Ancient genomic research - From broad strokes to nuanced reconstructions of the past

Kathrin Nägele[1], Maite Rivollat [1,2,3,4], He Yu[1,5] & Ke Wang[1,6]

1) *Max Planck Institute for Evolutionary Anthropology, Germany*
   e-mail: kathrin_naegele@eva.mpg.de
2) *Ghent University, Department of Archaeology, Belgium*
3) *Durham University, Department of Archaeology, UK*
4) *Bordeaux University, PACEA, France*
5) *State Key Laboratory of Protein and Plant Gene Research, School of Life Sciences, Peking University, Yiheyuan Rd. 5, Haidian District, Beijing 100871, China*
6) *Department of Anthropology and Human Genetics, School of Life Science, Fudan University, China*

Summary - *Ancient DNA (aDNA) studies have deployed genetic material from archaeological contexts to investigate human dispersals and interactions, corroborating some longstanding hypotheses and revealing new aspects of human history. After drawing the broad genomic strokes of human history, geneticists have discovered the exciting possibilities of applying this method to answer questions on a smaller scale. This review provides an overview of the commonly used methods, both in the laboratory and the analyses, and summarizes the current state of genomic research. It reviews human dispersals across the continents and additionally highlights some studies that integrated genomics to answer questions beyond biology to understand the cultural and societal traits of past societies. By shining a light from multiple angles, we gain a much better understanding of the real shape of the human past.*

Keywords - *Ancient DNA, Archaeogenomics, Migrations, Dispersals, Human history.*

Since the 1980s (Higuchi et al. 1984; Pääbo 1985), when ancient DNA (aDNA) (Hofreiter et al. 2001) recovery was the subject of skepticism, the field has grown to become a widely used, significant and robust line of evidence in reconstructing the past (Stoneking and Krause 2011).

Two types of DNA are present in animal cells. MtDNA is a small, haploid, circular genome found in the mitochondria. Because they are very abundant (Giles et al. 1980), and the circular nature of the genome stabilizes it, this type of DNA is more likely to preserve. However, mtDNA is inherited maternally, does not recombine and therefore reflects only the maternal genealogies and population history of an individual, but its fast mutation rate provides insight into relatively recent evolutionary timescales. The decades of work on this marker have resulted in well defined lineages, also called haplogroups,

and provide a great basis for comparative research (Bisso-Machado and Fagundes 2021).

To understand the genetic diversity of both parental lineages combined, it is necessary to study the nuclear genome. The nuclear genome consists of 23 pairs of chromosomes, of which two are the sex chromosomes. This genome is a recombination of the genomic information of both parents, with the exception of the non-recombining portion of the Y-chromosome. This region is inherited from fathers to sons, and can trace the paternal lineage of an individual. Despite the protection of the cell core, the large DNA molecules are only present in two copies per cell, and degrade faster after a cell's death. However, the large number of markers each provide an independent information about the genetic ancestry (Mathieson and Scally 2020), and provides more statistical power and

resolution to study genetic history (Stoneking and Krause 2011).

After refining the methods and tackling problems such as contamination (Llamas et al. 2017) and poor preservation, aDNA can today be retrieved from a variety of archaeological and palaeontological remains. Genomes recovered from skeletal tissue (Higuchi et al. 1984; Pääbo 1985), hair (Rasmussen et al. 2010), calcified dental biofilms (Warinner et al. 2014; Warinner et al. 2015), mummified soft tissues (Schuenemann et al. 2017), plants (Kistler et al. 2020, Swarts et al. 2017), coprolites (Poinar et al. 2003), sediment and ice cores (Dommain et al. 2020; Slon et al. 2017), among others (Bro-Jørgensen et al. 2018; Duggan et al. 2020; Hansson and Foley 2008; Hartnup et al. 2011; Jensen et al. 2019; LeBlanc et al. 2007; Oskam et al. 2010; Ramos-Madrigal et al. 2019; Schablitsky et al. 2019; Sullivan et al. 2021; Teasdale et al. 2015) have broadened our understanding of the evolution of various species, including humans (Orlando et al. 2021).

Ancient DNA retrieval

Ancient DNA preservation is impacted by a variety of factors and is difficult to predict. Time is an essential factor (Adler et al. 2011; Allentoft et al. 2012), but other environmental conditions can considerably impact the degradation process. The chemical properties of certain minerals interact with the DNA, leading to different preservation states depending on soil pH and mineral content. Additionally, the microclimate of a site impacts the degradation process. Cave sites provide a more stable environment and show better preservation compared to open-sites (Mendisco et al. 2014; Ramos Madrigal et al. forthcoming). Considering the macro-climate, regions with high humidity and with high temperature fluctuations show generally worse DNA preservation (Kistler et al. 2017). In areas with stable and cold conditions, much older ancient DNA can be retrieved (Orlando et al. 2013; van der Valk et al. 2021).

In an extract dominated by environmental contaminants such as bacterial, viral, fungal, plant and contemporary human DNA (Kazarina et al. 2019; Mann et al. 2018), the target molecules are drowned out. Targeting skeletal elements suited for the goals of an analysis are key to the success of ancient genomic studies. The petrous portion of the temporal bone, surrounding the inner ear, preserves DNA molecules better than other tissues (Hansen et al. 2017; Parker et al. 2020; Pinhasi et al. 2015), as do auditory ossicles (Sirak et al. 2020). Teeth have been shown to be a good source of ancient DNA, although less effectively preserving the molecules. In areas or sites with conditions beneficial for ancient DNA preservation, postcranial bones can be used to source ancient DNA. Regardless of the element, ancient DNA sampling is mostly destructive (Pinhasi et al. 2015; Sirak et al. 2017). Considering a variety of reasons (Charlton et al. 2019; Ponce de León et al. 2018) (See Box 1), alternative substrates can be considered (Parker et al. 2020).

The handling of the sample at the excavation site or in the curating facility can contribute to reducing the environmental contamination, i.e., by using gloves when retrieving elements, avoiding application of substances such as animal based glues and avoiding washing steps. These measures can substantially increase the likelihood of recovering sufficient genomic material and reduce cross contamination (Llamas et al. 2017). Using dedicated pre-and post-amplification facilities, UV-radiation of elements and control of contamination through negative controls (Pääbo 1989; Pääbo et al. 2004) contribute to the reduction of contamination. Post-sequencing, the sample is authenticated in silico through investigation of DNA damage and fragment size (Fellows Yates et al. 2021; Peltzer et al. 2016). Both measures are the result of the limited chemical stability of DNA molecules. After death, the absence of cellular repair mechanisms (Lindahl 1993) and beginning autophagy of cells (Darzynkiewicz et al. 1997) contribute to the decomposition process. Microbial digestive processes (Eglinton and Logan 1991; Lindahl 1993) further fragment DNA, as do hydrolytic

reactions altering the chemistry of the molecules (Dabney et al. 2013; Lindahl and Andersson 1972), which result in short fragment sizes of, on average, 40base pairs (Krause et al. 2010). Another typical type of DNA damage used for authentication is depurination, visible in the misincorporation patterns, particularly at the end of the reads, referred to as "the smiley plot" (Dabney et al. 2013). This type of damage can be repaired enzymatically (Rohland et al. 2015) or be removed bioinformatically (Skoglund et al. 2014) to reduce the systematic errors introduced into the analysis.

After selection of suitable samples, ancient DNA labs document the state of the received element, before sampling in dedicated ancient DNA laboratories (see also Figure 1). Sampling of ancient bones is a difficult step in which many considerations have to be weighed. Minimizing the impact on the sample is an ethical imperative, as other researchers, especially future generations, might want to study these irreplaceable samples with other - improved - methods. Therefore, most protocols aim to retrieve the most genomic material from a minimal amount of material (Bolnick et al. 2012; Dabney et al. 2013; Harney et al. 2021; Rohland and Hofreiter 2007). However, not all methods are equally suited for all types of samples, and the goals of retrieving DNA and minimally impacting the perhaps rare or culturally significant sample have to be balanced by the involved stakeholders (Austin et al. 2019; Fox and Hawks 2019; Nieves-Colón et al. 2021). Protocols combining samples for several types of analyses should be prioritized (Fagernäs et al. 2020; Korlević et al. 2018). Most importantly, double-sampling of an individual by several labs should be avoided to save the invaluable resources of human remains, but also those of the respective labs.

After sampling, DNA has to be extracted. Standardly, DNA is isolated and purified (Dabney et al. 2013; Glocke and Meyer 2017). Shorter molecules in a range between 25 and 45 base pairs are likely constituting the majority of authentic DNA fragments in the sample, usually referred to as "endogenous DNA", but

can also contain modern and ancient contaminants (Carpenter et al. 2013). To stabilize the fragments retrieved during extraction, they are converted into synthetic copies in sequencing libraries (Gansauge et al. 2017; Meyer and Kircher 2010). The synthetic strands contain adapters, which can be used to further increase the number of copies for this fragment during sequencing, and allow to store and rebuild the composition of the extract. In theory, the libraries are immortal, as they can be re-amplified and used again for a variety of downstream processes (Orlando et al. 2021). After stabilizing the molecules and equipping them with adapters, those can be used to finally "read" the sequences. In the early years of DNA sequencing, producing genomes was slow, cost intensive, and held great limitations. Today, Next-Generation-Sequencing (NGS) platforms can sequence massive amounts of (short) fragments at low costs, with a very low error rate, while identifying the sequences of all fragments in an extract in parallel (Goodwin et al. 2016). Due to the non-specific and non-targeted sequencing, this method has been dubbed "shotgun sequencing". This approach is well suited for modern DNA samples and well preserved ancient samples, allowing to retrieve data not only from the source, but to assess the presence of specific pathogens or commensal microbes (Orlando et al. 2021). However, for most aDNA purposes it is only the first step, after which levels of damage and amount of fragments of a certain organismic origin can be assessed, but genomic coverage is too low to perform reliable data analyses (Carpenter et al. 2013).

This shortcoming can be mitigated by targeting molecules of a certain organismic origin, such as humans or pathogens (Andrades Valtueña et al. 2017), enriching the mix for those while removing non-target fragments. By using complementary probes (Carpenter et al. 2013; Enk et al. 2014; González Fortes and Paijmans 2019) to capture specific fragments, this approach not only increases the yield of endogenous DNA, but also removes possible contaminants which are washed away. With this method, only the targeted fragments will be amplified and sequenced, allowing
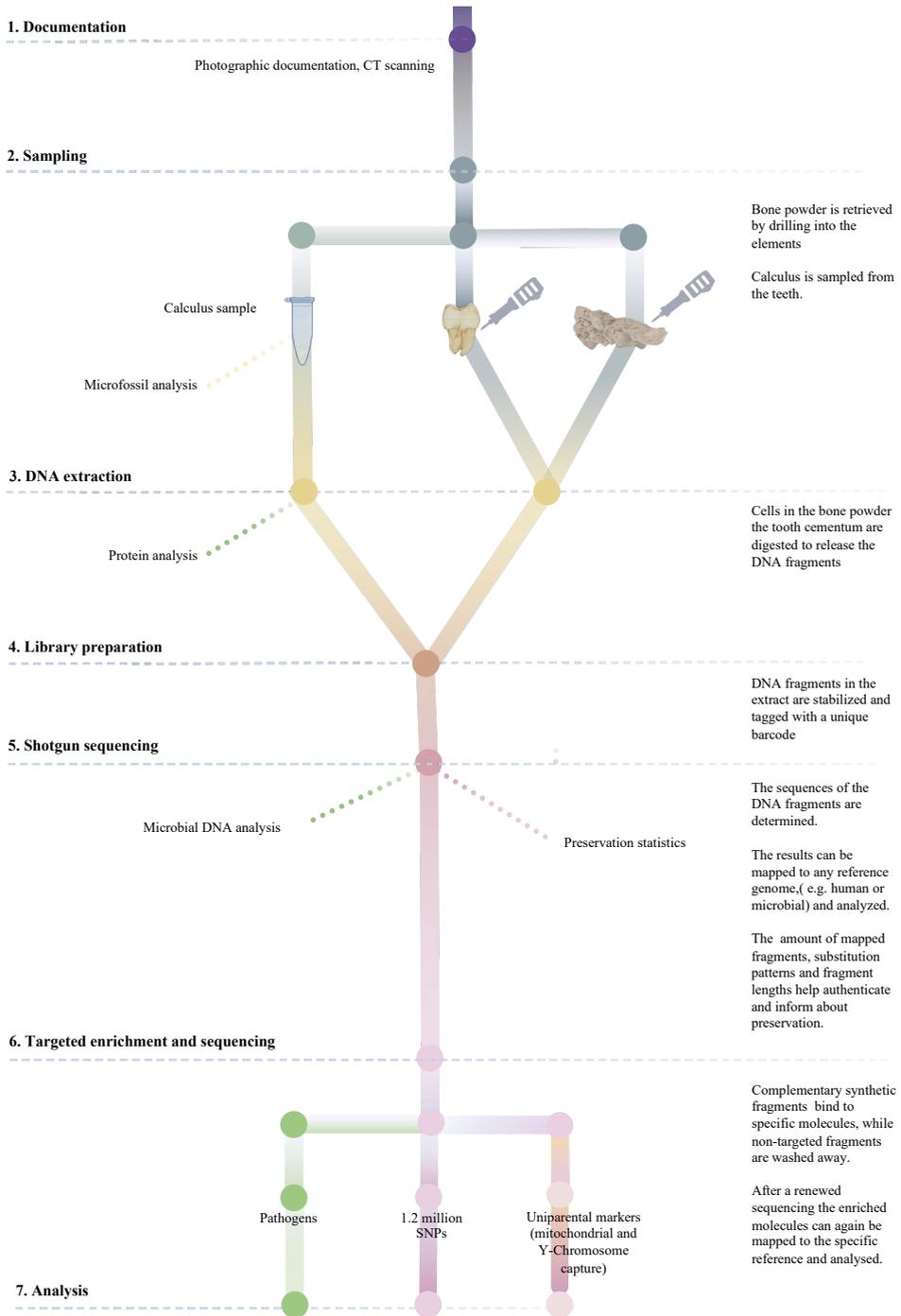
1. Documentation

Photographic documentation, CT scanning

2. Sampling

Bone powder is retrieved by drilling into the elements

Calculus is sampled from the teeth.

Calculus sample

Microfossil analysis

3. DNA extraction

Cells in the bone powder the tooth cementum are digested to release the DNA fragments

Protein analysis

4. Library preparation

DNA fragments in the extract are stabilized and tagged with a unique barcode

5. Shotgun sequencing

The sequences of the DNA fragments are determined.

Microbial DNA analysis

Preservation statistics

The results can be mapped to any reference genome,(e.g. human or microbial) and analyzed.

The amount of mapped fragments, substitution patterns and fragment lengths help authenticate and inform about preservation.

6. Targeted enrichment and sequencing

Complementary synthetic fragments bind to specific molecules, while non-targeted fragments are washed away.

After a renewed sequencing the enriched molecules can again be mapped to the specific reference and analysed.

