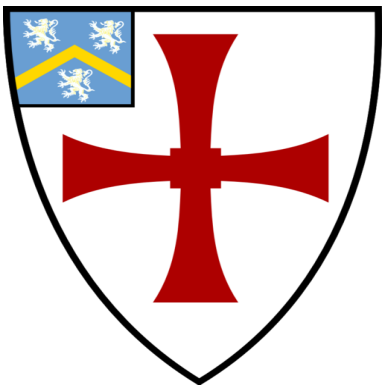
Investigating patterns of animal domestication using ancient DNA

Erik Linus Girdland Flink

A Thesis presented for the degree of
Doctor of Philosophy



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2013

Dedicated to

Julie, my family and friends.

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Abstract

Animal domestication is a continuous but nonlinear evolutionary process that follows different paths (trajectories) of human-animal relationships. These paths vary in structure and intensity over time and include processes like human intentionality (such as control and taming of wild animals), directed selection on behavioral and phenotypic traits and characters, human-mediated movement of domestic herds across space (migration), wild-domestic admixture, and adaptation. Because domestic animals are continuously shaped through complex interaction of these processes, gaining a better understanding of where, when and how these took place helps clarifying human prehistory and the practice and process of domestication.

Studies of modern and ancient DNA (aDNA) have recently disentangled the history of several domestic species. These studies have often shown that domestication processes were far more complex than previously thought, often encompassing more than one independent domestication event, and continuously shaped by migration and admixture. Importantly, ancient DNA studies have convincingly demonstrated that inferring the past (for example, where, when and how domestication and selection took place) from the present (modern contemporary domesticates) is biased by comparatively recent events such as modern breed formation. Ancient DNA is therefore a key component in the reconstruction of where, when and how animal domestication took place.

This thesis aims to shed new light on pig and chicken domestication by analysing ancient DNA extracted from archaeological specimens from Europe and the Near

and Middle East. First, I find that pig domestication took place over a much wider temporal and geographical range than previously thought, and secondly that the current reference framework for inferring where and when pigs were domesticated (wild boar mitochondrial phylogeography) must be revised. In addition, I find that genetic variation in modern domestic chickens, to a great extent, is the result of recent rather than ancient events of admixture and strong human driven selection. Overall, these finds strengthen the presumption that genetic signatures in modern contemporary populations often provide misleading estimates of their ancient history. Across genes and species, therefore, this thesis demonstrates the effectiveness of using ancient DNA for resolving a range of different aspects of human prehistory and animal domestication.

Declaration

The work in this thesis is based on research carried out at the Ancient DNA laboratory in the Department of Archaeology, Durham University, England. No part of this thesis has been submitted elsewhere for any other degree or qualification. Others carried out some of the work and results presented in this thesis as part of a larger collaborative research project. This is fully acknowledged in the text (see declaration preceding chapter 2).

Acknowledgements

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Abbrevations

aDNA	Ancient DNA
bp	Base pair
BP/BC	Before present/Christ
DNA	Deoxyribo nucleic acid
hg	haplogroup
ht	haplotype
LGM	Last Glacial Maximum
PCR	Polymerase chain reaction
PPNA	Pre-pottery Neolithic A
PPNB	Pre-pottery Neolithic B
PN	Pottery Neolithic
SNP	Single nucleotide polymorphism
LBK	Linearbandkeramik Culture
YBP	Years before the present

Chapter 1

Introduction

1.1 Overview

This thesis uses ancient DNA as a means to examine various aspects of animal domestication. The two main objectives are: (a) to gain a better understanding of where and when pig domestication took place in West Eurasia by exploring mitochondrial phylogeography and population history of wild and domestic pigs in Europe and the Near and Middle East, and, (b) to explore different domestication trajectories of pigs and chickens by analysing genetic markers that are directly linked to different aspects of the process of their domestication (MC1R, TSHR, BCDO2 and the mitochondrial d-loop). Analyses of ancient DNA allows for the investigation of molecular genetic aspects of domestication by monitoring genetic changes through time and provide a means to bridge theoretical and technological aspects of traditional archaeological (and archaeozoological) and genetic research.

The thesis comprises four case studies (chapters 2-5) that each address specific hypotheses of pig or chicken domestication. Chapter 1 provides a general introduction and background to methodology and the history of domestic pigs and chickens (and the processes through which they were domesticated). I sum up the thesis in chapter 6 by discussing the thesis aims in the light of the results and conclusions presented

in chapters 2-5.

1.2 A brief definition of domestication and domestic animals

Domestication is a much discussed and widely studied topic in both biology and archaeology; from preoccupying Darwin in his work on natural selection and evolutionary theory (Darwin 1868) to being a central theme in archaeology and the study of the Neolithic transition (Price 2000). The Neolithic (or New Stone Age) was a phase in human evolution and social development that in part was characterised by the domestication of some of the most common and well known domestic species such as pigs (*Sus scrofa domesticus*), goats (*Capra aegagrus hircus*), sheep (*Ovis aries*) and cattle (*Bos taurus* and *Bos indicus*) (Clutton-Brock 1989, pp 10; 1999).

Despite a long research tradition, and despite efforts to understand important mechanisms underpinning a domestication process (e.g. molecular mechanisms underlying phenotypic diversity in farm animals, Andersson 2001), some basic questions concerning the definition of domestication and domestic animals remains unresolved (Clutton-Brock 1989; pp 10; Russel 2002). The most crucial of these questions is how one should define domestication and domestic animals in a simple and straightforward manner (Russel 2002; Rowley-Conwy 2003; Dobney and Larson 2006; Vigne et al. 2011; Vigne 2011). For example, where do domestication begin or end, and how do we distinguish a domestic animal from its wild relative?

This issue becomes clear when considering the earliest steps of animal domestication. For example, although some researchers claim that significant changes in shape and size occur within a few generations of initial domestication (Peters et al. 1999; 2005), others have suggested that this process may take several millennia (Ervynck et al. 2001). Differences in size and shape (measurements) is the most useful method to

distinguish wild from domestic animals (Ervynck et al. 2001). If attempting to identify where and when domestication began it is important to fully understand how these changes develop during a domestication process, but since it is somewhat unclear how rapid the morphological changes occur, it is still unclear precisely when domestication first occurred (Peters et al. 1999; Ervynck et al. 2001). Consequently, our understanding of domestication from a theoretical and conceptual perspective relies to a great extent on interpretations drawn from archaeozoology and its account (or narrative) of the early domestication process.

In the broadest sense, the concept of domestication comes from the study of how people develop, adopt and embed technological artefacts into their daily lives (Harty 2007). People control and manage the domestic objects (including, then, domestic animals) incorporated into human society. The definition can be expanded to include various cultural (techno-economic and social-symbolic) contexts within human societies, suggesting there is a critical difference between animals as a resource and animals as property (Russel 2002; Vigne et al. 2011). In addition, because a domestic animal is a living organism, the process of animal domestication encompasses human control over a biological system (or an organism). Animal domestication is therefore both techno-cultural (techno-economic and social-symbolic) and biological (Russel 2002; Mignon-Grasteau et al. 2005).

Consequently, the most basic assumption underpinning any definition of what constitutes a domestic animal is that there is "wild" and "domestic". Together these opposites form a wild/domestic dichotomy (Uerpmann 2008; Vigne 2011). According to the Oxford dictionary, wild and domestic equals "not domesticated or cultivated" and "tame and kept by humans", respectively, clearly supporting the idea of wild/domesticated as a dichotomy. This definition therefore assumes that the negation of one term necessarily implies the other: an animal is either wild or domestic (Dobney and Larson 2006). However, the wild/domestic dichotomy is sometimes problematic and even misleading when considering animals that may live their lives under various degrees of human control (or various degrees of domestication). Some

researchers therefore prefer to ignore this narrow categorisation in favour of a continuum, or spectrum, of animal-human relationships, thereby accounting for the wide variety of possible "domestic" states an animal may be in (Russel 2002; Dobney and Larson 2006; Zeder et al. 2006; Zeder 2006).

Vigne (2011) presents a possible solution to this dilemma by considering varying states of intensity in the relationship between humans and animals along an axis of variation (a scheme similar to that of Zeder 2006) (figure 1.1). This model takes into consideration the dynamic nature of domestication and recognise that populations can move, over time, in both directions along the proposed axis.

For archaeozoological materials, one approach to identify the varying states or degrees of domestication is to identify demographic profiles comprising age/sex ratios (Zeder 2006; 2008). The method relies on the assumption that humans, by interfering with essentially wild populations, significantly alter the demographic profile as compared to that of a truly wild, or non-managed, population. This approach, including the definitions presented by Vigne (2011) (figure 1.1), could well reflect realistic situations known from anthropological data, such as a recent study of pig populations on contemporary Papua New Guinea (PNG) (Hide 2003).

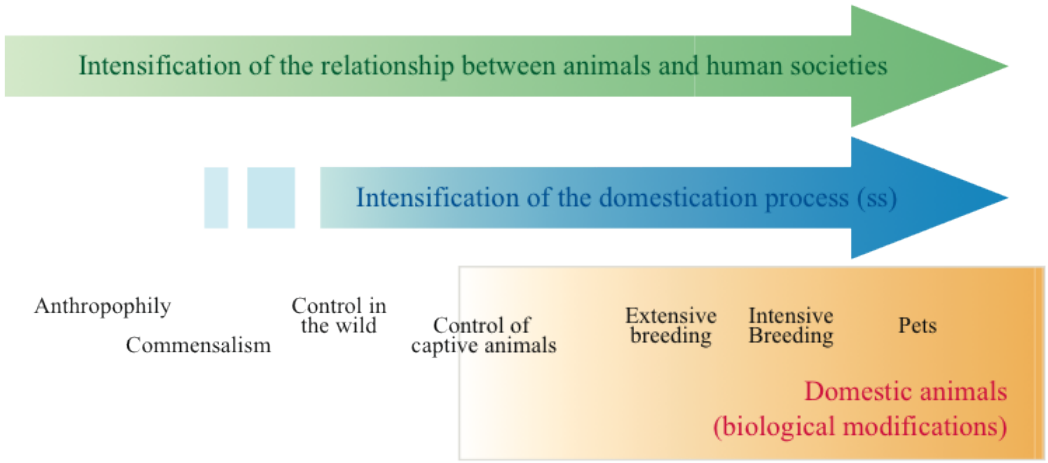


Figure 1.1: A dynamic framework that depict the varying states of domestication, (from Vigne 2011).

Hide (2003) surveyed domestic, and to some extent wild/feral, pig husbandry across PNG. He described a dynamic system where domestic pigs are captured as wild piglets and subsequently tamed, living the remaining of their lives as "domestic" pigs. He further describes a crossbreeding system in which domestic male offspring are castrated in order to avoid mating with domestic sows, allowing domestic sows to only mate with wild boar. Hide (2003) also provides examples of human management through castration of captured wild piglets that are subsequently earmarked, released and saved for future hunting, demonstrating that a rather complex system of human control and management is exerted over the reproduction cycles of the wild (or feral) populations. Importantly, he noted that while there was constant gene flow between the free roaming feral population and the village domestic populations, the physical appearance of domestic pigs remained similar to that of the feral (or wild) population. Morphological change, including traditional domestic traits such as coat colour and overall body shape, occurred rapidly in the absence of wild-domestic gene flow (Hide 2003). This observation is important to keep in mind in the light of the wild/domestic determination issues involved with archaeological materials (Albarella et al. 2006a, b; 2009; Vigne et al. 2009; 2011).

appearance of dwarf and giant varieties	all
piebald coat color	all
wavy or curly hair	sheep, poodles, donkeys, horses, pigs goats, mice, guinea pigs
rolled tails	dogs, pigs
shortened tails, fewer vertebrae	dogs, cats, sheep
floppy ears	dogs, cats, pigs, horses, sheep, goats, cattle
changes in reproductive cycle	all except sheep

Table 1.1: Morphological change associated with domestication and selection for tameness (from Trut 1999).

The definitions of domestication can also be more intricate and include a full suit of perquisites that must be fulfilled in order to consider an animal fully domestic

(as do Vigne 2011). For example, Diamond (2002) defines a domestic animal, and animal domestication, as:

> "[...]a species bred in captivity and thereby modified from its wild ancestors in ways making it more useful to humans who control its reproduction and (in the case of animals) its food supply. Domestication is thus distinct from mere taming of wild-born animals."

Uerpmann (2008) elaborates further on the function of taming during domestication by listing a three-stage model of a domestication process where taming is central:

1. Gaining complete control over individual animals, preferably by taming.
2. Assembling tamed (or otherwise controlled) groups of animals containing both sexes and keeping them together over periods long enough to start intra-group breeding.
3. Continued intragroup breeding of the tame (or otherwise controlled) stock and avoiding large-scale crossbreeding with the wild population.

Are the tamed wild pigs on PNG (Hide 2003) domestic, then? The main issue is that domestic animals are not necessarily tame (although probably derived from animals that were once tamed), and tame animals are not necessarily domestic (Clutton-Brock 1989, pp 10; Vigne 2011). Russel (2002) neatly summarise the differences between tame and domestic as follows:

> "[...]taming is a relationship between a particular person and a particular animal without long-term effects beyond the lifetime of that animal. Domestication is a relationship with a population of animals that often leads to morphological and behavioural changes in that population".

Interestingly, by selecting for mere tameness over 45 generations, a captive population of Russian silver fox (*Vulpes vulpes*) developed fully behaviourally and morphologically domestic traits, similar to those observed in domestic dogs (*Canis lupus familiaris*) and domestic pigs (table 1.1) (Trut 1999; Albarella et al. 2006a, b). The behavioural traits observed in the domestic population include reduced aggressiveness, seeking contact with humans at an early age, and prolonged periods of playfulness - characteristics resembling the retention of juvenile traits. The morphological traits included floppy ears, rolled tails, shorter tails, and changes in skull shape (shortening of the snout and crowded tooth rows), again in resemblance to what is observed in most domestic animals (Trut 1999). Some of these changes are analogue to morphological changes in the skeleton used to identify domestic animals in archaeozoological contexts (table 1.1) (e.g. Rowley-Conwy 2003; Albarella et al. 2006a, b). These observations indicate that the phenotypic changes observed during domestication could be linked with selection for tameness (Trut 1999).

Could this mean that the intricate definitions of domestication, as outlined above, are overly complex? The selection for tameness is perhaps analogue to the intensification step usually ascribed as the key turning point in the human-animal relationship that differentiate domestication from mere human control over wild populations (figure 1.1). This would include intense human control over all (or most) aspects of an animals life, including human-driven selection for tameness (or reduced aggressiveness). This fits to an extent with a three-stage model proposed by Uerpmann (2008). Uerpmann (2008) assumes that important aspects of the life of a domestic animal, like behaviour, nutrition, reproduction, range of movements and life span are in the hands of humans alone. Wild animals, on the other hand are independent (not under human influence) in all these aspects.

Recent archaeozoological data indicate that domestication is the end product of an intensification of animal-human relationships and that it primarily marks human intentionality (Zeder 2006; 2008; Vigne et al. 2009; 2011). According to this view, domestication is a phase following the management of essentially wild animals (a

management phase in which humans are actively in control of fundamental parts of an animals life cycle) (figure 1.1). In archaeolozoological materials, the intensification (or domestication) step is reflected in morphological (both size and shape) changes (Rowley-Conwy 2003).

In summary, domestication can be seen as the end product of the intensification of the relationship between animals and human societies (into which animals have been incorporated as domestic objects). Various management strategies of wild and domestic populations might lead to intermediate states in which animals are neither fully wild nor domestic (figure 1.1). Whether a model such as the three-stage model proposed by Uerpmann (2008) is necessary to account for the occurrence of fully behaviourally and morphologically domestic animals is questionable. However, it is clear that domestication is a process that takes place over several distinct phases and that animals diverge, both behaviourally and morphologically, from their wild ancestors at some stage during the domestication process.

1.3 Genetics of animal domestication

Domestication research has long-standing traditions in both zoology/evolutionary biology (e.g. Darwin 1868) and archaeology (Childe 1925; Rütimeyer 1862). As such, domestic animals are not only proxies for human-driven processes like domestication (as it occurred in relation to human evolution) and human migration, but also model organisms for evolutionary genetic studies (Darwin 1868; Wright 1978; Andersson 2001; Wiener and Wilkinson 2011). For example, domestic animals display a wide array of phenotypes in comparison to their wild ancestors (Andersson 2001), including coat color variability (Eriksson et al. 2008; Fang et al. 2009; Sheppy 2009), behaviour (Jensen 2006; Campler et al. 2009) and fat deposition (Van Laere et al. 2002). The short time-scale over which these phenotypes (or genetic mutations) have accumulated makes domestication and animal domestication a suitable model for studying evolutionary mechanisms underlying genotypic and phenotypic

variability (Andersson 2001; Ludwig et al. 2009; Galibert et al. 2011).

1.3.1 Genetic variation in domestic animals

Three major processes shape genetic variation in domestic populations (Mignon-Grasteau et al. 2005):

1. Inbreeding, which is the process by which genetic variability is reduced due to mating of genetically closely related individuals.
2. Selection (or artificial selection), which is the process by which humans control the breeding of animals in order to create a population with desired traits.
3. Genetic drift, which is stochastic variability in allele frequencies due to random sampling.

However, other evolutionary mechanisms have had impact on the genetic composition of domestic animals. For example, domestication leads to a relaxation of selective constraints that subsequently elevates the accumulation rate of non-synonymous mutations (phenotypes), which most often would have been subject to purifying selection and elimination in natural wild populations (Björnerfeldt et al. 2006; Cruz et al. 2008; Fang et al. 2009; Wang et al. 2011). Subsequent human-driven selection on novel mutations caused the wide variety of phenotypic variability present in domestic populations (Andersson 2001; Fang et al. 2009; Ludwig et al. 2009). Other human-driven processes that have shaped genetic and phenotypic variation in domestic animals include breed formation (a strict form of artificial selection where animals are divided into groups, or breeds, as defined by certain phenotypic traits) and wild-domestic admixture (Taberlet et al. 2008; Akey et al. 2010; Groeneveld et al. 2010).

Investigating these processes in a spatiotemporal context is useful for reconstructing the history of a domestic species. Svensson et al. (2007), for example, revealed small but significant decline over time of homo-, and heterozygosity in the IGF1 and MC1R genes in domestic cattle and was able to link this observation with historical records of human-driven selection and breed formation.

In some cases, domestic phenotypes can be directly associated with a single point mutation in a specific gene (a single nucleotide polymorphism or SNP). SNPs are suitable for aDNA studies, as they require only short fragments to be PCR amplified prior to sequencing (Svensson et al. 2007; Leonard 2008; Daskalaki et al. 2011). By genotyping SNPs linked with specific phenotypes in ancient materials, several recent studies have successfully examined phenotypic diversity in ancient populations (Götherström et al. 2005; Bollongino et al. 2008a; Svensson et al. 2008; Ludwig et al. 2009; Asplund et al. 2010; Malmström et al. 2010).

1.3.2 Phylogeography

A common methodological approach in animal domestication studies is phylogeography of the circular, non-recombining, and maternally inherited mitochondrial genome (mtDNA) (Savolainen et al. 2002; Larson et al. 2005; Liu et al. 2006; Naderi et al. 2006; Pang et al. 2009). The field of phylogeography connects genealogy and geography with the aim to reconstruct the historical events that led to the contemporary spatial arrangement of genetic lineages (Avise et al. 1987; Avise 2000; 2009). By comparing mtDNA signatures in domestic populations with those found in wild populations it is possible, in case there is a correlation between phylogenetic structure and geographic location, to identify the wild populations and geographic regions ancestral to domesticates (Giuffra et al. 2000; Larson et al. 2005).

The phylogeographic method has been useful in aDNA studies addressing the spatiotemporal origin and dispersal of domesticates in West Eurasia. For example,

Larson et al. (2007a), Bollongino et al. (2006; 2007), Edwards et al. (2007) and Beja-Pereira (2006) showed that the earliest domestic pigs and cattle in Europe were introduced from the Near East during the Neolithic transition. The early Neolithic domesticates were genetically dissimilar to the local wild boar and aurochs populations. In the former example the distinctive mtDNA Y1 haplotype is absent in modern contemporary domestics but ubiquitous across modern wild boar from the Near East and in ancient domestic pigs from Europe.

These papers, alongside studies of ancient dog mtDNA by Malmström et al. (2008) and Deguilloux et al. (2008), also show that mtDNA lineage replacement was common in pre-historic Europe and that ancient DNA is key for reconstructing an accurate population history. Recent studies of ancient DNA from horse (Cieslak et al. 2010; Lira et al. 2010) and goat (Fernandez et al. 2006) have also revealed detailed insights into these species early history. Fernandez et al. (2006), for example, found that two divergent mtDNA lineages (A and C) segregated in an early Neolithic population in southwest France and hypothesized that substantial gene flow occurred continuously during the Neolithic expansion in Europe.

1.4 Background to pig domestication

Where, when, how and why pigs were domesticated has been the focus of intense study and debate for nearly two centuries. The primary contribution to our understanding of pig domestication comes from traditional archaeozoological research (and methods) that relies on comparative metric and morphological analyses of ancient and modern bones (Albarella et al. 2006a; Rowley-Conwy and Dobney 2007). Recent methodological advances in geometric morphometrics (e.g. Cucchi et al. 2010) have broadened the possibilities to characterize and distinguish groups of ancient wild and domestic pigs, especially if coupled with ancient DNA (Larson et al. 2007b). More recently, the ongoing development of DNA sequencing techniques has allowed for large-scale genetic studies of pig domestication using modern spec-

imens (Larson et al. 2005; Ramirez et al. 2009). These studies have provided an interpretive framework for ancient DNA studies (Larson et al. 2007a, b; Haile et al. 2010).

1.4.1 Traditional archaeological perspectives

Pig domestication formed part of the Neolithic transition and has been subject of intense archaeozoological research. Perhaps the most well known early contribution was Rütimeyers in the 1860s. Rütimeyer (1862) investigated pig bone remains from Swiss Neolithic lake dwellings and determined the wild and domestic status of the remains based on biometric variability, assuming that wild boar could readily be separated from domestic pigs on size alone (effectively forming two separate, bimodal, groups with little overlap).

The reliability of size criteria to determine wild and domestic status has been crucial since unlike sheep and goats, whose wild ancestors are confined to a relatively small geographic region in the Near East, the natural range of wild boar covers most of Eurasia. Any sheep or goat remains found associated with archaeological contexts in Europe can be identified as domestic specimens given the geographic distance to the nearest wild ancestor (Clutton-Brock 1999). The ubiquity of wild boar, and the significant degree of size variability within wild populations across Eurasia (Albarella et al. 2009), however, has prevented archeologists from confidently assigning wild and domestic status calls to recovered *Sus* remains. This is especially true of long bones, though some teeth, particularly the M3 and M2 can more reliably be used as a domestication marker given the relative lack of plasticity in the dentition. This material, alongside additional methods that take into account demographic profiles of the studied population by investigating population statistics such as age and sex ratios and average species abundance (Bull and Payne 1982), have been used to bolster the robustness of status determinations (Rowley-Conwy and Dobney 2007).

However, domestication is a continuous process (Dobney and Larson 2006) and forcing bone and teeth remains into static and dichotomous categories denies that reality. Archaeozoology is uniquely placed to investigate the morphological shifts that occurred during the early stages of domestication. Ervynck et al. (2001) examined pig bones from early Neolithic layers from the eastern Anatolian site of Çayönü Tepesi, and by determining the relative sizes of lower M3s they found a gradual decrease in size over two millennia. This pattern, they suggested, was the result of a protracted domestication process in situ, and that fully domestic pigs only emerged approximately 9,000 cal BP.

The evidence at other sites in the Near East has also demonstrated that pig domestication took place there perhaps earlier than anywhere else, though the details remain contentious. It has been argued that the initial intensification of human-wild boar relationship at the southeastern Anatolian site of Hallan Çemi took place around 13,000-12,700 cal. BP (Redding and Rosenberg 1998; Rosenberg et al. 1998; Redding 2005), though these interpretations have been questioned (Peters et al. 1999; Ervynck et al. 2001). Clear evidence for the presence of domestic pigs has been argued for other Early Neolithic sites in the region including Hayaz Tepe, Tell Halula, and Gürcutepe (Peters et al. 1999) but these conclusions have also been questioned (Ervynck et al. 2001). Lastly, a rapid decrease in body size dated to approximately 10,500 cal. BP could suggest that humans controlled, and perhaps directed, breeding at the site of Nevali Çori in Eastern Anatolia (Peters et al. 2005).

Recently published radiocarbon dates on pig bones from the Cypriot site of Akrotiri Aetokremnos have shown that the remains date to at least 11,400 cal. BP (Vigne et al. 2009). These findings suggest that humans must have introduced a wild boar population when they colonised the island, which in turn implies an early, and strong relationship between humans and wild boar, and that this exertion of control over a wild boar population may have been an early phase of the domestication process.

A great deal of evidence suggests that prehistoric deliberate movement of wild and domestic populations of pigs, especially in the Mediterranean, was not unusual (Al-

barella et al. 2006a). The Cypriot (and Mediterranean) example is also similar to the situation on Gotland, an island in the Baltic Sea on which numerous Neolithic pig bones have been found (Rowley-Conwy and Dobney 2007). Whether or not the Gotland pigs were wild, wild-domestic hybrids, feral, or fully domestic pigs, has been subject of a long and intense debate. Radiocarbon dating suggests that pigs were brought to Gotland during the Neolithic (Lindqvist and Possnert 1997). Some favour the argument that these pigs were domestic based on the large quantities of skeletal remains in graves (Österholm 1989), or solely by the fact that they were brought to the island by humans (Jonsson 1986). Biometric analysis has led others (Ekman 1974) to suggest that the Gotland population was wild, and this was also argued in later work (Rowley-Conwy and Dobney 2007). Jonsson (1986) argued that the pigs were wild-domestic hybrids. Clearly, this is still an unresolved question that, when resolved, will allow us to gain a much better understanding of pig-human relationships in pre-historic Europe.

More generally, there is no question that wild boar were domesticated in the Near East and East Asia (Jing and Flad 2002), but the degree to which European wild boar were locally domesticated, either independently or as a consequence of earlier introduction of domestic pigs from the Near East (Albarella et al. 2006b; Larson et al. 2007a) remains uncertain. It has been argued that local domestication, or deliberate wild-domestication hybridisation, was rather common in prehistoric and historic Europe (Bökönyi 1974), though it is possible that the size variations on which Bökönyi relied upon to infer instances of local domestication were the result of natural size variation in wild *Sus* populations (Albarella et al. 2009). Dinu et al. (2006) investigated the hypothesis of Mesolithic and Early Neolithic pig domestication in the Iron gates region but found no evidence to support either domestication or human management of wild populations.

These examples demonstrate the difficulty archaeologists have had in determining the true status of pig remains, and because so many of the major questions related to pig domestication (when did it occur, did it take place independently in different

regions, etc.) require accurate status calls, the lack of certainty around this issue has prevented confident answers from being obtained. The archaeological approach has established the basic pattern of pig domestication across Eurasia, and has been particularly successful at investigating the domestication process and the effects of that process on gross morphology of individual pigs. What the archaeologists traditionally lacked, however, was an ability to unambiguously ascertain differences between geographically differentiated wild boar populations.

1.4.2 Modern genetic perspectives

The primary genetic marker used in pig domestication studies is the mitochondrial genome (usually the control region or the cytochrome b gene). These regions evolve fast enough to capture genetic variability in closely related populations, over relatively short time scales, but slowly enough to retain phylogenetic signals (Avise 2009). Our understanding of pig domestication from a genetics perspective is largely based on mitochondrial phylogenetic and phylogeographic studies (Alves et al. 2003; Giuffra et al. 2000; Larson et al. 2005; 2007a, b; 2010; Ramirez et al. 2009). Mitochondrial DNA is also suitable for ancient DNA studies because it is present in multiple copies per cell, and this increases the probability of its survival and retrieval (Binladen et al. 2006).

Giuffra et al. (2000) published the first major genetic study on wild and domestic pig phylogeography. By analysing mitochondrial DNA in addition to three nuclear genes, they found that European wild boar and East Asian wild boar were genetically distinct (comprising three main lineages; E1 and E2 in Europe and A in East Asia). Domestic pigs from these two regions possess genetic signatures that closely match the local populations of wild boar, supporting the hypothesis of separate origins for modern Eurasian pig breeds.

Larson et al. (2005) expanded upon this study by investigating the genetic variation

found in wild boar distributed across Eurasia. The increased resolution of the genetic data revealed that, despite the natural migration of wild boar and the long history of human-assisted movements of both wild and domestic populations, the vast majority of wild boar possessed a signature that was unique to the geographical area from which they derived. This strong phylogeographic structure revealed more than 14 distinct and well supported genetic groupings of wild boar (figure 1.2).

More significantly, by comparing the DNA of domestic pigs with that of the wild samples, Larson et al. (2005) were able to identify six different regions in which the local domestic pigs and the local wild boar shared unique mitochondrial lineages. This implied that either local wild boar had been independently domesticated, or that local wild boar had contributed maternal DNA to imported domestic stocks after they had been domesticated elsewhere (through wild-domestic hybridisation). For example, on a smaller geographical scale, certain mutation motifs in the mitochondrial genome suggest that some Iberian pig breeds can be distinguished from non-Iberian breeds (Alves et al. 2003; Ramirez et al. 2009). The process that led to this pattern remains unknown, but it could imply contribution of local genetic material to the domestic stock.

Another finding of the Larson et al. (2005) publication was the general lack of shared haplotypes between European domestic pigs and Near Eastern wild boar. The phylogeographic patterning suggested that wild boar from continental Europe differed significantly from those in the Anatolian peninsula and the Near East (marked red/orange and yellow, respectively, in figure 1.2), and the archaeozoological evidence suggested that, though pigs were first domesticated in the Near East, they were later introduced into Europe during the Neolithic expansion (marked specifically by the introduction of the Y1 and possibly Y2 haplotypes). Because modern European domestic breeds clustered with European wild boar (i.e. lacking the Y1 and Y2 haplotypes), this result implied that the first pigs introduced by Neolithic farmers had at some point been replaced by European pigs descended at least maternally from European wild boar.

This narrative rests on the assumption that the natural geographic ranges of wild boar possessing Near Eastern and European signatures have remained relatively isolated since at least the beginning of the Holocene (approximately 11,500 YBP). If the European genetic motif was naturally present in wild boar populations in the Near East, then Early Neolithic farmers from the Near East could have domesticated this type and a secondary domestication in Europe would no longer be necessary to explain the modern pattern (and vice versa).

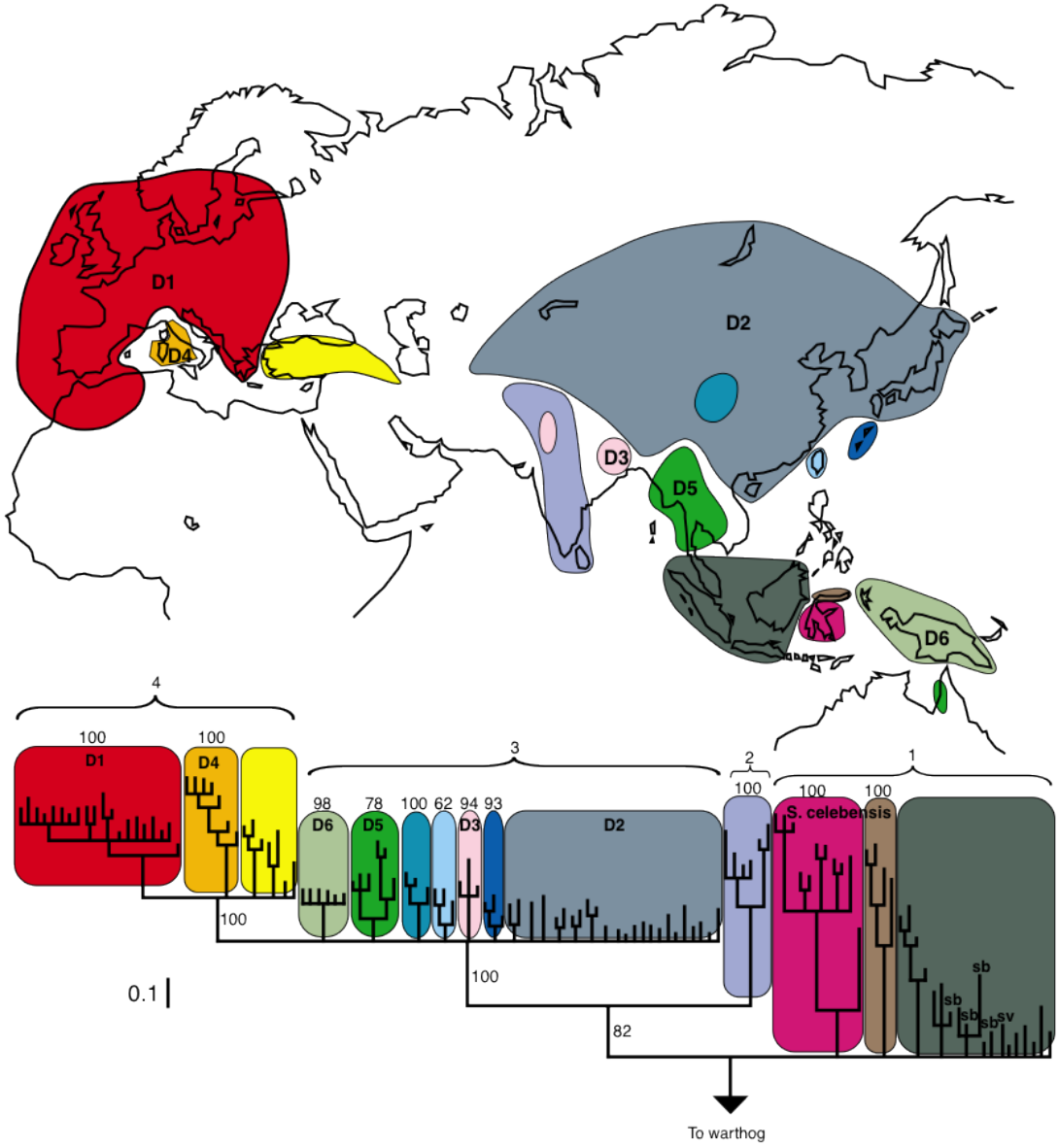


Figure 1.2: Modern mitochondrial phylogeographic structure of the Eurasian wild boar (*Sus scrofa*) (from Larson et al. 2005).

The low frequency of wild boar in the Near East with European signatures has led some to suggest that the phylogeographic structure is not as dichotomous as Larson et al. (2005; 2007a) proposed. Ramirez et al. (2009) suggested that the occasional inconsistency within the general phylogeographic pattern could be due to the natural admixture of wild boar populations, and not a consequence of human-mediated translocation of domestic pigs that subsequently became feral, as has been suggested by Larson et al. (2005; 2007a). Ramirez et al. (2009) supported their argument with a nuclear microsatellite analysis, the results of which demonstrated that European, Near and Middle Eastern, and North African wild boar populations cluster into a single group, despite the fact that the mitochondrial haplotype frequencies within these samples differ markedly. They argued that since mitochondrial DNA is more prone to extinction on shorter time scales (due to genetic drift), the observed haplotype frequencies in modern populations could be due to recent demographic events. Because domestic pigs have been known to become feral (Albarella et al. 2006a), ancient introgression, as suggested by Larson et al. (2007a), cannot be ruled out as the cause of the observed discrepancies within the phylogeographic pattern, or a combination of both hypotheses.

Regardless of whether the exceptions to the phylogeographic rule (or Bosporus barrier hypothesis) are the result of natural or human-mediated processes, the extent to which domestic pigs introgressed with European wild boar remains unknown. It would be impossible to resolve these issues using modern DNA alone (Larson et al. 2005; 2007a). Ancient DNA, derived from the bones of archaeological pig remains, however, could provide the necessary temporal framework to reveal not only the genetic affinities of the first domestic pigs introduced into Europe, but also, whether or not the process of European domestication was truly independent or facilitated by the introduction of Near Eastern pigs.

1.4.3 Ancient DNA perspectives

A great deal of the genetic understanding of Near Eastern and European pig domestication rests on the assumption of temporally consistent phylogeographic patterns (see above). By extracting DNA from archaeological material from the Near East to West Europe, and from 10,000 years ago to the present, Larson et al. (2007a) were able to directly test pig domestication hypotheses and reveal the temporal and geographic pattern of pig haplotypes.

Their results firstly demonstrated that no wild boar in Europe dated to before the arrival of the Neolithic possessed haplotypes hypothesised to be geographically restricted to the Near East (see Larson et al. 2005). In fact, the only Mesolithic wild pigs that did possess haplotypes that phylogenetically clusters with modern Near Eastern wild boar were from the Crimea, suggesting that the biogeographic boundary located near the Bosporus strait (figure 1.2) was intact at the beginning of the Holocene. This geographic split between the genetic signatures of wild boar on each side of the boundary then allowed for the test of whether the first domestic pigs in Europe were brought in from the Near East, or were domesticated from wild boar indigenous to Europe. In several archaeological sites from Romania near the Black Sea coast, and at the site of Eilsleben in Germany (Whittle 1990), every pig identified as domestic using morphometric criteria possessed haplotypes that are identical to haplotypes endemic to the Near East, and every wild boar possessed a genetic signature believed to be European. The same was true at the Neolithic site of Bercy in France (dated to approximately 4,000 cal. BC) (Balasse and Tresset 2002), except for a single domestic pig that possessed a haplotype that phylogenetically groups with European wild boar.

Both medieval and modern pigs from the island of Corsica, however, still retain a Near Eastern maternal genetic affinity (haplotype Y2), suggesting that they are the sole European pigs to retain the inheritance of the first pigs introduced to Europe during the Neolithic. Even more intriguingly, domestic pigs in the Near East re-

tained their Near Eastern ancestry until at least 700 cal. BC, after which, they too, were replaced by pigs derived from European wild boar. The presence of different haplotypes along the purported northern and southern Neolithic expansion routes into Europe also seemed to suggest that different lineages of pigs were transported along these two routes, but the number of samples was too small to conclusively demonstrate this potential correlation.

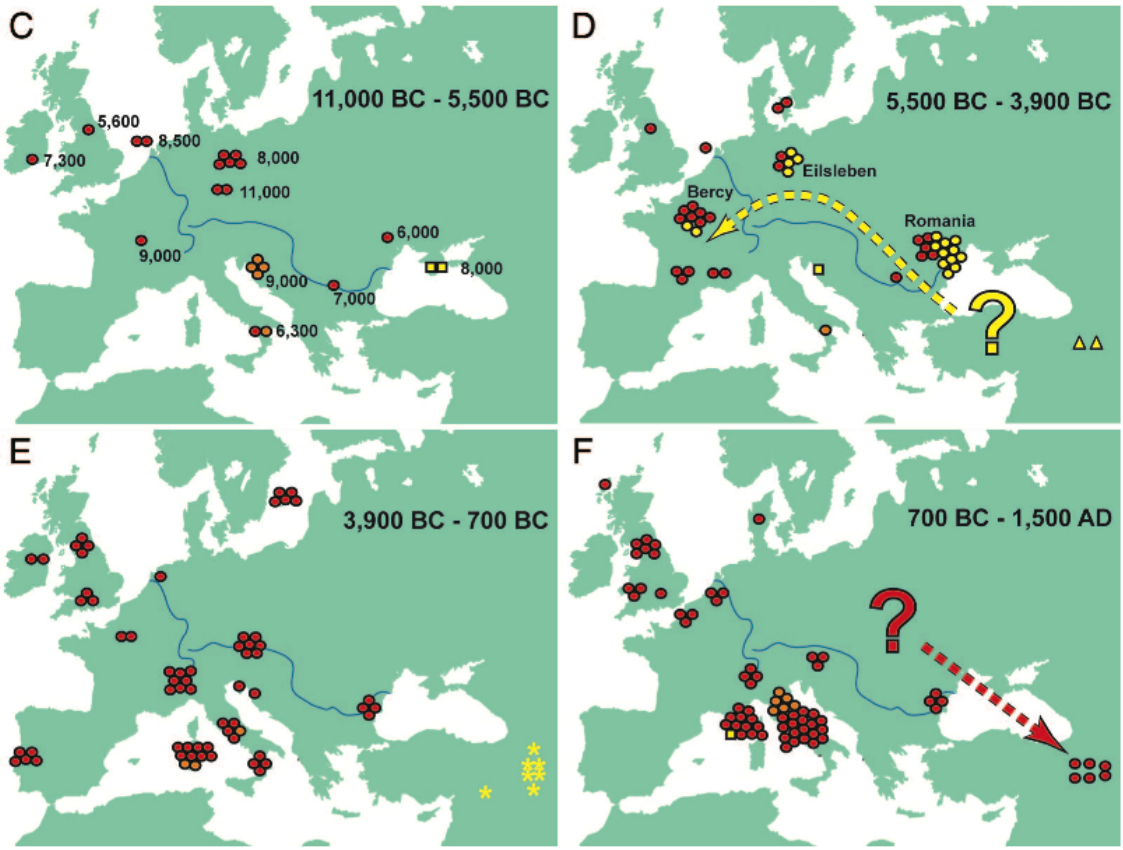


Figure 1.3: Previously published ancient pig mtDNA data from West Eurasia. Colour codes correspond to figure 1.2. From Larson et al. (2007a).

Despite the insights these ancient DNA studies on pigs revealed, a number of questions remain unanswered. First, it is entirely possible that additional genetically distinct populations existed in Europe and that the phylogeographic patterning of wild and domestic pigs will undergo additional revision as more samples are analysed. The increased temporal and geographical resolution of future studies will establish more firmly the genetic continuity between Europe and the Near East. These data will help to establish whether the observed modern genetic patterns are

due to admixture of wild populations without the involvement of humans, or human mediated translocations that also resulted in feralisation and subsequent admixture. Secondly, the extent to which the European pig domestication was independent or stimulated by the introduction of Near Eastern domestic pigs still remains unknown. The currently published data suggests that European domestication followed the introduction of Near Eastern domestic pigs, though it would only take the discovery of a single, clearly domestic pig remain from a securely dated context, which predates the introduction of Near Eastern pigs to Europe, to establish the independence of European pig domestication.

1.5 A brief history of domestic chickens

Domestic chickens (*Gallus gallus domesticus* or, alternatively, *Gallus domesticus*) are alongside dogs, pigs, cattle and sheep and goats, the most widespread and numerous domestic animals in the world (see further discussion on the naming of domestic chickens in Gentry et al. 2004 and Eriksson et al. 2008). Chickens have both socioeconomic (broiler and egg-layers) and cultural and symbolic value (e.g. cock fighting) (Zeuner 1963; Groeneveld et al. 2010). However, chickens were likely domesticated at a late stage relative to the most common domestic species, and their true origin, both spatiotemporal and biological, remains disputed (Zeuner 1963; West and Zhou 1988; Eriksson et al. 2008; Sawai et al. 2010). By addressing where, when and how chickens were domesticated and dispersed around the globe it is possible to gain detailed information of the patterns and timing of human migrations (West and Zhou 1988; Storey et al. 2007; 2010; Gongora et al. 2008).

Chicken domestication studies have relied on multiple lines of evidence to address these broadly defined questions (where, when and how). The attempts to decipher the true origin of chickens have included comparative studies of phenotypes, controlled breeding (cross-species hybridization) (see Darwin 1868), studies of mitochondrial and nuclear genomic DNA (Liu et al. 2006; Sawai et al. 2010) and

archaeozoology (West and Zhou 1988).

Despite the ongoing discussions, it was early recognized that chickens were domesticated from either of four species in the genus *Gallus*, which inhabits South and Southeast Asia: the Red jungle fowl (*G. gallus*), the Grey junglefowl (*G. sonnerati*), the Green junglefowl (*G. varius*), or La Fayettes junglefowl (*G. lafayetii*) (figure 1.3). The central question since Darwin (1868) has revolved around whether domestic chickens were domesticated from one or several subspecies; the single-species versus multiple-species hypothesis (Liu et al. 2006; Eriksson et al. 2008; Sawai et al. 2010), but also when domestication first took place (West and Zhou 1988).

A phylogeographic study of mitochondrial d-loop variation in wild Red junglefowl, comprising a sample of *G. g. gallus, G. g. spadiceus, G. g. bankiva*, combined with samples of Green and Grey junglewfowl, Lafayettes junglefowl, and several domestic populations indicated that domestic chickens are solely derived from the Red junglefowl. It was argued that chickens probably originated from a single domestication event from *G. g. gallus* in Thailand and adjacent regions (Fumihito et al. 1994; 1996). A more recent phylogeographic study comprising a large sample of worldwide domestic chicken populations and several species of *Gallus* revealed a large number of informative haplotypes structured in nine clades designated A-I (Liu et al. 2006). Based on the phylogenetic and phylogeographic structuring of the major clades, Liu et al. (2006) concluded that; (1) the sole maternal ancestor of the domestic chicken is the Red junglefowl (*Gallus gallus*), in agreement with Fumihito et al. (1996), and (2), that the geographic patterning of genetic variability probably reflects multiple independent domestication events stretching an area from the Indus Valley in the west to Southeast China or adjacent areas in Vietnam, Burma or Thailand, which is in contrast to the findings of Fumihito et al (1996).

In more detail, worldwide domestic chickens generally belongs to mitochondrial clusters (or haplogroups) A, B and E, with hg E probably representing a domestication event in South Asia (Indus valley), and hg A and B a possibly independent domestication event in Southeast China (Liu et al. 2006). The geographic distribution

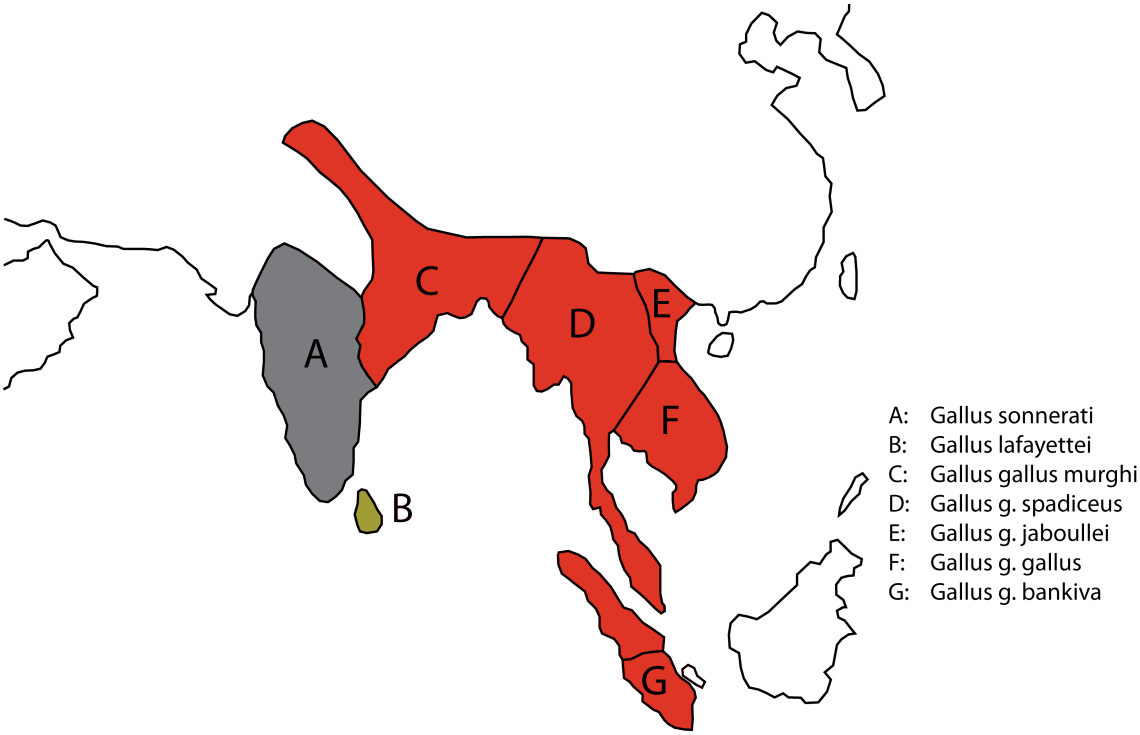


Figure 1.4: Geographic locations of wild junglefowl in South and Southeast Asia (modified from West and Zhou 1988). A=India, B=Sri Lanka, C=India, Bangladesh and South China, D=Burma (Myanmar), Thailand, Indonesia and South China, E=Vietnam, Laos and South China, F=Thailand, Laos, Cambodia and Vietnam, G=Indonesia.

of the remaining haplogroups is more restricted, but recent translocations and admixture with local breeds have seen a geographic spread of most haplogroups (Liu et al. 2006; Storey et al. 2007; 2010; Gongora et al. 2008; Dana et al. 2010). Following the discussion of Liu et al. (2006), however; the distribution of hg D is correlated with the occurrence of cockfighting in India, Indonesia, China and Japan, while haplogroup C is restricted to southeast China and Japan, solely containing domestic chickens and no wild Red junglefowl. Haplogroups F and G are exclusive to Southeast China and adjacent regions, while hgs H and I are restricted to a few specimens in Indonesia and Vietnam, respectively (Liu et al. 2006).

Phylogeographic studies incorporating ancient mitochondrial data from chickens has been of particular importance to the long-held discussion of the peopling of Island

Southeast Asia (ISEA) and Remote Oceania (Storey et al. 2007; 2010; Gongora et al. 2008). Temporally structured d-loop data recently provided direct insights into past and recent human migratory trajectories in Island South East Asia and Oceania (Storey et al. 2007; 2010), but the results, interpretations, and conclusions are fiercely debated (Gongora et al. 2008). One of the main disputes is whether the phylogenetically distinct E-clade was present in the region before the European arrival in the 16th century AD. Some argue that the E-clade was introduced with the first Europeans (Gongora et al. 2008) while others claim a much earlier introduction (Storey et al. 2007; 2010). However, despite the dispute surrounding the mode and timing of the arrival of E-clade chickens, both sides of the discussion make the underlying assumption that European chickens are historically associated with haplogroup E. This issue can only be resolved by direct sequencing of DNA extracted from ancient European chickens.

More recent genetic analyses of the chicken nuclear genome revealed that the Grey junglefowl also contributed genetic material to modern domestic chickens, thereby providing evidence in favour of the multiple-species hypothesis (Eriksson et al. 2008). Eriksson and colleagues found that the BCDO2 gene on chromosome 24 is associated with yellow skin pigmentation and identified a single SNP in complete linkage disequilibrium (non-random association) with the yellow skin phenotype across a panel of domestic breeds. Importantly, phylogenetic analysis of re-sequenced BCDO2 regions revealed that the *yellow skin* allele cluster with Grey junglefowl rather than Red junglefowl. Other nuclear regions provided no evidence of a hybrid origin and clustered with Red junglefowl, indicating that a minor genomic region isolated by subsequent recombination was selected for in a backcrossed domestic population of primarily Red junglefowl origin (Eriksson et al. 2008).

Mitochondrial data also somewhat surprisingly revealed that captive Grey junglefowl possess mitochondrial haplotypes derived from hybridisation with domestic chickens (haplotypes originally derived from Red junglefowl). Sawai et al. (2010) sequenced 30 introns at 25 different loci and showed that unidirectional gene flow have occurred

from domestic chickens to Green junglefowl and that, more importantly, continuous introgression of genetic material from the Red jungefowl into domestic chickens have occurred since the initial domestication. Thus, while the multi-species hypothesis seems plausible, the detailed account for number of introgression events, and from how many species, remains unknown (Sawai et al. 2010).

Genomic sequencing recently allowed the identification of a potential domestication locus; a gene variant that all domestic chickens carry at least one copy of. Specifically, Rubin et al. (2010) reported the identification of a SNP located in the thyroid stimulating hormone receptor locus (TSHR) on chromosome 5. They found that a variant (allele) of TSHR is fixed in virtually all domestic chickens, indicating that the sweep event occurred prior to any large-scale movements (human-mediated migration). The fixed allele is possibly linked with the absence of a strictly regulated reproductive season but further functional analysis of the TSHR region is required (Rubin et al. 2010). Importantly, however, the thyroid hormone was recently identified as possibly part of a series of regulatory changes in the endocrine system that seems to occur during the domestication process. These changes might be linked to domestic phenotypes and the retention of juvenile traits (Crockford 2002; Dobney and Larson 2006). The true function of the TSHR sweep allele remains hypothetical, despite the recent sequencing efforts. We therefore lack an empirical explanation for the fixation observed in all examined chicken populations.

1.6 Ancient DNA

Ancient DNA (aDNA) is a young research discipline. It was pioneered in the mid nineteen-eighties by Higuchi et al. (1984) who extracted and clonally amplified a 228bp mtDNA fragment from the extinct quagga (*Equus quagga*) and Pääbo (1985) who retrieved a *ca* 2,000bp fragment from an Egyptian mummy (although the results of the latter study were later re-interpreted as contamination, Pääbo et al. 2004). However, it was not until the advent of the PCR (polymerase chain reaction) amplification technique (Mullis and Faloona 1987) that aDNA research (and DNA sequencing overall) became more readily available.

Ancient DNA has three major properties that make it challenging to work with: contamination, fragmentation and degradation (Hofreiter et al. 2001a, b; Malmström et al. 2005; Gilbert et al. 2005; Briggs et al. 2007). All of these processes are somehow related to the taphonomic history of a bone (or any other source material used for ancient DNA extraction), i.e. all processes affecting an organism post-mortem (Lyman 1994; p 463).

Contamination is a common problem in aDNA studies and must be overcome in order to produce reliable sequence data (Cooper and Poinar 2001; Gilbert et al. 2005). The problem of contamination is predominantly restricted to human studies due to the abundance of modern, contaminant, human DNA in all steps of the analysis (Malmström et al. 2005; Linderholm et al. 2008), which leads to authentic DNA sequences becoming indistinguishable from contamination. This problem is less severe in studies of ancient animal DNA simply because modern animal DNA contaminants are less frequent. However, Leonard et al. (2007) observed low-level animal DNA contamination in PCR reagents and Bollongino et al. (2008b) found a sample of cattle bones to be contaminated by goat DNA. Contamination can occur at any stage of the aDNA analysis and it is therefore vital to minimise the risk of contamination at each step of the process.

DNA degrades over time. The age of a sample subject to aDNA analysis is of primary concern as time dependent processes of DNA degradation, like hydrolysis, are inevitable (Hofreiter et al. 2001a, b). However, the rate of degradation is first and foremost dependent on thermal conditions, salt levels and acidity of soil, background radiation and humidity (Lindahl 1993; Smith et al. 2003; Pruvost et al. 2008). Thus, age could be a very poor estimate of DNA preservation (Bollongino and Vigne 2008).

The degree of degradation (and therefore survival) of DNA is governed by a series of biological and chemical processes. Depurination and deamination through hydrolysis and digestion (fragmentation) caused by autolysis and bacterial attacks are among the most commonly occurring processes. The most common form of damage is deamination through hydrolysis resulting in the conversion of cytosine bases to uracil (alternatively hydroxyuracil). Uracil is read as thymine by DNA polymerases during PCR amplification and subsequently induce the common Type 2 (C->T/G->A transitions) damage (Höss et al. 1996; Gilbert et al. 2003; 2007). Hence, low template copy number combined with high frequencies of Type II damage can cause erroneous sequence data.

Fragmentation of DNA occurs post-mortem due to breaks in the sugar-phosphate backbone of the DNA molecule (Briggs et al. 2007). Though a poor estimate on its own (Briggs et al. 2009, but see Green et al. 2009), the shape of fragment length distribution may be regarded as a good proxy alongside other evidence of aDNA authenticity (Gilbert et al. 2005; Malmström et al. 2007; Green et al. 2009). The problem of fragmentation, and the inability to target long DNA fragments for PCR amplification, may be overcome by targeting specific SNPs. The short fragment length required for SNP genotyping could in turn allow for some flexibility in PCR primer design, and therefore specificity (Svensson et al. 2007; Daskalaki et al. 2011).

Most aDNA work follows the guidelines of Cooper and Poinar (2000) and Gilbert et al. (2005). The following list was published as a general framework for authenticating ancient DNA (Gilbert et al. 2005):

1. Isolation of work areas: to separate samples and extracted DNA from PCR amplied products.

2. Negative control extractions and amplications: to screen for contaminants entering the process at any stage.

3. Appropriate molecular behaviour: owing to DNA degradation, the successful amplication of large DNA fragments in ancient DNA studies should be treated with caution.

4. Reproducibility: multiple PCR and extractions should yield consistent results.

5. Cloning of products: to assess for damage, contamination and jumping PCR.

6. Independent replication: the generation of consistent results by independent research groups.

7. Biochemical preservation: preservation of other biomolecules that correlate with DNA survival (e.g. collagen or amino-acid racemization) should indicate good sample preservation.

8. Quantication: by competitive PCR or Real-Time PCR to give an indication of the number of starting templates in the reaction.

9. Associated remains: are associated remains equally well preserved, and do they show evidence of contamination?

1.7 Thesis outline and aims

The overall objectives of this thesis are (1) to gain a better understanding of where, when and how pigs were domesticated in West Eurasia (Europe and Southwest Asia) through analyses of mtDNA; and (2) to gain a better understanding of the mechanisms underlying the process of domestication (such as human intentionality and selection during early domestication) by examining genetic loci associated with domestic phenotypes. The second objective aims to provide a deeper understanding of animal domestication as a general biological and cultural process and comprises analysis of both chickens and pigs. To the extent that the objective of an analysis is to create a more comprehensive understanding of a particular course of events (domestication), it is important to portray specific events (such as selection and admixture) across species boundaries. This is especially important when dealing with genetic markers termed domestication genes (or domestication loci), which are believed to share a similar histories (selected for by people during the early course of domestication) irrespective of what species they belong to, but also important for general markers such as mtDNA, as these can provide important insights about the overall direction (or trajectory) of a domestication event of one species compared to that of other species. It is therefore possible that to some extent analyse genetic differences across different species with the objective of reaching a point where it is possible to discuss the process of domestication in general terms (such as described and discussed in section 1.2).

Chapter 2 concerns spatial and temporal mtDNA variation in wild and domestic pigs across Anatolia and the Near East. The main objective of this chapter is to gain a better understanding of where and when pigs were first domesticated by investigating genetic variation in ancient wild and domestic pigs from Anatolia (Near East) and the Middle East. I also test the hypothesis of whether people brought domestic pigs of European ancestry to Anatolia during the Iron Age, as proposed by Larson et al. (2007a).

Chapter 3 expands the narrative that was proposed in Chapter 2, by analysing ancient DNA extracted from archaeological pigs in Europe. The main objective is to examine and test a number of hypotheses about the Neolithic expansion into Europe, and whether pig mtDNA is in fact a good proxy to detect patterns of cultural and/or human demic diffusion, as previously suggested (Larson et al. 2007a). This chapter also examines an important mechanism behind the process of pig domestication: the selection process of domestic traits (specifically coat color variation due to non-synonymous mutations in the MC1R gene) and the process of admixture (introgression) with local European wild boar populations. Fang et al. (2009) hypothesised that the MC1R gene was subject to strong human-driven selection from the onset of domestication but it has not yet been empirically demonstrated. On the other hand, Larson et al. (2007a) conclusively showed that European domestic pigs acquired the genetic signature of the local wild boar some time after their initial introduction from the Near East but it remains uncertain when, where and how it happened. By contrasting mtDNA and MC1R data, I aim to provide a better understanding of these processes.

Chapter 4 examines the phylogeography and population structure of West Eurasian wild boar. The main objective of this chapter is to determine the processes that have shaped the spatial arrangement of genetic lineages across space and time. Because mitochondrial phylogeography is a common method for inferring domestication events (e.g. Giuffra et al. 2000; Larson et al. 2005), re-assessing the usefulness of that approach in the light of new research (chapters 2 and 3) is critical.

Chapter 5 is the fourth case study and test a number of specific hypotheses concerning three unlinked genetic loci in domestic chickens (TSHR, BCDO2 and mtDNA). The overall aim is to describe the domestication trajectory for these loci and to contrast these results with hypotheses formulated on the basis of modern data. For example, TSHR, and to some extent BCDO2, are hypothesised to be domestication genes (Rubin et al. 2010). By directly genotyping these markers in ancient chickens, it is possible to test (falsify or verify) hypotheses based solely on modern data.

It is also possible to get a good insight as to whether these genetic markers, and associated phenotypes, were a key component of the early domestication process (as with the MC1R gene in pigs, see chapter 3).

In addition to the overall aims and objectives, which are described above, I intend to test several hypotheses that are specific and directly linked to the overall objectives. These are specified at the end of the introductory section to each chapter.

Chapter 2

Ancient suid DNA and geometric morphometrics reveal migrations and population turnover in Anatolia during the Bronze and Iron Age

2.1 Declaration

The work presented in this chapter is the outcome of a collaboration between the author of the thesis (Linus Girdland Flink) and Dr. Claudio Ottoni (CO) (shared first co-authorship on a paper published on this data set: Ottoni and Girdland Flink et al. (2013) *Mol Biol Evol*: 30 (4): 824-832. doi: 10.1093/molbev/mss261). In addition, Dr. Allowen Evin (AE) made significant contributions by conducting all geometric morphometric analyses. The chapter contains novel genetic and morphometric data that were produced by CO and AE (in addition to the data produced by the author of this thesis). This is stated in full below (in materials and methods) and a complete track record of which samples were analysed by whom (and where) is shown in table 2.1. The version of the paper appearing in this thesis is not the published version but an early draft written primarily by the thesis author (though it also contains contributions from CO and AE, primarily on the methodological background of their work). The published version of this manuscript includes a third data set and has been revised by several co-authors. The published version is presented in Appendix B.

CO is currently based at the departments of 1: Center for Archaeological Sciences, Department of Earth and Environmental Sciences, University of Leuven, Leuven, Belgium, 2: Laboratory of Forensic Genetics and Molecular Archaeology, Department of Forensic Medicine, UZ Leuven, Belgium, and 3: Department of Imaging Pathology, University of Leuven, Leuven, Belgium.

AE is currently based at the departments of 1: Department of Archaeology, University of Aberdeen, Aberdeen, Scotland, United Kingdom, and at 2: 8UMR 7209 CNRS/Museum National dHistoire Naturelle, Paris, France.

2.2 Introduction

The transition from hunting and gathering to farming was one of the most important landmarks in human history (Diamond and Bellwood 2003). This process led not only to a radical change in human social evolution (largely because of emerging sedentism) but also to long term change in human biology (for example, the emergence of widespread lactase persistence and dairy consumption, Itan et al. 2009). Domestication processes formed an integral part of this transitional phase, which is partly characterised by an increasing intensification of relationships between humans and wild plants and animals (Vigne 2011; Zeder 2011). Determining the precise locations and timeframes over which domestication took place is crucial for the understanding of the development of complex human societies and patterns of human trade and migration (Diamond and Bellwood 2003; Zeder et al. 2006; Zeder 2008).

Animal domestication in the Near East took place in early sedentary human communities (permanent residence in villages, territorialism, Bar-Yosef 2011). Sedentism had first appeared within groups of semi-sedentary or sedentary foragers/hunter-gatherers in the Levant during the Early Natufian some 14,500-13,000/12,800 years BP (Bar-Yosef 1998; 2011). This period and cultural development, sometimes referred to as *the point of no return* (Belfer-Cohen and Bar-Yosef 2000), set the stage for the subsequent Neolithic Revolution (Price and Bar-Yosef 2011; Zeder 2011), which spread into Europe during the seventh millennium BC (Price 2000; Perles 2003).

The Near East was a key center for the earliest development of farming and stock-keeping in Western Eurasia, starting as early as the mid-tenth millennium BC (Zeder 2008; Zeder 2011). Of the four major livestock species (cattle, pig, sheep and goat) domesticated in the Near East (Zeder 2008; Conolly et al. 2011), pigs have proved to be one of the most useful proxies for tracking human networks (trade and migration) across Eurasia (Alves et al. 2003; Larson et al. 2007a, b; Haile et al. 2010).

Archeological evidence suggests that pigs were first domesticated in the Near East in Southeastern Anatolia by 8,500-8,000 BC (Zeder 2006; 2008; 2011), and that by the 7th millennium BC domestic pigs were present in the Levant, Iran, and along the Mediterranean coast (Hongo and Meadow 1998; Ervynck et al. 2001; Albarella et al. 2006a, b; Zeder 2008; Conolly et al. 2011; Arbuckle *in press*).

Traditional archaeozoological and archaeobotanical methods have generated significant quantities of data (Zeder 2011) that is now being added to by genetic techniques that possess even greater resolving power (Larson et al. 2005; Larson et al. 2007a, b; Haile et al. 2010; Larson et al. 2010). Genetic signatures derived from modern samples have been used to unravel the geographic origins and dispersal patterns of, for example, sheep (Fernandez et al. 2006; Chessa et al. 2009), goats (Fernandez et al. 2006; Chessa et al. 2009), grapes (Myles et al. 2011; van Heerwaarden et al. 2011) and maize (Myles et al. 2011; van Heerwaarden et al. 2011), while ancient DNA (aDNA) analyses have added a temporal component to understand the human-mediated movements of domesticates during Neolithic transition in Europe (e.g. Edwards et al. 2007; Larson et al. 2007a; Bollongino et al. 2008a). Similarly, morphological methods including geometric morphometrics (GMM) have addressed these same questions by documenting phenotypic differences between wild and domestic plants and animals (Bignon et al. 2005; Larson et al. 2007b; Cucchi et al. 2009; 2010; Terral et al. 2010). The emerging picture of the domestication process is geographically widespread, complex, and often independent (Zeder 2008; Vigne et al. 2009; Vigne 2011; Zeder 2011).

Genetic studies of modern pigs revealed a robust phylogeographic structure of wild boar populations and the existence of multiple domestication centers (Giuffra et al. 2000; Larson et al. 2005; Wu et al. 2007; Larson et al. 2010). Recent aDNA analyses have taken advantage of the strong phylogeographic structure and demonstrated, in agreement with archeological predictions, that the earliest domestic pigs in Europe possessed a genetic signature (mainly the mitochondrial haplotype Y1, but also the closely related haplotype Y2) that is absent in modern or ancient European suids,

but present in modern wild boar in Anatolia and the Near East (Larson et al. 2005; Larson et al. 2007a). This pattern suggested that domestic pigs were introduced to Europe from the Near East during the Neolithic transition, as early as 5,500 BC. This introduction may even have triggered the domestication of indigenous European wild boar (possessing E1 haplotypes), which, once domesticated, replaced the domestic pigs of Near Eastern ancestry by the early 4th millennium BC (Larson et al. 2007a). This same study demonstrated that by at least the 7th century BC, European domestic pigs were introduced into the Near East where they replaced the indigenous Near Eastern domestic pigs (Larson et al. 2007a).

The temporal and geographic patterns of shifting domestic pig haplotypes revealed by Larson et al. (Larson et al. 2007a) were based on relatively few samples and a number of essential questions remain unanswered. First, because the genetic turnover of pigs from those possessing Near Eastern signatures (Y1/Y2) to those with European ancestry (E1) was deduced from six pigs excavated at five archaeological sites in Armenia, when and where European pigs were first introduced into Anatolia is still unknown. Bronze Age and Iron Age Anatolia witnessed rapid changes in social structure and human demography, including large-scale migrations (Sagona and Zimansky 2009). Determining the precise temporal and geographic pattern over which the turnover took place would add important information to help resolve the complexity of this period.

Secondly, the Anatolian origin of the Y1 and Y2 haplotypes associated with the Neolithic movement into Europe has been inferred from modern phylogeographic patterns but never empirically demonstrated by sequencing ancient Y1 pigs from Anatolia (Larson et al. 2007a). Detecting the Y1/Y2 signatures in ancient pigs in Early Neolithic contexts from Anatolia is necessary to establish the origins of the earliest European pigs. Lastly, a comprehensive genetic survey of Anatolian pigs over several thousand years would establish the genetic signature of the earliest domestic pigs and help to resolve the question of whether pigs were domestic multiple times in this region (Arbuckle *in press*).

In order to address these questions, the genetic signatures of 350 suids from 44 Near East archeological sites spanning the Early Neolithic to the Medieval era were investigated (table 2.1). In addition, traditional and Geometric Morphometric (GMM) approaches were applied to 36 specimens from which DNA had been successfully extracted and sequenced. This allowed for the assessment of whether the observed genetic differences were reflected morphometrically (table 2.1).

2.3 Materials and methods

2.3.1 Ancient samples

Three hundred and fifty ancient pig bones and teeth representing 44 Near Eastern archaeological sites were analysed (table 2.1). Samples were chosen to represent Early Neolithic, Neolithic, Chalcolithic, Bronze Age, Iron Age and Medieval contexts (and further subdivisions within each of these groups) with the aim to maximise spatial and temporal coverage.

All associated dates are reported in calibrated radiocarbon years BC, BP or AD. The ages of the archaeological remains ranged from the 10th millennium BC to 1,300-1,400 AD. Dates were inferred either directly using AMS radiocarbon dating (Beta Analytic Inc. and University of Oxford) or upon stratigraphic associations with AMS dates and/or archaeological evidence of the context from which the bones were excavated (these dates were primarily provided by the archaeozoologists in charge of the materials). Specimens with European ancestry from the oldest stratigraphic layers were purposely selected for AMS dating in order to gain a better estimate of the time period during which the putative introduction took place. Additional sample details are presented in table 2.1.

Table 2.1: Samples and archaeological sites examined in this chapter. Red colour denotes failure to amplify while green colour indicates success.

ID sample	Reference ID / Find ID / Context	Site	Country	Period (Stratigraphy evidence)	Period (cal BC)	AMS ^{14}C dating cal BC (*indirect dating)	Period (AMS dating)	Status	Laboratory	ANC1 Haplogroup	Anc1	Anc2	Cloning	External replication	GMM Lower M2	GMM Lower M3	Source
LG005	MM-CHKH N106	Chiakho	Russia (Adygeya)	Chalcolithic	6,000-3,100 BC				Durham								Mashkour, M
LG006	MM-CHKH N107	Chiakho	Russia (Adygeya)	Chalcolithic	6,000-3,100 BC				Durham								Mashkour, M
LG007	MM-MSK05 N99	Mushki	Iran	Neolithic	7th millennium BC?				Durham								Mashkour, M
LG008	MM-MSK06 N100	Mushki	Iran	Neolithic	7th millennium BC?				Durham								Mashkour, M
LG009	MM-MSK07 N101	Mushki	Iran	Neolithic	7th millennium BC?				Durham								Mashkour, M
LG010	MM-GT01 N102	Gohar Tappeh	Iran	Bronze Age	~3,000BC				Durham								Mashkour, M
LG011	MM-GT01 N103	Gohar Tappeh	Iran	Bronze Age	~3,000 BC				Durham	Am1T*							Mashkour, M
LG012	MM-GT01 N104	Gohar Tappeh	Iran	Bronze Age	~3,000BC				Durham								Mashkour, M
LG013	MM-GKH01 N105	Ghar Khar	Iran	Palaeolithic/Epipaleolithic	n/a				Durham								Mashkour, M
LG014	JD-QR09 N108	Qaleh Rostam	Iran	Neolithic	7th millennium BC?				Durham								Mashkour, M
LG015	JD_QR10 N109	Qaleh Rostam	Iran	Neolithic	7th millennium BC?				Durham								Mashkour, M
LG016	JD-QR11 N110	Qaleh Rostam	Iran	Neolithic	7th millennium BC?				Durham								Mashkour, M
LG017	JD-QR12 N111	Qaleh Rostam	Iran	Neolithic	7th millennium BC?				Durham	Am1T*							Mashkour, M
LG059	EEL968	Ulucak Höyük	Turkey	Early Neolithic (Late Chalcolithic?)					Durham								Çakırlar, C.
LG060	EEL969	Ulucak Höyük	Turkey	Early Neolithic (Late Chalcolithic?)					Durham								Çakırlar, C.
LG061	EEL973	Ulucak Höyük	Turkey	Early Neolithic (Late Chalcolithic?)					Durham								Çakırlar, C.
LG064	L.3185 R:19	Tol e Spid	Iran	Chalcolithic	6,000-3,100 BC				Durham								Mashkour, M
LG065	L.3178 R:35	Tol e Spid	Iran	Chalcolithic	6,000-3,100 BC				Durham								Mashkour, M
LG066	L.3177 R:10	Tol e Spid	Iran	Chalcolithic	6,000-3,100 BC				Durham								Mashkour, M
LG067	Exc No. 33030	Qareh Doyub	Iran	Historical	5th -7th Century AD				Durham	Am1T*							Mashkour, M
LG068	SF No. 45	Qelich Qômeq	Iran	Achemend	8th -5th Centuries BC				Durham								Mashkour, M
LG069	SF No. 166	Qelich Qômeq	Iran	Achemend	8th -5th Centuries BC				Durham	Am1T*							Mashkour, M
LG070	SF No. 166	Qelich Qômeq	Iran	Achemend	8th -5th Centuries BC				Durham	Am1T*							Mashkour, M
LG071	SF No. P136	Qelich Qômeq	Iran	Achemend	8th -5th Centuries BC				Durham	Am1T*							Mashkour, M
LG072	SF No32	Dasht Qaleh	Iran	Historical	5th Century AD				Durham								Mashkour, M
LG073	SF No. 099	Dasht Qaleh	Iran	Historical	5th Century AD				Durham	Am1T*							Mashkour, M
LG074	CHI_aDNA_19	Çayönü	Turkey	PPNB					Durham								Hongo, H.
LG075	CHI_aDNA_23	Çayönü	Turkey	PPNB					Durham								Hongo, H.
LG076	CHI_aDNA_30	Çayönü	Turkey	PPNB					Durham								Hongo, H.
LG077	CHI_aDNA_09	Çayönü	Turkey	PPNA/PPNB					Durham								Hongo, H.
LG078	CHI_aDNA_25	Çayönü	Turkey	PPNB					Durham								Hongo, H.
LG079	Mun_013	Nevali Cori	Turkey	PPNB					Durham								Peters, J
LG080	Mun_014	Nevali Cori	Turkey	PPNB					Durham								Peters, J
LG081	Mun_017	Nevali Cori	Turkey	PPNB					Durham								Peters, J
LG082	Mun_018	Nevali Cori	Turkey	PPNB					Durham								Peters, J
LG083	Mun_020	Nevali Cori	Turkey	PPNB					Durham								Peters, J
LG109	Mun_022	Lidar Höyük	Turkey	MBA III/LBA I ?		1,291-1,055 BC	Late Bronze/Iron Age	domestic	Durham	Asidе*							Peters, J
LG110	Mun_023	Lidar Höyük	Turkey	MBA III/LBA I ?		1,370-1,119 BC	Late Bronze/Iron Age	domestic	Durham	Asidе*							Peters, J
LG111	Mun_024	Lidar Höyük	Turkey	MBA IIIII ? (uncertain)				domestic	Durham	Am1T*					X		Peters, J
LG112	Mun_025	Lidar Höyük	Turkey	MBA III/LBA I					Durham	Y2							Peters, J
LG113	Mun_026	Lidar Höyük	Turkey	MBA III/LBA I					Durham								Peters, J
LG114	Mun_033	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,296-1,055 BC	Late Bronze/Iron Age		Durham	Asidе*							Peters, J
LG115	Mun_034	Lidar Höyük	Turkey	Middle Bronze Age III	2,000-1,650 BC				Durham	Am1T*							Peters, J
LG116	Mun_009	Gurcutepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Durham								Peters, J
LG117	Mun_011	Gurcutepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Durham								Peters, J
LG118	Mun_010	Gurcutepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Durham								Peters, J
LG128	Mun_001	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG129	Mun_002	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG130	Mun_003	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG131	Mun_004	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG132	Mun_005	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG133	Mun_006	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG134	Mun_007	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG135	Mun_008	Gobekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Durham								Peters, J
LG136	Mun_015	Nevali Cori	Turkey	PPNB					Durham								Peters, J
LG137	Mun_028	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD	897-1,021 AD	Medieval	domestic	Durham	Asidе*							Peters, J
LG138	Mun_039	Lidar Höyük	Turkey	MBA III/ LBA I					Durham								Peters, J
LG139	Mun_040	Lidar Höyük	Turkey	MBA IIIII					Durham								Peters, J
LG140	Mun_042	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J
LG141	Mun_043	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J
LG142	Mun_044	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J

LG418	#14	Kohneh Tepesi	Iran	Early Bronze Age					Durham								Mashkour, M
LG419	#45	Kohneh Tepesi	Iran	Early Bronze Age					Durham								Mashkour, M
LG420	#377	Kohneh Tepesi	Iran	Early Bronze Age					Durham								Mashkour, M
LG450	CHI_aDNA_01	Çayönü	Turkey	PPNA					Durham								Hongo. H.
LG451	CHI_aDNA_04	Çayönü	Turkey	PPNA					Durham								Hongo. H.
LG452	CHI_aDNA_08	Çayönü	Turkey	PPNA/PPNB					Durham								Hongo. H.
LG454	CHI_aDNA_16	Çayönü	Turkey	PPNB					Durham								Hongo. H.
LG455	CHI_aDNA_21	Çayönü	Turkey	PPNB					Durham								Hongo. H.
LG456	CHI_aDNA_22	Çayönü	Turkey	PPNB					Durham								Hongo. H.
LG458	CHI_aDNA_29	Çayönü	Turkey	PPNB					Durham								Hongo. H.
LG459	CHI_aDNA_31	Çayönü	Turkey	PN					Durham	Arm1T*							Hongo. H.
LG460	CHI_aDNA_32	Çayönü	Turkey	PN					Durham								Hongo. H.
LG475	EDI-CAM 250-397b	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*							Bartosiewicz, L
LG476	EDI-CAM 273-868	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*							Bartosiewicz, L
LG477	EDI-CAM 778-5155b	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Y1					X		Bartosiewicz, L
LG479	EDI-CAM 891-5779	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Y1						X	Bartosiewicz, L
LG480	EDI-CAM 966-6042	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*					X	X	Bartosiewicz, L
LG485	EDI-CAM 247-372b	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Y1					X		Bartosiewicz, L
LG486	EDI-CAM 463-4067	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Y1						X	Bartosiewicz, L
LG487	EDI-CAN 906-5291	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	?	Durham								Bartosiewicz, L
LG488	EDI-CAM 796-5229	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*					X	X	Bartosiewicz, L
LG489	EDI-CAM 746-4982	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Y1					X	X	Bartosiewicz, L
LG491	EDI-CAM 56-252c	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*							Bartosiewicz, L
LG492	EDI-CAM 352-987	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*						X	Bartosiewicz, L
LG493	EDI-CAM 925-5377	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*					X	X	Bartosiewicz, L
LG495	EDI-CAM 858-5569	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic	domestic	Durham	Arm1T*						X	Bartosiewicz, L
LG496	EDI-CAN 263-724	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC*		Chalcolithic		Durham								Bartosiewicz, L
LG516	MUN_012	Nevali Çori	Turkey	PPNB					Durham								Peters, J.
LG517	MUN_016	Nevali Çori	Turkey	PPNB					Durham								Peters, J.
LG518	MUN_021	Nevali Çori	Turkey	PPNB					Durham								Peters, J.
LG520	MUN_035	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J.
LG521	MUN_041	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J.
LG522	MUN_045	Sirkeli Höyük	Turkey	Iron Age					Durham	Arm1T*							Peters, J.
LG523	MUN_046	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J.
LG524	MUN_047	Sirkeli Höyük	Turkey	Iron Age					Durham	Arm1T*							Peters, J.
LG526	MUN_048	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J.
LG527	MUN_049	Sirkeli Höyük	Turkey	Iron Age					Durham	Y1							Peters, J.
LG528	MUN_050	Sirkeli Höyük	Turkey	Iron Age					Durham								Peters, J.
LG529	MUN_051	Sirkeli Höyük	Turkey	Iron Age					Durham	Arm1T*							Peters, J.
LG531	MUN_052	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG532	MUN_053	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG533	MUN_054	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG534	MUN_055	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG536	MUN_056	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG537	MUN_057	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG538	MUN_058	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG539	MUN_059	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG540	MUN_060	Hassek Höyük	Turkey	Chalcolithic/Bronze					Durham								Peters, J.
LG773	Iran-CG-1	Chogha Gavaneh	Iran	Chalcolithic/Bronze Age	4th/3rd millenium BC				Durham	Arm1T*							Mashkour, M
LG775	KSB-01	Kalanan Sirlan Bi	Iran	Chalcolithic					Durham								Mashkour, M
LG776	L: 5/f:3	Cham Quleh	Iran	Chalcolithic	4th/3rd millenium BC				Durham								Mashkour, M
LG777	L: 5/R.5	Cham Quleh	Iran	Chalcolithic	4th/3rd millenium BC				Durham								Mashkour, M
LG779	KT-01	Kohneh Tepesi	Iran	Early Bronze Age					Durham								Mashkour, M
LG780	KT-29	Kohneh Tepesi	Iran	Early Bronze Age					Durham	Arm1T*					X		Mashkour, M
LG781	KT-32	Kohneh Tepesi	Iran	Early Bronze Age					Durham								Mashkour, M
LG782	KT-41	Kohneh Tepesi	Iran	Early Bronze Age					Durham								Mashkour, M
LG784	HV-08	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*						X	Mashkour, M
LG785	HV-09	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*					X	X	Mashkour, M
LG786	HV-10	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham								Mashkour, M
LG787	HV-13	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*							Mashkour, M
LG788	HV-33	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*					X	X	Mashkour, M
LG789	HV-34	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*						X	Mashkour, M
LG790	HV-35	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*					X	X	Mashkour, M
LG791	HV-36	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*						X	Mashkour, M
LG792	HV-37	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*					X	X	Mashkour, M

LG794	HV-39	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*						X	Mashkour, M
LG795	HV-45	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*						X	Mashkour, M
LG796	HV-46	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*						X	Mashkour, M
LG797	HV-47	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham								Mashkour, M
LG798	HV-54	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham	Arm1T*						X	Mashkour, M
LG799	HV-55	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC				Durham								Mashkour, M
BAD1		Bademağacı	Turkey	Early Neolithic I - 8	7,000-6,000 BC	7,050-6,690 BC*	Early Neolithic	domestic	Leuven								De Cupere, B.
BAD10		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic	domestic	Leuven	Y1				X			De Cupere, B.
BAD11		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic	wild	Leuven								De Cupere, B.
BAD12		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic	domestic	Leuven								De Cupere, B.
BAD13		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic	domestic	Leuven								De Cupere, B.
BAD14		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			wild	Leuven								De Cupere, B.
BAD15		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			domestic	Leuven	Y2				X			De Cupere, B.
BAD16		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			domestic ?	Leuven	Arm1T*				X			De Cupere, B.
BAD17		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			domestic	Leuven	Y1			X				De Cupere, B.
BAD18		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			domestic	Leuven	Arm1T*				X			De Cupere, B.
BAD19		Bademağacı	Turkey	Early Neolithic II - 1	7,000-6,000 BC	6,230-6060 BC*	Early Neolithic	domestic	Leuven								De Cupere, B.
BAD2		Bademağacı	Turkey	Early Neolithic I - 8	7,000-6,000 BC	7,050-6,690 BC*	Early Neolithic	domestic	Leuven								De Cupere, B.
BAD3		Bademağacı	Turkey	Early Neolithic I - 7	7,000-6,000 BC			wild	Leuven								De Cupere, B.
BAD30		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven	Y1							De Cupere, B.
BAD31		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD32		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven	Y1							De Cupere, B.
BAD33		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD34		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD35		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD36		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD38		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD39		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD4		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	wild	Leuven	Y1							De Cupere, B.
BAD47		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC			domestic	Leuven	Y1			X				De Cupere, B.
BAD5		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	wild	Leuven	Y1				X			De Cupere, B.
BAD50		Bademağacı	Turkey	Early Neolithic II - 4	7,000-6,000 BC	6,420-6,110 BC*	Early Neolithic	domestic	Leuven								De Cupere, B.
BAD52		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	domestic	Leuven	Arm1T*			X				De Cupere, B.
BAD54		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	domestic	Leuven	Arm1T*							De Cupere, B.
BAD6		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD60		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	domestic	Leuven								De Cupere, B.
BAD63		Bademağacı	Turkey	Early Neolithic II - 4B	7,000-6,000 BC			domestic	Leuven	Y1							De Cupere, B.
BAD7		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD73		Bademağacı	Turkey	Early Neolithic I - 6	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD8		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC			domestic	Leuven								De Cupere, B.
BAD82		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			wild	Leuven								De Cupere, B.
BAD83		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			domestic	Leuven	Y1							De Cupere, B.
BAD84		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			wild	Leuven	Y1							De Cupere, B.
BAD85		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			wild	Leuven	Y1							De Cupere, B.
BAD86		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			wild	Leuven	Y1			X				De Cupere, B.
BAD87		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			wild	Leuven	Y1							De Cupere, B.
BAD9		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC			wild	Leuven	Arm1T*							De Cupere, B.
F13	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC			domestic	Leuven	Aside*							De Cupere, B.
F15	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC	390-180 BC		domestic	Leuven	Aside*							De Cupere, B.
F20	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC			domestic	Leuven	Aside*							De Cupere, B.
F21	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC			domestic	Leuven	Cside*							De Cupere, B.
M100	1981; E 44 d; Abh. 18	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Aside*							Peters, J.
M101	1981; E 44 c, Abh. 18	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Arm1T*							Peters, J.
M11	S1 1. Steg 200/40; 4/49	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC			domestic	Leuven								Peters, J.
M113	GT Z; 1995; S 1; 1.1; 80/4	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC			wild	Leuven								Peters, J.
M115	GT Z; 1995; S 2; 1.1; 50/4	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC			wild	Leuven								Peters, J.
M116	GT W; 1995; 67/40	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC			wild	Leuven								Peters, J.
M118	GT W; S 2; 1.1; 50/40	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC			wild	Leuven								Peters, J.
M119	1985, BH 32; O 20; 7,00-1	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven								Peters, J.
M120	1985, BH 32; O 20; 7,00-1	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven	Arm1T*							Peters, J.
M121	1985, BH 32; O 20; 7,00-1	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven								Peters, J.
M122	1985, BH 32; O 20; 7,00-1	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven								Peters, J.
M123	1984; BH 110; R 21; 5,0-7	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven	Arm1T*				X			Peters, J.
M124	1984; BH 110; R 21; 5,0-7	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven	Y1				X			Peters, J.
M125	1985, BH 7; P 16; 0,60-9,	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven								Peters, J.
M126	1985, BH 7; P 16; 0,60-9,	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			domestic	Leuven								Peters, J.

M127	1985. BH 7: P 16: 0,60-9,	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC				domestic	Leuven										Peters, J.
M13	H 1984, Ash pit, BH 191 d	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven										Peters, J.
M14	H 1984, Ash pit, BH 191 d	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven										Peters, J.
M15	H 1984, Ash pit, BH 191 d	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven										Peters, J.
M16	H 1984, Ash pit, BH 191 d	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven										Peters, J.
M17	H 1984, Ash pit, BH 191 d	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven										Peters, J.
M18	H 1984, Ash pit, BH 191 d	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven	Am1T*									Peters, J.
M19	H 1984, Ash pit, BH 191 d	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven										Peters, J.
M40	1981; R 45 c/d; Abhub 14	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				domestic	Leuven	Am1T*									Peters, J.
M41	1981; R 45 d, Abh. 12	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				domestic	Leuven										Peters, J.
M42	1981; H 40 b/c; 4 OR u 2	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				domestic	Leuven	Aside*									Peters, J.
M43	1981; H 40 b/c; 4 OR u 2	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				domestic	Leuven										Peters, J.
M44	1981; H 40 b/c; 4 OR u 2	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				domestic	Leuven	Aside*									Peters, J.
M45	1981; H 40 b/c; 4 OR u 2	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				domestic	Leuven	Aside*									Peters, J.
M46	1981; R 45 c/d, Abh. 15	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				domestic	Leuven	Am1T*			X						Peters, J.
M47	1998; S 43 b; Abh. 15	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC				domestic	Leuven	Am1T*									Peters, J.
M48	1998; S 44 a/b; Abh. 54-53	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC				wild	Leuven	Y2									Peters, J.
M49	1998; O/P 50; Abh. 22; de	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC				domestic	Leuven	Am1T*									Peters, J.
M5	N-Wadi, W-Profil, A1	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				domestic	Leuven										Peters, J.
M50	1998; Q 44 c - R 44 b, 54	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC				domestic	Leuven	Am1T*									Peters, J.
M51	1998; R 44 d; Abh. Gr 182	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC	1,217-1,025 BC	Late Bronze/Iron Age		domestic	Leuven	Aside*									Peters, J.
M52	1998; R 44 b; Abh. 54 KV	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC				domestic	Leuven	Aside*									Peters, J.
M53	1980; Q 45 b; 8 GS 1; Lay	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD				domestic	Leuven	Aside*									Peters, J.
M54	1980; Q 45 b; 8 GS 1; Lay	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD				domestic	Leuven	Aside*									Peters, J.
M55	1980; Q 45 b; 8 GS 1; Lay	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD				domestic	Leuven	Aside*									Peters, J.
M56	1980; Q 45 b; 8 GS 1; Lay	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD				domestic	Leuven	Aside*									Peters, J.
M57	1980; Q 45 b; 8 GS 1; Lay	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD				domestic	Leuven	Aside*									Peters, J.
M58	1980; Q 45 b; 8 GS 1; Lay	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD				domestic	Leuven	Aside*									Peters, J.
M59	1980; Q 45 b; 8 GS 1; Lay	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD				domestic	Leuven	Aside*									Peters, J.
M6	N-Wadi, W-Profil, D4	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				domestic	Leuven										Peters, J.
M60	1987; N 50a; Abh. 27 R 7	Lidar Höyük	Turkey	Middle Bronze Age	2,000-1,650 BC				domestic	Leuven										Peters, J.
M61	1987; N 50a; Abh. 27 R 7	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven										Peters, J.
M62	1987; S 44/45 - R 44/45;	Lidar Höyük	Turkey	Middle Bronze Age	2,000-1,650 BC				domestic	Leuven										Peters, J.
M63	1987; S 44/45 - R 44/45;	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven										Peters, J.
M64	1987; S 46 a; Abh. 30 a; E	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven	Am1T*									Peters, J.
M65	1987; MB I/II (Phase)	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven										Peters, J.
M66	1987; R 45 c; Abh. 56; R	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven										Peters, J.
M67	1987; R 45 c; Abh. 56; u R	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven										Peters, J.
M68	1987; P 50 c/d; Abh. 27 R	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven	Y2									Peters, J.
M69	1987; P 50 c/d; Abh. 27 R	Lidar Höyük	Turkey	Middle Bronze Age	2,000-1,650 BC				domestic	Leuven										Peters, J.
M7	S2; 1,3; 260/40; 1/49	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				domestic	Leuven										Peters, J.
M70	1987; S 44/45; Abh. 57-58	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven										Peters, J.
M71	1987; S 44/45; Abh. 57-58	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven	Am1T*									Peters, J.
M72	1987; S 44/45; Abh. 57-58	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven										Peters, J.
M73	1987; S 43 d; Abh. 18	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven	Y2									Peters, J.
M74	1987; S 43 d; Abh. 18	Lidar Höyük	Turkey	Middle Bronze Age III/I	2,000-1,650 BC				domestic	Leuven	Am1T*									Peters, J.
M75	1998; R 44 b; Abh. 54 e F	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				domestic	Leuven	Y2									Peters, J.
M76	1998; Q 44 d; Abh. 53, 54	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,120-900 BC	Iron Age		domestic	Leuven	Aside*									Peters, J.
M77	1998; Q 44 d; Abh. 53, 54	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				domestic	Leuven	Am1T*									Peters, J.
M78	1998; R 44 d; Abh. 54 e F	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,270-1,050 BC	Late Bronze/Iron Age		domestic	Leuven	Aside*									Peters, J.
M79	1998; R 44 b; Abh. Mal. C	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				wild	Leuven	Am1T*									Peters, J.
M8	S1; 1,4; 340/40; 6/49	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				domestic	Leuven										Peters, J.
M80	1998; S 44 a; Abh. 54 e	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				wild	Leuven	Am1T*									Peters, J.
M81	1998; R 44 d; Abh. 54 e F	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				domestic	Leuven	Am1T*									Peters, J.
M82	1998; R 44 d; Abh. 54 e F	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,600-1,570/1540-1	Late Bronze Age		domestic	Leuven	Aside*									Peters, J.
M83	1998; Q 44 d; Abh. 53; S	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				domestic	Leuven	Am1T*									Peters, J.
M84	1998; O/R/S 44/45; Schic	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				domestic	Leuven										Peters, J.
M85	1981; G 34 a/F 34 d; Abh.	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC	2,835-2,478 BC	Early Bronze Age		domestic	Leuven	Am1T*									Peters, J.
M86	1981; F 34 b/c; Abh. 25 K	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven	Am1T*									Peters, J.
M87	1981; G 34 a; Abh. 26 nB	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven	Am1T*									Peters, J.
M88	1981; F 34 c/d - G 34 b; A	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven	Am1T*									Peters, J.
M89	1981; F 34 c/d - G 34 b; A	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven										Peters, J.
M9	S3; 1,1; 110/40;	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				domestic	Leuven										Peters, J.
M90	1981; G 33 b; Abh. 28 2,	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				domestic	Leuven	Am1T*									Peters, J.
M91	1998; S 48 a; Abh. 15	Lidar Höyük	Turkey	Iron Age	1,200-600 BC				domestic	Leuven										Peters, J.
M92	1998; S 48 a; Abh. 15	Lidar Höyük	Turkey	Iron Age	1,200-600 BC				domestic	Leuven										Peters, J.

M93	1986; S 48 a; Abh. 15	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Am1T*								Peters, J.
M94	1981; E 44 c; Abh. 23	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Am1T*								Peters, J.
M95	1981; E 44 c; Abh. 23	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Am1T*								Peters, J.
M96	1981; E 44 c; Abh. 19	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven				x					Peters, J.
M97	1981; E 44 c; Abh. 21	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Aside*								Peters, J.
M98	1981; E 44 c; -	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Aside*								Peters, J.
M99	1981; E 44 d; Abh. 18	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			domestic	Leuven	Y2							x	De Cupere
SA1193	SA 2003 DA 167	Sagalassos	Turkey	Early Byzantine	450-650 AD			domestic	Leuven	Aside*					x		x	De Cupere
SA1203	SA 2003 AP 208	Sagalassos	Turkey	Early to Mid Imperial	0-300 AD			domestic	Leuven	Aside*				x	x		x	De Cupere
SA1227	SA 2003 LA1 73	Sagalassos	Turkey	Early Byzantine	450-650 AD			domestic	Leuven	Aside*				x	x			De Cupere
SA1230	SA 2003 AP 191	Sagalassos	Turkey	Early to Mid Imperial	0-300 AD	160 BC - 60 AD		domestic	Leuven	Aside*				x			x	De Cupere
SA1301	SA 2004 AP 45/3	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			domestic	Leuven	Aside*							x	De Cupere
SA1302	SA 2004 AP 45/3	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			domestic	Leuven	Aside*								De Cupere
SA1315	SA 2004 AP 70/2	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD	250-430 AD		domestic	Leuven	LDomBritSaddle01					x	x	x	De Cupere
SA133	SA 2000 B3 198	Sagalassos	Turkey	Early Byzantine	450-650 AD	230-410 AD		domestic	Leuven	Aside*				x	x	x	x	De Cupere
SA139	SA 2001 NEG 113	Sagalassos	Turkey	Early Byzantine	450-650 AD	140-390 AD		domestic	Leuven	Aside*					x	x	x	De Cupere
SA223	SA 2000 B3 278	Sagalassos	Turkey	Early Byzantine	450-650 AD			domestic	Leuven	Aside*					x	x	x	De Cupere
SA295	SA 91 N 309	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			domestic	Leuven	Aside*			x			x		De Cupere
SA298	SA 91 N 309	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			domestic	Leuven	Aside*								De Cupere
SA398	SA 92 N 389	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD	260-520 AD		domestic	Leuven	Cside*								De Cupere
SA400	SA 92 N 389	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			domestic	Leuven	Aside*							x	De Cupere
SA405	SA 90 DT 2	Sagalassos	Turkey	0-1200 AD	0-1200 AD			domestic	Leuven	Aside*					x		x	De Cupere
SA406	SA 90 DT 2	Sagalassos	Turkey	0-1200 AD	0-1200 AD			domestic	Leuven	Aside*							x	De Cupere
SA510	SA 2000 B1 165	Sagalassos	Turkey	Early Byzantine	450-650 AD			domestic	Leuven	Aside*								De Cupere
SA791	SA 90 N 4	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			domestic	Leuven	Aside*				x				De Cupere
SA941	SA 96 B 262	Sagalassos	Turkey	Early Byzantine	450-650 AD			domestic	Leuven	Aside*				x			x	De Cupere
SA988	SA 95 UAN 216	Sagalassos	Turkey	Early Byzantine	450-650 AD			domestic	Leuven	Aside*							x	De Cupere

One-hundred and forty nine modern reference sequences are presented in table 2.2 and were compiled from Alves et al. (2003, GenBank accession numbers AY232868-AY232868), Giuffra et al. (2000, GenBank accession numbers AF136555, AF136556, AF136558 and AF136563), Gongora et al. (2003, GenBank accession numbers AF535163 and AF535164), Kijas and Andersson (2001, GenBank accession number AF304203), Larson et al. 2005, (GenBank accession numbers AY884609-AY884831), and Larson et al. (2007a, GenBank accession numbers DQ872931-DQ873203). 38 novel sequences originating from wild boar in Armenia, Iran, Turkey, Tunisia, Romania and Ukraine (Perez unpublished data, Everett unpublished data, were also included, see table 2.2). Marjan Mashkour provided one novel wild boar sequence from Iran (specimen LG778, table 2.2). These sequences were adjusted in length to match the ANC1 and ANC2 fragments (comprising approximately 160bp, see below).

ID sample	country	source	Clade	Network
GL52	Spain	Larson et al. 2005	European	
GL55	Turkey	Larson et al. 2005	Near Eastern - NE2	x
GL59	Iran	Larson et al. 2005	Near Eastern - NE2	x
GL63	Germany	Larson et al. 2005	European	
GL65 - feral	Italy	Larson et al. 2005	Italian	
GL71	France	Larson et al. 2005	European	
GL73	Morocco	Larson et al. 2005	European	
GL77	Iran	Larson et al. 2005	Asiatic	
GL107	Germany	Larson et al. 2005	European	
GL108	Germany	Larson et al. 2005	European	
GL109	Germany	Larson et al. 2005	European	
GL110 - feral	France	Larson et al. 2005	European	
GL111 - feral	Italy	Larson et al. 2005	European	
GL112	Holland	Larson et al. 2005	European	
GL113	Macedonia	Larson et al. 2005	European	
GL133 - feral	Norway	Larson et al. 2005	European	
GL141	Armenia	Larson et al. 2005	European	
GL142	Armenia	Larson et al. 2005	Near Eastern - NE2	x
GL143 - feral	France	Larson et al. 2005	European	
GL144	Italy	Larson et al. 2005	European	
GL190 - feral	Italy	Larson et al. 2005	Italian	
GL193	Armenia	Larson et al. 2005	Near Eastern - NE2	x
GL194	Armenia	Larson et al. 2005	Near Eastern - NE2	x
GL220 - feral	France	Larson et al. 2005	Near Eastern - NE2	
GL221	Spain	Larson et al. 2005	European	
GL222	Portugal	Larson et al. 2005	European	
GL236	Armenia	Larson et al. 2005	Near Eastern - NE2	x
GL242	Spain	Larson et al. 2005	European	
GL244	Italy	Larson et al. 2005	Italian	
GL245	Italy	Larson et al. 2005	Italian	
GL246	Italy	Larson et al. 2005	Italian	
GL247	Italy	Larson et al. 2005	Italian	
GL248	Italy	Larson et al. 2005	Italian	
GL249	Italy	Larson et al. 2005	Italian	
GL250	Italy	Larson et al. 2005	Italian	
GL251	Italy	Larson et al. 2005	Italian	
GL252	Italy	Larson et al. 2005	European	
GL254	Iran	Larson et al. 2005	Near Eastern - NE1	x
GL270	Armenia	Larson et al. 2005	Near Eastern - NE1	x
GL271	Armenia	Larson et al. 2005	Near Eastern - NE2	x
GL284 - feral	France	Larson et al. 2005	European	
GL285 - feral	France	Larson et al. 2005	European	
GL286 - feral	France	Larson et al. 2005	European	
GL287 - feral	France	Larson et al. 2005	European	
GL288 - feral	Italy	Larson et al. 2005	European	
GL289 - feral	Italy	Larson et al. 2005	European	
LCorsica82 - feral	France	Larson et al. 2005	European	
LNSardinia88 - feral	Italy	Larson et al. 2005	European	
French Wild Boar	France	Larson et al. 2005	European	
SWB1	Spain	Alves et al. 2003	European	
SWB2	Spain	Alves et al. 2003	European	
SWB3	Spain	Alves et al. 2003	European	
SWB6	Spain	Alves et al. 2003	European	
SWB4	Spain	Alves et al. 2003	European	
SWB5	Spain	Alves et al. 2003	European	
SWB7	Spain	Alves et al. 2003	European	
GiuPolEWB1	Poland	Giuffra et al. 2000	European	
GiuPolEWB2	Poland	Giuffra et al. 2000	European	
GiuItalEWB3	Italy	Giuffra et al. 2000	Italian	
GiuIsrealiWB	Israel	Giuffra et al. 2000	European	
Kijas01SwedishWB	Sweden	Kijas & Anderson 2001	European	
GongFinnish36	Finland	Gongora et al. 2003	European	
GongFinnish41	Finland	Gongora et al. 2003	European	
GL374	Romania Dubova, Iron Gates	Larson et al. 2007	European	
GL392	Romania	Larson et al. 2007	European	

Table 2.2: Modern reference sequences.

