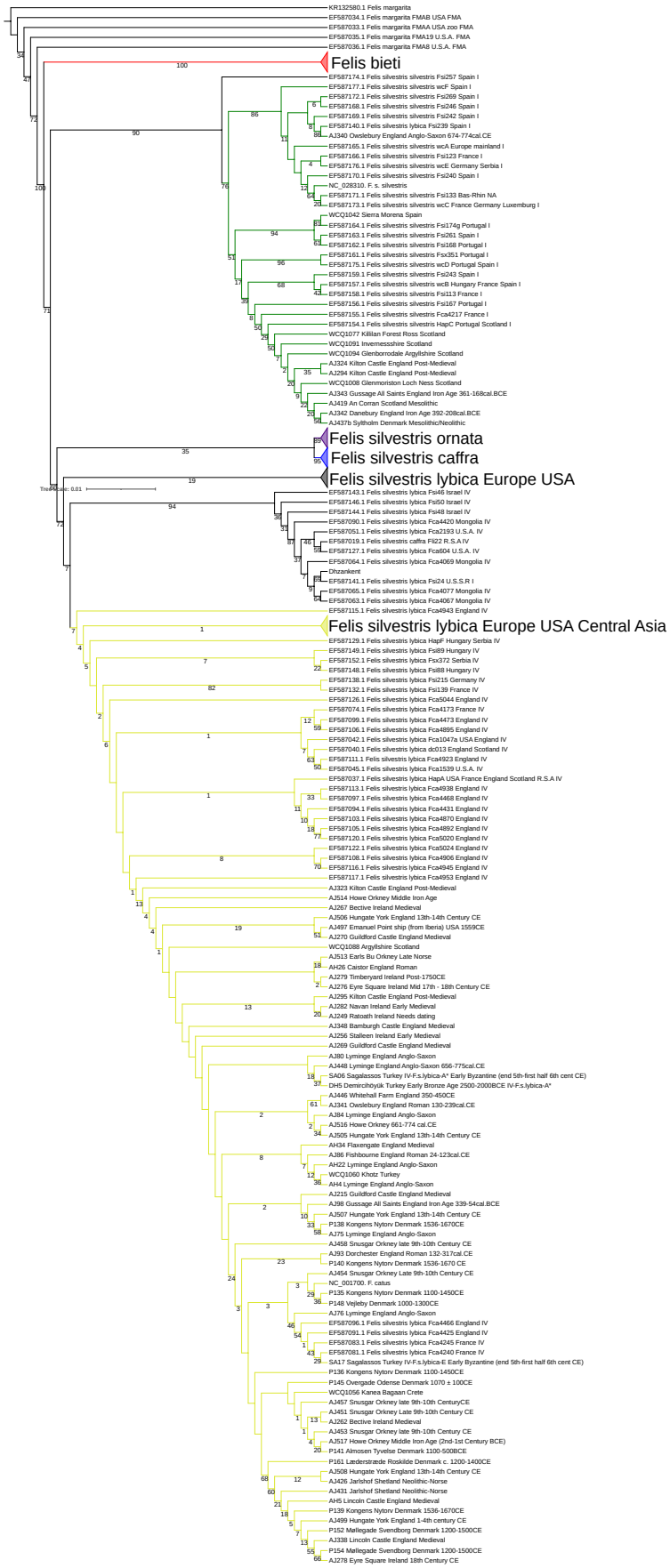


Figure S3.2 Bayesian tree of samples from this study with 60 % or more bases covered. All samples are above 4x depth of coverage, apart from those marked with † which are between 2x-4x. Those marked with a * are samples mentioned in the main text.

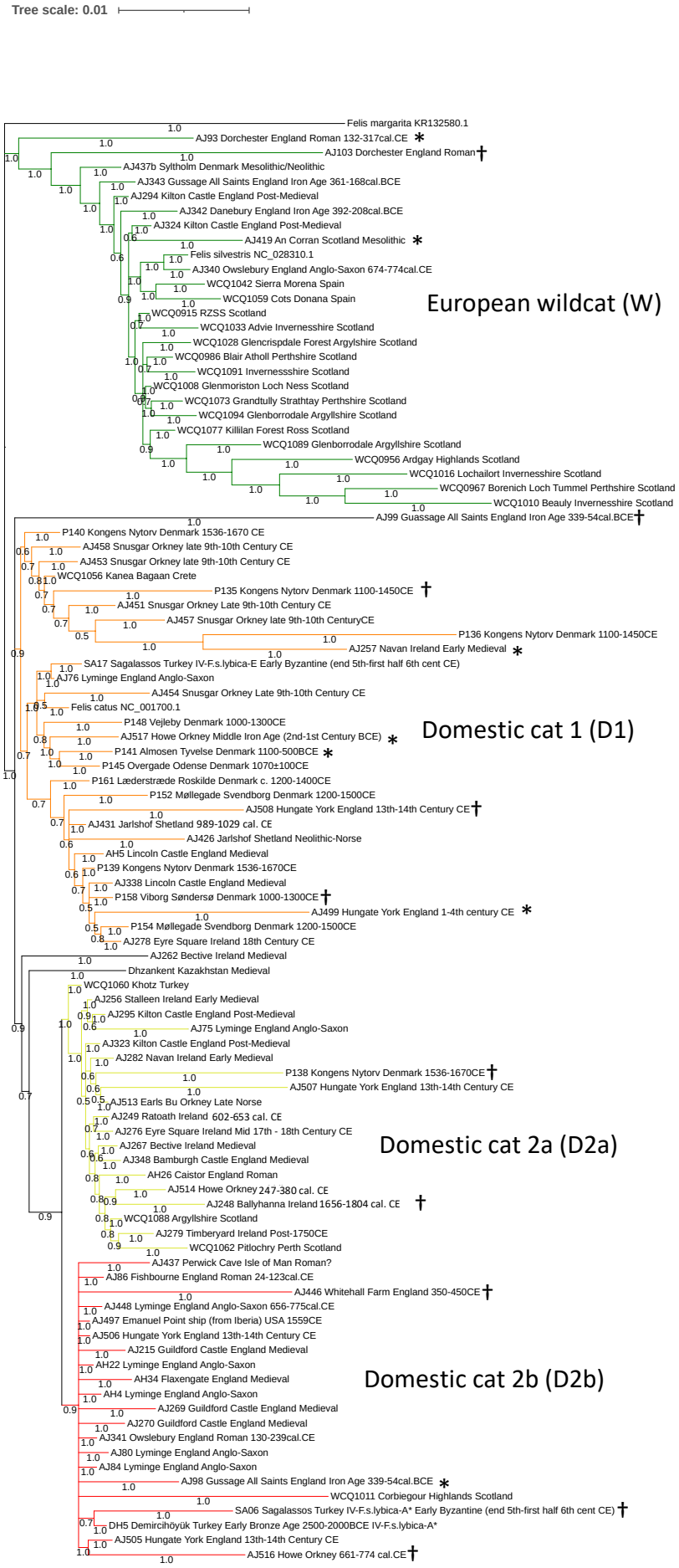


Figure S3.3 Maximum likelihood tree of samples from this study 60 % or more bases of bases covered. All samples are above 4x depth of coverage, apart from those marked with † which are between 2x-4x.

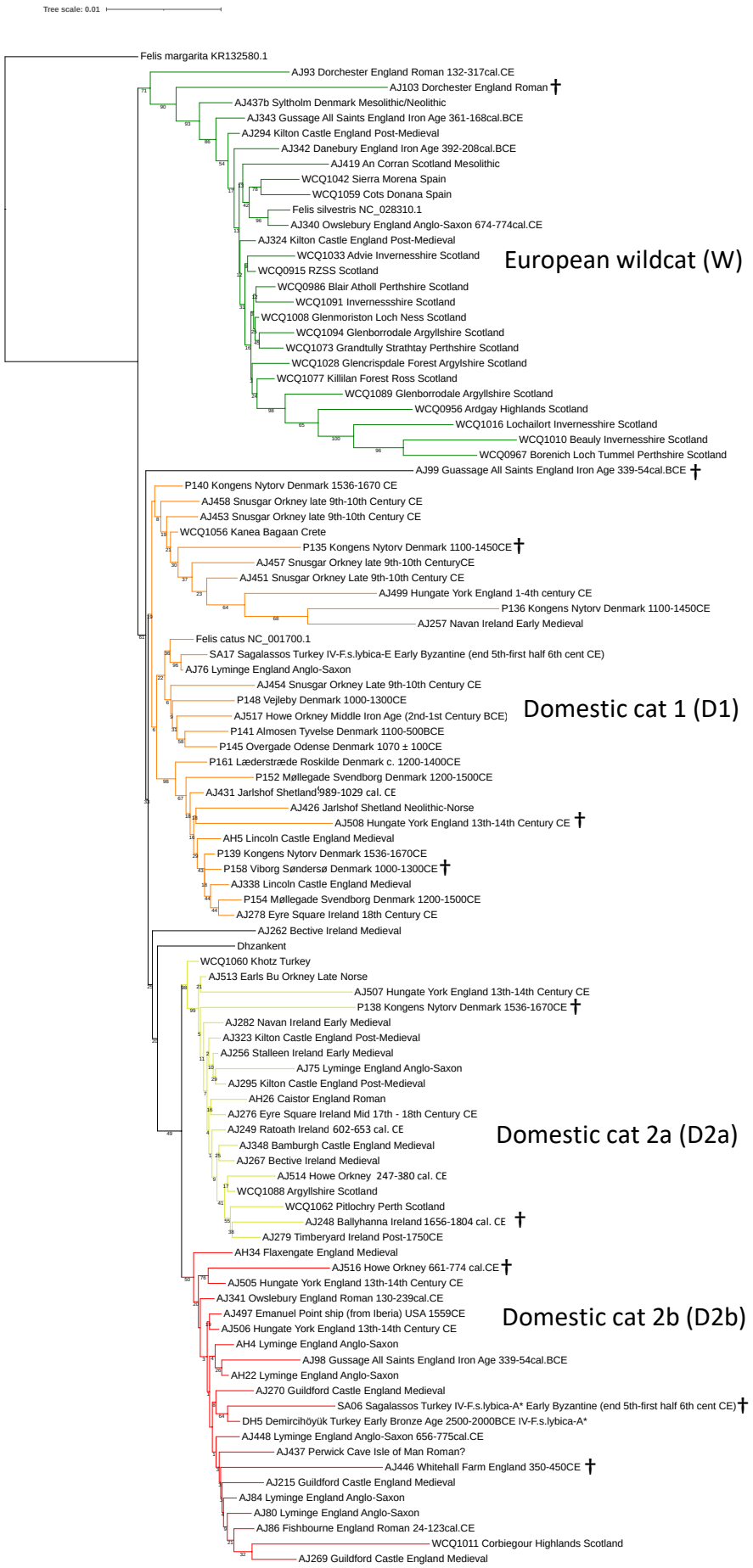


Figure S3.4a Admixture full plot of all samples included in the PCA, error bars have been omitted for clarity

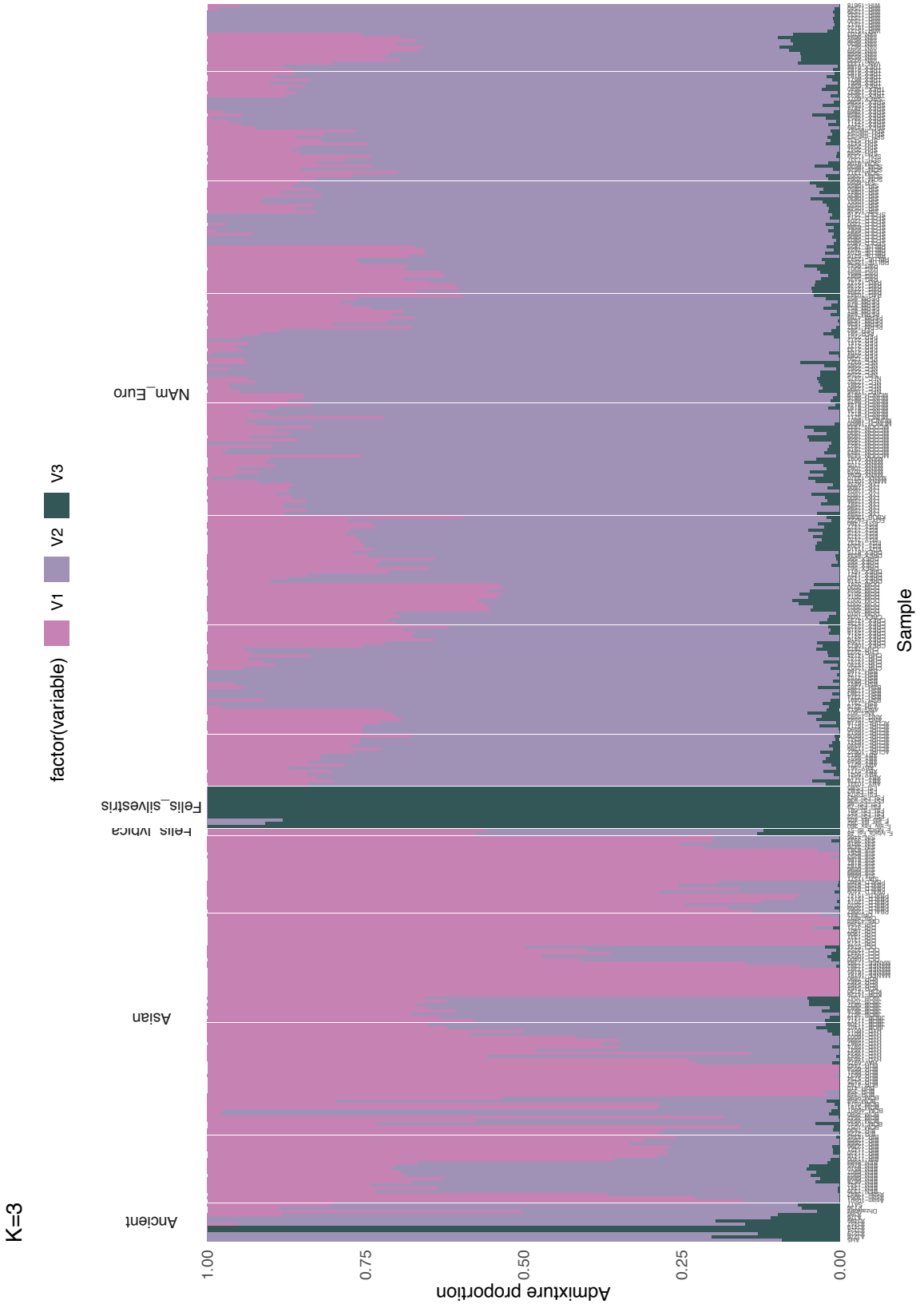


Figure S3.4b Admixture plot of the same subset as Figure 3.4 in the main text with error bars added

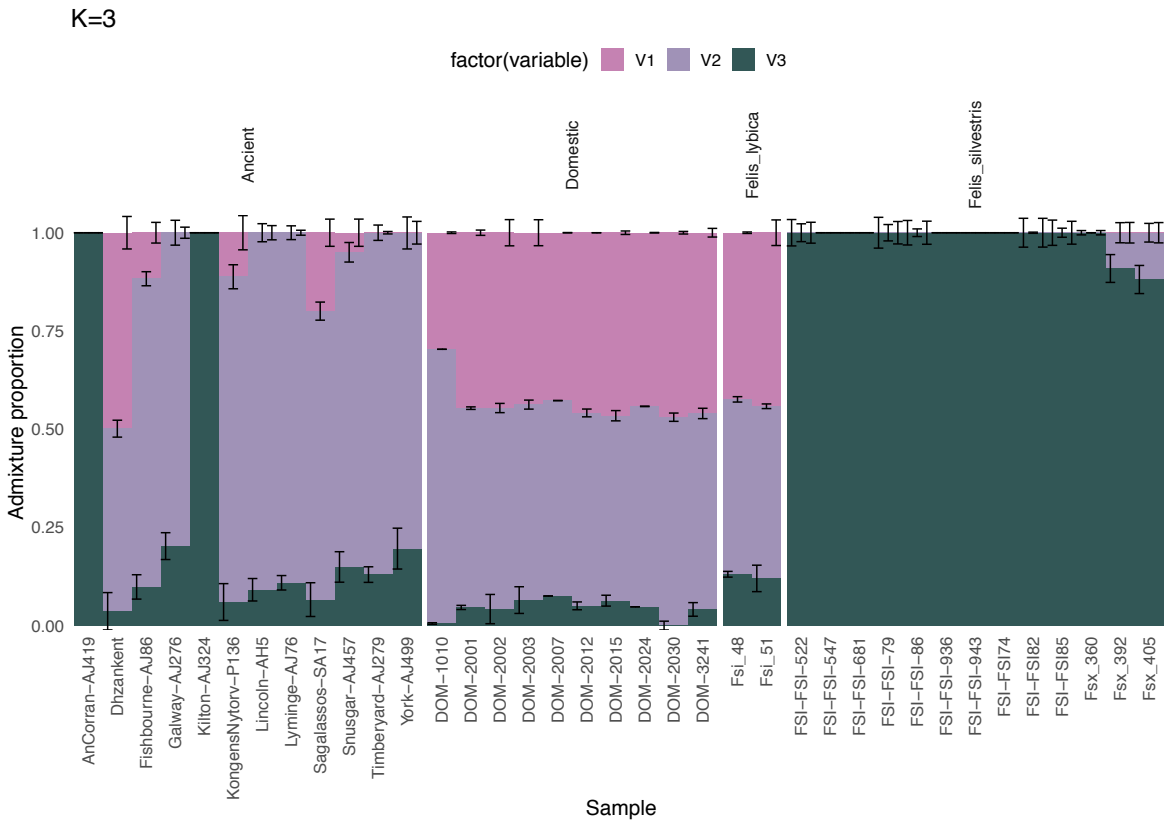
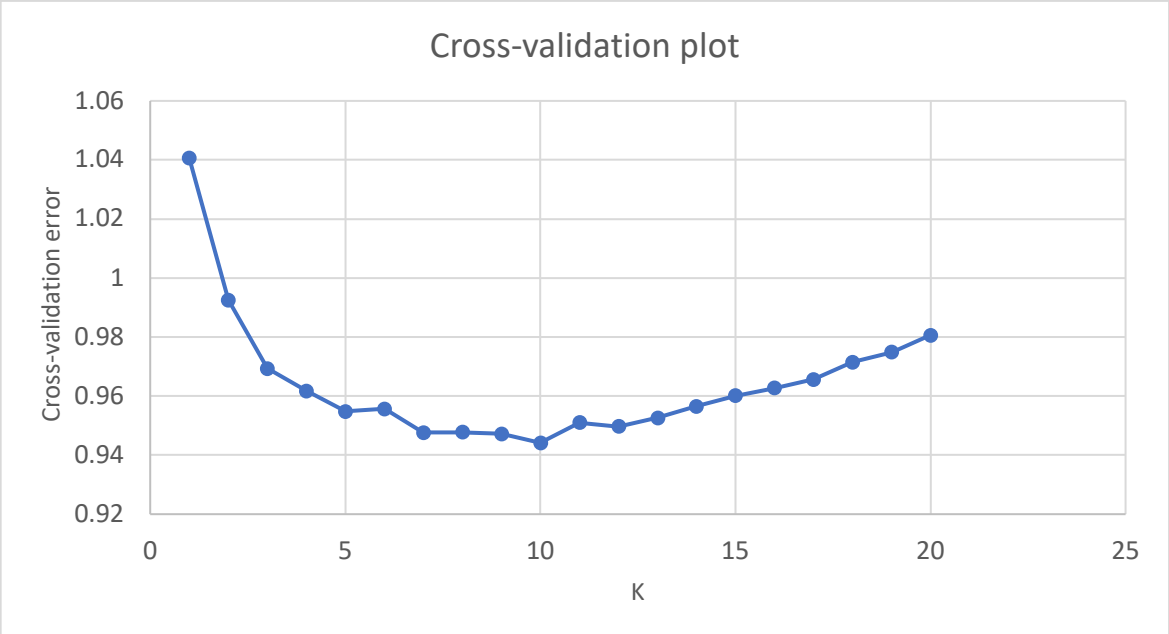


Figure S3.4c Cross Validation plot for ADMIXTURE analysis



3.10.2 Supplementary Information Tables

Table S3.1 List of ancient samples included in analysis and sequenced

Extract code	Sample ID/ information (if known)	Site	Country	Period	Element	Sample provider	Laboratory Performed extraction	Laboratory performed library building onwards	Mitochondrial final coverage (x)	Depth of sequencing	Full genome depth of coverage (x)	Included in analysis
DVIN1_II		Dvin	Armenia	Middle Age	cranium	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
P141		Almosen, Tyvelse	Denmark	1100-500 BCE	tibia	Anne Birgitte Gotfredsen	Oxford	Oxford	7	Capture/Screening		YES
P147		Gyngstruplund Nordøst	Denmark	c. 1-150 CE	tibia	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P133		Kongens Nytorv	Denmark	1100-1450 CE	tibia	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P135		Kongens Nytorv	Denmark	1100-1450 CE	tibia	Anne Birgitte Gotfredsen	Oxford	Oxford	3.8	Capture/Screening		YES
P136		Kongens Nytorv	Denmark	1100-1450 CE	tibia	Anne Birgitte Gotfredsen	Oxford	Oxford	9.6	Deeper sequencing	0.3	YES
P138		Kongens Nytorv	Denmark	1536-1670 CE	humerus	Anne Birgitte Gotfredsen	Oxford	Oxford	2.3	Capture/Screening		YES
P139		Kongens Nytorv	Denmark	1536-1670 CE	humerus	Anne Birgitte Gotfredsen	Oxford	Oxford	161.2	Capture/Screening		YES
P140		Kongens Nytorv	Denmark	1536-1670 CE	humerus	Anne Birgitte Gotfredsen	Oxford	Oxford	17.2	Capture/Screening		YES
P161		Læderstræde 4, Roskilde	Denmark	c. 1200-1400 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	13	Capture/Screening		YES
P163		Læderstræde 4, Roskilde	Denmark	c. 1200-1400 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	1.4	Capture/Screening		
P164		Læderstræde 4, Roskilde	Denmark	c. 1200-1400 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0.7	Capture/Screening		
P165		Læderstræde 4, Roskilde	Denmark	c. 1200-1400 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0.1	Screening		

P151		Møllegade 6, Svendborg	Denmark	1200-1500 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0.3	Screening		
P152		Møllegade 6, Svendborg	Denmark	1200-1500 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	7.3	Capture/Screening		YES
P153		Møllegade 6, Svendborg	Denmark	1200-1500 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P154		Møllegade 6, Svendborg	Denmark	1200-1500 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	48.2	Capture/Screening		YES
P142		Overgade, Odense	Denmark	1070 ± 100 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0.1	Screening		
P143		Overgade, Odense	Denmark	1070 ± 100 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P144		Overgade, Odense	Denmark	1070 ± 100 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P145		Overgade, Odense	Denmark	1070 ± 100 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	11.6	Capture/Screening		YES
P146		Overgade, Odense	Denmark	1070 ± 100 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P167		Ribe	Denmark	8th century	mandible	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
AJ437b	MLF00906-I x8876	Sylholm	Denmark	Mesolithic/Neolithic	tooth	Mikkel Sinding	Oxford	Oxford	19.5	Capture/Screening		YES
AJ440	MLF00906-I X7925	Sylholm	Denmark	Mesolithic/Neolithic	tooth	Mikkel Sinding	Oxford	Oxford	0.1	Screening		
AJ441	MLF00906-I X4908	Sylholm	Denmark	Mesolithic/Neolithic	tooth	Mikkel Sinding	Oxford	Oxford	0.1	Screening		
P168		Toftegård	Denmark	c. 650-1075 CE	radius	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P149		Unknown	Denmark	unknown	tibia	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P148		Vejleby	Denmark	1000-1300 CE	ulna	Anne Birgitte Gotfredsen	Oxford	Oxford	8.4	Capture/Screening		YES
P156		Viborg Søndersø	Denmark	1000-1300 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		

P157		Viborg Søndersø	Denmark	1000-1300 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P158		Viborg Søndersø	Denmark	1000-1300 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	3	Screening		YES
P159		Viborg Søndersø	Denmark	1000-1300 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0	Screening		
P160		Viborg Søndersø	Denmark	1000-1300 CE	femur	Anne Birgitte Gotfredsen	Oxford	Oxford	0.1	Screening		
BE01		Berenike	Egypt	Early Roman; 1st-2nd century CE	scapula	Claudio Ottoni	Paris/Leuven	Oxford	1.5	Capture/Screening		
BE02		Berenike	Egypt	Early Roman; 1st-2nd century CE	astragalus	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
BE04		Berenike	Egypt	Late Roman; late 4th - early 5th century CE	astragalus	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
BM02		British Museum	Egypt	Ptolemaic or Roman	skin	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
OXI3_II		Oxyrhynchus	Egypt	about 500 BCE to Roman period	vertebra	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
AJ345	ACR 0001	Ashton	England	Roman	ulna	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ344	BAL 0010	Baldock	England	Pre-Roman		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ348	BC09 0001	Bambrugh Castle	England	Medieval	mandible	Naomi Sykes	Oxford	Oxford	27.6	Capture/Screening		YES
AH13	BC09 0002	Bambrugh Castle	England	Medieval		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ337	CRT0001	Caistor Roman Town	England	Roman	pelvis	Naomi Sykes	Oxford	Oxford	0.1	Screening		
AH20	CRT0002	Caistor Roman Town	England	Roman	pelvis	Naomi Sykes	Oxford	Oxford	0.1	Screening		
AH11	CAS0003	Caistor Roman Town	England	Roman	pelvis	Naomi Sykes	Oxford	Oxford	0	Screening		
AH26	CRT003	Caistor Roman Town	England	Roman	pelvis	Naomi Sykes	Oxford	Oxford	10.1	Capture/Screening		YES

AJ342	DAB0001	Danebury	England	Iron Age	humerus	Naomi Sykes	Oxford	Oxford	13.6	Capture/Screening		YES
AJ90		Dorchester	England	Roman	mandible	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ91		Dorchester	England	Roman		Naomi Sykes	Oxford	Oxford	0.5	Capture/Screening		
AJ92		Dorchester	England	Roman	humerus	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ93		Dorchester	England	Roman		Naomi Sykes	Oxford	Oxford	4.5	Capture/Screening		YES
AJ95		Dorchester	England	Roman	Tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ96		Dorchester	England	Roman	femur	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ103		Dorchester	England	Roman		Naomi Sykes	Oxford	Oxford	2.5	Capture/Screening		YES
AJ104		Dorchester	England	Roman	vertebra	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ85	CHCFB:FBE02/CB401	Fishbourne	England	Iron Age	humerus	The Sussex Archaeological Society	Oxford	Oxford	0.5	Capture/Screening		
AJ86	CHCFB:FBE02/CB403	Fishbourne	England	Roman	mandible	The Sussex Archaeological Society	Oxford	Oxford	158	Deeper sequencing	4.6	YES
AJ87	CHCFB:FBE02/CB404	Fishbourne	England	Roman	canine	The Sussex Archaeological Society	Oxford	Oxford	0	Screening		
AJ88	CHCFB:FBE02/CB405	Fishbourne	England	Roman	tibia	The Sussex Archaeological Society	Oxford	Oxford	0	Screening		
AJ89	CHCFB:FBE02/CB406	Fishbourne	England	Roman	femur	The Sussex Archaeological Society	Oxford	Oxford	0	Screening		
AH33		Flaxengate	England	Medieval		Naomi Sykes	Oxford	Oxford	0	Screening		
AH36		Flaxengate	England	Medieval		Naomi Sykes	Oxford	Oxford	0	Screening		
AH38		Flaxengate	England	Medieval		Naomi Sykes	Oxford	Oxford	0	Screening		

AH35		Flaxengate	England	Medieval		Naomi Sykes	Oxford	Oxford	0	Screening		
AH34		Flaxengate	England	Medieval		Naomi Sykes	Oxford	Oxford	6.9	Capture/Screening		YES
AJ97	box 475 bone 59 feature 381	Guassage All Saints	England	Iron Age	long bone	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ98	box 490 bone 74 feature 424	Guassage All Saints	England	Iron Age	long bone	Naomi Sykes	Oxford	Oxford	5.1	Capture/Screening		YES
AJ99	box 490 bone 74 feature 424	Guassage All Saints	England	Iron Age	long bone	Naomi Sykes	Oxford	Oxford	2.6	Capture/Screening		YES
AJ100	box 490 bone 74 feature 424	Guassage All Saints	England	Iron Age	long bone	Naomi Sykes	Oxford	Oxford	0.5	Capture/Screening		
AJ101	box 435 feature 77	Guassage All Saints	England	Iron Age	femur	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ102	box 443 feature 157	Guassage All Saints	England	Iron Age	humerus	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ214	GCP 92 383	Guildford castle	England	Medieval	cranium	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ215	AG21367	Guildford castle	England	Medieval	femur	Naomi Sykes	Oxford	Oxford	17.4	Capture/Screening		YES
AJ216	LP89 1220	Guildford castle	England	Medieval	radius	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ217	GCP 93 621	Guildford castle	England	Medieval	tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ218	GCP92 396	Guildford castle	England	Medieval	humerus	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ219	GCP90 116	Guildford castle	England	Medieval	humerus	Naomi Sykes	Oxford	Oxford	0.1	Screening		
AJ220	AG21559	Guildford castle	England	Medieval	humerus	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ221	AG21558 CD 72.2.60	Guildford castle	England	Medieval	femur	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ268	AG21366	Guildford castle	England	Medieval	pelvis	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ269	AG21366	Guildford castle	England	Medieval	pelvis	Naomi Sykes	Oxford	Oxford	6.9	Capture/Screening		YES

AJ270	AG21418	Guildford castle	England	Medieval	radius	Naomi Sykes	Oxford	Oxford	10	Capture/Screening		YES
AJ343	GAS0001	Gussage All Saints	England	Iron Age	Tibia	Naomi Sykes	Oxford	Oxford	24.8	Capture/Screening		YES
AJ108	1986.155 1	Hod Hill	England	Roman	femur?	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ510	49646	Hungate, York	England	unknown	cranium	York Archaeological Trust	Oxford	Oxford	0.3	Screening		
AJ499	49014	Hungate, York	England	1-4th	humerus	York Archaeological Trust	Oxford	Oxford	7.7	Deeper sequencing	0.2	YES
AJ502	52192	Hungate, York	England	10th century	humerus	York Archaeological Trust	Oxford	Oxford	0	Screening		
AJ498	48060	Hungate, York	England	11th-12th century	humerus	York Archaeological Trust	Oxford	Oxford	0	Screening		
AJ503	48404	Hungate, York	England	12th-13th century	humerus	York Archaeological Trust	Oxford	Oxford	0.4	Screening		
AJ504	48404	Hungate, York	England	12th-13th century	ulna	York Archaeological Trust	Oxford	Oxford	0.4	Screening		
AJ505	49004	Hungate, York	England	13th-14th century	ulna	York Archaeological Trust	Oxford	Oxford	11.4	Capture/Screening		YES
AJ506	49073	Hungate, York	England	13th-14th century	Femur?	York Archaeological Trust	Oxford	Oxford	158	Capture/Screening		YES
AJ507	49438	Hungate, York	England	13th-14th century	humerus	York Archaeological Trust	Oxford	Oxford	5.1	Capture/Screening		YES

AJ508	50062	Hungate, York	England	13th-14th century	ulna	York Archaeological Trust	Oxford	Oxford	3.2	Capture/Screening		YES
AJ509	49459	Hungate, York	England	13th-14th century	pelvis	York Archaeological Trust	Oxford	Oxford	0.1	Screening		
AJ500	52552	Hungate, York	England	undated	femur	York Archaeological Trust	Oxford	Oxford	0.8	Screening		
AJ501	52776	Hungate, York	England	undated	humerus	York Archaeological Trust	Oxford	Oxford	0.1	Screening		
AJ511	53366	Hungate, York	England	undated	cranium	York Archaeological Trust	Oxford	Oxford	0.4	Screening		
AJ323	KC1	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	70.6	Capture/Screening		YES
AJ324	KC2	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	265.3	Deeper sequencing	0.9	YES
AJ325	KC3	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	1.1	Screening		
AJ291	KC4	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	0	Screening		
AJ326	KC5	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	0	Screening		
AJ293	KC6	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	0.5	Screening		
AJ294	KC7	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	24.4	Capture/Screening		YES
AJ295	KC8	Kilton Castle	England	Post-Medieval	mandible	David Orton/ Terry O'Connor	Oxford	Oxford	15	Capture/Screening		YES

AH5	LCNCC0002	Lincoln Castle	England	Medieval	femur	Naomi Sykes	Oxford	Oxford	79.3	Capture/Screening/ Deeper sequencing	0.4	YES
AJ338	LCNCC0003	Lincoln Castle	England	Medieval	tibia	Naomi Sykes	Oxford	Oxford	82.1	Capture/Screening		YES
AJ339	LCNCC0006	Lincoln Castle	England	Medieval	radius	Naomi Sykes	Oxford	Oxford	0	Screening		
AH30	1074	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0	Screening		
AH21	1263	Lyminge	England	Anglo-Saxon	femur	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ109	Lum12(3261)	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ112	Lum08(106)	Lyminge	England	Anglo-Saxon	tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ347	47	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ113	Lym08(197)	Lyminge	England	Anglo-Saxon	humerus	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ68	Lym08(232)	Lyminge	England	Anglo-Saxon	femur	Naomi Sykes	Oxford	Oxford	0.1	Screening		
AH23	717	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0.3	Screening		
AJ69	Lym08(546)	Lyminge	England	Anglo-Saxon	tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ70	Lym08(634)	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ71	Lym08(645)	Lyminge	England	Anglo-Saxon	metatarsal	Naomi Sykes	Oxford	Oxford	0.9	Screening		
AJ72	Lym08(658)	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0.3	Screening		
AJ73	Lym08(658)	Lyminge	England	Anglo-Saxon	radius	Naomi Sykes	Oxford	Oxford	1.1	Screening		
AJ74	Lym08(715)	Lyminge	England	Anglo-Saxon	radius	Naomi Sykes	Oxford	Oxford	0.9	Screening		
AJ82	Lym09(1037)	Lyminge	England	Anglo-Saxon	mandible	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ83	Lym09(1091)	Lyminge	England	Anglo-Saxon	mandible	Naomi Sykes	Oxford	Oxford	0	Screening		
AH2	2165	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ84	lym09(1095)	Lyminge	England	Anglo-Saxon	tibia	Naomi Sykes	Oxford	Oxford	41.5	Capture/Screening		YES
AJ75	Lym09(1101)	Lyminge	England	Anglo-Saxon	humerus	Naomi Sykes	Oxford	Oxford	5.3	Capture/Screening		YES

AJ76	Lym09(1333)	Lyminge	England	Anglo-Saxon	tibia	Naomi Sykes	Oxford	Oxford	461.1	Deeper sequencing	1.8	YES
AJ77	Lym09(1360)	Lyminge	England	Anglo-Saxon	mandible	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ78	Lym09(1362)	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ79	Lym09(1449)	Lyminge	England	Anglo-Saxon	ulna	Naomi Sykes	Oxford	Oxford	0.5	Screening		
AJ80	Lym09(1502)	Lyminge	England	Anglo-Saxon	femur	Naomi Sykes	Oxford	Oxford	28.3	Capture/Screening		YES
AJ334	602	Lyminge	England	Anglo-Saxon	humerus	Naomi Sykes	Oxford	Oxford	0	Screening		
AH22	1956	Lyminge	England	Anglo-Saxon	femur	Naomi Sykes	Oxford	Oxford	53.4	Capture/Screening		YES
AJ81	Lym09(1664)	Lyminge	England	Anglo-Saxon	tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ448	329 and 330	Lyminge	England	Anglo-Saxon	tibia	Naomi Sykes	Oxford	Oxford	38.8	Capture/Screening		YES
AJ449	1073 - 1076	Lyminge	England	Anglo-Saxon	ulna	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ450	1556	Lyminge	England	Anglo-Saxon		Naomi Sykes	Oxford	Oxford	0	Screening		
AH4	3027	Lyminge	England	Anglo-Saxon	metatarsal	Naomi Sykes	Oxford	Oxford	16.7	Capture/Screening		YES
AJ340	OWB0002	Owslebury	England	Anglo-Saxon	tibia	Naomi Sykes	Oxford	Oxford	21.9	Capture/Screening		YES
AJ341	OWB0001	Owslebury	England	Roman	metatarsal	Naomi Sykes	Oxford	Oxford	35.8	Capture/Screening		
AJ107	QF 634 box 71	Quarry field	England	Iron Age/Roman	femur	Naomi Sykes	Oxford	Oxford	0.1	Capture/Screening		
AJ349	E5810005	Whistler place	England	Post-Medieval	tibia	Naomi Sykes	Oxford	Oxford	0.7	Capture/Screening		
AJ350	E5810013	Whistler place	England	Post-Medieval	femur	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ105	WH 1965-76 1572.121	Whitcombe	England	Roman	tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ106	WH.1966.39.122	Whitcombe	England	Roman	tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ443	53366	Whitehall farm	England	Roman	humerus	Naomi Sykes	Oxford	Oxford	0.1	Screening		

AJ444	53366	Whitehall farm	England	Roman	tibia	Naomi Sykes	Oxford	Oxford	0	Screening		
AJ445	1982-0209	Whitehall farm	England	Roman		Naomi Sykes	Oxford	Oxford	0	Screening		
AJ446	CH1575	Whitehall farm	England	Roman		Naomi Sykes	Oxford	Oxford	3.8	Capture/Screening		YES
AJ447	CH1666	Whitehall farm	England	Roman		Naomi Sykes	Oxford	Oxford	0	Screening		
KA03_II		Kastanas	Greece	c. 200-400 BCE	mandible	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
KA1		Kastanas	Greece	c. 1250 BCE	radius	Claudio Ottoni	Paris/Leuven	Oxford	1.2	Capture/Screening		
AJ252	5791	Annaghdown	Ireland	11th-12th century	Femur	Fiona Beglane	Oxford	Oxford	0.1	Screening		
AJ248	184	Ballyhanna	Ireland	17^{th}-19^{th} century	Femur	Fiona Beglane	Oxford	Oxford	3.2	Screening		YES
AJ259	9552	Bective	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ260	7597	Bective	Ireland	Medieval	Mandible	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ261	7856	Bective	Ireland	Medieval	metatarsal	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ262	7492	Bective	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	4.1	Capture/Screening		YES
AJ263	8944	Bective	Ireland	Medieval	humerus	Fiona Beglane	Oxford	Oxford	0.6	Screening		
AJ264	9061	Bective	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ265	7558	Bective	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ266	11297	Bective	Ireland	Medieval	tibia	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ267	9947	Bective	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	42	Capture/Screening		YES
AJ244	10365	Bective	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ245	8883	Bective	Ireland	Medieval	metatarsal	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ246	11452	Bective	Ireland	Medieval	Radius	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ247	11355	Bective	Ireland	Medieval	tibia	Fiona Beglane	Oxford	Oxford	0.3	Screening		
AJ280	5962	Bective	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	0.1	Screening		