Pathogens

1.2 million SNPs

Uniparental markers (mitochondrial and Y-Chromosome capture)

7. Analysis

Fig. 1 Data generation scheme for aDNA. Details may vary between labs.

to retrieve more analyzable data at much lower cost. However, this method potentially introduces a bias (Seguin-Orlando et al. 2015), resulting from the ascertainment of markers based on and most informative about variation in present-day populations (Orlando et al. 2021). Analyzing with ancient DNA data, this can severely limit the detection of genetic diversity in in certain groups, and might introduce artifacts when comparing with other datasets where markers were ascertained differently.

Ancient DNA analysis

Once sequenced, a bouquet of methods can be deployed to analyze the ancient DNA data. The specific method needs to be chosen based on data quality, availability of reference data and the specific hypotheses to be tested. As part of the quality control, determining the genetic sex is a standard analysis. For molecular sexing, there are methods detecting the genetic elements unique to the X and Y chromosomes (Stone et al. 1996), or comparing the number of fragments aligning to the respective chromosome (Buonasera et al. 2020; Skoglund et al. 2013). Most males carry XY and most females an XX karyogram, although variations in this pattern exist (see also Box 4). After assessing the quality of the data, most population genetic analyses start with methods allowing a first understanding of the population composition and structure. Commonly used methods are principal component analyses (PCA), decomposing genetic distance between individuals into lower dimensions (Patterson et al. 2006), and clustering approaches, classifying separate individuals into clusters based on shared genetic ancestry and admixture patterns (Lawson et al. 2018). These methods provide a good basis for formulating hypothesis and determine further, more formal statistical tests and models to be used downstream. Formal statistics, e.g., *f*-statistics, compare allele frequencies to identify shared drift, the relative time two populations have evolved together, and can detect admixture between populations or genetic continuity by examining differential affinities (Durand et al. 2011; Patterson et al. 2012),

and estimate admixture times (Chintalapati et al. 2022; Loh et al. 2013). Measures of genetic distance and patterns of allelic diversity (Holsinger and Weir 2009) can be used to construct models of phylogenetic trees and networks (Bandelt et al. 1999; Bandelt et al. 1995; Mardulyn 2012) and investigate evolutionary relationships between groups. By adding ancient sequences of a known date, these trees can hold a temporal dimension, allowing estimations of group divergence, changes of mutation rates (Molak et al. 2012; Rieux and Balloux 2016) and other patterns of lineage diversification, speciation and admixture between lineages (Chang et al. 2017; Pickrell and Pritchard 2012; Reich et al. 2010). Large-scale palaeogenomic studies include substantial numbers of ancient genomes across wide temporal and geographic regions (Mathieson et al. 2018; McColl et al. 2018; Narasimhan et al. 2019), harvesting the power of aDNA to reconstruct demographic histories of continents, sub-continents and island regions (Fehren-Schmitz et al. 2017; Fernandes et al. 2021; Haak et al. 2015; Lazaridis et al. 2014; Matisoo-Smith 2015; Nägele et al. 2020; Olalde et al. 2018; Posth et al. 2018; Pugach et al. 2021; Raghavan et al. 2015; Skoglund et al. 2012). They aim to reconstruct origins, migration patterns, and interactions in human populations (Slatkin and Racimo 2016), and – related – ancient epidemics and transmission patterns and adaption to disease (Barquera and Krause 2020; Duchêne et al. 2020; Guzmán-Solís et al. 2021; Kerner et al. 2021; Kocher 2021), but also animal dispersals and domestication (see Box 3).

Ancient DNA analyses can also inform on demographic patterns on a smaller scale, focusing on local sites, communities, and investigate patterns of genetic relatedness among ancient individuals. Kinship is a complex social construct, but often pertains to genetic relation. By identifying genomic segments shared between individuals as a result of common descent (Feuerborn et al. 2021; Monroy Kuhn et al. 2018; Ringbauer et al. 2021; Vai et al. 2020), ancient family pedigrees can be reconstructed and questions about ancient social structures informed (See also Box Nr. 2). Extending this approach beyond a burial group or site can

BOX 1 - ETHICAL CONSIDERATIONS WHEN WORKING WITH ANCIENT DNA

The studies highlighted in this paper show that analytical methods of ancient DNA are a powerful tool in reconstructing many aspects of the human past. However, they have inherent challenges and limitations. Ethical challenges within biological anthropology, including bio-archeology, are becoming much more widely discussed. A variety of publications aims to discuss ethical issues in the field (Ávila-Arcos et al. 2022; Cortez et al. 2021; Nieves-Colón et al. 2021; Wagner et al. 2020) and provide guidance for sampling (Fox and Hawks 2019; Sirak and Sedig 2019), publication (Squires et al. 2022), community involvement and collaboration (Argüelles et al. 2022; Ávila-Arcos et al. 2022; Wagner et al. 2020). Ancient DNA sampling is destructive. Despite usage of only 50-100 mg of material, elements often have to be destroyed. In general, but especially when sampling unique individuals or poorly preserved elements, the reason and goals of the aDNA sampling need to be evaluated carefully, and double sampling should be avoided. The number of genetic markers analyzed is too high to be processed, illustrated and communicated easily. Hence, genetic science has to be reductive, introducing simplifications that are subjective to the hypothesis, methods, region and researcher. Therefore, the results produced by archaeogenetics will only ever be an approximation to the real events. Most approaches are sensitive to the reference populations used, the choice of parameters, significance thresholds and underlying assumptions, which will affect the interpretation of the data. Another limitation affecting specifically ancient DNA is that it has to be combined with datasets produced in different ways, often representing present-day individuals to be able to conduct comparative analyses. Preset-day populations are not the best proxy for ancestry in ancient people for chronological reasons (Pickrell and Reich 2014), especially in places impacted by large-scale population turnovers and cryptic displacements, i.e during the colonial period. Additionally, the different production styles of genomes (i.e., shotgun, capture) and the patterns of damage (Leonardi et al. 2017; Orlando et al. 2021) can result in artifacts in the analysis that have to be taken into account during analysis (Callaway 2016; Gallego Llorente et al. 2015). Despite the seemingly objective nature of genomics research, the reduction of complexity and particular processing of DNA leaves much of the interpretation to the researchers, introducing subjective biases. So eventually, contextualizing and integrating with other lines of evidence is imperative to reconstruct the human past. It becomes increasingly evident that narratives about the past, especially in countries impacted by colonialism and imperialism, have been and still are constructed often without inclusion of local perspectives, academic and non-academic. Even within Europe, power dynamics between western and eastern European countries can resemble the exploitation of cultural heritage in other countries, i.e., those impacted by the European invasion during the colonial period. By including indigenous perspectives like oral traditions, and local experts within the respective fields and regions (Pollard and Bray 2007), archaeogenetic studies are more sustainable, and foster academic sovereignty and knowledge exchange (Argüelles et al. 2022; Ávila-Arcos et al. 2022).

inform on inter-site interactions, reconstruct residence patterns (Bongers et al. 2020; Fernandes et al. 2021; Žegarac et al. 2021) and even elucidate ancient diets and activities (Obregon-Tito et al. 2015; Racimo et al. 2020; Warinner et al. 2015).

After ancient DNA studies had been deployed for investigations of human history on a macro-scale, adding the broad strokes of human history on the globe (Fig. 2), geneticists have discovered the interesting possibilities of applying this method to answer questions on a smaller scale, and advancing more into anthropological questions, including cultural and societal traits. Most studies summarized below do have the limitations mentioned in Box 1 and integrating genetic evidence with other lines of evidence can be very difficult to interpret. However, by shining a light from multiple angles we gain a much better understanding of the real shape of the human past. This paper aims to provide an overview of the findings on a continental scale, but presents case studies in which ancient DNA was integrated to answer questions beyond biology.
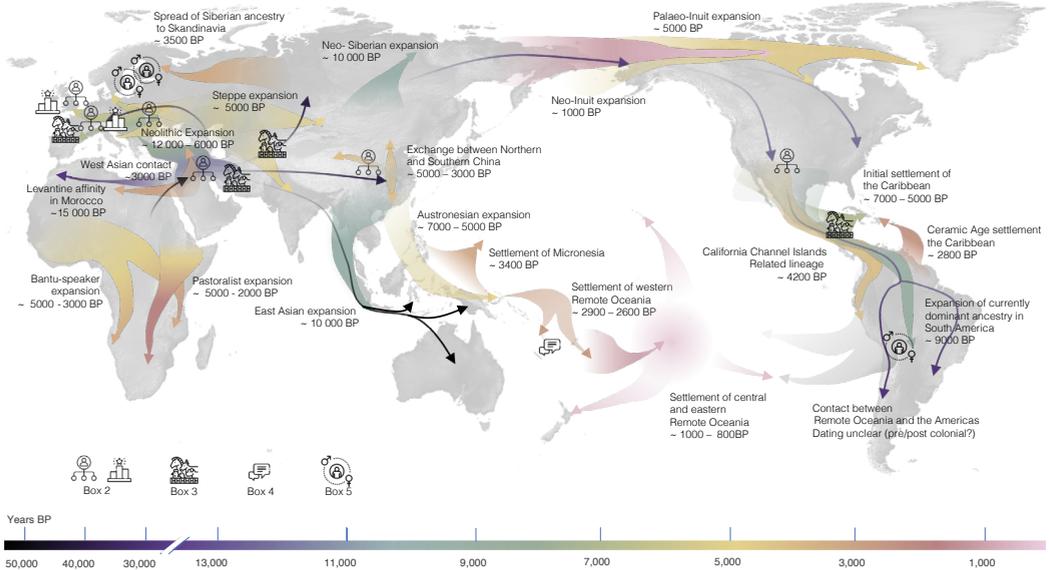
Fig. 2 Map of the World outlining a selection of major human dispersals in the current state of the research. Arrows do not indicate exact regions or migration routes. Locations of studies mentioned in Boxes indicated by icons.

Africa

The African continent harbors the greatest genetic diversity, and also the world's deepest populations divergence. The split among ancestral southern, central and eastern African hunter-gatherer communities formed the distinct genetic structure of present-day foraging societies in various regions of sub-Saharan Africa (Lipson et al. 2022; Skoglund et al. 2017). After the populations split, the spread of agriculturalists and pastoralists across the contitnent greatly altered the genetic landscape of Africa and shaped the genetic structure of present-day African populations (Lipson et al. 2022; Patin et al. 2017; Pickrell and Pritchard 2012; Schlebusch et al. 2017; Skoglund et al. 2017; Wang et al. 2020)

aDNA allows to trace the deep lineages of the hunter-gatherer populations back in time, revealing previously undescribed genetic ancestries and connections. The publication of a 4500-year-old Ethiopian individual "Mota" (Gallego Llorente et al. 2015) distinguished the genetic ancestry of ancient northeastern African individuals from present-day northeastern and eastern African populations. 3500-year-old genomes representing hunter-gathers from Nyarindi Rocksshelter in Kenya, along with Late Stone Age foragers from Kenya and Tanzania represent the core ancestry of ancient eastern African hunter-gatherers today. The ancient hunter-gatherers from eastern to southern Africa form a genetic cline in which the geographically intermediate ancient hunter-gatherer groups fall in between, corresponding with their proportion of eastern and southern genetic ancestries, their positions mirror their latitude and geographic location (Lipson et al. 2022; Prendergast et al. 2019; Skoglund et al. 2017; Wang et al. 2020). The ancient hunter-gatherers in western Africa, represented by 8000-year-old and 3000-year-old foragers from Shum Laka site in Cameroon, represent a distinct genetic lineage most similar to present-day western-central African hunter-gatherer ancestry (Lipson et al. 2022) and imply a separate deep lineage different from the east-to-south hunter-gatherer cline

Beyond defining the deep ancestral lineages, ancient genomes have recovered the continental connections between Africa and Eurasia. 15,000-year-old individuals from the Taforalt site in eastern Morocco show a genetic affinity to early Holocene Near Easterners represented by Levantine Natufians, linking the late Pleistocene north Africa with the early Holocene Levant (Van de Loosdrecht et al. 2018). The genetic link between North Africa and the Levant continues to be evident until early Neolithic in Morocco at 7000 BP, while late Neolithic individuals at 5000 BP appear to be associated with the European Mediterranean regions (Fregel et al. 2018). aDNA also revealed previously undescribed interregional connections within Africa, such as the long-range connection between eastern and central African hunter-gatherers, represented by an 3900-year-old genome from the Kakapel site in western Kenya who carries ancestry found in the present-day indigenous hunter-gatherer communities of the Central African rainforests (Wang et al. 2020). Such interregional connections are especially evident during the spread of Bantu-speaking farmers and northeastern African pastoralists across the continent. The 3000 year-old genome from the Luxmanda site in Tanzania records the first direct genetic evidence of the arrival of pastoralist ancestry in eastern Africa (Skoglund et al. 2017). Combined evidence from Prendergast et al. 2019 and Wang et al. 2020 reveals a rather complex genomic formation of ancient eastern African pastoralists. Groups carrying Levantine-related ancestry entered eastern Africa during the Pastoral Neolithic period and repeatedly mixed with local hunter-gatherers and Nilotic-related pastoralists, today represented by the Dinka from South Sudan. The three ancestral components persist to the Iron Age of eastern Africa ~2500 BP (Crowther et al. 2018; Lane et al. 2013), and notably, the Iron Age gene pool is marked by increased Nilotic ancestry (Prendergast et al. 2019; Wang et al. 2020). The ancient eastern African pastoralists further spread southwards, and reached their southernmost distribution in South Africa, recorded by a 1200-year-old genome with southern hunter-gatherer and eastern pastoralist ancestry (Skoglund et al. 2017). The arrival of pastoralists, together with the footprint of the Bantu-speaking famer's expansion into southern Africa, forms a notable mosaic pattern of farmer-pastoralist-hunter-gatherers today. Bantu-speaking farmers, who originated in western Africa, haves expanded across over half of the African continent, and arrived in eastern and southern Africa. However, the routes of their dispersal remain debated. Encouragingly, ancient DNA provides direct genetic evidence on the dispersal route, with the potential of resolving existing archaeological and linguistic debates. For instance, in South Africa, four 400-year-old n individuals are genetically indistinguishable from present-day southern Bantu-speaking populations, with little genetic contribution from indigenous southern African hunter-gatherers (Schlebusch et al. 2017). Contemporaneously, in eastern Africa, a 600-year-old individual from Pemba Island in Tanzania carries ancestry indistinguishable to southern Bantu-speaking Ovambo (Skoglund et al. 2017), together recording the arrival of Bantu-speaking farmers in eastern and southern Africa. In Botswana, 1400-year-old genomes from the Xaro site show the first genetic evidence that southern African foragers mixed with eastern African pastoralists, and later recieved genetic contribuition from Bantu-related farmers (Wang et al. 2020). This unique mosaic of genetic ancestry supports archeological and linguistical hypotheses of pastoralists arriveong in southern Africa first, and Bantu-speaking farmers later (Guldemann 2008; Isern and Fort 2019), corroborating previous inferences based on present-day African genomes (Pickrell and Pritchard 2012).

Europe

As a result of favourable climatic conditions and a particularly intense research dynamic, western Eurasia is the most intensively studied area of the world (Liu et al. 2021).