GL724	Estonia Restaurant in Tallinn	Larson et al. 2007	European	
GL748	Syria Amouk Plains	Larson et al. 2007	Near Eastern - NE2	
GL749	Poland Bialystok Prov Bialowieza* National Park	Larson et al. 2007	European	
GL750	Iraq Irbil, Baradost	Larson et al. 2007	Near Eastern - NE2	x
GL751	Iraq Baghdad, 3 mi S	Larson et al. 2007	Near Eastern - NE1	
GL752	Iran Fars, Yasuj, 10.9 mi SW	Larson et al. 2007	Near Eastern - NE2	x
GL753	Iran Kermanshahan Kermanshah	Larson et al. 2007	European	
GL754	Turkey Mersin (ifel) Tarsus Forest	Larson et al. 2007	Near Eastern - NE2	x
GL766	Iraq Maysan, Amara, nr; Chahala	Larson et al. 2007	European	
GL767	Iraq Diyala, Khanaquin, 10 mi from; Rhamalla	Larson et al. 2007	Near Eastern - NE1	
GL768	Syria Amouk Plains	Larson et al. 2007	Near Eastern - NE2	
GL769	Iran Esfahan, Kuh Rang	Larson et al. 2007	Near Eastern - NE2	x
GL771	Iran Fars, Yasuj	Larson et al. 2007	Near Eastern - NE1	x
GL779	Iraq As Sulaymaniyah; Darband area, Zagros Mts	Larson et al. 2007	European	
GL781	Iran Kermanshahan	Larson et al. 2007	Near Eastern - NE1	x
GL782	Iran Khuzistan, Ahwaz	Larson et al. 2007	Near Eastern - NE1	
GL783	Iran Khuzistan, Ahwaz-Andimeshk	Larson et al. 2007	Near Eastern - NE1	x
GL784	Iran Khuzistan, Ahwaz-Andimeshk	Larson et al. 2007	Near Eastern - NE1	
GL786	Iran Kermanshahan, Kermanshah	Larson et al. 2007	European	
GL787	Iran Mazandaran, Sama	Larson et al. 2007	Asiatic	
GL788	Iran Maku	Larson et al. 2007	Near Eastern - NE2	
GL789	Iran Mazandaran, Gorgan	Larson et al. 2007	Asiatic	
GL790	Iran Mazandaran, Gorgan	Larson et al. 2007	Near Eastern - NE2	
GL791	Iran Mazandaran, Gorgan	Larson et al. 2007	Asiatic	
GL792	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic	
GL793	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic	
GL794	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic	
GL795	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic	
GL799	Romania Dubova, Iron Gates	Larson et al. 2007	European	
GL912	NW Persia	Larson et al. 2007	Near Eastern - NE2	x
GL918	Russia Volga Delta	Larson et al. 2007	European	
GL919	Russia Volga Delta	Larson et al. 2007	European	
GL935	West Caucasus, north slope	Larson et al. 2007	European	
GL940	Turkey Smyrna (Izmir)	Larson et al. 2007	Near Eastern - NE2	x
GL942 - domestic	Sudan Nuba	Larson et al. 2007	Near Eastern - NE2	
GL943	Egypt Egyptian	Larson et al. 2007	Near Eastern - NE1	x
GL944	Georgia Kavkaz from tiflis (Tbilisi)	Larson et al. 2007	Near Eastern - NE1	x
GL945	Slovakia	Larson et al. 2007	European	
GL946	Hungary	Larson et al. 2007	European	
GL948 - unknown	Greece Kos	Larson et al. 2007	European	
GL949 - unknown	Greece Kos	Larson et al. 2007	European	
GL951	Bulgaria	Larson et al. 2007	European	
GL952 - wild?	Sudan	Larson et al. 2007	Near Eastern - NE2	x
GL1009	Turkmenistan	Larson et al. 2007	Asiatic	
AR 2	Armenia	Miguel Perez	European	x
AR 298	Armenia	Miguel Perez	European	x
East AR	Armenia	Miguel Perez	European	x
Northeast AR	Armenia	Miguel Perez	European	x
IR 1	Iran	Miguel Perez	Near Eastern - NE2	x
IR 2	Iran	Miguel Perez	Near Eastern - NE2	x
IR 4	Iran	Miguel Perez	Near Eastern - NE2	x
IR 5	Iran	Miguel Perez	Near Eastern - NE2	x
TK 107	Turkey	Miguel Perez	Near Eastern - NE2	x
TK 119	Turkey	Miguel Perez	Near Eastern - NE2	x
TK 126	Turkey	Miguel Perez	Near Eastern - NE2	x
Tp1	Turkey	Helen Everett	European	x
Tp10	Turkey	Helen Everett	Near Eastern - NE2	x
Tp11	Turkey	Helen Everett	Near Eastern - NE2	x
Tp12	Turkey	Helen Everett	Near Eastern - NE2	x
Tp2	Turkey	Helen Everett	Near Eastern - NE2	x
Tp3	Turkey	Helen Everett	Near Eastern - NE2	
Tp4	Turkey	Helen Everett	Near Eastern - NE2	x
Tp5	Turkey	Helen Everett	Near Eastern - NE2	x
Tp6	Turkey	Helen Everett	Near Eastern - NE2	
Tp7	Turkey	Helen Everett	Near Eastern - NE2	x
Tp8	Turkey	Helen Everett	Near Eastern - NE2	x

Tp9	Turkey	Helen Everett	Near Eastern - NE2	
WBTN 959	Tunisia	Miguel Perez	European	
WBTN 960	Tunisia	Miguel Perez	European	
WBTN 961	Tunisia	Miguel Perez	European	
WBTN 962	Tunisia	Miguel Perez	European	
WBTN 963	Tunisia	Miguel Perez	European	
WBTN 964	Tunisia	Miguel Perez	Near Eastern - NE2	
WBTN 965	Tunisia	Miguel Perez	European	
WBTN 966	Tunisia	Miguel Perez	European	
WBTR 514	Turkey	Miguel Perez	European	x
WBTR 515	Turkey	Miguel Perez	Near Eastern - NE2	x
WBTR 516	Turkey	Miguel Perez	Near Eastern - NE2	x
WBTR 517	Turkey	Miguel Perez	Near Eastern - NE2	x
WBRO 562	Romania	Miguel Perez	European	
WBUA 1267	Ukraina	Miguel Perez	European	
WBUA 1268	Ukraina	Miguel Perez	European	
LG778 KS1-3	Iran, Khuzestan	This study	Near Eastern - NE1	x

2.3.2 DNA extraction, PCR amplification and sequencing

Laboratory of Durham. DNA extraction was performed in a dedicated ancient DNA laboratory in the Archaeology department at Durham University following strict laboratory procedures as according to commonly applied guidelines (Gilbert et al. 2005; Cooper and Poinar 2001). This includes wearing protective lab coats and over-shoes, double gloves (outer pair of gloves are changed in between every step of the preparation/extraction procedure). All equipment and work surfaces were cleaned before and after each use with a dilute solution of bleach (10%) followed by ethanol (99%). A strict one-way system for entering the labs is in use in order to avoid introducing post-PCR contaminants. Although every person working in any lab cleanses the used equipment/work surfaces, a weekly lab clean of all surfaces/equipment is in place in order to ensure that the labs are kept clean.

The ancient pig bone remains were prepared for DNA extraction by removing an approximately two-millimeter layer of the outer bone surface by abrasion using a dremel drill with clean cut-off wheels (Dremel no 409), targeting compact cortical bone. The bone was then pulverized in a Micro-dismembrator (Sartorious-Stedim Biotech), followed by collection in 15mL Grainer tubes.

Bone powder was digested in 0.425M EDTA, 0.05% SDS, 0.05M Tris-HCI and 0.333/mg/ml proteinase K and incubated overnight on a rotator at 50 °C until fully dissolved. The reagent master mix, excluding proteinase K, was UV-irradiated at (254 nm) for an hour using a cross linker prior to use in the extraction buffer. 2mL of solution was then concentrated in a Millipore Amicon Ultra-4 30KDa MWCO to a final volume of 100μL. The concentrated extract was purified using the QIAquick PCR Purification Kit (Qiagen) following manufacturers recommendations, except that the final elution step was performed twice to produce a final volume of 100μL. One in five to ten negative extraction controls were performed alongside the ancient bone samples.

PCRs were setup in 25μL reactions using 1.25U Taq GOLD (Applied Biosystems), 1x Gold buffer (Applied Biosystems), 2.5mM $MgCl_2$, 0.5μg/μL BSA (Bovine Serum Albumine), 200μM of each dNTP, 0.8μM of each forward and reverse primers, and 2μL of aDNA extract. PCR primers ANC1 (Larson et al. 2007a), and U15697-L15787/U15775-L15864 (Rütze personal communication, but see also chapter 3 for full details) which two fragments overlaps the ANC2 fragment amplified in Leuven, were used to amplify target DNA. One PCR negative control was included for every 5-8 aDNA template PCRs. PCR cycling conditions were 95°C for 5min, 50 cycles of 94°C for 45 sec, 54°C for 45 sec and 72°C for 45 sec, followed by 72°C for 10 min. PCR products were stored at -20C.

An initial PCR using the ANC1 primers was performed in order to screen the extracts for preserved DNA. Successful amplifications was followed by Sanger sequencing on the Applied Biosystems 3730 DNA Analyser at the DNA sequencing service in the School of Biological and Biomedical Sciences at Durham University. Once preserved samples were identified we used 5 base pair 5′-tagged PCR primers (following Binladen et al. 2007) to re-amplify the ANC1 fragment and, in addition, the fragment corresponding to ANC2. In both instances PCR products were visualised on agarose gel and stained with GelRed (Life Technologies), and then pooled by eye into approximately equimolar concentrations using a reference series previously quantified on the Qubit fluorometer; approximately 12μg/μL of each PCR product was used for the final pool.

The pooled 5′ tagged PCR products were then concentrated using an Amicon Ultra-4 30KDa MWCO filter column to a final volume of 100μL. The concentrated amplicon pool was subsequently purified using the QIAquick PCR Purification Kit (Qiagen) following manufacturers recommendations, except that the final elute volume was 80μL. The concentrated PCR amplicon pool was then built into a paired-end library (Paired-End DNA Sample Prep Kit, Illumina) following manufacturers guidelines and subsequently sequenced on the Illumina GAII platform at the Department of Biology at Copenhagen University. Illuminas Genome Analyzer Sequencing Control

Software (SCS) v2.4 was used for base calling. A custom written PERL script (Rasmussen, M., University of Copenhagen) was used to filter out sequences containing the 5′ tag label and to mate paired-end reads into single lines containing both forward and reverse 5′ tag label information. A second custom written PERL script (Frantz, L., Wageningen University) was used to write a single fasta files for each tag label/amplicon. The resulting fasta files were assembled into contigs against a reference sequence (EU333163) in Geneious Pro 5.4.3 (Drummond et al. 2011). Assembly was performed using total quality score to call the best base (any base with a quality below 20, equivalent to PHRED scores, was called as N and therefore not considered in the consensus sequence).

Laboratory of Leuven. Genetic analyses were performed in the aDNA facilities of the Laboratory of Forensic Genetics and Molecular Archaeology in Leuven (Department of Human Genetics, Katholieke Universiteit Leuven, Belgium). Pre- and Post-PCR procedures were carried out in physically separated laboratories. Access to the pre-PCR laboratory is restricted to only two workers (CO and NV) and only after wearing clean overalls, gloves, over-shoes, surgical facemasks, plastic spectacles, and following an irreversible sequence of work steps to avoid contamination. Entry is not permitted if PCR products have been handled the same day.

The aDNA facilities are routinely cleaned with bleach and RNAse Away (Molecular BioProducts, San Diego, CA, USA). Dedicated equipment is used in the pre-PCR laboratory, laboratory plastic-ware is irradiated in a cross-linker (4 hours with ultraviolet (UV) light at 254 nm), and every item entering the room is extensively washed with RNAse Away and subsequently UV-irradiated (254 nm). Various reagents, i.e. nuclease-free water (Promega, Fitchburg, WI, USA), dNTPs (Promega), and PCR Gold Buffer (Applied Biosystems, Foster City, CA, USA), are filtered through 100 kDa Centricon micro-concentrators (Millipore, Billerica, MA, USA) and stored in small volume aliquots. Extractions are performed in a UV-irradiated workstation while preparation of amplification reactions is carried out in a UV-irradiated laminar flow cabinet (Esco, Breukelen, Netherlands).

For each ancient individual at least two extractions were undertaken at different time points, at least four amplifications for each extraction were made and both strands of the DNA were sequenced, to assess the reproducibility of the results. When possible, independent extractions of each individual were carried out from anatomically distant samples. To detect potential contamination by exogenous modern DNA, extraction and amplification blanks were used as negative controls.

Samples were submitted to decontamination procedures: the outer surface of bone and tooth samples was removed through sterile blades or by sanding with a Dremel tool (Dremel, Racine, WI, USA). Additionally, the surface of the teeth was gently wiped with 10% bleach and rinsed with bi-distilled water. Bone and tooth samples were then UV-irradiated (254 nm wavelength, 12 W and 5 cm distance) in a cross linker at each side for 60 min and subsequently ground to a fine powder in a 6750 Freezer Mill (SPEX CertiPrep, Metuchen, NJ, USA) and stored at 4 °C until use. Grinding vials were accurately decontaminated after use, by means of RNAse Away (Molecular BioProducts, San Diego, CA, USA) and subsequent UV-irradiation (254 nm in cross-linker). Nonetheless, hydroxyapatite powder was used as blank controls in each grinding batch to test for potential cross contamination of the grinding vials.

Aliquots of 0.3-0.4g powder were incubated over-night in a water bath at 56°C, followed by 24h at 37°C in a digestion solution of 0.5M EDTA pH 8 (Invitrogen, Carlsbad, CA, USA), 0.5% SDS (USB Affymetrix, Santa Clara, CA, USA) and 0.1mg/mL Proteinase K (Roche, Penzberg, Germany). DNA was extracted through silica-based spin columns (Yang et al. 1998) and resuspended in 100μL TE. Each independent extraction batch contained not more than 8 samples, including two blank controls and one hydroxyapatite control. Amplifications of the first and the second 80-bp fragments in the mtDNA control region (i.e. ANC1 and ANC2, (Larson et al. 2007a; Larson et al. 2007b) were performed in a final volume of 50μL, containing 1x PCR Gold Buffer (Applied Biosystems), 2.5mM $MgCl_2$ (Applied Biosystems), 0.2mM dNTPs mix (Promega), 0.1μM each primer (Eurogentec, Seraing, Belgium IDT, Leuven, Belgium), 0.05% BSA (Sigma Aldrich, St. Louis, MO, USA), 2.5U

AmpliTaq Gold DNA polymerase (Applied Biosystems), 5-10μL of aDNA extract. The following cycle conditions were used: 94°C for 10 min, 45 cycles of 94°C for 45 sec, 56°C for 1 min, 72°C for 1 min, and a final step of 72°C for 5 min. All the amplifications reactions were carried out on a GeneAmp PCR System (Applied Biosystems). The amplification products were visualised on a microchip electrophoresis system (MCE-202 MultiNA, Shimadzu Biotech).

Positive amplification products were purified with Microcon filter concentrators (Millipore) or through ExoSAP-IT (USB Affymetrix), according to manufacturers specifications. The purified amplicons were directly sequenced by means of ABI Prism BigDye Terminator Cycle Sequencing Kit (ver3.1, Applied Biosystems) according to the manufacturers specifications. Dyed products were ethanol precipitated and sequence reactions were performed on each strand by using 5′-tailed sequencing primer6. The products were detected by capillary electrophoresis on ABI PRISMTM 3130XL Genetic Analyzer (Applied Biosystems).

Cloning of the ANC1 products was carried out in six individuals (Bad17, Bad47, Bad52, Bad86, M46, M96) using the TOPO TA Cloning kit (Invitrogen), according to the manufacturers instructions. Up to 10 colonies from amplification products of two independent extracts were picked into 25μL nuclease free water (Promega), of which 1μL was used for PCR amplifications in a 25μL volume of 1x PCR Master Mix (Qiagen, Hilden, Germany), 0.5μM each of vector M13R and M13F primers. Amplification products were purified and sequenced as previously described and the sequences were aligned, analysed for artefacts induced by post-mortem miscoding lesions and the presence of contaminant DNA sequences. Sequences from independent experiments were aligned by using BioEdit 5.0.9 (Hall 1999).

2.3.3 Morphometric analyses

36 specimens (table 2.1) corresponding to 21 second (M2) and 27 third (M3) lower molars were analysed using traditional and GMM approaches based on pictures of the occlusal view of the teeth (figure 2.1). The GMM analyses were based on landmarks (N=7 for the M2, N=8 for the M3) located on the internal occlusal view and sliding-landmarks (N=68 for the M2, N=91 for the M3) located on the outline of the tooth (figure 2.1). In addition traditional metrics were measured : maximum length and widths (2 for the M2 and 3 for the M3, 22, figure 2.1).

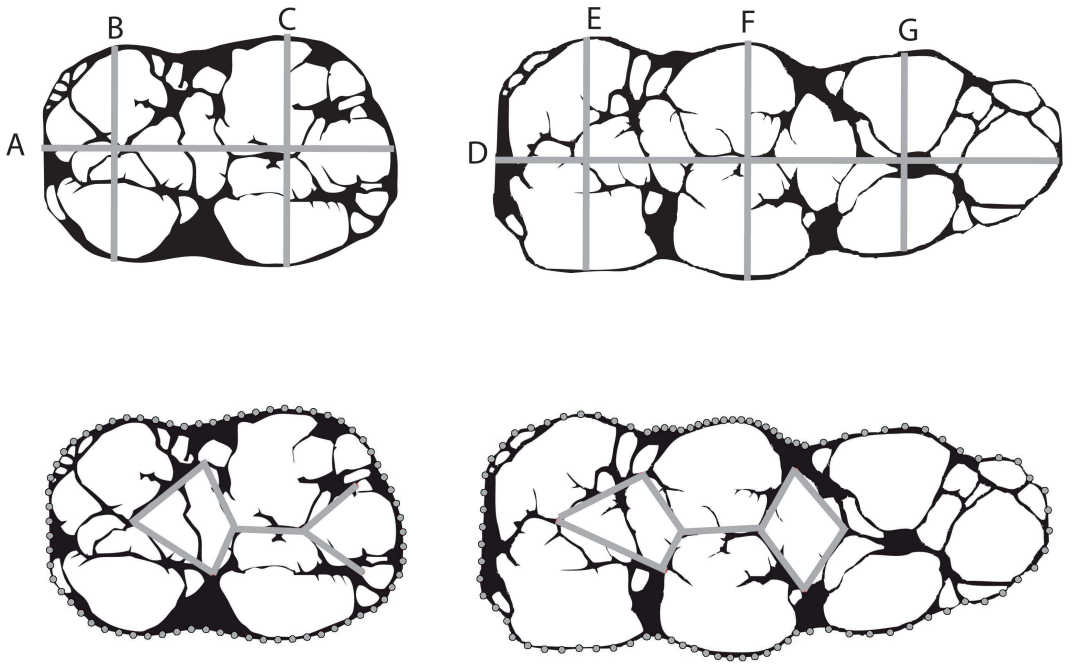


Figure 2.1: Morphometric variables.

Differences between genetic haplogroups (Near Eastern versus European) were tested using both traditional metric and GMM approach. For the GMM approach, shape and log-transformed centroid size were analysed for the overall teeth and then separately for the inside of the occlusal view and for the outline. Traditional measurements were analysed using a Log Shape Ratio approach (Mosimann and James 1979) that allows a separation of shape and isometric size.

Differences between haplogroups were tested with Kruskal-Wallis tests for sizes (centroid and isometric) coupled with boxplot and MANOVAs for shapes (from GMM and LSR) coupled with Linear Discriminant Analyses (LDAs) paired with leave-one-out cross-validation (CV).

The pictures were taken using a reflex camera (Nikon D90) coupled with a 60mm micro-length (AF-S Nikkor) to obtain images of the teeth in their occlusal view. Images were standardised for position and parallax. Two-dimensional coordinates of landmarks within the occlusal surfaceand sliding-landmarks along the outline of the teeth were recorded, as well as traditional measurements (maximum length and widths) using TpsDig (http://life.bio.sunysb.edu/morph/). 7 landmarks were recorded and 68 sliding-landmarks for the lower M2 and 8 landmarks and 91 sliding-landmarks for the lower M3 (figure 2.1).

The coordinates of the sliding-landmarks were recorded using the "Draw background curves" tool of TpDIG that allows to positioned equidistant points. The outline of the lower M2 was divided into two anterior and posterior curves composed by 28 and 38 points respectively plus 2 points in between. The outline of the lower M3 was divided into four curves (anterior (28 points), posterior (28 points), labial (18 points), lingual (13 points) plus 4 points in between). TpsRelw (http://life.bio.sunysb.edu/morph/) was used to slide the sliding-landmarks along their respective curves with the Procustes distance minimization criteria (Bookstein et al. 2002). The aligned coordinates and the centroid size, as well as the traditional measurements, were then analysed using R v2.13.1 (R Development Core Team 2011) and the "Rmorph" library (Baylac 2012). The first components of the Principal Component Analysis (PCA) realised on the coordinates after superimposition were analysed instead of the original dataset to minimise the number of variables compare to the number of specimens. Before discriminant analyses, a dimensionality reduction was applied on the scores of the PCA with the Baylac and Friess procedure (Baylac and Friess 2005) that selects the N firsts components that maximise the variability between the groups.

2.3.4 Phylogeographic analyses

To assess phylogenetic structure among specimens, a Maximum-Likelihood (ML) tree based on 661bp sequences of the mtDNA control region from the modern wild boar (table 2.2) was constructed using PhyML (Guindon and Gascuel 2003) as implemented in Geneious v5.4.3 (Drummond et al. 2011).

A median-joining (MJ) network (Bandelt et al. 1999) of the combined ANC1-ANC2 haplotypes was created using Network 4.6 (http://www.fluxus-engineering.com) in order to illustrate the degree of variation among modern and ancient haplotypes in Anatolia, Middle East and . All sequences were edited and aligned by eye using BioEdit 5.0.9 program (Hall 1999) or using MAFFT (Katoh et al. 2002) in Geneious v5.4 (Drummond et al. 2011). Haplotypes were assigned to haplogroups following ANC1 haplogroup designations published by Larson et al. (2007a).

2.3.5 Wild and domestic status determinations

The status (wild or domestic) of some of the specimens was provided following identification based on traditional metrics (Leuven specimens). 18 out of 197 specimens analysed in Durham had associated wild or domestic status information available (table 2.1). Specimens for which status identification was not available were left undetermined.

2.4 Results

The ML tree of modern sequences (figure 2.4, table 2.2) revealed an identical topology to that previously published (Larson et al. 2005; Larson et al. 2007a). The MJN (figure 2.3) show the relationships among ancient and modern specimens from Anatolia, Middle East and North Africa and support previous haplotype relationships.

Reproducible aDNA was obtained from 134 out of 350 specimens (38.2%, table 2.1). As expected for ancient samples following diagenetic trajectories (e.g. Smith et al. 2001; Smith et al. 2003; Allentoft et al. 2012), an inverse correlation between yields of successful DNA extraction and sequencing and age of the samples was observed (Spearmans rank correlation $r^2 = 0.87$, $p \leq 0.001$, n=9; figure 2.2).

Among ancient samples, nearly all observed ANC1 sequences matched haplotypes previously described in Larson et al. (2007a). Only four novel ANC1 sequences were observed (Bad9, M123 and M56, LG354/YellowStar or YS). The MJN indicate that YS is a novel NE2 haplotype (figure 2.3). As expected for temporally structured genetic sequence data, the oldest specimens tend to cluster at the central nodes the in network, whereas the more recent ones occupy derivative nodes, indicative of population expansion.

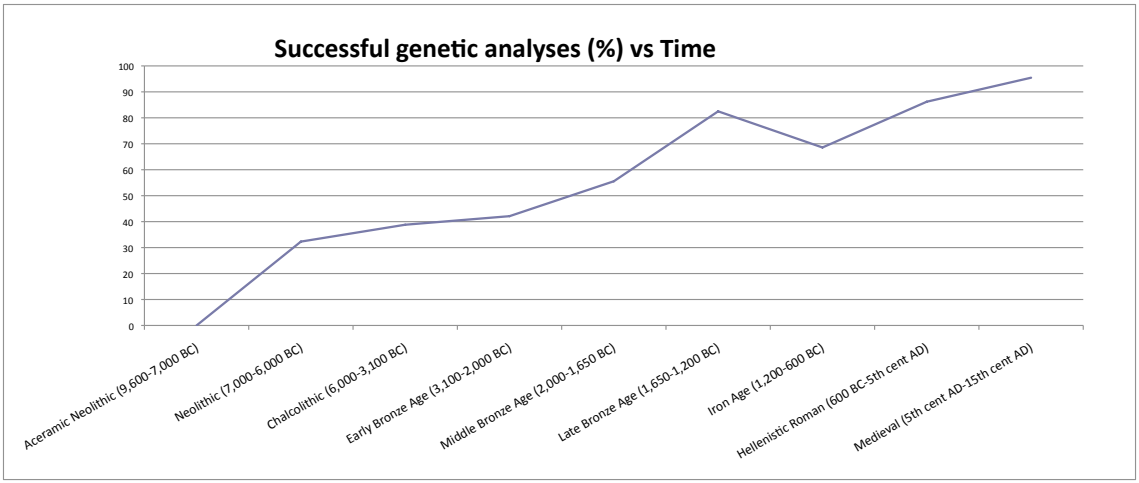


Figure 2.2: Rate of successful DNA extractions over time. $r^2 = 0.87$.

2.4.1 Assessing the authenticity of ancient DNA data

It is possible to exclude contamination with a high level of confidence on several grounds. The analyses were undertaken in dedicated aDNA laboratories, under strictly controlled conditions. A selection of samples was processed both in the laboratory of Durham and in the laboratory of Leuven, providing identical haplotypes.

A Fisher exact test was used to validate the ancient sequences produced in Leuven (Champlot et al. 2010). It has been observed that DNA from domestic animals (cattle, pig and chicken) commonly contaminates PCR reagents (Leonard et al. 2007; Champlot et al. 2010). These contaminants are present in very low amounts and may remain undetected unless a high number of blank controls are performed. In the present study, a high number of blank controls were used. No systematic contamination was ever observed in either the grinding (hydroxyapatite), extraction or amplification controls. Overall, 21 out of 927 blank controls produced positive amplification (2.3%). After sequencing, the positive blank controls always revealed a European haplotype, and in one instance an East Asian haplotype. To determine whether the sample PCR success rate is significantly different from the amplification rate due to contaminants and to ensure authenticity of the sample amplification with a 95% confidence level, we used Fishers exact test after pooling blank control data

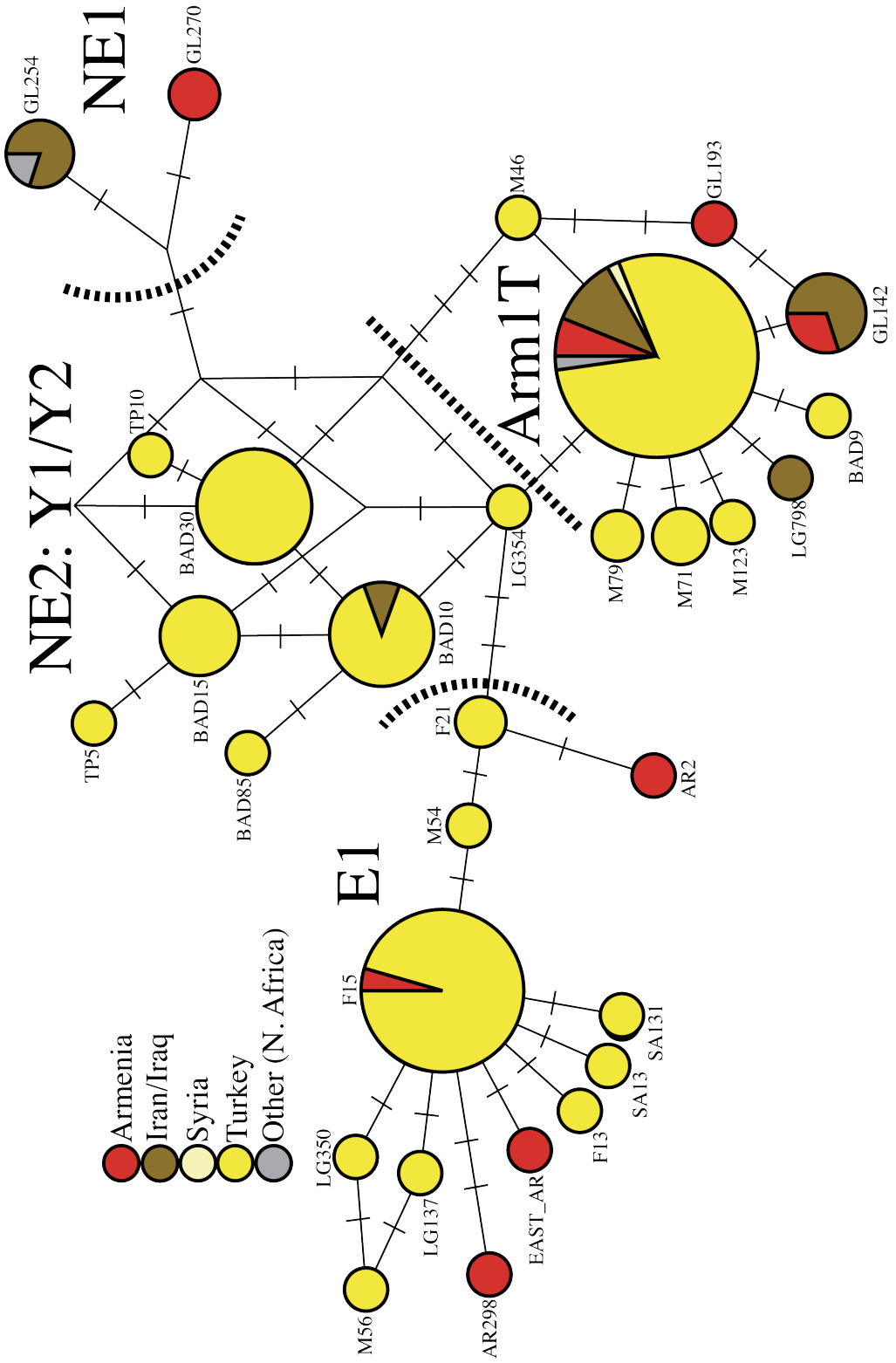


Figure 2.3: Median-joining network of concatenated ANC1 and ANC2 haplotypes from ancient and modern specimens from Anatolia, Middle East and North Africa.

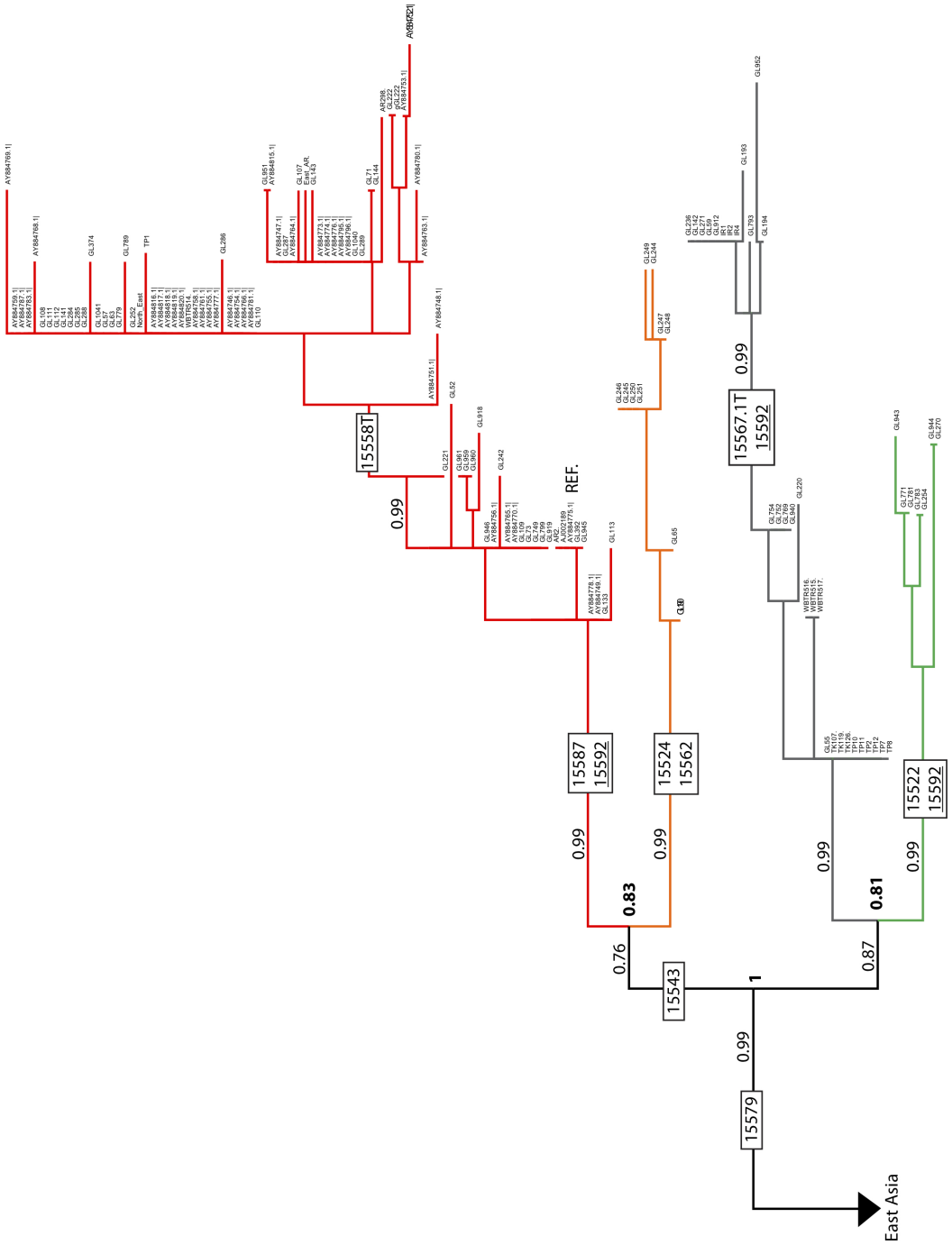


Figure 2.4: Maximum Likelihood tree of a 661bp d-loop fragment representing the modern reference samples in table 2.2. Nodal support is the chi-squared based support value implemented in Geneious Pro 5.4.3 (Drummond et al. 2011). Parsimony informative sites are highlighted relative to the Ursing and Arnasson (1998) reference sequence. Green=NE1, Grey=NE2, Orange=E2 and Red=E1.

obtained over many experiments with a given reagent batch (Champlot et al. 2010). After Bonferroni correction, only sequences with a 95% confidence interval were validated and considered authentic.

Overall validation of sequences is given by the high reproducibility among the extracts from at least three independent PCR experiments from two independent extracts (Leuven). In some instances, reproduced sequences were obtained from up to seven amplification attempts carried out from the same extract, and a third extraction was performed in order to give more consistency to the data. Fishers exact test was used to authenticate sequences produced in the laboratory of Leuven, which were analysed with standard PCR techniques. Of the total 153 samples analysed in Leuven, 60 resulted in unsuccessful genetic analyses (39% of the total individuals), 56 of which provided no DNA amplification after multiple attempts, whereas four gave low success rate which turned out to be non-significant in the Fisher exact test, likely because of poor DNA preservation.

Authenticity of sequences produced in the laboratory of Durham relied on the extensive cloning obtained by means of Illumina sequencing (see below and figure 2.5).

The molecular behavior of the PCR products is in agreement with what is expected from analyses of ancient samples, since higher yields of successful genetic analyses were observed in the younger samples (figure 2.1, table 2.1), whereas no DNA amplification at all was observed in the oldest samples (sites of Göbekli Tepe and Gürcütepe, or the Aceramic Neolithic). In addition, a higher number of amplification attempts (up to six) were necessary for DNA amplification of the oldest samples.

Results of the cloning experiments in six specimens (Leuven) confirmed the haplotypes determined through direct sequencing of the PCR products, with consistency of mutations ranging from 78% (Bad86) to 100%. The pattern of variation of the cloned sequences showed single substitutions (mostly C->T and G->A transitions)

that were interpreted as artifacts due to misincorporations during the amplification or miscoding lesions. The latter is likely the result of post-mortem hydrolytic deamination that is common and characteristic in ancient samples (Hofreiter et al. 2001a; Briggs et al. 2007; Gilbert et al. 2007). Average rate of C->T and G->A transitions ranges from 1% to 8%. Significantly, consistency of artifacts was higher in the oldest samples (Bad47 and Bad52, dated to Early Neolithic), compatible with a higher level of damage of nucleic acids and a lower number of template molecules initiating the amplification reaction.

A similar pattern was observed in a subset of the available sub-clonal data set from Durham (figure 2.5). Out of approximately 450-1000 randomly drawn ANC1 sequences (first 45bp forward read) from four specimens (LG281, LG459, LG477 and LG495) a total of 59 haplotypes were observed (N=12, 12, 10 25 respectively. C->T/G->A transitions (Type 2 transitions) are more common than other types of substitutions, including Type 1 transitions (83% and 17% respectively), and are interpreted to mainly represent postmortem damage-derived miscoding lesions (C->U deamination) (Gilbert et al. 2007). The other types of substitutions, including Type 1 transitions, are sporadic and most likely derive from nucleotide misincorporations or sequencing errors. In support for this argument is the lack of consistency of other types of substitutions in between clones as compared to Type 2 transitions. The average rate of Type 2 transitions, calculated as the total number of transitions over C/G bases in the total extracted sequences (not accounting for identical haplotypes that might derive from a single template molecule) ranged in between 1% to 14% with an average of 5%.

These observations, together with the above-mentioned laboratory procedures, make it highly unlikely that the haplotypes observed in the ancient samples arose from contamination or post-mortem damage and lend credibility to conclusions drawn below.

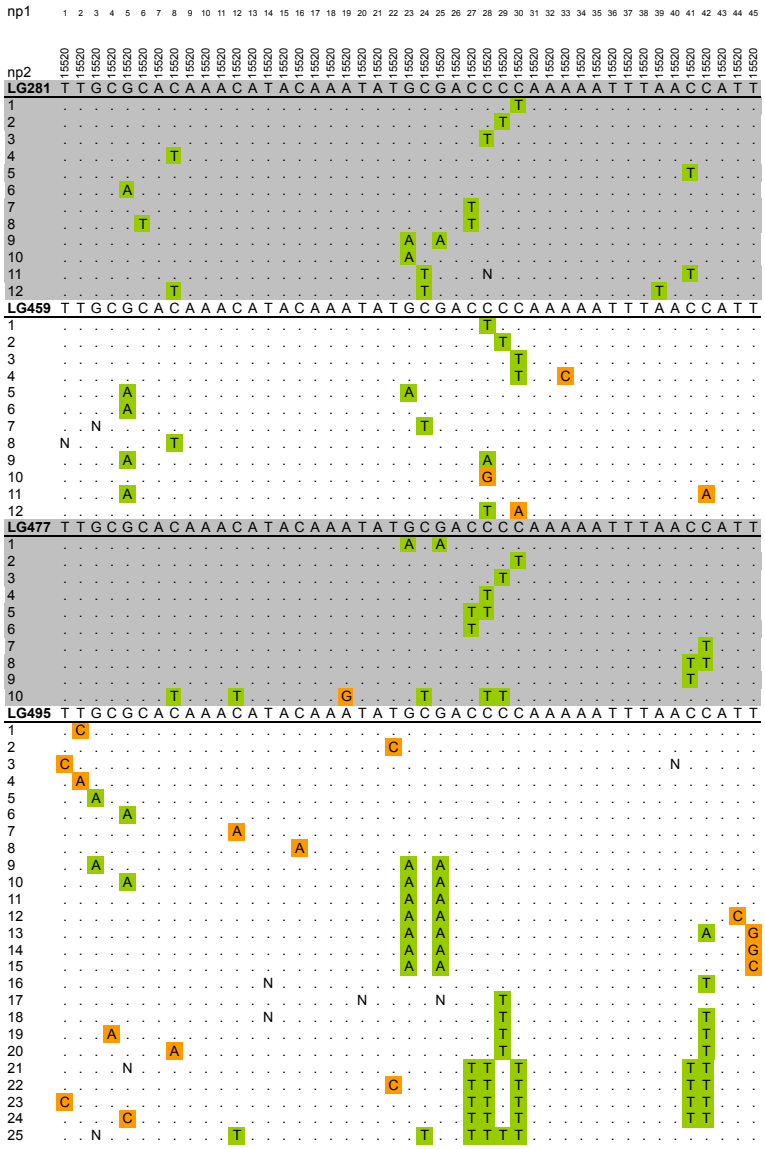


Figure 2.5: Unique haplotypes observed in the sub-clonal data set obtained through Illumina deep sequencing of PCR amplicons (Durham). Green colour indicates Type 2 damage and orange colour indicate other errors. Mutations are denoted relative to the Ursing and Arnasson (1998) reference sequence (np2).

2.5 Discussion

2.5.1 Timing the Anatolian Turnover

Larson et al. (2007a) hypothesised that domestic pigs carrying E1 (European) haplotypes were introduced to Anatolia no later than 700 BC. Because that study did not type any ancient pigs from modern day Turkey, it remained a possibility that European pigs had been introduced earlier than this date, followed by slow dispersion eastwards to Armenia. Alternatively, the low number of ancient samples published in Larson et al. (2007a) left the question open of whether the E1 clade had a natural range that stretched from Europe into Anatolia (Ramirez et al. 2009). The temporal (often using direct AMS dating) and geographic distribution of mtDNA haplotypes (figure 2.6) generated in this study, however, revealed that all 45 Neolithic specimens possessed one of two Near Eastern lineages Y1 or Arm1T, and that the first pig with European ancestry appeared at the beginning of the Late Bronze Age, $\sim 1,600 - 1,500$ BC at Lidar Höyük in Southeast Anatolia.

Though not corroborated by AMS dating, a pig possessing a European (E1) haplotype from Middle Bronze Age layers suggests that an even earlier appearance of European pigs in Lidar Höyük cannot be ruled out. Nevertheless, European pigs are unlikely to have arrived before 2,000 BC because all pigs from Early Bronze Age layers at Bademağaci and Lidar Höyük, in West and East Anatolia respectively, possessed only NE2 clade haplotypes. Following their initial introduction, European pigs increased in numbers considerably at Lidar Höyük, particularly towards the beginning of the Iron Age around 1,200 BC. This was the beginning of the so-called Anatolian turnover, which was completed when the Hellenistic and Medieval eras began across Anatolia and Armenia (figure 2.6).

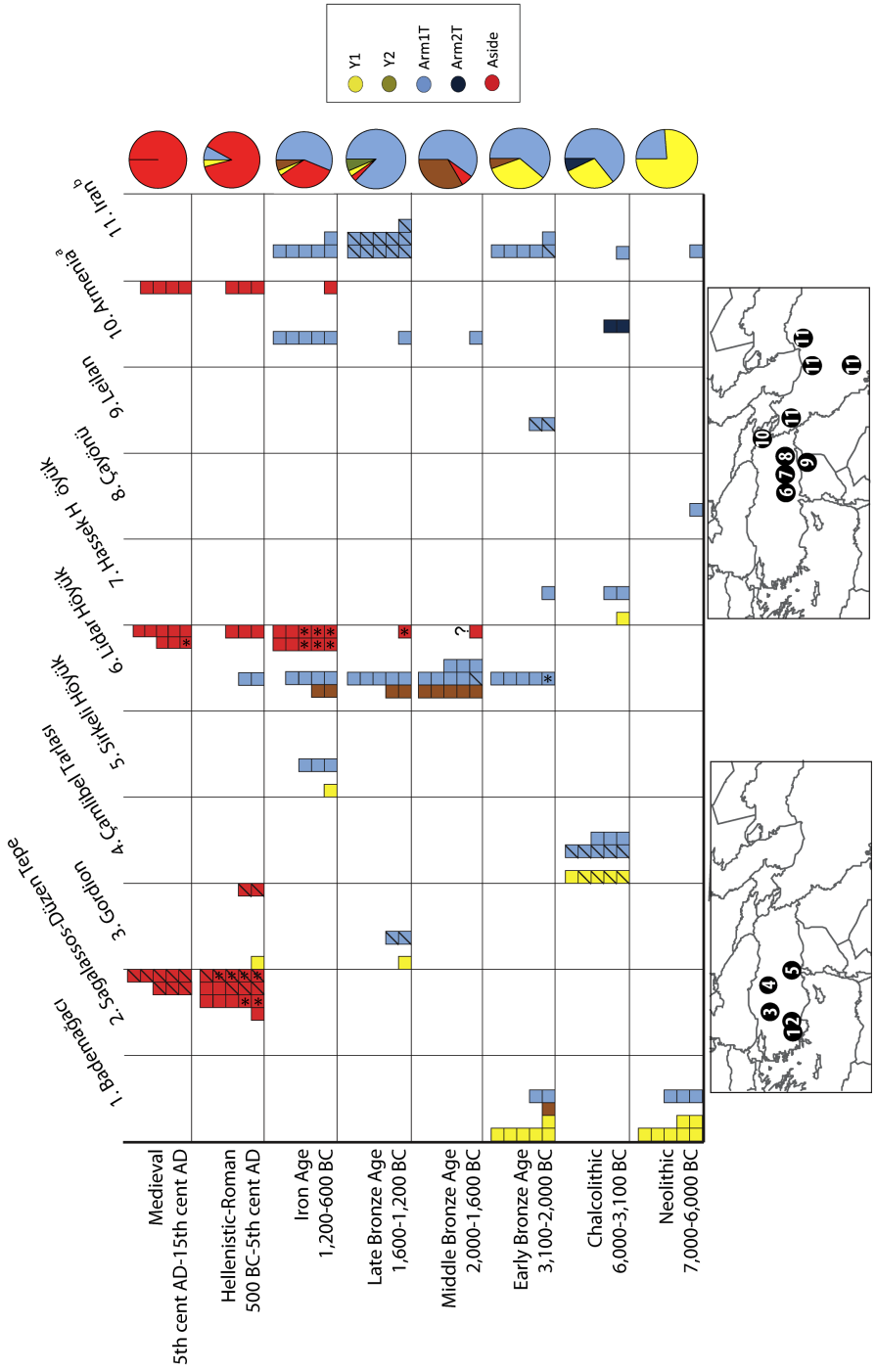


Figure 2.6: The spatio-temporal distribution of mtDNA d-loop haplotypes. Asterisks denote AMS dated samples, the question mark show the single specimen that failed to produce an AMS radiocarbon date, boxes crossed by a line show specimens for which GMM was obtained, and the A and B denotes bins for which several sites are represented.

If assuming the current sample size (table 2.1), it is not possible to eliminate the possibility that the E1 clade existed in Anatolia prior to the increase of E1 frequencies (given the current sample size, a binomial 95% confidence interval show that E1 pigs could have segregated at frequencies between 0-6.5% during the Neolithic without being detected in the sample). If, in fact, E1 pigs were indigenous to Anatolia, this signature could have been increased via drift or selection, thus eliminating the requirement of a human-driven introduction.

To address this issue, the morphometric differentiation among pigs of different mtDNA haplogroups was assessed using shape and size variation of the second and third lower molars. The expectation (or hypothesis) is that pigs of different haplogroups would be phenotypically indistinguishable if the full Anatolian sample represents one interbreeding population (as elaborated on in Larson et al. 2007b). However, GMM results show that the shape of the inside of the occlusal views discriminate European and Near Eastern haplogroups with a probability of 81% (table 2.3). Morphometric differences were also detected in the shape of the third molar and in the isometric size of the second molar (table 2.3). These results show that the European and Near Eastern populations, respectively, have distinct phenotypes, probably as a result of geographical separation (i.e. these were non-interbreeding populations) (figure 2.7). The combined GMM and aDNA results are therefore consistent with the hypothesis that people introduced domestic pigs to Anatolia from Europe. The full spatio-temporal structure of the data show that this introduction took place no later than the Late Bronze Age (1,600-1,200 BC), at least nine centuries earlier than previously thought (Larson et al. 2007a).

Establishing the time frame and geographic area over which the turnover took place is important for understanding the human cultural contexts in which it occurred. As the dataset covers Middle and Late Bronze Age layers mainly in Southeast Anatolia (and specifically at the site of Lidar Höyük), determining patterns and routes of the introduction of European domestic pigs to the Anatolian peninsula is difficult, and various equally plausible scenarios could be envisaged. The initial appearance

		Lower M2								Lower M3							
		X^2	Df	Pillai	approxF	numDf	denDf	p	CV	X^2	Df	Pillai	approxF	numDf	denDf	p	CV
Global (inside+outline)	Shape		1	0.5585	3.7947	5	15	0.0202	57%		1	0.5014	1.6088	10	16	0.1817	
	Centroid Size	2.6717	1					0.1021		3.2407	1					0.0718	
Inside	Shape		1	0.5066	3.0804	5	15	0.0414	81%		1	0.4367	5.9441	3	23	0.0037	81%
	Centroid Size	3.6818	1					0.0550		0.0423	1					0.837	
Outline	Shape		1	0.3329	1.497	5	15	0.2490			1	0.7554	2.6479	14	12	0.0493	74%
	Centroid Size	2.6717	2					0.1021		3.0582	1					0.0803	
Tradionnal metric	Shape		1	0.2217	1.6142	3	17	0.2232			1	0.1327	0.8418	4	22	0.5136	
	Isometric Size	3.9596	1					0.0466		1.7884	1					0.1811	

Table 2.3: Differences between haplogroups in size (Kruskall-Wallis test) and shape (MANOVA) based on global analysis, restricted to landmarks inside the occlusal view, restricted to sliding-landmarks along the outline, and to traditional metric data. Significant results are highlighted in grey.

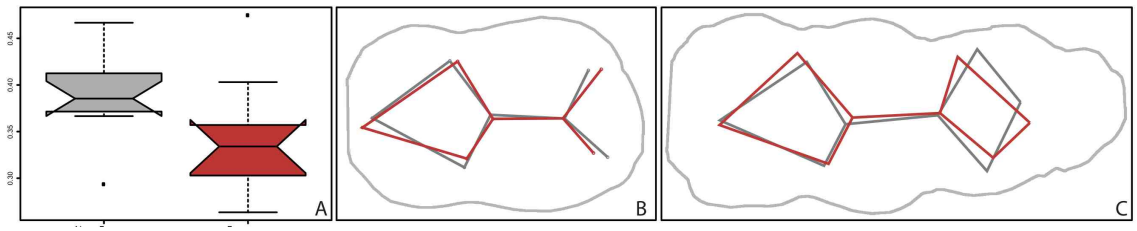


Figure 2.7: Significant molar differences between pigs of European (in red) and Near-Eastern (in grey) ancestry in isometric size of the lower M2 (A), and shape of the lower M2 (B) and M3 (C).

of pigs in Southeast Anatolia during the Late Bronze Age may have been the result of contacts and trading routes, direct or via Cyprus, between people in the Aegean and Northern Levant (Van Wijngaarden 2002). Cyprus was a Hittite outpost in the seaborne trade along the Eastern Mediterranean (Seeher 2011). The Hittites dominated central Anatolia from the beginning of Late Bronze Age (Bryce 2005), so if pigs were introduced a few centuries earlier, during the Middle Bronze Age, it is possible that they arrived with Indo-European speaking Proto-Hittite populations migrating through Caucasus into Anatolia. However, this is also difficult to assess because the precise time frame and geographic routes along which the migration of Indo-European speakers migrated into Anatolia remains uncertain (Melchert 2011).

The turnover to European pig haplotypes began during the transition between the Bronze and Iron ages, which also coincided with the sudden collapse of states and

empires in Central Anatolia, the Levant and the Aegean (Bryce 2005). Following the fall of the Hittite Empire, Neo-Hittite principalities developed in Northern Syria and Southeast Anatolia, whereas Central and West Anatolia witnessed the rise of the Phrygian Kingdom (Yücel Senyurt 2005). Phrygians, who spoke an Indo-European language, are believed to have arrived in Anatolia from the west, probably as part of large-scale migrations occurring at the transition between Bronze and Iron Age (Sagona and Zimansky 2009). Their arrival might explain the turnover trend observed at Gordion (the Phrygian capital).

The transition in Anatolia from indigenous pigs to those derived from Europe is similar to the genetic turnover in Europe (Larson et al. 2007a) where the turnover took place earlier (beginning about 3,900 BC) and may have taken as little as 500 years. In Anatolia and Armenia, the time between the first appearance of European pigs and the complete elimination of Near Eastern pigs in the late Roman or Early Medieval period lasted $\sim 2,000$ years. The underlying cause of the genetic turnovers is unclear, thus opening the possibility for a range of different explanation models. For example, pigs of European ancestry might have had a biological or cultural advantage relative to those of Near Eastern ancestry. For example, it is known that Romans selectively bred pigs with different phenotypes (White 1970; Peters 1998) suggesting that amenability to human selection could have played a role. Administrative officers in Mesopotamia recorded coat colours (Zeder 1994), and early farmers might have intentionally selected pigs on the basis of coat colouring (Fang et al. 2009).

Regardless of the underlying cause of the observed turnover, or the exact geographical routes along which European pigs were brought to Anatolia, it is clear is that domestic pigs possessing E1 haplotypes were deliberately introduced into Anatolia from Europe by 1,600-1,200 BC, and that they had out-competed the local indigenous pigs two millennia later (figure 2.6).

2.5.2 Anatolian origins of the Neolithic diffusion into Europe

A previous study (Larson et al. 2005) of modern wild boar showed that the Y1 and Y2 haplotypes are geographically restricted to the Near and Middle East (with few exceptions). A subsequent study of aDNA (Larson et al. 2007a) showed that no European wild pigs, from the Mesolithic to the present day, possessed Y1 or Y2 haplotypes (except two wild Y2 specimens from the Crimea) (Larson et al. 2005; 2007a). Neither of these studies, however, presented direct observations of either Y1 or Y2 haplotypes in ancient pigs from the Near East, thus leaving open the possibility that these haplotypes originated elsewhere. The ancient Anatolian data presented here show that both wild and domestic Early Neolithic pigs at Bademağaci in Southwestern Anatolia (6,400-6,100 BC) (De Cupere et al. 2008) possessed the Y1 haplotype (figure 2.6). These data support the hypothesis that the earliest domestic pigs in Europe were introduced from the Near East (Larson et al. 2007a). In addition, these data provide strong empirical evidence for a close link between the Neolithisation of Europe (and especially the LBK expansion into Central Europe, Larson et al. 2007a) with Neolithic cultures in West Anatolia (Perles 2003; Larson et al. 2007a; Özdogan 2011).

The fine geographic scale of the survey (figure 2.6) also allowed for the detection of a west to east cline in the frequency of Near Eastern haplogroups Y1 and Arm1T. The frequency of Y1 is significantly higher (Fisher exact test, $p<0.001$) in the west (32%) than in the east (1%) while Arm1T is more frequent in East Anatolia, Armenia and Iran. Even when focusing on the period before the European turnover (Early Neolithic to the Early Bronze Age) the frequency of the Y1 haplotype in Western Anatolia (56%) is significantly higher than in East Anatolia (8%, $p<0.01$).

In Southeastern Anatolia, the Y1 haplotype was absent from Lidar Höyük despite the $\sim 3,000$ year stratigraphic sequence. The easternmost pig that possessed the Y1 haplotype comes from Chalcolithic layers at Hassek Höyük (a domestic spec-

imen). These data therefore suggest that Y1 pigs were indigenous primarily to Western Anatolia, where they were possibly domesticated before being transported into Europe (Larson et al. 2007a; Özdogan 2011). Because the earliest archeological evidence for pig domestication comes from East Anatolia (Ervynck et al. 2001; Zeder 2008) and because Y1 pigs were not transported east into Armenia and Iran, this pattern suggests the possibility of two domestication centers in Anatolia, one primary center in East Anatolia (which is mainly supported by archaeozoology, see section 1.4.1) and one, possibly independent from the eastern one, in West Anatolia (see section 2.5.3 below).

The haplotype distribution (figure 2.6) also reveals a general scarcity of the Y2 lineage in Neolithic and Chalcolithic layers across Anatolia and raises questions about its geographic origin. The oldest specimen possessing the Y2 haplotype is a single pig from Bademağaci in Western Anatolia. It is dated (stratigraphically) to the Early Bronze Age. Y2 pigs also appear in Middle Bronze Age and Iron Age layers at Lidar Höyuk in Eastern Anatolia, alongside the earliest occurrence of pigs possessing European haplotypes. Despite the fact that no modern European wild boar possesses Y2 haplotypes, the pattern observed here could indicate that Y2 pigs are not indigenous to Anatolia but were introduced from Europe alongside E1 pigs.

2.5.3 Early pig domestication in Anatolia

The large sample size and chronological breadth of the data allows for an assessment of where domestication took place (figure 2.3, figure 2.6, and see section 2.5.2 above). All ancient domestic pigs (those predating the introduction of E1 pigs) exclusively possess haplotypes that cluster in the NE2 clade (figure 2.6), which is restricted primarily to Anatolia. All pigs possessing NE1 clade haplotypes are wild (or possibly feral in the case of African specimens) and come from the Caucasus, Iran or North Africa (table 2.2). These patterns strongly indicate that early pig domestication was restricted to Anatolia and to pigs possessing mtDNA lineages clustering in the

NE2 clade (Larson et al. 2005; 2007a).

This conclusion is also supported by the archaeozoological records available (Conolly et al. 2011). For example, by measuring size change in the lower M3 molars of pigs over a 2,000 year sequence at the Southeastern Anatolian site of Çayönü Tepesi, Ervynck et al. (2001) found a gradual decrease in size which they suggested was the result of an in situ domestication process that culminated with the appearance of fully domesticated pigs by 7,000 BC. The single specimen from this site that yielded amplifiable DNA was excavated from Pottery Neolithic layers that postdate the beginning of the domestication process (Ervynck et al. 2001). It possessed the Arm1T haplotype (belonging to the NE2 clade). The ubiquity of Arm1T across Anatolia, Armenia and Iran (figure 2.3), and its dominance in Eastern Anatolia around Çayönü Tepesi (and other sites that bear evidence of early domestication), suggests that Arm1T was a common haplotype amongst the early domestic pigs.

Arm1T haplotypes are also found in Western Anatolia in wild and domestic specimens, but only the Y1 signature was transported into Europe. The phylogeographic structure among these haplotypes suggests that regionally differentiated wild boar possessing the Arm1T and Y1 haplotypes were domesticated in Eastern and Western Anatolia, respectively, and though the processes may have been independent, it is also possible that the concept of pig domestication was transferred during the Neolithic diffusion by human groups migrating with small herds from the core domestication area in Southeastern Anatolia westward along a Mediterranean coastal route. This scenario is bolstered by the presence of domestic pigs in Neolithic layers of the coastal site of Yumuktepe and the general dearth of pigs during the same period in central Anatolia (Conolly et al. 2011; Arbuckle *in press*). If true, this sequence of events would be analogous to the European Neolithic when pigs domesticated from local wild boar eventually replaced the first domestic pigs to enter Europe from the Near East (Larson et al. 2007a).

2.6 Conclusions

This study addresses a number of unresolved questions regarding the origins and subsequent dispersals of domestic pigs in Anatolia and the Near East. The results contribute to the ongoing discussion about the earliest phases of domestication and prehistoric human movements. The combination of genetic and morphometric analyses on the same samples allowed for the analysis of variation at different levels of biological organization and the data add to the growing body of evidence that animal domestication in general, and pig domestication specifically, was a complex, non-linear process that took place over millennia in different Anatolian regions (Ervynck et al. 2001; Peters et al. 2005; Vigne et al. 2009).

More specifically, the data suggests that pigs possessing the Arm1T lineage were initially domesticated in Southeastern Anatolia at sites such as Çayönü Tepesi (Ervynck et al. 2001), and possibly dispersed with humans as the Neolithic expanded into Western Anatolia. Wild pigs indigenous to Western Anatolia possessing the Y1 haploype were also domesticated, however independently, and were subsequently transported into Europe along the northern Danubian route (Larson et al. 2007a). Once domestic pigs arrived into Europe, local domestication or introgression with local European wild boar led to a replacement of the Anatolian Y1 maternal genetic signature in local pigs. From at least the beginning of Late Bronze Age, and possible a few hundred years before, domestic pigs possessing European haplotypes were transported back into Anatolia where they completely replaced the endemic Y1 and Arm1T lineages by the 5th century AD (Larson et al. 2007a).

Whether the introduction of European pigs to Anatolia reflects human movement or trade is unclear. Cultural upheaval leading to invasions and migrations into Anatolia from the Late Bronze Age to the Iron Age suggests that human movement is certainly a possibility. This study presents the most nuanced picture of the timing and geography of pig domestication and human migration in pre-historic Anatolia to date.

Chapter 3

Ancient *Sus* DNA reveal patterns of migration, selection and local domestication in Europe and the Near East

3.1 Introduction

The pig (*Sus scrofa domesticus*) was independently domesticated from the Eurasian wild boar (*Sus scrofa* sp.) multiple times across Eurasia during the Holocene (Larson et al. 2005, and see chapter 2). Where, when, how and why domestication took place is better understood today than a decade ago. Nevertheless, the precise timing and location of pig domestication, and along which routes pigs spread from the earliest domestication centers, is still a question open to debate (Larson et al. 2011). Consequently, to what extent domestic pigs (and pig domestication, as a process) formed part of the "Neolithic package" remains somewhat unclear (Larson et al. 2007a; Conolly et al. 2011).

Archaeozoological data show that the earliest pig domestication took place in the primary area of Neolithisation in Southeast Anatolia as early as the tenth millennium BC (or during the Early Neolithic) (Rosenberg et al. 1998; Peters et al. 1999; Ervynck et al. 2001; Zeder 2008). The Neolithic package, probably including domestic pigs (see chapter 2), spread westward through Anatolia during a secondary Neolithic phase in the first half of the 7th millennium BC. From there, pigs were introduced to Europe towards the end of the 7th millennium BC (Perles 2003; Larson et al. 2007a; Zeder 2008; Özdogan 2011). Ancient genetic data has played an important role in this research in that it has provided a framework in which genealogical relationships among wild and domestic pigs can be mapped through space and time. This framework (the spatial and temporal arrangement of genetic lineages; phylogeography, Avise 2000; 2009) can be used to infer where and when domestication took place (Giuffra et al. 2000; Larson et al. 2005; 2007a).

In chapter 2, a $\sim$ 160bp mitochondrial d-loop fragment was analysed in wild and domestic pigs from Neolithic to contemporary modern contexts across the Near and Middle East. Two important observations were made: first, the low frequency of mtDNA haplotype Y2, and the complete lack of this haplotype in strata older than the Bronze Age, raised questions about the Near Eastern origin of this lineage (figure

2.6). It was previously hypothesised that the Y1 and Y2 haplotypes share a common origin in the Near East (Larson et al. 2005; 2007a), but the results of chapter 2 contradict this hypothesis. The Y2 haplotype was present in Mesolithic and Neolithic contexts in Crimea, Croatia and Corsica (Larson et al. 2007a), suggesting a geographic disconnect in the natural range of Y1 and Y2 haplotypes. Secondly, the spatial arrangement of mtDNA haplotypes showed that the earliest domestic pigs in Europe likely originated from pigs domesticated in West Anatolia (figure 2.6). The domestication of Y1 pigs was therefore probably related to the secondary Neolithic development in West Anatolia, which took place west of the primary Neolithisation zone in East Anatolia (Özdogan 2011).

3.1.1 Trajectories of domestication - determining the process of local domestication

If pigs were domesticated multiple times in prehistory, it is important to elucidate to which extent this was independent as opposed to the product of admixture (human-mediated or not) with local wild boar (Larson et al. 2007a). GMM (geometric morphometrics) solved this issue in chapter 2 by providing statistical evidence that pigs belonging to different mtDNA haplogroups had significantly different dental phenotypes. However, this is sometimes difficult to implement, particularly in a species like *Sus scrofa*, which harbour high levels of phenotypic variation among and within populations (Albarella et al. 2009). In the absence of clear morphological data (for example, clear wild/domestic status calls), determining whether prehistoric pigs were wild or domestic (and whether they had been subject to wild-domestic hybridisation) could be solved by genotyping mutations known to be associated with domestic phenotypes (such as black coat colour, Fang et al. 2009).

3.1.2 Genetics of domestication

Three main processes shape genetic variation in domestic populations (and during the domestication process): inbreeding, genetic drift and directed selection (Mignon-Grasteau et al. 2005). Genetic drift is mainly caused by a reduction of the effective number of breeding individuals in a population (effective population size). Inbreeding can be the result of a reduction in the effective population size or of directed selection (or both). Directed selection is a process through which people exert control over breeding with the objective of improving the population (like the behaviour or appearance) (Mignon-Grasteau et al. 2005; Fang et al. 2009; Rubin et al. 2010).

Domestication also leads to a relaxation of selective constraints: natural selection, which act on wild populations, is to a great extent put out of action during a domestication process (Fang et al. 2009). A relaxation of selective constraints results in the accumulation of non-synonymous (non-silent, protein changing, mutations) (Björnerfeldt et al. 2006; Cruz et al. 2006; Fang et al. 2009; Wang et al. 2011). Björnerfeldt et al. (2006), for example, found a higher frequency of non-synonymous mutations in the mitochondrial genome from dogs than those from wolves. The authors concluded that this variation is caused by a relaxation of purifying selection.

Similarly, Fang et al. (2009) found that non-synonymous mutations in the MC1R (Melanocortin Receptor 1) locus had accumulated at a much faster evolutionary rate in domestic pigs than in wild boar. In fact, all mutations in the wild boar populations were synonymous (not causing changes in the coat colour phenotype), indicating that the MC1R locus is subject to strong purifying selection. However, because of the fast rate at which non-synonymous mutations have accumulated in domestic populations (<10,000 years), the authors concluded that people had exerted strong directed selection (so-called cherry-picking) on novel phenotypes, rather than that only a relaxation of purifying selection had caused the abundance of coat colour variation. If this hypothesis is true, non-synonymous mutations in the MC1R gene should have been abundant, if not ubiquitous, in domestic pigs from very early on in

the domestication process. In short, it would imply that the domestication process was coupled with strong human-driven selection, which likely would have resulted in a selective sweep, rather than just a relaxation of selective constraints (Fang et al. 2009; Rubin et al. 2010).

The MC1R locus

The MC1R locus is directly linked to expression of coat colour pigment (phenotypes) (Fang et al. 2009). MC1R is a G-protein-coupled receptor that is expressed in melanocytes (melanin-producing cells located in the bottom layer of the skin's epidermis) and is important in melanogenesis (the process during which these cells produce melanin) by affecting the switch between production of red/yellow phenomelanin and darker eumelanin (Barsh 1996). The binding of melanocyte stimulating hormone (MSH) to MC1R induces synthesis of eumelanin. An absence of MC1R signaling causes the melanocytes to only produce pheomelanin. Loss-of-function mutations are associated with recessive red coat colour, while dominant black colouring is linked to mutations causing constitutive activation of MC1R signalling (Fang et al. 2009).

Fang et al. (2009) linked several SNPs to specific coat colour phenotypes. For pigs of European (West Eurasian) ancestry, the most basal mutation is the D124N substitution. This SNP causes dominant black coat colour and is the first in a series of mutations leading to various coat colour phenotypes. All domestic pigs from West Eurasia possessing a non-wild type phenotype (save recessive red coat colour) carry at least one copy of the dominant D124N mutation (Fang et al. 2009). The D124N substitution is therefore a suitable marker for bolstering assessments of whether individual pigs are wild or domestic, and for assessing wild-domestic hybridisation. Because MC1R is an autosomal (diploid) bi-parentally inherited genetic marker, this type of analysis overcomes the bias associated with mtDNA, which is a non-recombining, maternally inherited marker.

3.1.3 The Neolithic expansion in Europe

The Neolithisation of Europe has been debated for almost a century, gaining popularity by the early works of Childe (1925) and continuously debated since (Price 2000). These old questions have also been revived in the light of ancient DNA sequencing (Rowley-Conwy 2009; Burger and Thomas 2011). The main topic of debate has been how farming and animal husbandry, two processes that began in Southeast Anatolia around 11,500 years ago (Zeder 2011), spread across Europe. Two extreme scenarios (migration vs. acculturation) have been advocated, and a range of possible combinations of these two has been investigated over the years (e.g. Price 2000; Perles 2003; Robb and Miracle 2007). The first scenario, the acculturation theory, is based on the concept of cultural diffusion, where ideas of farming developed in East Anatolia and spread over Europe through the exchange of ideas rather than the exchange of people. The acculturation theory postulates that once the concept of farming reached Europe, accompanied by the technical skills necessary for of a sedentary lifestyle (including the rearing of domestic animals), it was adopted, spread, and locally developed by European hunter-gatherers. The second scenario, the migrationist theory, advocates large-scale population diffusion (demic diffusion) as the main cause for the transmission, where an already developed sedentary lifestyle spread with the migrating farmers that replaced hunter-gatherers in Europe (e.g. Ammerman and Cavalli-Sforza 1973; 1984; Bramanti et al. 2009; Burger and Thomas 2011).

One of the most popular explanation models for the Neolithic expansion in Europe is that it spread along two major migratory routes: the Northern Danubian route and the Southern Mediterranean route (e.g. Burger and Thomas 2011; Lacan et al. 2011). However, the question of whether the proposed two-route expansion model represents a single and continuous expansion event of peoples, or local developments initiated through small-scale migration and/or cultural exchange, has remained one of the most debated and controversial questions in archaeology since the early 20th century (Price 2000). The evidence suggests that, although the expansion coalesced

in West Anatolia (Perles 2003, Özdogan 2011), it was probably initiated by several independent small-scale migratory pulses that subsequently diverged and dispersed through Europe (Tringham 2000; Özdogan 2011). These small-scale expansions from West Anatolia to the European mainland, via the Aegan sea, began as early as the pre-pottery Neolithic (Perles 2003; Özdogan 2011). Secondary waves of more complete, or developed, Neolithic cultures (the phase of the Neolithic development linked to the term *Neolithic package*) expanded further into the Balkans during the mid-seventh millennium BC (Perles 2003). While it remains clear that both intra-, and inter-regional diversity of the Neolithic cultures was high (Tresset and Vigne 2007; 2011), the question of whether the early Neolithic development in Europe was homogenous and can be generalised in terms like *Neolithic package* is much debated (Price 2000; Oross and Banffy 2009; Tresset and Vigne 2007; 2011).

The LBK originated on the Hungarian plain and brought farming and animal husbandry to Central Europe around 5,500 BC. It is considered the most prominent example of the Danubian group of Neolithic cultures. The Cardial culture originated along the Adriatic coast of the Balkans around 6,000 BC and spread rapidly westward along the Mediterranean coastline. It is considered to be the pioneering culture that brought the Neolithic to Southern Europe. Despite marked differences in subsistence economy and material cultures, the question of interconnectedness (or shared ancestry) between the various groups, and whether the mode of expansion was primarily through demic or cultural diffusion, remains for the most part unclear (Tresset and Vigne 2007; 2011).

Genetic evidence

Recently published human ancient DNA has shed new light on these old issues and, on the whole, supports both demic diffusion and the two-route expansion hypothesis (Burger and Thomas 2011). Several studies of ancient mtDNA indicate that the earliest farmers in Central Europe (LBK) did not share a recent common ancestry with local hunter-gatherers (Bramanti et al. 2009, Haak et al. 2010). LBK farmers pos-

sessed haplotypes in high frequencies that were either very rare or completely absent in the local hunter-gatherer populations, suggesting that the onset of the Central European Neolithic was initiated by migrant farmers rather than local hunter-gatherers (Bramanti et al. 2009; Haak et al. 2010; Burger and Thomas 2011). Important to note, however, is that the mode of the LBK diffusion was probably not analogue to the wave-of-advance model that propose large-scale, continuous, migrations (e.g. Ammerman and Cavalli-Sforza 1973; 1984), but more likely a leap-frogging type dispersal among patchy low-density enclaves consisting of small pioneering farming communities (Robb and Miracle 2007). Together these data propose that the Neolithisation of Europe was neither genetically nor geographically uniform.

Haak et al. (2010) further demonstrated that Central European LBK farmers were genetically more similar to modern Anatolian populations than modern Europeans, and concluded that this observation supports the hypothesis of demic diffusion from the Near East. This observation is to some extent supported by human ancient autosomal DNA, which show that Scandinavian early farmers shared genetic affinity with populations from South Europe rather than local Scandinavian hunter-gatherers (Skoglund et al. 2012). On the contrary, recent human ancient DNA from Neolithic contexts (among them Cardial and Impressa ware) in Northeast Iberia and South France demonstrate that these populations were significantly differentiated from the central European LBK population. Furthermore, the results show that the Mediterranean Neolithic populations shared genetic affinity with modern (local) European populations. This observation could indicate that the acculturation theory (diffusion of technology rather than people) drove the Neolithisation along the Mediterranean route (Sampietro et al. 2007; Lacan et al. 2011).

Interestingly, the inconsistency among populations along the different expansion routes is, to an extent, mirrored in the genetic composition of some domestic animals in respective regions. Larson et al. (2007a) showed that the early Neolithic domestic pigs on the Balkans and in Central Europe (LBK) possessed the mtDNA haplotype Y1. The Y1 haplotype is not found in modern domestic pigs and was replaced by

local European E1 lineages towards the end of the Neolithic (a situation similar to that of LBK human genetic signatures, Bramanti et al. 2009). However, the question of whether domestic pigs along the Southern Mediterranean route were genetically distinct from the Danubian group remains unclear. Based on the presence of mtDNA haplotype Y2 in one Neolithic specimen from a cave site on the Adriatic coastline in Croatia, and in one medieval specimen from Corsica, Larson et al. (2007a) highlighted the possibility that this haplotype could mark the Neolithic expansion along the Mediterranean. However, this hypothesis was never directly tested because they lacked Neolithic samples from that area.

3.1.4 Aims and objectives

This chapter expands on the narrative and observations made in chapter 2 by analysing ancient DNA in pigs from Europe. The aim is to explore and test a series of hypotheses regarding the mode of the Neolithic expansion into Europe and whether pig DNA is in fact a good proxy to detect patterns of human movements (Larson et al. 2007a). This chapter also investigates two mechanisms of pig domestication: human-driven, directed, selection on phenotypes (MC1R), and the process of admixture (introgression) with local wild boar (Fang et al. 2009; Larson et al. 2007a, respectively). The questions and hypotheses are:

1. MtDNA haplogroups E1 and E2, and NE1 and NE2 do not share a natural range overlap, where the former two clades are geographically restricted to Europe and the latter two are geographically restricted to the Near and Middle East (Larson et al. 2005; 2007a). This hypothesis relies on the assumption that the Bosporus strait (and the Black Sea) has been a physical barrier to gene flow between wild boar in the Near East and Europe throughout the Holocene. It has been argued that this barrier gave rise to the spatial arrangement of phylogenetically distinct clades observed in modern West Eurasian wild boar populations (Larson et al. 2005).

Larson et al. (2007a) published ancient genetic data from Europe and the Near East that supported the hypothesis that the Bosporus is a barrier to gene flow. The authors showed that genetic variation in pre-Neolithic European wild boar was restricted to the major European clade (E1) and the Italian clade (E2). This observation was constructed into a pre-Neolithic comparative baseline for evaluating genetic variation in Europe from that period onwards. However, it is because of two reasons necessary to test the validity of the comparative baseline. First, certain geographic regions in close proximity to the Neolithic contact zone in Southeast Europe (Balkans) are poorly sampled (Larson et al. 2007a). Secondly, because the Y2 lineage is rare in the Near East but present in Mesolithic and Neolithic contexts on Crimea (Larson et al. 2007a) it remains a possibility that Y2 is in fact European (see chapter 2 and figure 2.6).

2. Neolithic migrant farmers brought domestic pigs possessing haplotype Y1 to Europe from the Near East (Larson et al. 2007a). This hypothesis relies on the validity of the pre-Neolithic comparative baseline and assumes that humans must have introduced pigs that possess non-E1 or non-E2 haplotypes to Europe.

3. The Y2 lineage was also introduced to Europe from the Near East by Neolithic migrant farmers, but dispersed along another expansion route than Y1 pigs (southern Mediterranean route and the northern Danubian route respectively) (Larson et al. 2007a).

4. The introduction of domesticated pigs from the Near East was followed by domestication of local European wild boar in Central Europe towards the end of the Neolithic. This hypothesis relies on the observation that domestic pigs possessing European E1 signatures replaced the introduced Y1 haplogroup at least by 3,900 BC, probably through introgression with local wild boar. The last domestic pig possessing the Y1 lineage was observed at Bercy in the Paris basin, a region highlighted as a putative center for local European domestication (Larson et al. 2007a).

This chapter also investigates a hypothesis that relates to the process of pig domestication: the D124N substitution in the MC1R locus arose and was selected for during the early domestication process in Anatolia, prior to the introduction of domestic pigs in Europe (Fang et al. 2009).

3.2 Materials and methods

DNA was extracted from 676 wild and domestic pigs from 102 archaeological sites, stretching Epipalaeolithic/Mesolithic to Iron Age contexts from across Europe, Anatolia and the Near East figure 3.1. The samples range in age from approximately 14,000 YBP to 500 YBP (table 3.1). Samples were chosen to represent the continuation of spatial and temporal regions outlined in chapter 2 and in Larson et al. (2007a): South and Central Europe, the Balkans, the Crimean peninsula, the Near East (Anatolia) and the Middle East. The specimens analysed in chapter 2 are included among the 676 samples, but an extra 325 - 406bp sequence data was included for 60 of those samples. Although the main body of work in this chapter relies on the analysis of a 486bp fragment (see below), previously published 80bp ANC1 sequences from Larson et al. (2007a) were included for comparative purposes (table 3.1, Genbank Accession numbers DQ872931-DQ873203).

Wild and domestic pigs were pooled in this chapter due to incomplete wild/domestic status determinations. Some preliminary status calls are provided in table 3.1 (Allowen Evin, personal communication, chapter 2, table 3.1) but these are to be considered only preliminary and the referral to in this chapter to domestic or wild should be interpreted with caution unless otherwise stated. Terms like *putatively domestic* is used throughout the discussion to highlight this inconsistency.

The age of the specimens were determined either through direct AMS radiocarbon dating (see below) or through relative stratigraphic dating by the archaeozoologists who provided the materials.

LG extract	Reference	Metric	GMM	Haplotype	Phylo group	MC1R 0.30.80bp	Reference ID	Stat group	Country	Site	Period	Culture	Date
A212	Larson et al. 2007	wild		n/a	E1		ANC-Cside	P2	UK	England	Carsington Pasture Cave	Mesolithic		4393 ± 41 cal BC
A213	Larson et al. 2007	wild		n/a	E1		ANC-Cside	P3	UK	England	Carsington Pasture Cave	Mesolithic		5678 ± 30 cal BC
A214	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	P4	UK	England	Carsington Pasture Cave	Bronze Age		1130 ± 63 cal BC
A215	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	P5	UK	England	Carsington Pasture Cave	Bronze Age		1158 ± 60 cal BC
A216	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	P6	UK	England	Carsington Pasture Cave	Neolithic		3457 ± 58 cal BC
A217	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	P7	UK	England	Carsington Pasture Cave	Neolithic		2327 ± 82 cal BC
A244	Larson et al. 2007	undet		n/a	E1		ANC-Aside	WB 07	UK	Ireland	Moynagh Crannog	Neolithic		3868 ± 60 cal BC
A352	Larson et al. 2007	wild		n/a	E1		ANC-Cside	WB 08	UK	Ireland	Kilgreany	Mesolithic		7358 ± 138 cal BC
ASPg15	Larson et al. 2007	wild		n/a	E1		ANC-Cside	15	Central Europe	Switzerland	2003 (year of excavation)	Neolithic	Plyn culture	38th - 36th century BC
ASPg4	Larson et al. 2007	domestic		n/a	E1		ANC-Cside	4	Central Europe	Switzerland	2001 (year of excavation)	Neolithic	Horgen culture	2610+/-50BC, 2630+/-50BC
ASPg9	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	9	Central Europe	Switzerland	1981 (year of excavation)	Neolithic	Horgen culture	29th/28th century BC
GL1000	Larson et al. 2007	wild		n/a	E1		ANC-Cside	49	Italy	Italy	Grotta Madonna	Mesolithic		7,000-6,800 BC cal
GL1022	Larson et al. 2007	domestic		n/a	E1		ANC-Cside	8	Central Europe	Switzerland	1981 (year of excavation)	Neolithic	Horgen culture	29th/28th century BC
GL1023	Larson et al. 2007	wild?		n/a	E1		ANC-Cside	10	Central Europe	Switzerland	1981 (year of excavation)	Neolithic	Horgen culture	29th/28th century BC
GL1024	Larson et al. 2007	wild		n/a	E1		ANC-Cside	11	Central Europe	Switzerland	2003 (year of excavation)	Neolithic	Corded Ware culture	27th - 25th century BC
GL1025	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	12	Central Europe	Switzerland	2003 (year of excavation)	Neolithic	Corded Ware culture	27th - 25th century BC
GL1026	Larson et al. 2007	wild		n/a	E1		ANC-Cside	14	Central Europe	Switzerland	2003 (year of excavation)	Neolithic	Corded Ware culture	27th - 25th century BC
GL1027	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	Fr1	Central Europe	France	Boulancourt;	Bronze Age		ca. 900-700 cal. BC
GL1028	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	Fr2	Central Europe	France	Boulancourt;	Bronze Age		ca. 900-700 cal. BC
GL1030	Larson et al. 2007	undet		n/a	E1		ANC-Aside	2	Balkans	Romania	Cârlomănești 2003, Cpl.	Bronze Age	Monteoru culture	3000-1600 BC
GL1032	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	4	Balkans	Romania	Popești	Bronze Age		3000-1600 BC*?
GL1034	Larson et al. 2007	wild?		n/a	E1		ANC-Aside	6	Balkans	Romania	Popești	Bronze Age	Hallstatt C	900 - 150 BC*?
GL1035	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	7	Balkans	Romania	Popești	Iron Age	La Tène	900 - 150 BC*?
GL1036	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	13	Balkans	Romania	Dunostorum	Roman		300-400 AD
GL1037	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	4	Balkans	Romania	Dunostorum	Roman		300-400 AD
GL115	Larson et al. 2007	wild		n/a	E1		ANC-Cside	1	Central Europe	Germany	Aldlendorf	Mesolithic	Epipalaeolithic	12,000-10,000 BC
GL116	Larson et al. 2007	wild		n/a	E1		ANC-Cside	2	Central Europe	Germany	Aldlendorf	Mesolithic	Epipalaeolithic	12,000-10,000 BC
GL119	Larson et al. 2007	wild		n/a	E1		ANC-Cside	7	Central Europe	Germany	Friesack	Mesolithic		8,500-7,500 BC cal
GL120	Larson et al. 2007	wild		n/a	E1		ANC-Cside	10	Central Europe	Germany	Friesack	Mesolithic		8,500-7,500 BC cal
GL121	Larson et al. 2007	wild		n/a	E1		ANC-Cside	12	Central Europe	Germany	Friesack	Mesolithic		8,500-7,500 BC cal
GL122	Larson et al. 2007	wild		n/a	E1		ANC-Aside	17	Central Europe	Germany	Friesack	Mesolithic		8,500-7,500 BC cal
GL123	Larson et al. 2007	wild		n/a	E1		ANC-Cside	21	Central Europe	Germany	Eilsleben	Neolithic	LBK	5,500-5,000 BC cal
GL126	Larson et al. 2007	wild		n/a	E1		ANC-Cside	1	Balkans	Moldova	Seroca III	Iron Age		6th millennium BC
GL128	Larson et al. 2007	wild		n/a	NE2		ANC-Cside	1	Russia/Ukraine	Ukraine	Span Kyba	Mesolithic		9th-8th mil BC cal
GL150	Larson et al. 2007	domestic		n/a	E1		ANC-Cside	2	Balkans	Romania	Popești	Bronze Age	Hallstat	10th century BC
GL157	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	6	UK	England	Fishergate	Roman		1st-5th cent AD
GL158	Larson et al. 2007	domestic		n/a	E1		ANC-Aside		Central Europe	Belgium	Montaigle	Roman		Late 2nd - 5th Century AD
GL159	Larson et al. 2007	domestic		n/a	E1		ANC-Aside		Central Europe	Hungary	Aquincum	Roman		
GL160	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside		Central Europe	Netherlands	Nijmegen	Roman		0-70 AD
GL183	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	86	Italy	Italy	Torre Mordillo 89	Bronze Age		Late 2nd - early 1st mil. BC
GL184	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	87	Italy	Italy	Torre Mordillo 87	Bronze Age		Late 2nd - early 1st mil. BC
GL185	Larson et al. 2007	domestic		n/a	E1		ANC-Aside		Central Europe	Hungary	Bajcsa-Torokvar	Medieval		AD 1578-1661
GL186	Larson et al. 2007	domestic		n/a	E1		ANC-Aside		Central Europe	Hungary	Bajcsa-Torokvar	Medieval		AD 1578-1661
GL187	Larson et al. 2007	domestic?		n/a	Arm		ANC-Arm1T	2	Middle East	Armenia	Lchashen	Bronze Age/Iron age		13th-9th cent. BC
GL188	Larson et al. 2007	domestic?		n/a	Arm		ANC-Arm1T	4	Middle East	Armenia	Lchashen	Bronze Age/Iron age		13th-9th cent. BC
GL206	Larson et al. 2007	undet		n/a	E1		ANC-Cside		Central Europe	Netherlands	Southern Bight	Mesolithic		
GL209	Larson et al. 2007	undet		n/a	E1		ANC-Cside		Central Europe	Netherlands	Southern Bight	Mesolithic		
GL210	Larson et al. 2007	wild?		n/a	E1		ANC-Cside	JG202	Central Europe	Netherlands	Southern Bight	Mesolithic		8435-8645 cal BC
GL211	Larson et al. 2007	wild?		n/a	E1		ANC-Cside		Central Europe	Netherlands	Southern Bight	Mesolithic		8415-8617 cal BC
GL212	Larson et al. 2007	undet		n/a	E1		ANC-Cside		Central Europe	Netherlands	Southern Bight	Mesolithic		
GL30	Larson et al. 2007	undet		n/a	E1		ANC-Cside	1	Central Europe	Czech Rep.	Homolka	Neolithic		c. 2700-2300 BC
GL306	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	9	Central Europe	Denmark	Trelleborg	Neolithic		c. AD 1000
GL308	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	33	Corsica/Sardinia	France	Ota	Medieval		15th cent. AD
GL311	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	93	Italy	Italy	Arco di Costantino	Roman		1st cent. AD
GL313	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	34	Corsica/Sardinia	France	Ota	Medieval		15th cent. AD
GL314	Larson et al. 2007	domestic		n/a	E1		ANC-Aside		Central Europe	Belgium	Oudenburg	Late Roman/Early Medieval		
GL316	Larson et al. 2007	undet		n/a	E1		ANC-Aside	7	Central Europe	Sweden	Ajvide	Neolithic	Pitted ware culture	2800-2500 cal BC
GL317	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	23	Corsica/Sardinia	France	Rostino	Medieval		13th cent AD
GL318	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	40	Corsica/Sardinia	France	Urtolo	Medieval		15th cent. AD
GL319	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	39	Corsica/Sardinia	France	Urtolo	Medieval		15th cent. AD
GL321	Larson et al. 2007	wild		n/a	E1		ANC-Aside	6	South Europe	France	Roucadour	Neolithic		c.4,200-3,500 BC cal
GL324	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	24	Corsica/Sardinia	France	Rostino	Medieval		13th cent AD
GL325	Larson et al. 2007	undet		n/a	E1		ANC-Aside	66	Italy	Italy	Crypta Balbi	Medieval		10th cent. AD
GL326	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	96	Italy	Italy	Cencelle	Medieval		14th-15th cent. AD
GL327	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	5	UK	England	Fishergate	Roman		1st-5th cent AD
GL329	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	77	Italy	Italy	Quirinale	Roman		1st cent. AD
GL33	Larson et al. 2007	undet		n/a	E1		ANC-Aside	4	Central Europe	Czech Rep.	Homolka	Neolithic		c.2700-2200 BC
GL330	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	1	UK	Scotland	Jarlshavins Flotty, Sandur	Medieval		c.AD1100

Table 3.1: The ancient specimens analysed in this chapter. The dates highlighted in green are novel calibrated AMS radiocarbon dates.