AJ287	12578	Chancellorsland	Ireland	unknown	Mandible	Fiona Beglane	Oxford	Oxford	1.5	Capture/Screening		
AJ278	5786	Eyre Square, Galway	Ireland	18th century CE	Femur	Fiona Beglane	Oxford	Oxford	27	Capture/Screening		YES
AJ251	5793	Eyre Square, Galway	Ireland	18th-19th century	Femur	Fiona Beglane	Oxford	Oxford	0.1	Screening		
AJ276	5712	Eyre Square, Galway	Ireland	Mid-17th - 18th century CE	Ulna	Fiona Beglane	Oxford	Oxford	72.6	Deeper sequencing	0.3	YES
AJ284	6139	Greencastle	Scotland	13th century CE		Fiona Beglane	Oxford	Oxford	0.3	Screening		
AJ277	5739	Mallin St. Wexford	Ireland	Post-Medieval	tibia	Fiona Beglane	Oxford	Oxford	0	Capture/Screening		
AJ273	5683	Market St Trim	Ireland	Medieval	tibia	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ274	5684	Market St Trim	Ireland	Medieval	tibia	Fiona Beglane	Oxford	Oxford	0.1	Screening		
AJ285	6181	Mountgorry	Ireland	11-12th century	humerus	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ281	6032	Navan 1	Ireland	9th century CE	Mandible	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ282	6095	Navan 2 & 3	Ireland	Early Medieval	humerus	Fiona Beglane	Oxford	Oxford	14.8	Capture/Screening		YES
AJ283	6118	Navan 2 & 3	Ireland	Early Medieval	humerus	Fiona Beglane	Oxford	Oxford	0.1	Screening		
AJ257	5827	Navan 2 +3	Ireland	Early Medieval	tibia	Fiona Beglane	Oxford	Oxford	4.6	Capture/Screening		YES
AJ275	5703	Nobber	Ireland	14th century	Mandible	Fiona Beglane	Oxford	Oxford	0.1	Screening		
AJ253	7643	Parknabinnia	Ireland	Early Neolithic	humerus	Fiona Beglane	Oxford	Oxford	1.6	Screening		
AJ250	5661	Ratoath	Ireland	Anglo Norman	Femur	Fiona Beglane	Oxford	Oxford	0.2	Screening		
AJ249	3923	Ratoath	Ireland	7th century CE	Femur	Fiona Beglane	Oxford	Oxford	30.5	Capture/Screening		YES
AJ256	6927	Stalleen	Ireland	Early Medieval	tibia	Fiona Beglane	Oxford	Oxford	68.6	Capture/Screening		YES
AJ254	6728	Stalleen	Ireland	Medieval	Ulna	Fiona Beglane	Oxford	Oxford	0	Screening		
AJ255	7057	Stalleen	Ireland	Medieval	Femur	Fiona Beglane	Oxford	Oxford	0	Screening		

AJ279	5850	Timberyard	Ireland	Post 1750	Femur	Fiona Beglane	Oxford	Oxford	32.9	Deeper sequencing	1.1	YES
AJ286	6338	Town parks South, Trim	Ireland	Medieval	cranium	Fiona Beglane	Oxford	Oxford	0.3	Screening		
AJ437	1982-0209	Perwick Cave	Isle of Man	Roman?	tooth	Manx Museum	Oxford	Oxford	4.6	Deeper sequencing	0	YES
AQ1_II		Aqaba	Jordan	Ottoman	humerus	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
Dzhankent	PRJEB38002	Dzhankent	Kazakhstan	Medieval		Ashleigh Haruda	Potsdam	Potsdam	22.9	Previously sequenced		YES
SID1_II		Sidon	Lebanon	Middle Bronze Age (2nd mill BCEE)	mandible	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
BM03_II		British Museum	N/A	Ptolemaic or Roman	hair	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
QAL3_II		Qalhat	Oman	Medieval, Islam.	axis	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
QAL1_II		Qalhat	Oman	Medieval, Islam.	mandible	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
PIE3_II		Pietrele	Roman/Iron Age	4550-4250 BCE (Gumelnița culture)	radius	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
AJ419	AC0247	An Corran	Scotland	Mesolithic	ulna	NHM Scotland	Oxford	Oxford	34.3	Deeper sequencing	0.2	YES
AJ423	HL 399/04	Druimvargie	Scotland	Mesolithic	tibia	NHM Scotland	Oxford	Oxford	0	Screening		
AJ424	HL 399/03	Druimvargie	Scotland	Mesolithic	tibia	NHM Scotland	Oxford	Oxford	0	Screening		
AJ425	X.HL 406.Z or 406.02	Druimvargie	Scotland	Mesolithic	fibula	NHM Scotland	Oxford	Oxford	0	Screening		
AJ421	Context 103 bag 384	Dundonald Castle	Scotland	Medieval	tibia	NHM Scotland	Oxford	Oxford	0	Screening		
AJ420	Context 103 bag 474	Dundonald Castle	Scotland	Medieval	tibia	NHM Scotland	Oxford	Oxford	0	Screening		
AJ433	Colin Coventry Jan 99	Loch Borralie	Scotland	2913 cal BP	humerus	NHM Scotland	Oxford	Oxford	0	Screening		
AJ422	354	MacArthur cave	Scotland	Mesolithic?	mandible	NHM Scotland	Oxford	Oxford	0	Screening		

AJ432	1940-20-4	Galson	Scotland, Isle of Lewis	500 CE	tibia	NHM Scotland	Oxford	Oxford	1	Capture/Screening		
AJ434	04/11/1940	Broch of Gurness	Scotland, Orkney	Iron Age	femur	NHM Scotland	Oxford	Oxford	0	Screening		
AJ512	469	Earls Bu	Scotland, Orkney	Late Norse	pelvis	Ingrid Mainland	Oxford	Oxford	0	Screening		
AJ513	363	Earls Bu	Scotland, Orkney	Late Norse	femur	Ingrid Mainland	Oxford	Oxford	58.3	Capture/Screening		YES
AJ516	499_4_5	Howe	Scotland, Orkney	Late Iron Age	maxilla	Ingrid Mainland	Oxford	Oxford	3.1	Capture/Screening		YES
AJ515	1214	Howe	Scotland, Orkney	Late Iron Age (Phase 8)	radius	Ingrid Mainland	Oxford	Oxford	0.1	Screening		
AJ517	5939	Howe	Scotland, Orkney	Viking/Late Norse	femur	Ingrid Mainland	Oxford	Oxford	5.2	Capture/Screening		YES
AJ514	3101b	Howe	Scotland, Orkney	Middle Iron Age	tooth	Ingrid Mainland	Oxford	Oxford	12	Deeper sequencing	0.1	YES
AJ442	OSB 95-031, area b	Old Scatness	Scotland, Orkney	Viking	mandible	Ingrid Mainland	Oxford	Oxford	0	Screening		
AJ451	1533	Snusgar	Scotland, Orkney	late 9th-10th century	cranium	Ingrid Mainland	Oxford	Oxford	21.6	Capture/Screening		YES
AJ452	2152	Snusgar	Scotland, Orkney	late 9th-10th century	lower jaw	Ingrid Mainland	Oxford	Oxford	0	Screening		
AJ453	2077	Snusgar	Scotland, Orkney	late 9th-10th century	ulna	Ingrid Mainland	Oxford	Oxford	12.3	Capture/Screening		YES
AJ454	2019	Snusgar	Scotland, Orkney	late 9th-10th century	femur	Ingrid Mainland	Oxford	Oxford	6.5	Capture/Screening		YES
AJ455	2118	Snusgar	Scotland, Orkney	late 9th-10th century	humerus	Ingrid Mainland	Oxford	Oxford	0.1	Screening		
AJ456	2175	Snusgar	Scotland, Orkney	late 9th-10th century	radius	Ingrid Mainland	Oxford	Oxford	0	Screening		
AJ457	2009	Snusgar	Scotland, Orkney	late 9th-10th century	femur	Ingrid Mainland	Oxford	Oxford	20.3	Deeper sequencing	0.4	YES
AJ458	2041	Snusgar	Scotland, Orkney	late 9th-10th century	humerus	Ingrid Mainland	Oxford	Oxford	10.5	Capture/Screening		YES

AJ459	2028	Snusgar	Scotland, Orkney	late 9th-10th century	humerus	Ingrid Mainland	Oxford	Oxford	0	Screening		
AJ460	687	The Cairn, South Romaldsay	Scotland, Orkney	late 9th-10th century	metacarpal	Ingrid Mainland	Oxford	Oxford	0	Screening		
AJ426	summer 1949-1-4	Jarlshof	Scotland, Shetland	Neolithic-Norse	humerus	NHM Scotland	Oxford	Oxford	4	Capture/Screening		YES
AJ427	1935-50-4 smaller	Jarlshof	Scotland, Shetland	Neolithic-Norse	femur	NHM Scotland	Oxford	Oxford	0	Screening		
AJ428	1935-50-4 larger	Jarlshof	Scotland, Shetland	Neolithic-Norse	femur	NHM Scotland	Oxford	Oxford	0	Screening		
AJ429	1952-1-1	Jarlshof	Scotland, Shetland	Neolithic-Norse	femur	NHM Scotland	Oxford	Oxford	0.3	Capture/Screening		
AJ430	1952-1-4 midden c	Jarlshof	Scotland, Shetland	Neolithic-Norse	femur	NHM Scotland	Oxford	Oxford	1.2	Capture/Screening		YES
AJ431	1952 R.P.A layer	Jarlshof	Scotland, Shetland	Viking/Late Norse	humerus	NHM Scotland	Oxford	Oxford	32.1	Capture/Screening		YES
AJ435	1940-17-4	Norby	Scotland, Shetland	Iron Age?		NHM Scotland	Oxford	Oxford	0	Screening		
GO2_II		Gorée	Senagal	after 18th century CE	radius	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
CF1_II		Cova Fosca	Spain	Neolithic	scapula	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
PK1		Mapangani Cave	Tanzania	10-12th century CE	calcaneus	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
SM2		Songo Mnara	Tanzania	end 14th-16th century CE	metapodial	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
UU1_II		Unguja Ukuu	Tanzania	7th-8th century CE	humerus	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
BA02t		Bademagaci	Turkey	Neolithic 6500-6000 BCE	tooth	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
BA02b		Bademagaci	Turkey	Neolithic 6500-6000 BCE	mandible	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
BA04		Bademagaci	Turkey	Neolithic 6500-6000 BCE	pelvis	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		

DH5		Demircihöyük	Turkey	2500-2000 BCE	ulna	Claudio Ottoni	Paris/Leuven	Oxford	94.9	Capture/Screening		YES
DH7		Demircihöyük	Turkey	3000-2500 BCE	tibia	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
DH3_II		Demircihöyük	Turkey	3000-2500 BCE	radius	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
KKG1_II		Kirklareli-Kangligeçit	Turkey	Early Bronze Age	humerus	Claudio Ottoni	Paris/Leuven	Oxford	1.6	Screening		
SA03		Sagalassos	Turkey	Early Byzantine	humerus	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
SA05		Sagalassos	Turkey	Early Byzantine	humerus	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
SA19		Sagalassos	Turkey	Early Byzantine	humerus	Claudio Ottoni	Paris/Leuven	Oxford	1.1	Capture/Screening		
SA20		Sagalassos	Turkey	Early Byzantine	humerus	Claudio Ottoni	Paris/Leuven	Oxford	1.5	Screening		
SA16		Sagalassos	Turkey	Early Byzantine (end 5th-first half 6th century CE)	humerus	Claudio Ottoni	Paris/Leuven	Oxford	0.1	Screening		
SA17		Sagalassos	Turkey	Early Byzantine (end 5th-first half 6th century CE)	humerus	Claudio Ottoni	Paris/Leuven	Oxford	44.5	Deeper sequencing	0.8	YES
SA02		Sagalassos	Turkey	Early Byzantine (end 5th-first half 6th century CE)	fibula	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
SA06		Sagalassos	Turkey	Early Byzantine (end 5th-first half 6th century CE)	mandible	Claudio Ottoni	Paris/Leuven	Oxford	3.7	Capture/Screening		YES
SA01		Sagalassos	Turkey	Late Roman	mandible	Claudio Ottoni	Paris/Leuven	Oxford	0	Screening		
SA18		Sagalassos	Turkey	unknown	humerus	Claudio Ottoni	Paris/Leuven	Oxford	0.3	Screening		
AJ496	14w 5103	Emanuel Point ship	USA	1559	vertebra	John Bratten	Oxford	Oxford	0.2	Screening		
AJ497	15w - 6096	Emanuel Point ship	USA	1559	vertebra	John Bratten	Oxford	Oxford	38.4	Capture/Screening		YES

Table S3.2 List of historic samples included in analysis and sequenced

UNIQUE_ID	Locality	Country	Period	Origin	Sample Provider	MT final coverage	Depth of sequencing	Included in analysis
WCQ1056	Kanea,Bagaan	Crete	1895-1985	NHM Scotland	Helen Senn	4.6	Screening	YES
WCQ1058	Bashuran, Dobrudscha	Romania	1895-1985	NHM Scotland	Helen Senn	1.6	Screening	
WCQ0948	Aberdeenshire	Scotland	1895-1985	NHM Scotland	Helen Senn	1.2	Screening	
WCQ0949	Aberdeenshire	Scotland	1895-1985	NHM Scotland	Helen Senn	1.1	Screening	
WCQ1033	Advie, Invernesshire	Scotland	1895-1985	NHM Scotland	Helen Senn	2.3	Screening	YES
WCQ0956	Ardgay, Highlands	Scotland	1895-1985	NHM Scotland	Helen Senn	2.6	Screening	YES
WCQ1027	Ardnamurchan estate, Invernesshire	Scotland	1895-1985	NHM Scotland	Helen Senn	1.3	Screening	
WCQ1088	Argyllshire	Scotland	1895-1985	NHM Scotland	Helen Senn	8	Screening	YES
WCQ1010	Beauly, Invernesshire	Scotland	1895-1985	NHM Scotland	Helen Senn	2.4	Screening	YES
WCQ1029	Ben Ghornaig, Argyll	Scotland	1895-1985	NHM Scotland	Helen Senn	0.6	Screening	
WCQ1031	Ben Ghornaig, Argyll	Scotland	1895-1985	NHM Scotland	Helen Senn	0.4	Screening	
WCQ1026	Ben Ghornaig, Argyll	Scotland	1895-1985	NHM Scotland	Helen Senn	0.5	Screening	
WCQ0986	Blair Atholl, Perthshire	Scotland	1895-1985	NHM Scotland	Helen Senn	4.1	Screening	YES
WCQ0967	Borenich, Perthshire	Scotland	1895-1985	NHM Scotland	Helen Senn	2.2	Screening	YES
WCQ1021	Braulen, Inverness	Scotland	1895-1985	NHM Scotland	Helen Senn	1.4	Screening	

WCQ1124	Connachan	Scotland	1895-1985	NHM Scotland	Helen Senn	0.6	Screening	
WCQ1011	Corbiegour, Highlands	Scotland	1895-1985	NHM Scotland	Helen Senn	2	Screening	YES
WCQ0965	Glen Ahee,Perthshire	Scotland	1895-1985	NHM Scotland	Helen Senn	1.6	Screening	
WCQ1125	Glen Tanar, Aberdeenshire	Scotland	1895-1985	NHM Scotland	Helen Senn	0.9	Screening	
WCQ1080	Glenborrodale, Argyllshire	Scotland	1895-1985	NHM Scotland	Helen Senn	0.2	Screening	
WCQ1089	Glenborrodale, Argyllshire	Scotland	1895-1985	NHM Scotland	Helen Senn	2.5	Screening	YES
WCQ1094	Glenborrodale, Argyllshire	Scotland	1895-1985	NHM Scotland	Helen Senn	4.1	Screening	YES
WCQ1023	Glencrispdale forest, Argylshire	Scotland	1895-1985	NHM Scotland	Helen Senn	0.2	Screening	
WCQ1028	Glencrispdale forest, Argylshire	Scotland	1895-1985	NHM Scotland	Helen Senn	3.2	Screening	YES
WCQ1030	Glencrispdale forest, Argylshire	Scotland	1895-1985	NHM Scotland	Helen Senn	0	Screening	
WCQ1008	Glenmoriston, Loch Ness	Scotland	1895-1985	NHM Scotland	Helen Senn	10.3	Screening	YES
WCQ1073	Grandtully,Perthshire	Scotland	1895-1985	NHM Scotland	Helen Senn	4.2	Screening	YES
WCQ1057	Invermoriston, Invernesshire	Scotland	1895-1985	NHM Scotland	Helen Senn	0.7	Screening	
WCQ1091	Invernessshire	Scotland	1895-1985	NHM Scotland	Helen Senn	3.5	Screening	YES
WCQ1077	Killilan forest, Ross	Scotland	1895-1985	NHM Scotland	Helen Senn	4.7	Screening	YES
WCQ0966	Loch Tummel, Perthshire	Scotland	1895-1985	NHM Scotland	Helen Senn	1.3	Screening	
WCQ1016	Lochailort, Invernesshire	Scotland	1895-1985	NHM Scotland	Helen Senn	2.4	Screening	YES

WCQ1061	Pitlochry	Scotland	1895-1985	NHM Scotland	Helen Senn	1.4	Screening	
WCQ1062	Pitlochry	Scotland	1895-1985	NHM Scotland	Helen Senn	2.1	Screening	YES
WCQ1123	Ross and Cromarty, Highlands	Scotland	1895-1985	NHM Scotland	Helen Senn	0.9	Screening	
WCQ0915	RZSS	Scotland	Modern	RZSS	Helen Senn	15.9	Screening	YES
WCQ1063	Strathtay, Perthshire	Scotland	1895-1985	NHM Scotland	Helen Senn	1.2	Screening	
WCQ1059	Andalucia	Spain	1895-1985	NHM Scotland	Helen Senn	3	Screening	YES
WCQ1042	Sierra Morena	Spain	1895-1985	NHM Scotland	Helen Senn	3.8	Screening	YES
WCQ1060	Khotz	Turkey	1895-1985	NHM Scotland	Helen Senn	10.3	Screening	YES

Table S3.3 Modern samples used in analysis

Sequence IDs	Species	Location	Analysis used in	Sequence provider
WCQ211	*Felis silvestris silvestris*	Scotland	mitochondrial	Senn
KR132580_1	*Felis margarita*	unknown	mitochondrial	NCBI
NC_001700_1	*Felis catus*	unknown	mitochondrial	NCBI
NC_028310_1	*Felis silvestris silvestris*	unknown	mitochondrial	NCBI
FSI_51	*Felis lybica lybica*	Nahal Zihor Israel	ALL	Driscoll
FSX-405	*Felis silvestris silvestris*	Scotland	ALL	Driscoll
FSX-392	*Felis silvestris silvestris*	Scotland	ALL	Driscoll
FSX-360	*Felis silvestris silvestris*	Portugal	ALL	Driscoll
FSI-48	*Felis lybica lybica*	Nahal Zihor Israel	ALL	Driscoll
FSI-47	*Felis lybica lybica*	Nahal Zihor Israel	ALL	Driscoll
FSI-1	*Felis silvestris silvestris*	Azerbaijan	mitochondrial	Murphy
FBI-4	*Felis bieti*	Qinghai, Huzhu County, Tibet	mitochondrial	Driscoll
FMA-8	*Felis margarita*	UAE	mitochondrial	Driscoll
FSI-204	*Felis lybica ornata*	Syr Daria Kazakhstan	mitochondrial	Driscoll
FSI-7	*Felis lybica lybica*	UAE	mitochondrial	Murphy
FSI-194	*Felis lybica lybica*	Ili River, kazakhstan	mitochondrial	Driscoll

Table S3.4 Sequences used for HAYSTAC custom database

Sequence IDs	Species	Coverage	Location	Sequence provider
FBI-4	*Felis bieti*	13X	Qinghai, Huzhu County, Tibet	Driscoll
WCQ211	*Felis silvestris silvestris*	13X	Scotland	Senn
SRR2062187	*Felis chaus*	18X	China	Yu
FSI-51	*Felis lybica lybica*	20X	Nahal Zihor Israel	Driscoll
FMA-8	*Felis margarita*	22X	UAE captive in Woodland park zoo	Driscoll
SRR5040117	*Felis catus*	19X	Italy	Yu

Table S3.5 Ancient results of both mitochondrial and nuclear species assignment. ML refers to maximum likelihood tree, D1 = Domestic 1, D2a = Domestic 2a. D2b = Domestic 2b and W= European wildcat. Uncertain = where there were two species assigned (when the first call is less than two times the abundance of the first) we have marked these as uncertain species identification.

Extract code	Site	Country	Period	Mitochondrial Coverage (x)	Mitochondrial species assignment	Mitochondrial haplogroup assignment	Method for assignment	Nuclear Species assignment	Method for assignment
P141	Almosen, Tyvelse	Denmark	1100-500 BCE	7	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC
P135	Kongens Nytorv	Denmark	1100-1450 CE	3.8	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC
P136	Kongens Nytorv	Denmark	1100-1450 CE	12.4	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F.catus*	PCA
P138	Kongens Nytorv	Denmark	1536-1670 CE	2.3	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian	*F. beiti*	HAYSTAC
P139	Kongens Nytorv	Denmark	1536-1670 CE	161.2	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
P140	Kongens Nytorv	Denmark	1536-1670 CE	17.2	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
P161	Læderstræd 4, Roskilde	Denmark	c. 1200-1400 CE	13	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F. beiti*	HAYSTAC
P152	Møllegade 6, Svendborg	Denmark	1200-1500 CE	7.3	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC
P154	Møllegade 6, Svendborg	Denmark	1200-1500 CE	48.2	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
P145	Overgade, Odense	Denmark	1070 ± 100 CE	11.6	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC

AJ437b	Sylthom	Denmark	Mesolithic/Neolithic	19.5	*Felis s. silvestris*	W	ML, Bayesian, strict Bayesian	*F.s.silvestris*	HAYSTAC
P148	Vejleby	Denmark	1000-1300 CE	8.4	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC
P158	Viborg Søndersø	Denmark	1000-1300 CE	3	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC
AJ348	Bambrugh Castle	England	Medieval	27.6	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
AH26	Caistor Roman Town	England	Roman	10.1	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
AJ342	Danebury	England	Iron Age	13.6	*Felis s. silvestris*	W	ML, Bayesian, strict Bayesian	*F.s.silvestris*	HAYSTAC
AJ93	Dorchester	England	Roman	4.5	*Felis s. silvestris*	W	ML, Bayesian	*F.s.silvestris*	HAYSTAC
AJ103	Dorchester	England	Roman	2.5	*Felis s. silvestris*	W	ML, Bayesian	uncertain	HAYSTAC
AJ86	Fishbourne	England	Roman	160.6	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AH34	Flaxengate	England	Medieval	6.9	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	*F.catus*	HAYSTAC
AJ215	Guildford castle	England	Medieval	17.4	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
AJ269	Guildford castle	England	Medieval	6.9	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	*F.catus*	HAYSTAC
AJ270	Guildford castle	England	Medieval	10	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	*F.catus*	HAYSTAC
AJ98	Gussage All Saints	England	Iron Age	5.1	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	*F.catus?*	HAYSTAC
AJ99	Gussage All Saints	England	Iron Age	2.6	*Felis catus/Felis l. lybica*	D	ML, Bayesian	*F.l.lybica*	HAYSTAC

AJ343	Gussage All Saints	England	Iron Age	24.8	*Felis s. silvestris*	W	ML, Bayesian, strict Bayesian	*F.s.silvestris*	HAYSTAC
AJ499	Hungate, York	England	1-4th century	8.4	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	*F.catus*	PCA
AJ505	Hungate, York	England	13th-14th century	11.4	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
AJ506	Hungate, York	England	13th-14th century	158	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
AJ507	Hungate, York	England	13th-14th century	5.1	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian	uncertain	HAYSTAC
AJ508	Hungate, York	England	13th-14th century	3.2	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	*F.catus*	HAYSTAC
AJ323	Kilton Castle	England	14th-15th century	70.6	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
AJ324	Kilton Castle	England	14th-15th century	265.3	*Felis s. silvestris*	W	ML, Bayesian, strict Bayesian	*F.s.silvestris*	PCA
AJ294	Kilton Castle	England	14th-15th century	24.4	*Felis s. silvestris*	W	ML, Bayesian, strict Bayesian	*F.s.silvestris*	HAYSTAC
AJ295	Kilton Castle	England	14th-15th century	15	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
AH5	Lincoln Castle	England	Medieval	79.3	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AJ338	Lincoln Castle	England	Medieval	82.1	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
AJ84	Lyminge	England	Anglo-Saxon	41.5	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
AJ75	Lyminge	England	Anglo-Saxon	5.3	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian	*F. chaus*	HAYSTAC

AJ76	Lyminge	England	Anglo-Saxon	461.1	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AJ80	Lyminge	England	Anglo-Saxon	28.3	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
AH22	Lyminge	England	Anglo-Saxon	53.4	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.s.catus*	HAYSTAC
AJ448	Lyminge	England	Anglo-Saxon	38.8	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
AH4	Lyminge	England	Anglo-Saxon	16.7	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
AJ340	Owslebury	England	Anglo-Saxon	21.9	*Felis s. silvestris*	W	ML, Bayesian, strict Bayesian	*F.s.silvestris*	HAYSTAC
AJ341	Owslebury	England	Roman	35.8	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F. beiti*	HAYSTAC
AJ446	Whitehall farm	England	Roman	3.8	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	*F.catus*	HAYSTAC
AJ248	Ballyhanna	Ireland	17th-19th century	3.2	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian	uncertain	HAYSTAC
AJ262	Bective	Ireland	Medieval	4.1	*Felis catus/Felis l. lybica*	D2	ML, Bayesian	uncertain	HAYSTAC
AJ267	Bective	Ireland	Medieval	42	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
AJ278	Eyre Square, Galway	Ireland	18th century CE	27	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
AJ276	Eyre Square, Galway	Ireland	17th - 18th century CE	72.6	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AJ282	Navan 2 & 3	Ireland	Early Medieval	14.8	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
AJ257	Navan 2 +3	Ireland	Early Medieval	4.6	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC

AJ249	Ratoath	Ireland	7th century CE	30.5	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
AJ256	Stalleen	Ireland	Early Medieval	68.6	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
AJ279	Timberyard	Ireland	Post 1750	32.9	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AJ437	Perwick Cave	Isle of Man	Roman?	4.2	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	uncertain	HAYSTAC
Dhzankent	Dhzankent	Kazakhstan	Medieval	22.9	*Felis catus/Felis l. lybica*	D2	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AJ419	An Corran	Scotland	Mesolithic	34.3	*Felis s. silvestris*	W	ML, Bayesian	*F.s.silvestris*	PCA
AJ513	Earls Bu	Scotland, Orkney	Late Norse	58.3	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian, strict Bayesian	*F.l.lybica*	HAYSTAC
AJ516	Howe	Scotland, Orkney	Late Iron Age	3.1	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	*F.catus*	HAYSTAC
AJ517	Howe	Scotland, Orkney	Viking/Late Norse	5.2	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC
AJ514	Howe	Scotland, Orkney	Middle Iron Age	12	*Felis catus/Felis l. lybica*	D2a	ML, Bayesian	uncertain	HAYSTAC
AJ451	Snusgar	Scotland, Orkney	late 9th-10th century	21.6	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
AJ453	Snusgar	Scotland, Orkney	late 9th-10th century	12.3	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
AJ454	Snusgar	Scotland, Orkney	late 9th-10th century	6.5	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	*F.catus*	HAYSTAC

AJ458	Snusgar	Scotland, Orkney	late 9th-10th century	10.5	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
AJ457	Snusgar	Scotland, Orkney	late 9th-10th century	21.6	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AJ426	Jarlshof, Shetland	Scotland, Shetland	Neolithic-Norse	4	*Felis catus/Felis l. lybica*	D1	ML, Bayesian	uncertain	HAYSTAC
AJ431	Jarlshof, Shetland	Scotland, Shetland	Viking/Late Norse	32.1	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	uncertain	HAYSTAC
DH5	Daemircihöyük	Turkey	2500-2000 BCE	94.9	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC
SA06	Sagalassos	Turkey	Early Byzantine (end 5th-first half 6th century CE)	3.7	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian	*F.catus*	HAYSTAC
SA17	Sagalassos	Turkey	Early Byzantine (end 5th-first half 6th century CE)	49.5	*Felis catus/Felis l. lybica*	D1	ML, Bayesian, strict Bayesian	*F.catus*	PCA
AJ497	Emanuel Point ship	USA	1559	38.4	*Felis catus/Felis l. lybica*	D2b	ML, Bayesian, strict Bayesian	*F.catus*	HAYSTAC

Table S3.6 Historic and modern mitochondrial results. D1 = Domestic 1, D2a = Domestic 2a. D2b = Domestic 2b and W= European wildcat

UNIQUE_ID	Locality	Country	Period	Mitochondrial final coverage (x)	Mitochondrial species assignment	Mitochondrial haplogroup assignment
WCQ1056	Kanea	Crete	1895-1985	4.63	Felis catus/Felis l. lybica	D1
WCQ1033	Advie, Invernesshire	Scotland	1895-1985	2.32	Felis silvestris silvestris	W
WCQ0956	Ardgay, Highlands	Scotland	1895-1985	2.56	Felis silvestris silvestris	W
WCQ1088	Argyllshire	Scotland	1895-1985	8.03	Felis catus/Felis l. lybica	D2a
WCQ1010	Beauly, Invernesshire	Scotland	1895-1985	2.37	Felis silvestris silvestris	W
WCQ0986	Blair Atholl, Perthshire	Scotland	1895-1985	4.08	Felis silvestris silvestris	W
WCQ0967	Borenich,Perthshire	Scotland	1895-1985	2.21	Felis silvestris silvestris	W
WCQ1011	Corbiegour, Highlands	Scotland	1895-1985	2.04	Felis catus/Felis l. lybica	D2b
WCQ1089	Glenborrodale Argyllshire	Scotland	1895-1985	2.54	Felis silvestris silvestris	W
WCQ1094	Glenborrodale Argyllshire	Scotland	1895-1985	4.07	Felis silvestris silvestris	W
WCQ1028	Glencrispdale forest, Argylshire	Scotland	1895-1985	3.17	Felis silvestris silvestris	W
WCQ1008	Glenmoriston, Loch Ness	Scotland	1895-1985	10.33	Felis silvestris silvestris	W
WCQ1073	Grandtully,Perthshire	Scotland	1895-1985	4.24	Felis silvestris silvestris	W
WCQ1091	Invernessshire	Scotland	1895-1985	3.51	Felis silvestris silvestris	W
WCQ1077	Killilan forest, Ross	Scotland	1895-1985	4.68	Felis silvestris silvestris	W
WCQ1016	Lochailort, Invernesshire	Scotland	1895-1985	2.39	Felis silvestris silvestris	W
WCQ1062	Pitlochry	Scotland	1895-1985	2.14	Felis catus/Felis l. lybica	D2a
WCQ0915	RZSS	Scotland	Modern	15.94	Felis silvestris silvestris	W
WCQ1059	Andalucia	Spain	1895-1985	3.03	Felis silvestris silvestris	W
WCQ1042	Sierra Morena	Spain	1895-1985	3.84	Felis silvestris silvestris	W
WCQ1060	Khotz	Turkey	1895-1985	10.28	Felis catus/Felis l. lybica	D2a

3.10.3 Supplementary Information Text

Text S3.1 q30 mapping and NUMTs

It is well known that within the nuclear genome of the cat there are fragments of mitochondrial DNA often referred to as NUMTs (nuclear mitochondrial DNA). This makes it difficult to map the cat mitochondrial genome, as it maps to both the nuclear as well as the mitochondrial regions. Any reads mapping to the nuclear genome are expected to be in much lower quantities than those mapping to the true mitochondrial genome, given the abundance of mitochondrial DNA compared to nuclear DNA and the ancient nature of the samples. To overcome this issue, we dropped the mapping quality score to 0. The divergence between the NUMT and the true mitochondrial DNA was great enough that NUMTs would not preferentially map to the mitochondrial DNA (Antunes et al. 2007). For example, the NUMT in Chromosome D2 was inserted 1.8 million years ago which was well before the split of European wildcat and North African wildcat, the two subspecies in this study. All other known NUMTs were inserted before the Chromosome D2 *NUMT* (Antunes et al. 2007).

Text S3.2 HAYSTAC method

There were no publicly available reference sequences for all but *Felis catus*. To ensure no bias towards the published *Felis catus* we did not use this reference and instead used one provided to us along with the other unpublished newly sequenced cat (*Felis*) species. The following species were included in the reference database: *Felis bieti*, *Felis silvestris silvestris*, *Felis chaus*, *Felis margarita*, *Felis lybica lybica* and *Felis catus*. Unfortunately, we were missing two subspecies, *Felis lybica ornata* and *Felis lybica cafra*. *Felis lybica ornata* was not included, as the coverage of the genome was too low to use for this analysis, and *Felis lybica cafra* was not included as we did not have access to a sequence from this species. As hybridisation is known between *Felis silvestris silvestris* and *Felis catus* in most of their present range at least to some degree, we ensure we selected a *Felis silvestris silvestris* with low levels of hybridisation. WCQ211 had a hybrid Q score of 0.884. A score of 1 is pure *Felis silvestris silvestris* however this is rarely seen. This individual had the highest score from the available full genomes. When interpreting the results the occurrence of hybridisation in all of the reference sequences needs to be considered.

Genotype calling was performed using ANGSD (Analysis of Next Generation Sequencing Data). The autosomal genes were extracted for use in all downstream analysis. This removed the mitochondrial genome and the sex chromosomes, as well as all the unplaced contigs. The mitochondrial genome was excluded as it is not nuclear and the sex chromosomes were also discarded as they do not recombine. A custom python script was then used to covert the GLF file into a FASTA file. As HAYSTAC is unable to read heterozygous sites, when there was an occurrence of a heterozygous site, one of the two bases was randomly chosen to avoid any bias. The percentage of Ns in each region was visualised using a graph to see the amount of missing data and how this compared between all the references (Figure S3.5). Next, we masked any areas of the genome not covered in another reference using BEDTools maskfasta. This was to ensure that the mapping was not biased between the different references. First, a bed file was created for each reference with the coordinates for all Ns. These were then merged. The distance between features to merge was set as 0, which meant that only overlapping or bookend features were merged. We tested the amount lost when the distance was set to 0, 10, 40 and 100 bp (base pair) (Table S3.7). These masked FASTA files were then used for the HAYSTAC nuclear reference database.

Distance	% loss average per chromosome
0	9
10	11
40	23
100	49

Table S3.7 BEDTools maskfasta distance between features testing

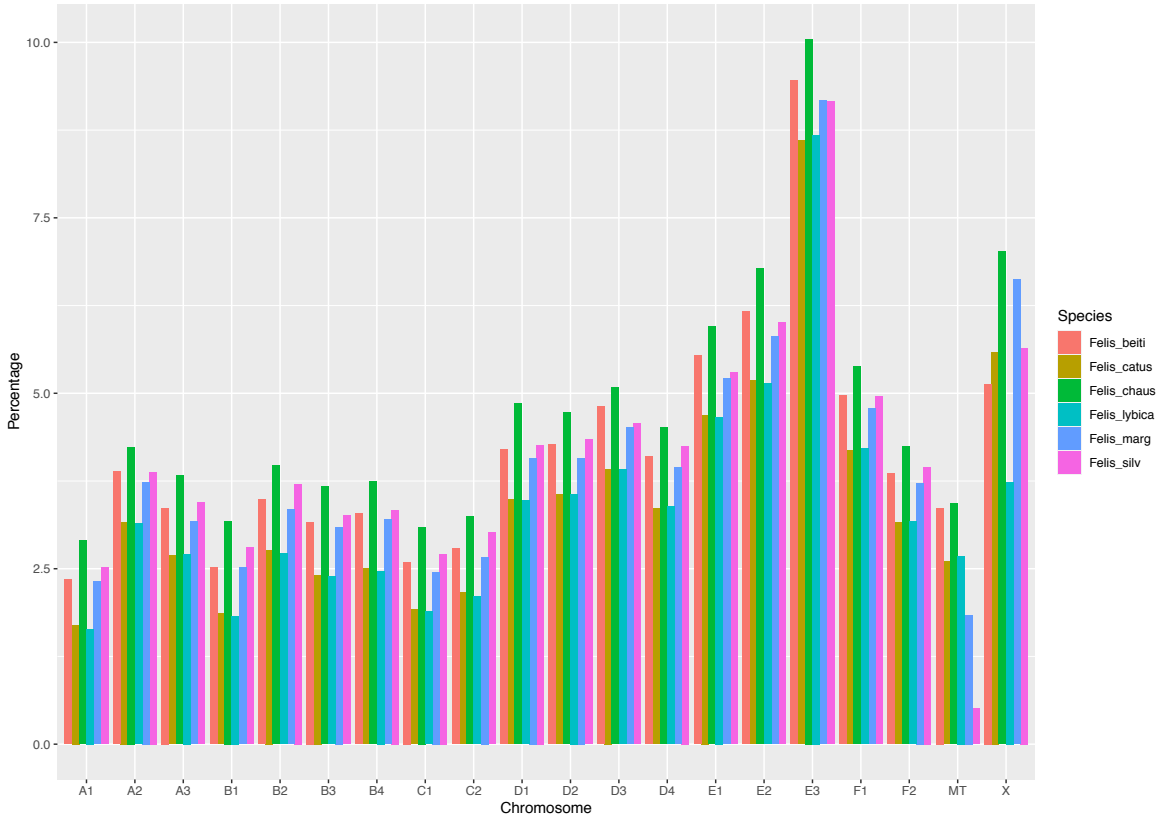


Figure S3.5 Comparison of the percentage of ns of each of the chromosomes from each of the felid reference sequences with distance set to 0.

The increase in Ns does not correlate to the divergence from the domestic cat or the coverage. The highest number of Ns was seen in the X chromosome and E3. The highest number of Ns being in chromosome E3 may be explained by it being the shortest chromosome. It is expected that there is a higher number of Ns in the sexual chromosome compared to the autosomes, as the sexual chromosome should differ more between closely related species. This promotes sexual incompatibility, which is part of the speciation mechanism. The sex chromosome was not used in the HAYSTAC analysis.

Text S3.3 HAYSTAC simulations with modern data

Before running the ancient samples through HAYSTAC, we first ran performance tests to check if HAYSTAC can differentiate between subspecies. To do this, we first simulated an ancient dataset using the modern reference sequences. The programme package 'gargammel', a set of programmes for simulating ancient datasets, was employed to create both a dummy ancient dataset and a dummy hybrid dataset. The amount of damage was set to 0.3 (slight damage) for one set of individuals and 0.9 (very damaged) for another, to

simulate moderate and high damage patterns. Hybrids were created at 50/50 and 75/25 from *Felis silvestris silvestris* and *Felis silvestris catus*. With 100% of the one subspecies, HAYSTAC was able to identify subspecies successfully with 0.9 and 0.3 damage. With the hybrid individuals, the two top hits were for the two subspecies making up the hybrid. However, this is difficult to interpret, as the abundance scores are all very low due to a lot of the reads going into the grey and dark matter, as the subspecies are very similar. For this study, we have only reported individuals which from the interpretation of the HAYSTAC results are 100% one species.

Reference

Antunes, Agostinho, Joan Pontius, Maria João Ramos, Stephen J. O'Brien, and Warren E. Johnson. 2007. "Mitochondrial Introgressions into the Nuclear Genome of the Domestic Cat." The Journal of Heredity 98 (5): 414–20.

3.11 Acknowledgments

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3.12 Permission from co-authors

I hereby give permission to Alexandra Jamieson to use our joint work as contribution towards her D. Phil thesis to be submitted for examination at Oxford University.

I confirm that to the best of my knowledge, the author contribution statement below is accurate and Alexandra Jamieson's contribution towards the work is greater or equal than that of any other co-author.

Chapter author contribution statement:
A.J, G.L. and N.S designed the project; A.J. generated data; A.J. and L.F analysed data; G.L., L.F., M.B., H.S, N.S, I.M and F.B provided material and support in interpreting results; A.J. wrote the paper with contributions from all other authors.

