



Approaching sheep herds origins and the emergence of the wool economy in continental Europe during the Bronze Age

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Abstract

In recent years, extensive archaeological studies have provided us with new knowledge on wool and woollen textile production in continental Europe during the Bronze Age. Concentrations of large numbers of textile tools, and of zooarchaeological evidence suggesting intense shepherding, hint at specialized centres of wool production during the Bronze Age. The aim of this paper is to discuss whether engagement with this economic activity was facilitated by the introduction of new foreign sheep types, possibly from the Eastern Mediterranean, where well-established wool economies existed, or by using local sheep, or a mixture of local and non-local types. A small-scale genetic pilot study, presented in this paper, primarily aimed at testing the DNA preservation, and thus the genomic potential in Bronze Age sheep remains provides evidence of both mitochondrial haplogroups A and B among Bronze Age sheep in Hungary. This result could hint at sheep herds with mixed origin but further in-depth studies are necessary to address this. We aim to promote scholarly interest in the issue and propose new directions for research on this topic.

Keywords Ancient wool · Breeding practices · Textile production · Ancient DNA · Second millennium BC

Introduction

The introduction of wool and of woollen textile production represented in all likelihood a major innovation in Bronze Age Europe during the 2nd millennium BCE. Wool was clearly becoming increasingly appreciated and widespread in Europe. This is demonstrated by the presence of woollen textile fragments in the archaeological record from various parts of the continent (see below). Despite the need for more data to better understand the characteristics of the continental wool economy, current research suggests that local production of wool and woollen products emerged and developed in Europe

during the Bronze Age (e.g. Becker et al. 2016; Bergerbrant 2018; Bergerbrant *in press*; Gleba 2017; Sabatini et al. 2018; Vretemark 2010). Moreover, recent strontium isotope analyses on wool textiles from the Early Bronze Age in Denmark suggest that the clothing found in a number of local elite graves was manufactured mainly with wool produced outside present-day Danish territory, the island of Bornholm excluded (Frei et al. 2015; Frei et al. 2017; see Thomsen and Andreasen 2019 for baseline discussion). These results show the existence of a continental trade of wool and/or of woollen textiles on a large scale (Kristiansen and Sørensen *in Press*).

Multiple factors must have contributed to this rise of continental wool economies, including technological exchange and a growing demand (e.g. Bender Jørgensen 2018; Frei et al. 2017; Harris 2012; Kristiansen 2016). However, the emergence of local production might have been triggered, or facilitated, in the first place by access to woollier animals. This could have happened through the introduction of new foreign animals or by extensive breeding in local sheep or maybe a mixture of both. To understand the development of the wool economy, it is therefore of critical importance to identify the type of sheep used for production. Supported by the results of our small-scale genetic study (see below), we argue that an interdisciplinary approach is essential to addressing this problem, and valuable insights are expected to come in the future through the study of ancient DNA (aDNA) from sheep.

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The emergence of wool production during the European Bronze Age

A wealth of archaeological evidence has shown that woollen textiles came into use across continental Europe at the onset of the second millennium BCE (Bender Jørgensen 1992; Bender Jørgensen and Rast-Eicher 2016; Bender Jørgensen and Rast-Eicher 2018; Gleba and Mannering 2012; Rast-Eicher and Bender Jørgensen 2013), and also that a local production emerged at some sites throughout the following centuries (Belanová Štolcova and Grömer 2010; Bergerbrant 2018; Bergerbrant *in press*; Earle and Kristiansen 2010b; Sabatini et al. 2018). Fully developed wool economies already existed in the Near East during the third millennium BCE as documented by archaeological, iconographical and written sources (e.g. Biga 2011; Breniquet and Michel 2014; Michel and Nosch 2010; Wisti Lassen 2010). A comparable combination of evidence shows that wool and woollen textile production also flourished in the Aegean during the second millennium BCE (e.g. Burke 2012; Del Frio et al. 2010; Killien 2015; Nosch 2014; Nosch 2015). Around the coasts of the north-eastern Mediterranean, the wool economy appears to have been an expansive activity involving large numbers of animals, intense labour, specialised artisans and meticulous administration. However, it is clear that written archive records from these areas represent a major source of information and we could not have gained such insights by relying only on archaeological evidence (see e.g. Burke 2012; Siennicka 2014; Skals et al. 2015; Tournavitou et al. 2015).

For the study of wool economy in the continental context, textual and archaeological evidence from the Mediterranean world, although politically and socio-culturally different, represent important contemporaneous references (Sabatini 2018). However, when lacking written sources, we must rely on three kinds of archaeological evidence to assess wool production in Bronze Age Europe: (1) the occurrence and distribution of tools related to the production of textiles, (2) the zooarchaeological remains revealing the presence of high proportions of sheep/goats among the domesticated animals, and (3) the presence of fragments of wool textiles. Textile tools attest to the production of textiles (e.g. Barber 1991; Gleba 2008), but how these can be used to assess the quality, type and origin of the fibres has been much debated (e.g. Andersson Strand et al. 2008; Andersson Strand and Nosch *In press*; Grömer 2006; Kania 2015). Zooarchaeological studies, in combination with the study of the archaeobotanical remains, are critical to our understanding of whether there was access to wool or plant fibres or both (e.g. Barber 1991; Bender Jørgensen 2018). A significant number of different textile tools and high percentages of sheep/goat among the faunal remains was recently demonstrated at the Hungarian Middle Bronze Age (c. 2000–1500/1400 BCE) site of Százhalombatta-Földvár (Bergerbrant 2018; Vretemark

2010) and at the Italian Middle and Recent Bronze Age (c. 1550–1200 BCE) Terramare settlement of Montale in the Po valley (De Grossi Mazzorin and Ruggini 2009; Sabatini et al. 2018). The characteristics of the local material suggest that both sites might have been centres of specialized wool manufacture, producing exports in exchange for locally unavailable raw materials such as metals.

We sampled sheep teeth from both areas to carry out a small-scale genetic pilot study (see below). The aim of the study was first and foremost to test the DNA preservation and thus assess the potential for a larger population genetic study, but also to hint at eventual genetic differences, similarities and possible links in the sheep between these two specific areas. For this last specific purpose, animal remains dated to about the same time (approximately sixteenth–fifteenth century BCE) were chosen.