GL333	Larson et al. 2007	wild?	n/a	E1		ANC-Cside	14	Spain	Portugal	Zambujal	Chalcolithic/Early Bronze	2,600-1,800 BC cal?
GL334	Larson et al. 2007	dom/fer	n/a	E1		ANC-Aside	13	Italy	Italy	SanTimbenia	Iron Age	c.900-600 BC
GL336	Larson et al. 2007	dom/fer	n/a	E1		ANC-Aside	18	Italy	Italy	Arrubiu	Bronze Age	Cortile B	c.1400-1200 BC cal
GL338	Larson et al. 2007	dom/fer	n/a	E1		ANC-Aside	7	Italy	Italy	Santu Antine	Bronze Age	Saggio Torre D	c.1400-1200 BC cal
GL34	Larson et al. 2007	undet	n/a	E1		ANC-Aside	5	Central Europe	Czech Rep.	Homolka	Neolithic		c.2700-2300 BC
GL341	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	2	Central Europe	Iceland	Hofstadir	Medieval		10th cent AD
GL343	Larson et al. 2007	wild	n/a	Arm		ANC-Arm2T	32	Middle East	Armenia	Khatunarkh	Chalcolithic		5th millennium BC cal?
GL344	Larson et al. 2007	dom/fer	n/a	E1		ANC-Aside	4	Italy	Italy	Santu Antine	Bronze Age	Saggio Torre D	c.1400-1200 BC cal
GL345	Larson et al. 2007	domestic?	n/a	E1		ANC-Aside	97	Italy	Italy	Cenicelle	Medieval		14th-15th cent. AD
GL346	Larson et al. 2007	dom/fer	n/a	E1		ANC-Cside	12	Italy	Italy	SanTimbenia	Iron Age		c.900-600 BC
GL355	Larson et al. 2007	domestic?	n/a	NE2		ANC-Y1-6A	61	Central Europe	France	Bercy	Neolithic	Chasen culture	early 4th Mil BC
GL36	Larson et al. 2007	undet	n/a	E1		ANC-Cside	7	Central Europe	Czech Rep.	Homolka	Neolithic	Homolka	c. 2700-2300 BC
GL361	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	4	Central Europe	Iceland	Hrisheimar	Medieval		9th-12th cent. AD
GL366	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	37	Middle East	Armenia	Tsaksektsi	Medieval		13th cent AD
GL367	Larson et al. 2007	domestic?	n/a	E1		ANC-Aside	99	Italy	Italy	Cenicelle	Medieval		14th-15th cent. AD
GL37	Larson et al. 2007	wild	n/a	E1		ANC-Cside	8	Central Europe	Czech Rep.	Homolka	Neolithic		c. 2700-2300 BC
GL371	Larson et al. 2007	domestic?	n/a	E1		ANC-Aside	41	Central Europe	Netherlands	Nijmegen Canabae	Iron Age		70-120 AD
GL372	Larson et al. 2007	wild	n/a	E2		ANC-Italy	94	Italy	Italy	Cenicelle	Medieval		14th-15th cent. AD
GL375	Larson et al. 2007	undet	n/a	E1		ANC-Aside	11	Balkans	Romania	Veterani cave	Neolithic	Starcevo culture	5300 - 5000 BC?
GL376	Larson et al. 2007	undet	n/a	Arm		ANC-Arm2T	15	Middle East	Armenia	Shengavit	Bronze Age		late 4th-early 3rd mill BC uncal?
GL38	Larson et al. 2007	wild?	n/a	E1		ANC-Cside	9	Central Europe	Czech Rep.	Homolka	Neolithic	Homolka	c. 2700-2300 BC
GL41	Larson et al. 2007	wild?	n/a	E1		ANC-Cside	12	Central Europe	Czech Rep.	Homolka	Neolithic	Homolka	c. 2700-2300 BC
GL429	Larson et al. 2007	wild	n/a	E1		ANC-Cside	4	Central Europe	Denmark	Flynderhage	Mesolithic		4500-3900 BC
GL431	Larson et al. 2007	wild	n/a	E1		ANC-Cside	2	Central Europe	France	Noyen - Sur Seine	Mesolithic		9th millennium cal BC
GL432	Larson et al. 2007	domestic	n/a	NE2		ANC-Y1-6A	7	Balkans	Romania	Cheia-nuele A	Chalcolithic	Gumelnita	mid.5th - mid.4th millennium BC
GL438	Larson et al. 2007	wild	n/a	E2		ANC-Italy	100	Italy	Italy	Cenicelle	Medieval		14th-15th cent. AD
GL439	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	73	Italy	Italy	Crypta Balbi	Roman		10th cent. AD
GL440	Larson et al. 2007	undet	n/a	E1		ANC-Aside	71	Italy	Italy	Crypta Balbi	Roman		10th cent. AD
GL442	Larson et al. 2007	domestic?	n/a	E1		ANC-Aside	2	UK	Ireland	Newgrange	Neolithic		3000 BC?
GL447	Larson et al. 2007	undet	n/a	E1		ANC-Cside	3	Balkans	Romania	Vărăşti	Neolithic	Boian & Gumelnita cu	5th Millennium BC?
GL453	Larson et al. 2007	undet	n/a	E1		ANC-Aside	2	Central Europe	Sweden	Ajvide	Neolithic	Pitted ware culture	2800-2500 cal BC
GL454	Larson et al. 2007	wild?	n/a	E1		ANC-Cside	1	Spain	Portugal	Zambujal	Chalcolithic/Early Bronze		2,600-1,800 BC cal?
GL455	Larson et al. 2007	undet	n/a	E1		ANC-Aside	69	Italy	Italy	Crypta Balbi	Medieval		10th cent. AD
GL456	Larson et al. 2007	domestic?	n/a	E1		ANC-Aside	101	Italy	Italy	Cenicelle	Medieval		14th-15th cent. AD
GL457	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	1	UK	Scotland	High Pasture Cave	Iron Age		350-100BC
GL459	Larson et al. 2007	undet	n/a	E1		ANC-Aside	6	Central Europe	Sweden	Ajvide	Neolithic	Pitted ware culture	2800-2500 cal BC
GL460	Larson et al. 2007	undet	n/a	E1		ANC-Aside	68	Italy	Italy	Crypta Balbi	Medieval		10th cent. AD
GL464	Larson et al. 2007	wild	n/a	E2		ANC-Italy	95	Italy	Italy	Cenicelle	Medieval		14th-15th cent. AD
GL465	Larson et al. 2007	domestic?	n/a	E1		ANC-Cside	27	Spain	Portugal	Zambujal	Chalcolithic/Early Bronze		2,600-1,800 BC cal?
GL467	Larson et al. 2007	domestic?	n/a	E1		ANC-Aside	84	Italy	Italy	Torre Mordillo 89	Bronze Age		Late 2nd - early 1st mil. BC
GL470	Larson et al. 2007	wild	n/a	E1		ANC-Aside	8	South Europe	France	Roucadour	Neolithic		c.4,200-3,500 BC cal
GL471	Larson et al. 2007	undet	n/a	E1		ANC-Aside	67	Italy	Italy	Crypta Balbi	Medieval		10th cent. AD
GL474	Larson et al. 2007	undet	n/a	E1		ANC-Aside	5	Central Europe	Sweden	Ajvide	Neolithic		2800-2500 cal BC
GL484	Larson et al. 2007	domestic	n/a	Arm		ANC-Arm1T	8	Middle East	Syria	CB00 (Chagar Bazar)	Iron Age		1st 1/2 2nd mill BC
GL485	Larson et al. 2007	wild	n/a	E1		ANC-Aside	10	South Europe	France	Roucadour	Neolithic		c.4,200-3,500 BC cal
GL488	Larson et al. 2007	undet	n/a	E1		ANC-Aside	4	Central Europe	Sweden	Ajvide	Neolithic	Pitted ware culture	2800-2500 cal BC
GL490	Larson et al. 2007	wild	n/a	E1		ANC-Cside		South Europe	France	B. Oulens	Neolithic	Cardial	6185 ± 68 [5306-4962] cal BC
GL491	Larson et al. 2007	wild	n/a	E1		ANC-Aside		South Europe	France	B. Oulens	Neolithic	Cardial	6,361 ± 66 [5471-5222] cal BC
GL496	Larson et al. 2007	wild?	n/a	E2		ANC-Italy	63	Italy	Italy	Crypta Balbi	Medieval		10th cent. AD
GL501	Larson et al. 2007	undet	n/a	E1		ANC-Aside	65	Italy	Italy	Crypta Balbi	Medieval		10th cent. AD
GL507	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	1	Central Europe	Switzerland	Grube 84 (1990.32)	Iron Age	La Tene	late 2nd - early 1st century BC
GL509	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	5	Central Europe	Switzerland	Grube 86 (1990.32)	Iron Age	La Tene	late 2nd - early 1st century BC
GL510	Larson et al. 2007	domestic	n/a	E1		ANC-Cside	1	Central Europe	Switzerland	Kastelen	Roman		0-50 AD
GL515	Larson et al. 2007	undet	n/a	E1		ANC-Cside		Central Europe	Netherlands	Southern Bight	?		
GL516	Larson et al. 2007	undet	n/a	E1		ANC-Cside		Central Europe	Netherlands	Southern Bight	?		
GL521	Larson et al. 2007	domestic	n/a	NE2		ANC-Y1-6A	1	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4500-3950 BC
GL522	Larson et al. 2007	domestic	n/a	NE2		ANC-Y1-6A	2	Balkans	Romania	Poduri	Chalcolithic	Cucuteni	4500-4250 BC cal
GL523	Larson et al. 2007	domestic	n/a	NE2		ANC-Y1-6A	3	Balkans	Romania	Poduri	Chalcolithic	Cucuteni	4500-4250 BC cal
GL524	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	11	UK	England	Durrington Walls 04	Neolithic		2800-2400 BC cal
GL525	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	12	UK	England	Durrington Walls 04	Neolithic		2800-2400 BC cal
GL526	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	16	UK	England	Durrington Walls 04	Neolithic		2800-2400 BC cal
GL527	Larson et al. 2007	wild	n/a	E1		ANC-Aside	17	UK	England	Chedworth Roman villa	Roman		1st-5th cent AD
GL528	Larson et al. 2007	wild	n/a	E1		ANC-Cside	19	UK	England	Wroxeter	Medieval		6th-7th cent AD
GL529	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	21	UK	England	Wroxeter	Medieval		6th-7th cent AD
GL530	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	25	UK	England	Coppergate	Roman		1st-5th cent AD
GL531	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	27	UK	England	Coppergate	Roman		1st-5th cent AD
GL532	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	29	UK	England	Swinegate	Roman		1st-5th cent AD
GL533	Larson et al. 2007	domestic	n/a	E1		ANC-Aside	31	UK	England	Swinegate	Roman		1st-5th cent AD
GL536	Larson et al. 2007	wild	n/a	NE2		ANC-Y2-5A	5	Russia/Ukraine	Ukraine	Spias-Koba	Neolithic		7th mil BC ca

GL538	Larson et al. 2007	wild		n/a	E1		ANC-Aside	9	Central Europe	Germany	Friesack	Mesolithic	8,500-7,500 BC cal
GL541	Larson et al. 2007	undet		n/a	E1		ANC-Cside	22	Central Europe	Germany	Eilsleben	Neolithic	LBK	5,500-5,000 BC cal
GL544	Larson et al. 2007	undet		n/a	E1		ANC-Cside		Central Europe	Netherlands	Southern Bight			
GL565	Larson et al. 2007	undet		n/a	NE2		ANC-Y1-6A	4	Balkans	Romania	Várdgá	Neolithic	Boian & Gumelnita c	5th Millennium BC?
GL566	Larson et al. 2007	wild		n/a	E1		ANC-Cside	5	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL567	Larson et al. 2007	wild		n/a	E1		ANC-Cside	6	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL568	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	8	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL571	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	36	Central Europe	France	Bercy	Neolithic	Chaseen culture	early 4th Mil BC
GL572	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	40	Central Europe	France	Bercy	Neolithic	Chaseen culture	early 4th Mil BC
GL573	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	44	Central Europe	France	Bercy	Neolithic	Chaseen culture	early 4th Mil BC
GL574	Larson et al. 2007	wild		n/a	E1		ANC-Cside	59	Central Europe	France	Bercy	Neolithic	Chaseen culture	early 4th Mil BC
GL575	Larson et al. 2007	wild		n/a	E1		ANC-Cside	12	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL576	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	10	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL688	Larson et al. 2007	wild		n/a	E1		ANC-Cside	4	Balkans	Romania	Peşteri	Chalcolithic	Cucuteni	4500-4230 BC cal
GL705	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	30	Italy	Italy	Crypta Balbi	Medieval		8th cent AD
GL706	Larson et al. 2007	undet		n/a	E1		ANC-Cside	34	Italy	Italy	Crypta Balbi	Medieval		7th cent AD
GL707	Larson et al. 2007	wild?		n/a	E2		ANC-Italy	35	Italy	Italy	Crypta Balbi	Medieval		8th cent AD
GL708	Larson et al. 2007	wild?		n/a	E2		ANC-Italy	36	Italy	Italy	Crypta Balbi	Medieval		8th cent AD
GL709	Larson et al. 2007	undet		n/a	E1		ANC-Aside	37	Italy	Italy	Crypta Balbi	Medieval		8th cent AD
GL720	Larson et al. 2007	undet		n/a	E1		ANC-Cside	38	Italy	Italy	Crypta Balbi	Medieval		8th cent AD
GL721	Larson et al. 2007	undet		n/a	E1		ANC-Aside	39	Italy	Italy	Crypta Balbi	Medieval		8th cent AD
GL722	Larson et al. 2007	undet		n/a	E2		ANC-Italy	40	Italy	Italy	Crypta Balbi	Medieval		7th cent AD
GL723	Larson et al. 2007	wild		n/a	E1		ANC-Cside	59	Italy	Italy	Crypta Balbi	Medieval		9th cent AD
GL726	Larson et al. 2007	wild?		n/a	E2		ANC-Italy	1	Balkans	Croatia	Pupicina Cave	Mesolithic		8500 cal BC
GL728	Larson et al. 2007	domestic?		n/a	NE2		ANC-Y2-5A	3	Balkans	Croatia	Pupicina Cave	Neolithic		4300 cal BC
GL729	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	4	Balkans	Croatia	Pupicina Cave	Bronze Age		1500 cal BC
GL730	Larson et al. 2007	wild?		n/a	E2		ANC-Italy	5	Balkans	Croatia	Pupicina Cave	Mesolithic		~9500 cal BC
GL731	Larson et al. 2007	undet		n/a	E1		ANC-Aside	60	Italy	Italy	Crypta Balbi	Medieval		9th cent AD
GL732	Larson et al. 2007	undet		n/a	E1		ANC-Aside	61	Italy	Italy	Crypta Balbi	Medieval		9th cent AD
GL733	Larson et al. 2007	undet		n/a	E1		ANC-Cside	62	Italy	Italy	Crypta Balbi	Medieval		9th cent AD
GL738	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	54	Italy	Italy	Grotta Madonna	Bronze Age		c.1,500 BC cal
GL803	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	14	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL804	Larson et al. 2007	wild		n/a	E1		ANC-Aside	20	UK	England	Worcester	Medieval		6th-7th cent AD
GL805	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	28	Spain	Portugal	Zambujal	Chalcolithic/Early Bronze		2,600-1,800 BC cal?
GL806	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside		Central Europe	Netherlands	Nijmegen	Roman		0-70 AD
GL810	Larson et al. 2007	wild?		n/a	E1		ANC-Aside		UK	England	Southrigs Lane	Bronze - Medieval		
GL811	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	16	Italy	Italy	SanTimbenia	Iron Age		c.900-600 BC
GL812	Larson et al. 2007	undet		n/a	E1		ANC-Aside	35	Middle East	Armenia	Beniamin	Roman		1st half 1st mill. AD
GL814	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	2	Central Europe	Switzerland	Kastelen	Roman		275-320 AD
GL822	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	36	Corsica/Sardinia	France	Ota	Medieval		15th cent. AD
GL824	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	42	Central Europe	France	Bercy	Neolithic	Chaseen culture	early 4th Mil BC
GL825	Larson et al. 2007	domestic		n/a	E1		ANC-Aside		Central Europe	Belgium	Oudenburg	Medieval		
GL834	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	15	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL837	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	26	Corsica/Sardinia	France	Rostino	Medieval		13th cent AD
GL840	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	2	Spain	Portugal	Zambujal	Chalcolithic/Early Bronze		2,600-1,800 BC cal?
GL846	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	14	Central Europe	France	Bercy	Neolithic	Chaseen culture	4323-4083 cal. BC
GL848	Larson et al. 2007	undet		n/a	E2		ANC-Italy	46	Italy	Italy	Grotta Madonna	Neolithic		5,500-4,900 BC cal
GL849	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	28	Corsica/Sardinia	France	Rostino	Medieval		14th cent. AD
GL857	Larson et al. 2007	dom/fer		n/a	E1		ANC-Cside	1	Corsica/Sardinia	Italy	Santi Antine	Bronze Age	Saggio Tore D	c.1400-1200 BC cal
GL858	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	42	Corsica/Sardinia	France	Urtolo	Medieval		15th cent. AD
GL859	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	20	Central Europe	France	Bercy	Neolithic	Chaseen culture	early 4th Mil BC
GL861	Larson et al. 2007	undet		n/a	E1		ANC-Aside	27	Middle East	Armenia	Tmhatir	Iron Age		6th-5th cent BC
GL864	Larson et al. 2007	undet		n/a	E1		ANC-Aside	38	Middle East	Armenia	Tsaksektsi	Medieval		13th cent AD
GL867	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	78	Italy	Italy	Quirinale	Roman		1st cent. AD
GL868	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	11	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL869	Larson et al. 2007	dom/fer		n/a	E1		ANC-Cside	35	Corsica/Sardinia	France	Ota	Medieval		15th cent. AD
GL871	Larson et al. 2007	dom/fer		n/a	E1		ANC-Cside	10	Italy	Italy	SanTimbenia	Iron Age		c.900-600 BC
GL874	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	53	Central Europe	France	Bercy	Neolithic	Chaseen culture	early 4th Mil BC
GL876	Larson et al. 2007	undet		n/a	Arm		ANC-Arm1T	28	Middle East	Armenia	Tmhatir	Iron Age		13th-9th cent. BC
GL877	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	29	Central Europe	Netherlands	Swifterbant - S3	Neolithic	Swifterband	4100-3400 BC cal
GL881	Larson et al. 2007	domestic?		n/a	E1		ANC-Aside	23	Middle East	Armenia	Pilorpat	Iron Age		6th-5th cent BC
GL882	Larson et al. 2007	undet		n/a	E2		ANC-Italy	52	Italy	Italy	Grotta Madonna	Neolithic		6,500-5,500 BC cal
GL884	Larson et al. 2007	domestic?		n/a	E1		ANC-Cside	25	Italy	Italy	Concordia Sagittaria	Bronze Age		13th-9th cent. BC
GL885	Larson et al. 2007	dom/fer		n/a	E1		ANC-Italy	21	Corsica/Sardinia	Italy	Arrubiu	Iron Age	Cortile B	c.1200-900 BC cal
GL891	Larson et al. 2007	undet		n/a	Arm		ANC-Arm1T	10	Middle East	Armenia	Lchashen	Iron Age		13th-9th cent. BC
GL892	Larson et al. 2007	dom/fer		n/a	E2		ANC-Italy	20	Corsica/Sardinia	Italy	Arrubiu	Iron Age	Cortile B	c.1200-900 BC cal
GL895	Larson et al. 2007	domestic		n/a	E1		ANC-Aside	17	Middle East	Armenia	Sevkar	Iron Age		7th-5th cent BC
GL896	Larson et al. 2007	domestic?		n/a	Arm		ANC-Arm1T	1	Middle East	Armenia	Lchashen	Iron Age		13th-9th cent. BC
GL900	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	4	Balkans	Romania	Măgura	Neolithic	Dudesti/Karanovo III	5500 BC

GL903	Larson et al. 2007	domestic		n/a	NE2		ANC-Y1-6A	3	Balkans	Romania	Măgura	Neolithic	Dudesti/Karanovo III	5500 BC
GL906	Larson et al. 2007	undet		n/a	E1		ANC-Aside	6	Balkans	Romania	Bucu 2004	Bronze Age	Hallstat	1000-800 BC
GL907	Larson et al. 2007	wild		n/a	E1		ANC-Cside	1	Central Europe	Denmark	Flyndebage	Mesolithic		4500-3900 BC
GL972	Larson et al. 2007	domestic?		n/a	NE2		ANC-Y1-6A	26	Central Europe	Germany	Eilsleben	Neolithic	LBK	5,500-5,000 BC cal
GL973	Larson et al. 2007	domestic?		n/a	NE2		ANC-Y1-6A	27	Central Europe	Germany	Eilsleben	Neolithic	LBK	5,500-5,000 BC cal
GL976	Larson et al. 2007	domestic?		n/a	NE2		ANC-Y1-6A	28	Central Europe	Germany	Eilsleben	Neolithic	LBK	5,500-5,000 BC cal
GL977	Larson et al. 2007	domestic?		n/a	NE2		ANC-Y1-6A	24	Central Europe	Germany	Eilsleben	Neolithic	LBK	5,500-5,000 BC cal
GL979	Larson et al. 2007	wild?		n/a	E2		ANC-Italy	2	Balkans	Croatia	Pupicina Cave	Mesolithic		9225-9310 cal BC
GL980	Larson et al. 2007	wild?		n/a	E2		ANC-Italy	1	Balkans	Croatia	Pupicina Cave	Mesolithic		8740-9220 cal BC
GL986	Larson et al. 2007	wild		n/a	E1		ANC-Aside	3	Balkans	Romania	Schela Cladovei	Mesolithic		7134-6851 BC cal.
GL987	Larson et al. 2007	domestic?		n/a	NE2		ANC-Y1-6A	4	Balkans	Romania	Căscioarele A	Chalcolithic	Gumelnita	mid 5th - mid 4th millennium BC
GL988	Larson et al. 2007	wild		n/a	E1		ANC-Cside	5	Balkans	Romania	Schela Cladovei	Mesolithic		
GL992	Larson et al. 2007	domestic?		n/a	Arm		ANC-Arm1T	25	Middle East	Armenia	Sevan	Iron Age		2nd millennium BC uncal?
GL996	Larson et al. 2007	dom/fer		n/a	NE2		ANC-Y2-5A	44	Corsica/Sardinia	France	Urtolo	Medieval		15th cent. AD
GL997	Larson et al. 2007	dom/fer		n/a	E1		ANC-Aside	46	Corsica/Sardinia	France	Urtolo	Medieval		15th cent. AD
LG011	This study	sus	Domestic	n/a	Arm		ANC-Arm-1T	MM-GT01 N103 (GOH_C	Middle East	Iran	Gohar Tappeh	Bronze Age		3300-1200 BC
LG017	This study	sus		n/a	Arm		ANC-Arm-1T	JD-QR12 N111 (QHA_04	Middle East	Iran	Qaleh Rostam	Neolithic		8000 BC?
LG053	This study	sus	Wild	n/a	NE2		ANC-Y2-5A	BB 01 4/71	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG054	This study	sus	Wild	n/a	NE2		ANC-Y2-5A	1/13598-V	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG056	This study	sus	Domestic	n/a	NE2		ANC-Y1-6A	4/19098-V	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG057	This study	sus	Domestic	n/a	NE2		ANC-Y1-6A	800/30	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG058	This study	sus	Domestic	n/a	NE2	T/T	ANC-Y1-6A	BB 02-37/11	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG067	This study			n/a	Arm		ANC-Arm-1T	Exc No. 33030	Middle East	Iran	Qara Divah	Historical		
LG069	This study			n/a	Arm		ANC-Arm-1T	SF No. 166	Middle East	Iran	Ghebleh Ghoyneh	Iron Age		1300 – 600 BC
LG070	This study			n/a	Arm		ANC-Arm-1T	SF No. 166	Middle East	Iran	Ghebleh Ghoyneh	Iron Age		1300 – 600 BC
LG071	This study			n/a	Arm		ANC-Arm-1T	SF No. P136	Middle East	Iran	Ghebleh Ghoyneh	Iron Age		1300 – 600 BC
LG073	This study			n/a	Arm		ANC-Arm-1T	SF No. 099	Middle East	Iran	Dasht Qaleh	Iron Age		1300 – 600 BC
LG084	This study			aM	NE2		ANC-Y2-5A	BK4-006 BKIV_08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG085	This study			aM	NE2		ANC-Y2-5A	BK4-116 BKIV_08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG087	This study			aM	NE2		ANC-Y2-5A	BK4-017 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG088	This study			aM	NE2		ANC-Y2-5A	BK4-121 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG090	This study			aM	NE2		ANC-Y2-5A	BK4-087 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG092	This study			aM	NE2	C/C	ANC-Y2-5A	BK4-080 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG093	This study			aM	NE2		ANC-Y2-5A	BK4-066 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG095	This study			aM	NE2		ANC-Y2-5A	BK4-075 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG096	This study			aM	NE2		ANC-Y2-5A	BK4-046 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG097	This study			aM	NE2		ANC-Y2-5A	BK4-014 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		Mid 6th millenium BC?
LG098	This study			LG098_BK	NE2	C/C	ANC-Y1-6A	BK4-025 BKIV-08	Russia/Ukraine	Ukraine	Buren Kaya 4	Neolithic		5664-5534 cal. BC
LG103	This study			n/a	E1		ANC-Cside	Mun_302	Central Europe	Germany	Stuttgart Mühlhausen	Neolithic	LBK	6th Millennium BC?
LG109	This study			A	E1	C/C	ANC-Aside	Mun_022	Near East	Turkey	Lidar Höyük	Bronze Age/Iron age		1,291-1,055 BC
LG110	This study		Domestic	A	E1	C/T	ANC-Aside	Mun_023	Near East	Turkey	Lidar Höyük	Bronze Age/Iron age		1,370-1,119 BC
LG111	This study		Domestic	aK	Arm	T/T	ANC-Arm-1T	Mun_024	Near East	Turkey	Lidar Höyük	Bronze Age/Iron age		?
LG112	This study		Domestic	n/a	NE2	C/T	ANC-Y2-5A				Lidar Höyük	Bronze Age/Iron age		?
LG114	This study			n/a	E1	C/C	ANC-Aside	Mun_033	Near East	Turkey	Lidar Höyük	Bronze Age/Iron age		1,296-1,055 BC
LG115	This study			BQ_A	Arm		ANC-Arm-1T	Mun_034	Near East	Turkey	Lidar Höyük	Bronze Age	II/III	2,000-1,650 BC
LG137	This study			AJ	E1		ANC-Aside	Mun_028	Near East	Turkey	Lidar Höyük	Medieval		897-1,021 AD
LG143	This study		Domestic	EF	NE2		ANC-Y1-6A	Mun_204	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC
LG145	This study		Domestic	E	E1		ANC-Cside	Mun_202	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC
LG147	This study			E	E1		ANC-Cside	Mun_196	Central Europe	Germany	Hetzenberg_Heilbronn	Neolithic	Michelsberger	4000-3500 BC
LG148	This study	Wild		LG148_KU	NE2		ANC-Y2-5A	Mun_061	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG153	This study	Domestic		EF	NE2		ANC-Y1-6A	Mun_074	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG155	This study	Domestic		EF	NE2		ANC-Y1-6A	Mun_083	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG156	This study	Wild		C	E1	C/C	ANC-Cside	Mun_085	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG159	This study	Wild		C	E1		ANC-Cside	Mun_089	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG161	This study		Domestic	BK	E1		ANC-Aside	Mun_133	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC - 100 AD
LG162	This study		Domestic	A	E1		ANC-Aside	Mun_150	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC - 100 AD
LG164	This study		Domestic	E	E1		ANC-Cside	Mun_174	Central Europe	Germany	Regensburg/Harting	Roman	Roman	AD
LG165	This study		Domestic	aF	E1		ANC-Aside	Mun_180	Central Europe	Germany	Regensburg/Harting	Roman	Roman	AD
LG166	This study		Domestic	aE	NE2	C/C	ANC-Y2-5A	Mun_185	Central Europe	Germany	Rottenburg Siebenlinden	Mesolithic		7692-99 cal. BC
LG167	This study		Wild	n/a	E1		ANC-Cside	Mun_188	Central Europe	Germany	Stuttgart Mühlhausen	Neolithic	LBK	5000 BC?
LG169	This study			EF	NE2		ANC-Y1-6A	Mun_191	Central Europe	Germany	Hetzenberg_Heilbronn	Neolithic	Michelsberger	4000-3500 BC
LG171	This study			A	E1		ANC-Aside	Mun_193	Central Europe	Germany	Hetzenberg_Heilbronn	Neolithic	Michelsberger	4000-3500 BC
LG173	This study			EF	NE2		ANC-Y1-6A	Mun_197	Central Europe	Germany	Hetzenberg_Heilbronn	Neolithic	Michelsberger	4000-3500 BC
LG174	This study	Wild		aE	NE2		ANC-Y2-5A	Mun_090	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG177	This study			EF	NE2		ANC-Y1-6A	Mun_120	Central Europe	Germany	Buxheim	Neolithic	Pollinger kultur	3650-3500 BC
LG178	This study	Domestic		aA	NE2		ANC-Y1-6A	800/29	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG179	This study	Domestic		aC	NE2		ANC-YcluvoNi	800/13	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG180	This study	Domestic		aB	NE2		ANC-Y1-6A	03-2102	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	4791-4598 cal. BC
LG181	This study	Domestic		A	E1		ANC-Aside	02-2061	Balkans	Serbia	Belo Brdo	Medieval	Medieval	429-577 AD

LG182	This study	Domestic		EF	NE2		ANC.Y1.6A_01-124/2	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG183	This study	Domestic		aC	NE2	C/C	ANC.YellowSki_830/416	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG184	This study	Domestic		EL	EI	C/C	ANC.Cside_02.1.2	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG185	This study	Wild		aE	NE2		ANC.Y2.5.A_45/25	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG186	This study	Wild		aE	NE2		ANC.Y2.5.A_01-1496/1	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG187	This study	Wild		aE	NE2		ANC.Y2.5.A_9/19/98.V	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG188	This study		Domestic	Y2_A	NE2		ANC.Y2.5.A_Cepan_01	South Europe	France	Fontrégoua	Neolithic	Cardial	5297-5087 cal. BC
LG191	This study			Y2_A	NE2		ANC.Y2.5.A_Cepan_04	South Europe	France	Fontrégoua	Neolithic	Cardial	6th Millennium BC?
LG194	This study		Domestic	aE	NE2		ANC.Y2.5.A_Cepan_07	South Europe	France	Fontrégoua	Neolithic	Cardial	5306-5071 cal. BC
LG195	This study			aE	NE2	T/T	ANC.Y2.5.A_Cepan_08	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG197	This study			BK	EI		ANC.Aside_Cepan_10	South Europe	France	Fontrégoua	Neolithic	Cardial	4828-4618 cal. BC
LG198	This study		Domestic	n/a	NE2		ANC.Y2.5.A_Cepan_11	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG200	This study		Domestic	A	EI		ANC.Aside_Cepan_13	South Europe	France	Fontrégoua	Neolithic	Cardial	6th Millennium BC?
LG204	This study		Domestic	BK	EI	T/T	ANC.Aside_Cepan_17	South Europe	France	Fontrégoua	Neolithic	Pontochasséen	4345-4238 cal. BC
LG208	This study		Domestic	Y2_AdE	NE2	T/T	ANC.Y2.5.A_Cepan_21	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG210	This study		Domestic	A	EI	T/T	ANC.Aside_Cepan_23	South Europe	France	Fontrégoua	Neolithic	Cardial	6th Millennium BC?
LG211	This study		Domestic	n/a	NE2		ANC.Y2.5.A_Cepan_24	South Europe	France	Fontrégoua	Neolithic	Pontochasséen	6th Millennium BC?
LG215	This study			LG215_PEN	E2		ANC.Italy_Cepan_34	South Europe	France	Pendimoun	Neolithic	VBQ1	6208-4947 cal. BC
LG217	This study			aJ	Arm		ANC.Arm-1T_MM-KTaS02	Middle East	Azerbaijan	Kolineh Tepesi	Bronze Age		3300-1200 BC
LG219	This study			aJ	Arm		ANC.Arm-1T_MM-KTaS04	Middle East	Azerbaijan	Kolineh Tepesi	Bronze Age		3300-1200 BC
LG221	This study			n/a	Arm		ANC.Arm-1T_MM-KTaS06	Middle East	Azerbaijan	Kolineh Tepesi	Bronze Age		3300-1200 BC
LG222	This study			aJ	Arm		ANC.Arm-1T_MM-KTaS07	Middle East	Azerbaijan	Kolineh Tepesi	Bronze Age		3300-1200 BC
LG223	This study			BQ_A	Arm		ANC.Arm-1T_MM-HTS01	Middle East	Azerbaijan	Hajiavan Tepe	Bronze Age/Iron age		1800-1200 B.C.
LG224	This study			BQ_A	Arm		ANC.Arm-1T_MM-HTS02	Middle East	Azerbaijan	Hajiavan Tepe	Bronze Age/Iron age		1800-1200 B.C.
LG225	This study			BQ_A	Arm		ANC.Arm-1T_MM-HTS03	Middle East	Azerbaijan	Hajiavan Tepe	Bronze Age/Iron age		1800-1200 B.C.
LG226	This study			aJ	Arm		ANC.Arm-1T_MM-DTS02	Middle East	Iran	Dashan Tepe	Iron Age		1300 - 600 BC
LG227	This study			BQ_A	Arm		ANC.Arm-1T_MM-DTS01	Middle East	Iran	Dashan Tepe	Iron Age		1300 - 600 BC
LG228	This study			aM	NE2	C/C	ANC.Y2.5.A_DNA sample 2	Russia/Ukraine	Ukraine	Shan koba	Mesolithic		9th millenium BC?
LG229	This study			aM	NE2		ANC.Y2.5.A_DNA sample 3	Russia/Ukraine	Ukraine	Shan koba	Mesolithic		9th millenium BC?
LG230	This study			aM	NE2		ANC.Y2.5.A_DNA sample 4	Russia/Ukraine	Ukraine	Shan koba	Mesolithic		9th millenium BC?
LG234	This study		Domestic?	BK	EI	C/C	ANC.Aside_DNA sample 7	Russia/Ukraine	Estonia	Narvalf	Mesolithic/Neolithic	Narva Culture	5000-4500 BC?
LG236	This study			BK	EI	C/C	ANC.Aside_DNA sample 11	Russia/Ukraine	Russia	Krasny Yar	Iron Age		108 BC - 50 AD
LG239	This study			E1_C	EI		ANC.Aside_DNA sample 9	Russia/Ukraine	Russia	Lake Ladoga	Historical		
LG241	This study			aJ	Arm		ANC.Arm-1T_DNA_4	Middle East	Armenia	Areni-1	Calcolithic or Medieval	n/a	n/a
LG247	This study			A	EI		ANC.Aside_DNA_15	Middle East	Armenia	Tsaksyeghtsi	Medieval		1300-1400 AD
LG248	This study			n/a	EI		ANC.Aside_DNA_16	Middle East	Armenia	Sevkar-4	Iron Age	n/a	1100-400 BC
LG249	This study			BQ_A	Arm		ANC.Arm-1T_DNA_18	Middle East	Armenia	Lehashen 2	Bronze Age	n/a	1700-1600 BC
LG251	This study		Domestic	BQ_A	Arm		ANC.Arm-1T_Mun_029	Near East	Turkey	Lidar Hoyük	Iron Age		1,200-600 BC
LG252	This study			aO	NE2	T/T	ANC.Y2.5.A_Mun_036	Near East	Turkey	Lidar Hoyük	Iron Age		1,200-600 BC
LG253	This study			aO	NE2		ANC.Y2.5.A_Mun_037	Near East	Turkey	Lidar Hoyük	Bronze Age		1,650-1,200 BC
LG254	This study			n/a	NE2		ANC.Y2.5.A_Mun_038	Near East	Turkey	Lidar Hoyük	Bronze Age		1,650-1,200 BC
LG255	This study	Domestic	Domestic	EF	NE2		ANC.Y1.6A_Mun_063	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG256	This study	Domestic	Domestic	EF	NE2		ANC.Y1.6A_Mun_065	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG260	This study	Wild		aE	NE2		ANC.Y2.5.A_BEO.VL_233.7	Balkans	Serbia	Vlasac	Mesolithic		7060-6799 cal. BC
LG261	This study	Wild		LG261_VLA	NE2		ANC.Y2.5.A_BEO.VL_224.sfind 4	Balkans	Serbia	Vlasac	Mesolithic		7134-6825 cal. BC
LG262	This study	Wild		aE	NE2		ANC.Y2.5.A_BEO.VL_206.1	Balkans	Serbia	Vlasac	Mesolithic		9th millenium BC?
LG263	This study	Wild		aE	NE2	C/C	ANC.Y2.5.A_(216).Ex-T-1.2007.X12	Balkans	Serbia	Vlasac	Mesolithic		7038-6796 cal. BC
LG276	This study			aK	Arm		ANC.Arm-1T_DNA sample 6, OP. B, Lo	Middle East	Iran	Mahyan	Bronze Age		3rd millenium BC?
LG281	This study			BQ_A	Arm		ANC.Arm-1T_DNA sample 2, Bag 959	Middle East	Syria	Leilan	Bronze Age		2,600-1,700 BC
LG289	This study			aK	Arm		ANC.Arm-1T_DNA sample 8, Bag 549	Middle East	Syria	Leilan	Bronze Age		2,600-1,700 BC
LG335_R1	This study			LG335R1_SA	E2		ANC.Italy_3864	Balkans	Croatia	Šandalja	Neolithic		?
LG343_R1	This study			aB	NE2		ANC.Y1.6A_XXXIII 17	Balkans	Croatia	Gudnja	Neolithic		6208-5728 BC (Budja 2009)
LG344_R1	This study	non diagnostic		aE	NE2		ANC.Y2.5.A_XXVI 8	Balkans	Croatia	Gudnja	Neolithic		6208-5728 BC (Budja 2009)
LG346_R1	This study	non diagnostic		aE	NE2		ANC.Y2.5.A_XXVIII 5	Balkans	Croatia	Gudnja	Neolithic		6208-5728 BC (Budja 2009)
LG347_R1	This study			aC	NE2		ANC.YellowSki_XXXII 5	Balkans	Croatia	Gudnja	Neolithic		6208-5728 BC (Budja 2009)
LG350	This study			E1_H	EI		I.Dom(Germany) PIN 23259 Bag 18	Near East	Turkey	Gordion	Hellenistic		IH-I centurs BC
LG351	This study			aK	Arm		ANC.Arm-1T_PIN 29955 Bag 22	Near East	Turkey	Gordion	Bronze Age		1650-1200 BC
LG352	This study			aK	Arm		ANC.Arm-1T_PIN 30618 Bag 220	Near East	Turkey	Gordion	Bronze Age		1,650-1,200 BC
LG353	This study			A	EI		ANC.Aside_PIN 29350 Bag 16	Near East	Turkey	Gordion	Phrygian		550-330 BC
LG354	This study			aC	NE2		ANC.YellowSki_PIN 29961 Bag 22	Near East	Turkey	Gordion	Bronze Age		1,650-1,200 BC
LG356	This study			LG356_Gor	NE2		ANC.Y1.6A_PIN 25020 Bag 35	Near East	Turkey	Gordion	Phrygian		550-330 BC
LG360	This study			A	EI		ANC.Aside_Cepan_39	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG361	This study			A	EI		ANC.Aside_Cepan_40	South Europe	France	Fontrégoua	Neolithic		5324-5081 cal. BC
LG362	This study		Domestic	n/a	NE2		ANC.Y2.5.A_Cepan_41	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG363	This study		Domestic	aE	NE2	C/C	ANC.Y2.5.A_Cepan_42	South Europe	France	Fontrégoua	Neolithic		4998-4800 cal. BC
LG367	This study			aE	NE2		ANC.Y2.5.A_Cepan_45	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG369	This study			A	EI		ANC.Aside_Cepan_46	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG370	This study		Domestic	H153	EI		ANC.Cside_Cepan_47	South Europe	France	Fontrégoua	Neolithic		6th Millennium BC?
LG387	This study			C	EI		ANC.Cside_Noy_08	Central Europe	France	Noyen	Mesolithic		9th millenium BC?

LG402_R1	This study	Wild		LG402_R1	NE1		Christmas	ICO_07	Balkans	Romania	Iceana	Mesolithic		8249-7964 cal. BC
LG404_R1	This study	Wild		n/a	NE2		ANC-Y2-5A	ICO_09	Balkans	Romania	Iceana	Mesolithic		8274-7967 cal. BC
LG410_R1	This study	Wild	Domestic	LG410_CII	EI		ANC-Cside	CLI_001	Balkans	Romania	Climente II	Mesolithic		?
LG411_R1	This study	Wild		LG411_CII	NE1		ANC-EI	CLI_002	Balkans	Romania	Climente II	Mesolithic		12968-12713 cal. BC
LG412_R1	This study	Wild		n/a	NE1		ANC-EI	CLI_003	Balkans	Romania	Climente II	Mesolithic		13th millennium BC?
LG413_R1	This study	Wild		LG413_CII	EI		ANC-Cside	CLI_004	Balkans	Romania	Climente II	Mesolithic		?
LG414	This study			LG414_MEHR	Arm		ANC-Arm-1T	MF06 TV/E4 PH1.1.APv1	Middle East	Iran	Mehr Ali	Chalcolithic		4000-3500 BC
LG418	This study			LG418_KOH	Arm		ANC-Arm-1T	#14	Middle East	Azerbaijan	Kohneh Tepesi	Bronze Age		3300-1200 BC
LG419	This study			aJ	Arm		ANC-Arm-1T	#45	Middle East	Azerbaijan	Kohneh Tepesi	Bronze Age		3300-1200 BC
LG422	This study			aA	NE2		ANC-Y1-6A	VIT_18	Balkans	Romania	Vitanesti	Chalcolithic	Gumelnita	4200-3900 BC?
LG423	This study			EL	EI	C/C	ANC-Cside	VIT_20	Balkans	Romania	Vitanesti	Chalcolithic	Gumelnita	4200-3900 BC?
LG424	This study		Domestic	EF	NE2	C/T	ANC-Y1-6A	VIT_22	Balkans	Romania	Vitanesti	Chalcolithic	Gumelnita	4200-3900 BC?
LG426	This study			K	EI		ANC-Cside	VIT_23	Balkans	Romania	Vitanesti	Chalcolithic	Gumelnita	4200-3900 BC?
LG427	This study			aB	NE2		ANC-Y1-6A	VIT_25	Balkans	Romania	Vitanesti	Chalcolithic	Gumelnita	4200-3900 BC?
LG430	This study		Domestic	aN	NE2		ANC-Y2-5A	VIT_29	Balkans	Romania	Vitanesti	Chalcolithic	Gumelnita	4200-3900 BC?
LG431	This study			Y2_A	NE2		ANC-Y2-5A	VIT_39	Balkans	Romania	Vitanesti	Chalcolithic	Gumelnita	4200-3900 BC?
LG432	This study			C	EI	C/C	ANC-Cside	MAG_01	Balkans	Romania	Magura	Neolithic	Precris	6200 BC?
LG434	This study			H153	EI		ANC-Cside	MAG_04	Balkans	Romania	Magura	Neolithic	Precris	6200 BC?
LG437	This study			C	EI		ANC-Cside	MAG_06	Balkans	Romania	Magura	Neolithic	Precris	6200 BC?
LG438	This study			EF/aB	NE2		ANC-Y1-6A	MAG_07	Balkans	Romania	Magura	Neolithic	Vadastra	5318-5078 cal. BC
LG440	This study			C	EI		ANC-Cside	MAG_08	Balkans	Romania	Magura	Neolithic	Vadastra	6200 BC?
LG441	This study			EF	NE2		ANC-Y1-6A	MAG_09	Balkans	Romania	Magura	Neolithic	Dudesti	6200 BC?
LG459	This study			aK	Arm		ANC-Arm-1T	#31	Near East	Turkey	Cayonii	Neolithic		7th millenium BC?
LG475	This study			aK	Arm		ANC-Arm-1T	EDI_CAN_250_397b	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG476	This study			aK	Arm		ANC-Arm-1T	EDI_CAN_273_868	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG477	This study		Domestic	aL	NE2	T/T	ANC-Y1-6A	EDI_CAN_778-5155b	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG479	This study			aL	NE2		ANC-Y1-6A	EDI_CAN_891-5779	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG480	This study		Domestic	aK	Arm		ANC-Arm-1T	EDI_CAN_966-6042	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG481	This study			Y2_A	NE2		S-EVA-4683		Balkans	Greece	Gioura	Mesolithic		7521-7321 cal. BC
LG482	This study		Domestic	EF	NE2		ANC-Y1-6A	S-EVA-4685	Balkans	Greece	Gioura	Neolithic		6232-6077 cal. BC
LG485	This study		Domestic	aL	NE2		ANC-Y1-6A	EDI_CAN_247-372b	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG486	This study			aL	NE2		ANC-Y1-6A	EDI_CAN_463-4067	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG488	This study		Domestic	aK	Arm		ANC-Arm-1T	EDI_CAN_796-5229	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG489	This study		Domestic	aL	NE2		ANC-Y1-6A	EDI_CAN_746-4982	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG491	This study			aK	Arm		ANC-Arm-1T	EDI_CAN_56-252c	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG492	This study			aK	Arm		ANC-Arm-1T	EDI_CAN_385-987	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG493	This study		Domestic	aK	Arm		ANC-Arm-1T	EDI_CAN_925-5377	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG495	This study		Domestic	aK	Arm		ANC-Arm-1T	EDI_CAN_858-5569	Near East	Turkey	Camlibel Tarlasi	Chalcolithic		3,590-3,470 BC*
LG497	This study			n/a	NE2		ANC-Y1-6A	POZ_ZEG-01	Central Europe	Poland	Zegotki 2	Neolithic	LBK	5th Millennium BC?
LG500	This study		Domestic	A	EI		ANC-Aside	POZ_CIE-01	Central Europe	Poland	Cieclrz 25	Neolithic	Globular amorpha	3400-2800 BC
LG501	This study		Domestic	aG	EI		ANC-Aside	POZ_CIE-02	Central Europe	Poland	Cieclrz 25	Neolithic	Globular amorpha	3400-2800 BC
LG502	This study		Domestic	A	EI		ANC-Aside	POZ_CIE-03	Central Europe	Poland	Cieclrz 25	Neolithic	Globular amorpha	3400-2800 BC
LG503	This study			A	EI		ANC-Aside	POZ_CIE-04	Central Europe	Poland	Cieclrz 25	Neolithic	Globular amorpha	3400-2800 BC
LG506	This study		Domestic	LG506_SIN1	NE2	C/C	ANC-Y1-6A	POZ_SIN-02	Central Europe	Poland	Siniarzewo 1	Neolithic	Band Pottery	5th Millennium BC?
LG507	This study			A	EI	C/T	ANC-Aside	POZ_SIN-03	Central Europe	Poland	Siniarzewo 1	Bronze Age	Lusatian Culture	3200-600 BC
LG508	This study		Domestic	A	EI		ANC-Aside	POZ_SIN-05	Central Europe	Poland	Siniarzewo 1	Bronze Age	Lusatian Culture	3200-600 BC
LG510	This study		Domestic	A	EI		ANC-Aside	POZ_SIN-06	Central Europe	Poland	Siniarzewo 1	Bronze Age	Lusatian Culture	3200-600 BC
LG511	This study		Domestic	A	EI		ANC-Aside	POZ_SIN-07	Central Europe	Poland	Siniarzewo 1	Bronze Age	Lusatian Culture	3200-600 BC
LG513	This study		Domestic	BK	EI		ANC-Aside	POZ_SIN-09	Central Europe	Poland	Siniarzewo 1	Bronze Age	Lusatian Culture	3200-600 BC
LG514	This study		Domestic	n/a	EI		ANC-Aside	POZ_SIN_10	Central Europe	Poland	Siniarzewo 1	Bronze Age	Lusatian Culture	3200-600 BC
LG522	This study			aK	Arm		ANC-Arm-1T	MUN_045	Near East	Turkey	Sirkeli Hoyuk	Iron Age		1300 – 600 BC
LG524	This study		Domestic	n/a	Arm		ANC-Arm-1T	MUN_047	Near East	Turkey	Sirkeli Hoyuk	Iron Age		1300 – 600 BC
LG527	This study			n/a	NE2		ANC-Y1-6A	MUN_049	Near East	Turkey	Sirkeli Hoyuk	Iron Age		1300 – 600 BC
LG529	This study		Domestic	n/a	Arm		ANC-Arm-1T	MUN_051	Near East	Turkey	Sirkeli Hoyuk	Iron Age		1300 – 600 BC
LG558	This study			n/a	EI		ANC-Aside	MUN_117	Central Europe	Germany	Baxheim	Neolithic	Pollinger kultur	3650-3500 BC
LG577	This study		Domestic	A	EI		ANC-Aside	MUN_132	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG578	This study		Domestic	F	EI		ANC-Cside	MUN_134	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG579	This study			C	EI		ANC-Cside	MUN_135	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG580	This study		Domestic	BK	EI		ANC-Aside	MUN_136	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG582	This study		Domestic	BK	EI		ANC-Aside	MUN_144	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG583	This study			BK	EI		ANC-Aside	MUN_145	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG584	This study		Domestic	R	EI		LDonGermany	MUN_146	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG585	This study		Domestic	E	EI		ANC-Cside	MUN_160	Central Europe	Germany	Altenburg	Iron Age	La Tene	450 BC -100 AD
LG588	This study			n/a	NE2		ANC-Aside	MUN_173	Central Europe	Germany	Regensburg/Harting	Roman	Roman	AD
LG589	This study		Domestic	BK	EI		ANC-Aside	MUN_178	Central Europe	Germany	Regensburg/Harting	Roman	Roman	AD
LG590	This study		Domestic	L590_REG	EI		ANC-Aside	MUN_181	Central Europe	Germany	Regensburg/Harting	Roman	Roman	AD
LG592	This study			aG	EI		ANC-Aside	MUN_198	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC
LG593	This study			A	EI		ANC-Aside	MUN_199	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC
LG595	This study			aB	NE2		ANC-Y1-6A	MUN_201	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC

LG598	This study			A	E1		ANC_Aside	MUN_205	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC
LG599	This study		Wild	E	E1		ANC_Cside	MUN_206	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC
LG600	This study		n/a	E1		ANC_Cside	MUN_208	Central Europe	Germany	Klingenberg	Neolithic	Michelsberger	4000-3500 BC	
LG602	This study	Domestic	Domestic	EF	NE2		ANC_Y1.6A	MUN_209	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG603	This study	Domestic	Domestic	n/a	E1		ANC_Cside	MUN_210	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG604	This study	Domestic		E	E1		ANC_Cside	MUN_211	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG606	This study			n/a	E1		ANC_Cside	MUN_213	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG608	This study	Domestic		aI	NE2		ANC_Y1.6A	MUN_214	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG609	This study	Domestic		E	E1		ANC_Cside	MUN_215	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG610	This study	Domestic		aI	NE2		ANC_Y1.6A	MUN_216	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG611	This study	Domestic	Wild?	A	E1		ANC_Aside	MUN_217	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG618	This study	Domestic		aI	NE2		ANC_Y1.6A	MUN_225	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG619	This study	Domestic		C	E1		ANC_Cside	MUN_227	Central Europe	Germany	Bruchsal	Neolithic	Michelsberger	4000-3500 BC
LG622	This study			E	E1		ANC_Cside	MUN_314	Central Europe	Germany	Grisstetten	Neolithic	?	4000-3500 BC?
LG624	This study			E	E1		ANC_Cside	MUN_356	Central Europe	Germany	Kurelburg	Bronze Age/Iron age	?	?
LG625	This study			E	E1		ANC_Cside	MUN_357	Central Europe	Germany	Kurelburg	Bronze Age/Iron age	?	?
LG626	This study		Domestic	E	E1		ANC_Cside	MUN_358	Central Europe	Germany	Kurelburg	Bronze Age/Iron age	?	?
LG628	This study	Domestic	Domestic	n/a	NE2		ANC_Y1.6A	MUN_069	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG629	This study	Domestic	Domestic	n/a	NE2		ANC_Y1.6A	MUN_071	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG633	This study			n/a	NE2		ANC_Y1.6A	MUN_078	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG634	This study	Wild		n/a	E1		ANC_Cside	MUN_088	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG635	This study	Wild		n/a	NE2		ANC_Y2.5A	MUN_091	Central Europe	Germany	Künzing Ünterberg	Neolithic	Rössen	4900-4500 BC
LG638	This study		Domestic	aH	E1		ANC_Aside*	MUN_247	Central Europe	Germany	Egeolsheim	Bronze Age/Iron age	?	?
LG639	This study		Domestic	aH	E1		ANC_Aside*	MUN_255	Central Europe	Germany	Egeolsheim	Bronze Age/Iron age	?	?
LG640	This study			C	E1		ANC_Cside	MUN_256	Central Europe	Germany	Egeolsheim	Bronze Age/Iron age	?	?
LG641	This study		Domestic	E	E1		ANC_Cside	MUN_259	Central Europe	Germany	Egeolsheim	Bronze Age/Iron age	?	?
LG643	This study		Domestic	n/a	E1		ANC_Aside	MUN_261	Central Europe	Germany	Egeolsheim	Bronze Age/Iron age	?	?
LG644	This study			n/a	E1		ANC_Cside	MUN_289	Central Europe	Germany	Egeolsheim	Bronze Age/Iron age	?	?
LG646	This study			n/a	E1		ANC_Aside	MUN_340	Central Europe	Germany	Rosstal	Bronze Age/Iron age	?	?
LG647	This study			n/a	E1		ANC_Aside	MUN_341	Central Europe	Germany	Rosstal	Bronze Age/Iron age	?	?
LG649	This study			n/a	E1		ANC_Aside	MUN_342	Central Europe	Germany	Rosstal	Bronze Age/Iron age	?	?
LG650	This study			n/a	E1		ANC_Cside	MUN_343	Central Europe	Germany	Rosstal	Bronze Age/Iron age	?	?
LG651	This study			aF	E1		ANC_Aside	MUN_344	Central Europe	Germany	Rosstal	Bronze Age/Iron age	?	?
LG652	This study			n/a	E1		ANC_Cside	MUN_347	Central Europe	Germany	Rosstal	Bronze Age/Iron age	?	?
LG654	This study			BK	E1		ANC_Aside	MUN_234	Central Europe	Germany	Fürmingen	Roman	Roman	AD
LG655	This study			A	E1		ANC_Aside	MUN_239	Central Europe	Germany	Fürmingen	Roman	Roman	AD
LG657	This study		Domestic	A	E1		ANC_Aside	MUN_242	Central Europe	Germany	Fürmingen	Roman	Roman	AD
LG658	This study		Domestic	aF	E1		ANC_Aside	MUN_245	Central Europe	Germany	Fürmingen	Roman	Roman	AD
LG660	This study			Y2_A	NE2		ANC_Y2.5A	CHE_001	Balkans	Romania	Cheia	Chalcolithic	Harmanga	4700 BC?
LG665	This study	Wild		EL	E1		ANC_Cside	BEO BB01-216.2	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG666	This study	Wild	Domestic	LG666_BB	NE2		ANC_Y2.5A	BEO BB03-216.2	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG668	This study			n/a	NE2		ANC_Y1.6A	BEO 1-19.98.V	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG669	This study	Wild		C	E1		ANC_Cside	BEO 97-10	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG671	This study	Wild		aN/aB	NE2		ANC_Y1.6A	BEO 1-28.98.V	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG673	This study	Domestic	Domestic	aC	NE2		ANC_YellowSk	BEO BB99-93.2	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG674	This study	Domestic		aA/aB	NE2		ANC_Y1.6A	BEO 15.17	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG675	This study	Domestic		aC	NE2		ANC_YellowSk	BEO 1-48	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG677	This study		Domestic	n/a	NE2		ANC_YellowSk	BEO BB01-117-4	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG678	This study			n/a	NE2		ANC_YellowSk	BEO 7-20	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG679	This study	Domestic	Domestic	EL	E1		ANC_Cside	BEO BB03-200.3	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG681	This study	Domestic	Domestic	EL	E1		ANC_Cside	BEO BB03-30-1	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG682	This study	Domestic		aC	NE2		ANC_YellowSk	BEO 1-45.98.V	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG683	This study			n/a	NE2		ANC_Y1.6A	BEO BB02-40-1	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG684	This study	Domestic	Domestic	aE	NE2		ANC_Y2.5A	BEO 79-1	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG685	This study			n/a	NE2		ANC_Y1.6A	BEO 82-42	Balkans	Serbia	Belo Brdo	Neolithic	Vinça Culture	5th Millennium BC?
LG691	This study		Domestic	n/a	E1		ANC_Aside	TWA_2204-1	Central Europe	Switzerland	Twann	Neolithic		5th Millennium BC?
LG707	This study		Domestic	E	E1		ANC_Cside	BJR_13	Central Europe	Switzerland	Bitsmatte	Mesolithic		?
LG711	This study		Domestic	n/a	E1		ANC_Aside	POZ_RAC_02	Central Europe	Poland	Racot	Neolithic		5th Millennium BC?
LG712	This study			n/a	E1		ANC_Aside	POZ_RAC_04	Central Europe	Poland	Racot	Neolithic		5th Millennium BC?
LG721	This study		Domestic	A	E1	1/7T	ANC_Aside	POZ_RAC_17	Central Europe	Poland	Racot	Neolithic		5th Millennium BC?
LG723	This study		Domestic	A	E1		ANC_Aside	POZ_DEB_01	Central Europe	Poland	Deby	Neolithic?	Lengyel	5th Millennium BC?
LG724	This study		Domestic	n/a	NE2		ANC_Y1.6A	POZ_LUD_02	Central Europe	Poland	Ludwinowo	Neolithic	LBK	5th Millennium BC?
LG726	This study		Domestic	n/a	NE2		ANC_Y1.6A	POZ_LUD_05	Central Europe	Poland	Ludwinowo	Neolithic	LBK	5th Millennium BC?
LG727	This study			n/a	NE2		ANC_Y1.6A	POZ_LUD_07	Central Europe	Poland	Ludwinowo	Neolithic	LBK	5th Millennium BC?
LG730	This study		Domestic	n/a	NE2		ANC_Y1.6A	POZ_ZEL_01	Central Europe	Poland	Zelepo	Neolithic	LBK	5th Millennium BC?
LG732	This study		Domestic	n/a	NE2		ANC_Y1.6A	POZ_ZEL_03	Central Europe	Poland	Zelepo	Neolithic	LBK	5th Millennium BC?
LG733	This study			n/a	NE2		ANC_Y1.6A	POZ_KUC_01	Central Europe	Poland	Kuchowo 5	Neolithic?	LBK?	5th Millennium BC?
LG735	This study			EF	NE2		ANC_Y1.6A	POZ_KUC_09	Central Europe	Poland	Kuchowo 5	Neolithic?	LBK?	5th Millennium BC?
LG736	This study		Domestic	n/a	E1		ANC_Aside	POZ_KUC_12	Central Europe	Poland	Kuchowo 5	Neolithic?	LBK?	5th Millennium BC?

LG737	This study		Domestic	n/a	NE2		ANC-Y1-6A	POZ-KUC-18	Central Europe	Poland	Kuckowo 5	Neolithic?	LBK?	5th Millennium BC?
LG738	This study		Domestic	A	E1		ANC-Aside	POZ-KUC-19	Central Europe	Poland	Kuckowo 5	Neolithic?	LBK?	5th Millennium BC?
LG739	This study			n/a	E1		ANC-Cside	POZ-KUC-20	Central Europe	Poland	Kuckowo 5	Neolithic?	LBK?	5th Millennium BC?
LG740	This study		Domestic	E1_C	E1		ANC-Aside	POZ-BOD-08	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG742	This study		Domestic	E1_C	E1		ANC-Aside	POZ-BOD-13	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG743	This study		Domestic	E1_A	E1		ANC-Aside	POZ-BOD-17	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG745	This study			aF	E1		ANC-Aside	POZ-BOD-22	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG748	This study			N	E1		ANC-Cside	POZ-BOD-28	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG750	This study		Domestic	E1_A	E1	T/T	ANC-Aside	POZ-BOD-32	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG751	This study		Domestic	aG	E1		ANC-Aside	POZ-BOD-33	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG752	This study		Domestic	BK	E1		ANC-Aside	POZ-BOD-36	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG753	This study		Domestic	A	E1		ANC-Aside	POZ-BOD-38	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG754	This study		Domestic	BK	E1		ANC-Aside	POZ-BOD-44	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG755	This study		Domestic	BK	E1		ANC-Aside	POZ-BOD-57	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG756	This study		Domestic	E	E1		ANC-Cside	POZ-BOD-58	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG758	This study		Domestic	BK	E1		ANC-Aside	POZ-BOD-66	Central Europe	Poland	BODZIA stan 1	Neolithic	LBK	5500-4600 BC
LG760	This study			LG760_BOZ	E1		ANC-Aside	POZ-BOZ-01	Central Europe	Poland	Bozegewice stan 28	Neolithic?	LBK?	5th Millennium BC?
LG761	This study		Domestic	aB	NE2		ANC-Y1-6A	POZ-BOZ-02	Central Europe	Poland	Bozegewice stan 28	Neolithic?	LBK?	5th Millennium BC?
LG762	This study			C	E1		ANC-Cside	POZ-BOZ-03	Central Europe	Poland	Bozegewice stan 28	Neolithic?	LBK?	5th Millennium BC?
LG763	This study		Domestic	n/a	E1		ANC-Aside	POZ-BOZ-04	Central Europe	Poland	Bozegewice stan 28	Neolithic?	LBK?	5th Millennium BC?
LG764	This study			A	E1		ANC-Aside	POZ-BOZ-05	Central Europe	Poland	Bozegewice stan 28	Neolithic?	LBK?	5th Millennium BC?
LG767	This study		Domestic	n/a	E1		ANC-Cside	POZ-BOZ-09	Central Europe	Poland	Bozegewice stan 22/23	Neolithic?	LBK?	5th Millennium BC?
LG770	This study			EF	NE2		ANC-Y1-6A	MDJ04 4074	Balkans	Macedonia	Madzhuri	Neolithic	Anzebegovo-Vršnik	first half of the 6th millennium BC
LG771	This study			EF	NE2		ANC-Y1-6A	MDJ04 4366	Balkans	Macedonia	Madzhuri	Neolithic	Anzebegovo-Vršnik	first half of the 6th millennium BC
LG773	This study			aK	Arm		ANC-Arm-1T	Iran CG-1	Middle East	Iran	Chogha Gavaneh	Calcolithic/Bronze Age	?	?
LG778	This study			LG778_KUZE	NE1		ANC-NE1	KS1-3	Middle East	Iran	Khuzestan	Modern		
LG779	This study			n/a	Arm		ANC-Arm-1T	K1-01	Middle East	Azerbaijan	Khoneh Tepesi	Bronze Age		3300-1200 BC
LG780	This study		Domestic	aJ	Arm		ANC-Arm-1T	K1-29	Middle East	Azerbaijan	Kohneh Tepesi	Bronze Age		3300-1200 BC
LG784	This study			BQ_A	Arm		ANC-Arm-1T	HV-08	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG785	This study		Domestic	aK	Arm		ANC-Arm-1T	HV-09	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG787	This study			aK	Arm		ANC-Arm-1T	HV-13	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG788	This study			BQ_A	Arm		ANC-Arm-1T	HV-33	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG789	This study		Domestic	BQ_A	Arm		ANC-Arm-1T	HV-34	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG790	This study		Domestic	n/a	Arm		ANC-Arm-1T	HV-35	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG791	This study		Domestic	BQ_A	Arm		ANC-Arm-1T	HV-36	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG792	This study		Domestic	BQ_A	Arm		ANC-Arm-1T	HV-37	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG794	This study			BQ_A	Arm	C/C	ANC-Arm-1T	HV-39	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG795	This study			BQ_A	Arm	C/C	ANC-Arm-1T	HV-45	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG796	This study			BQ_A	Arm		ANC-Arm-1T	HV-46	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG797	This study			n/a	Arm		ANC-Arm-1T	HV-47	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG798	This study			LG798_HAFT	Arm		ANC-Arm-1T	HV-54	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG799	This study			n/a	Arm		ANC-Arm-1T	HV-55	Middle East	Azerbaijan	Haftavan Tepe	Bronze Age		1800-1200 B.C.
LG802	This study		Domestic	aB	NE2		ANC-Y1-6A	L1A-03	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG803	This study			n/a	NE2		ANC-Y1-6A	L1A-04	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG804	This study		Domestic	n/a	NE2		ANC-Y1-6A	L1A-05	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG805	This study			n/a	NE2		ANC-Y1-6A	L1A-06	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG806	This study			n/a	NE2		ANC-Y1-6A	L1A-08	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG807	This study			n/a	NE2		ANC-Y1-6A	L1A-09	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG808	This study			n/a	NE2		ANC-Y1-6A	L1A-10	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG811	This study			n/a	NE2		ANC-YellowSki	L1A-12	Balkans	Romania	Lunca-vita	Chalcolithic	Gumelnita	4200-3900 BC?
LG815	This study			n/a	NE2		ANC-Y1-6A	CAS-BS-03	Balkans	Romania	Cascioarele	Chalcolithic	Boian-Spantov	4700-4300?
LG816	This study			n/a	NE2		ANC-Y1-6A	CAS-BS-05	Balkans	Romania	Cascioarele	Chalcolithic	Boian-Spantov	4700-4300?
LG817	This study			n/a	NE2		ANC-Y1-6A	CAS-BS-08	Balkans	Romania	Cascioarele	Chalcolithic	Boian-Spantov	4700-4300?
LG819	This study			n/a	NE2		ANC-Y1-6A	BORD_01	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG821	This study			aA/aB	NE2	C/C	ANC-Y1-6A	BORD_07	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG822	This study			EF	NE2		ANC-Y1-6A	BORD_11	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG823	This study			aB	NE2	C/C	ANC-Y1-6A	BORD_19	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG824	This study			aB	NE2		ANC-Y1-6A	BORD_24	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG825	This study			aB	NE2	C/C	ANC-Y1-6A	BORD_28	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG827	This study		Domestic	aA/aB	NE2		ANC-Y1-6A	BORD_44	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG828	This study			aB	NE2		ANC-Y1-6A	BORD_45	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG829	This study		Domestic	n/a	NE2		ANC-Y1-6A	BORD_47	Balkans	Romania	Bordusani	Chalcolithic	Gumelnita	4200-3900 BC?
LG831	This study			BK	E1		ANC-Aside	ROT_01	Balkans	Romania	Rothav	Bronze Age	Wietenberg	1500-1200 BC?
LG832	This study		Domestic	A	E1		ANC-Aside	ROT_02	Balkans	Romania	Rothav	Bronze Age	Wietenberg	1500-1200 BC?
LG833	This study			A	E1		ANC-Aside	ROT_04	Balkans	Romania	Rothav	Bronze Age	Wietenberg	1500-1200 BC?
LG834	This study		Domestic	A	E1		ANC-Aside	ROT_07	Balkans	Romania	Rothav	Bronze Age	Noua	1200-900 BC?
LG835	This study		Domestic	A	E1		ANC-Aside	ROT_09	Balkans	Romania	Rothav	Bronze Age	Noua	1200-900 BC?
LG836	This study			A	E1		ANC-Aside	ROT_10	Balkans	Romania	Rothav	Bronze Age	Noua	1200-900 BC?
LG837	This study			A	E1		ANC-Aside	ROT_12	Balkans	Romania	Rothav	Bronze Age	Noua	1200-900 BC?

LG838	This study		Domestic	A	E1		ANC_Aside	ROT_13	Balkans	Romania	Rothav	Bronze Age	Neua	1200-900 BC?	
LG839	This study		Domestic	A	E1		ANC_Aside	ROT_19	Balkans	Romania	Rothav	Bronze Age	Neua	1200-900 BC?	
RB465	This study			n/a	E1		ANC_Cside	7915	Central Europe	Switzerland	Frauenfeld	Neolithic		5th Millennium BC?	
RB468	This study			RB468_FRAU	E1		ANC_Aside	9143	Central Europe	Switzerland	Frauenfeld	Neolithic		5th Millennium BC?	
RB472	This study			n/a	E1		ANC_Cside	597	Central Europe	Switzerland	Frauenfeld	Neolithic		5th Millennium BC?	

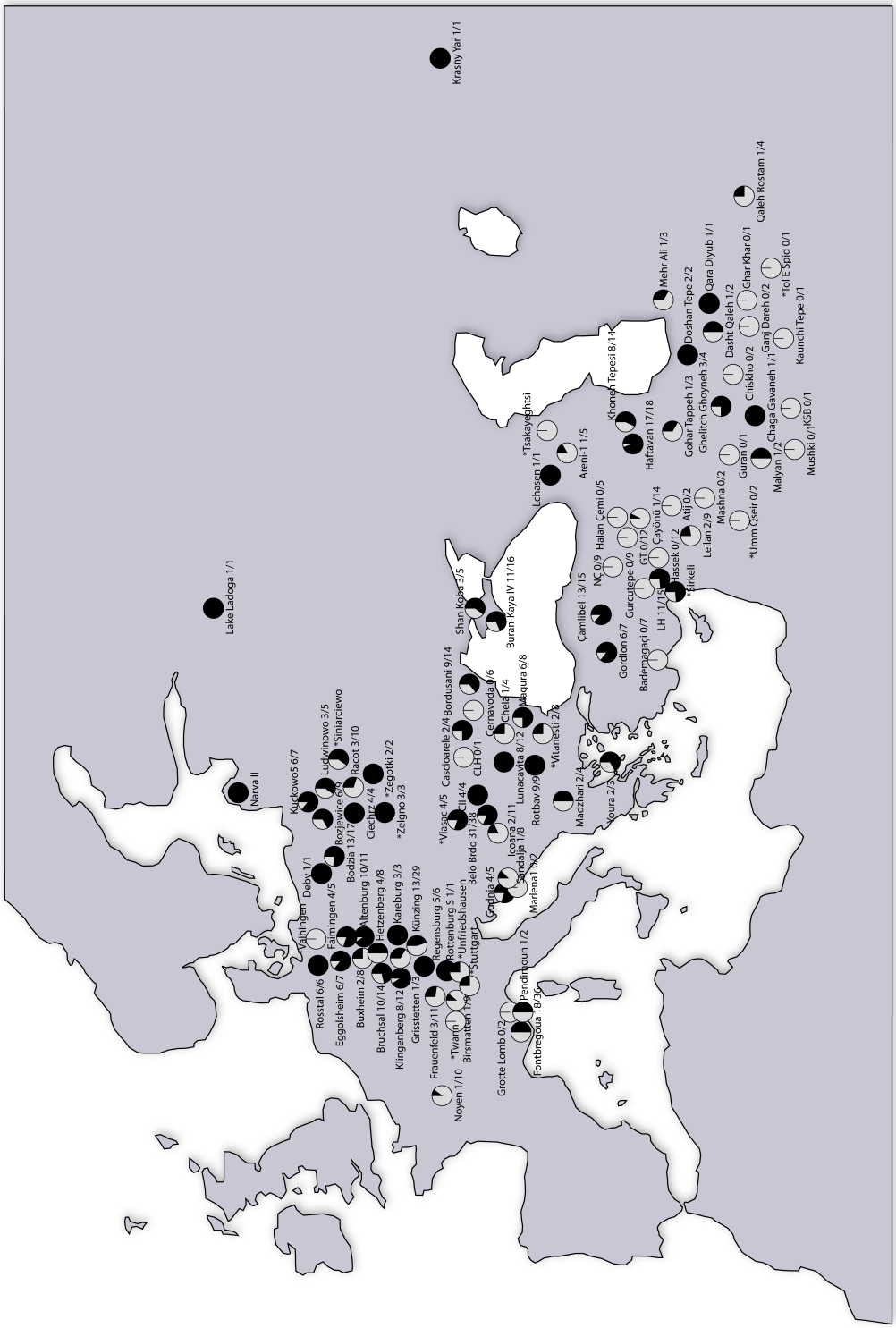


Figure 3.1: A map depicting the approximate geographic location of the archaeological sites sampled for this chapter. Black colour indicates successful retrieval of DNA and grey colour indicates failure to amplify DNA.

3.2.1 DNA extraction

DNA extraction was performed in a dedicated ancient DNA laboratory in the Archaeology department at Durham University following stringent laboratory procedures according to commonly applied guidelines (Cooper and Poinar 2001; Gilbert et al. 2005). This included wearing protective lab coats and over-shoes, double pairs of gloves (outer pair of gloves are changed in between every step of the preparation/extraction procedure). All equipment and work surfaces were cleaned before and after each use with a dilute solution of bleach (10%) followed by ethanol (99%). A strict one-way system for entering the labs is in use in order to avoid introducing post-PCR contaminants.

Compact cortical bone or dentine was prepared for DNA extraction by removing an approximately two-millimeter layer of the outer bone surface by abrasion using a dremel drill with clean cut-off wheels (Dremel no 409). The bone was then pulverized in a Micro-dismembrator (Sartorious-Stedim Biotech) followed by collection in 15mL Grainer tubes.

Bone powder was digested in 0.425M EDTA, 0.05% SDS, 0.05M Tris-HCI and 0.333/mg/ml proteinase K and incubated overnight on a rotator at 50 °C until fully dissolved. The reagent master mix, excluding proteinase K, was UV-irradiated at (254 nm) for an hour using a cross linker prior to use in the extraction buffer. 2mL of solution was then concentrated in a Millipore Amicon Ultra-4 30KDa MWCO to a final volume of 100μL. The concentrated extract was purified using the QIAquick PCR Purification Kit (Qiagen) following manufacturers recommendations, except that the final elution step was performed twice to produce a final volume of 100μL. One in five to ten negative extraction controls were performed alongside the ancient bone samples.

A selection of bones was also re-extracted and Sanger sequenced at Durham University in order to ensure authenticity (specimens with the R1 annotation in table

3.1).

3.2.2 PCR amplification and sequencing

Up to 6 mitochondrial d-loop fragments (approximately 120bp each) were amplified and sequenced (table 3.2). The ANC1 PCR primers were published previously (Larson et al. 2007a) and the remaining primers were designed by Dr. Christina Geörg at the Palaeogenetics Group in Mainz (http://www.uni-mainz.de/). The amplified fragment(s) corresponds to nucleotide positions 15520-16026 in the reference mitochondrion DNA sequence AJ002189 (Ursing and Arnason; 1998), omitting conserved bases in positions 15594-15613 for which no sequence data was obtained due to non-overlapping fragments. Numbers in the primer names refer to nucleotide positions in the Ursing and Arnason (1998) reference genome.

D-loop ANC I 5'-3'	
ANC1 F	CTTTAAAACAAAAAAACCCATAAAAA
ANC1 R	TTAATGCACGACGTACATAGG
D-loop Fragment II 5'-3'	
U15613	ARCCCTATGTACGTCGTGCATTA
L15704	GCATGTTGACTGGARTTATTTGAC
D-loop Fragment III 5'-3'	
U15697	CATATYATTATTGATCGTACATAGCACA
L15787	AAGAGGGATCCCTGCCAAG
D-loop Fragment IV 5'-3'	
U15775	AAYTACCATGCCGCGTGAAA
L15864	GTTCTTACTTCAGGACCATCTCACC
D-loop Fragment V 5'-3'	
U15852	TGGGGGTTTCTATTGATGAACTTTA
L15941	TATGTGTGAGCATGGGCTGATTA
D-loop Fragment VI 5'-3'	
U15932	CCCTTAAATAAGACATCTCGATGGA
L16027	TTTGACTGTGTTAGGGCCTTTGA
MC1R 0301 5'-3'	
MC1R_U234*	TGGTGCAGCAGCTGGACAA
MC1R_L246	TGGAGCCGCAGATGAGCA
MC1R_S	CCGCAGATGAGCAC

Table 3.2: PCR primers used to amplify d-loop fragments and the MC1R SNP. The asterisk denote biotinylation and the S denotes the sequencing primer.

PCRs for the D-loop fragments were setup in 25μL reactions using 1.25U Taq

GOLD (Applied Biosystems), 1x Gold buffer (Applied Biosystems), 2.5mM $MgCl_2$, 0.5μg/μL BSA (Bovine Serum Albumin), 200μM of each dNTP, 0.8μM of each forward and reverse primers, and 2μL of aDNA extract. One PCR negative control was included for every 5-8 aDNA template PCRs. PCR cycling conditions were 95°C for 5min, 50 cycles of 94°C for 45 sec, 54°C for 45 sec and 72°C for 45 sec, followed by 72°C for 10 min. PCR products were stored at -20C.

An initial PCR using the ANC1 primers was performed to screen the extracts for preserved DNA. If samples did not produce a PCR product during the second attempt, after failing the first, the extract was excluded from further analysis. Sanger sequencing on the Applied Biosystems 3730 DNA Analyser at the DNA sequencing service in the School of Biological and Biomedical Sciences at Durham University followed successful amplification of the ANC1 fragment. Sanger sequences were analysed by eye in Geneious Pro 5.4.3 (Drummond et al. 2011). Once preserved samples were identified 5bp 5′-tagged PCR primers (following Binladen et al. 2007) were used to re-amplify the full fragment. PCR products were visualized on agarose gel stained with GelRed (Life Technologies) and pooled by eye into approximate equimolar concentrations using a reference series previously quantified on the Qubit fluorometer; approximately 12μg/μL of each PCR product was used for the final pool.

The pooled 5′ tagged PCR products were then concentrated using an Amicon Ultra-4 30KDa MWCO filter column to a final volume of 100μL. The concentrated amplicon pool was then purified using the QIAquick PCR Purification Kit (Qiagen) following manufacturers recommendations, except that the final elute volume was 80μL. The concentrated PCR amplicon pool was then built into a paired-end library (Paired-End DNA Sample Prep Kit, Illumina) following manufacturers guidelines and sequenced on the Illumina GAII platform at the Department of Biology at Copenhagen University. Illuminas Genome Analyzer Sequencing Control Software (SCS) v2.4 was used for base calling. A custom written PERL script (Rasmussen, M., University of Copenhagen) was used to filter out sequences containing the 5′ tag label and to mate

paired-end reads into single lines containing both forward and reverse 5′ tag label information. A second custom written PERL script (Frantz, L., Wageningen University) was used to write a single fasta files for each tag label/amplicon. The resulting fasta files were assembled into contigs against a reference sequence (EU333163) in Geneious Pro 5.4.3. (Drummond et al. 2011) Assembly was performed using global total quality score to call the best base (any base with a quality below 20, which is equivalent to PHRED scores, was called as N and therefore not considered in the consensus sequence.

No.	Tags
1	ACAGT
2	AGACT
3	ATACG
4	ACGAG
5	ACTAG
6	AGCAT
7	ATCAG
8	AGTAC
9	ATGAT
10	ACGTA
11	AGCTG
12	ATCGC
13	AGTCA
14	ATGCA
15	CAGAT
16	CATAG
17	TAGCA
18	TACGC
19	CGATA
20	GCATG

Table 3.3: The 5′ tags used to assign the pooled PCR products to individuals.

3.2.3 MC1R PCR amplification and pyrosequencing

The D124N substitution, causative of dominant black coat colour (0301 SNP in the MC1R locus, Fang et al. 2009), was targeted using primers U243-L246 that amplify a 48bp fragment corresponding to nucleotide positions 344-391 in a MC1R reference sequence (EU443644). Dr. Christina Geörg at the Palaeogenetics Group in Mainz (http://www.uni-mainz.de/) designed the PCR primers. The Q24 sequencing primer (0301S) was designed in Durham using the PSQ Assay Design Software

(Biotage).

Attempts were made to amplify the D124N substitution in 48 ancient specimens representing 17 archaeological sites from the Near East (Anatolia) and Europe. The archaeological sites were selected to represent contexts ranging in age from the Mesolithic to Iron Age. Successful genotypings (after at least 4 replications) are presented in table 3.1.

PCRs for the MC1R SNP were setup in 25μL reactions using 1.0-1.25U Taq GOLD (Applied Biosystems), 1x Gold buffer (Applied Biosystems), 2.5mM MgCl2 , 0.5μg/μL BSA (bovine serum albumin), 1M betaine, 200M of each dNTP, 0.4M of each primer, and 2-5μL of aDNA extract. One PCR negative control was included for every 7 aDNA template PCRs. PCR cycling conditions were 95°C for 5min, 50 cycles of 94°C for 30 sec, 57°C for 30 sec and 72°C for 30 sec, followed by 72°C for 10 min.

Pyrosequencing was performed in-house at the Archaeology department in Durham using the PyroMark Q24 (Qiagen) following manufacturers guidelines and using Qiagen Q24 sequencing reagent kits. Results were analysed in the PyroMark Q24 software using modified settings: accepted peak deviation and minimum peak heights were set to *less strict* to account for minor errors associated with the degraded state of ancient DNA.

Due to the low template copy number in ancient DNA extracts, PCR amplification of diploid loci in ancient materials is susceptible to allelic dropout that increase the risk of falsely determining a true heterozygous individual as homozygous (Taberlet et al. 1996; Svensson et al. 2007; Ludwig et al. 2009; Daskalaki et al. 2011). In order to account for allelic drop out each SNP (or genotype) was confirmed by repeated genotypings from independent PCRs. The probability of falsely assigning a heterozygous individual as homozygous was calculated as follows: P(false homozygote)=K*(K/2)n-1, where n is the number of replicates and K is the observed number of allelic dropouts divided by the total number of genotypings of heterozygous individuals (Gagneux et al. 1997).

3.2.4 Analysis of mtDNA sequence data

Consensus sequences were aligned in Geneious Pro 5.4.3 (Drummond et al. 2011) using MAFFT (Katoh et al. 2002). Haplogroup and haplotype assignment was performed using previously published modern sequences (Alexandri et al. 2011, GenBank accession numbers JF774182-JF774393, Alves et al. 2003, GenBank accession numbers AY232868-AY232868, Alves et al. 2010, GenBank accession numbers HM747196, HM747198, HM747199, HM747201, HM747202, HM747206-HM747209, HM747211, HM747213, and HM747215, Fang and Andersson 2006, GenBank accession number DQ379232, Fang et al. 2006, GenBank accession numbers DQ379233-DQ379261, Giuffra et al. 2000, GenBank accession numbers AF136555, AF136556, AF136558 and AF136563, Gongora et al. 2003, GenBank accession numbers AF535163 and AF535164, Kijas and Andersson 2001, GenBank accession number AF304203, Larson et al. 2005, GenBank accession numbers AY884609-AY884831, Larson et al. 2007a, GenBank accession numbers DQ872931-DQ873203, and Randi et al. 2002, GenBank accession number AJ314544) (see also details in chapter 4).

If ancient haplotypes matched haplotypes published by Larson et al. (2005; 2007a) the published haplotype designation was used. If ancient haplotypes did not match Larson et al. (2005; 2007a) they were named according to matches in previous publications (see above). If haplotypes did not match any previously published modern sequence they were named arbitrarily to aA-aO. Alternatively, if haplotypes were only found in a single individual, the reference id describing that individual sample was used to name the haplotype. Ancient specimens from which one fragment was missing were defined to haplotype according a best fit against the reference sequences. In some instances it was not possible to define the specific haplotype but a label describing the closest matches (or putative haplotypes) were used. The modern sequences used for reference purposes are not presented in this chapter but co-analysed with the ancient sequences in chapter 4.

Haplotypes were divided into three groups for managerial purposes: haplotype (rep-

resenting the 486bp fragment), phylo group (corresponding to previously described haplogroups/clades E1, E2, NE1, NE2 and Arm, Larson et al. 2005; 2007a), or 80bp haplotype, which is the ANC1 corresponding haplotype (table 3.1). Therefore, the ANC1 80bp haplotypes denote both a specific haplotype but also a haplogroup. In addition, because there are several 486bp haplotypes possessing identical haplotypes in the ANC1 fragment (Larson et al. 2005; 2007a), the ANC1 fragment can also be used to describe sub-groups of haplotypes in each haplogroup (e.g. ANC1 haplotype Y1 corresponds to several 486bp haplotypes that all cluster within the NE2 clade. Therefore, ANC1 Y1 and ANC1 Y2, which are both part of the NE2 clade, are also haplogroups).

The genetic relationship among ancient individuals and populations was investigated using median joining networks (MJN) constructed using the NETWORK software (Bandelt et al. 1999).

3.2.5 Groups and statistical analysis

Archaeological samples for which the 80bp ANC1 fragment and the longer 486bp d-loop sequence were amplified were grouped into spatial and temporal bins corresponding to four major time periods (Mesolithic, Neolithic, Chalcolithic and Bronze Age, the latter of which comprise ancient samples from the Bronze Age and onwards and can be considered analogue to post-Neolithic/Chalcolithic). These groups were chosen to fit the time bins and hypotheses proposed by Larson et al. (2007a), the hypotheses tested in this chapter, and the results obtained in chapter 2. Consequently, they represent the pre-Neolithic diversity, the Neolithic and in some instances Chalcolithic diversity, and post-Neolithic diversity - time bins over which the most significant changes occurred in the genetic history of pigs according to previously published data (Larson et al. 2007a; chapter 2). These groups (Mesolithic, Neolithic/Chalcolithic and post-Neolithic) were also implemented when examining the spatial and temporal arrangement of individual specimens and sequences.

Archaeological samples were further grouped into spatial bins for statistical analysis (n denotes the number of samples for which the 486bp sequence is available): Bronze Age Balkans (BroBal, n=9) Bronze Age Central Europe (BroEu, n=31), Bronze Age Middle East (BroME, n=29), Bronze Age Near East (BroNE, n=15), Bronze Age Russia (BroRU, n=2), Buran-Kaya 4, which is an analogue to Crimean Neolithic (n=11), Çamlibel, which is an analogue to Calcolithic Anatolia/Near East (n=13), Chalcolithic Balkans (ChaBal, n=16), Mesolithic Balkans (MesBal, n=9), Mesolithic Crimea (MesCri, n=3), Mesolithic Central Europe (MesEu, n=3), Neolithic Balkans (NeoBal, n=39), Neolithic Central Europe (NeoEUn=56), Neolithic Middle East (NeoME, n=2), and Neolithic South Europe (NeoSEU, n=16). Individual archaeological sites and samples belonging to each group are listed in table 3.1. Note that the Near East is considered an analogue to Anatolia whereas the Middle East is considered the area east of Anatolia (sometimes bordering Anatolia).

Population pairwise Φ_{ST} was calculated in Arlequin v3.5.1.3 (Excoffier et al. 2005) using 10,000 permutations to test for statistical significance. Φ_{ST} is an analogue to traditional F_{ST} (Wright 1951) but with the addition that it incorporates both haplotype frequencies and distances between haplotypes (Excoffier et al. 1992). Distances between haplotypes were inferred from a distance matrix of pairwise differences. All p-values were adjusted using Bonferroni correction.

The population pairwise Φ_{ST}'s were analysed in a non-metric MDS (Multi Dimensional Scaling) plot in the Past software (Hammer et al. 2001). The MDS method attempts to place the data points in a two-dimensional coordinate system while preserving their original ranked differences. The ranked differences are the ranked order of the distances between data points (or populations). If, for example, population 2 and 5 have the 7th largest distance among all populations, these populations will ideally be placed so that their Euclidean distance (automatically transformed in the software from the original distance) in the 2D plane is still preserved. This method is implemented to visualize all population pairwise Φ_{ST} in a single figure and in so doing visualize the relative differentiation among populations. A Mini-

mal Spanning Tree (MST) was visualized on the MDS plot in order to deduce the shortest distances among populations. The MST is the shortest possible set of lines connecting all populations (the population/group pairwise Φ_{ST}'s and can be used to clarify relationships among groups, Hammer et al. 2001).

Summary genetic statistics were calculated for each putative population (or group). The number of haplotypes (Nei 1987), haplotype (gene) diversity (H, Nei 1987), and nucleotide diversity (π, Nei 1987) were calculated in DNAsp version 5 (Librado and Rozas 2009).

3.2.6 AMS radiocarbon dating

A selection of the bone material was AMS radiocarbon dated (n=29) at the Oxford Radiocarbon Accelerator Unit (ORAU). Prof. Tom Higham (Oxford) calibrated the raw dates with OxCal v4 (c14.arch.ox.ac.uk/oxcal.html) prior to use in this thesis (see also chapter 2). These dates are highlighted in green in table 3.1.

3.3 Results

The samples that yielded sequences are presented in detail in table 3.1. 335 samples out of 676 yielded PCR-reproducible 80bp ANC1 sequences, resulting in an overall success rate of 50%. 256 out of those had a good PCR success rate (at least 50%) for the remaining five overlapping fragments and were subsequently deep-sequenced on the Illumina platform in Copenhagen and analysed as outlined above.

33 samples out of 48 yielded reproducible MC1R genotypes (table 3.1), corresponding to a success rate of 69%. Note, however, that specimens were selected out of the group of DNA extracts that consistently yielded PCR products for the mtDNA fragments (suggesting good preservation and high number of starting template molecules). Therefore, the overall success rate for this locus must be considered significantly lower on average compared to a situation where no pre-screening for mtDNA is carried out. The probability of falsely assigning a heterozygous individual as homozygous after 4 successful genotypings was estimated to be <0.05. In table 3.1, T denotes the derived allele and C denotes the wild type allele.

3.3.1 Haplotypes and phylogenetic reconstruction

11 haplotypes were observed for the 80bp ANC1 fragment, one of which is previously undescribed (LG402 from Mesolithic contexts at the Iron Gates site Icoana), and one of which is previously unpublished but described in chapter 2 (a haplotype denoted, arbitrarily, YellowStar). The remaining ANC1 haplotypes correspond to previously published sequences (Larson et al. 2007a). 48 haplotypes were observed among the 256 specimens from which longer fragments were sequenced. 19 out of those were unique to individual specimens (singletons). 10 out of the 48 haplotypes were unique to populations but not to individuals.

A MJN (figure 3.2) revealed a phylogenetic structure that captures sequence varia-

tion in a resolution that is in accordance with previously defined haplogroups and clades (Larson et al. 2005; 2007a). A discrepancy in the relationship among clades was observed in that the E2 (Italian) clade is linked to the NE2 (Y2) group rather than the European (E1) group (Larson et al. 2007a). However, this observation has no bearing on the following discussion or conclusions (see below).

One discrepancy in the grouping of Y1 and Y2 haplotypes was observed (figure 3.2 and figure 3.3): a Neolithic specimen from the Crimean site Buran-Kaya 4 possessed an Y1 ANC1 haplotype while the remaining sequence is identical to the Y2 haplotype aM, which in turn is geographically restricted to the Crimean peninsula (these sequences are identical apart from the 5/6-mononucleotide indel that separate ANC1 Y1 from Y2). Although this observation could be indicative of homoplasy, the broader structure between the remaining ANC1 Y1 and Y2 haplotypes support haplogroup designations NE2 Y1 and NE2 Y2. Therefore, the overall grouping of ANC1 haplotypes into haplogroups is both supported and useful for taking into consideration the spatial and temporal arrangement of haplogroups (figure 3.2 and figure 3.3). Whether these haplogroups form unique phylogenetic clades, however, remains uncertain because of the low intra-group resolution: there are at least two putative evolutionary pathways between the Y1 and Y2 haplogroups. This question is discussed further in-depth in chapter 4.

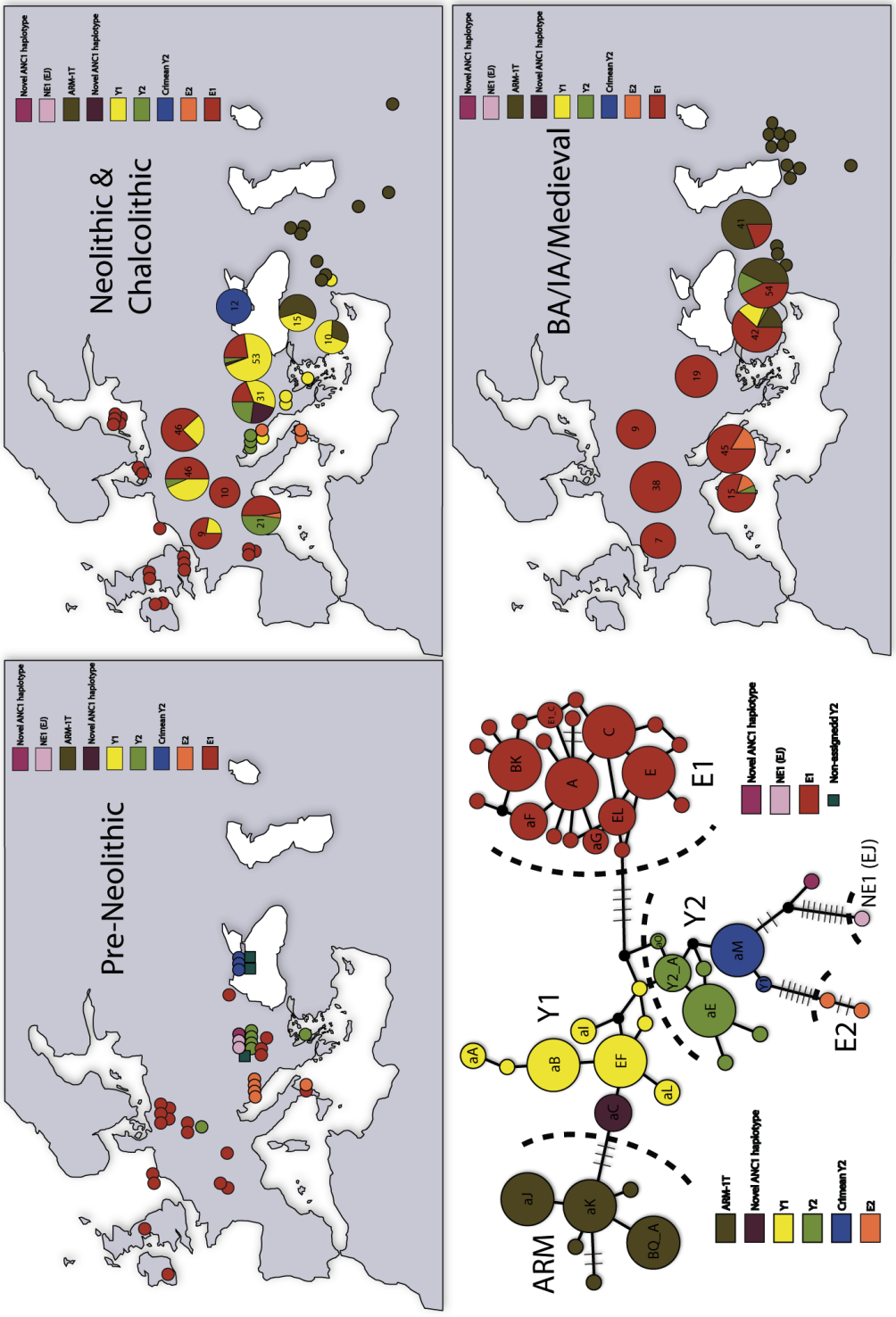


Figure 3.2: A median-joining network of 486bp haplotypes and the spatial and geographical distribution of ANC1 haplotypes. ANC1 haplotypes are from this study, from chapter 2 and from Larson et al. (2007a).

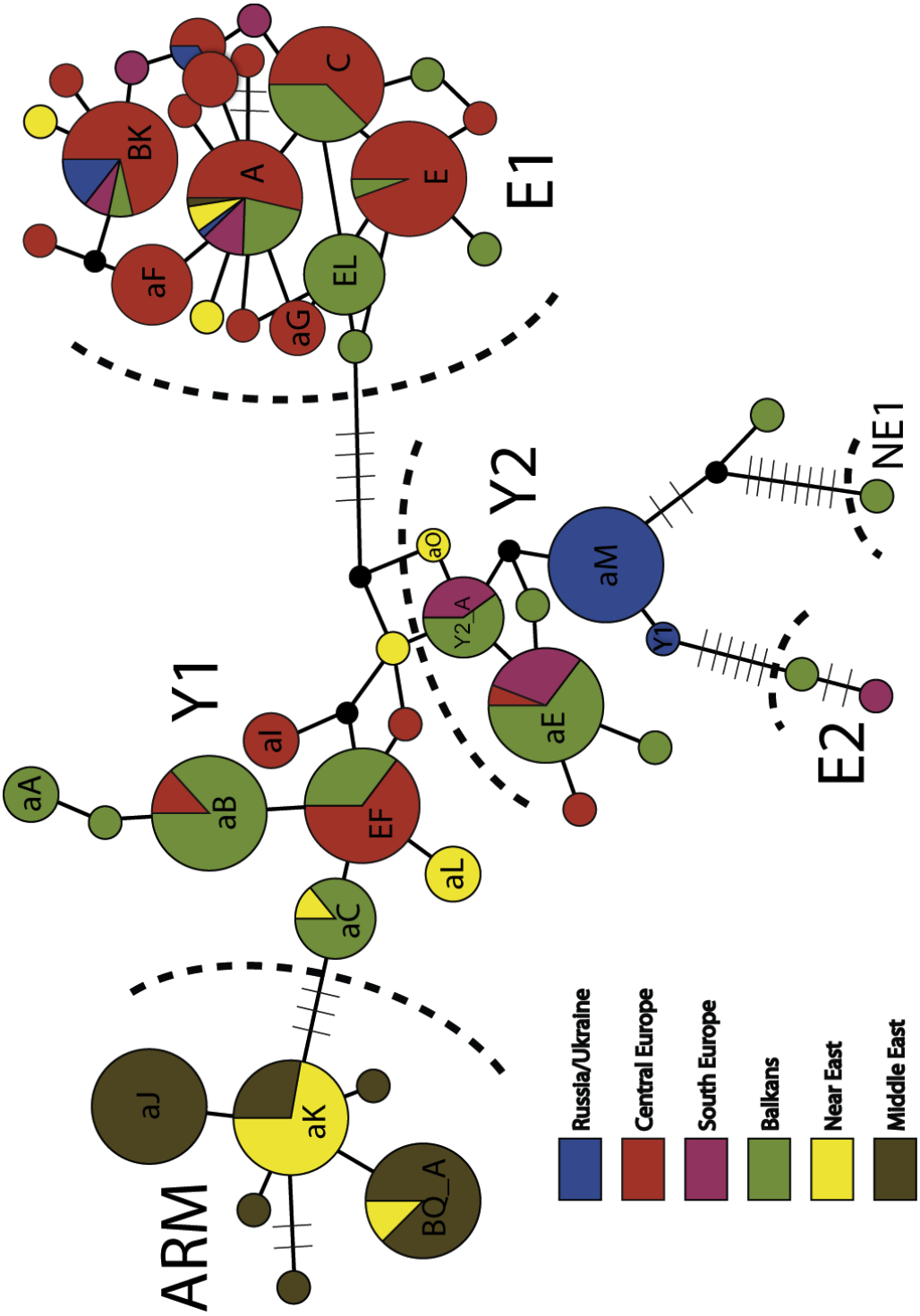


Figure 3.3: The distribution of 486bp haplotypes over geographic locations.

3.3.2 Genetic diversity and population differentiation

The genetic diversity within ancient populations varied from very low to very high (table 3.4). π (nucleotide diversity) ranged from $\pi = 0$ in Mesolithic Crimea (n=3) and Neolithic Crimea (represented by one archaeological site only, Buran Kaya 4, n=11) to $\pi = 12.6 \times 10^{-3}$ in the South European Neolithic group (consisting of samples from the archaeological sites Fontbregoua, n=15 and Pendimoun, n=1). Haplotype diversity (H) is also highly variable and ranged from 0.0 in the Crimean Mesolithic and Neolithic group to 1.0 in the groups representing Neolithic Middle East (n=2), Bronze Age Russia (n=2) and Mesolithic Europe (n=4) (the latter is an effect of small sample size). The highest observed value for groups representing a higher number of individuals (a statistically more valid sample) is found in the Bronze Age (or post-Neolithic and post-Chalcolithic) Near Eastern group (H=0.88, n=15).

	n	Hap	H	VarH	s.d.	Pi	s.d.
BroBal	9	2	0.222	0.02764	0.166	0.000457	0.00034
BroEU	31	8	0.839	0.00111	0.033	0.00339	0.00032
BroME	29	6	0.7	0.00406	0.064	0.00341	0.00116
BroNE	15	8	0.876	0.00354	0.06	0.011782	0.00118
BroRU	2	2	1	0.25	0.5	0.004115	0.00206
BuranKaya	11	1	0	0	0	0	0
Camlibel	13	2	0.513	0.00675	0.082	0.004247	0.00068
ChaBal	16	7	0.75	0.01148	0.107	0.006082	0.00185
MesBal	9	6	0.833	0.016	0.127	0.012241	0.00281
MesCri	3	1	0	0	0	0	0
MesEU	4	4	1	0.03125	0.177	0.010653	0.00391
NeoBal	39	9	0.872	0.0004	0.02	0.010352	0.00086
NeoEU	56	14	0.857	0.0009	0.03	0.009175	0.00068
NeoME	2	2	1	0.25	0.5	0.004107	0.00205
NeoSEU	16	6	0.833	0.00313	0.056	0.012584	0.00155

Table 3.4: Genetic diversity indices for ancient groups.

Population pairwise Φ_{ST}'s are presented in table 3.5. The MDS plot of population pairwise Φ_{ST}'s reveals both spatial and temporal structure among populations. The Φ_{ST} distances among groups show that Chalcolithic Near East (represented by the archaeological site Çamlibel from Central Anatolia, n=13) cluster with the Neolithic

Middle East sample (n=2) and the post-Neolithic (Bronze Age and onwards) sample from Middle East (n=29) (table 3.4). The post-Neolithic sample from the Near East (or Anatolia) is distanced closer to the European groups, probably reflecting the higher proportion of shared haplogroups (E1) previously observed in chapter 2 (and figure 3.2 and figure 3.3). This sample is closest to the Mesolithic group from Central Europe (Φ_{ST}=0.09, p>0.05), Neolithic Europe (Φ_{ST}=0.12, p>0.05) and Neolithic South Europe (Φ_{ST}=0.12, p>0.05).

The MDS and MST reveals close affinity between the Mesolithic (n=9), Neolithic (n=39, Φ_{ST}=0.10, p>0.05) and Chalcolithic (n=16, Φ_{ST}=0.27, p>0.05) groups from the Balkans, which could be indicative of temporal continuity. Mesolithic (n=3) and Neolithic (n=11) samples from the Crimea cluster by themselves (Φ_{ST}=0, p>0.05) and both share a shortest distance to the Mesolithic group from the Balkans (Φ_{ST}=0.13, p>0.05 and Φ_{ST}=0.35, p<0.05).

The MDS and MST also group Neolithic South Europe (n=16) with Neolithic Europe (n=56, Φ_{ST}=0.06, p>0.05) and Mesolithic Europe (n=4, Φ_{ST}=0, p>0.05) despite the discrepancy in haplotype frequencies (figure 3.3).

Lastly, the MDS and MST reveal a clustering of Bronze Age Russia (n=2), Bronze Age Europe (n=31) and Bronze Age Balkans (n=9). Population pairwise Φ_{ST}'s indicate a closest relationship to the Central European group, and the Mesolithic Central European group in particular (BroRU: Φ_{ST}=0, p>0.05, BroEU: Φ_{ST}=0.2, p>0.05 and BroBal: Φ_{ST}=0.37, p>0.05).

Table 3.5: Population pairwise Φ_{ST} values. Statistically significant values after Bonferroni correction are cursive and bolded.

Group	MesBal	MesCri	MesEU	NeoBal	NeoEU	NeoME	NeoSEU	ChaBal	BroBal	BroEU	BroME	BroNE	BroRU	BuranK	Camlibe
MesBal	-														
MesCri	0.130	-													
MesEU	0.091	0.533	-												
NeoBal	0.095	0.270	0.181	-											
NeoEU	0.244	0.448	0.000	0.184	-										
NeoME	0.396	0.933	0.541	0.343	0.482	-									
NeoSEU	0.057	0.294	0.000	0.143	0.057	0.462	-								
ChaBal	0.265	0.453	0.450	0.043	0.317	0.539	0.325	-							
BroBal	***0.589***	***0.981***	***0.375***	***0.516***	***0.191***	***0.961***	***0.309***	***0.760***	-						
BroEU	***0.617***	***0.837***	***0.200***	***0.526***	***0.174***	***0.843***	***0.344***	***0.734***	***0.060***	-					
BroME	***0.646***	***0.844***	***0.750***	***0.479***	***0.566***	***0.168***	***0.641***	***0.640***	***0.872***	***0.833***	-				
BroNE	0.164	0.392	0.089	0.108	0.123	0.117	0.122	0.248	0.424	0.457	0.348	-			
BroRU	0.333	0.925	0.000	0.393	0.018	0.818	0.057	0.649	0.394	0.002	0.833	0.193	-		
BuranKaya	***0.349***	***0.000***	***0.757***	***0.360***	***0.506***	***0.964***	***0.439***	***0.565***	***0.978***	***0.861***	***0.869***	***0.529***	***0.960***	-	
Camlibel	***0.449***	***0.739***	***0.619***	***0.265***	***0.463***	***0.169***	***0.492***	***0.370***	***0.848***	***0.807***	***0.207***	***0.205***	***0.760***	***0.811***	-

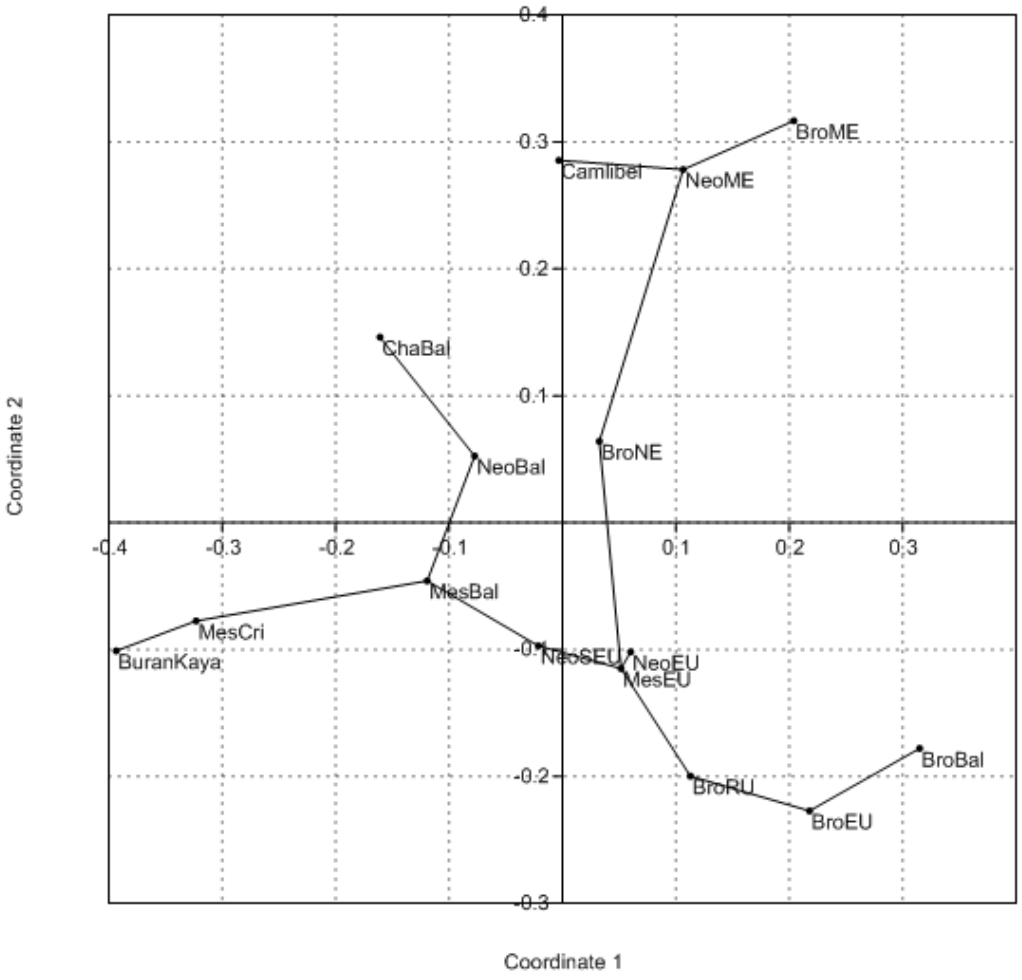


Figure 3.4: MDS plot and MST of population pairwise Φ_{ST} values.

3.3.3 AMS radiocarbon dating

29 AMS radiocarbon dates were obtained from ORAU. Calibrated AMS radiocarbon dates are presented in table 3.1 (highlighted in green).

3.4 Discussion

3.4.1 Selection and selective constraints during the domestication process

The spatial and temporal arrangement of the derived MC1R D124N substitution (Fang et al. 2009) reveals several new insights. Mesolithic wild boar from Rottenburg-Siebenlinden in Germany (LG166), Shan Koba on the Crimean peninsula (LG228) and Vlasac in Serbia (LG263), two of which are directly radiocarbon dated, were homozygous for the wild type allele (table 3.1), in agreement with their wild status (Fang et al. 2009). On the other hand, a single individual (LG477) from the Chalcolithic site Çamlibel Tarlasi in central Anatolia was homozygous for the derived D124N substitution. Because this individual belongs to a population that had not yet been admixed with pigs from Europe (see chapter 2), this observation supports a Near Eastern origin of the D124N substitution. It also supports the hypothesis that early domestic pigs possessed domestic phenotypes (chapter 2; Fang et al. 2009).

However, some European pigs carrying the mtDNA Y1 haplotype, and dating to the Neolithic/Chalcolithic, were homozygous for the wild type MC1R allele (table 3.1). Assuming that all Y1 pigs in European contexts were domestic (Larson et al. 2007a), this observation could indicate that people had not yet exerted positive selection on coat colour phenotypes at the time domestic pigs were first brought to Europe. MC1R data from younger contexts (the Bronze and Iron Ages) in both Europe and the Near East show that, even during these periods, it was not uncommon for (putatively) domestic pigs to be homozygous for the wild type allele. In fact, the D124N substitution lingered at low or intermediate frequency for the duration of the studied time period (Neolithic to Iron Age) (table 3.1). Because of this, the data does not immediately support the hypothesis of fast, directed, selection during the early domestication process, which likely would have driven the D124N substitution to fixation (Fang et al. 2009). Instead, a more plausible explanation

is that domestication led to a relaxation of selective constraints, which would allow non-synonymous mutations like the D124N substitution to accumulate relatively fast while segregating at low or intermediate frequency in the absence of positive selection (similar to the situation for mtDNA, Björnerfeldt et al. 2006; Wang et al. 2011).

An alternative, but not mutually exclusive, explanation could be constant gene flow between wild and domestic populations. It remains a possibility that Neolithic stock-keepers deliberately maintained gene flow from wild male boar to domestic sows in a manner similar to that observed in modern contemporary societies on Papua New Guinea. There, under certain breeding or management schemes, domestic sows are allowed only to mate with wild boar (Hide 2003). These sows retain wild characteristics (phenotypes) during levels of constant gene flow and acquired fully domestic traits only when the gene flow ceased (Hide 2003).

A third explanation model could be that these individuals were in fact wild. Preliminary wild/domestic data suggests that at least some of the European specimens carrying the Y1 haplotype were wild (table 3.1). In all, however, the data is too scarce to draw far-reaching conclusions about selection and admixture, particularly in the absence of a detailed morphological assessment of the wild or domestic status of the ancient specimens (see above).

3.4.2 Exploring the hypothesis of genetic continuity in Europe

Larson et al. (2005; 2007a) hypothesise that mitochondrial phylogenetic lineages E1 and E2, and NE1 and NE2 do not share a natural range overlap, where the former two clades are geographically restricted to Europe and the latter two are geographically restricted to the Near and Middle East. Furthermore, it has been suggested that the Y2 haplogroup was introduced to Europe from the Near East

by Neolithic migrant farmers but dispersed along an expansion route different to that of Y1 pigs (southern Mediterranean route and the northern Danubian route, respectively) (Larson et al. 2007a).

Phylogenetic analysis and direct AMS radiocarbon dating reveal that a large proportion of individuals from Mesolithic sites in Europe possessed NE1 or NE2 clade haplotypes (table 3.1, figure 3.2). Two pigs from the Iron Gates site Climente II, one of which is directly AMS dated to 12,540±427 cal. BC, possessed NE1 haplotypes that group closely with the EJ haplotype (Larson et al. 2005). These individuals are the only ones in the entire data set that carried haplotypes belonging to this rare haplogroup (table 3.1). However, the observation that NE1 pigs were present in Europe has no bearing on the further discussion because no domestic pigs have ever been found to possess NE1 haplotypes (Larson et al. 2005; 2007a, and see chapter 2). It does, however, provide a clear indication that there are structural errors in the current understanding of West Eurasian wild boar phylogeography (see Scandura et al. 2011a for a summary of previously published data). The two remaining specimens from Climente II carried unique haplotypes that cluster within the major E1 clade, which is ubiquitous among both ancient and modern European populations (figure 3.2, figure 3.3).

During the early Holocene, the NE2 clade Y2 haplogroup was seemingly far more widespread in Europe than the NE1 clade. A single pig, presumably wild, from the Mesolithic open-air site of Rottenburg Siebenlinden (directly AMS dated to 7,691.5±99 cal. BC) and four Mesolithic specimens from the Iron Gates site of Vlasac (with four tightly clustered corresponding AMS dates, representing three specimens, with a mean age of 6,924±157 cal. BC) possessed Y2 haplotypes that cluster closely together within NE2 (haplotype aE and a unique Y2 haplotype, LG261). A single specimen from the Mesolithic site Icoana (with two tightly clustered AMS dates with a mean age of 8,090±170 cal. BC) failed to amplify the full mtDNA fragment but successfully produced an Y2 ANC1 sequence (table 3.1).

Nine wild and possibly domestic pigs from the Middle Neolithic Vinça site Belo Brdo

in central Serbia, three wild and possibly domestic pigs from the Middle Neolithic Rössen culture site of Künzing/Unternberg in southeast Germany, and a one wild boar and domestic pig from the Chalcolithic and Neolithic sites Vitanesti and Cheia in Romania also possessed Y2 haplotypes that are either shared or closely linked to those found in the Mesolithic sample (figure 3.2). These observations together suggest long-term genetic continuity in Central Europe and the Balkan Peninsula, possibly linking the Y2 haplotype with local European domestication.

These data are also supported in the analysis of population pairwise Φ_{ST}'s in that the distances among groups indicate regional continuity between Mesolithic and Neolithic Crimean groups, Mesolithic, Neolithic and Chalcolithic groups in the Balkans and Mesolithic and Neolithic groups in south and central Europe (figure 3.4).

The abundance of Y2 pigs in Mesolithic Europe and the absence of Y2 pigs in old (Neolithic and Chalcolithic) strata from Anatolia and the Middle East (chapter 2) therefore falsify the hypothesis that migrant Neolithic farmers brought domesticated Y2 pigs to Europe from the Near East (Larson et al. 2007a). It also falsifies the hypothesis of undisturbed genetic continuity in Europe since the beginning of the Holocene (Larson et al. 2005; 2007a). However, the data show that the Y1 and Y2 haplogroups were geographically separated. This separation appears to be defined by the physical barrier between the Balkans and Anatolia (the Aegean Sea and the Bosporus strait) (figure 3.2), in agreement with the hypothesis of Larson et al. (2007a).

However, isolation-by-distance (a consequence of limited dispersal across space, Wright 1943), genetic drift and poor sampling in the contact zone between Southeast Balkans and Northwest Anatolia are factors that could explain the absence of wild Y1 pigs in the European sample (though preliminary wild/domestic status calls of Neolithic/Chalcolithic specimens reveal that some of these might have been wild, table 3.1). In fact, the formation of the phylogeographic structure (or barrier) between NE2 haplogroups could be linked with the rise of the Black Sea (the Black Sea deluge hypothesis) that took place possibly as early as 7,400 BC (Giosan and

Constantinescu 2009).

3.4.3 Mesolithic Aegean and the question of pre-domestic management of wild boar

A single specimen from the Mesolithic site of Cyclops cave on the Island of Youra (or Giuora) in the Aegean Sea (directly AMS dates to 7,691.5±99 cal. BC) carried the NE2 clade Y2A haplotype. The Y2A haplotype is only present in wild and domestic pigs from Neolithic and Chalcolithic contexts in Romania (Cheia and Vitanesti), Fontbregoua in Southern France (figure 3.6), and in one modern feral pig from Corsica (Larson et al. 2007a). Although based on only a few specimens, the spatial arrangement of the Y2A haplotype demonstrates a possible link between different Mediterranean island populations.

The question of whether wild boar naturally populated Youra, or whether people brought them there remains a topic of debate (Masseti 2009; Sampson 1998; Trantalidou 2008; Vigne et al. 2009; 2011). The main difficulty in determining the true history of this population lies in the fact that the sea level was considerably lower during the Last Glacial Maximum and Mesolithic than it is today (118 m to 60-40 m respectively) (Sampson 1998; Trantalidou 2008; and see figure 3.5). Because of that, it is not possible to rule out that wild pigs colonised the island naturally by means of swimming.

