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EVE RANNAMÄE

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UNIVERSITY OF TARTU
Press

Institute of History and Archaeology, Faculty of Arts and Humanities, University of Tartu, Estonia

The dissertation is accepted for the commencement of the degree of Doctor of Philosophy (in Archaeology) on September 13th 2016 by the Council of the Institute of History and Archaeology, University of Tartu.

Supervisors: Dr. Heiki Valk, Department of Archaeology, Institute of History and Archaeology, University of Tartu
Dr. Urmas Saarma, Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu
Dr. Lembi Lõugas, Archaeological Research Collection, Tallinn University

Opponent: Prof. PhD Laszló Bartosiewicz, Osteoarchaeological Research Laboratory, Stockholm University, Sweden

Commencement: November 18th 2016 at 16.15, Institute of History and Archaeology, Jakobi st. 2–224, Tartu, Estonia

This research was funded by the Estonian Science Foundation (ETF grants 8525 and 8526), institutional research funding (IUT20-32 and IUT20-7) and targeted funding (SF0130012s08) of the Estonian Ministry of Education and Research, the European Union through the European Regional Development Fund (the Centre of Excellence in Cultural Theory, the Centre of Excellence in Biodiversity Research) and the European Social Fund (Graduate School of Culture Studies and Arts), European Research Council (part of the European Union's Seventh Framework Programme [FP7/2007–2013] under grant agreement no. 263735), the Academy of Finland (FinnARCH-project, project decision no. 128451), Estonian and Polish Academies of Sciences, and the European Social Fund's Doctoral Studies and Internationalisation Programme DoRa and the Kristjan Jaak scholarships that are carried out by Foundation Archimedes. The research was based on finds stored in the archaeological research collections of the universities of Tallinn and Tartu, supported by the Estonian Ministry of Education and Research.

European Union
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ISSN 1736-2733
ISBN 978-9949-77-263-6 (print)
ISBN 978-9949-77-264-3 (pdf)

University of Tartu Press
www.tyk.ee

After all, the wool of a black sheep is just as warm.

Ernest Lehman

ACKNOWLEDGEMENTS

This thesis is the outcome of several years of challenging, yet splendid and inspiring work, for which first and foremost I want to thank my supervisors: Lembi Lõugas for introducing me to the field of zooarchaeology and discussing the background of the history of animal husbandry in Estonia; Urmas Saarma for guiding me in the world of genetics and lab work; and Heiki Valk for helping me to find a way into the exciting topic of the prehistoric societies and the 13th century crusades, and for teaching me to be a true archaeologist during the many unforgettable archaeological excavations.

I would also like to credit the people who have taught me a lot and helped me in so many ways. My sincere gratitude goes to Eha Järv (Estonian University of Life Sciences) for teaching me the basics of animal anatomy and osteology from 2009, when I first started with the assemblage from medieval Viljandi, and for always being willing to help me with any osteological 'mysteries'. Thanks to Eha and the preparation room in the University of Life Sciences I was able to build up a substantial part of the anatomical reference collection at the Department of Archaeology in the University of Tartu, which formed a crucial part of my zooarchaeological work. Eha has also analysed a vast amount of the animal bone assemblages considered in the present research. Thank you, Elisabeth Iregren (Lund University) for teaching me the very basics in analysing the osteological assemblages in spring 2010 during my five months of Master studies in the Lund University, Sweden – I am still guided by the knowledge I gained there. Thank you, Marianna Niemi (University of Helsinki) and Tuula-Marjatta Hamama (Natural Resources Institute Finland) for guiding me in the lab work and introducing me to genetic data analysis during the two months in 2011–2012 that I spent in the Natural Resources Institute Finland (at the time being MTT Agrifood Research Finland). A big thanks goes also to Arvi Haak (Tartu City Museum; Tallinn University) for the years long collaboration on the Viljandi material, and Aleks Pluskowski (University of Reading) for the fruitful collaboration on the topic of the Baltic Crusades. Anneli Ärmpalu-Idvand (MTÜ Kihnu Maalambakasvatajate Selts) is kindly appreciated for all her hard work with breeding and gaining the acknowledged breed status for our only formal native sheep breed in Estonia – the Kihnu native sheep, for welcoming me to her farm, and for discussing the matters of breed status and the traits of the native sheep. I cheerfully compliment my sister Anneli Rannamäe and her family's decision to start breeding the Kihnu sheep, because the visits to those fascinating animals, with a camera in one hand and a piece of bread in the other, gave me the final spark to truly attach to my research topic.

I would like to thank Liina Maldre and Kristi Tasuja (Tallinn University) for helping me to collect the specimens for DNA samples from the Archaeological Research Collection in Tallinn; and colleagues in Europe for providing the samples and contextual information: Rūta Kraukle and Jānis Ciglis (National History Museum of Latvia) in Latvia, Janusz Krzysztof Kozłowski (Jagiellonian

University) and Małgorzata Kaczanowska (Kraków Archaeological Museum) in Poland, Adamantios Sampson (Aegan University Rhodes) in Greece, and Olga Batchura (Zoological Institute of Russian Academy of Sciences), Boris Kharlashov and Tatiana Ershova (Archaeological Centre of Pskov) in Russia. I thank Ain Mäesalu and Andres Tvauri (University of Tartu) for helping with the archaeological contexts and dating of the deposits of some of my samples, Enn Küng (University of Tartu) for the information on Early Modern animal trade in Estonia, and Riina Rammo (University of Tartu) for discussions on medieval wool trade and sheep husbandry. I appreciate the help from Maria Smirnova with Russian, Madis Maasing and Riina Rammo with German, and John C. Mittermeier and John Davison with English texts. A special note of gratitude goes to Filipe Pereira (University of Porto) for his useful comments and edits on the final manuscript of this introductory part of the thesis. I would also like to draw attention to the co-authors and reviewers of my papers, whose contribution, criticism and advice was ever so educative. Last but not least I thank my friends and family who never got tired of my sheep stories, and with the right questions and encouraging words inspired me to aim forward.

This research would have not been possible without the funding of the Estonian Science Foundation (ETF grants 8525 and 8526), institutional research funding (IUT20-32 and IUT20-7) and targeted funding (SF0130012s08) of the Estonian Ministry of Education and Research, the European Union through the European Regional Development Fund (the Centre of Excellence in Cultural Theory, the Centre of Excellence in Biodiversity Research) and the European Social Fund (Graduate School of Culture Studies and Arts), European Research Council (part of the European Union's Seventh Framework Programme [FP7/2007–2013] under grant agreement no. 263735), the Academy of Finland (FinnARCH-project, project decision no. 128451), Estonian and Polish Academies of Sciences, and the European Social Fund's Doctoral Studies and Internationalisation Programme DoRa and the Kristjan Jaak scholarships that are carried out by Foundation Archimedes. The research was based on finds stored in the archaeological research collections of the universities of Tallinn and Tartu, supported by the Estonian Ministry of Education and Research.

In Tartu, September 2016

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Author contribution: conceptualization, methodology, analysis, investigation, writing and visualization of the zooarchaeological material represented on pp. 297–310. Additionally, the author contributed to writing a general introduction and discussion, a general review and editing of the full paper.

II – Rannamäe E. & Valk H. (2013) Some spatial and temporal aspects of animal utilisation in Viljandi, Medieval Livonia. In: A. Pluskowski, A.D. Brown, M. Stančikaitė & L. Daugnora (Eds.) *Archaeologia Baltica* 20. Klaipėda, Klaipėda University, 47–58.

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Author contribution: conceptualization, data collection, methodology, analysis, investigation, visualization, writing the first full manuscript with subsequent review and editing. Additional contribution to analysis, and review and editing of the full manuscript was provided by the co-authors.

IV – Rannamäe E. & Lõugas L. (forthcoming) Animal exploitation in Karksi and Viljandi (Estonia) in the Late Iron Age and Medieval Period. In: A.G. Pluskowski (Ed.) *The Ecology of Crusading, Colonisation and Religious Conversion in the Medieval Eastern Baltic: Terra Sacra II*. Turnhout, Brepols Publishers.

Author contribution: conceptualization, data collection, methodology, analysis, investigation, visualization, writing the first full manuscript (except the sections regarding fish) with subsequent review and editing. Additional contribution to analysis, investigation and visualization of fish data, and general review and editing of the full manuscript was provided by the co-author.

This paper has been accepted for publication in *Terra Sacra volume II* by Brepols Publishers. The volume is currently under peer review with the Editorial Board. Planned publication in 2017.

V – Rannamäe E., Lõugas L., Speller C.F., Valk H., Maldre L., Wilczyński J., Mikhailov A. & Saarma U. (forthcoming) Three thousand years of continuity in the maternal lineages of ancient sheep in Estonia. *PLoS ONE.*

Author contribution: conceptualization, data collection, methodology, analysis, investigation, visualization, writing the first full manuscript with subsequent review and editing. Additional contribution to conceptualization, data collection, methodology, analysis, investigation, and review and editing of the full manuscript was provided by the co-authors.

This paper has been accepted for publication in *PLoS ONE*. The paper is currently in the production department of the journal. Planned publication in 2016.

1. INTRODUCTION

According to the Food and Agriculture Organization of the United Nations (FAO), sheep is one of the most important and widely distributed domestic species, one of the so-called ‘big five’ – alongside with cattle, goats, pigs and chicken (FAO 2015, 28). Sheep have been an important animal resource for humans since their initial domestication 11,000 years ago. The high number of sheep breeds, their wide distribution across the world, and their long history alongside humans makes them a fascinating, yet difficult species to be studied.

Zooarchaeological material and the diversity and distribution of different characteristics (like those of wool fibres, horns and tails) provide the basis to investigate sheep history. Of these studies, the more than 800-paged *Sheep and Man* by Michael Ryder (1983) should be credited, as it is deemed to be *the book* of sheep history. Even more than thirty years after its first publication, it continues to provide valuable insights into the study of sheep, and inspires young researchers such as the author of this thesis. During the last few decades, archaeological methods have been supplemented with genetic research to better understand both modern and ancient populations. The major focus of research has not only been the domestication and distribution of sheep, but also unravelling the sheep genome.

Sheep have been studied in Estonia from several perspectives. Archaeofaunal assemblages have provided patterns of animal utilisation, archaeological textiles have stressed the importance of wool, and breeding history from the 18th century onwards has led to the management of present-day sheep husbandry and the existing breeds. Although the known data covers many aspects of sheep history, the uneven representation of osteological[1] material from different time periods, insufficient dating, and only partial analysis of many bone assemblages have hindered drawing wider conclusions on the development of sheep populations in Estonia.

This thesis describes the first archaeogenetic study on ancient sheep in Estonia. Although the study forms merely a small contribution to the vast sheep history, it adds to the previous knowledge of sheep husbandry in Estonia, and more broadly, in the Eastern Baltic Sea region, by joining the zooarchaeological and genetic evidence from the Bronze Age to present-day sheep husbandry.

1.1. Objectives of the research

The aim of this thesis is to study sheep husbandry in Estonia by exploring the origin, distribution, and exploitation of sheep from the Middle Bronze Age (*ca.* 1200 BC) to the present. The objectives are derived from two separate approaches – zooarchaeology and genetics, intertwined in many aspects, and complemented by the archaeological and historical record. The results of the research are summarised in five scientific papers (see Ch. 1.2).

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[1] Osteology – the scientific study of bones (Jobling *et al.* 2014, 630).

The zooarchaeological study presents an overview of the diachronic exploitation of faunal resources in two locations – Viljandi and Karksi, from the Late Iron Age to the Early Modern Period (10th/11th – 17th c.). Both sites are situated in the area of historical Livonia, present-day south-western Estonia. With castles in Viljandi and Karksi, these were two of the several power centres of the Teutonic Order during the Middle Ages. In Karksi the zooarchaeological material derives only from the medieval and early modern castle (2nd half of the 13th – 17th c.), while in Viljandi, in addition to the contemporary castle, the assemblages from the Late Iron Age Castle Hills (from the 10th/11th c. to the end of the first quarter of the 13th c.) and the medieval Hanseatic town (from the mid-13th to the late 17th c.) were also involved (for detailed descriptions on the sites see **Papers I**, **II** and **IV**). More than 46,000 bone and tooth specimens[2] from 46 assemblages, covering archaeological excavations from 1987–2012, were analysed from these sites. Roughly half of the material was identified by the author during 2009–2015 (for details on the assemblages see **Paper IV**, Table 1). The work considered the entire material, and only in the later phase of the doctoral studies was the necessary information about sheep extracted from the overall osteological data. The investigation of the archaeofaunal material addressed mainly the peculiarities of the dietary structure and evidence of activities secondary to food and diet, *i.e.* utilising animals for different by-products. To tackle these topics, attention was given to the following objectives:

- Domestic livestock – cattle, sheep, goat and pig as the most abundant meat providers, formed the basic source material and were analysed more closely in terms of proportion of each species in the material, body part representation, cut marks and age structures (*i.e.* consumption patterns), physical characteristics, size and health.
- The rest of the remains of domestic and wild mammals, birds and fish were assessed in terms of species diversity and proportion of each species in the material (*i.e.* reflection of animal husbandry versus the exploitation of natural resources), body part representation and cut marks (*i.e.* consumption patterns).
- The transition from the Late Iron Age to the Middle Ages in the 13th century was an important focus throughout the research, as this is the widely discussed period of changes in the power regime, society, economy and culture (*e.g.* Valk & Selart 2012). Distribution and diversity of species in prehistoric and medieval Viljandi led to questions about the differences in animal husbandry, and exploitation of domestic and wild animals in the societies of the prehistoric Late Iron Age and the Middle Ages. By comparing prehistoric assemblages to medieval material, it was possible to gauge the extent to which the 13th century crusades might have influenced the environment and economy in south-western

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[2] Specimen – in a context of zooarchaeological material a whole bone/tooth or a fragment thereof (see Lyman 2008, 27).

Estonia, of which the potential changes in animal husbandry and meat consumption are addressed in this study.

- As animal consumption is induced by social and cultural factors, one of the specific aims of this study was to compare faunal remains between the castle, town, suburban and rural regions in order to detect any differences in social structures and economic conditions.
- The role of trade and international contacts were taken into consideration in terms of detecting any imported species and by that referring to a certain activity or social privilege.

The main objectives of **the genetic study** were to assess the preservation of ancient DNA[3] (aDNA) in archaeological sheep remains, to gain data of ancient sheep in Estonia, and investigate the fluctuations of genetic diversity of sheep populations over time in comparison with modern data. These objectives were approached by analysing the mitochondrial genome in 134 ancient sheep specimens from Estonia, Latvia, Poland, Russia, and Greece, and from 44 modern samples of Kihnu native sheep (**Papers III**, **V**). Additionally, Y-chromosome was analysed for 27 samples among the Estonian samples. The research tasks were the following:

- To observe the development of sheep populations in Estonia from the Middle Bronze Age to recent breeding in the Modern Period using genetic diversity estimates.
- In case of fluctuations in genetic diversity in time and space, the diversity estimates were brought together with the known historical events and cultural shifts to evaluate the congruence between the archaeological and/or historical material and the genetic data.
- Within the previous task, the aim was to establish the degree of continuity between the ancient populations dating back to the Bronze Age and the present-day population of Kihnu native sheep.
- By using comparative material from ancient and modern sheep across Eurasia, it was important to assess the diversity of the indigenous sheep populations in Estonia in a wider phylogeographical[4] context. This task allows to position Estonia on the map of ancient migration routes and cultural contacts, and to position the ancient and extant sheep populations among other northern European sheep breeds.

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[3] DNA – a molecule of deoxyribonucleic acid, which is one of the two forms of nucleic acid in a living cell, and the genetic material for all cellular life forms and many viruses (the other is ribonucleic acid, RNA) (Brown & Brown 2011, 290, 298).

[4] Phylogeography – a discipline in which the geographical distribution of the genetic variation of natural or domesticated populations is studied in a historical context; intraspecific phylogeography helps to decipher spatial and temporal patterns of population structure (*i.e.*, genetic differences within and among populations) and to explain the ecological and evolutionary processes responsible for those patterns (Avise *et al.* 1987; Avise 2000; see also Gutiérrez-García & Vázquez-Domínguez 2011).

1.2. Overview of the conducted research and outline of the dissertation's introductory part

The research began in 2009 with a Master thesis project on a medieval faunal assemblage from Viljandi (Rannamäe 2010a; 2010b) and by that setting the geographical focus for the subsequent work in the following years. Several comprehensive faunal assemblages from Viljandi and Karksi proved to be the core of the osteological study and provided the main zooarchaeological background of livestock husbandry and management from the final centuries of the Late Iron Age to the Early Modern Period. Several papers about the consumption and utilisation of animals in medieval Viljandi and Karksi were published, including ***Worked and unworked bone from the Viljandi castle of the Livonian Order (13th–16th centuries)*** in *Lietuvos Archeologija* (**Paper I**) and ***Some spatial and temporal aspects of animal utilisation in Viljandi, Medieval Livonia*** in *Archaeologia Baltica* (**Paper II**). The concise analysis of the region was written as a comprehensive paper ***Animal exploitation in Karksi and Viljandi (Estonia) in the Late Iron Age and Medieval Period*** in the volume of *The Ecology of Crusading, Colonisation and Religious Conversion in the Medieval Eastern Baltic: Terra Sacra II* (**Paper IV**). Alongside with the analysis of faunal assemblages, the foundation for organising and systematising the zooarchaeological collections in the Department of Archaeology at the University of Tartu was established by the author (starting from 2009; with support from the Centre of Excellence in Cultural Theory).

The zooarchaeological analysis conducted over the years laid foundations towards the genetic studies initiated by the project *Genetic ancestries, breeding strategies and utilization of Estonian indigenous sheep and cattle from Prehistoric to Modern times* (budgeted by the Estonian Science Foundation ETF8526, Lembi Lõugas, 01.01.2011−31.12.2014). Opportunity to get 'deeper' into the bones, on to the molecular lever, seemed fascinating, and the focus of research was decided to be set on sheep. First experience in the laboratory work and data analysis of the aDNA was provided by the Green Technology, Natural Resources Institute Finland (Jokioinen, Finland; at the time named as MTT Agrifood Research Finland) during two months in 2011–2012, when the first set of ancient sheep samples from the Estonian Late Bronze Age to Early Modern Period were studied by the author. The outcome of the analysis was published in ***Maternal and paternal genetic diversity of ancient sheep in Estonia from the Late Bronze Age to the post-medieval period and comparison with other regions in Eurasia*** in the journal of *Animal Genetics* (**Paper III**). The results induced further questions, which led to the second phase of the aDNA work, now conducted in Estonia in an aDNA specific laboratory at the University of Tartu, Institute of Ecology and Earth Sciences. The lab had been constructed within the newly built Chemicum in 2009 and was fully equipped by 2013, when the studies on ancient sheep were started (funded by Estonian Science Foundation research grants ETF 8525 and 8526). The lab work with sheep samples lasted five months, and was followed by studies on genetic analyses, collecting and interpreting the background data, and exploring the written sheep history in Estonia. The results were written into a paper ***Three thousand years of continuity in the maternal lineages of ancient sheep in Estonia*** (**Paper V**), published in the journal *PLoS ONE*, and is considered to form the most important output of the dissertation.

The current introductory part of the thesis integrates those five scientific publications into a uniform approach and explains some of the aspects of the research that were not discussed in detail in the original publications. In Chapter 2, the domestication and development of sheep in the world and more specifically, in Estonia, are briefly described, as revealed by available zooarchaeological and genetic evidence. Here a special subchapter is dedicated to the genetics and archaeogenetics of sheep, introducing basic concepts used in this research field. In Chapter 3, the material and methods are described, including the principles for material selection and an overview of the applied zooarchaeological and genetic methods. The results of the study are presented in Chapter 4, where several topics relevant to the obtained data are discussed.

2. BACKGROUND – THE HISTORY AND GENETICS OF SHEEP

The taxonomy, diversity, and development of sheep are complex research subjects. Recent methodological advances are continuously producing new information that questions the previous hypotheses, opening new discussions on the domestication and subsequent development of sheep. Although ancient faunal remains and 'traditional' zooarchaeological methods (*i.e.* based on osteology and morphology[5]) continue to elucidate the field, the recent advances in genetics, and more precisely the studies on aDNA, have become one of the most influential tools for that purpose.

