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Redakcijos adresas / Editorial Board address:
Lietuvos istorijos institutas, Archeologijos skyrius
Kražių g. 5, LT-01108 Vilnius
Tel. (+370) 5 2614935, fax (+370) 5 2611433
e-mail: lietuvosarcheologija@gmail.com;
civilytea@gmail.com

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STUDIES OF ANCIENT DNA.
THE RACE FOR THE ULTIMATE ANSWER

INTRODUCTION

The outbreak of the Covid-19 virus has convincingly demonstrated the universal application of genetic technology, allowing effective diagnostics in the earliest stages of the illness. DNA research can indeed be regarded as one of the revolutions in modern times with significant groundwork occurring in the 1980s and today claiming new fields and areas of application. In archaeology, DNA research is playing an increasingly important role. From the groundbreaking results extracting DNA from the tissues of ancient mummified bodies (Hunan 1980; Pääbo 1984), it soon became evident that excavated bones, as well as teeth and hair, also contain preserved genetic material, making it possible to investigate their DNA (Hagelberg *et al.* 1989). In 2003 a high-quality, comprehensive sequence of the human genome was completed and opened unforeseen possibilities in genetic research (Collins et al. 2003). Today ancient DNA-based studies range from the identification of human gender, kinship and even physical characteristics (phenotypes) to population genetics and human ecology, including palaeobotany, zoology, and paleoepidemiology. Groundbreaking progress occurred in around 2000 with the development and application of next-generation sequencing (NGS) technologies, which made it possible to sequence the whole human genome in just one day (Straiton *et al.* 2019). For thorough overviews of the typing of ancient DNA, the methods, and the applications, there is a vast body of literature available for reference (e.g. Hummel 2003; Butler 2010; for readers in Lithuanian, see Kučinskas 2004).

Below, the author presents three examples of DNA research projects, in which she has participated and which demonstrate the enormous potential of DNA-based analysis as an exciting new source of information about the past. These projects were undertaken under the auspices of a broad interdisciplinary initiative 'The Genomic History of Denmark' by the University of Copenhagen (KU2016 initiative) with E. Willerslev as PI. She also shares some cautionary remarks regarding the uncritical acceptance of the results generated by the DNA studies.

DNA FROM PARASITE EGGS

The advancement of DNA research has opened doors for the elucidation of human epidemiology, including infections with intestinal worms. It has been known that parasite eggs may survive in the soil for several thousands of years, protected by their resilient shell. In Denmark, it was possible to find parasite eggs deriving from Bronze Age contexts, although no systematic attempts were made to find out the lowest limit for their recovery. Microscopy is a powerful tool for the morphological examination of parasite eggs; however, it is often not possible to achieve reliable identification beyond the genus level. DNA based analysis offers identification at the species level, which can then be attributed to specific hosts, i.e. from humans to various terrestrial and aquatic animals. In this way, the correct identification of parasite eggs serves as a marker for the presence of their intermediate and/or definitive hosts. The benefits of DNA analysis are thus evident. For instance, the *Trichuris* genus comprises more than ten distinct species with narrow host specificity where *T. trichiura* infects humans, *T. suis* pigs, and *T. muris* mice. Thus proper identification of parasites becomes a very informative source for understanding the environment and human-animal interaction.

The study designed by Martin J. Søe (Søe *et al.* 2018) focused on the identification of roundworm (*Ascaris lumbricoides*), the human whipworm (*Trichuris trichiura*), as well as tapeworms (*Taenia species*) and other helminths (i.e. parasitic worms) from contexts associated with human remains, coprolites and mixed waste deposits. Through the application of a novel approach of shotgun sequencing on ancient parasite eggs, it was possible to obtain a detailed insight into the parasitic infections of ancient human populations from several geographical areas and periods: Bahrain (500–400 BC), Jordan (AD 650–750), Denmark (AD 1018–1600s), The Netherlands (AD 1350–1850), and Lithuania (AD 1550–1580).

