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Institute of Genomics and Institute of Molecular and Cell Biology, University of Tartu, Estonia

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The author's contributions to the listed articles are as follows:

REF I: I was part of conceiving the study, performed the laboratory work, participated in data analysis except for isotopes, interpreted the results, and co-wrote the manuscript.

REF II: I performed the laboratory work of the pilot set (12 samples) and first raw data analysis, including mapping, estimating the average human coverage, and sex determination, provided the information to the first authors and reviewed the manuscript.

REF III: The compiled dataset for the screening for pathogens was done based on several projects in which I was involved and for which I performed laboratory work. I also performed the target capture for the specific viruses of interest.

REF IV: I was part of conceiving the study, performed the laboratory work, participated in data analysis focusing on raw data analysis and population genomic studies, interpreted the results, and co-wrote the manuscript.

ABBREVIATIONS

aDNA	ancient DNA (deoxyribonucleic acid)
BCE	Before the Common Era
bp	base pairs
CE	Common Era
CHG	Caucasus hunter-gatherer
CNE	continental northern European
cNSz	continental North Sea zone ancestry
cM	centimorgan
chrY	Y chromosome
ds	double-stranded library
EEF	Early European farmers
EHG	Eastern hunter-gatherers
HBV	hepatitis B virus
HRC	Haplotype Reference Consortium
HHV-6	Human betaherpesvirus 6
HHV-6A	Human betaherpesvirus 6A
HHV-6B	Human betaherpesvirus 6B
HSV-1	herpes simplex virus 1
IBD	identical-by-descent
LGM	Last Glacial Maximum
LSAI	Long shared allele intervals
mtDNA	mitochondrial DNA
NGS	next-generation sequencing
PCA	principal component analyses
PCR	polymerase chain reaction
PiC	individual connectedness score
sedaDNA	Sedimentary DNA
SHG	Scandinavian hunter-gatherer
ss	single stranded library
UMAP	Uniform Manifold Approximation and Projection
VARV	variola virus
WHG	Western Hunter-Gatherer

1. INTRODUCTION

Human evolution and the history of our species have long attracted academic interest and have been studied across multiple disciplines. Research from diverse fields has contributed to a deeper understanding of the major milestones of past events. In Europe, these include key phases such as the arrival of hunter-gatherer populations, the introduction of agriculture and animal domestication, and the emergence of the first major civilisations.

Within this broader research landscape, paleogenomics emerged as a complementary field around 45 years ago, with the aims to reconstruct human history and migration patterns through the analysis of ancient DNA. Driven by major technological advances, this discipline has enabled significant paleogenetic discoveries, culminating in the 2022 Nobel Prize in Physiology and Medicine being awarded to Svante Pääbo, in recognition of his fundamental contributions and groundbreaking findings.

Over the years, archaeogenomics has addressed a wide range of questions related to prehistoric and historical populations. More recently, however, genetic research has increasingly turned its attention to later periods, such as the post-Roman and medieval eras, with the aim of characterising changes in population structure and elucidating the extent and dynamics of admixture and relatedness within and between different groups.

At the same time, an increasingly interdisciplinary approach has emerged. It is now possible not only to study the genetics of past individuals directly, but also to test hypotheses and complement evidence derived from other disciplines, including archaeology, history, and linguistics. By integrating genetic data with these independent lines of evidence, archaeogenomics provides a more comprehensive and nuanced reconstruction of past societies.

This thesis provides a general overview of archaeogenetics, tracing the field's origins, outlining its main stages of development, identifying key challenges associated with the study of ancient DNA, and highlighting its most recent advances. It then focuses on investigating the demographic history of present-day Belgium and Estonia during the medieval period. Following the fall of the Western Roman Empire in 476 CE, Europe experienced profound transformations. In the territory of present-day Flanders (Belgium), the Merovingian Kingdom came to power, reshaping the region from a landscape of relatively small settlements into a more interconnected area through maritime trade networks. To better understand the social and genetic changes that occurred during this period, we investigated the ancestry of a Late Merovingian population from the coastal North Sea site of Koksijde (REF I). These results were then compared with data from a later population from the site of Sint-Truiden (REF II), also located in Belgium but situated further inland and characterised by a broader temporal transect. Over time, Sint-Truiden became an important pilgrimage centre, allowing us to examine how increased mobility and urban development influenced both population structure and individual health status. The emergence of cities around newly founded

abbeys was a common phenomenon in medieval Europe, reflecting the growing importance and widespread diffusion of Christianity. Besides the focus on human genetic variation, the thesis next examines the presence and evolutionary history of pathogens—particularly human betaherpesviruses (REF III)—in both the Sint-Truiden population and more broadly in Europe, including in medieval Estonian communities, providing insights into population health in the medieval period. In this broader European context, the Northern Crusades were launched in the 13th century, during which German forces conquered Estonia, introducing major social and genetic changes to the region. The final chapter of the thesis examines the genetic impact of these historic events on local urban and rural populations (REF IV).

2. LITERATURE OVERVIEW

The following chapter highlights innovations in ancient DNA research and provides an overview of historical events related to the demographic history of northern Europe during the medieval period.

2.1. Ancient DNA

2.1.1. History of ancient DNA studies

The era of ancient DNA (aDNA) began approximately 45 years ago, with the first attempts to extract DNA from various biological tissues. A major breakthrough occurred in 1984, when Higuchi and colleagues successfully extracted and sequenced 229 base pairs (bp) of mitochondrial DNA (mtDNA) from a museum sample of quagga (*Equus quagga*), an extinct equid closely related to modern zebras that disappeared in 1883 (Higuchi et al. 1984). The following year, Svante Pääbo reported cloning of DNA extracted from an Egyptian mummy (Pääbo 1985).

In subsequent years, the development of the polymerase chain reaction (PCR), which enabled rapid amplification of specific DNA fragments, led to a sharp increase in publications in the field (Rollo et al. 1988; Thomas et al. 1989; DeSalle et al. 1992; Woodward et al. 1994). However, this initial phase of enthusiasm was followed by a period of critical reassessment, during which many previously reported results were questioned and revised to test their authenticity. A notable example is the case of putative Cretaceous dinosaur DNA, first reported in (Woodward et al. 1994) and later retracted after being identified as contamination (Hedges & Schweitzer 1995; Zischler et al. 1995). Similarly, many researchers re-examined their discovery (Cooper & Poinar 2000; Pääbo et al. 2004). Despite these early challenges, this period was fundamental for highlighting the pervasive contamination issue and ultimately led to the establishment of the first standardised laboratory protocols specifically designed to minimise contamination in aDNA studies (Handt et al. 1996; Ward & Stringer 1997; Cooper & Poinar 2000; Knapp et al. 2012).

In 2005, the development of the next-generation sequencing (NGS) technology (Margulies et al. 2005) brought significant advances in the field: in 2006, Poinar and colleagues published 13 million bps of the genome sequence of the extinct woolly mammoth (Poinar et al. 2006), and in 2008, Miller and others managed to sequence more than 70% of its genome (Miller et al. 2008). In 2010, a draft Neanderthal genome was released (Green et al. 2010), followed shortly thereafter by the first full modern human and Denisovan genome sequences (Rasmussen et al. 2010; Reich et al. 2010). The first high-coverage Neanderthal genome was published in 2014 (Prüfer et al. 2014). In the last ten years, the field has made significant advances in developing laboratory methods and analyses (Orlando et al. 2021) and in the study of pathogens (Blevins et al. 2026). In 2021,

the DNA of a mammoth "Krestovka" that dated 1.2 million years ago was extracted and analysed, showing that genomic data can be recovered from Early Pleistocene specimens and highlighting the importance of perennially frozen environments for advancing the field (van der Valk et al. 2021).

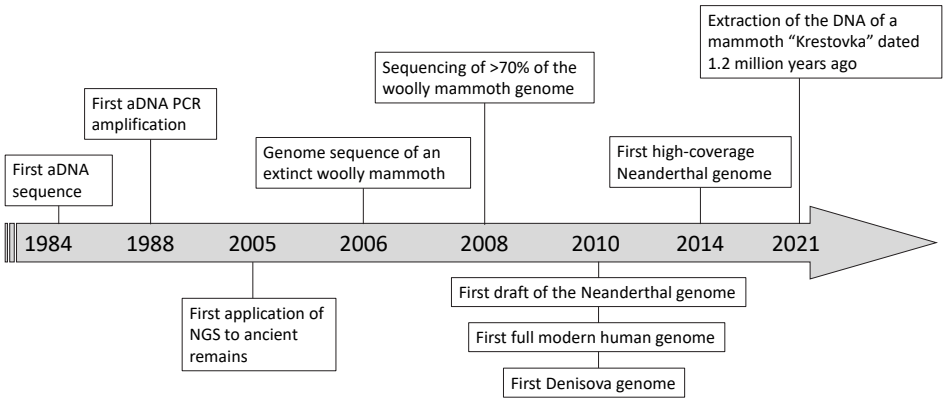

Figure 1. Major milestones in the history of ancient DNA studies.

2.1.2. Challenges in aDNA studies

In the aDNA studies, numerous challenges must be addressed, starting with the environmental conditions under which skeletal remains are preserved. DNA preservation depends on several factors, including climate, geographic location, the presence of exogenous DNA from surrounding organisms, and the degradation of the biomolecules over time (Green et al. 2010; Miller et al. 2012; Orlando et al. 2013; Der Sarkissian et al. 2015). Already in the 1990's, it was recognised that cool and stable preservation environments contribute to improved DNA preservation (Höss, Jaruga, et al. 1996; Höss, Dilling, et al. 1996; Hadly et al. 1998; Noro et al. 1998; Wayne et al. 1999). Evidence has shown that permafrost and cave environments provide optimal conditions for it, whereas warm climates have a negative impact. Studies on mummified remains and individuals of sub-Saharan African origin are an example: it was only recently possible to conduct successful studies on remains recovered from hot climates (Schuenemann et al. 2017; Skoglund et al. 2017; Gretzinger et al. 2024). However, it has not yet been possible to extract DNA from burned remains due to heat damage or from remains recovered from bog environments, owing to the severe degradation caused by the highly acidic soil.

In addition, various chemical and biological processes contribute to the decomposition of organisms or the human body after death. These processes also affect DNA, leading to its fragmentation into progressively smaller fragments (Pääbo 1989; Lindahl 1993; Deagle et al. 2006). One cause of this degradation is nucleolytic activity within cells: as decomposition begins, cellular DNA is digested by microorganisms (Eglinton & Logan 1991; Lindahl 1993). Furthermore, DNA is

inherently chemically unstable, leading to strand breakage and the need for continuous repair even in living cells (Lindahl 1993). However, DNA repair mechanisms cease to function upon the individual's death. The loss of purines (depurination) is an example of chemical decay in which purine bases are hydrolysed from the deoxyribose backbone, potentially leading to strand breakage. The outcome of these processes is random DNA fragmentation. The fragment length distribution is commonly used in aDNA studies as an indicator to assess whether a sample is genuinely ancient or shows evidence of modern contamination (Ginolhac et al. 2011; Jónsson et al. 2013; Allentoft et al. 2012).

A chemical process characteristic of aDNA is the post-mortem modification of cytosine (C) to thymine (T) and guanine (G) to adenine (A) within the DNA sequence. In particular, the substitution of cytosine by thymine is caused by cytosine deamination, in which the amino group of the nitrogenous base is hydrolysed, resulting in the formation of uracil (U) (Lindahl 1993). However, uracil is not available during DNA amplification and sequencing reactions and is therefore read as thymine (Hofreiter et al. 2001). Consequently, the substitution of guanine with adenine is more frequently observed during library preparation and DNA synthesis (Fogg et al. 2002). Similar to fragmentation, these characteristic base substitutions can serve as indicators of ancient DNA authenticity: they occur predominantly at the ends of DNA fragments, allowing ancient molecules to be distinguished from modern ones.

2.1.3 Advances in aDNA studies

The challenges discussed in the previous paragraph led to the development of dedicated laboratory protocols to maximise DNA extraction while minimising contamination risk with modern DNA.

2.1.3.1 Selection of samples for aDNA extraction

Another key factor to consider, particularly in light of the characteristics described above, is selecting the most suitable sample for DNA extraction. The petrous part of the temporal bone (*pars petrosa*) has been singled out for retaining a high degree of endogenous DNA preservation (Gamba et al. 2014). Specifically, the cochlea represents the most optimal region for obtaining high yields (Pinhasi et al. 2019). In recent years, it has also been shown that the three auditory ossicles (malleus, incus, and stapes) serve as excellent sources of human DNA (Sirak et al. 2020). Unfortunately, due to their very small size, they are frequently lost during archaeological excavations.