The Mesolithic specimen from Cyclops cave on Youra dates to the beginning of the Upper Mesolithic (the Mesolithic on Youra is dated to approximately 8,626-8,290 BC and lasts until 6,643-6,496 BC, Trantalidou 2008). That is before (but close in proximity to) the arrival of the early Neolithic settlements on mainland Greece (Perles 2003; Özdogan 2011). Importantly, there are no signs in the fossil record that *Sus* inhabited the island before humans arrived around 8,600 BC (Trantalidou 2008). Moreover, th possible introduction is roughly in the same time frame as the

known introduction to Cyprus, which also took place prior to the appearance of a fully developed Neolithic culture (including morphologically domestic pigs) as early as the 10th millennium BC (Vigne et al. 2009; 2011).

The Mesolithic pigs from Youra were small in size in comparison to their wild counterparts on mainland Europe. Trantalidou (2008) argue that neither early Holocene climate change nor insularity (the island effect) can fully explain their small (and continuously diminishing) size. Small pigs are common in the Mediterranean area around the Mesolithic/Neolithic transition, including pigs from Corsica (Albarella et al. 2006a), Italy (Albarella et al. 2006b) and Cyprus (Vigne et al. 2009; 2011). However, size change comparisons, particularly when involving island populations, should be interpreted with caution due to inherent problems with identifying the source of fluctuations in size (Albarella et al. 2009). It is therefore uncertain whether the Youra population was in an incipient phase of domestication, part of a managed herd or simply wild.

3.4.4 Genetic variation in wild and domestic pigs from the Cardial culture

Wild and possibly domestic pigs from the early to Middle Neolithic (Cardial and Protochassen culture) site of Fontbregoua in Southern France possessed only E1 and NE2 Y2 haplotypes. The single specimen from the VBQ1 (Square Mouthed Pottery-phase I) culture site Abri Pendimoun in Southern France that yielded DNA carried a haplotype that cluster in the E2 clade (figure 3.3). This clade has previously only been found in the North Mediterranean around Italy and Corsica, and the North Adriatic coastline in Croatia (Scandura et al. 2011a).

The Y1 haplogroup was not observed either at Fontbregoua or Abri Pendimoun, indicating that the southern pig population was genetically distinct from pigs along the Danubian route (Larson et al. 2007a), in similarity to what has been observed

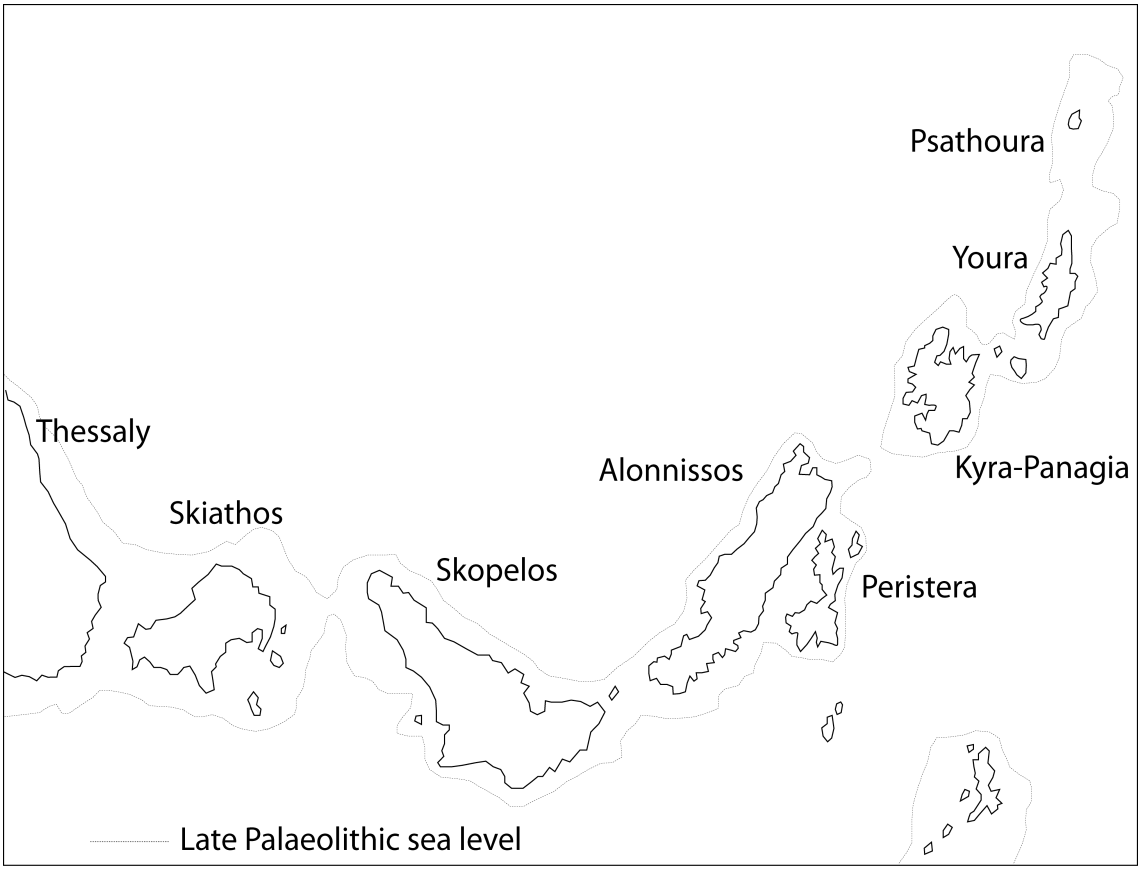


Figure 3.5: Sea level change in the Aegean sea surrounding Youra and Cyclops cave. Re-drawn after Sampson 1988.

in human Neolithic populations (Sampietro et al. 2007; Bramanti et al. 2009). The remaining samples at Fontbregoua (8/18) possessed three E1 haplotypes (the common A and BK haplotypes, and the rare H153 haplotype), all of which seem to be ubiquitously distributed across Europe (see further analysis in chapter 4). Population pairwise Φ_{ST}'s (table 3.5) show that this population is closely related to the Mesolithic Central European sample and the Neolithic Central European sample, despite differences in haplotype frequencies (figure 3.3).

3.4.5 The Danubian expansion

The onset of the Neolithic in the Balkans and Central Europe is linked to the emergence of pigs carrying Y1 haplotypes (Larson et al. 2007a). The earliest appearance

of the Y1 haplogroup (haplotype EF) comes from a directly AMS radiocarbon dated pig from Early Neolithic contexts in Cyclops cave on Youra island in the Aegean Sea (represented by two near identical AMS dates with a mean age of 6,151±77 cal. BC). The EF haplotype is also present in two pigs from the early Neolithic Anzabegovo culture site Madzhari in the Skopje basin (Macedonia), dated to the early 7th millennium BC (table 3.1). From there, it spread north to Central Balkans: it appears at the Neolithic site of Magura in Romania (probably dating to around 6,000 BC) and the Middle Neolithic site of Belo Brdo in Serbia, which dates to the mid 5th millennium BC (table 3.1). From the Balkans it spread into Central Europe with the LBK expansion and was retained at relatively high frequencies until the Late Neolithic. The Y1 haplogroup and its spread along the Danubian expansion route is also exemplified by haplotype aB, though the spatial and temporal distribution of that haplotype is not as clearly defined as that of haplotype EF (figure 3.2, figure 3.6). Other Y1 haplotypes are restricted to Central European Neolithic contexts (haplotype aI) or to Balkan Neolithic contexts (haplotype aA).

Although the morphometric wild/domestic status determinations of these pigs remains, to a great extent, uncertain and incomplete, the domestic status of at least some Y1 pigs is supported by the observation that they carried the derived MC1R D124N substitution (table 3.1). In addition, the spatial and temporal structure of the Y1 haplogroup in Europe (figure 3.6) demonstrates a direct genetic link between pigs in the primary Neolithisation zone in Greece (Perles 2003), Neolithic contexts in the Balkans, and LBK contexts in central Europe.

3.4.6 Wild-domestic hybridization and local European domestication

Mitochondrial and MC1R data from the Cardial Neolithic site of Fontbregoua in South France provides an important new insight to the process of local European domestication: the presence at this site of domestic pigs carrying E1 and Y2 haplo-

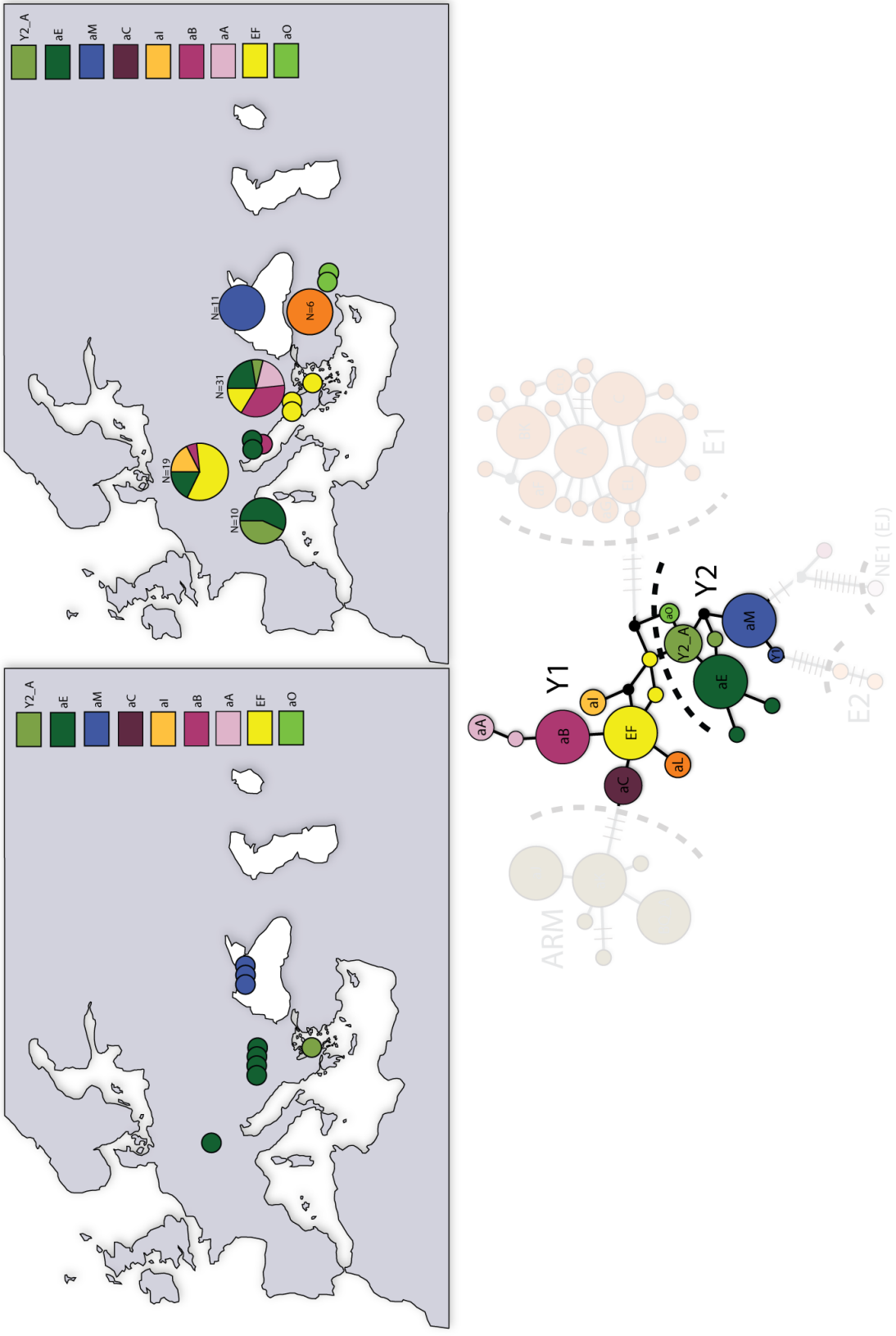


Figure 3.6: The distribution of 486bp NE2 haplotypes in Europe and the Near East. The left figure illustrate the pre-Neolithic variation and the right one the Neolithic and Chalcolithic variation.

types is strongly indicative of local European domestication, likely through a process of introgression between local European wild boar and domestic pigs that possessed the D124N MC1R substitution (which most probably originated in the Near East). The observation that domestic pigs at Fontbregoua had acquired genetic signatures from local European wild boar as early as 5,000 BC (table 3.1) suggests that the date by which local domestication took place could be pushed back by up to a millennium relative to that previously suggested (Larson et al. 2007a).

The first appearance of domestic pigs possessing genetic signatures matching those of local European wild pigs should correspond both in time and space to the Neolithic expansion routes (Larson et al. 2007a). The MDS plot of population pairwise Φ_{ST}'s (figure 3.4) and the geographic distribution of a number of E1 haplotypes (see below) is indicative of population continuity in both central Europe and the Balkans. Locally restricted haplotypes that are shared between wild and domestic pigs could be indicative of introgression from local wild boar. Hence, it is possible, given these data, that local European domestication (mediated through wild-domestic hybridisation) was an ongoing process, encompassing many different European wild boar populations.

For example, three possibly domestic pigs from the Middle Neolithic site Belo Brdo in Serbia possessed the rare E1 haplotype EL, which is only shared with two other pigs in the entire ancient data set, a wild pig from the Chalcolithic site Vitanesti in Romania and a wild pig from Belo Brdo. One putatively domestic EL pig and one wild EL pig were homozygous for the wild type D124N substitution, thereby failing to confirm whether the former specimen is in fact domestic (it cannot be ruled simply because this individual possessed the wild type MC1R phenotype) (table 3.1).

Central Europe is a second region where wild and putatively domestic pigs share geographically restricted haplotypes. The haplotype E is present in a wild boar from the Neolithic Michelsberger culture site of Klingenberg in Germany dated to approximately 4,000-3,500 BC. Haplotype E is also found in a range of putatively domestic pigs from Neolithic to Roman contexts (table 3.1), all geographically re-

stricted to Central Europe. Hence, albeit based on a handful samples and incomplete wild/domestic status determinations, the observation of local continuity combined with the observation that some wild and putatively domestic pigs share geographically restricted haplotypes could indicate that local domestication (introgression with local wild populations) took place more than once and over a large geographic region.

A complete genetic turnover is observed across the Balkans and Central Europe towards the late Neolithic/Calcholithic (figure 3.2), indicating a very fast movement of local peoples and/or cultures. The youngest Y1 pig in the Balkans is found at either of two Gumelnita culture sites Luncavita or Bordusani, dated to the late 5th or early 4th millennium BC, a date in very close proximity to that observed by Larson et al. (2007a) (3,900 BC). This shift of haplotypes later spread to the Near and Middle East, where European E1 pigs replaced native NE2 clade pigs (see chapter 2).

3.5 Conclusions

The data presented in this chapter show that the phylogeographic history of European wild boar was considerably different from currently held hypotheses (Scandura et al. 2011a). The NE2 haplogroup Y2 was present in several geographical regions in Europe (in Central Europe, the Balkans, including islands in the Aegean Sea, and on the Crimean peninsula) during the early to mid-Holocene (*ca* 10,000 to 5,000 years ago). The Y2 haplogroup vanished from most geographic regions in Europe during the mid-fifth millennium BC (or around 6,500 years ago). A single modern feral pig on Corsica retains a remnant of this once widespread, primarily European, haplogroup (Larson et al. 2005).

Likewise, the NE1 haplogroup was present in upper Palaeolithic contexts in the Balkans but vanished from the region probably during the early Holocene. Hence,

this haplogroup too had a much wider geographic distribution than previously thought (Scandura et al. 2011a). This haplogroup has not been identified in any other European specimens, ancient or modern, west of the Black Sea (Larson et al. 2007a).

Today, the spatial distribution of genetic lineages is upheld by the geographic barrier between Anatolia and Southeast Europe (the Bosporus barrier). However, it is unclear if this barrier was intact throughout the Holocene. The shifts in the spatial distribution of genetic lineages could be linked with sea level rise in the Black Sea, which would have caused a disrupt in west-east gene flow (Giosan and Constantinescu 2009).

Migrant Neolithic farmers brought the first domestic pigs to Southeast Europe, probably across the Aegean Sea, no later than 6,232-6,077 BC. From there, domestic pigs were brought north across the Balkans and into Central Europe (the Danubian expansion associated with LBK). This migration of pigs probably reflects a migration of people too (demic diffusion), as indicated by human ancient DNA (Burger and Thomas 2011). Following the introduction during the Early Neolithic, the genetic signature associated with the migration from the Near East (Y1) vanished from Europe, probably during the early to mid-fourth millennium BC, only to be replaced by genetic signatures acquired from local European wild boar. Pigs are therefore a useful proxy for tracking pre-historic human migration (and/or trading routes), in agreement with previous suggestions (Larson et al. 2007a, but see chapter 2).

Domestic pigs along the southern Mediterranean route carried different mtDNA haplotypes than those brought into Central Europe (figure 3.2). The South European (or Mediterranean) pigs possessed only mtDNA haplotypes matching those of European wild boar but they shared the derived (or domestic) MC1R allele with Danubian pigs (who in turn carried mtDNA haplotypes of Near Eastern ancestry). The former population could therefore have been the result of local domestication (through introgression with local wild boar; the incorporation of wild sows into the domestic stock). AMS radiocarbon dates suggests that this process took place at

least a millennium prior to previous estimates, possibly as early as 5,000 BC, and in different geographic locations than previously thought (Larson et al. 2007a). Because (putatively) domestic pigs and wild boar from the same geographical regions shared haplotypes restricted to these regions (indicative of wild-domestic gene flow), it is likely that this process took place independently over many geographic locations. That would reinforce the idea that domestication is an ongoing, continuous process (Dobney and Larson 2006) with no clear beginning or end (Vigne 2011, but see figure 1.1).

Lastly, the derived D124N substitution in the MC1R gene (which is linked to black coat colour, Fang et al. 2009) originated in the Near East, probably in one of the first domestic populations. The accumulation and retention of this phenotype was likely the result of a relaxation of selective constraints (the elimination of purifying selection) only, as opposed to a scenario in which the relaxation, and thereby its first appearance, was followed by cherry-picking and directed selection (in which case all domestic pigs would have possessed the derived, domestic, phenotype).

Chapter 4

West Eurasian wild boar phylogeography revisited

4.1 Introduction

The wild boar, or common Eurasian wild pig (*Sus scrofa*), is one of the most widespread and numerous mammals in Eurasia. Based on morphology, Groves (1981; 2007) identified up to 16.5 sub-species (the extra half being an anomaly from Sri Lanka). However, these classifications are disputed both on morphological (Albarella et al. 2009; Genov 1999) and genetic grounds (e.g. Scandura et al. 2011a). Western Eurasian wild boar, comprising the group of western races (Groves and Grubb 1993), are traditionally divided into at least three major subspecies; *Sus scrofa scrofa* (Central-Western Europe), *Sus scrofa attila* (Eastern Europe and the Balkans, into Khazakhstan to Iraq) and *Sus scrofa lybicus* (South Balkans to the Nile delta, to South Caucasus) (Groves 1981; 2007) (figure 4.1).

A fourth subspecies (*Sus scrofa meridionalis*) is endemic to Andalusia, and was possibly the source population for pigs introduced to Corsica and Sardinia (Albarella et al. 2006a). However, the true status and origin of the wild (or feral) pig of Corsica and Sardinia is disputed on the basis of metric data (Albarella et al. 2006a; 2009) and genetic data (Larson et al. 2007a; Scandura et al. 2011b). Autosomal microsatellite data indicate that the wild (or feral) population of Sardinia is likely admixed with wild boar from the Italian Peninsula, Central Europe and domestic stock, although the authors found no clear evidence of admixture with local free-ranging domestic pigs (Scandura et al. 2011b). Ancient genetic data (Larson et al. 2007a) and archaeozoological data (Albarella et al. 2006a) show that humans introduced pigs to Corsica from mainland Europe rather than the Iberian or Italian peninsulas, although genetic signatures from Iron Age contexts on Sardinia show that at least some pigs were introduced from the Italian Peninsula (Larson et al. 2007a). Worth noting, however, is that no ancient genetic data is available from Iberian contexts, which would allow a direct testing of these hypotheses (Scandura et al. 2011a).

Another proposed subspecies, which true origin and status is disputed, is the North

African *Sus scrofa algira* (Larson et al. 2005; Ramirez et al. 2009; Hajji and Zachos 2011) (figure 4.1). The Egyptian and Sudanese populations are possibly descendants from feral domestic pigs (Manilus et al. 1999) but carries a rare haplogroup (NE1) that has never been detected in any, ancient or modern, domestic pigs (Larson et al. 2005; 2007a; Scandura et al. 2011a). The demographic history and intra-population relationship among African populations is therefore somewhat unclear. Palaeontological records show that wild boar were present in the Maghreb (North/Northwestern part of Africa) during the Pleistocene and throughout the Holocene (Dobson 1998), suggesting that at least part of the African population could have a long demographic continuity. As revealed through mitochondrial DNA (Ramirez et al. 2009; Hajji and Zachos 2011) and autosomal sequence data from the FABP4 gene (Ojeda et al. 2006), the North African population is likely admixed with wild or domestic pigs from Europe, possibly as a result of gene flow across the Mediterranean, in similarity to the proposed human-mediated spread of snails (Jesse et al. 2011) and cattle (Beja-Perreira et al. 2006), or linked to the introduction of domestic pigs from Europe to Anatolia (chapter 2).

Other authors have suggested additional subspecies among the Western Races (e.g. Mayer and Brisbin 1991; Oliver et al. 1993); *Sus scrofa castilianus* (Spain and Portugal), *Sus scrofa baeticus* (Southern Spain) and *Sus scrofa majori* (South Italy). However, neither *Sus scrofa majori* nor *Sus scrofa castilianus* is supported among taxonomists (Groves 1981; Apollonio et al. 1988) although at least the former has been used *a priori* in taxonomic revisions (Genov 2004).

An important difference in karyotype, or chromosome number, exists between European (*S. s. scrofa* and *S. s. meridionalis*) and Asian wild boar (including *S. s. attila* and *S. s. lybicus*); the former have 2n = 36 while the latter 2n = 38 (Fang et al. 2006) (figure 4.1). The karyotype with 2n = 38 likely represent the ancestral state (Scandura et al. 2011a). The reduction in the number of chromosomes arose from a process called Robertsonian translocation and involves chromosomes 15 and 17 (McFee et al. 1966 in: Scandura et al. 2011a).

Crossings between individuals with 2n=36 and 2n=38 are known to create fertile offspring who have karyotypes with 2n=37 (Fang et al. 2006; Scandura et al. 2011a). Wild boar possessing karyotype with 2n=37 has been reported from the Netherlands, Spain, Italy, Poland, Lithuania, Byelorussia and Central Russia (the latter three corresponding to the border between (*S. s. scrofa* and *S. s. attila* possibly indicating natural gene flow, figure 4.1). In fact, for all geographic locations where wild boar possessing karyotypes with 2n=37, the 2n=36 and 2n=38 karyotypes are reported too. However, the crossings may in some instances be due to human movement of wild boar or wild-domestic hybridisation (Fang et al. 2006; Scandura et al. 2011a). Genetic variation appears to be distributed with no correspondence to the the geographic restriction of proposed subspecies (Larson et al. 2005), suggesting continuous gene flow across regions and between putative subspecies (Ramirez et al. 2009; Scandura et al. 2011a).

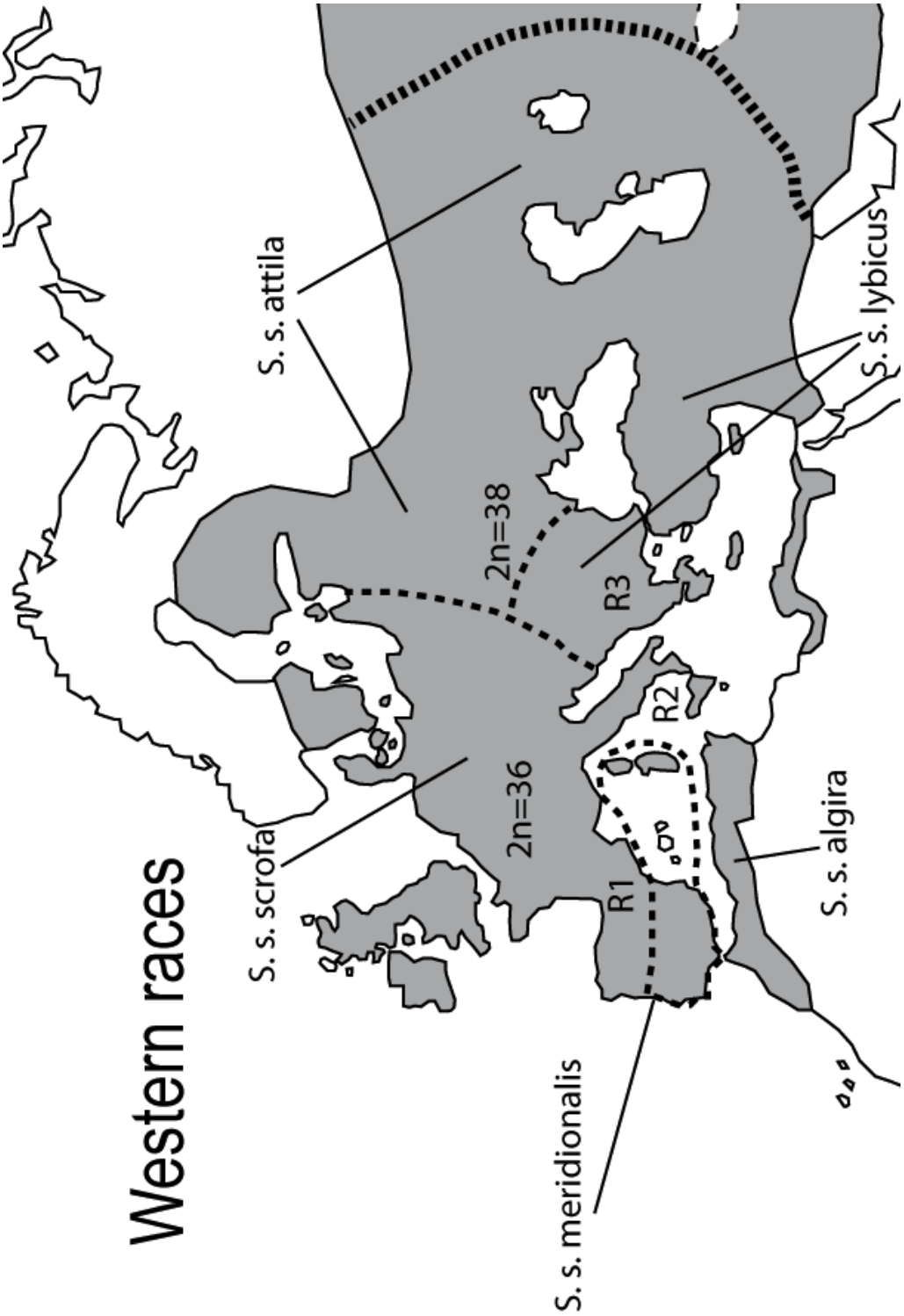


Figure 4.1: West Eurasian wild boar subspecies after Groves 1981; 2007 and Groves and Grubb (1993). R1-R3 is putative LGM refugia (Sommer and Nadachowski 2006) and 2n=36/38 is chromosome number after Fang et al. (2006) and Scandura et al. (2011a).

4.1.1 The West Eurasian wild boar - from past to present

The West Eurasian wild boar first colonised Europe during the Early Pleistocene (some 1,5-1,0 million years ago) (Rook and Martinez-Navarro 2010). The oldest records of *S. scrofa* in Europe are dated to the Late Villafranchian (Early Pleistocene) and comes from the central German site of Untermassfeld and the North Spanish site of Atapuerca (Rook and Martnez-Navarro 2010). The *S. scrofa* expansion into Europe was the culmination of a westward expansion across Eurasia that in turn followed a split of several lineages of the genus *Sus* in Southeast Asia during the Late Pliocene and Early Pleistocene (Larson et al. 2005; Mona et al. 2007).

European wild boar were probably restricted to glacial refugia during the last glacial maximum (LGM), 23,000-18,000 years ago (Sommer and Nadachowski 2006; Scandura et al. 2008; 2011, Alexandri et al. 2011). The putative refugia were located in the Iberian Peninsula, the Italian Peninsula and the Balkans (or R1-R3 respectively, Sommer and Nadachowski 2006, but see Taberlet et al. 1998) (figure 4.1). Nevertheless, some populations remained in northern-more refugia during the LGM, like in Dordogne in Southwest France (Sommer and Nadachowski 2006).

Sommer and Nadachowski (2006) summarise the presence and absence of common mammals at 47 LGM sites across putative refugia but also from more northerly sites in West, Central and East Europe (sometimes referred to as cryptic refugia, Provan and Bennet 2008). Wild boar were not among the species found in East/Central European refugia but these sites are mainly characterised by the presence of fox (*Vulpes vulpes*), bear (*Ursus arctus*) and reindeer (*Rangifer tarandus*) (species adapted to a colder climate) (Sommer and Nadachowski 2006). Apart from sites in Southwest France (confirmed presence at 7 of 9 investigated sites), wild boar was present in Italy (2 out of 4 sites) and Greece (3 out of 3 sites). It remains unclear whether gene flow occurred among refugial wild boar populations, similar to that of other species (e.g. bears, Valdiosera et al. 2008). Wild boar re-colonised Europe towards the end of the LGM, some 20,000-16,000 years ago, probably from all three putative refugia

(Sommer and Nadachowski 2006; Provan and Bennet 2008; Scandura et al. 2011a).

However, little is known about the process of post-glacial expansion of wild boar out of glacial refugia and to which extent populations from R1-R3 contributed to the re-colonization of Europe (Scandura et al. 2011a). The European wild boar has undergone a great deal of demographic change and population shifts since the post-glacial re-colonization, not least because of anthropogenic factors like local extinctions and re-introductions (thereby also relocations) and wild-domestic admixture (Fang et al. 2006; Scandura et al. 2011a, but see also chapter 3). These processes have to a great extent blurred genetic patterns of post-LGM re-colonisation (Scandura et al. 2008; 2011).

Scandura et al. (2008) used autosomal microsatellites and mtDNA to investigate whether the genetic structure and diversity in modern Italian wild boar was shaped by ancient or recent processes. The authors found that modern Italian wild boar preserve a high proportion of pre-glacial diversity and that demographic decline of local populations did not produce a noticeable reduction in overall genetic diversity. In general, levels of genetic diversity appear to be relatively high in Eurasian populations (e.g. Ramayo et al. 2010).

Taking one step back, analysis of mitochondrial sequence data from Eurasian wild boar have showed a robust phylogeographic grouping of lineages into two major clades: the East Asian and the European (Giuffra et al. 2000). While the initial work was carried out on few specimens (Giuffra et al. 2000), Larson et al. (2005) analysed sequence variation in several hundred Eurasian wild boar and found a number of previously uncharacterised clades. While the major West-East grouping of lineages remained intact, the observation of additional clades provided clues that helped deciphering regional variability across a geographic area stretching from Island Southeast Asia to Scandinavia (Larson et al. 2005; 2007a).

The mitochondrial variation in modern West Eurasian wild boar groups into four phylogenetic clades: the European (E1), the Near Eastern 1 and 2 (NE1 and NE2),

and the Italian (E2) (Giuffra et al. 2000; Larson et al. 2005, and see chapters 2 and 3). The European clade consists of wild boar from Europe, ranging from the Iberian Peninsula to Russia (Alves et al. 2004; Larson et al. 2005; Scandura et al. 2008; Ramirez et al. 2009), North Africa (Larson et al. 2005; Hajji and Zachos et al. 2011), and Israel and the Middle East (Giuffra et al. 2000; Larson et al. 2005). The NE clade 1 and 2 consists of wild boar from Anatolia, Caucasus, Middle East and North Africa (Larson et al. 2005; Ramirez et al. 2009; Hajji and Zachos et al. 2011), and a possibly feral individual on Corsica (Larson et al. 2005), while the E2 clade is restricted to the Italian Peninsula (Larson et al. 2005; 2007a; Scandura et al. 2011a).

However, ancient DNA has shown that the E2 clade occurred outside the Italian peninsula during the Early Holocene (reaching at least into Croatia) possibly reflecting post-LGM expansion (Larson et al. 2007a; Scandura et al. 2011a, chapter 3). Moreover, ancient DNA has shown that the geographic range of mitochondrial phylogenetic haplogroups E1, E2, NE1 and NE2 has shifted considerably during the Holocene (chapter 3). European wild boar possessed all of these haplogroups at some point between 5,000-15,000 YBP (chapter 3). These novel data (chapter 2 and 3) show that the post-LGM population history (and phylogeographic history) of wild boar was far more complex than previously thought.

4.1.2 Human influence on wild boar phylogeography

Pigs and humans have had an intense relationship since at least the early Holocene (Albarella et al. 2009; Vigne et al. 2009; 2011; Larson et al. 2011). Various wild boar-human interactions have led to shifts in, or expansions of, geographical ranges of wild boar (and therefore shifts in the spatial arrangement of genetic lineages). For example, humans have introduced wild boar to Cyprus (Vigne et al. 2009), and likely to Corsica and Sardinia (Albarella et al. 2009). In addition, humans possibly brought wild pigs to Youra Island in the Aegean Sea during the Mesolithic

(Trantalidou 2008, chapter 3). These processes are complicating factors that must be taken into account when inferring the past from modern genetic data (Avise 2000; 2009; Scandura et al. 2011a).

A second complicating factor is that of local extinction followed by repopulation. European local populations have gone extinct in the British Isles, Netherlands, Denmark, Sweden, the Baltic States, Czech Republic, Switzerland and Slovenia, and to some extent in West Russia and in the Italian, Iberian and Balkan Peninsulas. Relict populations in France, Germany, Poland, Slovakia, Hungary and Romania seem to have contributed to subsequent repopulation (Apollonio et al. 2010; Scandura et al. 2008).

A third complicating factor is that of wild-domestic hybridisation and feralisation of domestic animals (Albarella et al. 2009). Wild-domestic hybridisation is potentially easily identifiable through means of molecular approaches, utilising, for example, prior knowledge of phylogeographic expectations (Scandura et al. 2008) or genotyping SNPs that are associated with domestic phenotypes (Fajardo et al. 2008; Koutsogiannouli et al. 2010). However, ten thousand years of potential hybridisation of genetically very similar wild and domestic populations, in relation to, or followed by feralisation, could lead to cryptic phylogeographic patterns easily misidentified as natural variation (Larson et al. 2005; Scandura et al. 2011a).

4.1.3 Aims and objectives

The aim and objective of this chapter is to create a deeper understanding of the processes that have shaped the genetic variability of West Eurasian wild boar. On the whole, this chapter examines the phylogenetic and phylogeographic relationships among modern contemporary wild boar in the light of the ancient genetic data presented in chapters 2 and 3. Because mitochondrial phylogeography is a common method for inferring domestication events (e.g. Giuffra et al. 2000; Larson et al.

2005), re-assessing the usefulness of that approach in the light of new research is critical.

4.2 Materials and methods

4.2.1 Samples, populations and groups

Modern mitochondrial d-loop sequences from 658 wild *Sus scrofa* from across Europe, the Near and Middle East, and North Africa were compiled (table 4.1). The data set comprises previously published data (see below) and novel sequences (table 4.1). A small sample of domestic pigs (n=32, Larson et al. 2005) was included for comparative purposes. The novel sequences were extracted from a larger unpublished data set that was sequenced at the Animal Breeding and Genomics Centre, Wageningen University in The Netherlands as part of an ongoing pig "60k SNP chip" project (Groenen et al. 2011).

The modern data set consists of small samples from local populations which together form larger, regional, putative populations representing Africa, Balkans, Iberia, West Europe, Central Europe, Russia and East Europe, Italy, Corsica, Sardina, Anatolia (Near East) and Middle East (table 4.1). The small samples of local populations are considered random samples of variation from within geographical regions. Data collection was focused on geographic regions corresponding to locations from which ancient samples were collected (Central Europe, the Balkans and the Near and Middle East, see chapter 3).

The previously published modern samples were compiled from: Alexandri et al. 2011, GenBank accession numbers JF774182-JF774393, Alves et al. 2003, GenBank accession numbers AY232868-AY232868, Alves et al. 2010, GenBank accession numbers HM747196, HM747198, HM747199, HM747201, HM747202, HM747206-HM747209, HM747211, HM747213, and HM747215, Fang and Andersson 2006, GenBank accession number DQ379232, Fang et al. 2006, GenBank accession numbers DQ379233-DQ379261, Giuffra et al. 2000, GenBank accession numbers AF136555, AF136556, AF136558 and AF136563, Gongora et al. 2003, GenBank accession numbers AF535163 and AF535164, Kijas and Andersson 2001, GenBank accession

number AF304203, Larson et al. 2005, GenBank accession numbers AY884609-AY884831, Larson et al. 2007a, GenBank accession numbers DQ872931-DQ873203, and Randi et al. 2002, GenBank accession number AJ314544.

Modern putative populations (table 4.1) from Africa (n=12) consists of wild boar from Morocco (n=1), Egypt (n=1), Sudan (n=1) and Tunisia (n=9). Modern putative populations from Balkans (n=209) consists of wild boar from Bulgaria (n=10), Macedonia (n=1), Romania (n=8), Serbia (n=6) and Greece (n=183). Modern putative populations from Central Europe (n=107) consists of wild boar from Austria (n=12), Estonia (n=1), Germany (n=14), Hungary (n=4), Poland (n=30), Slovakia (n=1), Slovenia (n=24), Sweden (n=3), and Switzerland (n=18). (Note that Sweden was included due to a lack of other samples from that region. Note also that the Estonian specimen is omitted due to too short sequence length (table 4.1)). Modern putative populations from Corsica (n=13) consists of wild and feral individuals from several locations. Modern putative populations from Italy (n=52) consists of individuals from several locations. Modern putative populations from the Middle East (n=49) consists of wild boar from Armenia (n=11), Iran (n=26), Iraq (n=5), Israel (n=5), Syria (n=2), and Turkmenistan (n=1). Modern putative populations from the Near East (n=35) consists of wild boar from Samos/Greece (n=13) and Turkey (n=22). This population is primarily Anatolian and both definitions may be used below. Modern putative populations from East Europe (n=24) consists of wild boar from Finland (n=6), Georgia (n=1), Russia (n=8) and Ukraine (n=9). Modern putative populations from Sardinia (n=18) consists of wild and feral individuals from several locations. Modern putative populations from Iberia is referred to below as *Spain* (n=50) and consists of wild boar from Portugal (n=15), Spain (n=35). Lastly, modern putative populations from West Europe (n=46) consists of wild boar from Belgium (n=7), France (n=31), and Holland (n=8).

Archaeological samples (n=256) were kept in the same spatial and temporal bins as in chapter 3: Bronze Age Balkans (BroBal, n=9), Bronze Age Central Europe (BroEu, n=31), Bronze Age Middle East (BroME, n=29), Bronze Age Near East

(BroNE, n=15), Bronze Age Russia (BroRU, n=2), Buran-Kaya 4, which is an analogue to Crimean Neolithic (n=11), Çamlibel, which is an analogue to Calcolithic Anatolia/Near East (n=13), Chalcolithic Balkans (ChaBal, n=16), Mesolithic Balkans (MesBal, n=9), Mesolithic Crimea (MesCri, n=3), Mesolithic Central Europe (MesEu, n=3), Neolithic Balkans (NeoBal, n=39), Neolithic Central Europe (NeoEUn=56), Neolithic Middle East (NeoME, n=2), and Neolithic South Europe (NeoSEU, n=16).

Note that in the ancient samples, no clear distinction is made between wild and domestic individuals due to a lack of complete (and reliable) coverage of wild/domestic determinations (chapter 3). This is further highlighted in the discussion below.

ID sample	Haplotype	Short ID	Additional ID	Full		Continent/Stat group	Country	Included	source	Clade	Accession	included	Comment
tri514	K	1ri514			Wild	Balkans	Trikala, Greece	Trikala	Alexandri et al. 2011	E1	JF774259	x	Published
ait049	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774294	x	Published
ait072	A	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774186	x	Published
ait109	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774359	x	Published
ait126	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774350	x	Published
ait127	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774320	x	Published
ait261	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774308	x	Published
ait278	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774317	x	Published
ait286	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774290	x	Published
ait297	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774312	x	Published
ait305	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774289	x	Published
ait400	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774351	x	Published
ait440	ait440	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774348	x	Published
ait500	G	ai			Wild	Balkans	Aitoloakarnania, Greece	Aitoloakarnania	Alexandri et al. 2011	E1	JF774382	x	Published
ait432	ait432	ar			Wild	Balkans	Arcadia, Greece	Arcadia	Alexandri et al. 2011	E1	JF774212	x	Published
ait435	ait435	ar			Wild	Balkans	Arcadia, Greece	Arcadia	Alexandri et al. 2011	E1	JF774211	x	Published
ait438	ait438	ar			Wild	Balkans	Arcadia, Greece	Arcadia	Alexandri et al. 2011	E1	JF774375	x	Published
ait439	C	ar			Wild	Balkans	Arcadia, Greece	Arcadia	Alexandri et al. 2011	E1	JF774233	x	Published
Blg002	BL002	BL			Wild	Balkans	Bulgaria	n/a	Alexandri et al. 2011	E1	JF774375	x	Published
Blg003	H132	BL			Wild	Balkans	Bulgaria	n/a	Alexandri et al. 2011	E1	JF774206	x	Published
Blg004	K	BL			Wild	Balkans	Bulgaria	n/a	Alexandri et al. 2011	E1	JF774276	x	Published
Blg005	K	BL			Wild	Balkans	Bulgaria	n/a	Alexandri et al. 2011	E1	JF774278	x	Published
dra001	K	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774247	x	Published
dra005	K	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774271	x	Published
dra007	K	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774256	x	Published
dra009	K	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774279	x	Published
dra012	C	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774228	x	Published
Dra015	C	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774234	x	Published
dra035	C	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774229	x	Published
dra046	C	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774236	x	Published
drm015	C	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	n/a		Published
drm027	A	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774187	x	Published
drm129	drm129	dr			Wild	Balkans	Drama, Greece	Drama	Alexandri et al. 2011	E1	JF774232	x	Published
Ebr009	Ebr009	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774284	x	Published
Ebr010	H142	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774260	x	Published
Ebr014	H141 (alt. 140)	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774214	x	Published
Ebr017	A	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774188	x	Published
Ebr018	H142	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774261	x	Published
Ebr020	ait435	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774219	x	Published
Ebr022	H142	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774262	x	Published
Ebr025	K	eb			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774272	x	Published
Ebr701	ET01	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774252	x	Published
Ebr703	K	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774281	x	Published
Ebr704	K	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774283	x	Published
Ebr705	K	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774244	x	Published
Ebr711	ET11	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774255	x	Published
Ebr715	K	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774248	x	Published
Ebr718	ET01	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774253	x	Published
Ebr721	ET21	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774207	x	Published
Ebr722	ET01	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774254	x	Published
Ebr727	K	ET			Wild	Balkans	Ebros, Greece	Ebros	Alexandri et al. 2011	E1	JF774280	x	Published
eur061	eu061	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774305	x	Published
eur062	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774303	x	Published
eur088	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774336	x	Published
eur092	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774306	x	Published
eur307	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774333	x	Published
eur308	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774355	x	Published
eur310	eu310	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774335	x	Published
eur312	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774307	x	Published
eur316	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774334	x	Published
eur480	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774284	x	Published
eur492	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774285	x	Published
eur506	G	eu			Wild	Balkans	Evritania, Greece	Evritania	Alexandri et al. 2011	E1	JF774309	x	Published
fok046	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774298	x	Published
fok050	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774354	x	Published
fok055	fo055	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774323	x	Published
fok064	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774345	x	Published
fok115	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774297	x	Published
fok116	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774324	x	Published
fok290	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774358	x	Published
fok298	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	n/a		Published
fok308	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774302	x	Published
fok450	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774329	x	Published
fok452	G	fo			Wild	Balkans	Fokida, Greece	Fokida	Alexandri et al. 2011	E1	JF774339	x	Published
fth080	G	ft			Wild	Balkans	Fthiotida, Greece	Fthiotida	Alexandri et al. 2011	E1	JF774303	x	Published
fth082	?	ft			Wild	Balkans	Fthiotida, Greece	Fthiotida	Alexandri et al. 2011	E1	n/a		Published
fth084	G	ft			Wild	Balkans	Fthiotida, Greece	Fthiotida	Alexandri et al. 2011	E1	JF774338	x	Published
fth216	G	ft			Wild	Balkans	Fthiotida, Greece	Fthiotida	Alexandri et al. 2011	E1	JF774304	x	Published
fth217	G	ft			Wild	Balkans	Fthiotida, Greece	Fthiotida	Alexandri et al. 2011	E1	JF774331	x	Published

Table 4.1: The modern specimens analysed in this chapter.

fth250	G	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774337	x	Published
fth253	H167	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774363	x	Published
fth254	H167	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774362	x	Published
fth255	G	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774344	x	Published
fth259	H167	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774364	x	Published
fth268	H167	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774365	x	Published
fth269	H167	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774366	x	Published
fth274	G	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774326	x	Published
fth505	G	ft		Wild	Balkans	Fthiotida, Greece	Fthiotida		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774342	x	Published
Hlk001	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774220	x	Published
Hlk002	H142	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774263	x	Published
Hlk003	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774221	x	Published
Hlk004	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774222	x	Published
Hlk005	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774223	x	Published
Hlk006	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774224	x	Published
Hlk007	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774225	x	Published
Hlk008	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774226	x	Published
Hlk086	H141 (alt 140)	Hl		Wild	Balkans	Halkidiki, Greece	Halkidiki		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774227	x	Published
ioa211	G	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774295	x	Published
ioa212	G	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774347	x	Published
ioa317	K	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774282	x	Published
ioa319	8K	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774193	x	Published
ioa320	I320	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774371	x	Published
ioa322	H196	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774369	x	Published
ioa405	H171	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774370	x	Published
ioa406	K	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774249	x	Published
ioa507	K	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774257	x	Published
ioa509	G	I		Wild	Balkans	Ioannina, Greece	Ioannina		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774321	x	Published
Kb001	H142	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774264	x	Published
Kb002	H141 (alt 140)	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774215	x	Published
Kb004	H142	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774265	x	Published
Kb006	H142	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774266	x	Published
Kb007	H142	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774267	x	Published
Kb012	k012	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774241	x	Published
Kb021	k021	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774289	x	Published
Kb023	H176 (alt H177)	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774376	x	Published
Kb025	kb25	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774208	x	Published
Kb026	kb26	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774374	x	Published
Kb027	H176 (alt H177)	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774377	x	Published
Kb028	K	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774273	x	Published
Kb029	kb29	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774209	x	Published
Kb030	kb30	Kb		Wild	Balkans	Kavala, Greece	Kavala		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774378	x	Published
km124	G	Ko		Wild	Balkans	Korinthos, Greece	Korinthos		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774310	x	Published
km125	C	Ko		Wild	Balkans	Korinthos, Greece	Korinthos		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774235	x	Published
lar223	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774288	x	Published
lar224	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774311	x	Published
lar225	H168 (alt. H169)	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774360	x	Published
lar226	K	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774258	x	Published
lar228	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774291	x	Published
lar230	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774318	x	Published
lar231	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774292	x	Published
lar232	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774319	x	Published
lar234	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774349	x	Published
lar235	H168 (alt. H169)	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774361	x	Published
lar513	G	la		Wild	Balkans	Larisa, Greece	Larisa		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774322	x	Published
mag222	G	ma		Wild	Balkans	Magnisia, Greece	Magnisia		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774296	x	Published
mag227	G	ma		Wild	Balkans	Magnisia, Greece	Magnisia		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774316	x	Published
mag229	ma229	ma		Wild	Balkans	Magnisia, Greece	Magnisia		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774313	x	Published
mag518	G	ma		Wild	Balkans	Magnisia, Greece	Magnisia		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774346	x	Published
mag523	ma523	ma		Wild	Balkans	Magnisia, Greece	Magnisia		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774353	x	Published
mag524	G	ma		Wild	Balkans	Magnisia, Greece	Magnisia		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774315	x	Published
pel350	pe350	pe		Wild	Balkans	Pella, Greece	Pella		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774213	x	Published
pel351	pe351	pe		Wild	Balkans	Pella, Greece	Pella		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774373	x	Published
pel352	C	pe		Wild	Balkans	Pella, Greece	Pella		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774230	x	Published
pel353	pe353	pe		Wild	Balkans	Pella, Greece	Pella		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774210	x	Published
pel354	G	pe		Wild	Balkans	Pella, Greece	Pella		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774352	x	Published
pel355	A	pe		Wild	Balkans	Pella, Greece	Pella		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774204	x	Published
Ro1001	R132	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774205	x	Published
Ro1002	C	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774238	x	Published
Ro1003	C	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774239	x	Published
Ro1006	K	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774290	x	Published
Ro1007	K	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774214	x	Published
Ro1008	H141 (alt 140)	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774216	x	Published
Ro1010	H141 (alt 140)	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774217	x	Published
Ro1012	R012	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774185	x	Published
Ro1015	K	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774277	x	Published
Ro1017	H141 (alt 140)	R		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774218	x	Published
RodT08	C	RT		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774240	x	Published
RodT09	K	RT		Wild	Balkans	Rodopi, Greece	Rodopi		Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774245	x	Published

RodT10	K	RT		Wild	Balkans	Rodopi, Greece	Rodopi	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774246	x	Published
Sam001	EF_A	Sa001		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774381	x	Published
Sam002	EF_A	Sa002		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774382	x	Published
Sam004	Sa04	Sa004		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774392	x	Published
Sam005	Sa05	Sa005		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774393	x	Published
Sam006	EF_A	Sa006		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774383	x	Published
Sam007	EF	Sa007		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774384	x	Published
Sam008	EF	Sa008		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774385	x	Published
Sam010	EF	Sa010		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774386	x	Published
Sam012	EF	Sa012		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774387	x	Published
Sam013	EF	Sa013		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774388	x	Published
Sam014	EF	Sa014		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774389	x	Published
Sam015	EF	Sa015		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774390	x	Published
Sam016	EF	Sa016		Wild	Near East	Samos, Greece	Samos	Alexandri et al. 2011	Alexandri et al. 2011	NE2	JF774391	x	Published
thp407	H167	TH		Wild	Balkans	Thesprotia, Greece	Thesprotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774372	x	Published
thp408	H167	TH		Wild	Balkans	Thesprotia, Greece	Thesprotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774373	x	Published
Th001	H142	Th		Wild	Balkans	Thessaloniki, Greece	Thessaloniki	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774367	x	Published
Th002	H142	Th		Wild	Balkans	Thessaloniki, Greece	Thessaloniki	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774369	x	Published
Th003	Th003	Th		Wild	Balkans	Thessaloniki, Greece	Thessaloniki	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774198	x	Published
Th004	H142	Th		Wild	Balkans	Thessaloniki, Greece	Thessaloniki	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774270	x	Published
th1128	Th128	Th		Wild	Balkans	Thessaloniki, Greece	Thessaloniki	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774192	x	Published
tri357	K	tr		Wild	Balkans	Trikala, Greece	Trikala	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774251	x	Published
tri359	K	tr		Wild	Balkans	Trikala, Greece	Trikala	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774275	x	Published
tri360	G	tr		Wild	Balkans	Trikala, Greece	Trikala	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774299	x	Published
voi003	voi09	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774314	x	Published
voi011	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774325	x	Published
voi013	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774343	x	Published
voi014	H192	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774286	x	Published
voi056	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774356	x	Published
voi236	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774300	x	Published
voi237	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774327	x	Published
voi242	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774357	x	Published
voi264	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774341	x	Published
voi306	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774301	x	Published
voi420	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	n/a	x	Published
voi442	G	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774340	x	Published
voi445	H192	voi		Wild	Balkans	Voiotia, Greece	Voiotia	Alexandri et al. 2011	Alexandri et al. 2011	E1	JF774287	x	Published
tr441	A	tr441		Feral	Balkans	Trikala, Greece	Trikala	Alexandri et al. 2011	Alexandri et al. 2012	E1	JF774189	x	Published
SWB1	BY	SWB1		Wild	Spain	Spain	n/a	Alves et al. 2003	Alves et al. 2003	E1	AY232868	x	Published
SWB2	BY	SWB2		Wild	Spain	Spain	n/a	Alves et al. 2003	Alves et al. 2003	E1	AY232869	x	Published
SWB3	BY	SWB3		Wild	Spain	Spain	n/a	Alves et al. 2003	Alves et al. 2003	E1	AY232870	x	Published
SWB4	CA	SWB4		Wild	Spain	Spain	n/a	Alves et al. 2003	Alves et al. 2003	E1	AY232871	x	Published
SWB5	CA	SWB5		Wild	Spain	Spain	n/a	Alves et al. 2003	Alves et al. 2003	E1	AY232872	x	Published
SWB6	E	SWB6		Wild	Spain	Spain	n/a	Alves et al. 2003	Alves et al. 2003	E1	AY232873	x	Published
SWB7	H136	SWB7		Wild	Spain	Spain	n/a	Alves et al. 2003	Alves et al. 2003	E1	AY232874	x	Published
ALH1	N	ALH1		Wild	Central Europe	Austria	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747196	x	Published
ALH11	H153	ALH11		Wild	Spain	Spain	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747206	x	Published
ALH12	K	ALH12		Wild	Spain	Spain	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747207	x	Published
ALH13	H136	ALH13		Wild	Spain	Spain	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747208	x	Published
ALH14	E	ALH14		Wild	Spain	Spain	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747209	x	Published
ALH16	BY	ALH16		Wild	Spain	Spain	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747211	x	Published
ALH18	ALH18	ALH18		Wild	Spain	Spain	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747213	x	Published
ALH20	E	ALH20		Wild	Spain	Spain	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747215	x	Published
ALH3	BK	ALH3		Wild	Spain	Portugal/France	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747198	x	Published
ALH4	H135	ALH4		Wild	Spain	Iberia	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747199	x	Published
ALH6	K	ALH6		Wild	Spain	Iberia	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747201	x	Published
ALH7	C	ALH7		Wild	Spain	Iberia	n/a	Alves et al. 2010	Alves et al. 2010	E1	HM747202	x	Published
S4	BK	S4		Wild	West Europe	France	n/a	Fang & Andersson 2006	Fang & Andersson 2006	E1	DQ379232	x	Published
Sm10	BK	F1		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379233	x	Published
Sm9	A	F10		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379253	x	Published
96	I1_G	F11		Wild	West Europe	Belgium	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379238	x	Published
105	I1_G	F12		Wild	West Europe	Belgium	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379239	x	Published
mt51	H135	F13		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379242	x	Published
mt52	H135	F14		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379243	x	Published
mt53	F15	F15		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379244	x	Published
Sm1	H135	F16		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379245	x	Published
Sm2	H135	F17		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379246	x	Published
Sm3	H135	F18		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379247	x	Published
Sm4	H135	F19		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379248	x	Published
S1	H110	F2		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379254	x	Published
Sm5	H135	F20		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379249	x	Published
Sm6	H135	F21		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379250	x	Published
Sm7	H135	F22		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379251	x	Published
Sm8	H135	F23		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379252	x	Published
	81 H147	F24		Wild	West Europe	Belgium	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379235	x	Published
	83 H147	F25		Wild	West Europe	Belgium	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379236	x	Published
	89 H147	F26		Wild	West Europe	Belgium	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379237	x	Published
	78 F27	F27		Wild	West Europe	Belgium	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379234	x	Published
	114 E	F28		Wild	West Europe	Belgium	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379241	x	Published
S2	H110	F3		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379255	x	Published
S3	H110	F4		Wild	West Europe	France	n/a	Fang et al. 2006	Fang et al. 2006	E1	DQ379256	x	Published

S6	H110	F5		Wild	West Europe	France	n/a	Fang et al. 2016	E1	DQ379257	x	Published
S7	H110	F6		Wild	West Europe	France	n/a	Fang et al. 2016	E1	DQ379258	x	Published
S8	H110	F7		Wild	West Europe	France	n/a	Fang et al. 2016	E1	DQ379259	x	Published
S9	H110	F8		Wild	West Europe	France	n/a	Fang et al. 2016	E1	DQ379260	x	Published
S10	H110	F9		Wild	West Europe	France	n/a	Fang et al. 2016	E1	DQ379261	x	Published
GiuIsraelWB	n/a	Gisr	NO gap	Wild	Middle East	Israel	n/a	Giuffra et al. 2000	E1	AF136558	x	Published
GiuItalEW83	n/a	Gita	NO gap	Wild	Italy	Italy	n/a	Giuffra et al. 2000	E2	AF136563	x	Published
GiuPolEW81	n/a	GPol1	NO gap	Wild	Central Europe	Poland	n/a	Giuffra et al. 2000	E1	AF136555	x	Published
GiuPolEW82	n/a	GPol2	NO gap	Wild	Central Europe	Poland	n/a	Giuffra et al. 2000	E1	AF136556	x	Published
GongFinnish36	AF	GFin1		Wild	Russia/Ukraine	Finland	n/a	Gongora et al. 2003	E1	AF535163	x	Published
GongFinnish41	GFin2			Wild	Russia/Ukraine	Finland	n/a	Gongora et al. 2003	E1	AF535164	x	Published
Kijas01SwedishWB	Kijan	Kijan		Wild	Central Europe	Sweden	n/a	Kijas & Anderson 2001	E1	AF304203	x	Published
FrenchWild Boar/LeiffFrench	H100	FWB		Wild	West Europe	France	n/a	Larson et al. 2005	E1		x	Published
GL144	n/a	GL144	No	Wild	Sardinia	Sardinia	Near Tempio, Gallura	Larson et al. 2005	E1		x	Published
GL224	Barbatus	GL224		Wild	Outgroup/no stat	Malaysia		Larson et al. 2005			x	Published
AF084783	A	GL013441		Wild	Central Europe	Germany	n/a	Larson et al. 2005	E1		x	Published
UDomIberiaBlack01	A	UBl1		Domestic	Spain	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace01	C	UDe1		Domestic	Denmark	Denmark	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace04	BK	U04		Domestic	Denmark	Denmark	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace05	BK	U05		Domestic	Denmark	Denmark	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace06	N	U06		Domestic	Finland	Finland	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace09	E	U09		Domestic	Iceland	Iceland	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace10	BK	U10		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace12	BK	U12		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomLandrace14	A	U14		Domestic	Domestic	Germany	n/a	Larson et al. 2005	E1		x	Published
UDomBritSaddle01	LBS1	LBS1		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UCorsicaB2 - feral	BK	UCB2		Feral	Corsica	Corsica	n/a	Larson et al. 2005	E1		x	Published
UDomDuroc02	A	UDur2		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomGermanyAngler	E1_H	UGA		Domestic	Domestic	Germany	n/a	Larson et al. 2005	E1		x	Published
UDomGermBunter01	A	UGBu1		Domestic	Domestic	Germany	n/a	Larson et al. 2005	E1		x	Published
UDomHampshire01	A	UHa1		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomHampshire02	BK	UHa2		Domestic	Domestic	Germany	n/a	Larson et al. 2005	E1		x	Published
UDomSwedLinderod01	E1_C	Linder		Domestic	Domestic	Sweden	n/a	Larson et al. 2005	E1		x	Published
UDomLeicomel01	A	LL01		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomBritLop01	BK	LW01		Domestic	Domestic	Europe	n/a	Larson et al. 2005	E1		x	Published
UDomMeishan01_Jiangkai01	BK	UMei1		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomMeiNan01	A	UMW1		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomNegroCanaria01	E1_F	UNC1		Domestic	Domestic	Spain	n/a	Larson et al. 2005	E1		x	Published
UDomNegroCanaria12	E1_F	UNC12		Domestic	Domestic	Spain	n/a	Larson et al. 2005	E1		x	Published
UDomPietrain03	R	UP03		Domestic	Domestic	Germany	n/a	Larson et al. 2005	E1		x	Published
UDomPietrain04	E1_G	UP04		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomPietrain05	A	UP05		Domestic	Domestic	France	n/a	Larson et al. 2005	E1		x	Published
UDomPortBisaro01	A	UPB1		Domestic	Domestic	Portugal	n/a	Larson et al. 2005	E1		x	Published
USardinia88 - feral	BK	USa88		Feral	Sardinia	Sardinia	n/a	Larson et al. 2005	E1		x	Published
UDomLargeWhite05	A	UW05		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
UDomLargeWhite06	LW06	UW06		Domestic	Domestic	United Kingdom	n/a	Larson et al. 2005	E1		x	Published
GL220 - feral	Y2_A	GL220		Feral	Corsica	Corsica	Alta Roca	Larson et al. 2005	NE2		x	Published
GL284 - feral	A	GL284		Feral	Corsica	Corsica	Alta Roca	Larson et al. 2005	E1		x	Published
GL285 - feral	A	GL285		Feral	Corsica	Corsica	Alta Roca	Larson et al. 2005	E1		x	Published
GL110 - feral	A	GL110		Feral	Corsica	Corsica	Corsica	Larson et al. 2005	E1		x	Published
GL71	AU	GL71		Wild	West Europe	France	Cote D'Or, Ile-sur-Tille	Larson et al. 2005	E1		x	Published
GL252	A	GL252		Wild	Italy	Italy	Florence	Larson et al. 2005	E1		x	Published
GL143 - feral	BK_D	GL143		Feral	Corsica	Corsica	Leve	Larson et al. 2005	E1		x	Published
GL287 - feral	A	GL287		Feral	Corsica	Corsica	Leve	Larson et al. 2005	E1		x	Published
GL244 - feral	BK	GL244		Feral	Corsica	Corsica	Maremma Region	Larson et al. 2005	E1		x	Published
GL245	BH	GL245		Wild	Italy	Italy	Maremma Region	Larson et al. 2005	E2		x	Published
GL246	BH	GL246		Wild	Italy	Italy	Maremma Region	Larson et al. 2005	E2		x	Published
GL247	BG	GL247		Wild	Italy	Italy	Maremma Region	Larson et al. 2005	E2		x	Published
GL248	BG	GL248		Wild	Italy	Italy	Maremma Region	Larson et al. 2005	E2		x	Published
GL249	BG	GL249		Wild	Italy	Italy	Maremma Region	Larson et al. 2005	E2		x	Published
GL250	BH	GL250		Wild	Italy	Italy	Maremma Region	Larson et al. 2005	E2		x	Published
GL251	BH	GL251		Wild	Italy	Italy	Maremma Region	Larson et al. 2005	E2		x	Published
GL77	GL77			Wild	Middle East	Iran	Mazanderon, 25km East of Gorgon	Larson et al. 2005	East Asian		x	Published
GL107	GL107			Wild	Central Europe	Germany	n/a	Larson et al. 2005	E1		x	Published
GL108	A	GL108		Wild	Central Europe	Germany	n/a	Larson et al. 2005	E1		x	Published
GL109	C	GL109		Wild	Central Europe	Germany	n/a	Larson et al. 2005	E1		x	Published
GL112	A	GL112		Wild	West Europe	Holland	n/a	Larson et al. 2005	E1		x	Published
GL113	K	GL113		Wild	Balkans	Macedonia	n/a	Larson et al. 2005	E1		x	Published
GL133 - feral	n/a	GL133		Feral	None	Norway	n/a	Larson et al. 2005	E1		x	Published
GL141	A	GL141		Wild	Middle East	Armenia	n/a	Larson et al. 2005	E2		x	Published
GL142	BQ	GL142		Wild	Middle East	Armenia	n/a	Larson et al. 2005	NE2		x	Published
GL190 - feral	GL190			Feral	Sardinia	Sardinia	n/a	Larson et al. 2005	E1		x	Published
GL193	BQ_A	GL193		Wild	Middle East	Armenia	n/a	Larson et al. 2005	NE2		x	Published
GL194	BQ_A	GL194		Wild	Middle East	Armenia	n/a	Larson et al. 2005	NE2		x	Published
GL221	H153	GL221		Wild	Spain	Spain	n/a	Larson et al. 2005	E1		x	Published
GL222	H135	GL222		Wild	Spain	Portugal	n/a	Larson et al. 2005	E1		x	Published
GL236	BQ	GL236		Wild	Middle East	Armenia	n/a	Larson et al. 2005	NE2		x	Published
GL242	SP	GL242		Wild	Spain	Spain	n/a	Larson et al. 2005	E1		x	Published
GL254	EO	GL254		Wild	Middle East	Iran	n/a	Larson et al. 2005	NE1		x	Published
GL270	EJ	GL270		Wild	Middle East	Armenia	n/a	Larson et al. 2005	NE1		x	Published
GL271	BQ	GL271		Wild	Middle East	Armenia	n/a	Larson et al. 2005	NE2		x	Published

GL288 - feral	A	GL288			Feral	Sardinia	Sardinia	n/a	Larson et al. 2005	E1		x		Published
GL52	n/a	GL52		No	Wild	Spain	Spain	n/a	Larson et al. 2005	E1		x		Published
GL55	TU	GL55			Wild	Near East	Turkey	n/a	Larson et al. 2005	NE2		x		Published
GL59	9Q	GL59			Wild	Middle East	Iran	n/a	Larson et al. 2005	NE2		x		Published
GL73	C	GL73			Wild	Africa	Morocco	n/a	Larson et al. 2005	E1		x		Published
GL286 - feral	GL286	GL286			Feral	Corsica	Corsica	Ota	Larson et al. 2005	E1		x		Published
GL111 - feral	A	GL111			Feral	Sardinia	Sardinia	Sardinia	Larson et al. 2005	E1		x		Published
GL65 - feral	I1_A	GL65			Feral	Sardinia	Sardinia	Sinnai, Cagliari	Larson et al. 2005	E2		x		Published
GL289 - feral	BK	GL289			Feral	Sardinia	Sardinia	Uzzulei, Ogliastra	Larson et al. 2005	E1		x		Published
GL1009	EK		1009		Wild	Middle East	Turkmenistan	n/a	Larson et al. 2007	East Asian		x		Published
GL1040	BK		1040		Domestic		Cyprus	n/a	Larson et al. 2007	E1		x		Published
GL1041	A		1041		Domestic		Cyprus	n/a	Larson et al. 2007	E1		x		Published
GL374	E1_A	GL374			Wild	Balkans	Romania	n/a	Larson et al. 2007	E1		x		Published
GL392	N (alt. C in ref)	GL392			Wild	Balkans	Romania	n/a	Larson et al. 2007	E1		x		Published
GL724	n/a	GL724		80bp	Wild	Central Europe	Estonia	Nestaurm'in Tallinn	Larson et al. 2007	E1				Published
GL748	n/a	GL748		NO gap	Wild	Middle East	Syria	Amouk Plains	Larson et al. 2007	NE2		x		Published
GL749	n/a	GL749			Wild	Central Europe	Poland	Jeziorki near Bialowieza* National Park	Larson et al. 2007	E1		x		Published
GL750	GL750	GL750			Wild	Middle East	Iraq	Idil, Bardarat	Larson et al. 2007	NE2		x		Published
GL751	n/a	GL751		NO gap	Wild	Middle East	Iraq	Baghdad, 3 mi S	Larson et al. 2007	NE1		x		Published
GL752	EF	GL752			Wild	Middle East	Iran	Fars, Yasuj, 10.9 mi SW	Larson et al. 2007	NE2		x		Published
GL753	GL753	GL753			Wild	Middle East	Iran	Kermanshahan Kermanshah	Larson et al. 2007	E1		x		Published
GL754	EF_A	GL754			Wild	Near East	Turkey	Mersin (Icel) Tarsus Forest	Larson et al. 2007	NE2		x		Published
GL766	n/a	GL766		80bp	Wild	Middle East	Iraq	Diyala, Khanaquin, 10 mi from; Rhamaila	Larson et al. 2007	E1				Published
GL767	n/a	GL767		80bp	Wild	Middle East	Iraq	Amouk Plains	Larson et al. 2007	NE1				Published
GL768	n/a	GL768		80bp	Wild	Middle East	Syria	Amouk Plains	Larson et al. 2007	NE2				Published
GL769	EF	GL769			Wild	Middle East	Iran	Esfahan, Kuh Rang	Larson et al. 2007	NE2		x		Published
GL771	EP	GL771			Wild	Middle East	Iran	Fars, Yasuj	Larson et al. 2007	NE1		x		Published
GL779	A	GL779			Wild	Middle East	Iraq	As Sulaymaniyah; Darband area, Zagros Mt	Larson et al. 2007	E1		x		Published
GL781	EP	GL781			Wild	Middle East	Iran	Kermanshahan	Larson et al. 2007	NE1		x		Published
GL782	n/a	GL782		80bp	Wild	Middle East	Iran	Khuristan, Ahwaz-Andimeshk	Larson et al. 2007	NE1				Published
GL783	EO	GL783		80bp	Wild	Middle East	Iran	Khuristan, Ahwaz-Andimeshk	Larson et al. 2007	NE1		x		Published
GL784	n/a	GL784		80bp	Wild	Middle East	Iraq	Khuristan, Ahwaz-Andimeshk	Larson et al. 2007	NE1				Published
GL786	n/a	GL786		80bp	Wild	Middle East	Syria	Amouk Plains	Larson et al. 2007	NE2				Published
GL787	n/a	GL787		80bp	Wild	Middle East	Iran	Esfahan, Kuh Rang	Larson et al. 2007	East Asian		x		Published
GL788	EK	GL788			Wild	Middle East	Iran	Mazandaran, Sarra	Larson et al. 2007	NE2				Published
GL789	EK	GL789			Wild	Middle East	Iran	Nikalu	Larson et al. 2007	East Asian		x		Published
GL790	n/a	GL790		80bp	Wild	Middle East	Iran	Mazandaran, Gorgan	Larson et al. 2007	NE2		x		Published
GL791	EG	GL791			Wild	Middle East	Iran	Mazandaran, Gorgan	Larson et al. 2007	East Asian		x		Published
GL792	EG	GL792			Wild	Middle East	Iran	Sistan and Baluchistan, Zabol	Larson et al. 2007	East Asian		x		Published
GL793	GL793	GL793			Wild	Middle East	Iran	Sistan and Baluchistan, Zabol	Larson et al. 2007	East Asian		x		Published
GL794	GL794	GL794			Wild	Middle East	Iran	Sistan and Baluchistan, Zabol	Larson et al. 2007	East Asian		x		Published
GL795	n/a	GL795		80bp	Wild	Middle East	Iran	Sistan and Baluchistan, Zabol	Larson et al. 2007	East Asian				Published
GL799	C	GL799			Wild	Balkans	Romania	Dubova, Iron Gates	Larson et al. 2007	E1		x		Published
GL912	8Q	GL912			Wild	Middle East	Iran	NW Persia	Larson et al. 2007	NE2		x		Published
GL918	GL918	GL918			Wild	Russia/Ukraine	Russia	Volga Delta	Larson et al. 2007	E1		x		Published
GL919	C	GL919			Wild	Russia/Ukraine	Russia	Volga Delta	Larson et al. 2007	E1		x		Published
GL935	n/a	GL935		NO gap	Wild	Russia/Ukraine	West Caucasus, north slope	n/a	Larson et al. 2007	E1		x		Published
GL940	EF_A	GL940		NO gap	Wild	Near East	Turkey	Smyrna (Izmir)	Larson et al. 2007	NE2		x		Published
GL942 - domestic	n/a	GL942			Wild	Domestic	Sudan	Nuba	Larson et al. 2007	NE1		x		Published
GL943	GL943	GL943			Wild	Africa	Egypt	n/a	Larson et al. 2007	NE1		x		Published
GL944	EJ	GL944			Wild	Russia/Ukraine	Georgia	Kavkaz from tiflis (Tbilisi)	Larson et al. 2007	NE1		x		Published
GL945	N	GL945			Wild	Central Europe	Slovakia	n/a	Larson et al. 2007	E1		x		Published
GL946	9K	GL946			Wild	Central Europe	Hungary	n/a	Larson et al. 2007	E1		x		Published
GL948 - unknown	n/a	GL948			Wild	Balkans	Greece Kos	n/a	Larson et al. 2007	E1		x		Published
GL949 - unknown	n/a	GL949		80bp	Wild	Balkans	Bulgaria	n/a	Larson et al. 2007	E1				Published
GL951	n/a	GL951		NO gap	Wild	Balkans	Bulgaria	n/a	Larson et al. 2007	E1		x		Published
GL952 - wild?	GL952	GL952			Wild	Africa	Sudan	n/a	Larson et al. 2007	NE2		x		Published
GL959	EL	GL959			Domestic	Domestic	Sardinia	n/a	Larson et al. 2007	E1		x		Published
GL960	EL	GL960			Domestic	Domestic	Sardinia	n/a	Larson et al. 2007	E1		x		Published
GL961	EL	GL961			Domestic	Domestic	Sardinia	n/a	Larson et al. 2007	E1		x		Published
RandiSus3	A	RSus3			Wild	Sardinia	Sardinia	n/a	Randi et al. 2002	E1	AJ314544	x		Published
PORHAP02277	BK	BD001	SSBD001		Wild	Balkans	Romania	Basarabi, Constanta County	This study	dr. Gregor Larson,Durham | E1				Unpublished
PORHAP03131	BK	BD002	SSBD002		Wild	Balkans	Romania	Basarabi, Constanta County	This study	Gregor	E1			Unpublished
PORHAP02278	C	BD003	SSBD003		Wild	Russia/Ukraine	Russia	Russian Fed, Il'enko village	This study	dr. Gregor Larson,Durham | E1				Unpublished
PORHAP03132	C	BD005	SSBD005		Wild	Russia/Ukraine	Ukraine	Lugansk Region, Milova district	This study	Gregor	E1			Unpublished
PORHAP03133	AF	BD007	SSBD007		Wild	Russia/Ukraine	Ukraine	Lugansk Region, Trotck district on Russian	This study	Gregor	E1			Unpublished
PORHAP02281	C	BD008	SSBD008		Wild	Russia/Ukraine	Ukraine	Lugansk Region, Stanichno-Luganskiy distric	This study	Gregor	E1			Unpublished
PORHAP02282	C	BD009	SSBD009		Wild	Russia/Ukraine	Ukraine	Lugansk Region, Lutugino district	This study	Gregor	E1			Unpublished
PORHAP02283	AF	BD010	SSBD010		Wild	Russia/Ukraine	Ukraine	Lugansk Region, near Alchevsk city	This study	Gregor	E1			Unpublished
PORHAP02284	AF	BD011	SSBD011		Wild	Russia/Ukraine	Ukraine	Lugansk Region, Belovodsk district	This study	Gregor	E1			Unpublished
PORHAP03134	C	BD012	SSBD012		Wild	Russia/Ukraine	Ukraine	Lugansk Region, Kremmna district	This study	Gregor	E1			Unpublished
PORHAP03135	BK	BD013	SSBD013		Wild	Central Europe	Poland	Trechel bei Neugard	This study	Gregor	E1			Unpublished
PORHAP03136	n/a	BD014	SSBD014	No	Wild	Central Europe	Poland	Bialowies	This study	Gregor				Unpublished
PORHAP03137	n/a	BD015	SSBD015	No	Wild?	Africa	Tanzania	Tanzeno	This study	Gregor				Unpublished
PORHAP03138	n/a	BD016	SSBD016	No	Wild	Balkans	Serbia	Serbia	This study	Gregor				Unpublished
PORHAP03139	n/a	BD017	SSBD017	No	Wild	Russia/Ukraine	Russia	Kalkasus	This study	Gregor				Unpublished
PORHAP03140	n/a	BD018	SSBD018	No	Wild	Russia/Ukraine	Russia	Derbens, Caspian Sea	This study	Gregor				Unpublished
PORHAP03141	C	BD019	SSBD019		Wild	Russia/Ukraine	Russia	north of Moscow	This study	Gregor	E1			Unpublished
PORHAP03142	n/a	BD020	SSBD020	No	Wild	Russia/Ukraine	Russia	north of Moscow	This study	Gregor				Unpublished
PORHAP02288	A	BD027	SSBD027		Domestic	Domestic	Egypt	Cairo	This study	dr. Gregor Larson,Durham | E1				Unpublished
PORHAP03146	C	BD028	SSBD028		Domestic	Domestic	Egypt	Cairo	This study	dr. Gregor Larson,Durham | E1				Unpublished

PORHAP02289	K5	BJD029	SSBDD029		Domestic	Egypt	Cairo	This study	dr. Gregor Larson, Durham | E1			Unpublished
PORHAP02290	E	BJD030	SSBDD030		Domestic	Egypt	Cairo	This study	dr. Gregor Larson, Durham | E1			Unpublished
PORHAP03165	n/a	BJD054	SSBDD054	No	Wild	Middle East	Israel	na	dr. Gregor Larson, Durham | E1			Unpublished
PORHAP02860	C	K10	SSWB49F03		Wild	Central Europe	Austria	lower Austria	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02116	A	K100	SSWB40F11		Wild	Central Europe	Germany	Kirchhellen; Wilkebadiesen	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02117	A	K101	SSWB40M03		Wild	Central Europe	Germany	Kirchhellen; Stadtlohn	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02124	A	K102	SSWB41U31		Wild	Central Europe	Germany	Landau; Kestert	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02125	A	K103	SSWB41M02		Wild	Central Europe	Germany	Landau; Niedernhesen	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02127	A	K104	SSWB41M04		Wild	Central Europe	Germany	Landau; Neuweid, Stadt	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02132	A	K105	SSWB41M05		Wild	Central Europe	Germany	Landau; Lahnstein, Stadt	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02133	A	K106	SSWB41F01		Wild	Central Europe	Germany	Landau; Niederrisen	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02134	BK	K107	SSWB41F02		Wild	Central Europe	Germany	Landau; Zweibr¿cken, Stadt	This study	Dr. Richard Croojimans, A|E1		Unpublished
PORHAP02913	A	K108	SSWB64U01		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02914	A	K109	SSWB64U02		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02861	H135	K11	SSWB62F02		Wild	Central Europe	Austria	periphery of Vienna	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02915	C	K110	SSWB64U03		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02916	A	K111	SSWB64U04		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02917	A	K112	SSWB64U05		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02918	C	K113	SSWB64U06		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02919	H135	K114	SSWB64U07		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02920	C	K115	SSWB64U08		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02921	H135	K116	SSWB64U09		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02922	C	K117	SSWB64U10		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP02925	H135	K118	SSWB64U13		Wild	Central Europe	Poland	east poland	This study	katarzyna Chabros, national E1		Unpublished
PORHAP01263	C	K119	SSWB36M02		Wild	Central Europe	Hungary	N.hlik Andr s	This study	Miguel Perez-Enciso,Dept. C E1		Unpublished
PORHAP02862	E1_B	K12	SSWB62F03		Wild	Central Europe	Austria	periphery of Vienna	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP03007	K120	K120	SSWB36M03		Wild	Central Europe	Hungary	N.hlik Andr s	This study	Miguel Perez-Enciso,Dept. C E1		Unpublished
PORHAP03008	C	K121	SSWB36M04		Wild	Central Europe	Hungary	N.hlik Andr s	This study	Miguel Perez-Enciso,Dept. C E1		Unpublished
PORHAP00345	A	K122	SSWB26M01		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00346	A	K123	SSWB26M02		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00348	G	K124	SSWB26M03		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00349	C	K125	SSWB26M04		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00350	G	K126	SSWB26M05		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00351	BG	K127	SSWB26M06		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E2		Unpublished
PORHAP00352	E1_E	K128	SSWB26M07		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00353	E1_E	K129	SSWB26M08		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00863	E1_B	K13	SSWB62M03		Wild	Central Europe	Austria	periphery of Vienna	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP00354	E1_D	K130	SSWB26M09		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00356	BG	K131	SSWB26M10		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E2		Unpublished
PORHAP00359	A	K132	SSWB26M11		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP00362	E1_D	K133	SSWB26M13		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP02207	E1_E	K134	SSWB26M14		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP02208	BG	K135	SSWB26M15		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E2		Unpublished
PORHAP02209	E1_D	K136	SSWB26M16		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP02210	BG	K137	SSWB26M17		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E2		Unpublished
PORHAP02216	E1_E	K138	SSWB26M18		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP02218	C	K139	SSWB26M19		Wild	Central Europe	Switzerland	The Maicantone region	This study	Sem Genini, Parco technolo E1		Unpublished
PORHAP02864	N	K14	SSWB49M01		Wild	Central Europe	Austria	Lower Austria	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP01527	A	K140	SSWB39U02		Wild	Middle East	Israel	na	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP01528	A	K141	SSWB39U03		Wild	Middle East	Israel	na	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP01530	A	K142	SSWB39U05		Wild	Middle East	Israel	na	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP01531	A	K143	SSCOU03		Wild	Corsica	Corsica	Corsica, local	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP01532	A	K144	SSCOU05		Wild	Corsica	Corsica	Corsica, local	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP01533	A	K145	SSCOU07		Wild	Corsica	Corsica	Corsica, local	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP01534	E1_D	K146	SSCOU08		Wild	Corsica	Corsica	Corsica, local	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP01535	E1_D	K147	SSCOU09		Wild	Corsica	Corsica	Corsica, local	This study	dr. Gregor Larson, Durham | E1		Unpublished
PORHAP00249	A_D	K148	SSWB42M09		Wild	Italy	Italy	San Rossore, Pisa	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP00250	K149	K149	SSWB28M02		Wild	Sardinia	Sardinia	Sardinia, Campanedda , Sassari	This study	dr. Massimo Scandura,depa E2		Unpublished
PORHAP02865	H153	K15	SSWB62M04		Wild	Central Europe	Austria	periphery of Vienna	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP00251	EL	K150	SSWB28M03		Wild	Sardinia	Sardinia	Sardinia, Villasalto	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP00252	I1_A	K151	SSWB28U01		Wild	Sardinia	Sardinia	Sardinia, Muravera	This study	dr. Massimo Scandura,depa E2		Unpublished
PORHAP00384	BH	K152	SSWB42F01		Wild	Italy	Italy	San Rossore, Pisa	This study	dr. Massimo Scandura,depa E2		Unpublished
PORHAP01682	BK	K153	SSWB44M01		Wild	Italy	Italy	Arezzo, Tuscany	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP01683	H135	K154	SSWB44F01		Wild	Italy	Italy	Arezzo, Tuscany	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP01684	H135	K155	SSWB44M02		Wild	Italy	Italy	Arezzo, Tuscany	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02817	BK	K156	SSWB44M04		Wild	Italy	Italy	Arezzo, Tuscany	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02818	BK	K157	SSWB44M05		Wild	Italy	Italy	Arezzo, Tuscany	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02819	BK	K158	SSWB44F02		Wild	Italy	Italy	Arezzo, Tuscany	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02802	A	K159	SSWB42M01		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02866	N	K16	SSWB49F04		Wild	Central Europe	Austria	Lower Austria	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02803	A	K160	SSWB42M02		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02804	A	K161	SSWB42F02		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02805	A	K162	SSWB42M03		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02806	A	K163	SSWB42M04		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02807	A	K164	SSWB42M04		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02808	A	K165	SSWB42F04		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02809	A	K166	SSWB42U03		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02810	A	K167	SSWB42M05		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02811	A	K168	SSWB42F05		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02812	A	K169	SSWB42M08		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,depa E1		Unpublished
PORHAP02867	E1_B	K17	SSWB62M05		Wild	Central Europe	Austria	periphery of Vienna	This study	dr. Massimo Scandura,depa E1		Unpublished

PORHAP02813	A	K170	SSWB42M06		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02814	A	K171	SSWB42M07		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02815	A	K172	SSWB42F06		Wild	Italy	Italy	San Rossore	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02820	BK	K173	SSWB60U01		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02821	BK	K174	SSWB60U02		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02822	K175	K175	SSWB60U03		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02823	H135	K176	SSWB60U04		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02824	BK	K177	SSWB60U05		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02825	K179	K178	SSWB60U06		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02826	K179	K179	SSWB60U07		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02868	N	K18	SSWB49M02		Wild	Central Europe	Austria	Lower Austria	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02827	H135	K180	SSWB60U08		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02828	BG	K181	SSWB60U09		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E2		Unpublished
PORHAP02829	K179	K182	SSWB60U10		Wild	Italy	Italy	Cilento	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02830	E1_D	K183	SSWB45M03		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02831	E1_D	K184	SSWB45M04		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02832	E1_D	K185	SSWB45M05		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02833	E1_D	K186	SSWB45M06		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02835	E1_D	K187	SSWB45M08		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02836	E1_D	K188	SSWB45M09		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02837	E1_D	K189	SSWB45M10		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02869	BK	K19	SSWB62F04		Wild	Central Europe	Austria	periphery of Vienna	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02839	E1_D	K190	SSWB45M11		Wild	Italy	Italy	Goriția	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02873	E	K191	SSWB52U04		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02874	E	K192	SSWB52U05		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02875	E	K193	SSWB52U06		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02876	E	K194	SSWB52U07		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02877	E	K195	SSWB52U08		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02878	E	K196	SSWB52U09		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02879	E	K197	SSWB52U10		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02880	E	K198	SSWB52U11		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02881	E	K199	SSWB52U12		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP01715	EL	K2	SSPF96U01		Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP00365	E1_I	K20	SSWB23U07		Wild	Spain	Portugal	na	Deodália Dias, PhD,Universi E1			Unpublished
PORHAP02882	E	K200	SSWB52U13		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02884	E	K202	SSWB52U14		Wild	Spain	Spain	Coto Donana	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP00379	H153	K203	SSWB52U15		Wild	Spain	Spain	Asturias	This study	Miguel Perez-Ericko Dept. C E1		Unpublished
PORHAP00380	E	K204	SSWB27M01		Wild	Spain	Spain	Asturias	This study	Miguel Perez-Ericko Dept. C E1		Unpublished
PORHAP00383	K	K205	SSWB27M02		Wild	Spain	Spain	Cuenca	This study	Miguel Perez-Ericko Dept. C E1		Unpublished
PORHAP02840	C	K206	SSWB47U05		Wild	Central Europe	Poland	south-east	This study	dr. Massimo Scandura,dept E1		Unpublished
A2_WB47U01	C	K2107	SSWB47U01		Wild	Central Europe	Poland	south-east	This study	dr. Massimo Scandura,dept E1		Unpublished
B2_WB47U02	C	K2108	SSWB47U02		Wild	Central Europe	Poland	south-east	This study	dr. Massimo Scandura,dept E1		Unpublished
C2_WB47U03	N	K2109	SSWB47U03		Wild	Central Europe	Poland	south-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP00372	E1_I	K21	SSWB23U14		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
D2_WB47U04	N	K210	SSWB47U04		Wild	Central Europe	Poland	south-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP00374	E1_I	K22	SSWB23U16		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP00375	H136	K23	SSWB23U17		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP00376	H136	K24	SSWB23U18		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP00377	E1_J	K25	SSWB23U19		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP00378	SP	K26	SSWB23U20		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP01241	E1_I	K27	SSWB23U01		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP01242	E1_I	K28	SSWB23U02		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP01243	A1_I	K29	SSWB23U03		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP01716	EL	K3	SSPF96U03		Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP01244	E1_I	K30	SSWB23U04		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP01245	H136	K31	SSWB23U05		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP01246	E1_J	K32	SSWB23U06		Wild	Spain	Portugal	na	This study	Deodália Dias, PhD,Universi E1		Unpublished
PORHAP00329	E1_C	K33	SSWJ59U01		Wild	Central Europe	Sweden	na	This study	Department of medical Bio E1		Unpublished
PORHAP00330	BK	K34	SSWB59U02		Wild	Central Europe	Sweden	na	This study	Department of medical Bio E1		Unpublished
PORHAP00314	H135	K35	SSWB25U02		Wild	West Europe	France	Deux Serves	This study	Dr. Alain Duvro, Production E1		Unpublished
PORHAP00315	A	K36	SSWB25U03		Wild	West Europe	France	Deux Serves	This study	Dr. Alain Duvro, Production E1		Unpublished
PORHAP00316	H135	K37	SSWB25U04		Wild	West Europe	France	Deux Serves	This study	Dr. Alain Duvro, Production E1		Unpublished
PORHAP00317	H135	K38	SSWB25U05		Wild	West Europe	France	Deux Serves	This study	Dr. Alain Duvro, Production E1		Unpublished
PORHAP00319	H135	K39	SSWB25U07		Wild	West Europe	France	Deux Serves	This study	Dr. Alain Duvro, Production E1		Unpublished
PORHAP01717	K4	K4	SSPF96U03		Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP00326	H135	K40	SSWB25U14		Wild	West Europe	France	Deux Serves	This study	Dr. Alain Duvro, Production E1		Unpublished
PORHAP00328	H135	K41	SSWB25U16		Wild	West Europe	France	Deux Serves	This study	Dr. Alain Duvro, Production E1		Unpublished
PORHAP01427	E1_C	K42	SSWB43U04		Wild	Russia/Ukraine	Finland	na	This study	Dr. Jaime Gorgoro, REPROC E1		Unpublished
PORHAP01428	AF	K43	SSWB43U05		Wild	Russia/Ukraine	Finland	na	This study	Dr. Jaime Gorgoro, REPROC E1		Unpublished
PORHAP02841	C	K44	SSWB61U01		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02843	H135	K45	SSWB61U03		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02844	C	K46	SSWB61U04		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02846	C	K47	SSWB61U05		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02847	H135	K48	SSWB61U07		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02848	H135	K49	SSWB61U08		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP01718	K5	K5	SSPF96U04		Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02849	C	K50	SSWB61U09		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02850	C	K51	SSWB61U10		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02851	C	K52	SSWB61U11		Wild	Central Europe	Poland	north-east	This study	dr. Massimo Scandura,dept E1		Unpublished
PORHAP02947	AF	K53	SSWB46U05		Wild	Russia/Ukraine	Finland	na	This study	Dr. pekka Uimari, erikoistut E1		Unpublished

PORHAP02948	AF	K54	SSWB46U06	Wild	Russia/Ukraine	Finland	na	This study	Dr. pekka Ulmali, erikoistut	E1			Unpublished
PORHAP02135	C	K55	SSWB58U01	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02136	C	K56	SSWB58U02	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02137	C	K57	SSWB58U03	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02138	C	K58	SSWB58U04	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02139	C	K59	SSWB58U05	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP01720	K	K6	SSFP56U06	Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,depa	E1			Unpublished
PORHAP02146	C	K60	SSWB58U06	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02147	C	K61	SSWB58U07	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02148	N	K62	SSWB58U08	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02149	C	K63	SSWB58U09	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02151	C	K64	SSWB58U11	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02152	C	K65	SSWB58U12	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02153	N	K66	SSWB58U13	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02154	C	K67	SSWB58U14	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02155	C	K68	SSWB58U15	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP01721	A	K69	SSFP56U07	Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,depa	E1			Unpublished
PORHAP02966	E1_D	K7	SSFP56U07	Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,depa	E1			Unpublished
PORHAP02967	E1_D	K70	SSWB65U05	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02968	E1_D	K71	SSWB65U06	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02970	E1_D	K72	SSWB65U07	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02973	E1_D	K73	SSWB65U09	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02977	E1_D	K74	SSWB65U12	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02978	AF	K75	SSWB65U16	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02979	E1_D	K76	SSWB65U17	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP02981	E1_D	K77	SSWB65U18	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP00338	BK	K78	SSWB65U20	Wild	Central Europe	Slovenia	na	This study	Dr. Peter Dovž,Slovenia	E1			Unpublished
PORHAP01722	EL	K79	SSWB32F02	Wild	West Europe	Holland	Meinweg; Roerdalen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP00339	BK	K8	SSFP56U08	Wild	Sardinia	Sardinia	Sardinia	This study	dr. Massimo Scandura,depa	E1			Unpublished
PORHAP00340	BK	K80	SSWB32F03	Wild	West Europe	Holland	Meinweg; Roerdalen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP00341	BK	K81	SSWB32F04	Wild	West Europe	Holland	Meinweg; Roerdalen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP00342	BK	K82	SSWB32F05	Wild	West Europe	Holland	Meinweg; Roerdalen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP00343	BK	K83	SSWB32M03	Wild	West Europe	Holland	Meinweg; Roerdalen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP00344	BK	K84	SSWB32M04	Wild	West Europe	Holland	Meinweg; Roerdalen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP00257	BK	K85	SSWB32M05	Wild	West Europe	Holland	Meinweg; Roerdalen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP01845	A	K86	SSRO415	Wild	Balkans	Romania	Dubova	This study	Gregor Larson	E1			Unpublished
PORHAP01846	BK	K87	SSRO416	Wild	Balkans	Romania	Dubova	This study	Gregor Larson	E1			Unpublished
PORHAP01845	H132	K88	SSWB53F01	Wild	Balkans	Bulgaria	Burgas	This study	Professor Costas Triantaphy	E1			Unpublished
PORHAP01846	K	K89	SSWB53F02	Wild	Balkans	Bulgaria	Burgas	This study	Professor Costas Triantaphy	E1			Unpublished
PORHAP02858	E1_B	K9	SSWB62M02	Wild	Central Europe	Austria	periphery of Vienna	This study	dr. Massimo Scandura,decal	E1			Unpublished
PORHAP01847	H132	K90	SSWB53F03	Wild	Balkans	Bulgaria	Burgas	This study	Professor Costas Triantaphy	E1			Unpublished
PORHAP01848	K	K91	SSWB53F04	Wild	Balkans	Bulgaria	Burgas	This study	Professor Costas Triantaphy	E1			Unpublished
PORHAP01849	K	K92	SSWB53F05	Wild	Balkans	Bulgaria	Burgas	This study	Professor Costas Triantaphy	E1			Unpublished
PORHAP01850	BK	K93	SSWA02U01	Wild	Balkans	Serbia	Vojvodina province	This study	prof. Dr. Vesna Milicevie, hi	E1			Unpublished
PORHAP01851	C	K94	SSWB54U02	Wild	Balkans	Serbia	Vojvodina province	This study	prof. Dr. Vesna Milicevie, hi	E1			Unpublished
PORHAP01852	C	K95	SSWB54U03	Wild	Balkans	Serbia	Vojvodina province	This study	prof. Dr. Vesna Milicevie, hi	E1			Unpublished
PORHAP01853	C	K96	SSWB54U04	Wild	Balkans	Serbia	Kolubara District	This study	prof. Dr. Vesna Milicevie, hi	E1			Unpublished
PORHAP01854	C	K97	SSWB54U05	Wild	Balkans	Serbia	central Serbia	This study	prof. Dr. Vesna Milicevie, hi	E1			Unpublished
PORHAP02114	A	K98	SSWB40M02	Wild	Central Europe	Germany	kirchhellen; Bielefeld	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
PORHAP02115	A	K99	SSWB40F10	Wild	Central Europe	Germany	Kirchhellen;Wiebadessen	This study	Dr. Richard Croojimans, ABK	E1			Unpublished
Northeast AR	A	NEAR		Wild	Middle East	Armenia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBKO 3562	C	RO3562		Wild	Balkans	Romania	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
TK 107	TU	TK 107		Wild	Near East	Turkey	n/a	This study	Miguel Perez unpublished	NE2	Remaining TK's	x	Unpublished
TK 119	TU	TK 119		Wild	Near East	Turkey	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
TK 126	TU	TK 126		Wild	Africa East	Tunisia	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
WBTN 959	TN1	TN959		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBTN 960	TN1	TN960		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBTN 961	TN1	TN961		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBTN 962	TN1	TN962		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBTN 963	TN1	TN963		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBTN 964	TN2	TN964		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
WBTN 965	TN1	TN965		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBTN 966	TN1	TN966		Wild	Africa	Tunisia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
Tp1	A	Tp1		Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	E1		x	Unpublished
Tp10	TP10	Tp10		Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp11	TU	Tp11		Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp12	TU	Tp12		Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp2	TU	Tp2		Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp3	n/a	Tp3	NO gap	Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp4	n/a	Tp4	NO gap	Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp5	n/a	Tp5	NO gap	Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp6	n/a	Tp6	NO gap	Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp7	TU	Tp7		Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp8	TU	Tp8		Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
Tp9	n/a	Tp9	NO gap	Wild	Near East	Turkey	n/a	This study	Helen Everett unpublished	NE2		x	Unpublished
WBTR 514	A	TR514		Wild	Near East	Turkey	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBTR 515	TR	TR515		Wild	Near East	Turkey	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
WBTR 516	TR	TR516		Wild	Near East	Turkey	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
WBTR 517	TR	TR517		Wild	Near East	Turkey	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
WBUA 1267	C	U1267		Wild	Russia/Ukraine	Ukraine	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
WBUA 1268	C	U1268		Wild	Russia/Ukraine	Ukraine	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished

AR 2	N			Wild	Middle East	Armenia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
AR 298	AR 298			Wild	Middle East	Armenia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
East AR	East_AR			Wild	Middle East	Armenia	n/a	This study	Miguel Perez unpublished	E1		x	Unpublished
IR 1	BQ			Wild	Middle East	Iran	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
IR 2	BQ			Wild	Middle East	Iran	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
IR 4	BQ			Wild	Middle East	Iran	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
IR 5	BQ			Wild	Middle East	Iran	n/a	This study	Miguel Perez unpublished	NE2		x	Unpublished
Wat99ItW81	BH		WAT1	Wild	Italy	Italy	n/a	Watanobe et al. 1999	Watanobe et al. 1999	E2	AB015094	x	Published
Wat99ItW83	BG		WAT2	Wild	Italy	Italy	n/a	Watanobe et al. 1999	Watanobe et al. 1999	E2	AB015095	x	Published

4.2.2 Phylogeny

Sequences were aligned in Geneious v5.5.4 (Drummond et al. 2011) using MAFFT (Katoh et al. 2002). Alignments were subsequently adjusted in length to fit the 486bp amplified in ancient specimens (chapter 3). The adjusted fragment corresponds to nucleotide positions 15520-16026 in the reference mitochondrion DNA sequence AJ002189 (Ursing and Arnason 1998), omitting conserved bases in positions 15594-15613 for which no ancient DNA is available (chapter 3). Haplogroup and haplotype assignment was performed using previously published modern sequences as references (table 4.1).

The nucleotide substitution model was estimated using MrModeltest 2.3 (Nylander 2004) and PAUP* 4.0 (Swofford 2000) as implemented in MrMtGui (Nuin 2010). The best-fit model using both aLRT (approximate likelihood-ratio test) statistics and AIC (Akaike Information Criteria) was HKY+I+G.

Phylogentic analysis was performed on a collapsed data set of 152 unique haplotypes representing 874 samples (including the ancient sequences from chapter 3). A *Sus barbatus*, the Bornean bearded pig, was used as an outgroup (Genbank accession number AY884699).

A Maximum Likelihood tree was constructed in Geneious v5.5.4 (Drummond et al. 2011) using PhyML (Guindon et al. 2010). On every possible tree, a Maximum Likelihood method optimises model parameters and branch lengths to obtain a maximum likelihood estimate. The maximum likelihood tree is the tree topology that gives the highest likelihood under the given model (Guindon et al. 2010). Topology and node support was estimated using the aLRT statistic as estimated using both the SH-like support (Shimodaira-Hasegawa-like procedure, Shimodaira and Hasewaga 1999) and the chi-square-based interpretation (Guindon et al. 2010).

Secondly, a phylogenetic tree was constructed using Bayesian inference in MrBayes 3.2.0 (Ronquist et al. 2011). MrBayes is a model-based framework that estimates

the posterior probability of model parameters using Markov Chain Monte Carlo (MCMC) methods; the MCMC methods effectively search tree space (the probability landscape over which all possible tree topologies are represented) in a step wise or generational manner until it reach an optimal peak in the probability landscape (until the sampling reaches stationary). MrBayes was run for 20,000,000 generations using 2x cold chains with 2x4 corresponding warm chains. Diagnostic frequencies (the *diagnfreq* function) were recorded every 200,000 generations. The standard deviation of split frequencies (a similarity measure between the two cold chains and associated samples) was 0,0107, which is characteristic of good mixing and indicative of well supported topologies (Ronquist et al. 2011). As a further control to ensure that the posterior distribution was optimally sampled, the *sump* (summarise parameters) command (discarding 25% of the sample as burn-in) was used: the PSRF+ values of all parameters were close to 1,0 (0.999-1,007) which is in agreement with optimal sampling (Ronquist et al. 2011). The *sumt* command was used to output a tree annotated with posterior probabilities for each node, discarding 25% of the samples as burn-in. This tree was processed in FigTree (http://tree.bio.ed.ac.uk/software/figtree/).

The phylogenetic relationship among NE2 clade haplotypes was also assessed using a median-joining (MJ) network that was constructed in NETWORK 4.6 (Bandelt et al. 1999). The purpose of the MJN is to assess whether the Y1/Y2 dichotomy (as haplogroup designations) is phylogenetically valid.

4.2.3 Genetic diversity

Summary genetic statistics were calculated for each putative population: the number of haplotypes (Nei 1987), haplotype (gene) diversity (H, Nei 1987), and nucleotide diversity (π, Nei 1987). These were calculated in DNAsp version 5 (Librado and Rozas 2009).

4.2.4 Population structure over time and space

Hierarchical AMOVA (Analysis of Molecular VAriance) and population pairwise Φ_{ST}'s were calculated in Arlequin v3.5.1.3 (Excoffier et al. 2005) using 10,000 permutations of sequences among populations to test for significance of covariance components and fixation indices (Φ_{ST}, Φ_{CT} and Φ_{SC}). Φ_{ST} is an analogue to conventional F_{ST} (Wright 1951) but with the difference that it incorporates both haplotype frequencies and distances between haplotypes (Excoffier et al. 1992). Distances between haplotypes were inferred from a distance matrix of pairwise differences. P-values for the population pairwise Φ_{ST}'s were adjusted using Bonferroni correction.

AMOVA is used to assess correlations among haplotype distances at a variety of hierarchical levels with the aim to estimate the genetic structure among populations. Φ_{ST} is equal to the correlation of randomly drawn haplotypes within a group of populations relative to that of haplotypes drawn from the global population. Φ_{CT} is equal to the correlation of randomly drawn haplotypes within a group of populations (groups of populations are defined by the person conducting the analysis) relative to those in the global population. Φ_{SC} is equal to the correlation of randomly drawn haplotypes within populations relative to those drawn within a grouping of populations: it measures the proportion of variation among populations within each group. The grouping of populations that maximise Φ_{CT} values, and is significantly different from random distribution of individuals, is generally assumed to reflect the most probable subdivisions. The subdivisions (or groups) can be geographical or temporal (Excoffier et al. 1992; Dalén et al. 2007).

The population pairwise Φ_{ST}'s were analysed in a non-metric MDS (Multi Dimensional Scaling) plot in the Past software (Hammer et al. 2001). The MDS method attempts to place the data points in a two-dimensional coordinate system while preserving their original ranked differences. The ranked differences are the ranked order of the distances between data points (or populations). If, for example, popula-

tion 2 and 5 have the 7th largest distance among all populations, those populations will ideally be placed so that their Euclidean distance (automatically transformed original distance) in the 2D plane (MDS plot) is still preserved. This method is implemented to visualise the global population pairwise Φ_{ST} among ancient and modern populations. In addition, linear regressions of average geographic distances (estimated using the country in each group that contained the highest number of individual specimens and www.distancefromto.net/countries.php) and population pairwise Φ_{ST}'s were performed to make a crude assessment of how genetic variation is distributed across space (similar to isolation-by-distance, Wright 1943).