The DNA analysis helped to establish soil-borne parasites transmitted directly between humans (*A. lumbricoides*, *E. vermicularis*, and *T. trichiura*), which points to the faecal contamination of the immediate environment, and thus poor hygiene and varying levels of exposure. Other findings of specific helminth species indicate that humans were infected through the consumption of raw or undercooked fish and pork. Moreover, a range of different parasites attests to the presence of various domestic and synanthropic animals living in close proximity to humans. Finally, the reconstruction of full mitochondrial parasite genomes from whipworm (*T. trichiura* and *T. muris*) and roundworm species (*A. lumbricoides*) contributed towards an understanding of the genetic diversity of helminths. For instance, whipworms from Northern Europe and Jordan show greater affinity to whipworms from Asia than Africa. At the same time, human roundworms from samples from Northern Europe are closely related to African samples from Uganda, showing greater phylogenetic distance to samples from China. Consequently, the earlier hypotheses of the global dispersal of *T. trichiura* along with human migrations should be reconsidered (Araujo *et al.* 2008).

This study has also revealed that DNA analysis is not without limitations, and the best results are achieved through integration with other investigative methods. Traditional morphological identification was undertaken prior to the DNA analysis, which identified 78% of the microscopically identified taxa, i.e. 32 of 41. In contrast, while seven different helminth genera were identified through microscopic examination, DNA analysis revealed eight genera, including 11 distinct species. Most importantly, with the help of DNA analysis, in a number of cases, it was possible to identify both the parasitic worms and their definitive hosts. Microscopy did identify *Capillaria* eggs in one sample and *Toxocara* eggs in two samples that were not identified in the DNA analysis. The reason for this omission may be due to an insufficient DNA reference database.

DNA FROM SOIL

Another study was also focused on helminths but at the same time attempted to look more broadly on the total spectrum of the DNA sequencing (Tams *et al.* 2018). This study was carried out on 13 (of 19) soil samples collected in several vertical series from a man-made pond (approx. 15x18 m) at the famous Danish site of Hoby on Lolland (Fig. 1). Three separate horizons were recognised in the fill, spanning three centuries (c. 100 BC–AD 200). The samples were screened for the presence of parasite eggs by microscopy and analysed using NGS sequencing that helped to identify not only the parasites but also plant and animal DNA.

Hoby became famous after the 1920 discovery of a male burial containing one of the richest inventories of Roman imports in Northern Europe. Recently, the nearby Iron Age settlement was investigated, and it revealed the remains of 52 buildings within an area of 150x100 m; some of the buildings were of impressive dimensions and had an exceptional internal organisation of space (for more details, see Klingenberg *et al.* 2017). The excavations revealed many other archaeological features that