Date: 26 Jan 2021

Name: Mark Beaumont

Signature:

Date: 28/01/2021

Name: Laurent Frantz

Signature:

Date: 26 Jan 2021

Name: Greger Larson

Signature

Date: 01/02/2021

Name: Naomi Sykes

Signature

Date:29/01/21

Name: Helen Senn

Signature:

Date: 28/1/21

Name: FIONA BEGLANE

Signature:

Date: 4/2/21

Name: Ingrid Mainland

Signature:

4. Palaeogenomic analysis of black rat (*Rattus rattus*) reveals multiple European introductions associated with human economic history

4.1 Statement of Authorship

This work was the product of a large international collaboration, with two first authors leading separate parts of the project, myself leading the full mitochondrial DNA and cytochrome b (cytb) analysis and He Yu the nuclear DNA analysis and *de novo* assembly. This chapter is soon to be submitted for publication.

Research design: The project was designed by Greger Larson, David Orton and Johannes Krause

Data generation: I performed the genetic laboratory analysis at the University of Oxford from sample preparation to pooling for next-generation sequencing.

Analysis: I performed the computational analysis for the ancient mitochondrial full genomes under the guidance of He Yu and I performed all the cytochrome b analysis myself (results sections 4.5.2). He Yu performed all the computational analysis of the full ancient genomes and assembled the black rat modern *de novo* genome.

Manuscript: I wrote the manuscript along with He Yu and David Orton with input from all other co-authors.

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4.3 Abstract

The distribution of the black rat (*Rattus rattus*) has been heavily influenced by its association with human societies. The dispersal history of this commensal rodent across Europe, however, remains poorly understood, and different populations may have been introduced during the Roman and Medieval periods. Here, in order to reconstruct the population history of European black rats, we generated a *de novo* genome assembly of the black rat, 70 ancient black rat mitogenomes and 39 ancient nuclear genomes from sites spanning the 1st-17th century CE in Europe and North Africa. Analyses of the mitochondrial DNA indicate that black rats were introduced into Europe from Southwest Asia via the eastern Mediterranean. Genomic analyses of the ancient rats reveal a population turnover in temperate Europe between the 6th and 10th centuries CE, coincident with an archaeologically attested decline in the black rat population. The near disappearance and re-emergence of black rats may have been the result of the breakdown of the Roman Empire, the First plague Pandemic, and/or Post-Roman climatic cooling.

4.4 Introduction

The black rat (*Rattus rattus*) is one of three rodent species, along with the house mouse (*Mus musculus*) and brown rat (*Rattus norvegicus*), to have become globally distributed thanks to a close commensal relationship with humans. Collectively, these taxa are highly significant to human societies both as pests responsible for billions of euros of damage to food stores annually (Capizzi, Bertolino, and Mortelliti 2014), and as vectors and/or reservoirs that have contributed to the spread of numerous diseases, most infamously bubonic plague (Meerburg, Singleton, and Kijlstra 2009; McCormick 2003).

Despite its significance, our knowledge of the black rat's evolutionary history and taxonomy remains limited. Previous genetic studies described the *R. rattus* species complex involving multiple recognized species with potential introgression among different lineages (Aplin et al. 2003; Lack et al. 2012; Conroy et al. 2013). Mitochondrial DNA studies helped to resolve the taxonomic controversies by linking a monophyletic mitochondrial lineage to specific global and South Asian *R. rattus* populations that possess a 2n=38 karyotype (Robins et al. 2007; Pagès et al. 2010; Aplin et al. 2011). The Asian house

rat (*Rattus tanezumi*), endemic to Southeast Asia, has been identified as the closest sister lineage of the black rat. The divergence between the two has been dated to ~0.4 Mya (Robins et al. 2008) and the two species are suggested to be able to hybridise (Yosida et al. 1971; Lack et al. 2012; Conroy et al. 2013).

The ability of rats to colonise, and become dependent upon, anthropogenic niches (Hulme-Beaman et al. 2016) makes them ideal bioproxies to track historical processes (Boivin et al. 2016; Jones et al. 2013; Puckett, Orton, and Munshi-South 2020)**.** Archaeological specimens of rats and mice have thus been used to track human migrations, trade, and settlement types in a wide range of contexts (Jones et al. 2012; Cucchi 2008; Cucchi et al. 2013, 2020; Matisoo-Smith and Robins 2004; Matisoo-Smith and Robins 2009; West et al. 2017). Previous archaeological and genetic evidence suggests that the pre-commensal distribution of the Eurasian black rat (based on the taxonomic definition proposed by mitochondrial DNA studies (Robins et al. 2007; Pagès et al. 2010) and hereafter referred to as black rat, see Text S4.1 for discussion) was largely limited to South Asia (Aplin et al. 2011; Niethammer 1975; Baig et al. 2019). Black rat finds from late Pleistocene to early Holocene caves in the Levant indicate a possible western distribution (Tchernov 1984; Ervynck 2002), but these remains require direct dating given the subsequent absence of rats from settlement sites in this region for around eight millennia.

The earliest large concentrations of presumed commensal rat remains reported thus far derive from the late third, or early second millennium BCE settlements in both the Indus Valley and Mesopotamia (Ervynck 2002). Commensal black rats may also have reached the Levant and eastern Mediterranean region by the start of the first millennium BCE (Ervynck 2002). Based on archaeological evidence from Corsica, the Balearics, Italy and Morocco, black rats likely first appeared in the western Mediterranean basin towards the end of that same millennium (Ruffino and Vidal 2010; Vigne and Valladas 1996; Oueslati et al. 2020).

The colonisation of Europe by the black rat has been linked to the historical development of urbanism and trade networks, and is also important for understanding historical plague pandemics including the 6th century Justinianic Plague and the 14th century Black Death (McCormick 2003; Audoin-Rouzeau and Vigne 1994; Frédérique Audoin-Rouzeau and

Vigne 1997; Armitage 1994). The central role traditionally attributed to black rats and their fleas in the spread of the plague bacterium (*Yersinia pestis)* during these pandemics has been challenged on grounds including the historical distribution and abundance of rats, and it still continues to be debated (Hufthammer and Walløe 2013; Dean et al. 2018; Sloane 2011; Hardy 2019; White and Mordechai 2020).

Although surveys of zooarchaeological collections from archaeological sites across Europe reveal a relative paucity of remains, the data available indicates successive episodes of dispersal north of the Mediterranean associated first with Roman expansion (1st century BCE to 2nd century CE) and then with the emergence of Medieval economies from the 9th century CE, punctuated by a decline and possible range contraction (Armitage 1994). Rat remains are found throughout the Roman Empire in the 1st to 5th centuries CE but rarely beyond its northern borders, suggesting that rats were dependent on a Roman economic system characterised by a network of dense settlements connected by bulk transport via efficient road, river, and maritime routes (Audoin-Rouzeau and Vigne 1997; McCormick 2003).

With the breakdown of the Roman empire from the 5th century onwards, evidence for the existence of black rats becomes scarcer, even where bones of other small mammals have been reported. Rats may have been extirpated entirely from the northern provinces including Britain (O'Connor 1991; Armitage 1994; Rielly 2010), and the percentage of archaeological sites with rat remains declined even in the Western Empire's Italian core (Salvadori 2018). By contrast, rats remained common in the Balkans and Anatolia until at least the 6th century CE, presumably reflecting continued stability in the Eastern Roman Empire (De Cupere et al. 2009; Parfitt 2007; Davis 1981; Baron, Reuter, and Marković 2019). Since 5th-8th century zooarchaeological data is limited in many regions, the pattern of Post-Roman absence may partly represent both excavation and research bias (Benedictow 2010).

Black rats reappear at northern European trading settlements during the 9th century CE, including sites well beyond their Roman range, for example Hedeby in northern Germany and Birka in Sweden, as well as former Roman towns and high-status Saxon settlements

such as York and Flixborough in England (O'Connor 1989; Reichstein 1991; Wigh 2001). The subsequent expansion of urbanism and large-scale trade of bulk goods in Medieval Europe appears to have favoured rats, just as in the Roman period. By the 13th century CE, black rats were present throughout most of Europe (McCormick 2003) and they reached southern Finland by the late 14th century (Tourunen 2008). They seem to have remained widespread until at least the 18th century, before a decline likely caused by competition with the newly arrived brown rat (*Rattus norvegicus*), the dominant rat species in temperate Europe today (Ervynck 1989; Barrett-Hamilton and Hinton 1910; Mitchell-Jones 1999).

It remains unclear whether the black rat was actually extirpated from Post-Roman northern and western Europe; and whether Medieval rat populations in temperate Europe derived from the remnant population in southern Europe, or from another wave of rats that were introduced from beyond the Mediterranean (for example via Russian river trade (Armitage 1994; Savinetsky and Krylovich 2011)). These questions are relevant to several key debates in European economic and environmental history including:

1) the extent to which the end of the Western Roman Empire represented an economic as well as political collapse (Ward-Perkins 2005; Wickham 2005; Horden and Purcell 2000)
2) the role of easterly vs. westerly connections in the rise of northern European Medieval urban networks (Ambrosiani 2002; Hodges 2012)
3) the model of the spread of the Justinianic Plague and the subsequent First Pandemic. This pandemic started in the eastern Mediterranean in 541 CE, spread quickly across Europe, reached as far as England, and continued for approximately two centuries (Keller et al. 2019; Wagner et al. 2014; Feldman et al. 2016), a period that coincides with the gap in archaeological evidence for rats in north-west Europe.

Given the limitations of zooarchaeology and genetic studies of modern rat populations in addressing successive waves of contact after a species is established, ancient DNA may help to resolve these questions by directly revealing the historical genetic background.

Here, in order to understand the history of the black rat in Europe, especially its association with Roman expansion and trade, and its apparent extirpation and repopulation in temperate Europe during the early Medieval period, we first assembled a *de novo* reference genome of the black rat and investigated the demographic history of *Rattus rattus* in relation to other rat species. We then generated and analysed 39 nuclear genomes and 70 mitochondrial genomes of ancient black rats from Europe and North Africa spanning the Roman to early Post-Medieval periods (1^{st}-17^{th} century CE). We analysed these data alongside 132 cytochrome b sequences generated from modern and museum black rat specimens sampled from across western Eurasia, the Indian Ocean, and Africa. Our results reveal key aspects of the species' European dispersal history, and the black rat's connections to major historical processes.

4.5 Results and Discussion

4.5.1 Assembly of the *de novo* black rat genome and its relationship to closely related species

Using a wild-caught black rat from California, USA, we first generated a *de novo* genome assembly of *R. rattus*, which facilitated the study of the demographic history of the black rat in Europe. Combining shotgun, Chicago and Hi-C sequencing data with the Dovetail HiRise assembler pipeline (Putnam et al. 2016), we obtained a genome assembly with a total length of 2.25 Gb and a scaffold N50 reaching 145.8Mb. The 22 scaffolds with over 10 Mb covering 98.9% of the entire assembly (Table 4.1), with each of the 18 autosomes of *R. rattus* corresponding to one large scaffold each and over 90% of the X chromosome represented by four scaffolds (Figure S4.1, S4,2, Text S4.2). The average GC content is 42.1%, similar to the *R. norvegicus* reference genome *Rnor_6.0* (42.3%), and 38.4% of the assembly was identified as repetitive elements. Benchmarking Universal Single-Copy Orthologs (BUSCO) analysis (Simão et al. 2015) also revealed a high completeness of this genome assembly, with 90.1% complete BUSCOs identified using eukaryotic dataset, comparable with *Rnor_6.0* (91.4%).

Scaffold Number	6805
Scaffold N50 (Mb)	145.8
Largest Scaffold (Mb)	260.8
Assembly size (Gb)	2.25
Scaffold length >10 Mb (Gb)	2.23
GC content (%)	42.1
Repetitive region (%)	38.4

Table 4.1 Assembly statistics of the *de novo R. rattus* reference genome.

To address the demographic history of black rat, we applied the Pairwise Sequentially Markovian Coalescent (PSMC) analysis to estimate its population size dynamics alongside the brown rat and Asian house rat (Li and Durbin 2011). When calibrated with a mutation rate of $2.96*10^{-9}$ per generation and generation time of 0.5 years, the analyses revealed different dynamic patterns of population size changes amongst these rat species (Figure 4.1A) (Deinum et al. 2015). The brown rat experienced a population decline beginning ~1 Mya, as described previously by Deinum et al. (2015), while both the black rat and Asian house rat populations expanded until 300 - 400 thousand years ago (kya). The black rat population then experienced a bottleneck event with an 8-fold drop in effective population size until 100 kya, and a re-expansion from 100 kya to 40 kya. The Asian house rat, however, did not experience a population decline until ~40 kya, when both black rat and Asian house rat populations experienced declines that have continued to the present.

We further applied Generalized Phylogenetic Coalescent Sampler (G-PhoCS) to investigate the population sizes, split times, and migrations among these rat lineages (Gronau et al. 2011). The result revealed a similar population size dynamic pattern, with the effective population size (Ne) of black rat/Asian house rat ancestral lineage estimated to $1.25*10^{6}$, about ten-fold the Ne of black rat/Asian house rat/brown rat lineages (Table S4.7, Figure 4.1B). The split time between brown rat and black rat/Asian house rat lineages was estimated to be 1.94 million years ago (Mya), within the 95% Highest Posterior Density (HPD) range estimated based on a previous study using mitochondrial genomes (Robins et al. 2008), while the split of Asian house rat and black rat lineages took place 120 kya. Such a recent split time estimate relative to the coalescence time estimate based on mitochondrial genomes between these two lineages could be explained by the large ancestral population size of the black rat/Asian house rat lineage (Gronau et al. 2011).

Among these lineages, we only detected one instance of gene flow from the black rat/Asian house rat ancestral lineage into brown rat lineage, with an introgression proportion of 9.8%.

Taken together, we observed population expansions and bottlenecks in the black rat during the last one million years, and a smaller effective population size relative to the Asian house rat. This could be explained by the relatively limited geographic distribution of the black rat in southern Asia before the initiation of its commensal relationship with people, and the fact that the Asian house rat is endemic to a much greater area in southeastern Asia (Aplin et al. 2011). We did not detect any genomic introgression between the lineages leading to the black and Asian house rat, suggesting these two species were geographically isolated after their split from a common ancestor sufficiently long enough for them to become reproductively incompatible.

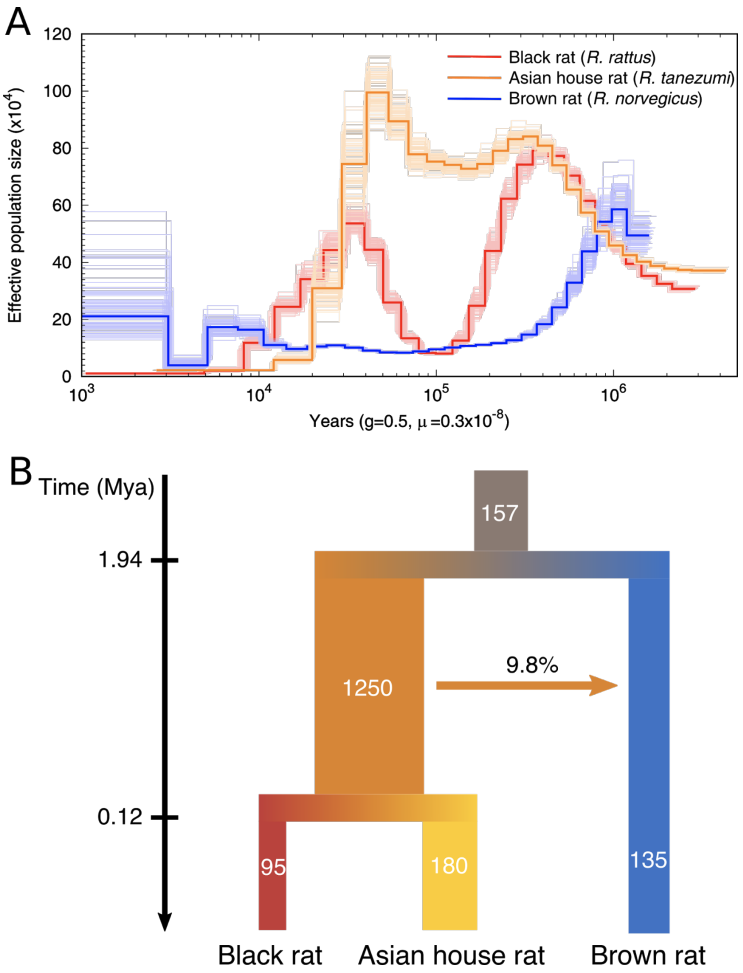

Figure 4.1 The demographic history of the black rat and its closely related species.
(A) Population dynamics of the black rat (*R. rattus*), Asian house rat (*R. tanezumi*) and brown rat (*R. norvegicus*) estimated by PSMC, with 100 bootstrap replicates.
(B) Demographic modelling of the divergence and migration among the black rat, Asian house rat and brown rat estimated by G-PhoCS. The orange arrow indicates the direction of introgression. The values represent the average estimates of effective population sizes (in thousands), population divergence times (Mya) and the total migration rate through time. The 95% HPD range of all estimates are listed in Table S4.7.

4.5.2 A global phylogeography of the black rat based on mitochondrial DNA

We collected 202 ancient black rat individuals from 36 archaeological sites across Europe and Africa dating from the 2nd century BCE to the 17th century CE (Table S4.8). After shotgun screening, we retrieved 70 mitochondrial genomes (with coverage spanning 3.5-300.0x) from samples excavated at 18 sites and identified 40 haplotypes (Table S4.8). The phylogenetic tree based on mitochondrial genomes showed that all the black rat samples group into two clades: 32 of them fell into the major clade, and eight haplotypes formed by 23 ancient samples from the 6th-century site of Caričin Grad, Serbia, formed the other (Figure S4.3). The phylogenetic resolution within each major clade was relatively poor,

though samples from the same or closely related sites occasionally formed sub-clades including the samples from early Byzantine Zembra (Tunisia) and Medieval central Europe.

In order to establish the relationship between the ancient rats and modern black rats from across their range, we analysed the cytochrome b region from our ancient samples alongside 132 previously unpublished modern cytochrome b sequences from across the Indian Ocean basin (Table S4.10), and sequences published in previous studies (Aplin et al. 2011; Colangelo et al. 2015; Baig et al. 2019; Etougbétché et al. 2020). Some of the same Indian Ocean basin samples were also sequenced as part of this study, however the coverage of the full mitochondrial genomes was too low for inclusion. Due to these being unusable we have used previously unpublished cytochrome b sequences from these same samples (Table S4.8, S4.10). The maximum likelihood tree of the cytochrome b region revealed that all the ancient rats from this study belong to the black rat lineage (Figure 4.2, S4.4, S4.5 and Table S4.11). We recapitulated the same substructure first demonstrated by Aplin that included five major black rat haplogroups (Aplin et al. 2011). In addition to these five, we revealed a new haplogroup that consists of modern samples from Sri Lanka and the Andaman Islands, and is basal relative to all other black rats and is likely to be *R. r. kandianus*. We have named these haplogroups A through F (Table S4.11, Figure 4.2).

Haplogroup A (previously described as the European ship rat (Baig et al. 2019)) was the most common among the analysed samples (89/203 samples). Members of this haplogroup include ancient and modern rats from Europe or regions of the world with a history of colonisation by and/or trade with European powers. The only additional haplogroup found in Europe was Haplogroup C (previously described as the Arab ship rat), which included 24 archaeological individuals from Caričin Grad, Serbia, as well as modern rats from India, East, South and West Africa and South America. None of the other haplogroups were present in Europe or the Mediterranean region. Haplogroups B and E only included modern samples from India and countries bordering the Indian Ocean. Haplogroup D included primarily samples from Madagascar and East Africa, and Haplogroup F consisted of samples from Sri Lanka and the Andaman Islands (Figure 4.2, Table S4.11).

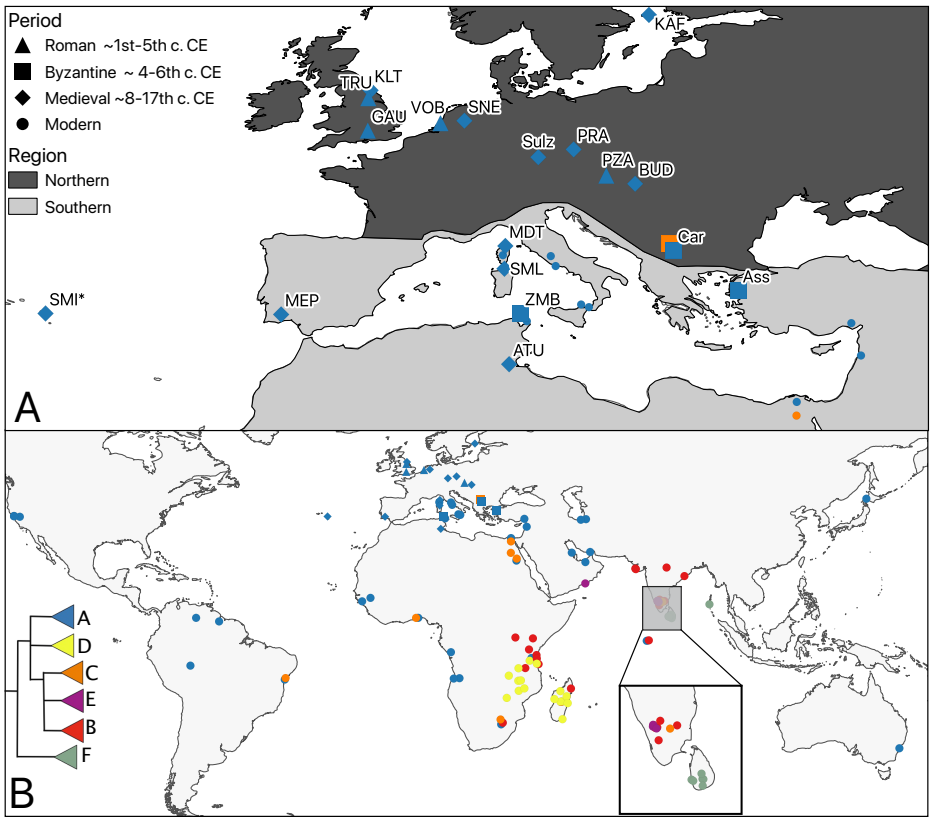

Figure 4.2 Sampling sites and mitochondrial phylogeographic patterns.
(A) Map of ancient sample locations. The ancient sample denoted with a * only has mitochondrial data, the rest have both nuclear and mitochondrial results. SMI (Villa Franca de Campo) MEP (Mertola) KLT (Kilton Castle) TRU (Tanner Row, York) GAU (Gatehampton Villa) VOB (Voorburg-Forum Hadriani) SNE (Deventer-Stadhuiskwartier) MDT (Monte di Tuda) SML (Santa Maria Lavezzi) ATU (Althiburos) ZMB (Zembra) Sulz (Castle Sulzbach) PRA (Prague Castle) PZA (Petronell-Zivilstadt) KAF (Kastelholm) BUD (Buda Castle-Teleki Palace) Car (Caričin Grad) Ass (Assos). (B) The phylogeographic pattern of black rat revealed by cytochrome b mitochondrial haplogroups (see Figure S4.4 for detailed phylogeny). The only modern nuclear genome is from the modern reference genome rat from California.

We performed an analysis of a mitochondrial fragment derived from globally distributed modern and ancient black rats to investigate their introduction into Europe. Previous studies indicated that the black rat originated in the Indian Peninsula (Aplin et al. 2011; Colangelo et al. 2015; Carleton, Musserand, and Musser 2005; Baig et al. 2019). Leaving aside the putative Terminal Pleistocene records from the eastern Levant, the earliest finds of presumed commensal rats derive from the Indus Valley and Mesopotamia in the 3rd/2nd millennium BCE, coincident with the emergence of urbanism and establishment of trade links between these regions (Ervynck 2002; Boivin 2017), though a more westerly limit to the black rat's natal range cannot be excluded. The source for dispersal to the Mediterranean and ultimately Europe remains unclear, with possibilities including overland communication routes between Mesopotamia and the Levant, or maritime trade

from India and/or the Arabian peninsula into the Red Sea and subsequently via Egypt, perhaps by taking advantage of the canal built under Darius in the mid first-millennium BCE (Armitage 1994; McCormick 2003; Cooper 2009).

While a coastal route is clearly implicated in the black rat's dispersal to East Africa (Prendergast et al. 2017; Tollenaere et al. 2010), our results favour an overland hypothesis for its dispersal to Europe, since both ancient and modern black rats from Europe and the eastern Mediterranean share the same haplogroups with sampled populations from Egypt, Iran and the Persian Gulf, and exclude Indian Ocean samples from southern India to Madagascar (Figure 4.2). The results also suggest a secondary dispersal route via Egypt, given the appearance of Haplogroup C at the 6th century CE Byzantine site of Caričin Grad, Serbia and in modern samples from the Nile valley. While tentative, this might reflect Egypt's central role in grain production for the Roman and early Byzantine Empires, as well as its links to Indian Ocean trade (McCormick 2003). Further investigation into ancient and modern rat populations from the Levant, Mesopotamia, Egypt and northern India is required to further test these hypotheses regarding the black rat's dispersal into the Mediterranean region.

4.5.3 The arrival of black rats in Europe

We shotgun sequenced 39 ancient black rat samples from 17 sites to 0.2-16x coverage for whole genome analysis from the larger dataset, including 18 females and 21 males determined by the coverage on sex chromosomes (Table S4.9, S4.12). The deeper sequenced samples covered three broad time periods, including nine from the Roman period (1st to 5th century CE), nine from Early Byzantine (4th to 7th century CE) and 21 from Medieval and Post-Medieval contexts (8th to 17th century CE). Geographically, all the samples were divided into two groups: a "northern" group of 25 samples from temperate Europe, and a "southern" group of 14 samples from the Mediterranean and Portugal (Figure 4.2). After mapping and genotyping, we identified 7,869,069 bi-allelic transversion variants in the autosomal non-repetitive regions for downstream population genetic analysis.

The phylogenetic tree constructed from autosomal SNPs revealed complex relationships among ancient black rats from different regions and time periods (Figure 4.3). Except for the late Medieval (14th century) to Ottoman (17th century) site of Buda Castle, Hungary, samples from the same site clustered together. All the samples from the northern group, together with one southern sample from the Medieval period - from 8th-9th century Althiburos, Tunisia formed a single clade, while all the other Byzantine to Medieval samples from the southern group formed several separate clades consistent with their local geographic region. Within the major northern cluster, samples were divided into two clusters representing Roman (and Byzantine) and Medieval (and Post-Medieval) periods respectively. The only exception was the Medieval Tunisian sample that falls in the Roman cluster. Within each cluster, these samples grouped together based upon their geographic location (central Europe, western/northern Europe, Serbia). These phylogenetic relationships suggest that the initial black rat population in temperate Europe was replaced by a genetically distinct population after the 6th century CE. The second population is first documented in early Medieval (8th to early 10th century CE) Sulzbach, Germany. The Roman-like gene pool was still present during the 8th-9th century in North Africa, though due to the lack of more recent samples we cannot address whether or when the second wave arrived there.

The phylogenetic tree based on Y-chromosome scpMSY regions similarly demonstrated that the Roman rats formed a single cluster. However, unlike the autosomal phylogeny, all the Byzantine and Medieval samples from both the northern and southern groups formed a separate cluster (Figure S4.6), without well supported substructures within the cluster. Given the male-biased dispersal pattern commonly described in the black rat and other rodent species (Ewer 1971; Pocock, Hauffe, and Searle 2005), this might indicate a male-specific replacement happening in both temperate Europe and Mediterranean regions.

A decline in the European black rat population during the 6th to 9th centuries has previously been suggested based on zooarchaeological evidence (Armitage 1994; Rielly 2010; O'Connor 1991). This collapse has been attributed to several causes including the demise of the Western Roman Empire's economic and urban system from the 5th century CE (McCormick 2003), climatic cooling in the 'Late Antique Little Ice Age' (Büntgen et al. 2016),

and the Justinianic Plague which began in 541 CE and is widely believed to have been spread by commensal rats that were highly susceptible to *Yersinia pestis* (Perry and Fetherston 1997; Spyrou et al. 2019; McCormick 2003). Our finding of a post-6th-century turnover corroborates this apparent decline, though the geo-temporal coverage of our sample set is not sufficient for us to distinguish between the potential causes. To understand how the Justinianic Plague influenced the rat population, further investigation should focus on black rats from contexts post-dating the mid-6th century in areas of the Byzantine Empire and wider Mediterranean where an urban settlement system persisted.

In contrast, the Medieval Tunisian (Althiburos) sample indicates a different population history of black rats in North Africa relative to temperate Europe. Black rats from a wider range of time periods in this region would allow us to test whether there was continuity within the black rat population from the Roman through to early Islamic periods, perhaps reflecting continuity in urban settlement even across major political transitions (Fenwick 2013).

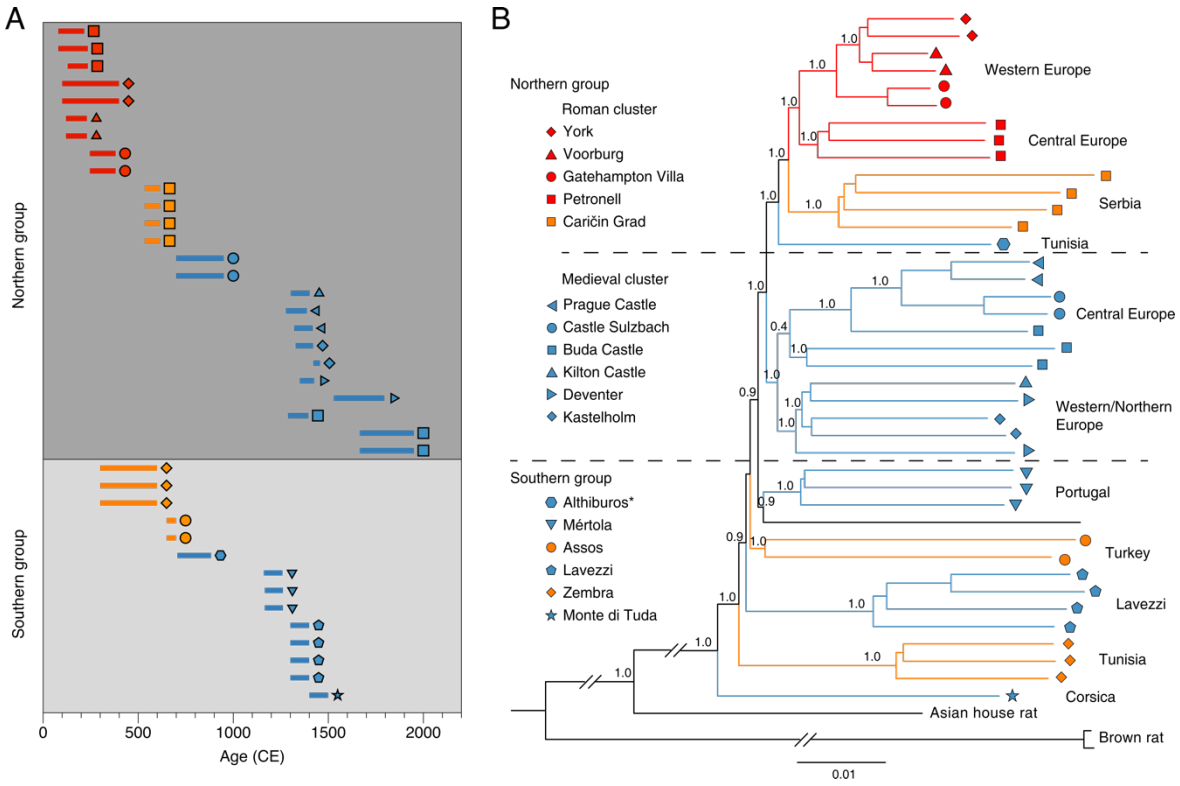

Figure 4.3 Relationships of the ancient black rats over time and space.
(A) Timespan for each of the samples from each site studied. The colours correspond to the sample ages and the symbols to the different sites. (B) The phylogenetic relationship among ancient black rats reconstructed with a neighbour joining method and pairwise genetic distances calculated based on autosomal variants. The support rates are based on 100 bootstrap replicates and are marked on the nodes. The branches are coloured by sample ages (see also panel A) and the tip symbols correspond to the different populations. Note that the medieval Tunisian (Althiburos) sample is geographically from the Southern group, though falls in the Roman cluster of the northern group in the phylogeny.

To further investigate the genetic diversity of black rats through time and space, we estimated the heterozygosity of ancient rat genomes and summarized the distributions across different time periods and regions (Figure S4.7). We found that in both Roman/Byzantine and Medieval/Post-Medieval time periods, the rats from the southern group possessed higher heterozygosity than rats from the northern group. The low genetic diversity in the northern group could be explained by the founder effect of limited waves of introduction into this region, likely related to the Roman expansion (McCormick 2003; Audoin-Rouzeau and Vigne 1994; Armitage 1994).This also corresponded to the clustering of all northern group rats together in the phylogenetic analysis (Figure 4.3). Conversely, the Mediterranean region has a longer history of rats, dating at least to the first millennium BCE (Ruffino and Vidal 2010; Ervynck 2002). Frequent contacts across the Mediterranean, and perhaps beyond to Asian regions with established rat populations, may have enabled

multiple waves of introduction into different sampling areas, as revealed by the multiple lineages of southern group rats in the phylogenetic analysis (Figure 4.3).

We further applied a series of *f*-statistics to investigate the genetic interaction between different rat populations. Based on the result of the f_4-statistics symmetry test, the ancient samples were divided into 18 groups, 16 of which correspond to samples from 16 different sites, and the three late/Post-Medieval samples from Buda Castle (Hungary) fell into two groups. These Buda Castle samples also corresponded to their different ages (Table S4.12), with BUD001/004 dated to the 17th century or later, while BUD003 dated to late 14th to 15th century.

First, we tested if any Roman population has contributed to the Byzantine or Medieval groups, with f_4(norvegicus, Byzantine/Medieval; Roman1, Roman2). The result suggested that the Roman groups from western Europe (Britain, the Netherlands) were significantly more closely related to all the Byzantine or Medieval groups than was the Roman central European population from Austria (Figure 4.4A, Figure S4.11). This suggested that despite the population turnover that occurred in temperate Europe after the Roman period, Roman black rats from western Europe may have contributed to populations that were introduced following the decline of the original population.

We then applied f_4(norvegicus, Roman; Byzantine/Medieval1, Byzantine/Medieval2) to test if there were any differences in the contribution level of Roman rat ancestry, in the Byzantine or Medieval populations. In agreement with the phylogenetic analysis, most temperate European groups were significantly more closely related to the Roman rat populations, compared to the Byzantine or younger Mediterranean groups (ZMB, SML, MDT, Ass), except for the two Post-Medieval samples from Buda Castle (BUD001/4), which were equally related to the Roman groups as well as the Assos (Ass) group of two samples from Byzantine Turkey (Figure 4.4). Among the temperate European groups, the Medieval rats from Åland (Finland), the UK and the Netherlands, as well as Early Byzantine rats from Serbia, were more closely related to the Roman rat populations than were most of the Medieval rats from central Europe (Germany, Czech Republic and Hungary).

The close affinity between Early Byzantine European rats and Roman rats corresponded to the phylogenetic relationship among these groups, again confirming that the population turnover in temperate Europe took place after the 6th century CE. The closer affinity of western/northern European Medieval rats with Roman rat populations, on the other hand, suggested that the genetic contribution from the Roman rats, specifically those in western Europe, is greater in the local western European Medieval rats than in those from other regions.

We also investigated the relationship between the Buda Castle (Hungary) samples from different time periods, by comparing them with the other Medieval rats from temperate Europe (Figure 4.4A, Figure S4.8). As revealed by the phylogenetic tree, both the German and Czech rats shared more genetic affinity with the 14th century Buda Castle (BUD003) sample, than with the 17th century or later specimens (BUD001/004). However, BUD001/004 still showed higher affinity to BUD003, when compared to all the other populations. This evidence suggests a black rat population transition in this region between the 14th century and the late 17th century, potentially related to the 16th-17th century Ottoman occupation of Buda Castle, while the local Medieval ancestry was still present in the later population.

We also generated an admixture graph of the ancient rat populations using Treemix (Pickrell and Pritchard 2012). This analysis revealed similar patterns of gene flow as suggested by the f_4-statistics. Using Asian house rat as an outgroup, the maximum-likelihood population tree without any admixture produced a similar topology to the neighbor-joining (NJ) autosomal phylogeny (Figure S4.9). The rats from the northern group and a Medieval Tunisian rat formed a clade, to which all the other Mediterranean rats were an outgroup, without any significant clustering pattern among the lineages. We further considered admixture events in the topology. The first two gene flow events detected were from the Medieval central European population to the Post-Medieval Buda Castle population, estimated to 18 +/- 3 %, and from the Roman western European population to the ancestral lineage of the Medieval European populations in the northern group, estimated to 8 +/- 0.8 % (Figure 4.4B, Figure S4.9).

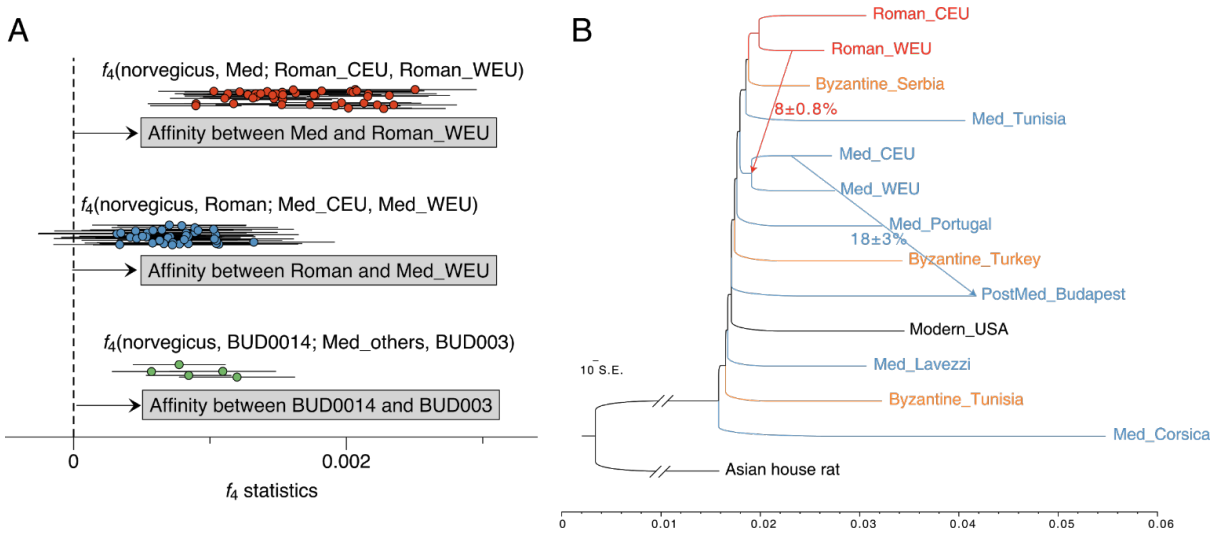

Figure 4.4 Gene flow among ancient rat populations.
(A) The *f*-statistics showing admixture between different ancient rat populations. The dots show all the combinations of f_4-values as described above each cluster, and the error bars show ± 3 Standard error (SE) of the estimates. The three clusters show the affinity between Medieval rats (Med) and western European Roman rats (Roman_WEU), Roman rats (Roman) and western European Medieval rats (Med_WEU), and Post-Medieval Buda Castle rats (BUD001/4) and the Medieval Buda Castle rat (BUD003), respectively.
(B) Admixture graph with two migration events fitted, estimated by Treemix. The migration edges are displayed by arrows, with the introgression fractions and standard errors noted. The colour of each branch represents the time period of each group: Roman (red), Byzantine (orange) and Medieval/post-Medieval (blue).