In this chapter, an overview of sheep domestication is given, followed by the development of sheep populations in Estonia as known from the previously analysed zooarchaeological and historical material. The last part of the chapter is dedicated to a brief introduction to genetics and archaeogenetics of sheep, which provides the necessary background to the material analysed in the current thesis.

2.1. Sheep domestication and modern day sheep breeds

Sheep – the genus *Ovis* – is part of the ruminant family *Bovidae*. The taxonomy of the sheep genus is complicated and no consensus among researchers has been reached. Different studies and classifications have presented a variable number of species and subspecies. In general, it has been agreed that the genus *Ovis* comprises seven species with several subspecies and hybrids, among which the wild sheep are the argali (*Ovis ammon*), urial (*Ovis vignei*) and Asiatic mouflon (*Ovis orientalis*) in Central and Southwest Asia, snow sheep (*Ovis nivicola*) in North Asia, and bighorn (*Ovis canadensis*) and Dall sheep (*Ovis dalli*) in North America (NCBI Taxonomy Database; Ryder 1983, 13–14; Rezaei *et al.* 2010). The domestic sheep (*Ovis aries*) is the most abundant species, being dispersed across the world, particularly in Asia and Africa, followed by Europe and the Caucasus and the rest of the regions (FAO 2015, 29). After cattle, sheep are one of the most exploited domestic livestock around the world. In 2014, it was estimated that 1.2 billion sheep exist distributed in more than 190 countries, and yielding over 1,100 breeds of wool, dairy, meat and hair sheep (FAO 2015[6], Table 1B2).

Sheep were initially domesticated in different parts of the Fertile Crescent in Southwest Asia, alongside the goat, pig and cattle. The accepted hypothesis states that sheep was domesticated between *ca.* 11,000 and 10,500 years ago in the high Euphrates basin on the high slopes of the Taurus Mountains (Peters *et*

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[5] Morphology – the characteristics of the form and structure of organisms (Jobling *et al.* 2014, 627).

[6] Statistics on the production of live animals is available at http://faostat3.fao.org/download/Q/QA/E (last accessed August 8th 2016).

al. 2005; Zeder 2008, 11598). The ancestral species of domestic sheep is now agreed to be the Asiatic mouflon based on the natural range of this species; moreover, *Ovis aries* and *Ovis orientalis* have similarities in their DNA (both maternal and paternal lineages) and karyotype[7], with both species presenting a diploid chromosome number of 2n = 54 (Shiwago 1931; Bunch *et al.* 1998, 267; Hiendleder *et al.* 2002; Bruford & Townsend 2006; Meadows & Kijas 2009). Goats (*Capra hircus*) were domesticated from the bezoar (*Capra aegagrus*) around the same time as sheep, and it has been suggested that both species had probably multiple domestication events (Zeder 2008, 11598). Pigs (*Sus scrofa domesticus*) were domesticated only slightly later, around 10,500–10,000 years ago, from the ancestral species of wild boar (*Sus scrofa*), while cattle (*Bos taurus*) was domesticated between 11,000–10,000 years ago from the wild aurochs (*Bos primigenius*) (Zeder 2008).

The first evidence of domestic sheep come from slaughtering profile and herd management (culling males and keeping females) in the faunal assemblages (*e.g.* Zohary *et al.* 1998; Peters *et al.* 2005; Zeder 2008), while morphological modifications followed well after the initial domestication (Zeder 2005; 2008; Dobney & Larson 2006, 265; Vigne 2011, 174), presumably roughly one thousand years later (Zeder 2008). Sheep retained their slender body build and hairy looks for several millennia, but when humans began to select the desired features, morphological changes were quick to follow: decrease in height, lengthening of the tail, reduction in horn size, changes in horn shape or complete loss of horns, changes in fleece colour and the disappearance of natural molt (Ryder 1983, 3, 28–29, 37; see also Bökönyi 1988, 159–163). Among these, changes in fleece, which first started in the area of the initial domestication, have proven to be the most drastic in the course of sheep breeding. The relevance of this morphological feature is expressed in the classification, evolution and affinity of the world sheep breeds, as these are defined based on the characteristics of wool (Ryder 1983, 28–29, 49). However, wool was not the first product sheep were valued for. It has been suggested that initially the ‘primitive’ (*i.e.* unimproved) populations of sheep were reared for meat and milk instead (Chessa *et al.* 2009, 532). These first domestic sheep populations came along with the first migrations of Neolithic communities that emerged from Southwest Asia. These populations spread via separate routes towards the west (Mediterranean route) and north (Danubian route and possibly through present-day Russia), appearing in the Mediterranean region 10,500–7,000 years ago, Britain around 6,000 years ago, and reaching northern Europe sometime between 5,500–4,000 years ago, including Estonia around 4,900–4,700 years ago (Ryder 1983, 29; Tapio *et al.* 2006, 1781; Lõugas *et al.* 2007; Zeder 2008; Clutton-Brock 2012, 35–36; Bläuer & Kantanen 2013). As new types of wool emerged in the Near East around five thousand years ago, sheep were dispersed across Eurasia, Africa and the rest of Asia in several migratory waves, gradually

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[7] Karyotype – a set of chromosomes of a cell or an individual (Heinaru 2012, 1013).

replacing the majority of primitive sheep populations and providing the foundation for most of the modern breeds (Chessa *et al.* 2009).

Nevertheless, relicts of these primitive populations are shown to have survived in isolated environments and not (or to a very small extent) mixed with other sheep breeds. These are, firstly, the European mouflon (*Ovis orientalis musimon*[8]) on the islands in the Mediterranean, the feral descendant of the first domestic sheep to enter Europe (Poplin 1979; Meadows *et al.* 2006, 451; Meadows & Kijas 2009, 123; Rezaei *et al.* 2010, 324–325), and secondly, old local breeds (so-called landraces) and strains (without a breed status) in peripheral northern European areas (Chessa *et al.* 2009, 535). The latter comprise the Northern European short-tailed sheep, who are distributed from Russia to Iceland across the Baltic and North Atlantic Sea regions (Dýrmundsson & Niżnikowski 2010, 1276). These breeds share a small hardy body build, short tail, large litters, double layered coat of outer hairy coat and woolly undercoat, primitive fleece structure, moderately fine wool, natural molt in the spring, and a range of colour from black and brown to grey and white – all characteristics referable to the ancestral wild sheep (Ryder 1981, 415; 1983, 28–29, 307–308). These breeds have also occasionally preserved behavioural and reproduction traits characteristic of their wild counterparts, like prolificacy and strong maternal instinct (*e.g.* Shillito & Hoyland 1971; Dýrmundsson & Niżnikowski 2010, 1276; KMKS 2015, 4). There are more than thirty short-tailed breeds of northern European origin, of which many are endangered or have already become extinct (Dýrmundsson & Niżnikowski 2010). Among these breeds, the Soay sheep in the island of St Kilda, Scotland, is believed to be the true relict from as early as the Bronze Age, and clearly linked to the Mediterranean and Asiatic mouflon (Boyd 1964; Ryder 1981, 382; 1983, 13; Chessa *et al.* 2009). The Icelandic sheep in Iceland is also believed to have survived rather intact for the last 1,100 years, from the time it was introduced by the Viking settlers (Musto 1979, 15–16; Ryder 1981, 400; Dýrmundsson 2002, 45). In the context of the current study, a few other Northern European short-tailed breeds are worth mentioning, as these have been used for comparison with Estonian ancient sheep (see **Paper III**, Table S2). These are, for example, Åland Island Sheep, Finnsheep and Kainuu Grey Sheep in Finland, Norwegian Speal Sheep in Norway, Polish Heath (Wrzosówka) in Poland, and Romanov Sheep and Russian Viena Sheep in Russia (Dýrmundsson & Niżnikowski 2010, Table 1). The Finnsheep and Romanov have gained a considerable distribution worldwide and are extensively used in breed improvement. Nonetheless, all primitive breeds contribute a valuable resource of genetic diversity, which is recognised as very important in international animal production, agriculture, conservation biology and cultural heritage (Scherf 2000, 22–36; Kantanen & Vilkki 2005; Tapio *et al.* 2005a; 2005b; Tapio 2006, 50; Dýrmundsson & Niżnikowski 2010; Lancioni *et al.* 2013; Räikkonen & Kurppa 2013).

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[8] According to Rezaei *et al.* (2010) the European mouflon (*Ovis orientalis musimon*) is a sub-species of the Asiatic mouflon (*Ovis orientalis*). Other sources like NCBI Taxonomy Database have represented the European mouflon as a sub-species of the domestic sheep (*Ovis aries*), named as *Ovis aries musimon*.

2.2. Sheep in Estonia from the Late Neolithic to the present-day

In Estonia, the development of ancient sheep populations has mainly been assessed together with the rest of the animal remains, with no special study objectives regarding sheep husbandry. Zooarchaeological research has relied on morphological methods, giving information about the consumption and utilisation of sheep and their by-products, as well as the overall size and body type of the individuals. For the few last centuries, where archaeological material becomes irrelevant or non-existent, the written documents and genetic data have started to contribute significantly to the sheep history.

In the following chapter, zooarchaeological and historical research conducted in Estonia is summarised. This is followed by a chronological overview of the available zooarchaeological material, as relevant from the point of sheep history. Although genetic data from the Bronze Age to the present day is the focus of the research, the background for the very first evidence of sheep from the Late Neolithic is presented as well (see also **Paper V**).

2.2.1. Research history: zooarchaeological studies and historical data

In Estonia, zooarchaeological research on a scientific level started with paleozoological interest, moved on to serve cultural historical purposes, and could now be considered as an integral part of archaeology. The origins of the studies of faunal remains in Estonia can be dated back to the end of the 19th century, when the results and methods from natural sciences were started to be used in archaeological studies (particularly on Stone Age material) by **Johann Heinrich Kawall** (1799–1881) and **Constantin Grewingk** (1819–1887). At the same time and into the 20th century the faunal assemblages were analysed by **Aleksander Rosenberg** (1839–1926), but after that, in the 1920s, the archaeofaunal studies were conducted only as minor tasks (Lõugas 1988, 17; Kriiska & Lõugas 2006, 270, 273).

The next important stage in Estonian zooarchaeology began in the 1930s with **Johannes Lepiksaar** (1907–2005), whose essential works are referred to and relied on even today. Lepiksaar worked with materials of both ancient and modern populations, producing a comprehensive list of publications on zoology and faunal history (*e.g.* Lepiksaar 1981; 1986; 1989; see Lõugas 2009, 65–79). Around the same time, at the end of the 1930s, interdisciplinary methods were applied to material from several important sites, worthy of mention, in terms of the study of sheep history, was the analysis of macro remains from Lõhavere hillfort. Namely, some 'harsh wools' in the partially burnt layer of sheep or goat dung were identified by the zoologists of that time (Moora & Saadre 1939, 158–159; Jaanits 1995, 40; Kriiska & Lõugas 2006, 273). It was not specified, whether the wool finds were of sheep or goat, but based on the Chronicle of Henry of Livonia (HCL), where foremost sheep have been mentioned, the archaeologists seem to have supported the idea of the finds belonging to sheep (Moora & Saadre 1939, 159).

The Second World War brought a low-point in the research field, because Lepiksaar was forced to emigrate to Sweden. He became an acknowledged osteologist throughout Europe, but continued to remain close to Estonian related topics. He published many zoological and zooarchaeological works (see Lõugas 2009). Meanwhile, help in the analysis of animal remains were provided by biologist L. Põder (see Kriiska & Lõugas 2006, 275), and by Russian and Latvian zoologists V. J. Tsalkin (Tsalkin 1952; Jaanits 1959, 24–25, 100; Tsalkin 1962), V. D. Lebedev (see Jaanits 1959, 24, 100; Lõugas 1988, 18), and J. Sloka (see Lõugas 1988, 18).

The next important researcher of the faunal history was zoologist **Kalju Paaver** (1921–1985), who from the 1950s specialised on ancient faunal remains (Lõugas 1988, 18). Paaver identified many faunal assemblages from archaeological sites (see Jaanits 1959, 25), and promoted the importance and understanding of archaeological animal bones (Paaver 1956). His main work was a thorough monograph on the faunal history of the eastern Baltic Holocene, which is still widely relied on (Paaver 1965). However, in the 1970s and 1980s, Paaver was not actively dealing with zooarchaeological research. Therefore, the concern, expressed by archaeologist Vello Lõugas in 1988 is pertinent. Lõugas wrote that there are no specialists to work with faunal remains, and there are no studies that would have approached animal remains from a more thorough perspective than merely identification of the species and description of the biological characteristics (Lõugas 1988, 18).

This concern started to be resolved when a new phase in Estonian zooarchaeology began in the 1990s. **Eha Järv** and **Paul Saks** (1918–2007) took on contractual works for the identification of many Late Iron Age and medieval assemblages from Viljandi and Tartu, and thus producing important data and knowledge regarding the history of animal breeding. Their identification reports were widely used for the current research, for which the author is highly thankful. Saks also published a few papers on his zooarchaeological reports (*e.g.* Saks 1993; Saks & Valk 2002), but a true scientific interest towards archaeofaunal material came with **Liina Maldre** and **Lembi Lõugas** in Tallinn University. While Lõugas has worked on the post-glacial development of Estonian fauna, first domesticates in Estonia, Stone Age animal utilisation, sea mammals and fish (*e.g.* Lõugas 1997; 2016; Lõugas *et al.* 2007), Maldre has concentrated on domestic animals, especially the use, breeding and population structure of livestock. Maldre's work is also essential in the frameworks of the current study because of her master thesis on domestic ungulates (Maldre 1993), and the following articles on animal husbandry (*e.g.* Maldre 1997a; 1997b; 1997c; 2007a; 2007b; 2008a; 2008b), including a short paper on a medieval four-horned sheep skull (Peets & Maldre 1995).

By using the foundation of the osteological work by Järv, the natural scientific approach by Lõugas, and data of domestic livestock by Maldre, the author of this thesis now continues to promote the study of zooarchaeology at the University of Tartu. Additionally, the first bachelor's thesis on archaeo-ornithology in Estonia was defended in 2016 at the University of Tartu by **Freydis Ehrlich** (Ehrlich 2016).

Another important source material regarding livestock husbandry would be the written documents, but these are very rare in Estonia. Moreover, archival sources considering the farms, where most of the livestock was actually bred, are missing altogether (E. Küng, personal communication, March 2016). One of the earliest works and widely referred to in the latest studies of sheep husbandry in Estonia, is the book by **Wilhelm Christian Friebe** (1761–1811), where he contrasts the local type of sheep with 'German' sheep, and describes the environmental conditions for sheep husbandry in Livonia and Estonia (Friebe 1794).

Inna Põltsam-Jürjo has analysed the available medieval documents for information about people's food menu (*e.g.* Põltsam 1999). Moreover, a comprehensive collection of historical studies is the **'Eesti talurahva ajalugu'** (Kahk *et al.* 1992; *The history of peasantry in Estonia* – author's translation), where mostly written data from medieval and early modern documents have been presented and analysed. Food habits in early modern farms and manors, including the consumption of meat and other products, have been covered, for example, by **Aliise Moora** (1900–1996) (Moora 1991, 218–245). It is not a straightforward task, however, to link the historical data with zooarchaeological data. These two sources of material can produce controversial information (see *e.g.* Albarella 1999). Despite not being addressed in the current thesis, it would be essential to include the written documents and the already published historical works into future zooarchaeological research objectives.

The more recent history of sheep has been treated in detail in the studies written by the researchers in animal sciences or sheep breeders. The aim of these books and booklets has been the improvement of animal husbandry, and therefore the historical background described is rather vague, while different sheep breeds, know-how of sheep keeping, diseases and production are covered in detail. One of the earliest booklets about the description and necessity to improve local sheep husbandry, comes from the beginning of the 1920s (Kallit 1924). Later, there have been several researchers compiling books and summaries on sheep husbandry in Estonia, of which the most relevant would be **Kristjan Jaama** (1904–1996) (*e.g.* Jaama 1984) and **Peep Piirsalu** (*e.g.* Piirsalu 2012).

The last, but not least, of the source materials for tackling sheep history are the sheep themselves. Parallels with extant local sheep in Estonia and elsewhere in northern Europe allow interpreting archaeological evidence in terms of the animals' morphology, but also their survival in certain environmental conditions, productivity, and quality of produce. Here the breeding programmes established by the breeders' associations provide data about the history and description of a breed, where, in case of Kihnu native sheep, work by **Anneli Ärmpalu-Idvand** must be acknowledged (Ärmpalu-Idvand 2009; KMKS 2015).

Initiated by the aim to study the origin of Estonian native sheep breed and other local types, there have been conjoined genetic studies by Estonian and Finnish scientists, especially by **Urmas Saarma** in the University of Tartu, and by the working group led by **Juha Kantanen** in the Natural Resources Institute Finland (Tapio *et al.* 2005a; 2005b; 2006; Tapio 2006; Saarma 2009; see Ch. 2.2.6 and 2.3.3).

2.2.2. Late Neolithic and Bronze Age

The beginning of animal husbandry in the Estonian area is associated with the **Late Neolithic (*ca.* 3000–1800 BC)** Corded Ware (2900–1800 BC) sites (*e.g.* Lõugas *et al.* 2007). The osteological evidence is very sketchy and dubious because of the thin occupation layers of this period and the fact that animal remains might get easily mixed and indistinguishable with the older or later material (Kriiska *et al.* 1998; Maldre 1999; Lõugas *et al.* 2007, 22, 25). The bone awl in the Ardu burial (North Estonia) made of a sheep metacarpal bone is the find that has been agreed to mark the beginning of animal husbandry in Estonia (Lõugas *et al.* 2007). The awl itself is not radiocarbon dated, but the distinctness of the archaeological context and radiocarbon dates from the accompanied human bones have placed it to a timeframe of 2,900–2,700 BC (Lõugas *et al.* 2007). However, two problematic aspects can be noted: firstly, the bone tools do not necessarily indicate animal husbandry on the spot, but could be imported items; and secondly, the non-worked remains might derive from deposits that are more recent and would therefore need direct dating. Moreover, from other Late Neolithic sites the sheep remains have not been radiocarbon dated (*e.g.* Akali and Tamula; Jaanits 1959, 24–25, 100; Paaver 1965, 440). The first migrants to the region were most probably small in numbers and early farmers had only small herds to maintain, indeed suggesting the appearance of the first domestic animals in the region, but not the fully established farming system dependent on domestic animals (Lõugas *et al.* 2007, 22). The latter phenomenon might have taken a long time in an area such as the East Baltic, because the geographic and climatic conditions did not favour a rapid development of animal husbandry (Lõugas *et al.* 2007, 26). This might be the reason why the following **Early (1800–1200 BC) and Middle (1200–850 BC) Bronze Age** in Estonia lack faunal remains. It is crucial to note though, that archaeological sites known and studied from these early metal periods are in general scarce, leaving room for open questions and different hypotheses. One of the prevailing opinions is that animal husbandry must have become predominant at that time, since the osteological material is numerous from the settlement sites of the following **Late Bronze Age (850–500 BC)**[9] (Maldre 1999, 322). These assemblages include sheep and goats who, based on the age structure of the bone assemblages, were kept for meat, wool and/or milk (Maldre

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[9] In **Paper III** the Late Bronze Age is defined to a time span of 1100–500 BC, while in **Paper V** and in the current text the period is defined to 850–500 BC. This change derives from a renewed periodization by the committee of the archaeology terminology (protocol of the meeting held in April 20th 2015, available in the archaeology archive of the University of Tartu).

2008a, 268). The largest sites of that period with recorded bone material are the Asva and Ridala settlements on Saaremaa Island, where the bones of domesticates constitute around 75–80% of the total osteological material (Lõugas 1994; Maldre 1999; 2008a). Although Asva is the oldest among the excavated sites in Saaremaa, where the bones of livestock have been found, it is still unknown when exactly the first domesticates were brought to the island (Lõugas 1994, 74). It is characteristic to the island that the remains of sheep and to a lesser extent goats tend to dominate in the osteological assemblages, but it must be remembered that the material from these old deposits is usually heavily fragmented and poorly preserved, thus making any conclusions speculative.