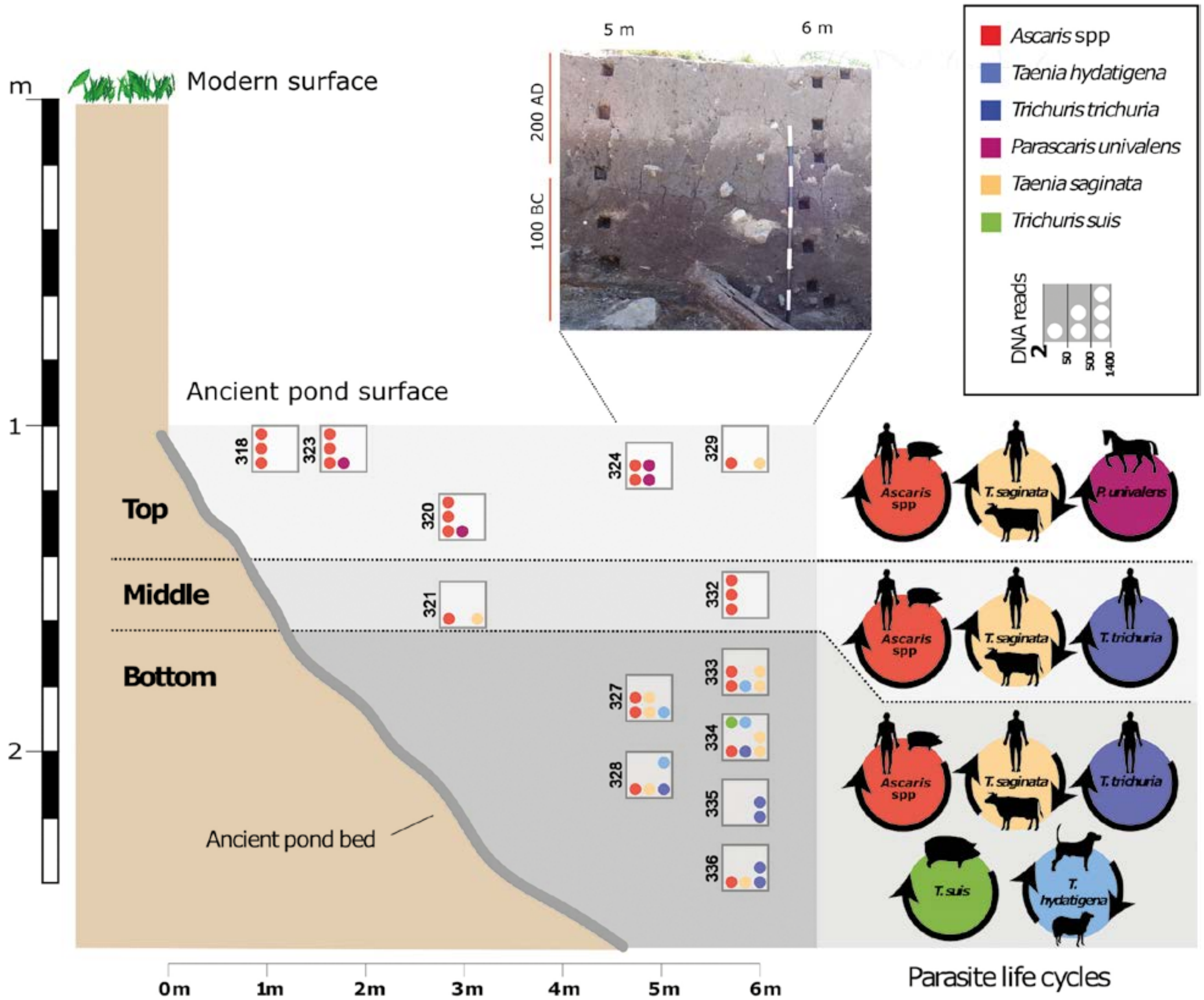

Fig. 1. Excavation of fill layers in an Iron Age man-made pond in Hoby, Island of Lolland, Denmark. Photo: Part of the cross-section of the pond with square holes after sampling. The drawing shows the corresponding position of samples. The numbered boxes show sample number and indicate the approximate position of sampling while the circles inside reflect the number of reads assigned to specific parasites (see legend box top right). Bottom right: typical lifecycles of the parasites in the three layers based on the DNA assignments. *After Tams et al. 2018.*

are interpreted as indicators for large gatherings of people. One of the unique findings was the discovery of an artificial pond. Overall, the material evidence merits the interpretation of Hoby as an important regional centre with a powerful magnate in charge. Therefore a variety of exploration projects were designed in tandem with archaeological excavations.

The artificial pond, oval in shape and measuring roughly 15x18 m was situated just 20 m north of the contemporary settlement. The pond was filled with household refuse such as animal bones (mainly of domestic livestock), pottery, wood and stones. Excavations revealed exceptionally good preservation conditions with even wood and bark being well preserved. Plant macrofossils collected from the settlement area and the pond suggest that the people who lived in the adjacent village were farming hulled barley (*Hordeum vulgare subsp. vulgare*), bread wheat (*Triticum aestivum*), rye (*Secale cereale*), oats (*Avena sativa*), and flax (*Linum usitatissimum*). The discovered animal bones suggest the rearing of pigs, cattle, sheep, and horses.