However, one limitation of using the *pars petrosa* is that it is challenging to obtain material suitable for metagenomic studies, as the pathogens found there are significantly fewer than those retrievable from teeth (Sikora et al. 2025). The *pars petrosa* of the temporal bone is the hardest structure in the human body and is composed of highly compact bone tissue, which is characterised by a relatively

low blood supply. In contrast, teeth possess an extensive vascular network and are therefore more directly exposed to blood-borne pathogens that can be recovered from the dentine (Margaryan et al. 2018)(Bos et al. 2011; Margaryan et al. 2018) (Margaryan et al. 2018). Teeth are also considered an excellent source of aDNA, as they are particularly well protected from environmental degradation (Alvarez García et al. 1996; Schwarz et al. 2009). Several studies have shown that root cementum preserves high levels of DNA (Adler et al. 2011; Damgaard et al. 2015). A comparison between different skeletal sources for aDNA extraction has shown that the *pars petrosa* consistently yields the highest amounts of endogenous material, whereas cancellous tissue should generally be avoided. Nonetheless, it has also been demonstrated that the use of alternative skeletal elements is promising. Cortical bone from the vertebral body, as well as the junction between the lamellae and the spinous process, yields high average proportions of human DNA, as do the talus and the distal phalanx. This makes these anatomical elements ideal substitutes from which reliable results can be obtained when *pars petrosa* or teeth are unavailable (Parker et al. 2020).

2.1.3.2 Laboratory methods for aDNA

In addition to selecting an appropriate source for DNA extraction, a proper workspace and efficient laboratory protocols are also essential. The extraction of aDNA must be carried out in dedicated clean laboratory facilities to minimise contamination risk. Moreover, it is crucial to consider the historical and cultural significance of the samples being analysed. For this reason, minimally destructive sampling strategies have been proposed to maximise the preservation of archaeological remains (Sirak et al. 2017; Harney et al. 2021).

Over time, protocols have been optimised and adapted at each experimental step to accommodate different sample types and preservation states. In particular, improvements in DNA extraction and genomic library construction strategies for recovering short fragments have been proven crucial for the successful characterisation of DNA from samples with extensive molecular degradation. Subsequently, customised adjustments to the protocols have been adopted by different laboratories to reduce contaminations and increase the availability of targeted aDNA (Pinhasi et al. 2015; Margaryan et al. 2018; Rohland et al. 2018). One example is the Institute of Genomics at the University of Tartu, which applies publicly available protocols that are continuously updated and adapted to ancient DNA research (Dabney et al. 2013; Scheib et al. 2018; Keller & L Scheib 2021).

The final laboratory step consists of library preparation for NGS. Two main approaches are available: single- (ss) and double-stranded (ds) library preparation. In the ds-method, DNA molecules undergo end-repair and are ligated to ds adapters (Meyer & Kircher 2010; Kircher et al. 2012), whereas in ss-library preparation, the aDNA templates are heat-denatured and adapters are ligated as ss-molecules (Gansauge & Meyer 2013; Gansauge et al. 2020). In both cases, a short unique identifying sequence (index) is incorporated into the adapters to

ensure sample traceability. Moreover, indexing allows multiple samples to be pooled together and reduces the risk of cross-contamination.

2.1.4. Modern applications of ancient DNA

With the advent of NGS technologies, DNA has been extracted and analysed not only from skeletal remains but also from other sample sources (Figure 1). This has substantially expanded the amount of available information and enabled a more detailed investigation of human population history.

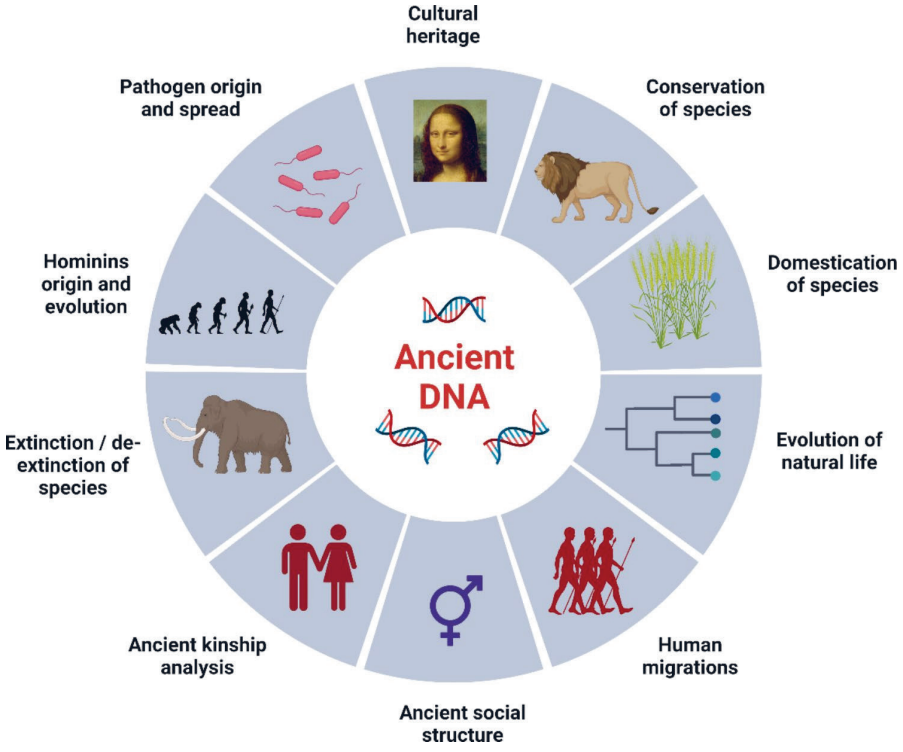

Figure 2. Possible areas of ancient DNA method implementation for anthropological and paleobiological material. Figure reprinted with permission from Figure 1 (Chen & Nedoluzhko 2023), Springer Nature.

2.1.4.1 Sediment DNA

Sedimentary ancient DNA (sedaDNA) refers to genetic material preserved in environmental substrates such as soil, sediments, or ice, enabling the detection of hominin groups at sites and in areas where no skeletal remains are found. It originates from a wide range of organisms, including plants, animals, and micro-organisms, and can be used to reconstruct past ecosystems, biodiversity, and environmental changes. As such, sedaDNA provides a powerful tool for investigating species presence, population turnover, and ecological dynamics through

time. The first studies on DNA extracted from sediments date back to 2003 (Willerslev et al. 2003). Sedimentary DNA fragments containing taxonomic information were amplified using PCR and subsequently analysed, with the aim of investigating changes in flora and fauna. More recently, the field of ancient sedimentary DNA has expanded considerably and is now frequently applied in interdisciplinary studies. In 2017, a study analysed 85 cave sediment samples from seven different archaeological sites, demonstrating that mitochondrial DNA can be efficiently retrieved from cave sediments, thereby enabling the detection of hominin presence at specific sites (Slon et al. 2017). Subsequent work successfully extracted and analysed nuclear DNA from sediments, allowing more detailed investigations into Neanderthal population history. These advances enabled the identification of population turnover approximately 100,000 years ago at a site in Spain (Vernot et al. 2021).

2.1.4.2 Dental calculus

Dental calculus is a mineralised form of dental plaque that forms on the surface of teeth during life and persists in the archaeological record. Diverse microremains and biomolecules, including DNA, protein, and metabolites, are preserved within it. Interest in the study of dental calculus as a source of information for reconstructing past diets began to gain traction in the 1990s, when the first work dedicated entirely to this material appeared (Arensburg 1996). Early investigations relied primarily on microscopy (Hardy et al. 2009), which allowed the identification of microremains but offered limited insight into broader biological patterns. These early studies highlighted the remarkable potential of calculus as a reservoir of microremains, offering insights into the dietary habits of past populations, like Neanderthals (Henry et al. 2011).

Subsequently, the introduction of metagenomic approaches expanded the field. Scientists began extracting both DNA and proteins from dental calculus, opening new ways for investigating its biological and ecological complexity. The study of commensal microbes has provided important insights into two of the most significant dietary shifts in human history: the adoption of carbohydrate-rich Neolithic farming diets and the more recent advent of industrially processed flour and sugar (Adler et al. 2013). Other studies have provided direct evidence of past diets, as demonstrated by dental calculus analyses of five Neanderthal individuals, which enabled the reconstruction of regional differences in Neanderthal ecology (Weyrich et al. 2017). In addition, the human oral microbiome has long served as a reservoir for a wide range of opportunistic pathogens implicated in both local and systemic diseases (Warinner et al. 2014). Because dental calculus forms incrementally, layer by layer (Jin & Yip 2002), it provides information not only from the period immediately preceding an individual's death but also from earlier life stages. This multi-temporal nature has made it a valuable archive for understanding long-term biological processes, such as the effects of sustained tobacco consumption on individual health (Velsko et al. 2022).

More recently, the field has benefited from the creation and implementation of large-scale reference datasets, which have substantially increased comparative power and analytical resolution. Among these, the extensive archaeological dental calculus dataset, published by (Standeven et al. 2025)), represents a major milestone, providing a robust framework for interpreting biomolecular signals across time and space. Overall, dental calculus represents a uniquely rich and temporally resolved archive for the study of past human biology and behaviour.

2.1.4.3 Pathogens

The 1990s marked the beginning of the first systematic attempts to investigate ancient pathogens. Early research relied primarily on traditional paleopathological methods, focusing on the morphological examination of skeletal remains and mummified tissues. These approaches allowed researchers to identify macroscopic signs of disease but offered limited resolution regarding the specific pathogens involved. Shortly thereafter, the introduction of PCR-based techniques marked a major methodological shift in the identification of specific pathogens, including those causing skeletal lesions, like tuberculosis (Salo et al. 1994). These approaches eventually led to the reconstruction of the first historical pathogen genome, the 1918 influenza virus (Taubenberger et al. 2005). More recently, capture-based approaches enabled the selective enrichment of highly degraded pathogenic DNA, facilitating the reconstruction of complete pathogen genomes, such as *Yersinia pestis*, the causative agent of plague (Bos et al. 2011). As a result, research on ancient pathogens offers a powerful framework for reconstructing the origins, spread, and long-term evolution of pandemic-causing human pathogens, as well as for investigating host–pathogen interactions over deep time. In particular, aDNA studies allow the assessment of pathogen-driven selective pressures on the human genome (Kerner et al. 2021) and the exploration of patterns of resistance and susceptibility to infection across different periods (Blevins et al. 2026).

Bacterial pathogens have been the subject of extensive research, with particular emphasis on their transmission between vectors and host organisms. One of the primary drivers of infectious disease transmission is zoonotic jumps, in which an agent crosses from an animal reservoir to a human host. This process has been investigated across a wide range of infections. An example is *Yersinia pestis*, whose evolutionary history is exceptionally well documented. Genetic evidence indicates that plague was already widespread during the Late Neolithic period (Spyrou et al. 2018; Rascovan et al. 2019; Susat et al. 2024), coinciding with the emergence of permanent settlements and the domestication of animals. *Mycobacterium leprae*, the bacterium that causes leprosy, has been isolated from both medieval human and red squirrel remains, with all analysed genomes belonging to the same lineage, suggesting interspecies transmission (Urban et al. 2024). Other pathogens, by contrast, appear to have spread primarily through human mobility and colonisation. An illustrative case is tuberculosis: although the disease was already present in the Americas as *Mycobacterium pinnipedii*, this lineage was

later replaced by another following European colonisation (Bos et al. 2014; Torres Ortiz et al. 2021).

Viruses have also been the subject of extensive research. However, their study is particularly challenging, as they lack conserved genomic regions—such as the bacterial 16S region—that facilitate taxonomic identification. In addition, viral detection is often hindered by poor preservation and tissue-specific tropism, especially when the target tissues are unavailable for sampling. Nevertheless, recent technological advances have enabled large-scale screening of numerous ancient samples and the development of extensive reference databases, substantially improving our ability to investigate viral diversity and evolution in ancient contexts (de-Dios et al. 2023). An illustrative example is herpes simplex virus 1 (HSV-1), which currently infects approximately two-thirds of the global population, typically from early childhood. This virus has also been identified in four individuals from archaeological sites across northern Europe, spanning the last 2,000 years. Ancient HSV-1 genomes show no major structural or functional differences compared to modern strains; however, they indicate that present-day HSV-1 diversity results from relatively recent lineage replacement events during the Late Neolithic and Bronze Age, rather than long-term virus–host codivergence (Guellil et al. 2022). Another interesting example is the variola virus (VARV), the causative agent of smallpox. It is one of the most lethal human pathogens known and the only human virus to have been completely eradicated through vaccination. The study of its evolution relies on a combination of historical sources, museum specimens, and aDNA data, as the virus is now extinct in nature. Early genomic analyses of historical VARV strains initially suggested a relatively recent origin of viral diversity, with a common ancestor dating to the 16th or 17th century, likely associated with a bottleneck. A major shift in this view emerged with the application of metagenomics to ancient human remains from Viking Age Europeans (600-1050 CE), enabling the identification of VARV in Europe. These genomes belong to a distinct ancient clade that is not directly ancestral to historical and modern smallpox strains. Phylogenetic analyses indicate that multiple VARV lineages coexisted in the past, sharing a common ancestor approximately 1,700 years ago, highlighting processes of lineage extinction and replacement over time (de-Dios et al. 2023).