4.2.5 Demographic analysis

BEAST (Bayesian Evolutionary Analysis by Sampling Trees) is a Bayesian framework in which MCMC (Markov Chain Monte Carlo) analysis is implemented for testing evolutionary hypotheses: BEAST uses MCMC to average over tree space so that each tree is weighted proportional to its posterior probability (Drummond and Rambaut 2007). BEAST v1.7.4 (Drummond and Rambaut 2007) was first used to estimate the nucleotide substitution rate in units of substitutions/site/year and to reconstruct effective population size (*Ne*) through time using the full ancient DNA data set from chapter 3. In addition, regional demographic analyses were carried out for: (1) the Balkans (pooled ancient and modern data), (2) the Near and Middle East (pooled ancient and modern data), and (3) Central and West Europe (pooled ancient and modern data). Effective female population size at different time points were estimated from the lineage coalescent rate through time using the Skyride model (Minin et al. 2008) (see further details below).

The full ancient DNA data set used to estimate the nucleotide substitution rate consists of 254 individual 486bp mtDNA sequences (or, in some instances, a shorter fragment due to missing data) (data from chapter 3). These sequences correspond to individual specimens for which a haplotype (column 5, *haplotype*) is specified in

table 3.1. Two specimens were removed from the analyses due to missing sequence data (more than one of six fragments missing). The mutation rate estimates were calibrated using the ages of the specimens/sequences. These were obtained by direct radiocarbon dating or through an estimation based on stratigraphic association. The stratigraphic associations and relative ages of the specimens were provided by the archaeozoologists who provided samples. A mean age was calculated for each sequence for which no direct radiocarbon date was available (e.g. LG217 is an Azerbaijani specimen stratigraphically dated to the Bronze Age. This specimen has a date estimate of 3,300-1,200 BC, which corresponds to approximately 5,300-3,200 YBP. The average date is therefore approximately 4,250 YBP). For specimens ambiguously labeled Bronze/Iron Age (or similar), the average age of the remaining specimens dated to those periods, from that geographic region, was used. The regional data sets were constructed as follows: (1) Balkans (280 taxa of which 73 were ancient, time-stamped, sequences), (2) Near and Middle East (127 taxa of which 58 were ancient, time-stamped, sequences), and (3) Central and West Europe (245 taxa of which 100 were ancient, time-stamped, sequences). The geographical bin to which each specimen belongs to is specified in table 3.1 and table 4.1.

The input files were generated in BEAUti version 1.7.4 (Drummond and Rambaut 2007). The BEAST analyses were performed using the estimated nucleotide substitution model (HGY+I+G, see above). The analyses used a strict clock, a random starting tree, empirical base frequencies, an age-dependent error model accounting for transitions only (assuming that Type 2 errors, see figure 2.5, are the most common errors, if any) using the default uniform prior, a default uniform prior on the clock rate parameter, and the tree prior for estimating the root height parameter (TMRCA).

BEAST was first run using only ancient sequences in order to estimate the nucleotide substitution rate and to assess global (among all populations) trajectory of effective population size through time. Two demographic coalescent models were implemented: *constant population size* that assumes a population under a constant ef-

fective population size (*Ne*) (Drummond and Rambaut 2007), and *Bayesian Skyride Plot* (Minin et al. 2008), which estimates effective population sizes (*Ne*) over time. The latter method decides on how many time points to estimate *Ne* based on the individual data set, unlike the Bayesian Skyline plot method in which the user predefines the number of temporal bins over which *Ne* is estimated (Minin et al. 2008). All BEAST results were analysed in Tracer v1.5 (Rambaut and Drummond 2007). Bayes factors were calculated through estimating the harmonic mean of the sampled marginal likelihood. This method was used to determine which demographic model best fitted the data. These were calculated in Tracer v1.5 using the likelihood trace. Analyses were run for 80 million generations (for the ancient data set) or 40 million generations (for the pooled, regional, data sets). Analyses were run at least twice (but sometimes more) to control for consistency between runs, but only one run was used in the final analyses. Efficiency of parameter estimation was assessed using ESS (effective sample size). 25% of the samples were discarded as burn-in.

4.3 Results

Of the 658 compiled modern DNA sequences (table 4.1) 618 (of which 266 is previously unpublished) were suitable for analysis. The remaining sequences (n=40) were either geographical outliers (e.g. GL133 which is the only specimen from Norway) or not fully matching the 486bp fragment obtained from the ancient specimens (chapter 3).

4.3.1 Phylogeny

The 486bp region of mitochondrial DNA control region surveyed in ancient wild and domestic pigs (n=255) from the Near and Middle East, Balkans, and East, Central and South Europe, modern wild boar or feral pigs from Africa, Balkans, Central Europe, Corsica, Italy, Middle East, Near East, Russia/Ukraine/Finland, Sardinia, Spain and West Europe (n=586), and a selection of domestic pigs (n=32) revealed a total of 152 haplotypes (but up to 160, including some sequences for which there are ambiguities or minor missing data, table 4.1). The ancient specimens were not divided into wild or domestic subsections because the status determinations are incomplete (see chapter 3). The haplotype terminology follows Larson et al. (2005; 2007a), where haplotypes are defined first according to their 80bp ANC1 fragment haplotype, which in turn is used to define haplogroups corresponding to supported clades in a phylogeny (Larson et al. 2007a) (but see a detailed explanation in chapter 3).

The phylogenetic reconstruction of the 152 haplotypes revealed a topology near identical to that published by Larson et al. (2005; 2007a, chapter 2) (figure 4.2). Nodes with poor support or inconsistent groupings between tree building methods were collapsed. See Appendix A for a full list of unique haplotypes (table 3.1 and 4.1).

The median-joining network of NE2 clade haplotypes sheds light on the issue concerning the Y1/Y2 dichotomy (chapter 3). Although the intra-clade relationship among haplotypes in NE2 remains unresolved, with several plausible evolutionary pathways between Y1 haplotypes and Y2 haplotypes, there is clustering among groups of Y1 and Y2 haplotypes, respectively (figure 4.3). One discrepancy between Y1/Y2 is observed in that the haplotype EF A (Y2) is identical to haplotype EF (Y1) apart from the 5/6-mononucleotide indel that separate Y1 from Y2 (a situation identical to that of ancient Y2 haplotype aM and a single individual, LG098, which display the Y1 indel but retains the rest of the aM haplotype, chapter 3, figure 4.3). (The EF A haplotype is only encountered in modern wild boar from Samos (Alexandri et al. 2011) and western Turkey (Larson et al. 2007a)). Intra-clade variability therefore indicates homoplasy at the indel used for differentiating ANC1 haplotypes Y1 and Y2 (Larson et al. 2007a). Lastly, a very small number of wild boar possessing East Asian lineages (not shown in phylogenetic tree) were observed in the Eastern most part of the Middle East (Larson et al. 2005) (table 4.1).

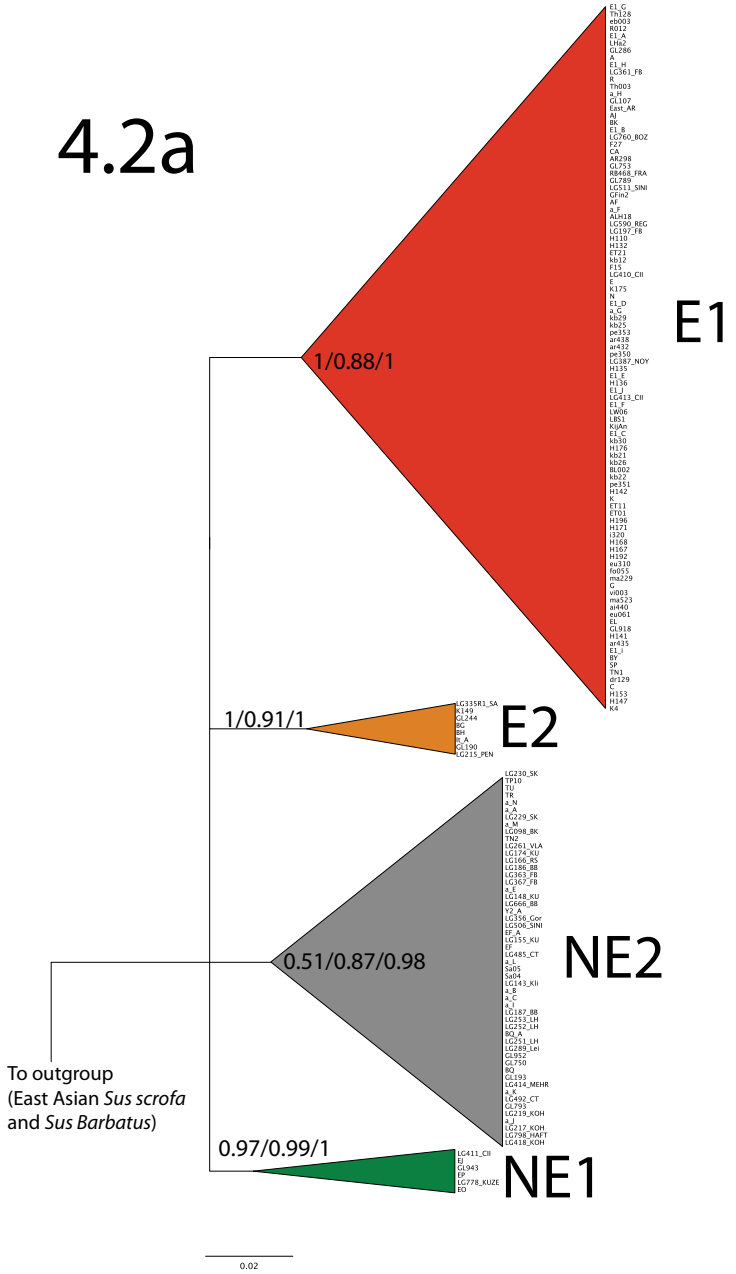
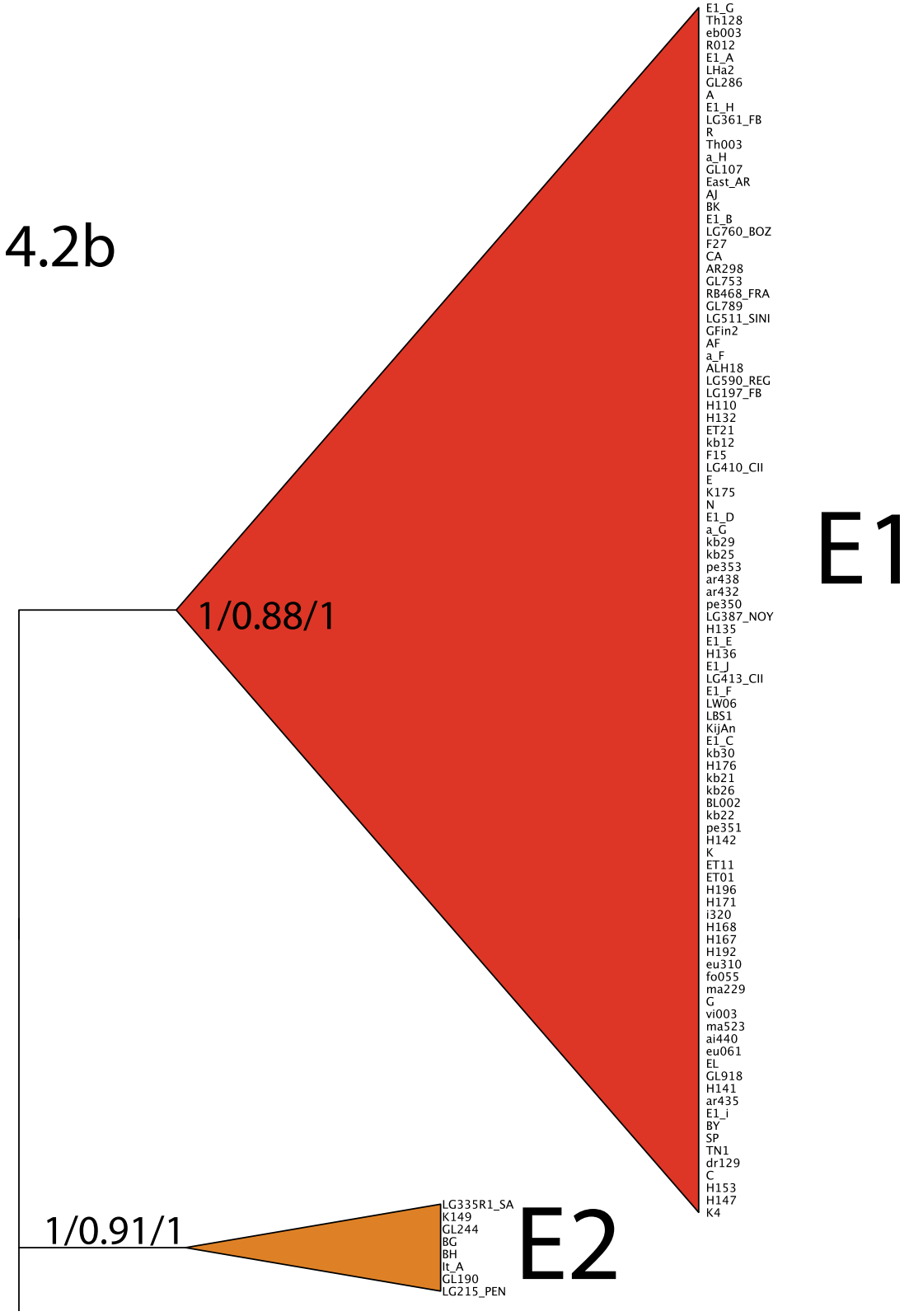
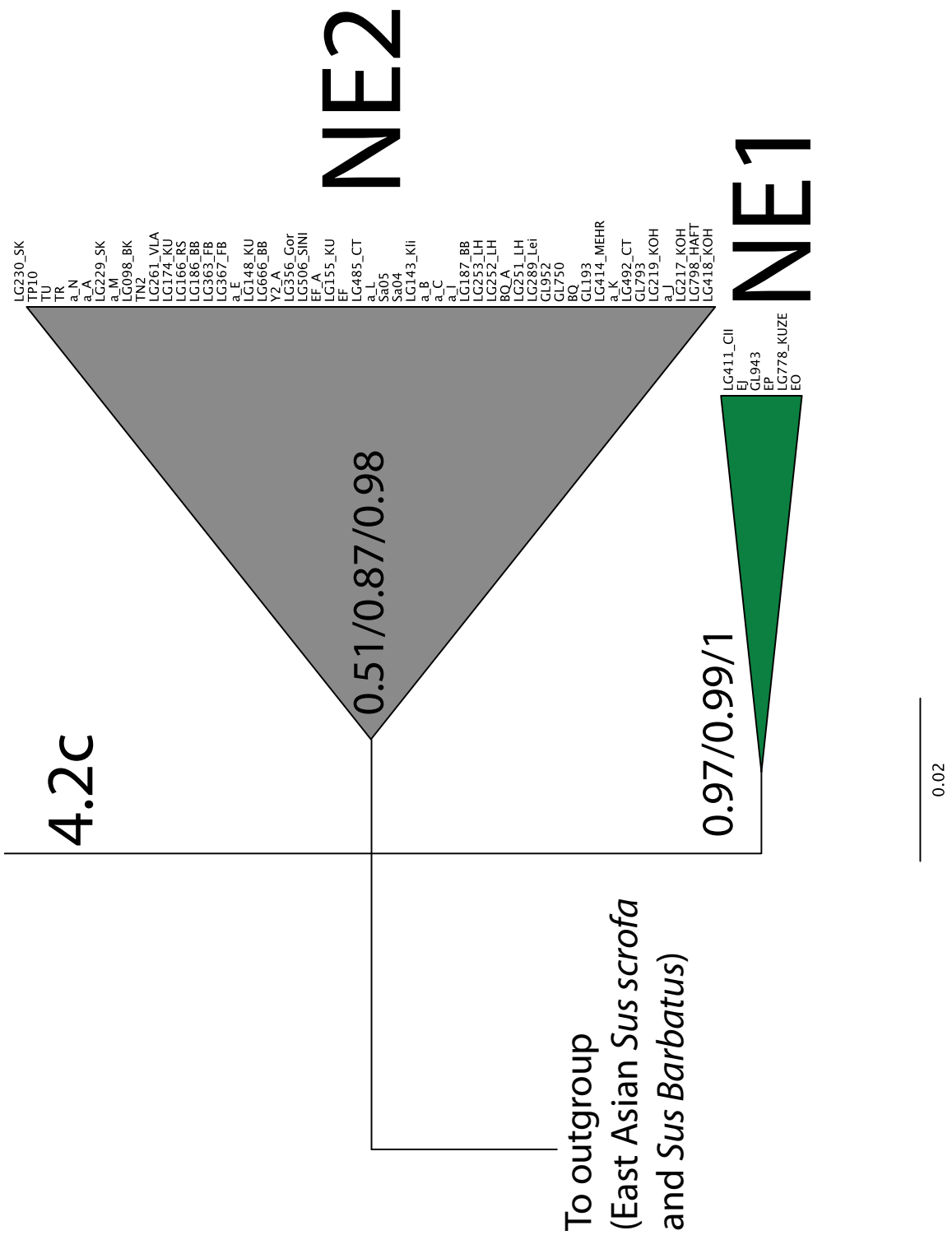


Figure 4.2: a: Phylogenetic tree constructed of the 152 unique haplotypes found in the global (ancient and modern) data. Nodal support values represent those obtained in MrBayes (posterior probability) and PhyML (SH-like and chi-square), respectively. The colour codes correspond to the colour codes used in figure 2.4. A magnified version (figure 4.2b and 4.2c) is depicted on the following two pages.


4.2b
1/0.88/1
E1_G
Th128
eb003
R012
E1_A
LHa2
GL286
A
E1_H
LG361_FB
R
Th003
a_H
GL107
East_AR
AJ
BK
E1_B
LG760_BOZ
F27
CA
AR298
GL753
RB468_FRA
GL789
LG511_SINI
GFin2
AF
a_F
ALH18
LG590_REG
LG197_FB
H110
H132
ET21
kb12
F15
LG410_CII
E
K175
N
E1_D
a_G
kb29
kb25
pe353
ar438
ar432
pe350
LG387_NOY
H135
E1_E
H136
E1_J
LG413_CII
E1_F
LW06
LBS1
KijAn
E1_C
kb30
H176
kb21
kb26
BL002
kb22
pe351
H142
K
ET11
ET01
H196
H171
i320
H168
H167
H192
eu310
fo055
ma229
G
vi003
ma523
ai440
eu061
EL
GL918
H141
ar435
E1_i
BY
SP
TN1
dr129
C
H153
H147
K4
E1
1/0.91/1
LG335R1_SA
K149
GL244
BG
BH
It_A
GL190
LG215_PEN
E2


NE2
NE1
4.2c
0.51/0.87/0.98
0.97/0.99/1
LG230_SK
TP10
TU
TR
a_N
a_A
LG229_SK
a_M
LG098_BK
TN2
LG261_VLA
LG174_KU
LG166_RS
LG186_BB
LG363_FB
LG367_FB
a_E
LG148_KU
LG666_BB
Y2_A
LG356_Gor
LG506_SiNI
EF_A
LG155_KU
EF
LG485_CT
a_L
Sa05
Sa04
LG143_Kli
a_B
a_C
a_I
LG187_BB
LG253_LH
LG252_LH
BQ_A
LG251_LH
LG289_Lei
GL952
GL750
BQ
GL193
LG414_MEHR
a_K
LG492_CT
GL793
LG219_KOH
a_J
LG217_KOH
LG798_HAFT
LG418_KOH
LG411_CII
EJ
GL943
EP
LG778_KUZE
EO
To outgroup
(East Asian Sus scrofa
and Sus Barbatus)
0.02

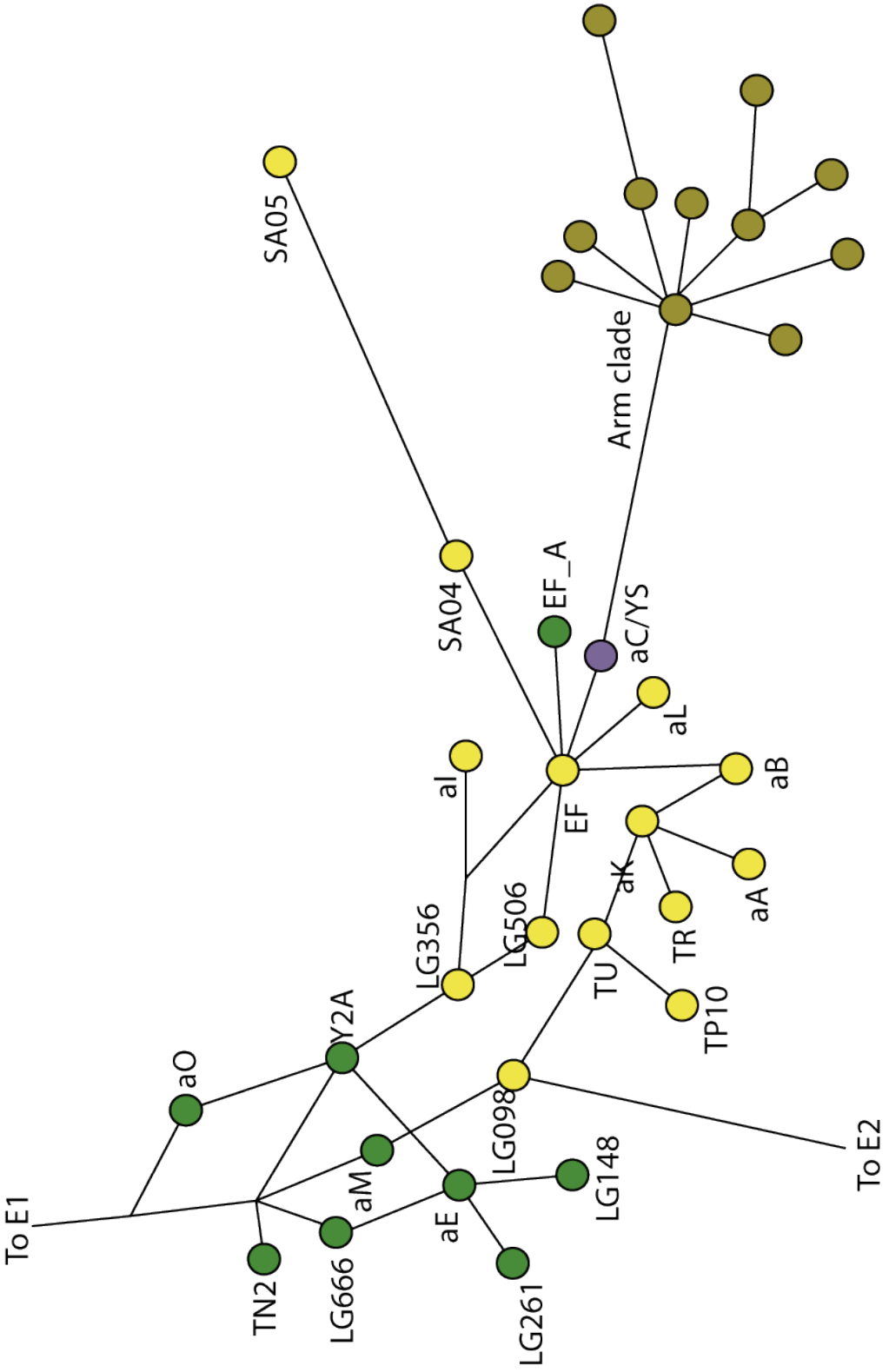


Figure 4.3: MJN of NE2 clade haplotypes. Only Y1 and Y2 haplotypes are named (and the novel YS). Green = Y2, Yellow = Y1, Purple = YS.

4.3.2 Genetic diversity

Results for H and π is displayed in table 4.2. The relationship between H and π is depicted in figure 4.4.

	n	Hap	H	VarH	s.d.	Pi	s.d.
Africa	15	8	0.79	0.01101	0.105	0.012314	0.00337
Balkans	207	24	0.753	0.00035	0.019	0.003882	0.00017
BroBal	9	2	0.222	0.02764	0.166	0.000457	0.00034
BroEU	31	8	0.839	0.00111	0.033	0.00339	0.00032
BroME	29	6	0.7	0.00406	0.064	0.00341	0.00116
BroNE	15	8	0.876	0.00354	0.06	0.011782	0.00118
BroRU	2	2	1	0.25	0.5	0.004115	0.00206
BuranKaya	11	1	0	0	0	0	0
Camlibel	13	2	0.513	0.00675	0.082	0.004247	0.00068
CentralEU	99	17	0.839	0.00065	0.025	0.006558	0.00093
ChaBal	16	7	0.75	0.01148	0.107	0.006082	0.00185
Corsica	13	6	0.821	0.00668	0.082	0.004601	0.00122
Domestic	32	12	0.827	0.00288	0.054	0.003421	0.00047
Italy	51	9	0.841	0.00086	0.029	0.013008	0.00145
MesBal	9	6	0.833	0.016	0.127	0.012241	0.00281
MesCri	3	1	0	0	0	0	0
MesEU	4	4	1	0.03125	0.177	0.010653	0.00391
MiddleEast	36	21	0.93	0.00102	0.032	0.0184	0.00127
NearEast	33	6	0.742	0.00212	0.046	0.008726	0.00148
NeoBal	39	9	0.872	0.0004	0.02	0.010352	0.00086
NeoEU	56	14	0.857	0.0009	0.03	0.009175	0.00068
NeoME	2	2	1	0.25	0.5	0.004107	0.00205
NeoSEU	16	6	0.833	0.00313	0.056	0.012584	0.00155
RussiaUkraine	20	6	0.7	0.00539	0.073	0.005398	0.00168
Sardinia	17	9	0.89	0.00293	0.054	0.011829	0.00222
Spain	49	13	0.858	0.00128	0.036	0.004833	0.00037
WestEU	46	10	0.808	0.00133	0.036	0.005789	0.0003

Table 4.2: Nucleotide diversity indices for the modern putative populations and ancient samples (see section 4.2.1).

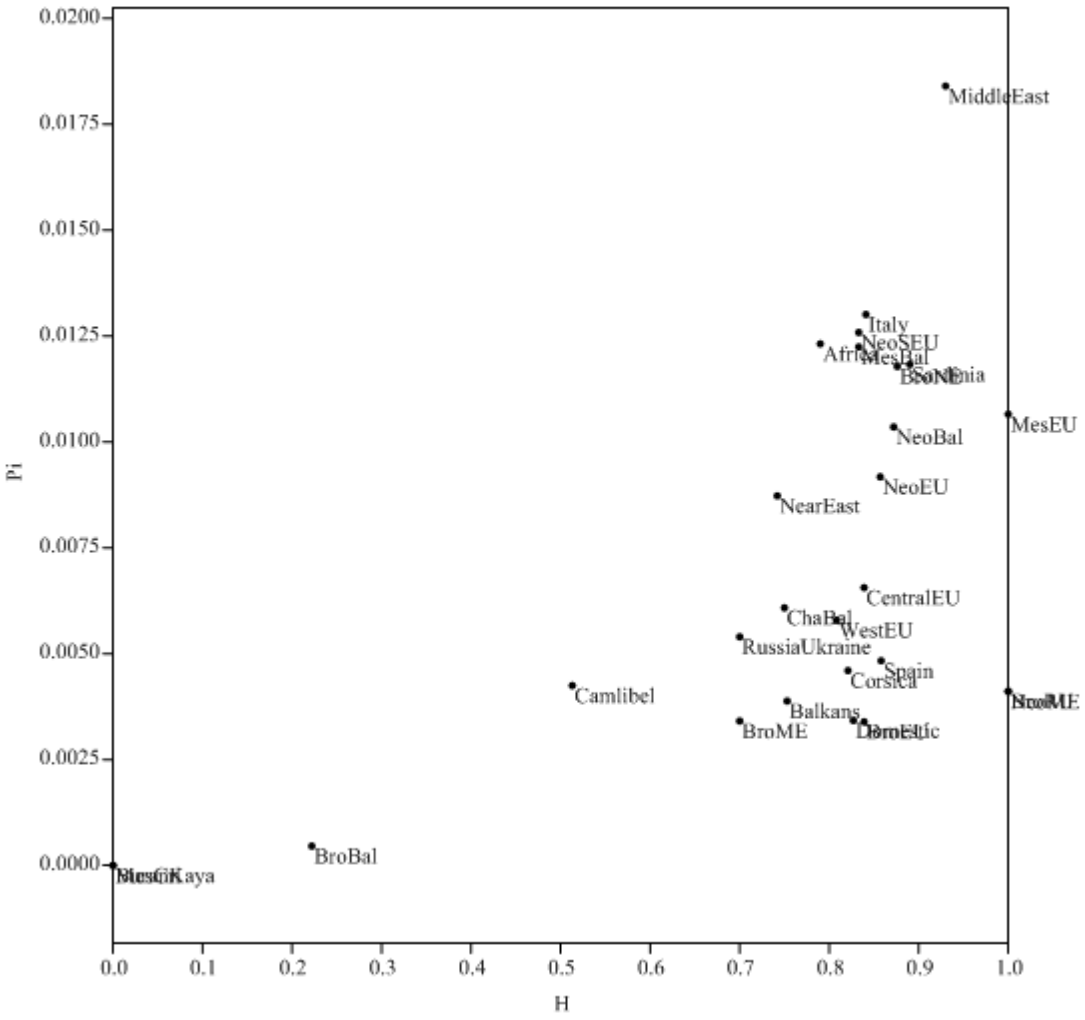


Figure 4.4: Relationship between π and H.

4.3.3 AMOVA

Results from AMOVA is displayed in table 4.3 and population pairwise Φ_{ST} in table 4.4.

Structure tested	Source of variation	φ Statistics		P-values	Variation (%) explained
Global West Eurasia modern (no groups)	Among populations	φST =	0.309	<0.001	30.94
	Within populations				69.06
Two groups (Europe vs. non-Europe)	Among groups	φCT =	0.319	<0.01	31.92
	Among populations within groups	φSC =	0.212	<0.001	14.43
	Within populations	φST =	0.463	<0.001	53.65
Global only Europe (no groups)	Among populations	φST =	0.206	<0.001	20.55
	Within populations				79.45
Four groups (1:Ru, Bal 2:CEU, WEU 3:Iberia 4: Co, Sa, It)	Among groups	φCT =	0.116	<0.05	11.69
	Among populations within groups	φSC =	0.111	<0.001	9.87
	Within populations	φST =	0.215	<0.001	78.43
Global West Eurasia Modern and Ancient		φST =	0.395	<0.001	39.47
					60.53
Two groups (Ancient vs. Modern)	Among groups	φCT =	0.127	<0.5	12.68
	Among populations within groups	φSC =	0.355	<0.001	30.96
	Within populations	φST =	0.436	<0.001	56.36
Global Balkans (no groups)	Among populations	φST =	0.522	<0.001	52.23
	Within populations				47.77
Two Groups (Ancient vs. Modern)	Among groups	φCT =	0.226	>0.10	22.58
	Among populations within groups	φSC =	0.397	<0.001	30.74
	Within populations	φST =	0.533	<0.001	46.68
Three groups (1:Mes, Neo, Cha 2: BA 3: Modern)	Among groups	φCT =	0.453	>0.05<0.10	45.34
	Among populations within groups	φSC =	0.153	<0.01	8.34
	Within populations	φST =	0.537	<0.001	46.32
Four groups (1: Mes 2: Neo, Cha 3: Bro 4: Modern)	Among groups	φCT =	0.493	>0.05<0.10	49.33
	Among populations within groups	φSC =	0.075	>0.10	3.78
	Within populations	φST =	0.531	<0.001	46.89
Four groups (1: Mes, Neo 2: Cha 3: Bro 4: Modern)	Among groups	φCT =	0.422	>0.10	42.16
	Among populations within groups	φSC =	0.181	<0.05	10.5
	Within populations	φST =	0.527	<0.001	47.35
Global Near/Middle East (no groups)	Among populations	φST =	0.268	<0.001	26.84
	Within populations				73.16
Two Groups (Ancient vs. Modern)	Among groups	φCT =	0.117	>0.10	11.73
	Among populations within groups	φSC =	0.206	<0.001	18.21
	Within populations	φST =	0.299	<0.001	70.06
Three groups (1: Neol, Chal 2: Bronze 3: Modern)	Among groups	φCT =	0.052	>0.10	5.22
	Among populations within groups	φSC =	0.239	<0.001	22.61
	Within populations	φST =	0.278	<0.001	72.18
Global Europe Ancient and Modern	Among populations	φST =			13.52
	Within populations				86.48
Two Groups (Ancient vs. Modern)	Among groups	φCT =	0.049	>0.10	4.92
	Among populations within groups	φSC =	0.105	<0.001	10.02
	Within populations	φST =	0.149	<0.001	85.06
Three groups (1: Mes, Neol 2: Bronze 3: Modern)	Among groups	φCT =	0.122	>0.05<0.10	12.23
	Among populations within groups	φSC =	0.044	<0.05	3.84
	Within populations	φST =	0.161	<0.001	83.93

Table 4.3: Results from AMOVA. See description of groups in section 4.2.1.

Population	MesBal	MesCri	MesEU	NeoBal	NeoEU	NeoME	NeoSEU	ChaBal	BroBal	BroEU	BroME	BroNE	BroRU	BuranKaya	Camlibel	Africa	Balkans	CentralEurope	Corsica	Domestic	Italy	MiddleEast	NearEast	RussiaUkraine	Sardinia	Spain	WestEurope
MesBal	0.000																										
MesCri	0.130	0.000																									
MesEU	0.091	0.533	0.000																								
NeoBal	0.095	0.270	0.181	0.000																							
NeoEU	0.244	***0.448***	0.000	0.184	0.000																						
NeoME	0.396	0.933	0.541	0.343	0.482	0.000																					
NeoSEU	0.057	0.294	0.000	0.143	0.057	0.462	0.000																				
ChaBal	0.265	0.453	0.450	0.043	***0.317***	0.539	***0.325***	0.000																			
BroBal	***0.589***	0.981	0.375	***0.516***	0.191	0.961	0.309	***0.760***	0.000																		
BroEU	***0.617***	0.837	0.200	***0.526***	0.174	***0.843***	***0.344***	***0.734***	0.060	0.000																	
BroME	***0.646***	***0.844***	***0.750***	***0.479***	***0.566***	0.168	***0.641***	***0.640***	***0.872***	***0.833***	0.000																
BroNE	0.164	0.392	0.089	0.108	0.123	0.117	0.122	***0.248***	0.424	***0.457***	***0.348***	0.000															
BroRU	0.333	0.925	0.000	***0.393***	0.018	0.818	0.057	0.649	0.394	0.002	0.833	0.193	0.000														
BuranKaya	***0.349***	0.000	***0.757***	***0.360***	***0.506***	0.964	***0.439***	***0.565***	***0.978***	***0.861***	***0.869***	***0.529***	0.960	0.000													
Camlibel	***0.449***	0.739	***0.619***	***0.265***	***0.463***	0.169	***0.492***	***0.370***	***0.848***	***0.807***	***0.207***	0.205	0.760	***0.811***	0.000												
Africa	0.264	0.475	0.000	***0.294***	0.098	0.503	0.127	***0.457***	0.253	***0.238***	***0.668***	0.190	0.037	***0.599***	***0.563***	0.000											
Balkans	***0.552***	***0.725***	0.174	***0.519***	***0.272***	***0.720***	***0.364***	***0.656***	***0.332***	***0.278***	***0.726***	***0.440***	0.304	***0.736***	***0.702***	***0.275***	0.000										
CentralEurope	***0.515***	***0.683***	0.041	***0.483***	***0.155***	0.716	***0.272***	***0.625***	0.107	0.056	***0.733***	***0.402***	0.000	***0.705***	***0.702***	0.125	***0.215***	0.000									
Corsica	***0.456***	0.761	0.038	***0.427***	0.098	0.778	0.188	***0.645***	0.116	0.023	***0.807***	0.322	0.000	***0.828***	***0.747***	0.170	***0.296***	0.080	0.000								
Domestic	***0.611***	***0.828***	0.212	***0.529***	0.184	0.836	***0.333***	***0.734***	0.022	0.022	***0.831***	***0.459***	0.000	***0.853***	***0.804***	***0.242***	***0.260***	0.044	0.078	0.000							
Italy	0.310	0.455	0.002	***0.337***	***0.115***	0.513	0.128	***0.449***	0.122	0.130	***0.602***	***0.233***	0.000	***0.518***	***0.530***	0.119	***0.291***	***0.095***	0.062	***0.122***	0.000						
MiddleEast	0.152	0.232	0.117	***0.151***	***0.205***	0.042	***0.168***	***0.198***	***0.347***	***0.386***	***0.265***	0.035	0.158	***0.336***	0.175	0.179	***0.497***	***0.404***	***0.287***	***0.398***	***0.254***	0.000					
NearEast	0.228	0.286	0.362	0.053	***0.296***	0.439	0.284	0.000	***0.628***	***0.637***	***0.565***	***0.230***	0.524	***0.378***	***0.328***	***0.419***	***0.628***	***0.587***	***0.542***	***0.642***	***0.426***	***0.203***	0.000				
RussiaUkraine	***0.504***	0.762	0.175	***0.438***	***0.189***	0.757	***0.313***	***0.644***	***0.389***	***0.286***	***0.786***	***0.370***	0.291	***0.813***	***0.734***	0.133	***0.268***	***0.148***	***0.323***	***0.287***	***0.208***	***0.313***	***0.555***	0.000			
Sardinia	0.273	***0.464***	0.000	***0.300***	0.071	0.511	0.091	***0.459***	0.176	0.175	***0.665***	0.189	0.000	***0.581***	***0.558***	0.064	***0.259***	0.076	0.083	***0.163***	0.000	***0.198***	***0.416***	***0.199***	0.000		
Spain	***0.545***	***0.753***	0.109	***0.485***	***0.189***	0.771	***0.336***	***0.671***	***0.333***	***0.218***	***0.783***	***0.434***	0.282	***0.780***	***0.750***	***0.141***	***0.215***	***0.071***	***0.251***	***0.215***	***0.181***	***0.384***	***0.609***	***0.173***	***0.160***	0.000	
WestEurope	***0.574***	***0.748***	0.190	***0.531***	***0.234***	0.762	***0.345***	***0.689***	0.161	0.124	***0.784***	***0.454***	0.000	***0.778***	***0.753***	0.225	***0.322***	0.059	0.148	0.097	***0.124***	***0.397***	***0.633***	***0.274***	***0.166***	***0.204***	0.000

Table 4.4: Population pairwise Φ_{ST}. Significant values are highlighted in bold.

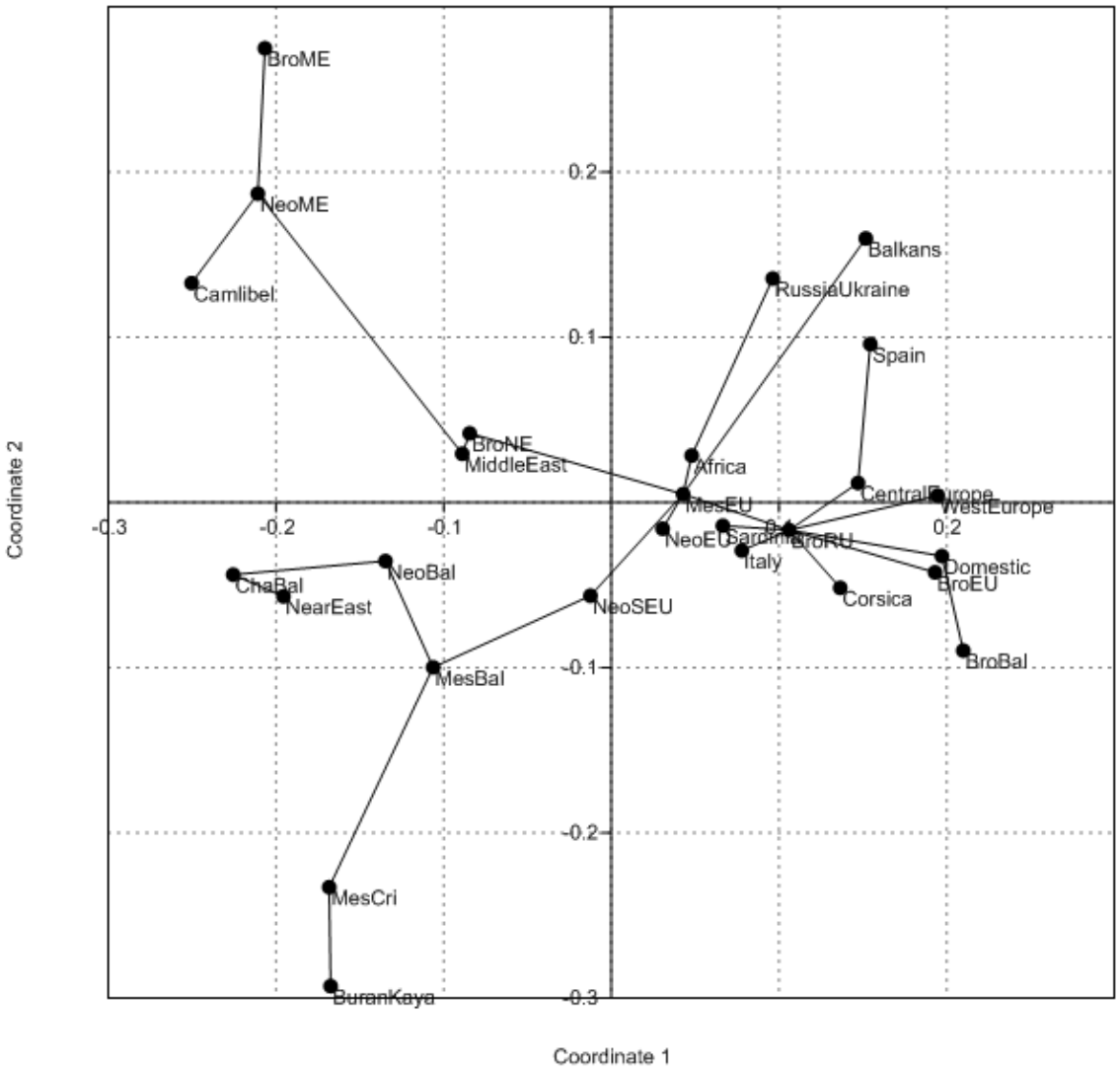


Figure 4.5: Non-metric MDS plot of the relationship among populations based on population pairwise Φ_{ST}.

4.3.4 Demographic analysis

The best fit model according to Bayes factor analysis of the harmonic mean of the sampled marginal likelihoods was Bayesian skyride model over the constant size model (ln P(model over data) -1225 and -1228 respectively) (table 4.5).

The mean nucleotide substitution rate was estimated to be 6.51E-07 (3.50E-07 95% HPD lower and 9.94E-07 95% HPD upper, ln Bayes factor: 2.233 for Skyride over constant size) (table 4.5, figure 4.7). This rate is similar to rate estimates in other mammals (e.g. horse (1.11E-07) and cave lion (2.02E-07), Ho et al. 2007) but different to previous estimates of boar (mean of 2.90E-06, low HPD: 1.60E-06, high HPD: 4.40E-06, Ho et al. 2007).

	Clock rate mean	Standard error	Median	95% HPD lower	95% HPD upper
Constant (only ancient)	7.98E-07	8.26E-09	7.75E-07	4.69E-07	1.17E-06
Skyride (only ancient)	6.51E-07	7.90E-09	6.31E-07	3.50E-07	9.94E-07

Table 4.5: Nucleotide substitution rate estimate based on the 486bp ancient DNA data set from chapter 3.

The Bayesian Skyride Plot (BSP) (figure 4.6) reveals a reduction in effective population size starting around 8,000 years before the present (YBP) and lasting until the mid-Holocene, approximately 5,500-6,000 YBP. The plot shows an increase in effective population size from the mid Holocene that appears to plateau between 3,000-4,000 YBP.

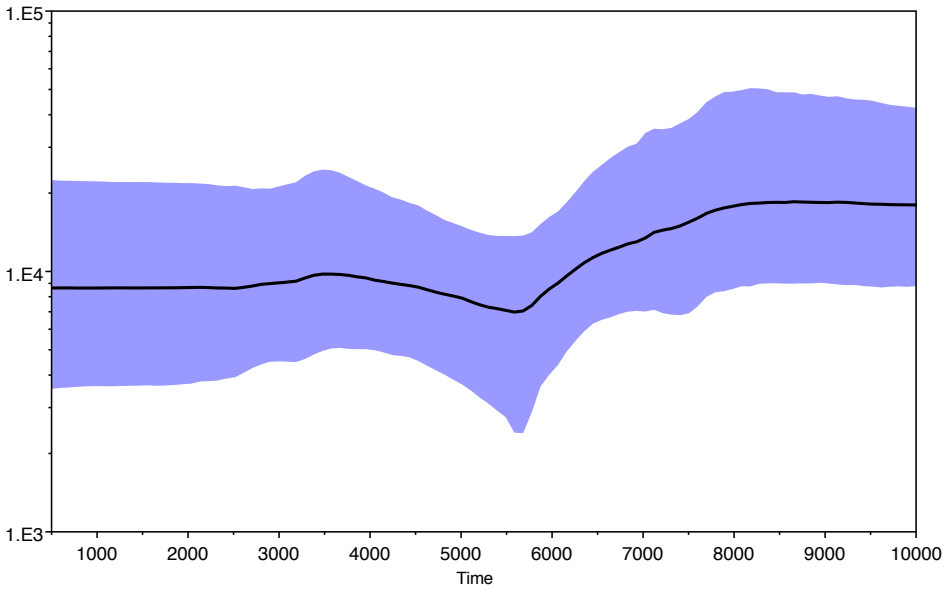


Figure 4.6: A Bayesian Skyride Plot based on 254 ancient, time-stamped, sequences from Europe and the Near and Middle East. The specimens are dated, through direct AMS radiocarbon dating or by stratigraphic association, to approximately 14,500 - 500 YBP (table 3.1). See section 4.2.5 for a detailed description of the analysis.

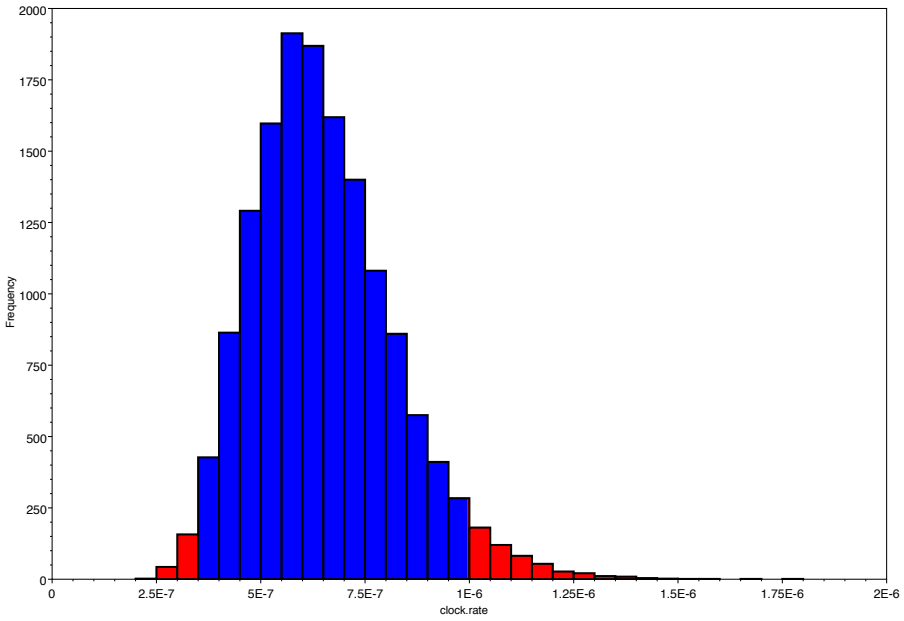


Figure 4.7: Estimation of nucleotide substitution rate based on the ancient only data set (see figure 4.6 and section 4.2.5).

4.3.5 Regional demographic fluctuations

The BSP plot for the Balkan population (using ancient and modern data, figure 4.8) shows a reduction of effective population size starting around 10,000 YBP (roughly corresponding to the onset of the Holocene). This trajectory is continued until the mid Holocene around 5,000 YPB, when the plot reveals that a rapid expansion lasting until 1,000 YBP. The reduction in effective size between 500 - 1,000 YPB could be an artifact due to a low number of specimens/sequences (this time bin contains only 3 specimens).

The BSP plot for the Central European population (using ancient and modern data) reveals a stable population at constant effective sizes throughout the Holocene (figure 4.9), and the BSP plot for the Near and Middle Eastern population (using ancient and modern data) shows an increase in the effective number of females starting around 3,000-4,000 YBP (figure 4.10).

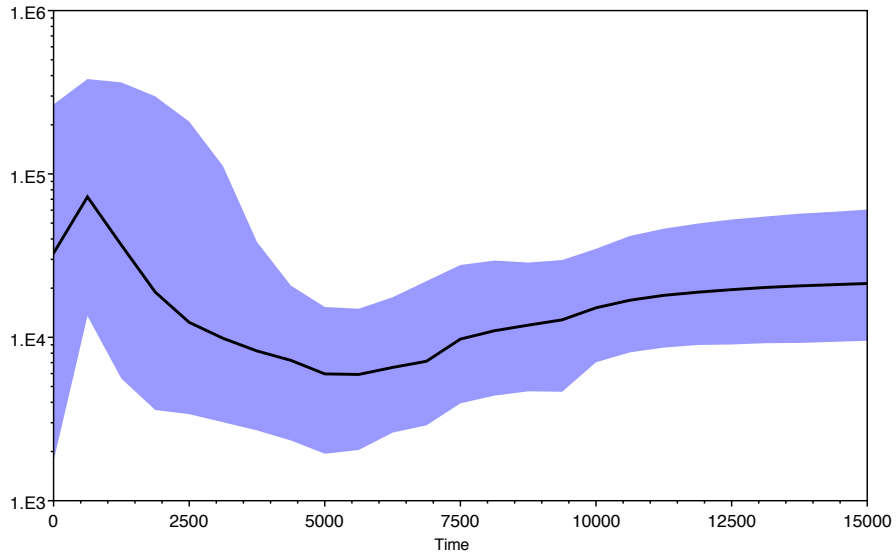


Figure 4.8: BSP plot for Balkan modern and ancient specimens (representing 280 taxa of which 73 were ancient, time-stamped, sequences). The ancient specimens are dated, through direct AMS radiocarbon dating or by stratigraphic association, to approximately 14,500 - 1,500 YBP (table 3.1, table 4.1).

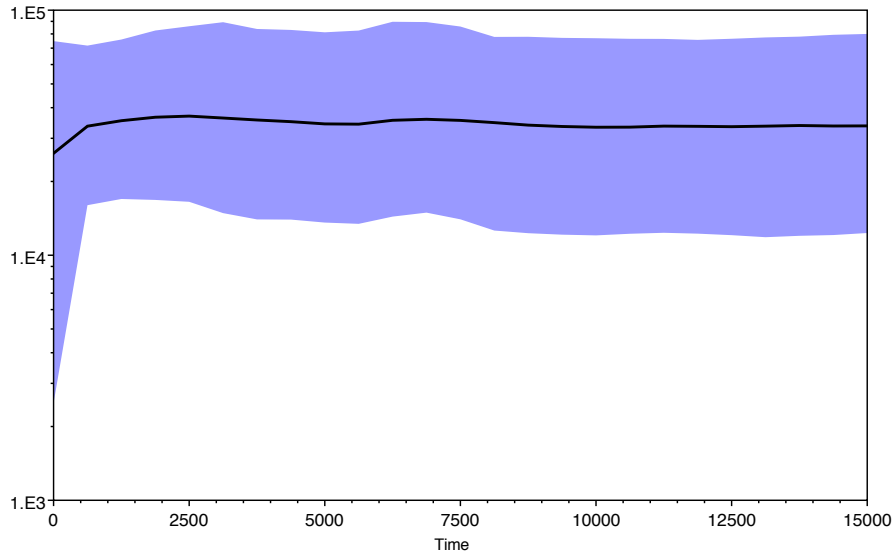


Figure 4.9: BSP plot for Central European modern and ancient specimens (representing 245 taxa of which 100 were ancient, time-stamped, sequences). The ancient specimens are dated, through direct AMS radiocarbon dating or by stratigraphic association, to approximately 9,700 - 2,000 YBP (table 3.1, table 4.1).

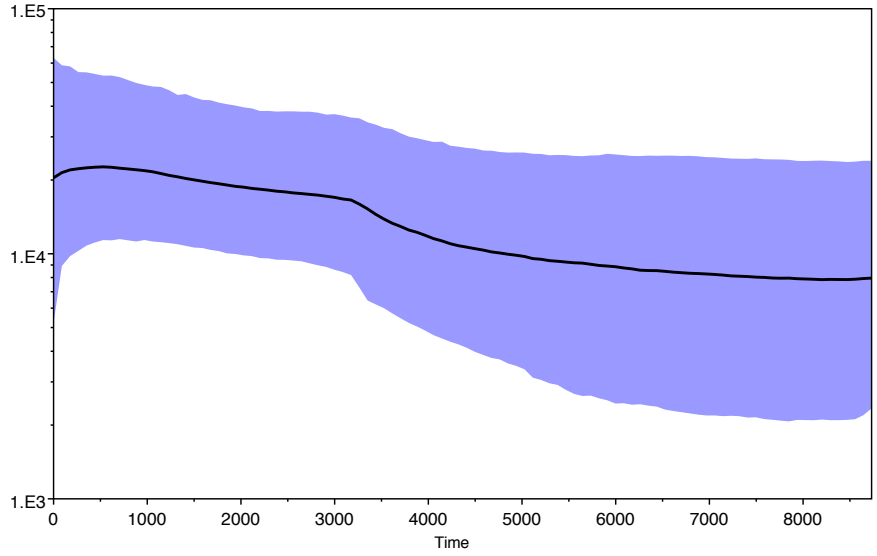


Figure 4.10: BSP plot for Near and Middle Eastern modern and ancient specimens (representing 127 taxa of which 58 were ancient, time-stamped, sequences). The ancient specimens are dated, through direct AMS radiocarbon dating or by stratigraphic association, to approximately 8,500 - 500 YBP (table 3.1, table 4.1).

4.4 Discussion

4.4.1 Geographical distribution of haplogroups and haplotypes

The spatial distribution of haplogroups (and phylogenetic clades) in modern populations corresponds to patterns observed previously (Larson et al. 2005; 2007a, Ramirez et al. 2009; Scandura et al. 2011a). The E1 clade (European) is ubiquitous across all European populations and also present in wild or feral pigs from North Africa and Anatolia and the Middle East (Morocco and Tunisia, Israel, Iran, Iraq and Armenia) (table 4.1). The modern contemporary wild boar in Spain, Central, West and East Europe, and the Balkans possess only E1 haplotypes. Both the E1 and E2 haplogroup is present in wild pigs from Italy, Southern Switzerland (the Malcantone region bordering to Italy) and feral pigs from Sardinia. The E2 clade is restricted to these two populations in the modern samples. Likewise, the geographic distribution of the NE1 and NE2 is geographically restricted to the Near and Middle East (Larson et al. 2005; 2007a; Alexandri et al. 2011).

Spatial and temporal distribution of haplogroups and haplotypes

Modern wild boar from the Balkans carries only the E1 haplogroup. Ancient DNA from Upper Palaeolithic, Mesolithic and Neolithic contexts in the Iron Gates (Balkans) (chapter 3, table 3.1) showed that wild boar in this region possessed all major haplogroups (E1, E2, NE1 and NE2) during these periods. The Balkan population has since then experienced a successive (slow but steady) loss of haplogroups NE1, NE2 and E2 (chapter 3). Continuously, since the onset of the Holocene approximately 10,000-12,000 years ago, this population has simultaneously experienced a slow decline in the female effective population size (figure 4.11). A rapid population expansion began in this region about 5,000-6,000 YBP (figure 4.11), corresponding

approximately in time to the last known occurrence of Y2 wild boar in the Balkans (approximately 6,500 years ago, chapter 3). This chain of events could suggest a scenario in which the local Balkan population, which retained relatively high levels of genetic diversity despite the slow demographic decline (table 4.2, figure 4.4), went extinct only to be replaced (possibly over centuries) by a new population that thrived and rapidly expanded (and continued to expand for several millennia). Whether this population came from elsewhere in the Balkans (for example from remnants of refugia in Greece, Alexandri et al. 2011) can only be speculated in because spatial arrangement of E1 haplotypes varies over space and time. Because the NE2 Y2 haplotype was also present in Neolithic wild boar from Central Europe, the Aegean and the Crimean peninsula, and in putatively domestic pigs and possibly wild boar from Southern France (chapter 3), the question is raised as to why this lineage vanished almost simultaneously (around the mid Holocene) over a wide geographic area.

The rapid population growth (figure 4.8) could be analogue to that previously inferred from mismatch analysis on d-loop sequences from a large sample of Greek modern wild boar (Alexandri et al. 2011) (table 4.1). This group of local populations possesses a high number of unique haplotypes (24 haplotypes in a sample of 207, table 4.1). However, π and H is amongst the lowest for all putative populations (table 4.2, figure 4.4), consistent with a population possessing only closely related haplotypes. The rate of coalescent is fast (and the time to the most recent common ancestor is short) among the haplotypes in these local Greek populations, consistent with a recent demographic expansion (Kingman 1982). The geographic origin of this expansion event is therefore uncertain. Note also that the rapid expansion event (figure 4.8) corresponds in time to the genetic turnover usually ascribed to local European domestication: the process through which domestic Y1 pigs were exchanged for local E1 pigs (chapter 3, Larson et al. 2007a). Importantly, it also corresponds to the demise of both wild and domestic Y2 lineages in Europe.

Re-colonisation from putative refugia

The presence of NE2 Y2 haplotype in Central European Mesolithic contexts raises the question of re-colonisation of Central Europe from the Balkans (Stuart et al. 2009; Alexandri et al. 2011; Scandura et al. 2011a). Because of putative gene flow among populations restricted to southern refugia (Valdiosera et al. 2008), which is a process that cannot be ruled out for wild boar, it remains a possibility that Central European Y2 wild boar were present too in refugia R1 and R2. However, because of poor sampling of Mesolithic sites in those two regions, the current data set does not allow that question to be resolved.

4.4.2 Genetic variation across space

Linear regression analysis of average geographic distances between populations and population pairwise Φ_{ST}'s (4.4) show that geographic distance is a poor predictor of genetic differentiation (r^2= 0.10 for the whole of West Eurasia, excluding Africa, Sardinia and Corsica since these populations were primarily shaped through human-driven dispersal of pigs, Albarella et al. 2009, Manilus et al. 1999), and within Europe (r^2= 0.0009) (omitting the islands of Sardinia and Corsica) (figure 4.11, figure 4.12, respectively). These results show that isolation-by-distance, the process through which genetic distances are increased as a function of geographic distance (Wright 1943), is not a primary factor in shaping genetic variation among West Eurasian wild boar. On the contrary, the main factor in shaping spatial distribution of genetic variation appears to be physical barriers such as the Black Sea and the Bosporus, in agreement with previous observations (Larson et al. 2005; 2007a; Scandura et al 2008; 2011).

Wild pigs possessing E1 haplotypes do occur in the Near and Middle East (table 4.1, Ramirez et al. 2009), suggesting that gene flow along dispersal routes east to the Black Sea could have occurred in addition to human-mediated dispersal (see

chapter 2). While it is difficult to support the former scenario based on the present data (particularly based on shared haplotypes, the Anatolian and Middle Eastern populations possess only the common and geographically widespread A or N haplotypes, table 4.1), it is worth highlighting that additional, natural, mechanisms can be responsible for the spatial distribution of genetic variation.

For example, large movements and spatial re-arrangement of genetic lineages in Europe is supported by the linear regression of Φ_{ST}'s over geographic distances (figure 4.12). These processes were to some extent visualised in chapter 3 by sequencing ancient DNA. For instance, the rapid spread of haplogroup E1 across Europe towards the Late Neolithic or Early Bronze Age, corresponding to the demise of haplotype Y2 in Europe, show that fast movements of wild boar over great geographic distances (in this case coupled with a rapid increase of the effective number of females, figure 4.8) have taken place. (However, take note that the process observed in chapter 3 is based on analyses of combined wild and domestic pigs, which bias the overall picture).

In addition, because the MDS coupled with MST (figure 4.5) show some support for regional continuity, it is likely that a range of processes have shaped the spatial structure of genetic variation in modern contemporary populations. These processes include population continuity, lineage replacements coupled with rapid population expansions, and fast, human-driven movements of domestic pigs over great geographic distances. If taking into account that additional processes are common, such as wild-domestic hybridization and feralisation (see section 4.1.2), the complexity of wild boar phylogeography becomes clear.

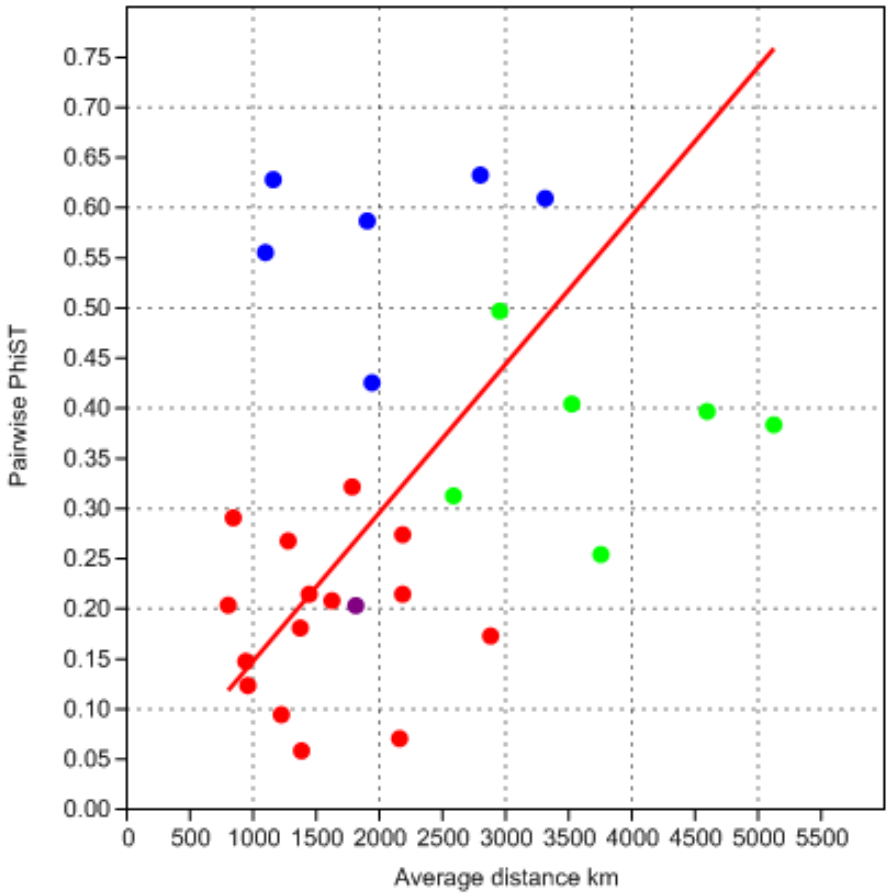


Figure 4.11: Relationship between population pairwise Φ_{ST} and geographic distance for putative populations in West Eurasia. Red = Europe vs. Europe, Blue = Europe vs. Near East, Green = Europe vs. Middle East and Purple = Near East vs. Middle East. r^2= 0.10.

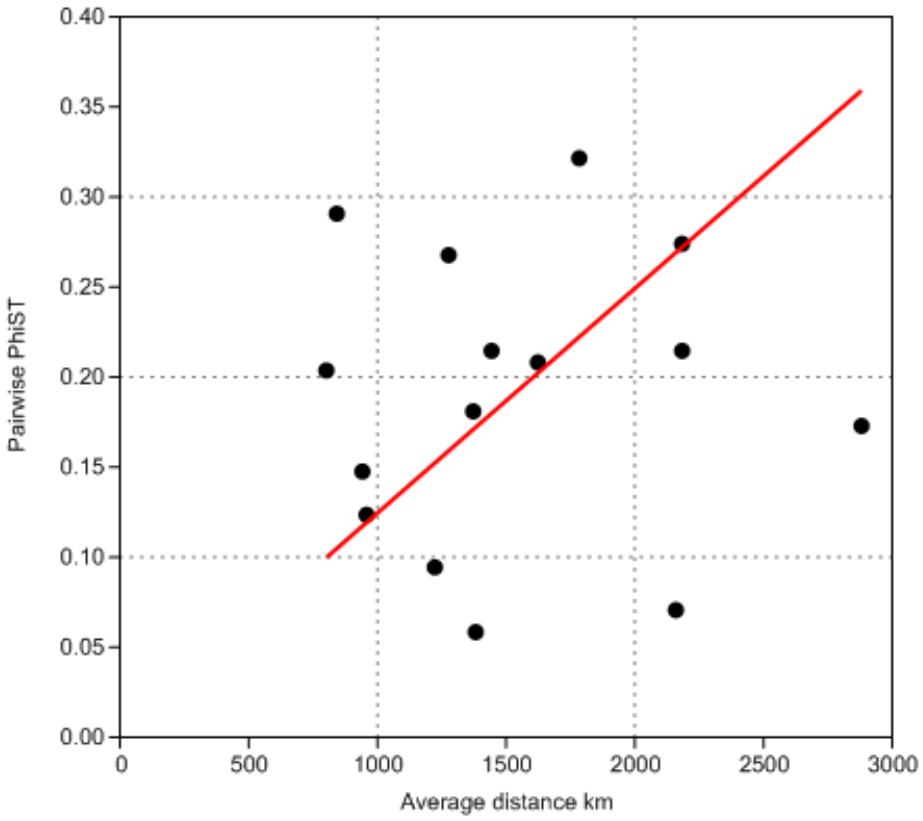


Figure 4.12: Relationship between population pairwise Φ_{ST} and geographic distance for putative populations in Europe. $r^2 = 0.0009$.

4.4.3 Genetic diversity

The genetic diversity in West Eurasian populations (table 4.2) is similar to that observed in other wild boar populations (e.g. Ramayo et al. 2010). π (nucleotide diversity) ranged from $\pi = 3.8 \times 10^{-3}$ in wild boar from the Balkans to $\pi = 18.4 \times 10^{-3}$ in wild boar from the Middle East. However, in the modern sample, the overall lowest observed nucleotide diversity was for the domestic group ($\pi = 3.4 \times 10^{-3}$). Haplotype diversity (H) is consistently high and ranged from 0.7 in the Russia/Ukraine/Finland group to 0.93 in wild boar from the Middle East. The eastern part of the Middle Eastern population is admixed with wild boar possessing East Asian mitochondrial lineages (Larson et al. 2005, table 4.1), which is the likely cause for the high diversity.

The relationship between H and π is depicted in figure 4.4. Modern populations appear to be relatively homogenous (equal relative to each other) in relation to both H and π although populations possessing multiple haplogroups tend to display higher π values (Africa, Italy, Middle East, Sardina and the Near East) than populations possessing only a single haplogroup (Central Europe, West Europe, Spain/Iberia and the Balkans). Corsica is the exception and possesses haplotypes from three different haplogroups ($\pi = 4.601 \times 10^{-3}$).

At least two populations (Mesolithic Crimea and Neolithic Crimea) show exceptionally low H (H=0, H=0 respectively) and π (π=0, π=0 respectively) despite having sample sizes comparable to other regions (n=3 and 11 respectively, see chapter 3 and table 3.1). This could be indicative of a pre-Holocene bottleneck followed by isolation with no or little gene flow until at least the early mid-Holocene (one direct AMS radiocarbon date from Buran-Kaya 4 place this individual between 5,664-5,534 cal. BC, one sigma, chapter 3). Note that no Crimean wild boar are present in the modern reference population from Ukraine (n=9, table 4.1).

4.4.4 Population structure across time and space

AMOVA was used to investigate population structure among West Eurasian populations (table 4.3). Populations were first partitioned into European and non-European groups (1: Spain, Sardinia, Corsica, Italy, West and Central Europe, the Balkans and Russia/Ukraine/Finland, and 2: Near and Middle East and Africa). The results of this analysis revealed substantial genetic differentiation between European and non-European populations (Φ_{CT}=0.319, p<0.01) and great genetic differentiation among populations within the same geographical region (Φ_{SC}=0.212, p<0.001), consistent with the observations and discussions above (sections 4.4.2 and 4.4.3).

In another AMOVA, European populations were partitioned into four groups (1= Balkans, and Russia/Ukraine/Finland, 2=Central and West Europe, 3=Spain/Iberia, and 4=Corsica, Sardinia and Italy), four principal areas separating putative subspecies (figure 4.1). The results revealed significant but moderate genetic differentiation among regions (Φ_{CT}=0.116, p<0.05) and highly significant moderate differentiation among populations within the same geographical region (Φ_{SC}=0.111, p<0.001). A non-hierarchical AMOVA showed that the differentiation among all populations is substantial (Φ_{ST}=0.206, p<0.001) but lower than for the whole of West Eurasia. Intra-European structure is therefore not as pronounced as the overall genetic structure in West Eurasia when also considering North Africa, Near East and Middle East, consistent with the overall geographic distribution of major haplogroups (Larson et al. 2005, and see figure 4.11). In addition, population pairwise Φ_{ST} (table 4.4) reveals substantial and highly significant genetic differentiation between populations in the Near East/Anatolia and the Middle East (Φ_{ST}=0.203, p<0.001). Again, these observations are consistent previous results (see figure 4.5 and 4.11).

Ancient vs. Modern: Global

Several AMOVAs were carried out to examine the distribution of genetic variation among ancient and modern populations (table 4.3). Considering only ancient vs. modern putative populations (simply grouped into two groups), the between-group genetic differentiation was moderate (Φ_{CT}=0.127, p<0.05), though variation among populations within each group was substantially higher (Φ_{SC}=0.355, p<0.001). These results show that the overall temporal structure of genetic variation (Φ_{CT}) is considerably less important than geographic partitioning or sub-structuring of populations within temporal groups (Φ_{SC}). Consequently, a much higher proportion of total genetic variation is found among populations within temporal strata than among temporal strata, consistent with observations made in chapters 2 and 3.

Ancient vs. Modern: Balkans

On a regional level, partitioning of genetic variation among populations in the Balkans (Mesolithic, Neolithic, Chalcolithic, Bronze Age and Modern), assuming no groups, is very high (Φ_{ST}=0.522, p<0.001). The highest population pairwise Φ_{ST} values were observed among the Mesolithic sample and the Bronze Age and Modern sample (Φ_{ST}=0.589, p<0.001 and Φ_{ST}=0.552, p<0.001 respectively, table 4.4). The differentiation between the Mesolithic sample and the Neolithic and Chalcolithic samples is non-significant (Φ_{ST}=0.095, p>0.05 and Φ_{ST}=0.265, p>0.05 respectively), indicative of regional (temporal) continuity between these strata (one continuous population). The pairwise Φ_{ST}'s in table 4.4 further reveals that the differentiation between the Bronze Age and Modern sample is highly significant (Φ_{ST}=0.332, p<0.001) whereas the differentiation between the Neolithic and Chalcolithic samples is small and non-significant (Φ_{ST}=0.043, p>0.05).

Hierarchical AMOVA (Ancient vs. Modern) reveal non-significant differentiation between groups (Φ_{CT}=0.226, p>0.10) but substantial and highly significant variation

among populations within groups (Φ_{SC}=0.397, p<0.001). Three different hierarchical AMOVAs reveal very similar but non-significant Φ_{CT} values (table 4.3). The grouping that minimise Φ_{SC} and maximise Φ_{CT} (despite being non-significant) is (1: Mesolithic, 2: Neolithic/Chalcolithic, 3: Bronze Age and 4: Modern). Again, this is reflected in population pairwise Φ_{ST}'s, which is consistent with previous observations (chapter 3).

Ancient vs. Modern: The Near and Middle East

AMOVA show that the overall temporal partitioning of genetic variation in the Near and Middle East (Ancient vs. Modern) is moderate (though non-significant) (Φ_{CT}=0.117, p>0.10). Genetic variation among populations within groups is substantial and highly significant (Φ_{SC}=0.206, p<0.001). Variation among all populations (no groups) is substantial (Φ_{ST}=0.206). Furthermore, AMOVA using a more clearly defined temporal structure (1: Çamlibel/Neolithic/Chalcolithic, 2: Bronze Age, including samples up to medieval times, and 3: Modern) in fact reinforces the observation that there is relatively little differentiation among temporal groups (Φ_{CT}=0.052, p>0.10) whereas the variation among populations within temporal groups is substantial (Φ_{SC}=0.239, p<0.001).

Thus, the temporal structure in these regions appears to be largely defined by the genetic composition of individual, local, populations and constantly shifting distributions of haplotypes across space and time. (It is also consistent with the presence of East Asian genetic lineages in the eastern most regional populations in the Middle Eastern group (table 4.1) though the very small proportion of these haplotypes is unlikely to severely bias the overall interpretations). ANC1 haplotype variation across time (chapter 2) reveals that at least parts of the global Near and Middle Eastern population experienced a shift in genetic composition (chapter 2). In addition, the MDS and MST support the interpretation of shifting haplotypes across time and space (figure 4.5). Hence, although there is substantial geographic structure among modern populations, the population pairwise Φ_{ST}'s is indicative of gene

flow between the Near and Middle East at some point in the past.

Ancient vs. Modern: West and Central Europe

There is little and non-significant differentiation between ancient and modern European populations (Φ_{CT}=0.049, p>0.10) and moderate variation among populations within groups (Φ_{SC}=0.105, p<0.001) (assuming two groups; ancient and modern). However, a second AMOVA using a more defined temporal structure (1: Mesolithic Europe and Neolithic Europe, 2: Bronze Age Europe, and 3: modern West Europe and modern Central Europe) reveal a higher but still non-significant variation among groups (Φ_{CT}=0.122, p=0.067). Although non-significant, these results suggest that the three-group division can explain a substantially higher proportion of the total genetic variation. This is consistent with the observation that a genetic turnover takes place in Europe towards the end of the Neolithic (Larson et al. 2007a, but see chapter 3). Pairwise population Φ_{ST}'s confirm this observation (table 4.4) and it is also supported through AMOVA in that the variation among populations within groups is reduced using the three group partitioning (Φ_{SC}=0.043, p<0.05).

4.5 Conclusion

First, based on the spatio-temporal structure of genetic variation, there is little evidence to support the hypothesis that there are several sub-species in West Eurasia (see figure 4.1, and Groves et al. 1981; 2007). In fact, there is very little correspondence between geographic and genetic distances at all (figure 4.11 and 4.12). This implies high levels of constant gene flow across mainland Europe, possibly coupled with local extinctions followed by repopulation; a process that is known to have occurred many times in Europe (Scandura et al. 2011a). Instead, the genetic structure among European and West Asian populations is to a great extent governed by physical barriers to gene flow such as the Bosporus strait.

The data presented in chapter 3, combined with previously published and novel genetic sequences presented in this chapter, show that the genetic structure among modern European and West Asian (Near and Middle Eastern) wild boar is relatively young: haplogroup sharing, geographic structure of haplogroups over time, AMOVA and population pairwise Φ_{ST}'s are all indicative of continuous gene flow across the region during the first half of the Holocene (see also the conclusion of chapter 3). The modern day genetic structure among European and West Asian populations is likely a consequence of the formation of physical barriers to gene flow in West Anatolia (or Southeast Europe): the rise of the Black Sea possibly as early as 7,400 BC (Giosan and Constantinescu 2009). Importantly, this date roughly corresponds to the demise of NE2 Y2 wild boar in Europe but also to the rapid expansion of Balkan, and primarily Greek, E1 wild boar (figure 4.8) (Alexandri et al. 2011).

However, because not a single Y2 specimen was found in Neolithic layers from Anatolia and the Middle East (chapter 2), and because there are question marks surrounding the natural range of the Y1 mtDNA lineage (preliminary wild/domestic status calls for some Neolithic/Chalcolithic specimens from the Balkans indicate that its range might have reached into Southeast Anatolia, though it is premature to draw far-reaching conclusions from that data, see chapter 3), it is unclear whether gene

flow occurred directly between Anatolia and Southeast Europe prior to the formation of the Bosporus barrier.

Because European and West Asian wild boar populations have experienced shifts in the haplotype/haplogroup composition, on both local and regional levels (figure 4.5), it is reasonable to conclude that a combination of ancient and recent factors have shaped the current distribution of genetic variation. Humans are responsible for some spatial re-arrangement of genetic lineages (see chapter 2), but some level of natural gene flow between geographically distant populations cannot be ruled out. In the light of these results, caution should be taken if using mtDNA phylogeography for identifying geographic regions where domestication took place (see chapter 3). In addition, these finds will be important for reconstructing a more complete Holocene population history. In fact, the results show that it is impossible to use only modern sequences to reconstruct, for example, the re-colonisation of Europe from peninsular refugia.

Chapter 5

Ancient DNA reveals timing of selection and introgression in domestic chickens

5.1 Introduction and background

Mitochondrial DNA phylogeography has shown that chickens were domesticated from the Red junglefowl (*Gallus gallus gallus*) multiple times in Southeast Asia (Fumihito et al. 1994; Fumihito et al. 1996; Liu et al. 2006; Kanginakudru et al. 2008; Sawai et al. 2010). In contrast, the BCDO2 (beta-carotene dioxygenase 2) gene show evidence of past introgression (admixture) with the Grey junglefowl (*Gallus sonneratii*) (Eriksson et al. 2008). In fact, recent genetic analyses have shown that chickens have a widespread history of hybridisation with various *Gallus* subspecies in Southeast Asia (Nishibori et al. 2005; Berthouly-Salazar et al. 2010; Sawai et al. 2010). These data show that, like pigs (chapter 2,3 and 4), the domestication trajectory of chickens was non-linear and complex, probably encompassing many diffuse stages of varying degrees of human interaction and intentionality (for example, directed selection and deliberate admixture) (Zeder 2006; 2008; Vigne 2011, and see figure 1.1).

Research on modern domestic animals has shown that human-driven positive (directed) selection on certain genes (so-called domestication genes) might have played an important role in the first steps of animal domestication (Fang et al. 2009; Rubin et al. 2010; Wright et al. 2010). For example, whole genome sequencing of domestic chickens recently allowed the identification of a selective sweep at the TSHR locus on chromosome 5. Because the derived allele is swept to fixation in all modern chicken breeds, Rubin et al. (2010) hypothesised that the TSHR locus was actively selected for by people during the initial (or early) domestication process, prior to the expansion of chickens to other geographical regions. The TSHR sweep is particularly important because chickens harbour comparatively high levels of genetic variation, bolstering the assumption of strong, early human-driven selection on the derived TSHR allele (Muir et al. 2008; Wright et al. 2010; Kerstens et al. 2011). Because chickens harbour high levels of genomic variability, strong selection and fixation of specific alleles (like TSHR) could theoretically induce patterns of similarity among seemingly unrelated populations (for example, ancient breeds versus modern

commercial breeds): one model to explain these patterns is human driven selection during the early domestication process (cherry-picking; Fang et al. 2009; Rubin et al. 2010). An alternative explanation model is that relaxation of purifying selection, which allowed novel mutations to remain in populations even at relatively low frequencies (Björnerfeldt 2009; Wang et al. 2011), followed by recent human-driven selection and rapid global dispersal and admixture, led to fixation across all modern breeds.

Ancient DNA has recently shed important light on the issue of domestication genes. For example, Asplund et al. (2010) analysed a SNP in the *NAM-B1* gene (also a proposed domestication gene) in historical wheat seeds and showed that recent human-driven selection caused the sweep, not ancient selection as previously thought (Asplund et al. 2010). Moreover, ancient DNA analyses of autosomal SNPs (located in the TLR4, LEP and MC1R genes) in cattle, linked to specific phenotypes, revealed temporal structure in allele frequencies and a decline in heterozygosity over time (Svensson et al. 2007). These studies show that gene frequencies observed in modern, contemporary populations are poor estimates of past diversity. Chickens have likely experienced recent admixture and selection, which bolster the presumption that recent events, like breed formation, have had great impact on the genetic composition of modern chickens (Dana et al. 2010).

In this chapter, ancient chicken DNA is used to resolve the history of three, unlinked, genetic loci (mtDNA, BCDO2 and TSHR). The aim of the study is to assess whether patterns of variability in modern populations resulted from ancient or recent processes and, in doing so, gain a better understanding of the domestication trajectories that have shaped modern chickens.

The high occurrence of the mtDNA E-clade in European domestic chickens is assumed to reflect ancient diversity, while the occurrence of other haplogroups should reflect recent admixture with East Asian breeds (Dana et al. 2010). The question of whether the high frequency of mtDNA clade E in modern European chickens (it is ubiquitous across all breeds, Dana et al. 2010) reflect ancient diversity is open

to debate because studies of ancient DNA in domestic animals often reveal ancient, rapid, and geographically widespread population shifts (chapter 2, 3, but see Malmstrm et al. 2008; Deguilloux et al. 2008; Larson et al. 2007a). Moreover Dana et al. (2010) hypothesise that relatively low frequencies of clades A-D reflects recent, directed, introgression of East Asian lineages as part of breed improvement.

The *Y* BCDO2 allele (causative of the yellow skin phenotype and common in modern breeds) originated in the Grey junglefowl, which natural range is restricted to the Indian subcontinent (Liu et al. 2006; Kanginakudru et al. 2008). The common yellow skin phenotype is caused by the recessive *Y* BCDO2 allele (Eriksson et al. 2008). The BCDO2 gene is a catalyst for the asymmetric oxidative cleavage of beta-carotene in carotene metabolism encodes the beta-carotene dioxygenase 2 enzyme that cleaves colorful carotenoids into colorless apocarotenoids (Kiefer et al. 2001). Expression of the dominant *W* allele in skin tissue subsequently results in white skin color. The introgressed Gray junglefowl *Y* allele contains one or more cis-acting and tissue-specific regulatory mutations that inhibit expression of the BCDO2 gene in skin tissue. This reduces cleavage of carotenoids and allows for the carotenoids to be deposited in skin tissue, causing yellow skin color provided that enough carotenoids are available in the food (Eriksson et al. 2008). Because a great number of chicken breeds worldwide still possesses the wild type *W* allele, but commercial breeds tend to be fixed for the *Y* allele (Eriksson et al. 2008), it is unclear when past introgression and selection took place.

Lastly, the TSHR gene (thyroid stimulating hormone receptor gene) has undergone a selective sweep at some point in the past (Rubin et al. 2010). The ubiquity of the sweep haplotype across worldwide populations suggests that the sweep event took place during the initial stages of the domestication process, prior to the major expansion of chickens around the globe (Rubin et al. 2010). Thyroid hormones (TH) and domestication are probably linked closely in complex patterns of gene regulation and gene expression, cell structure and cell architecture, by means which are not yet fully understood (Crockford 2002; 2004; 2009; Dobney and Larson 2006). Whether

TSHR is a domestication gene or a result of breed formation (like NAM-B1, Asplund et al. 2010) is unclear.

Specifically, this chapter examines the following questions:

1. Did ancient Europan chickens possess exclusively E-clade haplotypes as previously hypothesised (Liu et al. 2006 and Dana et al. 2010)?

2. Did introgression with Grey Junglefowl, and following selection for yellow skin colour (BCDO2), occur prior to the expansion of domestic chickens into Europe?

3. Did the derived (sweep) TSHR allele, which is fixed in modern domestic chickens, undergo selection during the early domestication process?

5.2 Materials and methods

In order to address these questions, DNA was extracted from 61 ancient European chickens collected from 10 archaeological sites in Germany, Austria and the UK (figure 5.1, table 5.1). The age of samples were determined by stratigraphic association (as provided by archaeozoologists). They range in date from Iron Age La Tene C and D (*ca* 285-15 BC), to post-medieval layers dated to the 16th-18th centuries AD (table 5.1).

The BCDO2 and TSHR SNPs were genotyped using Pyrosequencing (Q24). Because of allelic dropout, which is a problem in ancient DNA studies due to extremely low amounts of starting template molecules, the risk of falsely determining a heterozygous individual as homozygous is significantly higher than when genotyping modern DNA (Svensson et al. 2007; Ludwig et al. 2009). Multiple replicates were performed to ensure genotype authenticity. Likewise, at least two but often three mtDNA amplicons from independent PCR's were sequenced to ensure sequence authenticity.

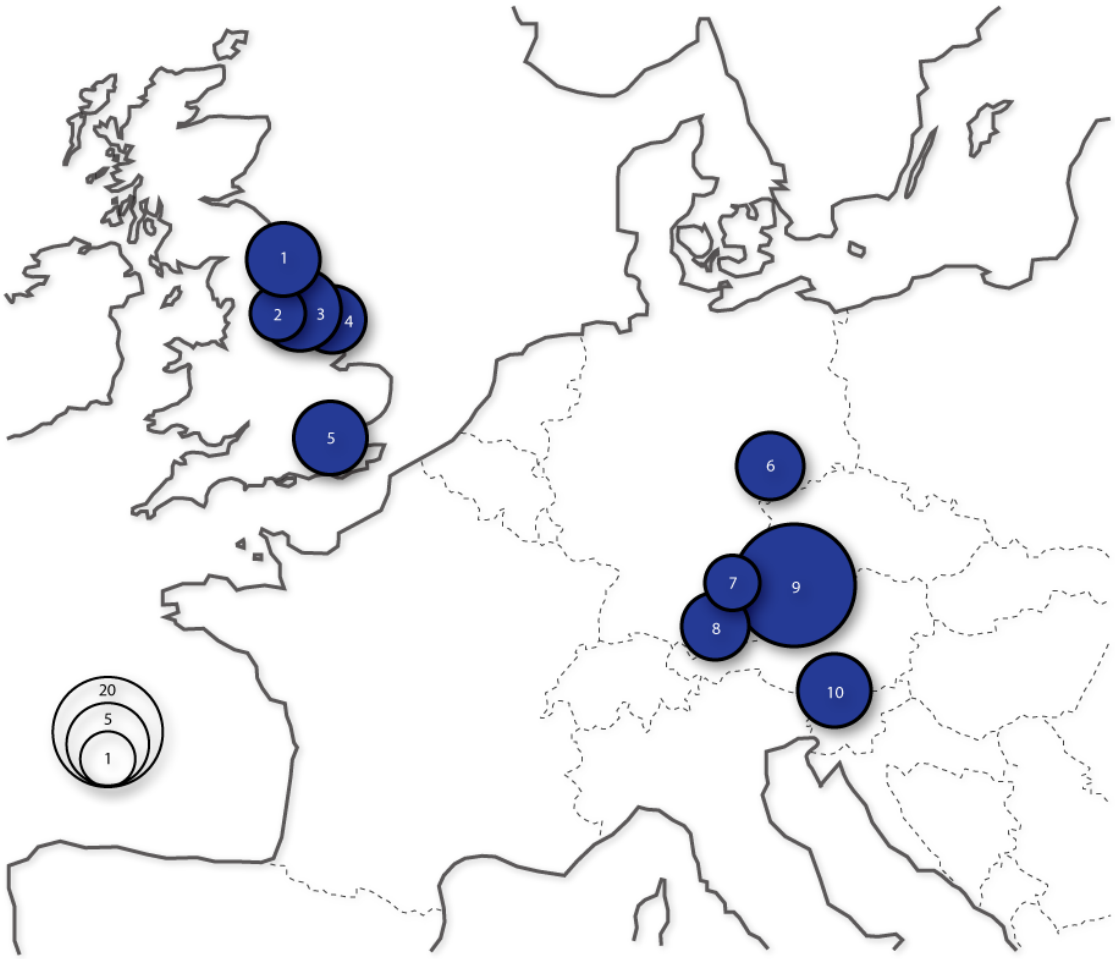


Figure 5.1: A map depicting sample locations. Numbers in circles corresponds to archaeological sites: 1: Arbeia, Roman, 120-400 AD, 2: Scott lane Whetherby, 11th/12th century AD, 3: York, 10th-14th century AD, 4: Beverly Playhouse, 12th-18th century AD, 5: London Wall, Roman, 6: Altenburg, 280-15 BC, 7: Manching, 200-30 BC, 8: Künzing Kaserfeld, Roman, 2nd century AD, 9: Epfach, Roman, 50 AD, 10: Magdalensberg, Roman, 100 BC-1600 AD.

5.2.1 DNA extraction, purification and concentration

DNA extraction was performed in a dedicated ancient DNA laboratory in the Archaeology department at Durham University following stringent laboratory procedures according to commonly applied guidelines (Cooper and Poinar 2001; Gilbert et al. 2005). This included wearing protective lab coats and over-shoes, double pairs of gloves (outer pair of gloves are changed in between every step of the prepa-

ration/extraction procedure). All equipment and work surfaces were cleaned before and after each use with a dilute solution of bleach (10%) followed by ethanol (99%). A strict one-way system for entering the labs is in use in order to avoid introducing post-PCR contaminants.

Chicken bones were prepared for DNA extraction by removing an approximately one-millimeter layer of the outer bone surface by abrasion using a dremel drill with clean cut-off wheels (Dremel no 409). The bone was then pulverized in a Micro-dismembrator (Sartorious-Stedim Biotech) followed by collection in 15mL Grainer tubes.

Bone powder was digested in 0.425M EDTA, 0.05% SDS, 0.05M Tris-HCI and 0.333/mg/ml proteinase K and incubated overnight on a rotator at 50 °C until fully dissolved. The reagent master mix, excluding proteinase K, was UV-irradiated at (254 nm) for an hour using a cross linker prior to use in the extraction buffer. 2mL of solution was then concentrated in a Millipore Amicon Ultra-4 30KDa MWCO to a final volume of 100μL. The concentrated extract was purified using the QIAquick PCR Purification Kit (Qiagen) following manufacturers recommendations, except that the final elution step was performed twice to produce a final volume of 100μL. One in five to ten negative extraction controls were performed alongside the ancient bone samples.

5.2.2 PCR amplification

One 201bp mitochondrial HV1R mtDNA fragment (Storey et al. 2007) and two 40-50bp fragments targeting one SNP in each of two autosomal nuclear loci (BCDO2 and TSHR) were amplified (table 5.1). PCR setup was conducted in a fume hood in a dedicated ancient DNA PCR setup room. One in eight PCR reactions were PCR negative controls. One positive control (a modern Grey junglefowl) was included for each PCR round. In order to avoid contaminating the PCR reactions

containing ancient DNA, the modern positive control was stored in the dedicated PCR/post-PCR laboratory and added to the reaction when tubes had been placed on the thermo cycler. PCRs were visualized on a 1-2% agarose gel using GelRed and UV illumination. For d-loop sequencing, the PCR products were purified using Qiagen's PCR purification kit. All PCR products were stored at -20°C prior to sequencing. Pyrosequencing PCR primers were developed in PyroMark Assay Design 2.0 (Qiagen).

D-loop

PCRs were setup in 25μL reactions using 1U Taq GOLD (Applied Biosystems), 1x Gold buffer (Applied Biosystems), 2.5mM MgCl2 , 0.5μg/μL BSA (bovine serum albumine), 200μM of each dNTP, 0.4μM of each forward and reverse primers, and 2-5μL of aDNA extract. One PCR negative control was included for every 7 aDNA template PCRs. PCR cycling conditions were 95°C for 5min, 50 cycles of 94°C for 30 sec, 54°C for 30 sec and 72°C for 30 sec, followed by 72°C for 10 min.

BCDO2

PCRs were setup in 25μL reactions using 1.0-1.25U Taq GOLD (Applied Biosystems), 1x Gold buffer (Applied Biosystems), 2.5mM MgCl2 , 0.5μg/μL BSA (bovine serum albumine), 1M betaine, 200μM of each dNTP, 0.4μM of each primer, and 2-5μL of aDNA extract. One PCR negative control was included for every 7 aDNA template PCRs. PCR cycling conditions were 95°C for 5min, 50 cycles of 94°C for 30 sec, 57°C for 30 sec and 72°C for 30 sec, followed by 72°C for 10 min.

TSHR

PCRs were setup in 25μL reactions using 1.0-1.25U Taq GOLD (Applied Biosystems), 1x Gold buffer (Applied Biosystems), 2.5mM MgCl2 , 0.5μg/μL BSA (bovine serum albumine), 200μM of each dNTP, 0.6μM of the biotinylated forward primer and 0.8μM of the reverse primer, and 2-5μL of aDNA extract. One PCR negative control was included for every 7 aDNA template PCRs. PCR cycling conditions were 95°C for 5min, 50 cycles of 94°C for 30 sec, 56°C for 30 sec and 72°C for 30 sec, followed by 72°C for 10 min.

5.2.3 DNA sequencing

Sanger sequencing was performed on the Applied Biosystems 3730 DNA Analyser at the DNA sequencing service in the School of Biological and Biomedical Sciences at Durham University. Trace files were manually inspected using 4Peaks (Mekentosj) or Geneious v5.4 (Drummond et al. 2011) and built into contigs by hand in Se-Al (http://tree.bio.ed.ac.uk/software/seal/).

Pyrosequencing was performed in-house at the Archaeology department in Durham using the PyroMark Q24 (Qiagen) following manufacturers guidelines and using Qiagen Q24 sequencing reagent kits. Results were analysed in the PyroMark Q24 software using modified settings: accepted peak deviation and minimum peak heights were set to the less strict option.

5.2.4 Analysis of sequence and SNP data

A collapsed alignment of the haplotypes published by Liu et al (2006) combined with the E-clade haplotypes published by Dana et al. (2010) was used as a reference to identify haplotypes. Sequences were aligned in Geneious v5.4 using the MAFFT

alignment software (Katoh et al. 2002). Phylogentic analysis was performed using PhyML (Guindon. et al. 2010) as implemented in Geneious v5.4. The nucleotide substitution model was estimated in using MrModeltest 2.3 (Nylander 2004) and PAUP* 4.0 (Swofford 2000) as implemented in MrMtGui (Nuin 2010). The best-fit model using both aLRT statistics and AIC was HKY+I+G.

In order to account for allelic dropout, which is common in ancient DNA studies (Svensson et al. 2007; Daskalaki et al. 2011), each SNP was confirmed by repeated genotyping from independent PCRs. The probability of falsely assigning a heterozygous individual as homozygous was calculated as: P(false homozygote)=K*(K/2)n-1, where n is the number of replicates and K is the observed number of allelic dropouts divided by the total number of genotypings of heterozygous individuals (Gagneux et al. 1997).

Fisher exact test, as implemented in R v2 (R Development Core Team 2011) using the *dbinom* and *gbinom* functions, was used to examine differences in allele frequencies between ancient and modern samples. The binomial probability distribution was also implemented as ancient DNA authenticity criteria, assuming that possible contamination would reflect genotype frequencies in modern populations.

5.2.5 Ancient DNA replication

Independent replication of 10 chicken remains (HVR1/D-loop and TSHR) was conducted in a dedicated ancient DNA laboratory at EBC, Uppsala University, Sweden, by Helena Malmström. Bones were UV irradiated 1J/cm2 per side. 40 to 80mg powder incubated in 1mL Yang-Urea buffer (0.5M EDTA, pH 8 and 1M Urea) and 10μL Proteinase K for 22 hours at 38°C together with 4 extraction blanks. An additional 10μL Proteinase K was then added and the samples were incubated for 3 more hours at 55°C. DNA was further extracted using Qiagen's PCR Purification Kit and finally eluted in 100μL elution buffer. A slightly modified PCR protocol was used:

addition of RSA (rabbit serum albumine) was used instead of BSA. Apart from following the PCR cycling conditions described above, PCRs were also performed following Storey et al. (2007).

Locus	Primer sequence (5'-3')	Name	Reference
D-loop	ACCCATTATATGTATACGGGCATTAA	GG144F	Storey et al. (2007)
D-loop	CGAGCATAACCAAATGGGTTAGA	GG387R	Storey et al. (2007)
TSHR	CTTTCTTCTTGCCCTTTT	TSHR-F biotin	This study
TSHR	GATGCTGACTTTGCTGTA	TSHR-R	This study
TSHR	TGCTGTAGCTGCTGACTC	TSHR-S	This study
BCDO2	ACTCTTGCATGGATCTGG	BCDO2-F biotin	This study
BCDO2	TGTGGTCTCAGAATTTGG	BCDO2-R	This study
BCDO2	TCAGAATTTGGGACG	BCDO2-S	This study

Table 5.1: PCR primers used to amplify and sequence the three loci investigated in this chapter: D-loop (or HVR1), TSHR, and BCDO2. Single letter appendices after primer names denote; F: forward, R: reverse and, S: sequencing. Biotin is an abbreviation of biotinylated.

5.3 Results

The overall success rate of mtDNA retrieval was 67%. The ancient European sample (n=34) comprised three haplotypes that cluster within the E-clade. Two haplotypes were identified as E3 (N=1) and E6 (N=2) according Liu et al. (2006) but E3 and E5 according Dana et al. (2010). The third haplotype is identical to the E1 haplotype but due to the shortened total sequence length (Storely et al. 2007) it was not possible to differentiate between E1, E15 (after Liu et al. 2006, but E1 and E12 according Dana et al. 2010). The topology of the Maximum likelihood tree constructed from an alignment of ninety seven 201bp haplotypes capture the topology of the Neighbour Joining tree produced by Liu et al. (2006), indicating that the short 201bp fragment is sufficient for determining overall genetic variation in the chicken d-loop. However, one discrepancy in internal branching order between clades C and E was observed (figure 5.2, figure 5.3).

The overall success rate for the BCDO2 locus was comparatively low (36%). The probability of falsely determining a heterozygous individual as homozygous after five replications was estimated to be <0.01.

The success rate for the TSHR SNP was higher than for both HVR1 and BCDO2 SNP (72%). The frequency of the derived TSHR allele in the ancient sample was significantly lower than frequencies reported previously for modern populations (Fisher exact test, p=<0.0001) (264 out of 271 birds representing 36 global breeds were shown to be homozygous for the sweep allele and the remaining seven were heterozygous, Rubin et al. 2010). Six ancient individuals were homozygous for the derived C>T allele, while 12 were homozygous for the wild type C allele. 24 individuals were heterozygous. Allelic dropout was observed in 20 out of 24 heterozygous specimens. The probability of falsely assigning a heterozygous individual as homozygous after 5 replications was estimated to be <0.01.

No PCR contaminants were detected.

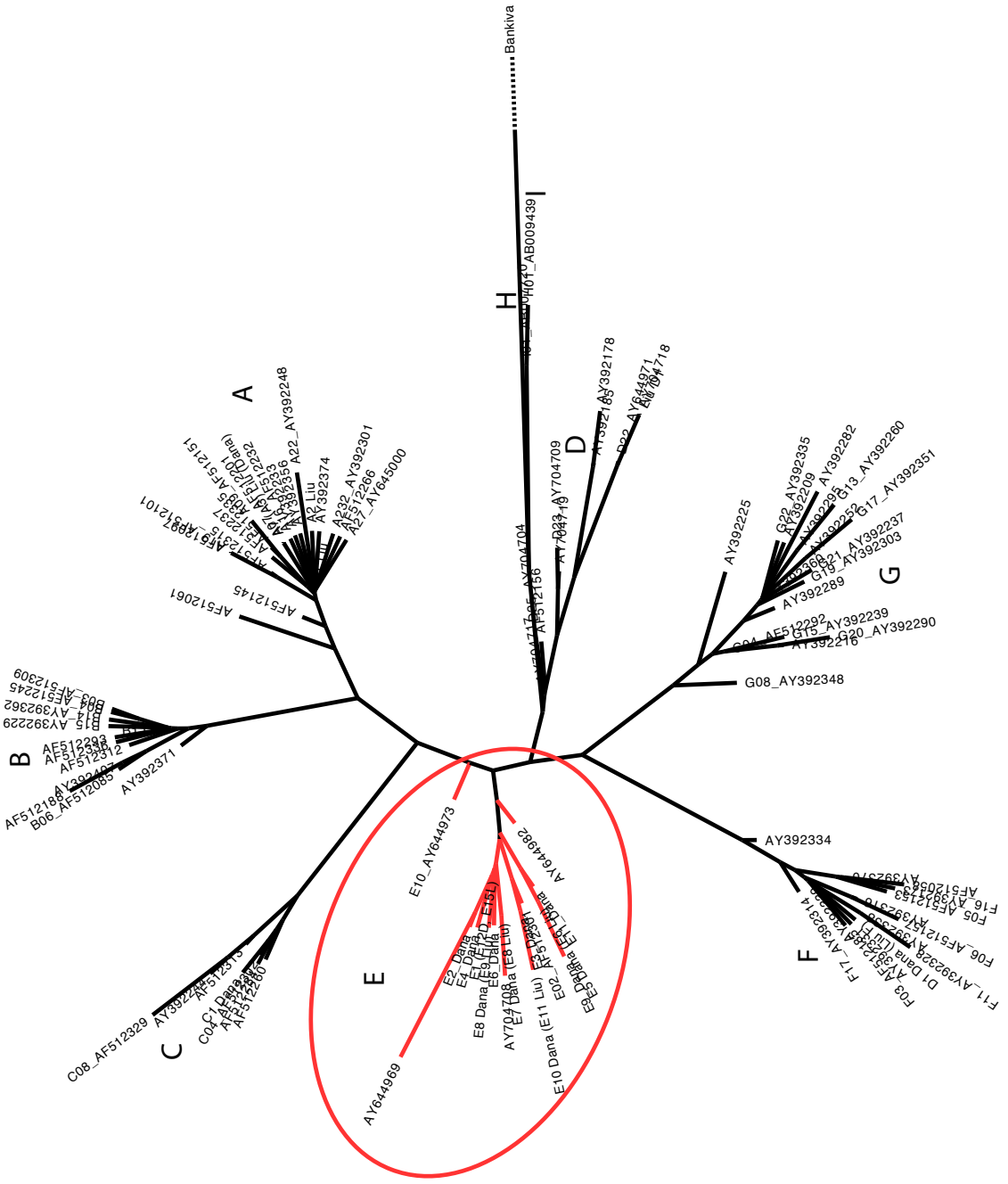


Figure 5.2: A Maximum Likelihood tree constructed from a collapsed mtDNA sequence data comprising the 201bp fragment (Storey et al. 2007) of the haplotypes published by Liu et al. (2006) and a representative sample of the haplotypes published by Dana et al. (2010).