The sediments accumulated in the pond provided an opportunity to review the resource economy of the Iron Age settlement over 300 years, roughly represented by three major blocks of layers. The DNA analysis of soil samples has revealed varying deposition patterns over time. The lowest block shows great contamination with human faeces through the abundant presence of whipworm (*Trichuris trichiura*) and tapeworms (*Taenia saginata*). Roundworms (*Ascaris spp.*) were encountered in each layer, but more abundantly in the upper. The identification of the helminth species shows that the lower layers produced evidence of parasites deriving from pigs, cattle, canines, and felines, the middle layers, of pigs and cattle, and the upper layers, also the presence of *Parascaris univalens* which parasitise horses (Fig. 1). The presence of horses underlines the importance of Hoby as a regional power centre. Horses remain otherwise unaccounted for in the bone collections from Hoby. Also, the presence of tapeworm (*Taenia saginata*) indicates high-status consumption based on (undercooked) domestic cattle.

The DNA typing has also revealed a number of other wild and domestic animals based on direct samples from the soil, for instance, wild boar, frog, turtle, lizard, etc. (unpublished data). All but the pigs and sheep were excluded from the final publication as contaminations or misassignments. Of course, a question could be raised as to why fowl or junglefowl (*Gallus gallus*), which is a predecessor of the domesticated chicken and was lavishly represented in the upper layers, was dismissed as contamination. It is exactly in places like Hoby that one expects all such novelties to be present, and recent studies do indicate that fowl were kept in domestic settings much earlier than previously anticipated, i.e. well before the year 0 (Kyselý 2010).

The genera and distribution of the identified edible plants also show different compositions between the layers. Rosemary (*Rosmarinus*) was only detected in the bottom layer. Strawberry (*Fragaria*), hazelnut (*Corylus*), stone fruits (*Prunus*), berries (*Vaccinium*), lettuce (*Lactuca*), buckwheat (*Fagopyrum*), barley (*Hordeum*), carrot (*Daucus*), and wheat (*Triticum*) were found in all three layers but predominantly in the bottom layer. Similarly, it is not entirely obvious what criteria were used in the sorting process of the results produced by the DNA analysis. A DNA damage profile for hazelnut was satisfactory, while for spinach (*Spinacia*), which was detected in all the samples, the DNA damage profile was not consistent with the ancient DNA, which led to its omission from the catalogue of Hoby plants (Tams *et al.* 2018, Fig. 2). Other plants listed in the publication were not authenticated through the investigation of the DNA damage patterns.

The original raw data contains evidence from a much longer list of identified plants, which were not included in the published inventories. For instance, among the edible plants, walnut (*Junglans*) and rhubarb (*Rheum*) are found in all three layers, although predominantly in the bottom layer. Both may be problematic to reconcile with contemporary pollen or macrobotanical data. At the same time, it is interesting to note, with some reservation, the presence of carrots (likely wild varieties), lettuce, rosemary, and buckwheat. These as yet controversial findings may inspire researchers to search for the 'hard' evidence in archaeological contexts (De Klerk *et al.* 2015).

The potential of the method is great. The same process identified many other relics, such as trees, herbs, and various microorganisms. The correlation of this data may shed light on the seasonality of the deposits. For instance, samples nos. 324 and 327 seemingly reflect summer accumulations. But as in the case with edible plants, it is evident that DNA studies should be carried out in tandem with