With both *f*-statistics and Treemix analyses, we revealed a degree of Roman rat ancestry preserved in the Medieval populations, more closely related to the Roman rat populations from the Netherlands and Britain (Figure 4.4). This signal suggests a reservoir of black rat population in western Europe, that admixed with the re-introduced Medieval population. The stronger affinity of Medieval western European populations to Roman populations also suggested that this relict population was more likely distributed in western and not central Europe. This result suggests that rats from the northernmost Roman provinces may not have been extirpated, despite their absence in zooarchaeological assemblages. Alternatively, and in our view more likely, the inferred relict population may have been located in an unsampled region of France or southwest Europe. The observation that Medieval rats from temperate Europe fall into the same cluster with Roman rats also suggests that the second (Medieval) wave of introduction to temperate Europe probably originated from the same source population as the first (Roman) dispersal. Considering the zooarchaeological evidence that rat populations in southern Europe persisted after the

collapse of the Western Roman Empire, notably in Italy (Salvadori 2018), it is likely that southern Europe was the source of reintroduced rats in temperate Europe.

Given the presence of rats in 9th century northern *emporia* (proto-urban trading sites) around the North and Baltic Seas (O'Connor 1989; Wigh 2001; Reichstein 1991), this argument emphasises the importance of the Carolingian Empire (the Frankish polity which controlled much of western and central Europe as well as northern Italy in the 9th century CE) and routes such as the Rhône and Rhine corridors in re-establishing large-scale trade links between the Mediterranean and northern Europe (McCormick 2007). This connection remains tentative until samples can be studied from mainland Italy and Iberia, and from the early *emporia* themselves.

4.6 Conclusion

Utilising a *de novo* genome assembly for the black rat and ancient genomes from North Africa and across Europe, our study explores the historic dispersal of this commensal species in Europe. We suggest that the black rat was introduced to the eastern Mediterranean from Southwest Asia, and we identify two waves of rat introduction into temperate Europe. The first wave likely accompanied Roman northward expansion around the first centuries BCE/CE. The second wave, which took place in the Medieval period, was likely derived from the same ancestral rat population, and admixed with a western or southern European relict population of the first wave.

Considered alongside the scarcity of archaeological rat finds from the 6th-8th centuries CE, particularly in western Europe, this population turnover suggests a black rat population decline and commensurate range contraction in the early Medieval period. This may have been associated with the breakdown of the Roman Empire, from the 5th century CE in western Europe and the early 7th century CE in the Balkans, and with it the network of well-connected settlements that had previously supported rat populations. Alternatively, or additionally, European rat populations may have been impacted by the First Plague Pandemic and/or the climatic cooling of the Late Antique Little Ice Age, both of which began in the mid 6th century CE. To disentangle these scenarios, further zooarchaeological

and genomic studies of ancient rats are required that span these centuries across a wider geographic range.

The Medieval introduction is detected at the latest by the early 10th century in Germany, coinciding with an increase in rat bone finds across the continent. Our results point to a repopulation of temperate Europe from the south, perhaps linked with the development of trade routes in Carolingian western Europe, and probably not via early Russian riverine trade. Black rats appear to have been a continuous presence in Europe from this point until the Post-Medieval period, spanning the 14th century Black Death and extending to the 17th century. This population may also have been supplemented by localised introductions including one potentially associated with the Ottoman occupation of Buda Castle.

The much-reduced distribution of black rats in present-day Europe is probably linked to competition with the brown rat (*Rattus norvegicus*) following its apparent arrival from Asia in the early 18th century (Ervynck 1989; Barrett-Hamilton and Hinton 1910). The genetic and demographic impact of this dispersal on black rat is an important area for future investigations: by the late 18th century naturalists in several European countries already attributed a marked decline in *R. rattus* to competition from *R. norvegicus* (Buffon 1760; Smith 1768; Pennant 1776; Rutty 1772), but the former's persistence into the present-day in many areas, particularly in towns, suggests a degree of niche partitioning (O'Connor 2017).

Overall, these results demonstrate how human-commensal species can undergo population dispersal and demographic fluctuations. In fact, because these dynamic evolutionary processes are tightly correlated with the characteristics of the human niche, the palaeogenomic assessment of commensal species provides ideal proxies to interpret the history of human movement and cultural change.

4.7 Methods

4.7.1 Radiocarbon dating and calibration

Eighteen samples were analysed by accelerator mass spectrometry (AMS) at Manheim (MAMS), University of Waikato (Wk) or Oxford University (OxA) for radiocarbon dating (Table S4.13). All the radiocarbon dates were calibrated using the IntCal20 calibration curve (Reimer et al. 2020).

4.7.2 *De novo* genome assembly

The black rat genome was sequenced and assembled using DNA extracted from the liver of a male wild-caught individual from California, USA. Shotgun, Chicago and Dovetail Hi-C libraries were prepared and sequenced on Illumina HiSeq 4000 platform and the genome was assembled using Meraculous (Chapman et al. 2011) and HiRise scaffolding pipeline (Putnam et al. 2016). The detailed information of genome assembly is provided in Text S4.2.

The repetitive regions were identified using RepeatMasker 4.0.7 (Smit, Hubley & Green 2013-2015) with Repbase 20170127 and the query species set as *rattus*, and TRF 4.09 (Tandem repeats finder) (Benson 1999), with parameters set as "2 7 7 80 10 50 12". The completeness of genome assembly was assessed by BUSCO 3.0.2 (Simão et al. 2015), using the 303 orthologs in Eukaryota odb9 dataset. The new genome assembly was aligned to the brown rat reference genome *Rnor_6.0* using nucmer 4.0.0 in MUMmer tool package (Kurtz et al. 2004), to investigate the synteny between *R. rattus* and *R. norvegicus* genomes, using both masked assemblies and anchor matches that are unique in both reference and query (Text S4.2, Text S4.5).

4.7.3 Mitochondrial cytochrome b fragment sequencing

Overall, 292 tissue samples identified as *R. rattus* were included for analysis, including 263 museum specimens and 29 modern specimens collected in the field. The sampling area comprises different places of the mainland and islands around the Indian Ocean.

DNA extraction and sequencing were conducted in the modern laboratory at the Archaeology Department of Durham University, following standard protocols (Text S4.4). The cytochrome b region was amplified in 10 overlapping fragments and a variety of primer

combinations were used depending on the nature of the sample (Table S4.5). The sequencing reaction was carried out by the DNA Sequencing Service at the School of Biological and Biomedical Sciences at Durham University. The sequencing chromatograms were edited manually, subsequently assembled, and a consensus sequence per individual exported using Geneious R6 version 6.0.6 (Drummond et al. 2011). Standard anti-contamination guidelines were followed. We successfully amplified cytochrome b sequences from 202 of 292 samples. Only those from the *Rattus rattus* lineage I and II (after Aplin et al.) and those with greater than 90% gene coverage were used in this study, leaving 132 sequences available for analysis.

4.7.4 Ancient DNA extraction and processing

We sampled 202 ancient black rat individuals from 36 archaeological sites across Europe and Africa (Table S4.8). Where multiple samples were taken from the same or related archaeological contexts, care was taken to ensure that these represented discrete individuals, either by sampling the same skeletal element and side or on the basis of differing size and/or age.

Ancient DNA extraction was performed in the dedicated ancient DNA facilities at the University of Oxford, the Max Planck Institute for the Science of Human History in Jena and the University of York with all the laboratories following the standard ancient DNA laboratory practices to minimise contamination. All material analysed at Oxford underwent the following treatment. Due to the small size of rat bones, the outer surface of the bones was not removed prior to extraction. With any bones which weighed under 50mg the whole bone was used for extraction. The bone or tooth was cut using a Dremel drill with a clean cutting wheel per sample (Dremel no 409) and pulverised in a Micro-dismembrator (Sartorious-Stedim Biotech). Materials analysed at York were subject to bleach treatment (6% sodium hypochlorite for 5 minutes, and then rinsed with ultrapure water 3 times) prior to powdering following the same procedure as Oxford.

Extractions performed in Jena followed a silica-based Dabney protocol (Dabney et al. 2013) with 50 mg of bone powder. Extractions performed at the University of Oxford were conducted using the Dabney protocol with a modification of the addition of a 30 minute

pre-digestion stage (Damgaard et al. 2015). Extractions performed at the University of York were conducted using Yang et al. (1998) modified in Speller et al. (2010).

For each sample processed in Jena, a double-stranded DNA sequencing library was prepared from 20 µL of extract, with partial uracil-DNA-glycosylase (UDG) treatment (hereafter denoted as ds_halfUDG) or without UDG treatment (ds_nonUDG), following a published protocol (Rohland et al. 2015). Sample-specific index combinations were added to the sequencing libraries (Gansauge et al. 2020; Kircher, Sawyer, and Meyer 2012). The indexed libraries were shotgun sequenced on an Illumina HiSeq 4000 instrument for screening, with 75 single-end-run cycles for ds_halfUDG libraries and 75 double-end-run cycles for ds_nonUDG libraries. After screening, one ds_nonUDG library and seven ds_halfUDG libraries were deep sequenced in the University of Kiel, on an Illumina HiSeq 4000 platform with 75 double-end-run cycles using the manufacturer's protocol.

All extracts performed at the University of Oxford and the University of York had double stranded Illumina libraries built following the Blunt-End Single-Tube Illumina library building (BEST) protocol as described in Carøe et al. (Carøe et al. 2018) at the University of Oxford (ds_nonUDG). The libraries had an additional barcode added to the IS1_adapter.P5 adapter resulting in them having double external indexing. The libraries were then amplified on an Applied Biosystems StepOnePlus Real-Time PCR system, to determine both the success of the library build and the number of optimum cycles to use for the indexing PCR reactions. These 164 libraries were pooled at equimolar concentrations ready for sequencing. The pool of libraries was sequenced on an Illumina HiSeq 4000 platform at the Danish National High-Throughput Sequencing Centre for screening and at Novogene, Sacramento.

Single-stranded libraries were also prepared for ten extracts from Oxford. The experiment was performed at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. The libraries were built from 30 µl of DNA extract in the absence of uracil DNA glycosylase (ss_nonUDG) followed by double indexing, using an automated version of the protocols described in Gansauge et al. (2020) and Kircher, Sawyer, and Meyer (2012) on a liquid handling system (Agilent Technologies Bravo NGS Workstation). From the initial

screening run results 31 ds_nonUDG libraries from Oxford were included for deeper sequencing in Jena, together with the ten ss_nonUDG libraries, on an Illumina HiSeq 4000 platform with 75 single-end-run cycles (Table S4.12).

4.7.5 Genotyping and dataset preparation

The shotgun sequencing reads from 39 ancient rats were cleaned and mapped to the *R. rattus* genome assembly from this study, using the EAGER pipeline 1.92.55 (Peltzer et al. 2016). Within the pipeline, the adapters were removed by AdapterRemoval 2.2.0 (Schubert, Lindgreen, and Orlando 2016), reads were mapped with BWA 0.7.12 aln/samse algorithm (Li and Durbin 2009), duplications were removed by DeDup 0.12.1 (https://github.com/apeltzer/DeDup) and damage patterns of each library were checked with mapDamage 2.0.6 (Jónsson et al. 2013). For the seven ds_halfUDG libraries, we masked 2bp from both ends of the reads using trimBam in bamUtil 1.0.13 (Jun et al. 2015) to remove the damaged sites.

The shotgun sequencing reads from four modern individuals, including the Californian black rat for *de novo* genome assembly, two published *R. norvegicus* individuals (Accession: ERS215789, ERS215791) (Deinum et al. 2015) and one published *R. tanezumi* individual (Accession: SRS1581480, individual name HXM4) (Teng et al. 2017) were mapped to the genome assembly using BWA 0.7.12 mem algorithm. After mapping quality filtering of 30 and removing reads with multiple hits, the duplications were further removed using DeDup. Then we performed indel realignment for cleaned bam files of both ancient and modern individuals, using RealignerTargetCreator and IndelRealigner in The Genome Analysis Toolkit (GATK) v3.5-0 (McKenna et al. 2010).

For the demographic history analysis, we called diploid genotypes from three modern genomes with highest coverage of each of the species: *R. rattus* (CP-5999), *R. norvegicus* (ERS215791) and *R. tanezumi* (HXM4). Each of the bam files were piled up using samtools mpileup, using reads with mapping quality and base quality over 30, and BAQ disabled. Then bi-allelic SNPs were individually called using bcftools call -m mode and filtered for SNPs with phred-scaled quality score (QUAL) over 30, sequence depth between 0.5-2x mean coverage, and not within 5bp of an indel. After masking for repetitive regions, the

consensus sequences of 18 largest autosomal scaffolds were generated, with heterozygous sites represented by IUPAC nucleotide code.

The sequencing reads of ancient and modern black rats after AdapterRemoval were also mapped to *R. rattus* reference mitochondrial sequence NC_012374.1 with BWA 0.7.12 aln/samse algorithm and realigned with CircularMapper (Peltzer et al. 2016). The reads of *R. norvegicus* and *R. tanezumi* individuals were mapped to mitochondrial references of *R. norvegicus* (NC_001665.2) and *R. tanezumi* (NC_011638.1), respectively. After removing duplication using DeDup, the consensus sequences were generated by Schmutzi with a quality threshold of 30 (Renaud et al. 2015).

We called the pseudo-haploid genotypes in autosomal regions, from all modern and ancient individuals using ANGSD 0.931 (Korneliussen, Albrechtsen, and Nielsen 2014), with parameter "-doHaploCall 1" to randomly sample one base. As the 18 longest autosomal scaffolds covered over 99% of the autosomal assembly, we only called genotypes on the non-repetitive regions of these 18 scaffolds. We applied "-remove_bads 1 -uniqueOnly 1 -minMapQ 30 -minQ 30 -C 50 -baq 1" parameters to filter out reads that had multiple hits, with mapping quality or base quality less than 30, perform base alignment quality (BAQ) computation and adjust mapping quality based for excessive mismatches (Li 2011). To remove the deamination-induced damages in ancient DNA molecules, we only keep transversion variants for downstream analysis. The genotypes on single-copied male-specific Y-chromosome regions (scpMSY) were called from all male individuals using ANGSD 0.931, with the same filters as autosomal genotyping, and -doHaploCall 2 to get the major call. The detailed information of scpMSY regions identification was provided in Text S4.2.

To estimate the heterozygosity rates of ancient rat samples, the cleaned reads with base quality and mapping quality over 30 were piled up with mpileup in SAMtools 1.3 (Li et al. 2009). Then we called pseudo-diploid genotypes with pileupCaller 1.2.2 under random diploid calling mode, which randomly sampled two reads at each site, on the transversion variants identified in ANGSD. The heterozygosity rates calculated from pseudo-diploid genotypes were half of the real heterozygosity rates of the samples on these variants.

4.7.6 Demographic history analysis

The population size dynamics was estimated using PSMC 0.6.5 (Li and Durbin 2011), with parameter "-N25 -t20 -r5 -p "4+25*2+4+6"" and 100 bootstrap replicates. The PSMC output was visualized with generation time of 0.5 years and mutation rate $\mu = 3*10^{-9}$ site/generation, based on the previous study on *R. norvegicus* (Deinum et al. 2015).

G-PhoCS (Gronau et al. 2011) was applied to estimate the population sizes, population divergence times and migration rates among three rat species, using the three high-coverage diploid genomes. The analysis was performed on 38,078 loci of 1kb length, identified in non-repetitive, autosomal regions. A preliminary analysis with all possible migration events was first run for 250,000 generations, then two parallel runs for 500,000 generations with one migration event were carried out for parameter estimation. Finally, the estimated parameters were converted to effective population sizes (Ne), divergence times (T) and total migration rates (m_total) as described in Gronau et al. (2011): theta = $4*Ne*\mu$, tau = $T*\mu/g$ and m_total=m*tau, with mutation rate $\mu=2.96*10^{-9}$ site/generation and generation time (g) of 0.5 years. The detailed information for loci selection and analysis is provided in Text S4.3.

4.7.7 Phylogenetic analysis

The ancient mitochondrial genomes were analysed alongside seven modern references, including the modern Californian black rat from the reference genome assembly, two published *R. norvegicus* individuals (Deinum et al. 2015), one published *R. tanezumi* individual (Teng et al. 2017) and the published mitochondrial genome references of the three species (*R. rattus* NC_012374.1, *R. tanezumi* NC_011638.1, *R. norvegicus* NC_001665.2). The haplotypes were aligned using MUSCLE v3.8.1551 (Edgar 2004) with default parameters, and the best-fit model was selected based on Akaike Information Criterion (AIC) calculated by jmodeltest v2.1.10 (Darriba et al. 2012). Then Maximum Likelihood (ML) tree was built using RAxML v8.2.12 (Stamatakis 2014), with GTR+I+G model and 100 bootstrap replicates.

The cytochrome b region of the mitochondrial genome haplotypes was extracted using MEGA7 and combined with modern cytochrome b haplotypes from previous publications

(Aplin et al. 2011; Colangelo et al. 2015; Baig et al. 2019; Etougbétché et al. 2020) and this study. We aligned the data using MAFFT v7.123b (Katoh and Standley 2013), then built a ML tree using RAxML v8.2.9 (Stamatakis 2014), with GTR+I+G model and 100 bootstrap replicates.

The autosomal phylogeny was reconstructed using a neighbor-joining method implemented in package Ape 5.3 in R 3.5.1. The distance matrix was calculated based on 3,393,710 autosomal transversion variants, after removing singletons, using the genetic distance described in Gronau et al. (2011). Bootstrapping was performed by resampling the variants from 100 kb non-overlapping windows, and the support on each node was calculated based on 100 bootstrap replicates. The phylogenetic tree based on Y-chromosome scpMSY regions was built with RaxML 8.2.12 (Stamatakis 2014), using GTR substitution model, ML estimation of base frequencies and 100 rapid bootstrapping replicates.

4.7.8 Population genetics analysis

The f_4-statistics was calculated by *qpDstat* 755 in ADMIXTOOLS 5.1 package (Patterson et al. 2012), with parameter "f4 mode: YES", and the two *R. norvegicus* individuals were used as outgroup in all the analysis.

We also applied Treemix 1.13 (Pickrell and Pritchard 2012) to collaboratively infer the population structure and admixture events among black rat samples. The black rat samples were grouped based on the geographic location, time period and phylogenetic pattern identified in previous analysis (Table S4.12). The allele frequency was calculated by PLINK and 1,145,713 sites covered in at least one sample from each group were included in the analysis. We built the admixture graph assuming 0 to 10 migration events, with parameters "-k 500 -global -se -noss -root tanezumi" to group 500 SNPs per block for covariance matrix estimation and we used *R. tanezumi* as the root of the resulting topology.

4.7.9 Data availability

The *R. rattus* genome assembly is available in the NCBI under the accession number GCA_011800105.1. Aligned reads from the 39 newly reported ancient black rats are

available at the ENA archive under the accession number (provided upon publication). The mitochondrial genome haplotypes are available under the accession number (provided upon publication).

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4.10 Supplementary material

4.10.1 Supplementary Information Text

Text S4.1 Taxonomy of the black rat and mitochondrial phylogeny based on cytochrome b region

Taxonomy of the black rat

Rattus rattus (also known as the black rat, roof rat or ship rat) and *Rattus tanezumi* belong to the '*Rattus rattus* species complex' within *Rattus*; these species and their relatives all form an extremely taxonomically complicated set of closely related (and interrelated, see below) taxa belonging to a number of genera (the Rattini tribe) within Rodentia. The *Rattus* genus comprises approximately 66 currently recognised species (Musser and Carleton 2005). It is the most diverse genus of rodents and the largest of mammalian genera with a range of highly adaptive specialists and also multiple generalists (Rowe et al., 2011). The fossil and subfossil record for *Rattus* is sparse and an inability to identify between closely related species precludes confident assessment of ancestral taxa (Ervynck 2002; Hulme-Beaman et al. 2019). As a result, assessment of species divergences and radiations within *Rattus* using the fossil record has generally only been possible on the large scales, such as the assessment to the arrival of *Rattus* to New Guinea and Australia (for example see Sahulian *Rattus* (Rowe et al. 2011)). Biomolecular and morphological advances have helped clarify the taxonomic complexity within this genus and its closest relatives (Hulme-Beaman et al. 2019; Fabre et al. 2012; Pagès et al. 2010; Rowe et al. 2008; Rowe et al. 2011), but questions still hang over the association of many of these species; for example *Bandicota* sp. and *Rattus* sp. (Pagès et al. 2010).

Within the Rattus genus a number of lineages and/or species form the Rattus rattus species complex (Aplin et al. 2011; Pagès et al. 2010). This is possibly the most complicated species complex within mammals, with more than 150 different species names having been previously assigned to populations and lineages within it, the resulting number of synonyms continue to cause taxonomic confusion in modern studies (Aplin et al. 2011). Biomolecular methods (when considered as encompassing both single marker studies and multi marker studies) have helped resolve a number of these taxonomic problems, but in

a number of instances, where they have used single or few markers (e.g. studies using only mtDNA) they have revealed even greater complexity, and raised numerous questions, which directly reflects the nature of these species' evolutionary past. For example, the *Rattus* genus harbours a number of deeply divergent lineages, some reflect likely real taxonomic division (e.g. the split between *Rattus rattus* and *Rattus tanezumi* as examined here) but others reflect deeply divergent lineages that exist within single populations of the same species (e.g. the finding of the mtDNA lineage for Rattus clade 3 (Pagès et al. 2010), which microsatellite evidence showed had no taxonomic support (Pagès et al. 2013)). Even more complicated still are species within the *Rattus rattus* species complex that appear to have diverged more recently than most lineages within the complex, yet have developed distinct morphological differences and correspondingly show little to no signs of gene flow; therefore forming distinct taxonomic units. For example, *Rattus sakeratensis* (formerly one population of a number previously identified as *Rattus losea* (Pagès et al. 2010; Aplin et al. 2011)) appears to have rapidly diverged and is now considered a distinct species (Pagès et al. 2013). In light of the complex evolution of these taxa, resolving the systematics of *Rattus* requires in-depth biomolecular and genomic approaches.

Within the *Rattus rattus* species complex the two major commensal taxa with the most extensive human associated distributions are *Rattus rattus* (identified as mtDNA lineage I in Aplin et al. (2011), see overview below in section on mitochondrial phylogeny) and *Rattus tanezumi* (the east Asian house rat, identified as mtDNA lineage II in (Aplin et al. 2011)). *Rattus rattus* (the primary subject of this study) is widely distributed and appears to be associated with global trade routes associated with European imperialism; *Rattus tanezumi* has an almost exclusively east Asian distribution, east of the Tibetan plateau (Aplin et al. 2011). These two species represent some taxonomic uncertainty, both appear morphologically similar, though with some variation in pelage colour (Kambe et al. 2011). However, pelage colour (coat colour of belly and/or back) is highly variable both among populations, but also within population; furthermore, taxonomic divisions based on coat colour within *Rattus rattus* have led to some of the proliferation of weak taxonomic divisions (Aplin et al. 2011; Aplin et al. ; Pagès et al. 2010; Musser and Carleton 2005). An initial basis for division, and most likely a restriction on gene-flow between these lineages

stem from chromosomal rearrangements (Baverstock et al. 1983; Yosida et al. 1971; Yosida 1973). Chromosomal variation is often considered an unsatisfactory criteria for species definition in mammals, but can be considered an indicator of potential accelerated rates of speciation and a possible restriction of gene-flow (Ayala & Coluzzi, 2005; Corti & Rohlf, 2001; Navarro & Barton, 2003; Rieseberg, 2001; Saïd et al., 1999; Searle, 1998); within *Rattus* the majority of species are 2N=42, which is as a result thought to be the ancestral arrangement for the genus (Rickart and Musser 1993). *Rattus tanezumi* has a karyotype arrangement of 2N=42; in contrast *Rattus rattus* (lineage I) has at least 3 karyotype races, but the primary configuration is 2N=38; an additional karyotype race in Mauritius has the same number as the ancestral form (2N=42), though in a different arrangement; and a further race with 2N=40 is found in Sri Lanka (Baverstock et al. 1983; Baverstock et al. 1977; Bianchi et al. 1969; Capanna and Civitelli 1971; Capanna and Civitelli 1971; Yosida et al. 1971; Yong 1971). However, these differences in karyotype arrangement are not a complete gene-flow barrier and in fact the two mtDNA lineages associated with each taxon, *Rattus rattus* and *Rattus tanezumi*, are found in anthropogenically introduced and mixed populations in Sri Lanka, South Africa, California and Japan (Conroy et al. 2013; Lack et al. 2012; Aplin et al. 2011; Robins et al. 2007). With evidence for admixture between karyotype races and animals with the separate mtDNA showing free gene-flow in human introduced populations, the question of the taxonomic division between *Rattus rattus* and *Rattus tanezumi* requires a greater and in-depth analysis of multiple lines of evidence to test this division; here we examine whole genomic evidence.

Earliest *Rattus rattus* commensalism and its western natural occurrence: Natufian rats

The presence of *Rattus sp.* (cf. *Rattus rattus*) is often cited as an indication of a shift to more sedentary settlements of the Natufian period (~15,000–10,000BP) in the Levant region (Tchernov 1968; Weissbrod et al. 2013). If correct, these *Rattus* specimens would be the furthest and earliest western range of *Rattus* post the Last Glacial Maximum (~20,000 ± 2,000 BP for Europe, prior to 40,000–20,000BP a rat species cf. *Rattus haasi* is reported from central and western Eurasia, but its relationship to other major *Rattus* species is unclear (Tchernov 1968)). Furthermore, the link between Natufian *Rattus rattus* with Natufian sedentism is based upon the suggestion that these early *Rattus rattus* finds are also commensal, which would also make these the earliest examples of commensal

Rattus. In this way *Rattus rattus* finds are combined with a suite of other likely commensal species including house mouse (*Mus musculus*), and house sparrows (*Passer domesticus*) to bolster support for Natufian shifts towards sedentary settlements and the first steps towards domestication of cereal grains (Bar-Yosef and Tchernov 1966). However, amongst these species displaying early commensal behaviour, *Rattus rattus* remains are usually recovered in the smallest numbers and most sporadically and none of these *Rattus rattus* remains have been directly dated (Weissbrod et al. 2013). Therefore, although this might represent some of the earliest steps of *Rattus rattus* toward commensal behaviour the earliest evidence for intense and large-scale commensal behaviour appears to be from Indus Valley sites (Ervynck 2002).

S4.2 *De novo* assembly of *Rattus rattus* reference genome

Autosomal chromosome assembly

For the *de novo* assembly of *R. rattus* reference genome, an individual male black rat was caught in California, USA, where an invasive black rat population was established in the early 18th century (Lantz 1909). This rat is now catalogued at the Museum of Vertebrate Zoology, UC Berkeley. Genomic DNA was extracted from the liver and one shotgun sequencing library was prepared using Illumina TruSeq DNA PCR-free kit. The shotgun library was sequenced on Illumina HiSeq 4000 platform to produce 900M 150 bp paired-end sequencing reads, and a *de novo* assembly was generated using Meraculous (Chapman et al. 2011), with k-mer size of 55, minimum k-mer frequency cut-off of 9 and diploid mode.

Three Chicago libraries and three Dovetail Hi-C libraries were further prepared following published procedures (Putnam et al. 2016; Lieberman-Aiden et al. 2009), and sequenced on Illumina HiSeq 4000 platform. A total of 498M PE150 reads were produced from the three Chicago libraries, providing an estimated physical coverage of 55.5x, which is the average number of read pairs of 1-100kb spanning a certain position in the genome. The Hi-C libraries were sequenced for 512M PE150 reads and provided an estimated physical coverage (10-10,000 kb pairs) of 15,256x. The *de novo* genome assembly from Meraculous and Chicago sequencing reads were first used as input data for HiRise scaffolding pipeline (Putnam et al. 2016), then the output assembly, together with Hi-C sequencing reads were used for a second round of HiRise scaffolding.

Sex chromosome assembly

To retrieve the assembly from both sex chromosomes, we first mapped the shotgun sequencing reads to *Rattus norvegicus* reference genome Rnor_6.0 using BWA (Li and Durbin 2009), and extracted reads mapped to the X chromosome (NC_005120.4) and Y chromosome (NC_024475.1), respectively.

Then we used Meraculous 2.2.5.1 (Chapman et al. 2011) to get the *de novo* assembled scaffolds for both sex chromosomes, with k-mer size set to 55, minimum size cut-off as 9 and diploid mode disabled. The average and standard deviation of insert size was set to 400 bp and 10 bp, with average read length as 150 bp and the approximate genome sizes were 120 Mb for X chromosome and 2 Mb for Y chromosome. After Meraculous assembly, we reconstructed 9984 scaffolds from X chromosome, with a total length of 110.0 Mb and N50 length of 18.9 kb, and 440 scaffolds from Y chromosome, with a total length of 2.0 Mb and N50 length of 8.9 kb (Table S4.1).

Chromosome	N Scaffold	Total length	Min length	Max length	N50	L50
ChrX	9984	110.0 Mb	1.0 kb	228.2 kb	18.9Kb	1644
ChrY	440	2.0 Mb	1.0 kb	45.7 kb	8.9Kb	69

Table S4.1 Meraculous *de novo* assembly of the sex chromosomes

These *de novo* scaffolds were then further assembled with Chicago and Hi-C data using HiRise genome assembly pipeline from Dovetail (Table S4.2). After combing the sex chromosomes and autosomes assembly, we got the genome assembly of *R. rattus* consisted of 6805 scaffolds, with a total length of 2.25 Gb.

	Total length	N scaffold	N50	L50	N90	L90
Autosomes	2137.8 Mb	5604	145.8 Mb	6	73.3 Mb	15
ChrX	110.9 Mb	781	68.0 Mb	1	1.5 Mb	5
ChrY	2.1 Mb	420	9.8 kb	50	1.8 kb	260

Table S4.2 Statistics of the HiRise genome assembly

Identification of scpMSY regions

The single-copied scaffolds in the MSY region (scpMSY) were identified following a published strategy (Wallner et al. 2017), using ten male and ten female *R. rattus* individuals with average genomic coverage over 1x (Table S4.12). The mean coverage on each scaffold

of each individual was calculated using reads with mapping quality and base quality over 30 and normalized by the mean coverage on all the 420 Y-chromosome scaffolds. The average normalized mean coverage (ANMC) of each scaffold was calculated as the average of normalized coverage in ten male individuals. The scaffolds with the average of coverage/nuclear mean coverage < 0.01 on the female individuals, and 0.1 < ANMC < 1.5 were considered as scpMSY scaffolds. Finally, we identified 321 scpMSY scaffolds, with a total length of 1,925,316 bp.

Assessment of the genome assembly

The repetitive regions were identified using RepeatMasker 4.0.7 (http://repeatmasker.org) (Smit, AFA, Hubley, R & Green, P 2013-2015) using Repbase 20170127 and the query species set as rattus (Table S4.3), and TRF 4.09 (Tandem repeats finder) (Benson 1999), with parameters set as "2 7 7 80 10 50 12".

	Percentage of sequence (%)
Total	38.34
SINEs	7.21
LINEs	16.39
LTR elements	9.87
DNA elements	1.24
Unclassified	0.4
Small RNA	0.03
Satellites	0.02
Simple repeats	2.87
Low complexity	0.33

Table S4.3 RepeatMasker summary for the *R. rattus* genome assembly

The completeness of genome assembly was assessed by BUSCO 3.0.2 (Simão et al. 2015), using the 303 orthologs in Eukaryota odb9 dataset, and compared to the *Rnor_6.0* reference genome (Table S4.4).

Assembly		**Complete**	**Fragmented**	**Missing**	**Total**
R. rattus	unmask	273	11	19	303
	mask	269	13	21	303
Rnor_6.0	unmask	277	10	16	303
	mask	270	14	19	303

Table S4.4 Comparison of BUSCO output between *R. rattus* genome assembly and *Rnor_6.0*

We aligned the new genome assembly with Rnor_6.0 reference genome using nucmer 4.0.0 in MUMmer tool package (Kurtz et al. 2004), to investigate the synteny between *R.*

rattus and *R. norvegicus* genomes, using both masked assemblies and anchor matches that are unique in both reference and query. The 18 longest *R. rattus* scaffolds in autosomal assembly and 20 *R. norvegicus* chromosomes were well aligned (Figure S4.1). As described in previous karyotype study, *R. rattus* has a diploid number of 2n=38. Chr5/7 and chr9/11 of *R. norvegicus* correspond to chr1 and chr2 of *R. rattus*, respectively (Cavagna, Stone, and Stanyon 2002). The 9 largest scaffolds (>0.5 Mb) of the X chromosome assembly were also aligned to *R. norvegicus* chrX (Figure S4.2).

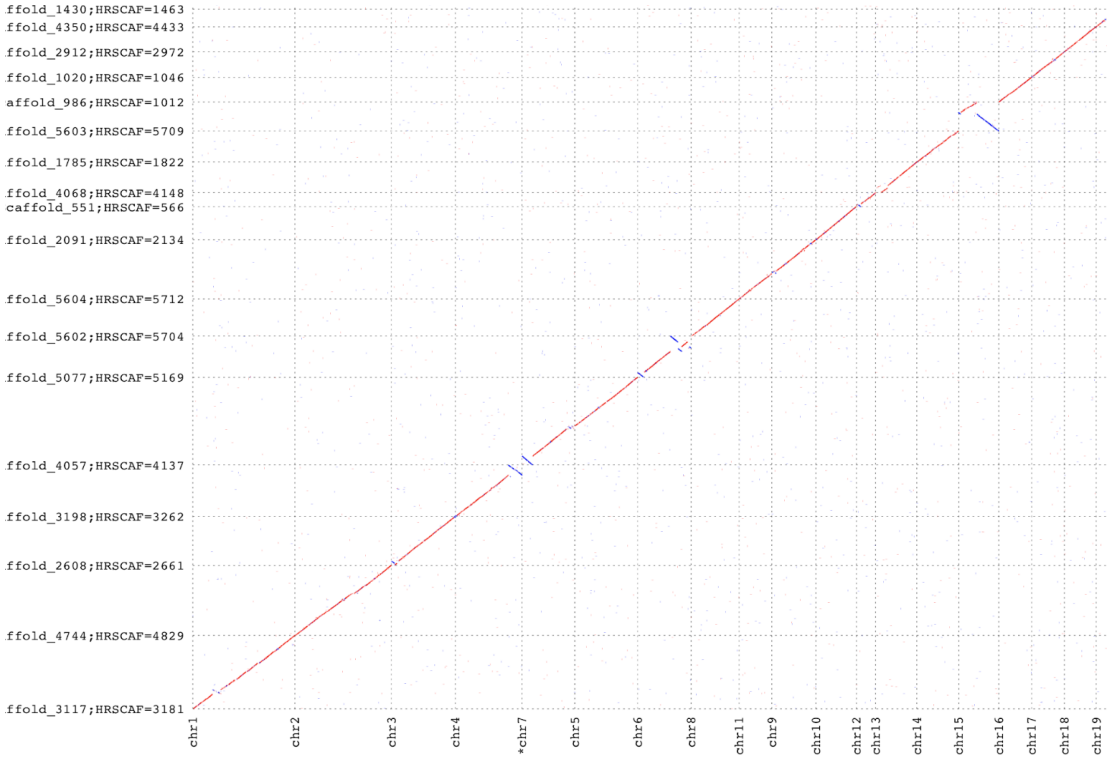


Figure S4.1 Pairwise alignment between the *R. rattus* genome assembly and *Rnor_6.0* on autosomes. The X-axis shows 20 autosomal chromosomes of Rnor_6.0 and the Y-axis shows the 18 largest autosomal scaffolds of the new genome assembly, each corresponding to one autosomal chromosome of the black rat. Forward matches are shown in red and reverse matches are shown in blue. The scaffolds with asterisk marked on Y-axis are plotted in a flipped orientation.

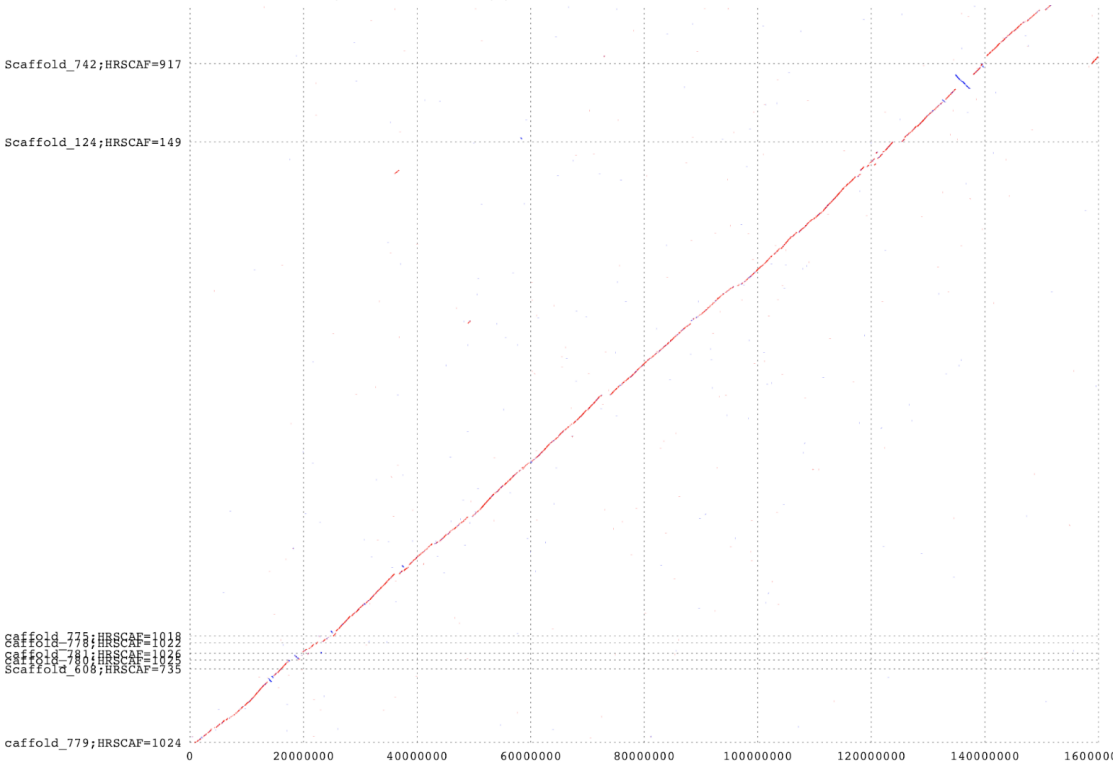


Figure S4.2 Pairwise alignment between the *R. rattus* genome assembly and *Rnor_6.0* on chrX. The X-axis shows X chromosome of *Rnor_6.0* and the Y-axis shows the 9 scaffolds over 0.5Mb of the new X-chromosome assembly. Forward matches are shown in red and reverse matches are shown in blue. The scaffolds with asterisk marked on Y-axis are plotted in a flipped orientation.

Text S4.3 Demographic analysis using G-PhoCS

The Generalized Phylogenetic Coalescent Sampler (G-PhoCS) was applied to estimate the population sizes, population divergence times and migration rates among the three rat species (Gronau et al. 2011), using high-coverage, diploid genomes. After masking out the repetitive regions identified by RepeatMasker and TRF, we identified 38,078 loci of 1kb length on autosomal regions, with less than 10% masked sites and interlocus distance over 50 kb, allowing for sufficient recombination.