2.2.3. Iron Age and the Middle Ages

The **Early Iron Age (500 BC – AD 550)** yields little osteological evidence for animal husbandry, which could be attributed both to the mixed nature of archaeological deposits and the dispersed settlement pattern characteristic to this period (which makes it difficult to locate sites on the landscape). Much of the animal remains of this period come from the burial sites, but since they hardly can be associated with being grave goods, their true age and depositional reason remains dubious (*e.g.* Mägi *et al.* 1998, 106–108; Maldre 2000a; Ots *et al.* 2003; Laneman *et al.* 2015; Vedru *et al.* 2015, 119). From the **Late Iron Age (AD 550–1225)** onwards animal remains, especially of domesticates, again become numerous and are hereafter abundant in the archaeological deposits. Most of the known material comes from the hillforts, while the settlements hold only poor evidence – the latter are not often excavated and the Late Iron Age occupation layers cannot easily be distinguished from the later ones. Sheep (and to a lesser extent goats) have been one of the most exploited animals (*e.g.* Lõugas 1994; Maldre 2000b; 2007b) with the focus on meat and wool production (Maldre 2007b, 68). It is interesting to note that as for the Late Bronze Age, sheep in Viking Age (AD 800–1050) Saaremaa and western Estonia continued to be the most numerously exploited livestock, although towards the end of the Iron Age their importance there started to decrease (Maldre 2012a). At the same time in southern Estonia, however, sheep and goat breeding evidently increased (Maldre 2012a).

The time of the crusades in Estonia (AD 1208–1227), which marks the transition from the prehistoric to the historic era and the beginning of the **Middle Ages (AD 1225–1550)**, brought significant changes in power structures and settlement. The decades of crusades are illustrated by the Chronicle of Henry of Livonia, where he describes ‘countless’ numbers of sheep or ‘other livestock’ besides cattle, oxen and horses, that were taken from the local inhabitants during the campaigns (*e.g.* HCL XIV.10, XXVIII.5). Medieval zooarchaeological material, however, comes predominantly from urban deposits; rural assemblages tend to be rarely excavated and/or poorly preserved. Although there have been several large-scale excavations in rural settlement sites (*e.g.* Olustvere in central Estonia), the material is disorganised and lacks contextual information.

In addition, as rural sites tend to be more disturbed with ploughing and other ground works, the material collected is usually of mixed context. In the towns, while still being influenced by construction works, the material is usually more often and systematically collected and documented. Still, as common to the Middle Ages, it is difficult to separate different deposits, even if historically different periods would hypothetically be present (*e.g.* Lõugas *et al.* 2012). Medieval urban assemblages are dominated by domestic mammals like cattle, pig, sheep and to a lesser extent goat, while the exploitation of wild game is practically non-existent, in comparison to prehistoric times (*e.g.* Maldre 1997b, 111; 2007a; 2008b; **Paper IV**). Usually the sheep/goat bones form around 25–30% from the total assemblage (*e.g.* Lõugas *et al.* 2012, 84), but sometimes they can dominate over cattle and pig (*e.g.* Maldre 2000b, 443). In Saaremaa, the previously observed trend of having more sheep (and goats) continues into the Middle Ages (*e.g.* Peets *et al.* 2013b; Saage *et al.* 2015). Widening trade (*e.g.* through the German Hanse), the development of towns, and the growing human population all influenced animal husbandry, supposedly increasing the number of livestock. The local livestock populations may have been augmented by imported individuals, although this practice would have been rather exceptional and occurred only in wealthy manors as known from the later periods.

2.2.4. Early Modern and Modern Period

In Estonia, the Middle Ages came to an end with the Livonian War (1558–1583). Well-dated zooarchaeological material from the 17th and 18th centuries is scant – evidently, because of limited archaeological interest in the **Early Modern Period (1550–1800)** and difficulties in archaeologically separating the layers of this period from more recent times. The same applies to the following **Modern Period (1800 – first half of the 20th c.)** which also marks the beginning of large-scale breeding. However, the history of sheep starts to be elucidated by written sources. From the 17th and 18th centuries, there are documents about breeding attempts in the manors. From the 1630s, documentation exists about some new pig breeds introduced to Estonia (Soom 1954, 129), but more important than the pigs was the need for improved, better milk producing cattle breeds. In the 1620s–1630s, dairy cattle of Dutch, German and Swedish origin (Liiv 1935, 146; Soom 1954, 129) and in the 1640s–1650s beef cattle also (Soom 1954, 129) were imported by the local landlords. Apparently, the animal trade was not one sided – around the same time horses were exported from Estonia to Russia (Liiv 1935, 146). Any export of livestock, however, is unknown.

The import of some new sheep breeds from Prussia to Latvia and by some Swedish aristocracy into Estonia in the mid-17th century was planned, but probably no significant breeding occurred (Soom 1954, 131). Firmer document evidence of imported sheep appear a few decades later, from the 1670s, when ‘English’ sheep were brought to the Viimsi manor in North Estonia (Soom 1954, 131). There are also some, though scarce, documents of local sheep trade from that time, for example, concerning the 17th century livestock movements from the western islands to northern or eastern part of the Estonian mainland, with the purpose to consume them as food or, possibly, to transfer them to some mainland manor for breeding (E. Küng, personal communication, March 2016). Not until a hundred years later, at the end of the 18th century, were the first attempts made to improve the local sheep with Spanish sheep (Friebe 1794, 300; Jaama 1959, 16). True breeding of fine-wool sheep with extensive improvement of local flocks began in Estonia in 1824 in wealthier manors – first with Merino and then with other breeds like Shropshire and Cheviot; the latter two were used to develop the modern-day Estonian breeds – Estonian Blackhead and Estonian Whitehead, respectively (Jaama 1959, 16, 19, 24; Piirsalu 2012, 17–19; see also Viinalass *et al.* 2006, 20; Luik *et al.* 2011, 4–6). Among peasants, breed improvement started later and at a more limited scale at the beginning of the 19th century (Porga 1979, 7–8), but more likely in the second half of the 19th or the beginning of the 20th century (Jaama 1959, 17). Improvement with the Merinos and large-scale breeding started at different times in rest of the Europe. For example, Spanish Merino rams were used to improve local sheep in Italy as early as the beginning of the 15th century (Lancioni *et al.* 2013), in Finland in the 16th (Niemi *et al.* 2013), in Hungary at the beginning of the 17th (Bökönyi 1988, 189), in Sweden at the beginning of the 18th (Ryder 1983, 524) and in Russia at the beginning of the 19th century (Jaama 1946, 83), and in the area of former Czechoslovakia improvement of the native sheep was carried out from 1900 onwards (Ryder 1983, 359).

2.2.5. 20th century sheep husbandry

In the last hundred years, sheep populations in Estonia have gone through a decline, being the largest at the beginning of the 20th century: in 1922 there were 745,000 sheep in the country, including the lambs born that year (Piirsalu 2012, 9). The 1920s was also the decade when the Estonian Sheep Breeders' Association (*Eesti Lambakasvatajate Selts*) was founded (in 1928; Piirsalu & Kalda 2004, 36). The sheep populations were also in a good state just before the Second World War in 1939, reaching 695,700 in numbers (Jaama 1959, 25), but just after the war in 1945 they dropped to 243,000 individuals (Jaama 1946, 4; Porga 1979, 8). The sheep populations continued to decrease in the following decades, mostly because of the favouring of milk production, where cattle husbandry was more productive (Porga 1979, 3, 8), and reached the low point in 1999 with only 28,200 individuals (Piirsalu 2012, 9). However, by 2016 the number of sheep in Estonia had grown to around 88,300 individuals, yielding 25 sheep breeds, of which three – the Estonian Blackhead, Whitehead, and Kihnu sheep – are local (ARIB = Estonian Agricultural Registers and Information Board).

In the 20th century, several books were written on sheep husbandry, and although the local native sheep were acknowledged for their hardy characteristics, the prevailing suggestion was to improve them with breeds that were more profitable in order to gain longer wool and larger amounts of meat and milk (*e.g.* Kallit 1924, 6; Jaama 1959, 24–30).

2.2.6. Present-day native sheep

In Estonia, the native cattle and horse breeds were mostly acknowledged in the beginning of the 20th century: the Estonian Native Cattle Breeders Association was established in 1920; the studbook for the Estonian native horse in 1921, for Tori horse in 1892, and for Estonian heavy draught horse in 1953 (VFB = The Veterinary and Food Board). The native breed status for sheep remained unestablished at the time. In spite of the introgression of improved and imported breeds, especially during the Soviet period in state and collective farms, the local populations survived in peripheral areas of Estonia, especially in the islands of Saaremaa, Ruhnu and Kihnu (the last two in the Riga Bay), and are often referred to as 'Estonian native sheep'. In 1990s, the population on Kihnu Island was 'discovered' and started to recovered. In January 2016, Kihnu native sheep (named after the founder population) gained acknowledged breed status (VFB). Other populations of indigenous sheep of Estonia lack breed status and have not been incorporated into the existing breeding programme.

Although Estonian local sheep have occasionally been thought to be part of the Northern European short-tailed sheep (*e.g.* KMKS 2015, 6; online sources like Wikipedia), firm affiliation to this group is still not proved (*e.g.* Tapio 2006, Table 1). As surmised, the determinative trait would be a short tail, which, in the phenotype[10] of local Estonian sheep is unclear (tail length is variable or intermediate) and probably a result of being crossed with long-tailed breeds (Tapio *et al.* 2005a; Dýrmundsson & Niżnikowski 2010, 1276). This debate, however, is still open, as the breeding and status affirmation of the Kihnu sheep is an ongoing process. Kihnu sheep express the 'primitive' features of body build, wool and behaviour characteristic to northern European native sheep (see Ch. 2.1; Ärmpalu-Idvand 2009; **Paper III**, Fig. 2; **Paper V**, Fig. 2), of which the presence of horns and wattles have been witnessed to correlate with the presence of a shorter tail (A. Ärmpalu-Idvand, personal communication, June 2016). In addition, regular measurements of the tail in live sheep (averagely 21–22 cm; KMKS 2015, 9) and the number of caudal vertebrae[11]

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[10] Phenotype – the observable traits of an organism that are determined by the coeffect of its genotype (a description of the genetic composition of an organism) and the environmental factors (Brown & Brown 2011, 292; Heinaru 2012, 991).

[11] The Kihnu sheep specimen in the anatomical reference collections of the Department of Archaeology, University of Tartu, has 13 caudal vertebrae (as counted by the author), which is considered a short tail among domestic sheep and a trait for primitive Northern European short-tailed sheep (Bökönyi 1988, 162). During the animal's lifetime the length of the tail had been *ca.* 20–21 cm (A. Ärmpalu-Idvand, personal communication, July 2016), which correlates with the length measured in other flocks of the Kihnu sheep (KMKS 2015). Certainly, more documentation on tail measurements and counts of caudal vertebrae are needed to make firmer conclusions on the tail type of the Kihnu sheep.

suggest ancestral affinity with Northern European short-tailed sheep. Since morphological similarities or differences do not necessarily provide the same results as molecular data, more genetic analyses are needed to unravel this issue (*e.g.* Casellas *et al.* 2004; Tapio *et al.* 2005b, 455).

2.3. Genetics and archaeogenetics of sheep

In this chapter, a brief introduction to the genetics and archaeogenetics of sheep is presented in order to explain the material, chosen methods and objectives of the current research. The genetic markers relevant to the study are briefly introduced, followed by the advantages and disadvantages of the aDNA. Finally, a short overview of the genetic diversity of the world's sheep breeds is summarised.

2.3.1. Genetic markers in animal studies

Genetic studies of domestic animals became more common in the early 1990s owing to advances in DNA sequencing and bioinformatics (Bruford *et al.* 2003). Cattle, sheep and goats, pigs, horses, dogs, chicken and turkeys are examples of species whose phylogenetics[12] have been extensively studied. The rapid developments in DNA extraction and sequencing[13] methods within the last decade have increased significantly the amount of available data, opening new research questions and reassessing old ones. The main research issues in animal studies have remained the same, namely revolving around initial domestication and dispersal, with the focus on genetic variability and population history. Although the aim is to study events and animals from the past, usually modern specimens are used to tackle these issues. These studies are possible because the DNA of each individual contains a record of ancestry and past evolution (Brown & Brown 2011, 6).

Because different genetic markers may show different relationships among breeds, they are usually applied simultaneously to study one species (Kantanen & Vilkki 2005, 4). One of the most used genetic markers in population genetic studies are the few base pairs (bp)[14] long microsatellites[15] (see Kantanen &

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[12] Phylogenetics – evolutionary relationships between individuals, species, or other taxa (Brown & Brown 2011, 297).

[13] DNA sequencing – process of determining the nucleotide order of a given DNA fragment (Heinaru 2012, 1068).

[14] Base pair – the hydrogen-bonded structure in the DNA helix formed by two complementary nucleotides, where adenine (A) always pairs with thymine (T) and cytosine (C) always pairs with guanine (G); when abbreviated to 'bp', it indicates the shortest unit of length for a double-stranded DNA molecule (Brown & Brown 2011, 14, 288) and is used to express the length of the amplified fragment. In the current study, for example, a 599 bp fragment of mtDNA D-loop region was analysed.

[15] Microsatellites or short tandem repeats (STRs) – a DNA sequence containing a number (usually ≤50) of tandemly repeated short (2–6 bp) sequences (Jobling *et al.* 2014, 626).

Vilkki 2005, 4). Microsatellites can be located on autosomes[16] or sex chromosomes and have proved to be especially useful for studying close genetic relationships – mostly the evolution and affinities between modern day breeds (Kantanen & Vilkki 2005, 4; Brown & Brown 2011, 24). Other genetic markers located in the Y-chromosome and in the mitochondrial DNA (mtDNA) are used to provide a complete picture of the genetic diversity of livestock (see Bruford *et al.* 2003; Tapio 2006).

In the current study, the main focus was on mtDNA (**Papers III**, **V**) and to some extent on data from Y chromosome (**Paper III**).

Mitochondrial DNA

Mitochondria are small organelles in a cell responsible for cellular energy production and yield their own DNA – a closed-circular double-stranded biomolecule named mitochondrial DNA (Taanman 1999, 103–104). In mammals, the average length of the mtDNA is 16.6 kb[17] (*e.g.* Gustafsson *et al.* 2016, 135). While nuclear DNA is located only in the nucleus of the cell, and each nuclear locus is represented by two copies, there are usually thousands of mitochondria in one somatic[18] cell on average, each containing several mitochondrial genomes (*e.g.* Wilson *et al.* 1985, 381, 388). For this reason, the amount of mtDNA per cell is more numerous than the nuclear DNA. Unlike nuclear DNA, which is inherited from both parents, the mitochondrial genome is a maternally inherited molecule; and since mtDNA does not undergo recombination[19] and usually presents only a single haplotype[20] for an individual, the history of its lineage is rather straightforward to interpret (Wilson *et al.* 1985, 379; Bruford *et al.* 2003, 902).

The mtDNA control region (also known as the displacement loop or D-loop) is a non-coding[21] segment that regulates mtDNA expression. The control region has a rate of nucleotide[22] substitution (that is, the accumulation of mutations) five to ten times higher than that of nuclear DNA (*e.g.* Brown *et al.* 1979; Wilson *et al.* 1985, 379; Taanman 1999, 106). Moreover, this section of the mtDNA is often regarded as neutral, meaning that the occurring mutations have

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[16] Autosomal – inherited from the autosomal chromosome, which is common for both sexes (Heinaru 2012, 974). In sheep there are 27 pairs of chromosomes, of which 26 pairs are of autosomes and one pair of sex chromosomes (*e.g.* Cockett *et al.* 2001, 69).

[17] Kb = kilo base pairs = 1,000 base pairs.

[18] Somatic cell – a non-reproductive cell (Brown & Brown 2011, 299).

[19] Recombination – a large-scale rearrangement of a DNA molecule (Brown & Brown 2011, 298).

[20] Haplotype – the combination of allelic states of a set of polymorphisms lying on the same DNA molecule, for example, a chromosome, or region of a chromosome (Jobling *et al.* 2014, 620). Individuals with identical SNPs share a haplotype.

[21] Non-coding or pseudogene – a nonfunctional DNA sequence that shows a high degree of similarity to a non-allelic homologous gene (Jobling *et al.* 2014, 633).

[22] Nucleotide – the unit of DNA; based on its chemical structure there are four nucleotides – adenine (A), cytosine (C), guanine (G) and thymine (T) (Brown & Brown 2011, 11, 296) and these form the base pairs in a DNA sequence.

not been affected by natural or artificial selection, and therefore, the overall patterns of the demographic processes, *e.g.* a recent demographic expansion can be easily assessed (*e.g.* Bruford *et al.* 2003, 901–902; Tapio 2006, 20). The rapid and simple mode of mutation accumulation (mainly base substitutions and length mutations) makes it easier to trace the changes that occurred within the last 10,000 years, which is also the time since the origin of the domestic sheep (Wilson *et al.* 1985, 379; Dobney & Larson 2006, 268). The mutation rate is not uniformly distributed throughout the molecule, with a high number of rapidly evolving sites confined to the control region, which is usually organised into three different domains: a highly conserved central domain and two flanking adenine-rich segments with high intra- and interspecific genetic variability, known as hypervariable regions I and II (HVRI and HVRII) (see *e.g.* Matson & Baker 2001). The popularity of control region sequencing analysis over the past two decades results from the high proportion of genetic variation concentrated in a very small and easily sequenced stretch. The cytochrome *b* gene is another section of the mtDNA used in phylogenetic and population genetic studies of livestock species, although presenting a slower rate and mode of evolution when compared with the control region (Bruford *et al.* 2003, 902).

The described features of mtDNA makes it suitable for the analysis of both distant past and relatively recent (less than 10,000 years) evolutionary processes, and to determine the levels of genetic diversity, phylogenetic structure and the interspecies variability, dispersal and phylogeography, gene flow, demographic expansion, genetic drift and hybridization (Villablanca 1994, 32; Bruford *et al.* 2003, 902; Henkes *et al.* 2005, 60). Moreover, the high copy-number of mtDNA has made this biomolecule especially suitable for aDNA studies. When compared to the fast-evolving microsatellites, mtDNA allows studying broader affinities within thousands of years (Meadows *et al.* 2006; Brown & Brown 2011, 24). In addition, there is a rich worldwide mtDNA data set available in contrast to the nuclear genomic data still negligible for domestic sheep (Larson & Burger 2013, 200).

Nevertheless, mtDNA has limited capacity to resolve overall genomic diversity (Hauser & Ward 1998; Bruford *et al.* 2003, 902) and the phylogenetic relationship between closely related breeds (Meadows *et al.* 2005; Lv *et al.* 2015). The mtDNA gives insights only into the maternal lineages, which might be substantially different from the nuclear ones (Pamilo & Nei 1988; Villablanca 1994, 32). The phylogenetic networks used in many mtDNA-based studies have been argued to be a random result of the inheritance process and only partially reflect the complex demographic histories (Nielsen & Beaumont 2009; Larson & Burger 2013, 200). Therefore, it is important to remember that genetic distance estimates can vary greatly according to the genetic marker used. The recent demographic history of the breed, such as whether the subject population has passed through a population bottleneck, may have been influenced by a male-mediated gene flow (Bruford *et al.* 2003, 902, 908), and therefore Y-chromosome genetic markers should also be used.

Y chromosome

The Y chromosome has two main components in mammals: a small pseudo-autosomal region which frequently recombines with the X chromosome, and a male-specific region (MSY), which forms the majority of the chromosome and does not undergo recombination, similar to mtDNA (Meadows *et al.* 2004, 379; Ferencakovic *et al.* 2013, 184). There are different genetic markers on the Y chromosome that could be used for phylogenetic inferences, including microsatellites and single nucleotide polymorphisms (SNP). However, most Y chromosome markers are not as variable within a species as other markers (Bruford *et al.* 2003, 902; Hellborg & Ellegren 2004; Lindgren *et al.* 2004; Meadows *et al.* 2004; Ferencakovic *et al.* 2013; Zhang *et al.* 2014) due to the low male effective population size, meaning that there are usually fewer males contributing to the development of domestic stock (Lindgren *et al.* 2004, 336; Meadows *et al.* 2004, 384). In addition, analysis of the Y chromosome has proved to be technically challenging due to the presence of several repeated genomic regions, resulting in a low number of polymorphic markers available for characterization of male-mediated processes (Niemi *et al.* 2013, 12). Nevertheless, the genetic information provided by the Y chromosome is important to study the domestication process and breed development, as it complements or even gives a contrasting evolutionary perspective to the information gained from the maternal genetic data provided by the mtDNA (*e.g.* Meadows *et al.* 2004; Ferencakovic *et al.* 2013).