Bronze Age wool and wool textiles from continental Europe

Extensive studies of textile tools and bone assemblages combined with investigations of the environmental conditions that have allowed for the survival and preservation of a significant number of Bronze Age woollen fabrics and clothing have provided us with an increasingly detailed understanding of the continental wool production. These remains are scattered both geographically and chronologically, but can provide precious insights into local spinning and weaving traditions (e.g. Bender Jørgensen 1992; Gleba 2017). Some of the most famous European Bronze Age woollen textiles are represented by the oak-log coffins excavated in Denmark (Bergerbrant 2007; Broholm and Hald 1940), generally dated between the end of the 15th and the thirteenth century BCE (Holst et al. 2001). Another important collection of woollen textiles has been retrieved from the Hallstatt salt mines in present-day Austria, dated between the fifteenth and twelfth century BCE (Grömer 2012; Grömer 2016; Grömer et al. 2013). A large (at least 300 × 170 cm) piece of cloth was also found in Pustopolje in Bosnia-Herzegovina (Bender Jørgensen and Grömer 2013; Grömer et al. 2018; Harding 1995; Marić Baković and Car 2014), radiocarbon dated to 3195 ± 30 BP (Marić Baković and Car 2014), or 1517–1414 BCE (2 sigma, calibrated with Oxcal v4 3,2 (Bronk Ramsey 2009)). A few sites in Italy (Bazzanella 2012; Gleba 2008; Gleba 2012) and a limited number of other European areas (Bender Jørgensen and Rast-Eicher 2015; database 2013; Gleba and Mannering 2012) complete the picture. Despite the lack of written records, there is sparse but significant evidence for the use of woollen textiles starting from the second millennium BCE. A recent study (Gleba 2017) argued for a continental textile tradition that produced fabrics that are different from those of the Mediterranean region, thus indirectly supporting our hypothesis of a continent-based production (see also Sabatini 2018).

However, due to the estimated limited annual wool yield per sheep per year (see discussion below), in order to have an economically sustainable wool production during the Bronze Age, it was necessary to have access to large numbers of woolly-fleeced sheep. We believe that the characteristics of sheep and sheep fleeces had a determinant role in relation to the emergence of local wool economies. Therefore, the study of sheep evolution is of utmost importance for understanding the political economy of the continent during the Bronze Age.

Scientific approaches to the study of prehistoric sheep and wool

In addition to the information offered by Aegean and Near Eastern written sources, the study of prehistoric sheep has often been pursued within two main spheres: textile archaeology (e.g. Bender Jørgensen 1992; Breniquet and Michel 2014; Ryder 1983) and zooarchaeology (e.g. Becker et al. 2016; Benecke 1994; Greenfield 2014). In recent times, new possibilities for investigating prehistoric sheep have become available, thanks to advances in aDNA analyses (Brandt 2014; Niemi et al. 2013; O’Sullivan et al. 2016; Olivieri et al. 2012; Rannamäe et al. 2016a; Rannamäe et al. 2016b). We here present and discuss some of the main results from each of these disciplines relating to the study of sheep and sheep fleece.

Textile archaeology and fibre analysis

Through textile archaeology, and in particular the study of prehistoric textiles, an interest in the characteristics of early sheep/goat has emerged. One of the main goals for textile archaeologists has often been to obtain a better understanding of the characteristics and quality of the fibres used in the textiles. Important and eagerly debated results concerning these early fibres have been achieved using scanning electron microscopy (SEM) (Gleba 2012; Rast-Eicher 2016; Ryder 1969; Ryder 1988; Skals et al. 2018). Such fibre analyses can provide information on the source of a fibre, vegetable or animal, and assist in identifying the species (Rast-Eicher 2016). Most analysed Bronze Age fibres are from sheep wool (Gleba 2012; Rast-Eicher and Bender Jørgensen 2013) or from plant material, in particular flax (Bazzanella et al. 2003; database 2013). The use of goat hair is known (e.g. Barber 1991; Bender Jørgensen and Rast-Eicher 2018; Del Freo et al. 2010; Frangipane et al. 2009), but to our knowledge, there are no published examples of goat hair fibres from the European Bronze Age (Rast-Eicher 2016). Goat skin, however, has been identified in both Neolithic and Chalcolithic contexts (Hollemeier et al. 2012; O’Sullivan et al. 2016; Rast-Eicher 2012). Fibre analyses have also demonstrated how fleeces have developed over time (e.g. Gleba

2012; Rast-Eicher and Bender Jørgensen 2013; Ryder 1983), although there are inherent problems in discussing fleece qualities based on ancient textile remains, and some studies have reached contradictory conclusions (e.g. Gleba 2012; Rast-Eicher and Bender Jørgensen 2013; see also Skals et al. 2018). One consistent problem may be linked to the fact, documented by ancient written sources from Mesopotamia, that before spinning the yarn, the fleeces were sorted, and likely mixed, to obtain the required wool quality (e.g. Andersson Strand and Cybulska 2013; Waetzoldt 1972).

The challenging aspects of fibre analyses were exemplified recently during the reconstruction work of an Early Nordic Bronze Age cloak (Hammarlund and Bergerbrant *Manuscript*). The fibre analyses (SEM) carried out on the unworked fleece demonstrated a fibre composition closely resembling compositions found in Bronze Age textiles (Rast-Eicher 2013). However, analyses of the same fleece, but using yarn prepared and spun in different ways, yielded results that for the most part were comparable in character to those obtained when analysing textiles from Iron Age contexts (Hammarlund and Bergerbrant *Manuscript*; Rast-Eicher 2013). The distinct preparation and spinning methods produced spun fibre of very different quality from categories B to F in the classification proposed by Rast-Eicher (Rast-Eicher 2013). Fibre analyses provide a wealth of precious information about the applied textile technology (see Rast-Eicher 2016; Skals *in Press*), but it remains unresolved whether it is possible to use such an approach to discriminate between various types of fleece and to discuss fleece quality and/or the development of it (cf. Skals et al. 2018).

Zooarchaeology

In contrast to textile archaeology and fibre analyses, zooarchaeology is concerned with the study of animal bones in multifarious ways. While zooarchaeological studies cannot offer data as to the quality and characteristics of prehistoric sheep fleece, they do provide detailed insights into the physical characteristics of the animals, and have been widely used to investigate the development and breeding of sheep through time (e.g. Benecke 1994; Bökönyi 1974; Ryder 1983). Morphological studies of central European faunal assemblages from the Neolithic to the Early Bronze Age show for instance that there was a large variety in sheep sizes and that some regional differences existed (Bökönyi 1974; Grömer and Saliari 2018; Pipes et al. 2014; Schmölcke et al. 2018). Although such data cannot provide information as to the eventual variety of sheep fleeces, it suggests that different types of sheep were already present in the area at the end of the third millennium BCE.