The genomes recovered from anatomically modern humans dating to before 40,000 BP (Fu

et al. 2015; Fu et al. 2014; Hajdinjak et al. 2021; Prüfer et al. 2021), have not directly contributed to the subsequent European gene pool. However, the Neandertal ancestry found in variable amounts amongst them marks the main difference between sub-Saharan African populations and those outside sub-Saharan Africa (Green et al. 2010; Petr et al. 2019; Prüfer et al. 2014).

In western Europe, the Aurignacian, the first Upper Palaeolithic culture in western Europe, is genetically represented by a single individual from Belgium (Fu et al. 2016), which is genetically distinct from an individual from western Russia, Kostenki 14 (Fu et al. 2016; Seguin-Orlando et al. 2015). From 34,000 to 26,000 cal BP, the Gravettian culture spans the entire European continent (Conard and Moreau 2004), but the associated people's ancestry, derived from Kostenki 14, is represented only in central and southern Europe (Fu et al. 2016), and refered to as the Věstonice cluster. The discontinuity between the genetic ancestries from the Věstonice cluster and individuals in Western Europe, associated with the Aurignacian, has been interpreted as the result of a replacement by Gravettian associated groups (Fu et al. 2016). During the Last Glacial Maximum (LGM), a period of drastic climatic cooling between 26,000 and 19,000 cal BP, massive glaciers pushed human groups to retreat to southern areas. From 19,000 BP, two different material cultures expanded at the same time, the Epigravettian in the Italian Peninsula and southeastern Europe, and the Magdalenian in central, western and southwestern Europe. All known individuals associated with the Epigravettian culture constitute the Villabruna genetic cluster, showing no affinity with the previous Věstonice cluster, but with the Near-East (Fu et al. 2016). The genetic turnover mirrors the discontinuity observed in the archaeological records and is possibly linked to the climatic LGM event. During the LGM, the Solutrean archaeological culture is present in western and southwestern Europe. Following the Solutrean, the Magdalenian culture was present in most of Western and Central Europe as far as Poland. Individuals associated with the Magdalenian carry an ancestry linked to

the Aurignacian individual - in different proportions - and affinity to hunter-gatherers in southern Europe, forming the Goyet Q2 cluster and suggesting northward population expansions during the post-LGM period (Fu et al. 2016; Haak et al. 2015; Olalde et al. 2019; Posth et al. 2016; Villalba-Mouco et al. 2019). During the following warming period, from 14,000 cal. BP, the Magdalenian-related gene pool in most of Europe is almost completely replaced by an Epigravettian-related component, the western hunter-gatherer (WHG) cluster (Fu et al. 2016; Haak et al. 2015). This event is also detected at the mitochondrial level (Bramanti et al. 2009; Fu et al. 2013; Posth et al. 2016) where the previously dominant haplogroups U2'3'4'7'8'9 and M are dwindling in frequency while haplogroups U5a and U5b become dominant. In eastern Europe, the Eastern Hunter-gatherer (EHG) cluster is contemporaneous to the WHG cluster. Individuals in this cluster are genetically a mixture of a Villabruna-related ancestry and the Ancient North Eurasian (ANE) ancestry of Upper Palaeolithic Siberians (Fu et al. 2016; Haak et al. 2015; Raghavan et al. 2014). Meanwhile, a new cluster appears in the Caucasus consisting of two individuals from Georgia, referred to as Caucasus Hunter-Gatherers (CHG). Dated between 13,400 and 9,500 cal BP, this cluster separated from European Paleolithic groups around 45,000 years ago and from the ancestors of Neolithic farmers around 25,000 years ago (Jones et al. 2015). It also shares genetic affinity with Iranian Mesolithic individuals (Narasimhan et al. 2019), related to a basal Eurasian genetic component. From 14,000 cal BP onward, all individuals from Europe show genetic affinity with ancient individuals from Anatolia and the Levant, as well as with CHG (Feldman et al. 2019; Fu et al. 2016; Jones et al. 2015; Lazaridis et al. 2016).

From 8,000 years ago, genetic and geographic proximity increasingly correlate (Mathieson et al. 2018). In the east, the EHG ancestry dominates, including Russian and Ukrainian individuals, while in the west, the WHG ancestry is the predominant ancestry, in different proportions

corresponding with geography (Günther et al. 2018; Haak et al. 2015; Jones et al. 2017; Lazaridis et al. 2014; Mathieson et al. 2018; Mittnik et al. 2018).

Around 12,000 BP, the transition from a hunter-gathering subsistence to a sedentary lifestyle based on animal and plant domestication starts in the fertile crescent. Ancient DNA closed the debate about the modalities of the "Neolithic revolution" in Europe. Instead of a cultural diffusion, genomic studies favour the demic diffusion hypothesis. Neolithic populations derive ancestry from Anatolian, Caucasus, and Levantine hunter-gatherers (Feldman et al. 2019; Lazaridis et al. 2022a,b; Lazaridis et al. 2016; Lipson et al. 2017; Omrak et al. 2016). Their ancestry spread westward from Anatolia along two routes, one through Central Europe, the other along the Mediterranean coasts, with an important diversity in the admixture processes with local Mesolithic hunter-gatherers (Antonio et al. 2019; Brace et al. 2019; Brunel et al. 2020; Hofmanová et al. 2016; Lipson et al. 2017; Marchi et al. 2022; Mathieson et al. 2015, 2018; Olalde et al. 2015, 2019, Rivollat et al. 2020; Villalba-Mouco et al. 2019). Specific Y-chromosome sub-haplogroups trace each route (Rohrlach et al. 2021), and groups in the Iberian peninsula show an additional Iranian Neolithic or Levant component, admixed with the Anatolian Neolithic source (Skourtanioti et al. 2020; Villalba-Mouco et al. 2021). In south-western Europe, the residual *Goyet Q2* component remains present in the Neolithic populations (Brunel et al. 2020; Rivollat et al. 2020; Villalba-Mouco et al. 2019). By around 6000 years ago, the Neolithic ancestry reached all parts of the continent. However, already after a farming lifestyle had been established, an increase in hunter-gatherer genetic ancestry is observed in farming groups (Brandt et al. 2013; Haak et al. 2015; Olalde et al. 2019). Several examples of this increase can be found in present-day Germany and France (Bollongino et al. 2013; Immel et al. 2021; Lipson et al. 2017; Rivollat et al. 2020; Seguin-Orlando et al. 2021). Overall, the Neolithic and Chalcolithic across Europe show genetic continuity (Brace et al. 2019; Haak et al. 2015; Lipson et al. 2017; Mathieson et al. 2015; Olalde et al. 2018; Villalba-Mouco et al. 2021), before the transition to the Bronze Age in western Eurasia around 5000 BP marks the second major shift in cultural and demographic aspects.

The Pontic-Caspian steppe pastoralist cultures of Yamnaya and Afanasievo appear around 5300-4600 BP. Their genepool formed through contributions of *Sidelkino*, *CHG* and Iranian Neolithic ancestries (Jones et al. 2017; Narasimhan et al. 2019; Wang et al. 2019) and led to a strong genetic shift all over Europe most significantly visible in the change of Y-chromosomal frequencies, when R1a and R1b haplogroups massively dominate after the third millennium dispersals (Allentoft et al. 2015; Haak et al. 2015; Olalde et al. 2018, 2019; Papac et al. 2021; Villalba-Mouco et al. 2021).

Dispersals of various groups, mostly associated to the Corded Ware culture, carried this steppe-related ancestry into different parts of Europe (Allentoft et al. 2015; Brunel et al. 2020; Dulias et al. 2022; Furtwängler et al. 2020; Haak et al. 2015; Lazaridis et al. 2022a,b; Linderholm et al. 2020; Malmström et al. 2019; Mathieson et al. 2015; Moore et al. 2022; Papac et al. 2021; Patterson et al. 2022; Saag et al. 2017, 2021; Villalba-Mouco et al. 2021). In the western Mediterranean area, the Iranian Neolithic/Levant component can also be tracked in Bronze Age island populations in the Mediterranean and south-eastern Iberia as part of the local Neolithic ancestry (Fernandes et al. 2020; Lazaridis et al. 2017; Villalba-Mouco et al. 2021). By around 5000 BP, the steppe ancestry reached the Iberian Peninsula and the British and Irish Isles, while African ancestry in Iberian individuals reveals contacts over the Mediterranean Sea (Olalde et al. 2018, 2019; Patterson et al. 2022; Villalba-Mouco et al. 2021).

The three genetic components inherited from Mesolithic hunter-gatherers, Neolithic farmers from Anatolia, and pastoralists from the Steppes represent the three main components of most Europeans today (Haak et al. 2015).

BOX 2 - WHEN ANCIENT DNA CONTRIBUTES TO DISCUSSIONS ON SOCIAL STRUCTURES

Recently, the integration of large numbers of individuals from the same site marks an evolution of the field from geographically broad sampling to analyses at local scales, allowing to explore kinship and site organization, with enough power and resolution to investigate social structures, such as residence patterns, sex-biased mobility, consanguinity, funerary practices. Biological relatedness or affinities are only one aspect of human relationships among others, and ideas of kinship are not necessarily tied to genetic relatedness. However, these elements can contribute to the discussion of the connection between biological and social kinship.

Several Early Neolithic villages in Anatolia provide evidence of group structure through confirmation of close genetic relatedness in house-related co-burials in the earliest sedentary communities around 10,000 BP. A heterogeneity observed in the kin structures among different communities likely reflects a transition from the Aceramic to the Ceramic period in Anatolia (Yaka et al. 2021). In monumental sites in the Neolithic period (Cassidy et al. 2020) and (Sánchez-Quinto et al. 2019) show the individuals buried in passage tombs are connected to some degree to each other, implying a non-random mating across large territories. The genome of one individual points to a mating between first degree related parents, and was interpreted as 'royal' or 'dynastic' incest. The second group of individuals, buried in simple court and portal tombs with no artwork and less prestigious grave goods, do not show these links, and seem to represent smaller-scale societies. In contrast, in the megalithic monument Hazelton North in England (Fowler et al. 2022), the genetic relationships suggest the burial of a complex family. One male produced offspring with four female partners, all buried within their female lineage. In monumental burials Fleury-sur-Orne, each monument was built for one or two individuals, dedicated to a genetically independent lineage, suggesting a male-mediated transmission of socio-political authority (Rivollat et al. 2022). In the late Neolithic period, the mass grave of Koszyce in Poland revealed a large extended family violently killed (Schroeder et al. 2019). The individuals' position corresponded with their genetic relationship, evidently buried by someone who knew the deceased. Evidence for patrilineal, patrilocal, and female exogamic systems are found across Europe from the Neolithic to the Bronze Age (Furtwängler et al. 2020; Sjögren et al. 2020; Žegarac et al. 2021). An exceptional example of interdisciplinary work reveals patrilocality and female exogamy at the Lech Valley in southern Germany, revealing social inequality based on kinship (Mittnik et al. 2019) in households consisted of high-status core families, buried in the same site as low-status unrelated individuals, a system that lasted at least 700 years.

Outside of Europe, a study on a Late Neolithic site in China associated with Longshan culture suggested the extended family served as the basic household unit during this Late Neolithic transitional stage, and showed consanguineous mating patterns from at least 4,000 BP (Ning et al. 2021). In the southern United States, archaeogenetic research suggests a matrilineal system for the societies inhabiting the Chaco Canyon between 1,200 - 900 BP (Kennett et al. 2017).

In medieval times, individuals with northern and central ancestries in Longobard cemeteries in Italy and Hungary are buried with significantly more grave goods than individuals with southern ancestries (Amorim et al. 2018). In Bavaria, six sites show heterogenous ancestries for females, some of them with artificial cranial modifications, carrying south-eastern European ancestry (Veeramah et al. 2018). An interesting pattern can be found in the Alemannic cemetery of Niederstotzingen in southern Germany. Five genetically related males were buried with grave goods associated with three different cultural origins (O'Sullivan et al. 2018).

Overall, a high variability of practices is observed across regions and periods, highlighting diverse social practices in the past, and cautioning for reflection on the biases researchers bring from their own societal organization when interpreting the results of archaeological and genetic analysis.

The Iron Age overall shows genetic continuity from the Bronze age period throughout Europe, although as a result of an increase in cremation of human remains, few data are available at the moment (Allentoft et al. 2015; Antonio et al. 2019; Brunel et al. 2020; Fischer et al. 2022; Furtwängler et al. 2020; Gamba et al. 2014; Martiniano et al. 2016; Mathieson et al. 2018; Olalde et al. 2019; Patterson et al. 2022; Schiffels et al. 2016). Specific migrations from Siberia to eastern Scandinavia have been identified, correlated to Uralic language spread 3500 years ago (Lamnidis et al. 2018). In continental Europe, dispersals to the British Isles at the early Iron Age support archaeological evidence of contact (Patterson et al. 2022). In the Mediterranean area, Greek and Phoenician/Punic migrations trace dispersals west starting in the Near East and the Levant (Feldman et al. 2019; Fernandes et al. 2020; Marcus et al. 2020; Matisoo-Smith et al. 2018; Olalde et al. 2019). Evidence of mercenaries with diverse ancestries fighting for the Greek armies in Sicily shows how participation in war played a role in large-scale mobility during this period (Reitsema et al. 2022). From the Roman Empire period, Near-Eastern ancestry increases significantly the coasts, linked to dispersals within the Empire as reported in historical sources (Antonio et al. 2019; Posth et al. 2021).

During the first years of research in archaeogenetics, the majority of publications investigated prehistoric societies, with no textual sources. Recently, studies have focused more on historical periods, often uncovering mismatches with the historic narratives. During the late Antiquity and the early Middle Ages historical sources describe the "Barbarian migrations" leading to population shifts from northern and central Europe toward West and South, which are mirrored in ancestry shifts (Amorim et al. 2018; Antonio et al. 2019; O'Sullivan et al. 2018; Olalde et al. 2019; Veeramah et al. 2018). Moving from northern continental Europe and southern Scandinavia to England, these migrations involved entire communities, and not war bands or elite men, shaping the early Medieval English populations (Gretzinger et al. 2022). During the 7th century

CE, genetic ancestries associated to the East Asian steppe appears in the Carpathian Basin, proving rapid trans-Eurasian migrations. This ancestry remains present for over 200 years in local Avar elites (Gnecchi-Ruscone et al. 2022). At the end of the first millennium CE, gene flow in and out of Scandinavia characterises the Viking period, with genetic structure within Scandinavia, and evidence of migration to England, Ireland, Iceland, and Greenland (Ebenesersdóttir et al. 2018; Krzewińska et al. 2018; Margaryan et al. 2020).