The G-PhoCS analysis was performed based on a given topology (norvegicus, (rattus, tanezumi)), using the modern black rat CP-5999 and ERS215791, HXM4 from published study to represent for *R. rattus*, *R. norvegicus* and *R. tanezumi*, respectively. We first ran a preliminary analysis with all eight possible migration bands added in the model, for 250,000 generations and sampled every 100 generations. The prior for all migration events set to alpha=0.001, beta=0.0001 and all theta and tau parameters were set to alpha=3, beta=1000. The result was checked and summarized with Tracer 1.6.0 (Rambaut et al. 2018) and the first 50,000 generations were burn-in. In this preliminary run we identified only one migration event with total migration rate (m_total=m*tau) over 0.01, that is, the gene flow from rattus/tanezumi ancestral population into norvegicus lineage (Table S4.7).

Based on the preliminary results, we performed two parallel runs for 500,000 generations and sampled every 100 generations, with one migration event and priors for theta and tau parameters set as Table S4.6. Finally, the estimated parameters were converted to effective population sizes (Ne), divergence times (T) and total migration rates (m_total) as described in Gronau *et al.* (Gronau et al. 2011): theta = 4*Ne*μ, tau = T*μ/g and m_total=m*tau, with mutation rate $\mu=2.96*10^{-9}$ site/generation and generation time (g) of 0.5 years.

Text S4.4 Details on cytochrome b laboratory analysis

Mitochondrial phylogeny based on the cytochrome b region

For an overview of the relationship between the ancient rats and modern black rats from across their range, 292 tissue samples of *R. rattus* were collected and analysed for mitochondrial cytb region. Among them 263 specimens were obtained from various museums (Field Museum, Chicago; American Museum of Natural History, New York; British National History Museum, London) and additional 29 modern specimens were collected in the field by Dr. J. Chris Hillman. The museum material is composed mainly of dried tissue, skins or ethanol-fixed samples, modern specimens were stored in ethanol. The sampling area comprises different places of the mainland and islands around the Indian Ocean, including countries from the East and West African coast, the Arabian Peninsula, as well as the Indian subcontinent and South-East Asia.

DNA extraction was performed in dedicated ancient and modern DNA laboratories in the Archaeology Department at Durham University. The different sample types (wet and dried tissue, skin) used in this analysis were prepared prior to DNA extraction in order to minimise the risk of coextracting exogenous contaminants and to remove preservative chemicals that can inhibit subsequent PCR, respectively. Dried skin samples were washed several times with Tween 20, ethanol- or formalin-fixed specimens were washed several times with purified water in order to increase the quality of DNA recovery. Afterwards, samples were placed on a petri dish and finely chopped with a sterile, disposable blade before transferral of ~ 10 mg into a 1.5 ml Eppendorf tube. The different DNA extraction protocols for each sample type are stated below. One in ten extractions were blank controls in order to detect possible contamination.

DNA extraction of dried tissue samples was carried out using the Qiagen MicroKit, following the manufacturer's recommendations. DNA extraction of ethanol-fixed tissue samples was carried out using the following protocol.

Day 1: Add 300 µl Extraction buffer (1M NaCl, Tris-HCl pH 8.0, 10% SDS, H2 O) to each sample, add 3 µl Proteinase K to each sample, vortex 15 sec, incubate samples on a rotary shaker overnight at 50°C

Day 2: Add 80 µl of saturated NaCl to remove DNA byproducts, vortex centrifuge 10 min at 9.000 rpm, transfer supernatant without touching the pellet, discard pellet repeat step until the supernatant is clear. Add 800 µl ethanol (97-100%) to precipitate the DNA pellet, mix by inverting the tubes several times, centrifuge 45 min at 13.000 rpm. Pour off the supernatant of each sample and remove any fluids with a small pipette, but mind the DNA pellet. Leave the tube open to dry the pellet, wait until all fluids are dissolved. Add 200 µl 1xTE, incubate 5 min, centrifuge 1 min at 14.000 rpm, end up with one elution E1 á 200 µl, freeze at -20°C until further use.

The cytochrome b region of the mitochondrial DNA was targeted for PCR amplification. PCR set-up was conducted under a fume hood in a dedicated ancient DNA room. Every PCR set-up included a negative control in order to detect possible contamination. Additionally, a positive control (modern material of each particular species) was included in each PCR to exclude that possible failure of the reaction is due to reagents or the thermal cycler.

Standard protocols of PCR set-up and thermal cycler programs are stated below. To ensure optimal PCR success, modification of the reaction conditions was repeatedly needed. Modification included altering the amount of DNA extract added or adjusting the final concentration of the other reagents used. Furthermore, cycling conditions were changed decreasing the times and numbers of cycle repetitions. PCRs were visualised on a 1.5% agarose gel, using GelRed and UVillumination.

The first set of primer pairs U1/L1 to U4/L4 has been designed by Trinks (Table S4.5). The second set of primer pairs Cyt b Rr1 to Cyt b Rr10 have been designed in equal parts by Eager and Trinks. Primer pairs F1 and F2 were taken from Aplin et al. (2011). The design is based on the sequence of a whole mitochondrial genome of *Rattus rattus* (NCBI accession number NC_012374).

Fragment Ref_NC_012374	Primer forward 5'-3'	Primer Position		Primer reverse 5'-3'	Primer Position		Product Length	°C
Cyt b U1/L1	AATTTGTCATTATTTCTACACAGCATT	14043	14069	TAGGGTTGCTTTGTCTACTGAGAA	14628	14652	559 bp	56
Cyt b U2/L2	CATCTGCCGAGACGTAAACTAC	14330	14352	GTCTCCTAGTAAGTCTGGGAAGAAT	14858	14883	507 bp	56
Cyt b U3/L3	AGGATCAAACAACCCCACAG	14735	14755	TGTTGATGGTGGGGAGTTAGT	15353	15374	599 bp	56
Aplin Museum F1 (2011)	ATCACACCCTCTACTCAAAA	14144	14164	GGCATGTAAGTATCGRATTAG	14358	14378	194 bp	56
Aplin Museum F2 (2011)	TCATCAGTTACYCACATCTGC	14316	14337	CCTCAGATTCATTCGACTAGRGT	14601	14624	264 bp	56
Cytb b Rr1	ACACAGCATTTAACTGTGACCA	14060	14082	GGGCGGGAAGGTCAATGAAGG	14176	14197	94 bp	56
Cytb b Rr2	TTAATCACTCCTTCATTGACCTTCC	14167	14192	AGCCGTAGTTTACGTCTCGGCAG	14333	14356	141 bp	56
Cytb b Rr3	TTAACAGCATTCTCATCAGTTAC	14304	14327	GTTGCTATGACTGCAAATA	14485	14504	158 bp	56
Cytb b Rr4	TCCTACACCTTCTTAGAAACATGAAAC	14442	14469	AGCCTCCTCAGATTCATTCGAC	14607	14629	138 bp	56
Cytb b Rr5	CAAACCTATTATCAGCCATTCCCTA	14566	14590	AGTTTAGTCCTGTGGGGTTGTT	14742	14764	151 bp	56
Cytb b Rr6	GCCCTTGCAATTGTACATCTCCT	14697	14720	TGGGTCTCCTAGTAAGTCTGGGAA	14862	14886	142 bp	56
Cytb b Rr7	GACTTACTTGGAGTATTCATGTTAC	14808	14833	GGGATGGAGCGTAGAATAGCG	14960	14980	127 bp	56
Cytb b Rr8	ACCCCACCACATATTAAGCCAGA	14916	14939	TGGGCGGAATGTTAGACTGCGT	15062	15084	123 bp	56
Cytb b Rr9	TTCTAATCTTAGCCTTTCTACCA	15019	15042	AACTRATGGATGCTAGTTGG	15179	15199	137 bp	56
Cytb b Rr10	AGCCAACCTCTTCATTTTAAC	15113	15134	GCTCTTCATTTTTGGTTTACAA	15300	15322	166 bp	56

Supplementary Table S4.5 Primers for mitochondrial fragment amplification.

All samples were analysed in the facilities at the Archaeology Department of Durham University. Because of the recent age of most of the specimens, the samples were treated as modern material. Each workstep, from DNA extraction to sequencing set-up, was conducted in the modern laboratory, following standard extraction protocols. The sequencing reaction was carried out by the DNA Sequencing Service at the School of Biological and Biomedical Sciences at Durham University. Mitochondrial DNA was amplified in 10 overlapping fragments for cytochrome b, whereas a variety of primer combinations was used depending on the nature of the sample. The sequencing chromatograms were edited manually, subsequently assembled, and a consensus sequence per individual exported using Geneious R6 version 6.0.6 (Drummond et al. 2011). Standard anti-contamination guidelines were followed.

Text S4.5 Assessment of the *R. tanezumi* introgression in the modern black rat

The modern *R. rattus* sample (CP-5999) sequenced for reference genome assembly was collected from California, USA, where admixture between *R. rattus* and *R. tanezumi* was proposed by microsatellite studies (Conroy et al. 2013; Lack et al. 2012). To test whether the CP-5999 sample carried introgression from *R. tanezumi*, we applied f_4-statistics in the form of f_4(norvegicus, tanezumi; CP-5999, Testpop) for all the ancient rat groups (Table S4.6). We found that the modern rat is equally related to *R. tanezumi* with all ancient rats, ruling out the possibility of genetic introgression in this individual.

Testpop	F4	Z	nBABA	nABBA	nSNPs
Ass	-0.000011	-0.283	27364	27442	6835117
ATU	-0.000011	-0.236	12710	12754	4072243
BUD0014	0.000044	1.151	19356	19110	5592353
BUD003	0.000053	1.154	12420	12218	3810370
Car	-0.000044	-1.12	28332	28641	6973691
GAU	-0.000009	-0.203	8852	8882	3244499
KAF	-0.000038	-0.878	12086	12233	3920611
KLT	-0.000031	-0.683	14471	14607	4326576
MDT	-0.000092	-2.129	16759	17200	4783967
MEP	-0.000025	-0.692	18856	18997	5679673
PRA	-0.000026	-0.632	17674	17811	5221123
PZA	-0.000057	-1.428	14156	14419	4592312
SML	-0.000091	-2.26	27357	27980	6819026
SNE	-0.000045	-0.792	10224	10366	3120163
Sulz	-0.000025	-0.6	23211	23365	6225331
TRU	-0.000047	-1.107	16714	16958	5157166
VOB	-0.000011	-0.261	15900	15955	5081887
ZMB	-0.000089	-2.129	26124	26707	6593161

Table S4.6 F_4-statistics of the affinity to *R. tanezumi* in black rats

4.10.2 Supplementary Information Figures

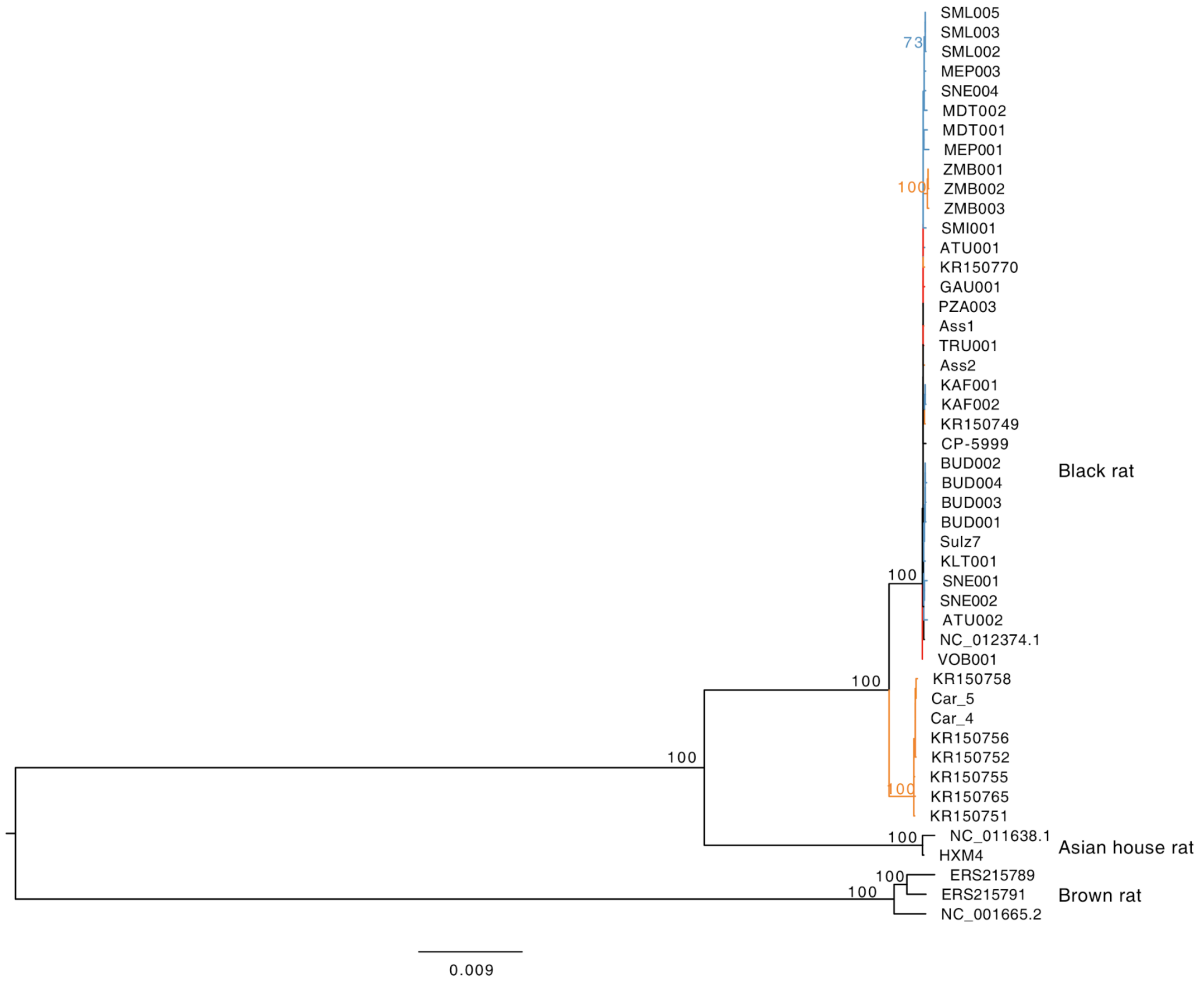
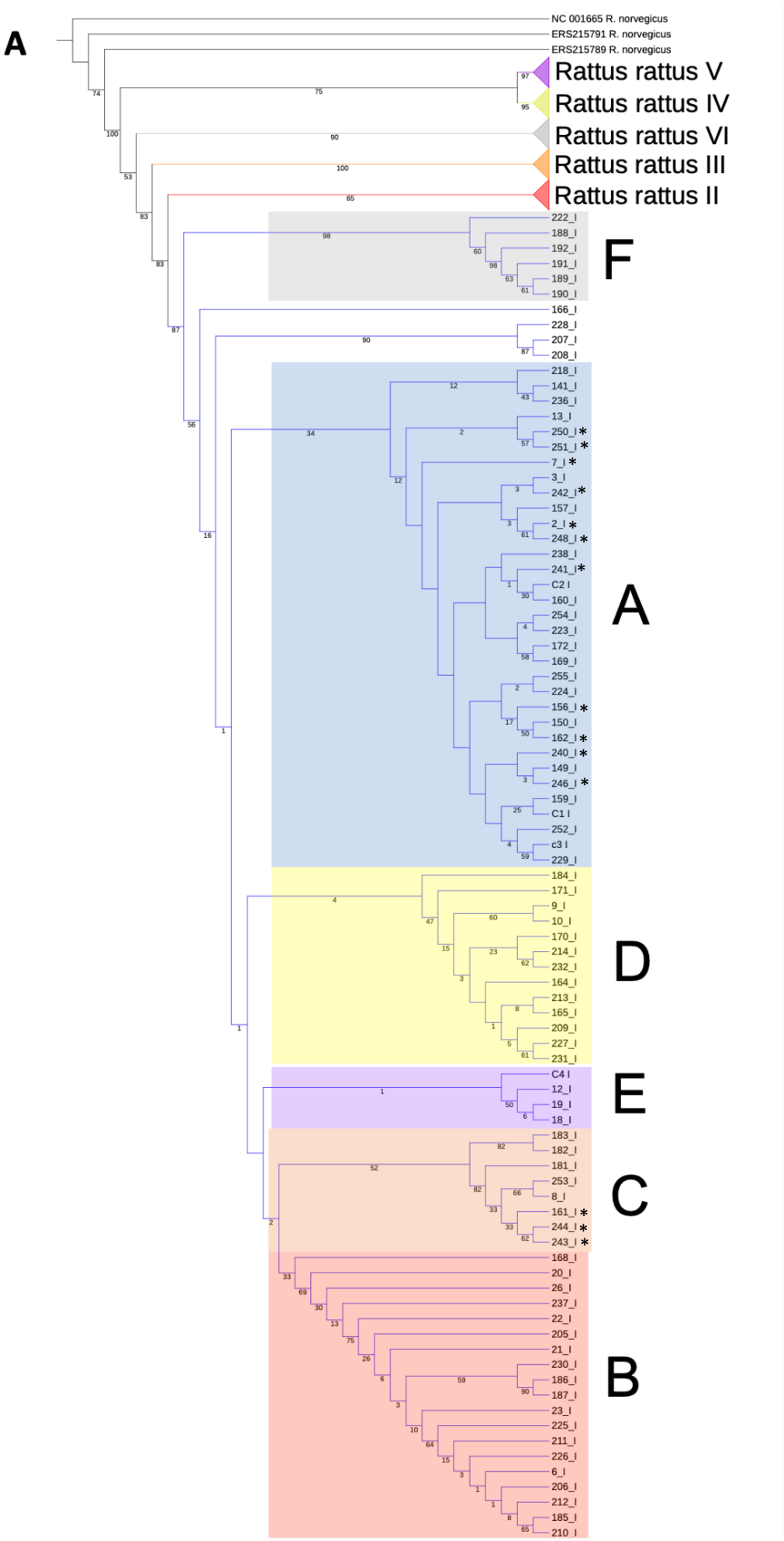


Figure S4.3 Phylogenetic relationship among ancient black rats on mitochondrial genomes.


A
NC 001665 R. norvegicus
ERS215791 R. norvegicus
ERS215789 R. norvegicus
Rattus rattus V
Rattus rattus IV
Rattus rattus VI
Rattus rattus III
Rattus rattus II
F
A
D
E
C
B

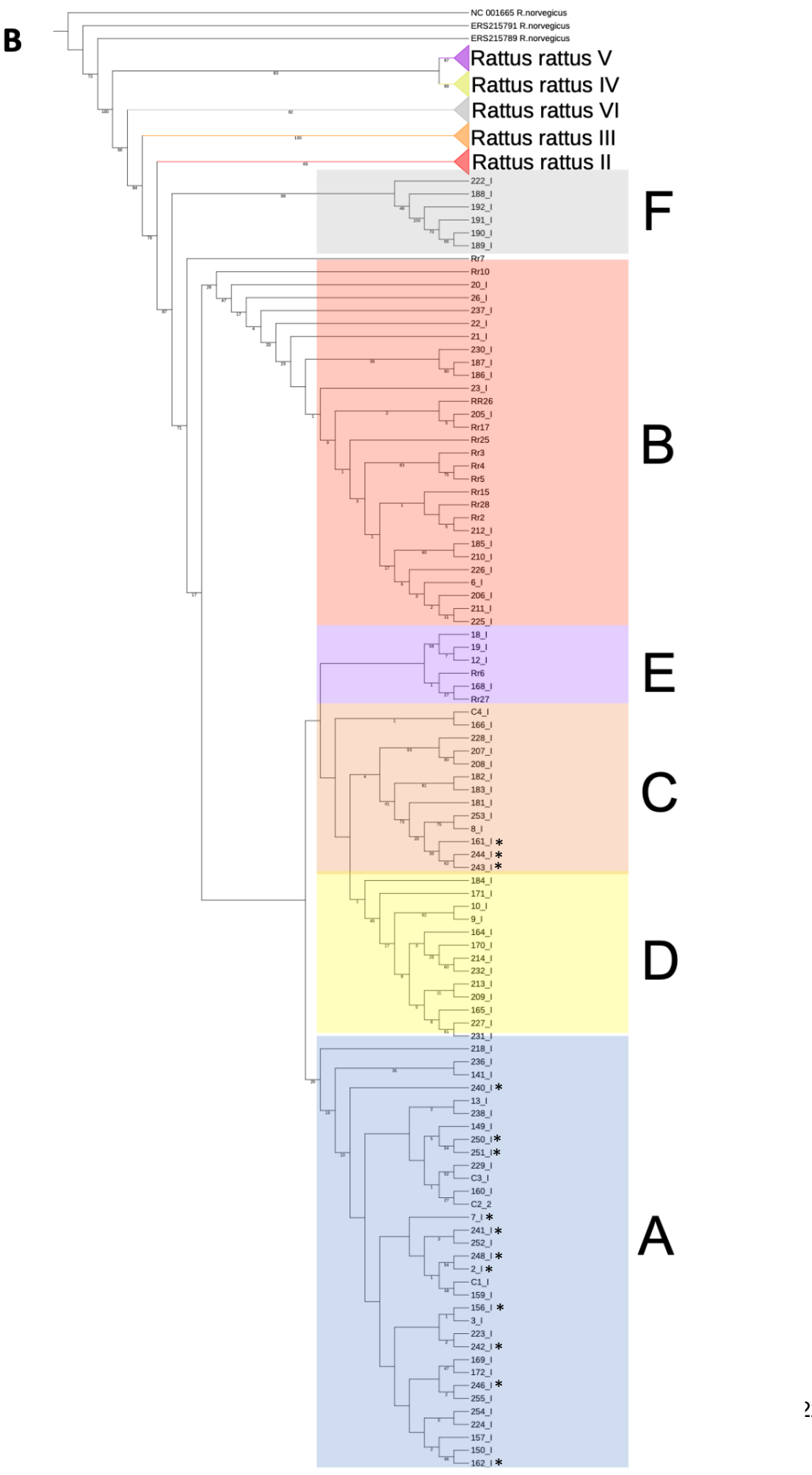

B
NC 001665 R.norvegicus
ERS215791 R.norvegicus
ERS215789 R.norvegicus
Rattus rattus V
Rattus rattus IV
Rattus rattus VI
Rattus rattus III
Rattus rattus II
222_I
188_I
192_I
191_I
190_I
189_I
F
Rr7
Rr10
20_I
26_I
237_I
22_I
21_I
230_I
187_I
186_I
23_I
RR26
205_I
Rr17
Rr25
Rr3
Rr4
Rr5
Rr15
Rr28
Rr2
212_I
185_I
210_I
226_I
6_I
206_I
211_I
225_I
B
18_I
19_I
12_I
Rr6
168_I
Rr27
E
C4_I
166_I
228_I
207_I
208_I
182_I
183_I
181_I
253_I
8_I
161_I *
244_I *
243_I *
C
184_I
171_I
10_I
9_I
164_I
170_I
214_I
232_I
213_I
209_I
165_I
227_I
231_I
D
218_I
236_I
141_I
240_I *
13_I
238_I
149_I
250_I *
251_I *
229_I
C3_I
160_I
C2_2
7_I *
241_I *
252_I
248_I *
2_I *
C1_I
159_I
156_I *
3_I
223_I
242_I *
169_I
172_I
246_I *
255_I
254_I
224_I
157_I
150_I
162_I *
A

Figure S4.4 Maximum likelihood tree (GTR+GAMMA) of rat samples based on CYTB region
a. This figure includes ancient samples from this study alongside haplotypes from Aplin, Colangelo, Etougbétché as well as modern samples from Trinks and Eager. See Table S4.11 for a list of samples corresponding to each haplotype. Haplotypes denoted with a * have at least one ancient sample found with this haplotype.
b. This figure includes samples above and the addition of modern samples from India. They were not included in the main tree due to their sequence lengths being less than 90% however due to their importance we built this second tree. They are all the samples starting Rr.

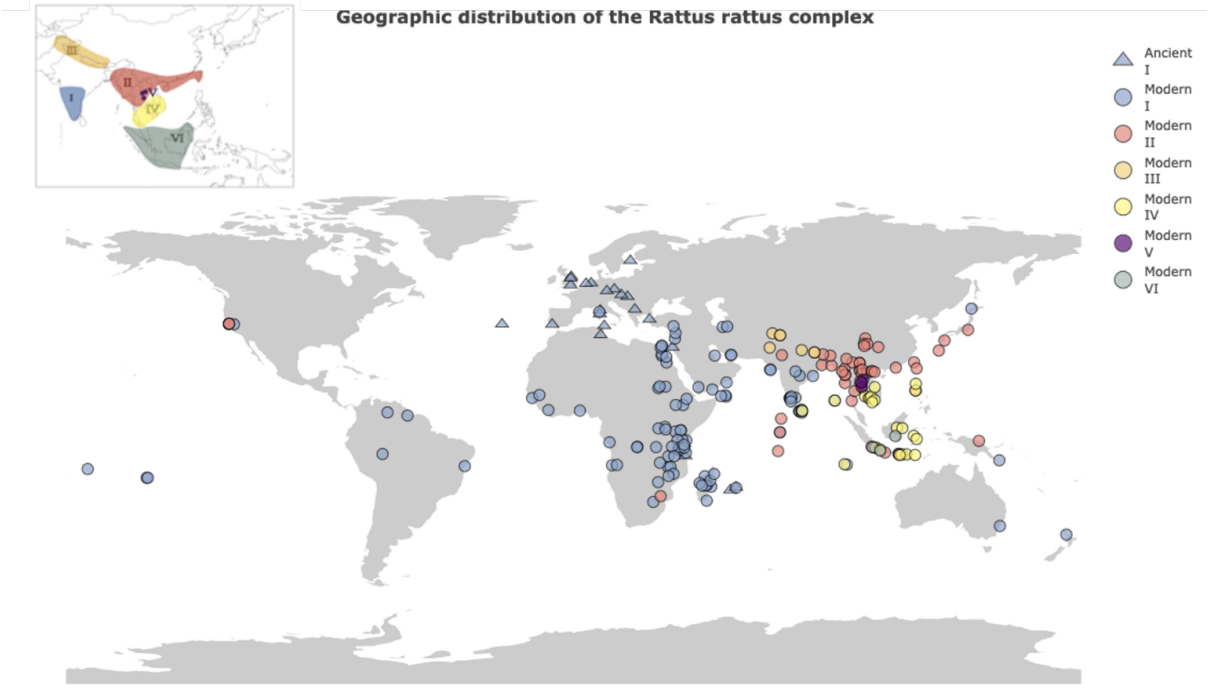


Figure S4.5 Map showing the mitochondrial lineage included in the cytochrome b analysis. Triangles depict ancient samples and circles modern, colours depict the different mitochondrial lineages within the *Rattus rattus* complex. The insert in the top left is an image from Aplin et al. (2011) showing the modern distribution of the *Rattus rattus* complex. Lineage I and lineage II are the only samples to be seen outside their natural range with lineage I being the main lineage moved around the world.

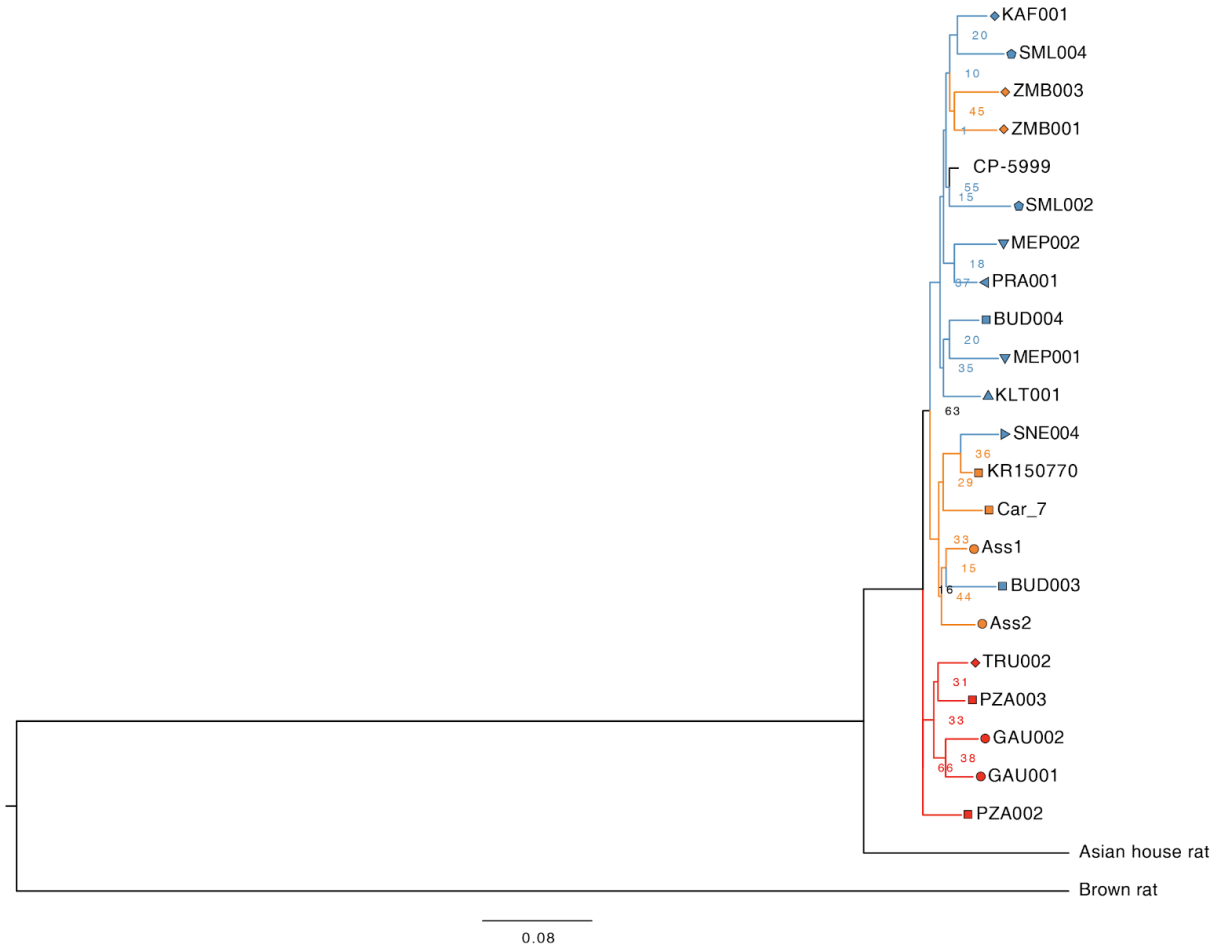


Figure S4.6 Phylogenetic relationship among ancient black rats on Y-chromosome.

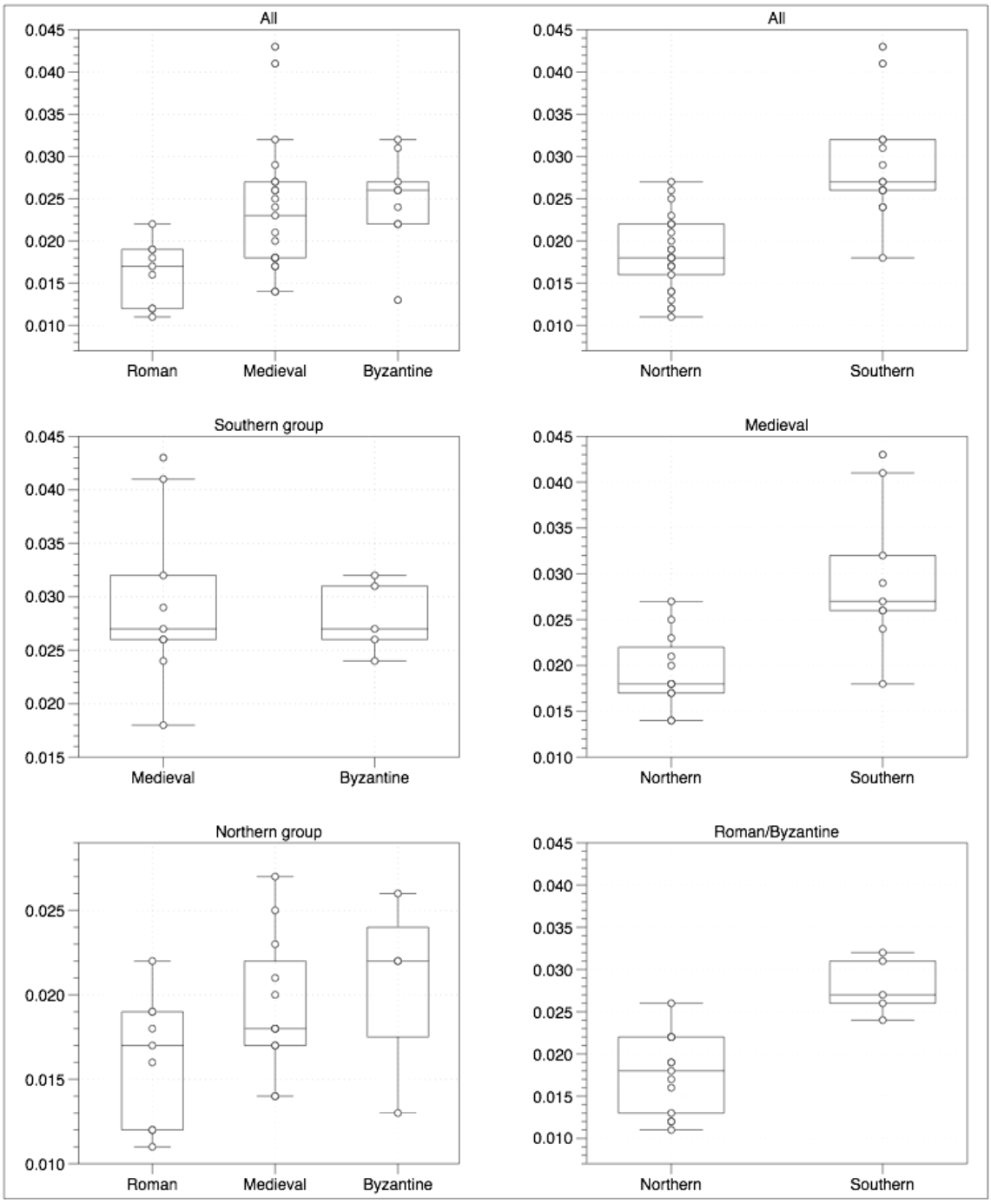


Figure S4.7 Heterozygosity of ancient black rats on autosomal variants.

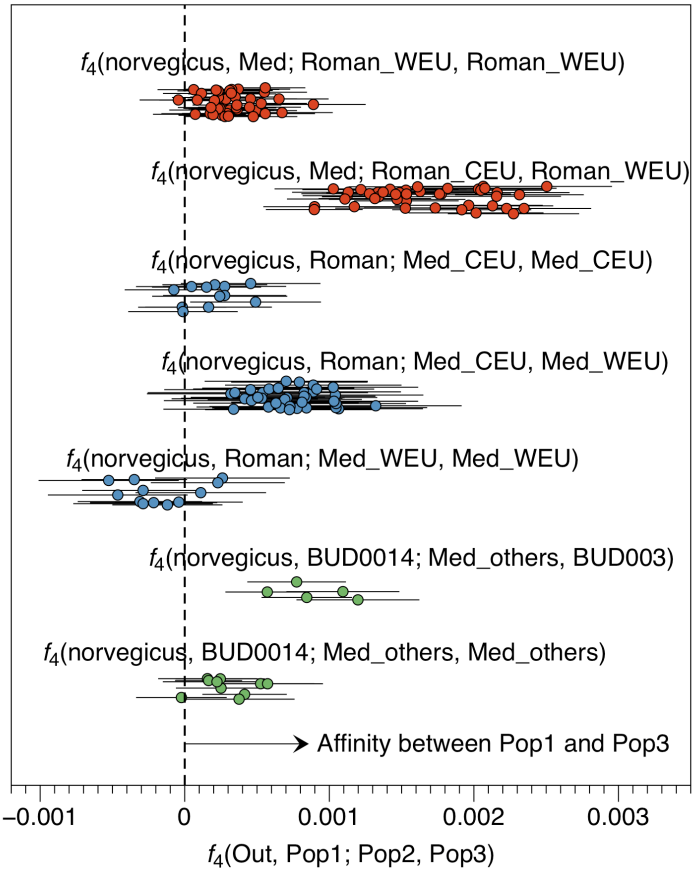


Figure S4.8 The *f*-statistics showing admixture between different ancient rat populations. The dots show all the combinations of f_4-values as described above each cluster, and the error bars show ± 3SE of the estimates. Here the red clusters show that the Medieval rats (Med) are closer related to western European Roman rats (Roman_WEU), compared to central European Roman rats. The blue clusters show that the Roman rats (Roman) are closer related to western European Medieval rats (Med_WEU), compared to central European Medieval rats (Med_CEU). The green clusters show that the Post-Medieval Buda Castle rats (BUD001/4) are closer related to the Medieval Buda Castle rat (BUD003), compared to other Medieval rats from continent Europe (Med_others).

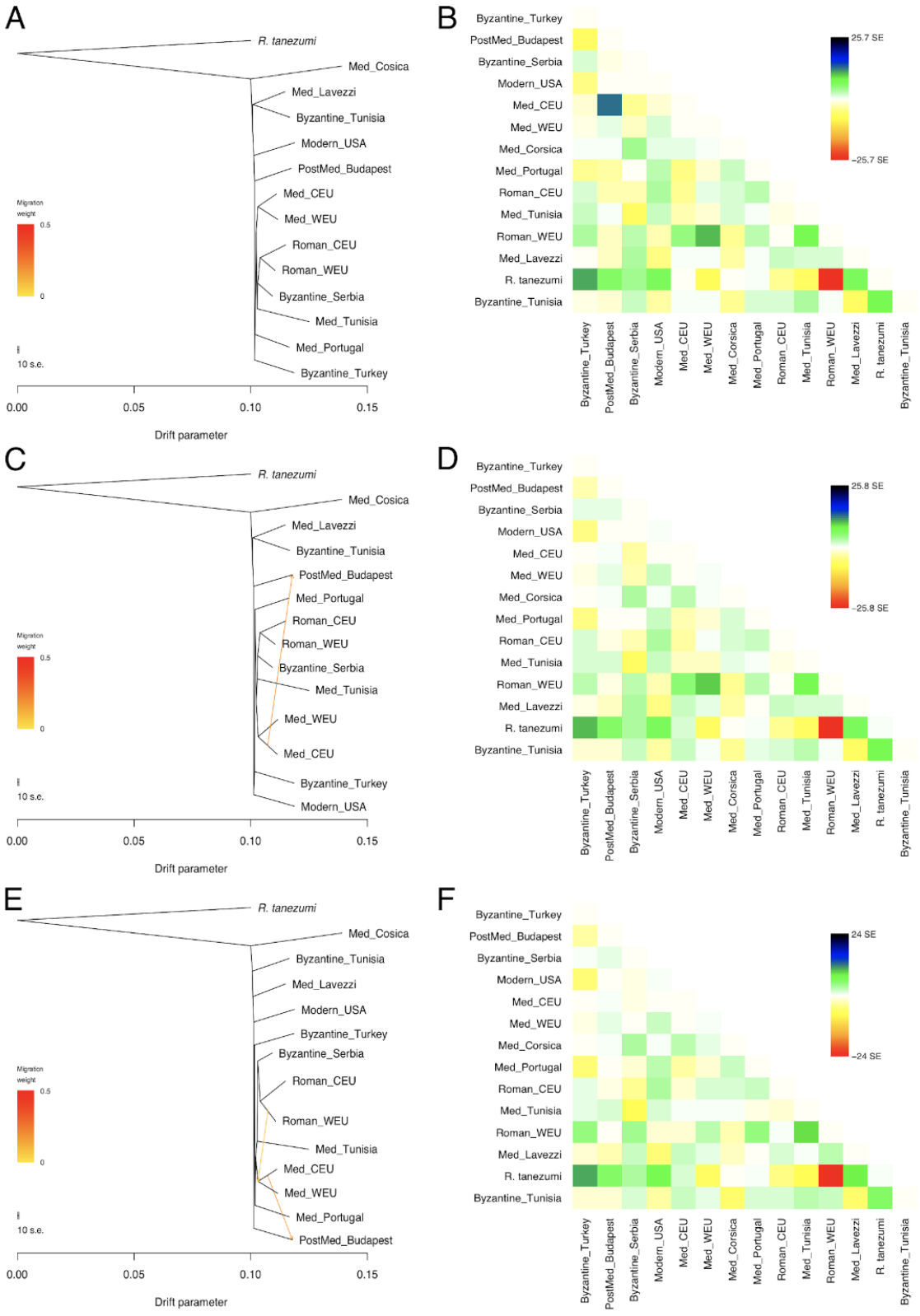


Figure S4.9 Admixture graph among ancient black rat populations. The ML trees estimated by Treemix with (A) no (C) one and (E) two migration edges fitted are plotted with the Asian house rat individual as outgroup. The corresponding residue covariance matrices are shown in (B), (D) and (F).