In relation to wool production and textile manufacture, one of the most prominent achievements of zooarchaeological studies derives from the analysis of slaughtering patterns. It

has been demonstrated that difference in the prevailing slaughtering age can indicate the primary economic role of sheep at a given site (Greenfield 2014; Payne 1973). For example, the fact that older wethers normally produce the most wool (Barber 1991) suggests their presence in a herd could be a sign of wool production. Ancient written texts from the Mediterranean Bronze Age (e.g. Barber 1991; Del Frio et al. 2010; Killen 1964) show that local economies were well aware of the amount of wool that one could obtain from different categories of sheep and that such specialized herds existed. Nevertheless, a mixed economy, exploiting other products in addition to wool, seems the most common practice, which makes it difficult to draw definitive conclusions about the wool economy based solely on zooarchaeological data (see Halstead 1998; Payne 1973).

Zooarchaeological analyses also hold the possibility of estimating the relative proportion of sheep and goat bones in an assemblage. Although not in equal proportions, there is clear evidence that the two species often coexisted in the same managed herd (see e.g. Becker et al. 2016; De Grossi Mazzorin 2013; De Grossi Mazzorin and Ruggini 2009; Greenfield 2005). Since goat hair has not yet been detected in Bronze Age textiles from European mainland, the presence of goats represents an important feature to factor in when discussing wool production, since a significant number of animals may not have been kept for wool. We are confronted by two major difficulties when attempting to estimate the ratio between these two taxa based on the old excavated bones. In general, the taxonomic representation in faunal assemblages may be biased and therefore not directly display the relative proportions of the species as they appeared in a given prehistoric landscape (e.g. Albarella 2017; see also Allentoft et al. 2010). Moreover, it can be very difficult to distinguish sheep from goat osteologically, unless there is access to the diagnostic bones, of which there are only a few (Gillis et al. 2011; Halstead et al. 2002; Salvagno and Albarella 2017). When these particular bones are missing one talks about sheep/goats. Today, due to the discovery of a type 1 collagen peptide with a differing sequence between sheep and goat, the two species can be easily distinguished based on their peptide mass fingerprints (PMF) (Buckley et al. 2010; Campana et al. 2013). This technology is also often referred to as ZooMS (Zooarchaeology by Mass Spectrometry) (see Buckley et al. 2009). Ancient DNA technology (as discussed below) offers another means to distinguish between the two species.

Despite these caveats, a growing volume of zooarchaeological evidence suggests that some major economic changes occurred at the beginning of the second millennium BCE in southeastern Europe. Culling strategies, and thus likely secondary product exploitation patterns, seem to undergo a significant transformation (Becker et al. 2016; Bökönyi 1974; Greenfield 2005; Vretemark 2010), which suggests that wool was becoming an appreciated product. A

thorough investigation of the factors that facilitated these changes should be a priority for future research. It is here argued that the introduction of new sheep, possibly with woollier fleeces, would fit well with the archaeological evidence showing the emergence of a continental wool production at this time. Of course, changes in sheep fleece may also have occurred due to changes in local breeding practices. Indeed, according to Ryder (Ryder 1983), the morphological changes (from size decrease, to alteration of the shape of the horns, to development of lighter fleece) seen in sheep during prehistory could be due to both domestication and breeding.

Genetic studies

Genetic research has great potential to detect changes in the population structure in space and time within any given species. Genetic population studies of sheep have so far had a main focus on modern sheep, and in particular on analyses of their mitochondrial DNA (mtDNA), revealing a great complexity and intense breeding throughout history (Alberto et al. 2018; Fernández et al. 2006; Guo et al. 2005; Hiendleder et al. 1998a; Hiendleder et al. 1998b; Larson et al. 2007; Larson et al. 2005; Luikart et al. 2001; Meadows et al. 2007; Pedrosa et al. 2005; Tapio et al. 2006; Wood and Phua 1996). Recently, analyses of mtDNA have been conducted on prehistoric sheep bone samples as well (Demirci et al. 2013; Niemi et al. 2013; O'Sullivan et al. 2016; Olivieri et al. 2012; Rannamäe et al. 2016a; Rannamäe et al. 2016b), confirming that breeding was commonly practised in early times.

Analysis of archaeological wool has also been attempted with success for mtDNA, but is dependent on treatment processes and environment (Brandt et al. 2011; Sinding et al. 2017). Nuclear DNA has not yet been successfully retrieved from ancient textiles. This may be due to a low amount of nuclear DNA in hair, combined with a more rapid degradation compared to mtDNA. Next-generation sequencing technology will hopefully change this in the future (Brandt and Allentoft *in Press*). Given the increasing possibility of working on highly degraded aDNA, we anticipate many insights into the ancient sheep gene pools in the future. Ancient DNA provides information on the genetic diversity of ancient populations (e.g. Allentoft et al. 2015; Larson et al. 2007; Larson et al. 2005) but in order to properly understand migratory patterns (whether artificially moved around by humans or by natural events) and detect changes in the gene pool, one preferably needs access to a broad reference database. The number of published mtDNA sequences from ancient sheep is still limited and further studies are therefore required to document genetic changes in the past (Brandt and Allentoft *in Press*). For instance, according to Brandt and Allentoft (Brandt and Allentoft *in Press*) one should consider that there might be a number of mtDNA haplogroups that have disappeared with

time and which cannot be detected when only investigating modern sheep populations.

Additionally, while mtDNA and Y-chromosome studies may help us trace back the lineages of specific sheep, they cannot provide information on the sheep's appearance such as the nature of the fibres and the coat colour, which must have had crucial significance in the breeding practices. For this, we need knowledge on specific genes, which, for example, can be obtained by sequencing the complete genomes of the animals. So far, there have only been a few studies that can help us on the way. Though research on modern sheep (Seroussi et al. 2017), suggested candidate genes for affecting fibre diameter (*KATNAL1*) and coat pigmentation (*FRY*). In the future, when more studies have confirmed these genetic influences in modern sheep, we can potentially investigate the same gene sequences in ancient sheep, before and after various key events related to domestication and wool production. This will allow us to gain a much deeper understanding of the relationships between the evolution and domestication of sheep, their fleece, and eventually of textile production.