While the study of ancient DNA pathogens has advanced over time, there are many limitations in ancient RNA research. It degrades very rapidly, and relatively little work has been done on its preservation and degradation from ancient samples (Duchêne et al. 2020).

2.1.5. Principal methods and statistical tools in aDNA population genetic research

Several approaches have been developed over time to investigate population structure, individual ancestry, and the relationships between ancient and modern individuals. Among these, allele-frequency-based methods are widely used to characterise genetic differences across populations. One of the most commonly applied techniques is principal component analysis (PCA) (Patterson & Alkes n.d.; Novembre et al. 2008), which is based on a covariance matrix. The resulting principal components—or eigenvectors—represent axes of maximal genetic variance, allowing individuals to be grouped into clusters that reflect broad patterns of population structure. An alternative clustering method, ADMIXTURE (Alexander et al. 2009), partitions individuals into ancestries based on genotype frequencies. These groupings serve as a foundation for subsequent, more targeted analyses, such as f4-statistics (Patterson et al. 2012), which consist of formal tests of shared genetic drift between populations and can detect signatures of admixture by evaluating allele-frequency correlations across four groups.

Another class of methods are the haplotype-based ones, which analyse shared chromosomal segments inherited from common ancestors, providing high temporal resolution and enabling the detection of recent gene flow and demographic events that are often invisible to allele-frequency-based approaches. Among these, the analysis of long identical-by-descent (IBD) segments has gained particular importance, as it can reveal fine-scale demographic processes such as regional mating patterns (Ralph & Coop 2013). IBD analyses typically focus on segments ≥7 centimorgan (cM); however, informative signals can also be obtained from shorter segments (>5 cM). In this context, such segments are referred to as long shared allelic intervals (LSAI) and can be especially informative for resolving complex demographic scenarios involving recent population splits. From the LSAI, it is possible to calculate the probability of individual connectedness (PiC) score. It summarises the proportion of individuals within a given group that share detectable genomic segments with a focal individual, thereby providing a population-level measure of recent genetic connectedness (Kivisild et al. 2021). More recently, genotype imputation has also gained considerable prominence in aDNA studies (Martiniano et al. 2017; Antonio et al. 2019; Sousa da Mota et al. 2023). Imputation methods infer missing genotypes in low-coverage ancient DNA by using haplotype information from high-quality reference panels, thereby increasing marker density and improving the resolution of downstream population-genetic analyses. Several imputation tools have been developed and systematically evaluated in recent years (Ausmees et al. 2022; Çubukcu & Kılınç 2024; Davies et al. 2021), and they have been successfully applied in several studies. Among these, QUILT 2 stands out for its strong performance even when applied to very low-coverage genomes, with reliable results reported at coverage levels as low as ~0.1× (Li et al. 2025).

The investigation of a population's social organisation can be greatly informed by methods for detecting kinship relationships. Archaeological evidence—such

as burial practices and spatial organisation—can already provide preliminary insights into interpersonal relationships within past communities, while genetic analyses enable a more refined reconstruction of kinship patterns. Recently, a comparative study assessed the performance and robustness of several software tools for kinship inference (Lefeuvre et al. 2026). Among these is READv2 (Relationship Estimation from Ancient DNA, version 2; (Alaçamlı et al. 2024)), an allele-sharing–based method that estimates genetic relatedness by quantifying the proportion of mismatching SNPs between pairs of individuals and subsequently normalising this mismatch rate. According to the authors, READv2 is a robust and reliable approach that can detect kinship relationships even in low-coverage ancient DNA data. Although its performance depends strongly on the availability and quality of samples, it has been effectively applied to reconstruct genealogical connections within archaeological groups with reported effectiveness at coverage levels as low as ~0.04×. Additional information on maternal and paternal lineages is provided by uniparentally inherited mitochondrial DNA (mtDNA) and the Y chromosome (chrY), which trace inheritance through the maternal and paternal lines, respectively.

Table 1: Main methods used in the thesis

Allele-frequency-based methods		
Category	**Method**	**References**
Detecting population structure and ancestry proportions	Principal component analyses (PCA)	(Patterson & Alkes n.d.; Novembre et al. 2008)
	ADMIXTURE	(Alexander et al. 2009)
Inferring population splits and mixture	f4-statistics	(Patterson et al. 2012)
Haplotype-based methods		
Detecting population structure and ancestry proportions	Identity-by-descent (IBD)	(Ralph & Coop 2013)
	Long shared allelic intervals (LSAI)	(Kivisild et al. 2021)
	individual connectedness (PiC) score	(Kivisild et al. 2021)
Kinship analysis		
	READv2 (Relationship Estimation from Ancient DNA, version 2)	(Alaçamlı et al. 2024)

2.2 The demographic history of Europe from an archaeogenomics perspective

Genetic studies have shown that present-day European populations derive from admixture among three major ancestral components: Mesolithic hunter–gatherer, Anatolian Neolithic farmers, and steppe-related groups (Haak et al. 2015; Skoglund & Mathieson 2018). After the early Neolithic and Bronze Age periods, the genetic composition of populations across parts of Europe had already become similar to that of modern-day groups in those regions (Gretzinger & Schiffels 2022). In contrast, subsequent periods are characterised by increasingly complex social and political transformations, which played a central role in shaping population dynamics. The details of each period are discussed below.

2.2.1 Genetic and demographic processes in prehistoric Europe

Around 45,000 years ago, anatomically modern humans appeared in what is now Europe (Benazzi et al. 2011; Fu et al. 2014; Hublin et al. 2020). Genetic evidence indicates that they all carried a small amount of Neanderthal admixture. Signals of additional introgression have been identified in individuals from Bacho Kiro (Bulgaria, 47,000–43,999 years) and Oase 1 (Romania, 41,716–37,656 years) (Hajdinjak et al. 2021; Fu et al. 2015). In contrast, other individuals from the same period, such as Zlatý kůň (Czechia, ≥45,000 years) and Ust'-Ishim (Russia, 47,556–42,636 years), do not exhibit significantly higher levels of Neanderthal ancestry than later populations of Europe (Fu et al. 2014; Prüfer et al. 2021), suggesting heterogeneous interactions between Neanderthals and early modern humans during the initial phases of their expansion across Eurasia. Notably, however, none of these pre-40,000 years ago individuals appears to have contributed substantially to the genetic makeup of present-day Eurasian populations (Posth et al. 2023). Around 33,000 years ago, the Palaeolithic Hunter-Gatherers had to cope with ongoing environmental deterioration. Summer insolation in northern latitudes began to decline, coinciding with the onset of glaciation processes that culminated in the peak ice sheets of the Last Glacial Maximum (25,000–19,000 years ago, LGM) (Maier & Zimmermann 2017). At that time, the region was predominantly cold and inhospitable, so humans living in this environment had settlements restricted to specific refuge areas, located in southern latitudes.

Around 14,000 years ago, during the Mesolithic period, two main hunter-gatherer groups were predominant across Europe: Western Hunter-Gatherers (WHG) and Eastern Hunter-Gatherers (EHG). The WHG group displayed genetic regional variability, whereas the EHG group showed additional admixture with a Siberian source (Allentoft et al. 2024). Different studies have identified a third group, the Scandinavian hunter-gatherer (SHG), who are an admixed group between WHG and EHG (Haak et al. 2015; Mittnik et al. 2018; Günther et al. 2018).

Approximately 7,500 years ago, a new type of ancestry related to the Neolithic of northwest Anatolia (Mathieson et al. 2015; Omrak et al. 2016) and to early

farming populations of the Levant and northern Iran (Broushaki et al. 2016; Lazaridis et al. 2016) started to expand rapidly throughout Europe. Its appearance was closely linked in time and space to the adoption of an agricultural lifestyle, and it is now clear that this major transition was, at least in part, driven by migration. However, the Anatolian Neolithic migrants did not completely replace the hunter–gatherer populations. Over the next 4,000 years, the two populations merged, and by 4,500 years ago, almost all European populations were mixed between both Mesolithic hunter-gatherers and the Anatolian Neolithic (Skoglund & Mathieson 2018).

The next substantial change occurred approximately 5,000 years ago and is closely related to the arrival of individuals associated with the Yamna culture from the Eurasian steppe. Yamna ancestry (that is, 'steppe' ancestry) has been characterised as a mix between EHG and Caucasus hunter-gatherer (CHG) ancestries, formed in a hypothetical admixture between a 'northern' steppe source and a 'southern' Caucasus (Lazaridis et al. 2022). By 3000 years ago, in a period known as the Bronze Age, Yamna ancestry had become widespread across Europe through large-scale migrations. One of the most notable genetic shifts during this transition is the marked increase in chrY haplogroups R1a and R1b, which today represent some of the most common paternal lineages in Europe (Haak et al. 2015) (Figure 2). Alongside these genetic transformations, the Bronze Age was also characterised by profound cultural changes. This period is associated with a new concept of family, property, and personhood, accompanied by the emergence of long-distance trade networks and increased human mobility. It was further marked by a shift in funerary practices, with cremation becoming the predominant burial rite in many regions of Europe (Harding 2000).

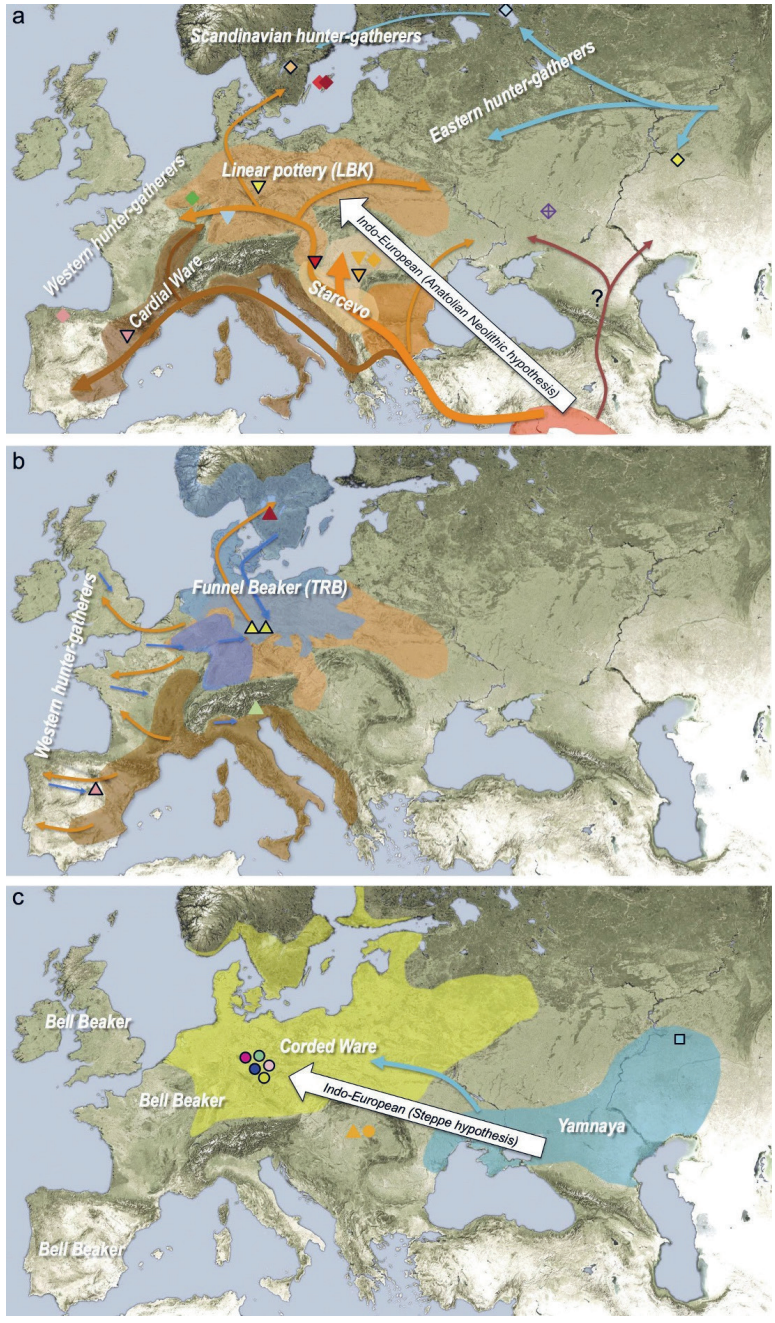

Figure 3. Geographic distribution of archaeological cultures and graphic illustration of proposed population movements/turnovers discussed in the main text.
a. Proposed routes of migration by Early farmers into Europe, 9,000–27000 years ago. **b.** Resurgence of hunter-gatherer-related ancestry during the Middle Neolithic, 7,000–25,000 years ago. **c.** Arrival of Steppe-related ancestry in central Europe during the Late Neolithic, 4,500 years ago. White arrows indicate the two possible scenarios of the arrival of Indo-European language groups.
Figure reprinted with permission from Extended data figure 4 (Haak et al. 2015), Springer Nature.