Asia

Asia has received more and more attention on its important role in understanding modern human dispersals. A series of anatomically modern human remains dating back to 100-60 ka have been discovered in West, East and Southeast Asia (Bae et al. 2017). Based on these remains, multiple early human dispersals have been proposed, including the "Southern dispersal route" hypothesis that suggested an early migration happened between 130-70 ka along the Asian coast from the Arabian Peninsula, via South Asia to Southeast Asia, finally reaching Oceania (Bae et al. 2017; López et al. 2015). However, genetic studies on both present-day and ancient human DNA have shown that the majority of the ancestry of non-Africans is shaped by a major dispersal event around 60-50 ka (Bergström et al. 2020). So far, an ~45,000-year-old individual from western Siberia (Fu et al. 2014) represents the oldest Asian genome, followed by the 40,000-year-old individual from Tianyuan Cave in East Asia. Genetically similar is the 32 000 year old individual AR33K (Mao et al. 2021), and both show a genetic link to present-day East Eurasians (Yang et al. 2017).

From West Asia, modern humans dispersed into different parts of Asia, following at least two routes (Bae et al. 2017). Via North and East Asia, the northern dispersal reached the Tibetan plateau (Zhang et al. 2018, 2022) and Japanese archipelago (Nakazawa 2017) around 40,000 -30,000 years ago. Jomon hunter-gatherers from

Japan and an 11,000-year-old hunter-gatherer individual from southern China represent early lineages among North and East Asians (Kanzawa-Kiriyama et al. 2019; McColl et al. 2018). Their genetic ancestry is distinct from those who dispersed to South and Southeast Asia (Bae et al. 2017; Macaulay et al. 2005), represented by Andamanese hunter-gatherers (Onge) from South Asia and Hòabìnhian hunter-gatherers from Southeast Asia (Lipson et al. 2018; McColl et al. 2018).

In addition to the East Eurasian lineages, the Palaeolithic landscape of Siberia from ~ 30,000 years ago was home to a group of people genetically more closely related to present-day West Eurasians (Sikora et al. 2019). They carried the "Ancient North Eurasian" (ANE) ancestry, which spread across Siberia and Central Asia during the Upper Palaeolithic, and left genetic traces in people across Eurasia and the Americas today (Fu et al. 2016; Raghavan et al. 2014). Starting from at least 16 ky ago, they mixed with Northeast Asian hunter-gatherer groups and formed various ancient Siberian populations (Kılınç et al. 2021; Sikora et al. 2019; Yu et al. 2020). One lineage constitutes the ancestral population to the dispersal through Beringia and reached the American continents (Moreno-Mayar et al. 2018). This First American lineage was likely widely distributed in Siberia, the ancestry present in a 14 000-year-old individual from the Lake Baikal region in southern Siberia (Yu et al. 2020).

Admixture with Neandertals likely first occurred in the Near East (Green et al. 2010), so similar to Europeans, ancient and present-day Asian populations carry around 2% Neanderthal introgression, including the individuals older than 40 ka (Fu et al. 2014; Yang et al. 2017). Additionally, most Asian people carry introgression from the Denisovan, today only known from few sites in the Altai region and the Tibetan plateau (Chen et al. 2019; Reich et al. 2010). This archaic human lineage contributed between 0.1-3% to the gene pool of present-day populations (Bergström et al. 2020; Prüfer et al. 2014; Reich et al. 2011; Sankararaman et al. 2016), the earliest evidence found in the Tianyuan individual and a ~34 000-year-old individual from Salkhit in Mongolia (Massilani et al. 2020; Yang et al. 2017). The Denisovan introgression likely happened multiple times from different sources, indicating complex interactions between these two human groups (Browning et al. 2018; Choin et al. 2021; Jacobs et al. 2019) and introgressed genes led to adaptations in anatomically modern humans (Choin et al. 2021; Dannemann and Racimo 2018). However, the paucity of genetic data from Pleistocene East Eurasia, especially Southeast Asia, limits our understanding of when, where and how these interactions happened.

Home to multiple agriculture centers and language groups, ancient DNA studies in Asia have shed light on a series of key anthropological and archaeological questions, including the spread of Neolithization, emergence of language groups and ancient social organization among others. In East Asia, farming emerged between 10,000 and 8000 years ago in two major centers: the Yangtze River and the Yellow River Basins (Yang et al. 2012; Zuo et al. 2017). From the Yellow River Basin, farmers cultivating domesticated millet spread across East Asia including Tibet (Wang et al. 2021; Zhang et al. 2019, 2022), likely spreading the Sino-Tibetan language. Genetic studies on ancient and present-day Tibetan people have shown they predominantly derive their genetic ancestry from Late Neolithic farmers in the Upper Yellow River region, but additionally a minor contribution from an unknown deeply divergent East Eurasian ancestry (Jeong et al. 2016; Liu et al. 2022). The West Liao River in Northeast Asia is recognized as another early center of millet farming (Lu et al. 2009; Yang et al. 2012). Farmers there interacted with those from the Yellow River, but also with hunter-gatherers of the Amur River (Ning et al. 2020). Whether they also spread the Transeurasian, also known as "Altaic" languages across Northeast Asia (Robbeets et al. 2021), is a controversial theory still under debate (Robbeets et al. 2022; Tian et al. 2022).

In the millenia after, population growth and technology development triggered migrations

BOX 3 - HOW ANCIENT DNA OF DOMESTICATED ORGANISMS HELPS TRACE HUMAN MIGRA-TIONS AND CULTURAL CHANGES.

The domestication of plants and animals has impacted human societies, history and living environments as much as the genomes of the domesticated organisms themselves. By altering the evolution of certain domesticates, humans have constructed ecological niches they became dependent on. This in turn has altered human genetic makeup to adapt to the newly created environments (e.g., Lactase persistence adapted to the dairy consumption). Studying the past of domesticated organisms can therefore inform about the past of the closely associated human populations. While some aspects can be understood from the analysis of modern domesticate DNA, ancient DNA can shed light on ancestors today extinct in the wild, gene flow between domesticates and their wild ancestors, and the development of human domestication practices (reviewed in detail in (Frantz et al. 2020; MacHugh et al. 2017).

Through in an interdisciplinary study of domesticated sheep and goat in Central Asian Kyrgyzstan, (Taylor et al. 2021) showed sheep and goats had already been domesticated and seasonally slaughtered 8,000 years ago in Central Asia. Genetic analysis revealed their affinity to breeds in Anatolia and South Asia today, indicating human movement or technology exchange between these areas. Not only did this finding suggest pastoralism had been practised three millennia earlier than previously assumed, but also that networks of pastoral mobility had been in place much earlier, and potentially drove exchange across Central Asia. Another species associated with pastoral practice are horses. Extensive ancient genomic studies revealed the expansion of Persian-related horse lineage associated with Islamic conquests (Fages et al. 2019) and connections between Anatolia, Caucasus and Eurasian steppe through the introduction of horses to Anatolia in the Bronze Age (Guimaraes et al. 2020). However, the origin of modern horses remains unclear, as several candidates (Iberia, Anatolia, Central Asia Botai) were ruled out by these studies (Gaunitz et al. 2018).

Dogs are likely the earliest domesticated animals, and have accompanied humans since more than 10,000 years. Along with their owners, they dispersed to new regions, and mirror the dispersals of humans from the Mesolithic, with some notable exceptions. In Europe, German and Irish Neolithic dogs retained the genetic make-up of their ancestors who accompanied the hunter-gatherers of Europe, while humans in the region show a large contribution of Anatolian farmer ancestry (Bergström et al. 2020). Similar exceptions are found in ancient European pigs. Although the oldest European pigs ~ 8,000 BP carried significant genetic contribution from Near Eastern wild boars, later populations until today show limited to no Near Eastern ancestry. This indicates that after introduction of domestic pigs by Neolithic farmers, local European wild boars were quickly involved in the domestication practice (Frantz et al. 2019).

In the Americas, Maize was an influential driver of subsistence change for many groups the continents. Originally domesticated ~ 9000 years ago, the use of a semi-domesticated version spread to South America, possibly with people moving south. However, analysis of ancient Maize genomes suggests that the highly domesticated versions spread back north prior to ~2000 BP (Kistler et al. 2020), likely mediated by Indigenous farmers. Human population genomics suggests a reintroduction after 5600 BP, when an ancestry shift in Belize, related to ancestry today found in Chibchan speakers from Costa Rica and Colombia coincides with evidence for Maize horticulture (Kennett et al. 2022).

Ancient DNA analysis of domesticated organisms add to the adaption capacity of humans, and can provide another line of evidence about past human movements. This might allow understanding of some domesticates that are not used by humans anymore and be extended to non-domesticated organisms that might have also influenced - or been influenced by - human migrations and history, like commensal species (e.g., the black rat: Yu et al. 2022)

and interactions between farmers from northern and southern East Asia, leading to a North-South genetic cline in present-day East Asians (Yang et al. 2020). From southern East Asia, people dispersed into Southeast Asia, bringing their farming practices, genetic ancestry, and perhaps languages. There, they interacted with local hunter-gatherer groups, evident in ~4,000 year old early farmers in mainland Southeast Asia, who carried southern East Asian and local hunter-gatherer ancestries, similar to that in present-day Austroasiatic language speakers, supporting the "two-layer" hypothesis of the peopling of Southeast Asia (Lipson et al. 2018; McColl et al. 2018; Wang et al. 2021). The genetic link of ~8,000-year-old southern Chinese individuals with ancient and present-day Austronesian speakers suggests southern China as the origin of Austronesian languages, today mainly found in Island Southeast Asia (Yang et al. 2020).

Unlike Southeast Asia, where farming was probably introduced from East Asia, farming in South Asia likely emerged from local hunter-gatherers. The genetic study of an individual associated with the Harappan, or Indus Valley Civilization, revealed that this 4,000-year-old ancient South Asian farmer didn't carry Anatolian or Iranian farmer ancestry. Instead, they were a mixture of Iranian and South Asian hunter-gatherers, suggesting the rise of farming in South Asia didn't involve large-scale migrations (Shinde et al. 2019). The "steppe" ancestry only arrived in South Asia after the Indus Valley Civilization period, around 3900-3500 BP (Narasimhan et al. 2019). Additionally, these findings provide insights on the origin of Indo-European languages in South Asia, by concordantly supporting the Steppe origin of these languages (Narasimhan et al. 2019; Shinde et al. 2019).

Since the Early Bronze Age, the increase of human mobility stimulated genetic and cultural interactions across different parts of Eurasia, especially in Central Asia - crossroads between eastern and western Eurasia (Allentoft et al. 2015; Damgaard et al. 2018a,b; Narasimhan et al. 2019; Sikora et al. 2019). Before the Bronze Age, Central Asian local hunter-gatherers carried ANE ancestry similar to the Siberians, and Neolithic ancestry from Anatolia and Iran, which also spread westward towards Europe (Lazaridis et al. 2014, Narasimhan et al. 2019). The Steppe ancestry expanded into Central Asia and reached Mongolia and southern Siberia as early as 5,000 BP, giving rise to a series of Bronze Age archaeological cultures like Afanasievo and Andronovo (Allentoft et al. 2015; Jeong et al. 2020; Jeong et al. 2018; Yu et al. 2020). The spread of pastoralism and dairy consumption is highly correlated with the unique Steppe ancestry and lactase persistence phenotype in western Eurasia. In contrast, various studies showed that in Central and East Asia, many ancient pastoralist groups practised pastoralism and consumed dairy but carried limited to no Steppe ancestry and the genetic variation related to lactase persistence (Jeong et al. 2018; Zhang et al. 2022). Exemplary are the mummies from the Tarim Basin in southern Xinjiang. Combining genomic and proteomic evidence, researchers revealed that these earliest residents in the Tarim Basin carried genetic ancestry inherited from local Upper Palaeolithic hunter-gatherers, carried no steppe-related ancestry, but consumed milk products, indicating communications of persistence practices independent from genetic exchange (Zhang et al. 2021).

Pacific

During the Pleistocene, the first anatomically modern humans to settle in the Pacific region were the ancestors of present-day Australo-Melanesian speakers, including Papuans, Aboriginal Australians and Torres Strait Islanders, and some groups in Near Oceania and Island South East Asia. More than 55,000 years ago, they mixed with Denisovans (see "Asia") and crossed the waters dividing the ancient land-masses of Sunda (the Asian mainland and Western Indonesia) and Sahul (today New Guinea and Australia) (Clarkson et al. 2017; O'Connell et al. 2018; Summerhayes et al. 2010). A cornerstone of their route is represented by the ancestry present in an

individual from Sulawesi, whos ancestry mainly derives from a lineage related to this early dispersal (Carlhoff et al. 2021). They dispersed to the islands of the Bismarck Archipelago (Leavesley 2006; Leavesley et al. 2002) and the Solomon Islands (Walter and Sheppard 2017; Wickler and Spriggs 1988) during the late Pleistocene. Present-day genomes show genetic diversification and regional structure in the following millennia (Bergström et al. 2017, 2020). Together with ancient genomic data (Carlhoff et al. 2021; Tobler et al. 2017), they add evidence to the long cultural continuity of Indigenous cultures in Papua and Australia, but also show the influence of later dispersals.

The archaeological record, present-day genomics, and linguistics (Blust 2019), provide good documentation for a dispersal associated with Austronesian-speaking seafaring farmers, starting on the Asian mainland somewhen between 7,000 and 5,000 years BP (Bellwood 1995; Bellwood et al. 2006; Blust 2019; Klamer 2019; Ko et al. 2014; Lansing et al. 2011; Soares et al. 2016). From Taiwan, this Austronesian-speaker associated ancestry spread across the islands of South East Asia to the shores of New Guinea and the islands offshore. Ancient genomics have only just started to contribute to these questions (Oliveira et al. 2022; Pugach et al. 2021), but the initial settlement of Western Remote Oceania by descendants of groups genetically most similar to present-day Indigenous Taiwanese has been confirmed by aDNA (Skoglund et al. 2016). Ancient genomes show people with almost exclusively Asian ancestry eventually settled Remote Oceania. There is still debate about the details of this expansion, and increasing critiques of Taiwan as the "homeland" of this expansion (Choin et al. 2021; Soares et al. 2016). The expansion was seemingly fast, and some evidence suggests there was not much interaction with the local populations met along the way. Still, much evidence suggests this "Fast train model" is too simplistic, and – perhaps additionally – interaction happened in Island South East Asia and Papua New Guinea (Bergström et al. 2017; Oliveira et al. 2022). The

Lapita cultural complex formed in the Bismarck Archipelago around 3,300 years BP as part of the Austronesian expansion. Identified in the archaeological record by their distinct ornate pottery, they quickly expanded into Remote Oceania, bringing with them a cultural landscape of agriculture, seafaring technologies, and Austronesian languages, and reached Vanuatu and Tonga in Western Remote Oceania around 2,900 – 2,500 years BP (Petchey et al. 2014). Archaeological evidence suggests that this initial expansion halted here, and material culture changed in the millennium after.

In the north-western region of Remote Oceania, often referred to as "Micronesia", archaeological sites show people navigated to the Marianna Islands and Palau around 3,000 – 3,400 BP. The mosaic of languages, cultural practices, and genetic affinities today (Liu et al. 2022; Petersen 2009) reflects the complex history, and the origins and details of the settlement are still a matter of debate. Archaeogenetic insights show that multiple dispersals contributed to the formation of the different societies and that a settlement via the Philippines – deemed unlikely because of unfavorable currents – cannot be excluded (Liu et al. 2022; Pugach et al. 2021).