Domestication and spread of sheep

Much literature is available on issues of domestication and the early exploitation of secondary products (e.g. Becker et al. 2016; Benecke 1994; Demirci et al. 2013; Greenfield 2010; Greenfield 2014; Larson and Burger 2013; Lawson Handley et al. 2007; Legge 1996; Marciniak 2011; Sherratt 1981; Sherratt 1983; Wang et al. 2015). Sheep/goats were probably initially domesticated for meat consumption and eventually their skin and milk became valuable too. Throughout the Neolithic period all over Eurasia, with possible exceptions (Grabundžija and Russo 2016; Pipes et al. 2014; Shislina et al. 2003), there is no conclusive evidence for the use of wool (e.g. Barber 1991; Greenfield 2010; Marciniak 2011) in textile production, while both sheep and goat skins were clearly exploited for clothing (Hollemeyer et al. 2012; O'Sullivan et al. 2016; Rast-Eicher 2012).

It is believed that sheep were domesticated from wild Mouflon (*Ovis orientalis*), or rather a minimum of three ancestral sub-species of the wild Mouflon (Lawson Handley et al. 2007; Ryder 1983). Later analyses have suggested that the European Mouflon is a remnant after an early domestication event, so more investigations are needed before understanding the relationship between the Asian Mouflon and our current domesticated sheep (Meadows et al. 2011). Sheep were probably initially domesticated in the 10th millennium BCE (Alberto et al. 2018; Demirci et al. 2013; Hole 1996; Larson and Fuller 2014; Legge 1996; Naderi et al. 2008; Zeder 2012), but Meadows (Meadows et al. 2011) argues that the domestication must have occurred through at least five domestication processes. Goats seem to have been preferred

over sheep on some of the sites with evidence of early domestication in southwest Asia (Legge 1996; Naderi et al. 2008), while other southwest Asian locations demonstrate a dominance of sheep bones (Stiner et al. 2014). The latter focus is typical in Early Neolithic sites in Greece (Halstead 1996) and can also be seen in most of continental Europe during the Bronze Age (e.g. Bartosiewicz 2013; Becker et al. 2016; De Grossi Mazzorin 2013; Greenfield 2005).

While most scholars agree that domestication took place somewhere in southwest Asia, there have been different suggestions as to the routes along which domesticated sheep spread from Asia into Europe. During the Neolithic period (approximately 6th to 4th millennium BCE) domesticated animals spread to the rest of Europe (Bökönyi 1974; Ryder 1983). One suggested route for the spread of the first farmers into continental Europe is via the Danube, and another is a marine route through the Mediterranean Sea (Ryder 1983). Some studies support the hypothesis of a maritime route for the specific case of the Iberian Peninsula (Pereira et al. 2006; Zilhão 2001). The importance of the Danube route for the spread of domesticated sheep into central and northern Europe has been emphasised by Kijas (Kijas et al. 2012). Since aDNA analyses of pig indicate that domesticated pigs spread from Asia via the Danube to central and northern Europe (Larson et al. 2007), we might imagine that domestic caprines were introduced in a similar way. Neolithic sheep/goats from continental Europe also appear to have been morphologically different (size, presence and shape of the horns) through time and regions, and environmental factors, among other things, possibly affected health and characteristics of the sheep/goat population (Bökönyi 1974; Grömer and Saliari 2018; Pipes et al. 2014). Such factors may have had an impact on the success of different waves of introductions (cf. Gronenborn 2009).

Disregarding the exact route, analyses of endogenous retroviruses (ERV = part of the genome that contains an active or inactive element of a retrovirus (see Brown 2012)) as genetic markers, Chessa et al. (2009) have argued that there must have been two migrations of sheep from the Near East to Europe. Remnants of the first wave of sheep are breeds such as Sardinian and Corsican Mouflons, or Scottish Soay and Nordic short-tailed sheep (Chessa et al. 2009). A second migration of sheep with 'improved production traits' occurred at a non-specified later time. These later sheep are regarded as the antecedents of many modern sheep (Chessa et al. 2009).

Wool, sheep breeding and fleece development

Today over 1155 local (present only in one country) and 227 transboundary sheep breeds exist in the world (Baumung and Wieczorek 2015). Although the total number has drastically

increased since the early modern period (Kijas et al. 2012), these figures clearly show how important sheep are for societies across the world. Generally, it is believed that the ancient sheep moulted sometime during the spring and summer months (Ryder 1983) and the wool that was first used was therefore wool that was ‘naturally’ released by the animals. So-called primitive sheep breeds such the Soay sheep from the St Kilda archipelago in northern Scotland, still moult (Clutton-Brock et al. 2004), but most modern breeds do not moult (Ryder 1983). It is often considered that the appearance of the first iron shears during the first millennium BCE is connected to non-moulted wool-producing sheep (Barber 1991); conversely the invention and use of shears might have made it more feasible to breed sheep that did not moult (e.g. Gleba 2008).

It has been highlighted that according to Mesopotamian written records, clipping was used in the production of goat hair, thus both plucking and clipping were to a certain extent already known practices during the Bronze Age (Barber 1991, p. 29). A need for wool has driven sheep breeding practices all over the world, and even today, there are races such as the Peppin Merino, which can produce an average of c. 10 kg fine quality wool per animal per year with picks over 18 kg for specific stud rams (breeders n.d.). However, these numbers are unthinkable for a prehistoric wool economy. Thanks to a body of ancient written sources from the Near Eastern and the Aegean, we have rather precise indications as to quantity and quality of the prehistoric wool production (e.g. Breniquet and Michel 2014; Del Frio et al. 2010). Archive documents from the Aegean show for instance that a general standard weight of a sheep fleece was 700–750 g (e.g. Nosch 2014). Based on preserved ancient texts Killen (Killen 1964) was able to demonstrate in a seminal work that specialized wool-producing sheep flocks existed in Bronze Age Crete and would have been composed of 100 wethers, which were expected to deliver 25 LANA, i.e. 75 kg or c. 750 g per animal (see also Del Frio et al. 2010). A mixed herd supposedly consisting of c. 120 sheep, 60 ewes and 60 lambs, was to produce a total of 12 LANA, i.e. about 36 kg or c. 300 g per animal (Del Frio et al. 2010); if the latter was calculated only on the ewes then the differences expected between ewes and wethers was c. 600 g versus 750 g (Rougemont 2014). Written sources also show that well-documented Bronze Age wool economies in the wider Mediterranean area (including the Near East) relied on a huge number of sheep, up to over 100,000 animals directly owned by the producing institutions. It also seems clear that the sheep were carefully managed into smaller herds assigned to individual shepherds throughout the year (Biga 2014; Firth 2014; Foster 2014; Matoian and Vita 2014; Rougemont 2014). Finally, Mesopotamian written sources (Andersson Strand 2014: 44) suggest that woollier sheep existed there, and were able to provide a yearly wool yield between 0.7 and 1.12 kg. Thus, sheep breeding attempting to gain woollier

sheep was likely to have been commonly practised, and with noteworthy results.