2.3.2. Ancient DNA

Ancient DNA is undoubtedly one of the ground-breaking fields of molecular genetics of the last few decades and has become an integral part of most phylogenetic research projects. The rapid development of DNA extraction, sequencing and data analysis techniques, including sequencing of the whole genomes, and the study of aDNA has allowed researchers to understand our past from a different perspective, complementing conventional archaeological work and changing previous conceptions. Ancient DNA analyses are now widely used for resolving many questions concerning the past of many species.

Ancient DNA allows the study of extinct populations and comparison with extant ones, forging an empirical link between the two (Herrmann & Hummel 1994, 31). The genetic variability can be quantified at the DNA level and measured over long time spans. According to Brown and Brown (2011, 10), modern and aDNA analyses are important to identify unknown species, to study the individual's characteristics and the individual's ancestry. The latter is probably the most widely used both in human and other animal studies, and a recurrent issue in the current thesis. The possibility to infer the relationships among past populations before recent admixture events is another advantage of aDNA (Larson & Burger 2013, 200), which can be quite useful in the study of sheep populations.

Many phylogenetic studies on the past diversity and distribution of livestock species are conducted on modern DNA of extant populations. However, inferences from these studies can be biased by selective breeding, hybridization and introgression that have taken place throughout the millennia (Zeder *et al.* 2006, 149). Therefore, the use of ancient faunal remains allows a direct comparison between contemporary and historical patterns of genetic variability, which reveals the temporal changes within the populations of that time (Speller *et al.* 2012, 2). Genetic analyses of archaeological material using aDNA have greatly advanced the studies of livestock domestication and their evolutionary and demographic history, contributing to the data gained from modern populations (Bruford *et al.* 2003, 908). Ancient DNA from diverse domestic species have revealed complex migration patterns which are not accessible if only the modern context of breeds is explored (*e.g.* Larson *et al.* 2007; Svensson & Götherström 2008; Cieslak *et al.* 2010; Niemi *et al.* 2015).

Several studies have shown that ancient specimens hold a great deal of preserved DNA in their tissues, particularly in bones, teeth, hair, and skin. The DNA replication process occurring during the organism's lifetime ceases when an organism dies, and the DNA present in its cells starts to degrade immediately. Due to the autolytic and diagenetic processes, the aDNA degrades over hundreds and thousands of years, leaving only traces or fragments of it (Hermann & Hummel 1994, 2). It has been stated that the level of preservation is not dependant on the age of the specimen, but more on the environment where it has been preserved (Colson *et al.* 1997; Brown & Brown 2011, 6). Ancient DNA can be very fragile and easily contaminated. Radiation (mainly UV), temperature, moisture, pH, oxidative agents, and mechanical stress are among the most important factors influencing the survival of aDNA under diagenesis (Herrmann & Hummel 1994, 3). Although potential contamination (especially from humans) could be kept to a minimal level during fieldwork, usually samples from the already stored archaeological collections are analysed. In addition, animal bones are rather abundant during archaeological fieldwork and usually are not collected in any special sterile method.

Both mtDNA and nuclear DNA can be analysed from ancient osseous material, but in both cases the fragmented nature of old DNA molecules makes the extraction and amplification of aDNA challenging. However, the high copy number of mtDNA per cell prove to be especially useful in these investigations, making it a straightforward first step for aDNA analyses (see Bruford *et al.* 2003, 901; Matisoo-Smith & Horsburgh 2012, 33–38). For this reason, mtDNA is more likely to have been preserved relatively intact in ancient tissues, making it easier to amplify from different molecules in order to obtain a consensus sequence[23] (Villablanca 1994, 32–33; Dobney & Larson 2006).

The first successful extraction of animal aDNA was in 1984 from a 140-year-old museum quagga specimen (Higuchi *et al.* 1984), followed by the first

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[23] Consensus sequence – unambiguous result of the overlapping DNA fragments from multiple sequences.

extracted human aDNA from a two thousand year old Egyptian mummy in 1985 (Pääbo 1985). Nevertheless, studies using aDNA started to rapidly progress only with the development of the *Polymerase Chain Reaction* (PCR)[24] method in the mid-1980s (Mullis *et al.* 1987; see also Bartlett & Stirling 2003). The PCR method, which was also used for DNA amplification in the present thesis, allows to exponentially amplify the short DNA fragments that are typically found in an ancient sample, making it possible to get a consensus sequence long enough for the statistical analyses. The amplification nature of the PCR technique can also be a limitation (Hermann & Hummel 1994, 3). First, one must have some previous information about the genomic region to be amplified by PCR. Second, the exponential nature of PCR makes it prone to contamination, since it can work on only a few molecules present in a sample. Third, only a tiny section of the all DNA from a species is targeted by PCR, meaning that only partial genetic information is obtained.

Nevertheless, analyses of short fragments amplified by PCR, such as the mtDNA control region, both in modern and ancient samples have contributed remarkably to the studies of genetic diversity in several species. Although the advent of whole-genome sequencing has opened up new possibilities to study complete ancient genomes (Edwards *et al.* 2010; Lari *et al.* 2011; Paijmans *et al.* 2013), mtDNA data has remained sufficiently informative to study matrilineal evolutionary processes, especially for degraded samples with short amplifiable DNA sequences.

2.3.3. Genetic diversity of the world's sheep in the past and present

Studies on sheep karyotype and genetics can be traced back to the early 20th century (*e.g.* Oguma & Makino 1937). The first sequencing of a sheep mtDNA control region (1,181 bp) was achieved in 1996 (Wood & Phua). In 1997 a comprehensive book *The Genetics of Sheep* was published (Piper & Ruvinsky 1997). The complete mitochondrial genome (~16.6 kb) was first sequenced in 1998 (Hiendleder *et al.* 1998a) and nuclear genome (~2.6 Gb[25]) in 2010 (International Sheep Genomics Consortium *et al.* 2010; GenBank[26] accession no.

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[24] The purpose of PCR is the amplification of the DNA fragment of interest, often starting with a very small number of DNA copies. First, the DNA needs to be denaturated, *i.e.* separated into single strands by heating the sample. Then two key components are needed: 1) an enzyme that synthesises new strands of DNA using an existing strand as a template, and 2) a pair of region-specific primers that attach to a target region of a single-stranded DNA and with the help of the enzyme start copying the sequences with the single nucleotides that have been added to the sample. This cycle of denaturation and amplification is repeated several times, resulting in millions of copies of the target DNA template (Brown & Brown 2011, 26, 28).

[25] Gb = giga base pairs = 1,000,000,000 base pairs.

[26] GenBank® (http://www.ncbi.nlm.nih.gov) – a comprehensive genetic sequence database that contains the majority of publicly available nucleotide sequences (Benson *et al.* 2013).

PRJNA179263). The sequencing of the sheep genome is an ongoing field involving several research groups throughout the world. Revealing the sheep history, genetic diversity and genes responsible for useful traits (*e.g.* productivity, better wool quality and resistance to diseases) would aid the breeding programmes all over the world and speed up selective breeding, advancing the field of animal husbandry (see *e.g.* Jiang *et al.* 2014; Lv *et al.* 2015).

Over the last few years, several studies have elucidated the evolution and diversity of sheep populations remarkably, relying on different genetic markers such as a mtDNA control region and cytochrome *b* gene (*e.g.* Lv *et al.* 2015), autosomal and Y chromosomal SNPs and microsatellites (*e.g.* Meadows *et al.* 2004; 2006; Tapio *et al.* 2005b; Lawson Handley *et al.* 2007; Peter *et al.* 2007; Kijas *et al.* 2009; Meadows & Kijas 2009; Oner *et al.* 2011). An increasing number of studies are being published on whole genome analysis (*e.g.* Kijas *et al.* 2009; Meadows *et al.* 2011; Lancioni *et al.* 2013; Jiang *et al.* 2014; Teasdale *et al.* 2014; Lv *et al.* 2015). The main topics addressed by all these works have been the wild ancestry, number and location of domestications, and genetic structure towards conservation studies.

Tackling the history and archaeology of sheep using ancient samples have been exploited as well. For example, information has been gained from Iron Age and medieval Finland (Niemi *et al.* 2013), medieval Norway (Bollvåg 2010) and Italy (Gabbianelli *et al.* 2015), Bronze Age Turkey (Demirci *et al.* 2013) and from prehistoric sites in South Africa (Horsburgh & Rhines 2010) and China (Cai *et al.* 2007; 2011). Ancient wool has been analysed from Scandinavia and the rest of Europe (Brandt *et al.* 2011; Rast-Eicher & Bender Jørgensen 2013), including the famous Ötzi find complex in the Alps (Olivieri *et al.* 2012). One of the latest widely discussed source material for aDNA is parchment that has opened up exceptional potential for whole genome analyses and for revealing the 18th–19th century's complex sheep breeding (Teasdale *et al.* 2014).

Genetic studies have shown that past and present sheep populations belong to at least five major maternal (mtDNA) lineages named as haplogroups[27] A–E (Meadows *et al.* 2007). The formation of the two major groups, A and B, occurred approximately at the same time during the initial domestication process (Tapio 2006, 35) and are now common in Asia and Europe, respectively. The same pattern of haplogroup distribution is seen in Baltic and Nordic sheep, where around 70–90% of the population belongs to haplogroup B and the minority to haplogroup A (*e.g.* Kantanen & Vilkki 2005; Tapio *et al.* 2006; Niemi *et al.* 2013). Other mtDNA lineages are less common, with C found across Eurasia, and D and E in a geographically more restricted area in the Middle East (*e.g.* Lv *et al.* 2015; for additional references see **Paper V**). These five lineages have several genetic differences resulting from the accumulation

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[27] Haplogroup – a group of similar haplotypes that share a common ancestor. Usually applied to a set of mtDNA haplotypes that is defined by relatively slowly mutating polymorphisms (*i.e.* any sequence variants) (Jobling *et al.* 2014, 620).

of several mutations across the mitochondrial genome. Nevertheless, sheep breeds have an extensive haplotype sharing, often including animals from different mtDNA haplogroups (Kijas *et al.* 2012). The existence of different haplogroups may result from multiple independent domestication events from different *Ovis orientalis* subspecies, a broad genetic base during domestication, and/or result from a later introgression of wild individuals to the stocks of domestic sheep (*e.g.* Wood & Phua 1996; Hiendleder *et al.* 1998b; 2002; Luikart *et al.* 2001, 5930; Bruford *et al.* 2003; Pedrosa *et al.* 2005; Bruford & Townsend 2006, 315; Tapio 2006; Tapio *et al.* 2006; Zeder *et al.* 2006; Meadows *et al.* 2007; Kijas *et al.* 2012; Singh *et al.* 2013; Lv *et al.* 2015). It was thought that after the initial domestication there was a continuous interbreeding with the wild counterparts, both naturally and induced by man (Ryder 1983, 3, 26; Tapio 2006, 49). This hypothesis has also been suggested by a recent study where the expansion of lineage C around 4,500 years ago has been associated with a deliberate mating of domestic and wild sheep (Lv *et al.* 2015). However, the introgression hypothesis has been put in doubt in some of the recent studies, which suggest that the domestic sheep are free from wild sheep introgression (Meadows & Kijas 2009; Zhang *et al.* 2012, 480). It is possible that a combination of introgression and migrations, facilitated by the small size and versatility of sheep, shaped the vast distribution of genetic diversity seen in today's modern breeds. The last 200 years of intensive breeding practice also contributed to the weak phylogeographic structure observed in sheep (Bruford *et al.* 2003; Tapio *et al.* 2005a; Tapio 2006; Kijas *et al.* 2009; 2012).

The genetic diversity has shown to decrease with the increasing distance from the domestication centre in sheep (*e.g.* Bruford & Townsend 2006; Lawson Handley *et al.* 2007; Peter *et al.* 2007; Tapio *et al.* 2010) and in cattle (*e.g.* Loftus *et al.* 1999; Niemi *et al.* 2015) and goat (Cañón *et al.* 2006). This scenario would be expected as Neolithic farmers who migrated out of Southwest Asia only took some of the animals with them (Bruford *et al.* 2003), but also because the sheep breeds originating in the Near East have retained more variation from their ancestral species (*e.g.* Tapio *et al.* 2006, 1781; Peter *et al.* 2007; Ćinkulov *et al.* 2008). This pattern is also seen in northern European sheep populations that are characterised by lower genetic diversity than the ones closer to the domestication region (*e.g.* Lawson Handley *et al.* 2007; Tapio *et al.* 2010). The pattern of genetic diversity decrease is not always clear and could be caused by widespread recent introgression, especially with the oldest defined sheep breed after the Middle Ages – the Merino (Bruford & Townsend 2006; Kijas *et al.* 2012; Tapio 2006, 17; see also **Paper V**). This influence can explain the homogeneous genetic diversity in modern populations (Tapio *et al.* 2005b, 453). In northern sheep, however, introgression has been minimal and they are repeatedly shown to be genetically more distinct from the modern breeds. Based on a microsatellite study, Estonian local sheep populations have shown recent population size reduction and high within-population inbreeding (especially the population on Ruhnu island), but nevertheless yield an important genetic diversity among the northern European sheep breeds (Tapio *et al.* 2005a). Kihnu sheep have also been shown to be genetically distinct from modern breeds and from other primitive northern European native breeds (Saarma 2009; Tapio *et al.* in preparation). Although the native breeds have not shown to form tight groups, they have a common origin and similar genetic construction (Tapio *et al.* 2005a, 3961). Native breeds are very much valued for conservation of genetic variability among the world's sheep breeds because of their distinctiveness (*e.g.* Lawson Handley *et al.* 2007; Tapio *et al.* 2010). Nevertheless, direct evidence of ancient populations would facilitate the study of ancient genetic diversity.

The expansion of domestic sheep from the Near East into Europe revealed by the archaeological evidence is also seen at the genetic level in ancient and modern populations. The divergence observed in present-day European breeds has been suggested to result from a major migration route from Southwest Asia to the Mediterranean region and via central Europe to Britain and the Nordic regions (Pereira *et al.* 2006; Kijas *et al.* 2012). Based on the observed population expansions, the first major sheep migratory wave across eastern Eurasia – of lineages A and B – probably occurred roughly 6,400–6,800 years ago, and influenced by prehistoric west-east commercial trade (Lv *et al.* 2015; see also Tapio *et al.* 2006). Migrations from an eastern origin, such as from Russian areas, may have influenced northern European sheep populations, most likely, in the time of the Vikings and their extensive trade – this influence might be reflected in the present distribution of haplogroup A (Tapio 2006, 36; Tapio *et al.* 2006, 1781), although later introgressions from the east might had occurred as well, shaping modern day breeds (Bruford & Townsend 2006, 315).

Recently, the Y chromosome has gained attention in scientific research of livestock species (Meadows *et al.* 2004; 2006; Meadows & Kijas 2009; Oner *et al.* 2011; Zhang *et al.* 2012; 2014; Niemi *et al.* 2013). Geographical distribution of Y chromosome haplotypes revealed a correlation with historically known colonial migration and the migration out of the domestication centre to Africa (Meadows *et al.* 2006, 451; Kijas *et al.* 2012, 9–10). It has also shown a paternal genetic homogeneity (Ferencakovic *et al.* 2013, 188; Zhang *et al.* 2014) and suggested that domestic sheep are free from signatures of wild sheep introgression (Meadows & Kijas 2009).

Currently, sheep mtDNA and Y chromosome data have been analysed simultaneously only in a few studies (Ferencakovic *et al.* 2013; Niemi *et al.* 2013), yet it is important to combine the data gained from different markers. These studies have raised new questions, although sharing information from both is a complex issue. Nevertheless, new insights regarding the distribution of haplotypes and lineages, or the affinities between certain breeds continue to be revealed as research continues with the growing number of sampled individuals, populations, breeds and genetic markers (*e.g.* Zhang *et al.* 2014).

3. MATERIAL AND METHODS

This thesis combines zooarchaeological material and genetic data. The faunal assemblages and zooarchaeological methods (detailed descriptions in **Papers I**, **II**, **IV**) are firstly described, followed by the aDNA analyses (detailed descriptions in **Papers III**, **V**) in line with the outlined objectives.

3.1. Principles for the selection of the osteological assemblages and aDNA samples

Faunal remains are an important part of almost every archaeological fieldwork project, yielding special value for historical source and cultural inheritance information (Lõugas *et al.* 2008, 42). Osteological collections in Estonia are mostly stored in Tallinn University[28] and in the University of Tartu, and to a lesser extent in some of the museums (for the museum collections incorporated in this study see **Paper III**, 210; **Paper V**, S1 Table).

The faunal assemblages analysed in this study represent the majority of the osteological material excavated within the last few decades in Viljandi and Karksi. **Selection of assemblages for osteological analysis** was induced by the following factors (for the total incorporated assemblages in the osteological research see **Paper IV**, Table 1):

1. <u>Spatial principle and state of research</u>: subject to the previous zooarchaeological work (Saks & Valk 2002; Haak 2007; Rannamäe 2010a, 2010b; for the list of unpublished identification reports by E. Järv and P. Saks see **Paper IV**), the focus was on Late Iron Age and medieval Viljandi – an important centre, largely investigated in 1987–2004 – where the settlement-castle-town-suburb differentiation allowed analysing the various consumption patterns with historically and socially different contexts (see **Paper I**, Fig. 1; **Paper II**, Fig. 1; **Paper IV**, Fig. 1). Viljandi's medieval material was complemented with the nearby contemporaneous Karksi castle, where archaeological excavations in 2011–2012 allowed the author to be part of the exploration and documentation of the exceptional faunal material, mainly from the late 13th century (**Paper IV**, Fig. 1; see also Valk *et al.* 2012; 2013).

2. <u>Temporal principle</u>: assemblages from the final part of the Late Iron Age to the first century of the Early Modern Period were incorporated, and divided into four periods in order to investigate the changes in animal consumption over time:

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[28] In 2012 most of the bone collections of the Tallinn University were packaged and moved to a rented storehouse with no access to the bone boxes – a fact that has substantially influenced the zooarchaeological research in the last few years in Estonia, including the current study.

a) time before the crusades (from the late 10th/11th c.[29] until *ca.* AD 1225) (**Papers II**, **IV**);
b) first century of the Middle Ages (from *ca.* AD 1225 to the mid-14th c.), as during the excavations these deposits have often been possible to separate from the rest of the medieval deposits (Haak & Rannamäe 2014; **Papers I**, **II**, **IV**);
c) Middle Ages (from the mid-13th to the mid-16th c.) (Rannamäe 2010a; 2010b; **Paper IV**);
d) Post-Medieval / Early Modern Period – Livonian War and the following century (from the 2nd half of the 16th to the end of the 17th c.).

Samples for aDNA analyses were selected from an ample geographical and temporal coverage from all Estonia, and additionally from several countries in Europe. However, the selection was constrained by standard archaeological contingencies of preservation and accessibility, plus the limitations of taxonomical identification of sheep remains. A total number of 134 ancient sheep specimens were sampled. Several principles were followed considering the sample selection (for details see **Paper III**, Tables S1, S2; **Paper V**, S1 Table):

1. State of research: assemblages that had been previously identified were favoured; unidentified assemblages were browsed for suitable sheep samples.
2. State of preservation: completeness of a specimen in order to separate sheep from goats, and sufficient condition of a bone structure based on visual inspection.
3. Spatial principle: samples had to cover a wide geographical range, including both rural and urban assemblages – from towns, castles, manors, monasteries, hillforts, settlement sites, field remains and burials in mainland Estonia, as well as on Saaremaa Island (see **Paper III**, Fig. 1; **Paper V**, Fig. 1). Because of the osteological focus on Viljandi and Karksi material, a large part of the samples (n = 22) for aDNA analysis were selected from those collections.
4. Temporal principle: samples had to cover a wide period, *i.e.* from the Middle Bronze Age to Modern Period (1200 BC to AD 1900s) plus the present-day Kihnu native sheep. The earliest evidence from the Late Neolithic was deliberately left out because of the complexity of the matter of first domesticates in Estonia and a need for additional radiocarbon dating and the intent to keep the valuable samples for future whole-genome studies. The final dataset analysed in **Paper V** was divided into four temporal cohorts, which were different from the periods concerned

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[29] In **Paper II** the occupation in Viljandi settlement has been stated to start from the 10th century. In the present thesis the formation of occupation layers in Viljandi started in the 11th century (Valk & Rannamäe 2015, 127).

in the zooarchaeological analysis (due to the differences in source material and the level of analysis):

a) Middle/Late Bronze Age and Iron Age (1200 BC – AD 1225);
b) Middle Ages (AD 1225–1550);
c) Early Modern and Modern Period (AD 1550 – first half of the 20th c.);
d) present-day Kihnu native sheep.