Similarities in the ceramic tradition and exchange of resources show that the communities across western Remote Oceania - in Samoa, Tonga and Fiji - remained in contact in the millennium after initial settlement (Green and Kirch 1997). In the archaeological record, a shift in material culture is visible. From decorated Lapita-style pottery to "Polynesian-plainware" to the absence of pottery, these shifts have been interpreted as a changing society, settling in and adapting to the environment (Kirch 2017). In the last millennium, intensified food production and specialized and monumental architecture suggest a population growth before an expansion to the remaining areas of the Pacific Ocean. Radiocarbon dates of early sites in Central and Eastern Oceania suggest that the Cook Islands, Society Islands, and the Marquesas Islands were settled in rapid sequence starting from 1,000 BP (Spriggs and Anderson 1993), and served

BOX 4 - HOW ANCIENT DNA PROVIDED A KEY TO UNDERSTANDING THE DISSENT OF LANGUAGE AND GENETICS IN VANUATU

The ancestry of present-day Pacific Islanders shows, in addition to the ancestries introduced with the colonial invasion, ancestry related to the present-day inhabitants of the Papuan Highlands. The amount of Papuan ancestry varies across the Pacific region. While Polynesians carry around 40 %, some Archipelagos in Western Remote Oceania have much higher proportions. At the same time, the languages spoken across Remote Oceania are most closely related (Gray et al. 2009). Still, they have isolated speakers in various islands across Near Oceania, and the cultural, linguistic and genetic diversity in the region show that the population history of the region is much more complex. In Vanuatu, where first record of Lapita pottery in Remote Oceania was recovered, the Ni-Vanuatu (as people self-identify today) speak a plethora of Austronesian languages, linking them to the earliest settlers in the region. However, cultural aspects and genetic composition suggest relations to Near Oceania. The genetic ancestry of Ni-Vanuatu is most similar to that of present-day Baining-speaking people from the Bismarck Archipelago. This peculiar mismatch in genetic and linguistic evidence is rare, if not unprecedented, in human history. A potential explanation is the succession of events in the settlement of the archipelago and the subsequent interactions. From ancient genomes, spanning the close to 3000 years of occupation of the islands, the connections to other regions within the Pacific could be traced by inferring mixture events. Individuals from the Teuoma cemetery with almost exclusively Austronesian-related ancestry (Posth et al. 2018; Skoglund et al. 2016), dating to ~2,900 BP are followed by a genetically diverse population displaying variable proportions of Austronesian-related and Papuan-related ancestry between 2,600 and 2,100 BP, including one individual with exclusively Bismarck-related ancestry. In the period from 2,000 BP to 1,100 BP today, the Austronesian-related component declines to levels similar to those in Ni-Vanuatu. The dating of the admixture event showed a particular pattern: the older the individuals were, the farther back in time the admixture event was inferred, suggesting that there were multiple such events. A single, substantial migration, as observed in other parts of the world, not only would have led to a complete change in the genetic signal within a very short timeframe, but also very likely changed the language spoken to that of the new-coming group. In this case, the region should have shifted to languages spoken in the Bismarck Archipelago today. Perhaps the repeated arrival of people with Bismarck-related ancestry over millennia, and their integration into the local society led to the genetic turnover, while retaining the local languages.

as a hub for the navigation to other islands in eastern Oceania. A recent study on the genomes of people living in the region today shows sequential bottlenecks retracing the settlement sequence. Although the inferred dates should be interpreted cautiously and are partly in conflict with the radiocarbon sequences for this region, the study adds detail to the settlement history (Ioannidis et al. 2021). The oldest reliable dates in the most remote islands suggest the settlement of Hawaii (910 – 731 BP), Rapa Nui (900 – 600 BP), and Aotearoa (700 – 650 BP) mark the end of the last initial settlement period of human history. One aspect of the genetic landscape of the

Pacific is still debated. Present-day inhabitants of Rapa Nui and Central Oceania carry Native American ancestry proportions from different source populations in the Americas (Ioannidis et al. 2020; Moreno-Mayar et al. 2014). The ancestry dominant in the Native American proportion in Rapa Nui was likely introduced in the late 19th century after Chile's annexation of Rapa Nui. In addition to this ancestry, a second one is more similar to that of populations in the Pacific region of Colombia. Various Islanders in Central Oceania carry the same ancestry, but the inferred date of this introgression sparks controversy. An inference from present-day genomes suggests a

very early introduction starting from 800 BP. However, this result conflicts with the archaeological record, that lacks evidence for an early American influence. Only two ancient genomes are recovered from this region, and while those do not show a Native American proportion, they are too few to rule out this possibility with certainty. The great seafarers of the Pacific were likely able to navigate to the Americas and perhaps brought innovations and even people or their ancestry with them. For now, it seems less likely that the journey was undertaken in the opposite direction, although many Indigenous peoples of the Americas are and were skilled in water navigation.

Americas

The ancestors of the indigenous peoples of the Americas were at home in Asia (Yu et al. 2020). During the last glacial maximum, around 26,000 to 19,000 BP, the lower sea-level exposed a landmass bridging what is today Siberia and northern America (Lambeck et al. 2014). Massive glaciers bordered this landmass, preventing passage into the American continents (Meltzer 2004). Into this area, the ancestors of Native Americans moved, and were likely isolated from their ancestral population in Asia (Moreno-Mayar et al. 2018a,b; Sikora et al. 2019; Yu et al. 2020). This isolated population differentiated into three lineages: the merely inferred "unsampled Population A", the "ancient Beringian", genetically represented by genomes from Alaska with equal genetic affinity to all Native American populations, and "Ancestral Native Americans" (Moreno-Mayar et al. 2018a,b). How these populations differentiated while occupying the same region is still unknown, but perhaps they occupied different environments within Beringia. The lower sea levels likely exposed a number of islands south of Beringia between 30,000 and 8,000 years ago, providing marine resources and perhaps inspiring the development of seafaring techniques. Some groups in Beringia might have exploited the marine and coastal environment,

others specialized in the hunting of megafauna, leading to different lifestyles, adaptions, and a differentiation of the gene pool.

Towards the end of the LGM the glaciers retreated to open a corridor along the Rocky Mountains (Perego et al. 2010; Potter et al. 2018), but only after the first occupational sites were established, this corridor was viable enough to allow human passage (Pedersen et al. 2016). Therefore, the earliest settlers of the Americas will likely have taken a different route into the continents. Along coastal shore lines of the Pacific (Davis and Madsen 2020), the productive Kelp forests provided subsistence, and possibly facilitated the dispersal along the coasts (Erlandson et al. 2007). Around 15,000 years ago, the "Ancestral Native American" lineage split. Where exactly this split happened is still unclear, and both north and south of the ice shield are options (Moreno-Mayar et al. 2018a,b; Willerslev and Meltzer 2021). Since only few genomes are recovered from this time and region, it is difficult to discern if the observed ancestry pattern is a result of later (re)dispersals, or if it reflects the geography of the branching pattern. One lineage likely remained in North America, and most groups there are descendants of this lineage. The other spread southward. Again, different ways of dispersal are possible. The Pacific coast provided resources facilitating a coastal expansion. Individuals buried with arrowheads and other goods implying a hunter-lifestyle suggest hunting megafauna was part of the subsistence, and facilitated an inland dispersal to the south.

A treelike model of ancient individuals suggests that the dispersal south happened very fast, and the currently oldest confirmed sites show that at least by 14,000 BP (Dillehay et al. 2008; Prates et al. 2020), people had settled the southern cone of the Americas. Additionally, the genomes of people who lived in South and Central America around 10,000 BP show close genetic links, despite their geographical distance (Moreno-Mayar et al. 2018a,b; Posth et al. 2018). However, there is variability in the ancestry observed through time in South America, and assuming an initial expansion followed by

BOX 5 - HOW ANCIENT DNA HELPS RE-EXAMINING GENDER CONSTRUCTIONS IN THE PAST

Gender has become an important field of study in many disciplines. Heated discussions about what gender is, how many there are and what this means for our societies permeate newspapers, political debate and nearly all public exchange platforms. The definition of gender roles and their impact on lived experiences have resurged during the pandemic, where many found themselves in constellations reminiscent of what they had believed lay in the past. Understanding gender roles in the distant past is incredibly difficult, seeing evidence is usually interpreted from the experiences with the topic of today.

Ancient genomes allow us to infer the genetic sex, and in the Americas, this was applied to an individual that had been buried with an impressive amount of burial goods, suggesting the person had been an expert hunter, well respected by their community (Haas et al. 2020). Initially assuming it was the grave of a male leader, the genetic sex provided reason to re-examine other hunter burials, and close to half of all burials suggestive of a "hunter burial" were in fact genetically female. This result shattered the "man the hunter – woman the gatherer" hypothesis that has shaped narratives about gender roles in the present-day, which in turn "inform" interpretations of such and similar contexts in archaeology.

In Europe, the graves of high-status Viking warriors were mostly interpreted as those of men. The genome of one such individual, excavated near the Swedish town of Birka, proved this practice to be improper (Hedenstierna-Jonson et al. 2017). The genetic sexing revealed this individual to be female, and the grave goods showed she was of high rank. Critiques of this paper included the objection that this person might have been genetically female, but it was unknown which gender she identified with. Seeing transgender, in the sense that someone does not identify with the (binary) gender connected to their reproductive sex, is a concept known and accepted in cultures on nearly every continent and throughout recorded history, this argument is valid. However, to understand the complicated details of gender constructions in the past, more than grave goods and genetic sex are necessary.

The idea of a binary biological sex is something that does not fit with the many variations in the sex Chromosomes. While most females carry two X-Chromosomes, and most males an X- and a Y-Chromosome, other combinations are observed in human populations. X, XXX, XXY, XYY, XXXY are all possibilities. They do somewhat determine the level of hormones, which lead to the external representation of the reproductive sex, but not always do they correspond with what would be expected from the karyotype.

In Finland, a grave featuring two swords and dress accessories and jewelry gendered feminine was interpreted by some as the burial of a powerful female warrior. Others were doubtful, believing the Swords should not be part of a female burial. A detailed analysis of the grave (Moilanen et al. 2021) included Chromosomal analyses, and revealed that this individual showed a karyotype of XXY, today known as Klinefelter Syndrome, one of the most common sex-chromosome aneuploidies. The physical appearance of this karyotype is male, and in other individuals found with this aneuploidy from Iceland and Germany, the contexts are not ambiguous. It is still difficult to interpret this evidence, because – as mentioned above – biological sex has several variations, and chromosomal sex is different from gender. This individual might have identified anywhere on the gender spectrum, but this evidence cautions us not to impose modern "western" binary gender constructs onto the past.

long periods of no dispersal and interactions is too simplistic. Some groups from Central America show affinity to both Northern and Southern Native American lineages. Genomes from the site of Los Rieles in today's Chile show affinity to a genome associated with the Clovis-culture (Posth et al. 2018; Rasmussen et al. 2014). In the Central Andes, ancestry related to individuals from the California Channel Islands is present before 4,200 BP (Posth et al. 2018)

and might be linked to the spread of agriculture from Mesoamerica (Sutter 2021). When examined on a local scale, South and Central America are a mosaic of genetic continuity and ancestry shifts. In some parts, for example in Peru and in the Southern cone, genetic continuity through millennia links some Indigenous groups inhabiting the regions today with the ancient individuals studied through ancient genomics (Posth et al. 2018). In other regions, the lack of continuity suggests additional dispersals or complex interactions between groups with different genetic ancestries. In Belize, an ancestry shift in individuals occupying the area between 9,600–7,300 cal. BP and 5,600–3,700 cal. BP shows that dispersals were bi-directional, also occurring south to north (Kennett et al. 2022). In the Andes, the abovementioned affinity to the Anzik individual vanishes before 5,000 BP, and in Brazil, ancient individuals show no, or complex relations to later groups, including Indigenous People in the Amazon today (Posth et al. 2018; Ferraz da Silva et al. forthcoming) One ancestry signal was first described in present-day groups from the Amazon and the Central Brazilian Plateau, (Skoglund et al. 2015), but has since been detected in ancient individuals from Lagoa Santa in Brazil (Moreno-Mayar et al. 2018a,b) and present-day groups from the Central-Western Brazilian region and Peru (Castro e Silva et al. 2021). The low excess affinity to Australasians was assumed to derive from an unsampled population, named "Ypikuéra", or "Population Y" (Skoglund et al. 2015). Originally linked to the presence of certain cranial features carried by the "Palaeoamericans", a group of first inhabitants of South America (Neves and Hubbe 2005), their ancestry does not differ markedly from other ancient Native Americans. The "Population Y" ancestry remains a conundrum, but each ancient genome recovered showing this affinity (Campelo dos Santos et al. 2022) helps understanding the link between the populations today and the deep past of South America.

In the Caribbean, there is only very little continuity between the ancient genomes and people today. The colonial atrocities committed altered the cultural, linguistic and genetic landscape to an extreme extend. However, the assessment of ancient genomes and their affinity to the American ancestry proportion in people living in some parts of Cuba and Puerto Rico today – and more obviously the Indigenous groups such as the Kalinago and Garifuna - show that the common narrative of the extinction of the Indigenous peoples of the Caribbean is not true. Still, a reconstruction of the settlement history of the Caribbean was only possible through archaeological evidence, including ancient genomics. The origin of the first settlers of the Caribbean is a continuing debate. The oldest sites date to ~ 7,000 – 5,000 BP, the Archaic Age in the Caribbean. The combined pattern of sites, dates and material culture does not allow to trace the origins to one geographical region on the mainlands, and neither do ancient genomes. North-, Central and South America remain potential regions. The genomes of the early settlers of the western Caribbean show equal affinity to ancient and present-day Central- and South Americans (Nägele et al. 2020) and can be modeled as part of the South and Central American radiation (Fernandes et al. 2021), but also as a mixture of South American ancestry, mixed with a more ancestral lineage (Nägele et al. 2020), suggesting multiple dispersals. Starting from 2,800 BP, an additional dispersal from northeastern South America into the islands is well supported by archaeological, linguistic and genetic evidence. The dispersal of groups crafting decorated ceramics and practicing larger-scale agriculture heralds the Ceramic Age in the Caribbean. They are surprisingly homogenous in their genomic affinities, seeing the multiple ceramic traditions have been interpreted as originating from multiple dispersals, and accounts of the colonizer's chroniclers mention many groups with different continental origins. Genetically they are clearly distinct from the previous populations, and surprisingly little mixture between the two has been reported so far.