To summarize, sheep/goats are common domesticated animals that have been living close to humans since at least the 10th millennium BCE, when initially they were used for their meat, milk and skin. Interest in sheep wool must have manifested rather early but the first real evidence of wool production is from the 4th millennium BCE in the Mesopotamian region. Early sheep did not have a particularly woolly fleece with staples long enough to allow successful spinning. Our assumption is that in order to be able to produce wool for textile production it is necessary to have access to sheep with a specific type of fleece. A series of events must have led to the woollier fleece and breeding practices would surely have been an essential part of this development. Various disciplines have contributed to our present understanding of the relationship between sheep and sheep fleeces and wool production. Fibre analyses suggest that fleece quality and colour have changed through time. Zooarchaeological assessments have proven that deliberate culling strategies were employed to optimize the production, but also that the morphological characteristics of sheep changed significantly thanks to domestication and breeding practices. Modern DNA studies have confirmed that sheep breeding must have been widespread (Alberto et al. 2018), but whether this involved moving a large number of animals or instead conducting intense targeted breeding on the sheep already present in Europe remains unresolved. It seems that breeding practices aiming to improve specific traits such as woollier fleeces can be successful with the introduction of just one individual/ram with the required characteristics into a given flock (e.g. Munro 2003). In other words, relevant changes could have been implemented by just introducing a small number of animals into the existing herds, followed by heavy breeding among these newcomers.

We believe that it was a change in the sheep population, and in particular of sheep fleeces, that facilitated the rise of the continental wool economies. It is reasonable to expect that access to new sheep with improved productive characteristics (e.g. relating to wool and length/characteristics of the staples) would have a significant economic impact. It is hoped that future DNA analyses can be used to test these hypotheses and allow us to also investigate more quantitative questions regarding the numbers of new animals being imported. Did this concern only specifically selected rams that were introduced into existing populations, or did it involve the translocation of large populations of sheep? Or was it simply the breeding technology and strategy that was adopted in Europe during the Bronze Age, applying this to the existing local populations of sheep rather than introducing new foreign animals?

Ancient DNA analyses of eight Bronze Age samples from the Po (Italy) and the Danubian (Hungary) plains

For the aDNA part of this study we sampled eight sheep from two Bronze Age archaeological sites: the Hungarian Middle Bronze Age site of Százhalombatta-Földvár and the Italian Middle and Recent Bronze Age Terramare area in the central part of the Po valley. The overall aim was to assess the DNA preservation in these samples allowing us to evaluate the potential for conducting genome-scale studies of the Bronze Age sheep populations. Species identification of all ancient samples was carried out by experienced archaeologists and a zooarchaeologist.

For aDNA extraction, teeth were taken from different archaeological contexts within the chosen sites to ensure (as far as possible) the sampling of different individuals.

The archaeological context of the samples

Baggiovara (Modena province) is an early Terramare settlement from the Po plain. It was c. 1 ha in size and was fortified like most of the Terramare settlements. Terramare populations inhabited the central Po plain from the beginning of the Italian Middle Bronze Age until the end of the local Recent Bronze Age, c. 1700/1650–1200/1150 BCE (see Bernabò Brea et al. 1997). At the end of the Recent Bronze Age, this apparently prosperous system collapses for reasons that are widely debated (Cardarelli 2009a; Cremaschi et al. 2006). In contrast to other sites of the Po plain, Baggiovara was occupied for a relatively short period of time between the Italian Middle Bronze Age 1 and 2 or c. 1650–1450 BCE (Cardarelli 2009b; Cardarelli et al. 2013). The site was chosen for sampling due to its very early date in the Terramare context, which would enable the mapping of the first sheep in the area close to Montale from which consistent evidence has been found for intensive shepherding and textile production during the rest of the Middle Bronze Age (De Grossi Mazzorin and Ruggini 2009; Sabatini et al. 2018).

Százhalombatta-Földvár is a fortified Bronze Age tell settlement strategically placed overlooking a bend of the river Danube (Earle and Kristiansen 2010a; Vicze 2013). The tell site has well-preserved occupation layers between 3 and 6 m thick and dates between c. 2300 and 1500/1400 BCE (Earle and Kristiansen 2010a; Vicze 2013). It has been seen as strategically located between central Europe and the Mediterranean world (Earle and Kristiansen 2010a). Zooarchaeological studies (Vretemark 2010) of the faunal remains from the site show at the onset of the second millennium BCE a marked shift in composition of livestock (sheep from below 20% of the examined faunal remains before 2000 BCE rise to over 40% in the following periods). Slaughtering patterns indicate also a shift from meat

production before 2000 BCE (sheep are slaughtered at a young age) to secondary product (wool?) production (many sheep kept to an old age). They therefore confirm, at least for the Hungarian plain, earlier suggestions, according to which the general rise of the number of sheep and their prolonged life-time in Bronze Age Eastern Europe was an indication of wool production (Bökönyi 1974). The teeth (Table 1) analysed in this study derive from ongoing excavations and are all dated to the Classical Koszider Phase of the Vatyá Cultural complex dating them to 1500–1400 BCE (Vicze 2013).

aDNA extraction

The aDNA work was carried out in a special clean-room laboratory at the Centre for GeoGenetics, Natural History Museum of Denmark, according to strict aDNA standards (Gilbert et al. 2005; Willerslev and Cooper 2005). All the samples were mechanically cleaned by removing the surface area with diamond-dust-coated disks. We drilled out between 179 and 305 mg powder from the sheep teeth targeting the cementum-rich layer of the roots (though this is complicated by the folded structure of sheep teeth), which has been demonstrated to contain elevated amounts of endogenous DNA compared to the inner dentine (Damgaard et al. 2015).

Depending on the sample size of the initial material, the bone powder was dissolved in 3–4 ml of extraction buffer (0.463 M EDTA, 10 mM TE buffer 100×, 0.14–0.22 mg/ml Proteinase K, 0.5% N-laurylsarcosine (10%) and 1/1000 vol. Phenol red). For the first 15–20 min, a pre-digestion step was introduced to enrich for endogenous DNA (Damgaard et al. 2015) and this was followed by an overnight incubation at 37 °C in an identical buffer. The samples were centrifuged and DNA was extracted by incubating the supernatant with a 10× vol. of binding buffer (4.88 M GuHCl, 29.3% 2-propanol, 1/1000 vol. phenol red, 24.88 mM NaCl, 87.6 mM Na Acetate (adjusted to pH 4.5~)) and 100 µl silica beads (prepared as in Rohland and Hofreiter 2007 which was used in: Orlando et al. 2013, 2011) for 1 h. Following DNA-binding, the silica was pelleted by centrifugation and the supernatant removed. The pellet was then first washed with 1 ml of the binding buffer and then twice with 1 ml 80% EtOH. After removing the supernatant and letting the pellet dry (15 min), the pellet was resuspended in 75 µl TEB buffer (Qiagen EB supplemented with 0.05% Tween-20) and incubated at 37 °C for 15 min. The supernatant (the pure DNA extract) was transferred to a new low-bind tube and was used for preparing a DNA library as required for Next Generation Sequencing.