There is a potential bias in this temporal grouping since Kihnu sheep represent a contemporaneous 'living population', while the ancient samples are drawn from a group of individuals living over several centuries, and thus may have artificially inflated diversity values. Nevertheless, these matters did not seem to have played a substantial role in the interpretation of the results (see **Paper V**).

5. Chronological/micro-regional principle: micro-regions of Viljandi-Karksi (south-western Estonia), Tartu-Lohkva (eastern Estonia) and Saaremaa Island (western Estonia) were selected to study the fluctuations of genetic diversity over a long chronological time span. The selection followed the principles of having a sufficient amount of successfully amplified samples and having both the mainland and an island represented.
6. Comparative principle: to include regions outside Estonia, samples from neighbouring areas of contemporaneous periods were favoured (from Russia and Latvia), but further contacts (from Poland) were also of interest, covering a time span from AD 0–1700. The Neolithic Greek samples from around 6800 BC were included as background data since the GenBank database still lacks ancient reference material for sheep (for details see **Paper V**, S1 Table). Additional data from GenBank was chosen to reflect potential ancient and modern affinities with Estonian sheep and plausible connections to Estonia in both prehistoric and modern times from different Eurasian regions (for details see **Paper III**, 3, Table S2; **Paper V**).
7. Bridging the ancient populations to present-day native sheep: blood samples from modern Kihnu native sheep had been previously collected (by A. Ärmpalu-Idvand), extracted and sequenced (by U. Saarma), and resequenced for the current study (**Paper V**). Kihnu sheep were integrated as an important part of the research in order to study the continuity of ancient lineages into present-day populations.

Naturally, the temporal and chronological aspects of the osteological material are very much dependent on dating accuracy. Age of the faunal remains is usually designated based on archaeological stratigraphy from which the remains are collected, but direct dating has also proven to be a crucial part of the research (*e.g.* Bläuer & Kantanen 2013; Niemi *et al.* 2013). Generally, the contextual dating is reliable and the interpretations made on large assemblages would not be substantially biased with some mixing of the material. However, a single specimen should be more critically assessed and radiocarbon dating applied for detailed analyses. The present work shows how important it is to date the faunal specimens and not rely solely on the contextual data, as many radiocarbon dated samples turned out to be substantially younger than expected when compared to the archaeological context (for details see **Paper V**, S1 Table, S2 Text).

3.2. Applied zooarchaeological methods

The level of documentation, identification and analysis of the faunal remains are dependent on several factors, of which the following are highlighted: 1) fieldwork methods (excavation, collection and documentation of the zooarchaeological material); 2) preservation of the material; 3) researcher's methods and objectives. Methods used in the current study could be regarded as the most commonly applied in zooarchaeological studies. Part of the study relies on previously analysed material from the Late Iron Age Viljandi settlement site and some of the castle assemblages (for details see **Paper IV**, Table 1). Here the methods applied to the assemblages identified by the author[30] are briefly reacquainted (for details see **Papers I**, **II**, **IV**).

The specimens were identified by morphological features with the help of the reference collections of the Zoomedicum of the Estonian University of Life Sciences, the Department of Archaeology of the University of Tartu, and the Archaeological Research Collection of the Tallinn University. In addition, bone atlases were used (Schmid 1972; Lepiksaar 1981; Barone 1999; Ernits 2000; Ernits & Saks 2004; Tomek & Bocheński 2009a; 2009b; Ernits & Nahkur 2013). First, the taxonomy, anatomical element and level of fragmentation of the specimen were recorded as usually done in the identification of every faunal assemblage. Data was quantified as the number of identified specimens (NISP) and the minimum number of individuals (MNI). These quantification methods, however, are not free of problems (see also Lyman 2008, 29–45). NISP does not determine the assemblage, but represents only a fraction of the once deposited remains, which in turn form only part of what really was consumed. Therefore, the commonly used estimate of MNI could be inconsistent and not reflect the real number of animals kept or slaughtered at a site during a period of time (*e.g.* Wigh 2001, 45). NISP and MNI are also very dependent on the fragmenta-

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[30] The incorporated bone assemblages identified and analysed by the author in 2009–2015: Viljandi castle (VM 10922) and town (Vaksali Str. [VM 11090], Viljandi Museum [VM 10942], Pikk Str. [no code given]), Karksi castle (TÜ 1929), Tartu town (Botanical Garden [TM 2032]), Jõelähtme stone-cist graves (AI 5306), Väo Jaani stone graves (AI 5220), Alt-Laari settlement site (TÜ 1695), Aakre Kivivare hillfort (TÜ 1928), Kiltsi manor (RM 6782/A 160), Proosa field remains (TÜ 1770), as well as Vybuty settlement site (no code given) and Pskov town (no code given) in Russia. Other assemblages mentioned in the study have previously been identified by Eha Järv and Paul Saks (Estonian University of Life Sciences), and Liina Maldre and Lembi Lõugas (Tallinn University).

tion of the material, which in turn is affected by various taphonomic[31] processes. The assessment of NISP and MNI for sheep is even more complicated because it is often interfered by the presence of goat bones. The skeletal elements of these two species have very similar morphology and are therefore difficult to distinguish, especially if the material is extensively fragmented. There are several studies about distinguishing sheep and goat by skeletal elements, of which the ones by Boessneck (1969) and Boessneck *et al.* (1964) were most often used here, but still, they have mostly been analysed together. Therefore, it must be borne in mind that as the recorded diversity of species and distribution of body parts forms the basis of the consumption patterns, the shortcoming of recognizing the sheep specimens in the material might alter our knowledge on the importance of the species.

Consumption of animals is reflected in the presence and structure of the faunal remains. Typical material comes from the waste of everyday butchery and food preparation, as evident from the presence of cut and gnawing marks, and the distribution of skeletal elements. Sometimes atypical assemblages like butchering and bone processing waste occur as well. In general, cranial fragments and extremities reflect the process of slaughtering and processing the animal, and parts of the body as well as the upper parts of the limbs tend to reflect cooking and eating. It is then possible to deduce which activities occurred on the site based on the character of these assemblages. Zooarchaeological material, though, is hardly ever clear-cut, and it must be remembered that the interpretations usually apply only to the particular excavation site, and cannot be extrapolated to the whole object or area. Moreover, the period of deposition covers often several centuries, which reduces the relevance of the counted NISP and MNI.

Ageing and sexing of the faunal specimens help to assess the herd management. The culling time can not only imply whether the flock was used for meat or milk, but also for evaluating the degree of social differences, as is the case, for example, with the consumption of juvenile animals (Valk *et al.* 2013, 80–82; **Paper I**, 303–304; **Paper II**, 55; **Paper IV**). There are many methods developed for determining the age for sheep and goats based on their bones and teeth (*e.g.* Moran & O'Connor 1994; Greenfield & Arnold 2008) but these can be quite variable and yield difficulties. For example, the methods that are based on modern populations and breeds, may not be appropriate to apply to ancient domestic animals (see *e.g.* Zeder 2006c). The development of the skeletal system is very much dependent on the environmental conditions and the nutrition of the animal – factors that have changed over time. Of great relevance are also the individual changes in the body that affect the development of every single individual documented, and the fact that only partial evidence of an animal is available for the researcher. Known methods of epiphyseal fusion by Silver

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[31] Taphonomy – study of the processes by which animal bones are transformed by human and natural processes during their incorporation into archaeological deposits, their subsequent long-term preservation within those deposits, and their recovery by archaeologists (Darvill 2008, 448).

(1969, 285–286), and teeth eruption by Schmid (1972, Table X) were used in the current study. Although these methods are occasionally considered as outdated, they have been considered sufficient for the purposes of this research, because the questions regarding the age structures were covered only slightly. Sex structure is even more difficult to assess, because usually it is calculated only based on available measurements on specific skeletal elements and is therefore dependent on large series of data. Within the current material, sex has been estimated only for cattle and goat populations in one urban assemblage in Viljandi (Rannamäe 2010a). The assignment of a bone specimen to a ram or ewe has only been possible for single individuals because both male and female sheep can have horns, and sheep specimens are only occasionally separable from goats. No sex estimations on metrical series have been conducted.

Standardised measures (according to the method established by von den Driesch 1976) were taken, mainly because these lay the grounds for the future morphometrical studies, and were also used in a current study to calculate the withers heights of six species – cattle, sheep, goat, pig, horse and dog. The withers height calculations for sheep followed the method established by Teichert (1975) and aimed at a general overview of the probable size of the animals and possible temporal fluctuations therein.

Every bone specimen was examined individually to document the taphonomical features. Although there are various aspects regarding the preservation and utilisation of the bone or tooth find, in the current study only thanatic processes were studied. These processes comprise the factors that bring about the death and deposition of the remains of animals – mostly slaughtering, butchering, cooking and consuming, of which, in the course of the current study, the cut and gnawing marks were most often recorded (see also Rannamäe 2010a, 12–13).

Traces of pathologies and any anomalies were recorded when detected. These features yielded, for example, healed bone fractures, developmental disorders, abnormally worn teeth, and age-specific wear of joints. It is important to note though that the documentation of anomalies is most probably incomplete, as this kind of data might be left unseen to an untrained eye. The material would need to be reexamined for any additional pathologies and anomalies for future studies on the health of past sheep populations.

3.3. aDNA work

The focus of the current study – the diversity of mtDNA lineages – has been not only defined by the research possibilities in Estonia, but also by the characteristics of mtDNA discussed above, the existing reference material in the genetic databases and cost-efficient laboratory work.

Ancient DNA work comprised two major components conducted in separate laboratories: 1) the bone or tooth specimen was sampled in a sterile aDNA lab, followed by the extraction and amplification of DNA; 2) post-PCR work and

DNA sequencing were conducted in regular laboratories. The detailed protocols for the lab work have been described in **Papers III** and **V**, while here some of the general tendencies are provided for what was considered when extracting aDNA and analysing sequences.

3.3.1. Sampling, DNA extraction and sequence amplification

Sheep specimens were sampled for analysis of a ~599 bp section of the hypervariable mtDNA control region and the 130 bp sequence in the 5'-promoter region of the sex determining protein (*SRY*) gene on the ovine Y-chromosome. Sample preparation and DNA extraction of archaeological sheep bones were conducted in the dedicated aDNA laboratories at the Natural Resources Institute Finland, Jokioinen, Finland (for details see **Paper III**) and at the University of Tartu, Estonia (for details see **Paper V**). Sample preparation and DNA extraction followed strict protocols for in-laboratory contamination control and detection (Cooper & Poinar 2000; Poinar 2003; Yang & Watt 2005). Both in Estonia and Finland, the post-PCR work was done in separate laboratories, located in separate buildings. In Finland, both lab works were conducted by the author in strict order to avoid the cross-contamination between the labs[32]. In Estonia, sampling, extraction and pre-PCR work was done by the author, while post-PCR work was conducted by U. Saarma. Sterile workplaces with UV treatment and bleach[33]/ethanol[34], whole body protection and negative controls in extraction and PCR were a routine part of the work.

DNA was extracted using silica spin column protocols (Yang *et al.* 1998; amended by Niemi *et al.* 2013) with slight modifications (see **Paper III; Paper V**, S1 Text). Briefly, the sample was prepared by removing the outer layer of the bone and drilling 0.5 ml of bone powder. The powder was dissolved in an extraction buffer and incubated overnight in a shaker. The sample was then concentrated using Amicon Filter Units (Merck Millipore, Germany). The resulting supernatant was then bound to the silica-based column, washed and eluted with the buffers of QIAquick PCR Purification Kit (Qiagen, Germany). The mtDNA control region and the *SRY* gene of the Y-chromosome were then amplified in separate PCRs using a HotStarTaq DNA polymerase Kit (Qiagen, Sweden). The sheep-specific primer pairs (designed by M. Niemi, see Niemi *et al.* 2013; **Paper III**, Table S3; **Paper V**, S2 Table) yielding overlapping sequences were used. Each of the samples was amplified at least twice. The

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[32] After working in the post-PCR lab, it was not allowed to go to the sterile aDNA lab on the same day. In Finland, M. Niemi and T.-M. Hamama very much guided and helped with the lab work.

[33] Bleach – sodium hypochlorite (NaOCl), one of the most commonly used agencies for the decontamination in aDNA work (see also Kemp & Smith 2005; Fukuzaki 2006; Barta *et al.* 2013).

[34] Two kind of ethanols were used: 1) 96 % EtOH; 2) 70 % EtOH, 30 % 2-Propanol (Flore HD, Flore Keemia OÜ, Estonia).

success of the PCR was checked by electrophoresis[35]. All samples were sequenced in both directions to reduce the probability of sequencing errors. The purification and sequencing of the PCR products was performed following Niemi *et al.* (2013) and Keis *et al.* (2013), using the same primers for sequencing as for the initial PCR. Sequencing products were further analysed by service-providers (Natural Resources Institute Finland; Core Laboratory, Estonian Biocentre).

3.3.2. DNA preservation and authentication

There are two major difficulties in extracting aDNA: the contamination of the sample and the degradation of DNA (Villablanca 1994, 34). The first threat was avoided with careful handling of the ancient samples in a dedicated sterile lab. Extraction of the aDNA is much more difficult than from a tissue of a contemporary organism because only short fragments of DNA are left in ancient material. Moreover, extraction of endogeneous DNA might be inhibited by the presence of other organism DNA in a sample, such as bacteria, fungi, traces of human and other animals (Herrmann & Hummel 1994, 11; Brown & Brown 2011, 7, 25). The second threat – the degradation of DNA – could not be avoided because the diagenetic modification and DNA fragmentation starts immediately after the death of the organism (see also Pääbo 1989; 1990; Brown & Brown 2011, 7). Therefore, extreme caution should be taken when working with ancient samples.

It is important to ensure that the target DNA (and not any contaminant) is amplified to obtain authentic sequences. Several extractions and amplifications of each sample were conducted, negative controls and blank extracts added and only reproducible results included in the analyses. The existence of contaminated or damaged DNA comes to light in two possible ways (see also Herrmann & Hummel 1994, 3). Firstly, no intact target region is available for PCR, the primers fail to amplify and no amplified product is obtained. Secondly, nucleotide modifications in the primer-binding sites may affect PCR efficiency. The mutations may also occur on the sequenced region. To confirm that the mutations are authentic and not chemical alteration post-mortem or during PCR, additional extraction and/or amplification is needed. The mutation can only be regarded as authentic if it is detected in the majority of sequences. A DNA titration test was performed to ascertain the optimal volume of aDNA for sequencing and to avoid an excessive number of inhibitors (by the author and U. Saarma). The test included different volumes of extracted aDNA and the PCR followed essentially the protocol described above and was conducted on

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[35] Electrophoresis – PCR products are run on an agarose gel plate with an electrical charge that separates DNA molecules by length (Brown & Brown 2011, 28; see also Epplen 1994, 15), and visualised with ethidium bromide (EtBr) and UV illumination. In current research electrophoresis was performed in a 1 % or 2 % agarose gel consisting of 1xTBE or 1xTAE buffer and EtBr.

two samples (54OaKir3, 95OaVec1) in a total reaction of 25 µl: 15 µl of HotStarTaq Master-mix (Qiagen, Sweden) was added to 10 µl of aDNA extract and H_2O mix (where the ratio of aDNA and H_2O changed with a pace of 0, 1, 2, 3, 4, 5, 7, 10 µl). The results of the titration test showed the optimal volume of DNA to be 3 µl.

No significant differences in the preservation of DNA were detected in temporal or spatial cohorts (**Paper V**, S3 Table). The success rate for DNA amplification was as high as 76–77 %, which is a very good result regarding the fact that the samples originated from old collections with various storing conditions (**Paper III**, 212, Table S1; **Paper V**, S1 Table; all sequences are available in GenBank, accession nos. KP052792–KP052815, KU670230–KU670319; Kihnu sheep sequences KX056139–KX056146).

3.3.3. Sequence analysis

The obtained sequences[36] had some base errors that by comparing the different amplifications were edited and trimmed to a consensus sequence using Geneious v.6.1.6. / v.6.1.7. (Kearse *et al.* 2012; http://www.geneious.com). The sequences were pooled into different groupings (spatial or temporal populations) and subjected to further analyses. Several measures of molecular variation were used (for details on data analysis see **Paper III**, 211; **Paper V**):

1. Genetic parameters – number of individuals, segregating (variable) sites and haplotypes, as well as haplotype diversity, nucleotide diversity and Tajima's D values (Tajima 1989) for each cohort were calculated using DnaSP v.5 / v.5.10. (Librado & Rozas 2009). Genetic variability among ancient and modern cohorts was mainly quantified in terms of nucleotide and haplotype diversities (**Paper III**, Tables 1, 2, S4; **Paper V**, Fig. 6, Tables 1, S5, S6).

2. Median-joining networks of the obtained haplotypes were produced using Network v.4.6 / v.4.6.1.3. (Bandelt *et al.* 1999; www.fluxus-engineering.com). This method gave the ability to graphically illustrate the relationships and genetic differences (depicted as mutations on branches) between the haplotypes (depicted as nodes) (**Paper III**, Fig. 3; **Paper V**, Fig. 3, S1).

3. Temporal and geographical patterns were analysed by comparing haplotype groups within geographical regions (**Paper III**, Fig. 4, Table 3). The

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[36] Three samples (IDs 2OaKivi1, 3OaOrdu1, 26OaSuu1) were included in a pilot data in **Paper III** but omitted from the final analysis in **Paper V**, because they shared an identical sequence with another sample from the same site; also the morphological analysis failed to assign the identical sequences to separate individuals. Two samples (IDs 54OaKir3, 134OaKar2) were omitted from the analysis in an early phase because of the same reasons.

differences in frequencies in all temporal and geographical approaches were tested with Pearson's chi-square test in SPSS v.11.5.0.

4. Continuity of haplotypes through time was assessed using a three-dimensional statistical parsimony network through TempNet (Prost & Anderson 2011) implemented through the R package v.3.1.2 (R Core Team 2014) (**Paper V**, Figs. 4, 5).
5. The phylogenetic relationship between the temporal cohorts, pairwise population fixation index values (Reynolds *et al.* 1983) and analysis of molecular variation were calculated using Arlequin v.3.5.1.2 (Excoffier & Lischer 2010) (**Paper V**, Tables 2, S4).

The data analysis was approached from two perspectives. The primary focus was on Estonian material in order to assess the presence, continuity, and changes of unique and shared haplotypes through time. The secondary perspective of the analysis was the comparison of Estonian data with other regions in Eurasia in an attempt to advance our understanding of the origins of the maternal lineages that contributed to the formation of the ancient sheep populations in Estonia. The geographical and temporal cohorts were pooled and analysed according to these perspectives (for details see **Paper III**, 210–211; **Paper V**).

4. RESULTS AND DISCUSSION

Zooarchaeological and genetic analyses provided new data regarding the development of the local sheep populations in Estonia and affinities to rest of the European breeds. Additionally, pieces of evidence attained during the course of the study made it possible to draw a picture of the possible appearance of our past sheep. These topics are discussed in detail in the papers included in this dissertation, and complemented below.

4.1. Genetic diversity in Estonian sheep

The first populations of domesticates in Late Neolithic Estonia were probably small, and since being far from the domestication centre, with a reduced genetic diversity compared to the south-eastern sheep populations (see Ch. 2.3.3). It has been suggested that the number and diversity of lineages decreases as the distance increases from the domestication areas since only a subset of animals disperse during migrations. The scarcity of rarer haplotypes and dominance of old haplotypes was evident in the present study (**Paper III**, Fig. 4, Table 3), a result of the spread of sheep from Southwest Asia to Northern Europe. The ancient haplotypes of Estonian sheep observed in phylogenetic networks (**Paper III**, Fig. 3; **Paper V**, Figs. 3, S1) were found in modern sheep breeds from different regions across Eurasia, confirming that these populations share their origin with the sheep from the domestication centre (**Paper III**, 213). Similar to ancient and modern sheep from other European regions (including Baltic and Nordic sheep breeds), Estonian ancient sheep show a high haplotype diversity belonging to haplogroups A (10 %) and B (90 %) (**Paper III**, Fig. 3; **Paper V**, Fig. 3). Moreover, Estonian sheep carry the SNP *G-oY1* of the Y-chromosome characteristic to northern European sheep (**Paper III**, 216; see also Niemi *et al.* 2013, Fig. 2; Zhang *et al.* 2014).