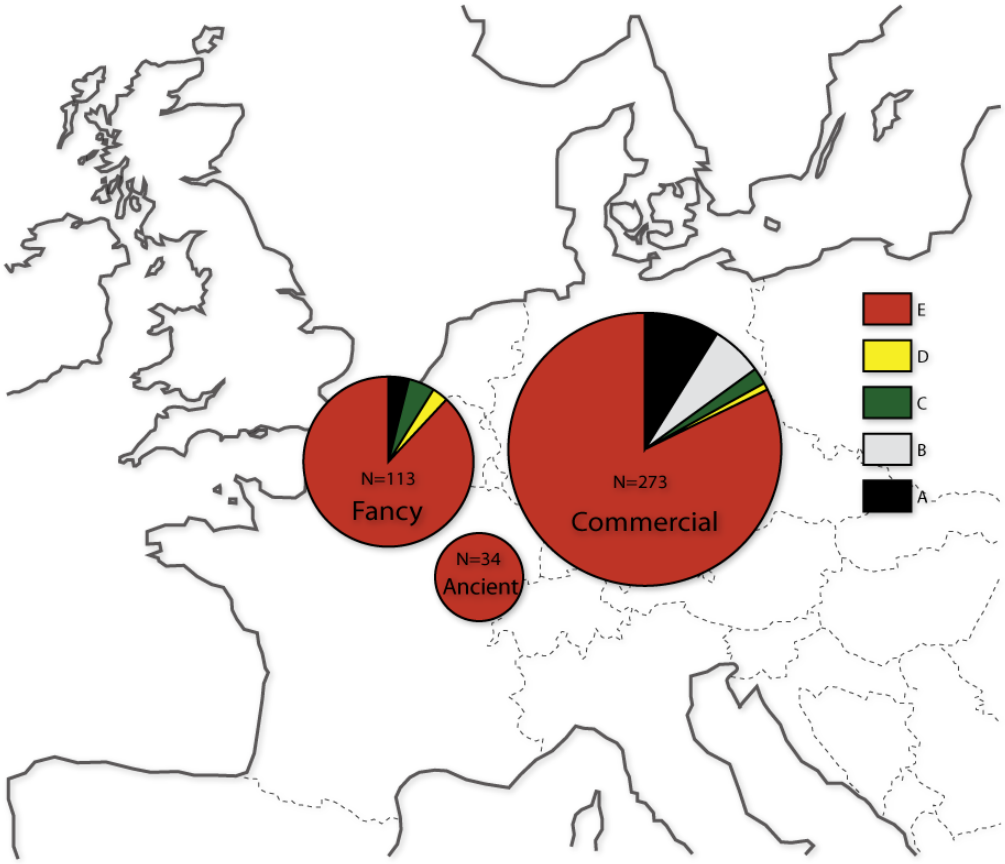


Figure 5.3: Haplogroup proportions in modern chickens (Dana et al. 2010).

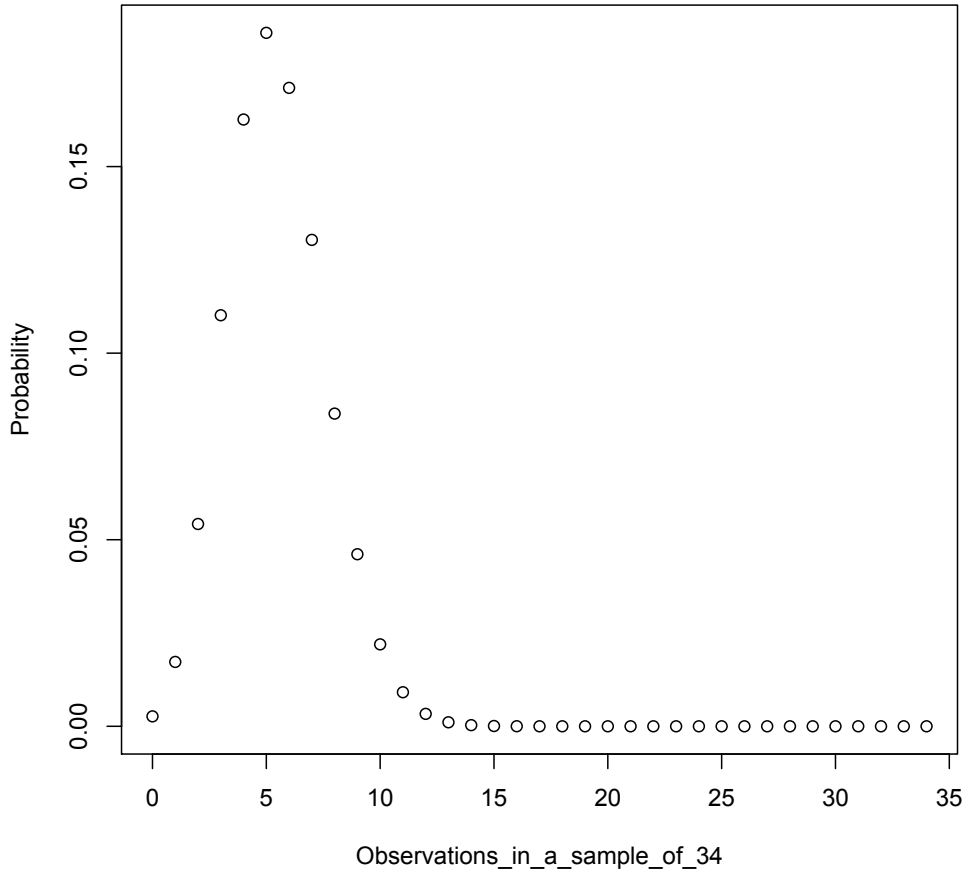


Figure 5.4: The binomial probability distribution of number of observations in a sample of 34 given a frequency (or probability) of 0.16.

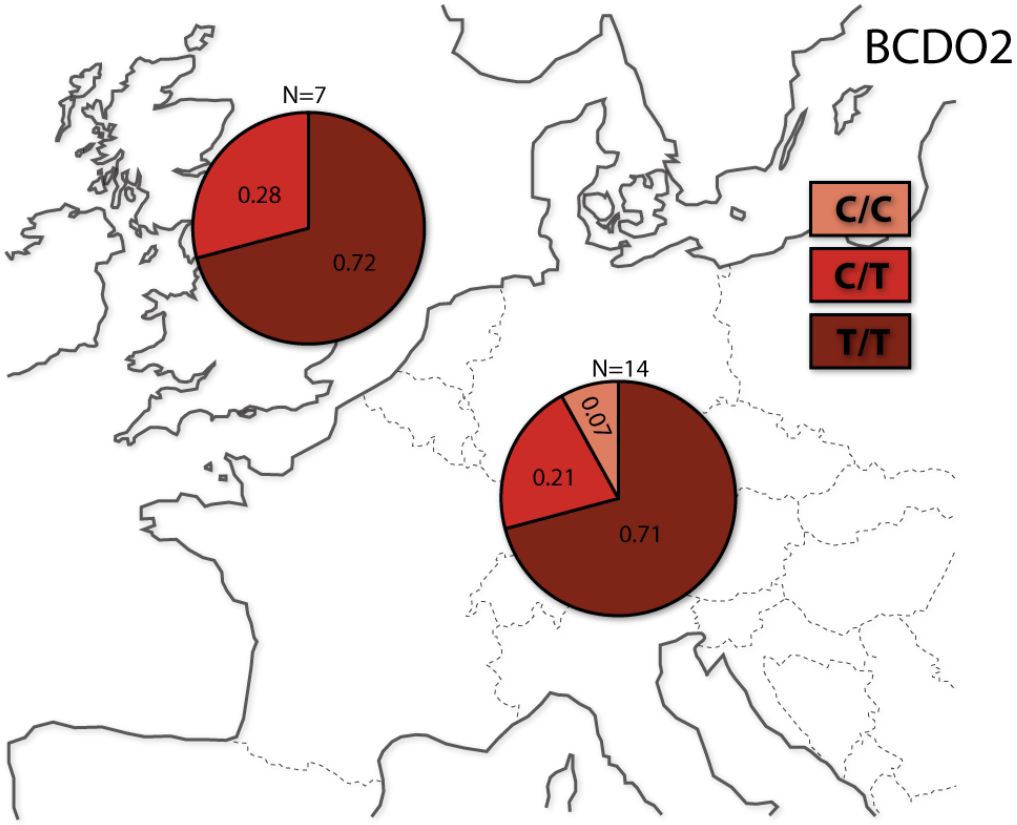


Figure 5.5: Pie chart diagrams depicting the relative proportion of BCDO2 alleles in the ancient UK and German/Austria sample. The T allele corresponds to the wild type W allele and the C allele corresponds to the Gray junglefowl Y allele (Eriksson et al. 2008).

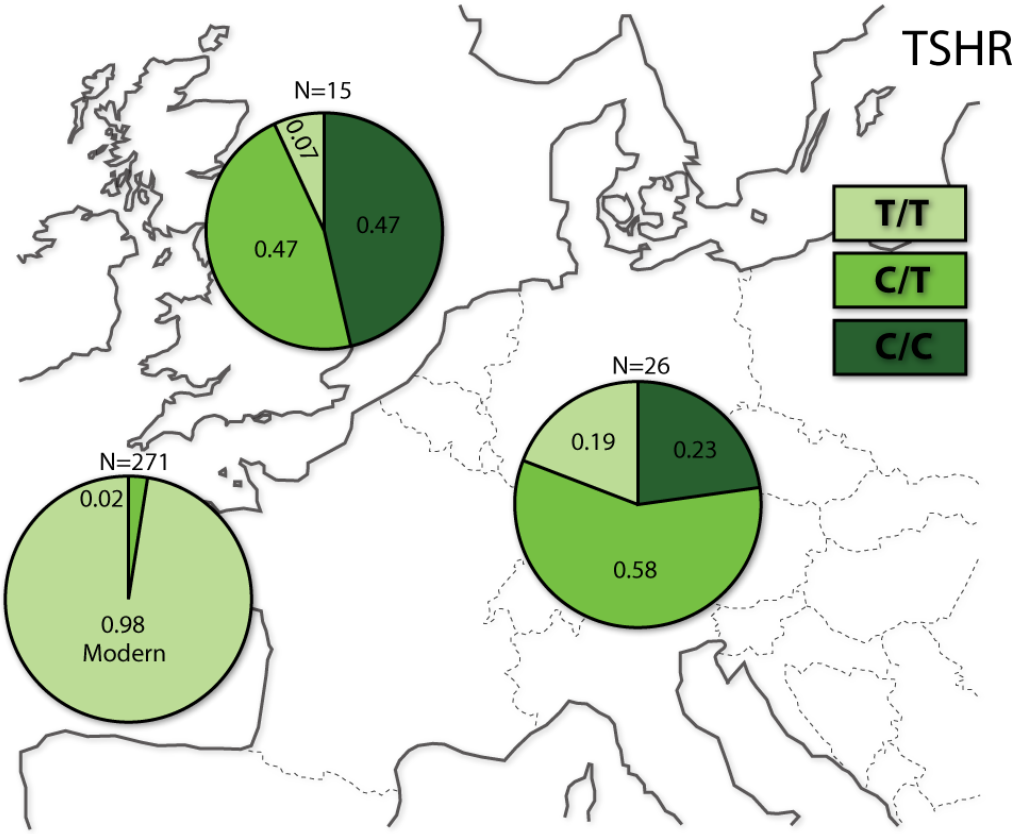


Figure 5.6: The relative proportion of TSHR alleles in the UK and Germany/Austria sample. The modern sample comprises 271 chickens from 36 populations worldwide (Rubin et al. 2010). The discrepancy in allele frequency between the ancient and modern sample is highly significant (Fisher exact test, p=0.0001).

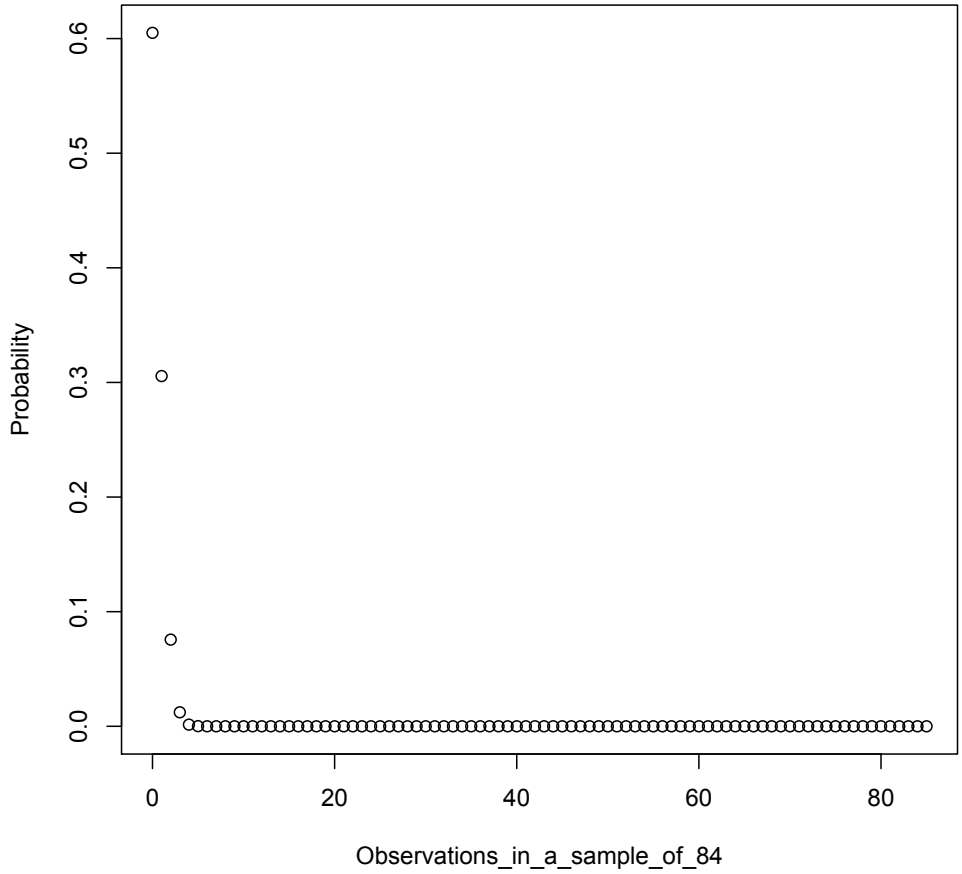


Figure 5.7: The binomial probability distribution of number of observations in a sample of 84 given a frequency (or probability) of 0.01.

Extract ID	Reference ID	Country	Site	Age estinate	Contact	mtDNA	TSHR	BCDO2
Ch1	Nr D553771 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1		
Ch2	Nr D553771 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1		
Ch3	Nr D53772 ob 1513B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/C	C/T
Ch4	Nr D53772 ob 1513B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	T/T	T/T
Ch5	Nr D53830 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1		
Ch6	Nr D53739 ob 1509	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters			
Ch7	Nr D53760 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	T/T	
Ch8	Nr D53760 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1		
Ch9	Nr D53760 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1		
Ch10	Nr D53771 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/C	T/T
Ch11	Nr D53772 ob 1513 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1		
Ch12	Nr D53772 ob 1513 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/T	C/T
Ch13	Nr D53772 ob 1513 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/T	T/T
Ch14	Nr D53772 ob 1513 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/C	
Ch15	Nr D53772 ob 1513 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/T	T/T
Ch16	Nr D53772 ob 1513 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/T	T/T
Ch17	Nr D53772 ob 1513 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/T	
Ch18	Nr D53884 ob 1509 B	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1		
Ch19	Nr D53858 ob 1509	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	T/T	
Ch20	Nr D53858 ob 1509	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/T	T/T
Ch21	Nr D53771 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/C	T/T
Ch22	Nr D53771 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters		C/T	
Ch23	Nr D53771 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters		C/C	
Ch24	Nr D53771 ob 1513 A	Germany	Künzing Kaserfeld	2nd centrury AD Roman	J. Peters	E1	C/T	
Ch25	56/1121*	Germany, Bavaria	Abodiacom, Epfach	50 AD?	J. Peters	E1	C/T	
Ch26	56/554	Germany, Bavaria	Abodiacom, Epfach	50 AD?	J. Peters		C/C	
Ch27	56/1009	Germany, Bavaria	Abodiacom, Epfach	50 AD?	J. Peters	E1	C/T	T/T
Ch28	56/1121*	Germany, Bavaria	Abodiacom, Epfach	50 AD?	J. Peters			
Ch29	?/367	Germany	Manching	200-30 BC La Tene C2/D2	J. Peters			
Ch30	62/336	Germany	Manching	200-30 BC La Tene C2/D3	J. Peters			
Ch31	239	Germany	Manching	200-30 BC La Tene C2/D4	J. Peters	E1	C/C	T/T
Ch32	395	Germany	Manching	200-30 BC La Tene C2/D5	J. Peters			
Ch33	55	Austria	Magdalensberg	100 BC- 50 AD Early Roman	J. Peters	E1	C/T	C/T
Ch34	24	Austria	Magdalensberg	100 BC- 50 AD Early Roman	J. Peters		C/T	
Ch35	3	Austria	Magdalensberg	100 BC- 50 AD Early Roman	J. Peters		T/T	
Ch36	38	Austria	Magdalensberg	100 BC- 50 AD Early Roman	J. Peters		C/T	T/T
Ch37	A140-431	Germany	Altenburg	280 - 15 BC La Tene C and D	J. Peters		C/T	
Ch38	A115-406	Germany	Altenburg	280 - 15 BC La Tene C and D	J. Peters	E1	T/T	C/C
Ch39	A147-439	Germany	Altenburg	280 - 15 BC La Tene C and D	J. Peters			
Ch40	A46-202	Germany	Altenburg	280 - 15 BC La Tene C and D	J. Peters		C/T	
RB367	8209/5589	UK	Arbeia	120 AD - 400 AD Roman	A. Croom			
RB368	2413/5589	UK	Arbeia	120 AD - 400 AD Roman	A. Croom	E1	C/C	C/T
RB369	712/5589	UK	Arbeia	120 AD - 400 AD Roman	A. Croom	E1	C/C	T/T
RB370	3522/89	UK	Arbeia	120 AD - 400 AD Roman	A. Croom	E1	C/C	T/T
RB371	702/5589	UK	Arbeia	120 AD - 400 AD Roman	A. Croom			
RB372	219/5589	UK	Arbeia	120 AD - 400 AD Roman	A. Croom	E1	C/T	
RB373	Chick2	UK	London Wall	Roman?	F. Grew		C/C	
RB374	Chick12	UK	London Wall	Roman?	F. Grew		C/T	C/T
RB375	Chick5	UK	London Wall	Roman?	F. Grew		C/T	T/T
RB376	Chick11	UK	London Wall	Roman?	F. Grew		C/T	T/T
RB378	SLW04 [169]	UK	Scott Lane, Wetherby	11th/12th century AD	Jaques	E1	C/C	
RB379	1995.434 [114]	UK	St. Saviourgate, York	Late medieval 14th/15th century AD	Jaques			
RB380	1995.434 [115]	UK	St. Saviourgate, York	Late medieval 14th/15th century AD	Jaques		C/T	T/T
RB381	2000.584 [3029]	UK	Spurriergate York	11th/12th century AD	Jaques	E6	C/C	
RB382	2000.584 [7004]	UK	Spurriergate York	?	Jaques			
RB383	2000.584 [3080]	UK	Spurriergate York	10th/11th century AD	Jaques		C/C	
RB384	2000.584 [3757]	UK	Spurriergate York	12th/14th century AD	Jaques	E6	T/T	
RB385	[1146]	UK	Beverley Playhouse	Post-medieval 16th-18th century AD	Jaques		C/T	
RB386	[1216]	UK	Beverley Playhouse	Medieval 12th-15th century AD	Jaques			
RB387	[1209]	UK	Beverley Playhouse	Medieval 12th-15th century AD	Jaques			
RB388	[1109]	UK	Beverley Playhouse	Post-medieval 16th-18th century AD	Jaques	E3	C/T	

Table 5.2: A table of the samples, including results, analysed in this chapter.

5.4 Discussion and conclusions

5.4.1 Mitochondrial DNA diversity: was haplogroup E ubiquitous across ancient Europe?

Mitochondrial control region data is the most commonly used genetic marker in chicken domestication studies (Liu et al. 2006; Dana et al. 2010). By sequencing a 201bp control region fragment that captures the overall structure in clades A-I (Liu et al. 2006; Storey et al. 2007; 2010) from temporally structured samples from two major locations in Europe this chapter address the hypotheses of genetic continuity and recent introgression of East Asian breeds (Dana et al. 2006).

No significant difference in control region haplotype frequencies was observed between ancient and modern chickens when grouping the data strictly into A-I haplogroups (one group for each haplogroup) (Dana et al. 2010) (Fisher exact test, p=0.28). There is a significant difference in haplotype frequencies between the ancient and modern sample if pooling non E-clade haplotypes into a single bin (Fisher exact test, p=<0.005). It is therefore possible to reject the null hypothesis that the proportion of haplotypes A, B, C, D (bin 1, N(modern)=63, N(ancient)=0) and E (bin 2, N(modern)=323, N(ancient)=34) were equal in ancient and modern European populations. If expressed as a binomial probability distribution, the probability of observing precisely zero non E-clade haplotypes is 0.0026 (zero observations in a sample of 34, with a probability of 0.16 (the frequency of non E-clade haplotypes in the Dana et al. 2010 modern reference data) (figure 5.4).

These results support the hypothesis that ancient European chickens possessed the E haplogroup and lend weight to the hypothesis that clades A-D were introgressed recently (Liu et al. 2006; Storey et al. 2007; 2010; Dana et al. 2010). The haplogroup structure across breeds reported by Dana et al. (2010) suggests that commercial breeds in particular are heavily admixed with exotic Asiatic breeds,

represented primarily by haplogroups A and B. The timing of this admixture most likely coincided with known breed formation in the last centuries (Darwin 1868; Muir et al. 2008; Dana et al. 2010).

5.4.2 Did early European domestic chickens possess the Gray junglefowl BCDO2 allele?

The frequency of the introgressed *Y* allele in ancient European chickens (7 out of 42 genotyped chromosomes, or 16%) show that the *Y* allele was rare in Europe throughout the studied time period. Secondly, the data show that the yellow skin phenotype was near absent in the populations that were analysed. A single chicken from Altenburg (La Tene C and D) was homozygous for the *Y* allele and is therefore the only individual in the ancient sample that could even express the yellow skin phenotype (Eriksson et al. 2008). The overall dominance of the *W* allele, even in medieval and post-medieval individuals from the UK, show that human-driven selection for the yellow skin phenotype did not take place until recently (assuming that the European population reflects modern commercial breeds, Eriksson et al. 2008, and see also Rubin et al. 2010). In total, 15 ancient chickens were homozygous for the *W* allele, while 5 were heterozygous (figure 5.5).

Because the Grey junglefowl *Y* allele was present in ancient Europe, the GJF/domestic chicken hybridisation event (Eriksson et al. 2008) occurred prior to the introduction of domestic chickens to Europe. The natural range of *G. g. murghi* is restricted to India (West and Zhou 1988; Liu et al. 2006; Eriksson et al. 2008) so the early domestic chickens in Europe must therefore have at least partial ancestry in domestic chickens from the Indian sub-continent (West and Zhou 1988).

5.4.3 Is TSHR a domestication gene?

The low frequency of the derived TSHR allele (figure 5.6) show that TSHR is not a domestication gene: TSHR was not subject to human-driven selection during the early domestication process in East Asia, prior to the expansion of chickens worldwide. The temporal structure of the ancient European data shows no obvious correlation between time and allele frequencies, or time and homozygosity, suggesting that the selective sweep is very recent relative to the age of the ancient specimens (table 5.1). Interestingly, Rubin et al. (2010) genotyped TSHR in 271 birds representing 36 populations and found only 6 wild types in the whole panel, all of which were heterozygous. The TSHR sweep is therefore probably linked to recent breed formation.

Chapter 6

Summary and conclusion

Thesis aims

This thesis uses ancient DNA as a means to examine various aspects of animal domestication. The two main objectives are: (a) to gain a better understanding of where and when pig domestication took place in West Eurasia by exploring mitochondrial phylogeography and population history of wild and domestic pigs in Europe and the Near and Middle East, and, (b) to explore different domestication trajectories of pigs and chickens by analysing genetic markers that are directly linked to different aspects of the process of their domestication (MC1R, TSHR, BCDO2 and the mitochondrial d-loop). Analyses of ancient DNA allows for the investigation of molecular genetic aspects of domestication by monitoring genetic changes through time and provide a means to bridge theoretical and technological aspects of traditional archaeological (and archaeozoological) and genetic research.

Short summary of findings

This thesis demonstrates that ancient DNA is a useful tool for resolving different types of questions of animal domestication, and in doing so, gaining a better understanding of human prehistory. Animal domestication is a continuous but nonlinear evolutionary process that follows different paths (trajectories) of human-animal relationships, which vary in makeup and intensity over time (Dobney and Larson 2006; Zeder 2006; 2008; Vigne 2011, and see figure 1.1). These trajectories (and processes) comprise adaptation to new and changing environments, human intentionality (control and taming of wild animals and selection on behaviour and phenotypic traits), human-mediated movement of domestic herds across space, and wild-domestic admixture (and how that was mediated by people). Because modern domestic animals are (and were) continuously shaped by a complex interaction of these processes, gaining a better understanding of where, when and how these took place helps clarifying not only specific aspects of human prehistory but also the very concept of domestication. The case studies in this thesis show that domestication, in general, is a very complex and non-linear process. Consequently, inferring the past from present-day DNA is unavoidably biased by comparatively recent events that have changed, or even eliminated, genetic signatures from prehistoric events.

6.1 Summary of chapter aims and main findings

6.1.1 Chapter 2

Background

This chapter concerns spatial and temporal mtDNA variation in wild and domestic pigs from Anatolia and the Near East. The main objectives of this study were to gain a better understanding of where and when pigs first were domesticated and

whether people brought domestic pigs of European ancestry to Anatolia during the Iron Age, as previously hypothesised by Larson et al. (2007a).

It has long been recognized that pigs were first domesticated in East Anatolia during the Neolithic (e.g. Ervynck et al. 2001; Peters et al. 2005); a process that was probably the culmination of a several millennia long relationship between humans and local wild boar (Vigne et al. 2009; 2011). Therefore, the first appearance of morphologically domestic pigs during the mid-seventh millennium BC (Ervynck et al. 2001) probably reflected intensification, or an end product, of a much longer and not very well understood process of human interaction with wild (but managed) animals (Vigne et al. 2009).

The relationship between these early domestic pigs and other domestic populations in West Eurasia is not very well understood. Larson et al. (2007a) showed that Neolithic farmers first brought domestic pigs to Europe from the Near East at the onset of the Neolithic revolution. The authors supported this claim on two grounds: first they established the pre-Neolithic diversity in Europe and concluded that spatial arrangement of genetic lineages had remained intact throughout the Holocene. Because modern contemporary wild boar from the Near East predominantly possesses NE2 haplotypes while European wild boar possesses E1 or E2 haplotypes, it would be theoretically possible to detect human-mediated movements of pigs to Europe from the Near East.

Because the Early Neolithic pigs in Europe in fact did possess genetic signatures matching those of modern Near Eastern wild boar, and not the local European wild boar, the authors concluded that humans had brought these from the Near East during the Neolithic expansion into Europe. This fits theoretical expectations but the authors never demonstrated empirically the presence of those specific genetic signatures in ancient pigs from the Near East. The ancient Near Eastern specimens they did analyse possessed other haplotypes, one of which clusters with those found in European wild boar (haplotypes from the E1 clade). The specimens with haplotypes matching European wild boar were Iron Age pigs from Armenia. This finding

provided the basis for their second major hypothesis: that of the Anatolian Turnover event. The hypothesis is that people brought domestic pigs of European ancestry to Anatolia, following their domestication in Europe (which in turn followed the introduction of domestic pigs to Europe, which originally possessed Near Eastern haplotypes).

Summary and main findings

By sequencing DNA extracted from wild and domestic pigs from Neolithic to Medieval times across a geographic area stretching from West Anatolia to Eastern Iran (using small consecutive time bins in which individual specimens were grouped), a good cross-section of the whole region (Anatolia and Middle East) was obtained. Overall success rate of DNA extractions was approximately 40%, which, for the geographical region, is very high (compare for example with Larson et al. 2007a; Bollongino and Vigne 2008). More importantly, the results showed a near-perfect inverse relationship between sample ages and DNA retrieval success rate, suggesting time dependent DNA fragmentation (Allentoft et al. 2012).

Several important observations were made regarding pig domestication in Anatolia. First, the empirical observation that both wild and domestic pigs possessed the Y1 haplotype strongly supports the hypothesis that the first domestic pigs in Europe came originally from the Near East (Larson et al. 2007a). Secondly, the Y1 haplotype was very rare (and often completely absent) at archaeological sites in East Anatolia but very common in West Anatolia (figure 2.6). This finding indicates that the Y1 haplotype was probably domesticated as part of a secondary Neolithic movement in West Anatolia, either independently or as a consequence of westward dispersal of Neolithic peoples and cultures.

The Anatolian turnover hypothesis was also confirmed. People clearly brought domestic pigs possessing E1 haplotypes to Anatolia no later than the Late Bronze Age (figure 2.6). Once these pigs had been brought to Anatolia, they rapidly increased

in numbers (or frequency) until they had replaced all other (domestic) lineages.

Lastly because of a complete absence of the NE2 Y2 haplogroup in temporal bins older than the Middle Bronze Age (4,000-2,600 BP), the Near Eastern origin of this type (Larson et al. 2005; 2007a) could be questioned. Because the Y2 haplotype was previously hypothesised to have originated in the Near and Middle East, where it was domesticated and brought to Europe alongside Y1 pigs, this finding added new important dimensions to further research (see summary of chapter 3, below).

6.1.2 Chapter 3

Background

This chapter expands on the narrative and observations made in chapter 2 by analysing DNA in ancient pigs from Europe. The main objective was to explore and test a series of hypotheses regarding the mode of the Neolithic transmission into Europe and whether pig DNA is a good proxy for detecting patterns of cultural and/or demic diffusion (Larson et al. 2007a). This chapter also investigated two mechanisms that were important during the process of pig domestication: the process of selection on domestic traits (specifically coat colour variability) and the process of admixture (introgression) with local wild boar populations (Fang et al. 2009; Larson et al. 2007a).

1. MtDNA haplogroups E1 and E2, and NE1 and NE2 do not share a natural range overlap, where the former two clades are geographically restricted to Europe and the latter two are geographically restricted to the Near and Middle East (Larson et al. 2005; 2007a). This hypothesis relies on the assumption that the Bosporus strait (and the Black Sea) has been a physical barrier to gene flow between wild boar in the Near East and Europe throughout the Holocene. It has been argued that this barrier gave rise to the spatial arrangement of

phylogenetically distinct clades observed in modern West Eurasian wild boar populations (Larson et al. 2005).

Larson et al. (2007a) published ancient genetic data from Europe and the Near East that supported the hypothesis that the Bosporus is a barrier to gene flow. The authors showed that genetic variation in pre-Neolithic European wild boar was restricted to the major European clade (E1) and the Italian clade (E2). This observation was constructed into a pre-Neolithic comparative baseline for evaluating genetic variation in Europe from that period onwards. However, it is because of two reasons necessary to test the validity of the comparative baseline. First, certain geographic regions in close proximity to the Neolithic contact zone in southeast Europe (Balkans) are poorly sampled (Larson et al. 2007a). Secondly, because the Y2 lineage is rare in the Near East but present in Mesolithic and Neolithic contexts on Crimea (Larson et al. 2007a) it remains a possibility that Y2 is in fact European (see chapter 2 and figure 2.6).

2. Neolithic migrant farmers brought domestic pigs possessing haplotype Y1 to Europe from the Near East (Larson et al. 2007a). This hypothesis relies on the validity of the pre-Neolithic comparative baseline and assumes that humans must have introduced pigs that possess non-E1 or non-E2 haplotypes to Europe.

3. The Y2 lineage was also introduced to Europe from the Near East by Neolithic migrant farmers, but dispersed along another expansion route than Y1 pigs (southern Mediterranean route and the northern Danubian route respectively) (Larson et al. 2007a).

4. The introduction of domesticated pigs from the Near East was followed by domestication of local European wild boar in Central Europe towards the end of the Neolithic. This hypothesis relies on the observation that domestic pigs possessing European E1 signatures replaced the introduced Y1 haplogroup at least by 3,900 BC, probably through introgression with local wild boar. The last domestic pig possessing the Y1 lineage was observed at Bercy in

the Paris basin, a region highlighted as a putative center for local European domestication (Larson et al. 2007a).

Summary and main findings

Because wild boar from several Mesolithic (and Upper Palaeolithic) sites in the Iron Gates (often directly radiocarbon dated), at some point during the first half of the Holocene, possessed all four major haplogroups E1, E2, NE1 and NE2 (although never NE2 haplotypes Y1 or Arm1T, assuming that all Y1 pigs from chapter 3 are domestic) the hypothesis of genetic continuity in Europe and the Near and Middle East throughout the Holocene (Larson et al. 2007a) could be falsified. However, this finding did not imply that the hypothesis of a physical barrier to gene flow between Europe and the Near East is false. Further research into the wild/domestic status of European Y1 pigs must be carried out to resolve that question. Were some of these pigs in fact wild (which preliminary wild/domestic status calls could suggest), it would imply that gene flow occurred between Anatolia and Southeast Europe to the mid-Holocene.

This chapter also shed new light on the introduction and dispersal of domestic pigs to Europe from the Near East. A spatial and temporal survey of wild and domestic pigs, coupled with direct AMS radiocarbon dating, provided evidence that pigs carrying the Y1 haplotype spread from the Aegean and Southwest Balkans into North and Central Balkans, and further into Central Europe, mirroring the Danubian LBK expansion (Burger and Thomas 2011). However, the Y1 haplotype was not found in pigs from Neolithic South Europe, but those pigs carried only haplotypes matching those of local European wild boar (E1 and NE2 Y2). Their domestic status was bolstered by the fact that they carried a derived, domestic, variant of the MC1R gene. Because these were domestic pigs carrying European haplotypes, dating to up to 5,000 BC, and because they possessed a domestic MC1R phenotype (which was shown to have originated in the Near East), the timing and location of local domestication could be pushed back by up to a millennium (the previous estimate

was 3,900 BC, Larson et al. 2007a). It is probable that the Cardial (South European) population reflects admixture that took place in the Balkans prior to their westward expansion along the Mediterranean coastline.

MC1R

Mesolithic European wild boar (n=3) possessed the wild type phenotype while a Chalcolithic pig from Central Anatolia was homozygous for the derived, domestic, allele. Because chapter 2 indicated that no gene flow took place from Europe to Anatolia before the human introduction of E1 pigs during the Bronze Age, it is safe to conclude that this mutation arose in Anatolia, probably during the Early Neolithic.

However, the D124N substitution (the domestic allele) was not fixed among European Y1 pigs, suggesting that relaxed purifying selection only (as opposed to directed selection, Fang et al. 2009) allowed the D124N substitution to be maintained in the domestic population at low frequency. Alternatively, though not mutually exclusive, the low frequency among Y1 pigs could be explained by male-mediated gene flow to domestic Y1 sows, a breeding practice known from modern PNG (Hide 2003). The admixture scenario also fit the hypotheses of early local European domestication that followed the first introduction of pigs from the Near East, suggesting that both male and female gene flow took place.

6.1.3 Chapter 4

Background

Chapter 4 examines the phylogeography and population structure of West Eurasian wild boar. The main objective of this chapter was to determine the processes that

have shaped the spatial arrangement of genetic lineages across space and time. Because mitochondrial phylogeography is a common method for inferring domestication events (e.g. Giuffra et al. 2000; Larson et al. 2005), re-assessing the usefulness of that approach in the light of new research (chapters 2 and 3) is critical.

Summary and main findings

The findings in this chapter confirm the picture that West Eurasian wild boar have a very complex and dynamic history of gene flow and lineage replacement. There is very little geographic structure to the genetic variation in mainland Europe (geographic distances do not correspond to genetic distances) and local populations, primarily the Balkans, have experienced major shifts in haplogroup frequencies. The modern structure is likely the result of physical barriers to gene flow (hence an absence of gene flow from areas East and South to the Balkans) combined with rapidly expanding local populations.

6.1.4 Chapter 5

Background

This chapter is the fourth case study and test a number of specific hypotheses concerning three unlinked genetic loci in domestic chickens (TSHR, BCDO2 and mtDNA). The overall aim is to describe the domestication trajectory for these loci and to contrast these results with hypotheses formulated on the basis of modern data. For example, TSHR, and to some extent BCDO2, are hypothesised to be domestication genes (Rubin et al. 2010). By directly genotyping these markers in ancient chickens, it is possible to test (falsify or verify) hypotheses based solely on modern data. It is also possible to get a good insight as to whether these genetic markers, and associated phenotypes, were a key component of the early

domestication process (as with the MC1R gene in pigs, see chapter 3).

Summary and main findings

This study show that the domestication trajectory of chickens, like that of pigs, was non-linear and complex, probably encompassing many diffuse stages of varying degrees of human interaction and intentionality (Zeder 2006; 2008; Vigne 2011, and see figure 1.1). For example, because the results of this chapter show that TSHR was not a domestication gene (Rubin et al. 2010), two conclusions can be drawn: gene frequencies in modern populations are poor markers for inferring ancient processes (as shown for a similar genetic markers in wheat, Asplund et al. 2010). Secondly, because TSHR was not a domestication gene, the relationship between the function of this gene (a phenotype that is still not understood, Rubin et al. 2010) and the mechanisms underlying the process of early domestication are not necessarily linked. To clarify: if this study *would* have confirmed that TSHR underwent a selective sweep during the early domestication process, it would have been possible to build on that finding and hypothesise that the function and phenotype of the sweep allele was an important trait for people who first domesticated chickens.

6.1.5 Future work

Because of the complex population history of wild boar and domestic pigs in West Eurasia, it would be useful to step away from the classical phylogeographic framework of reference (Giuffra et al. 2000; Larson et al. 2005; 2007a). Mitochondrial DNA (mtDNA phylogeography) is useful for detecting and characterising population dynamics across time and space (like the Bayesian skyride, chapter 4), and to some extent to track major shifts in populations across time and space (see chapters 2 and 3). However, an approach similar to that of Skoglund et al. (2012) would be a feasible method to pursue (for chickens, pigs and other domestic species). In that study,

high-throughput shotgun sequencing captured random nuclear SNPs in a number of human ancient DNA extracts. Because those SNPs are randomly spread across the (diploid) genome, the power to resolve complex questions such as admixture and long-term population trajectories is increased significantly compared to that of mtDNA. This type of study is feasible in pig domestication studies not least because of the vast number of preserved specimens available (chapter 2 and 3), but also because of the massive amount of modern reference data that is currently available (with whole genomes and genome wide SNP data becoming readily available). In addition, further (morphometric) research will also clarify the wild/domestic status of many of the ancient specimens analysed for this thesis. Those results will allow for more specific analyses in which wild and domestic pigs are separated. By doing so, the data presented in chapters 2-4 will undoubtedly shed even more light on the hypotheses and questions addressed in this thesis.

Chapter 7

Bibliography

Akey, J. M., Ruhe, A. L., Akey, D., Wong, A. K., Connelly, C. F., Madeoy, J., Nicholas T. J., and Neff, M. W. 2010. Tracking footprints of artificial selection in the dog genome. *Proc Natl Acad Sci U S A.* 1073: 1160.

Albarella, U., Manconi, F., Rowley-Conwy, P., and Vigne, J-D. 2006a. Pigs of Corsica and Sardinia: a biometrical re-evaluation of their status and history. In U. Tecchiati, U., and Sala, B. (Eds.), *Archaeozoological Studies in Honour of Alfredo Riedel.* Province of Bolzano, Bolzano. Pp. 285-302.

Albarella, U., Tagliacozzo, A., Dobney, K., and Rowley-Conwy, P. 2006b. Pig hunting and husbandry in prehistoric Italy: a contribution to the domestication debate. *Proceedings of the Prehistoric Society* 72: 193- 227.

Albarella, U., Dobney, K., Rowley-Conwy, P. 2009. Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology*, 14: 103-136.

Alves, E., Vilo, C., Rodrguez, M.C., Sili, L. 2003. Mitochondrial DNA sequence variation and phylogenetic relationships among Iberian pigs and other domestic and wild pig populations. *Animal Genetics* 34: 319-324.

Alves, P.C., Pinheiro, I., Godinho, R., Vicente, J., Gortazar., C. and Scandura, M. 2010. Genetic diversity of wild boar populations and domestic pig breeds (*Sus scrofa*) in Southwestern Europe. *Biological Journal of the Linnean Society* 101: 797–822.

Alexandri, P., Triantafyllidis, A., Papakostas, S., (et al.). 2011. The Balkans and the colonization of Europe: the post-glacial range expansion of the wild boar, *Sus scrofa*. *Journal of Biogeography* 39: 713-723.

Allentoft, M. E., Collins, M., Harker, D., (et al.). 2012 The half-life of DNA in bone: measuring decay kinetics in 158 dated fossils. *Proceedings of the Royal Society B* 279: 4224-4733.

Andersson, L. 2001. Genetic dissection of phenotypic diversity in farm animals. *Nature Reviews Genetics* 2, 130-138.

Ammerman, AJ., and Cavalli-Sforza LL. 1973. A population model for the diffusion of early farming in Europe. In: Renfrew, C. (Ed.) *The explanation of culture change.* London: Duckworth. Pp. 343–357.

Ammerman, AJ., and Cavalli-Sforza, LL. 1984. *The Neolithic transition and the genetics of populations in Europe.* Princeton: Princeton University Press. 176.

Asplund, L., Hagenblad, J., and Leino, M. 2010. Re-evaluating the history of the wheat domestication gene NAM-B1 using historical plant material. *Journal of Archaeological Science*: 37(9): 2303-2307.

Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A., Saunders, N.C., 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Ann. Rev. Ecol. Syst.* 18: 489–522.

Avise, J.C. 2000. *Phylogeography: the History and Formation of Species.* Harvard University Press: MA, USA.

Avise, J.C. 2009. Phylogeography: retrospect and prospect. *Journal of Biogeography*, 36: 3-15.

Apollonio M., Randi E. & Toso S. 1988. The systematics of the wild boar (*Sus scrofa* L.) in Italy. *Bollettino di Zoologia* 3: 213–21.

Apollonio M, Andersen R, Putman R. 2010. (Eds.) European Ungulates and Their Management in the 21st Century. Cambridge University Press, Cambridge, UK.

Arbuckle, BS. (*in press*) Pigs at Köşk Höyük: An ethnic or ecological marker? *Anadolu.*

Balasse, M., and Tresset, A. 2002. Early weaning of Neolithic domestic cattle (Bercy, France) revealed by intra-tooth variation in nitrogen isotope ratios. *Journal of Archaeological Science* 29: 853-859.

Bandelt, HJ., Forster, P., Rohl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* 16: 37-48.

Barsh GS. 1996. The genetics of pigmentation: from fancy genes to complex traits. *Trends in Genetics* 12: 299–305.

Bar-Yosef, O. 1998. The Natufian Culture in the Levant, Threshold to the Origins of Agriculture. *Evolutionary Anthropology* 6: 159-177.

Bar-Yosef, O. 2011. Climatic Fluctuations and Early Farming in West and East Asia. *Current Anthropology* 52: 175-193.

Baylac M. 2012. Rmorph: a R geometric and multivariate morphometrics library.

Baylac, M., and Friess, M. 2005. Fourier descriptors, procrustes superimposition and data dimensionality: an example of cranial shape analysis in modern human populations. In: Slice, D.E. (Ed.), *Modern Morphometrics in Physical Anthropology*. Springer-Verlag, New York. Pp. 145-165.

Beja-Pereira, A., Caramelli, D., Lalueza-Fox, C., (et al.). 2006. The origin of European cattle: evidence from modern and ancient DNA. *Proc Natl Acad Sci USA* 103:8113–8118.

Belfer-Cohen, A, and Bar-Yosef, O. 2000. Early sedentism in the Near East: a bumpy ride to village life. In *Life in Neolithic farming communities: social organization, identity, and differentiation.* Ian Kuijt, (ed.). Pp. 19–37. New York: Plenum.

Berthouly-Salazar, C., Rognon, X., Nhu Van, T., (et al.) 2010. Vietnamese chickens: a gate towards Asian genetic diversity. *BMC genetics* 11:53.

Bignon, O., Baylac, M., Vigne, J-D, & Eisenmann, V. 2005 Geometric morphometrics and the population diversity of Late Glacial horses in Western Europe (*Equus caballus arcelini*): phylogeographic and anthropological implications. *Journal of Archaeological Science* 32: 375-391.

Binladen, J., Wiuf, C., Gilbert, M. T .P., (et al.). 2006. Assessing the Fidelity of Ancient DNA Sequences Amplified From Nuclear Genes. *Genetics* 172: 733-741.

Binladen, J., Gilbert, M.T.P., Bollback, J.P., (et al.). 2007. The Use of Coded PCR Primers Enables High-Throughput Sequencing of Multiple Homolog Amplification Products by 454 Parallel Sequencing. *PLoS ONE* 2(2).

Björnerfeldt, S., Webster, MT., Vila C. 2006. Relaxation of selective constraints in dog mitochondrial DNA following domestication. *Genome research* 16: 990-994.

Bollongino, R., Edwards, C., and Alt. K., (et al.). 2006. Early history of European domestic cattle as revealed by ancient DNA. *Biology Letters* 22: 155–159.

Bollongino, R., and Burger, J. 2007. Neolithic cattle domestication as seen from ancient DNA. *Proceedings of the British Academy* 144: 165-187.

Bollongino, R., Elsner J., Vigne, J-D., Burger, J. 2008a. Y-SNPs Do Not Indicate Hybridisation between European Aurochs and Domestic Cattle. *PLoS ONE* 3(10).

Bollongino, R., Tresset, A., and Vigne, J-D. 2008b. Environment and excavation: Pre-lab impacts on ancient DNA analyses. *Comptes Rendus Palevol* 7: 91-98.

Bollongino, R., and Vigne, J-D. 2008. Temperature monitoring in archaeological animal bone samples in the Near East arid area, before, during and after excavation. *Journal of Archaeological Science* 35: 873-881.

Bökönyi, S. 1974. *History of domestic mammals in Central and Eastern Europe*, Budapest, Akadmiai Kiad.

Bramanti, B., Thomas, M. G., Haak, W., (et al.). 2009. Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. *Science* 326: 137-140.

Briggs, A. W., Stenzel, U., Johnson, P. L. (et al.). 2007. Patterns of damage in genomic DNA sequences from a Neandertal. *Proc Natl Acad Sci USA*. 104: 14616-14621.

Briggs, AW., Good, JM., Green, RE., Krause, J., Maricic, T., (et al.). 2009. Targeted retrieval and analysis of five Neandertal mtDNA genomes. *Science* 325: 318–321.

Bryce, T. 2005. *The kingdom of the Hittites*. Oxford University Press, Oxford. New Ed pp xix, 554p.

Bull, G., Payne, S. 1982. Tooth eruption and epiphysial fusion in pigs and wild boar. In Wilson, B, Grigson, C. Payne S. (Eds.), *Ageing and sexing animal bones from archaeological sites*. British Archaeological Reports, British Series 109. Archeopress, Oxford: 55-71.

Burger, J., and Thomas, M. G. 2011. Palaeopopulationgenetics of man, cattle, and dairying in Neolithic Europe. In: Pinhasi R. and Stock J (Eds.) *Human Bioarchaeology of the Transition to Agriculture*. Wiley-Liss. Pp. 371-384.

Campler, M. and M. Jngren (et al.). 2009. Fearfulness in red junglefowl and domesticated White Leghorn chickens. *Behavioural processes* 81:39-43.

Cieslak, M., Pruvost, M., Benecke, N., Hofreiter, M., Morales, A., Reissmann, M., and Ludwig, A. 2010. Origin and History of Mitochondrial DNA Lineages in Domestic Horses. *PLoS One* 5(12).

Champlot, S., Berthelot, C., Pruvost, M., Bennett. EA., Grange, T., (et al.). 2010. An efficient multistrategy DNA decontamination procedure of PCR reagents for hypersensitive PCR applications. *PLoS One*(5).

Chessa, B., Pereira, F., Arnaud, F, (et al.). 2009. Revealing the history of sheep domestication using retrovirus integrations. *Science* 324: 532–536.

Childe, V. G. 1925. *The Dawn of European Civilization.* Kegan Paul, London.

Clutton-Brock, J. 1999. *A natural history of domesticated mammals*. Cambridge, Cambridge University Press.

Clutton-Brock, J. 1989. Introduction to domestication, in Clutton-Brock, J. (ed.) In *The Walking Larder: Patterns of Domestication, Pastoralism, and Predation.* Unwin Hyman, London. Pp. 10-19.

Cruz, F. Vila, C. Webster, MT. 2008. The legacy of domestication: accumulation of deleterious mutations in the dog genome. *Molecular biology and Evolution* 25: 2331-2336.

Cucchi T, Fujita M, Dobney K. 2009. New insights into pig taxonomy, domestication, and human dispersal in Island South East Asia: molar shape analysis of Sus remains from Niah Caves, Sarawak. *Int. J. Osteoarchaeol.* 19: 508–530.

Cucchi, T., Hulme-Beaman, A. Yuan, J., Dobney, K. 2010. Early Neolithic pig domestication at Jiahu, Henan Province, China: Clues from molar shape analyses using geometric morphometric approaches. *Journal of Archaeological Science* 38: 11-22.

Conolly, J., Colledge, S., Dobney. K., Vigne, J-D., Peters, J., Stopp, B., Manning, K., Shennan, S. 2011. Meta-analysis of zooarchaeological data from SW Asia and SE Europe provides insight into the origins and spread of animal husbandry. *Journal of Archeological Science* 38: 538–545.

Cooper, A., and Poinar, H. 2000. Ancient DNA: do it right or not at all. *Science* 289: 1139.

Cruz, F., Vila, C., Webster, MT. 2008. The legacy of domestication: accumulation of deleterious mutations in the dog genome. *Molecular biology and Evolution* 25: 2331-2336.

Crockford, S.J. 2002. Animal domestication and heterochronic speciation: the role of thyroid hormone. pg. 122-153. In: N. Minugh-Purvis & K. McNamara (Eds.) *Human Evolution Through Developmental Change.* Baltimore, Johns Hopkins University Press.

Crockford, S. 2004. Animal domestication and vertebrate speciation: a paradigm for the origin of species. (dspace.library.uvic.ca.)

Crockford, S. 2009. Evolutionary roots of iodine and thyroid hormones in cell-cell signaling. *Comp. Biol.* 49 (2): 155-166.

Dalén L, Nyström V, Valdiosera C, (et al.). 2007. Ancient DNA reveals lack of postglacial habitat tracking in the arctic fox. *Proc Natl Acad Sci U S A.* 104: 6726-6729.

Dana, N., Megens, H-J., Crooijmans, R. P. M. A. O. (et al.). 2010. East Asian contributions to Dutch traditional and western commercial chickens inferred from mtDNA analysis. *Animal genetics* 42(2): 125-133.

Darwin, C. 1868. *The variation of animals and plants under domestication*, Volume 1, London: John Murray.

Daskalaki, E., Anderung, C., and Humphrey, L. 2011. Further developments in molecular sex assignment: A blind test of 18th and 19th century human skeletons. *Journal of Archaeological Science* 38: 1326–1330.

De Cupere, B., Duru, R., Umurtak, G. 2008. Animal husbandry at the Early Neolithic to Early Bronze Age site of Bademağacı (Antalya province, SW Turkey): evidence from the faunal remains. In: Vila, E., Gourichon, L., Choyke, AM., Buitenhuis, H., (Eds). *Proceedings of the eight International Symposium on the Archaeozoology of southwestern Asia and adjacent areas*: Archéorient, Maison de l'Orient et de la Méditerranée. p. 367-405.

Deguilloux, M. F., Moquel, J., Pemonge, M. H., and Colombeau, G. 2008. Ancient DNA supports lineage replacement in European dog gene pool: insight into Neolithic southeast France. *Journal of Archaeological Science* 36: 513-519.

Diamond, J. 2002. Evolution, consequences and future of plant and animal domestication. *Nature* 418: 700-707.

Diamond J, and Bellwood P. 2003. Farmers and their languages: the first expansions. *Science* 300: 597–603.

Dinu A., Meiggs D., Balasescu A., Boroneant A., Soficaru D. A. and Miritoiu N. 2006. On Men and Pigs: Were Pigs Domesticated at Mesolithic Iron Gates of the Danube? Part One: Teeth Metrics. *Studii de Preistorie* 3: 77-98.

Dobney, K. Larson, G. 2006. Genetics and animal domestication: new windows on an elusive process. *Journal of Zoology*, 269, 261-271.

Dobson, M. 1998. Mammal distributions in the western Mediterranean: the role of human intervention. *Mammal Review* 28(2): 77–88.

Drummond, A. J. and Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214.

Drummond, AJ., Ashton, B., Buxton, S., (et al.). 2011. Geneious v5.4: Available from http://www.geneious.com/.

Edwards, C., Bollongino, R. (et al.). 2007. Mitochondrial DNA analysis shows a Near Eastern Neolithic origin for domestic cattle and no indication of domestication of European aurochs. *Proc Royal Soc B*. 274:1377-85.

Ekman, J. 1974. Djurbensmaterialet frn stenlderslokalen Ire, Hangvar sn, Gotland. In Janzon, G. (ed.), *Gotlands Mellanneolitiska Gravar*, Almqvist and Wiksell, Stockholm (Acta Universitatis Stockholmiensis, Studies in North-European Archaeology 6). Pp. 212-246.

Eriksson, J., Larson, G., Gunnarsson, U., Bedhom, E., Tixier-Boichard, M., Strömstedt, L., Wright, L., Jungerius, A., Vereijken, A., and Randi, E. 2008. Identification of the yellow skin gene reveals a hybrid origin of the domestic chicken. *PLoS Genetics* 4.

Ervynck, A., Hongo, H., Dobney, K., Meadow, R. 2001. Born free? New evidence for the status of *Sus scrofa* at Neolithic Cayönü Tepesi. *Paléorient*, 27, 47-73.

Excoffier. L., Smouse, P.E. and Quattro, J.M. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 131: 479-491.

Excoffier, L., and Lischer H. 2005. Arlequin ver. 3.5. An Integrated Software Package for Population Genetics Data Analysis. *Computational and Molecular, Population Genetics Lab (CMPG).*

Fajardo, V., Gonzalez, I., Martin, I., Rojas, M., Hernandez, P.E., Garcia, T., Martin, R., 2008. Differentiation of European wild boar (*Sus scrofa scrofa*) and domestic swine (*Sus scrofa domestica*) meats by PCR analysis targeting the mitochondrial D-loop and the nuclear melanocortin receptor 1 (MC1R) genes. *Meat Sciences* 78: 314-322.

Fang, M., and Andersson, L. 2006. Mitochondrial diversity in European and Chinese pigs is consistent with population expansions that occurred prior to domestication. *Proceedings of the Royal Society B* 273: 1803-1810.

Fang, M., Berg, F., Ducos, A. and Andersson, L. 2006. Mitochondrial haplotypes of European wild boars with 2n = 36 are closely related to those of European domestic pigs with 2n = 38. *Animal Genetics* 37: 459–464.

Fang, M., Larson, G., Soares Ribeiro, H., Li, N., Andersson, L. 2009. Contrasting Mode of Evolution at a Coat Color Locus in Wild and Domestic Pigs. *PLoS Genetics* 5.

Fernandez, H., Hughes, S., Vigne, J-D., (et al.). 2006. Divergent mtDNA lineages of goats in an Early Neolithic site, far from the initial domestication areas. *Proc Natl Acad Sci U S A.* 103: 15375-15379.

Fumihito, A., Miyake, T., and Sumi, S. 1994. One subspecies of the red junglefowl (*Gallus gallus gallus*) suffices as the matriarchic ancestor of all domestic breeds. *Proc Natl Acad Sci USA* 91: 12505-12509.

Fumihito, A., Miyake, T., Takada, M., (et al.). 1996. Monophyletic origin and unique dispersal patterns of domestic fowls. *Proc Natl Acad Sci USA* 93: 6792-5.

Galibert, F., P. Quignon and C. Hitte (et al.) 2011. Toward understanding dog evolutionary and domestication history. *Comptes Rendus Biologies* 334:190-6.

Gagneux, P., Boesch, C., and Woodruff, D. S. 1997. Microsatellite scoring errors associated with noninvasive genotyping based on nuclear DNA amplified from shed hairs. *Molecular Ecology* 6: 861–868.

Genov, P.V. 1999. A review of the cranial characteristics of the wild boar (*Sus scrofa* Linnaeus 1758), with systematic conclusions. *Mammal Review* 29: 205–238.

Genov., P.V. 2004. Craniometric charachteristics of the subgenus *Sus* Linneaus, 1758 and a systematic conclusion. *Galemys* 16 (n^{o} especial): 9-23.

Giuffra, E., Kijas, J.M.H., Amarger, V., Carlborg, O., Jeon, J.T. & Andersson, L. 2000. The origin of the domestic pig: independent domestication and subsequent introgression. *Genetics* 154: 1785–1791.

Gilbert, M.T.P., Willerslev, E., Hansen, A., Barnes, I., Rudbeck, L., Lynnerup, N., Cooper, A., 2003. Distribution patterns of postmortem damage in human mitochondrial DNA. *Am. J. Hum. Genet* 72: 32-47.

Gilbert, M.T.P., Bandelt, H. J., Hofreiter, M., Barnes, I. 2005. Assessing ancient DNA studies. *Trends Ecol Evol* 20:5414.

Gilbert, M.T.P., Binladen, J., Miller, W., (et al.). 2007. Recharacterization of ancient DNA miscoding lesions: insights in the era of sequencing-by-synthesis. *Nucleic Acids Res.* 35: 1–10.

Giosan, L., F, F., and Constantinescu, S. 2009. Was the Black Sea catastrophically flooded in the early Holocene? *Quaternary Science Reviews* 28(1-2): 1-6.

Gentry, A., Clutton-Brock, J., and C. Groves. 2004. The naming of wild animal species and their domestic derivatives. *Journal of Archaeological Science* 31: 645–651.

Gongora, J., Peltoniemi, O.A.T., Tammen, I., Raadsma, H. & Moran, C. 2003. Analyses of possible domestic pig contribution in two populations of Finnish farmed wild boar. *Acta Agriculturae Scandinavica, Section A – Animal Science*, 53: 161–165.

Gongora, J., Rawlence, N. J. Mobegi, V. A. (et al.). 2008. Indo-European and Asian origins for Chilean and Pacific chickens revealed by mtDNA. *Proc Natl Acad Sci U S A.* 105: 10308-10313.

Green, R., Briggs, A., Krause, J., (et al.). 2009. The Neandertal genome and ancient DNA authenticity. *EMBO Journal* 28: 2494-2502.

Groeneveld, L. F., Lenstra, J. A., Eding, H. (et al.). 2010. Genetic diversity in farm animals - a review. *Animal genetics* 41: 6-31.

Groves, C. 1981. *Ancestors for the Pigs: Taxonomy and Phylogeny of the Genus Sus*. Research School of Pacific Studies, Australian National University, Canberra, Australia.

Groves, C. 2007. Current views on taxonomy and zoogeography of the genus *Sus*. In: Albarella U., Dobney K., Ervynck A. & Rowley-Conwy P. (Eds.), *Pigs and Humans. 10,000 years of interaction.* Oxford: Oxford University Press. Pp. 15-29.

Groves, C.P., and Grubb, P. 1993. The Eurasian suids: *Sus* and *Babyrousa*. In: Oliver, W.L.R. (ed.) *Pigs, Peccaries and Hippos*. International Union for Conservation of Nature (IUCN), Gland, Switzerland. Pp. 107–111.

Guindon, S., and Gascuel, O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst Biol* 52: 696-704.

Guindon S., Dufayard J.F., Lefort V., Anisimova M., Hordijk W. and G. O. 2010. New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0 *Systematic Biology* 59(3): 307-321.

Groenen, M. AM., Megens, H-J., Zare, Y., 2011. The development and characterization of a 60K SNP chip for chicken. *BMC Genomics* 12:274.

Götherström, A., Anderung, C., Hellborg, L., Elburg, R., Smith, C., Bradley D. G., and Ellegren, H. 2005. Cattle domestication in the Near East was followed by hybridization with aurochs bulls in Europe. *Proceedings of the Royal Society B* 272: 2345-50.

Haak, W., Balanovsky, O., Sanchez, JJ., (et al.). 2010. Ancient DNA from European Early Neolithic Farmers Reveals Their Near Eastern Affinities. *PLoS Biology* 8(11).

Hajji, G., and Zachos, F.E. 2011. Mitochondrial and nuclear DNA analyses reveal pronounced genetic structuring in Tunisian wild boar *Sus scrofa*. *European Journal of Wildlife Research* 57(3): 449-456.

Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl Acids Symp Ser* 41: 95-98.

Hammer, Ø., Harper, D.A.T., Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Haile, J., Larson, G., Owens, K., (et al.). 2010. Ancient DNA typing of archaeological pig remains corroborates historical records. *Journal of Archaeological Science* 37: 174-177.

Harty, C. 2007. Implementing Innovation: Transforming Practices and Technologies in Construction Work. *CIB World Building Congress*: 357-370.

Hide, R. 2003. Pig husbandry in New Guinea. A literature review and bibliography. *ACIAR Monograph* No. 108.

Higuchi, R., Bowman, B., Freiberger, M., Ryder, OA., Wilson, AC. 1984. DNA sequences from the quagga, an extinct member of the horse family. *Nature* 312: 282-284.

Ho, S.Y.W., Kolokotronis, S.O., and Allaby, R.G. 2007. Elevated substitution rates estimated from ancient DNA sequences. *Biology letters* 18: 1-5.

Hofreiter, M., Jaenicke, V., Serre, D., Haeseler, A., Pääbo, S. 2001a. DNA sequences from multiple amplifications reveal artifacts induced by cytosine deamination in ancient DNA. *Nucleic Acids Res* 29: 4793-4799.

Hofreiter, M., D. Serre, H. N. Poinar, M. Kuch and S. Paabo. 2001b. Ancient DNA. *Nature Reviews Genetics* 2: 353-359.

Hongo, H. and Meadow, R. 1998. Pig exploitation at Neolithic Çayönü Tepesi (Southeastern Anatolia). In: Nelson, SM. (Ed.) *Ancestors for the pigs: pigs in prehistory.* Philadelphia (PA): Penn Press. p. 77–98.

Höss, M., Jaruga, P., Zastawny, TH., Dizdaroglu, M., Pääbo, S. 1996. DNA damage and DNA sequence retrieval from ancient tissues. *Nucleic Acids Res* 24: 1304-1307.

Itan, Y,. Powell, A., Beaumont, M. A., Burger, J., Thomas, M. G. 2009. The origins of lactase persistence in Europe. *PLoS Comput. Biol.* 5(8).

Jensen, P. 2006. Domestication - From behaviour to genes and back again. *Applied animal behaviour science* 97: 3–15.

Jesse, R., Véla, E., Pfenninger, M. .2011. Phylogeography of a Land Snail Suggests Trans-Mediterranean Neolithic Transport. *PLoS ONE* 6(6).

Jing, Y., and Flad, R. 2002. Pig domestication in ancient China. *Antiquity* 76: 724-732.

Jonsson, L. 1986. From wild boar to domestic pig - a reassessment of Neolithic swine of northwestern Europe. In Knigsson, L.-K. (ed.), *Nordic Late Quaternary Biology and Ecology*, Striae 24. Pp. 125-129.

Kanginakudru, S., Metta, M., Jakati, R., and Nagaraju, J. 2008. Genetic evidence from Indian red jungle fowl corroborates multiple domestication of modern day chicken. *BMC Evol Biol* 8(1): 174.

Katoh, K., Misawa, K., Kuma, K., Miyata, T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucl. Acids Res.* 30: 3059-3066.

Kerstens, H.D.H., Crooijmans, R., Dibbits., B.W. (et al.). 2011. Structural variation in the chicken genome identified by paired-end next-generation DNA sequencing of reduced representation libraries. *BMC Genomics* 2011, 12:94

Kijas, J.M.H., and Andersson, L. 2001. A phylogenetic study of the origin of the domestic pig estimated from the near- complete mtDNA genome. *Journal of Molecular Evolution*, 52, 302–308.

Kingman J. F. C. 1982. The coalescent. *Stochastic Process. Appl*. 13: 235–248.

Koutsogiannouli, E.A., Moutou, K.A., Sarafidou, T., Stamatis, C., Mamuris, Z. 2010. Detection of hybrids between wild boars (*Sus scrofa scrofa*) and domestic pigs (*Sus scrofa f. domestica*) in Greece, using the PCR-RFLP method on melanocortin-1 receptor (MC1R) mutations. *Mammal Biology* 75: 69-73.

Lacan, M., Keyser, K., Ricaut., F-X., (et al.). 2011. Ancient DNA reveals male diffusion through the Neolithic Mediterranean route. *Proc Natl Acad Sci USA*.108: 9788–9791.

Larson, G., Dobney, K., Albarella, U, (et al.). 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science* 307: 1618–1621.

Larson, G., Albarella, U., Dobney, K., (et al.). 2007a. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *Proc Natl Acad Sc*i *U S A*. 104: 15276–15281.

Larson, G., Cucchi, T., Fujita, M., (et al.). 2007b. Phylogeny and ancient DNA of Sus provides insights into neolithic expansion in Island Southeast Asia and Oceania. *Proc Natl Acad Sci U S A* 104: 4834–4839.

Larson, G. Liu, R. Zhao, X. Yuan, J. (et al.). 2010. Patterns of East Asian pig domestication, migration, and turnover revealed by modern and ancient DNA. *Proc Natl Acad Sci USA* 107: 7686-91.

Larson, G., Cucchi, T., and Dobney, K. 2011. Genetic aspects of pig domestication. In M. F. Rothschild & A. Ruvinsky (Eds.), *The genetics of the pig* (2nd ed., pp. 14–37). Wallingford: CAB International.

Leonard, J. A., Shanks, O., Hofreiter, M., (et al.). 2007. Animal DNA in PCR reagents plagues ancient DNA research. *Journal of Archaeological Science* 34: 1361-1366.

Leonard, J. A. 2008. Ancient DNA applications for wildlife conservation. *Molecular Ecology* 17, 4186–4196.

Librado, P., and Rozas, J., 2009. DnaSP v. 5, A software for comprehensive analyses of DNA polymorphism data. *Bioinformatics* 25: 1451-1452.

Lindahl, T., 1993. Instability and decay of the primary structure of DNA. *Nature* 362: 709-715.

Linderholm, A., Malmström, H., Lidén, K., Holmlund, G., and Götherström. A. 2008. Cryptic contamination and phylogenetic nonsense. *PloS One*(3): 2316.

Lindqvist, C., and Possnert, G. 1997. The subsistence economy and diet at Jakobs/Ajvide, Eksta parish and other prehistoric dwelling and burial sites on Gotland in long-term perspective. In Burenhult, G. (ed.), *Remote Sensing vol. I*, Institute of Archaeology, University of Stockholm (Theses and Papers in North European Archaeology 13a). Pp. 29-90.

Lira, J., Linderholm, A., Olaria, C., (et al.). 2010. Ancient DNA reveals traces of Iberian Neolithic and Bronze Age lineages in modern Iberian horses. *Molecular ecology* 19: 64-78.

Liu, Y., Wu, G., Yao, Y., Miao, Y., and Luikart, G. 2006. Multiple maternal origins of chickens: out of the Asian jungles. *Molecular phylogenetics* 38: 12-19.

Ludwig, A., Pruvost, M,. Reissmann, M., and Benecke, N. (et al.). 2009. Coat color variation at the beginning of horse domestication. *Science* 324: 485.

Lyman, L.R. 1994. *Vertebrate taphonomy*. Cambridge University Press, Cambridge.

Malmström, H., Stor, J., Dalén, L., Holmlund, G., and Götherström. A. 2005. Extensive human DNA contamination in extracts from ancient dog bones and teeth. *Molecular biology and Evolution* 22: 2040-7.

Malmström, H., Svensson, E., and Gilbert, M. T. P. (et al.). 2007. More on contamination: the use of asymmetric molecular behavior to identify authentic ancient human DNA. *Molecular biology and Evolution* 24(4): 998-1004.

Malmström, H., Vila, C., Gilbert, M. T. P., (et al.). 2008. Barking up the wrong tree: modern northern European dogs fail to explain their origin. *BMC Evol Biol* 8: 71.

Malmström H, Linderholm A, Lidén K, Storå J, Molnar P, (et al.). 2010. High frequency of lactose intolerance in a prehistoric hunter-gatherer population in northern Europe. *BMC Evolutionary Biology* 10: 89.

Manilus, N. 1999. Le sanglier en gypte [The wild boar in Egypt]. *Comptes Rendus de l'Academie des Sciences* Paris, Series III, Sciences de la vie 322, 573-577.

Masseti, M. 2009. A possible approach to the conservation of the mammalian populations of ancient anthropochorous origin of the Mediterranean islands. *Folia Zool.* 58(3): 303-308.

Mayer, J. J., and I. L. Brisbin, Jr. 1991. *Wild pigs in the United States: their history, comparative morphology, and current status.* Univ. of Georgia Press, Athens. Pp. 313.

Melchert, HC. 2011 Indo-Europeans. *The Oxford handbook of ancient Anatolia: 10,000-323 B.C.E* Steadman, SR. and McMahon, JG. (Eds.) (Oxford University Press, New York). Pp. 705-716.

Mignon-Grasteau, S,. Boissy, A., Bouix, J. (et al.). 2005. Genetics of adaptation and domestication in livestock. *Livestock Production Science* 93, 3-14.

Mona, S., Randi, E., Tommaseo-Ponzetta, M. 2007. Evolutionary history of the genus Sus inferred from cytochrome b sequences. *Molecular Phylogenetics and Evolution* 45: 757–762.

Mosimann, JE., and James, FC. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* 33: 444-459.

Muir, W. M., Wong, G. K-H., Zhang, Y., (et al.). 2008. Genome-wide assessment of worldwide chicken SNP genetic diversity indicates significant absence of rare alleles in commercial breeds. *Proc Natl Acad Sci U S A.* 105(45): 17312–17317.

Mullis, KB., and Faloona, FA. 1987. Specific synthesis of DNA in vitro via a polymerase-catalyzed chain reaction. *Methods Enzymol* 155: 335-350.

Myles, S., Boyko, A.R., Owens, C.L., (et al.). 2011. Genetic structure and domestication history of the grape. *Proc Natl Acad Sci U S A.* 108: 3530–3535.

Naderi, S., Rezaei, H.R., Pompanon, F. (et al.). 2008. The goat domestication process inferred from large-scale mitochondrial DNA analysis of wild and domestic individuals. *Proc Natl Acad Sci U S A.* 105: 17659.

Nei, M. 1987. *Molecular Evolutionary Genetics*. Columbia University Press, New York, NY, USA.

Nishibori, M., Shimogiri, T., Hayashi, T., Yasue, H. 2005 Molecular evidence for hybridization of species in the genus *Gallus* except for *Gallus varius*. *Animal Genetics* 36(5): 367-375.

Nuin, P. 2010. ”http://www.genedrift.org/files/mrmtgui.zip.”

Nylander, J. 2004. Modeltest: testing the model of DNA substitution, Evolutionary Biology Centre, Uppsala University, Sweden.

Ojeda, A., Rozas, J., Folch, JM., Perez-Enciso, M. 2006. Unexpected high polymorphism at the FABP4 gene unveils a complex history for pig populations. *Genetics* 174: 2119–2127.

Oliver, W.L.R., Groves, C.P., Cox, C.R. and Blouch, R.A. 1993. Origins of domestication and the pig culture. In: Oliver, W.L.R. (ed.) *Pigs, Peccaries, and Hippos*. International Union for Conservation of Nature (IUCN), Gland, Switzerland. Pp. 171–179.

Oross, K., and Bánffy, E. 2009. Three successive waves of Neolithisation. LBK development in Transdanubia. *Documenta Praehistorica* 36: 175-189.

Österholm, I. 1989. *Bosttningsmnstret på Gotland under stenåldern. En analys av fysisk miljö, ekonomi och social struktur.* Stockholm, University of Stockholm.

Özdogan M. 2011. Archaeological evidence on the westward expansion of farming communities from eastern Anatolia to the Aegean and the Balkans. *Current Anthropology* 52: 415–430.

Pääbo, S. 1985. Molecular cloning of ancient Egyptian mummy DNA. *Nature* 314: 644-645.

Pääbo, S., Poinar, H., Serre, D., Jaenicke-Despres, V., Hebler, J., Rohland, N., Kuch, M., Krause, J., Vigilant, L., Hofreiter, M. 2004. Genetic analyses from ancient DNA. *Annual Review Genetics* 38: 645-679.

Pang, J., Kluetsch, C., Zou, X., (et al.). 2009. MtDNA data indicate a single origin for dogs south of Yangtze River, less than 16,300 years ago, from numerous wolves. *Molecular Biology and Evolution* 26: 2849.

Perlès, C. 2003. An Alternate (and old-fashioned) view of Neolithisation in Greece. In M Budja (ed.), *10th Neolithic Studies.* Documenta Praehistorica 30: 99-114.

Peters, J. (Ed.). 1998. *Römische tierhaltung und tierzucht* (Verlag Marie Leidorf GmbH, Rahden/Westf), Vol 5.

Peters, J., Helmer, D., Von Den Driesch, A., and M. Saa Segui. 1999. Early animal husbandry in the northern Levant. *Paléorient* 25, 27-48.

Peters, J., Von Den Driesch, A. Helmer, D. 2005. The upper Euphrates-Tigris basin: cradle of agro-pastoralism? In: Vigne, J-D., Peters, J. Helmer, D. (Eds.) *The First Steps of Animal Domestication: New Archaeological Approaches.* Oxford: Oxbow Books. Pp. 96-124.

Price, T. D. 2000. Europe's first farmers: an introduction. In *Europe's first farmers.* T. D. Price (ed.) Pp. 1–18. Cambridge: Cambridge University Press.

Price, D. T. and Bar-Yosef, O. 2011. The Origins of Agriculture: New Data, New Ideas. *Current Anthropology* Volume 52: 163-174.

Pruvost, M., Schwarz, R., Correia, VB., Champlot, S., Grange, T., (et al.). 2008. DNA diagenesis and palaeogenetic analysis: Critical assessment and methodological progress. *Paleogeography, Paleoclimatology and Paleoecology* 266: 211–219.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randi, E., D'Huart, J-P., Lucchini, V., Aman., R. 2002. Evidence of two genetically deeply divergent species of warthog, *Phacochoerus africanus* and *P. aethiopicus* (Artiodactyla: Suiformes) in East Africa. *Mammalian Biology - Zeitschrift für Säugetierkunde* 67(2): 91-96.

Ramayo, Y., Shemeret'eva, I. N., Pérez-Enisco, M. 2010. Mitochondrial DNA diversity in wild boar from the Primorsky Krai Region (East Russia). *Animal Genetics* 42(1): 96-99.

Rambaut, A. and Drummond, A. J. 2007. Tracer v 1.4. University of Edinburgh, UK.

Provan, J., and Bennett, K.D. 2008. Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution* 23, 564-571.

Ramirez, O., Ojeda, A., Tomas A., (et al.) 2009) Integrating Y-chromosome, mitochondrial, and autosomal data to analyze the origin of pig breeds. *Molecular Biology and Evolution* 26: 2061–72.

Redding, R. 2005. Breaking the mold: a consideration of variation in the evolution of animal domestication In: Vigne, J.-D., Peters, J. Helmer, D. (Eds.) *The First Steps of Animal Domestication: New Archaeological Approaches*. Oxford: Oxbow books. Pp. 41-49.

Redding, R., and Rosenberg, M. 1998. Ancestral Pigs: A New (Guinea) Model for Pig Domestication in the Near East. In *Ancestors for the pigs: pigs in prehistory.* Sarah M. Nelson (ed.). Pp. 65-76. MASCA Research Papers in Science and Archaeology 15. Philadelphia: University of Pennsylvania Museum.

Ronquist, F. (et al.) 2011. MrBayes 3.2 http://mrbayes.sourceforge.net/

Robb, J., and Miracle, P. 2007. Beyond migration versus acculturation: new models for the spread of agriculture. *Proceedings of the British Academy* 144: 99-115.

Rook, L., and Martínez-Navarro, B. 2010. Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International* 219: 134–144.

Rosenberg, M., Redding., R.W., Nesbitt, R., Peasnall, B.L. 1998. Hallan Çemi, pig husbandry, and post-pleistocene adaptations along the Taurus-Zagros Arc (Turkey). *Paléorient* 24: 25-41.

Rowley-Conwy, P. 2003. Early domestic animals in Europe: imported or locally domesticated? In: *The Widening Harvest. The Neolithic Transition in Europe: Looking Back, Looking Forward.* Ammerman A. Biagi P. (Eds.) Boston: Archaeological Institute of America. AIA Colloquia and Conference Papers 6: 99-117.

Rowley-Conwy, P. 2009. Human prehistory: hunting for the earliest farmers. *Current Biology* 19: 948-949.

Rowley-Conwy, P., and Dobney, K. 2007. Wild boar and domestic pigs in Mesolithic and Neolithic southern Scandinavia. In: Albarella, U., Dobney, K., Ervynck, A. Rowley-Conwy, P. (Eds.) *Pigs and humans: 10,000 years of interaction* Oxford University Press. Pp. 131-155.

Rubin, C., Zody, M., Eriksson, J., and J. Meadows. (et al.). 2010. Whole-genome resequencing reveals loci under selection during chicken domestication. *Nature* 464: 587–591.

Russell, N. 2002. The wild side of animal domestication. *Society and Animals*, 10, 285-302.

Rűtimeyer, L. 1862. *Die Fauna der Pfahlbauten der Schweiz, Bürkli, Zrich (Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft fr die Gesammten Naturwissenschaften).* Basel.

Sagona, AG., and Zimansky, P. 2009. *Ancient Turkey*. New York: Routledge.

Sampietro, M.L., Lao, O., Caramelli, D., Lari, M., Pou, R., Marti, M., Bertranpetit, J., Lalueza-Fox, C. 2007. *Proc Biol Sc*i 274: 2161-2167.

Sampson, A. 1998. The Neolithic and Mesolithic Occupation of the Cave of Cyclope, Youra, Alonnessos, Greece. *The Annual of the British School at Athens* 93: 1-22.

Savolainen, P., Zhang, Y.P., Luo, J., Lundeberg, J., and Leitner, T. 2002. Genetic evidence for an East Asian origin of domestic dogs. *Science* 298: 1610-1613.

Sawai, H., Kim, H-L., Kuno, K.. (et al.). 2010. The Origin and Genetic Variation of Domestic Chickens with Special Reference to Junglefowls *Gallus g. gallus* and *G. varius*. *PLoS One*(5).

Scandura, M., Iacolina, L., Crestanello, B., (et al.). 2008. Ancient vs. recent processes as factors shaping the genetic variation of the European wild boar: are the effects of the last glaciation still detectable? *Molecular Ecology* 17: 1745-1762.

Scandura, M., Iacolina, L., Apollonio., M. 2011a. Genetic diversity in the European wild boar *Sus scrofa*: phylogeography, population structure and wild x domestic hybridization. Mammal Review 41(2): 125-137.

Scandura, M., Iacolina, L., Cossu, A., Apollonio, M. 2011b. Effects of human perturbation on the genetic make-up of an island population: the case of the Sardinian wild boar. *Heredity* 106(6): 1012-1020.

Seeher, J. 2011. The plateau: the Hittites. In: Steadman, SR., McMahon, JG, (Eds). *The Oxford handbook of ancient Anatolia: 10,000–323 B.C.E.* New York: Oxford University Press. p. 376–392.

Sheppy, A. 2009. The colour of domestication and the designer chicken. *Optics Laser Technology*. 86: 885–899.

Shimodaira H., Hasegawa M. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Mol. Biol. Evol.* 16: 1114-1116.

Skoglund, P., Malmström, H., Raghavan, M., (et al.). 2012. Origins and Genetic Legacy of Neolithic Farmers and Hunter-Gatherers in Europe. *Science* 336: 466-469.

Smith, CI., Chamberlain, AT., Riley, MS., Stringer, C., Collins, MJ. 2003. The thermal history of human fossil remains and the likelihood of successful DNA amplification. *Journal of Human Evolution* 45: 203-217.

Sommer, RS., and Nadachowski, A. 2006. Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Review* 36: 251–265.

Storey, A. A., Ramrez, J. M., Quiroz, D., (et al.). 2007. Radiocarbon and DNA evidence for a pre-Columbian introduction of Polynesian chickens to Chile. *Proc Natl Acad Sci U S A.* 104: 10335-10339.

Storey, A. A, Spriggs, M., Bedford, S., (et al.). 2010. Mitochondrial DNA from 3000- year old chickens at the Teouma Site, Vanuatu. *Journal of Archaeological Science*: 37: 2459-2468.

Svensson, E.M., Anderung, C., Baubliene, J., Persson, P., Malmström, H., Smith, C., Vretemark, M., Daugnora, L., Götherström, A. 2007. Tracing genetic change over time using nuclear SNPs in ancient and modern cattle. *Animal Genetics* 38: 378-383.

Svensson, E. and A. Götherström. 2008. Temporal fluctuations of Y-chromosomal variation in Bos taurus. *Biology Letters* 4: 752.

Swofford, D. .2000. PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer, Sunderland, Mass.

Taberlet, P., S. Friffin, B., Goossens, S., Questiau, V., Manceau (et al.). 1996. Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Res*. 24: 3189–3194.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.G., Cossons, F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, 7: 453–464.

Taberlet, P,. Valentini, A., Rezaei. (et al.). 2008. Are cattle, sheep, and goats endangered species? *Molecular Ecology* 17:275-284.

Terral, J-F., Tabard, E., Bouby, L., (et al.). 2010. Evolution and history of grapevine (*Vitis vinifera*) under domestication: new morphometric perspectives to understand seed domestication syndrome and reveal origins of ancient European cultivars. *Ann Bot.* 105 :443–455.

Trantalidou, K. 2008. Glimpses of Aegean Island Communities during the Mesolithic and Neolithic Periods: the Zooarchaeological Point of View. In N. Brodie, J. Doole, G. Gavalas, and C. Renfrew (Eds.), *ORIZON. A Colloquium on the Prehistory of the Cyclades.* Cambridge pp. 19-27.

Tresset, A, and Vigne, J-D. 2007. Substitution of species, techniques and symbols at the Mesolithic-Neolithic transition in Western Europe. *Proceedings of the British Academy* 144: 189-210.

Tresset, A., and Vigne, J-D. 2011. Last hunter-gatherers and first farmers of Europe. *Computes Rendes Biologies* 334: 182-189.

Tringham, R., 2000. Southeastern Europe in the transition to agriculture in Europe: bridge, buffer or mosaic. In T. D. Price (ed.), *Europe's First Farmers*. Cambridge University Press, Cambridge. Pp. 19-56.

Trut, L.N. 1999 Early Canid domestication: The Farm Fox Experiment. *American Scientist* 87. 160-169.

Uerpmann, H-P. 2008. Domestication of animals. In Pearsall, D, M. (Ed.) *Encyclopedia of Archaeology*. Elsevier. Pp. 434-445.

Ursing, B.M., and Arnason, U. 1998. The complete mitochondrial DNA sequence of the pig (*Sus scrofa*). *Journal of Molecular Evolution* 47: 302–306.

Valdiosera, C. E., Garcia-Garitagoitia, J. L.. Garcia, N. (et al.). 2008. Surprising migration and population size dynamics in ancient Iberian brown bears (*Ursus arctos*). *Proc. Natl Acad. Sci. USA*. 105(13): 5123-5128.

Van Heerwaarden, J., Doebley, J., Briggs, W.H., Glaubitz, J.C., Goodman, M.M., de Jesus Sanchez Gonzalez, J., Ross-Ibarra, J. 2011. Genetic signals of origin, spread, and introgression in a large sample of maize landraces. *Proc Natl Acad Sci U S A*. 108: 1088–1092.

Van Laere, A-S, Minh Nguyen, (et al.). 2002. A regulatory mutation in IGF2 causes a major QTL effect on muscle growth in the pig. *Nature* 425: 832-836.

Van Wijngaarden, J.G. 2002 *Use and Appreciation of Mycenaean Pottery in the Levant, Cyprus and Italy (1600–1200 BC)*. Amsterdam: Amsterdam University Press.

Vigne, J-D., Zazzo, A., Salige, J.-F., Poplin, F., Guilaine, J. and Simmons, A. 2009. Pre-Neolithic wild boar management and introduction to Cyprus more than 11,400 years ago. *Proc Natl Acad Sci U S A*. 106: 16135-8.

Vigne, J-D. 2011. The origins of animal domestication and husbandry: a major change in the history of humanity and the biosphere. *Comptes Rendus Biologies* 334: 171–181.

Vigne, J-D., Carrre, I., Briois, F., Guilaine, J. 2011. The early process of the mammal domestication in the Near East: new evidence from the Pre-Neolithic and Pre-Pottery Neolithic in Cyprus. *Current Anthropology* 52(4): 255-271.

Wang, ZF., Yonezawa, T., Liu, B., Ma, T., Shen, X., (et al.). 2011. Domestication Relaxed Selective Constraints on the Yak Mitochondrial Genome. *Molecular Biology and Evolution* 28: 1553–1556.

West, B., and B. X. Zhou. 1988. Did chickens go north? New evidence for domestication. *Journal of Archaeological Science* 15: 515-533.

White, K. D. 1970. *Roman farming*. Cornell University Press, Ithaca, New York, USA.

Whittle, A. 1990. Radiocarbon dating of the Linear Pottery culture: the contribution of cereal and bone samples. *Antiquity* 64: 297-302.

Wiener, P., Wilkinson, S. 2011. Deciphering the genetic basis of animal domestication. *Proc. R. Soc. B* 278, 3161-3170.

Wright, S. 1978. The relation of livestock breeding to theories of evolution. *Journal of Animal Science* 46, 1192-1200.

Wright, S. 1943. Isolation by distance. *Genetics* 28: 114–138.

Wright, S. 1951. The genetic structure of populations. *Annals of Eugenics* 15: 323-354.

Wright, D., Rubin, C-J., Barrio., A. (et al.) 2010. The genetic architecture of domestication in the chicken: effects of pleiotropy and linkage. *Molecular Ecology* 19(23): 5140-46.

Wu, G-S., Yao, Y-G., Qu, K-X. (et al.) 2007. Population phylogenomic analysis of mitochondrial DNA in wild boars and domestic pigs revealed multiple domestication events in East Asia. *Genome Biology* 8:245.

Yücel Senyurt, S. 2005. Büyükardic - An Early Iron Age hilltop settlement in Eastern Anatolia. *In Publications of archaeological salvage excavations: 2* (Gazi Universtity research center for Archaeology, Ankara).

Zeder, M. 1994. Of Kings and Shepherds: Specialized Animal Economy in Ur III Mesopotamia, In: *Chiefdoms and Early States in the Near East: The Organizational Dynamics of Complexity*. Pp. 175-191. Stein, G. and Rothman, M. (Eds). Prehistory Press: Madison, WI.

Zeder, M. 2006. Central Questions in the Domestication of Plants and Animals. *Evolutionary Anthropology* 15, 105-177.

Zeder, M. A., Emshwiller, E., Smith, B-D., and Bradley, D.. 2006. Documenting domestication: the intersection of genetics and archaeology. *Trends in Genetics* 22: 139-155.

Zeder, M. 2008. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *Proc Natl Acad Sci U S A.* 105. 33: 11597-11604.

Zeder M. 2011. The origins of agriculture in the Near East. *Current Anthropology* 52: 221–235.

Zeuner, F. E. 1963. *A history of domesticated animals*. London, Hutchinson Co. Ltd.

Websites

4Peaks (nucleobytes.com/4peaks)

www.distancefromto.net/countries.php

FigTree (http://tree.bio.ed.ac.uk/software/figtree/)

Geneious (http://www.geneious.com/)

Network 4.6 (http://www.fluxus-engineering.com)

MrBayes 3.2 http://mrbayes.sourceforge.net/

MrMtGui (http://www.genedrift.org/files/mrmtgui.zip.)

OxCal v4 (c14.arch.ox.ac.uk/oxcal.html)

PAST (http://palaeo-electronica.org/2001_1/past/issue1_01.htm)

Se-Al (http://tree.bio.ed.ac.uk/software/seal/)

Chapter 8

Appendix A

The 152 unique haplotypes analysed in chapters 3 and 4 (table 3.1 and 4.1) are depicted below (table 8.1) relative to the Ursing and Arnasson (1998) reference sequence (AJ002189).

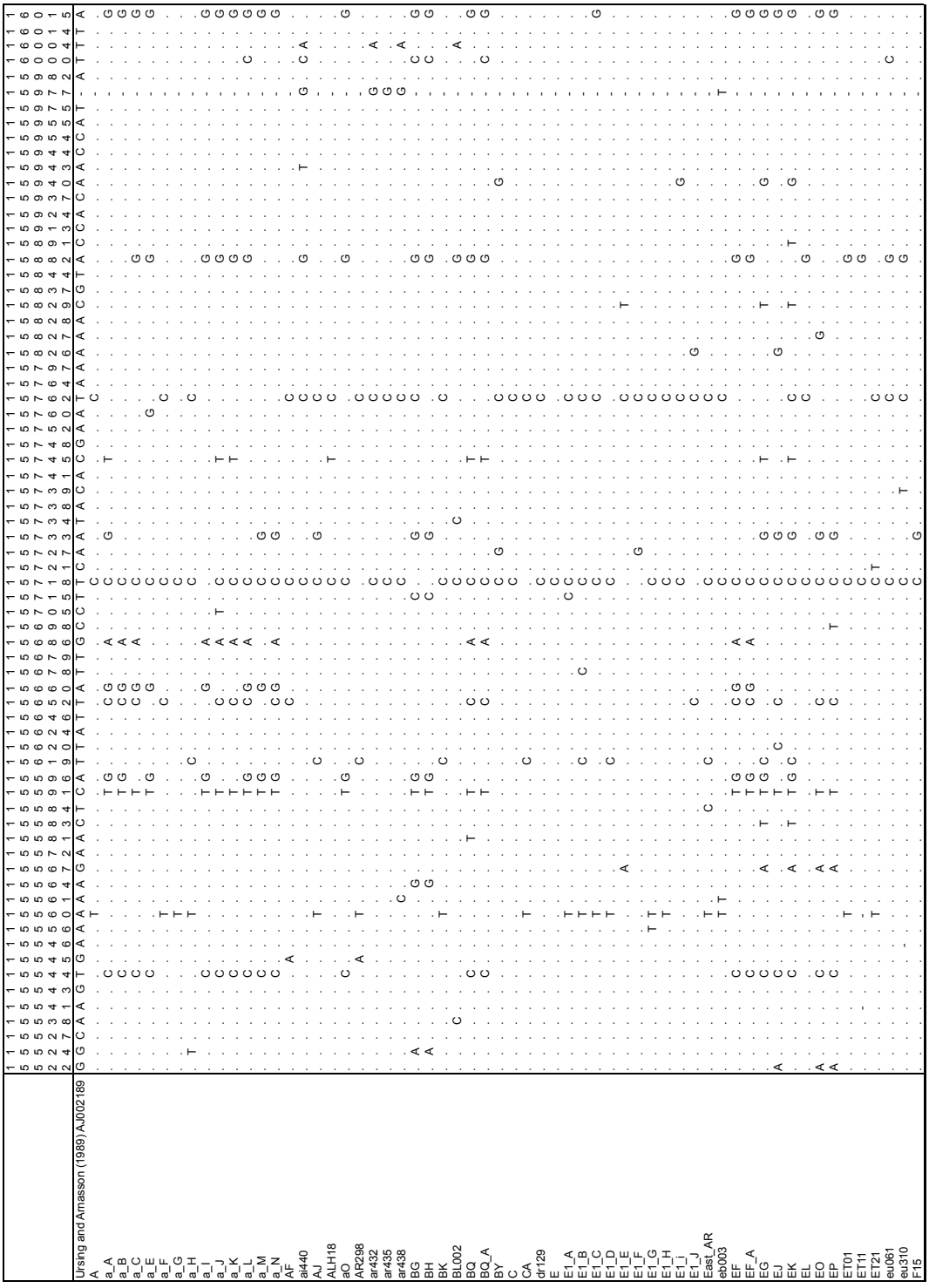


Table 8.1: The 152 unique haplotypes relative to the Ursing and Arnasson (1998) reference sequence (AJ002189).

Chapter 9

Appendix B

The published version of chapter 2. Ottoni and Girdland Flink et al. (2013) Mol Biol Evol: 30 (4): 824-832. doi: 10.1093/molbev/mss261).

Pig Domestication and Human-Mediated Dispersal in Western Eurasia Revealed through Ancient DNA and Geometric Morphometrics

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Article

Abstract

Zooarcheological evidence suggests that pigs were domesticated in Southwest Asia ~8,500 BC. They then spread across the Middle and Near East and westward into Europe alongside early agriculturalists. European pigs were either domesticated independently or more likely appeared so as a result of admixture between introduced pigs and European wild boar. As a result, European wild boar mtDNA lineages replaced Near Eastern/Anatolian mtDNA signatures in Europe and subsequently replaced indigenous domestic pig lineages in Anatolia. The specific details of these processes, however, remain unknown. To address questions related to early pig domestication, dispersal, and turnover in the Near East, we analyzed ancient mitochondrial DNA and dental geometric morphometric variation in 393 ancient pig specimens representing 48 archeological sites (from the Pre-Pottery Neolithic to the Medieval period) from Armenia, Cyprus, Georgia, Iran, Syria, and Turkey. Our results reveal the first genetic signatures of early domestic pigs in the Near Eastern Neolithic core zone. We also demonstrate that these early pigs differed genetically from those in western Anatolia that were introduced to Europe during the Neolithic expansion. In addition, we present a significantly more refined chronology for the introduction of European domestic pigs into Asia Minor that took place during the Bronze Age, at least 900 years earlier than previously detected. By the 5th century AD, European signatures completely replaced the endemic lineages possibly coinciding with the widespread demographic and societal changes that occurred during the Anatolian Bronze and Iron Ages.

Key words: **pig domestication, wild boar, Neolithic, phylogeography.**

Introduction

The transition from hunting and gathering to agriculture is one of the most important biocultural processes in human history (Diamond and Bellwood 2003). Though this transition took place in numerous locations across the globe (Purugganan and Fuller 2009), the earliest stages of animal domestication in western Eurasia are recorded in the northern Fertile Crescent in the 9th millennium BC (Zeder 2008, 2011). Recent evidence suggests that the establishment of food production was followed by rapid population growth (Bocquet-Appel 2011) and agropastoral economies often spread through demic diffusion (Gignoux et al. 2011). This was certainly the case for Southwest Asia where, following the development of agricultural economies, farmers migrated into Europe during the Neolithic bringing with them domestic crops and livestock (Bramanti et al. 2009).

The increased resolving power of new genetic and morphometric techniques has allowed for the identification of fine-scale population differences across wide temporal and geographic contexts and the capability of tracking these differences through time and space. For example, DNA derived from modern animal (Naderi et al. 2008; Chessa et al. 2009) and plant (Myles et al. 2011; van Heerwaarden et al. 2011) domesticates have been used to unravel geographic origins and dispersal patterns. The use of modern data alone, however, can be problematic. Past domestic populations often underwent dramatic bottlenecks, demographic fluctuations (including complete replacement), and admixture with wild relatives, thus obscuring the genetic signatures of earlier populations (Larson, Albarella, et al. 2007; Larson et al. 2012).

Analyses of ancient DNA (aDNA) have overcome this issue by typing (pre)historic populations and allowing for the direct observation of genetic signatures through time. This approach has generated new insights related to past genetic diversity (Fernandez et al. 2006), wild–domestic hybridization (Bollongino et al. 2008), and human migration (Larson, Albarella, et al. 2007; Larson, Cucchi, et al. 2007). Similarly, novel morphometric methods, including geometric morphometrics (GMM), have been successfully applied to document changes between wild and domestic animals (Larson, Cucchi, et al. 2007) and plants (Terral et al. 2010) and to track the phenotypic evolution of past populations (Cucchi et al. 2009).

Zooarcheological evidence demonstrates that wild boar were domesticated independently in the Near East by at least 8,500 BC (Conolly et al. 2011; Ervynck et al. 2001). By examining pig bones recovered from the Pre-Pottery Neolithic layers at Cayonu Tepesi (10,000–6,300 BC, Erim-Özdoğan 2011) in southeastern Anatolia, Ervynck et al. (2001) identified a disproportionate decrease in molar tooth size over two millennia. They interpreted this pattern to be the result of a long-term in situ domestication process that led to the emergence of morphologically domestic pigs by 6,800 BC (early Pottery Neolithic). Similar, though contentious, claims for human controlled pig breeding between 8,200 and 7,500 BC have been made at Cafer Höyük (Helmer 2008) and Nevali Çori (Peters et al. 2005) in southeastern Anatolia. The introduction of wild boar to Cyprus by at least 9,700–9,400 BC, however, indicates that humans were actively manipulating wild boar populations for millennia before the emergence of domestic pigs (Vigne et al. 2011; Vigne et al. 2009).

Though the zooarcheological evidence demonstrates that pigs were first domesticated in Southwest Asia, virtually all modern domestic pigs from western Eurasia possess mitochondrial signatures similar (or identical) to European wild boar (Larson et al. 2005). Ancient DNA extracted from early Neolithic domestic pigs in Europe resolved this paradox by demonstrating that early domestic pigs in the Balkans and central Europe shared haplotypes with modern Near Eastern wild boar (Larson, Albarella, et al. 2007). The absence of Near Eastern haplotypes in pre-Neolithic European wild boar suggested that early domestic pigs in Europe must have been introduced from Anatolia by the mid 6th millennium BC before spreading to the Paris basin by the early 4th millennium BC (Larson, Albarella, et al. 2007).

By 3,900 BC, however, virtually all domestic pigs in Europe possessed haplotypes originally only found in European wild boar. This genetic turnover may have resulted from the accumulated introgression of local female wild boar into imported domestic stocks or from an indigenous European domestication process (Larson, Albarella, et al. 2007). After the genetic turnover had taken place in Europe, aDNA from Armenian pigs indicated that European domestic pigs were present in the Near East by the 7th century BC at the end of the Iron Age where they replaced indigenous Near Eastern domestic mtDNA lineages (Larson, Albarella, et al. 2007). Crucially, the archeological record attests to rapid demographic and societal changes during the Late Bronze Age (1,600–1,200 BC) and Iron Age (1,200–600 BC), including large-scale migrations and the expansion of trade and exchange networks across the Mediterranean and the Black Sea region (Sagona and Zimansky 2009).

To establish a more precise geographic and temporal framework of mitochondrial *Sus* haplotypes in Anatolia and to address questions related to the mitochondrial turnover in Armenia at the end of the Iron Age, we obtained mitochondrial sequences from 39 modern wild boar and 393 archeological wild and domestic pigs from 48 Near Eastern sites spanning the Pottery Neolithic (~7,000 BC) to the 15th century AD from western Turkey to southwestern Iran (fig. 1, supplementary fig. S1*a* and table S1, Supplementary Material online). We analyzed our novel data alongside previously published ancient and modern sequences (supplementary table S2, Supplementary Material online). In addition, we performed a dental morphological assessment of 46 archeological specimens (with known genetic haplotypes) using traditional osteometric and GMM methods to assess the correlation between genetic and morphometric variation (fig. 2).

Results and Discussion

Genetic Signatures of Early Anatolian Domestic Pigs

Remains of the earliest domestic livestock are found in Southwest Asia ~9,000–8,000 BC (Zeder 2008). Unlike sheep, goats, and cattle that likely became domesticated through a prey pathway, pigs (like dogs and cats) probably followed a commensal pathway that began with an initial habituation phase before proceeding to a partnership that ended in controlled breeding (Ervynck et al. 2001; Zeder 2012). The protracted time over which pig domestication took place likely included a predomestic management phase that may have been widespread across the region (Vigne 2011).

We first tested the geographic correspondence between archeological and genetic evidence for pig domestication by mapping the geographic distribution of genetic signatures derived from modern wild boar in Anatolia and the Near East (fig. 2). A phylogenetic tree, based on 661 bp (base pairs) of the mitochondrial DNA (mtDNA) control region, revealed a previously observed topology (Larson, Albarella, et al. 2007) that included three well-supported phylogeographic clades: two clades with pigs found exclusively in the Near East (NE1 and NE2) and a European clade. Of the 192 novel ancient sequences (supplementary table S4, Supplementary Material online), all those that possessed one of three Anatolian/Near Eastern mtDNA lineages (Arm1T, Y1, or Y2) (Larson, Albarella, et al. 2007) belonged to the NE2 clade (supplementary fig. S2*a*, Supplementary Material online). In modern animals, the NE1 clade has been identified only in Near Eastern wild boar (supplementary table S2, Supplementary Material online) and is yet to be found in any modern or ancient domestic pigs. The geographic distributions of the NE1 and NE2 clades overlap only in Iran, Iraq, and in the Caucasus (fig. 2 and supplementary fig. S2*b*, Supplementary Material online). Given the absence of NE1 boar in Anatolia, and the complete lack of NE1 signatures in modern or ancient domestic pigs, it is plausible that the first domestic pigs in Anatolia belonged to the NE2 clade.

To establish the specific mtDNA lineage of one of the earliest domestic pig populations, we successfully extracted and sequenced DNA from one specimen excavated from an early Pottery Neolithic layer (~6,800–6,500 BC) at Çayönü Tepesi, representing the final stages of the proposed in situ domestication process (Hongo and Meadow 1998; Ervynck et al. 2001). This specimen possessed the Arm1T haplotype that (along with the Y1 haplotype) is the dominant signature in other Neolithic and Bronze Age Anatolian *Sus* remains (fig. 1).

We then contrasted the frequencies of NE2 lineages across Southwest Asia (fig. 1). Like numerous other pig clades distributed across the Old World (Larson et al. 2005), the distributions of Y1 and Arm1T are geographically partitioned. Y1 is significantly more frequent in western Anatolia (Fisher's exact test; $P < 0.001$), whereas Arm1T has a much wider distribution and dominates in southeastern Anatolia, Armenia, Syria, Georgia, and Iran (Fisher's exact test; $P < 0.001$) (fig. 1). Despite the limited sample size, the combined zooarcheological and genetic data suggest that at least the Arm1T lineage was present in the first domestic pigs in western Eurasia.