4.10.3 Supplementary Information Tables

Table S4.7a – G-phocs results

Summary Statistic	mean	Std error of mean	Standard deviation (stdev)	variance	median	geometric mean
theta_rattus	1.14E-03	3.44E-07	1.28E-05	1.63E-10	1.14E-03	1.14E-03
theta_tanezumi	2.17E-03	7.76E-07	2.68E-05	7.21E-10	2.17E-03	2.17E-03
theta_norvegicus	1.60E-03	3.52E-07	1.15E-05	1.33E-10	1.60E-03	1.60E-03
theta_rattus_tanezumi	0.0148	1.77E-06	7.45E-05	5.55E-09	0.0148	0.0148
theta_rat	2.06E-03	7.21E-06	8.68E-05	7.54E-09	2.06E-03	2.06E-03
tau_rattus_tanezumi	7.36E-04	2.94E-07	9.52E-06	9.06E-11	7.40E-04	7.36E-04
tau_rat	0.0114	4.37E-06	4.52E-05	2.04E-09	0.0114	0.0114
m_rattus->tanezumi	0.0121	1.14E-03	0.032	1.02E-03	8.00E-04	8.20E-04
m_tanezumi->rattus	0.0173	4.12E-03	0.0538	2.90E-03	1.11E-03	1.11E-03
m_rattus_tanezumi->norvegicus	5.6735	0.0621	0.3225	0.104	5.667	5.6645
m_norvegicus->rattus_tanezumi	1.16E-03	1.63E-04	2.43E-03	5.90E-06	2.10E-04	2.31E-04
m_tanezumi->norvegicus	9.53E-03	2.75E-03	0.0232	5.39E-04	7.00E-04	7.56E-04
m_norvegicus->tanezumi	3.13E-03	1.82E-04	8.12E-03	6.60E-05	3.60E-04	3.91E-04
m_rattus->norvegicus	3.8634	0.1582	0.5307	0.2817	3.8364	3.8264
m_norvegicus->rattus	3.1141	0.065	0.3941	0.1553	3.0567	3.0894
m_tot_rattus->tanezumi	8.91E-06	3.35E-10	3.05E-07	9.27E-14	5.92E-07	6.03E-07
m_tot_tanezumi->rattus	1.27E-05	1.21E-09	5.12E-07	2.63E-13	8.21E-07	8.15E-07
m_tot_rattus_tanezumi->norvegicus	6.05E-02	2.53E-07	1.15E-05	2.03E-10	6.04E-02	6.04E-02
m_tot_norvegicus->rattus_tanezumi	1.24E-05	6.63E-10	8.66E-08	1.15E-14	2.24E-06	2.47E-06
m_tot_tanezumi->norvegicus	7.01E-06	8.10E-10	2.21E-07	4.88E-14	5.18E-07	5.57E-07
m_tot_norvegicus->tanezumi	2.30E-06	5.34E-11	7.73E-08	5.98E-15	2.66E-07	2.88E-07
m_tot_rattus->norvegicus	2.84E-03	4.66E-08	5.05E-06	2.55E-11	2.84E-03	2.27E-03
m_tot_norvegicus->rattus	2.29E-03	1.91E-08	3.75E-06	1.41E-11	2.26E-03	2.27E-03

Table S4.7b G-phocs results

Summary Statistic	mean	stdev	median	95% HPD lower	95% HPD Upper	effective sample size (ESS)
theta_rattus	1.12E-03	1.27E-05	1.12E-03	1.10E-03	1.14E-03	4747
theta_tanezumi	2.13E-03	2.70E-05	2.13E-03	2.08E-03	2.18E-03	4754
theta_norvegicus	1.60E-03	1.14E-05	1.60E-03	1.58E-03	1.62E-03	6550
theta_rattus/tanezumi	1.48E-02	7.63E-05	1.49E-02	1.47E-02	1.50E-02	6075
theta_rat	1.86E-03	9.48E-05	1.86E-03	1.66E-03	2.03E-03	607
tau_rattus/tanezumi	7.20E-04	9.36E-06	7.20E-04	7.00E-04	7.30E-04	4683
tau_rat	1.15E-02	4.99E-05	1.15E-02	1.14E-02	1.16E-02	755
m_rattus/tanezumi->norvegicus	9.10E+00	3.34E-01	9.10E+00	8.45E+00	9.74E+00	2321
Variance-Mut	4.37E-01	2.57E-03	4.37E-01	4.32E-01	4.42E-01	742
Ne_rattus	9.48E+04	1.07E+03	9.46E+04	9.29E+04	9.63E+04	
Ne_tanezumi	1.80E+05	2.28E+03	1.80E+05	1.76E+05	1.84E+05	
Ne_norvegicus	1.35E+05	9.61E+02	1.35E+05	1.33E+05	1.37E+05	
Ne_rattus_tanezumi	1.25E+06	6.45E+03	1.26E+06	1.24E+06	1.27E+06	
Ne_rat	1.57E+05	8.00E+03	1.57E+05	1.40E+05	1.71E+05	
T_rattus/tanezumi (Mya)	0.122	0.002	0.122	0.118	0.123	
T_rat (Mya)	1.940	0.010	1.940	1.930	1.960	
Total migration rate_rattus/tanezumi->norvegicus	0.098	0.004	0.098	0.090	0.106	

Table S4.8 Sample information for all samples screened

Sample ID	Extract Name	Location	Site	Country	Contextual dating	Processing lab	% endogenous DNA	Included in analysis	Approximate latitude	Approximate longitude
	AJ222	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.87		54.5	-0.9
	AJ224	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.07		54.5	-0.9
	AJ225	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.25		54.5	-0.9
	AJ226	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.35		54.5	-0.9
	AJ227	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.37		54.5	-0.9
	AJ228	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.05		54.5	-0.9
	AJ229	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	1.38		54.5	-0.9
	AJ230	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	3.55		54.5	-0.9
	AJ231	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.05		54.5	-0.9
	AJ232	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.26		54.5	-0.9
KLT001	AJ233	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	61.23	MT/nuclear	54.5	-0.9
	AJ234	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.02		54.5	-0.9
	AJ235	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.13		54.5	-0.9
	AJ236	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.09		54.5	-0.9
	AJ237	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	1.32		54.5	-0.9
	AJ238	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.04		54.5	-0.9
	AJ239	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	7.44		54.5	-0.9
	AJ240	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	8.52		54.5	-0.9
	AJ241	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	0.1		54.5	-0.9
	AJ242	Kilton Castle	Kilton Castle	England, UK	17th century	Oxford	5.75		54.5	-0.9
	AJ296	Monte di Tuda	Monte di Tuda Cave	Corsica, France	15th century CE	Oxford	0.27		42.6	9.4
	AJ297	Monte di Tuda	Monte di Tuda Cave	Corsica, France	15th century CE	Oxford	0.34		42.6	9.4

	AJ298	Monte di Tuda	Monte di Tuda Cave	Corsica, France	15th century CE	Oxford	0.07		42.6	9.4
MDT001	AJ299	Monte di Tuda	Monte di Tuda Cave	Corsica, France	15th century CE	Oxford	9.5	MT	42.6	9.4
MDT002	AJ300	Monte di Tuda	Monte di Tuda Cave	Corsica, France	15th century CE	Oxford	32.63	MT/nuclear	42.6	9.4
	AJ301	Monte di Tuda	Monte di Tuda Cave	Corsica, France	15th century CE	Oxford	0.41		42.6	9.4
SML001	AJ303	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	85.78	MT/nuclear	41.3	9.3
SML002	AJ304	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	83.72	MT/nuclear	41.3	9.3
	AJ305	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	85.59		41.3	9.3
SML003	AJ306	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	82.64	MT	41.3	9.3
	AJ307	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	51.17		41.3	9.3
	AJ308	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	60.89		41.3	9.3
SML004	AJ309	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	89.14	MT/nuclear	41.3	9.3
	AJ310	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	65.48		41.3	9.3
SML005	AJ311	Lavezzi	Santa Maria Chapel	Lavezzi archipelago, Italy	14th century CE	Oxford	88.04	MT/nuclear	41.3	9.3
ZMB001	AJ313	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	32.33	MT/nuclear	37.1	10.8
ZMB002	AJ314	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	39.43	MT/nuclear	37.1	10.8
	AJ315	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	17		37.1	10.8

ZMB003	AJ317	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	66.51	MT/nuclear	37.1	10.8
	AJ319	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	33.91		37.1	10.8
	AJ320	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	29.13		37.1	10.8
	AJ321	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	21.54		37.1	10.8
	AJ322	Zembra	Abri du Casino	Tunisia	4th-6th century CE	Oxford	11.35		37.1	10.8
	AJ359	Tróia	Tróia	Portugal	Late 4th / early 5th century CE	Oxford	1.1		38.5	-8.9
	AJ360	Tróia	Tróia	Portugal	Late 4th / early 5th century CE	Oxford	5.88		38.5	-8.9
	AJ361	Tróia	Tróia	Portugal	Late 4th / early 5th century CE	Oxford	8.65		38.5	-8.9
	AJ363	Karksi Castle	Karksi Castle	Estonia	1266-1290 CE	Oxford	1.49		58.1	25.6
	AJ366	Karksi Castle	Karksi Castle	Estonia	1266-1290 CE	Oxford	0.14		58.1	25.6
	AJ37	Panga Ya saidi		Kenya	7th-10th century CE	Oxford	0.09		-3.7	39.7
	AJ38	Panga Ya saidi		Kenya	7th-10th century CE	Oxford	0.56		-3.7	39.7
	AJ40	Songo Mnara		Tansania	14th-15th century CE	Oxford	0.17		-9	39.6
	AJ41	Chombo		Kenya	8th century CE	Oxford	0.43		-4.1	39.5
	AJ42	Chombo		Kenya	8th century CE	Oxford	0.19		-4.1	39.5
	AJ43	Fort Frederick		Mauritius	late 17th century AD	Oxford	6.11		-20.2	57.5
	AJ44	Fort Frederick		Mauritius	late 17th century AD	Oxford	2.13		-20.2	57.5
	AJ45	ed-Dur		UAE	1st-4th century AD	Oxford	0.11		25.7	55.8
	AJ46	Mbuyuni		Kenya	Unknown	Oxford	0		-4.1	39.7
	AJ48	Paithan		India	Unknown	Oxford	0.01		19.5	75.4
	AJ49	Aqaba		Jordan	End 13th - 15th century CE	Oxford	4.86		29.5	35
	AJ50	Kantharodai		Sri Lanka	unknown	Oxford	0.5		9.8	80
	AJ51	Manthai		Sri Lanka	unknown	Oxford	0.01		9	80
	AJ52	Manthai		Sri Lanka	unknown	Oxford	0		9	80
	AJ53	Shenhour		Egpyt	unknown	Oxford	0.01		25.9	32.8

	AJ54	Kalba		Oman	Multi-period	Oxford	0		25.1	56.3
	AJ55	Kalba		Oman	Multi-period	Oxford	0		25.1	56.3
	AJ461	Deventer	Stadhuiskwartier	Netherlands	1350-1400 CE	Oxford	1.78		52.3	6.2
SNE001	AJ462	Deventer	Stadhuiskwartier	Netherlands	1350-1400 CE	Oxford/Jena	23.21	MT	52.3	6.2
	AJ463	Deventer	Stadhuiskwartier	Netherlands	1350-1425 CE	Oxford	0.26		52.3	6.2
SNE002	AJ464	Deventer	Stadhuiskwartier	Netherlands	1350-1425 CE	Oxford/Jena	30.7	MT/nuclear	52.3	6.2
	AJ465	Deventer	Stadhuiskwartier	Netherlands	1350-1425 CE	Oxford	18.77		52.3	6.2
SNE003	AJ466	Deventer	Stadhuiskwartier	Netherlands	1620-1650 CE	Oxford/Jena	23.16		52.3	6.2
	AJ467	Deventer	Stadhuiskwartier	Netherlands	1620-1650 CE	Oxford	14.86		52.3	6.2
SNE004	AJ468	Deventer	Stadhuiskwartier	Netherlands	1620-1650 CE	Oxford/Jena	42.46	MT/nuclear	52.3	6.2
VOB001	AJ469	Voorburg	Forum Hadriani	Netherlands	170-270 CE	Oxford/Jena	59.05	MT/nuclear	52.1	4.4
VOB002	AJ470	Voorburg	Forum Hadriani	Netherlands	170-270 CE	Oxford/Jena	28.85		52.1	4.4
	AJ471	Voorburg	Forum Hadriani	Netherlands	170-270 CE	Oxford	0.57		52.1	4.4
VOB003	AJ472	Voorburg	Forum Hadriani	Netherlands	170-270 CE	Oxford/Jena	64.08	MT/nuclear	52.1	4.4
PZA001	AJ473	Petronell	Carnuntum Zivilstadt	Austria	4th century CE	Oxford/Jena	59.86	MT/nuclear	48.1	16.9
	AJ474	Petronell	Carnuntum Zivilstadt	Austria	Roman	Oxford	11.9		48.1	16.9
	AJ475	Petronell	Carnuntum Zivilstadt	Austria	Roman	Oxford	33.16		48.1	16.9
	AJ476	Petronell	Carnuntum Zivilstadt	Austria	Last decades of 3rd century CE	Oxford	39.74		48.1	16.9
PZA002	AJ477	Petronell	Carnuntum Zivilstadt	Austria	Last decades of 3rd century CE	Oxford/Jena	53.26	MT/nuclear	48.1	16.9
	AJ478	Petronell	Carnuntum Zivilstadt	Austria	Roman	Oxford	49.84		48.1	16.9
	AJ479	Petronell	Carnuntum Zivilstadt	Austria	Roman	Oxford	34.43		48.1	16.9

	AJ480	Petronell	Carnuntum Zivilstadt	Austria	Last decades of 3rd century CE	Oxford	48.55		48.1	16.9
	AJ481	Petronell	Carnuntum Zivilstadt	Austria	Last decades of 3rd century CE	Oxford	1.34		48.1	16.9
PZA003	AJ482	Petronell	Carnuntum Zivilstadt	Austria	Last decades of 3rd century CE	Oxford/Jena	52.9	MT/nuclear	48.1	16.9
	AJ483	Petronell	Carnuntum Zivilstadt	Austria	Last decades of 3rd century CE	Oxford	16.17		48.1	16.9
	AJ484	Prague Castle	Old Probostry	Czech Republic	10-11th century CE	Oxford	0.81		49.7	13.6
	AJ485	Prague Castle	Old Probostry	Czech Republic	10-11th century CE	Oxford	52.37		49.7	13.6
	AJ486	Prague Castle	Old Probostry	Czech Republic	10-11th century CE	Oxford	26.39		49.7	13.6
PRA001	AJ487	Prague Castle	Old Probostry	Czech Republic	10-11th century CE	Oxford/Jena	69.7	MT/nuclear	49.7	13.6
	AJ488	Prague Castle	Old Probostry	Czech Republic	10-11th century CE	Oxford	65.22		49.7	13.6
	AJ489	Prague Castle	Old Probostry	Czech Republic	10-11th century CE	Oxford	60.05		49.7	13.6
	AJ490	Prague Castle	Old Probostry	Czech Republic	10-11th century CE	Oxford	3.65		49.7	13.6
	AJ491	Prague Castle	Old Probostry	Czech Republic	14-15th century CE	Oxford	12.06		49.7	13.6
	AJ492	Prague Castle	Old Probostry	Czech Republic	14-15th century CE	Oxford	52.29		49.7	13.6
	AJ493	Prague Castle	Old Probostry	Czech Republic	14-15th century CE	Oxford	26.21		49.7	13.6
	AJ494	Prague Castle	Old Probostry	Czech Republic	14-15th century CE	Oxford	1.36		49.7	13.6
PRA002	AJ495	Prague Castle	Old Probostry	Czech Republic	14-15th century CE	Oxford/Jena	66.31	MT/nuclear	49.7	13.6
	RA3	York	Coppergate	England, UK	c. 930/935–c. 955/6 CE	York/Oxford	0.09		54	-1.1
	RA4	York	Coppergate	England, UK	Anglo-Scandinavian	York/Oxford	52.33		54	-1.1
	RA5	York	Coppergate	England, UK	Anglo-Scandinavian	York/Oxford	3.42		54	-1.1
	RA20	York	Coppergate	England, UK	mid-late 800s/early 900s CE	York/Oxford	37		54	-1.1
	RA21	York	Coppergate	England, UK	Anglo-Scandinavian	York/Oxford	15.75		54	-1.1
	RA22	York	Coppergate	England, UK	Anglo-Scandinavian	York/Oxford	2.07		54	-1.1
TRU002	RA6	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford/ Jena	40.31	MT/nuclear	54	-1.1

	RA7	York	Coppergate	England, UK	mid-late 800s/early 900s CE	York/Oxford	0.39		54	-1.1
	RA8	York	Coppergate	England, UK	mid-late 800s/early 900s CE	York/Oxford	0.66		54	-1.1
TRU003	RA9	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford/ Jena	25.37	MT	54	-1.1
	RA10	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford	17.3		54	-1.1
	RA11	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford	4.28		54	-1.1
	RA12	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford	4.75		54	-1.1
	RA13	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford	64.53		54	-1.1
	RA14	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford	12.15		54	-1.1
	RA17	York	Coppergate	England, UK	5th–mid-9th CE	York/Oxford	13.81		54	-1.1
	RA4	York	Coppergate	England, UK	c. 955/6–early/mid-1000s CE	York/Oxford	52.33		54	-1.1
TRU001	RA19	York	Tanner Row	England, UK	Roman (2nd-4th CE)	York/Oxford/ Jena	70.88	MT/nuclear	54	-1.1
MEP001	AJ523	Mértola	Mértola	Portugal	1200-1225 CE	Oxford/Jena	38.92	MT/nuclear	37.6	-7.7
	AJ524	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	4.39		37.6	-7.7
	AJ525	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	14.57		37.6	-7.7
	AJ526	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	6.37		37.6	-7.7
	AJ527	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	7.67		37.6	-7.7
MEP002	AJ528	Mértola	Mértola	Portugal	1200-1225 CE	Oxford/Jena	47.35	MT/nuclear	37.6	-7.7
	AJ529	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	6.89		37.6	-7.7
MEP003	AJ530	Mértola	Mértola	Portugal	1200-1225 CE	Oxford/Jena	38.36	MT/nuclear	37.6	-7.7
	AJ531	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	0.6		37.6	-7.7
	AJ532	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	4.73		37.6	-7.7
	AJ533	Mértola	Mértola	Portugal	1200-1225 CE	Oxford	20.76		37.6	-7.7
ATU001	AJ534	Althiburos	Althiburos	Tunisia	250-400 CE	Oxford/Jena	26.16	MT	33.9	9.5
ATU002	AJ535	Althiburos	Althiburos	Tunisia	250-400 CE	Oxford/Jena	56.2	MT/nuclear	33.9	9.5

	AJ392	Buda Castle	Teleki Palace	Hungary	14th-15th century CE	Oxford	2.95		47.5	19
	AJ388	Buda Castle	Teleki Palace	Hungary	Turkish phase (1541-1699 CE)	Oxford	44.03		47.5	19
BUD002	AJ390	Buda Castle	Teleki Palace	Hungary	14th-15th century CE	Oxford/Jena	41.86	MT	47.5	19
BUD003	AJ391	Buda Castle	Teleki Palace	Hungary	14th-15th century CE	Oxford/Jena	59.87	MT/nuclear	47.5	19
BUD001	AJ389	Buda Castle	Teleki Palace	Hungary	Turkish phase (1541-1699 CE)	Oxford/Jena	54.92	MT/nuclear	47.5	19
BUD004	AJ393	Buda Castle	Teleki Palace	Hungary	Turkish phase (1541-1699 CE)	Oxford/Jena	50.38	MT/nuclear	47.5	19
	AJ394	Gatehampton Villa	Gatehampton Villa	England, UK	Roman	Oxford	10.06		51.5	-1.1
GAU001	AJ395	Gatehampton Villa	Gatehampton Villa	England, UK	Roman	Oxford/Jena	36.11	MT/nuclear	51.5	-1.1
	AJ396	Gatehampton Villa	Gatehampton Villa	England, UK	Roman	Oxford	32.14		51.5	-1.1
	AJ397	Gatehampton Villa	Gatehampton Villa	England, UK	Roman	Oxford	3.49		51.5	-1.1
	AJ398	Gatehampton Villa	Gatehampton Villa	England, UK	Roman	Oxford	9.28		51.5	-1.1
GAU002	AJ399	Gatehampton Villa	Gatehampton Villa	England, UK	Roman	Oxford/Jena	34.91	MT/nuclear	51.5	-1.1
SMI001	AJ400	São Miguel Island	Vila Franca do Campo	Azores, Portugal	pre 1522	Oxford/Jena	8.98	MT	37.7	-25.4
	AJ401	São Miguel Island	Vila Franca do Campo	Azores, Portugal	pre 1522	Oxford	2.09		37.7	-25.4
	AJ402	São Miguel Island	Vila Franca do Campo	Azores, Portugal	pre 1522	Oxford	9.56		37.7	-25.4
SMI002	AJ403	São Miguel Island	Vila Franca do Campo	Azores, Portugal	pre 1522	Oxford/Jena	25.71		37.7	-25.4

KAF001	AJ404	Kastelholm	Kastelholm	Åland, Finland	1400-1500 CE	Oxford/Jena	59.79	MT/nuclear	60.2	20.1
	AJ405	Kastelholm	Kastelholm	Åland, Finland	1400-1450 CE	Oxford	20.85		60.2	20.1
	AJ406	Kastelholm	Kastelholm	Åland, Finland	1400-1500 CE	Oxford	41.83		60.2	20.1
	AJ407	Kastelholm	Kastelholm	Åland, Finland	1400-1500 CE	Oxford	47.07		60.2	20.1
	AJ408	Kastelholm	Kastelholm	Åland, Finland	1400-1500 CE	Oxford	48.44		60.2	20.1
KAF002	AJ409	Kastelholm	Kastelholm	Åland, Finland	15th century CE	Oxford/Jena	56.04	MT/nuclear	60.2	20.1
	AJ410	Rirha	Rirha	Morocco	1st C BCE	Oxford	11.65		33.2	-8.5
	AJ411	Rirha	Rirha	Morocco	1st C BCE	Oxford	16.28		33.2	-8.5
	AJ412	Rirha	Rirha	Morocco	1st C BCE	Oxford	0.61		33.2	-8.5
	AJ413	Rirha	Rirha	Morocco	1st C BCE	Oxford	0.08		33.2	-8.5
	AJ414	Rirha	Rirha	Morocco	1st C BCE	Oxford	0.32		33.2	-8.5
	AJ415	Chersonesos	Chersonesos	Ukraine	1st BCE to 1st century CE	Oxford	2.52		44.6	33.5
	AJ416	Chersonesos	Chersonesos	Ukraine	1st BCE to 1st century CE	Oxford	2.98		44.6	33.5
	AJ417	Chersonesos	Chersonesos	Ukraine	1st BCE to 1st century CE	Oxford	1.59		44.6	33.5
	AJ418	Chersonesos	Chersonesos	Ukraine	1st BCE to 1st century CE	Oxford	1.05		44.6	33.5
Car_1	Car_1	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	21.32		43	21.7
Car_2	Car_2	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	25.97	MT	43	21.7
Car_3	Car_3	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	0.19		43	21.7
Car_4	Car_4	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	50.48	MT/nuclear	43	21.7
Car_5	Car_5	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	52.08	MT/nuclear	43	21.7
Car_6	Car_6	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	27.6	MT	43	21.7
Car_7	Car_7	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	58.1	MT/nuclear	43	21.7
Car_8	Car_8	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	5.34		43	21.7
Car_9	Car_9	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	52.76	MT	43	21.7

Ass_1	Ass_1	Assos	Assos	Turkey	End of the 7th century CE	Jena	83.13	MT/nuclear	39.4	26.9
Ass_2	Ass_2	Assos	Assos	Turkey	End of the 7th century CE	Jena	16.43	MT/nuclear	39.4	26.9
KR150754_2	KR150754_2	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	25.93		43	21.7
Nurn_1	Nurn_1	Nürnberg Castle	Nürnberg Castle	Germany	2nd half of the 12th century CE	Jena	16.56		49.5	11.1
Sulz_3	Sulz_3	Castle Sulzbach	Castle Sulzbach	Germany	8th to early 10th century CE	Jena	79.1	MT/nuclear	49.5	11.7
Sulz_4	Sulz_4	Castle Sulzbach	Castle Sulzbach	Germany	8th to early 10th century CE	Jena	38.34		49.5	11.7
Sulz_5	Sulz_5	Castle Sulzbach	Castle Sulzbach	Germany	8th to early 10th century CE	Jena	43.5		49.5	11.7
Sulz_6	Sulz_6	Castle Sulzbach	Castle Sulzbach	Germany	8th to early 10th century CE	Jena	55.59		49.5	11.7
Sulz_7	Sulz_7	Castle Sulzbach	Castle Sulzbach	Germany	8th to early 10th century CE	Jena	71.37	MT/nuclear	49.5	11.7
KR150749	KR150749	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	61.63	MT	43	21.7
KR150750	KR150750	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	84.75	MT	43	21.7
KR150751	KR150751	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	24.14	MT	43	21.7
KR150752	KR150752	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	66.69	MT	43	21.7
KR150753	KR150753	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	25.35	MT	43	21.7

KR150754	KR150754	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	22.54	MT	43	21.7
KR150755	KR150755	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	28.15	MT	43	21.7
KR150756	KR150756	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	3.73	MT	43	21.7
KR150757	KR150757	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	43	MT	43	21.7
KR150758	KR150758	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	18.06	MT	43	21.7
KR150759	KR150759	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	7.22	MT	43	21.7
KR150760	KR150760	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	7.61	MT	43	21.7
KR150761	KR150761	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	42.83	MT	43	21.7
KR150762	KR150762	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	24.84	MT	43	21.7
KR150763	KR150763	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	5.08	MT	43	21.7
KR150764	KR150764	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	7.89	MT	43	21.7
KR150765	KR150765	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	75.84	MT	43	21.7
KR150766	KR150766	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	50.45	MT	43	21.7
KR150767	KR150767	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	22.85	MT	43	21.7

KR150768	KR150768	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	57.31	MT	43	21.7
KR150769	KR150769	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	71.84	MT	43	21.7
KR150770	KR150770	Caričin grad	Caričin grad	Serbia	535-615 CE	Jena	79.27	MT/nuclear	43	21.7

Table S4.9 Information on the mitochondrial genomes generated in this study

Sample ID	Location	Site	Length	Missing	Coverage	Haplotype name	Species
Ass1	Assos	Assos	16305	1	54.1	Ass1	rattus
Ass2	Assos	Assos	16306	1	45.8	Ass2	rattus
ATU001	Althiburos	Althiburos	16305	1771	5.9	ATU001	rattus
ATU002	Althiburos	Althiburos	16306	1	76.6	ATU002	rattus
BUD001	Buda Castle	Teleki Palace	16306	1	77.2	BUD001	rattus
BUD002	Buda Castle	Teleki Palace	16305	181	10.3	BUD002	rattus
BUD003	Buda Castle	Teleki Palace	16305	1	59.2	BUD003	rattus
BUD004	Buda Castle	Teleki Palace	16305	1	41.1	BUD004	rattus
Car_2	Caričin Grad	Caričin Grad	16305	636	7.4	KR150770	rattus
Car_4	Caričin Grad	Caričin Grad	16306	1	275.5	Car_4	rattus
Car_5	Caričin Grad	Caričin Grad	16307	1	234.4	Car_5	rattus
Car_6	Caričin Grad	Caričin Grad	16307	1482	6.2	Car_4	rattus
Car_7	Caričin Grad	Caričin Grad	16307	1	228.5	Car_5	rattus
Car_9	Caričin Grad	Caričin Grad	16307	269	10.0	Car_5	rattus
CP-5999			16310	1	962.6	CP-5999	rattus
ERS215789			16313	2	269.2	ERS215789	norvegicus
ERS215791			16313	1	331.2	ERS215791	norvegicus
GAU001	Gatehampton Villa	Gatehampton Villa	16305	1	94.3	GAU001	rattus
GAU002	Gatehampton Villa	Gatehampton Villa	16305	1	22.3	GAU001	rattus
HXM4			16305	0	409.4	HXM4	tanezumi
KAF001	Kastelholm	Kastelholm	16308	1	66.6	KAF001	rattus
KAF002	Kastelholm	Kastelholm	16308	1	30.9	KAF002	rattus
KLT001	Kilton Castle	Kilton Castle	16305	1	23.9	KLT001	rattus
KR150749	Caričin Grad	Caričin Grad	16305	62	20.2	KR150749	rattus

KR150750	Caričin Grad	Caričin Grad	16307	3302	6.4	KR150765	rattus
KR150751	Caričin Grad	Caričin Grad	16307	1712	9.6	KR150751	rattus
KR150752	Caričin Grad	Caričin Grad	16307	1	60.5	KR150752	rattus
KR150753	Caričin Grad	Caričin Grad	16307	1604	8.7	Car_4	rattus
KR150754	Caričin Grad	Caričin Grad	16306	2	44.1	Car_4	rattus
KR150755	Caričin Grad	Caričin Grad	16308	14	25.5	KR150755	rattus
KR150756	Caričin Grad	Caričin Grad	16307	40	20.1	KR150756	rattus
KR150757	Caričin Grad	Caričin Grad	16307	127	25.2	Car_4	rattus
KR150758	Caričin Grad	Caričin Grad	16307	572	13.3	KR150758	rattus
KR150759	Caričin Grad	Caričin Grad	16307	66	33.5	Car_4	rattus
KR150760	Caričin Grad	Caričin Grad	16307	758	11.7	Car_4	rattus
KR150761	Caričin Grad	Caričin Grad	16307	41	39.0	Car_4	rattus
KR150762	Caričin Grad	Caričin Grad	16307	260	26.6	Car_5	rattus
KR150763	Caričin Grad	Caričin Grad	16307	254	16.7	Car_4	rattus
KR150764	Caričin Grad	Caričin Grad	16305	708	13.5	KR150770	rattus
KR150765	Caričin Grad	Caričin Grad	16307	55	31.2	KR150765	rattus
KR150766	Caričin Grad	Caričin Grad	16307	405	21.2	Car_4	rattus
KR150767	Caričin Grad	Caričin Grad	16305	251	17.8	KR150770	rattus
KR150768	Caričin Grad	Caričin Grad	16308	4	32.8	Car_4	rattus
KR150769	Caričin Grad	Caričin Grad	16307	12	33.0	Car_4	rattus
KR150770	Caričin Grad	Caričin Grad	16305	1	367.6	KR150770	rattus
MDT001	Monte di Tuda	Monte di Tuda Cave	16306	2577	4.9	MDT001	rattus
MDT002	Monte di Tuda	Monte di Tuda Cave	16305	1	152.7	MDT002	rattus
MEP001	Mértola	Mértola	16305	1	58.4	MEP001	rattus
MEP002	Mértola	Mértola	16305	1	28.1	MEP001	rattus
MEP003	Mértola	Mértola	16305	1	74.3	MEP003	rattus

PRA001	Prague Castle	Old Probostry	16305	1	36.5	Sulz7	rattus
PRA002	Prague Castle	Old Probostry	16305	5	14.0	Sulz7	rattus
PZA001	Petronell	Carnuntum Zivilstadt	16305	31	16.0	PZA003	rattus
PZA002	Petronell	Carnuntum Zivilstadt	16305	1	29.3	PZA003	rattus
PZA003	Petronell	Carnuntum Zivilstadt	16305	1	84.0	PZA003	rattus
SMI001	São Miguel Island	Vila Franca do Campo	16305	2	20.1	SMI001	rattus
SML001	Lavezzi	Santa Maria Chapel	16305	1	62.5	SML002	rattus
SML002	Lavezzi	Santa Maria Chapel	16305	1	110.3	SML002	rattus
SML003	Lavezzi	Santa Maria Chapel	16305	288	11.4	SML003	rattus
SML004	Lavezzi	Santa Maria Chapel	16305	1	75.1	SML005	rattus
SML005	Lavezzi	Santa Maria Chapel	16305	1	91.1	SML005	rattus
SNE001	Deventer	Stadhuiskwartier	16305	3215	4.6	SNE001	rattus
SNE002	Deventer	Stadhuiskwartier	16305	6	14.6	SNE002	rattus
SNE004	Deventer	Stadhuiskwartier	16305	2	16.5	SNE004	rattus
Sulz3	Castle Sulzbach	Castle Sulzbach	16306	1	89.6	Sulz7	rattus
Sulz7	Castle Sulzbach	Castle Sulzbach	16306	1	111.9	Sulz7	rattus
TRU001	York	Tanner Row	16305	1	19.2	TRU001	rattus
TRU002	York	Tanner Row	16305	33	12.0	TRU001	rattus
TRU003	York	Tanner Row	16305	5518	3.5	PZA003	rattus
VOB001	Voorburg	Forum Hadriani	16305	1	21.5	VOB001	rattus
VOB003	Voorburg	Forum Hadriani	16305	239	9.2	PZA003	rattus
ZMB001	Zembra	Abri du Casino	16305	1	130.8	ZMB001	rattus
ZMB002	Zembra	Abri du Casino	16305	1	133.6	ZMB002	rattus
ZMB003	Zembra	Abri du Casino	16306	1	80.4	ZMB003	rattus

Table S4.10 Previously unpublished cytochrome b sequences made available for this study

Sample	Country	Location	Lineage	Provider
R042	Afghanistan	Jalalabad	III	Field Museum Chicago
R230	Andaman	BrotherIsland	I	British National History Museum
R191	Angola	Benguela Lobito Bay	I	American Museum of Natural History
R134	Angola	Huambo Luimbale Mt Verdun	I	American Museum of Natural History
R137	Angola	Huambo Luimbale Mt Verdun	I	American Museum of Natural History
R133	Angola	Huambo Luimbale Mt Verdun	I	American Museum of Natural History
R170	Australia	Cocos Keeling New Selma Island	IV	American Museum of Natural History
R116	Myanmar	Gova	II	American Museum of Natural History
R099	Myanmar	Mergus Ban Sadein	II	American Museum of Natural History
R098	Myanmar	Mergus Ban Sadein	II	American Museum of Natural History
R119	Myanmar	Tawmaw	II	American Museum of Natural History
R069	Ceylon	Dehiwala	I	Field Museum Chicago
R071	Ceylon	Gonapola	I	Field Museum Chicago
R131	China		II	American Museum of Natural History
R084	China	Sezchuan KaoKu	II	Field Museum Chicago
R140	China	Szechuan Chengtu	II	American Museum of Natural History
R141	China	Szechuan Chengtu	II	American Museum of Natural History
R142	China	Szechuan Chengtu	II	American Museum of Natural History
R143	China	Szechuan Tsao Wenchwan	II	American Museum of Natural History
R113	China	Szechuan Wanksien Yen Ching Kao	II	American Museum of Natural History
R082	China	Yunnan	II	Field Museum Chicago
R196	Congo	Dolisie	I	American Museum of Natural History
R270	Egypt		I	American Museum of Natural History
R068	Egypt	Aswan	I	Field Museum Chicago

R021	Egypt	Aswan	I	Field Museum Chicago
R067	Egypt	Cairo	I	Field Museum Chicago
R025	Egypt	Giza	I	Field Museum Chicago
R265	Ethiopia	AddisAbbaba	I	Field Museum Chicago
R066	Ethiopia	AddisAbbaba	I	Field Museum Chicago
R077	Zimbabwe	Gatooma	I	Field Museum Chicago
R282	India		II	American Museum of Natural History
R279	India		II	American Museum of Natural History
R280	India		II	American Museum of Natural History
R059	India	Alapalli	I	Field Museum Chicago
R061	India	ManipurAssam	II	Field Museum Chicago
R008	India	ManipurAssam	II	Field Museum Chicago
R045	India	MangpuBengal	II	Field Museum Chicago
R038	India	Benhope	I	Field Museum Chicago
R003	India	MadrasNilgiriHillsKalhatti	I	American Museum of Natural History
R103	India	MadrasNilgiriHillsKalhatti	I	American Museum of Natural History
R104	India	MadrasNilgiriHillsKalhatti	I	American Museum of Natural History
R202	India	MysoreBiligiriranganHillsHonnametti	I	American Museum of Natural History
R203	India	MysoreBiligiriranganHillsHonnametti	I	American Museum of Natural History
R108	India	SonaripurKheriForest	III	American Museum of Natural History
R086	India	TamilNaduAnaimalaiHills	I	American Museum of Natural History
R123	Indonesia	BaliNusaPenida	IV	American Museum of Natural History
R120	Indonesia	BaliSelatTseh	II	American Museum of Natural History
R180	Indonesia	BorneoKalimantanTimurBoelongean	IV	American Museum of Natural History
R122	Indonesia	JavaCheribon	IV	American Museum of Natural History
R126	Indonesia	JavaCheribon	IV	American Museum of Natural History
R127	Indonesia	JavaCheribon	IV	American Museum of Natural History
R183	Indonesia	SulawesiRoeroekan	IV	American Museum of Natural History

R184	Indonesia	SulawesiRoeroekan	IV	American Museum of Natural History
R181	Iran	DarKalehAstarabadMazandaran	I	American Museum of Natural History
R182	Iran	DarKalehAstarabadMazandaran	I	American Museum of Natural History
R028	Iran	Gorgan	I	Field Museum Chicago
R204	Iran	Gorgan	I	Field Museum Chicago
R285	Kenya		I	American Museum of Natural History
R287	Kenya		I	American Museum of Natural History
R032	Kenya	Njoro	I	Field Museum Chicago
R031	Kenya	Njoro	I	Field Museum Chicago
R012	Laos	Phong Saly	II	Field Museum Chicago
R215	Lebanon	Akkar Halba	I	Field Museum Chicago
HE006	Madagascar		I	Field Museum Chicago
HE009	Madagascar		I	Field Museum Chicago
HE007	Madagascar		I	Field Museum Chicago
HE025	Madagascar		I	Field Museum Chicago
HE026	Madagascar		I	Field Museum Chicago
HE028	Madagascar		I	Field Museum Chicago
HE008	Madagascar		I	Field Museum Chicago
HE011	Madagascar		I	Field Museum Chicago
HE014	Madagascar		I	Field Museum Chicago
HE022	Madagascar		I	Field Museum Chicago
HE010	Madagascar		I	Field Museum Chicago
HE013	Madagascar		I	Field Museum Chicago
HE027	Madagascar		I	Field Museum Chicago
HE020	Madagascar		I	Field Museum Chicago
HE021	Madagascar		I	Field Museum Chicago
HE024	Madagascar		I	Field Museum Chicago
R006	Madagascar	Ambantondrazaka	I	Field Museum Chicago