The maternal genetic diversity from different periods observed in Estonia suggests that the development of sheep populations has been rather homogeneous from the Middle Bronze Age until the large-scale breeding in the 19th century. The comparison of haplotype and nucleotide diversity indices revealed no significant differences among the ancient temporal cohorts (**Paper V**, Fig 6, Table 1), including the analysed micro-regions (**Paper V**, Fig. 5). However, while the general homogeneity remained valid, some evidence for changes in the genetic diversity appeared in further data analyses (**Paper V**), opening up a discussion on a wider zooarchaeological and historical scale. Changes in genetic diversity – the suggested population expansion in the 13th century, and decrease of haplotype diversity in Kihnu native sheep – were associated with the possible animal exchange due to the widening trade at the beginning of the Middle Ages, and the beginning of large-scale breeding in the 19th century, respectively.

4.2. Effect of animal exchange on the local sheep populations

The frequent animal exchange, particularly of breeding ewes, through ancient trade routes is believed to have contributed to the observed geographic pattern of sheep lineages in Asia (Lv *et al.* 2015). Similar widespread movements of livestock are not known in the northern fringe of Europe, where sheep husbandry was economically less relevant, and trade probably played only a marginal part in forming the local gene pool. Only in the case of the Viking Age traders it has been hypothesised that live animals might have been distributed across northern Europe (see Ch. 2.3.3). The livestock trade is very hard to follow in (zoo)archaeological evidence. Thus, a sheep sample from a Viking Age burial of Scandinavian origin in Saaremaa Island (Salme I ship; Peets *et al.* 2011; 2013a) was chosen for aDNA analysis to address the possibility of foreign connections. It is believed that trade in Viking Age Estonia occurred mostly between north-western Russia and northern Latvia, which belonged to the same cultural sphere (Tvauri 2012, 231). Additionally, agricultural products could have been exported to northern areas of present-day Finland and Karelia, where the natural conditions were poorer (Tvauri 2012, 233), though connections towards Scandinavia are not excluded. It is unknown whether the traded products might have yielded any livestock, but it should be considered very unlikely due to the primitive means of transportation (Tvauri 2012, 233). In Salme, the sheep remains of an unknown number of individuals were scattered around the burial (Konsa *et al.* 2009, 61), coming mostly from the meaty trunk parts of the animals, and were therefore associated with the goods used in the burial ritual (Allmäe *et al.* 2011, 103, 111; see also Maldre 2011). A sheep sample (ID 25OaSal1) was tested for the mtDNA haplotype to verify if the mutton for the deceased might have had a Scandinavian origin. The obtained haplotype was compared with the rest of the Estonian ancient sheep in a median-joining network (**Paper V**, Fig. 3). The results placed Salme sheep in the predominating haplogroup B with close relations to other ancient and modern sheep, and showed no specific signals of being distant to other archaeological sheep sequences. Therefore, sheep remains in the burial were most probably of local origin. This result supports the previously proposed archaeological interpretation of placing only parts of the carcass into the grave, therefore, the animal(s) slaughtered and consumed most likely came from the nearby local herders.

Sheep wool has played an important role in the economy and wealth of different societies in Europe from the Bronze Age to the Medieval Period (Ryder 1983, 72, 75, 137, 158; Bökönyi 1988, 189). In Livonia, the western European wool textiles were favoured among the urban inhabitants (Rammo 2015, 70), while use of local wool prevailed in the rural areas all through the Middle Ages (Rammo 2015, 64). The extensive wool trade suggests a high value for sheep, but the animals themselves were most probably traded sparingly. It is believed that live animals were a luxury good (Hurley 1999, 17). The occasional import of rams for breeding with local sheep might have occurred in Livonia based on examples from other regions in Europe (*e.g.* Lancioni *et al.* 2013; Niemi *et al.* 2013). In such cases, those individuals would probably have had only a limited effect on the local gene pool (Kijas *et al.* 2012; Niemi *et al.* 2013), and certainly would not be visible in the maternal lineages, as is the case in the current study. Although colonists may have brought in new livestock, the subsequent development of sheep populations was most probably autonomic, especially in the first centuries after the crusades (see also Ryder 1983, 76). Trade had probably a role of higher importance for other livestock such as cattle, because of a demand for more productive dairy and beef cattle (see Ch. 2.2.3).

4.3. Transition to the Middle Ages

The transition from the Late Iron Age to the Middle Ages in the 13th century, associated with the crusades and the newly established power regime, had certainly an effect on animal husbandry. This effect on domestic sheep is briefly overviewed here and has been discussed in more detail in **Papers II**, **IV** and **V**.

The demand for food and the involvement of broader networks of communication increased with the beginning of the Middle Ages. The need for food supplies grew as the human population increased twofold from around AD 1200 to AD 1550 (Palli 1996, 92), raising the demand and subsequently the expansion of local livestock populations. Based on only a number of archaeofaunal assemblages, the increase in the actual abundance of the livestock is difficult to access. Nevertheless, it is possible to calculate the proportional differences between the periods before and after the transition to the Middle Ages. Despite the presumed changes in Estonian society associated with the crusades, the general character of meat consumption seems not to have changed much in Viljandi (**Papers II**, **IV**). The Late Iron Age Estonian settlement had a greater diversity of game species and the presence of horse remains when compared with the 13th century German castle and the earliest occupation layers of the medieval town. However, bones of domestic animals form the overwhelming majority in both periods. Despite the 'countless' amounts of livestock that were taken during the 13th century crusades (*e.g.* HCL XIV.10) and the degree of social polarisation between the colonists and the colonised, most of the local farmers and their livestock remained intact, and the economic basis remained consistent, with the new power centres dependent on the indigenous population and their farming (Pluskowski & Valk 2016; Pluskowski *et al.* forthcoming; see also Ryder 1983, 182–183; Põltsam 1999, 35). In particular, sheep husbandry has been stated to bloom in the 13th century, and continued to be prevalent throughout the Middle Ages (Põltsam 1999, 32 and references therein). It must be remembered though that the analysed assemblages reflect only the medieval urban consumption, and even if the animals consumed in the town originated from the nearby farms, there might be different patterns revealed with rural assemblages included in future studies. Nevertheless, the findings of the current analysis are in agreement with the genetic data that shows the expanding sheep population in the first centuries of the Middle Ages: while the genetic diversity over time remained rather unchanging, the calculations on molecular variation revealed a potential population expansion (**Paper V**, Table 1).

The obtained genetic data initially suggested that the haplotype diversity increased in the Middle Ages, which led to the idea of a probable recurrent import of animals during the Iron Age and the Middle Ages (**Paper III**, 215, Table 2). However, calculations based on a larger sample size in a subsequent study did not confirm the high haplotype diversity during the Middle Ages when compared to previous periods. Instead, the results of this latter study suggested a probable population expansion (**Paper V**, Table 1). Moreover, both works agreed that changes in the development of sheep husbandry after the crusades did occur and in either case reflect the increasing utilisation of livestock.

Slight changes also occurred when analysing the micro-regions Viljandi-Karksi, Saaremaa Island and Tartu-Lohkva, as in case of the first two, interestingly no prehistoric haplotypes continued into the medieval period (**Paper V**, Fig. 5). However, since the sample sizes are small, caution should be taken not to over interpret the results.

The changing environment might have also affected the observed population expansion. It has been suggested that the expanding agriculture and changes in land use right after the crusades would reflect in the paleoenvironmental indicators (Pluskowski *et al.* forthcoming; see also Põltsam 1999, 35). For example, opening landscapes could be connected with the expanding livestock populations, because sheep and cattle tend to graze in open grasslands. However, the evidence (*e.g.* pollen), is still very vague and complicated. Changes in vegetation have been noted in the vicinity of Karksi castle right after the crusades (Saarse *et al.* 2010; Reitalu *et al.* 2013), but only later, from the second half of the 14th century onwards, can be directly linked to the increase of pastoral land (Valk *et al.* 2009; Pluskowski *et al.* forthcoming). After deforestation, suitable conditions for cattle and sheep husbandry by any means increased (see Maltby 2013, 235). However, open landscapes and sheep pastures should not be necessarily equated, because from historic times we know that the local primitive sheep managed well on 'forest pastures' (Michelson 2013, 64). Therefore, changes in the cultural landscape witnessed in palaeoenvironmental data could have had only a limited effect on sheep husbandry.

4.4. Sheep consumption as indicated by faunal remains

In this thesis, the utilisation and pattern of consumption of livestock was mainly assessed using the distribution of species and skeletal elements, and the age structures on two sites: Viljandi and Karksi. As typical for most to the archaeofaunal assemblages, the material was determined to originate from the everyday butchering and food waste, with an addition from the bone processing remains.

The presence of sheep remains is often biased with those from goats. The remains of both species are often handled together as they are difficult to distinguish, especially in case of extensively fragmented material and/or if the material consists of large numbers of juveniles (*e.g.* **Paper I**, 304). Therefore, it is often difficult to draw conclusions on sheep husbandry alone and assess the details of utilisation. However, sheep usually form the majority of sheep/goat specimens in cases where identification is possible (see Ch. 2.2). This idea implies that sheep husbandry dominated over goat keeping. Therefore, the sheep/goat remains in the faunal assemblages from the Bronze Age to the Middle Ages could be considered to reflect specifically sheep husbandry.

In Viljandi and Karksi, sheep/goat remains constitute around 10–39 % of the total analysed material (**Paper V**, Fig. 2 – note that the lowest sheep/goat proportions in Karksi castle would be complemented by additional specimens, because the identification of a large part of small ungulates remained on sheep/goat/pig level, and therefore the 10 % stated above is most probably biased), which coincides with the known data from medieval assemblages in Estonia (see Ch. 2.2.3). Sheep were consumed mostly for meat, as suggested by the presence of butchering waste of animals from various age structures, and wool as suggested by the remains of older animals. Milk is another by-product of sheep, which was very much valued in Europe during the Middle Ages (see *e.g.* Ryder 1983, 275, 354, 389), but in Estonia the respective evidence is dubious. In the descriptions by W. C. Friebe (1794, 159), sheep were not milked in the 18th century. It is difficult to assess based on osteological material, if this tradition could be traced back to the Middle Ages.

The zooarchaeological material from different contexts in Viljandi provides evidence for differences in livestock consumption, both temporal and spatial, including the reflections of social differences. Usually the socially higher status sites yield a longer list of species, more game (although in very small amounts) and larger consumption of juvenile animals (**Paper I**, 300, 304, 309; **Paper II**, 53). This kind of socially higher level of meat consumption, connected to the feasting activities within the castle, were especially seen in Karksi (Valk *et al.* 2013, 80–82; **Paper V**), but also in Viljandi (**Paper I**). A completely different picture emerged in the town of Viljandi, where game and juvenile animals were less accessible than beef, pork, and mutton. However, it is important to note that when considering the profiling of social status, comparisons between the townspeople and castle inhabitants must be made cautiously – both of these communities included people of varying status (**Paper V**).

The distribution of main livestock species – cattle, sheep/goat, pig – remained roughly the same during the whole Middle Ages and the subsequent century (**Paper V**; see also Haak 2007). However, some fluctuations can be noted. The overall decrease of sheep and goat bones in the medieval period is evident in Viljandi town, while in the castles the relative proportion of this domesticate is higher than in the town and suburbs (**Paper V**, Fig. 2). At first, this partially opposes the genetic data of expanding sheep populations. It is difficult to assess whether the fluctuations reflect changes in animal husbandry, economic factors or simply the incidental characteristics of the bone assemblages. However, several aspects should be considered. First, the osteological data comes only from urban assemblages in one region while genetic data covers a wider time span from the whole of Estonia. Second, some of the analysed periods and sites yielded only a single excavation site that could reflect only a specific consumption. Third, the faunal assemblages cover only a fraction of the several centuries of animal utilisation. Fourth, the faunal assemblages reflect only the final consumption of the animal, *i.e.* for meat. Further analyses on age and sex structures could clarify this issue.

Although consumption for meat tends to be apparent in the archaeological material, sheep carcasses were also exploited for different by-products: horns, hides and bones (**Paper I**, 297, 301; see Oras 2015 for bone pipes made from sheep bones). This possibility was observed in Viljandi castle, where a specific assemblage refers to bone and horn processing (**Paper I**). The evidence is not direct because the large number of cranial fragments from cattle, sheep and goat came with almost no horn cores (**Paper I**, 298, 300; **Paper II**, 53). The pattern has been explained by the removal of horns with skinning and/or taking to some other location for processing (**Paper I**, 301, 304). It has also been suggested that lack of horn cores could indicate that sheep were mostly polled (see also Maldre 2007b, 63). However, this scenario seems unlikely because the horn cores of cattle are missing as well (see **Paper I**, 300) and there is no archaeological evidence of polled cattle from any time period in Estonia (Maldre 2007b, 63). The same pattern of missing horn cores has been recorded in other prehistoric and medieval sites in Estonia (*e.g.* Maldre 2007a, 33; 2007b, 63; 2012a, 115; 2012b, 81; Lõugas *et al.* 2012), and, for example, in Russia (Maltby 2013, 237) and Sweden (Lepiksaar 1980, 16).

4.5. The harsh times from the 16th to 19th century and the present situation

The zooarchaeological material from the Middle Ages is often well framed within two decisive events – the crusades in the 13th century and the Livonian War in the 16th century. However, the following periods are not as well defined in the matter of clarity of archaeological stratigraphy. The excavated deposits of Early Modern and Modern Period often consist of debris and redeposited soils, making the contextual dating of associated faunal remains difficult (**Paper I**, 296; **Paper V**). The complex times of warfare and famines in the Early Modern and Modern Periods are not evident in the genetic data, which would require more extensive sampling from such periods and the analysis of additional genetic markers. The inability to assign a precise archaeological context for the sample might also affect the genetic results.

The indigenous sheep populations in Estonia most probably continued to expand after the Middle Ages, and seem not to have been affected by the great wars and several famines as would be assumed, at least in the long term. For example, the great famine of 1695–1697 followed by the events of the Great Northern War (1700–1710 in Estonia) and the following plague were devastating to human populations (see Palli 1996, 92; 1997, 27). Yet, these events have been relatively short and are therefore not reflected in the analysed osteological data. Despite being a period of warfare, no significant changes in animal exploitation are evident, based on the distribution of consumed species. The preferences for meat in the castles remained roughly the same as it had been in the Middle Ages. In the town an increase in cattle bones over the remains of small ungulates did become evident, but this could just reflect the bias of a small sample size (see **Paper IV**). Several harsh winters, crop failures, famine and murrain are known in the 19th century, causing lack of fodder and animal diseases, which resulted in the deaths of enormous amounts of sheep and other livestock (Karelson 1981, 14; Lust 2015, 151–152). Lust (2015, 9) pointed out that the 19th century famines affected only certain peasants, depending on their agrarian status, and therefore more to do with the problems in the society and economy than crops failure and unfavourable climate. This fact means that the pattern of urban consumption, where most of the faunal evidence derives, could fail to reflect the occasional economical low-points that had taken place in the rural hinterlands. It has also been stated that the recovery of the livestock population after these events were rather rapid (Karelson 1981, 11). This situation might have been aided by the traits of the primitive and hardy sheep, who were more likely to survive harsh climatic conditions and able to survive winters with only dry leaves for feed (Michelson 2013, 64). Moreover, the general homogeneity and continuity of sheep populations through time may reflect their hardiness.

In the 20th century, because of large-scale breed improvement, the population of local sheep started to gradually decline and reached its low point in the last few decades. This process may explain the low genetic diversity observed for the Kihnu sheep analysed in this study, with lower haplotype diversity than ancient populations (**Paper V**, Tables 1, 2). Nevertheless, affinities between the Kihnu sheep and ancient populations seem to have prevailed. First, Kihnu sheep showed affinity to the haplotypes characteristic of ancient sheep as early as from the Bronze Age, suggesting that there has been continuity in some of the 'dam lineages' in Estonia for around 3,000 years (**Paper III**, 214–216; **Paper V**). This extensive continuity of core mtDNA haplotypes may result from husbandry practices favouring the maintenance of female animals, which were kept in large numbers for population reproduction and wool production. Secondly, a large portion of Kihnu sheep share common ancestry with sheep from broad geographical and temporal distribution as revealed by median-joining network (**Paper V**, Fig. 3), including medieval Russian and Iron Age Estonian sheep. Ancient samples from Estonia show an affinity with eastern, southern, and northern European ancient sheep, as well as modern Kihnu sheep, based on the genetic differentiation estimates (**Paper V**, Tables 2, S4). However, the Kihnu sheep appear to be genetically more distinct from the other groups. This finding is in agreement with the beginning of large-scale breeding in the 19th century and decline in the native sheep population. This pattern was caused probably by recent population contraction and a small founding population of the present-day native breed, being in accordance with studies on northern European local breeds, including Estonian Ruhnu sheep (see Ch. 2.3.3). The primitive breeds of these regions have a small genetic diversity, while being at the same time genetically distinct from the modern breeds (Tapio *et al.* 2005a; 2005b, 455). It has been suggested, at the molecular level, that there was an initial founder population formed by northern European sheep types who had a common origin with similar genetic structure. This founder population was fragmented into isolated breeds during recent history, with a decrease in the effective population size (Tapio *et al.* 2005a, 3960). In other words, it seems that the group of present-day Northern European short-tailed sheep shared the same basis in the past, but recent breeding differentiates the breeds within this group. The current research did not prove a firm affiliation of the Kihnu sheep to this group of northern breeds, and consequently left open the question whether Estonian native sheep descend from the first migratory wave of the 'primitive' sheep populations (see Ch. 2.1). Nonetheless, the affinities between the maternal lineages of Estonian and other northern European sheep demand further investigation.

4.6. Implications on the appearance of sheep

The available zooarchaeological and genetic data and the early descriptions of local sheep contribute to understanding the appearance of sheep in the past. These findings suggest that the 'local native' appearance prevailed until the large-scale breeding in the 19th century and beyond. The observed affinities (mitochondrial lineages going back from the modern native sheep to the Bronze Age population) suggest that ancient Estonian sheep may have resembled contemporary Kihnu sheep. On the other hand, there is little direct archaeological evidence for how the sheep might have looked like. It is rare to find complexes where animals have been discarded as a whole, allowing study of the individuals more closely – calculate the withers height, assess the body proportions and examine the pathologies. These find contexts are, for example, medieval cesspits (*e.g.* Maldre 1997a; Õunapuu & Maldre 2010), and burials, where (parts of) the animals have been sacrificed as grave goods (*e.g.* Maldre 2003; 2011; Allmäe & Maldre 2005; Allmäe *et al.* 2007; 2009). However, single skeletons reflect traits of only one individual and should be tentatively extrapolated to the whole population.

It has been described how native sheep could survive well grazing on forest pastures and feeding on dry leaves during winters (Vohlonen 1927, 88–91; Jaama 1946, 26–27; Michelson 2013, 64). Other primitive sheep (like Soay) have been described as being very efficient getting nutriments even from a limited diet compared to modern breeds (Ryder 1983, 80–81). The harsh environmental conditions have probably defined the appearance and hardy traits the primitive sheep possess. There are initial descriptions of local sheep from the

18th century as being small and with coarse black wool (Friebe 1794, 158, 298). In the 19th and 20th centuries, local types of sheep retained their primitive looks and were valued for their unpretentious traits and high prolificacy (Jaama 1959, 17). They were described as with poor and uneven quality wool of black and white colours, short tail, little heights, and rams often horned (Jaama 1959, 19). The same traits of wool have also been seen in the archaeological textiles: two-layered, semi-coarse and variable in fibre coarseness, resembling the wool of the modern Kihnu native sheep (see Rammo 2015). Compared to modern-day breeds, the primitive type of sheep truly are small. While modern Estonian breeds could weigh up to 76–95 kg (Piirsalu 2012, 20), the Kihnu rams weigh around 50 kg with withers height around 59–60 cm, and Kihnu ewes weigh 25–40 kg with withers height around 55–57 cm (KMKS 2015, 9).