2.2.2 Genetic and demographic processes in historic Europe

The fundamental distinction between prehistory and history lies in the availability of written sources: while prehistory is reconstructed primarily through archaeological and biological evidence, history is characterised by the emergence of written records.

2.2.2.1 The Iron Age

The Iron Age in Europe began approximately 1200 years BC and saw the development of major ancient civilisations in southern Europe, such as the Greeks and Romans. Written sources from this period also provide the first references to populations that would later play significant roles in European history, including the Celts, Gauls, Sarmatians, and Germanic groups. In regions such as France, the Netherlands, and Britain, which were not yet under Roman rule, seafaring began to develop, and the sea shifted from being a barrier to becoming a unifying element. In present-day Belgium, sandy settlements were located along the northern and southern parts of the Rhine River. These settlements were characterised by dispersed farmsteads that regularly shifted location (Haselgrove et al. 2023). In the Baltic region, in Eastern Europe, however, the cultural landscape differed markedly. Here, populations were predominantly organised into small, mainly agrarian villages, reflecting a distinct settlement structure and socioeconomic organisation (Lang 2007).

From a genetic perspective, the Iron Age broadly in Europe is characterised by substantial mobility and high levels of diversity, suggesting relatively stable population structures despite increased movement (Antonio et al. 2024), as shown for regions such as Viking Age Scandinavia (Rodríguez-Varela et al. 2023) and Iron Age England (Schiffels et al. 2016). Evidence points to a southward and/or eastward expansion of individuals who likely spoke Germanic languages and carried Scandinavian-related ancestry during the late Iron Age. These processes may have originated in north-central Europe and may be consistent with the attraction of greater wealth among Rome's immediate neighbours, which may have played a major role in driving migration dynamics within communities living beyond the Roman frontier. In later periods, patterns of gene flow appear to have shifted northwards, with the spread of Iron Age Central Europe–related ancestry into Scandinavia (Speidel et al. 2025). In the eastern Baltic, aDNA evidence indicates the appearance of a minor Siberian-related ancestry component during the Iron Age, which has also been associated with the arrival of Finnic languages in the area. This genetic input is limited in scale but persisted through time, becoming a stable element of the local population (Tambets et al. 2018; Saag et al. 2019; Kivisild et al. 2021).

2.2.2.2 The Medieval time

Conventionally, the beginning of the Middle Ages in most of Europe is dated to 476 CE, marked by the fall of the Western Roman Empire. This event initiated the emergence of a series of polities ruled by so-called barbarian kings, signalling a shift from a Mediterranean-centred imperial system to a mosaic of kingdoms that would ultimately lay the foundations for modern European states.

By the early sixth century, Italy was under Ostrogothic control; the Alemanni, Bavarians, and Frisians shared territory corresponding to present-day Germany, and France was divided between the Burgundians and Visigoths, the latter also ruling Spain. Part of France, as well as present-day Belgium, was inhabited by the Frankish population, ruled by the Merovingian kings (Wood 2016).

Because the conventional beginning of the Middle Ages is closely linked to the collapse of Roman authority, its application to regions beyond the Roman frontier, such as Scandinavia and the eastern Baltic, is less straightforward. In these areas, medieval periodization is often tied instead to Christianization, state formation, and the appearance of written sources. Until that time, the region corresponding to present-day Estonia was inhabited by rural communities, which gradually developed into small, more permanent settlements (Lang 2007).

2.2.2.3 The Merovingian era

Gallia (Gaul) was a vast region of west-central Europe inhabited by Celtic tribes (Gauls), extending from the Pyrenees to the Rhine, the Alps, and the Atlantic Ocean. Conquered and annexed to the Roman Empire between 59 and 50 BCE, the region subsequently came under prolonged Roman control. From a genetic perspective, the Gaul population, as well as those who followed, is difficult to study due to their widespread practice of cremating the dead. However, a study showed that Iron Age Gaulish populations exhibit strong genetic continuity with the communities of the preceding Bronze Age, indicating that no major migrations or population replacements occurred during this transition. Rather than being shaped by significant external influxes, Gaulish groups appear to have developed predominantly from long-established local populations, with the cultural transformations observed during the Iron Age reflecting internal dynamics and gradual evolution instead of demographic disruptions (Fischer et al. 2022).

In 476 CE, the Roman *Gallia* (Gaul) region essentially covered what is now France, Belgium, Germany (west of the Rhine) and most of Switzerland. After the fall of the Roman Empire, the Franks (an alliance of several groups settled along the left bank of the Lower Rhine) sought to take control of the region. Their consolidation of power culminated in 451 CE under the leadership of Merovech, whose name later gave rise to the ruling Merovingian dynasty (Saint Bishop of Tours Gregory 2022; Raffensperger & Curta 2025).

During the Merovingian era, the internal economy flourished, largely due to the development of agriculture. However, there is evidence that, in its coastal areas, the Merovingian kingdom also maintained commercial relations with other

cities located along the North Sea coast (Raffensperger & Curta 2025). Initially driven by trade, these contacts gradually fostered cultural influence across these areas, as reflected in material culture and settlement organisation. The region of Flanders, today within modern Belgium, played a particularly active role in trade networks across the North Sea. This is evidenced by archaeological findings of imported goods, shared building traditions, and settlement patterns comparable to those of other coastal regions. England, especially its southern regions, was likewise strongly influenced by exchange networks in the North Sea zone (Deckers & Tys 2012).

However, despite the substantial cultural evidence documenting the expansion of the so-called "North Sea culture," relatively little was known until recently about its genetic dimension. (Gretzinger et al. 2022) conducted the first investigation of population movements associated with this period, examining whether trade routes not only facilitated the exchange of goods but also promoted human mobility between ports. Their results indicate that these migrations began earlier than previously assumed, as demonstrated by individuals with continental northern European (CNE) ancestry identified in later Roman contexts, and continued throughout the Middle Anglo-Saxon period. Evidence from Middle Saxon sites such as Sedgeford suggests that the arrival of CNE ancestry may have persisted as late as the eighth century and overlapped with interpersonal mobility from Sweden and other Scandinavian regions during the later Viking expansions and settlements. Taken together, these findings suggest a sustained movement of people across the North Sea into Britain from the late Roman period through the 11th century CE.

2.2.2.4 Diffusion of Christianity

The Medieval period was marked not only by political change, but also by a major cultural transformation that would deeply shape European societies: the spread of Christianity. This was not a single, uniform process, but rather occurred in a fragmented manner and at different times across various regions of Europe. The Merovingian Empire was ruled throughout its existence by Christian kings, under whose authority monks began to disseminate the new faith—initially through itinerant preaching and later by founding monasteries. These monastic foundations often gave rise to small settlements, as at Bobbio in present-day Italy or Stavelot in present-day Belgium (Wood 2016).

The early eighth century witnessed further significant changes in the European political and religious landscape, including the transition from the Merovingian to the Carolingian dynasty and a more systematic consolidation of Christianity. In this context, monastic orders gradually became less itinerant and increasingly settled in permanent monasteries, which played a crucial role throughout the Middle Ages. Abbeys frequently developed into focal points around which pilgrimage centres and small communities emerged, eventually growing into towns (Wickham 2010).

Initially, this phase had only a limited impact on regions such as Germany, where pagan practices persisted, and the spread of Christianity proceeded slowly. The effective conversion of Germany occurred following its incorporation into the Holy Roman Empire, within which adherence to the Roman Church was the only permitted religious framework (Flierman 2019). Over the centuries, through a series of ecclesiastical reforms and religious transformations, the idea of Christianisation became deeply embedded and increasingly perceived as a mission. Within this ideological context, the Teutonic Order was founded in 1198 CE, supported by German nobility, with the explicit aim of spreading Christianity in regions where paganism was still prevalent (Urban 2002).

From a genetic perspective, by this time the composition of populations across most of Europe had already become broadly similar to that of present-day groups inhabiting the same regions (Günther & Jakobsson 2016). The growing population and density during the Middle Ages likely reduced the demographic impact of migration, as incoming groups constituted a progressively smaller proportion of the overall population. As a result, the demographic change was driven primarily by individual and small-scale mobility rather than by large-scale population replacements, with strong regional continuity already established by the early Middle Ages (Gretzinger & Schiffels 2022).

2.2.2.5 Baltic crusades

The Middle Ages were an extremely fragmented period, during which Europe was organised in markedly different ways across regions. In Estonia, for example, until around 1200 CE the population remained largely organised into predominantly local communities, primarily based on fishing, agriculture, and animal husbandry. These were pagan societies in which the sacred was closely connected to the natural world (Lang 2007).

Between the eleventh and twelfth centuries, the political structure began to be reorganised with the introduction of counties (*maakond*), although the most significant transformation occurred around 1200 CE with the onset of the Baltic Crusades. These campaigns were strongly promoted by the Teutonic Order, with the aims of conquering the Baltic territories, spreading Christianity, and expanding its territorial power. The Teutonic Order, composed mainly of German soldiers and nobles, invaded Estonia in 1208 and fully conquered it by 1227 (Selart 2015). From that point onward, Estonia's cultural and political landscape changed profoundly. Pagan cults were prohibited, and the population was forced to convert to Christianity. The previous organisation of small, largely autonomous communities was replaced by a feudal system, marked by the imposition of a German-origin noble and ecclesiastical elite (Selart 2015).

2.2.2.6 Genomic evidence of infectious diseases in Medieval Times

The Middle Ages, in addition to profound changes in Europe's political structure, were marked by recurrent epidemics and high mortality rates. The first major pandemic documented in historical sources is the Justinianic Plague (caused by *Yersinia pestis*), which began in 541 CE and persisted until around 750 CE. Originating in Egypt, it rapidly spread throughout the Mediterranean basin (Adapa et al. 2025).

The second plague pandemic began in the mid-fourteenth century. It likely originated in Asia and expanded swiftly along major trade routes, reaching Europe via the Silk Road. This pandemic is estimated to have caused the death of roughly half of the European population (Raffensperger & Curta 2025). Recent studies of ancient *Y. pestis* DNA from medieval plague victims have provided insights into the early stages of the pandemic. Specifically, mid-14th-century *Y. pestis* genomes reconstructed from France, Spain, England and Sweden were shown to be identical, suggesting the rapid dispersal of a single strain across Europe (Spyrou et al. 2019).

Plague, however, was not the only infectious threat of the medieval period. Leprosy also became widespread across Europe between the twelfth and fourteenth centuries, likely facilitated by poor hygienic conditions, its long incubation period, and close contact with animal reservoirs (Schuenemann et al. 2018).

While information on bacterial diseases is often more available across different historical periods, viruses are generally more difficult to investigate. This is because they rarely leave detectable traces on skeletal remains, often possess RNA genomes that degrade rapidly, and typically occur at low copy numbers in hard tissues. Nevertheless, a study of a Merovingian-period site identified three distinct viruses, demonstrating that viral pathogens were already circulating during the Early Middle Ages. These include Parvovirus B19, hepatitis B virus (HBV), and Variola virus. Parvovirus B19, which is associated with erythema infectiosum and, in severe cases, anaemia and fetal complications, was found to be genetically indistinguishable from other medieval European strains, indicating low genetic diversity at the time. HBV, a blood-borne DNA virus causing acute or chronic liver infection that may lead to liver cirrhosis and hepatocellular carcinoma, shows similarly limited divergence when compared with other viral genomes from the same period. In contrast, Variola virus—the causative agent of smallpox—occupies an intermediate phylogenetic position among early medieval smallpox strains and exhibits substantial genetic heterogeneity within the same period (Bonczarowska et al. 2022).