Anatolian Origins of European Neolithic Pigs

A previous DNA study of modern and ancient, wild and domestic pigs demonstrated that the earliest domestic pigs in Europe possessed one of two NE2 clade haplotypes: Y1 or Y2. Because both of these haplotypes clustered with others found in modern Anatolian and Near Eastern wild boar, the authors concluded that Y1 and Y2 lineages were indigenous to Anatolia and were later transported into Europe by migrating farmers at the onset of the European Neolithic. The lack of ancient Anatolian samples, however, precluded a direct demonstration of that assertion (Larson, Albarella, et al. 2007).

The ancient Anatolian data presented here reveal that both morphologically wild and domestic Neolithic pigs (distinguished using logarithmically indexed linear osteometrics) possessed Y1 haplotypes (fig. 1, supplementary fig. S3*a* and table S5, Supplementary Material online) and were present at three archeological sites in western Anatolia: Bademağacı (6,400–6,100 BC) (De Cupere et al. 2008), Ulucak Höyük

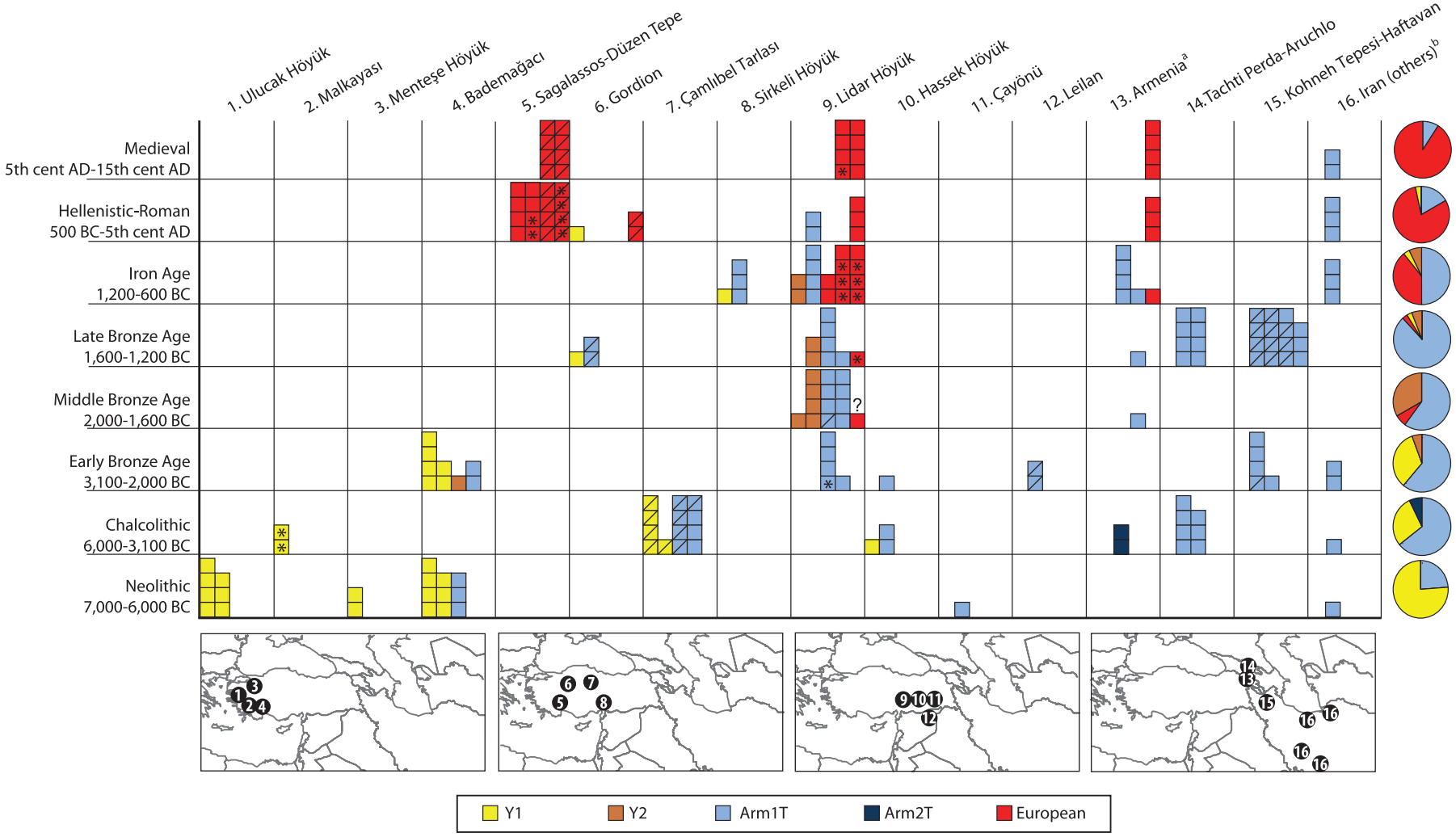

Fig. 1. A spatiotemporal depiction of ancient pig haplotypes. Rows represent eight chronological periods, and columns pertain to sites organized along a longitudinal axis from west to east. Approximate locations of the archeological sites from which the samples are derived are shown as numbered circles on maps beneath the horizontal axis. Asterisks indicate directly AMS-dated samples. The question mark signifies not enough material was available for AMS dating. Slashed boxes indicate samples on which GMM analyses were performed. Pie charts to the right of each row summarize the haplotype frequencies for each chronological period across all sites. Columns pertain to one or two sites except for two columns that consist of several sites: Armenia (Sevkar-4, Areni-1, Khatunarkh, Shengevit, Lchashen, Tmbatir, Pilorpat, Beniamin, and Tsakaektsi) and Iran (Qaleh Rostam, Qare Doyub, Qelīch Qōīneq, Dasht Qal'eh, Doshan Tepe, Malyan, Mehr Ali, Chogha Gavaneh, and Gohar Tepe).

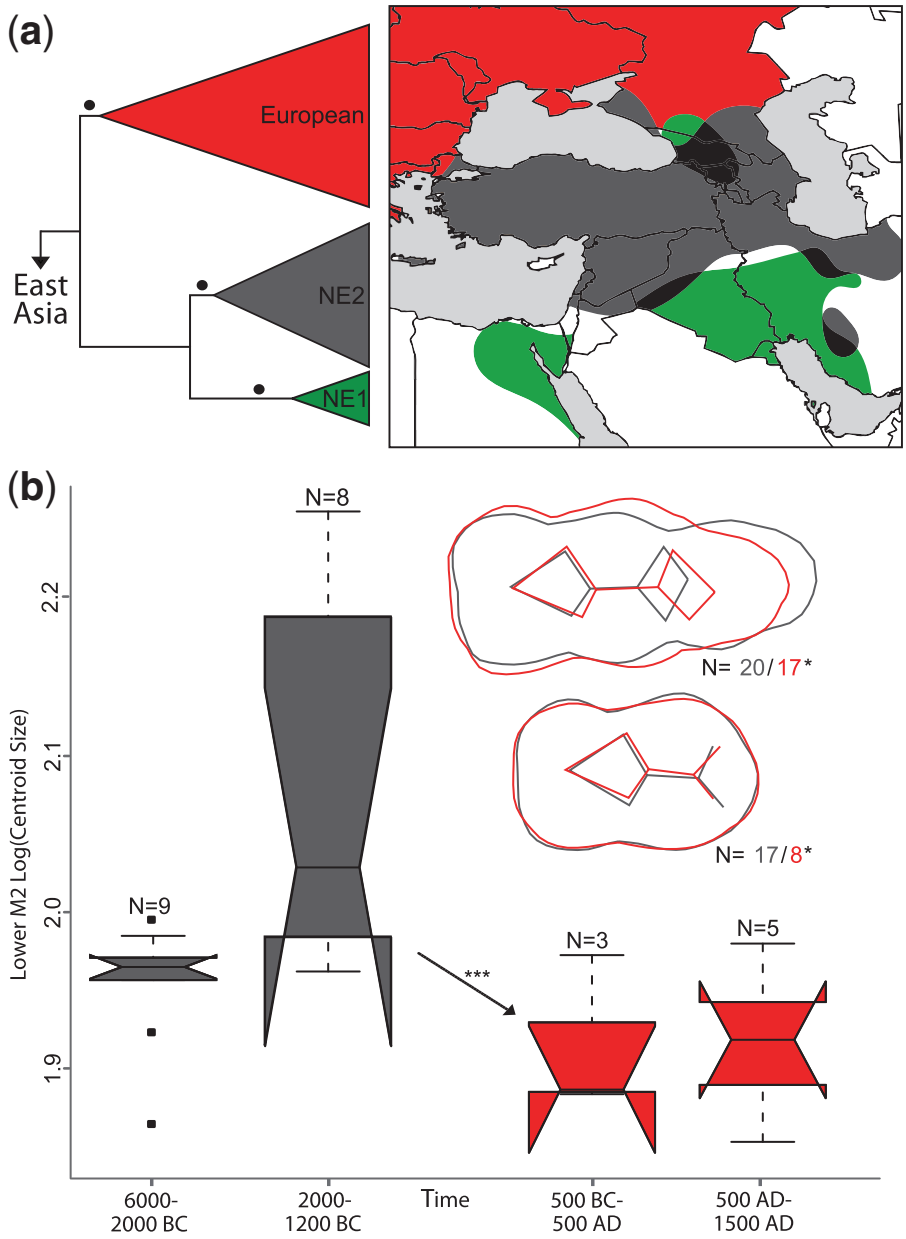

Fig. 2. Panel (*a*) depicts a schematic phylogenetic tree derived from an alignment of 267 modern wild boar from western Eurasia. Red, green, and gray triangles refer to the well-supported European, Near Eastern 1 (NE1), and Near Eastern 2 (NE2) clades, respectively. Branches supported by $P > 0.99$ are indicated by a black circle. A more detailed representation of the tree including support values is presented in supplementary figure S2*a*, Supplementary Material online. The NE2 clade includes all ancient Near Eastern haplotypes depicted in figure 1. Panel (*a*) also shows the approximate geographic distribution of modern wild boar belonging to these clades. Areas with overlapping distributions are represented in dark. A more detailed depiction is presented in supplementary figure S2*b*, Supplementary Material online. Panel (*b*) presents molar size (M_2) and shape (M_2 and M_3) differences between ancient pigs assigned to European (red) and Near Eastern (gray) mtDNA clades. Differences in shape calculated along linear discriminant analysis (LDA) axes are displayed in overlapping shapes in the upper right. The arrow indicates a statistically significant size reduction in the M_2 between European and Near Eastern pigs. Numbers following "*N*=" represent sample sizes, and single and triple asterisks represent significance to the $P < 0.05$ and $P < 0.01$ levels.

(6,400–5,900 BC) (Çakırlar 2012), and Menteşe Höyük (~6,000 BC). The presence of these lineages corroborates the supposition that the earliest domestic pigs in Europe originated from populations originally domesticated in the Near East, conclusively linking the Neolithization of Europe with Neolithic cultures of western Anatolia (Larson, Albarella, et al. 2007; Özdoğan 2005).

The Y1 haplotype does not appear to be associated with either wild boar or early domestic pigs in eastern parts of Anatolia, and it is completely absent in Iranian and Caucasian pigs where the Arm1T lineage dominates. Intriguingly, though Arm1T is present in early domestic pigs in eastern Turkey, this lineage has yet to be identified in either ancient or modern European pigs. This temporal and geographic pattern (fig. 1) could be the result of two different processes. First, it is possible that genetically differentiated wild boar populations in eastern and western Anatolia were domesticated independently. More likely, however, is a

scenario in which southeastern Anatolian wild boar were initially domesticated and subsequently transported west out of the Neolithic "core zone" (Özdoğan 2011). Then, following admixture with female wild boar indigenous to western Turkey, they acquired the local Y1 lineage that prevailed over the Arm1T lineage in this area.

The route along which domestic pigs traveled to arrive in western Anatolia remains unknown. The presence of morphologically domestic pig remains by the 7th millennium BC (Pottery Neolithic layers) at the site of Yumuktepe, in south-central Turkey (Buitenhuis and Caneva 1998), and at the early 7th millennium BC layers of Ulucak (Çakırlar 2012; Çilingiroğlu 2012) near the eastern Aegean coast, contrasted with the general dearth of pigs during the same period in central Anatolia (Conolly et al. 2011), however, suggest that one of the possible routes was along the Mediterranean coast.

Timing and Nature of the Anatolian Pig Turnover

A previous study (Larson, Albarella, et al. 2007) demonstrated that domestic pigs with mitochondrial haplotypes predominantly found in Europe replaced mitochondrial lineages in Armenia that possibly originated from the early domestic swine herds in the Neolithic core zone by 700 BC. Because that study did not include ancient pigs from central or western Anatolia, the scale and timing of this proposed eastward dispersal and replacement by European domestic pigs remained unresolved.

The temporal and geographic distribution of genetic haplotypes presented in our study demonstrates that the first AMS radiocarbon-dated pig with European ancestry (haplotype A) appeared almost 1,000 years earlier than the Armenian samples, in a Late Bronze Age context (~1,600–1,440 BC) at Lidar Höyük (fig. 1). An apparently even earlier Middle Bronze Age specimen from the same site also possessed a European signature, but a direct radiocarbon date for this specimen could not be obtained.

Our data also show that European pigs are unlikely to have arrived in Anatolia before 2,000 BC since the Early Bronze Age layers at Bademağacı and Lidar Höyük (in southwestern and southeastern Anatolia, respectively) only possess indigenous Near Eastern pig lineages. The frequency of pigs with European ancestry increased rapidly from the 12th century BC onwards, and by the 5th century AD, domestic pigs possessing a Near Eastern genetic signature had all but disappeared across Anatolia and the southern Caucasus. Though we did not detect European signatures in the ancient Iranian samples (fig. 1), the eastward spread of European lineages may have continued into Iran later than the Iron Age, since European lineages have been found in wild caught modern Iranian samples (Larson, Albarella, et al. 2007).

If European pig haplotypes were present in Anatolia at <5% before the Middle Bronze Age, our sample size (binomial distribution, $n = 73$, confidence interval = 95%) would not have allowed us to detect them. To assess the possibility that haplotypes so far found exclusively in Europe were indigenous to Anatolia and the Near East, we analyzed the morphometric differentiation in molar size and shape between archeological samples that possessed European and Anatolian/Near Eastern genetic signatures. Single interbreeding populations have been shown to possess deeply divergent mitochondrial haplotypes (e.g., yaks [Guo et al. 2006]) demonstrating that maternal genetic differentiation alone is not sufficient to infer geographic separation. Statistically significant phenotypic differences between pigs possessing Anatolian/Near Eastern and European haplotypes, however, would indicate that the two populations had been evolving in isolation from one another and that pigs with a European genetic signature were not present in Anatolia before being introduced by people.

A GMM analysis of 46 pigs with known genetic signatures revealed significant differences in both molar size ($P < 0.01$) and shape ($P < 0.05$) between European and Anatolian/Near Eastern pigs (fig. 2 and supplementary table S6, Supplementary Material online). European pigs possessed overall smaller teeth and proportionally shorter and laterally widened third molars. The concordance between genetic and GMM signatures strongly suggests that pigs possessing European and Anatolian/Near Eastern mtDNA lineages are morphologically different and that European pigs were, therefore, introduced to Anatolia. The DNA evidence suggests that this process may have taken place (at the latest) during the Middle to Late Bronze Age, at least 900 years earlier than previously inferred.

Establishing a more precise temporal and geographic pattern for the initial introduction and subsequent dominance of European pigs allows for the turnover to be assessed in its cultural context, though the limited archeological coverage of pigs in western Anatolia precludes a definitive identification of an entrance route. Minoans and Mycenaeans may have initially introduced pigs during the Bronze Age when they colonized the western Anatolian coast from the 16th to 12th centuries BC. Alternatively, pigs may have been imported by the Hittites (Seeher 2011) whose kingdom extended from central Anatolia to the northern Levant from the 17th to 13th centuries BC (Bryce 2005). The lack of pigs possessing European signatures in Bronze Age contexts from sites in Georgia suggests that pigs did not arrive via the Caucasus (fig. 1). Regardless of the exact routes of their arrival, European domestic pigs were deliberately introduced into Anatolia. Within two millennia, European mitochondrial lineages had replaced their Near Eastern domestic counterparts that were present, and grew in frequency in the early domestic herds of the Near East over the previous 6,000 years.

Conclusions

This study addresses questions regarding the origins and dispersal of domestic pigs in Southwest Asia by combining genetic and morphometric analyses often on the same archeological samples. The data presented here add to the growing body of evidence suggesting that pig domestication was a complex, nonlinear process that took place over several millennia and involved multiple Southwest Asian wild boar populations (Ervynck et al. 2001; Peters et al. 2005; Vigne et al. 2009).

More specifically, our data suggest a narrative that begins with the domestication of pigs in Southwest Asia, at Upper Tigris sites including Çayönü Tepesi (Ervynck et al. 2001) and possibly Upper Euphrates sites including Cafer Höyük (Helmer 2008) and Nevali Çori (Peters et al. 2005). Early domestic pigs likely possessed at least the Arm1T haplotype (indigenous to Southwest Asia) and dispersed with humans as the Neolithic expanded away from these centers. Once introduced to western Anatolia, domestic swineherds acquired a mitochondrial signature (Y1) associated with the local wild boar most likely through admixture. The eastern Anatolian mitochondrial lineage (Arm1T) became less frequent likely as a result of this admixture process, small population sizes, and genetic drift.

This same turnover pattern was evident after pigs possessing domestic Y1 lineages were subsequently transported west into Europe as far as the Paris Basin (Larson, Albarella, et al. 2007). Once domestic pigs orientating from southeastern Anatolia but possessing the western Anatolian Y1 haplotype arrived in Europe, they acquired European wild boar genetic signatures and lost the Y1 haplotype through introgression of resident wild boar mitochondria into the imported domestic pig population. From at least the beginning of the Late Bronze Age, and possibly several centuries before, domestic pigs of European wild boar origin now all carrying European wild boar mtDNA lineages were introduced to Anatolia. On this occasion, however, swineherds did not take on the genetic characteristics of the local populations. Instead, by the 5th century AD, European domestic pig haplotypes had completely replaced the endemic Y1 and Arm1T lineages.

The movement of domestic pigs from western Anatolia into Europe is consistent with recent aDNA studies of human remains that support a demic diffusion model of the initial Central European Neolithic (Bramanti et al. 2009). Whether the back migration of European pigs into Anatolia reflects human migration or trade and exchange remains unclear. Addressing these and other questions can be accomplished by incorporating both mitochondrial and nuclear markers in combination with large-scale morphological analyses.

Material and Methods

Ancient Samples

We analyzed 393 ancient pig bone and tooth specimens excavated from 48 Anatolian archeological sites (supplementary fig. S1*a* and table S1, Supplementary Material online). All dates are reported in calibrated radiocarbon years BC. The ages of the archeological remains ranged from the 10th millennium BC to the medieval era and were determined using direct accelerator mass spectrometry (AMS) radiocarbon dating (Beta Analytic Inc. and University of Oxford), stratigraphic associations with AMS dates, and contextual archeological evidence. Samples dated at Oxford were treated using standard protocols as described by Brock et al. (2010).

Genetic Analyses

Analyses were carried out in aDNA facilities in three separate institutions: the Forensic Genetics and Molecular Archeology department in Leuven (Belgium), the Department of Archaeology at Durham University (United Kingdom), and the Institute of Anthropology in Mainz (Germany) using standard contamination precautions (Gilbert et al. 2005). Two ~120 bp fragments of the control region of the mitochondrial genome were amplified (Larson, Albarella, et al. 2007) and sequenced. Some fragments were cloned (supplementary table S3, Supplementary Material online). Larger control region fragments (up to ~800 bp) were generated from DNA extracts of 39 modern wild boar from the greater geographic region (supplementary table S2, Supplementary Material online). Modern sequences were generated at the Department of Animal Sciences, Universitat Autònoma de Barcelona (Spain). A maximum likelihood (ML) tree was created from an alignment of 661 bp of the control region of 267 modern wild boar using PhyML (Guindon and Gascuel 2003) in Geneious 5.5 (Drummond et al. 2011) (supplementary text, Supplementary Material online). Variations in substitution model and analytical framework did not affect the topology of the main clades. Details regarding methods, contamination avoidance procedures, authentication, and phylogenetic analyses are described in the supplementary text, Supplementary Material online.

Reproducible aDNA sequences were obtained from 192 of 393 specimens (48.9%, supplementary table S4, Supplementary Material online). As expected for ancient samples (Smith et al. 2003), we observed an inverse correlation between aDNA success frequency and sample age in nine time bins (Spearman's rank correlation $r^2 = 0.87$, $P < 0.001$; supplementary fig. S1*b*, Supplementary Material online). All sequences have been deposited in GenBank (JX893958–JX894188). Variable positions of the two concatenated ANC1 and ANC2 fragments are presented in supplementary table S4, Supplementary Material online. As shown in the ML tree (supplementary fig. S2*a*, Supplementary Material online), the majority of the diagnostic variation is present in the ANC1 fragment (Larson, Albarella, et al. 2007). Given the greater resolving power of this fragment, the relatively low variation within the ANC2 fragment, and to be consistent with the terminology developed by Larson et al. (Larson, Albarella, et al. 2007), haplotype assignments for each specimen were based on the ANC1 terminology. Additional information regarding haplotype assignment and terminology is present in the supplementary text, Supplementary Material online. The haplotype distribution across Southwest Asia was tested using a Fisher's exact test. Western Anatolia included sites from Ulucak Höyük to Çamlibel Tarlası and eastern Anatolia included sites from Sirkeli Höyük to Çayönü.

Morphometric Analyses

A total of 62 mandibular molars (25 M_2 and 37 M_3) from 46 ancient specimens were analyzed using traditional biometrical and GMM approaches from standardized photographs taken from the occlusal view (supplementary fig. S3*b*, Supplementary Material online). For the traditional metrical approach, we measured maximum length and width metrics (two for the M_2 and three for the M_3, supplementary fig. S3*b*,

Supplementary Material online). Two-dimensional GMM methods (based on coordinates) were used to separately analyze size and shape variables. In total, we analyzed 7 landmarks (homologous points) for the M_2, 8 for the M_3, 68 sliding semilandmarks (points along the outline of the tooth) for the M_2, and 91 for the M_3 (Cucchi et al. 2011; Evin et al. forthcoming) (supplementary fig. S3*b*, Supplementary Material online).

Differences between ancient pigs assigned to Near Eastern mtDNA clade NE2 and European mtDNA clades were tested using traditional metric and GMM approaches that analyzed both shape and log-transformed centroid size. Traditional measurements were analyzed using a log-shape ratio (LSR) approach (Mosimann and James 1979) that allowed a separation of shape and isometric size. Differences between clades were tested with Kruskal–Wallis tests for size indices (centroid and isometric) paired with boxplots and multivariate analyses of variance for shape measures (from GMM and LSR) coupled with linear discriminant analyses paired with leave-one-out cross-validation percentages. Details are described in the supplementary text, Supplementary Material online.

Supplementary Material

Supplementary text, figures S1–S3, and tables S1–S6 are available at *Molecular Biology and Evolution* online (http://mbe.oxfordjournals.org/).

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References

Bocquet-Appel JP. 2011. When the world's population took off: the springboard of the Neolithic Demographic Transition. *Science* 333: 560–561.

Bollongino R, Elsner J, Vigne JD, Burger J. 2008. Y-SNPs do not indicate hybridisation between European aurochs and domestic cattle. *PLoS One* 3:e3418.

Bramanti B, Thomas MG, Haak W, et al. (16 co-authors). 2009. Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. *Science* 326:137–140.

Brock F, Higham TFG, Ditchfield P, Bronk Ramsey C. 2010. Current pretreatment methods for AMS radiocarbon dating at the Oxford Radiocarbon Accelerator Unit (ORAU). *Radiocarbon* 52:103–112.

Bryce T. 2005. The kingdom of the Hittites. Oxford: Oxford University Press.

Buitenhuis H, Caneva I. 1998. Early animal breeding in southeastern Anatolia: Mersin-Yumuktepe. In: Anreiter P, Bartosiewicz L, Jerem E, Meids W, editors. Man and the animal world. Budapest (Hungary): Archaeolingua. p. 122–130.

Çakırlar C. 2012. Evolution of animal husbandry in Neolithic Central-West Anatolia, the archaeozoological record from Ulucak Höyük (ca. 7040–5660 cal. BC, İzmir, Turkey). *Anatolian Studies* 62:1–33.

Chessa B, Pereira F, Arnaud F, et al. (33 co-authors). 2009. Revealing the history of sheep domestication using retrovirus integrations. *Science* 324:532–536.

Çilingiroğlu.Ç. 2012. The Neolithic pottery of Ulucak in Aegean Turkey: organization of production, interregional comparisons, and relative chronology. *British Archaeological Reports* (International Series) pp. 2426.

Conolly J, Colledge S, Dobney K, Vigne J-D, Peters J, Stopp B, Manning K, Shennan S. 2011. Meta-analysis of zooarchaeological data from SW Asia and SE Europe provides insight into the origins and spread of animal husbandry. *J Archaeol Sci.* 38:538–545.

Cucchi T, Fujita M, Dobney K. 2009. New insights into pig taxonomy, domestication, and human dispersal in Island South East Asia: molar shape analysis of *Sus* remains from Niah Caves, Sarawak. *Int J Osteoarchaeol.* 19:508–530.

Cucchi T, Hulme-Beaman A, Yuan J, Dobney K. 2011. Early Neolithic pig domestication at Jiahu, Henan Province, China: clues from molar shape analyses using geometric morphometric approaches. *J Archaeol Sci.* 38:11–22.

De Cupere B, Duru R, Umurtak G. 2008. Animal husbandry at the Early Neolithic to Early Bronze Age site of Bademağacı (Antalya province, SW Turkey): evidence from the faunal remains. In: Vila E, Gourichon L, Choyke AM, Buitenhuis H, editors. Proceedings of the 8th International Symposium on the Archaeozoology of Southwestern Asia and Adjacent Areas. Lyon (France): Archéorient, Maison de l'Orient et de la Méditerranée. p. 367–405.

Diamond J, Bellwood P. 2003. Farmers and their languages: the first expansions. *Science* 300:597–603.

Drummond AJ, Ashton B, Buxton S, et al. (15 co-authors). 2011. Geneious v5.4. Available from: http://www.geneious.com/ (last accessed December 10, 2012).

Erim-Özdoğan A. 2011. Çayönü. In: Özdoğan M, Basglen N, editors. The Neolithic in Turkey: New Excavations & New Research: The Tigris Basin. Istanbul: Archaeology and Art Publications. p. 185–269.

Ervynck A, Dobney K, Hongo H, Meadow R. 2001. Born free? New evidence for the status of *Sus* scrofa at Neolithic Çayönü Tepesi (southeastern Anatolia, Turkey). *Paléorient* 27:47–73.

Evin A, Cucchi T, Cardini A, Strand Vidarsdottir U, Larson G, Dobney K. 2013. The long and winding road: identifying pig domestication through molar size and shape. *J Archaeol Sci.* 40:735–743.

Fernandez H, Hughes S, Vigne JD, Helmer D, Hodgins G, Miquel C, Hanni C, Luikart G, Taberlet P. 2006. Divergent mtDNA lineages of goats in an Early Neolithic site, far from the initial domestication areas. *Proc Natl Acad Sci U S A.* 103:15375–15379.

Gignoux CR, Henn BM, Mountain JL. 2011. Rapid, global demographic expansions after the origins of agriculture. *Proc Natl Acad Sci U S A.* 108:6044–6049.

Gilbert MT, Bandelt HJ, Hofreiter M, Barnes I. 2005. Assessing ancient DNA studies. *Trends Ecol Evol.* 20:541–544.

Guindon S, Gascuel O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst Biol.* 52: 696–704.

Guo S, Savolainen P, Su J, Zhang Q, Qi D, Zhou J, Zhong Y, Zhao X, Liu J. 2006. Origin of mitochondrial DNA diversity of domestic yaks. *BMC Evol Biol.* 6:73.

Helmer D. 2008. Révision de la faune de Cafer Höyük (Malatya, Turquie): apports des méthodes de l'analyse des mélanges et de l'analyse de Kernel à la mise en évidence de la domestication. In: Vila E, Gourichon L, Choyke AM, Buitenhuis H, editors. Archaeozoology of the Near East VIII: Proceedings of the 8th International Symposium on the Archaeozoology of Southwestern Asia and Adjacent Areas. Lyon (France): Maison de l'Orient et de la Méditerraneé. p. 169–195.

Hongo H, Meadow R. 1998. Pig exploitation at Neolithic Çayönü Tepesi (Southeastern Anatolia). In: Nelson SM, editor. Ancestors for the pigs: pigs in prehistory. Philadelphia (PA): Penn Press. p. 77–98.

Larson G, Albarella U, Dobney K, et al. (19 co-authors). 2007. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *Proc Natl Acad Sci U S A.* 104:15276–15281.

Larson G, Cucchi T, Fujita M, et al. (32 co-authors). 2007. Phylogeny and ancient DNA of *Sus* provides insights into neolithic expansion in Island Southeast Asia and Oceania. *Proc Natl Acad Sci U S A.* 104: 4834–4839.

Larson G, Dobney K, Albarella U, et al. (13 co-authors). 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science* 307:1618–1621.

Larson G, Karlsson EK, Perri A, et al. (20 co-authors). 2012. Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proc Natl Acad Sci U S A.* 109:8878–8883.

Mosimann JE, James FC. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* 33: 444–459.

Myles S, Boyko AR, Owens CL, et al. (12 co-authors). 2011. Genetic structure and domestication history of the grape. *Proc Natl Acad Sci U S A.* 108:3530–3535.

Naderi S, Rezaei HR, Pompanon F, et al. (12 co-authors). 2008. The goat domestication process inferred from large-scale mitochondrial DNA analysis of wild and domestic individuals. *Proc Natl Acad Sci U S A.* 105:17659–17664.

Özdoğan M. 2005. The expansion of the Neolithic way of life: what we know and what we do not know. In: Lichter C, editor. *How did farming reach Europe? Anatolian-European relations from the second half of the 7th through the first half of the 6th millennium cal BC* (Proceedings of the International Workshop Istanbul, 20–22 May 2004; Byzas 2): 13–27. Istanbul: Deutsches Archäologisches Institut.

Özdoğan M. 2011. Archaeological evidence on the westward expansion of farming communities from eastern Anatolia to the Aegean and the Balkans. *Curr Anthropol.* 52:S415–S430.

Peters J, von den Driesch A, Helmer D. 2005. The upper Euphrates-Tigris basin: cradle of agro-pastoralism? In: Vigne JD, Peters J, Helmer D, editors. The first steps of animal domestication: new archaeological approaches. Proceedings of the 9th ICAZ Conference. Oxford (United Kingdom): Oxbow Books. p. 96–124.

Purugganan MD, Fuller DQ. 2009. The nature of selection during plant domestication. *Nature* 457:843–848.

Sagona AG, Zimansky P. 2009. Ancient Turkey. New York: Routledge.

Seeher J. 2011. The plateau: the Hittites. In: Steadman SR, McMahon JG, editors. The Oxford handbook of ancient Anatolia: 10,000–323 B.C.E. New York: Oxford University Press. p. 376–392.

Smith CI, Chamberlain AT, Riley MS, Stringer C, Collins MJ. 2003. The thermal history of human fossils and the likelihood of successful DNA amplification. *J Hum Evol.* 45:203–217.

Terral J-F, Tabard E, Bouby L, et al. (15 co-authors). 2010. Evolution and history of grapevine (*Vitis vinifera*) under domestication: new morphometric perspectives to understand seed domestication syndrome and reveal origins of ancient European cultivars. *Ann Bot.* 105:443–455.

van Heerwaarden J, Doebley J, Briggs WH, Glaubitz JC, Goodman MM, de Jesus Sanchez Gonzalez J, Ross-Ibarra J. 2011. Genetic signals of origin, spread, and introgression in a large sample of maize landraces. *Proc Natl Acad Sci U S A.* 108:1088–1092.

Vigne JD. 2011. The origins of animal domestication and husbandry: a major change in the history of humanity and the biosphere. *C R Biol.* 334:171–181.

Vigne JD, Carrère I, Briois F, Guilaine J. 2011. The early process of mammal domestication in the Near East. *Curr Anthropol.* 52:S4.

Vigne JD, Zazzo A, Saliege JF, Poplin F, Guilaine J, Simmons A. 2009. Pre-Neolithic wild boar management and introduction to Cyprus more than 11,400 years ago. *Proc Natl Acad Sci U S A.* 106:16135–16138.

Zeder MA. 2008. Domestication and early agriculture in the Mediterranean Basin: origins, diffusion, and impact. *Proc Natl Acad Sci U S A.* 105:11597–11604.

Zeder M. 2011. The origins of agriculture in the Near East. *Curr Anthropol.* 52:S221–S235.

Zeder MA. 2012. The domestication of animals. *Journal of Anthropological Research* 68:161–190.

Pig domestication and human-mediated dispersal in western Eurasia revealed through ancient DNA and geometric morphometrics

Supplementary text

The DNA analyses reported in this study were carried out in three ancient DNA facilities: Durham University (UK), Mainz University (Germany), and Leuven University (Belgium). Specific details about the analytical procedures carried out in each lab are described below.

1.0 Ancient DNA procedures and sample preparation

Leuven. Genetic analyses were performed in the aDNA facilities of the Laboratory of Forensic Genetics and Molecular Archaeology in Leuven (Department of Human Genetics, University of Leuven, Belgium). Pre- and post-PCR procedures were carried out in physically separated laboratories. Access to the pre-PCR laboratory was restricted to only two people (CO and NV) and only after wearing clean overalls, gloves, over-shoes, surgical facemasks, plastic spectacles, and following an irreversible sequence of work steps to avoid contamination. Entry was not permitted if PCR products had been handled the same day.

The aDNA facilities were routinely cleaned with bleach and RNAse Away (Molecular BioProducts, San Diego, CA, USA). Dedicated equipment was used in the pre-PCR laboratory, laboratory plastic-ware was irradiated in a cross-linker (four hours with ultraviolet (UV) light at 254nm, 5cm distance), and every item entering the room was extensively washed with bleach or RNAse Away and subsequently UV-irradiated. Various reagents including nuclease-free water (Promega, Fitchburg, WI, USA), dNTPs (Promega), and PCR Gold Buffer (Applied Biosystems, Foster City, CA, USA), were filtered through 100 kDa Centricon micro-concentrators (Millipore, Billerica, MA,

USA) and stored in small volume aliquots. Extractions were performed in a UV-irradiated workstation while preparation of amplification reactions was carried out in a UV-irradiated laminar flow cabinet (Esco, Breukelen, Netherlands).

For each ancient individual at least two extractions were undertaken at different time points. At least three amplifications for each extraction were performed and both strands of the DNA were sequenced in order to assess the reproducibility of the results. When possible, independent extractions of each individual were carried out from anatomically distant samples. To detect potential contamination by exogenous modern DNA, extraction and amplification blanks were used as negative controls.

To extract DNA from teeth and bone, one sample was prepared at a time. Samples were subjected to the following decontamination procedures. The outer surface of bone and teeth samples was removed through sterile blades or by sanding with a Dremel drill (Dremel, Racine, WI, USA). Additionally, the surfaces of the teeth were gently wiped with 10% bleach and rinsed with bi-distilled water. Bone and teeth samples were then UV-irradiated (254nm wavelength, 12W and 5cm distance) in a cross-linker on each side for 60 minutes and subsequently ground into a fine powder in a 6750 Freezer Mill (SPEX CertiPrep, Metuchen, NJ, USA) and stored at 4°C. Grinding vials were decontaminated using RNAse Away (Molecular BioProducts, San Diego, CA, USA) and subsequent UV-irradiation (254nm in cross-liker). To test for potential cross contamination in the grinding vials, hydroxyapatite powder was used as blank control in each grinding batch.

Durham. DNA extraction was performed in a dedicated ancient DNA laboratory in the Archaeology department at Durham University following strict laboratory procedures as according to commonly applied guidelines (Cooper and Poinar 2000; Gilbert et al. 2005). All equipment and work surfaces were cleaned before and after each use with a dilute solution of bleach (5-10%)

followed by ethanol (99%). Pipettes and plastic racks were subsequently UV-irradiated in a dedicated cross-linker (254 nm wavelength) prior to and after use. Pre- and post-PCR laboratories are physically isolated and access to the pre-PCR laboratories is restricted to Ancient DNA lab users only; access is also prohibited if the lab user had entered post-PCR areas the same day. Ancient DNA lab users wear clean lab coats, double set of gloves (nitrile and latex) and over-shoes in order to avoid introducing contamination from post-PCR areas.

The ancient pig remains were prepared for DNA extraction by removing an approximately two-millimeter layer of the outer bone surface by abrasion using a Dremel drill with clean cut-off wheels (Dremel no 409), targeting compact cortical bone or dental dentine. The bone was then pulverized in a Micro-dismembrator (Sartorious-Stedim Biotech), followed by collection in 15ml Grainer tubes. Milling containers and grinding balls were subsequently suspended and cleaned in 1% virkon and rinsed in absolute ethanol.

Mainz. The samples were analyzed in the facilities of the Institute of Anthropology (AG Palaeogenetics) in a laboratory dedicated for ancient DNA-work (free of molecular work). Laboratory rooms for Pre- and Post-PCR-work were strictly separated and persons were not allowed to enter the Pre-PCR-laboratory after working in the Post-PCR-rooms (including offices) the same day. All samples were subjected to the same procedures for ancient DNA analysis. The work was carried out while wearing clean overalls, disposable facemasks, face shields, gloves and over-shoes. All benches and rooms were routinely treated with soap and bleach or DNA-Exitus® (AppliChem) and UV-irradiated overnight. Additionally, the majority of the steps were carried out in special UV-irradiated work stations. The surface of all equipment entering the clean rooms was intensively washed and UV-irradiated (10h). The HPLC-water (Acros Organics) used for extraction and PCR was also UV-irradiated for at least 15h with a special waterproof UV-bulb. To detect contamination, extraction and amplification blanks were routinely used as negative controls.

The ancient specimens were prepared for DNA extraction as follows. Every sample was UV-irradiated for at least 1h (30min each side) before the outer surface was removed with sand blasting equipment (Harnisch and Rieth) and the samples were cut into pieces with a diamond drill (Dremel). The small pieces were UV-irradiated again and finally ground to a fine powder using a mixer mill (Retsch).

1.1 Assessing the authenticity of ancient DNA data

We can exclude contamination and demonstrate the authenticity of mtDNA results on the following grounds:

1. The analyses were undertaken in dedicated aDNA laboratories under strictly controlled conditions. A selection of samples (supplementary table S1) was processed in two independent laboratories (Leuven and Durham) and those samples generated identical haplotypes.

2. The molecular behavior of the PCR amplifications agrees with what we expect from the analysis of ancient samples. Younger samples were more likely to produce a greater proportion of successful amplifications (supplementary fig. S1b) while all DNA amplifications failed in the oldest samples (Aceramic Neolithic). Interestingly, despite variation in success rates of recovery between sites (supplementary table S1, supplementary fig. S1a) the recovery rate is nearly linear through time (supplementary fig. S1b). It is worth mentioning that the slight increase in success rate in Late Bronze Age (BA) layers compared to the Iron Age (IA) layers could be the result of mistaken contextual dating at Lidar Höyük, the site from which the majority of samples in this temporal bin come from. The re-assignments from LBA to IA of nearly all directly radiocarbon-dated samples from this site/time bin (supplementary table S1) support this observation.

Furthermore, in all instances, sequences were reproduced in multiple experiments, at least in two (and up to three) independent PCR experiments from up to two independent extracts. In some instances, particularly in the oldest samples, several amplification attempts (up to seven) were necessary to reproduce sequences. When this was the case, data were reproduced in a third extraction.

3. Results of the cloning experiments in six specimens (Leuven) confirmed the haplotypes determined through direct sequencing of the PCR products, with consistency of mutations ranging from 78% (Bad86) to 100% (supplementary table S3). The pattern of variation of the cloned sequences showed single substitutions (mostly C→T and G→A transitions) that were interpreted as artifacts due to misincorporations during the amplification or miscoding lesions. The latter is likely the result of *post-mortem* hydrolytic deamination that is common and characteristic in ancient samples (Hofreiter et al. 2001; Briggs et al. 2007; Gilbert et al. 2007). Average rate of C→T and G→A transitions ranges from 1% to 8%. Significantly, consistency of artifacts was higher in the oldest samples (e.g. Bad47 and Bad52, dated to Early Neolithic), compatible with a higher level of damage of nucleic acids and a lower number of template molecules initiating the amplification reaction.

A similar pattern was observed in a subset of the available 'sub-clonal' data set from Durham (supplementary table S3). Out of ~450-1000 randomly drawn ANC1 sequences (first 45bp forward read) from four specimens (LG281, LG459, LG477 and LG495) a total of 59 haplotypes were observed (N=12, 12, 10 & 25 respectively, supplementary table S3). C→T/G→A transitions (Type 2 transitions) are more common than other types of substitutions, including Type 1 transitions (83% and 17% respectively), and are interpreted to mainly represent post-mortem damage-derived miscoding lesions (C→U deamination). The other types of

substitutions, including Type 1 transitions, are sporadic and most likely derive from nucleotide misincorporations or sequencing errors. In support for this argument is the lack of consistency of other types of substitutions in between clones as compared to Type 2 transitions (supplementary table S3). The average rate of Type 2 transitions, calculated as the total number of transitions over C/G bases in the total extracted sequences (not accounting for identical haplotypes that might be derived from a single template molecule) ranged in between 1% to 14% with an average of ~5%.

4. The phylogenetic consistency between sequences produced independently in three different laboratories, and the phylogeographic consistency observed in the total data set (temporal and geographic), again consistent in all three laboratories, strongly indicate that the observed data are authentic.

These findings together with the above-mentioned laboratory procedures make it highly unlikely that the haplotypes observed in our samples arose from contamination or post-mortem damage, and lend credibility to the molecular results obtained in this study.

2. Molecular analyses

Leuven. Aliquots of 0.3-0.4 g powder were incubated overnight in a water bath at 56°C, followed by 24h at 37°C in a digestion solution of 0.5 M EDTA pH 8 (Invitrogen, Carlsbad, CA, USA), 0.5% SDS (USB Affymetrix, Santa Clara, CA, USA) and 0.1mg/mL Proteinase K (Roche, Penzberg, Germany). DNA was extracted through silica-based spin columns (Yang et al. 1998) and re-suspended in 100µL TE. Each independent extraction batch contained not more than eight samples, including two blank controls and one hydroxyapatite control.

Amplifications of the first and the second ~120bp fragments in the mtDNA control region (ANC1 and ANC2, (Larson et al. 2007a; Larson et al. 2007b)) were performed in a final volume of 50µL, containing 1x PCR Gold Buffer (Applied Biosystems), 2.5mM $MgCl_2$ (Applied Biosystems), 0.2mM dNTPs mix (Promega), 0.1µM each primer (Eurogentec, Seraing, Belgium – IDT, Leuven, Belgium), 0.05% BSA (Sigma Aldrich, St. Louis, MO, USA), 2.5 U AmpliTaq Gold® DNA polymerase (Applied Biosystems), 5-10µL of aDNA extract. The following cycle conditions were used: 94°C for 10 min, 45 cycles of 94°C for 45 sec, 56°C for 1 min, 72°C for 1 min, and a final step of 72°C for 5 min.

All the amplification reactions were carried out on a GeneAmp PCR System (Applied Biosystems). The amplification products were visualized on a microchip electrophoresis system (MCE-202 MultiNA, Shimadzu Biotech).

Positive amplification products were purified with Microcon filter concentrators (Millipore) or through ExoSAP-IT (USB Affymetrix), according to manufacturer's specifications. The purified amplicons were directly sequenced by means of ABI Prism BigDye Terminator Cycle Sequencing Kit (ver3.1, Applied Biosystems) according to the manufacturer's specifications. Dyed products were ethanol precipitated and sequence reactions were performed on each strand by using 5'-tailed sequencing primer (Binladen et al. 2007a). The products were detected by capillary electrophoresis on ABI PRISM™ 3130XL Genetic Analyzer (Applied Biosystems). The two ~120bp fragments in the control region of the mtDNA were successfully amplified in 93 out of the 153 specimens from Anatolia, except for one (Bad4) in which the second fragment could not be amplified.

Cloning of the ANC1 products was carried out in six individuals (Bad17, Bad47, Bad52, Bad86, M46, M96) using the TOPO TA Cloning kit (Invitrogen), according to the manufacturer's instructions. Up to 10 colonies from amplification products of two independent extracts were picked

into 25μL nuclease free water (Promega), of which 1μL was used for PCR amplifications in a 25 uL volume of 1x PCR Master Mix (Qiagen, Hilden, Germany), 0.5μM each of vector M13R and M13F primers. Amplification products were purified and sequenced as previously described and the sequences were aligned, analyzed for artefacts induced by *post-mortem* miscoding lesions and the presence of contaminant DNA sequences (supplementary table S3). Sequences from independent experiments were aligned by using BioEdit v5.0.9 (Hall 1999).

Overall, 21 out of total 927 blank controls produced positive amplification (2.3%). After sequencing, the positive blank controls always revealed a European haplotype, and in one instance an East Asian haplotype. To determine whether the PCR success rate of the archeological samples is significantly different from the amplification rate due to potential contaminants in the reagents (Leonard et al. 2007; Champlot et al. 2010), and to ensure authenticity of the sample amplification with a 95% confidence level, we used the Fisher's exact test (Champlot et al. 2010). Blank control data obtained over many experiments with a given reagent batch were pooled, and after Bonferroni correction, only sequences with a 95% confidence interval were validated and considered authentic. Of the 153 samples analyzed, 60 resulted in unsuccessful genetic analyses (39% of the total individuals), 56 of which did not produce any amplification products after multiple attempts, whereas four gave low success rate which turned out to be non-significant to the Fisher's exact test, likely because of poor DNA preservation.

Durham. Bone powder (100-400mg) was digested in 0.425 M EDTA, 0.05% SDS, 0.05 M Tris-HCI and 0.333 mg/mL proteinase K and incubated overnight (18-24 hours) on a rotator at 50°C, or until fully dissolved. The digestion buffer, excluding proteinase K, was UV-irradiated (254 nm wavelength) for an hour in a dedicated cross-linker prior to use. 2mL of extract solution was then concentrated in a Millipore Amicon Ultra-4 30 KDa MWCO (Millipore) to a final volume of 100μL. The concentrated extract was purified using silica spin-columns (QIAquick PCR

Purification Kit, Qiagen) following manufacturers recommendations, except that the final elution step was performed twice to produce a final volume of 100µL. One in five or one in ten negative extraction controls were performed alongside the ancient bone samples. All extraction blank controls were negative when screened for the ANC1 fragment.

PCRs were setup in 25µL reactions using 1.25U Taq GOLD (Applied Biosystems), 1x Gold buffer (Applied Biosystems), 2.5mM $MgCl_2$, 0.5µg/µL BSA (Bovine Serum Albumine), 200µM of each dNTP, 0.8µM of each forward and reverse primers, and 2µL of aDNA extract. We used PCR primers ANC1 (Larson et al. 2007a), and the two primer pairs:

- U15697 (5'-CATATYATTATTGATCGTACATAGCACA-3')
- L15787 (5'-AAGAGGGATCCCTGCCAAG-3'), and
- U15775 (5'-AAYTACCATGCCGCGTGAAA)
- L15864 (5'GGTGAGATGGYCCTGAAGTAAGAAC-3') (Geörg, this study),

that target two fragments overlapping the ANC2 fragment amplified in Leuven. One PCR negative control was included for every 5-8 aDNA template PCRs. PCR cycling conditions were 95°C for 5min, 50 cycles of 94°C for 45 sec, 54°C for 45 sec and 72°C for 45 sec, followed by 72°C for 10 min. PCR products were stored at -20°C.

An initial PCR using the ANC1 primers was performed in order to screen the extracts for preserved DNA. Successful amplifications were Sanger sequenced on the Applied Biosystems 3730 DNA Analyser at the DNA sequencing service in the School of Biological and Biomedical Sciences at Durham University. Once preserved samples were identified we used 5bp 5'-tagged PCR primers (Binladen et al. 2007b) to re-amplify the ANC1 fragment and, in addition, the fragment corresponding to ANC2. In both instances PCR products were visualized on agarose gel and stained with GelRed, and then pooled by eye into approximately equimolar concentrations using a reference series of PCR products previously quantified on the Qubit fluorometer; approximately 12µg/µL of

each PCR product was used for the final pool. The pooled 5' tagged PCR products were then concentrated using an Amicon Ultra-4 30KDa MWCO filter column to a final volume of 100µL. The concentrated amplicon pool was subsequently purified using the QIAquick PCR Purification Kit following manufacturers recommendations, except that the final elute volume was 80µL. The concentrated PCR amplicon pool was then built into a paired-end library (Paired-End DNA Sample Prep Kit, Illumina) following manufacturers guidelines and subsequently sequenced on the Illumina GAII platform at the Department of Biology at Copenhagen University.

Illumina's Genome Analyzer Sequencing Control Software (SCS) v2.4 was used for base calling. A custom written PERL script (Rasmussen, M., University of Copenhagen) was used to filter out sequences containing the 5' tag label and to mate paired-end reads into single lines containing both forward and reverse 5' tag label information. A second custom written PERL script (Frantz, L., Wageningen University) was used to write a single fasta file for each tag label/amplicon. The resulting fasta files were assembled into contigs against a reference sequence (EU333163) in Geneious Pro 5.4.3 (Drummond et al. 2011). Assembly was performed using total quality score to call the best base (any base with a quality <20, equivalent to PHRED scores, was called as N and subsequently excluded from further analysis). All resulting haplotypes corresponded to the ANC1 fragment previously sequenced using Sanger sequencing at Durham University and we observed consistency in the extended ANC2 haplotype with sequences produced in Leuven and Mainz. At least one hundred sub-clones per sample were obtained for each re-sequenced PCR product, although we reached an average of several thousand copies per PCR amplicon. Nucleotide positions that could not be resolved despite the deep coverage were discarded from further analysis and called according the IUPAC nucleotide code.

Mainz. For each specimen two independent extractions were carried out. Aliquots of 0.3-1g of bone powder were incubated in a decalcifying and digestive solution containing 0.5M EDTA (pH 8.3,

Applied Biosystems), 30-60µL Proteinase K (Roche) and 1/10 volume of 0.5M N-lauryl sarcosine (Merck) on a rotary mixer over night at 37°C. DNA was extracted using phenol / chloroform-isoamylalcohol (Roth). The supernatant was transferred to an Amicon Ultra-15 filter unit (50kDa, Millipore) and washed with at least 5ml of UV-irradiated water before concentrated to a final volume of 100-200µL. Extracts were stored at -20°C. Each extraction contained at least two blank controls to detect contamination. PCR was performed in a final volume of 50µL containing 2.5U AmpliTaq Gold® DNA Polymerase (Applied Biosystems), 1x Gold Buffer (Applied Biosystems), 2.5mM $MgCl_2$ (Applied Biosystems), 20µg BSA (Roche), 0.2mM dNTP-Mix (Quiagen), 0.2µM of each primer (Biospring) and 2-8µL of bone or teeth aDNA extract. The PCR thermal cycling conditions were 94°C for 6min and 50 cycles of 94°C for 30sec, 57°C for 30sec and 72°C for 40sec. The products were stored at -20°C. All PCR reactions were carried out on a Mastercycler (Eppendorf). The primers used overlapped the ANC1 and ANC2 fragments amplified in Leuven and Durham: U15516/L15620 and U15697/L15787 (Geörg, this study, see primer sequences above). At least one negative control was included for every 10-15 amplified templates.

Positive PCR products were visualized on an agarose gel (Ultra Pure™, Invitrogen) stained with bromophenol blue (Fermentas). Purification of the amplified products were done with MSB Spin PCRapace Kit (Invitrogen) according to manufacturer´s specification or trough enzymatic digesting using 0.5U SAP and 2U EXO (30min incubation at 37°C followed by 15min of denaturation at 80°C). The purified fragments were directly sequenced using ABI Prism® Big DyeTM Terminator Cycle Sequencing Kit (vers. 3.1, Applied Biosystems) on a ABI Prism® 3130 Genetic Analyzer (Applied Biosystems) with dye products purified using Sephadex G50-fine (GE Healthcare) on Multiscreen-plates (Millipore) following manufacturer´s instructions.

None of the blank controls produced a positive amplification. In 25 of 43 samples it was possible to reproduce at least four sequences out of two independent extractions for every fragment analyzed.

One sample from Ulucak (Ulu28) failed in one part of the 80bp fragment. The resulting sequences were edited using Lasergene software (DNASTAR Lasergene, Version 7.1, GATC Biotech AG).

Modern sequences. Modern wild boar mtDNA sequences were processed at the Department of Animal Sciences and Aliments, University of Barcelona (Spain). We used previously described methods (Alves et al. 2009) except for the use of a reverse primer (5'-GTAACCATTGACTGAATAGCACCT-3') to avoid amplifying NUMTs.
There are few published reports on *Sus* NUMTs (Fang et al. 2011) and no database readily available for screening putative NUMT sequences (if not undertaking NUMT identification through previously published pig nuclear genomic sequences). By applying the strict authentication criteria described in section 1.1 we have minimized the confounding effect of co-amplifying NUMTs.

3. Phylogeographic analyses

Haplotype assignment for each specimen was based on the ANC1 variation using the same terminology proposed in Larson et al. (Larson et al. 2007a). It is worth noting that we have defined the variable site diagnostic for haplotype Arm1T as an insertion (15567.1T in ANC1), which is a more parsimonious phylogenetic marker. Fragment ANC2 is less variable and possesses less discriminating power because of some recurrent mutations (e.g. np 15714) (supplementary table S4).

All the ANC1 sequences in this study matched haplotypes previously described in Larson et al. (Larson et al. 2007a). Only three novel ANC1 sequences were observed (Bad9, M123 and M56), but they were only one mutation distant from the motif of Arm1T (Bad9 and M123) and A (M56), and were therefore assigned to these haplotypes. Overall, 141 specimens possessed Near Eastern

ancestry (haplotypes Arm1T, Y1, Y2, Yellow star) and 51 possessed European ancestry (haplotypes A, C, LDomBritSaddle01 and LDomGermanyAngler).

We constructed a Maximum-Likelihood tree based on 661 bp sequences of the mtDNA control region of 267 modern wild boar (present study, (Larson et al. 2005; Larson et al. 2007a) from Near-Middle East, Europe, and East Asia (supplementary fig. S2a) using PhyML (Guindon and Gascuel 2003) in Geneious (Drummond et al. 2011). The same topology was obtained using different substitution models (GTR, HKY85) and support values were calculated using a chi-squared test. The same topology of the main clades was obtained in three Bayesian trees run for up to 5,000,000 iterations using MrBayes (Ronquist and Huelsenbeck 2003) in Geneious. The general topology of the tree confirmed the clades that were observed in previous phylogeographic analyses (Larson et al. 2007a). Within the large European clade (fig. 2a) two main sub-clades were observed including the Italian-specific sub-clade (supplementary fig. S2a). The Near Eastern sequences are structured in two main sub-clades that we termed NE1 and NE2. Genetic variation contained in the fragment ANC1 allowed for the assignment of all the ancient Near Eastern haplotypes observed in this study to the NE2 clade. Crucially, the topology of the tree within clade NE2 shows that the mutations 15567.1T and 15592 contained in the ANC1 provide strong phylogenetic support to the definition of the two main Near Eastern ancient haplotypes that we encountered in our study, Arm1T and Y1 (supplementary fig. S2a, supplementary table S4).

To assess the phylogeography of the mtDNA clades, the place of origin and genetic signature of the modern wild boar used in this study (supplementary table S2) were plotted on a map (supplementary fig. S2b). The geographic distribution of mtDNA clades NE1 and NE2 in the Near East shown in figure 2b was designed after calculating the spatial distribution of their absolute frequencies in modern wild boar mtDNA haplotypes (as in supplementary fig. S2b) with Surfer 6

(http://www.goldensoftware.com/) using the Kriging method. Regions that were not sampled (*e.g.* the Arabian peninsula) were removed from the analysis.

4. Morphometric analyses

We used 2D landmarks and sliding-semi-landmarks based GMM approaches to describe the molar size and shape variation. Photographs were taken using a reflex camera (Nikon D90) coupled with a 60mm micro-length (AF-S Nikkor) to obtain images of the teeth in their occlusal view. Images were standardized for position and parallax. Two-dimensional coordinates of landmarks within the occlusal surface and sliding-landmarks along the outline of the teeth were recorded (Cucchi et al. 2011), as well as traditional measurements (maximum length and widths) using TpsDig (http://life.bio.sunysb.edu/morph/, (Rohlf 2010b). We recorded 9 landmarks and 66 sliding semi-landmarks for the lower M2 and 12 landmarks and 87 sliding semi-landmarks for the lower M3 (supplementary fig. S3b). The coordinates of the semi-landmarks were recorded using the "Draw background curves" tool of TpDIG that allows for the positioning of equidistant points. The outline of the lower M2 was divided into two anterior and posterior curves composed of 28 and 38 points respectively plus two landmarks in between.

The outline of the lower M3 was divided into four curves (anterior (28 points), posterior (28 points), labial (18 points), lingual (13 points) plus 4 landmarks in between). We used TpsRelw (http://life.bio.sunysb.edu/morph/ (Rohlf 2010a) to slide the semi-landmarks along their respective curves with the Procustes distance minimization criteria (Bookstein et al. 2002). The aligned coordinates and the centroid size, as well as the traditional measurements, were then analyzed using R v2.13.1 (R Development Core Team 2011) and the "Rmorph" library (Baylac 2012). The first components of the Principal Component Analysis (PCA) realized on the coordinates after superimposition were analyzed instead of the original dataset to minimize the number of variables compared to the number of specimens. Before discriminant analyses were carried out, a

dimensionality reduction was applied on the scores of the PCA with the Baylac & Friess procedure (Baylac and Friess 2005) that selects the N firsts components that maximize the variability between the groups. Traditional measurements of maximum lengths and widths (supplementary fig. S3b) were analyzed using the isometric size and shape parameters calculated following the Mosimann log shape ratio approach (Mosimann 1970; Mosimann and James 1979).

It is worth noting that using traditional metrics, the only significant result that was obtained was the difference in the isometric size of the lower M3 between the pigs with European and Near Eastern mtDNA lineages (supplementary table S6, fig. 2b). In this analysis, the pigs with European mtDNAs show smaller lower M3 than the pigs with Near-Eastern lineages.

5. Brief descriptions of key archeological sites

Ancient pig specimens analyzed in this study were excavated from 48 archeological sites in modern day Armenia, Cyprus, Georgia, Iran, Syria and Turkey (supplementary fig. S1a). Supplementary tables S1 and S4 list additional details and statistics regarding the results of the genetic analyses in each archeological site. Below we provide background information for key sites mentioned in the main text.

Turkish sites

Bademağacı Höyük is located in the south of the Lake District (Pisidia), southwest Anatolia, about 50 Km north of Antalya. The mound lies at an altitude of 780m above sea level (asl) just north of the pass (ancient Klimax) in the Taurus Mountains, which links this region with the coastal plain of Pamphylia. The site was excavated from 1993 until 2010 (Duru and Umurtak 2011) and a study of

the faunal material was published (De Cupere et al. 2008). A total of 41 ancient pig specimens were genetically analyzed dated to the Early Neolithic and the Early Bronze Age on the basis of AMS dates or the associated archeological context from which the bones were unearthed. Fourteen specimens were identified as wild boars on the basis of metric analyses. Radiocarbon dating previously carried out on animal bones unearthed from the levels 3 and 4A of the Early Neolithic, in which some of the pig specimens of this study were also found (supplementary table S1), provided an age ranging in 6,450-6,240 BC (De Cupere et al. 2008). Of the 41 analyzed specimens, 19 yielded reproducible amplifications.

Lidar Höyük & Hassek Höyük. Hassek Höyük and Lidar Höyük are located in the Karababa Basin in the Urfa and Adiyaman provinces respectively (southeastern Anatolia). Altitudes range between 400 and 600m asl. Studies of the faunal material has been published (Kussinger 1988; Stahl 1989; Boessneck 1992). Based upon stratigraphical sequencing of the sites and AMS radiocarbon dating, pig samples from Hassek Höyük were dated to the Calcholithic and Early Bronze Age, and those from Lidar Höyük to a large time frame spanning the Early Bronze Age to the Middle Ages. Nine specimens from Lidar Höyük were directly AMS dated (supplementary table S1). In two instances (M51 and M76) the AMS dates did not support the chronological assignment based on stratigraphy, whereas in the other samples a total or partial agreement within the range of two-sigma calibrated results was observed. A total of 25 specimens from Hassek Höyük were analyzed, of which four yielded positive and reproducible amplifications of DNA. Sequences from 57 out of 77 specimens from Lidar Höyük were successfully generated.

Sagalassos & Düzen Tepe. The antique site of Sagalassos is located 7km north of the small city of Ağlasun on a steep, south-facing slope of the Ağlasun Dağları (Western Taurus range, Southwest Turkey) at an altitude of 1,450 to 1,650m asl. In Imperial times it was the main city of ancient Pisidia, and was continuously inhabited from the 5th century BC until the earlier 13th century. On a

lower plateau, ~1.8km southwest of Sagalassos, lies the Classical/Hellenistic proto-urban site of Düzen Tepe (5th-later 2nd century BC). Excavations of both sites are ongoing (e.g. www.sagalassos.be (Degryse and Waelkens 2009; Vanhaverbeke et al. 2010; Vyncke 2012) and the fauna is being studied (De Cupere 2001). Based upon AMS dating and stratigraphical sequencing of the site, pig specimens from Sagalassos and Düzen Tepe range from the 5th century BC to the 12th century AD (Ricaut and Waelkens 2008; Ottoni et al. 2011). A total of 24 ancient specimens were analyzed in this study all of which generated reproducible results.

Gordion was the capital of the Kingdom of the Phrygians (10th-early 7th century BC), located along the Sakarya River, on a mound (700m asl) known as Yassıhüyük, ca 80km west-southwest of Ankara. The mound was rebuilt and refortified several times and contained mainly 'megara' used as audience halls, shrines and storage buildings. The mound is surrounded by dozens of tumuli. The major periods represented here are the Bronze Age (~2500–1200 BCE) and the Early Iron Age (~1200–550 BC), when, at the latest from the 10th century BC, it became the capital of the Phrygian kingdom, but from the early 7th century BC onward was subjected first to the kingdom of the Lydians, and subsequently to that of the Achaemenid Persians (or "Late Phrygian") period (546-333 BC). After its conquest by Alexander the Great (333 BC), the site declined becoming a village during the Hellenistic period (3rd century to 25 BC), the Roman Imperial (25 BC – mid 6th century AD), the Byzantine (mid 6th century – early 15th century), and the Ottoman period (early 15th century– 1923). At the time of the formation of the Republic of Turkey in 1923, the mound was no longer inhabited. Genetic analyses were successful in six out of seven ancient pigs, recovered in layers associated to the Late Bronze Age, the Late Phrygian and the Late Hellenistic period.

Çamlıbel Tarlası is located on the Anatolian Plateau, approximately 1,000m asl. It is located on a ridge overlooking a river in what was once a heavily forested area. Excavations focused on a rural Late Chalcolithic settlement dated to 3,590-3,470 BC (Schoop 2009). The faunal material of this

site was studied and pigs are found in much greater frequency than goats and sheep (Bartosiewicz and Gillis 2011). Genetic analyses were carried out on 15 pig specimens, 13 of which were successful.

Çayönü Tepesi is an Early Neolithic site located in the upper Tigris valley, in Southeast Turkey, dated to 10,000-6,500 BC. It has been considered one of the oldest pig domestication sites in Western Asia and possesses evidence that the *Sus* population around Çayönü lived in an intermediary relationship with humans between 'wild' and 'domestic' (Ervynck et al. 2001). A total of 14 pigs were genetically analyzed though only one was successfully amplified and sequenced.

Ulucak Höyük Ulucak Höyük is favorably situated along one of the main arteries between the Aegean coast and inland Anatolia in the Izmir province. This settlement mound covers about 3 ha and rises about 6m above the plain. Well-preserved Neolithic deposits represent a material culture akin both with the Lake District and the Greek Neolithic (Çilingiroğlu 2012). Altogether 19 specimens were analyzed, 17 of which associated with levels IV and V that date from 6,400-5,900 BC (Çakırlar 2012). Six of these samples, all identified as domestic pigs, were successfully analyzed.

Malkayası. This cave, discovered in 2001, is located upon the northern fringe of the Beşparmak Mountain (ancient Latmos) in Ionia on the coast of Western Anatolia. In prehistoric times, Mount Latmos was a holy place. The Malkayası cave and several other sites in that area show similarity to the Hacilar-culture (Plain of Burdur, territory of classical Sagalassos) and were therefore dated to the Chalcolithic period. AMS-dates of two wild boar analyzed in this study support this classification (5,000-4,500 BC). These two specimens provided successful amplification of their DNA though five others did not.

Menteşe. This tell is located in the northern part of Western Anatolia next to the dried-out lake Yenişehir, about 25km south of the archeological site of Ilıpınar. The mound is four meters in height and has a diameter of ~150m. It encompasses three different strata. The youngest layer is associated with the Roman Imperial period, the other two date to the Bronze Age and the Chalcolithic. The oldest stratum of this latest phase was dated to 6,400 BC and is older than Ilıpınar. The three analyzed specimens, all identified as domestic pig on the basis of bone traditional metrics, were recovered from the Chalcolitic layer and date around 6,000 BC. Two samples yielded reproducible products.

Sirkeli Höyük. This is one of the biggest settlement mounds in Cilicia at the interface between Syria, Cyprus and Anatolia. The site is located approximately 40km east of the modern city of Adana, close to the Ceyhan River, which represented a trade route between Syria and the Central Anatolian Plateau. The site was occupied from the Chalcolithic throughout the Bronze and Iron Ages but was abandoned in Hellenistic times. A total of 12 Iron Age individuals were genetically analyzed, four of which generated reproducible data.

Göbekli Tepe and Gürcütepe. The Early Neolithic site of Göbekli Tepe is located on a limestone ridge overlooking the Harran plain, northeast of the town of Sanhurfa, in Southeastern Turkey (Schmidt 1995,2000), at an altitude of 770 m above sea level (asl). Twelve specimens dating back to the 10th millennium BC (Aceramic Neolithic), of which at least four were identified as wild boar, were analyzed in the present study, resulting in unsuccessful DNA amplification. Gürcütepe is located south to Göbekli Tepe, in the Harran plain (Schmidt 1995), at the altitude of about 450 m asl. A total of 9 pig specimens from Gürcütepe, dated to the 8th millennium BC, were analysed in the present study, providing no successful amplification of DNA.

Syrian sites

Samples from four archeological sites were analyzed (see supplementary table S1). DNA sequences were obtained from **Tell Leilan** located in Northeast Syria in the Khabur River Basin at an altitude of ~390-400m asl. It is one of the largest archeological sites in Syria and was one of the most important cities in Northern Mesopotamia during the second and third millennia BC (http://leilan.yale.edu/index.html). A total of eight ancient pig specimens were genetically analyzed. Samples were collected from two different areas: the Acropolis Northwest and the Lower Town South dated to 2,600-2,200 BC when the settlement was abandoned following an abrupt aridification. Two out of eight samples were successfully analyzed.

Armenian sites

Samples from six archeological sites were analyzed (supplementary table S1) and we obtained aDNA from four of these (Areni-1, Tsakaektsi, Sevkar-4, Lchashen-2).

Areni 1 (Wilkinson et al. 2012) is a cave located in south-central Armenia in the Vayots Dzor district (the Arpa River valley), on the border with Nakhijevan (Azerbaijan). The main focus of the excavations in 2007 were the Late Chalcolithic layers dating to the late 5th - Mid 4th Millennium BC, though later medieval intrusions were also present. The only pig that yielded DNA from Areni 1 (supplementary tables S1 and S4) has an uncertain date (Pinhasi et al. 2010).

Tsakaektsi is a settlement located in north-east Armenia in the Tavush district, 5 km east from the Sarigyugh village (the Aghstev River valley). The main focus of the excavations in 1983-1985 (Yesayan 1992) were the medieval constructions dating to 12 - 13th centuries AD (High Medieval period).

Sevkar 4 (Surb Nahatak) is a fortified settlement located in north-east Armenia in the Tavush district, south from the Sarigyugh village (the Aghstev River valley). The main focus of the excavations between 1960-1972 were the Iron Age structures dating to VII - VI centuries BC (Yesayan 1976).

Lchashen is a village close to Lake Sevan in the Gegharkunik Province (supplementary fig. S1a). A large, 55-hectare complex of archeological remains possesses dates ranging over several millennia with the oldest belonging to the Neolithic, is located close to the village (Smith et al. 2009). We successfully extracted DNA from one specimen belonging to the Bronze Age.

Shengavit settlement is located in south-central Armenia (in the northern proximity of Ararat valley in the Ayrarat province) and the inhabited phase is dated to between the 4th millennium BC to the 2nd century BC. The town covered approximately six hectares and was probably the commercial and cultural center for a number of satellite settlements in the region. Through cultural objects including ritual obelisks in particular, the town of **Mokhrablur** is closely connected to Shengavit (http://www2.widener.edu/~msrothma/shengavitweb2.html).

Georgian sites

Aruchlo is located ~50km southwest of the town Tiflis, the capital city of Georgia, and close to the small village Nachiduri. The rivers Chrami and Masavera converge in sight of the mound. The Neolithic tell is 6m high and is made up of several phases of later occupations and has been assigned to the "Sulaveri-Somutepe" group of settlements typical for the region. The AMS dates for the Neolithic layers provide an age ranging from 6,000-5,300 BC. The nine analyzed samples date

to ~5,600-5,300 BC, a time frame associated with the Early Neolithic in Caucasia. Seven domesticated animals from this site were successfully analyzed.

Tachti Perda. The multilayered site of Tachti Perda lies in a settlement chamber in the centre of the southern Caucasus and is surrounded by the Great and Small Caucasus Mountain ranges. This area functions as an important travel route connecting the Eurasian steppe with Asia Minor and Central Asia. The mound is ~20m in height and encompasses several layers dated to the Iron and Bronze Age. Eight domestic pigs dating back to the Late Bronze Age (1,400-1,200 BC) were analyzed and all yielded reproducible products.

Iranian sites

Haftavan Tepe was excavated in the 1970s by Charles Burney. It is one of the largest sites in the Province of Azerbaijan and was occupied from the Late Bronze Age (Trans Caucasian) to the Early Islamic period. The site is located north of Lake Urmia. The fauna of this site has been recently studied as part of a PhD Thesis (Mohaseb Karimlu 2012). The six AMS dates were performed on animal bones and range between 2,000 cal BC and 730 AD.

Kohneh Tepesi. The site, near the city of Khomarlu in the Arax River Basin, is a large mound (77m by 44m, 7m high) with multiple occupation layers from the Bronze Age to the Iron Age. The site was excavated as part of an archeological program related to the construction of the Khoda Afarin Dam in the province of Eastern Azerbaijan. Kohneh Tepesi is located in a forested area limited in the south by the Arax River Basin and in the north by the Arasbaran Mountains. Archeological investigations have revealed cultural interactions and important ties with the Caucasus and Eastern Anatolia.

The Gorgan Wall sites. The recent joint Iranian and British archeological expedition along the Gorgān Wall, a historical wall extending over 195km in the north-east of Iran shed light into poorly understood periods in Iranian archeology including the Sassanian era (AD 235-7th century). The sites of **Qelīch Qōīneq**, **Dasht Qal'eh** and **Qareh Dōyūb** belong to the Achaemenid (the first) and to the Sasanian period (the two last sites). An extensive zooarcheological study revealed insights into the subsistence economies of various type of sites (urban, rural, military) along this wall (Omrani Rekavandi et al. 2007; Mashkour 2012).

The other samples belong Neolithic and Chalcolthic sites along the Zagros Mountains. **Ganj Dareh**, **Tepe Guran**, and **Qaleh Rostam** are the oldest Iranian sites that were analyzed and only the latter has provided a single sequence. **Qaleh Rostam** is located in the Central Zagros and is dated to the mid-Neolithic period. **Chogha Gavaneh** is a Chalcolithic/Bronze Age site in the Central Zagros excavated by Kamyar Abdi (Abdi 1999). The fauna report is being prepared for publication. **Tepe Mehr Ali** is a Chalcolithic site in the Fars Province excavated by A. Sardari as a rescue excavation necessitated by the construction of a dam. The site is located at a high altitude and has a high pastoral component. **Malyan** is also in the Fars Province and belongs to the subsequent Bronze /Iron Age periods. The fauna was studied by Melinda Zeder (Zeder 1985,1991). **Doshan Tepe** is another Bronze Age/ Iron Age site in the northern part of the central plateau near Tehran and was excavated between 2000 and 2002 by Youssef Madjidzadeh within the Ozbaki archeological Zone Project. The abundant animal bones of the site are very well preserved and suitable for genetic studies (Mashkour and Mohaseb Karimlu 2011).

Cypriot sites

Shillourokambos. We attempted to extract DNA from a single bone from this PPNB (pre-pottery Neolithic B) site located six kilometers east of Limassol in southern Cyprus. This site is one of the

largest and most important PPN sites in the region. The site is key for understanding the chronology of animal domestication and human management during the early domestication process (Vigne et al. 2011).

Supplementary Table Descriptions

Supplementary table S1. List of all the ancient specimens from Middle and Near East analysed in the present study. In the AMS indirect dating, upper and lower bounds determined from AMS dating carried out on associated bones from the same stratigraphic layer is reported. The status (wild versus domestic) of some of the specimens was provided following identification based on traditional metrics. Specimens for which status identification was not possible are left blank. Because traditional metrical methods for determining status are not necessarily conclusive (Evin et al. submitted), some of the status calls reported here may be subject to revision.

Supplementary table S2. List of modern wild boars mapped in supplementary figure S2. Each specimen was assigned to a mtDNA clade (Larson et al. 2007a) on the basis of genetic variation in long stretches of the mtDNA control region (380-661bp).

Supplementary table S3. Variable positions in ANC1 clone sequences from 10 ancient pig specimens obtained with Topo-TA Cloning kit (Invitrogen) and Illumina GAII platform. Cloned sequences (in grey) are aligned to the consensus of each specimen. In Topo-TA cloned sequences, direct sequences from PCR products are shown in white and used to create a consensus sequence. A frequent occurrence of some artifacts appeared in the oldest samples (BAD47, BAD52), most likely due to a low initial number of template molecules. Names for the sequenced clones are given as follow: SAMPLE NAME_EXTRACTION_PCR FRAGMENT_# CLONE. Positions are numbered according to Ursing and Arnason (Ursing and Arnason 1998).

Supplementary table S4. Polymorphic sites and associated haplotypes detected in the fragments ANC1 and ANC2 of the mtDNA control region in ancient pig specimens from the Near East. Alignment was done with a reference sequence, in bold (AJ002189, (Ursing and Arnason 1998)). Colors of mtDNA haplotypes and clades (NE2, Near Eastern clade 2; E, European) mimic those in figures 1 and 2. Positions are numbered according to Ursing and Arnason (Ursing and Arnason 1998). Haplotype assignment is based on Larson et al. (Larson et al. 2007a). The status (wild versus domestic) of some of the specimens was provided following identification based on traditional metrics. Specimens for which status identification was not possible are left blank. Because traditional metrical methods for determining status are not necessarily conclusive (Evin et al. submitted), some of the status calls reported here may be subject to revision.

Supplementary table S5. Ancient pig specimens analyzed in the timeframe 6,500-3,000 BC depicted in supplementary figure S3. An asterisk indicated dates based upon direct AMS dating of pig samples unearthed from the same layer.

Supplementary table S6. Differences between pigs with Near Eastern and European lineages in size (Kruskall-Wallis test) and shape (MANOVA) based on geometric and traditional morphometrics. Significant results are in bold for lower M2 and M3 with sample size in parentheses (EU: European lineages, NE: Near East lineages).

Supplementary Figures Legends

Supplementary fig. S1. Panel a) pie charts indicate approximate locations of the archeological sites investigated in the present study. Size of the pie charts is proportional to the number of specimens

analyzed from each site. Colors indicate the fraction of haplotypes encountered (as in figure 1) and the rate of unsuccessful samples (in white). Sites are numbered on the map as follows: 1, Ulucak Höyük; 2, Malkayası; 3, Menteşe; 4, Bademağacı; 5, Sagalassos; 6, Gordion; 7, Çamlıbel Tarlası; 8, Düzen Tepe; 9, Lidar Höyük; 10, Hassek Höyük; 11, Sirkeli Höyük; 12, Göbekli Tepe; 13, Gürcütepe; 14, Nevali Çori; 15, Çayönü Tepesi; 16, Halan Çemi; 17, Tell Leilan; 18, Atij; 19, Mashnaqua; 20, Umm Qseir; 21, Tachti-Perda; 22, Aruchlo; 23, Shengavit; 24, Mokhrablur; 25, Tsakaektsi; 26, Sevkar 4; 27, Lchashen 2; 28, Areni-1; 29, Kohneh Tepesi; 30, Haftavan Tepe; 31, Kalanan Sirlan Bijar; 32, Doshan Tepe; 33, Gohar Tappeh; 34, Dasht Qaleh; 35, Qareh Doyub; 36, Qelīch Qōīneq; 37, Chishko; 38, Choga Gavaneh; 39, Ghar-i-Khar; 40, Ganj Dareh; 41, Guran Tepe; 42, Cham Quleh; 43, Qaleh Rostam; 44, Malyan; 45, Mushki; 46, Mehr Ali; 47, Tol-e-Spid; 48, Shillourokambos. Panel b) yields of successful genetic analyses of the ancient samples plotted against the chronological age of the specimen. The fraction of successful specimens in each chronological period is reported.

Supplementary fig. S2. Panel a) Maximum-Likelihood tree based on 661bp sequences of the mtDNA control region of 267 modern wild boar (including novel sequences and those from previous studies (Larson et al. 2005; Larson et al. 2007a)) from Europe, the western Eurasia and East Asia, the latter of which were used to root the tree . Diagnostic SNPs in the ANC1 fragment that define the main clades are shown on the tree. SNPs are numbered to a reference sequence (AJ002189 (Ursing and Arnason 1998), indicated as 'REF' in the tree and are all transitions unless specified. Recurrent mutations are underlined. It worth noting that mutations 15567.1T and 15592 discriminate halotypes Arm1T and Y1. Statistical support (chi-squared p-values) is indicated in the branches of the main clades. The same topology of the main clades of the tree was obtained in Bayesian trees. Posterior probabilities are indicated in bold in correspondence of the nodes separating the main clades. Panel b) geographic distribution within the west Eurasian continent of modern wild boar mtDNA haplotypes from literature and the present study (supplementary table

S2). In total, 150 specimens are displayed, and colors designate the clade affiliation, as reported in legend. Specifically for the specimens with Near Eastern ancestry, the color designate to one of the two Near Eastern clades (NE1 and NE2, in green and grey) detected by sequencing 661 bp of the D-Loop region. All the ancient pigs possessing one of three Near Eastern mtDNA lineages (Arm1T, Y1 or Y2) (Larson et al. 2007a) belonged to the NE2 clade.

Supplementary fig. S3. Panel a) Geographic distribution and frequency of ancient pig ANC1-haplotypes in the time frame 6,500-3,000 BC analyzed in the present study and in literature (Larson et al. 2007a). A total of 78 pig specimens are included in the map (supplementary table S5). Pie size is proportional to the number of specimens genetically analyzed in each region. Asterisks indicate the fraction of wild specimens. ANC1-haplotypes are represented by different colors as follows (clade assignation is also reported): yellow, Y1 (Near Eastern); light blue, Arm1T (Near Eastern); brown, Y2 (Near Eastern); brown, Arm2T (Near Eastern); red, A and C (European); orange, Italian specific haplotype (Italian). Dates are reported on the map in the areas where Y1 is present. An inset illustrating the geographic distribution of ANC1-haplotype in Europe in the time frame 3,000 BC-1,500 AD, as from Larson et al. (Larson et al. 2007a), has been included on top right. Dots in the inset indicate exclusively the presence of the haplotypes and not the frequency. Panel b) Traditional measurement (maximum tooth lengths and widths) and location of the 2D landmarks (in grey), connected by lines to emphasize their relative positions, and sliding semi-landmarks (in white) along the outlines of the second (left) and third (right) lower molars of *Sus scrofa*.

Literature cited

Abdi K. 1999. Archaeological Research in the Islamabad Plain, Central Western Zagros Mountains: Pre- liminary Results of the First Season, Summer 1998. Iran 37:33-43.

Alves E, Fernandez AI, Fernandez-Rodriguez A, Perez-Montarelo D, Benitez R, Ovilo C, Rodriguez C, Silio L. 2009. Identification of mitochondrial markers for genetic traceability of European wild boars and Iberian and Duroc pigs. Animal 3:1216-1223.

Bartosiewicz L, Gillis R. 2011. Preliminary Report on the Animal Remains from Camlıbel Tarlası, Central Anatolia. In: Schachner A, editor. Die Ausgrabungen in Boğazköy-Hattuša 2010. p. 76-79.

Baylac M, Friess M. 2005. Fourier descriptors, procrustes superimposition and data dimensionality: an example of cranial shape analysis in modern human populations. Modern morphometrics in physical anthropology:145-165.

Baylac M. 2012. Rmorph: a R geometric and multivariate morphometrics library.

Binladen J, Gilbert MT, Campos PF, Willerslev E. 2007a. 5'-tailed sequencing primers improve sequencing quality of PCR products. Biotechniques 42:174-176.

Binladen J, Gilbert MT, Bollback JP, Panitz F, Bendixen C, Nielsen R, Willerslev E. 2007b. The use of coded PCR primers enables high-throughput sequencing of multiple homolog amplification products by 454 parallel sequencing. PLoS One 2:e197.

Boessneck J. 1992. Besprechung der Tierknochen- und Molluskenreste von Hassek Höyük. Istanbuler Forschungen 38:58-74.

Bookstein FL, Streissguth AP, Sampson PD, Connor PD, Barr HM. 2002. Corpus callosum shape and neuropsychological deficits in adult males with heavy fetal alcohol exposure. Neuroimage 15:233-251.

Briggs AW, Stenzel U, Johnson PL, et al. (11 co-authors) 2007. Patterns of damage in genomic DNA sequences from a Neandertal. Proc Natl Acad Sci U S A 104:14616-14621.

Çakırlar C. 2012. Evolution of animal husbandry in Neolithic Central-West Anatolia, the archaeozoological record from Ulucak Höyük (ca. 7040-5660 cal. BC, İzmir, Turkey). Anatolian Studies 62:1-33.

Champlot S, Berthelot C, Pruvost M, Bennett EA, Grange T, Geigl EM. 2010. An efficient multistrategy DNA decontamination procedure of PCR reagents for hypersensitive PCR applications. PLoS One 5.

Çilingiroğlu Ç. 2012. The Neolithic pottery of Ulucak in Aegean Turkey: organization of production, interregional comparisons and relative chronology. British Archaeological Reports (International Series) 2426.

Cooper A, Poinar HN. 2000. Ancient DNA: do it right or not at all. Science 289:1139.

Cucchi T, Hulme-Beaman A, Yuan J, Dobney K. 2011. Early Neolithic pig domestication at Jiahu, Henan Province, China: clues from molar shape analyses using geometric morphometric approaches. Journal of Archaeological Science 38:11-22.

De Cupere B. 2001. Animals at ancient Sagalassos. Evidence of the faunal remains. Turnhout: Brepols.

De Cupere B, Duru R, Umurtak G. 2008. Animal husbandry at the Early Neolithic to Early Bronze Age site of Bademağacı (Antalya province, SW Turkey): evidence from the faunal remains. In: Vila E, Gourichon L, Choyke AM, Buitenhuis H, editors. Proceedings of the eight International Symposium on the Archaeozoology of southwestern Asia and adjacent areas: Archéorient, Maison de l'Orient et de la Méditerranée. p. 367-405.

Degryse P, Waelkens M. 2009. Sagalassos VI. Geo- and bio-archaeology at Sagalassos and in its territory. Leuven: Leuven University Press.

Drummond AJ, Ashton B, Buxton S, et al. (15 co-authors) 2011. Geneious v5.4: Available from http://www.geneious.com/.

Duru R, Umurtak G. 2011. Excavations at Bademağacı in 2010. ANMED 9:7-15.

Ervynck A, Dobney K, Hongo H, Meadow R. 2001. Born Free? New Evidence for the Status of Sus scrofa at Neolithic Çayönü Tepesi (Southeastern Anatolia, Turkey). Paléorient:47-73.

Evin A, Cucchi T, Cardini A, Strand Vidarsdottir U, Larson G, Dobney K. (2013). The long and winding road: Identifying pig domestication through molar size and shape. J Archaeol Sci 40 (1): 735-743.

Fang C, Liu Y-F, Zhao X-B. 2011. Distribution of Nuclear Mitochondrial DNA in Pig Nuclear Genome. Chinese Journal of Animal Science 17.

Gilbert MT, Bandelt HJ, Hofreiter M, Barnes I. 2005. Assessing ancient DNA studies. Trends Ecol Evol 20:541-544.

Gilbert MT, Binladen J, Miller W, Wiuf C, Willerslev E, Poinar H, Carlson JE, Leebens-Mack JH, Schuster SC. 2007. Recharacterization of ancient DNA miscoding lesions: insights in the era of sequencing-by-synthesis. Nucleic Acids Res 35:1-10.

Guindon S, Gascuel O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst Biol 52:696-704.

Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl Acids Symp Ser 41:95 - 98.

Hofreiter M, Jaenicke V, Serre D, Haeseler Av A, Paabo S. 2001. DNA sequences from multiple amplifications reveal artifacts induced by cytosine deamination in ancient DNA. Nucleic Acids Res 29:4793-4799.

Kussinger S. 1988. Tierknochenfunde vom Lidar Höyük in Südostanatolien (Grabungen 1979-86).

Larson G, Dobney K, Albarella U, et al. (13 co-authors) 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. Science 307:1618-1621.

Larson G, Albarella U, Dobney K, et al. (19 co-authors) 2007a. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. Proc Natl Acad Sci U S A 104:15276-15281.

Larson G, Cucchi T, Fujita M, et al. (32 co-authors) 2007b. Phylogeny and ancient DNA of Sus provides insights into neolithic expansion in Island Southeast Asia and Oceania. Proc Natl Acad Sci U S A 104:4834-4839.

Leonard J, Shanks O, Hofreiter M, Kreuz E, Hodges L, Ream W, Wayne R, Fleischer R. 2007. Animal DNA in PCR reagents plagues ancient DNA research. Journal of Archaeological Science 34:1361-1366.

Mashkour M, Mohaseb Karimlu A. 2011. Hunting and husbandry in the Ozbaki archaeological Zone (Savojbolagh plain) from the 6th millennium until the Iron Age: Archaeozoological study of Jeiran Tepe, Maral Tepe, Doshan Tepe and Tepe Ozbaki. In: Majidzadeh Y, editor. Final report of the Ozbaki archaeological excavations. Tehran: ICHTO Editions. p. 273-302 and 597-601.

Mashkour M. 2012. Animal exploitation during the Iron Age to Achaemenid, Sasanian and Early Islamic periods along the Gorgan Wall. In: Sauer E, Omrani Rekavandi H, Wilkinson T, Nokandeh J, editors. Persia's Imperial Power in Late Antiquity: The Great Gorgan Wall and the Frontier Landscapes of Sasanian Iran: Oxbow Books. p. 354-378.

Mohaseb Karimlu AF 2012. Exploitation des animaux de l'Âge du Bronze au début de la période Islamique dans le Nord-ouest de l'Iran : L'étude archéozoologique de Haftavan Tepe. [PhD]. [Paris]: Université de Paris I Panthéon Sorbonne.

Mosimann JE. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. Journal of the American Statistical Association 65:930-945.

Mosimann JE, James FC. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. Evolution:444-459.

Omrani Rekavandi H, Sauer EW, Wilkinson T, et al. (16 co-authors) 2007. An Imperial Frontier of the Sasanian Empire: Further Fieldwork at the GreatWall of Gorgan. Iran 45:95-136.

Ottoni C, Ricaut FX, Vanderheyden N, Brucato N, Waelkens M, Decorte R. 2011. Mitochondrial analysis of a Byzantine population reveals the differential impact of multiple historical events in South Anatolia. Eur J Hum Genet 19:571-576.

Pinhasi R, Gasparian B, Areshian G, Zardaryan D, Smith A, Bar-Oz G, Higham T. 2010. First direct evidence of chalcolithic footwear from the near eastern highlands. PLoS One 5:e10984.

R Development Core Team. R: A Language and Environment for Statistical Computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2011.

Ricaut FX, Waelkens M. 2008. Cranial discrete traits in a Byzantine population and eastern Mediterranean population movements. Hum Biol 80:535-564.

Rohlf FJ. Relative warps v1.49 [Internet]. State University of New York at Stony Brook, Stony Brook, NY; 2010a.

Rohlf FJ. tpsDig v2.16 [Internet]. State University of New York at Stony Brook, Stony Brook, NY.; 2010b.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572-1574.

Schmidt K. 1995. Investigations in the Upper Mesopotamian Early Neolithic: Göbekli Tepe and Gürcütepe. Neo-Lithics:9-10.

Schmidt K. 2000. Göbekli Tepe, Southeastern Turkey. A Preliminary Report on the 1995-1999 Excavations. Paléorient:45-54.

Schoop UD. 2009. Ausgrabungen in Camlibel Tarlasi 2007. Archäologischer Anzeiger 1:148-157.

Smith AT, Badalyan RS, Greene A, Minc L, Avetisyan P. 2009. The foundations of research and regional survey in the Tsaghkahovit Plain, Armenia. In. The Archaeology and Geography of Ancient Transcaucasian Societies. Chicago: Oriental Institute Publications. p. 410.

Stahl U. 1989. Tierknochenfunde vom Hassek Höyük (Südostanatolien).

Ursing BM, Arnason U. 1998. The complete mitochondrial DNA sequence of the pig (Sus scrofa). J Mol Evol 47:302-306.

Vanhaverbeke H, Waelkens M, Vyncke K, et al. (17 co-authors) 2010. The “Pisidian” culture? The Classical-Hellenistic site Düzen Tepesi near Sagalassus (SW Turkey). Anatolian Studies 60:105-128.

Vigne JD, Carrère I, Briois F, Guilaine J. 2011. The Early Process of Mammal Domestication in the Near East. Current Anthropology 52.

Vyncke K. 2012. The Classical-Hellenistic settlement at Düzen Tepe (SW Turkey): “the story of two settlements” or “two sides to a story”? Uluslararası Genç Bilimciler Buluşması / International Young Scholars Conference; 04-07 November 2009; Antalya: International Young Scholars Conference. p. 497-508.

Wilkinson KN, Gasparian B, Pinhasi R, Avetisyan P, Hovsepyan R, Zardaryan D, Areshian GE, Bar-Oz G, Smith A. 2012. Areni-1 Cave, Armenia: A Chalcolithic-Early Bronze Age settlement and ritual site in the southern Caucasus. Journal of Field Archaeology 37:20-33.

Yang DY, Eng B, Waye JS, Dudar JC, Saunders SR. 1998. Improved DNA extraction from ancient bones using silica-based spin columns. American Journal of Physical Anthropology 105:539-543.

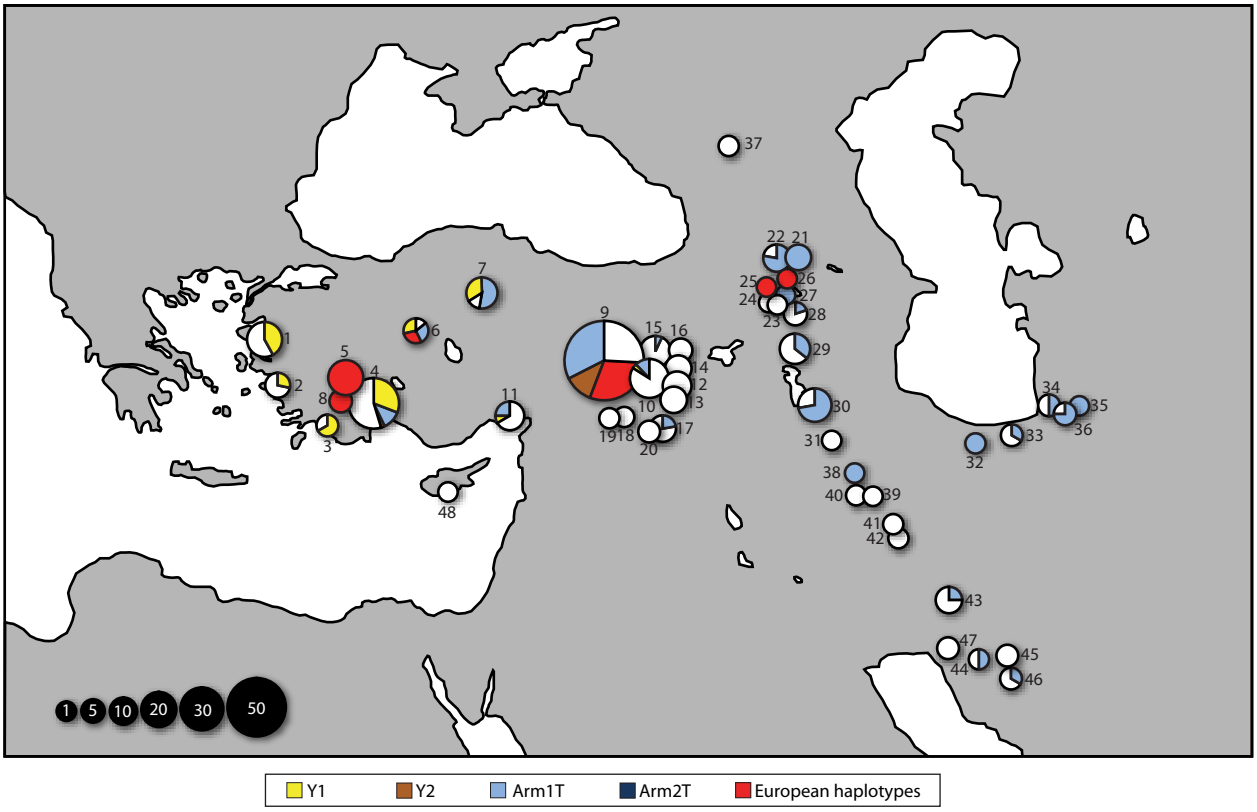
Yesayan GS. 1992. The Material Culture of the Aghstev River Basin in Developed Medieval Period. Yerevan: Yerevan State University Publishing House.

Yesayan SA. 1976. The Ancient Culture of tribes settling the Northeastern Armenia (III - I Millennia BC). Yerevan: Armenian SSR Academy of Sciences Publishing House.

Zeder M. 1985. Urbanism and animal exploitation in Southwest Highland Iran 3400-1500 BC: University of Michigan.