The last major dispersal in the Americas occurred around 5,000 BP in the far north,

and is represented by the Paleo-Inuit archaeological traditions. Only few genomes from this period are preserved, but individuals recovered from this context (Raghavan et al. 2014; Sikora et al. 2019) show genetic similarities to ancient Siberian populations, and suggest bi-directional interactions. Their tradition persisted until 500 BP, when a suite of technologies present from about 1,800 BP both east and west of the Bering strait - the Thule culture - became the only material culture found in the Arctic. From 800 BP, this culture rapidly spread through the Arctic to Greenland. Many of the cultural artefacts and tools present in the Thule context are still produced and used by Arctic people today, and their oral traditions tell of links to the past populations (Raff 2022). However, their relations to ancient groups is still unresolved. Many groups, in the Arctic, among them Inuit from Siberia through Greenland, and interestingly also Na-Dene speakers from further south, do harbour ancestry also present in Palaeo-Inuit. Whether this represents a direct link to these populations, or is a reflection of additional gene flow from Siberia is currently a disagreement between different studies (Flegontov et al. 2019; Moreno-Mayar et al. 2018a,b; Sikora et al. 2019).

The past decade of archaeogenomic research has mainly focused on the broad strokes, and inferred the dispersal of humans on a large scale, but from few anchor points in space in time. In recent years, studies with a more regional focus have increased, and the results have almost always shown that the narratives based on the broad-scale investigations are too simple. Additionally, we are now moving into periods where written sources are available, and ancient genomics can provide alternative insights, questioning the narratives of the chroniclers. In the next few years, we can expect a steeper rise in such studies, discussing societal changes and drivers, possibly leading to the observations from the broader picture. The true power of the smaller scale studies comes not from ancient genomics alone, but from the integration of all available lines of evidence, creating a better sense of the true shape and fabric of human history.

References

Adler CJ, Haak W, Donlon D, et al (2011) Survival and recovery of DNA from ancient teeth and bones. J Archaeol Sci 38:956-964. https://doi.org/10.1016/j.jas.2010.11.010

Allentoft ME, Collins M, Harker D, et al (2012) The half-life of DNA in bone: measuring decay kinetics in 158 dated fossils. Proc Biol Sci 279:4724-4733. https://doi.org/10.1098/rspb.2012.1745

Allentoft ME, Heller R, Holdaway R, et al (2015) Ancient DNA microsatellite analyses of the extinct New Zealand giant moa (*Dinornis robustus*) identify relatives within a single fossil site. Heredity 115:481. https://doi.org/10.1038/hdy.2015.48

Allentoft ME, Sikora M, Sjögren K-G, et al (2015) Population genomics of bronze age Eurasia. Nature 522:167-172. https://doi.org/10.1038/Nature14507

Amorim CEG, Vai S, Posth C, et al (2018) Understanding 6th-century barbarian social organization and migration through paleogenomics. Nature 9:1-11. https://doi.org/10.1038/s41467-018-06024-4

Andrades Valtueña A, Mittnik A, Key FM et al (2017) The Stone Age plague and its persistence in Eurasia. Curr biol 27:3683-3691.e3688. https://doi.org/10.1016/j.cub.2017.10.025

Antonio ML, Gao Z, Moots HM, et al (2019) Ancient Rome: A genetic crossroads of Europe and the Mediterranean. Science 366:708-714. https://doi.org/10.1126/Science.aay6826

Argüelles JM, Fuentes A, Yáñez B (2022) Analyzing asymmetries and praxis in aDNA research: A bioanthropological critique. Am Anthropol 124:130-40. https://doi.org/10.1111/aman.13692

Austin RM, Sholts SB, Williams L, et al (2019) Opinion: to curate the molecular past, museums need a carefully considered set of best practices. Proc Natl Acad Sci USA 116:1471-1474. https://doi.org/10.1073/pnas.1822038116

Ávila-Arcos MC, de la Fuente Castro C, Nieves-Colón MA, et al (2022) Recommendations

for sustainable ancient DNA research in the Global South: voices from a new generation of paleo geneticists. Front Genet 13:880170 https://doi.org/10.3389/fgene.2022.880170

Bae CJ, Douka K, Petraglia MD (2017) On the origin of modern humans: Asian perspectives. Science 358:eaai9067. https://doi.org/10.1126/Science.aai9067

Bandelt H-J, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. Mol Biol Evol 16:37-48. https://doi.org/10.1093/oxfordjournals.molbev.a026036

Bandelt H-J, Forster P, Sykes BC, et al (1995) Mitochondrial portraits of human populations using median networks. Genetics 141:743-753. https://doi.org/10.1093/genetics/141.2.743

Barquera R, Krause J (2020) An ancient view on host pathogen interaction across time and space. Curr Opin Immunol 65:65-69. https://doi.org/10.1016/j.coi.2020.05.004

Bellwood P (1995) Austronesian prehistory in Southeast Asia: homeland, expansion and transformation, ANU E Press, Canberra. https://doi.org/10.22459/A.09.2006.05

Bellwood P, Fox JJ, Tyron D (2006) The Austronesians: Historical and comparative perspectives, ANU Press, Canberra.

Bergström A, Frantz L, Schmidt R, et al (2020) Origins and genetic legacy of prehistoric dogs. Science 370:557-564. https://doi.org/10.1126/Science.aba9572

Bergström A, McCarthy SA, Hui R, et al (2020) Insights into human genetic variation and population history from 929 diverse genomes. Science 367:eaay5012. https://doi.org/10.1126/Science.aay5012

Bergström A, Oppenheimer SJ, Mentzer AJ, et al (2017) A Neolithic expansion, but strong genetic structure, in the independent history of New Guinea. Science 357:1160-1163. https://doi.org/10.1126/Science.aan3842

Bisso-Machado R, Fagundes NJ (2021) Uniparental genetic markers in Native Americans:A summary of all available data from ancient and contemporary populations.

Am J Phys Anthropol 176:445-458. https://doi.org/10.1002/ajpa.24357

Blust R (2019) The Austronesian homeland and dispersal. Annu Rev Appl Linguist 5:417-434. http://doi.org/10.1146/annurev-linguistics-011718-012440

Bollongino R, Nehlich O, Richards MP, et al (2013) 2000 years of parallel societies in Stone Age Central Europe. Science 342:479-481. https://doi.org/10.1126/Science.1245049

Bolnick DA, Bonine HM, Mata-Míguez J, et al (2012) Nondestructive sampling of human skeletal remains yields ancient nuclear and mitochondrial DNA. Am J Phys Anthropol 147:293-300. https://doi.org/10.1002/ajpa.21647

Bongers JL, Nakatsuka N, O'Shea C, et al (2020) Integration of ancient DNA with transdisciplinary dataset finds strong support for Inca resettlement in the south Peruvian coast. Proc Natl Acad Sci USA 117:18359-18368. https://doi.org/10.1073/pnas.2005965117

Brace S, Diekmann Y, Booth TJ, et al (2019) Ancient genomes indicate population replacement in Early Neolithic Britain. Nat Ecol Evol 3:765-771. https://doi.org/10.1038/s41559-019-0871-9

Bramanti B, Thomas MG, Haak W, et al (2009) Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. Science 326:137-140. https://doi.org/10.1126/Science.1176869

Brandt G, Haak W, Adler CJ, et al (2013) Ancient DNA reveals key stages in the formation of central European mitochondrial genetic diversity. Science 342:257-261. https://doi.org/10.1126/Science.1241844

Bro-Jørgensen MH, Carøe C, Vieira FG, et al (2018) Ancient DNA analysis of Scandinavian medieval drinking horns and the horn of the last aurochs bull. J Archeol Sci 99:47-54. https://doi.org/10.1016/j.jas.2018.09.001

Browning SR, Browning BL, Zhou Y, et al (2018) Analysis of human sequence data reveals two pulses of archaic Denisovan admixture. Cell 173:53-61.e59. https://doi.org/10.1016/j.cell.2018.02.031

Brunel S, Bennett EA, Cardin L, et al (2020) Ancient genomes from present-day France unveil 7,000 years of its demographic history. Proc Natl Acad Sci USA 117:12791-12798. https://doi.org/10.1073/pnas.1918034117

Buonasera T, Eerkens J, de Flamingh A, et al (2020) A comparison of proteomic, genomic, and osteological methods of archaeological sex estimation. Sci Rep 10:1-15. https://doi.org/10.1038/s41598-020-68550-w

Callaway E (2016) Error found in study of first ancient African genome. Nature 29:19258. https://doi.org/10.1038/Nature.2016.19258

Campelo dos Santos AL, Owings A, Sullasi HSL, et al (2022) Genomic evidence for ancient human migration routes along South America's Atlantic coast. Proc Biol Sci 289:20221078. https://doi.org/10.1098/rspb.2022.1078

Carlhoff S, Duli A, Nägele K, et al (2021) Genome of a middle Holocene hunter-gatherer from Wallacea. Nature 596:543-547. https://doi.org/10.1038/s41586-021-03823-6

Carpenter ML, Buenrostro JD, Valdiosera C, et al (2013) Pulling out the 1%:whole-genome capture for the targeted enrichment of ancient DNA sequencing libraries. Am J Hum Genet 93:852-864. https://doi.org/10.1016/j.ajhg.2013.10.002

Cassidy LM, Maoldúin RÓ, Kador T, et al (2020) A dynastic elite in monumental Neolithic society. Nature 582:384-388. https://doi.org/10.1038/s41586-020-2378-6

Chang D, Knapp M, Enk J, et al (2017) The evolutionary and phylogeographic history of woolly mammoths:a comprehensive mitogenomic analysis. Sci Rep 7:1-10. https://doi.org/10.1038/srep44585

Charlton S, Booth T, Barnes I (2019) The problem with petrous? A consideration of the potential biases in the utilization of pars petrosa for ancient DNA analysis. World Archeol 51:574-585. https://doi.org/10.1080/00438243.2019.1694062

Chen F, Welker F, Shen C-C, et al (2019) A late middle Pleistocene Denisovan mandible from the Tibetan Plateau. Nature 569:409-412. https://doi.org/10.1038/s41586-019-1139-x

Chintalapati M, Patterson N, Moorjani P (2022) The spatiotemporal patterns of major human admixture events during the European Holocene. eLife 11:e77625. https://doi.org/10.7554/eLife.77625

Choin J, Mendoza-Revilla J, Arauna LR, et al (2021) Genomic insights into population history and biological adaptation in Oceania. Nature:1-7. https://doi.org/10.1038/s41586-021-03236-5

Clarkson C, Jacobs Z, Marwick B, et al (2017) Human occupation of northern Australia by 65,000 years ago. Nature 547:306-310. https://doi.org/10.1038/Nature22968

Conard NJ, Moreau L (2004) Current research on the Gravettian of the Swabian Jura. Mitteilungen der Gesellschaft für Urgeschichte 13:29-57. https://doi.org/10.1016/j.jas.2021.105335

Cortez AD, Bolnick DA, Nicholas G, et al (2021) An ethical crisis in ancient DNA research:Insights from the Chaco Canyon controversy as a case study. J Soc Archeol 21:157-178. https://doi.org/10.1177/1469605321991600

Crowther A, Prendergast ME, Fuller DQ, et al (2018) Subsistence mosaics, forager-farmer interactions, and the transition to food production in eastern Africa. Quat Intl 489:101-120. https://doi.org/10.1016/j.quaint.2017.01.014

Dabney J, Knapp M, Glocke I, et al (2013) Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. Proc Natl Acad Sci USA 110:15758-15763. https://doi.org/10.1073/pnas.1314445110

Damgaard PdB, Marchi N, Rasmussen S, et al (2018a) 137 ancient human genomes from across the Eurasian steppes. Nature 557:369-374. https://doi.org/10.1038/s41586-018-0094-2

Damgaard PdB, Martiniano R, Kamm J, et al (2018b) The first horse herders and the impact of early Bronze Age steppe expansions into Asia. Science 360:eaar7711. https://doi.org/10.1126/Science.aar7711

Dannemann M, Racimo F (2018) Something old, something borrowed: admixture and

adaptation in human evolution. Curr Opin Genet Dev 53:1-8. https://doi.org/10.1016/j.gde.2018.05.009

Darzynkiewicz Z, Juan G, Li X, et al (1997) Cytometry in cell necrobiology:analysis of apoptosis and accidental cell death (necrosis) Cytometry 27:1-20. https://doi.org/10.1002/(SICI)1097-0320(19970101)27:1<1::AID-CYTO2>3.0.CO;2-L

Davis LG and Madsen DB (2020) The coastal migration theory: Formulation and testable hypotheses. Quat Sci Rev 249:106605. https://doi.org/10.1016/j.quascirev.2020.106605

Dillehay TD, Ramírez C, Pino M, et al (2008) Monte Verde:seaweed, food, medicine, and the peopling of South America. Science 320:784-786. https://doi.org/10.1126/Science.1156533

Dommain R, Andama M, McDonough MM, et al (2020) The challenges of reconstructing tropical biodiversity with sedimentary ancient DNA:a 2200-year-long metagenomic record from Bwindi impenetrable forest, Uganda. Front Ecol Evol 8:2296. https://doi.org/10.3389/fevo.2020.00218

Duchêne S, Ho SY, Carmichael AG, et al (2020) The recovery, interpretation and use of ancient pathogen genomes. Curr Biol 30:R1215-R1231. https://doi.org/10.1016/j.cub.2020.08.081

Duggan AT, Klunk J, Porter AF, et al (2020) The origins and genomic diversity of American Civil War Era smallpox vaccine strains. Genome Biol 21:1-11. https://doi.org/10.1186/s13059-020-02079-z

Dulias K, Foody MGB, Justeau P, et al (2022) Ancient DNA at the edge of the world Continental immigration and the persistence of Neolithic male lineages in Bronze Age Orkney. Proc Natl Acad Sci USA 119:e2108001119. https://doi.org/10.1073/pnas.2108001119

Durand EY, Patterson N, Reich D, et al (2011) Testing for ancient admixture between closely related populations. Mol Biol Evol 28:2239-2252. https://doi.org/10.1093/molbev/msr048

Ebenesersdóttir SS, Sandoval-Velasco M, Gunnarsdóttir ED, et al (2018) Ancient genomes from Iceland reveal the making of a human population. Science 360:1028-1032. https://doi.org/10.1126/Science.aar2625

Eglinton G, Logan GA (1991) Molecular preservation. Philos Trans R Soc Lond B Biol Sci 333:315-328. https://doi.org/10.1098/rstb.2016.0525

Enk JM, Devault AM, Kuch M, et al (2014) Ancient whole genome enrichment using baits built from modern DNA. Mol Biol Evol 31:1292-1294. https://doi.org/10.1093/molbev/msu074

Erlandson JM, Graham MH, Bourque BJ, et al (2007) The kelp highway hypothesis marine ecology, the coastal migration theory, and the peopling of the Americas. J Island Coast Archaeol 2:161-174. https://doi.org/10.1080/15564890701628612

Fagernäs Z, García-Collado MI, Hendy J, et al (2020) A unified protocol for simultaneous extraction of DNA and proteins from archaeological dental calculus. J Archeol Sci 118:105135. https://doi.org/10.1016/j.jas.2020.105135

Fages A, Hanghøj K, Khan N, et al (2019) Tracking five millennia of horse management with extensive ancient genome time series. Cell 177:1419-1435. https://doi.org/10.1016/j.cell.2019.03.049

Fehren-Schmitz L, Harkins KM, Jarman CL (2017) Paleogenomic investigations of human remains from Rapa Nui. Am J Phys Anthropol 27:3209-3215.e6. https://doi.org/10.1016/j.cub.2017.09.029

Feldman M, Fernández-Domínguez E, Reynolds L, et al (2019) Late Pleistocene human genome suggests a local origin for the first farmers of central Anatolia. Nature 10:1-10. https://doi.org/10.1038/s41467-019-09209-7

Fellows Yates JA, Lamnidis TC Borry M, et al (2021) Reproducible, portable, and efficient ancient genome reconstruction with nf-core/eager. PeerJ 9:e10947. https://doi.org/10.7717/peerj.10947

Fernandes DM, Mittnik A, Olalde I, et al (2020) The spread of steppe and Iranian-related ancestry in the islands of the western

Mediterranean. Nat Ecol Evol 4:334-345. https://doi.org/10.1038/s41559-020-1102-0.