3. AIMS OF THE STUDY

This thesis examines the period spanning the Early Medieval (675–750 AD) to the Early Modern (1600 AD) era in North and East Europe, focusing on Belgium and Estonia, regions that have so far been understudied from an aDNA perspective. It aims to provide an in-depth investigation of population structure, demographic changes, and individual health during that period. Using NGS, new genome-wide data on ancient individuals and pathogens from archaeological sites in Belgium and Estonia were generated at the Ancient DNA Laboratory of the Institute of Genomics at the University of Tartu and analysed within a broader European context. The specific aim of each study is reported below:

- **REF I:** This study investigates the origins, genetic structure, and kinship of the coastal Late Merovingian site of Koksijde (Belgium). For this reason, we generated 30 whole-genome shotgun sequences from individuals found in the Koksijde archaeological site, alongside 18 remains from two additional Early and Medieval sites in present-day Flanders, Belgium. These data are analysed together with previously published genomes from medieval and modern populations.

- **REF II**: This study examines the genetic and social structure through time, as well as the health status, of the population from the medieval European town of Sint-Truiden (Belgium). To conduct it, 372 genomes have been sequenced and analysed, and subsequently contextualised through comparison with other published ancient individuals from the same period and with relevant modern populations.

- **REF III**: This study aims to reconstruct the first ancient genomes of human betaherpesvirus 6 (HHV-6A and HHV-6B). After screening ~4000 individuals, the virus has been identified in 11 ancient human samples spanning the 8th century BCE to the 14th century CE and subsequently enriched using capture-based approaches. The recovered viral strains have then been analysed to investigate the mechanisms of viral integration into the human genome and to reconstruct genetic patterns of viral spread over time.

- **REF IV**: This work focuses on understanding population dynamics in the territory of Medieval Estonia. For this, we analyse genomic data from 164 individuals across different social classes in society, representing the populations of three medieval towns and rural communities. With this dense local genetic dataset, the aim is to determine whether the known sociocultural changes, such as increased social stratification, elite formation, and urbanisation, are reflected in the biomolecular data (genetic ancestries, pathogen presence, dental calculus metagenomic data, and stable isotope data) of medieval individuals.

4. MATERIALS AND METHODS

For the four publications of the thesis, a dataset combining new genome-wide data (generated in the ancient DNA Laboratory at the Core facilities of the Institute of Genomics, University of Tartu, Estonia) and published data from ancient and present-day individuals was compiled.

The samples of REF I and REF II were collected with permission from the relevant archaeological authorities (City Councils of Koksijde and Sint-Truiden) and handled in accordance with established professional guidelines for the respectful treatment of human remains (https://www.vlaanderen.be/publicaties/ethisch-verantwoord-omgaan-bij-onderzoek-van-menselijk-botmateriaal-in-vlaanderen). Ancient DNA samples of REF IV were obtained through a collaboration with the University of Tartu's archaeologists. The samples were collected in accordance with the Code of Ethics of Estonian archaeologists (https://arheoloogideliit.ee/kasulik-teada/eetikakoodeks/).

The following paragraphs summarise materials and methods used in each publication. Additional information about the experimental and computational methods can be found in the original publications and/or their supplemental materials.

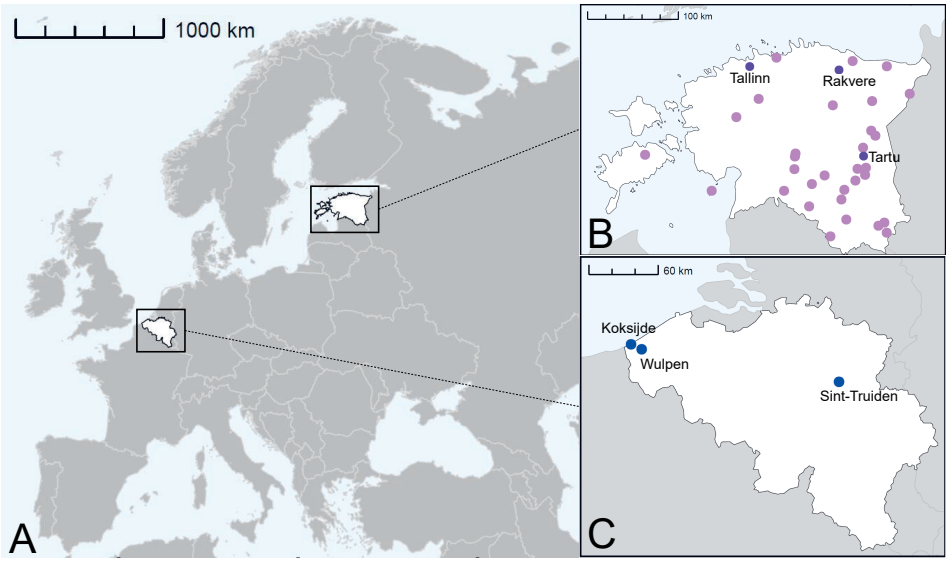

Figure 4. Overview of the newly generated data from Belgium and Estonia. A – Map of Europe. B – Map and archaeological sites of Estonia. C – Map and archaeological sites of Belgium

4.1 Reference I

New genome-wide data were obtained from the remains of 30 individuals from the Early Medieval site of Koksijde, 6 individuals from the Medieval site of Wulpen, and 12 individuals from the Early Medieval site of Sint-Truiden, recovered from the Flanders region of Belgium (Figure 3C, Table 1). Due to poor preservation conditions, DNA was extracted from different sources, including tooth roots, petrous bones, and talus bones, to achieve the highest possible aDNA concentration. After quality control and additional sequencing of the selected library, the genome-wide coverage reached 10.7×.

To explore the genetic ancestry of the individuals, we first imputed the newly generated data using QUILT 1.0.2 (Davies et al. 2021) with the Haplotype Reference Consortium (HRC) reference panels (McCarthy et al. 2016). Then we performed principal component analyses (PCA; (Alexander et al. 2009)), F statistics (Patterson et al. 2012), qpAdm (Patterson et al. 2012), long shared allele intervals (LSAI), probability of individual connectedness (PiC) scores (Kivisild et al. 2021), and UMAP (Uniform Manifold Approximation and Projection, (McInnes et al. 2018) for visualisation on the imputed data. Kinship estimation was inferred with the software READ (Monroy Kuhn et al. 2018), and mtDNA haplogroups were determined using HaploGrep2. Later, the results were checked by looking at all identified polymorphisms and confirming the hgs assignments in PhyloTree mtDNA build 17 (van Oven & Kayser 2009). The chrY haplogroups were determined by assessing the proportion of derived allele calls in a set of primary haplogroups (Karmin et al. 2015) and then were confirmed and specified using pathPhynder (Martiniano et al. 2022). The phenotypes of individuals have been studied using 39 SNPs from the HirisPlex-S (Chaitanya et al. 2018) set to predict eye, hair, and skin colours. As health-related phenotypes, 25 SNPs involved in diet adaptation and metabolism, and 50 involved in immunity response were studied.

4.2 Reference II

DNA was extracted from 404 human remains, dated from the 8th to the 18th century, all originating from the archaeological site of Sint-Truiden, in the Flanders region of Belgium (Figure 3C, Table1). After screening and additional sequencing phases, the newly generated data were imputed using QUILT 1.0.2 (Davies et al. 2021) with the HRC reference panel (McCarthy et al. 2016). To investigate the changes in the population structure during the Middle Ages transition in the Flanders region, PCA (Alexander et al. 2009), Admixture (Alexander et al. 2009), qpAdm (Patterson et al. 2012), and IBD (Seidman et al. 2020) (see methods, REF II) on imputed data were performed. In addition, the genetic relatedness of the ancient individuals was estimated using the software READ (Monroy Kuhn et al. 2018). Phenotypes of the newly generated individuals were studied as in REF I. For this study, individuals were also screened for pathogens to gain insights into the population's health.

4.3 Reference III

In this study, after an initial screening of ~4000 individuals across different population genetic projects, 11 individuals were identified as positive for signals of human betaherpesvirus 6A and 6B (HHBV-6A and HHBV-6B). The libraries were then selected for target enrichment to isolate the viral strains. After sequencing, KrakenUniq (Breitwieser et al. 2018),(Breitwieser et al. 2018) was used for initial metagenomic screening (see methods, REF III). Samples confirmed as HHV-6–positive by KrakenUniq were validated by mapping the reads to HHV-6A and HHV-6B reference genomes and by excluding closely related herpesviruses such as HHV-7. Phylogenetic analyses were performed by reconstructing ancient HHV-6A and HHV-6B consensus genomes, removing recombinant regions, and inferring maximum-likelihood trees together with modern reference genomes, allowing the placement of ancient sequences within known viral integration clades.

4.4 Reference IV

The new genome-wide data were obtained from 164 Medieval individuals recovered from 31 sites across Estonia (Figure 3A, Table 1). At first, the new data were imputed using QUILT 1.0.2 (Davies et al. 2021) and the HRC reference panel (McCarthy et al. 2016). To investigate the ancestry of the individuals and the structure of the Medieval Estonia population, PCA (Alexander et al. 2009), supervised admixture (Alexander et al. 2009), f4 statistics (Patterson et al. 2012), qpADM (Patterson et al. 2012), and LSAI (Kivisild et al. 2021) were performed on the imputed data. The kinship of the individuals was investigated using READ v2 (Alaçamlı et al. 2024). In addition, 116 SNPs related to diet, immunity and pigmentation variants were analysed. The individuals were also screened for pathogens, and dental calculus screening was performed for 23 individuals.

Table 2. Overview of the samples of the thesis.

REF I			
Archaeological site	**Period**	**Date range**	**Individuals**
Koksijde	Late Merovingian	7th–8th centuries	30
Sint-Truiden	Early Medieval	8th–13th centuries	12
Wulpen	High to Late Medieval	11th–14th centuries	6
REF II			
Sint-Truiden	Early Medieval	700–100 CE	87
	High Medieval	1000–1286 CE	207
	Later Medieval	1286–1600 CE	80
	post-medieval	1600+ CE	30
REF III			
Ordona (Italy)		780–540 BCE	1
Ezhol (Russia)		75–220 CE	1
Edix Hill (England)	Medieval	545–640 CE	1
St. Johns (England)	Medieval	1280–1390 CE	1
Sint-Truiden (Belgium)	Medieval	660–1155 CE	4
Valjala (Estonia)	Late Iron Age	1045–1260 CE	1
Karja (Estonia)	Late IA/Medieval	1175–1275 CE	1
Kukruse (Estonia)	Medieval	1300–1400 CE	1
REF IV			
Rural sites	Late IA/Early Modern	12th–17th centuries	107
Rakvere	Medieval	1043–1408 CE	7
Tartu	Medieval/Early modern	13th–17th centuries	39
Tallinn	Medieval/Early modern	1407–1638 CE	10

5. RESULTS AND DISCUSSION

This section provides an overview of how the structure and health status of medieval populations in Belgium and Estonia have been investigated. The transition to the medieval period occurred at different times and under different historical circumstances in the two regions, shaping patterns of population structure, mobility, and genetic diversity. In this thesis, population health was also examined, leading to the identification of pathogens in medieval individuals for the first time. The specific outcomes for each publication are the following:

5.1 Genetic structure, kinship, and health in Merovingian Flanders (REF I)

This study focuses on the Late Merovingian coastal population of Koksijde (675–750 CE), from Flanders, Belgium. During this period, the Merovingian kingdom was a vast polity, characterised by dense trade networks, particularly maritime ones. Archaeological research has identified two distinct cultural groups in the Flanders region: the first, comprising populations living along the coast, is commonly referred to as the "North Sea Culture". These communities, settled along the North Sea coastline, developed extensive trade networks with nearby countries through which they gradually came to share dialects and material culture. The second group consisted of inland river-basin communities, which were culturally more closely aligned with northern France, the Meuse valley, and the Rhineland (Deschepper & De Clercq 2021).

5.1.1 Population structure in Merovingian Flanders

We compared the newly generated genome-wide data from Koksijde sites with new data from the Early and Medieval sites of Sint-Truiden and Wulpen and with previously published ancient and modern reference populations (Fischer et al. 2022; Gretzinger et al. 2022; Sudlow et al. 2015; 1000 Genomes Project Consortium et al. 2015). Both newly analysed sites are located in present-day Belgium; however, Wulpen (dated to the 11th–14th centuries CE) lies in close proximity to Koksijde, whereas the site of Sint-Truiden (8th–13th centuries CE) is situated further inland, in the province of Limburg.