R263	Madagascar	Ambantondrazaka	I	Field Museum Chicago
R051	Madagascar	Ambohimahavelona	I	Field Museum Chicago
R171	Madagascar	Toamasina Maroantsetra	I	American Museum of Natural History
R172	Madagascar	Mahajanga Antsalova Tsiandro	I	American Museum of Natural History
R096	Malawi	Kasungu	I	American Museum of Natural History
R097	Malawi	Kasungu	I	American Museum of Natural History
R187	Malawi	KotaKota	I	American Museum of Natural History
R188	Malawi	Zomba	I	American Museum of Natural History
R237	Maldives	Addu Atoll Gan Island	I	British National History Museum
R236	Maldives	Addu Atoll Gan Island	I	British National History Museum
R232	MaldivesMale	Atoll	II	British National History Museum
R233	MaldivesMale	Atoll	II	British National History Museum
R235	MaldivesMululay	Island	II	British National History Museum
R246	Mozambique	Tete	I	British National History Museum
R063	Nepal		III	Field Museum Chicago
R034	Saudi Arabia	Halat Mahish	I	Field Museum Chicago
R079	Siam	KamPangThailand	II	Field Museum Chicago
R076	Siam	KamPangThailand	II	Field Museum Chicago
R173	Sri Lanka		I	American Museum of Natural History
R106	Sri Lanka	CentralProvinceHakgala	I	American Museum of Natural History
R102	Sri Lanka	CentralProvinceHortonPlains	I	American Museum of Natural History
R101	Sri Lanka	CentralProvinceHortonPlains	I	American Museum of Natural History
R155	Sri Lanka	SabaragamuwaEmbilipitiya	I	American Museum of Natural History
R174	Sri Lanka	UvaWelimada	I	American Museum of Natural History
R036	Tanzania	ArushaTengeru	I	Field Museum Chicago
R075	Tanzania	ArushaTengeru	I	Field Museum Chicago
R192	Tanzania	Kilosa	I	American Museum of Natural History
R193	Tanzania	Kilosa	I	American Museum of Natural History

R129	Tanzania	Kilosa	I	American Museum of Natural History
R004	Tanzania	Kilosa	I	American Museum of Natural History
HE001	Tanzania	Mafia	I	Field Museum Chicago
HE002	Tanzania	Mafia	I	Field Museum Chicago
HE018	Tanzania	Mafia	I	Field Museum Chicago
HE019	Tanzania	Mafia	I	Field Museum Chicago
HE003	Tanzania	Pemba	I	Field Museum Chicago
HE004	Tanzania	Pemba	I	Field Museum Chicago
HE023	Tanzania	Pemba	I	Field Museum Chicago
HE015	Tanzania	Pemba	I	Field Museum Chicago
HE016	Tanzania	Pemba	I	Field Museum Chicago
R093	Tanzania	Rungwe	I	American Museum of Natural History
R189	Tanzania	SingidaManyoni	I	American Museum of Natural History
HE005	Tanzania	Zanzibar	I	Field Museum Chicago
R080	Tanzania	Tanga	I	Field Museum Chicago
R057	Tanzania	Tanganyika Loljoro	I	Field Museum Chicago
R049	Turkey	AdanaHaruniye	I	Field Museum Chicago
R197	UAE	YemenMukala	I	American Museum of Natural History
R198	UAE	YemenMukala	I	American Museum of Natural History
R136	Uganda	Kampala	I	American Museum of Natural History
R072	Vietnam	Tonkin	II	Field Museum Chicago
R208	Vietnam	Tonkin	II	Field Museum Chicago
R095	Zambia	LakeChiyauaBongweuluLulingila	I	American Museum of Natural History
R094	Zambia	LakeChiyauaBongweuluLulingila	I	American Museum of Natural History

Table S4.11 All cytochrome b sequences included in analysis

Sample name	Haplotype	Lineage	Haplogroup tree	Ancient or Modern	Date	Location	Region	Reference
LN554986.1	Hap_C1	I	A	Modern	Modern	Italy	Europe	Colangelo et al. 2015
LN554987.1	Hap_C2	I	A	Modern	Modern	Italy	Europe	Colangelo et al. 2015
LN554988.1	Hap_C3	I	A	Modern	Modern	Italy	Europe	Colangelo et al. 2015
LN554989.1	Hap_C4	I	A?	Modern	Modern	Italy	Europe	Colangelo et al. 2015
DQ191488	126	IV		Modern	Modern	Philippines		Jansa et al. 2006
JN675622	126	IV		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675623	126	IV		Modern	Modern	Philippines		Aplin et. al. 2011
R124	126	IV		Modern	1929	Indonesia		Trinks/Eager
R125	126	IV		Modern	1929	Indonesia		Trinks/Eager
JN675603	28	IV		Modern	Modern	Sri Lanka		Aplin et. al. 2011
JN675616	115	IV		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675619	118	IV		Modern	Modern	Indonesia		Aplin et. al. 2011
R184	118	IV		Modern	1978	Indonesia		Trinks/Eager
JN675620	118	IV		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675621	124	IV		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675624	128	IV		Modern	Modern	Philippines		Aplin et. al. 2011
JN675605	65	IV		Modern	Modern	Cambodia		Aplin et. al. 2011
JN675611	74	IV		Modern	Modern	Vietnam		Aplin et. al. 2011
JN675607	68	IV		Modern	Modern	Cambodia		Aplin et. al. 2011
JN675608	69	IV		Modern	Modern	Cambodia		Aplin et. al. 2011
JN675609	70	IV		Modern	Modern	Cambodia		Aplin et. al. 2011

JN675617	116	IV		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675618	117	IV		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675613	82	IV		Modern	Modern	Vietnam		Aplin et. al. 2011
JN675606	67	IV		Modern	Modern	Cambodia		Aplin et. al. 2011
JN675610	73	IV		Modern	Modern	Cambodia		Aplin et. al. 2011
JN675612	75	IV		Modern	Modern	Vietnam		Aplin et. al. 2011
R180	75	IV		Modern	1931	Indonesia		Trinks/Eager
JN675614	83	IV		Modern	Modern	Vietnam		Aplin et. al. 2011
JN675604	64	IV		Modern	Modern	Laos		Aplin et. al. 2011
JN675625	58	V		Modern	Modern	Laos		Aplin et. al. 2011
JN675628	48	V		Modern	Modern	Thailand		Aplin et. al. 2011
JN675626	59	V		Modern	Modern	Laos		Aplin et. al. 2011
JN675627	38	V		Modern	Modern	Thailand		Aplin et. al. 2011
JN675516	121	VI		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675515	110	VI		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675599	31	III		Modern	Modern	Nepal		Aplin et. al. 2011
JN675600	14	III		Modern	Modern	Pakistan		Aplin et. al. 2011
JN675601	15	III		Modern	Modern	Pakistan		Aplin et. al. 2011
DQ439819	5	II		Modern	Modern	South Africa		Bastos et al. 2011
JN675554	33	II		Modern	Modern	Bangladesh		Aplin et. al. 2011
JN675562	49	II		Modern	Modern	Thailand		Aplin et. al. 2011
JN675570	61	II		Modern	Modern	Laos		Aplin et. al. 2011
R012	61	II		Modern	1929	Laos		Trinks/Eager
JN675571	62	II		Modern	Modern	Laos		Aplin et. al. 2011
JN675558	37	II		Modern	Modern	Myanmar		Aplin et. al. 2011
JN675566	54	II		Modern	Modern	Laos		Aplin et. al. 2011
JN675577	101	II		Modern	Modern	China		Aplin et. al. 2011
R143	101	II		Modern	1956	China		Trinks/Eager

JN675560	40	II		Modern	Modern	Thailand		Aplin et. al. 2011
JN675563	51	II		Modern	Modern	Laos		Aplin et. al. 2011
JN675568	56	II		Modern	Modern	Laos		Aplin et. al. 2011
JN675569	57	II		Modern	Modern	Laos		Aplin et. al. 2011
JN675565	53	II		Modern	Modern	Laos		Aplin et. al. 2011
JN675561	41	II		Modern	Modern	Thailand		Aplin et. al. 2011
JN675564	52	II		Modern	Modern	Laos		Aplin et. al. 2011
JN675575	98	II		Modern	Modern	China		Aplin et. al. 2011
JN675555	34	II		Modern	Modern	Bangladesh		Aplin et. al. 2011
JN675556	35	II		Modern	Modern	Myanmar		Aplin et. al. 2011
JN675572	87	II		Modern	Modern	Vietnam		Aplin et. al. 2011
JN675573	90	II		Modern	Modern	Vietnam		Aplin et. al. 2011
JN675590	135	II		Modern	Modern	Taiwan		Aplin et. al. 2011
JN675594	135	II		Modern	Modern	Japan		Aplin et. al. 2011
JN675596	135	II		Modern	Modern	USA		Aplin et. al. 2011
R131	135	II		Modern	?	China		Trinks/Eager
R140	135	II		Modern	1930	China		Trinks/Eager
R141	135	II		Modern	1930	China		Trinks/Eager
JN675588	133	II		Modern	Modern	Taiwan		Aplin et. al. 2011
JN675593	139	II		Modern	Modern	Japan		Aplin et. al. 2011
JN675578	104	II		Modern	Modern	China		Aplin et. al. 2011
JN675589	134	II		Modern	Modern	Taiwan		Aplin et. al. 2011
JN675595	142	II		Modern	Modern	Papua New Guinea		Aplin et. al. 2011
JN675559	39	II		Modern	Modern	Thailand		Aplin et. al. 2011
JN675567	55	II		Modern	Modern	Laos		Aplin et. al. 2011
R072	55	II		Modern	1929	Vietnam		Trinks/Eager
JN675574	55	II		Modern	Modern	Vietnam		Aplin et. al. 2011
JN675557	36	II		Modern	Modern	Myanmar		Aplin et. al. 2011

JN675583	113	II		Modern	Modern	Indonesia		Aplin et. al. 2011
JN675584	114	II		Modern	Modern	Indonesia		Aplin et. al. 2011
R120	114	II		Modern	1932	Indonesia		Trinks/Eager
JN675598	114	II		Modern	Modern	USA		Aplin et. al. 2011
JN675586	129	II		Modern	Modern	Philippines		Aplin et. al. 2011
JN675591	137	II		Modern	Modern	Taiwan		Aplin et. al. 2011
JN675587	130	II		Modern	Modern	Philippines		Aplin et. al. 2011
JN675597	153	II		Modern	Modern	USA		Aplin et. al. 2011
JN675585	127	II		Modern	Modern	Philippines		Aplin et. al. 2011
DQ439830	6	I	B	Modern	Modern	South Africa	Southern Central Africa	Bastos et al. 2011
HE027	6	I	B	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
R136	6	I	B	Modern	1935	Uganda	East Africa	Trinks/Eager
HE018	6	I	B	Modern	modern	Tanzania	East Africa	Trinks/Eager
HE019	6	I	B	Modern	modern	Tanzania	East Africa	Trinks/Eager
R036	6	I	B	Modern	1956	Tanzania	East Africa	Trinks/Eager
R057	6	I	B	Modern	1956	Tanzania	East Africa	Trinks/Eager
DQ439833	7	I	A	Modern	Modern	South Africa	Southern Central Africa	DQ439833
JN675536	7	I	A	Modern	Modern	Australia	Oceania	Aplin et. al. 2011
JN675519	7	I	A	Modern	Modern	Guinea	West Africa	Aplin et. al. 2011
JN675543	7	I	A	Modern	Modern	USA	Americas	Aplin et. al. 2011
JN675547	7	I	A	Modern	Modern	Venezuela	Americas	Aplin et. al. 2011
R134	7	I	A	Modern	1922	Angola	Southern Central Africa	Trinks/Eager
R133	7	I	A	Modern	1922	Angola	Southern Central Africa	Trinks/Eager
R196	7	I	A	Modern	?	Democratic Republic of the Congo	Southern Central Africa	Trinks/Eager
R197	7	I	A	Modern	1979	UAE	Near East	Trinks/Eager
R198	7	I	A	Modern	1979	UAE	Near East	Trinks/Eager
R067	7	I	A	Modern	1961	Egypt	Near East	Trinks/Eager

R028	7	I	A	Modern	1962	Iran	Near East	Trinks/Eager
R204	7	I	A	Modern	1962	Iran	Near East	Trinks/Eager
R181	7	I	A	Modern	1934	Iran	Near East	Trinks/Eager
NC_12374	7	I	A	Modern	Modern	New Zealand	Oceania	Robins et al. 2008
Ass1	7	I	A	Ancient	6th century CE	Assos, Turkey	Ancient	this study
Ass2	7	I	A	Ancient	6th century CE	Assos, Turkey	Ancient	this study
ATU001.A01	7	I	A	Ancient	250-400 CE	Althiburos, Tunisia	Ancient	this study
ATU002.A01	7	I	A	Ancient	250-400 CE	Althiburos, Tunisia	Ancient	this study
BUD001.A01	7	I	A	Ancient	16-17th century CE	Budapest, Hungary	Ancient	this study
BUD003.A01	7	I	A	Ancient	14-15th century CE	Budapest, Hungary	Ancient	this study
BUD004.A01	7	I	A	Ancient	16-17th century CE	Budapest, Hungary	Ancient	this study
GAU001.A01	7	I	A	Ancient	Roman	Gatehampton, England	Ancient	this study
GAU002.A01	7	I	A	Ancient	Roman	Gatehampton, England	Ancient	this study
TRU001.A01	7	I	A	Ancient	Roman or Viking	Tanner Row, York, England	Ancient	this study
TRU002.A01	7	I	A	Ancient	Roman	Tanner Row, York, England	Ancient	this study
TRU003.A01	7	I	A	Ancient	Roman	Tanner Row, York, England	Ancient	this study
KAF001	7	I	A	Ancient	1400-1500 CE	Kastelholm, Aland, Finland	Ancient	this study
KAF002	7	I	A	Ancient	c.1400 CE	Kastelholm, Aland, Finland	Ancient	this study
KR150770	7	I	A	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150764	7	I	A	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150767	7	I	A	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
PRA001	7	I	A	Ancient	14th century CE	Prazsky Hrad, Czech Republic	Ancient	this study
PRA002	7	I	A	Ancient	13-14th century CE	Prazsky Hrad, Czech Republic	Ancient	this study
PZA001	7	I	A	Ancient	4th century CE	Petronell, Zivilstadt, Austria	Ancient	this study
PZA002	7	I	A	Ancient	Last decades of 3rd century CE	Petronell, Zivilstadt, Austria	Ancient	this study
PZA003	7	I	A	Ancient	Last decades of 3rd century CE	Petronell, Zivilstadt, Austria	Ancient	this study

Car_2	7	I	A	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
Sulz7	7	I	A	Ancient	middle ages	Castle Sulzbach, Germany	Ancient	this study
Sulz3	7	I	A	Ancient	middle ages	Castle Sulzbach, Germany	Ancient	this study
MEP001.A01	7	I	A	Ancient	12th-13th century CE	Mertola, Portugal	Ancient	this study
MEP002.A01	7	I	A	Ancient	12th-13th century CE	Mertola, Portugal	Ancient	this study
MEP003.A01	7	I	A	Ancient	12th-13th century CE	Mertola, Portugal	Ancient	this study
SNE002.A01	7	I	A	Ancient	1350-1425	Deventer-Stadhuiskwartier, Neatherlands	Ancient	this study
VOB001.A01	7	I	A	Ancient	Roman	Voorburg – Forum Hadriani, Neatherlands	Ancient	this study
VOB003	7	I	A	Ancient	Roman	Voorburg – Forum Hadriani, Neatherlands	Ancient	this study
MDT001	7	I	A	Ancient	15th century CE	Monte di Tuda, Corsica, France	Ancient	this study
DQ439834	8	I	C	Modern	Modern	South Africa	Southern Central Africa	Aplin et. al. 2011
JN675517	2	I	A	Modern	Modern	France	Europe	Aplin et. al. 2011
SML005.A01	2	I	A	Ancient	14th century CE	Santa maria, Lavezzi, Lavezzi archipelago	Ancient	this study
SML002.A01	2	I	A	Ancient	14th century CE	Santa maria, Lavezzi, Lavezzi archipelago	Ancient	this study
SML001	2	I	A	Ancient	14th century CE	Santa maria, Lavezzi, Lavezzi archipelago	Ancient	this study
SML004	2	I	A	Ancient	14th century CE	Santa maria, Lavezzi, Lavezzi archipelago	Ancient	this study
JN675518	3	I	A	Modern	Modern	Senegal	Western Africa	Aplin et. al. 2011
JN675534	141	I	A	Modern	Modern	Japan	East Asia	Aplin et. al. 2011
R182	141	I	A	Modern	1934	Iran	Near East	Trinks/Eager
JN675541	149	I	A	Modern	Modern	USA	Americas	Aplin et. al. 2011
JN675546	157	I	A	Modern	Modern	Brazil	Americas	Aplin et. al. 2011
JN675549	160	I	A	Modern	Modern	Guyana	Americas	Aplin et. al. 2011
JN675542	150	I	A	Modern	Modern	USA	Americas	Aplin et. al. 2011
JN675544	150	I	A	Modern	Modern	USA	Americas	Aplin et. al. 2011
JN675545	156	I	A	Modern	Modern	USA	Americas	Aplin et. al. 2011
SMI001.A01	156	I	A	Ancient	1522	Vila Franca do Campo, Azores	Ancient	this study

JN675551	162	I	A	Modern	Modern	Brazil	Americas	Aplin et. al. 2011
SNE004.A01	162	I	A	Ancient	1350-1400	Deventer-Stadhuiskwartier, Neatherlands	Ancient	this study
R191	162	I	A	Modern	1921	Angola	Southern Central Africa	Trinks/Eager
JN675524	13	I	A	Modern	Modern	Iran	Near East	Aplin et. al. 2011
JN675548	159	I	A	Modern	Modern	Guyana	Americas	Aplin et. al. 2011
JN675520	9	I	D	Modern	Modern	Madagascar	Madagascar and islands	Aplin et. al. 2011
JN675521	10	I	D	Modern	Modern	Madagascar	Madagascar and islands	Aplin et. al. 2011
JN675522	10	I	D	Modern	Modern	Madagascar	Madagascar and islands	Aplin et. al. 2011
JN675523	12	I	E	Modern	Modern	Oman	Near East	Aplin et. al. 2011
JN675525	18	I	E	Modern	Modern	India	India	Aplin et. al. 2011
R038	18	I	E	Modern	1921	India	India	Trinks/Eager
JN675552	164	I	D	Modern	Modern	Madagascar	Madagascar and islands	Aplin et. al. 2011
R096	164	I	D	Modern	1942	Malawi	Eastern Africa	Trinks/Eager
R187	164	I	D	Modern	1942	Malawi	Eastern Africa	Trinks/Eager
R188	164	I	D	Modern	1942	Malawi	Eastern Africa	Trinks/Eager
R077	164	I	D	Modern	1961	Zimbabwe	Eastern Africa	Trinks/Eager
R094	164	I	D	Modern	1942	Zambia	Eastern Africa	Trinks/Eager
HE006	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE009	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE007	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager

HE025	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE026	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE028	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE008	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE011	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
R172	164	I	D	Modern	1925	Madagascar	Madagascar and islands	Trinks/Eager
HE014	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE024	164	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE001	164	I	D	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
HE002	164	I	D	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
R093	164	I	D	Modern	1925	Tanzania	Eastern Africa	Trinks/Eager
JN675553	165	I	D	Modern	Modern	Madagascar	Madagascar and islands	Aplin et. al. 2011
JN675550	161	I	C	Modern	Modern	Brazil	Americas	Aplin et. al. 2011
R270	161	I	C	Modern	1957	Egypt	Near East	Trinks/Eager
R025	161	I	C	Modern	?	Egypt	Near East	Trinks/Eager
Car_4	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
Car_5	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
Car_6	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
Car_7	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study

Car_9	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150752	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150755	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150756	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150765	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150750	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150753	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150754	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150757	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150759	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150760	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150761	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150762	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150763	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150766	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150768	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150769	161	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
JN675527	20	I	B	Modern	Modern	India	India	Aplin et. al. 2011
JN675528	21	I	B	Modern	Modern	India	India	Aplin et. al. 2011
JN675531	21	I	B	Modern	Modern	India	India	Aplin et. al. 2011
JN675530	23	I	B	Modern	Modern	India	India	Aplin et. al. 2011
JN675532	26	I	B	Modern	Modern	India	India	Aplin et. al. 2011
JN675533	26	I	B	Modern	Modern	India	India	Aplin et. al. 2011
JN675529	22	I	B	Modern	Modern	India	India	Aplin et. al. 2011
JN675526	19	I	E	Modern	Modern	India	India	Aplin et. al. 2011
R265	166	I	?	Modern	1929	Ethiopia	Eastern Africa	Trinks/Eager
R066	166	I	?	Modern	1929	Ethiopia	Eastern Africa	Trinks/Eager
R099	167	II		Modern	1924	Myanmar		Trinks/Eager

R237	168	I	B	Modern	?	Maldives	India	Trinks/Eager
R137	169	I	A	Modern	1922	Angola	Southern Central Africa	Trinks/Eager
R097	170	I	D	Modern	1942	Malawi	Eastern Africa	Trinks/Eager
R095	170	I		Modern	1942	Zambia	Eastern Africa	Trinks/Eager
R246	171	I	D	Modern	?	Mozambique	Eastern Africa	Trinks/Eager
R034	172	I	A	Modern	1963	Saudi Arabia	Near East	Trinks/Eager
R098	173	II		Modern	1924	Myanmar		Trinks/Eager
R116	174	II		Modern	1931	Myanmar		Trinks/Eager
R119	175	II		Modern	1931	Myanmar		Trinks/Eager
R063	176	II		Modern	1960	Nepal		Trinks/Eager
R113	177	II		Modern	?	China		Trinks/Eager
R142	178	II		Modern	1930	China		Trinks/Eager
AT001	179	II		Modern	2009	Diego Garcia Island		Trinks/Eager
AT012	179	II		Modern	2009	Diego Garcia Island		Trinks/Eager
AT021	179	II		Modern	2009	Diego Garcia Island		Trinks/Eager
AT006	180	II		Modern	2009	Diego Garcia Island		Trinks/Eager
R068	181	I	C	Modern	1929	Egypt	Near East	Trinks/Eager
R003	182	I	C	Modern	1943	India	India	Trinks/Eager
R103	183	I	C	Modern	1937	India	India	Trinks/Eager
R059	184	I	C?	Modern	?	India	India	Trinks/Eager
R104	185	I	B	Modern	1943	India	India	Trinks/Eager
R202	186	I	B	Modern	1943	India	India	Trinks/Eager
R203	187	I	B	Modern	1943	India	India	Trinks/Eager
R102	188	I	F	Modern	1925	Sri Lanka	India	Trinks/Eager
R069	189	I	F	Modern	1966	Sri Lanka	India	Trinks/Eager
R106	189	I	F	Modern	1940	Sri Lanka	India	Trinks/Eager
R101	190	I	F	Modern	?	Sri Lanka	India	Trinks/Eager
R173	190	I	F	Modern	1944	Sri Lanka	India	Trinks/Eager

R071	190	I	F	Modern	1960	Sri Lanka	India	Trinks/Eager
R155	191	I	F	Modern	1940	Sri Lanka	India	Trinks/Eager
R174	192	I	F	Modern	?	Sri Lanka	India	Trinks/Eager
R061	193	II		Modern	1950	India		Trinks/Eager
R108	194	II		Modern	1919	India		Trinks/Eager
R008	195	II		Modern	1950	India		Trinks/Eager
R045	196	II		Modern	1930	India		Trinks/Eager
R282	197	II		Modern	1965	India		Trinks/Eager
R279	198	II		Modern	1960	India		Trinks/Eager
R280	199	II		Modern	1961	India		Trinks/Eager
R122	200	IV		Modern	1930	Indonesia		Trinks/Eager
R123	201	IV		Modern	1934	Indonesia		Trinks/Eager
R183	202	IV		Modern	1927	Indonesia		Trinks/Eager
R127	202	IV		Modern	1929	Indonesia		Trinks/Eager
R126	203	IV		Modern	1928	Indonesia		Trinks/Eager
R042	204	III		Modern	1965	Afganistan		Trinks/Eager
R285	205	I	B	Modern	1956	Kenya	Eastern Africa	Trinks/Eager
R287	206	I	B	Modern	1956	Kenya	Eastern Africa	Trinks/Eager
R032	207	I	D	Modern	1948	Kenya	Eastern Africa	Trinks/Eager
R031	208	I	D	Modern	1948	Kenya	Eastern Africa	Trinks/Eager
HE022	209	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE010	210	I	B	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE013	210	I	B	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
R171	211	I	B	Modern	1926	Madagascar	Madagascar and islands	Trinks/Eager

HE020	212	I	B	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
HE021	213	I	D	Modern	modern	Madagascar	Madagascar and islands	Trinks/Eager
R051	214	I	D	Modern	1948	Madagascar	Madagascar and islands	Trinks/Eager
R232	215	II		Modern	?	Maldives		Trinks/Eager
R233	216	II		Modern	?	Maldives		Trinks/Eager
R235	217	II		Modern	?	Maldives		Trinks/Eager
R236	218	I	A	Modern	?	Maldives	India	Trinks/Eager
R079	219	II		Modern	1949	Thailand		Trinks/Eager
R076	220	II		Modern	1949	Thailand		Trinks/Eager
R208	221	II		Modern	1929	Vietnam		Trinks/Eager
R230	222	I	F	Modern	?	Andaman	India	Trinks/Eager
HE003	223	I	A	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
HE023	223	I	A	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
HE004	223	I	A	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
HE015	224	I	A	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
HE016	224	I	A	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
HE005	225	I	B	Modern	modern	Tanzania	Eastern Africa	Trinks/Eager
R075	226	I	B	Modern	?	Tanzania	Eastern Africa	Trinks/Eager
R192	227	I	D	Modern	1917	Tanzania	Eastern Africa	Trinks/Eager
R004	227	I	D	Modern	1916	Tanzania	Eastern Africa	Trinks/Eager
R193	228	I	D	Modern	1917	Tanzania	Eastern Africa	Trinks/Eager
R189	228	I	D	Modern	?	Tanzania	Eastern Africa	Trinks/Eager
R049	229	I	A	Modern	1954	Turkey	Europe	Trinks/Eager
R080	230	I	B	Modern	2006	Tanzania	Eastern Africa	Trinks/Eager
R129	231	I	D	Modern	1917	Tanzania	Eastern Africa	Trinks/Eager

R006	232	I	D	Modern	1915	Madagascar	Madagascar and islands	Trinks/Eager
R263	232	I	D	Modern	1915	Madagascar	Madagascar and islands	Trinks/Eager
R082	233	II		Modern	1917	China		Trinks/Eager
R084	234	II		Modern	1932	China		Trinks/Eager
R170	235	IV		Modern	1935	Australia		Trinks/Eager
R021	236	I	A	Modern	1962	Egypt	Near East	Trinks/Eager
R086	237	I	B	Modern	1985	India	India	Trinks/Eager
R215	238	I	A	Modern	1961	Lebanon	Near East	Trinks/Eager
BUD002.A01	240	I	A	Ancient	14th-15th century CE	Budapest, Hungary	Ancient	this study
KLT001	241	I	A	Ancient	14th century CE	Kilton Castle, England	Ancient	this study
KR150749	242	I	A	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150751	243	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
KR150758	244	I	C	Ancient	6th century CE	Carcin grad, Serbia	Ancient	this study
MDT002	246	I	A	Ancient	15th century CE	Monte di Tuda, Corsica, France	Ancient	this study
NC_11638	247	II		Modern	Modern	Japan	Asia	Robins et al. 2008
SML003.A01	248	I	A	Ancient	14th century CE	Santa maria, Lavezzi, Lavezzi archipelago	Ancient	this study
SRR2917427	249	II		Modern	Modern	China	Asia	unpublished
ZMB001	250	I	A	Ancient	4th-6th century CE	Zembra, Tunisia	Ancient	this study
ZMB002	250	I	A	Ancient	4th-6th century CE	Zembra, Tunisia	Ancient	this study
ZMB003	251	I	A	Ancient	4th-6th century CE	Zembra, Tunisia	Ancient	this study
MT294322.1	252	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294351.1	252	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294355.1	253	I	C	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294366.1	254	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294395.1	255	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294363.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020

MT294364.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294365.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294348.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294349.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294350.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294336.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294311.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294312.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294313.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294314.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294315.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294316.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294317.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294318.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294319.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294320.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294321.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294323.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294324.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294325.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294326.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294327.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294328.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294329.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294330.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294331.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294332.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294333.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020

MT294334.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294335.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294337.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294338.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294339.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294340.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294341.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294342.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294343.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294344.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294345.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294346.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294347.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294352.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294353.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294354.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294356.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294357.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294358.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294359.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294360.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294361.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294362.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294367.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294368.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294369.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294370.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294371.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020

MT294372.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294373.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294374.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294375.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294376.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294377.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294378.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294379.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294380.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294381.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294382.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294383.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294384.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294385.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294386.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294387.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294388.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294389.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294390.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294391.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294392.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294393.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294394.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294396.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294397.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294398.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294399.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020
MT294400.1	7	I	A	Modern	Modern	Benin	West Africa	Etougbétché 2020

KT221805.1	Rr2	I	B	Modern	Modern	Porbandar (Gujarat)	India	Baig et. al 2018
KT221808.1	Rr3	I	B	Modern	Modern	Porbandar (Gujarat)	India	Baig et. al 2018
KT221810.1	Rr4	I	B	Modern	Modern	Porbandar (Gujarat)	India	Baig et. al 2018
KT221809.1	Rr5	I	B	Modern	Modern	Navi Bandar (Gujarat)	India	Baig et. al 2018
KT221803.1	Rr6	I	B	Modern	Modern	Navi Bandar (Gujarat)	India	Baig et. al 2018
KT221819.1	Rr25	I	B	Modern	Modern	Brahmapur (Orissa)	India	Baig et. al 2018
KT221804.1	Rr27	I	B	Modern	Modern	Brahmapur (Orissa)	India	Baig et. al 2018
KT221811.1	Rr28	I	B	Modern	Modern	Brahmapur (Orissa)	India	Baig et. al 2018
KT221820.1	Rr10	I	B	Modern	Modern	India	India	Baig et. al 2018
KT221813.1	Rr15	I	B	Modern	Modern	India	India	Baig et. al 2018
KT221828.1	Rr17	I	B	Modern	Modern	India	India	Baig et. al 2018
KT221812.1	Rr26	I	B	Modern	Modern	India	India	Baig et. al 2018

Table S4.12 Ancient whole genome sequencing information

Sample name	Other ID	Location	Site	Country	Sample Age	Age description	Sex	Library type	UDG treatment	Endogenous DNA (%)	Mean Coverage	Treemix group
KLT001	AJ233	Kilton Castle	Kilton Castle	England, UK	1303-1402 CE	indirect C14	M	double	nonUDG	64.38	1.08	Med_WEU
MDT002	AJ300	Monte di Tuda	Monte di Tuda Cave	Corsica, France	15th century CE	contextual	F	single	nonUDG	23.81	1.384	Med_Corsica
SML001	AJ303	Lavezzi	Santa Maria Chapel	Lavezzi archipelago	14th century CE	contextual	F	single	nonUDG	87.41	0.897	Med_Lavezzi
SML002	AJ304	Lavezzi	Santa Maria Chapel	Lavezzi archipelago	14th century CE	contextual	M	single	nonUDG	86.87	1.599	Med_Lavezzi
SML004	AJ309	Lavezzi	Santa Maria Chapel	Lavezzi archipelago	14th century CE	contextual	M	single	nonUDG	91.08	1.036	Med_Lavezzi
SML005	AJ311	Lavezzi	Santa Maria Chapel	Lavezzi archipelago	14th century CE	contextual	F	single	nonUDG	86.22	1.525	Med_Lavezzi
ZMB001	AJ313	Zembra	Abri du Casino	Tunisia	4th-6th century CE	contextual	M	single	nonUDG	56.42	1.118	Byzantine_Tunisia
ZMB002	AJ314	Zembra	Abri du Casino	Tunisia	4th-6th century CE	contextual	F	single	nonUDG	57.32	1.266	Byzantine_Tunisia
ZMB003	AJ317	Zembra	Abri du Casino	Tunisia	4th-6th century CE	contextual	M	single	nonUDG	81.31	1.874	Byzantine_Tunisia
BUD001	AJ389	Buda Castle	Teleki Palace	Hungary	1666-1950 CE	indirect C14	F	double	nonUDG	69.77	1.11	PostMed_Budapest
BUD003	AJ391	Buda Castle	Teleki Palace	Hungary	1288-1395 CE	direct C14	M	double	nonUDG	75.44	0.946	Med_CEU
BUD004	AJ393	Buda Castle	Teleki Palace	Hungary	1666-1950 CE	direct C14	M	double	nonUDG	64.77	0.874	PostMed_Budapest
GAU001	AJ395	Gatehampton Villa	Gatehampton Villa	England, UK	246-381 CE	indirect C14	M	double	nonUDG	47.9	0.61	Roman_WEU
GAU002	AJ399	Gatehampton Villa	Gatehampton Villa	England, UK	246-381 CE	indirect C14	M	double	nonUDG	47.11	0.195	Roman_WEU

KAF001	AJ404	Kastelholm	Kastelholm	Åland, Finland	1328-1420 CE	direct C14	M	double	nonUDG	73.85	0.608	Med_WEU
KAF002	AJ409	Kastelholm	Kastelholm	Åland, Finland	1422-1456 CE	direct C14	F	double	nonUDG	70.83	0.359	Med_WEU
SNE002	AJ464	Deventer	Stadhuiskwartier	Netherlands	1350-1425 CE	contextual	F	double	nonUDG	38.83	0.547	Med_WEU
SNE004	AJ468	Deventer	Stadhuiskwartier	Netherlands	1529-1794 CE	direct C14	M	double	nonUDG	52.34	0.155	Med_WEU
VOB001	AJ469	Voorburg	Forum Hadriani	Netherlands	120-230 CE	direct C14	F	double	nonUDG	77.95	0.879	Roman_WEU
VOB003	AJ472	Voorburg	Forum Hadriani	Netherlands	120-230 CE	indirect C14	F	double	nonUDG	81.79	0.706	Roman_WEU
PZA001	AJ473	Petronell	Carnuntum Zivilstadt	Austria	129-235 CE	direct C14	F	double	nonUDG	78.73	0.23	Roman_CEU
PZA002	AJ477	Petronell	Carnuntum Zivilstadt	Austria	80-216 CE	direct C14	M	double	nonUDG	66.85	0.241	Roman_CEU
PZA003	AJ482	Petronell	Carnuntum Zivilstadt	Austria	80-235 CE	indirect C14	M	double	nonUDG	68.94	0.834	Roman_CEU
PRA001	AJ487	Prague Castle	Old Probostry	Czech Republic	1321-1417 CE	indirect C14	M	double	nonUDG	87.27	1.237	Med_CEU
PRA002	AJ495	Prague Castle	Old Probostry	Czech Republic	1277-1387 CE	indirect C14	F	double	nonUDG	85.04	0.473	Med_CEU
MEP001	AJ523	Mértola	Mértola	Portugal	1161-1259 CE	direct C14	M	double	nonUDG	50.68	0.562	Med_Portugal
MEP002	AJ528	Mértola	Mértola	Portugal	1166-1261 CE	direct C14	M	double	nonUDG	60.77	0.748	Med_Portugal
MEP003	AJ530	Mértola	Mértola	Portugal	1166-1261 CE	indirect C14	F	double	nonUDG	51.31	0.774	Med_Portugal
ATU002	AJ535	Althiburos	Althiburos	Tunisia	706-883 CE	direct C14	F	double	nonUDG	72.82	1.022	Med_Tunisia
Ass_1		Assos	Assos	Turkey	End of the 7th century CE	contextual	M	double	halfUDG	82.42	6.275	Byzantine_Turkey
Ass_2		Assos	Assos	Turkey	End of the 7th century CE	contextual	M	double	halfUDG	16.54	0.617	Byzantine_Turkey
Car_4		Caričin Grad	Caričin Grad	Serbia	535-615 CE	contextual	F	double	halfUDG	49.89	16.286	Byzantine_Serbia
Car_5		Caričin Grad	Caričin Grad	Serbia	535-615 CE	contextual	F	double	halfUDG	53.01	1.229	Byzantine_Serbia

Car_7		Caričin Grad	Caričin Grad	Serbia	535-615 CE	contextual	M	double	halfUDG	58.24	2.336	Byzantine_Serbia
KR150770		Caričin Grad	Caričin Grad	Serbia	535-615 CE	contextual	M	double	nonUDG	80.43	1.7	Byzantine_Serbia
TRU001	RA19	York	Tanner Row	England, UK	Roman (2nd-4th century CE)	contextual	F	double	nonUDG	89.46	1.263	Roman_WEU
TRU002	RA6	York	Tanner Row	England, UK	Roman (2nd-4th century CE)	contextual	M	double	nonUDG	52.2	0.322	Roman_WEU
Sulz3		Castle Sulzbach	Castle Sulzbach	Germany	8 to early 10th century CE	contextual	F	double	halfUDG	77.75	1.818	Med_CEU
Sulz7		Castle Sulzbach	Castle Sulzbach	Germany	8 to early 10th century CE	contextual	F	double	halfUDG	72.99	1.327	Med_CEU

Table S4.13– Radiocarbon dating results

Location	Site	Country	Contextual dating	Date lab reference	Uncal date	Stdev	d13C	d13C_method	d15N	Date cal CE (95.4%, overall range)	Sample ID (direct)	Sample IDs (indirect)	Notes	Reference
Gatehampton Villa	Gatehampton Villa	England, UK	Roman	Beta-37717	1760	30	-17.9	AMS		246-381		GAU001, GAU002	Rat bone from same deposit dated	Walker et al. 2019
Gatehampton Villa	Gatehampton Villa	England, UK	Roman	UBA-40928	1755	27	-19.3	AMS		247-379		GAU001, GAU002	Rat bone from same deposit dated	Walker et al. 2019
Kilton Castle	Kilton Castle	England, UK	17th century CE	OxA-36673	604	23	-20.27	IRMS	10.2	1303-1402		KLT001	Rat bone from same deposit dated	
Kastelholm	Kastelholm	Aland, Finland	15th century CE	Wk-51518	569	21	-18.71	IRMS	11.58	1328-1420	KAF001			
Kastelholm	Kastelholm	Aland, Finland	15th century CE	Wk-51519	463	21	-17.4	IRMS	11.79	1422-1456	KAF002			
Buda Castle	Teleki Palace	Hungary	14th-15th Century CE	Wk-51520	642	21	-18.76	IRMS	6.9	1288-1395	BUD003	BUD002		
Buda Castle	Teleki Palace	Hungary	Turkish phase (1541-1699 CE)	MAMS-46369	175	19	-21.2	AMS		1662-1950	BUD004	BUD001		
Deventer	Stadhuiskwartier	Netherlands	1350-1425 CE	Wk-51521							SNE002		Failed	
Deventer	Stadhuiskwartier	Netherlands	1620-1650 CE	MAMS-46370	263	19	-21.8	AMS		1527-1794	SNE004			
Voorburg	Forum Hadriani	Netherlands	170-270 CE	Wk-51522	1877	20	-19.8	AMS		120-230	VOB001	VOB002, VOB003		
Petronell	Carnuntum Zivilstadt	Austria	4th C CE	Wk-51523	1854	20	-18.03	IRMS	11.88	129-235	PZA001			
Petronell	Carnuntum Zivilstadt	Austria	Last decades of 3rd century CE	MAMS-46371	1869	20	-21.9	AMS		125-229	PZA002	PZA003		

Prague Castle	Old Probostry	Czech Republic	14-15th century CE	Wk-51524	679	21	-18.6	IRMS	7.25	1277-1387		PRA002	Rat bone from same deposit dated	
Prague Castle	Old Probostry	Czech Republic	10-11th century CE	OxA-39167	571	19	-21.7	IRMS	7.2	1321-1417		PRA001	Rat bone from same deposit dated	
Mértola	Mértola	Portugal	1200-1225 CE	Wk-51525	852	21	-18.23	IRMS	8.92	1161-1259	MEP001			
Mértola	Mértola	Portugal	1200-1225 CE	Wk-51526	843	21	-17.48	IRMS	9.08	1166-1261	MEP002	MEP003		
Althiburos	Althiburos	Tunisia	250-400 CE	Wk-51527	1222	21	-18.49	IRMS	8.89	706-883	ATU001	ATU002		
Chersonesos	Chersonesos	Ukraine	1-2nd century BCE	BRAMS-3373	1825	25	-16.9	AMS		130-320			Rat bone from same deposit as screened samples	

4.10.4 Supplementary Information References

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I hereby give permission to Alexandra Jamieson to use our joint work as contribution towards her D. Phil thesis to be submitted for examination at Oxford University.