Fernandes DM, Sirak KA, Ringbauer H, et al (2021) A genetic history of the pre-contact Caribbean. Nature 590:103-110. https://doi.org/10.1038/s41586-020-03053-2

Feuerborn TR, Carmagnini A, Losey RJ, et al (2021) Modern Siberian dog ancestry was shaped by several thousand years of Eurasian-wide trade and human dispersal. Proc Natl Acad Sci USA 118: e2100338118. https://doi.org/10.1073/pnas.2100338118

Fischer C-E, Pemonge M-H, Ducoussau I, et al (2022) Origin and mobility of Iron Age Gaulish groups in present-day France revealed through archaeogenomics. IScience 25:104094. https://doi.org/10.1016/j.isci.2022.104094

Flegontov P, Altınışık NE, Changmai P, et al (2019) Palaeo-Eskimo genetic ancestry and the peopling of Chukotka and North America. Nature 570:236-240. https://doi.org/10.1038/s41586-019-1251-y

Fowler C, Olalde I, Cummings V, et al (2022) A high-resolution picture of kinship practices in an Early Neolithic tomb. Nature 601:584-587. https://doi.org/10.1038/s41586-021-04241-4

Fox K, Hawks J (2019) Use ancient remains more wisely. Nature 583:31462783. https://doi.org/10.1038/d41586-019-02516-5

Frantz LA, Bradley DG, Larson G, et al (2020) Animal domestication in the era of ancient genomics. Nat Rev Genet 21:449-460. https://doi.org/10.1038/s41576-020-0225-0

Frantz LA, Haile J, Lin AT, et al (2019) Ancient pigs reveal a near-complete genomic turnover following their introduction to Europe. Proc Natl Acad Sci USA 116:17231-17238. https://doi.org/10.1073/pnas.1901169116

Fregel R, Méndez FL, Bokbot Y, et al (2018) Ancient genomes from North Africa evidence prehistoric migrations to the Maghreb from both the Levant and Europe. Proc Natl Acad Sci USA 115:6774-6779. https://doi.org/10.1073/pnas.1800851115

Fu Q, Hajdinjak M, Moldovan OT, et al (2015) An early modern human from Romania with a recent Neanderthal ancestor. Nature 524:216-219. https://doi.org/10.1038/Nature14558

Fu Q, Li H, Moorjani P, et al (2014) Genome sequence of a 45,000-year-old modern human from western Siberia. Nature 514:445-449. https://doi.org/10.1038/Nature13810

Fu Q, Mittnik A, Johnson PLF, et al (2013) A revised timescale for human evolution based on ancient mitochondrial genomes. Curr Biol 23:553-559. https://doi.org/10.1016/j.cub.2013.02.044

Fu Q, Posth C, Hajdinjak M, et al (2016) The genetic history of Ice Age Europe. Nature 534:200-205. https://doi.org/10.1038/Nature17993.

Furtwängler A, Rohrlach AB, Lamnidis TC, et al (2020) Ancient genomes reveal social and genetic structure of Late Neolithic Switzerland. Nature 11:1-11. https://doi.org/10.1038/s41467-020-15560-x

Gallego Llorente M, Jones E, Eriksson A, et al (2015) Ancient Ethiopian genome reveals extensive Eurasian admixture throughout the African continent. Proc Am Assoc Adv Sci.

Gamba C, Jones ER, Teasdale MD, et al (2014) Genome flux and stasis in a five millennium transect of European prehistory. Nature 5:1-9. https://doi.org/10.1038/ncomms6257

Gansauge M-T, Gerber T, Glocke I, et al (2017) Single-stranded DNA library preparation from highly degraded DNA usingT4DNA ligase. Nucleic Acids Res 45:e79. https://doi.org/10.1093/nar/gkx033

Gaunitz C, Fages A, Hanghøj K, et al (2018) Ancient genomes revisit the ancestry of domestic and Przewalski's horses. Science 360:111-114. https://doi.org/10.1126/Science.aao3297

Giles RE, Blanc H, Cann HM, et al (1980) Maternal inheritance of human mitochondrial DNA. Proc Natl Acad Sci USA 77:6715-6719. https://doi.org/10.1073/pnas.77.11.6715

Glocke I, Meyer M (2017) Extending the spectrum of DNA sequences retrieved from ancient bones and teeth. Genome Res 27:1230-1237. https://doi.org/10.1101/gr.219675.116

Gnecchi-Ruscone GA, Szecsenyi-Nagy A, Koncz I, et al (2022) Ancient genomes reveal origin

and rapid trans-Eurasian migration of 7th century Avar elites. Cell 185:1402-1413.e1421. https://doi.org/10.1016/j.cell.2022.03.007

González Fortes G, Paijmans JL (2019) Whole-genome capture of ancient DNA using homemade baits. In: Shapiro B, Barlow A, Heintzman P, Hofreiter M, Paijmans J, Soares A (eds) Ancient DNA. Methods in Molecular Biology, vol 1963, Humana Press, New York, NY, p. 93-105. https://doi.org/10.1007/978-1-4939-9176-1_11

Goodwin S, McPherson JD, McCombie WR (2016) Coming of age: ten years of next-generation sequencing technologies. Nat. Rev. Genet 17:333-351. https://doi.org/10.1038/nrg.2016.49

Gray RD, Drummond AJ, Greenhill SJ (2009) Language phylogenies reveal expansion pulses and pauses in Pacific settlement. Science 323:479-483. https://doi.org/10.1126/Science.1166858

Green RC, Kirch PV (1997) Lapita exchange systems and their Polynesian transformations Seeking explanatory models. Prehistoric long-distance interaction in Oceania an interdisciplinary approach. Curr Anthropol 52:19-37. https://doi.org/10.1086/662201

Green RE, Krause J, Briggs AW, et al (2010) A draft sequence of the Neandertal genome. Science 328:710-722. https://doi.org/10.1126/science.1188021.

Gretzinger J, Sayer D, Justeau P, et al (2022) The Anglo-Saxon migration and the formation of the early English gene pool. Nature 610:112-119. https://doi.org/10.1038/s41586-022-05247-2

Guimaraes S, Arbuckle BS, Peters J, et al (2020) Ancient DNA shows domestic horses were introduced in the southern Caucasus and Anatolia during the Bronze Age. Sci Adv 6:eabb0030. https://doi.org/10.1126/sciadv.abb0030

Guldemann T (2008) A linguist's view Khoe-Kwadi speakers as the earliest food-producers of southern Africa. Southern African Humanities 20:93-132. https://doi.org/10.10520/EJC84798

Günther T, Malmström H, Svensson EM, et al (2018) Population genomics of Mesolithic Scandinavia Investigating early postglacial migration routes and high-latitude adaptation. PLoS Biol 16:e2003703. https://doi.org/10.1371/journal.pbio.2003703

Guzmán-Solís AA, Villa-Islas V, Bravo-López MJ, et al (2021) Ancient viral genomes reveal introduction of human pathogenic viruses into Mexico during the transatlantic slave trade. eLife 10:e68612. https://doi.org/10.7554/eLife.68612

Haak W, Lazaridis I, Patterson N, et al (2015) Massive migration from the steppe was a source for Indo-European languages in Europe. Nature 522:207-211. https://doi.org/10.1038/Nature14317

Haas R, Watson J, Buonasera T, et al (2020) Female hunters of the early Americas. Sci Adv 6:eabd0310. https://doi.org/10.1126/sciadv.abd0310

Hajdinjak M, Mafessoni F, Skov L, et al (2021) Initial Upper Palaeolithic humans in Europe had recent Neanderthal ancestry. Nature 592:253-257. https://doi.org/10.1038/s41586-021-03335-3

Hansen HB, Damgaard PB, Margaryan A, et al (2017) Comparing ancient DNA preservation in petrous bone and tooth cementum. PLoS One 12:e0170940. https://doi.org/10.1371/journal.pone.0170940

Hansson MC, Foley BP (2008) Ancient DNA fragments inside Classical Greek amphoras reveal cargo of a 2400-year-old shipwreck. J Archeol Sci 35:1169-1176. https://doi.org/10.1016/j.jas.2007.08.009

Harney É, Cheronet O, Fernandes DM, et al (2021) A minimally destructive protocol for DNA extraction from ancient teeth. Genome Res 31:472-483. https://doi.org/10.1101/gr.267534.120

Hartnup K, Huynen L, Te Kanawa R, et al (2011) Ancient DNA recovers the origins of Māori feather cloaks. Mol Biol Evol 28:2741-2750. https://doi.org/10.1093/molbev/msr107

Hedenstierna-Jonson C, Kjellström A, Zachrisson T, et al (2017) A female Viking

warrior confirmed by genomics. Am J Phys Anthropol 164:853-860. https://doi.org/10.1002/ajpa.23308

Higuchi R, Bowman B, Freiberger M, et al (1984) DNA sequences from the quagga, an extinct member of the horse family. Nature 312:282-284. https://doi.org/10.1038/312282a0

Hofmanová Z, Kreutzer S, Hellenthal G, et al (2016) Early farmers from across Europe directly descended from Neolithic Aegeans. Proc Natl Acad Sci USA 113:6886-6891. https://doi.org/10.1073/pnas.1523951113

Hofreiter M, Serre D, Poinar HN, et al (2001) ancient DNA. Nat Rev Genet 2:353-359. https://doi.org/10.1038/35072071

Holsinger KE, Weir BS (2009) Genetics in geographically structured populations defining, estimating and interpreting FST. Nat Rev Genet 10:639-650. https://doi.org/10.1038/nrg2611

Immel A, Pierini F, Rinne C, et al (2021) Genome-wide study of a Neolithic Wartberg grave community reveals distinct HLA variation and hunter-gatherer ancestry. Cummun Biol 4:1-10. https://doi.org/10.1038/s42003-020-01627-4

Ioannidis AG, Blanco-Portillo J, Sandoval K, et al (2020) Native American gene flow into Polynesia predating Easter Island settlement. Nature 583:572-577. https://doi.org/10.1038/s41586-020-2487-2

Ioannidis AG, Blanco-Portillo J, Sandoval K, et al (2021) Paths and timings of the peopling of Polynesia inferred from genomic networks. Nature 597:522-526. https://doi.org/10.1038/s41586-021-03902-8

Isern N, Fort J (2019) Assessing the importance of cultural diffusion in the Bantu spread into southeastern Africa. PLoS One 14:e0215573. https://doi.org/10.1371/journal.pone.0215573

Jacobs GS, Hudjashov G, Saag L, et al (2019) Multiple deeply divergent Denisovan ancestries in Papuans. Cell 177:1010-1021.e1032. https://doi.org/10.1016/j.cell.2019.02.035

Jensen TZ, Niemann J, Iversen KH, et al (2019) A 5700-year-old human genome and oral microbiome from chewed birch pitch. Nature 10:1-10. https://doi.org/10.1038/s41467-019-13549-9

Jeong C, Nakagome S, Di Rienzo, A (2016) Deep history of East Asian populations revealed through genetic analysis of the Ainu. Genetics 202:261-272. https://doi.org/10.1534/genetics.115.178673

Jeong C, Wang K, Wilkin S, et al (2020) A dynamic 6,000-year genetic history of Eurasia's Eastern Steppe. Cell 183:890-904.e829. https://doi.org/10.1016/j.cell.2020.10.015

Jeong C, Wilkin S, Amgalantugs T, et al (2018) Bronze Age population dynamics and the rise of dairy pastoralism on the eastern Eurasian steppe. Proc Natl Acad Sci USA 115:E11248-E11255. https://doi.org/10.1073/pnas.1813608115

Jones ER, Gonzalez-Fortes G, Connell S, et al (2015) Upper Palaeolithic genomes reveal deep roots of modern Eurasians. Nature 6:1-8. https://doi.org/10.1038/ncomms9912

Jones ER, Zarina G, Moiseyev V, et al (2017) The Neolithic transition in the Baltic was not driven by admixture with early European farmers. Curr Biol 27:576-582. https://doi.org/10.1016/j.cub.2016.12.060

Kanzawa-Kiriyama H, Jinam TA, Kawai Y, et al (2019) Late Jomon male and female genome sequences from the Funadomari site in Hokkaido, Japan. Anthropol Sci 127:190415. https://doi.org/10.1537/ase.190415

Kazarina A, Gerhards G, Petersone-Gordina E, et al (2019) Analysis of the bacterial communities in ancient human bones and burial soil samples Tracing the impact of environmental bacteria. J Archeol Sci 109:104989. https://doi.org/10.1016/j.jas.2019.104989

Kennett DJ, Lipson M, Prufer KM, et al (2022) South-to-north migration preceded the advent of intensive farming in the Maya region. Nature 13:1-10. https://doi.org/10.1038/s41467-022-29158-y

Kennett DJ, Plog S, George RJ, et al (2017) Archaeogenomic evidence reveals prehistoric matrilineal dynasty. Nature 8:1-9. https://doi.org/10.1038/ncomms14115

Kerner G, Patin E, Quintana-Murci, L (2021) New insights into human immunity from ancient genomics. Curr Opin Immunol 72:116-125. https://doi.org/10.1016/j.coi.2021.04.006

Kılınç GM, Kashuba N, Koptekin D, et al (2021) Human population dynamics and Yersinia pestis in ancient northeast Asia. Sci Adv 7:eabc4587. https://doi.org/10.1126/sciadv.abc4587

Kirch PV (ed) (2017) Polynesia: origins and dispersals. On the Road of the Winds, University of California Press, Berkley, p.184-212. https://doi.org/10.1525/9780520968899-013

Kistler L, Bieker VC, Martin MD, et al (2020a) Ancient plant genomics in archaeology, herbaria, and the environment. Annu Rev Plant Biol 71:605-629. https://doi.org/10.1146/annurev-arplant-081519-035837

Kistler L, Thakar HB, VanDerwarker AM, et al (2020b) Archaeological Central American maize genomes suggest ancient gene flow from South America. Proc Natl Acad Sci USA 117:33124-33129. https://doi.org/10.1073/pnas.2015560117

Kistler L, Ware R, Smith O, et al (2017) A new model for ancient DNA decay based on paleogenomic meta-analysis. Nucleic Acids Research 45:6310-6320. https://doi.org/10.1093/nar/gkx361

Klamer M (2019) The dispersal of Austronesian languages in island South East Asia. Current findings and debates. Language and Linguistics Compass 13:e12325. https://doi.org/10.1111/lnc3.12325

Ko AM-S, Chen C-Y, Fu Q, et al (2014) Early Austronesians into and out of Taiwan. Am J Hum Genet 94:426-436. https://doi.org/10.1016/j.ajhg.2014.02.003

Kocher Aea (2021) Ten millennia of hepatitis B virus evolution. Science 374:182–188. https://doi.org/10.1126/science.abi5658

Korlević P, Talamo S, Meyer M (2018) A combined method for DNA analysis and radiocarbon dating from a single sample. Sci Rep 8:1-10. https://doi.org/10.1038/s41598-018-22472-w

Krause J, Fu Q, Good JM, et al (2010) The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature 464:894-897. https://doi.org/10.1038/Nature08976

Krzewińska M, Kjellström A, Günther T, et al (2018) Genomic and strontium isotope variation reveal immigration patterns in a Viking Age town. Curr Biol 28:2730-2738. e2710. https://doi.org/10.1016/j.cub.2018.06.053

Lambeck K, Rouby H, Purcell A, et al (2014) Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. Proc Natl Acad Sci USA 111:15296-15303. https://doi.org/10.1073/pnas.1411762111

Lamnidis TC, Majander K, Jeong C, et al (2018) Ancient Fennoscandian genomes reveal origin and spread of Siberian ancestry in Europe. Nature 9:1-12. https://doi.org/10.1038/s41467-018-07483-5

Lane P, Bollig M, Schnegg M, et al (2013) Pastoralism in Africa Past, Present and Future. Afr Health Sci 7:55-60. https://doi.org/10.5555/afhs.2007.7.1.55.