Already from the PCA it is visible that the Koksijde genomes mainly cluster with Early Medieval populations from England, Denmark, and the Netherlands (Gretzinger et al. 2022), as well as with individuals from Wulpen. In addition, the PCA reveals a small cluster of outliers that overlaps with Late Iron Age French Gaul genomes (Fischer et al. 2022), while individuals from Sint-Truiden occupy an intermediate position between the Gauls and Northern European Early Medieval populations (Figure 1, REF I). LSAI-based analyses and PiC scores, visualised through UMAP, further confirm the affinity of the medieval Flemish population with an Early Medieval England one (Gretzinger et al. 2022), distinguishing a

well-integrated core of individuals from the small number of genetically distinct outliers (Figure 2A and 2B, REF I). Also F-statistics and qpADM highlight an increased shared genetic drift of the Koksijde individuals with Early Medieval genomes from England (Gretzinger et al. 2022), whereas the outliers—consistently identified across all analytical frameworks—show a stronger affinity to Late Iron Age individuals from France (Fischer et al. 2022), characterised by minimal North Sea–related ancestry (Supplementary Figures 2–3; Supplementary Table 5; REF I) and likely serving as the proxy for local Gaulish ancestry.

Taken together, our results point to the presence of at least two distinct ancestry components at Koksijde: one closely related to Early Medieval populations of the North Sea zone (the so-called continental North Sea zone ancestry, cNSz), and another more plausibly associated with local Gaulish groups. The fact that most Koksijde individuals cluster with contemporaneous English and Dutch genomes indicates that the spread of North Sea zone ancestry during the Early Medieval period was not confined to the northern coastlines, but also extended to the southern shores of the North Sea.

Although our analyses do not allow us to precisely determine when this North Sea zone ancestry was introduced along the Flemish coast, we demonstrated that by the 7th century, it was present in the majority of Koksijde individuals. Further support for a stepwise integration process comes from comparing Koksijde with the Early Medieval sites in present-day Flanders. At Wulpen, which dates to a later period, differences in ancestry are no longer detectable, and the individuals appear genetically homogeneous and comparable to the present-day regional population, suggesting that, at this stage, the two components were well integrated. In contrast, the inland cemetery of Sint-Truiden shows lower affinity to the North Sea zone cluster, consistent with a different stage in the integration of ancestry components (Figure 2D, REF I).

5.1.2 Kinship of the Koksijde site

To better understand the population's social structure, we investigated kinship relationships among individuals from the Koksijde site. The analysis of chrY and mtDNA revealed high diversity for both (Supplementary tables 1 and 14, REF I). READ identified three pairs of first-degree relatives and one pair of second-degree relatives (Figure 4, REF I). A closer examination of these relationships highlights an interesting case: within a mother–daughter pair (samples KOS034 and KOS035A, Supplementary table 1, REF I), the mother exhibits a predominantly Gaulish genetic component and a terrestrial diet, whereas the daughter shows only a minor Gaulish ancestry component and a marine-based diet (Supplementary table 1, Supplementary figure 4, REF I). This suggests that in the Koksijde site, individuals with different ancestries could be incorporated into the same family unit, implying that integration across ancestry groups could occur within a single generation. This is evidence that social relationships such as marriage and family played a key role in mediating the fusion of populations, contributing to the gradual process of genetic and social integration.

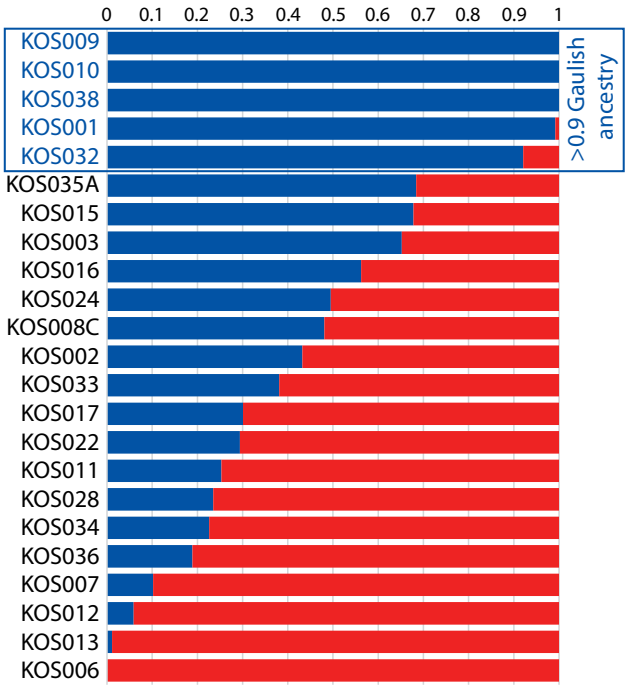

Figure 5. qpAdm-based Gaulish and North Sea zone ancestry estimates in Koksijde burials. Presented Gaulish (blue) and North Sea zone (red) ancestry proportions represent the best fit qpAdm model for each individual tested. Figure Reprinted with permission from figure 3 (REF I), PNAS.

5.1.3 Phenotypes

The analysis of pigmentation- and health-related variants also revealed differences between the two groups with distinct ancestral backgrounds. Ten variants (including two lactase-persistence variants, one associated with leprosy, one with celiac disease risk, and six pigmentation-related variants involved in lighter eyes, hair and skin pigmentation) showed higher frequencies ($P < 0.00001$) in the Early Medieval English, Koksijde, and modern Dutch and Belgian genomes compared to Iron Age France (Supplementary tables 16–18, REF I). In contrast, the outliers identified in the previous analyses displayed allele frequencies more similar to those observed in Iron Age France, consistent with their distinct ancestry profiles. These results suggest that genetic ancestry shifts in the North Sea region were associated with at least some phenotypic consequences.

5.2 Population dynamics and health in the medieval city of Sint-Truiden, Belgium

This study focuses on the Medieval site of Sint-Truiden, in the modern province of Limburg, Belgium. The site, which initially was a settlement called Sarchinum, became a highly popular pilgrimage destination after the 7th century, when Saint Trudo founded an abbey (Boes 1970). By the 12th century, the settlement evolved into a thriving town named after its founder, Sint-Truiden (Charles 1965). The long-term use of the cemetery (from 700 to 1600 CE) provides a unique opportunity to investigate the genetic structure and health of the Sint-Truiden population over time.

5.2.1 Population structure of Sint-Truiden

Most analyses were restricted to 332 individuals sequenced at 0.1x or higher, imputed, and further analysed alongside a selection of published ancient and present-day genomes (Methods, REF II). Our results indicate a change in the population's genetic composition over time. During the Early and High Middle Ages, it appeared more heterogeneous, with individuals distributed across Scandinavian, Dutch, and French clusters. In contrast, during the Late Medieval period, the Sint Truiden individuals became more homogeneous and clustered more tightly in the PCA (Figure 2, REF II) (Figure 5). To investigate their ancestry, we used genomes from Late Iron Age France (Fischer et al. 2022) and Early Medieval Netherlands (Gretzinger et al. 2022) as proxies for Gaulish and Germanic ancestries, respectively. qpADM and admixture show that the Gaulish ancestry is predominant in the population, with only a minimal Germanic contribution, even though inter-individual variance is significantly higher during the Early and High Middle Ages (Figure 3, Supplementary tables 2 and 3, REF II). Our results also show that Sint-Truiden was more genetically differentiated from surrounding regional populations, while genetic distances decreased over time, reflecting increasing regional homogenization (Figure 4, REF II).

What emerges is that Sint-Truiden, after an initially more heterogeneous phase during the Early and High Middle Ages, experienced gene flow that became increasingly local, with fewer long-distance migrants contributing to the gene pool.

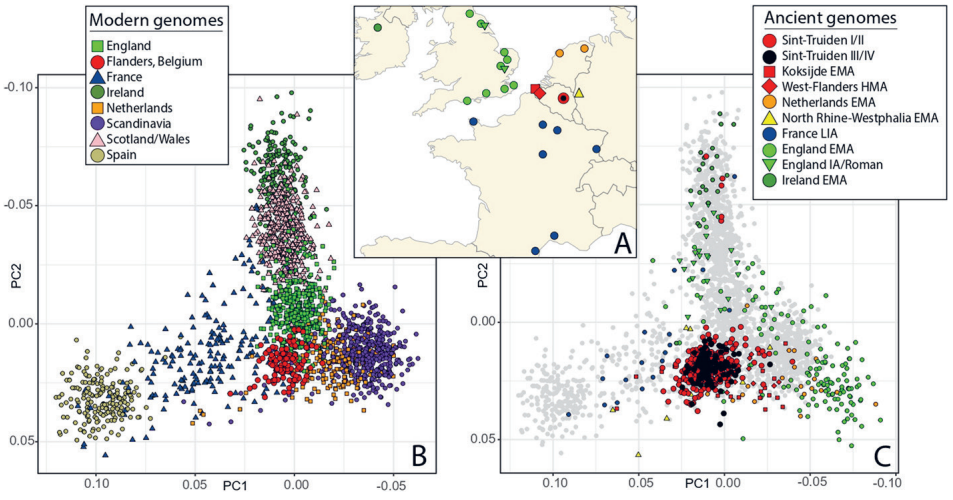

Figure 6. Sampling locations and genetic ancestry of the studied populations. **(A)** A map of the North Sea region with archaeological sites used in data analyses, including genomes from Sint-Truiden (red), and available reference data. PCA of selected modern **(B)** and ancient **(C)** genomes from Europe. Figure reprinted with permission from figure 1 (REF II), Springer Nature.

5.2.2 Genetic outliers of Sint-Truiden

From the PCA (Figure 5), it is also visible the presence of five outliers, which cluster at the top of the medieval and modern Irish and Scottish populations (Gretzinger et al. 2022; Sudlow et al. 2015) (Figure 2, REF II). To test the ancestry of these individuals, we perform f3 statistics, which confirm their origin. The results show that they share more genetic drift with the main group than with Early Medieval Ireland and Viking Age Orkney individuals (Gretzinger et al. 2022) (Supplementary table S4, REF II). These two populations also represent the most suitable proxies for modelling the outlier group under a two-way admixture model. The Sint-Truiden outliers can be modelled as mainly derived from a Scottish/Irish source, with little Germanic contribution and no detectable Gaulish ancestry (Supplementary table S5, REF II). We also estimated the inter-individual sharing of IBD segments, which supports the previous results. The analyses show that the five Sint-Truiden outliers share very little recent genetic ancestry with the main local population, indicating that they were not integrated into local kinship networks. Instead, they display higher levels of IBD sharing with medieval and modern populations from Scotland and Ireland. Moreover, no substantial IBD sharing is detected among the outliers themselves, suggesting that they do not represent a single family group or a coordinated migration event (Figure 5, REF II). Together, these results support the interpretation that the outliers correspond to independent, recent migrants from the British Isles.

5.2.3 Health status of the Sint-Truiden individuals

Individuals from Sint-Truiden were screened for the presence of human-associated microbial pathogens. Ten cases of hepatitis B virus (HBV) were identified, along with five cases of *Yersinia pestis* (Supplementary Figure 11), six cases of *Borrelia recurrentis*, three cases of human betaherpesvirus 6A (HHV-6A), one case of human betaherpesvirus 6B (HHV-6B), two cases of *Leptospira interrogans*, and two cases of herpes simplex virus (HSV-1). These pathogens were widespread during the medieval period, and in particular, *Borrelia* is commonly associated with poor hygiene and unfavourable living conditions. Interestingly, concerning plague, historical sources—although generally detailed—do not report its presence in this region. However, our results show that at least some individuals living in the fourteenth century were infected with *Yersinia pestis and* probably died because of plague.

5.3 Long-term evolution of human betaherpesvirus 6

This study focuses on the Human betaherpesviruses 6A (HHV-6A) and 6B (HHV-6B), which were first found in the 1980s in patients with lymphoproliferative disorders (Salahuddin et al. 1986). They were speculated to have a much longer history within the human population than modern data suggests. We investigated for the first time 11 recovered sequences matching HHV-6 species spanning from the 8th to the 6th BCE to the 14th CE to trace their evolution over 2500 years.