NGS library preparation and sequencing

DNA extracts (20 µl) were built into blunt-end DNA libraries using Illumina-specific adapters and NEBNext DNA

Table 1 The samples from Százhalombatta-Földvár with contextual data from the excavation (courtesy of Magdolona Vicze, Matrica Museum, Százhalombatta, Hungary)

| Sample | Excavation unit (ID) | Contextual ID | Description of contextual ID | Level |
|--------|----------------------|---------------|--|-------|
| LOEB6 | 4247 | ID 4014 | A house in the middle of the excavated area | 11 |
| LOEB7 | 4229 | | | |
| LOEB5 | 4385 | ID 4348 | A debris layer above house with ID 4348 north of house ID 4014 | 11 |
| LOEB8 | 4371 | ID 4213 | Found in the general fill outside a house | 11 |

Sample Pre Master Mix (E6070) kit according to manufacturer's instructions with some modification (see Margaryan et al. 2017). The DNA libraries were quantified using qPCR and indexed with barcoded primers in subsequent PCR reactions with a sample-dependent number of cycles. The libraries were purified and run on an Agilent Bioanalyzer 2100 to assess DNA concentration and length distribution. The libraries were then pooled (roughly equimolarly) and sequenced at the National High-throughput DNA Sequencing Centre, University of Copenhagen on one lane on the Illumina HiSeq 2500 platform using 100 bp single-read mode.

DNA data analysis

To remove the adaptor sequences and stretches of Ns at both ends from the ancient DNA reads we used AdapterRemoval 1.5.2 (Lindgreen 2012). Only DNA sequences with a minimum length of 30 bp were considered for downstream analysis. The trimmed reads were mapped against the sheep mitochondrial reference genome (GenBank: AF010406.1) and whole (GenBank: GCA_000298735.2) reference genomes using BWA 0.6.2 aligner (Li and Durbin 2009) with the seed disabled allowing higher sensitivity (Schubert et al. 2012). Only DNA reads with mapping quality > 30 were used and sorted using Picard (<http://picard.sourceforge.net>) and samtools (Li et al. 2009). Duplicate reads at library level were removed by Picard MarkDuplicates (<http://picard.sourceforge.net>).

The consensus mtDNA sequence for each ancient sample was called using Geneious® v. 9. We considered only sites with a sequencing depth of at least 2×. At each position a base was called only if it was observed in at least 75% of the reads covering that site.

For compatibility purposes, we also analogously analysed four previously published ancient sheep DNA sequences by O'Sullivan et al. (2016) relevant for this study and previously published modern sheep sequences assigned to haplogroups A, B, C, D, and E (Lancioni et al. 2013; Meadows et al. 2011).

Ancient DNA damage parameters, namely the C/T transition rates (typical for aDNA) (Briggs et al. 2007), were estimated using mapDamage 2.0 (Jonsson et al. 2013).

DNA results

A total of 164,809,125 DNA reads were generated for all eight ancient samples combined. After mapping our DNA reads to the sheep mitochondrial reference genome (GenBank: AF010406.1), we identified practically no DNA sequences of sheep mitochondrial origin in the case of the four samples from the Italian site Baggiovara. Hence, we did not engage in any further analyses concerning these samples. However, the four samples from Százhalombatta-Földvár (Hungary) contained enough mtDNA sequences (ranging from 517 to 3958 sequences) to yield low coverage mitochondrial genomes with varying depth of coverage ranging from 1.7× to 14.4× (Table 2). The average mapped read length ranged from 53.8 to 61.5 bp and this high level of fragmentation is expected for ancient samples (e.g. Allentoft et al. 2012; Lindahl 1993).

The DNA mapping stats against the sheep whole reference genome are presented in the Table 3. The endogenous DNA content for the four ancient samples from Százhalombatta-Földvár studied in this paper ranged from 0.3 to 9.6%.

The mapped sequences from the four successful samples showed increased C to T deamination rates at the 5' end of sequencing reads compared to the sheep reference mitochondrial genome sequence (Table 2). This observation confirms that the profiled DNA molecules were of ancient origin.

In an attempt to assign mtDNA haplogroup categories (previously observed and published genetic variants) to the four ancient sheep samples from Százhalombatta-Földvár, we constructed a Neighbour Joining tree using previously published sheep mitogenome haplogroup sequences (Lancioni et al. 2013; Meadows et al. 2011; O'Sullivan et al. 2016). The nomenclature of haplogroups is adopted from Lancioni et al. (Lancioni et al. 2013) as also seen in O'Sullivan et al. (2016).

For the two ancient samples LOEB5 and LOEB7 which had the lowest mtDNA coverage, we were only able to reconstruct a partial mitogenome consensus sequence (52% and 57%, respectively, see Table 2). This restricted the use of these two ancient samples in a combined phylogenetic analysis, and we therefore constructed additional phylogenetic trees for each of these two ancient samples separately.

The results indicate that three (LOEB6, LOEB7, LOEB8) out of four ancient sheep clustered with various

Table 2 Summary statistics of the analysed samples. The four samples from Baggiovara yielded too few sheep sequences to conduct any meaningful summary statistics. *e*: mass of tooth material used for DNA extraction, *Total*: total number of DNA sequences, *Retained*: number of retained sequences after initial bioinformatical filtering, *Mapped*: number of sequences that could be mapped to the sheep reference mitochondrial