A characteristic of the archaeological sheep is the small size that reflects the primitive animal husbandry of the past (*e.g.* Bökönyi 1988, 136; Maldre 2007a, 33). The scarce evidence available from the Late Bronze Age Asva settlement in Saaremaa Island, for example, has given the estimated withers height of around 56–69 cm (Lõugas 1994, 79). Data is also sparse from the Late Iron Age. For example, the average height of sheep in the Pada settlement in northern Estonia was around 60 cm (Maldre 2007b, 70) and in Viljandi 54–62 cm (**Paper V**, Fig. 6). The size of animals has been easier to estimate in medieval material, gauging the size for sheep to be 50–69 cm (Maldre 1993; 2008b, 296–297; Rannamäe 2010a, 41–42; **Paper V**, Fig. 6). Osteometric analysis of the material from Viljandi and Karksi revealed that the size of sheep decreased at the beginning of the Middle Ages but then began to increase, and finally exceeded the size of the prehistoric mean (**Paper IV**, Fig. 6). Despite the documented changes in size, there is no evidence for morphological modifications within those species, with the 'local native' appearance probably prevailing until large-scale breeding began in the 19th century. Whether those changes could be due to changes in environmental conditions, nutrition, or even imported additions to the local herds, is impossible to say in the current state of the research. It has been suggested by morphological analyses that medieval sheep in Estonia resembled more those from Russia than from Scandinavia (Maldre 2008b, 301). However, estimations for size must be treated with caution due to the uneven and insufficient sample sizes, sexual differences, and the extensive possibilities for individual variation (see also **Paper I**, 304).

The presence or absence of horns is an integral part of the sheep's appearance. The loss of horns is likely one of the oldest morphological modifications that accompanied domestication (*e.g.* Zeder 2006a, 172; 2006b, 182; Kijas *et al.* 2012, 10). Lack of horn cores and extreme fragmentation of the skulls in faunal assemblages is quite usual (*e.g.* in Viljandi, see Ch. 4.3), and therefore it is often hard to assess how much of the animals were polled, scarred or horned (see *e.g.* Maldre 1997b, 113–114). There have been both horned and hornless ewes recorded in the Late Iron Age (*e.g.* Maldre 2007b, 69) and in the Middle Ages in Estonia, although polled ewes have been prevalent (Maldre 1997a, 103; 2012b, 86). This observation has been speculated as evidence of Estonian medieval sheep to be interbreeding with primitive fur sheep from the west (horns on both sexes) and later with the wool sheep from the east (polled ewes) (Maldre 1997b, 114). The presence or absence of horns in both sexes is also characteristic of extant native sheep (Ärmpalu-Idvand 2009, 7–8; KMKS 2015, 9; see also **Paper V**, Fig. 2), although males have been described to be horned more often than not (Jaama 1946, 81).

Four-hornedness is an interesting feature recorded in Estonian archaeological material. Multi-horned is characteristic of domestic sheep and is known from several sites in Europe before the current era (*e.g.* Ryder 1983, 139; Maldre 2007a, 35). Four-hornedness is a rare trait today, being common only in a few northern European primitive breeds (see Boyd 1964, 132; Peets & Maldre 1995; Dyrmundsson 2005). In Estonian material, this characteristic has been documented in two cases from medieval Tallinn (Maldre 2007a, 35). There has been discussion whether these four horned individuals might either have been imported or could have been a form of mutation of the local animals (Maldre 2007a, 35). These two specimens were incorporated into the aDNA analysis, but revealed no peculiar information (**Paper V**).

5. CONCLUDING REMARKS

This thesis presents zooarchaeological and genetic data of sheep in Estonia from the Bronze Age to the present-day. The data was investigated in order to assess the consumption and utilisation of one of the most common livestock species and to establish a baseline for genetic diversity in ancient sheep in Estonia. Both osteological material and aDNA results suggest an excellent preservation of sheep remains in various archaeological sites in Estonia. Fluctuations in the development and utilisation of sheep populations were assumed at the beginning of this study, as suggested by the archaeological and historical data. The assumptions derived from the known events and shifts (*e.g.* migrations, cultural changes) that had occurred in Estonia from the Bronze Age onwards, particularly during the Late Iron Age and Medieval Period. Instead, a relative stability was revealed – both in the consumption patterns of the local sheep populations, and in the genetic diversity from the Middle Bronze Age to modern native sheep. Therefore, it seems that sheep husbandry has been persistent and relatively autochthonous in the territory of Estonia.

Nevertheless, some changes were observed in the first half of the Middle Ages when sheep populations seem to have expanded due to the growing human populations and the need for subsistence. The analysis of the distribution of species, the age structures of the assemblages, animals' physical characteristics, size and health of different species and the importance of game and fish provided an overview of the availabilities and preferences for faunal resources in the studied locations – Viljandi and Karksi, from the end of the Late Iron Age through to the Early Modern Period. Results on animal exploitation showed continuous dominance of cattle and small ungulates in the faunal assemblages. Historical and archaeological data corroborate the genetic evidence for population expansion of local sheep during the Middle Ages, rather than a significant introduction of imported animals. The current study did not find any evidence of new sheep populations arriving to Estonia in any time period from the Middle Bronze Age to the Middle Ages. There might have been some occasional imports and exports of sheep to neighbouring, and perhaps to more distant areas, but additional data is needed to demonstrate such connections. The first attempts of introducing new breeds occurred from the 17th century onwards, with large-scale breeding programmes starting at the beginning of the 19th century. This introduction led to a population decrease of the local native sheep during the last centuries, which has resulted in a lower genetic diversity in the sampled Kihnu sheep compared to the ancient populations. On the other side, the Kihnu sheep also reveal genetic distance of the extant modern breeds, characteristic to northern European primitive sheep breeds. A connection between the earliest studied sheep and the Kihnu breed suggests a continuity of some of the maternal lineages for roughly three thousand years.

In conclusion, the results concur with existing data from the rest of Europe, in that there has been a wide admixture between sheep breeds during different time periods, and this has led to high diversity in mitochondrial haplotypes.

Overall, the results of the current study suggest that in spite of the observed fluctuations in ancient sheep populations, and changes in ecology, power regime, and other influential historical events, the utilisation of local sheep has been constant, displaying matrilineal continuity from the Middle Bronze Age through the Modern Period, and into modern native sheep.

The study introduced new data in the context of already existing information and contributed to the worldwide GenBank with new data of sheep mtDNA and Y-chromosome. The study outlined general trends concerning the development of sheep populations from the Middle Bronze Age onwards and provided a model to be subsequently tested and complemented by new finds using advanced methods. The current thesis provides a baseline for subsequent studies by bringing together the zooarchaeological and genetic background of sheep history in Estonia and elucidating the origin and historical expansion of local sheep populations in northern Europe. The study provides valuable archaeogenetic data accessible to all researchers with interest in sheep genetics and contributes to the understanding of the history of sheep husbandry not only in Estonia but also in broader areas in the north-eastern part of Europe. The results are expected to be relevant to the modern day breeders of Estonian native sheep, as the overview of the maternal evolutionary history of local sheep provides suggestions for how the present-day state in Estonian native sheep populations have developed and could therefore help in subsequent breeding programmes. Moreover, understanding the structure and the origin of the genetic resources of ancient sheep is hoped to be of aid in the conservation of the valuable resource of genetic diversity of the native breed(s).

The results presented in this thesis are far from representing a total reconstruction of sheep populations in Estonia, but raised several questions to be addressed in the future. Subsequent works should combine data from different genetic markers, including those of nuclear DNA, by high-throughput sequencing and improved aDNA extraction methods. Further genetic, archaeological, and historical studies of modern and ancient sheep in Estonia and neighbouring regions would expand the understanding of both the early stages of the first domesticates in the region as well as the subsequent development of the populations. With additional material and advanced methods, the topic of sheep history would undoubtedly provoke new research challenges.

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SUMMARY IN ESTONIAN

Lambapopulatsioonide kujunemine Eestis pronksiajast tänapäevani zooarheoloogilise leiuainese ning mitokondriaalse DNA liinide põhjal

Sissejuhatus

Lammas kuulub maailmas enimlevinud kariloomade hulka ja on tähtis loomne ressurss inimeste elutegevuses alates tema kodustamisest u 11 000 aastat tagasi. Tänu oma arvukusele, laiale levikule ja pikale ajaloole – st ajale, mil teda on peetud koduloomana – on lammas huvipakkuv, kuid samas keeruline uurimisobjekt. Enamasti põhinevad lammaste minevikku käsitlevad uurimused zooarheoloogilisel materjalil, aga ka tänapäevaste lammaste iseloomulikel tunnustel nagu villa, sarvede ja saba omadused. Viimaste aastakümnete jooksul on lisandunud geneetilised uuringud, kus põhiküsimusteks on kodustamise, leviku ja lambagenoomiga seotud teemad. Eestis on lammaste ajalugu uuritud mitmest aspektist: lambakasvatust ja toiduks tarvitamist on analüüsitud arheoloogiliste loomaluude, villa olulisust arheoloogiliste tekstiilide ning viimase paarisaja aasta tõuaretust kirjalike allikate põhjal. Lisaks on tegeletud tänapäevaste maalammastega – nii nende ajaloo kui ka geneetilise mitmekesisusega Põhja-Euroopa vanade tõugude kontekstis. Siiski on allikad olnud katkendlikud ja ei ole pakkunud piisavat ülevaadet lambapopulatsioonide kujunemise kohta Eestis.

Käesolevas doktoritöös ühendatakse zooarheoloogiline ja geneetiline materjal, et uurida lambakasvatust ning kohalike lammaste emaliinide ajalugu Eestis ja ka laiemalt Läänemere kultuuriruumis keskmisest pronksiajast (u 1200 eKr) tänapäevani. Ühtlasi on see esimene uurimistöö lammaste vana DNA (= *ancient DNA* = aDNA) kohta Eestis. Doktoritöö tulemused on avaldatud viies teadusartiklis.

Doktoritöö zooarheoloogia osa (põhjalikum esitus artiklites I, II, IV) keskendub lammaste kasutamisele Viljandis ja Karksis (ajallooline Liivimaa, praegune Edela-Eesti) hilisrauaajast uusajani – Viljandis 10.-11. sajandi viikingiaegsest asustusest kuni 17. sajandini ja Karksis alates 13. sajandi keskelt kuni 17. sajandini. Mõlemas paigas oli keskajal ordulinnus, mis oli tol ajal oluline võimukeskus. Kokku on analüüsitud enam kui 46 000 luuleidu, millest ligikaudu pooled on määranud töö autor. Osteoloogilise materjali põhjal oli põhiline eesmärk hinnata loomade kasutust toiduks ja kõrvalproduktideks (nt nahad ja luud). Luukogumite määramisel ja analüüsimisel olid aluseks liigiline ja anatoomiline jaotumus ning lihakeha töötlemise jäljed. Kariloomi nagu veis, lammas, kits ja siga, kes moodustasid luujäätmetest enamuse, oli võimalik uurida põhjalikumalt ning nende puhul hinnati peale liigilise ja anatoomilise jaotumuse ka vanuselist struktuuri, luude morfoloogilisi tunnuseid, loomade turjakõrgust ja tervislikku seisukorda. Töös on pööratud tähelepanu eri sotsiaalse taustaga piirkondadele Viljandis (asulakoht, linnus, linn, eeslinn) ja Karksis (linnus), et uurida, kuidas erines ning muutus loomade kasutus ühiskonna gruppides läbi aja. Põhitähelepanu on suunatud üleminekule hilisrauaajalt keskajale koos 13. sajandi alguse ristisõdadega, mil toimusid muutused keskkonnas ja majanduses. Samuti püütakse vastata küsimusele, kas ja kuidas on mõjutanud loomakasvatust kaubanduskontaktid.

Doktoritöö geneetika osa (põhjalikum tutvustus artiklites III, V) keskendub lammaste emaliinide kujunemisele ja geneetilisele mitmekesisusele Eesti alal pronksiajast tänapäevani. Geneetilise analüüsi eesmärk oli jälgida, kuidas lambapopulatsioonid on Eestis kujunenud ja kas muutused geneetilises mitmekesisuses on kokku viidavad arheoloogilise materjali ja/või ajalooliste sündmuste/perioodidega. Omaette eesmärk oli hinnata, mil viisil tänapäevased Kihnu maalambad on seotud mineviku lambapopulatsioonidega ning kuidas mineviku geneetiline mitmekesisus ja mitokondriaalsed liinid on tänapäevastes maalammastes säilinud. Lisaks analüüsiti arheoloogilisi lambaid võrdluses Euraasia (eeskätt Soome) andmestikuga, et paigutada Eesti vanad ja tänapäevased lambad laiemasse geneetilisse ning ajaloolisesse konteksti. Selleks analüüsiti DNA-meetoditega 599 aluspaari pikkune lõik mitokondriaalse DNA (mtDNA) kontrollregioonist 134 arheoloogilisel lambaproovil Eestist, Lätist, Venemaalt, Poolast ja Kreekast ning 44 Kihnu maalamba proovil. Lisaks uuriti osadel vanadel proovidel 130 aluspaari pikkust lõiku Y-kromosoomil, et saada teavet isaliinide päritolu kohta.

Taust

Lamba kodustamine ja levik üle Euroopa. Maailmas on kokkuleppeliselt seitse lambaliiki, millest kodustatud lammas (*Ovis aries*) on arvukaim. Levinud arvamuse kohaselt on kodulamba lähteliigiks Aasia muflon (*Ovis orientalis*), kes kodustati u 11 000–10 500 aastat tagasi Lähis-Idas. Inimeste valiku tulemusel muutusid lambad aastatuhandete jooksul väiksemaks, nende saba pikenes ning sarved vähenesid või kadusid hoopis. Aja jooksul on suurimad muutused toimunud karvkatte omadustes, ehkki algul olid villast olulisemad saadused liha ja piim. Koos inimestega jõudsid kodustatud lambad Euroopa eri paigusse vahemikus 10 500–4000 aastat tagasi, sh Eestisse umbes 4900–4700 aastat tagasi. Lähis-Aasiast lähtuvad migratsioonilained jätkusid veel aastatuhandeid hiljem, tuues kaasa juba parandatud omadustega lammaste tüübid ja asendades varasemad „primitiivsed“ populatsioonid. Äärealadel need primitiivsed tüübid siiski säilisid ja on tänapäevani esindatud väikesearvuliste populatsioonidena Euroopas, näiteks muflonid Sardiinias, Korsikal ja Küprosel, aga ka maalambad Suurbritannias ja Põhja-Euroopas. Euroopa põhjaosa, sh Kihnu maalambaid, iseloomustavad suures osas esimestele kodustatud lammastele omased tunnused: väike ja vastupidav kehaehitus, suhteliselt lühike saba, hea viljakus ja tugev emahool, kahekihiline villak ja varieeruv värvus. Oma vastupidavuse ja geneetilise mitmekesisuse tõttu on primitiivsed lambatõud väga hinnatud tänapäevases tõuaretuses.

Uurimislugu. Eestis ulatub zooarheoloogiline uurimistöö 19. sajandi lõpukümnenditesse ja 20. sajandi algusesse (C. Grewingk, A. Rosenberg). Alates 1930ndatest uuris siinset faunat Johannes Lepiksaar ning alates 1950ndatest Kalju Paaver. Uus etapp sai alguse 1990ndatel, mil luid hakkasid määrama Eha Järv ja Paul Saks. Teaduslikuks huviobjektiks sai zooarheoloogia aga taas seoses Lembi Lõugase ja Liina Maldre tegevusega. Nemad on praegu tegevad zooarheoloogid Tallinna ülikoolis. Tartu ülikoolis tegeleb zooarheoloogilise uurimistööga käesoleva doktoritöö autor. Varem ei ole lambaid zooarheoloogilisest aspektist Eestis spetsiaalselt uuritud. Tavaliselt on seda tehtud üldkäsitlustes koos teiste koduloomadega. Küll aga on lambaliha ning muid produkte käsitletud toiduajaloo seisukohast (Inna Põltsam-Jürjo, Aliise Moora), samuti on kirjutatud mitmeid raamatuid lambakasvatusest (Kristjan Jaama, Peep Piirsalu). Allikmaterjalina saab käsitleda ka lambaid endid, eriti just maalambaid, kelle välimik ja käitumisharjumused annavad vihjeid selle kohta, millised võisid olla kunagised lambakarjad. Tänapäevaseid, sh Kihnu maalambaid, on uuritud ka geneetiliselt (Urmas Saarma Tartu Ülikoolist ning Juha Kantaneni töörühm Soome Loodusressursside Instituudist).

Lambakasvatus kiviajast tänapäevani. Lambakasvatuse alguseks Eestis võib pidada hilisneoliitikumi (u 3000–1800 eKr), mil esimesed tõendid koduloomade kohta pärinevad nöörkeraamika asulakohtade kultuurkihist (u 2900–2700 eKr). Seda, kuidas varane lambakasvatus Eesti aladel kujunes, on allikmaterjali nappuse tõttu raske hinnata. Samuti pole eriti materjali teada vara- ja keskmisest pronksiajast (1800–850 eKr). Esimesed arvukad tõendid koduloomade kohta pärinevad alles hilispronksiajast (850–500 eKr). Kuigi sellele järgnevast varasest ja vanemast rauaajast (500 eKr–550 pKr) tõendeid taas napib, on kogutud rohkesti luuleide noorema rauaaja (550–1225 pKr) linnustest ja keskaja (1225–1550 pKr) linnadest. Varauusajast (1550–1800 pKr) ja uusajast (1800–20. sajandi esimene pool) on luumaterjali vähe, kuna nii hilised kihid ei pälvi tihtipeale arheoloogide tähelepanu. Samuti on need kihid sageli sõjategevuse ja hilisema ehitustööga lõhutud. Uusajast on juba rohkem ka kirjalikke allikaid, mis kõnelevad esimestest katsetest 17. sajandi lõpuosas siinset kohalikku lambatõugu parandada. Ulatusliku tõuaretuse alguseks peetakse 19. sajandi algust. Tõuaretuse tõttu kahanes kohalike maalammaste arvukus 20. sajandi jooksul drastiliselt ning arvati, et selle tulemusena hävis maalammas meil täielikult (segunes moodsate tõugudega). Ent 1990ndatel märgati, et Eesti äärealadel, peamiselt Kihnu saarel, võib maalammas veel säilinud olla. Eestimaa Looduse Fondi eestvedamisel ja UNESCO toel korraldati 2006. aastal seitse suuremat ekspeditsiooni, mille käigus koguti proove ligi viiekümnest talust või majapidamisest, kus teati võimalikke maalambaid veel alles olevat ning geneetilise analüüsi tulemusel tuvastati (Urmas Saarma ning Juha Kantaneni töörühmade koostöö tulemusena), et maalammas on Eestis tõepoolest säilinud. Algas maalammaste taastamisprotsess, mis põhines peamiselt Kihnu saarelt toodud populatsioonil ning 2016. aasta alguses sai Kihnu maalammas ametlikult tunnustatuks tõuks. Väike, värvuselt väga varieeruva kahekihilise villakuga ning haiguste ja raskete keskkonntingimuste suhtes vastupidav Kihnu maalammas on oma omadustelt sarnane Põhja-Euroopa primitiivsetele lammastele ning on lambakasvatajate seas populaarsust koguv tõug.

Geneetikat ja arheogeneetikat rakendatakse aina enam loomade kodustamise, populatsioonide kujunemise ja mitmekesisusega tegelevates uuringutes. Selleks kasutatakse erinevaid geneetilisi markereid, millest mtDNAd ja Y-kromosoomi käsitleti ka käesolevas uurimistöös. MtDNA on rakus asuvate mitokondrite DNA, mida erinevalt tuuma DNAst on rakus mitmeid kordi rohkem ja see on reeglina päritav vaid emaliini pidi. MtDNAs on enim analüüsitud kontrollregiooni, mida iseloomustab kõrge mutatsioonikiirus ja enamikku mutatsioonidest ei mõjuta selektiivne aretus. Need omadused teevad mtDNAst hea vahendi, et uurida populatsioonides toimunud demograafilisi protsesse ja geneetilist mitmekesisust, sh ka aDNA meetoditega. Siiski peab arvestama, et mtDNA annab infot vaid emaliinide evolutsiooni kohta, mis ei pruugi alati kattuda loomaliigiga toimunud komplekssete demograafiliste sündmustega, eriti nende liikide puhul, kus isaliini roll on olnud märkimisväärne. Tihti mõjutab populatsiooni kujunemist just isassugupool, kelle geneetiline ajalugu on talletatud Y-kromosoomi. Seni kariloomade uurimisel kasutusel olevad Y-kromosoomi markerid on paraku vähevarieeruvad, peamiselt seetõttu, et aretuses on kasutatud piiratud arvul isasloomi. Kuigi liikide ja populatsioonide ajalugu sisaldub ka tänapäeval elavate isendite DNAs, on just vana materjali uurimine eelistatud, kuna sel viisil välditakse hilisema tõuaretuse mõju geneetilisele mitmekesisusele. Vana DNAd saab eraldada erinevatest kudedest, peamiselt luudest, hammastest, karvadest ja nahast. Seda on aga töömahukas analüüsida, kuna see on sageli lagunenud lühikesteks fragmentideks. Kuivõrd mtDNAd sisaldub rakus oluliselt rohkem kui tuuma DNAd, on selle eraldamist vanadest kudedest peetud pikka aega kõige otstarbekamaks.