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I confirm that to the best of my knowledge, the author contribution statement below is accurate and Alexandra Jamieson's contribution towards the work is greater or equal than that of any other co-author.

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J.K., G.L. and D.O. designed the project; A.J., B.K.-K., B.K., C.S., H.A-J., H.E., A.T. generated data; H.Y., A.J. and D.O. analysed data; N.B., H.B., A.C., C.J.C., T.C., K.E., L.G., E.G., P.G., S.H.-D., H.K., Z.K., K.K., R.K., A.L., A.M., M.N., T.Oc., T.Ou, K.P., E.R., J.B.S., E.T., S.V., I.van der J., J.-D. V. and J.Z. provided material and support; H.Y., D.O., A.J., A.H.-B., G.L. and J.K. wrote the paper with contributions from all other authors.

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5. Sample preservation and sequencing success

5.1 Sample collection and sequencing success across all three taxa

The three papers that constitute this thesis are all the first to sequence full ancient mitochondrial genomes for each of the three species. Additionally, the black rat and domestic cat papers are the first to sequence ancient full genomes (mitochondrial and nuclear) for these species. In total, across all three projects, 207 ancient full mitochondrial genomes have been generated at ≥2x coverage, of which 143 are ≥10x (Table 5.1). An additional 22 ancient full nuclear genomes were generated at ≥1x. Of the data from historic specimens (1895-1985), 20 full mitochondrial genomes were generated at ≥2x, with two of these over ≥10x.

In terms of modern genomes, 92 modern hare full mitochondrial genomes were generated at ≥10x with a further three at ≥2x. One modern Scottish European wildcat full mitochondrial genome was generated at 15x coverage as part of the Scottish cats provided as a comparison to the ancient dataset. For the black rat project, one modern black rat genome was generated by other collaborators in the project. This is the first full nuclear genome of a black rat to be sequenced.

5.1.1 Ancient

Taxa	Number of samples analysed	Overall success rate	Mitochondrial genomes at ≥2x coverage	Mitochondrial genomes at ≥10x coverage	Full genomes ≥1x coverage
Mountain hare	235	24.7%	58	32	0
European wildcat and domestic cat	258	29%	75	47	3
Black rat	202	36.6%	74	64	19

Table 5.1 Breakdown of ancient sequences generated as part of each project.

The success rate for obtaining useable full mitochondrial genomes using ancient data was low, but as the samples were taken from a wide range of locations and site types, across multiple periods, not all of which were optimal for the recovery of DNA, this is not unexpected. The petrous bone is known to contain a high endogenous DNA content and is

thus generally considered the optimal element to sample but none were available for the three taxa in this study due to skull scarcity and size (Charlton, Booth, and Barnes 2019). Long bones, which are often the thickest elements, were therefore preferentially chosen for analysis, unless unavailable, in which case another element was chosen.

Three factors were indicative of sequencing success: element type analysed, age of sample and location. With element selection, there were two elements seen to have greater success of sequencing for the cats and hares studied, the ulna and tooth samples (Figure 5.1). The tooth was expected given its density and the ulna was not unexpected given it is a relatively thick long bone. The more relevant indicators of sequencing success were age and latitude (Table 5.2 and Figure 5.2). As would be expected, on average, the older the sample the lower the success and samples from hot arid climates had a very low success rate.

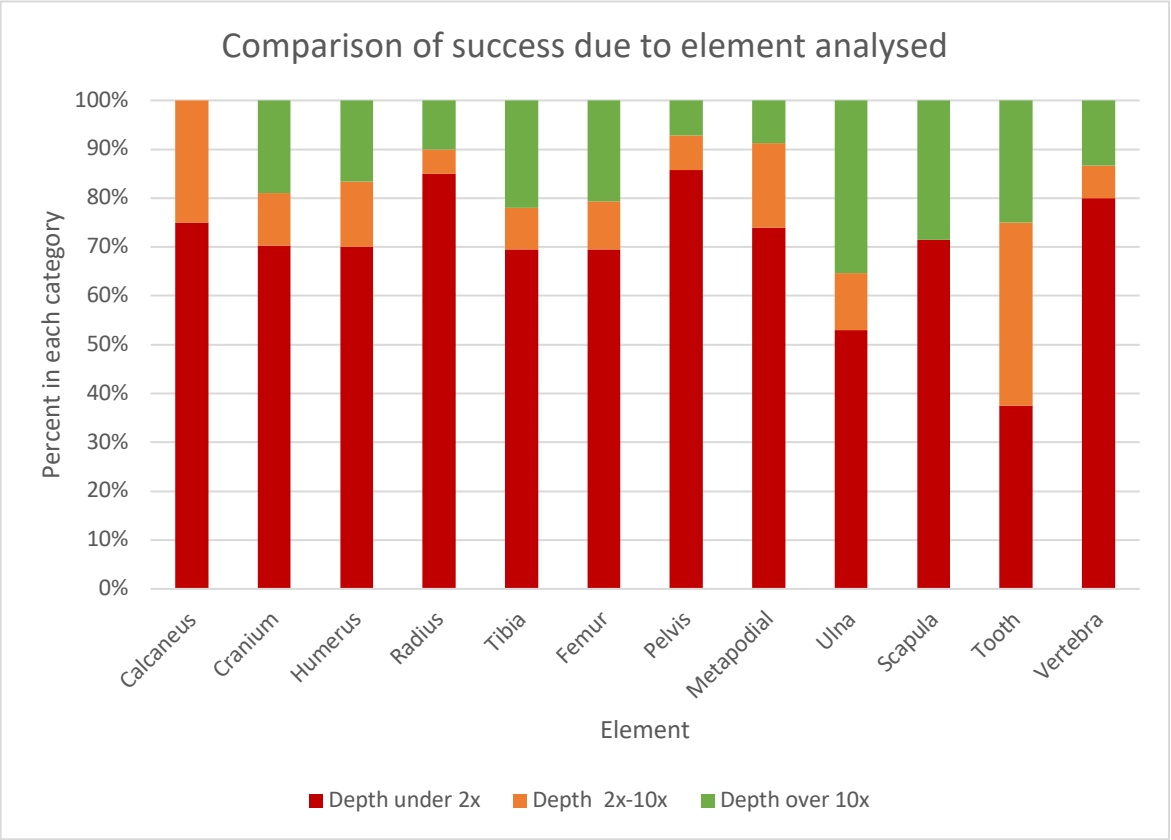

Figure 5.1 Percentage of each element from each category of success. Data was produced from cat and mountain hare data only as they were subject to roughly the same level of deeper sequencing. Success is categorised as a sample yielding enough mitochondrial DNA for analysis.

Table 5.2a - Overall					
Period	Dates	Successful	Unsuccessful	Total	Success rate
Late Pleistocene	57,000-11,700 BP	16	25	41	39%
Holocene	11,700-100 BP	76	89	165	46%

Table 5.2b - Hares					
Period	Dates	Successful	Unsuccessful	Total	Success rate
Late Pleistocene	57,000-11,700 BP	16	25	41	39%
Early Holocene	10,00-2,000 BP	15	21	36	42%
Late Holocene	2,000- 100 BP	8	15	23	35%

Table 5.2c - Cats					
Period	Dates	Successful	Unsuccessful	Total	Success rate
Mesolithic - Bronze Age	10,000 - 2,000 BP	5	12	17	29%
Iron Age - Roman	2,000 - 1,500 BP	9	13	22	41%
Medieval - Post-Medieval	1,500 - 100 BP	25	18	43	58%

Table 5.2d - Rats					
Period	Dates	Successful	Unsuccessful	Total	Success rate
Roman	100 BCE - 700 CE	5	4	10	50%
Medieval	700-1600 CE	14	6	19	74%

Table 5.2 Tables of the breakdown of success rate by time intervals for all studied samples together (Table 5.2a) and each species separately (Table 5.2b-5.2d). Success is categorised as a sample yielding enough mitochondrial DNA for analysis. Only samples with known dates have been included.

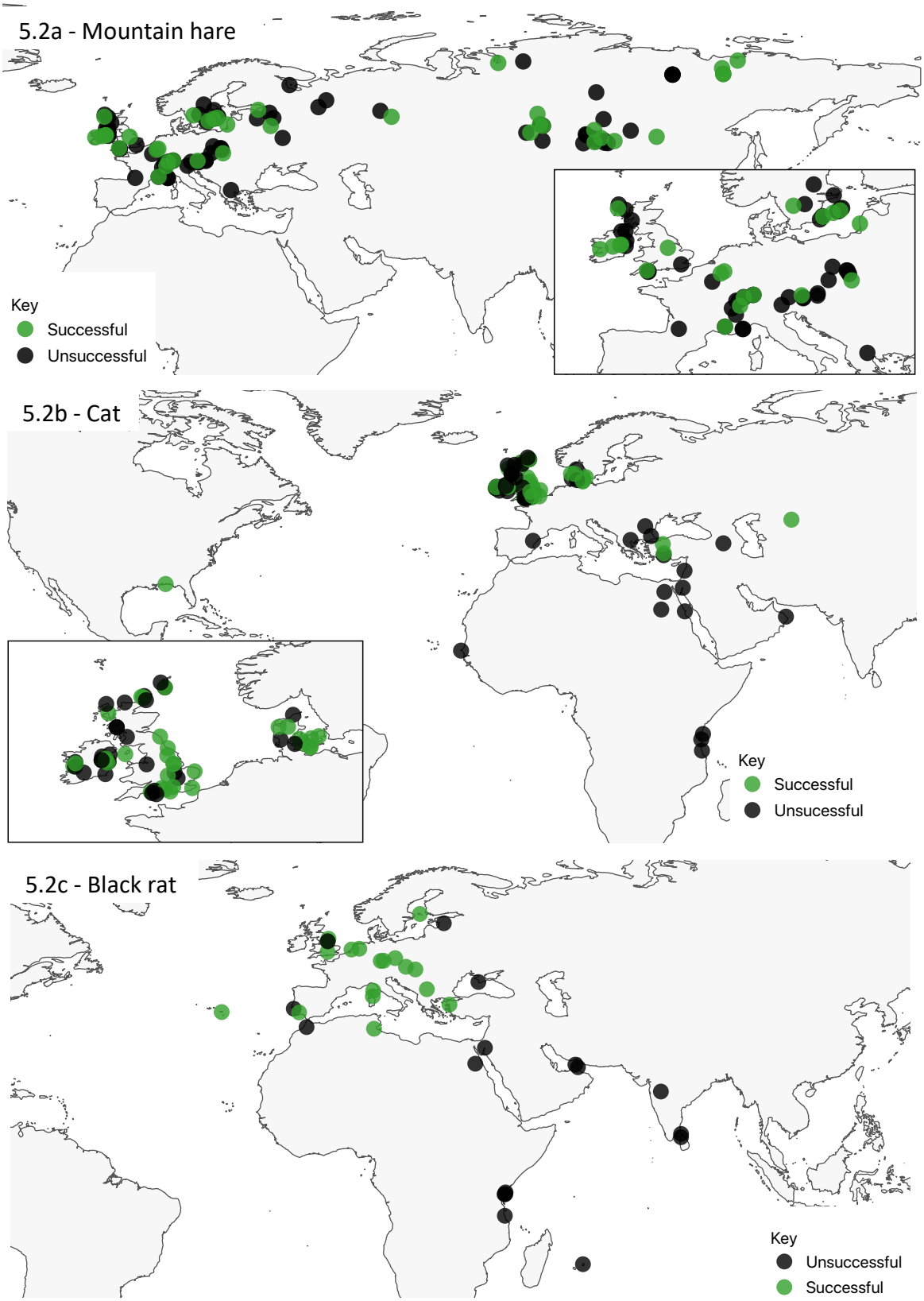

Figure 5.2 Maps of sites sampled for each of the three taxa. Successful = at least one sample from the site yielded enough mitochondrial DNA for analysis.

Of the three taxa, the success rate was highest for the black rat samples. This is due to two reasons:

1. Rat samples were from the 2nd century BCE onwards, making them the most recent samples across all three taxa.
2. The rat samples were sequenced the most thoroughly, with samples of interest deeper sequenced multiple times to ensure the greatest depth of coverage. This was not within the budget of the other two projects.

The lowest success rate was seen with the mountain hares. Being mostly older samples from the late Pleistocene and early Holocene, this can therefore be attributed to sample age. Among those that were successful in the earliest group, the Late Pleistocene, the oldest sample sequenced was that of a mountain hare from Caverne Marie-Jeanne, Belgium indirectly dated to around 44,000 years ago. The earliest directly-dated, successfully-sequenced sample in the study was from Church Hole, Creswell Crags, England dated to 14,606 ± 338 cal. BP (OxA-19163, 12430 ± 55 BP). These are the oldest dated mountain hares sequenced to date. Of all periods covered in the hare study, the lowest success rates of all were for samples from the late Holocene. This is unexpected given that these were the most recent samples from the study. There is currently no explanation for this discrepancy. Of the complete nuclear genomes sequenced with coverage ≥1x across all taxa, the oldest was a domestic cat directly dated to 24-123 cal. CE (OxA-38877, 1950 ± 17 BP) from Fishbourne, England.

From all three studies, the African continent produced only two sites from which samples were successfully sequenced, black rats from the island of Zembra, off the coast of Tunisia, from the 4th-6th century CE and Althiburos on the mainland from the 3rd to 5th century CE (Figure 5.2). All other samples from Africa, the Arabian Peninsula and India were unsuccessful. Only the samples from Tunisia were collected directly for this thesis, with all other cat and black rat samples from Africa, the Arabian Peninsula and India having been collected and extracted for previous projects over the last decade (Eager 2014; Trinks 2014; Ottoni et al. 2017). Very little is understood about how long extracts keep and the effects of freeze-thawing on their degradation, therefore it is not possible to draw conclusions on whether the length of time the extract has been stored had an effect on the sequencing

success of the samples in this study (Ivanova and Kuzmina 2013; Lee, Crouse, and Kline 2013). DNA was successfully extracted in the previous studies through targeting short regions of the mitochondrial genome and replicating them directly. This thesis utilises a different technique, targeting the whole mitochondrial genome for enrichment and then sequencing all the reads regardless of if they were mitochondrial or nuclear. In the future, a more targeted approach could be used on these unsuccessful samples to see if this yields usable results.

5.1.2 Modern

All modern samples sequenced successfully yielded mitochondrial DNA for analysis, with mitochondrial coverage varying from 4.1x to 106,304x. The highest coverage was from the Western Isles mountain hare which was deep sequenced along with seven ancient samples on a S4 NovaSeq lane. The achieved coverage of 106,304x is significantly higher than needed for this study's analysis. The full nuclear genome coverage on this sample is 51x. For this thesis only mitochondrial DNA was required to answer the research questions posed but due to the success in sequencing the full genome this data will be available for use in future projects. The only other published full mountain hare genome is the *de novo* draft reference genome with a coverage of 77x (GCA_009760805.1).

6. Conclusions

6.1 Review of the goals of this thesis

This thesis set out to further our understanding of the movement of animals in the past using detailed, targeted studies of three species moved by three different mechanisms: climate fluctuation (mountain hares), intentional human assisted movement (domestic cats) and unintentional human assisted movement (black rats). All three studies have added to our general understanding of species movements, as well as furthering our understanding of each of the species individually. Furthermore, each study is the most comprehensive of its kind to date, combining findings from previously published research alongside new data, which has been generated using the most up-to-date genetic and absolute dating techniques.

The combination of ancient and modern DNA analysis with radiometric dating allows for accurate mapping of the presence and genetic distribution of a species through time, leading to new insights into the past distribution and movements of these species. This deep-time perspective can also provide information that could inform conservation decisions for these species in the future, such as the long-term effects of introductions of non-native species and an understanding of a species' ability to adapt to a changing climate.

Across all three studies, we have shown that:

1. A deep-time perspective is key to reconstructing past movements of species.
2. In order to understand human translocations of animals, it is first important to establish the natural range of movements of a species, as demonstrated with the detailed investigation of the arrival of mountain hares to the Western Isles of Scotland.
3. Human translocations are complex as there are often multiple waves of introduction and sometimes complete or partial population replacement, again demonstrating the importance of a temporal perspective alongside modern data.

6.2 Key findings and implications for the study of the past

6.2.1 Natural movement of mountain hares across their species range

The study of mountain hares is the most comprehensive study to date on the changing species range from the end of the Pleistocene to the modern-day. It shows the advantages of using a combination of ancient and modern DNA to fully understand past movements, particularly when sampling throughout the species range to cover the full spatial and temporal extent of the population. Without sufficient coverage of the spatial and temporal range of the population, inferences are harder to draw, as has been shown in this study with the lack of success with ancient samples from mainland Scotland, where only modern mountain hare samples from this region yielded usable results.

We have added further evidence to demonstrate that a cold-adapted species, the mountain hare, was able to maintain its population diversity by habitat tracking. We have also shown that the species was highly adaptable, surviving in unfavourable conditions, most probably in refugia off the coast of Ireland. Since the retreat of the ice sheet, mountain hares have been able to adapt to the varying climate in Ireland, where they have been present at all elevations up to the present day. We have also demonstrated that mountain hares in Ireland have been genetically distinct from the rest of the species range throughout the Holocene, being most closely related to those in the Austrian/Italian Alps, which were also separated from the rest of the range with the warming climate since the Last Glacial Maximum. This again adds to the evidence that supports their survival in refugia off the coast of Ireland, cutting them off from the rest of the species range. We have found evidence for the early presence of mountain hares in the Western Isles of Scotland. One of these samples is basal to those found in Ireland. At present, there is no knowledge of contact between the Mesolithic peoples of Scotland and Ireland, making the introduction of mountain hare to the Western Isles by humans during this period improbable. This evidence supports the Montgomery et al. (2014) argument for mountain hares, in addition to other species, surviving the Last Glacial Maximum at the extreme western edge of Europe. The resilience and adaptability of this species allowed them to thrive, unlike other cold-adapted species, such as the Arctic fox, that went extinct in more southerly latitudes as the climate warmed (Dalén et al. 2007). We have shown that the mountain hares in Ireland and Scotland were genetically distinct from those that lived in

England, which were most probably part of the continuum population that lived on the edge of the ice sheet. This means that mountain hares can be added to the growing list of possible 'Celtic fringe' species.

6.2.2 Intentional human-assisted movement of domestic cats

Cats are among the earliest animals intentionally moved by people. Their movement to Britain was relatively early, which not only reflects the importance of cats to people but also how connected Britain was with the rest of Europe. Our findings show that domestic cats arrived in Britain at a similar time to other northern European locations, aside from the one example of the very early arrival of one recorded domestic cat in Denmark in the Bronze Age (Bitz-Thorsen and Gotfredsen 2018). Domestic cats first arrived in Britain during the Iron Age, with the earliest known example found at Gussage All Saints (339-54 cal. BCE) on the south coast of England, which was contemporary with the Roman civilisation in southern Europe. Domestic cats are well known in the Roman world, and trade between the Roman Empire and the neighbouring Gauls is well documented (Cunliffe 2010). At least one cat, which had a litter of kittens, was brought to the south coast of Britain before the Roman invasion of the island. Whether this cat was brought directly from the Roman world or through trade with Gaul or other European regions is unknown, but its presence shows further evidence that Iron Age Britain had well established trade routes to the European mainland.

Gussage All Saints is currently the only Iron Age site found to have domestic cats present, with all other Iron Age sites containing only European wildcats. While domestic cats may have been present at unsampled sites, this cat is the earliest known to be introduced to Britain. Gussage All Saints was just 20 miles away from the contemporary Iron Age trading port of Hengistbury Head, which is known to have traded in Roman goods. This further supports Gussage All Saints as being one of the earliest locations to house a domestic cat in Britain and presents a potential importation route. Analysis of cat remains from other important Iron Age trading posts with known Roman contact may reveal other early domestic cats and would further add to our understanding of their initial introduction to Britain.

This work has confirmed, using absolute dating and ancient and modern DNA analysis, that domestic cats were first introduced to mainland Britain during the Iron Age, but that it was during the Roman period that they became more widespread. There is also evidence to suggest separate introductions of domestic cats to Britain and Ireland by the Vikings. We have shown that in Denmark (part of the Viking Kingdom) one particular domestic cat lineage was dominant (D1). In samples found in Britain, in locations known to have Viking influence such as York and the Orkneys, this same lineage is found in higher proportions than in the other areas of the country. The lack of sampling of central European cats means introductions from this region cannot be discounted, but the correlation between areas of Viking influence and the presence of D1 lineage cats suggests that these cats were introduced by the Vikings rather than directly via the Roman Empire. We therefore have evidence of domestic cat introductions from both the Viking and Roman worlds.

Before this study very little was known about domestic cats in the Northern Isles. The Northern Isles of Scotland show a similar history to mainland Britain, with the initial arrival of cats occurring after the Roman invasion of Britain, followed by a later arrival with the Vikings from the Norse world. While in mainland Britain all lineages of domestic cats are found after the arrival of the Vikings, in the Northern Isles the arrival of Viking cats resulted in the complete replacement of the earlier cat lineage. This observed replacement could show the adoption of Norse culture by the people of Orkney and Shetland, or potentially even the settlement of Norse peoples and the subsequent replacement of the previous Orcadian and Shetlander human populations, if it is possible to use the cats as an indicator of what might have happened. A detailed genetic study of human remains from these islands during this period is needed to confirm this possible scenario. Further study of more recent cat specimens would reveal whether the predominance of the Viking D1 lineage continues to this day.

Domestic cats were first introduced to Ireland in the early Medieval period from the 7th century CE, with two of the three lineages found. These lineages were already present throughout mainland Britain, the Northern Isles and continental Europe before their introduction to Ireland, making the origin of the introduced cats uncertain. This demonstrates the difficulties in reconstructing past events in animal population

movements. In order to gain a better understanding of the origin of domestic cats in Ireland, earlier samples from sites contemporary with the beginning of the Roman Empire in the south of Europe are needed, however currently there is an absence of any known cat bones from this period.

This domestic cat study has also resulted in the addition of radiocarbon dates for sites or strata previously undated by absolute radiometric methods. For example, through the use of radiocarbon dating we have updated the known age for stratigraphic layers at the site of Howe, Orkney. For example, the dates for one of these specimens changed by many centuries as a result of the absolute dating conducted as part of this thesis. This one specimen from the stratigraphic dating had been dated to around 500-200 BCE in the Middle Iron Age. It has now been redated with radiocarbon dating by this study to 661-774 cal. CE, the Late Iron Age. These dates along with the others generated in this study will be useful for future interpretations of the sites which have had direct dates obtained.

This study has shown that a combination of ancient and modern DNA analysis provides us with a thorough understanding of the movement of animals by people in the past. Continuation of this work using additional samples from geographic areas and time periods that would enhance further this study have the potential to further our insights into the movement of domestic cats around Europe, and particularly Britain and Ireland.

6.2.3 Unintentional human-assisted movement of black rats

Black rats arrived in the eastern Mediterranean during the Roman period from south-west Asia (Ervynck 2002). Their exact route of introduction to Europe is unclear, but our results suggest that they were most probably introduced via an overland route from the Near East and/or Egypt, as these locations contain the same haplogroups as are found in the ancient European samples. From the samples in this study, not all lineages of black rat found around the world today were present in Europe in the past. We have also shown, alongside previous work, that Europeans were responsible for spreading black rats throughout their empires (Aplin et al. 2011). This has ultimately resulted in haplogroup A, the predominant haplogroup in Europe, being found on all continents today with the exception of Antarctica.

The other major finding from this work is that there were two waves of rat introductions into temperate (Northern) Europe, the first in the Roman period and the second in the Medieval period. Rat populations stayed relatively constant in the southern regions (around the Mediterranean). The first dispersal wave to the temperate regions was in the Roman period, then as the Roman Empire contracted the number of rats declined (McCormick 2003). This population decline also coincided with the Justinian Plague in addition to a climatic cooling event (McCormick 2003; Büntgen et al. 2016). It therefore may have been a combination of all three factors that led to the decline of the rat population at this time, with further study of rats from these periods needed to confirm this.

6.3 Key findings and implications for future conservation efforts

6.3.1 Mountain hares

Our first main finding which has implications for conservation is that the mountain hares that are currently found on the Western Isles are not the first on the islands. The genetic results suggest that introduction via humans in the Mesolithic is improbable, showing instead that they possibly migrated to the islands after the Last Glacial Maximum when the island became habitable. If confirmed, such a finding would change their conservation status, classifying the current population as reintroduced instead of introduced. This finding would also make mountain hares the only land mammal to be native to the Western Isles of Scotland, with all other mammals believed either to have arrived with early prehistoric people or to have been even more recently introduced (Berry 1979).

We have also been able to further demonstrate the adaptability of mountain hares during times of climate change. That the species has survived through such challenging conditions makes them more adaptable than most other cold-adapted species which have been studied. The paleontological/archaeological record, our findings and previous studies have shown that mountain hares are well suited to habitat tracking, and that when this is not possible, they are often able to adapt, making them more resilient to climate change (Smith et al. 2017). An example of this is their survival in Ireland, where they were cut off from the rest of the species range, forming an isolated population that survived on the island throughout the Holocene, and potentially even before. They are found at every elevation

today, and our study has confirmed that this also was true throughout the Holocene (Caravaggi et al. 2017). An example of these adaptations is that Irish mountain hares have subsequently adapted to the lower elevations by no longer changing their coat colour during the winter (Angerbjörn and Flux 1995).

6.3.2 Cats

Hybridisation between European wildcats and domestic cats is a well-known problem in the Scottish population with regards to the conservation and continuation of the Scottish European wildcat. This contrasts with other areas in the European wildcat range on mainland Europe where hybridisation is not as severe an issue (Mattucci et al. 2016; Steyer et al. 2018). The reason for the Scottish population being more susceptible to this hybridisation is unclear. A previous study of Scottish historic cats (1895-1985) has shown that levels of hybridisation were lower in the recent past compared to today (Senn et al. 2018). Our study has pushed back this time boundary to before the arrival of domestic cats, from the Mesolithic to the Medieval period. By measuring admixture in cat samples since the introduction of domestic cats in Britain and Ireland, we have so far found little evidence for significant hybridisation between the wildcat and domestic cat populations over the period studied however further analysis of these samples, in particular deeper nuclear analysis is needed to strengthen any conclusions made. Additionally, further study of the Medieval period, where the persecution of wildcats accelerated, is needed to confirm that high levels of hybridisation are a very recent occurrence as the present study only looked at a small subset of individuals with limited nuclear analysis. Studying from the start of their persecution would also demonstrate the relationship between relative wildcat population sizes and the extent of hybridisation.

Another significant output of this work is the generation of two ‘pure’ European wildcat genomes, which can be used as the natural baseline for European wildcats in Britain. Along with generating these two genomes, our ancient and modern DNA analysis also has shown that the genetic diversity of Britain’s wildcats was greater in the past. Ancient British wildcats were found throughout the European wildcat clade, whereas this was not the case with the historic and modern British European wildcats, which formed their own sub-clade within the larger European wildcat clade. This shows that the genetic diversity in the British

population was reduced at some point from the 14/15th to the 19th century, the 14/15th century being the date of the latest wildcat in this study's dataset. This coincides with their largescale persecution from around the 18th to the early 20st century, where wildcats were wiped out from most of Britain, only surviving in the remote parts of the Highlands today (Langley and Yalden 1977). These results have implications for where conservation managers could source populations for reintroduction. As the ancient wildcats show that the diversity of the British population was much higher in the past, it could be argued that future introductions should not be made using the most genetically similar cats from mainland Europe, instead introducing a more genetically-varied population in order to restore the previously seen genetic diversity. In order to do this, more work needs to be conducted on comparing the modern populations on the continent with these ancient and modern individuals from Britain. Additionally, analysis of samples from before and during the period of persecution would confirm whether this loss of diversity did in fact coincide with their rapid population loss.

6.3.3 Black rats

The impact of this study on the modern conservation of black rats is limited, but further investigation of samples from the 5th to 7th century CE may reveal the cause of the rat population decline and provide more conclusive evidence on the role black rats played, if any, in the spread of the Justinian plague as well as their reliance on humans for dispersal.

6.4 Future Perspectives

In each of the sections above, future directions of research have been suggested to add weight to the analysis already conducted. On top of these, there are several more general future enquiries which would add considerable knowledge to the understanding of movements of animals in the past and move beyond the work already conducted.

6.4.1 General

Ancient DNA research has many challenges, but recent advances over the last few years have helped overcome them and have made these projects possible. This includes the routine use of Next-Generation sequencing technology and its ever reducing cost, allowing for full mitochondrial and even full nuclear genome sequences to be generated (Hagelberg,

Hofreiter, and Keyser 2015). The ability to successfully extract DNA from samples below 200 mg was instrumental in the success of the black rat study, as most samples were under this mass (Orlando et al. 2013; Barnes, Matisoo-Smith, and Hunt 2006). Additionally, the availability of modern full reference sequences, one of which, the black rat, was generated for the study, have meant that full nuclear as well as mitochondrial genomes could be used for analysis.

Survival of DNA in the archaeological record is the most prominent challenge and an area which needs further research, with hot humid environments posing the greatest challenge for preservation (Campana, Bower, and Crabtree 2013; Horsburgh, Moreno-Mayar, and Gosling 2016; Prendergast et al. 2017). Due to this, we did not successfully extract any DNA south of 30 degrees north. Many of these more equatorial samples are key to understanding the movement of the black rat, in addition to other species moved around the Indian Ocean basin region, such as cattle and chickens (Prendergast et al. 2017; Horsburgh, Moreno-Mayar, and Gosling 2016). Until techniques can overcome this challenge, these studies prove less successful than for other areas of the world.

There is increasing understanding that archaeologists can help with conservation, as highlighted by Hofman et al. (2015), but more work is needed to evaluate how archaeology could be best used to face present day issues. The archaeological record, along with natural history and paleontological collections, are a largely untapped resource for studying species histories in deep time and we have demonstrated their potential uses, including quantifying the hybridisation of cats in Britain since their introduction (Brunson and Reich 2019; Hambrecht 2017). Future studies of animals in the past should endeavour to have a cross-disciplinary approach to ensure that the findings can be best used by relevant conservationists and policymakers.

6.4.2 Mountain hares

The results of this thesis begin to help us understand more about the past range of mountain hares in Europe and Russia, however there is still much left unanswered. For example, when did mountain hares first appear in Britain and Ireland and did they survive on the south coast of Britain in an ice-free zone through the last glaciation? These

questions could be answered with absolute dating of the earliest known mountain hare remains in Britain and Ireland on the southern coasts of both islands.

More targeted region studies would enhance our understanding of particular areas of interest. For the Western Isles samples, nuclear analysis and further deeper sequencing of the mitochondrial genomes could potentially improve our understanding of how hares arrived in this region, from refugia or by rafting. Nuclear analysis would not only build upon the mitochondrial results by providing information on the whole ancestry, as opposed to only the maternal inheritance, but would also allow for other types of analysis such as exploring demographic history. There may be limitations with the remains from the Western Isles as the percentage endogenous DNA was low for all the studied specimens. Additional samples from other Western Isles excavations may need to be taken with techniques employed to further enhance DNA recovery. Similarly, further research is also needed in the Alps region to clarify if there was a genetic divide between the east and west in the past. Ancient samples from the both the Pleistocene and Holocene of the Italian Alps would be beneficial to answer this question. Another possible target area for region study is the Iberian Peninsula. The results of this thesis have shown that the ancestral lineage is found only in the modern-day Iberian hare populations. Sampling mountain hares from the Iberian Pleistocene would have the potential to improve our understanding of the ancestral lineage, if samples can be found and DNA recovery allows.

One limitation of the research on mountain hares was the lack of nuclear analysis, therefore future studies including both the nuclear and mitochondrial DNA would allow for more in-depth population genetic studies of the whole ancestry. Demographic history analysis could be applied to explore population size, divergence and gene flow between each of the populations. This would greatly enhance the understanding of the population structure of mountain hares in the past which could aid in understanding their ability to habitat track. Further study of the nuclear data would also allow for the study of specific genes such as those selecting for seasonal coat colour change.

Another area of research on mountain hares which would be beneficial to pursue is their demise in southern Britain. This study focused on the early natural movements of

mountain hares. There is far more research needed into their disappearance and interaction with the anthropogenically-introduced European hare. This would benefit from both the research of historic texts alongside archaeological research to reconstruct the disappearance of the mountain hare from southern Britain and lower elevations of Europe.

Finally, there is still much to learn about refugial zones in the Atlantic Ocean surrounding Ireland, western Scotland and the south coast of Britain. In order to fully understand where species may have been present in the past, greater knowledge of the currently submerged land that was once above sea level may add to our understanding. Work similar to that conducted on Doggerland in the North Sea could be applied, if techniques allow, to the Bay of Biscay region (Weninger et al. 2008; Balin et al. 2007).

6.4.3 Cats

The research conducted for this thesis was the first to explore the movements of domestic cats and their interactions with the European wildcat in Britain. There are therefore many further research directions that could be studied in the future. The first is continued research into levels of hybridisation in the past, including gaining a greater understanding into why levels may have changed from the past to today. This research would benefit from using techniques such as D-statistics, in addition to a detailed study of historic records to provide context to the archaeological and genetic results.

Both Ireland and the Northern Isles would benefit from focused studies of these regions, specifically researching the presence of European wildcats in the past. It is known that European cats were present in Ireland, but currently it is unknown when they disappeared (see 3.4.3.1). Similarly, wildcats may have been present in the Northern Isles, although no evidence for their presence has been found so far (see 3.6.3.1.1). Focused studies of both regions would greatly enhance the understanding of the native range of European wildcats and how this has been affected by human action, by persecution or the introduction of the domestic cat or other species which may affect their survival. Further archaeological studies would be needed to identify potential wildcat specimens.

A limitation of this study was the lack of samples from mainland Europe available for comparison. Once sourced, these could be used to reconstruct the possible source populations of cats in Britain and Ireland. Full mitochondrial and nuclear genomes from ancient European cats would allow for further interpretations of the findings from this thesis. Additionally, more European samples could be used to gain a greater understanding of past hybridisation levels across Europe, which could then be compared to measured modern levels across the continent. This would not only have implications for current day conservation management of wildcats across Europe and influence their reintroduction to Scotland, but could also help to explain why wildcat numbers declined so dramatically in Scotland compared to elsewhere across their native range.

6.4.4 Black rats

The rat study contained in this thesis is the first large-scale study of ancient rats, the results of which reveal many further avenues for research. These include exploring the source population for the second wave of rats to northern Europe, studying when between the 6th and 10th century the turnover event occurred, and whether it occurred earlier in the western regions of northern and central Europe than it did in the eastern regions. All of these research questions posed can be answered with the inclusion of additional samples from the 6-10th century in the northern region as well as the addition of more samples from unsampled parts of the southern region (such as France and northern Spain) which could be used to reveal the source of the second wave.

We now have an initial dataset of full genomes of ancient black rats from Europe. To fully contextualise the findings from Europe, full genomes of black rats from their native range in southern Asia, specifically India, would greatly benefit the understanding of the movement of black rats to Europe. The inclusion of full genomes from possible stopping points on route to Europe, such as port towns in the Arabian Peninsula, would also aid understanding. There may be challenges associated with DNA recovery given the locations, therefore this research may require enhanced techniques.

Another area of great interest to black rat research is the spread of zoonotic diseases. Future genetic work specifically looking for pathogens would be of great value to the

archaeology community and modern pathogen research. This work would have the potential to enhance the understanding of past pandemic events and diseases spread by host species.

6.5 Concluding remarks

The geographical range of species commonly fluctuates throughout time, largely due to natural pressures. We have demonstrated this with our study of mountain hares in Britain and Ireland, finding that the Irish mountain hares were isolated from the rest of the range for at least the Holocene and possibly from the Last Glacial Maximum. More recently species ranges have also been affected by human actions, for example with translocation events. By exploring the past movements of domestic cats and black rats, we have gained a better understanding of their early distributions through Britain, Ireland and the rest of Europe, respectively. Of the many findings of our three studies, the power of ancient DNA is evident. With the use of ancient DNA alongside other lines of evidence we have shown when domestic cats arrived in Britain. We have begun to investigate levels of hybridisation between domestic cats and European wildcats in the past, with further work needed to give more certainty to our conclusions. We have also shown that rats in northern Europe underwent two separate waves of introduction during the Roman and Medieval periods. We have furthered the understanding of two past human-mediated translocation events, of cats and black rats, which has given us greater insight into the beginnings of people moving animals, the precursor to what we now see today with globalisation. The effects of such translocations have been significant, with these two species, black rats and domestic cats, found throughout the world today, on nearly every continent. Much remains to be learned about the past and how it can inform the future. The study of archaeology is well placed to make these unique contributions and further our understanding of both species' histories and aid in future conservation efforts.

5.7 References

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7. Appendix

In addition to the research I have conducted and presented in the main body of this DPhil thesis, I have also contributed to other research projects. Below is a list of the published research I have been involved in over the course of my doctoral studies.

Publication 1 – Book chapter

Irving-Pease, Evan K., Hannah Ryan, Alexandra Jamieson, Evangelos A. Dimopoulos, Greger Larson, and Laurent A. F. Frantz. 2018. "Paleogenomics of Animal Domestication." In *Population Genomics*, 225–72. Cham: Springer International Publishing.

Publication 2 – Site report

Crégut-Bonnoure, Evelyne, Jacqueline Argant, Nicolas Boulbes, Jessica Cohen, Emmanuel Desclaux, Jean Fietzke, Alexandra Jamieson, Adam Nadachowski, Sophie Montuire, Maxime Pelletier, Florent Rivals, Thierry Roger, Loïs Woodthorpe. 2018. "Coulet des Roches (Monieux, Vaucluse)." *Rapport de fouille intermediaire.*

Publication 3 - Peer-reviewed article

Bergström, Anders, Laurent Frantz, Ryan Schmidt, Erik Ersmark, Ophelie Lebrasseur, Linus Girdland-Flink, Audrey T. Lin, et al. 2020. "Origins and Genetic Legacy of Prehistoric Dogs." Science, 370 (6516): 557–64.

Publication 4 – Peer-reviewed article

Perri, Angela R., Kieren J. Mitchell, Alice Mouton, Sandra Álvarez-Carretero, Ardern Hulme-Beaman, James Haile, Alexandra Jamieson, et al. 2021. "Dire Wolves Were the Last of an Ancient New World Canid Lineage." *Nature*, January.