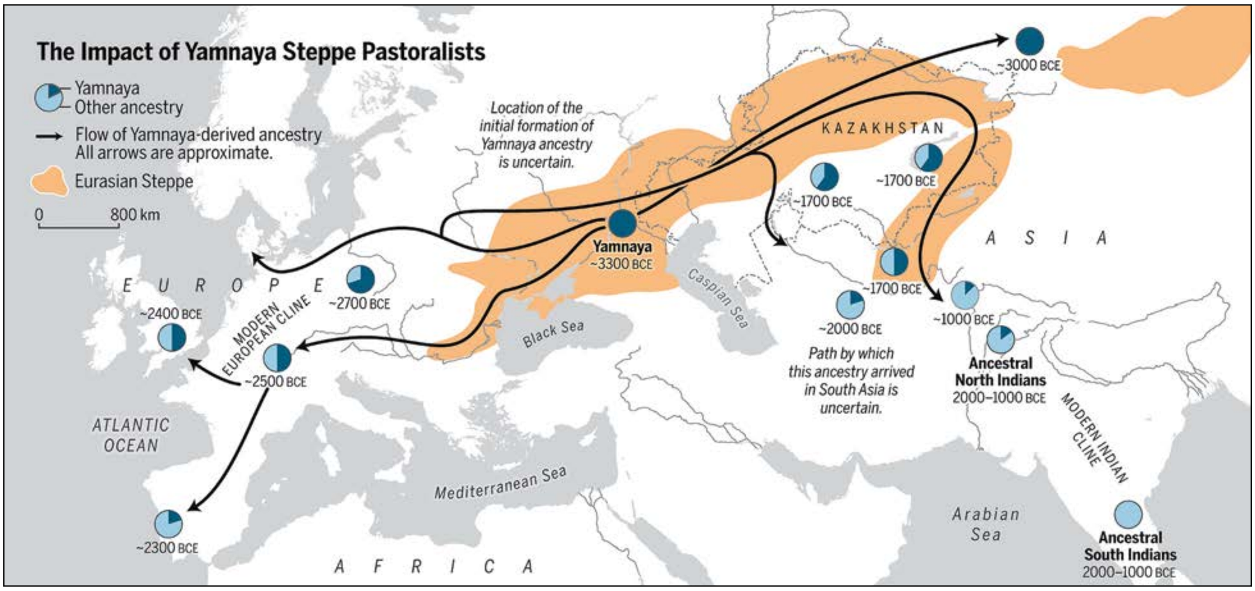

Fig. 2. The Bronze Age spread of Yamnaya Steppe pastoralist ancestry into two subcontinents—Europe and South Asia. *After Narasimhan et al. 2019.*

other studies, such as zoology and archaeobotany. In the present case, the discovery of rye, oat, and flax macrofossils were not mirrored in the DNA identifications.

EXTRACTION OF DNA FROM ANCIENT HUMAN REMAINS

The true significance of archaeogenetic studies became evident in 2015. Two studies were published almost simultaneously, both with the same message: the ancestors of modern Europeans were nomadic pastoralists roaming the steppes between the Caspian and Black Seas and known as bearers of the Yamnaya or Pit-Grave culture (Allentoft *et al.* 2015; Haak *et al.* 2015). As a member of the Copenhagen group (cf. Allentoft *et al.* 2015), the author witnessed hitherto unknown secrecy and haste towards producing results combined with a determination to unquestionably accept them. Many archaeologists and culture historians were overtaken by the simplicity of the presented models, which also included the spread of the Proto-Indo-European language. But the fact that two separate teams were seemingly working unaware of each other's research and yet producing overlapping results have bestowed reliability to the principal findings, which could not be sidelined.

These results have now become the point of departure for any Eurasian archaeogenetic study and can be summarised as two axioms: a) the expansion of farming across Europe was brought about by Early Neolithic migrants from Anatolia joined by a limited admixture of resident hunter-gatherers (cf. also Lazaridis *et al.* 2014) and b) the Indo-European languages spread through a massive migration by Bronze Age herders from the Pontic Steppe around 4 500 years ago, which generated the Corded Ware Culture (CWC) and related cultural phenomena (Fig. 2).