Zeder M. 1991. Feeding Cities. Specialized Animal Economy in the Near East. Washington and London: Smithsonian Institution Press.

a)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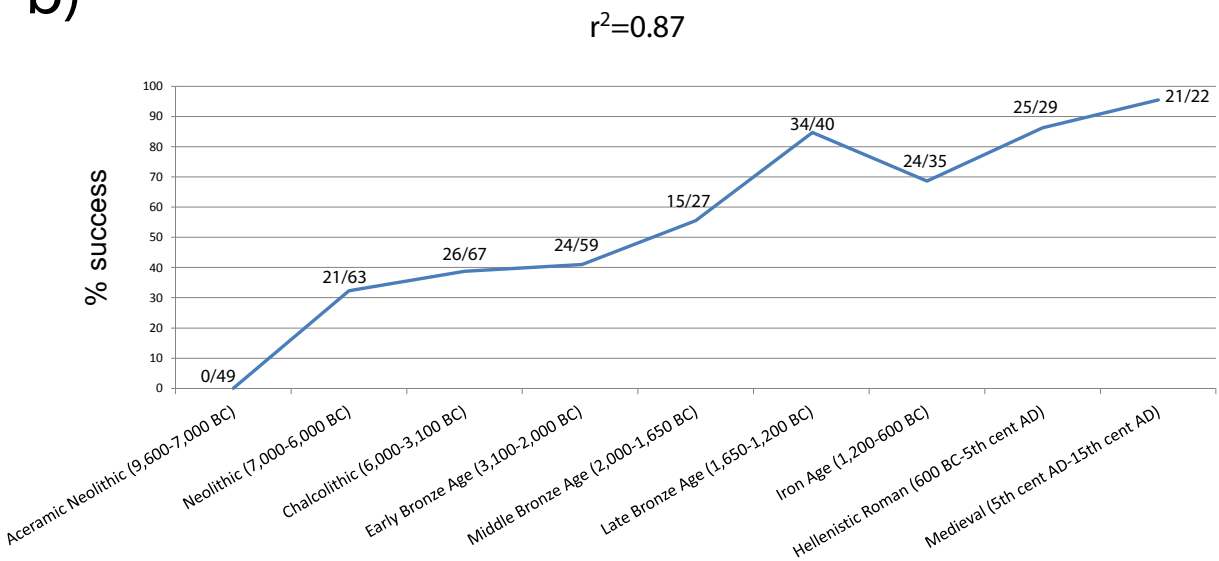
Y1
Y2
Arm1T
Arm2T
European haplotypes

b)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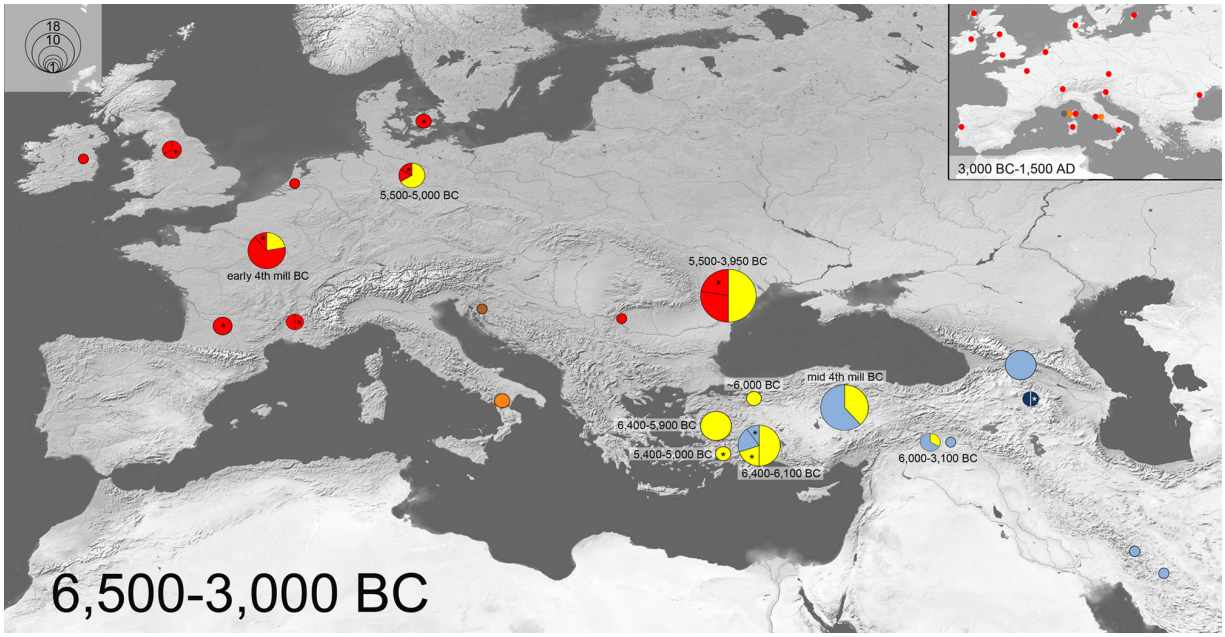
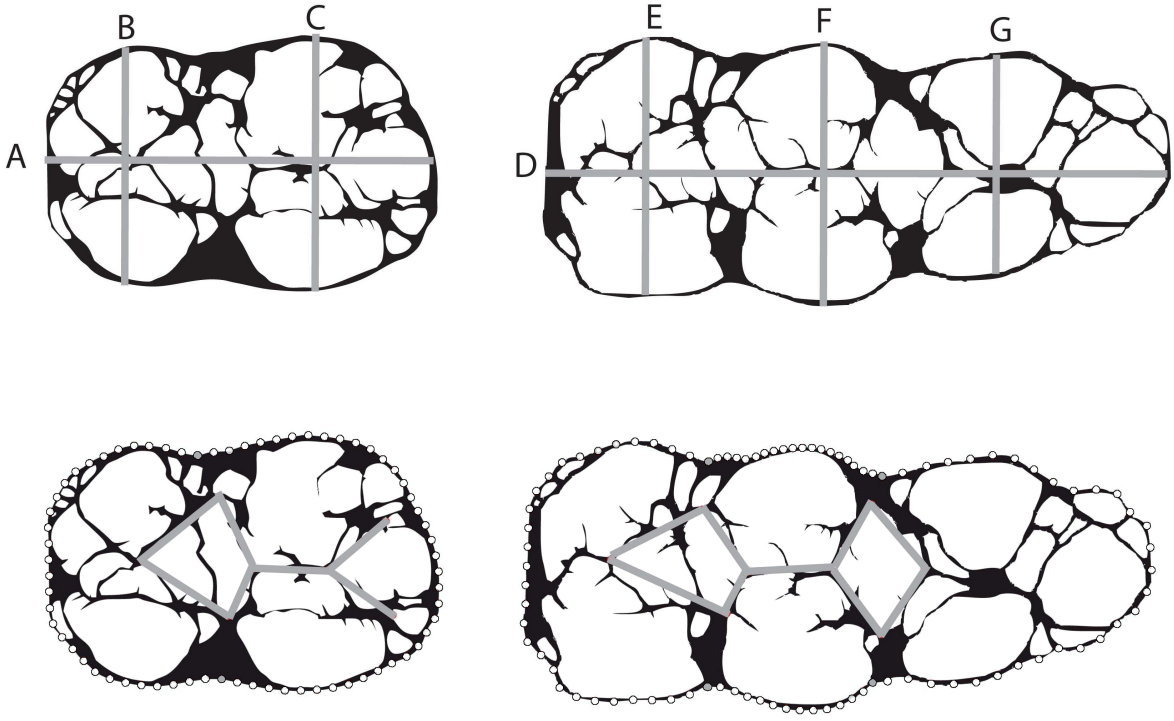
0/49
21/63
26/67
24/59
15/27
34/40
24/35
25/29
21/22
Aceramic Neolithic (9,600-7,000 BC)
Neolithic (7,000-6,000 BC)
Chalcolithic (6,000-3,100 BC)
Early Bronze Age (3,100-2,000 BC)
Middle Bronze Age (2,000-1,650 BC)
Late Bronze Age (1,650-1,200 BC)
Iron Age (1,200-600 BC)
Hellenistic Roman (600 BC-5th cent AD)
Medieval (5th cent AD-15th cent AD)

a)


18
10
1
3,000 BC-1,500 AD
5,500-5,000 BC
early 4th mill BC
5,500-3,950 BC
~6,000 BC
mid 4th mill BC
6,400-5,900 BC
5,400-5,000 BC
6,400-6,100 BC
6,000-3,100 BC
6,500-3,000 BC

b)


A
B
C
D
E
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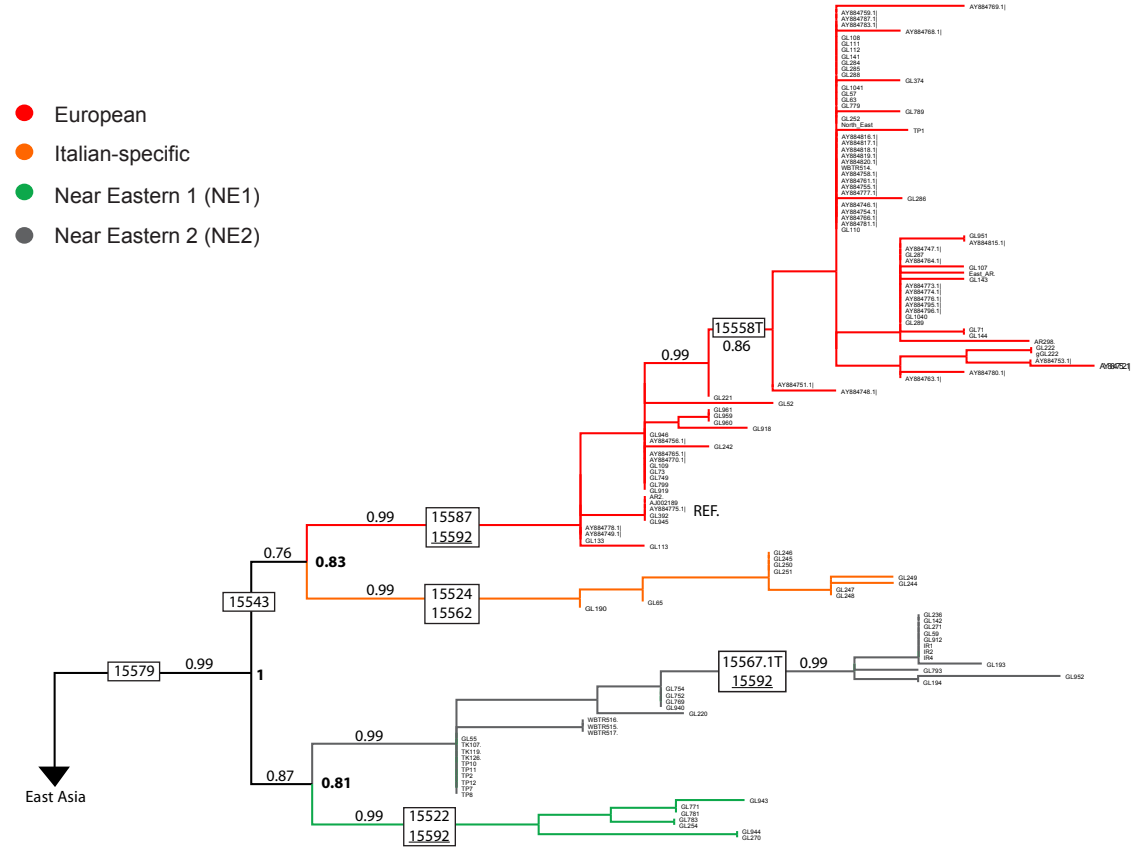
G

a)


European
Italian-specific
Near Eastern 1 (NE1)
Near Eastern 2 (NE2)
15579
15543
15587
15592
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15562
15522
15592
15558T
15567.1T
East Asia
REF.

b)

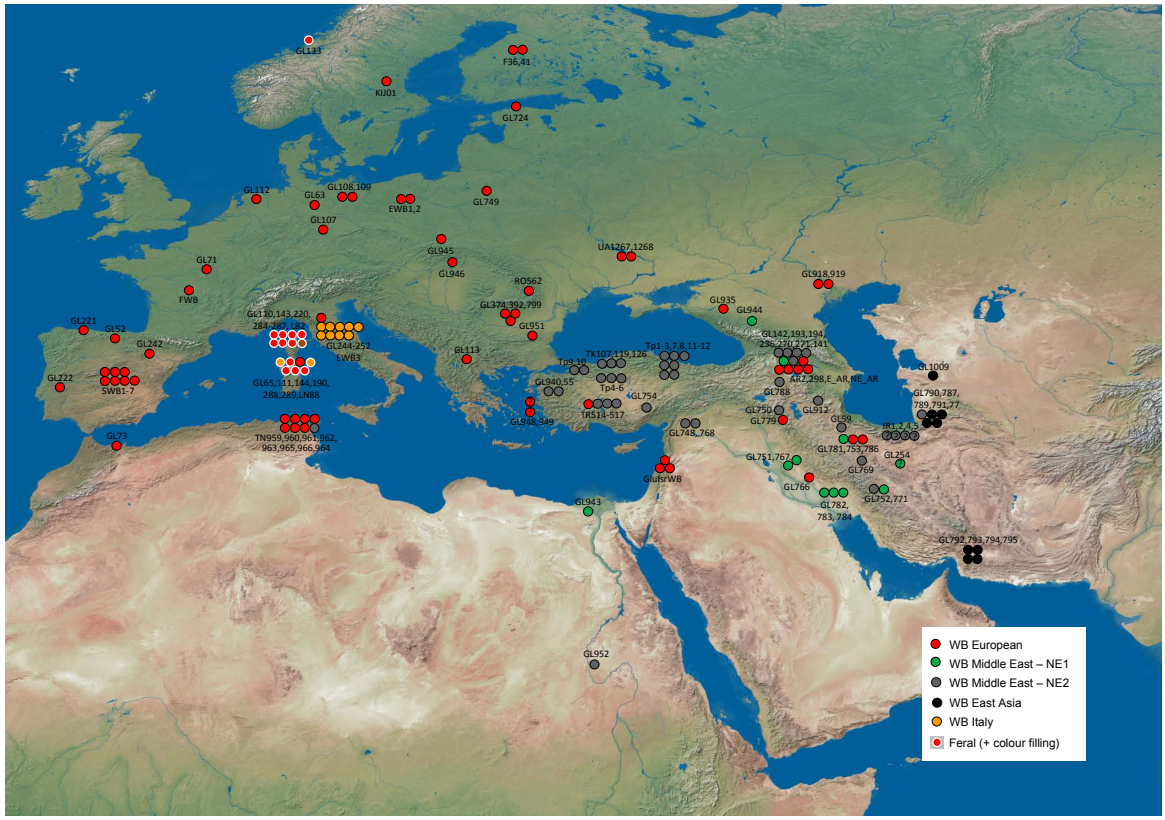
WB European
WB Middle East – NE1
WB Middle East – NE2
WB East Asia
WB Italy
Feral (+ colour filling)

Table S1. List of all the ancient specimens from Middle and Near East analysed in the present study. In the AMS indirect dating, upper and lower bounds determined from AMS dating carried out on associated bones from the same stratigraphic layer is reported. The status (wild versus domestic) of some of the specimens was provided following identification based on traditional metrics. Specimens for which status identification was not possible are left blank. Because traditional metrical methods for determining status are not necessarily conclusive (Evin et al. 2013), some of the status calls reported here may be subject to revision.

ID sample	Ref. ID / Find ID / Context	Site	Country	Period (Stratigraphy evidence)	Period (cal BC)	AMS dating cal BC (*indirect dating)	Period (AMS dating)	Period in fig.1	Element	Status	Lab	ANC1 Haplogroup	ANC 1	ANC 2	Cloning	Ext. replication	GMM Lower M2	GMM Lower M3	Reference-Source
LG005	MM-CHKH N106	Chiskho	Russia (Adygeya)	Chalcolithic	6,000-3,100 BC						Durham								Mashkour, M
LG006	MM-CHKH N107	Chiskho	Russia (Adygeya)	Chalcolithic	6,000-3,100 BC						Durham								Mashkour, M
LG007	MM-MSK05 N99	Mushki	Iran	Neolithic	7th millennium BC?						Durham								Mashkour, M
LG008	MM-MSK06 N100	Mushki	Iran	Neolithic	7th millennium BC?						Durham								Mashkour, M
LG009	MM-MSK07 N101	Mushki	Iran	Neolithic	7th millennium BC?						Durham								Mashkour, M
LG010	MM-GT01 N102	Gohar Tappeh	Iran	Bronze Age	~3,000BC						Durham								Mashkour, M
LG011	MM-GT01 N103	Gohar Tappeh	Iran	Bronze Age	~3,000 BC			Early Bronze Age			Durham	Arm1T							Mashkour, M
LG012	MM-GT01 N104	Gohar Tappeh	Iran	Bronze Age	~3,000BC						Durham								Mashkour, M
LG013	MM-GKH01 N105	Ghar Khar	Iran	Palaeolithic/Epipalaeolithic	n/a						Durham								Mashkour, M
LG014	JD-QR09 N108	Qaleh Rostam	Iran	Neolithic	7th millennium BC?						Durham								Daujat and Mashkour In prep Proceedings of 10th ASWA
LG015	JD_QR10 N109	Qaleh Rostam	Iran	Neolithic	7th millennium BC?						Durham								Daujat and Mashkour In prep Proceedings of 10th ASWA
LG016	JD-QR11 N110	Qaleh Rostam	Iran	Neolithic	7th millennium BC?						Durham								Daujat and Mashkour In prep Proceedings of 10th ASWA
LG017	JD-QR12 N111	Qaleh Rostam	Iran	Neolithic	7th millennium BC?			Neolithic			Durham	Arm1T							Daujat and Mashkour In prep Proceedings of 10th ASWA
LG059	EEL968	Ulucak Höyük	Turkey	Late Neolithic	~6,000 BC				Radius		Durham								Çakırlar, C. 2008, 2009
LG060	EEL969	Ulucak Höyük	Turkey	Late Neolithic	~6,000 BC				Mandible with teeth		Durham								Çakırlar, C. 2008, 2009
LG061	EMR573	Ulucak Höyük	Turkey	Late Neolithic	~6,000 BC				Mandible with teeth		Durham								Çakırlar, C. 2008, 2009
LG064	L: 3185 R:19	Tol e Spid	Iran	Chalcolithic	6,000-3,100 BC						Durham								Mashkour, M
LG065	L:3178 R:35	Tol e Spid	Iran	Chalcolithic	6,000-3,100 BC						Durham								Mashkour, M
LG066	L:3177 R:10	Tol e Spid	Iran	Chalcolithic	6,000-3,100 BC						Durham								Mashkour, M
LG067	Exc No: 33030	Qareh Doyub	Iran	Historical	5th -7th Century AD			Medieval			Durham	Arm1T							Mashkour, M
LG068	SF No: 45	Qelïch Qöïneq	Iran	Achemenid	8th -5th Centuries BC						Durham								Mashkour, M
LG069	SF No: 166	Qelïch Qöïneq	Iran	Achemenid	8th -5th Centuries BC			Hellenistic-Roman			Durham	Arm1T							Mashkour, M
LG070	SF No: 166	Qelïch Qöïneq	Iran	Achemenid	8th -5th Centuries BC			Hellenistic-Roman			Durham	Arm1T							Mashkour, M
LG071	SF No: P136	Qelïch Qöïneq	Iran	Achemenid	8th -5th Centuries BC			Hellenistic-Roman			Durham	Arm1T							Mashkour, M
LG072	SF No:32	Dasht Qaleh	Iran	Historical	5th Century AD						Durham								Mashkour, M
LG073	SF No: 099	Dasht Qaleh	Iran	Historical	5th Century AD			Medieval			Durham	Arm1T							Mashkour, M
LG074	CHI_aDNA_19	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG075	CHI_aDNA_23	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG076	CHI_aDNA_30	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG077	CHI_aDNA_09	Çayönü	Turkey	PPNA/PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG078	CHI_aDNA_25	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG079	Mun_013	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG080	Mun_014	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG081	Mun_017	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG082	Mun_018	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG083	Mun_020	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG109	Mun_022	Lidar Höyük	Turkey	MBA III/LBA I ?		1,291-1,055 BC	Late Bronze/Iron Age	Iron Age		domestic	Durham	A							Peters, J
LG110	Mun_023	Lidar Höyük	Turkey	MBA III/LBA I ?		1,370-1,119 BC	Late Bronze/Iron Age	Iron Age		domestic	Durham	A							Peters, J
LG111	Mun_024	Lidar Höyük	Turkey	MBA II/III ? (uncertain)				not included		domestic	Durham	Arm1T					X		Peters, J
LG112	Mun_025	Lidar Höyük	Turkey	MBA III/LBA I				Late Bronze Age			Durham	Y2							Peters, J
LG113	Mun_026	Lidar Höyük	Turkey	MBA III/LBA I							Durham								Peters, J
LG114	Mun_033	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,296-1,055 BC	Late Bronze/Iron Age	Iron Age			Durham	A							Peters, J
LG115	Mun_034	Lidar Höyük	Turkey	Middle Bronze Age III	2,000-1,650 BC			Middle Bronze Age			Durham	Arm1T							Peters, J
LG116	Mun_009	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC						Durham								Peters, J
LG117	Mun_011	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC						Durham								Peters, J
LG118	Mun_010	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC						Durham								Peters, J
LG128	Mun_001	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG129	Mun_002	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG130	Mun_003	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG131	Mun_004	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG132	Mun_005	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG133	Mun_006	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG134	Mun_007	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG135	Mun_008	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC						Durham								Peters, J
LG136	Mun_015	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG137	Mun_028	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD	897-1,021 AD	Medieval	Medieval		domestic	Durham	A							Peters, J

ID sample	Ref. ID / Find ID / Context	Site	Country	Period (Stratigraphy evidence)	Period (cal BC)	AMS dating cal BC (*indirect dating)	Period (AMS dating)	Period in fig.1	Element	Status	Lab	ANC1 Haplogroup	ANC 1	ANC 2	Cloning	Ext. replication	GMM Lower M2	GMM Lower M3	Reference-Source
LG138	Mun_039	Lidar Höyük	Turkey	MBA III/ LBA I							Durham								Peters, J
LG139	Mun_040	Lidar Höyük	Turkey	MBA II/III							Durham								Peters, J
LG140	Mun_ 042	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J
LG141	Mun_043	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J
LG142	Mun_044	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J
LG216	MM-KTsiS01	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG217	MM-KTsiS02	Kohneh Tepesi	Iran	Early Bronze Age				Early Bronze Age			Durham	Arm1T							Mashkour, M
LG218	MM-KTsiS03	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG219	MM-KTsiS04	Kohneh Tepesi	Iran	Early Bronze Age				Early Bronze Age			Durham	Arm1T							Mashkour, M
LG220	MM-KTsiS05	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG221	MM-KTsiS06	Kohneh Tepesi	Iran	Early Bronze Age				Early Bronze Age			Durham	Arm1T							Mashkour, M
LG222	MM-KTsiS07	Kohneh Tepesi	Iran	Early Bronze Age				Early Bronze Age			Durham	Arm1T							Mashkour, M
LG223	MM-HTS01	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T							Mashkour, M
LG224	MM-HTS02	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T							Mashkour, M
LG225	MM-HTS03	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T							Mashkour, M
LG226	MM-DTS02	Doshan Tepe	Iran	Iron Age				Iron Age			Durham	Arm1T							Mashkour, M
LG227	MM-DTS01	Doshan Tepe	Iran	Iron Age				Iron Age			Durham	Arm1T							Mashkour, M
LG240	DNA_1	Areni-1	Armenia	Chalcolithic							Durham								Pinhasi, R.
LG241	DNA_4	Areni-1	Armenia	Chalcolithic or Medieval				not included			Durham	Arm1T							Pinhasi, R.
LG242	DNA_5	Areni-1	Armenia	Chalcolithic							Durham								Pinhasi, R.
LG243	DNA_8	Areni-1	Armenia	Chalcolithic							Durham								Pinhasi, R.
LG244	DNA_9	Areni-1	Armenia	Chalcolithic							Durham								Pinhasi, R.
LG245	DNA_11	Shengavit	Armenia	Early Bronze Age							Durham								Pinhasi, R.
LG246	DNA_13	Mokhrablur	Armenia	Early Bronze Age							Durham								Pinhasi, R.
LG247	DNA_15	Tsakaektsi	Armenia	Medieval				Medieval			Durham	A							Pinhasi, R.
LG248	DNA_16	Sevkar 4	Armenia	Iron Age				Iron Age			Durham	A							Pinhasi, R.
LG249	DNA_18	Lchashen 2	Armenia	Middle Bronze Age				Middle Bronze Age			Durham	Arm1T							Pinhasi, R.
LG250	Mun_027	Lidar Höyük	Turkey	MBA II/III							Durham								Peters, J
LG251	Mun_029	Lidar Höyük	Turkey	MBA III				Middle Bronze Age			Durham	Arm1T					X		Peters, J
LG252	Mun_036	Lidar Höyük	Turkey	Iron Age				Iron Age			Durham	Y2							Peters, J
LG253	Mun_037	Lidar Höyük	Turkey	MBA II/III				Middle Bronze Age			Durham	Y2							Peters, J
LG254	Mun_038	Lidar Höyük	Turkey	MBA II/III				Middle Bronze Age			Durham	Y2							Peters, J
LG265	DNA sample 1	Ganj Dareh	Iran	Neolithic							Durham								Zeder, M
LG266	DNA sample 2	Ganj Dareh	Iran	Neolithic							Durham								Zeder, M
LG267	HC94 5E23-2232	Halan Çemi	Turkey	PPNA							Durham								Rosenberg et al.1998. Paléorient 24, 1:25-41
LG268	HC94 5E14-2211	Halan Çemi	Turkey	PPNA							Durham								Rosenberg et al.1998. Paléorient 24, 1:25-41
LG269	HC94 5E23-2227	Halan Çemi	Turkey	PPNA							Durham								Rosenberg et al.1998. Paléorient 24, 1:25-41
LG270	HC94 5E18-2250	Halan Çemi	Turkey	PPNA							Durham								Rosenberg et al.1998. Paléorient 24, 1:25-41
LG271	HC94 5H75-2039	Halan Çemi	Turkey	PPNA							Durham								Rosenberg et al.1998. Paléorient 24, 1:25-41
LG272	DNA sample 21, E-3-8	Umm Qseir	Syria	Chalcolithic (post-Neolithic)							Durham								Zeder 1994. Amer. Anthr., New Ser., 96, 1:97-126
LG273	E-1-6	Umm Qseir	Syria	Chalcolithic (post-Neolithic)							Durham								Zeder 1994. Amer. Anthr., New Ser., 96, 1:97-126
LG274	E-1-4	Umm Qseir	Syria	Chalcolithic (post-Neolithic)							Durham								Zeder 1994. Amer. Anthr., New Ser., 96, 1:97-126
LG275	DNA sample 5, B14	Malyan	Iran	Bronze Age/iron Age							Durham								Miller, Zeder and Arter 2009 (Curr. Anthr. 50, 6:915-924)
LG276	DNA sample 6, OP. B. Lot 12	Malyan	Iran	Bronze Age/iron Age				Iron Age			Durham	Arm1T							Miller, Zeder and Arter 2009 (Curr. Anthr. 50, 6:915-924)
LG277	DNA sample 23, Bag 9	Atij	Syria	Bronze Age							Durham								Zeder 1994. Amer. Anthr., New Ser., 96, 1:97-126
LG278	DNA sample 22, Bag 189	Atij	Syria	Bronze Age							Durham								Zeder 1994. Amer. Anthr., New Ser., 96, 1:97-126
LG279	DNA sample 24, Bag 381	Mashnaqua	Syria	Bronze Age							Durham								Zeder, M
LG280	DNA sample 25, Bag 353	Mashnaqua	Syria	Bronze Age							Durham								Zeder, M
LG281	DNA sample 2, Bag 959	Leilan	Syria	Early/Middle Bronze Age				Early Bronze Age			Durham	Arm1T					X		Zeder, M
LG282	DNA sample 9, Bag 549	Leilan	Syria	Early/Middle Bronze Age							Durham								Zeder, M
LG283	DNA sample 5, Bag 814	Leilan	Syria	Early/Middle Bronze Age							Durham								Zeder, M
LG284	DNA sample 7, Bag 405	Leilan	Syria	Early/Middle Bronze Age							Durham								Zeder, M
LG285	DNA sample 1, Bag 478	Leilan	Syria	Early/Middle Bronze Age							Durham								Zeder, M
LG286	DNA sample 3, Bag 1048	Leilan	Syria	Early/Middle Bronze Age							Durham								Zeder, M
LG287	DNA sample 10, Bag 350	Leilan	Syria	Early/Middle Bronze Age							Durham								Zeder, M
LG288	DNA sample 2, Bag 1051	Leilan	Syria	Early/Middle Bronze Age							Durham								Zeder, M
LG289	DNA sample 8, Bag 549	Leilan	Syria	Early/Middle Bronze Age				Early Bronze Age			Durham	Arm1T					X	X	Zeder, M
LG290	DNA sample 10, Level K	Guran Tepe	Iran	Neolithic							Durham								Zeder 1999 (Paléorient vol. 25/2 pp. 11-25)

ID sample	Ref. ID / Find ID / Context	Site	Country	Period (Stratigraphy evidence)	Period (cal BC)	AMS dating cal BC (*indirect dating)	Period (AMS dating)	Period in fig.1	Element	Status	Lab	ANC1 Haplogroup	ANC 1	ANC 2	Cloning	Ext. replication	GMM Lower M2	GMM Lower M3	Reference-Source
LG291	DNA sample 11, Level F	Guran Tepe	Iran	Neolithic							Durham								Zeder 1999 (Paléorient vol. 25/2 pp. 11-25)
LG350	PIN 23259 Bag18	Gordion	Turkey	Late Hellenistic				Hellenistic			Durham	LDomGermanyAngler					X	X	M-M, Voigt and R-C, Henrickson 2000 Anatolian Studies, 50: 37-54
LG351	PIN 29955 Bag 22	Gordion	Turkey	Late Bronze Age?				Late Bronze Age			Durham	Arm1T					X		M-M, Voigt and R-C, Henrickson 2000 Anatolian Studies, 50: 37-54
LG352	PIN 30618 Bag 220	Gordion	Turkey	Late Bronze Age				Late Bronze Age			Durham	Arm1T					X		M-M, Voigt and R-C, Henrickson 2000 Anatolian Studies, 50: 37-54
LG353	PIN 29550 Bag 16	Gordion	Turkey	Late Phrygian				Hellenistic			Durham	A					X	X	M-M, Voigt and R-C, Henrickson 2000 Anatolian Studies, 50: 37-54
LG354	PIN 29961 Bag 22	Gordion	Turkey	Late Bronze Age				Late Bronze Age			Durham	Yellow star							M-M, Voigt and R-C, Henrickson 2000 Anatolian Studies, 50: 37-54
LG355	PIN 28944 Bag 16	Gordion	Turkey	Late Phrygian							Durham								M-M, Voigt and R-C, Henrickson 2000 Anatolian Studies, 50: 37-54
LG356	PIN 25020 Bag 35	Gordion	Turkey	Late Phrygian				Hellenistic			Durham	Y1							M-M, Voigt and R-C, Henrickson 2000 Anatolian Studies, 50: 37-54
LG357	168-5	Shillourokambos	Cyprus	PPNB							Durham								Vigne, J-D
LG414	MF06 TV:E4 PH:LAPvi	Mehr Ali	Iran	Late Chalcolithic				Chalcolithic			Durham	Arm1T							Mashkour, M
LG415	TV:F10 PH:5	Mehr Ali	Iran	Late Chalcolithic							Durham								Mashkour, M
LG416	TV:F10 LOC:40-58 PH:6	Mehr Ali	Iran	Late Chalcolithic							Durham								Mashkour, M
LG418	#14	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG419	#45	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG420	#377	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG450	CHI_aDNA_01	Çayönü	Turkey	PPNA							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG451	CHI_aDNA_04	Çayönü	Turkey	PPNA							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG452	CHI_aDNA_08	Çayönü	Turkey	PPNA/PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG454	CHI_aDNA_16	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG455	CHI_aDNA_21	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG456	CHI_aDNA_22	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG458	CHI_aDNA_29	Çayönü	Turkey	PPNB							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG459	CHI_aDNA_31	Çayönü	Turkey	PN				Neolithic			Durham	Arm1T							Ervynck et al. 2001. Paléorient 27, 2:47-73
LG460	CHI_aDNA_32	Çayönü	Turkey	PN							Durham								Ervynck et al. 2001. Paléorient 27, 2:47-73
LG475	EDI-CAM 250-397b	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T							Bartosiewicz, L
LG476	EDI-CAM 273-868	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T							Bartosiewicz, L
LG477	EDI-CAM 778-5155b	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Y1					X		Bartosiewicz, L
LG479	EDI-CAM 891-5779	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Y1						X	Bartosiewicz, L
LG480	EDI-CAM 966-6042	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T					X	X	Bartosiewicz, L
LG485	EDI-CAM 247-372b	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Y1					X		Bartosiewicz, L
LG486	EDI-CAM 463-4067	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Y1						X	Bartosiewicz, L
LG487	EDI-CAN 906-5291	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic			?	Durham								Bartosiewicz, L
LG488	EDI-CAM 796-5229	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T					X	X	Bartosiewicz, L
LG489	EDI-CAM 746-4982	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Y1					X	X	Bartosiewicz, L
LG491	EDI-CAM 56-252c	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T							Bartosiewicz, L
LG492	EDI-CAM 352-987	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T						X	Bartosiewicz, L
LG493	EDI-CAM 925-5377	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T					X	X	Bartosiewicz, L
LG495	EDI-CAM 858-5569	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic	Chalcolithic		domestic	Durham	Arm1T						X	Bartosiewicz, L
LG496	EDI-CAN 263-724	Çamlıbel Tarlası	Turkey	Chalcolithic	3,590-3,470 BC		Chalcolithic				Durham								Bartosiewicz, L
LG516	MUN_012	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
G517	MUN_016	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG518	MUN_021	Nevali Çori	Turkey	PPNB							Durham								Helmer, Peters et al. 1999 Paléorient 25, 2:27-48
LG520	MUN_035	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG521	MUN_041	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG522	MUN_045	Sirkeli Höyük	Turkey	Iron Age				Iron Age			Durham	Arm1T							Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG523	MUN_046	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG524	MUN_047	Sirkeli Höyük	Turkey	Iron Age				Iron Age			Durham	Arm1T							Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG526	MUN_048	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html

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LG527	MUN_049	Sirkeli Höyük	Turkey	Iron Age				Iron Age			Durham	Y1							Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG528	MUN_050	Sirkeli Höyük	Turkey	Iron Age							Durham								Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG529	MUN_051	Sirkeli Höyük	Turkey	Iron Age				Iron Age			Durham	Arm1T							Peters, J. Personal communication+http://www.sirkeli-project.info/en/site_sirkeli.html
LG531	MUN_052	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG532	MUN_053	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG533	MUN_054	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG534	MUN_055	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG536	MUN_056	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG537	MUN_057	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG538	MUN_058	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG539	MUN_059	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG540	MUN_060	Hassek Höyük	Turkey	Chalcolithic/Bronze							Durham								Peters, J. Personal communication
LG773	Iran-CG-1	Chogha Gavaneh	Iran	Chalcolithic/Bronze Age	4th/3rd millenium BC			Early Bronze Age			Durham	Arm1T							Mashkour, M
LG775	KSB-01	Kalanan Sirlan Bijar	Iran	Chalcolithic							Durham								Mashkour, M
LG776	L: 5/f:3	Cham Quleh	Iran	Chalcolithic	4th/3rd millenium BC						Durham								Mashkour, M
LG777	L: 5/R.5	Cham Quleh	Iran	Chalcolithic	4th/3rd millenium BC						Durham								Mashkour, M
LG779	KT-01	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG780	KT-29	Kohneh Tepesi	Iran	Early Bronze Age				Early Bronze Age			Durham	Arm1T					X		Mashkour, M
LG781	KT-32	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG782	KT-41	Kohneh Tepesi	Iran	Early Bronze Age							Durham								Mashkour, M
LG784	HV-08	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T						X	Mashkour, M
LG785	HV-09	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T					X	X	Mashkour, M
LG786	HV-10	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham								Mashkour, M
LG787	HV-13	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T							Mashkour, M
LG788	HV-33	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T					X	X	Mashkour, M
LG789	HV-34	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T						X	Mashkour, M
LG790	HV-35	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T					X	X	Mashkour, M
LG791	HV-36	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T						X	Mashkour, M
LG792	HV-37	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T					X	X	Mashkour, M
LG794	HV-39	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T						X	Mashkour, M
LG795	HV-45	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T						X	Mashkour, M
LG796	HV-46	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T						X	Mashkour, M
LG797	HV-47	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham								Mashkour, M
LG798	HV-54	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham	Arm1T						X	Mashkour, M
LG799	HV-55	Haftavan Tepe	Iran	Middle & Late Bronze Age	1,800-1,200 BC			Late Bronze Age			Durham								Mashkour, M
BAD1		Bademağacı	Turkey	Early Neolithic I - 8	7,000-6,000 BC	7,050-6,690 BC*	Early Neolithic		scapula prox F	domestic	Leuven								De Cupere, B.
BAD10		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic	Neolithic	scapula prox F	domestic	Leuven	Y1				X			De Cupere, B.
BAD11		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic		tibia dist F	wild	Leuven								De Cupere, B.
BAD12		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic		tibia dist F	domestic	Leuven								De Cupere, B.
BAD13		Bademağacı	Turkey	Early Neolithic II - 3	7,000-6,000 BC	6,460-6,220 BC*	Early Neolithic		radius prox	domestic	Leuven								De Cupere, B.
BAD14		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC				humerus dist F	wild	Leuven								De Cupere, B.
BAD15		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	mandible	domestic	Leuven	Y2				X			De Cupere, B.
BAD16		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	mandible	domestic ?	Leuven	Arm1T				X			De Cupere, B.
BAD17		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	maxilla	domestic	Leuven	Y1			X				De Cupere, B.
BAD18		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	maxilla	domestic	Leuven	Arm1T				X			De Cupere, B.
BAD19		Bademağacı	Turkey	Early Neolithic II - 1	7,000-6,000 BC	6,230-6060 BC*	Early Neolithic		mandible	domestic	Leuven								De Cupere, B.
BAD2		Bademağacı	Turkey	Early Neolithic I - 8	7,000-6,000 BC	7,050-6,690 BC*	Early Neolithic		scapula prox F	domestic	Leuven								De Cupere, B.
BAD3		Bademağacı	Turkey	Early Neolithic I - 7	7,000-6,000 BC				calc voll F	wild	Leuven								De Cupere, B.
BAD30		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			Neolithic	mandible	domestic	Leuven	Y1							De Cupere, B.
BAD31		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC				mandible	domestic	Leuven								De Cupere, B.
BAD32		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC			Neolithic	mandible	domestic	Leuven	Y1							De Cupere, B.
BAD33		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC				mandible	domestic	Leuven								De Cupere, B.
BAD34		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC				mandible	domestic	Leuven								De Cupere, B.
BAD35		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC				mandible	domestic	Leuven								De Cupere, B.
BAD36		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC				mandible	domestic	Leuven								De Cupere, B.
BAD38		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC				maxilla	domestic	Leuven								De Cupere, B.
BAD39		Bademağacı	Turkey	Early Neolithic II - 2	7,000-6,000 BC				maxilla	domestic	Leuven								De Cupere, B.
BAD4		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	Neolithic	tibia dist F	wild	Leuven	Y1							De Cupere, B.
BAD47		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC			Neolithic	mandible	domestic	Leuven	Y1			X				De Cupere, B.
BAD5		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	Neolithic	talus compl	wild	Leuven	Y1				X			De Cupere, B.

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BAD50		Bademağacı	Turkey	Early Neolithic II - 4	7,000-6,000 BC	6,420-6,110 BC*	Early Neolithic		maxilla	domestic	Leuven								De Cupere, B.
BAD52		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	Neolithic	mandible	domestic	Leuven	Arm1T			X				De Cupere, B.
BAD54		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic	Neolithic	maxilla	domestic	Leuven	Arm1T							De Cupere, B.
BAD6		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC				scapula prox F	domestic	Leuven								De Cupere, B.
BAD60		Bademağacı	Turkey	Early Neolithic II - 4A	7,000-6,000 BC	6,405-6,235 BC*	Early Neolithic		maxilla	domestic	Leuven								De Cupere, B.
BAD63		Bademağacı	Turkey	Early Neolithic II - 4B	7,000-6,000 BC			Neolithic	mandible	domestic	Leuven	Y1							De Cupere, B.
BAD7		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC				scapula prox F	domestic	Leuven								De Cupere, B.
BAD73		Bademağacı	Turkey	Early Neolithic I - 6	7,000-6,000 BC				M2 maxillar	domestic	Leuven								De Cupere, B.
BAD8		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC				scapula prox F	domestic	Leuven								De Cupere, B.
BAD82		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC				radius prox	wild	Leuven								De Cupere, B.
BAD83		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	Ph1 compl, F	domestic	Leuven	Y1							De Cupere, B.
BAD84		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	humerus dist, F	wild	Leuven	Y1							De Cupere, B.
BAD85		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	mandible	wild	Leuven	Y1							De Cupere, B.
BAD86		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	MT III compl, F	wild	Leuven	Y1			X				De Cupere, B.
BAD87		Bademağacı	Turkey	Early Bronze Age II	3,100-2,000 BC			Early Bronze Age	MC II compl, F	wild	Leuven	Y1							De Cupere, B.
BAD9		Bademağacı	Turkey	Early Neolithic II - 3A	7,000-6,000 BC			Neolithic	radius prox F	wild	Leuven	Arm1T							De Cupere, B.
F13	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC			Hellenistic	Mandibula	domestic	Leuven	A							De Cupere, B., Van Neer, W., http://www.sagalassos.be/
F15	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC	390-180 BC		Hellenistic	Mandibula	domestic	Leuven	A							De Cupere, B., Van Neer, W., http://www.sagalassos.be/
F20	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC			Hellenistic	Tibia	domestic	Leuven	A							De Cupere, B., Van Neer, W., http://www.sagalassos.be/
F21	SA2007 TD 12-9	Düzen Tepe	Turkey	6th-3rd century BC	6th-3rd cent BC			Hellenistic	Mp	domestic	Leuven	C							De Cupere, B., Van Neer, W., http://www.sagalassos.be/
M100	1981; E 44 d; Abh. 18	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Radius	domestic	Leuven	A							Peters, J.
M101	1981; E 44 c, Abh. 18	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Mc IV	domestic	Leuven	Arm1T							Peters, J.
M11	S1 1. Steg 200/40; 4/49	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Mandibula	domestic	Leuven								Peters, J.
M113	GT Z; 1995; S 1; 1.1; 80/40; 4/49	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Talus	wild	Leuven								Peters, J.
M115	GT Z; 1995; S 2; 1.1; 50/46	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Scapula	wild	Leuven								Peters, J.
M116	GT W; 1995; 67/40	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Radius	wild	Leuven								Peters, J.
M118	GT W; S 2; 1.1; 50/40	Göbekli Tepe	Turkey	10th millenium BC	9,600-7,000 BC				Talus	wild	Leuven								Peters, J.
M119	1985, BH 32; O 20; 7,00-10,00; 4,30 - 9,80; Niv. 4,18-3,90; Nordhälfte	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC				Mc III	domestic	Leuven								Peters, J.
M120	1985, BH 32; O 20; 7,00-10,00; 4,30 - 9,80; Niv. 4,18-3,90; Nordhälfte	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			Chalcolithic	Radius	domestic	Leuven	Arm1T							Peters, J.
M121	1985, BH 32; O 20; 7,00-10,00; 4,30 - 9,80; Niv. 4,18-3,90; Nordhälfte	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC				Radius	domestic	Leuven								Peters, J.
M122	1985, BH 32; O 20; 7,00-10,00; 4,30 - 9,80; Niv. 4,18-3,90; Nordhälfte	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC				Scapula	domestic	Leuven								Peters, J.
M123	1984; BH 110; R 21; 5,0-7,0 (S) 0,6-7,0 (N); 0,6-9,4; Niv. 7,39-6,81	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			Chalcolithic	Ncr	domestic	Leuven	Arm1T				X			Peters, J.
M124	1984; BH 110; R 21; 5,0-7,0 (S) 0,6-7,0 (N); 0,6-9,4; Niv. 7,39-6,81	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC			Chalcolithic	Ncr	domestic	Leuven	Y1				X			Peters, J.
M125	1985, BH 7; P 16; 0,60-9,40; 0,60-9,40; Niv. 6,01	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC				Pelvis	domestic	Leuven								Peters, J.
M126	1985, BH 7; P 16; 0,60-9,40; 0,60-9,40; Niv. 6,01	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC				Radius	domestic	Leuven								Peters, J.
M127	1985, BH 7; P 16; 0,60-9,40; 0,60-9,40; Niv. 6,01	Hassek Höyük	Turkey	Chalcolithic	6,000-3,100 BC				Maxilla	domestic	Leuven								Peters, J.
M13	H 1984, Ash pit, BH 191 (cont.), Layer T 20; 360-760/060-500; Niv 0817-0777	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				Maxilla	domestic	Leuven								Peters, J.

ID sample	Ref. ID / Find ID / Context	Site	Country	Period (Stratigraphy evidence)	Period (cal BC)	AMS dating cal BC (*indirect dating)	Period (AMS dating)	Period in fig.1	Element	Status	Lab	ANC1 Haplogroup	ANC 1	ANC 2	Cloning	Ext. replication	GMM Lower M2	GMM Lower M3	Reference-Source
M14	H 1984, Ash pit, BH 191 (cont.), Layer T 20; 360-760/060-500; Niv 0817-0777	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				Maxilla	domestic	Leuven								Peters, J.
M15	H 1984, Ash pit, BH 191 (cont.), Layer T 20; 360-760/060-500; Niv 0817-0777	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				Mandibula	domestic	Leuven								Peters, J.
M16	H 1984, Ash pit, BH 191 (cont.), Layer T 20; 360-760/060-500; Niv 0817-0777	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				Humerus	domestic	Leuven								Peters, J.
M17	H 1984, Ash pit, BH 191 (cont.), Layer T 20; 360-760/060-500; Niv 0817-0777	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				Pelvis	domestic	Leuven								Peters, J.
M18	H 1984, Ash pit, BH 191 (cont.), Layer T 20; 360-760/060-500; Niv 0817-0777	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC			Early Bronze Age	Pelvis	domestic	Leuven	Arm1T							Peters, J.
M19	H 1984, Ash pit, BH 191 (cont.), Layer T 20; 360-760/060-500; Niv 0817-0777	Hassek Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				Mt IV	domestic	Leuven								Peters, J.
M40	1981; R 45 c/d; Abhub 14	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD			Hellenistic	Talus	domestic	Leuven	Arm1T							Peters, J.
M41	1981; R 45 d, Abh. 12	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				Femur (shaft)	domestic	Leuven								Peters, J.
M42	1981; H 40 b/c; 4 OR u 2 'ges'	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD			Hellenistic	Cranial frgt.	domestic	Leuven	A							Peters, J.
M43	1981; H 40 b/c; 4 OR u 2 'ges'	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD				Pelvis	domestic	Leuven								Peters, J.
M44	1981; H 40 b/c; 4 OR u 2 'ges'	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD			Hellenistic	Mandibula	domestic	Leuven	A							Peters, J.
M45	1981; H 40 b/c; 4 OR u 2 'ges'	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD			Hellenistic	P4, M1 inf.	domestic	Leuven	A							Peters, J.
M46	1981; R 45 c/d, Abh. 15	Lidar Höyük	Turkey	Hellenistic-Roman	600 BC-5th cent AD			Hellenistic	Maxilla	domestic	Leuven	Arm1T			X				Peters, J.
M47	1986; S 43 b; Abh. 15	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC			Middle Bronze Age	Humerus	domestic	Leuven	Arm1T							Peters, J.
M48	1986; S 44 a/b; Abh. 54-55	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC			Middle Bronze Age	Femur (shaft)	wild	Leuven	Y2							Peters, J.
M49	1986; O/P 50; Abh. 22; östl. Stegunterfüllung R.c.	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC			Middle Bronze Age	Mt III	domestic	Leuven	Arm1T							Peters, J.
M5	N-Wadi, W-Profil, A1	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Maxilla	domestic	Leuven								Peters, J.
M50	1986; Q 44 c - R 44 b; 54 K4	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC			Middle Bronze Age	Maxilla	domestic	Leuven	Arm1T							Peters, J.
M51	1986; R 44 d; Abh. Gr 182	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC	1,217-1,025 BC	Late Bronze/Iron Age	Iron Age	Mandibula	domestic	Leuven	A							Peters, J.
M52	1986; R 44 b; Abh. 54 KV	Lidar Höyük	Turkey	Middle Bronze Age II	2,000-1,650 BC			Middle Bronze Age	Mandibula	domestic	Leuven	A							Peters, J.
M53	1980; Q 45 b; 8 GS 1; Layer 1	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD			Medieval	Maxilla	domestic	Leuven	A							Peters, J.
M54	1980; Q 45 b; 8 GS 1; Layer 1	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD			Medieval	Maxilla	domestic	Leuven	A							Peters, J.
M55	1980; Q 45 b; 8 GS 1; Layer 1	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD			Medieval	Maxilla	domestic	Leuven	A							Peters, J.
M56	1980; Q 45 b; 8 GS 1; Layer 1	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD			Medieval	Maxilla	domestic	Leuven	A							Peters, J.
M57	1980; Q 45 b; 8 GS 1; Layer 1	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD			Medieval	Scapula	domestic	Leuven	A							Peters, J.
M58	1980; Q 45 b; 8 GS 1; Layer 1	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD			Medieval	Radius	domestic	Leuven	A							Peters, J.
M59	1980; Q 45 b; 8 GS 1; Layer 1	Lidar Höyük	Turkey	Medieval	5th cent AD-15th cent AD			Medieval	Pelvis	domestic	Leuven	A							Peters, J.
M6	N-Wadi, W-Profil, D4	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Radius	domestic	Leuven								Peters, J.
M60	1987; N 50a; Abh. 27 R 7 u. Fb	Lidar Höyük	Turkey	Middle Bronze Age	2,000-1,650 BC				Humerus	domestic	Leuven								Peters, J.
M61	1987; N 50a; Abh. 27 R 7 u. Fb	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC				Tibia	domestic	Leuven								Peters, J.
M62	1987; S 44/45 - R 44/45; Abh. 59	Lidar Höyük	Turkey	Middle Bronze Age	2,000-1,650 BC				Tibia	domestic	Leuven								Peters, J.
M63	1987; S 44/45 - R 44/45; Abh. 59	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC				Mt IV	domestic	Leuven								Peters, J.
M64	1987; S 46 a; Abh. 30 a; BF 4+3	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC			Middle Bronze Age	Atlas	domestic	Leuven	Arm1T							Peters, J.
M65	1987; MB I/II (Phase)	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC				Altas	domestic	Leuven								Peters, J.

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M66	1987; R 45 c; Abh. 56 u R 322	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC				Radius	domestic	Leuven								Peters, J.
M67	1987; R 45 c; Abh. 56 u R 322	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC				Mandibula	domestic	Leuven								Peters, J.
M68	1987; P 50 c/d; Abh. 27 R 18	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC			Middle Bronze Age	Maxilla	domestic	Leuven	Y2							Peters, J.
M69	1987; P 50 c/d; Abh. 27 R 18	Lidar Höyük	Turkey	Middle Bronze Age	2,000-1,650 BC				Humerus	domestic	Leuven								Peters, J.
M7	S2; 1,3; 260/40; 1/49	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Tibia	domestic	Leuven								Peters, J.
M70	1987; S 44/45; Abh. 57-58	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC				Maxilla	domestic	Leuven								Peters, J.
M71	1987; S 44/45; Abh. 57-58	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC			Middle Bronze Age	Mandibula	domestic	Leuven	Arm1T							Peters, J.
M72	1987; S 44/45; Abh. 57-58	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC				Maxilla	domestic	Leuven								Peters, J.
M73	1987; S 43 d; Abh. 18	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC			Middle Bronze Age	Maxilla	domestic	Leuven	Y2							Peters, J.
M74	1987; S 43 d; Abh. 18	Lidar Höyük	Turkey	Middle Bronze Age II/I	2,000-1,650 BC			Middle Bronze Age	Talus	domestic	Leuven	Arm1T							Peters, J.
M75	1986; R 44 b; Abh. 54 e Fr. 2	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC			Late Bronze Age	Humerus	domestic	Leuven	Y2							Peters, J.
M76	1986; Q 44 d; Abh. 53, 54 - Fr	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,120-900 BC	Iron Age	Iron Age	Humerus	domestic	Leuven	A							Peters, J.
M77	1986; Q 44 d; Abh. 53, 54 - Fr	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC			Late Bronze Age	Talus	domestic	Leuven	Arm1T							Peters, J.
M78	1986; R 44 d; Abh. 54 e Fr 2	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,270-1,050 BC	Late Bronze/Iron Age	Iron Age	Tibia	domestic	Leuven	A							Peters, J.
M79	1986; R 44 b; Abh. MaL (?)	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC			Late Bronze Age	Humerus (shaft)	wild	Leuven	Arm1T							Peters, J.
M8	S1; 1.4; 340/40; 6/49	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Scapula	domestic	Leuven								Peters, J.
M80	1986; S 44 a; Abh. 54 e	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC			Late Bronze Age	Tibia	wild	Leuven	Arm1T							Peters, J.
M81	1986; R 44 d; Abh. 54 e Fr 2	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC			Late Bronze Age	Scapula	domestic	Leuven	Arm1T							Peters, J.
M82	1986; R 44 d; Abh. 54 e Fr 2 + Gr	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC	1,600-1,570/1540-1440	Late Bronze Age	Late Bronze Age	Mandibula	domestic	Leuven	A							Peters, J.
M83	1986; Q 44 d; Abh. 53; S.M 315	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC			Late Bronze Age	Scapula	domestic	Leuven	Arm1T							Peters, J.
M84	1986; Q/R/S 44/45; Schicht 7	Lidar Höyük	Turkey	Late Bronze Age	1,650-1,200 BC				Mc IV	domestic	Leuven								Peters, J.
M85	1981; G 34 a/F 34 d; Abh. 24 Fr. 1	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC	2,835-2,478 BC	Early Bronze Age	Early Bronze Age	Mandibula	domestic	Leuven	Arm1T							Peters, J.
M86	1981; F 34 b/c; Abh. 25 R e	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC			Early Bronze Age	Mandibula	domestic	Leuven	Arm1T							Peters, J.
M87	1981; G 34 a; Abh. 26 nB1	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC			Early Bronze Age	Phalanx 2 H	domestic	Leuven	Arm1T							Peters, J.
M88	1981; F 34 c/d - G 34 b; Abh. 26 R j	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC			Early Bronze Age	Mandibula	domestic	Leuven	Arm1T							Peters, J.
M89	1981; F 34 c/d - G 34 b; Abh. 26 R j	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC				Mt IV	domestic	Leuven								Peters, J.
M9	S3; 1.1; 110/40;	Gürcütepe II	Turkey	Aceramic Neolithic	9,600-7,000 BC				Tibia	domestic	Leuven								Peters, J.
M90	1981; G 33 b; Abh. 28 2. Eimer	Lidar Höyük	Turkey	Early Bronze Age	3,100-2,000 BC			Early Bronze Age	Mandibula	domestic	Leuven	Arm1T							Peters, J.
M91	1986; S 48 a; Abh. 15	Lidar Höyük	Turkey	Iron Age	1,200-600 BC				Mp	domestic	Leuven								Peters, J.
M92	1986; S 48 a; Abh. 15	Lidar Höyük	Turkey	Iron Age	1,200-600 BC				Pelvis	domestic	Leuven								Peters, J.
M93	1986; S 48 a; Abh. 15	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Mp N	domestic	Leuven	Arm1T							Peters, J.
M94	1981; E 44 c; Abh. 23	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Scapula	domestic	Leuven	Arm1T							Peters, J.
M95	1981; E 44 c; Abh. 23	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Maxilla	domestic	Leuven	Arm1T							Peters, J.
M96	1981; E 44 c; Abh. 19	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Mandibula	domestic	Leuven	A			X				Peters, J.
M97	1981; E 44 c; Abh. 21	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Tibia	domestic	Leuven	A							Peters, J.
M98	1981; E 44 c; -	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Humerus (shaft)	domestic	Leuven	A							Peters, J.
M99	1981; E 44 d; Abh. 18	Lidar Höyük	Turkey	Iron Age	1,200-600 BC			Iron Age	Scapula	domestic	Leuven	Y2							Peters, J.
SA1193	SA 2003 DA 167	Sagalassos	Turkey	Early Byzantine	450-650 AD			Medieval		domestic	Leuven	A						X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA1203	SA 2003 AP 208	Sagalassos	Turkey	Early to Mid Imperial	0-300 AD			Hellenistic		domestic	Leuven	A				X		X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA1227	SA 2003 LA1 73	Sagalassos	Turkey	Early Byzantine	450-650 AD			Medieval		domestic	Leuven	A				X	X		De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA1230	SA 2003 AP 191	Sagalassos	Turkey	Early to Mid Imperial	0-300 AD	160 BC - 60 AD		Hellenistic		domestic	Leuven	A				X		X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA1301	SA 2004 AP 45/3	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			Hellenistic		domestic	Leuven	A						X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA1302	SA 2004 AP 45/3	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			Hellenistic		domestic	Leuven	A							De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA1315	SA 2004 AP 70/2	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD	250-430 AD		Hellenistic		domestic	Leuven	LDomBritSaddle01					X	X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA133	SA 2000 B3 198	Sagalassos	Turkey	Early Byzantine	450-650 AD	230-410 AD		Hellenistic		domestic	Leuven	A				X	X	X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/

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SA139	SA 2001 NEG 113	Sagalassos	Turkey	Early Byzantine	450-650 AD	140-390 AD		Hellenistic		domestic	Leuven	A					X	X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA223	SA 2000 B3 278	Sagalassos	Turkey	Early Byzantine	450-650 AD			Medieval		domestic	Leuven	A					X	X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA295	SA 91 N 309	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			Hellenistic		domestic	Leuven	A				X		X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA298	SA 91 N 309	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			Hellenistic		domestic	Leuven	A							De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA398	SA 92 N 389	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD	260-520 AD		Hellenistic		domestic	Leuven	C							De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA400	SA 92 N 389	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			Hellenistic		domestic	Leuven	A						X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA405	SA 90 DT 2	Sagalassos	Turkey	0-1200 AD	0-1,200 AD			Medieval		domestic	Leuven	A					X	X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA406	SA 90 DT 2	Sagalassos	Turkey	0-1200 AD	0-1,200 AD			Medieval		domestic	Leuven	A						X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA510	SA 2000 B1 165	Sagalassos	Turkey	Early Byzantine	450-650 AD			Medieval		domestic	Leuven	A						X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA791	SA 90 N 4	Sagalassos	Turkey	Late Roman (Imperial)	300-450 AD			Hellenistic		domestic	Leuven	A				X			De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA941	SA 96 B 262	Sagalassos	Turkey	Early Byzantine	450-650 AD			Medieval		domestic	Leuven	A				X		X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
SA988	SA 95 UAN 216	Sagalassos	Turkey	Early Byzantine	450-650 AD			Medieval		domestic	Leuven	A						X	De Cupere, B., Van Neer, W., http://www.sagalassos.be/
Aru10	2006, D07	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300			Neolithic		domestic	Mainz	Arm1T							Benecke, N.
Aru11	2006, D08	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300			Neolithic		domestic	Mainz	Arm1T							Benecke, N.
Aru12	2006, D12	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300			Neolithic		domestic	Mainz	Arm1T							Benecke, N.
Aru13	2006, D38	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300			Neolithic		domestic	Mainz	Arm1T							Benecke, N.
Aru24	2005, D30	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300			Neolithic		domestic	Mainz	Arm1T							Benecke, N.
Aru25	2005, A 21 D	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300			Neolithic		domestic	Mainz	Arm1T							Benecke, N.
Aru7	2006, B14	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300			Neolithic		domestic	Mainz	Arm1T							Benecke, N.
Aru8	2006, B21	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300					domestic	Mainz								Benecke, N.
Aru9	2006, C28	Aruchlo	Georgia	Early Neolithic, Šulveri-Šomutepe-Group	5,600-5,300					domestic	Mainz								Benecke, N.
Mal12	2004, Bef. 69	Malkayası, Latmos mountains	Turkey	Chalcolithic	5,000-4,500	5189 ± 84 calBC	Chalcolithic	Chalcolithic		wild	Mainz	Y1							Benecke, N.
Mal4	2002, Bef. 127	Malkayası, Latmos mountains	Turkey	Chalcolithic	5,000-4,500					wild	Mainz								Benecke, N.
Mal5	2002, Bef. 122	Malkayası, Latmos mountains	Turkey	Chalcolithic	5,000-4,500					wild	Mainz								Benecke, N.
Mal6	2004, Bef. 58	Malkayası, Latmos mountains	Turkey	Chalcolithic	5,000-4,500					wild	Mainz								Benecke, N.
Mal7	2004, Bef. 48	Malkayası, Latmos mountains	Turkey	Chalcolithic	5,000-4,500					wild	Mainz								Benecke, N.
Mal8	2002, Bef. 22	Malkayası, Latmos mountains	Turkey	Chalcolithic	5,000-4,500					wild	Mainz								Benecke, N.
Mal9	2002, Bef. 54	Malkayası, Latmos mountains	Turkey	Chalcolithic	5,000-4,500	4254 ± 61 calBC	Chalcolithic	Chalcolithic		wild	Mainz	Y1							Benecke, N.
Men 2	Mentese 2000, 26/7, OPER 2000, 21, 122, 678 / Probe #17	Menteşe	Turkey	Neolithic	~6,000				rechter Metacarpus II	domestic?	Mainz								Pinhasi, R.
Men 4	Mentese 2000, 14/7, OPER 2000, 12, 101, 604 / Probe #10	Menteşe	Turkey	Neolithic	~6,000			Neolithic	linker Metacarpus III	domestic?	Mainz	Y1							Pinhasi, R.
Men 5	Mentese 2000, 16/7, OPER 2000, 11, 101, 619 / Probe #5	Menteşe	Turkey	Neolithic	~6,000			Neolithic	Rechter Humerus	domestic?	Mainz	Y1							Pinhasi, R.
Tac10	UD 2005, 025D / Bef. 197	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Tac13	Ud2005, 025D / Bef.197	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Tac14	Ud2005, 025D / Bef.197	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Tac15	Ud2005, 025D / Bef.197	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Tac16	Ud2005, 025D / Bef. 197	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Tac17	Ud2005, 025D / Bef. 197	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Tac6	Ud2005, 025 / Bef. 196	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Tac8	Ta2006, 025B / Bef. 270	Tachti-Perda	Georgia	Late Bronze Age	1,400-1,200			Late Bronze Age		domestic	Mainz	Arm1T							Benecke, N.
Ulu1	DIE5920	Ulucak Höyük	Turkey	Neolithic	6,400-5,900			Neolithic	Metapodium	domestic	Mainz	Y1							Çakırlar, C. 2008, 2009

ID sample	Ref. ID / Find ID / Context	Site	Country	Period (Stratigraphy evidence)	Period (cal BC)	AMS dating cal BC (*indirect dating)	Period (AMS dating)	Period in fig.1	Element	Status	Lab	ANC1 Haplogroup	ANC 1	ANC 2	Cloning	Ext. replication	GMM Lower M2	GMM Lower M3	Reference-Source
Ulu17	Vd FFO / Fundnr. 3548	Ulucak Höyük	Turkey	Neolithic	6,400-5,900				Metapodium	wild?	Mainz								Çakırlar, C. 2008, 2009
Ulu2	IVb DOT	Ulucak Höyük	Turkey	Neolithic	6,400-5,900				Mandibula	domestic	Mainz								Çakırlar, C. 2008, 2009
Ulu20	FLI2929	Ulucak Höyük	Turkey	Neolithic	6,400-5,900			Neolithic	Scapula	domestic	Mainz	Y1							Çakırlar, C. 2008, 2009
Ulu21	Vc EUF / Fundnr. 1595	Ulucak Höyük	Turkey	Neolithic	6,400-5,900				Maxilla with teeth	wild?	Mainz								Çakırlar, C. 2008, 2009
Ulu24	EUS1209	Ulucak Höyük	Turkey	Neolithic	6,400-5,900			Neolithic	Maxilla with teeth	domestic	Mainz	Y1							Çakırlar, C. 2008, 2009
Ulu27	EHE875	Ulucak Höyük	Turkey	Neolithic	6,400-5,900			Neolithic	Maxilla with teeth	domestic	Mainz	Y1							Çakırlar, C. 2008, 2009
Ulu28	Vb EGN	Ulucak Höyük	Turkey	Neolithic	6,400-5,900			Neolithic	Maxilla with teeth	domestic	Mainz	Y1							Çakırlar, C. 2008, 2009
Ulu29	Vb EEL	Ulucak Höyük	Turkey	Neolithic	6,400-5,900				Ulna	domestic	Mainz								Çakırlar, C. 2008, 2009
Ulu30	DBF	Ulucak Höyük	Turkey	Early Bronze Age					Maxilla with teeth	domestic	Mainz								Çakırlar, C. 2008, 2009
Ulu32	CPI520-4	Ulucak Höyük	Turkey	Early Bronze Age					tibia	wild?	Mainz								Çakırlar, C. 2008, 2009
Ulu33	IVb BOF / Fundnr. 2392	Ulucak Höyük	Turkey	Neolithic	6,400-5,900				Tibia	wild?	Mainz								Çakırlar, C. 2008, 2009
Ulu34	Vc EUV / Fundnr. 1971	Ulucak Höyük	Turkey	Neolithic	6,400-5,900				Metacarpus	wild?	Mainz								Çakırlar, C. 2008, 2009
Ulu48	Vc EUR / Fundnr. 1261	Ulucak Höyük	Turkey	Neolithic	6,400-5,900			Neolithic	Astragalus	domestic	Mainz	Y1							Çakırlar, C. 2008, 2009
Ulu49	Vb EEL / Fundnr. 967	Ulucak Höyük	Turkey	Neolithic	6,400-5,900			Neolithic	Ulna	domestic	Mainz	Y1							Çakırlar, C. 2008, 2009
Ulu50	Vb EHE / Fundnr. 874	Ulucak Höyük	Turkey	Neolithic	6,400-5,900				Maxilla with teeth	domestic	Mainz								Çakırlar, C. 2008, 2009

Evin A, Cucchi T, Cardini A, Strand Vidarsdottir U, Larson G, Dobney K. (2013). The long and winding road: Identifying pig domestication through molar size and shape. J Archaeol Sci 40 (1): 735-743.

Supplementary table S2. List of modern wild boars mapped in supplementary figure S2. Each specimen was assigned to a mtDNA clade (Larson et al. 2007) on the basis of genetic variation in long stretches of the mtDNA control region (380-661bp).

ID sample	GenBank	country	source	Clade
GL52	AY884616.1	Spain	Larson et al. 2005	European
GL55	AY884619.1	Turkey	Larson et al. 2005	Near Eastern - NE2
GL59	AY884622.1	Iran	Larson et al. 2005	Near Eastern - NE2
GL63	AY884626.1	Germany	Larson et al. 2005	European
GL65 - feral	AY884628.1	Italy	Larson et al. 2005	Italian
GL71	AY884633.1	France	Larson et al. 2005	European
GL73	AY884635.1	Morocco	Larson et al. 2005	European
GL77	AY884638.1	Iran	Larson et al. 2005	Asiatic
GL107	AY884664.1	Germany	Larson et al. 2005	European
GL108	AY884665.1	Germany	Larson et al. 2005	European
GL109	AY884666.1	Germany	Larson et al. 2005	European
GL110 - feral	AY884667.1	France	Larson et al. 2005	European
GL111 - feral	AY884668.1	Italy	Larson et al. 2005	European
GL112	AY884669.1	Holland	Larson et al. 2005	European
GL113	AY884670.1	Macedonia	Larson et al. 2005	European
GL133 - feral	AY884672.1	Norway	Larson et al. 2005	European
GL141	AY884679.1	Armenia	Larson et al. 2005	European
GL142	AY884680.1	Armenia	Larson et al. 2005	Near Eastern - NE2
GL143 - feral	AY884681.1	France	Larson et al. 2005	European
GL144	AY884682.1	Italy	Larson et al. 2005	European
GL190 - feral	AY884690.1	Italy	Larson et al. 2005	Italian
GL193	AY884693.1	Armenia	Larson et al. 2005	Near Eastern - NE2
GL194	AY884694.1	Armenia	Larson et al. 2005	Near Eastern - NE2
GL220 - feral	AY884696.1	France	Larson et al. 2005	Near Eastern - NE2
GL221	AY884697.1	Spain	Larson et al. 2005	European
GL222	AY884698.1	Portugal	Larson et al. 2005	European
GL236	AY884710.1	Armenia	Larson et al. 2005	Near Eastern - NE2
GL242	AY884714.1	Spain	Larson et al. 2005	European
GL244	AY884716.1	Italy	Larson et al. 2005	Italian
GL245	AY884717.1	Italy	Larson et al. 2005	Italian
GL246	AY884718.1	Italy	Larson et al. 2005	Italian
GL247	AY884719.1	Italy	Larson et al. 2005	Italian
GL248	AY884720.1	Italy	Larson et al. 2005	Italian
GL249	AY884721.1	Italy	Larson et al. 2005	Italian
GL250	AY884722.1	Italy	Larson et al. 2005	Italian
GL251	AY884723.1	Italy	Larson et al. 2005	Italian
GL252	AY884724.1	Italy	Larson et al. 2005	European
GL254	AY884725.1	Iran	Larson et al. 2005	Near Eastern - NE1
GL270	AY884726.1	Armenia	Larson et al. 2005	Near Eastern - NE1
GL271	AY884727.1	Armenia	Larson et al. 2005	Near Eastern - NE2
GL284 - feral	AY884728.1	France	Larson et al. 2005	European
GL285 - feral	AY884729.1	France	Larson et al. 2005	European
GL286 - feral	AY884730.1	France	Larson et al. 2005	European
GL287 - feral	AY884731.1	France	Larson et al. 2005	European
GL288 - feral	AY884732.1	Italy	Larson et al. 2005	European
GL289 - feral	AY884733.1	Italy	Larson et al. 2005	European
LCorsica82 - feral	AY884796.1	France	Larson et al. 2005	European
LNSardinia88 - feral	AY884795.1	Italy	Larson et al. 2005	European
French Wild Boar	AY884815.1	France	Larson et al. 2005	European
SWB1	AY232868	Spain	Alves et al. 2003	European
SWB2	AY232869	Spain	Alves et al. 2003	European
SWB3	AY232870	Spain	Alves et al. 2003	European
SWB6	AY232871	Spain	Alves et al. 2003	European
SWB4	AY232872	Spain	Alves et al. 2003	European
SWB5	AY232873	Spain	Alves et al. 2003	European
SWB7	AY232874	Spain	Alves et al. 2003	European
GiuPolEWB1	AF136555	Poland	Giuffra et al. 2000	European
GiuPolEWB2	AF136556	Poland	Giuffra et al. 2000	European
GiuItalEWB3	AF136563	Italy	Giuffra et al. 2000	Italian
GiuIsrealiWB (3)	AF136558	Israel	Giuffra et al. 2000	European
Kijas01SwedishWB	AF304203	Sweden	Kijas & Anderson 2001	European
GongFinnish36	AF535163	Finland	Gongora et al. 2003	European
GongFinnish41	AF535164	Finland	Gongora et al. 2003	European
GL374	DQ872931.1	Romania Dubova, Iron Gates	Larson et al. 2007	European
GL392	DQ872932.1	Romania	Larson et al. 2007	European
GL724	DQ872933.1	Estonia Restaurant in Tallinn	Larson et al. 2007	European
GL748	DQ872934.1	Syria Amouk Plains	Larson et al. 2007	Near Eastern - NE2
GL749	DQ872935.1	Poland Bialystok Prov Bialowieza* National Park	Larson et al. 2007	European
GL750	DQ872936.1	Iraq Irbil, Baradost	Larson et al. 2007	Near Eastern - NE2
GL751	DQ872937.1	Iraq Baghdad, 3 mi S	Larson et al. 2007	Near Eastern - NE1
GL752	DQ872938.1	Iran Fars, Yasuj, 10.9 mi SW	Larson et al. 2007	Near Eastern - NE2
GL753	DQ872939.1	Iran Kermanshahan Kermanshah	Larson et al. 2007	European
GL754	DQ872940.1	Turkey Mersin (ifel) Tarsus Forest	Larson et al. 2007	Near Eastern - NE2
GL766	DQ872959.1	Iraq Maysan, Amara, nr; Chahala	Larson et al. 2007	European
GL767	DQ872960.1	Iraq Diyala, Khanaquin, 10 mi from; Rhamalla	Larson et al. 2007	Near Eastern - NE1
GL768	DQ872943.1	Syria Amouk Plains	Larson et al. 2007	Near Eastern - NE2
GL769	DQ872944.1	Iran Esfahan, Kuh Rang	Larson et al. 2007	Near Eastern - NE2
GL771	DQ872945.1	Iran Fars, Yasuj	Larson et al. 2007	Near Eastern - NE1
GL779	DQ872946.1	Iraq As Sulaymaniyah; Darband area, Zagros Mts	Larson et al. 2007	European
GL781	DQ872947.1	Iran Kermanshahan	Larson et al. 2007	Near Eastern - NE1
GL782	DQ872948.1	Iran Khuzistan, Ahwaz	Larson et al. 2007	Near Eastern - NE1
GL783	DQ872949.1	Iran Khuzistan, Ahwaz-Andimeshk	Larson et al. 2007	Near Eastern - NE1
GL784	DQ872950.1	Iran Khuzistan, Ahwaz-Andimeshk	Larson et al. 2007	Near Eastern - NE1
GL786	DQ872951.1	Iran Kermanshahan, Kermanshah	Larson et al. 2007	Asiatic
GL787	DQ872952.1	Iran Mazandaran, Sama	Larson et al. 2007	Asiatic
GL788	DQ872953.1	Iran Maku	Larson et al. 2007	Near Eastern - NE2
GL789	DQ872954.1	Iran Mazandaran, Gorgan	Larson et al. 2007	Asiatic
GL790	DQ872955.1	Iran Mazandaran, Gorgan	Larson et al. 2007	Near Eastern - NE2
GL791	DQ872956.1	Iran Mazandaran, Gorgan	Larson et al. 2007	Asiatic
GL792	DQ872957.1	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic
GL793	DQ872958.1	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic
GL794	DQ872959.1	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic
GL795	DQ872960.1	Iran Sistan and Baluchistan, Zabol	Larson et al. 2007	Asiatic
GL799	DQ872961.1	Romania Dubova, Iron Gates	Larson et al. 2007	European
GL912	DQ872962.1	NW Persia	Larson et al. 2007	Near Eastern - NE2
GL918	DQ872963.1	Russia Volga Delta	Larson et al. 2007	European

GL919	DQ872964.1	Russia Volga Delta	Larson et al. 2007	European
GL935	DQ872965.1	West Caucasus, north slope	Larson et al. 2007	European
GL940	DQ872966.1	Turkey Smyrna (Izmir)	Larson et al. 2007	Near Eastern - NE2
GL942 - domestic	DQ872967.1	Sudan Nuba	Larson et al. 2007	Near Eastern - NE2
GL943	DQ872968.1	Egypt Egyptian	Larson et al. 2007	Near Eastern - NE1
GL944	DQ872969.1	Georgia Kavkaz from tiflis (Tbilisi)	Larson et al. 2007	Near Eastern - NE1
GL945	DQ872970.1	Slovakia	Larson et al. 2007	European
GL946	DQ872971.1	Hungary	Larson et al. 2007	European
GL948 - unknown	DQ872972.1	Greece Kos	Larson et al. 2007	European
GL949 - unknown	DQ872973.1	Greece Kos	Larson et al. 2007	European
GL951	DQ872975.1	Bulgaria	Larson et al. 2007	European
GL952 - wild?	DQ872976.1	Sudan	Larson et al. 2007	Near Eastern - NE2
GL1009	DQ872980.1	Turkmenistan	Larson et al. 2007	Asiatic
AR 2		Armenia	present study	European
AR 298		Armenia	present study	European
East AR		Armenia	present study	European
Northeast AR		Armenia	present study	European
IR 1		Iran	present study	Near Eastern - NE2
IR 2		Iran	present study	Near Eastern - NE2
IR 4		Iran	present study	Near Eastern - NE2
IR 5		Iran	present study	Near Eastern - NE2
TK 107		Turkey	present study	Near Eastern - NE2
TK 119		Turkey	present study	Near Eastern - NE2
TK 126		Turkey	present study	Near Eastern - NE2
Tp1		Turkey	present study	European
Tp10		Turkey	present study	Near Eastern - NE2
Tp11		Turkey	present study	Near Eastern - NE2
Tp12		Turkey	present study	Near Eastern - NE2
Tp2		Turkey	present study	Near Eastern - NE2
Tp3		Turkey	present study	Near Eastern - NE2
Tp4		Turkey	present study	Near Eastern - NE2
Tp5		Turkey	present study	Near Eastern - NE2
Tp6		Turkey	present study	Near Eastern - NE2
Tp7		Turkey	present study	Near Eastern - NE2
Tp8		Turkey	present study	Near Eastern - NE2
Tp9		Turkey	present study	Near Eastern - NE2
WBTN 959		Tunisia	present study	European
WBTN 960		Tunisia	present study	European
WBTN 961		Tunisia	present study	European
WBTN 962		Tunisia	present study	European
WBTN 963		Tunisia	present study	European
WBTN 964		Tunisia	present study	Near Eastern - NE2
WBTN 965		Tunisia	present study	European
WBTN 966		Tunisia	present study	European
WBTR 514		Turkey	present study	European
WBTR 515		Turkey	present study	Near Eastern - NE2
WBTR 516		Turkey	present study	Near Eastern - NE2
WBTR 517		Turkey	present study	Near Eastern - NE2
WBRO 562		Romania	present study	European
WBUA 1267		Ukraina	present study	European
WBUA 1268		Ukraina	present study	European
LG778 KS1		Iran	present study	Near Eastern - NE1

Alves E, Ovilo C, Rodriguez MC, & Silio L (2003) Mitochondrial DNA sequence variation and phylogenetic relationships among Iberian pigs and other domestic and wild pig populations. Anim Genet 34(5):319-324.

Giuffra E, et al. (2000) The origin of the domestic pig: independent domestication and subsequent introgression. Genetics 154(4):1785-1791.

Kijas JM & Andersson L (2001) A phylogenetic study of the origin of the domestic pig estimated from the near-complete mtDNA genome. J Mol Evol 52(3):302-308.

Gongora J, et al. (2008) Indo-European and Asian origins for Chilean and Pacific chickens revealed by mtDNA. Proceedings of the National Academy of Sciences of the United States of America 105(30):10308-10313.

Larson G, et al. (2005) Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. Science 307(5715):1618-1621.

Larson G, et al. (2007) Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. Proc Natl Acad Sci U S A 104(39):15276-15281.

Supplementary table S3. Variable positions in ANC1 clone sequences from 10 ancient pig specimens obtained with Topo-TA Cloning kit (Invitrogen) and Illumina GAII platform. Cloned sequences (in grey) are aligned to the consensus of each specimen. In Topo-TA cloned sequences, direct sequences from PCR products are shown in white and used to create a consensus sequence. A frequent occurrence of some artifacts appeared in the oldest samples (BAD47, BAD52), most likely due to a low initial number of template molecules. Names for the sequenced clones are given as follow: SAMPLE NAME_EXTRACTION_PCR FRAGMENT_# CLONE. Positions are numbered according to Ursing and Arnason (1998).

		np	15520	15521	15522	15523	15524	15525	15527	15529	15530	15531	15535	15536	15538	15541	15542	15543	15544	15546	15547	15548	15549	15552	15555	15558	15560	15561	15563	15564	15565	15567	15567.1T	15568	15569	15570	15571	15573	15574	15575	15576	15577	15577.1A	15578	15579	15582	15583	15584	15587	15588	15589	15591	15592	15593	15594
BAD17	Consensus		T	T	G	C	G	C	C	A	A	C	C	A	A	T	G	C	G	C	C	C	C	A	T	A	C	C	T	T	G	A	-	A	A	C	C	A	A	A	A	A	-	T	C	A	T	A	T	T	A	A	G	C	C
BAD17_I_XXXII_1_BO	Direct		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
BAD17_I_XXXII_1_BQ	Direct		.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
BAD17_I_XXXII_1_BM	Direct		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
BAD17_I_XXXII_1_BN	Direct		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
BAD17_II_XXXIV_1_BS	Direct		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Y	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Y	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
BAD17_II_XXXIV_1_BU	Direct		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
BAD17_I_XXXII CO	Direct		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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BAD52	Consensus		T	T	G	C	G	C	C	A	A	C	C	A	A	T	G	C	G	C	C	C	C	A	T	A	C	C	T	T	G	A	T	A	A	C	C	A	A	A	A	A	-	T	C	A	T	A	T	T	A	A	A	C	C
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M46_I_4	Topo-TA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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M46_I_2	Topo-TA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M46_I_1	Topo-TA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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M96	Consensus	T	T	G	C	G	C	C	A	A	C	C	A	A	T	G	T	G	C	C	C	C	A	T	T	C	C	T	T	G	A	-	A	A	C	C	A	A	A	A	A	-	T	C	A	T	A	C	T	A	A	A	C	C
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M96_II_4	Topo-TA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M96_II_3	Topo-TA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M96_II_2	Topo-TA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M96_II_5	Topo-TA	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M96_II_1	Topo-TA	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
LG281	Consensus	T	T	G	C	G	C	C	A	A	C	C	A	A	T	G	C	G	C	C	C	C	A	T	A	C	C	T	T																									
LG281_I_1	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.																									
LG281_I_2	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.																									
LG281_I_3	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.																									
LG281_I_4	GAII	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG281_I_5	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.																									
LG281_I_6	GAII	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG281_I_7	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.																									
LG281_I_8	GAII	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.																									
LG281_I_9	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.																									
LG281_I_10	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG281_I_11	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	N	.	.	.	.	.	T	.	.	.																									
LG281_I_12	GAII	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	.																									
LG459	Consensus	T	T	G	C	G	C	C	A	A	C	C	A	A	T	G	C	G	C	C	C	C	A	T	A	C	C	T	T																									
LG459_I_1	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.																									
LG459_I_2	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.																									
LG459_I_3	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.																									
LG459_I_4	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	.	.	.	.	.	.																									
LG459_I_5	GAII	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG459_I_6	GAII	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG459_I_7	GAII	.	.	N	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.																									
LG459_I_8	GAII	N	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG459_I_9	GAII	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.																									
LG459_I_10	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.																									
LG459_I_11	GAII	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.																									
LG459_I_12	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	A	.	.	.	.	.	.	.																									
LG477	Consensus	T	T	G	C	G	C	C	A	A	C	C	A	A	T	G	C	G	C	C	C	C	A	T	A	C	C	T	T																									
LG477_I_1	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.																									
LG477_I_2	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.																									
LG477_I_3	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.																									
LG477_I_4	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.																									
LG477_I_5	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	.	.	.	.	.	.	.	.																									
LG477_I_6	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.																									
LG477_I_7	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.																									
LG477_I_8	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	.																									
LG477_I_9	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.																									
LG477_I_10	GAII	.	.	.	.	.	.	T	.	.	T	.	.	G	.	.	T	.	.	T	T	.	.	.	.	.	.	.	.																									
LG495	Consensus	T	T	G	C	G	C	C	A	A	C	C	A	A	T	G	C	G	C	C	C	C	A	T	A	C	C	T	T																									
LG495_I_1	GAII	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_2	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_3	GAII	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_4	GAII	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_5	GAII	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_6	GAII	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_7	GAII	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_8	GAII	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_9	GAII	.	.	A	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_10	GAII	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_11	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.																									
LG495_I_12	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	C	.																									
LG495_I_13	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	A	.	G																									
LG495_I_14	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	G																									
LG495_I_15	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	C																									
LG495_I_16	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.																									
LG495_I_17	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	N	.	.	T	.	.	.	.	.	.	.	.																									
LG495_I_18	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	T	.	.																									
LG495_I_19	GAII	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	T	.	.																									
LG495_I_20	GAII	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	T	.	.																									
LG495_I_21	GAII	.	.	.	.	N	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	T	.	.	.	T	T	.	.																									
LG495_I_22	GAII	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	T	T	.	T	.	.	.	T	T	.	.																									
LG495_I_23	GAII	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	T	.	.	.	T	T	.	.																									
LG495_I_24	GAII	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	T	.	.	.	T	T	.	.																									
LG495_I_25	GAII	.	.	N	.	.	.	.	.	.	T	.	.	.	.	.	T	.	T	T	T	T	.	.	.	.	.	.	.																									

Ursing BM, Arnason U. (1998) The complete mitochondrial DNA sequence of the pig (Sus scrofa). J Mol Evol 47:302-306.

Supplementary table S4. Polymorphic sites and associated haplotypes detected in the fragments ANC1 and ANC2 of the mtDNA control region in ancient pig specimens from the Near East. Alignment was done with a reference sequence, in bold (AJ002189, (Ursing and Arnason 1998)). Colors of mtDNA haplotypes and clades (NE2, Near Eastern clade 2; E, European) mimic those in figures 1 and 2. Positions are numbered according to Ursing and Arnason (1998). Haplotype assignment is based on Larson (2007). The status (wild versus domestic) of some of the specimens was provided following identification based on traditional metrics. Specimens for which status identification was not possible are left blank. Because traditional metrical methods for determining status are not necessarily conclusive (Evin et al. 2013), some of the status calls reported here may be subject to revision.

		ANC1										ANC2											
		15522	15543	15546	15557	15558	15567.1T	15577	15577.1A	15587	15592	15714	15723	15724	15729	15733	15741	15744	15758				
ID sample	Site	G	T	C	T	A	-	A	-	C	A	T	A	C	A	C	C	G	T	Haplotype	Clade	Date	Status
BAD4	Bademağacı	G	C	C	T	A	-	A	-	T	G									Y1	NE2	Early Neolithic II - 4A	wild
BAD5	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Early Neolithic II - 4A	wild
BAD52	Bademağacı	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic II - 4A	domestic
BAD54	Bademağacı	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic II - 4A	domestic
BAD63	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Early Neolithic II - 4B	domestic
BAD10	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Early Neolithic II - 3	domestic
BAD9	Bademağacı	A	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic II - 3A	wild
BAD47	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Early Neolithic II - 3A	domestic
BAD30	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Early Neolithic II - 2	domestic
BAD32	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Early Neolithic II - 3	domestic
BAD15	Bademağacı	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	T	Y2	NE2	Early Bronze Age II	domestic
BAD16	Bademağacı	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age II	domestic ?
BAD17	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Early Bronze Age II	domestic
BAD18	Bademağacı	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age II	domestic
BAD83	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Early Bronze Age II	domestic
BAD84	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Early Bronze Age II	wild
BAD85	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	G	C	A	C	C	G	T	Y1	NE2	Early Bronze Age II	wild
BAD86	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Early Bronze Age II	wild
BAD87	Bademağacı	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Early Bronze Age II	wild
M120	Hassek Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	domestic
M123	Hassek Höyük	G	C	C	C	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	domestic
M124	Hassek Höyük	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Chalcolithic	domestic
M18	Hassek Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age	domestic
M85	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age (AMS)	domestic
M86	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age	domestic
M87	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age	domestic
M88	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age	domestic
M90	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Bronze Age	domestic
M64	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle Bronze Age II/I	domestic
M68	Lidar Höyük	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	T	Y2	NE2	Middle Bronze Age II/I	domestic
M71	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	C	Arm1T	NE2	Middle Bronze Age II/I	domestic
M73	Lidar Höyük	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	T	Y2	NE2	Middle Bronze Age II/I	domestic
M74	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle Bronze Age II/I	domestic
M47	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle Bronze Age II	domestic
M48	Lidar Höyük	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	T	Y2	NE2	Middle Bronze Age II	wild
M50	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle Bronze Age II	domestic
M49	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle Bronze Age II	domestic
M51	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Bronze/Iron Age (AMS)	domestic
M52	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Middle Bronze Age II	domestic
M75	Lidar Höyük	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	T	Y2	NE2	Late Bronze Age	domestic
M76	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Iron Age (AMS)	domestic
M77	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
M78	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Bronze/Iron Age (AMS)	domestic
M79	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	T	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	wild
M80	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	T	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	wild
M81	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	C	Arm1T	NE2	Late Bronze Age	domestic
M82	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Bronze Age (AMS)	domestic
M83	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
M93	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	domestic
M94	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	domestic
M95	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	domestic
M96	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Iron Age	domestic
M97	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Iron Age	domestic
M98	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Iron Age	domestic

		ANC1										ANC2											
		15522	15543	15546	15557	15558	15567.1T	15577	15577.1A	15587	15592	15714	15723	15724	15729	15733	15741	15744	15758				
ID sample	Site	G	T	C	T	A	-	A	-	C	A	T	A	C	A	C	C	G	T	Haplotype	Clade	Date	Status
M99	Lidar Höyük	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	T	Y2	NE2	Iron Age	domestic
M100	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Iron Age	domestic
M101	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	domestic
M40	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Hellenistic-Roman	domestic
M42	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Hellenistic-Roman	domestic
M44	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Hellenistic-Roman	domestic
M45	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Hellenistic-Roman	domestic
M46	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	G	C	T	G	T	Arm1T	NE2	Hellenistic-Roman	domestic
M53	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Medieval	domestic
M54	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	T	A	E	Medieval	domestic
M55	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Medieval	domestic
M56	Lidar Höyük	G	T	C	T	T	-	A	A	C	A	C	A	C	G	C	C	G	C	A	E	Medieval	domestic
M57	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Medieval	domestic
M58	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Medieval	domestic
M59	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Medieval	domestic
F13	Düzen Tepe	G	T	C	T	T	-	A	-	C	A	C	A	C	A	T	C	G	C	A	E	6th-3rd cent BC	domestic
F15	Düzen Tepe	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	6th-3rd cent BC	domestic
F20	Düzen Tepe	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	6th-3rd cent BC	domestic
F21	Düzen Tepe	G	T	C	T	A	-	A	-	C	A	C	A	C	A	C	C	G	T	C	E	6th-3rd cent BC	domestic
SA133	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA139	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA223	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA510	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA941	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA988	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA1193	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA1227	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early Byzantine (450-650 AD)	domestic
SA295	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Roman (Imperial) (300-450 AD)	domestic
SA298	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Roman (Imperial) (300-450 AD)	domestic
SA398	Sagalassos	G	T	C	T	A	-	A	-	C	A	C	A	C	A	C	C	G	T	C	E	Late Roman (Imperial) (300-450 AD)	domestic
SA400	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Roman (Imperial) (300-450 AD)	domestic
SA791	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Roman (Imperial) (300-450 AD)	domestic
SA1301	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	T	G	C	A	E	Late Roman (Imperial) (300-450 AD)	domestic
SA1302	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Roman (Imperial) (300-450 AD)	domestic
SA1315	Sagalassos	G	T	C	T	T	-	A	-	T	A	C	A	C	A	C	C	G	C	LDomBritSaddle01	E	Late Roman (Imperial) (300-450 AD)	domestic
SA1203	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early to Mid Imperial (0-300 AD)	domestic
SA1230	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Early to Mid Imperial (0-300 AD)	domestic
SA405	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	0-1200 AD	domestic
SA406	Sagalassos	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	0-1200 AD	domestic
LG011	Gohar Tappeh	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Early Bronze Age	
LG017	Qaleh Rostam	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Neolithic	
LG067	Qareh Doyub	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Historical	
LG069	Qelïch Qöïneq	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Achemenid	
LG070	Qelïch Qöïneq	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Achemenid	
LG071	Qelïch Qöïneq	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Achemenid	
LG073	Dasht Qaleh	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Achemenid	
LG109	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Bronze/Iron Age (AMS)	
LG110	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Bronze/Iron Age (AMS)	
LG111	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	MBA II/III ? (uncertain)	
LG112	Lidar Höyük	G	C	C	T	A	-	-	-	T	G									Y2	NE2	Late Bronze Age	
LG114	Lidar Höyük	G	T	Y	T	T	-	A	-	C	A									A	E	Late Bronze/Iron Age (AMS)	
LG115	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle Bronze Age II/I	
LG137	Lidar Höyük	G	T	C	T	T	-	A	-	C	A	C	A	C	G	C	C	G	C	A	E	Medieval (AMS)	
LG217	Kohneh Tepesi	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Bronze Age	
LG219	Kohneh Tepesi	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Bronze Age	

		ANC1										ANC2											
		15522	15543	15546	15557	15558	15567.1T	15577	15577.1A	15587	15592	15714	15723	15724	15729	15733	15741	15744	15758				
ID sample	Site	G	T	C	T	A	-	A	-	C	A	T	A	C	A	C	C	G	T	Haplotype	Clade	Date	Status
LG221	Kohneh Tepesi	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Bronze Age	
LG222	Kohneh Tepesi	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Bronze Age	
LG223	Haftavan	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG224	Haftavan	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG225	Haftavan	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG226	Doshan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	
LG227	Doshan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	
LG241	Areni-1	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG247	Tsakayeghtsi	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Medieval	
LG248	Sevkar 4	G	T	C	T	T	-	A	-	C	A									A	E	Iron Age	
LG249	Lehashen 2	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle Bronze Age	
LG251	Lidar Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	
LG252	Lidar Höyük	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	T	Y2	NE2	Iron Age	
LG253	Lidar Höyük	G	C	C	T	A	-	-	-	T	G	C	A	C	A	C	C	G	Y	Y2	NE2	Late Bronze Age	
LG254	Lidar Höyük	G	C	C	T	A	-	-	-	T	G									Y2	NE2	Late Bronze Age	
LG276	Malyan	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Bronze Age/iron Age	
LG281	Leilan	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Early/Middle Bronze Age	
LG289	Leilan	G	C	C	T	A	T	A	-	T	A	C	A	Y	A	C	T	G	T	Arm1T	NE2	Early/Middle Bronze Age	
LG350	Gordion	G	T	C	T	T	-	A	A	C	A	C	A	C	A	C	C	G	C	LDomGermanyAngler	E	Late Hellenistic	
LG351	Gordion	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age?	
LG352	Gordion	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	
LG353	Gordion	G	T	C	T	T	-	A	-	C	A	C	A	C	A	C	C	G	C	A	E	Late Phrygian	
LG354	Gordion	G	C	C	T	A	-	A	-	T	A	C	A	C	A	C	C	G	T	Yellow star	NE2	Late Bronze Age	
LG356	Gordion	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Late Phrygian	
LG414	Mehr Ali	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Chalcolithic	
LG459	Çayönü	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Pottery neolithic	
LG475	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG476	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG477	Çamlıbel Tarlası	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Chalcolithic	
LG479	Çamlıbel Tarlası	G	C	C	T	A	-	A	-	T	G									Y1	NE2	Chalcolithic	
LG480	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG485	Çamlıbel Tarlası	G	C	C	T	A	-	A	-	T	G									Y1	NE2	Chalcolithic	
LG486	Çamlıbel Tarlası	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Chalcolithic	
LG488	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Chalcolithic	
LG489	Çamlıbel Tarlası	G	C	C	T	A	-	A	-	T	G									Y1	NE2	Chalcolithic	
LG491	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG492	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG493	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG495	Çamlıbel Tarlası	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic	
LG522	Sirkeli Höyük	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Iron Age	
LG524	Sirkeli Höyük	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Iron Age	
LG527	Sirkeli Höyük	G	C	C	T	A	-	A	-	T	G									Y1	NE2	Iron Age	
LG529	Sirkeli Höyük	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Iron Age	
LG773	Chaga Gavaneh	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Chalcolithic/Bronze Age	
LG780	Kohneh Tepesi	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Bronze Age	
LG784	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG785	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG787	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Middle & Late Bronze Age	
LG788	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG789	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG790	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A									Arm1T	NE2	Middle & Late Bronze Age	
LG791	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG792	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG794	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG795	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG796	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Middle & Late Bronze Age	
LG798	Haftavan Tepe	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	A	T	Arm1T	NE2	Middle & Late Bronze Age	
Aru7	Aruchlo	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic	domestic
Aru10	Aruchlo	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic	domestic
Aru11	Aruchlo	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic	domestic
Aru12	Aruchlo	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic	domestic
Aru13	Aruchlo	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic	domestic
Aru24	Aruchlo	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic	domestic

		ANC1										ANC2											
		15522	15543	15546	15557	15558	15567.1T	15577	15577.1A	15587	15592	15714	15723	15724	15729	15733	15741	15744	15758				
ID sample	Site	G	T	C	T	A	-	A	-	C	A	T	A	C	A	C	C	G	T	Haplotype	Clade	Date	Status
Aru25	Aruchlo	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Early Neolithic	domestic
Tac6	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
Tac8	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
Tac10	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
Tac13	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
Tac14	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	C	Arm1T	NE2	Late Bronze Age	domestic
Tac15	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
Tac16	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
Tac17	Tachti-Perda	G	C	C	T	A	T	A	-	T	A	C	A	C	A	C	T	G	T	Arm1T	NE2	Late Bronze Age	domestic
Mal9	Malkayası	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Chalcolithic	wild
Mal12	Malkayası	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Chalcolithic	wild
Men 4	Menteşe	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Chalcolithic	domestic?
Men 5	Menteşe	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Chalcolithic	domestic?
Ulu1	Ulucak Höyük	G	C	C	T	A	-	A	-	T	G	C	A	C	G	C	C	G	T	Y1	NE2	Neolithic	domestic
Ulu20	Ulucak Höyük	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Neolithic	domestic
Ulu24	Ulucak Höyük	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Neolithic	domestic
Ulu27	Ulucak Höyük	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Neolithic	domestic
Ulu28	Ulucak Höyük	G	C	C	T	A	-	A	-	T	G									Y1	NE2	Neolithic	domestic
Ulu48	Ulucak Höyük	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Neolithic	domestic
Ulu49	Ulucak Höyük	G	C	C	T	A	-	A	-	T	G	C	A	C	A	C	C	G	T	Y1	NE2	Neolithic	domestic

Evin A, Cucchi T, Cardini A, Strand Vidarsdottir U, Larson G, Dobney K. (2013). The long and winding road: Identifying pig domestication through molar size and shape. J Archaeol Sci 40 (1): 735-743.

Larson G, et al. (2007) Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. Proc Natl Acad Sci U S A 104(39):15276-15281.

Ursing BM, Arnason U. (1998) The complete mitochondrial DNA sequence of the pig (Sus scrofa). J Mol Evol 47:302-306.

Supplementary table S5. Ancient pig specimens analyzed in the timeframe 6,500-3,000 BC depicted in supplementary figure S3. An asterisk indicated dates based upon direct AMS dating of pig samples unearthed from the same layer.

ID sample	Country	Site	Phase	Dating	State	Anc haplotype	References
Bad4	Turkey	Bademağacı	EN II-4A	6,390-6,250 BC*	Wild	Y1	Present study
Bad5	Turkey	Bademağacı	EN II-4A		Wild	Y1	Present study
Bad10	Turkey	Bademağacı	EN II-3	6,450-6,240 BC*	Domestic	Y1	Present study
Bad30	Turkey	Bademağacı	EN II-2		Domestic	Y1	Present study
Bad32	Turkey	Bademağacı	EN II-2		Domestic	Y1	Present study
Bad47	Turkey	Bademağacı	EN II-3A		Domestic	Y1	Present study
Bad63	Turkey	Bademağacı	EN II-4B		Domestic	Y1	Present study
Bad9	Turkey	Bademağacı	EN II-3A		Wild	Arm1T*	Present study
Bad52	Turkey	Bademağacı	EN II-4A		Domestic	Arm1T*	Present study
Bad54	Turkey	Bademağacı	EN II-4A		Domestic	Arm1T*	Present study
Ulu1	Turkey	Ulucak Höyük	Neolithic	6,400-5,900	Domestic	Y1	Present study
Ulu20	Turkey	Ulucak Höyük	Neolithic	6,400-5,900	Domestic	Y1	Present study
Ulu24	Turkey	Ulucak Höyük	Neolithic	6,400-5,900	Domestic	Y1	Present study
Ulu27	Turkey	Ulucak Höyük	Neolithic	6,400-5,900	Domestic	Y1	Present study
Ulu28	Turkey	Ulucak Höyük	Neolithic	6,400-5,900	Domestic	Y1	Present study
Ulu48	Turkey	Ulucak Höyük	Neolithic	6,400-5,900	Domestic	Y1	Present study
Ulu49	Turkey	Ulucak Höyük	Neolithic	6,400-5,900	Domestic	Y1	Present study
Men4	Turkey	Menteşe	Neolithic	~6.000	Domestic?	Y1	Present study
Men5	Turkey	Menteşe	Neolithic	~6.000	Domestic?	Y1	Present study
Mal9	Turkey	Malkayası	Chalcolithic	5,000-4,500	Wild	Y1	Present study
Mal12	Turkey	Malkayası	Chalcolithic	5,000-4,500	Wild	Y1	Present study
#31	Turkey	Çayönü	Pottery Neolithic	6,500 BC?	Domestic	Arm1T*	Present study
M120	Turkey	Hassek Höyük	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
M123	Turkey	Hassek Höyük	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
M124	Turkey	Hassek Höyük	Chalcolithic	mid 4th mill BC	Domestic	Y1	Present study
EDI-CAN 778-5155b	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Y1	Present study
EDI-CAN 891-5779	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic?	Y1	Present study
EDI-CAN 247-372b	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Y1	Present study
EDI-CAN 463-4067	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic?	Y1	Present study
EDI-CAN 746-4982	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Y1	Present study
EDI-CAN 250-397b	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
EDI-CAN 273-868	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
EDI-CAN 966-6042	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
EDI-CAN 796-5229	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
EDI-CAN 56-252c	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
EDI-CAN 352-987	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
EDI-CAN 925-5377	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
EDI-CAN 858-5569	Turkey	Çamlıbel Tarlası	Chalcolithic	mid 4th mill BC	Domestic	Arm1T*	Present study
GL343	Armenia	Khatunarkh	5th mill	5th mill BC uncal ?	Wild	Arm2T*	Larson et al. 2007
GL376	Armenia	Shengevit	Late 4th-early 3rd mill	late 4th-early 3rdmill BC uncal?	undetermined	Arm2T*	Larson et al. 2007
ARU7	Georgia	Aruchlo	Early Neolithic	5,600-5,300	domestic	Arm1T*	Present study
ARU10	Georgia	Aruchlo	Early Neolithic	5,600-5,300	domestic	Arm1T*	Present study
ARU11	Georgia	Aruchlo	Early Neolithic	5,600-5,300	domestic	Arm1T*	Present study
ARU12	Georgia	Aruchlo	Early Neolithic	5,600-5,300	domestic	Arm1T*	Present study
ARU13	Georgia	Aruchlo	Early Neolithic	5,600-5,300	domestic	Arm1T*	Present study

ID sample	Country	Site	Phase	Dating	State	Anc haplotype	References
ARU24	Georgia	Aruchlo	Early Neolithic	5,600-5,300	domestic	Arm1T*	Present study
ARU25	Georgia	Aruchlo	Early Neolithic	5,600-5,300	domestic	Arm1T*	Present study
LG017	Iran	Qaleh Rostam	Neolithic	7th millennium BC?		Arm1T*	Present study
LG414	Iran	Mehr Ali	Late Chalcolithic	4th millennium BC		Arm1T*	Present study
GL728	Croatia	Pupicinia cave	Late Neolithic	4,300 BC	Domestic?	Y2-5A	Larson et al. 2007
GL123	Germany	Eilsleben	LBK	5,500-5,000 BC	Wild	Cside	Larson et al. 2007
GL541	Germany	Eilsleben	LBK	5,500-5,000 BC	Undetermined	Cside	Larson et al. 2007
GL977	Germany	Eilsleben	LBK	5,500-5,000 BC	Domestic?	Y1-6A	Larson et al. 2007
GL972	Germany	Eilsleben	LBK	5,500-5,000 BC	Domestic?	Y1-6A	Larson et al. 2007
GL973	Germany	Eilsleben	LBK	5,500-5,000 BC	Domestic?	Y1-6A	Larson et al. 2007
GL976	Germany	Eilsleben	LBK	5,500-5,000 BC	Domestic?	Y1-6A	Larson et al. 2007
GL882	Italy	Grotta Madonna	Mesolithic	6,500-5,500 BC	Undetermined	Italy	Larson et al. 2007
GL848	Italy	Grotta Madonna	Mid Neolithic	5,500-4,500 BC	Undetermined	Italy	Larson et al. 2007
GL900	Romania	Măgura	Neolithic	5,500 BC	Domestic	Y1-6A	Larson et al. 2007
GL903	Romania	Măgura	Neolithic	5,500 BC	Domestic	Y1-6A	Larson et al. 2007
GL375	Romania	Veterani cave	Neolithic	5,300-5,000 BC		Aside	Larson et al. 2007
GL521	Romania	Bordusani	Chalcolithic	4,500-3,950 BC	Domestic	Y1-6A	Larson et al. 2007
GL522	Romania	Poduri	Chalcolithic	4,500-4,250 BC	Domestic	Y1-6A	Larson et al. 2007
GL523	Romania	Poduri	Chalcolithic	4,500-4,250 BC	Domestic	Y1-6A	Larson et al. 2007
GL688	Romania	Poduri	Chalcolithic	4,500-4,250 BC	Wild	Cside	Larson et al. 2007
GL566	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Wild	Cside	Larson et al. 2007
GL567	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Wild	Cside	Larson et al. 2007
GL432	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Domestic	Y1-6A	Larson et al. 2007
GL568	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Domestic	Y1-6A	Larson et al. 2007
GL576	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Domestic	Y1-6A	Larson et al. 2007
GL868	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Domestic	Y1-6A	Larson et al. 2007
GL575	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Wild	Cside	Larson et al. 2007
GL803	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Domestic	Y1-6A	Larson et al. 2007
GL834	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	Domestic	Y1-6A	Larson et al. 2007
GL987	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	undetermined	Y1-6A	Larson et al. 2007
GL447	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	undetermined	Cside	Larson et al. 2007
GL565	Romania	Căscioareale	Chalcolithic	mid 5th-mid 4th mill BC	undetermined	Y1-6A	Larson et al. 2007
GL429	Denmark	Flynderhage	Late Mesolithic	4,500-3,900 BC	Wild	Cside	Larson et al. 2007
GL907	Denmark	Flynderhage	Late Mesolithic	4,500-3,900 BC	Wild	Cside	Larson et al. 2007
A212	England	Carsington Pasture cave	Mesolithic	4,393 ± 41 BC	Wild	Cside	Larson et al. 2007
A213	England	Carsington Pasture cave	Mesolithic	5,678 ± 30 BC	Wild	Aside	Larson et al. 2007
A216	England	Carsington Pasture cave	Mesolithic	3,457 ± 58 BC	Domestic	Aside	Larson et al. 2007
GL846	France	Bercy	Chaseen culture	early 4th mill BC	Domestic	Y1-6A	Larson et al. 2007
GL859	France	Bercy	Chaseen culture	early 4th mill BC	Domestic?	Aside	Larson et al. 2007
GL571	France	Bercy	Chaseen culture	early 4th mill BC	Domestic	Aside	Larson et al. 2007
GL572	France	Bercy	Chaseen culture	early 4th mill BC	Domestic	Aside	Larson et al. 2007
GL824	France	Bercy	Chaseen culture	early 4th mill BC	Domestic	Aside	Larson et al. 2007
GL573	France	Bercy	Chaseen culture	early 4th mill BC	Domestic	Aside	Larson et al. 2007
GL874	France	Bercy	Chaseen culture	early 4th mill BC	Domestic	Aside	Larson et al. 2007
GL574	France	Bercy	Chaseen culture	early 4th mill BC	Wild	Cside	Larson et al. 2007
GL355	France	Bercy	Chaseen culture	early 4th mill BC	Domestic	Y1-6A	Larson et al. 2007

ID sample	Country	Site	Phase	Dating	State	Anc haplotype	References
GL321	France	Roucador	Mid Neolithic	4,200-3,500 BC cal?	Wild	Aside	Larson et al. 2007
GL470	France	Roucador	Mid Neolithic	4,200-3,500 BC cal?	Wild	Aside	Larson et al. 2007
GL485	France	Roucador	Mid Neolithic	4,200-3,500 BC cal?	Wild	Aside	Larson et al. 2007
GL490	France	B. Oulens	Neolithic (cardial)	5,306-4,962 BC	Wild	Cside	Larson et al. 2007
GL491	France	B. Oulens	Neolithic (cardial)	5,471-5,222 BC	Domestic?	Aside	Larson et al. 2007
A244	Ireland	Moynagh Crannog		3,866 ± 60	undetermined	Aside	Larson et al. 2007

Larson G, et al. (2007) Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. Proc Natl Acad Sci U S A 104(39):15276-15281.

Supplementary table S6. Differences between pigs with Near Eastern and European lineages in size (Kruskall-Wallis test) and shape (MANOVA) based on geometric and traditional morphometrics. Significant results are in bold for lower M2 and M3 with sample size in parentheses (EU: European lineages, NE: Near East lineages).

		Lower M2 (EU=8 ; NE=17)								**Lower M3 (EU=17 ; NE=20)**							
		X^2	Df	Pillai	approxF	numDf	denDf	p	CVP	X^2	Df	Pillai	approxF	numDf	denDf	p	CVP
Geometric morphometrics	Shape		**1**	**0.53**	**3.34**	**6**	**18**	**0.021**	**80%**		**1**	**0.51**	**3.11**	**9**	**27**	**0.011**	**76%**
	Centroid Size	**6.87**	**1**					**0.009**	**80%**	**14.75**	**1**					**0.0001**	**76%**
Traditional metrics	Shape		1	0.29	2.91	3	21	0.06			1	0.15	1.46	4	32	0.24	
	Isometric Size	**8.83**	**1**					**0.003**	**80%**	**13.37**	**1**					**0.0003**	**78%**