| Sample ID | Museum ID | Mass, mg | Total | Retained | Mapped | DoC | Length, bp | Damage | Coverage |
|-----------|-----------------------------|----------|------------|------------|--------|------|------------|--------|----------|
| LOEB1 | Baggiovara 1 | 305 | 11,218,963 | 9,460,935 | 6 | NA | NA | NA | NA |
| LOEB2 | Baggiovara 2 | 179 | 10,593,574 | 9,765,729 | 11 | NA | NA | NA | NA |
| LOEB3 | Baggiovara 3 | 286 | 10,200,474 | 8,961,707 | 18 | NA | NA | NA | NA |
| LOEB4 | Baggiovara 4 | 231 | 11,926,685 | 11,106,591 | 1 | NA | NA | NA | NA |
| LOEB5 | Százhalombatta-Földvár 4385 | 183 | 16,212,838 | 14,685,010 | 517 | 1.7 | 55.7 | 27% | 52% |
| LOEB6 | Százhalombatta-Földvár 4247 | 259 | 45,390,062 | 41,143,421 | 3958 | 14.4 | 60.5 | 32% | 99% |
| LOEB7 | Százhalombatta-Földvár 4229 | 202 | 34,902,463 | 32,128,900 | 657 | 2.1 | 53.8 | 36% | 57% |
| LOEB8 | Százhalombatta-Földvár 4371 | 184 | 24,364,066 | 21,136,884 | 2886 | 10.7 | 61.5 | 28% | 98% |

genome, after removing duplicate reads, *DoC*: Estimated depth of coverage of the mtDNA genome, *Length*: average length of the mapped sequences, *Damage*: C-T transition rate at the first nucleotide position of the 5' end of the reads, *Consensus coverage*: fraction of the mitochondrial genome with enough DNA reads to call a consensus sequence

sub-lineages within haplogroup B (99% bootstrap support) while LOEB5 belonged within the haplogroup A lineages (Fig. 1) with 100% bootstrap support for the haplogroup A branch (the separate tree with LOEB7 sample is not shown but again the bootstrap support for a haplogroup B affinity was very high—100%).

Similar patterns were observed when using other methods for phylogenetic reconstructions such as Maximum Parsimony or Maximum Likelihood (data not shown). Since the sample LOEB5 had low mtDNA coverage we also used a stricter approach for calling the consensus mtDNA sequence, namely calling a nucleotide only if it was supported by at least 3 reads and observed with > 75% frequency. This more conservative method resulted in fewer informative but more reliable sites, and again the analysis confirmed the relationship of LOEB5 with haplogroup A with > 95% bootstrap support.

Discussion of the DNA results

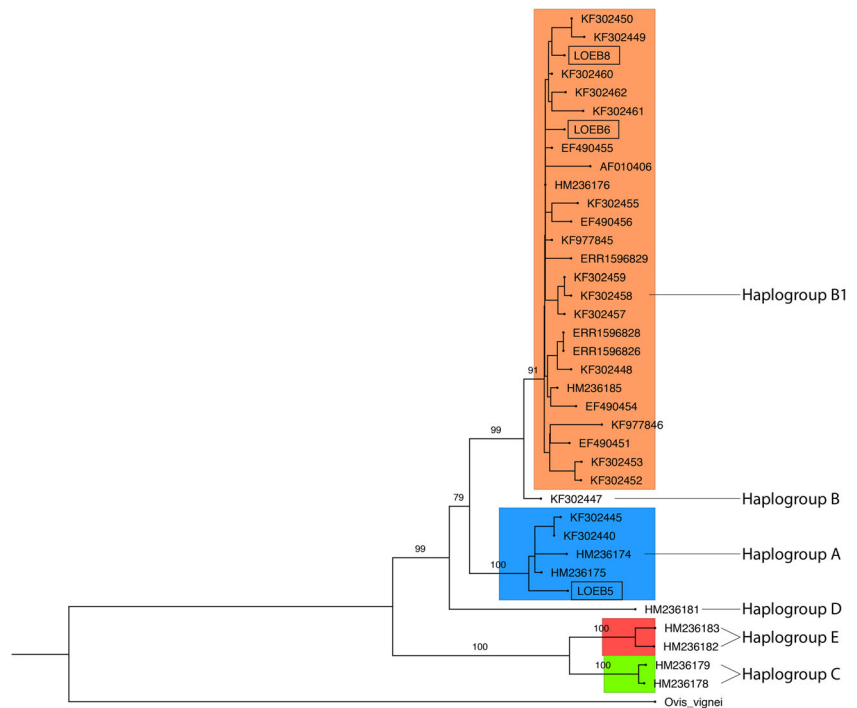
First and foremost, our results have demonstrated that the preservation of aDNA in the sheep teeth from Baggiovara in Italy is very problematic. Based on the methods used here, we can only detect marginal levels of endogenous sheep mtDNA. In contrast, Százhalombatta-Földvár in Hungary seems to constitute a highly promising site for studying the genomics of sheep development. It is well known from human aDNA projects that DNA preservation in warm regions such as the Mediterranean is often highly problematic. The quality of DNA in the samples from Százhalombatta-Földvár however is also rather variable in terms of endogenous DNA content, and it is therefore crucial to apply an initial screening process, in which several-to-many individuals are tested with low coverage shot-gun sequencing before selecting individuals for

Table 3 Sequencing statistics. Shotgun sequencing data of eight ancient sheep samples. *Total* is the total number of DNA reads per sample. *Trimmed* is the number of sequences passing quality and length filtering. *Mapped* represents the number of sequences mapping to the sheep reference genome - GCA_000298735.2, and *Final* is the same

number but with all duplicate sequences removed. *Endo%* is the proportion of sequences after trimming that could be identified as sheep, and *Duplicates%* shows the proportion of identical reads (clones) in this sheep DNA fraction

| Sample | Total | Trimmed | Mapped | Final | Duplicates% | Endo% |
|--------|------------|------------|-----------|-----------|-------------|-------|
| LOEB1 | 11,218,963 | 9,500,192 | 1905 | 1899 | 0.3 | 0.0 |
| LOEB2 | 10,593,574 | 9,800,152 | 5908 | 5901 | 0.1 | 0.1 |
| LOEB3 | 10,200,474 | 8,997,960 | 41,672 | 41,259 | 1.0 | 0.5 |
| LOEB4 | 11,926,685 | 11,143,732 | 332 | 326 | 1.8 | 0.0 |
| LOEB5 | 16,212,838 | 14,746,583 | 125,828 | 113,375 | 9.9 | 0.9 |
| LOEB6 | 45,390,062 | 41,307,284 | 3,858,103 | 3,707,517 | 3.9 | 9.3 |
| LOEB7 | 34,902,463 | 32,253,264 | 110,146 | 101,539 | 7.8 | 0.3 |
| LOEB8 | 24,364,066 | 21,221,786 | 2,043,301 | 1,926,147 | 5.7 | 9.6 |

Fig. 1 Neighbour joining tree based on three ancient samples from this study and previously published sheep mitogenomes. The numbers above major branches indicate bootstrap support values. The three ancient samples from this study (LOEB5, LOEB6 and LOEB8) are indicated with rectangular boxes. *Ovis vignei* mtDNA sequence was used as the outgroup



deeper sequencing. Alternatively, full genome or mitogenome capture approaches could be attempted (e.g. Carpenter et al. 2013) in order to minimize sequencing costs of problematic samples. Moreover, petrous bones could be sampled in future aDNA sheep studies, since these have been shown to yield very good DNA preservation in for example humans and horses—and also from ‘problematic’ regions such as the Mediterranean (Gallego Llorente et al. 2015; Lazaridis et al. 2016; Skoglund et al. 2016).