Despite the bluntness of these findings, there seems to be considerable confusion among the archaeologists. Indeed, the two big themes: the spread of farming and the historical background of the formation of the Indo-European languages have been on scientific agendas for two centuries. Different scenarios have been put forward and advocated (for a review, see Renfrew 1987), and painstakingly the evidence for the complexity of such processes has been accumulated, which illuminates both the social interactions and the impetus behind them, although never arriving at a wide-ranging consensus. But now genomics has provided an exciting shortcut that gives an air of redundancy to the earlier endeavours. Some have enthusiastically embraced the archaeogenetic findings (e.g. Anthony, Brown 2017; Kristiansen *et al.* 2017), some have dismissed them all together (e.g. Klejn 2017), others have made prized efforts to bridge the gap between the natural and humanistic sciences (e.g. Heyd 2017; Booth 2019), while others have questioned the interpretations based on apparent theoretical shortages (e.g. Vander Linden 2016; Furholt 2018). Yet for many culture historians these new, seemingly unshakable discoveries became a question of belief. They either believe or do not believe. As Furholt (2018) has rightly noticed, culture historians are too often being diminished to sample suppliers, while the whole palaeogenetic agenda is being formulated as it goes or in accordance with whatever makes the headlines and opens funding prospects. Serious dialogue often dissipates when geneticists retreat behind a 'shield of statistics', where most archaeologists find themselves on unfamiliar ground.

Several authors have compared the impact of the ancient DNA studies to the radiocarbon revolution. Indeed, the application of radiocarbon dating methods to archaeological materials has caused a drastic revision of the chronologies from the very beginning of the application of 14C dating. For instance, R. Braidwood's date for the earliest phase of the Jarmo multilayered early agricultural settlement in Iraq shifted from 4500 BC in 1954 to about 7000 BC in 1958 (Braidwood 1958; the accepted date today is 7090 BC). In Europe, all prehistoric chronologies were also pushed back, creating a comparable divide among the accepting and rejecting archaeologists. Even today articles are being produced that 'rewrite chronologies' (e.g. Stockhammer *et al.* 2015) or discover new and unexpected factors that influence the calibration curves (e.g. Manning *et al.* 2018). Since the 1950s when radiocarbon became a standard dating tool, researchers have made numerous adjustments to the calibration curves and also acknowledged a number of sources of errors, such as the effect of old wood, marine/freshwater, sea spray, etc. Already Braidwood had observed that 'the cutting edge of radiocarbon dating as a research tool is still blunt because of our difficulties with the "geobiological" contamination factor' (Braidwood 1958, p. 424). It is not accidental that DNA samples are routinely being directly dated in connection with DNA sequencing. The dating method is still evolving, including related statistical packages. Can we predict a similarly winding development for aDNA studies?

Modern and ancient contamination and bone diagenesis along with the degradation of endogenous DNA, which causes a deamination of the molecules, is well-acknowledged and addressed in standard sample evaluation procedures. Time will show if the confidence formulated by Der Sarkissian and her colleagues (2015) will prevail in the future.

Another component of the aDNA studies that most certainly will see advancement is statistics. D-statistics, F-statistics, Principal Component Analysis (PCA), ADMIXTURE, qpWave, qpAdm, and other quantitative and qualitative statistical packages are at the core of the archaeogenetic reconstructions. Most refer to them as the ultimate tool for the validation of the findings while ignoring that statistics are based on mathematical *models* that rely on theoretically formulated assumptions or hypotheses. For instance, the most commonly applied D-statistics was invented to analyse gene flow between Neanderthals and anatomically modern humans (Green *et al.* 2010). It is generally considered to be a powerful tool but not without limitations (Zheng, Janke 2018). To date, there is no proper validation of D-statistics based on simulation-based studies and, with the current technological capacity, that would require a running time of several years (ibid). Equally problematic is the use of PCA, which is used to discover and display patterns in SNP data from humans. A recent analysis has identified several irregularities in its application, which may have implications for the interpretation of genomics data (Gauch *et al.* 2019; see also Harney *et al.* 2020 regarding qpAdm).