Lamba geneetika. Esimene lamba mitogenoom järjestati 1998. aastal ja esimene tuumagenoom 2010. aastal. Arheoloogilisi lambaleide on geneetiliselt uuritud mitmes Euroopa riigis, sh Põhjamaades. Uuringud on näidanud, et Euraasia lambad – nii tänapäevased kui ka mineviku populatsioonid – kuuluvad viide suurde emaliini (haplogruppi), millest kaks (A ja B) on enamlevinud. Lambad on geneetiliselt väga mitmekesised, mis võib viidata sellele, et kodustamispiirkonnas kodustati neid mitmeid kordi või mitmes kohas. Geneetilised analüüsid on täiendanud lammaste migratsiooniteede ajalist ja ruumilist kulgu Lähis-Idast Aasiasse, Euroopasse ning Aafrikasse. Arvatakse, et lisaks lõunapoolsetele mõjudele võib osa Põhja-Euroopa lammaste geneetilistest liinidest pärineda ka idapoolsetelt stepialadelt. Samuti on praeguse geneetilise jaotuse kujunemisel võinud oma osakaal olla viikingiaegsel tihedal kaubavahetusel. Põhja-Euroopa lammaste kohta tehtud uuringud on näidanud, et vastavalt kauguse suurenemisega kodustamiskeskusest väheneb lammaste geneetiline mitmekesisus. Teisalt on nad aga geneetiliselt erinevad modernsetest tõugudest ning seetõttu tõuaretuses hinnatud kui geneetilise mitmekesisuse allikas.

Materjal ja metoodika

Osteoloogiline materjal ja zooarheoloogilised meetodid. Osteoloogilise materjali valikuprintsiipideks olid Viljandi ja Karksi luukogumid kui doktorantuuri jooksul põhjalikult analüüsitud materjal, mis lubasid peale ajalise läbilõike hilisrauaajast varauusajani (hilisrauaaeg, keskaja esimene sajand, üldine keskaeg, varauusaja algus) uurida sotsiaalselt eri taustaga piirkondi (muinasaegne asulakoht, linnus, linn, eeslinn). Osteoloogiline määrang hõlmas endas liigi, skeletielemendi ja fragmenteerituse dokumenteerimist. Saadud andmete põhjal arvutati määratud luuleidude koguarv (vastavalt liigile ja skeletielemendile) ja minimaalne isendite arv. Skeletielementide jaotumuse ning lõike- ja tükeldamisjälgede järgi analüüsiti luukogumi kasutusvaldkonda ehk seda, kas tegemist oli tapa-, toidu- või mõnd muud sorti jäätmetega. Karjakasvatuse eesmärkide (liha, vill, piim) uurimiseks analüüsiti ka luukogumite vanuselist ning soolist struktuuri. Loomade turjakõrguste arvutamiseks võeti standardiseeritud mõõtmed igalt luuleiult, kus võimalik. Teatud määral dokumenteeriti ka nähtavad anomaaliad, sh patoloogilised ilmingud.

DNA proovid ja geneetiline analüüs. DNA proovide puhul oli ajaline ja ruumiline valikukriteerium laiem kui osteoloogilise materjali puhul. Proove võeti arheoloogilistest leiukollektsioonidest üle Eesti, kattes ajavahemiku keskmisest pronksiajast 20. sajandi keskpaigani. Lisaks analüüsiti 44 Kihnu maalamba geneetilist järjestust. Ajaperioodide omavahelise analüüsi jaoks jaotati proovid nelja suuremasse ajalisse gruppi (pronksi- ja rauaaeg, keskaeg, varauus- ja uusaeg, tänapäevased Kihnu maalambad). Et hinnata kronoloogilisi muutusi kitsamal alal, analüüsiti omaette proove kolmest piirkonnast: Viljandi-Karksi, Tartu-Lohkva ja Saaremaa. Selleks, et lülitada Eesti proovid suuremasse Euraasia võrgustikku, eraldati DNAd ka mitmest Läti, Poola, Vene ja Kreeka lambaluust. Lisaks kasutati avalikes andmebaasides olevaid tänapäevaste lammaste andmeid. Kogu laboritöö tehti vastavalt aDNA töö nõuetele vastavates laborites Eestis (Tartu Ülikool) ja Soomes (Soome Loodusressursside Instituut). Saadud mtDNA järjestusi analüüsiti erinevate geneetiliste parameetrite osas ning evolutsiooniliste seoste tuvastamiseks kasutati fülogeneetiliste võrgustike rekonstrueerimist.

Uurimistöö tulemused ja diskussioon

Geneetilised näitajad. Esimesed koduloomade populatsioonid, kes koos inimestega Eesti alale jõudsid, olid tõenäoliselt väikesed ja võrreldes Lähis-Ida populatsioonidega madalama geneetilise mitmekesisusega. Sellega on kooskõlas ka käesoleva töö tulemused, kus on näha, et Eesti vanade lammaste geneetiline mitmekesisus on võrreldes Lõuna-Euroopa poolsemate lambapopulatsioonidega madalam. Samuti on kooskõlas enamiku analüüsitud lammaste kuulumine Euroopas levinud haplogruppi ehk emaliini B, samas kui vaid mõned üksikud isendid kuulusid haplogruppi A, mis on rohkem levinud Aasias. Y-kromosoomi uuringute tulemusedki kattusid seni Põhja-Euroopas enimlevinud

Y-kromosoomi haplotüübiga (SNP *G-oY1*). Geneetilise analüüsi tulemustest selgub, et lambapopulatsioonide kujunemine Eestis on olnud üsna homogeenne alates pronksiajast kuni 19. sajandil levinud tõuaretuseni. Siiski ilmnesid mõned murranguajad, millele tuleb seletust otsida laiemal arheoloogilisel ja ajaloolisel taustal. Need muudatused seostuvad kahe perioodiga. Esiteks üleminek muinasajalt keskajale koos 13. sajandi alguse ristisõdadega. Geneetilises andmestikus väljendub see lambapopulatsiooni suurenemises. Teine murrang ilmneb seoses suure tõuaretusega 19. sajandil, mille tagajärjel on vähenenud tänapäevaste maalammaste geneetiline mitmekesisus.

Kaubanduse mõju lambapopulatsioonidele. Põhja-Euroopa äärealadel ei olnud lambakasvatus veisekasvatusega võrreldes majanduslikult nii tähtis ja seega ei ole kaubandus kohalike lambakarjade kujunemisel tõenäoliselt olnud eriti märkimisväärne. Keskajal oli Euroopas käimas laialdane villakaubandus, mis näitab lambakasvatuse ulatuslikkust ning väärtust tollases ühiskonnas, kuid elusloomadega kaubeldi tõenäoliselt üsna vähe. Pealegi peeti imporditud elusloomi pigem luksuseks kui tavaks. Ka zooarheoloogilises materjalis on tõendeid elusloomade kaubandusest väga raske leida. Võimalik, et vähemal määral seda ette tuli, kuid sellisel juhul kaubeldi pigem üksikute isasloomadega, kellel oli kohalikule geneetilisele mitmekesisusele väike mõju ja mis uurimistöös vaadeldud emaliinides ei kajastu. Pigem võib arvata, et kohaliku lambapopulatsiooni produktiivsus oli järjepidev.

Üleminekut keskajale 13. sajandil on peetud ühiskonnas suureks murranguks. Koos inimpopulatsiooni kasvuga suurenes kindlasti kariloomade kasvatus ja kasutus. Seda toetavad käesoleva uurimuse geneetilised tulemused, mis näitasid samuti lambapopulatsioonide kasvu keskaja esimestel sajanditel. Mil määral võis see olla mõjutatud keskajal laienenud kaubandusest, on raske hinnata. Emaliinide geneetiline mitmekesisus jääb keskajal üsna samale tasemele võrreldes hilisrauaajaga, kuid nagu eespool öeldud, ei välista see imporditud tõujäärasid. Ei maksa aga kahelda, et loomakasvatusliku baasi moodustas suurima tõenäosusega ikkagi kohalik talumajandus, mis jäi püsima ka pärast 13. sajandi vallutusi.

Uurimistöös saadud Viljandi-Karksi ja Saaremaa mikroregioonide tulemus võib eelneva küll kahtluse alla seda, kuna nendes piirkondades ei kandu ükski pronksi- ja rauaaegne haplotüüp edasi keskaega. Siiski peab siinkohal arvestama, et analüüsitud proovide arv on piiratud ning tulemus võib olla juhuslik. Mingil määral võisid loomakasvatuse laienemist soodustada ka keskkondlikud muutused, nagu näiteks maastiku avanemine. Vastavad teaduslikud uurimused on küll näidanud taimestiku muutust keskaegse Karksi linnuse läheduses, kuid otsene seos käesoleva töös pakutud karjakasvatuse suurenemisega jääb hetkel siiski puudulikuks.

Lambasaaduste tarbimine. Lambaid kasvatati eelkõige liha ja villa pärast, mida tõendab luukogumite anatoomiline jaotus koos lõike- ja tükeldamisjälgedega (tapa- ja toidujäätmed) ja vanuseline struktuur, kus noorloomade luud võib spetsiaalselt liha eesmärgil kasvatatud loomadele omistada, samas kui vanemate isendite luud pärinevad loomadelt, keda enne toiduks tarvitamist villalammastena peeti. Talleliha ulatuslikku tarbimist võib tõlgendada ka kui kõrgema sotsiaalse klassi privileegi. Näiteks Karksi ordulinnuse 13. sajandi lõpu materjal koosneb suures osas just tallede ja põrsaste luudest, mis koos muu leiumaterjaliga viitab üheselt linnuses toimunud pidusöömingutele. Lisaks noorloomade liha tarvitamisele eristas kõrgemaid ühiskonnakihte (selle töö kontekstis eelkõige linnuste materjal) ka sagedasem jahilkäik ning tihtipeale ka linnuliha ja -munade söömine. Seevastu keskaegses Viljandi linnas oli noorloomade ja ulukite luuleide märksa vähem.

Luukogumite analüüsimisel vaadati ka liikide suhtelise arvukuse muutusi ajas, st kuidas muutus liigiline mitmekesisus ja mil määral suurenes/vähenes eri liikide tarvitamine. Ilmnes, et keskajal ja varauusajal märkimisväärseid muudatusi ei toimunud. Võis küll täheldada, et keskaja vältel kahanes Viljandi linnas lambaluude osakaal, kuigi linnuses oli see läbivalt kõrgem võrreldes linna ja eeslinna luukogumitega. Osaliselt on see vastuolus geneetilise andmestikuga, mis näitas lambapopulatsioonide arvukuse kasvu keskajal, kuid siin peab arvestama, et zooarheoloogilise materjali analüüs ning tõlgendus oleneb väga mitmest faktorist ning on tihtipeale raskesti üheselt kokkuviidav muu allikmaterjaliga.

Lisaks lihale ja villale saadi lammastelt teisigi tooraineid. Lambaid võidi pidada piima saamise eesmärgil, kuid kuigi Euroopas oli lambapiim keskajal kõrgelthinnatud produkt, ei ole seda Eesti kontekstis siiani väga uuritud. Küll aga on osteoloogilisi tõendeid lammaste sarvede, nahkade ja luude kasutamisest. Näiteks Viljandi ordulinnuselt analüüsitud luukogumis olid peaasjalikult veiste, lammaste ja kitsede koljufragmendid, millest mitmed olid pikuti poolitatud koljud ja mitmelt olid sarvjätked eemaldatud. Lisaks oli jäsemeluudel nahanülgimisele iseloomulikke lõikejälgi. Sellised spetsiifilise iseloomuga kogumid viitavad tavaliselt mõnele kindlale tegevusele, antud juhul nahkade ning luu- ja sarvede toormaterjali kasutamisele.

16.–19. sajandi keerulised ajad ja tänapäeva tõuaretus. Osteoloogilises materjalis on varauusaegset materjali väga raske eristada, kuna sõja- ja ehitustegevus on kultuurkihti seganud või hävitanud, samuti ei ole nii hiline aeg tihti olnud arheoloogide uurimisobjektiks. Vaadeldavat perioodi iseloomustavad ka suured näljahädad ning loomataudid. Siiski on arvatud, et kohalikud kariloomade populatsioonid toibusid nendest üsna kiiresti. Seda toetavad ka käesoleva uurimuse tulemused, kus võrreldes keskajaga ei ole varauusajal näha olulisi muudatusi ei loomade kasutusharjumustes ega ka geneetilises mitmekesisuses. Osaliselt võib see näidata kohalike lammaste vastupidavust taudidele ning ebasoodsatele elutingimustele.

Siiski ei peetud kohalikke lambaid majanduslikult piisavalt tulusaks ning alates 17. sajandist on teateid imporditud „hispaania lammaste“ ja esimeste tõuparanduse katsete kohta. Aktiivsem tõuaretus algas 19. sajandil, mil aretuses hakati kasutama eelkõige inglise lambatõuge. Kohalikud maalambad moodustasid lambakarjadest siiski enamuse kuni 20. sajandini ja on säilinud kuni tänapäevani. Praeguseks tunnustatud tõug Kihnu maalammas kuulus käesoleva uurimistöö fülogeneetilistes võrgustikes osaliselt samadesse haplotüüpidesse koos vanade lambaproovidega. Analüüsides ilmnes Kihnu lammaste seoseid isegi pronksiaegsete lammastega, mis viib kohalikud emaliinid 3000 aasta tagusesse aega. See võiks tuleneda osaliselt lambakasvatuse järjepidevusest ning sellest, et enamuse karjast moodustasid emasloomad, keda kasutati karja taastootmiseks. Teisalt aga on Kihnu maalammaste geneetiline mitmekesisus võrreldes varasemate populatsioonidega palju madalam. See peegeldab omakorda 19. sajandi tõuaretuse ning sellele järgneva 20. sajandi mõju, kus kohalikke lambaid ei peetud loomakasvatuses prioriteetseks. Samuti on madalama geneetilise mitmekesisuse põhjuseks asjaolu, et praegune Kihnu maalamba tõug pärineb ühest väikesest populatsioonist Kihnu saarelt. Need tulemused kattuvad teadaolevate uurimustega ülejäänud Põhja-Euroopa lambapopulatsioonide kohta, keda iseloomustab samuti ühelt poolt madal geneetiline mitmekesisus, kuid teisalt erisus võrreldes modernsete tõugudega.

Lammaste välimus. 18. sajandi lõpu kirjutistes kirjeldatakse kohalikke lambaid kui väikseid ja karmi musta villaga loomi. 19. ja 20. sajandist on kirjeldused veidi pikemad: väiksed, vastupidavad, viljakad, ebaühtlase musta ja valge kirju villaga, suhteliselt lühikese saba ja jäärade puhul tihti sarvedega. Samasugused villa omadused – kahekihiline, ebaühtlase pooljämeda villakiuga – on ilmnenud ka arheoloogiliste tekstiilide uurimisel ning sarnane on ka Kihnu maalammaste vill. Ka lammaste suuruse puhul on võimalik tõmmata paralleele tänapäeva ja mineviku vahel. Arheoloogiliste luude põhjal tehtud turjakõrguste arvutused näitavad, et lambad olid 50–69 cm kõrged, kusjuures Kihnu lammaste turjakõrgus jääb keskmiselt 55–60 cm kanti. Üheks primitiivsete lammaste iseloomulikuks tunnuseks on sarved. Kuigi arheoloogilises materjalis on enamjaolt nudipäised uted, esineb siiski ka sarvilisi emasloomi. Sarvede olemasolu nii isas- kui ka emasloomadel iseloomustab ühtlasi tänapäevaseid maalambaid. Lisaks on Eesti keskaegses materjalis kaks neljasarvelist lambakoljut, mis on väga harv nähtus, kuid siiski Euroopas mitmel pool kohatud. Tavapärane on neljasarvelisus vaid paarile Põhja-Euroopa lambatõule. Kas Eesti neljasarvelised leiud võisid olla kohalike lammaste mutatsioonid või pärit hoopis imporditud loomadelt, käesoleva uurimistöö raames tehtud geneetiline analüüs kahjuks välja ei selgitanud.

Kokkuvõte

Hoolimata muutustest keskkonnas, võimukorralduses ja majanduses on lambakasvatus Eestis olnud järjepidev. Seda tõendab nii geneetiline kui ka zooarheoloogiline andmestik. Siiski ilmnesid mõned „murrangud“, millele tuleb seletust otsida laiemal ajaloolisel taustal. Need muudatused seostuvad kahe perioodiga. Esiteks seostub see üleminekuga muinasajalt keskajale koos 13. sajandi alguse ristisõdadega. Geneetilises andmestikus väljendub see lambapopulatsiooni suurenemises, mis võib olla tingitud asjaolust, et keskajal kasvas koos rahvaarvuga ka kariloomade hulk. Samas on see toimunud kohaliku talumajanduse ja olemasolevate loomade baasil, mida tõendab ka zooarheoloogiline materjal:

lammaste tarvitamine toiduks on läbi aegade püsinud ühe olulisema liha-allikana. Teine murrang ilmnes seoses suure tõuaretusega 19. sajandil, mil läänest sisse toodud tõugudega hakati kohalike lammaste liha- ja villatootlikkust parandama. Hoolimata sellest säilisid Eesti alal algupärased põliste tunnustega maalambad osaliselt tänapäevani, kuigi mõnevõrra väiksema geneetilise mitmekesisusega. Töö tulemused ei ole kindlasti lõplikud ja tõstatasid kohati rohkem küsimusi kui pakkusid üheseid vastuseid. Edaspidi tuleks eri perioodidest kaasata veelgi enam materjali ja kasutada ülegenoomseid analüüse nii tuumagenoomi kui mitokondri genoomi osas, et saada täiendavat infot nii ema- kui isaliinide ning nende koosmõju kohta lambapopulatsioonide ajaloolisel kujunemisel, aga ka mitmekesisemate zooarheoloogiliste meetoditega (nt morfomeetria ja paleopatoloogia abil). Samuti oleks vajalik rahvusvahelise koostöövõrgustiku moodustamine, et analüüsida lammaste kodustamise ja hilisemate muutuste ajalugu laiemas fülogeograafilises kontekstis.

CURRICULUM VITAE

Name: Eve Rannamäe
Date of birth: 24.07.1985
Nationality: Estonia
Contact: eve.rannamae@ut.ee
Jakobi 2, Tartu 51014, Estonia

Education:

2010–2016	University of Tartu, doctoral studies (archaeology)
2007–2010	University of Tartu, master studies (archaeology)
2004–2007	University of Tartu, bachelor studies (archaeology)
1991–2003	Laagna High School, Tallinn

Career:

2010–…	University of Tartu, Institute of History and Archaeology, Department of Archaeology; technician/referent

Field of research: zooarchaeology and archaeogenetics

Publications connected with the thesis:

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ELULOOKIRJELDUS

Nimi: Eve Rannamäe
Sünniaeg: 24.07.1985
Kodakondsus: Eesti
Kontakt: eve.rannamae@ut.ee
Jakobi 2, Tartu 51014, Estonia

Hariduskäik:

2010–2016	Tartu Ülikool, doktoriõpe (arheoloogia)
2007–2010	Tartu Ülikool, magistriõpe (arheoloogia)
2004–2007	Tartu Ülikool, bakalaureuseõpe (arheoloogia)
1991–2003	Tallinna Laagna Gümnaasium

Teenistuskäik:

2010 – …	Tartu Ülikool, Ajaloo ja arheoloogia instituut, Arheoloogia osakond; tehnik/referent

Peamised uurimisvaldkonnad: zooarheoloogia ja arheogeneetika

Doktoriväitekirjaga seotud publikatsioonid:

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DISSERTATIONES ARCHAEOLOGIAE UNIVERSITATIS TARTUENSIS

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3. **Gurly Vedru.** Põhja-Eesti arheoloogilised maastikud. Archaeological landscapes of North-Estonia. Tartu, 2011.
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