5.3.1 Overview of the virus

Human betaherpesviruses 6A (HHV-6A) and 6B (HHV-6B) are two distinct but closely related large double-stranded DNA viruses restricted to humans. They have been linked to a wide range of conditions, like female infertility, myocarditis and multiple sclerosis. Despite being very closely related, they are epidemiologically and immunologically distinct: HHV-6A is estimated to be phylogenetically older but less prevalent in the human population today, and it infects mostly adults, whereas HHV-6B infects mainly children.

The different ways of viral transmission (acquired infections, noninherited chromosomal integrations, and inherited chromosomal integrations) led to distinct evolutionary dynamics across clades. Although HHV-6B is very common in modern populations, detecting it in historical remains is difficult because it typically persists in a limited number of somatic cells unless it is inherited through the germ line. In the latter case, HHV-6B can be detected in a wider range of body tissues, including hard tissues such as bones and teeth, which are commonly used for ancient DNA extraction.

5.3.2 HHV-6 clades

To avoid misidentification, we mapped all datasets to HHV-6A, HHV-6B, and HHV-7, the phylogenetically closest herpesviruses (supplementary text, REF III). All samples were classified as HHV-6A or HHV-6B, which matched the original Kraken Uniq classification in all cases (Table 1, REF III). For the phylogenetic analyses, we used only the 9 genomes that achieved sufficient depth of coverage to be analysed (Supplementary table 3, REF III). Our results show that the phylogenetic position of all ancient genomes is well supported and clearly nested within known clades that exhibit distinct evolutionary dynamics.

The HHV-6A clades are represented in the European population by the 14th Century at the latest, but they have a much older evolutionary history (Figure 3, REF III). Clade A2 is represented by one English sample, clade A3 by one Belgian genome and clade A4 by four genomes from Estonia and Belgium (Figure 6).

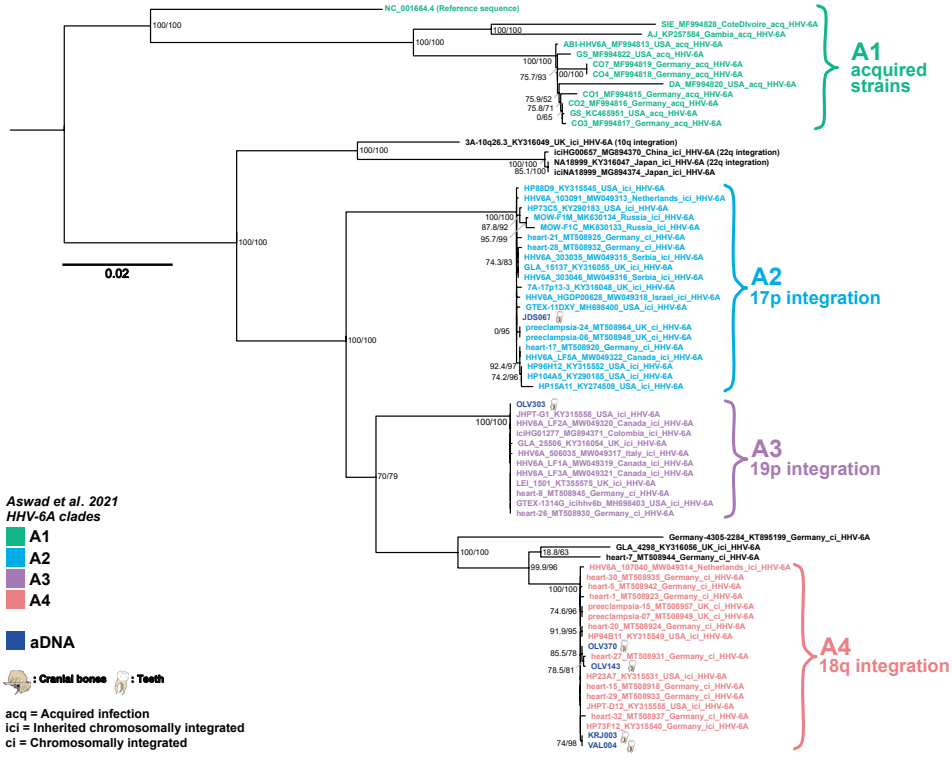

Figure 7. Midpoint-rooted maximum likelihood phylogeny for HHV-6A using 66 modern and 6 ancient genomes. Node labels show SH-aLRT support (%)/ultrafast bootstrap support (%) based on 10,000 replicates each in IQ-Tree2. Tip labels are coloured according to clade groupings, and integration locations are shown as defined in (Aswad et al. 2021). aDNA samples are shown in purple, with illustrations of the types of samples from which the genomes were extracted. Strains are only noted as ici if they are known to be inherited. Figure reprinted with permission from Figure 3 (REF III), Science.

For the HHV-6B phylogeny, our study yielded termini ante quem of the 1st to 6th and 6th to 7th century CE for clade B8 and B5, respectively (Figure 4, REF III).

An exception is OLV225, who cluster with two genomes from the United States with likely European ancestry. This clade is less well supported and more sensitive to pruning.

5.4 Genetic structure and social stratification in medieval Estonia

This study investigates the genetic structure of the medieval Estonian population by analysing individuals from 31 archaeological sites, including 28 rural cemeteries and three urban centres: Tallinn, Tartu, and Rakvere. In Estonia, the medieval period developed later than in many other parts of Europe, with its onset marked by the arrival of the Northern Crusades led by German forces in the 13th century. After conquering the present-day Estonian territory, the Germans initiated the Christianisation of the local population, establishing an ecclesiastical elite in the main urban centres and promoting the spread of the new religion. At the same time, they contributed to the expansion of trade networks, particularly through Estonia's integration into the Hanseatic League (Selart 2015).

5.4.1 Genetic ancestries in the Medieval Estonian populations

To investigate the population structure of medieval Estonia and assess the presence of a ruling elite of non-local origin, genome-wide data from newly generated individuals were analysed alongside selected published ancient and present-day genomes (Veeramah et al. 2018; Margaryan et al. 2020; Haller et al. 2021; Gretzinger et al. 2022; Rodríguez-Varela et al. 2023; Anon n.d.; Milani et al. 2025). The results confirm substantial heterogeneity in the genetic backgrounds of the analysed individuals. The PCA reveals two distinct clusters: a main one in which individuals overlap with present-day Estonians, a smaller cluster closer to modern Central European populations, and a third one comprising three individuals on top of present-day Finns, suggesting the presence of individuals with both local and non-local origin (Figure 1, REF IV). More fine-scale analyses allowed us to investigate the ancestry of the population, showing that the *locals* (individuals with a local ancestry) share genetic drift with Northeastern European and Scandinavian populations (Margaryan et al. 2020; Rodríguez-Varela et al. 2023), while those *non-locals* (with Central-Western European ancestry) show greater allele sharing with Central-Western Europeans and Anglo-Saxons (Gretzinger et al. 2022). We also used qpAdm to assess the genetic origin of the analysed individuals. The results show that the *local* ones share an ancestry profile dominated by a Yamnaya-related steppe component, with additional contributions from Early European farmers (EEF) and Western hunter-gatherers (WHG), and a minor Siberian component. On the contrary, *non-locals* are characterised by higher EEF contributions and little to no detectable

Siberian ancestry, distinguishing them from the local groups and supporting their non-local origin. The three individuals with a North European ancestry profile are characterised by balanced contributions of WHG, Yamna, and EF ancestry, along with a small but consistent Siberian component (Figure 7). Altogether, our results indicate that medieval urban communities were considerably more heterogeneous than rural ones, with local and non-local origins living in the same city. Our results also show that at least some people from Northern Europe migrated into the Baltic and integrated into the local population.

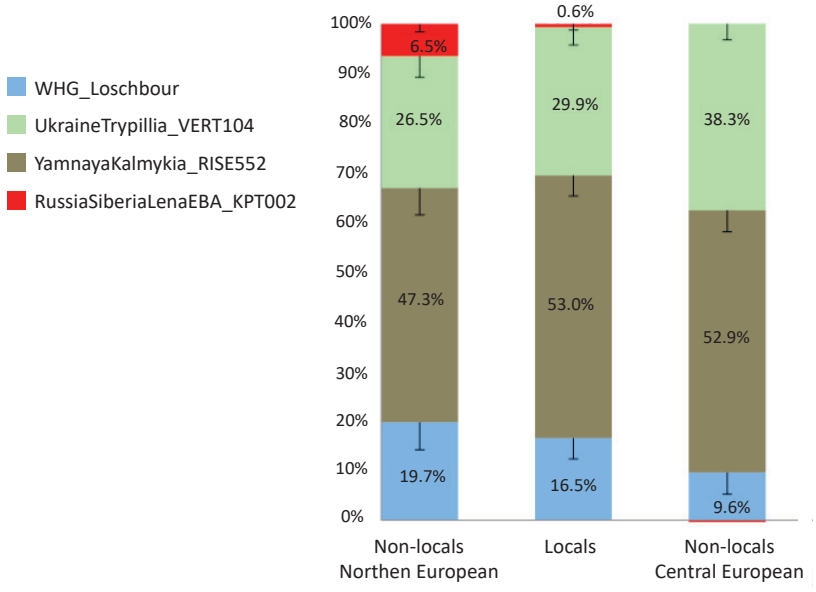

Figure 8. qpAdm results showing ancestry composition of different Estonian medieval genetic groups. Error bars indicate one standard error.

5.4.2 Regional structure across different time periods

The PCA reveals another noteworthy trend among individuals of local origin (Figure 8). Medieval individuals from southern regions cluster more closely with present-day southern Estonians, whereas those from northern regions show greater affinity with present-day northern Estonians (Figure 1, REF IV). This pattern indicates that the current internal geographic structure was already present during the Middle Ages. LSAI analyses and PiC scores further support these findings. PiC scores reveal that rural medieval individuals exhibit greater genetic connectivity with modern populations from the same macro-region (north or south). Specifically, medieval individuals from northern regions display higher PiC scores with present-day northern Estonians and Finns, while medieval individuals from southern regions show higher PiC scores with present-day southern Estonians and a relatively greater affinity with Latvians. Medieval individuals from eastern regions occupy an intermediate position, consistent with the same north–south gradient.

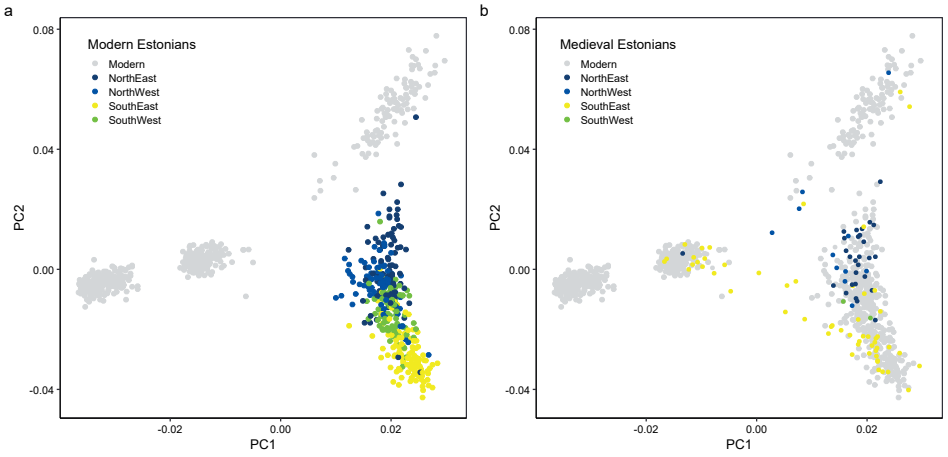

Figure 9. Principal component analyses of modern (A) genomes from Europe and ancient (B) genomes from Medieval Estonia. The panels show how the regional structure has been retained across time.

5.4.3 Health status of Estonian medieval individuals

All individuals included in the study were also screened for common pathogens. Evidence for *Borrelia recurrentis* was detected in several samples. Targeted enrichment was used to increase sequencing coverage and confirm the pathogen's presence in some cases, while other detections remained inconclusive due to low coverage. Additional pathogens identified include *Yersinia pestis* in multiple individuals from different sites, as well as *Staphylococcus aureus*, *Streptococcus pneumoniae*, Human betaherpesvirus 6B, and low-coverage reads matching *Treponema pallidum pallidum*.

Metagenomic analyses of 23 dental calculus samples showed no clear separation by cemetery or social group, although social origin explained a moderate proportion of the observed variance. Two samples exhibited distinct microbial profiles characterised by low species richness and an enrichment of taxa associated with periodontal disease.