Considerations concerning statistics inevitably lead toward a well-known problem of replicability. In existing publications this is hardly addressed, most recent studies referring to the older studies in terms of refining the results of sampled individuals with a higher coverage of genome-wide DNA sequence data (e.g. Mathieson *et al.* 2018; Jeong *et al.* 2019). However, some discrepancies might be discovered in the lengthy supplementary information of the articles. For instance, the human remains of a child from Obłaczkowo feature E8-A dated to 2870–2580 cal BC (95.4%) were determined to be those of a male who belongs to Y-chromosomal haplogroup R1b and to mtDNA haplogroup K1b1a1 (Allentoft *et al.* 2015), while another team determined the same individual to be female carrying a mtDNA haplogroup U3a'c profile (Malmström *et al.* 2019, Supp. Inf., 5-6).

Another issue is now also becoming pertinent, namely the exclusive use of a petrous portion of the temporal bone (*pars petrosa*) or alternatively, molar teeth. This has led to the increased destruction of petrous bones and crania (Charlton *et al.* 2019). Biomolecular studies are destructive, but the advancement of techniques and procedures may remain unverified due to a shortage of informative samples in the future.

While the aDNA data increases exponentially, the two axioms are accordingly being modified. As expected, complexity increases with the growth of data. A single source for the genetic ancestry of farmer populations is now being contested. Already Mathieson *et al.* (2018) have noticed that hunter-gatherers from the Iron Gates sites have ancestry that is not present among the dominant western hunter-gatherers (WHG) or eastern hunter-gatherers (EHG), suggesting a more varied genetic background in Europe than expected. Other studies reveal that the Mediterranean genetic pool was partly a result of Late Glacial expansions from a Near Eastern refuge and that this formed an important genetic source pool for subsequent Neolithic expansions into the rest of Europe (Hofmanová *et al.* 2016; Pereira *et al.* 2017). The Neolithic package is still seen as having been introduced from the Near East, but the present genetic interferences comply better with archaeological models proposing the demic diffusion of minor groups of pioneers, that genetically could have become more visible due to already existing 'farmer' lineages in Southern Europe. The major hindrance for a more comprehensive analysis is the general lack of Mesolithic human remains in Southern Europe. Also, as demonstrated by Rivollat *et al.* (2020), a nuanced regional sampling, as well as increasing numbers of samples, reveal far more diverse patterns of cultural and biological interaction between the first farmers and the indigenous hunter-gatherers than have been formulated by the broad-brush models.

Turning to the second major finding, namely the genetic turnover created by the steppe populations subscribing to the Yamnaya cultural traditions, including their role in the dissemination of the Proto-Indo-European languages, redefinition of social organisation and focus on male identity, there have also been several adjustments to this grand narrative, in particular with regard to the links between the steppe populations and the CWC. The CWC has been recognised over vast regions of Europe, not as a homogenous and clearly bounded social entity but rather as one of the elements in a diverse social landscape (SMPH 2020; see also Müller *et al.* 2009). According to proposed palaeogenetic models, the CWC was 79% (Haak *et al.* 2015) or 75% (Mathieson *et al.* 2018) Yamnaya-like. Based on such statements, we may deduce that the CWC was a version of the Yamnaya that have kept the language but adjusted its cultural appearance to central European conditions. Not many would agree with this. Steppe-related ancestry has now been detected in individuals predating the Yamnaya by 2000 years, from Copper Age burials in Bulgaria and Ukraine, including Varna cemetery (Mathieson *et al.* 2018). Having in mind the abrupt termination of the Copper Age in Southeastern Europe, more attention should be given to demographic dynamics in the 4th millennium BC which may in turn explain the high percentage of steppe ancestry in the samples from mid-3rd millennium BC.