Prior to this study, only a few analyses of full mitochondrial genomes from sheep have been carried out and also the number of published partial mitochondrial genomes is limited. Previous studies of the mtDNA Control Region and/or the cytochrome b gene of modern domesticated sheep breeds distributed over a wide geographical area have identified five sheep haplogroups A, B, C, D and E (Guo et al. 2005; Hiendleder et al. 2002; Hiendleder et al. 1998b; Meadows et al. 2011; Meadows et al. 2005; Meadows et al. 2007; Pedrosa et al. 2005; Wood and Phua 1996), which have been tentatively proposed to each represent a separate domestication event (Meadows et al. 2011; Pedrosa et al. 2005). Among these, haplogroups A and B are the most frequent ones and have been identified in modern sheep from all sampled geographical regions. Haplogroup A occurs particularly frequently in Asian sheep, whereas haplogroup B dominates in European sheep (Hiendleder et al. 1998b; Wood and Phua 1996). Haplogroup C is less prevalent, but has been located within both Asia, the Fertile Crescent and Europe (Guo et al. 2005; Pedrosa et al. 2005; Pereira et al. 2006; Tapio et al. 2006). Haplogroups D and E are the least frequent and have

only been identified in samples from Turkey and the Caucasus (Meadows et al. 2007; Tapio et al. 2006). Sheep haplogroups have also been identified in a number of studies on ancient teeth (Cai et al. 2007) and bone samples (Brandt 2014; Cai et al. 2011; Horsburgh and Rhines 2010; Niemi et al. 2013; Rannamäe et al. 2016a; Rannamäe et al. 2016b).

The earliest samples so far analysed from Europe derive from sheep hair from the skin garments of the Copper Age Iceman Otzi (c. 3350–3120 BCE), who was found extremely well-preserved in a glacier on the border between Austria and Italy in 1991 (Egg and Spindler 2009; O’Sullivan et al. 2016; Olivieri et al. 2012). The permafrozen layer in which the Iceman was preserved provided highly favourable conditions for DNA preservation. O’Sullivan et al. (2016) applied NGS technology to sequence DNA from the samples and managed to assemble three complete and one partial mitochondrial genome (O’Sullivan et al. 2016). All individuals were placed within the sheep mitochondrial haplogroup B, which is dominant in Europe still today. Sheep bones from the Early Neolithic Period and Roman Iron Age of the Danish prehistory also fall within haplogroup B (Brandt 2014). Likewise, the DNA in the sheep wool, from a textile sample from the tenth to fifteenth century CE from Greenland, could also be assigned to haplogroup B (Sinding et al. 2017).

In previous analyses of sheep bone samples from present-day Finland dating to the Iron Age, Medieval, and Post-Medieval periods haplogroup B was observed in most instances, whereas haplogroup A was only observed in the medieval and more recent post-medieval samples (Niemi et al. 2013). In sheep samples from present-day Estonia,

haplogroup A was observed from the Iron Age and Middle Ages, whereas B was observed in the earlier Bronze Age (Rannamäe et al. 2016a). So far it thus seems that haplogroup B is the oldest in Europe with haplogroup A arriving at a later stage; the oldest traces of haplogroup A have been documented in Asia. Demirci et al. (Demirci et al. 2013) can show the presence of both haplogroups A and B in sheep samples from the site Oylum Höyük in present-day Turkey dating from 1800 BCE. While further east Schröder et al. (2016) demonstrated the presence of both haplogroups A and B in sheep leather clothing from the Wupu cemetery in Xinjiang Uyghur Autonomous Region of north-western China dating to Bronze Age (eighth–sixth century BCE). Haplogroup C has been found in modern Tsigai sheep in Hungary (Tapio et al. 2006), but not yet in prehistoric samples from Europe. Since the Tsigai sheep is introduced in Hungary during historical periods (Bökönyi 1974), it is possible that haplogroup C was a generally late introduction in the continent.

To our knowledge, our sample LOEB5 is by far the oldest sheep sample in Europe assigned to haplogroup A (c. 1500–1400 BCE). This observation is highly interesting as the sample comes from a site that is most likely among the earliest continental centres of wool production that started at the beginning of the second millennium BCE (Vretemark 2010). In the light of these genetic results and the discussion above concerning wool production in Bronze Age Europe, it is worth speculating that the haplogroup A sheep from Százhalombatta-Földvár may represent evidence of new sheep tentatively introduced into Europe during the Bronze Age in order to improve production traits. We believe that the preliminary results presented here provide an excellent foundation for future genetic research, aimed at examining many more Bronze Age sheep remains from across Europe. This will allow us to understand how the spread of domesticated sheep from different parts of the world could have contributed to the development of woolly fleeces and thus of wool economies in general.

Concluding remarks

In recent years, extensive archaeological studies have provided us with new knowledge on wool and woollen textile production in continental Europe during the Bronze Age. The discovery of large numbers of textile tools, combined with zooarchaeological evidence suggesting intense sheepherding, has been used to pinpoint specialized centres of wool production during this period. One of the aims of this paper is to propose new directions for research in order to grasp the mechanisms that facilitated Bronze Age societies' engagement in wool economy. We argue that sheep breeding oriented towards improvement of specific productive traits, such as woollier fleeces, must have had a major role in the process.

Our genetic analyses showed a great molecular potential in the sheep remains from Hungary. Moreover, the observation of both haplogroups A and B in this population is highly interesting. This could hint at foreign sheep being imported to improve specific productive traits. In order to generate sufficient data to support such preliminary conclusions, and eventually detect other possible haplogroups as well as of course trying to identify the genes responsible for the characteristics of the wool, it would be necessary to analyse a large sample from both the chronological phases predating any evidence of wool production and phases contemporary with it.

An important direction for future research is therefore to investigate the relationship between the characteristics of local sheep populations and the archaeological evidence for continental wool production. We believe that it is a crucial issue, and that transformations of productive traits in the animal population had great consequences on the economy of those regions/areas that were able to exploit or facilitate the change. We believe that the combined effort between archaeological investigations and aDNA studies will bring fundamental results and greatly enhance our understanding of the Bronze Age political economy in general and the wool economy in particular.

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