6. CONCLUSIONS

The results presented in this thesis demonstrate that ancient genomic data can shed light on complex demographic processes during historical periods. This work aims to investigate the population history of medieval communities from different parts of medieval Europe, specifically in Belgium and Estonia. It shows how the historical processes can unfold differently across regions characterised by distinct genetic and historical backgrounds. In addition, this thesis illustrates how ancient genomic data enable the investigation of population health–related aspects and reveal the presence of so far undetected in ancient material pathogens, as illustrated by the case of human betaherpesvirus 6. In contrast, in case of the absence of extensive datasets, detecting pathogens and reconstructing their evolutionary history remains challenging.

The specific conclusions for each publication are the following:

REF I: The newly generated data of Merovingian-period burials from Koksijde, in present-day Flanders, Belgium, reveal a predominant ancestry component shared with early medieval genomes from England and the Netherlands, together with a smaller contribution likely traceable to earlier Gaulish ancestry. Notably, individuals representing these two ancestry components were buried together, and the identification of a mother–daughter pair provides direct evidence of admixture between them. This suggests that in Koksijde, the individuals were integrated into the community regardless of their different ancestries.

The comparison between Koksijde and the Early and medieval sites of Sint-Truiden and Wulpen shows different stages in the formation of the medieval Flemish population. Koksijde captures a structured stage with coexisting but not yet fully integrated ancestry groups, while Sint-Truiden, which is close in time but more inland, reflects an early phase of heterogeneous admixture and shows lower affinity to the North Sea–related genetic cluster. Wulpen, more closely but later in time, has a genetically homogeneous population in which the different ancestry components are already well integrated.

REF II: Analyses of genetic variation in the Sint-Truiden population across a time transect spanning more than a millennium reveal a progressive homogenisation of two distinct ancestry components during a phase of intensive urbanisation in the Low Countries. During the Early and High Middle Ages, the Sint-Truiden population was genetically more heterogeneous, with a predominance of Gaulish ancestry and a minor presence of Germanic ancestry. Genetic diversity decreased over time, with ancient genomes increasingly resembling those of present-day populations from the surrounding region. This pattern indicates that admixture between Gaulish and Germanic ancestries was a gradual process unfolding over several centuries rather than a single, abrupt event.

The only exception to this predominantly local ancestry profile is a distinct group of five individuals showing genetic affinities with populations from Ireland and Scotland, suggesting a more recent migration.

REF III: This study demonstrates that human betaherpesviruses HHV-6A and HHV-6B have been present in human populations for at least 2500 years, with ancient genomes dating back to the Iron Age. Phylogenetic analyses show that much of the genetic diversity observed today was already established by the medieval period, indicating long-term evolutionary continuity. The results further reveal that chromosomally integrated HHV-6 lineages, particularly HHV-6A, originate from ancient founder events and were already widespread in historical populations, suggesting that such integrations are no longer actively occurring in populations of European ancestry. Moreover, the study highlights distinct evolutionary dynamics between HHV-6A, which displays stable and clearly differentiated integration clades, and HHV-6B, which exhibits more complex evolutionary patterns. Overall, the findings emphasise deep host–virus coevolution and demonstrate the value of ancient DNA in reconstructing the long-term evolutionary history of persistent human viruses.

REF IV: This study shows that the medieval population of Estonia displayed clear differences between urban and rural contexts. In rural communities, most individuals exhibit local genetic origins, whereas urban centres include both locally derived individuals and others with Central-Western European ancestry, likely representing the dominant elite. This interpretation is supported by their burial context – some of these non-local individuals were members of the clergy and were buried in the cathedral.

Our analyses also reveal a regional genetic structure of the medieval population. Individuals of local origin show greater genetic affinity with modern populations from the same county, and more broadly, northern individuals display stronger affinities with modern Finland, while southern individuals are closer to present-day Latvia. This pattern indicates that regional population structure was already established during the medieval period and has been maintained over time.

SUMMARY IN ESTONIAN

Rahvastiku dünaamika ja tervis keskaegses Euroopas: arheogenoomiline vaatenurk

Inimese evolutsioon ja meie liigi ajalugu on pikka aega pakkunud akadeemilist erialadeülest huvi. Arheogeneetika kui teadusvaldkond kujunes välja ligikaudu 45 aastat tagasi ühe eesmärgiga rekonstrueerida inimkonna ajalugu ja rändemustreid vana DNA analüüsi abil. Teise põlvkonna sekveneerimistehnoloogiate kasutuselevõtt ning meetodite arendamine vana DNA eraldamiseks inimjäänustest on võimaldanud lõimida ajaloo, arheoloogia, antropoloogia ja geneetika andmestikke, et paremini mõista inimkonna ajalugu ja demograafilisi muutusi. Samas piiravad vana DNA uuringuid mitmed tegurid: DNA ebaühtlane säilimine erinevates keskkonnatingimustes, huvipakkuvatest piirkondadest pärit proovide vähesus, DNA lagunemine ajas ning uuringute kõrge maksumus. Seetõttu arendavad teadlased järjepidevalt uusi laboratoorseid töövooge ja bioinformaatilisi meetodeid, et suurendada andmehulkasid ning luua teadmisi, mida on võimalik nii teaduskogukonnaga kui ka laiemalt jagada.

Arheogeneetika on oluliselt süvendanud meie arusaamist inimkonna ajaloo peamistest verstapostidest. Euroopas hõlmavad need muuhulgas kütikorilaste populatsioonide saabumist, põllumajanduse ja loomade kodustamise levikut ning esimeste keerukate ühiskondade kujunemist.

Käesolev väitekiri annab esmalt üldise ülevaate arheogeneetikast, käsitledes valdkonna kujunemist, kirjeldades selle peamisi arenguetappe, tuues esile vana DNA uurimisega seotud olulisemad väljakutsed ning võttes kokku eriala viimased arengusuunad. Seejärel keskendub töö tänapäeva Belgia ja Eesti alade demograafilise ajaloo uurimisele keskajal.

Pärast Lääne-Rooma impeeriumi langust 476. aastal pKr toimusid Euroopas ulatuslikud muutused. Tänapäeva Flandria (Belgia) alal tõusis võimule Merovingide kuningriik, mis kujundas piirkonna suhteliselt hajusate asulate võrgustikust tihedamalt seotud ruumiks, eelkõige tänu merenduslikele kaubandusvõrgustikele. Aja jooksul vahetusid võimulolijad ning religiooni roll ühiskonnas kasvas, viies kloostriordude ja kloostrite rajamiseni. Linnade teke kloostrite ümber oli keskaja Euroopas laialt levinud nähtus, peegeldades kristluse kasvavat tähtsust ja levikut. Sint-Truiden kujunes Belgias oluliseks palverännukeskuseks, mis võimaldab uurida, kuidas suurenenud liikuvus ja linnastumine mõjutasid nii populatsiooni struktuuri kui ka tolleaegsete elanike tervist. Laiemas kontekstis käivitati 13. sajandil Euroopas Põhja ristisõjad, mille käigus ristisõdijate väed vallutasid Eesti, tuues piirkonda märkimisväärseid sotsiaalseid ja geneetilisi muutusi. Lisaks uuriti nii Sint-Truideni populatsioonis kui ka keskaegsetes Eesti kogukondades patogeenide—eelkõige inimese beeta-herpesviiruste—esinemist ja evolutsioonilist ajalugu, pakkudes uusi vaatenurki keskaja rahvastiku terviseseisundile. Peamised järeldused on järgmised:

REF I: Belgia keskaja sotsiaalsete ja geneetiliste muutuste paremaks mõistmiseks analüüsisime Põhjamere rannikul Flandrias asuva Koksijde Merovingide perioodi hilisesse etappi kuuluva arheoloogilise leiukoha populatsiooni geneetilist päritolu. Võrdlesime tulemusi piirkondlikult Sint-Truideni ja Wulpeni, mida kasutati pikema aja jooksul, andmetega. Geneetilised analüüsid näitasid, et Merovingide perioodil esines Koksijdesse maetud indiviidide populatsioonis kaks selgelt eristatavat päritolukomponenti. Neist domineeriv pärines varakeskaegselt Inglismaalt ja Madalmaadest, samas kui teine seostus varasema Gallia päritoluga. Seega esindab Koksijde elanikkond etappi, kus need kaks päritolukomponenti eksisteerisid populatsioonis samaaegselt, kuid siiski eristatavalt. Võrdlus Sint-Truideni ja Wulpeni materjaliga näitab seevastu erinevaid etappe keskaegse flaami populatsiooni kujunemisel.

REF II: Sint-Truideni populatsiooni geneetilise struktuuri uurimiseks enam kui tuhande aasta pikkuse perioodi jooksuli analüüsiti kokku 332 indiviidi andmeid. Populatsiooni geneetilise varieeruvuse analüüsid näitasid kahe päritolukomponendi järkjärgulist ühtlustumist intensiivse linnastumise perioodil Madalmaades. Keskaja esimeses pooles oli populatsioon geneetiliselt heterogeensem, domineeris gallia päritolu ning germaani päritolu osakaal oli väiksem. Aja jooksul geneetiline mitmekesisus vähenes ning keskaegsete genoomide sarnasus tänapäeva piirkondlike populatsioonidega suurenes. See viitab asjaolule, et gallia ja germaani päritolu segunemine toimus järk-järgult mitme sajandi vältel, mitte ühe järsu sündmusena. Erandiks sellele valdavalt lokaalsele mustrile oli viiest indiviidist koosnev rühm, mis sarnanes geneetiliselt Iirimaa ja Šotimaa populatsioonidega, viidates ka hilisemale rändele.

REF III: Inimese beeta-herpesviirused HHV-6A ja HHV-6B on kaks omavahel lähedalt suguluses olevat ning peremeesorganismi genoomi integreeruvat viirust, mis nakatavad üksnes inimesi. Neid on seostatud mitmesuguste haigustega, kuid nad erinevad immunoloogiliselt: HHV-6A nakatab peamiselt täiskasvanuid, HHV-6B aga lapsi, põhjustades väikelaste roseooli.

Vana DNA analüüs näitas, et mõlemad viirused on Euroopas esinenud vähemalt 2500 aastat, alates rauaajast, kuid tõenäoliselt väga palju kauem. Viirusegenoomide fülogeneetiline analüüs viitas sellele, et suur osa tänapäeval täheldatavast viiruse geneetilisest mitmekesisusest oli välja kujunenud juba keskajaks, mis osutab pikaajalisele evolutsioonilisele järjepidevusele.

Lisaks näitavad tulemused, et kromosoomidesse integreerunud HHV-6 liinid, eriti HHV-6A, pärinevad iidsetest asutajasündmustest ning olid ajaloolistes populatsioonides juba laialt levinud, viidates sellele, et sellised integratsioonid Euroopa päritolu populatsioonides enam aktiivselt ei toimu.

Samuti ilmnevad selged erinevused viiruste evolutsioonilises dünaamikas: HHV-6A puhul esinevad stabiilsed ja selgelt eristuvad integreerunud klaadid, samas kui HHV-6B puhul on evolutsioonilised mustrid keerukamad. Üldjoontes

rõhutavad tulemused peremehe ja viiruse läbipõimunud evolutsiooni ning kinnitavad vana DNA uuringute olulisust viiruste, aga ka teiste patogeenide evolutsiooni uurimisel.

REF IV: Põhjala ristisõdade (u 1200 pKr) käigus vallutasid Eesti alad ristisõdijate väed, kes kehtestasid uue valitseva eliidi ning asusid kohaliku elanikkonna seas kristlust levitama.

Genoomiandmete analüüs näitab, et keskaegses Eesti populatsioonis esinesid selged erinevused linna ja maapiirkondade elanike vahel. Maapiirkondades on enamik indiviide kohaliku geneetilise päritoluga, samas kui linnakeskustes esineb nii kohaliku päritoluga kui ka Kesk-Lääne-Euroopa päritolu inimesi, kes tõenäoliselt esindasid siinset valitsevat eliiti. Seda tõlgendust toetab ka uuritud indiviidide matuste kontekst – osa mittekohaliku päritoluga keskaegsetest indiviididest oli maetud katedraali ja kuulus vaimulikkonda.

Analüüs tõi esile ka keskaegse populatsiooni peeneteralisema regionaalse geneetilise struktuuri. Kohaliku päritoluga indiviidid on geneetiliselt lähedasemad sama piirkonna tänapäeva populatsioonidele; laiemalt eristub muster, kus põhjaeestlased on suurema geneetilise sarnasusega tänapäeva Soome populatsioonidega, samas kui lõunaeestlased on lähedasemad tänapäeva Läti populatsioonidele. See viitab, et Eesti alade regionaalne geneetiline struktuur oli välja kujunenud juba keskaja alguseks ning on püsinud ajas suhteliselt stabiilsena.

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