One of the problems that may explain the divide between archaeogenetics and archaeology is that the two operate on different time-scales. What may be 'sudden' for a geneticist can correspond to several centuries, if not more, for an archaeologist. Despite the fact that most of the genetic samples are being directly dated, the population reconstructions are being made on a vague attribution to an archaeological culture, with little consideration of its diachronic development. For instance, the expansion of steppe DNA is seen as instrumented by males (Goldberg *et al.* 2017; Kristiansen *et al.* 2017; Narasimhan *et al.* 2019), with approximately 5–14 migrating males for every migrating female (Goldberg *et al.* 2017). Moreover, this ongoing male migration from the steppe to central Europe continued over a period of multiple generations (ibid.). Other studies, focusing on the CWC have proposed a social organisation accompanied by patrilocality and female exogamy, a new family organisation mediated by the proto-Indo-Europeans of Yamnaya (Haak *et al.* 2008, Sjögren *et al.* 2016; Kristiansen *et al.* 2017). It is worth mentioning here the results of isotopic provenancing carried by Sjögren *et al.* (2016) as they tend to be erroneously cited. The analysis included 25 individuals from the Lauda-Königshofen burial site and 19 from the Bergrheinfeld burial site (a total of 44; both in southern Germany). Seven individuals from Lauda-Königshofen, of whom only five were determined to be females were of non-local origin, while at Bergrheinfeld eight individuals of whom five were anthropologically determined to be females had spent their childhood outside the region (ibid.). Following these observations, it seems highly relevant to learn when do the migrating males transform into locals and start a genetically less detectable (shorter range?) migration of females? On the other hand, mitogenomes reveal that it was females with steppe ancestry who contributed to the formation of the Baltic CWC (Juras *et al.* 2018). This implies that 'massive migrations' followed by 'brutal violence' (Barras 2019) was a more layered process than a uniform demographic phenomenon as suggested by paleogenomic ancestral reconstructions, displaying the need for the refinement of a sampling and reporting mesh in terms of chronology and geography that may narrow the divide between geneticists and archaeologists.

Genomic studies fail to explain the linkage between the observed 'gene flow' and the postulated 'massive migration'. Was it a single event (or wave, sensu Gimbutas 1977)? Was it unidirectional? What demographic capacity is needed to enable the genetic transformation of Central Europe that subsequently encompassed the whole continent, including west and south Asia? What social conditions inspired such movement? Why were European farmers and hunters so easily overtaken by herders? Was it attributable to demographic superiority or the scenario of crisis (Kristiansen et al. 2017; Barras 2019)? As Furholt has rightly argued, a unidimensional interpretation of molecular data has exposed the need to review the mobility models and their use as an explanatory framework (2018).

CONCLUSIONS

DNA typing is still an evolving discipline. Only a decade ago the first ancient human genome was fully and successfully sequenced; it came from the hair of a man who lived in Greenland 4000 years ago, with an A+ blood type, brown eyes and a predisposition to baldness (Rasmussen *et al*. 2010). In 2018 there were more than 1300 genome sequences that have been produced from the remains of ancient humans (Callaway 2018). Ancient genomics has allowed an unprecedented approach towards past populations providing exciting possibilities to unravel the complex web of local and regional interactions. This has a needed positive effect on archaeology, culture history, linguistics, mythology, etc. that have now received a robust testing and evaluation tool for theoretical insights and cultural and linguistic reconstructions. Genomic findings have enthused fundamental archaeological controversies related to migration, acculturation, technological and cultural innovations, ethnicity, the significance of material expressions, warfare, etc. that most certainly lead towards a qualitative improvement of the discipline.

Millar & Lambert (2019) have made an interesting prediction analysing the ontogeny of molecular science. They envisage three stages for new fields of science: a descriptive stage, followed by a focus on mechanisms/functions, and finally, the formulation of experiments and hypothesis testing. Archaeogenetics is currently at the descriptive stage, and accordingly, population dynamics are solely understood as admixture between distinct groups. It is the obligation of the archaeologists to 'reclaim the past' and provide alternatives to such overtly simplistic analyses and formulate theory-based scientific research agendas.

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Inga MERKYTĖ,
University of Copenhagen, Saxo Institute,
Karen Blixens Plads 8, 2300 Copenhagen, Denmark
merkyte@hum.ku.dk