Lansing JS, Cox MP, Therese A, et al (2011) An ongoing Austronesian expansion in island Southeast Asia. J Anthropol Archaeol 30:262-272. https://doi.org/10.1016/j.jaa.2011.06.004

Lawson DJ, Van Dorp L, Falush D (2018) A tutorial on how not to over-interpret structure and admixture bar plots. Nature 9:1-11. https://doi.org/10.1038/s41467-018-05257-7

Lazaridis I, Alpaslan-Roodenberg S, Acar A, et al (2022a) Ancient DNA from Mesopotamia suggests distinct pre-pottery and pottery Neolithic migrations into Anatolia. Science 377:982-987. https://doi.org/10.1126/science.abq0762

Lazaridis I, Alpaslan-Roodenberg S, Acar A, et al (2022b) A genetic probe into the ancient and medieval history of Southern Europe and West Asia. Science 377:940-951. https://doi.org/10.1126/science.abq0755

Lazaridis I, Mittnik A, Patterson N, et al (2017) Genetic origins of the Minoans and

Mycenaeans. Nature 548:214-218. https://doi.org/10.1038/Nature23310

Lazaridis I, Nadel D, Rollefson G, et al (2016) Genomic insights into the origin of farming in the ancient Near East. Nature 536:419-424. https://doi.org/10.1038/Nature19310

Lazaridis I, Patterson N, Mittnik A, et al (2014) Ancient human genomes suggest three ancestral populations for present-day Europeans. Nature 513:409-413. https://doi.org/10.1038/Nature13673

Leavesley M (2006) Late Pleistocene complexities in the Bismarck archipelago. Archaeology of Oceania Australia and the Pacific islands 8:189. https://doi.org/10.1002/9780470773475.ch9

Leavesley MG, Bird MI, Fifield LK, et al (2002) Buang Merabak:early evidence for human occupation in the Bismarck Archipelago, Papua New Guinea. Aust Archeol 54:55-57. https://doi.org/10.1080/03122417.2002.11682070

LeBlanc SA, Cobb Kreisman LS Kemp BM, et al (2007) Quids and aprons Ancient DNA from artifacts from the American Southwest. J Field Archaeol 32:161-175. https://doi.org/10.1179/009346907791071610

Leonardi M, Librado P, Der Sarkissian C, et al (2017) Evolutionary patterns and processes lessons from ancient DNA. Syst Biol 66:e1-e29. https://doi.org/10.1093/sysbio/syw059

Lindahl T (1993) Instability and decay of the primary structure of DNA. Nature 362:709-715. https://doi.org/10.1038/362709a0

Lindahl T, Andersson A (1972) Rate of chain breakage at apurinic sites in double-stranded deoxyribonucleic acid. Biochemistry 11:3618-3623. https://doi.org/10.1021/bi00769a019

Linderholm A, Kılınç GM, Szczepanek A, et al (2020) Corded Ware cultural complexity uncovered using genomic and isotopic analysis from south-eastern Poland. Sci Rep 10:1-13. https://doi.org/10.1038/s41598-020-63138-w

Lipson M, Cheronet O, Mallick S, et al (2018) Ancient genomes document multiple waves of migration in Southeast Asian prehistory. Science 361:92-95. https://doi.org/10.1126/science.aat3188

Lipson M, Sawchuk EA, Thompson JC, et al (2022) Ancient DNA and deep population structure in sub-Saharan African foragers. Nature 603:290-296. https://doi.org/10.1038/s41586-022-04430-9

Lipson M, Szécsényi-Nagy A, Mallick S, et al (2017) Parallel palaeogenomic transects reveal complex genetic history of early European farmers. Nature 551:368-372. https://doi.org/10.1038/Nature24476

Liu C-C, Witonsky D, Gosling A, et al (2022) Ancient genomes from the Himalayas illuminate the genetic history of Tibetans and their Tibeto-Burman speaking neighbors. Nature 13:1-14. https://doi.org/10.1038/s41467-022-28827-2.

Liu Y, Mao X, Krause J, et al (2021) Insights into human history from the first decade of ancient human genomics. Science 373:1479-1484. https://doi.org/10.1126/science.abi8202

Liu Y-C, Hunter-Anderson R, Cheronet O, et al (2022) Ancient DNA reveals five streams of migration into Micronesia and matrilocality in early Pacific seafarers. Science 377:72-79. https://doi.org/10.1126/science.abm6536

Llamas B, Valverde G, Fehren-Schmitz L, et al (2017) From the field to the laboratory Controlling DNA contamination in human ancient DNA research in the high-throughput sequencing era. STAR 3:1-14. https://doi.org/10.1080/20548923.2016.1258824

Loh P-R, Lipson M, Patterson N, et al (2013) Inferring admixture histories of human populations using linkage disequilibrium. Genetics 193:1233-1254. https://doi.org/10.1534/genetics.112.147330

López S, Van Dorp L, Hellenthal G (2015) Human dispersal out of Africa: a lasting debate. Evol Bioinform 11:57-68. https://doi.org/10.4137/EBO.S33489

Lu H, Zhang J, Liu K-b, et al (2009) Earliest domestication of common millet (Panicum miliaceum) in East Asia extended to 10 years ago. Proc Natl Acad Sci USA 106:7367-7372. https://doi.org/10.1073/pnas.0900158106

Macaulay V, Hill C, Achilli A, et al (2005) Single, rapid coastal settlement of Asia

revealed by analysis of complete mitochondrial genomes. Science 308:1034-1036. https://doi.org/10.1126/science.1109792

MacHugh DE, Larson G, Orlando L (2017) Taming the past ancient DNA and the study of animal domestication. Annu Rev Anim Bio Sci 5:329-351. https://doi.org/10.1146/annurev-animal-022516-022747

Malmström H, Günther T, Svensson EM, et al (2019) The genomic ancestry of the Scandinavian Battle Axe Culture people and their relation to the broader Corded Ware horizon. Proc Biol Sci 286:20191528. https://doi.org/10.1098/rspb.2019.1528

Mann AE, Sabin S, Ziesemer K, et al (2018) Differential preservation of endogenous human and microbial DNA in dental calculus and dentin. Sci Rep 8:1-15. https://doi.org/10.1038/s41598-018-28091-9

Mao X, Zhang H, Qiao S, et al (2021) The deep population history of northern East Asia from the Late Pleistocene to the Holocene. Cell 184:3256-3266.e3213. https://doi.org/10.1016/j.cell.2021.04.040

Marchi N, Winkelbach L, Schulz I, et al (2022) The genomic origins of the world's first farmers. Cell 185:1842-1859.e18. https://doi.org/10.1016/j.cell.2022.04.008

Marcus JH, Posth C, Ringbauer H, et al (2020) Genetic history from the Middle Neolithic to present on the Mediterranean island of Sardinia. Nature 11:1-14. https://doi.org/10.1038/s41467-020-14523-6

Mardulyn P (2012) Trees and/or networks to display intraspecific DNA sequence variation? Mol Ecol 21:3385-90. https://doi.org/10.1111/j.1365-294X.2012.05622.x

Margaryan A, Lawson DJ, Sikora M, et al (2020) Population genomics of the Viking world. Nature 585:390-396. https://doi.org/10.1038/s41586-020-2688-8

Martiniano R, Caffell A, Holst M, et al (2016) Genomic signals of migration and continuity in Britain before the Anglo-Saxons. Nature 7:1-8. https://doi.org/10.1038/ncomms10326

Massilani D, Skov L, Hajdinjak M, et al (2020) Denisovan ancestry and population history of early East Asians. Science 370:579-583. https://doi.org/10.1126/science.abc1166

Mathieson I, Alpaslan-Roodenberg S, Posth C, et al (2018) The genomic history of southeastern Europe. Nature 555:197-203. https://doi.org/10.1038/Nature25778

Mathieson I, Lazaridis I, Rohland N, et al (2015) Genome-wide patterns of selection in 230 ancient Eurasians. Nature 528:499-503. https://doi.org/10.1038/Nature16152

Mathieson I, Scally A (2020) What is ancestry? PLoS Genet 16:e1008624. https://doi.org/10.1007/s11892-018-1107-0

Matisoo-Smith E (2015) Ancient DNA and the human settlement of the Pacific A review. J Hum Evol 79:93-104. https://doi.org/10.1016/j.jhevol.2014.10.017

Matisoo-Smith E, Gosling A, Platt D, et al (2018) Ancient mitogenomes of Phoenicians from Sardinia and Lebanon A story of settlement, integration, and female mobility. PLoS One 13:e0190169. https://doi.org/10.1371/journal.pone.0190169

McColl H, Racimo F, Vinner L, et al (2018) The prehistoric peopling of Southeast Asia. Science 361:88-92. https://doi.org/10.1126/science.aat3628

Meltzer DJ (2004) Modeling the Initial Colonization of the Americas. In: CM Burton, GA Clarks, DR Yesner et al (eds) The settlement of the American continents a multidisciplinary approach to human biogeography, The University of Arizona Press, Tucsson, p.123-137.

Mendisco F, Keyser C, Seldes V, et al (2014) Genetic diversity of a late prehispanic group of the Quebrada de Humahuaca, northwestern Argentina. Ann Hum Genet 78:367-380. https://doi.org/10.1111/ahg.12075

Meyer M, Kircher M (2010) Illumina sequencing library preparation for highly multiplexed target capture and sequencing. Cold Spring Harb Protoc pdb prot5448. https://doi.org/10.1101/pdb.prot5448

Mittnik A, Massy K, Knipper C, et al (2019) Kinship-based social inequality in Bronze Age Europe. Science 366:731-734. https://doi.org/10.1126/science.aax6219

Mittnik A, Wang C-C, Pfrengle S, et al (2018) The genetic prehistory of the Baltic Sea region. Nature 9:1-11. https://doi.org/10.1038/s41467-018-02825-9

Moilanen U, Kirkinen T, Saari N-J, et al (2021) A Woman with a sword? –Weapon grave at Suontaka Vesitorninmäki, Finland. Europ J Archeol 1-19. https://doi.org/10.1017/eaa.2021.30

Molak M, Lorenzen ED, Shapiro B, et al (2012) Phylogenetic estimation of timescales using ancient DNA the effects of temporal sampling scheme and uncertainty in sample ages. Mol Biol Evol 30:253-262. https://doi.org/10.1093/molbev/mss232

Monroy Kuhn JM Jakobsson M, Gunther T (2018) Estimating genetic kin relationships in prehistoric populations. PLoS One 13:e0195491. https://doi.org/10.1371/journal.pone.0195491

Moore H, Wilson G, Challanain MN, et al (2022) Migration and community in Bronze Age Orkney innovation and continuity at the Links of Noltland. Antiquity 96:541-559. https://doi.org/10.15184/aqy.2021.185

Moreno-Mayar JV, Rasmussen S, Seguin-Orlando A, et al (2014) Genome-wide ancestry patterns in Rapanui suggest pre-European admixture with Native Americans. Curr Biol 24:2518-2525. https://doi.org/10.1016/j.cub.2014.09.057

Moreno-Mayar JV, Potter BA, Vinner L, et al (2018a) Terminal Pleistocene Alaskan genome reveals first founding population of Native Americans. Nature 553:203-207. https://doi.org/10.1038/Nature25173

Moreno-Mayar JV, Vinner L, de Barros Damgaard P, et al (2018b) Early human dispersals within the Americas. Science 362:eaav2621. https://doi.org/10.1126/science.aav2621

Nägele K, Posth C, Orbegozo MI, et al (2020) Genomic insights into the early peopling of the Caribbean. Science 369:456-460. https://doi.org/10.1126/science.aba8697

Nakazawa Y (2017) On the Pleistocene population history in the Japanese Archipelago. Curr Anthropol 58:S539-S552. https://doi.org/10.1038/s41598-021-91357-2

Narasimhan VM, Patterson NJ, Moorjani P, et al (2019) The formation of human populations in South and Central Asia. Science 365:eaat7487. https://doi.org/10.1126/science.aat7487

Neves WA, Hubbe M (2005) Cranial morphology of early Americans from Lagoa Santa, Brazil implications for the settlement of the New World. Proc Natl Acad Sci USA 102:18309-18314. https://doi.org/10.1073/pnas.0507185102

Nieves-Colón MA, Blevins KE, Contreras-Sieck MÁ, et al (2021) Paleogenómica y bioarqueología en México, Cuicuilco, Revista de Ciencias Antropologicas, Vol. 28.

Ning C, Li T, Wang K, et al (2020) Ancient genomes from northern China suggest links between subsistence changes and human migration. Nature 11:1-9. https://doi.org/10.1038/s41467-020-16557-2

Ning C, Zhang F, Cao Y, et al (2021) Ancient genome analyses shed light on kinship organization and mating practice of Late Neolithic society in China. IScience 24:103352. https://doi.org/10.1016/j.isci.2021.103352

O'Connell JF, Allen J, Williams MA, et al (2018) When did *Homo sapiens* first reach Southeast Asia and Sahul? Proc Natl Acad Sci USA 115:8482-8490. https://doi.org/10.1073/pnas.1808385115

O'Sullivan N, Posth C, Coia V, et al (2018) Ancient genome-wide analyses infer kinship structure in an Early Medieval Alemannic graveyard. Sci Adv 4:eaao1262. https://doi.org/10.1126/sciadv.aao1262

Obregon-Tito AJ, Tito RY, Metcalf J, et al (2015) Subsistence strategies in traditional societies distinguish gut microbiomes. Nature 6:1-9. https://doi.org/10.1038/ncomms7505

Olalde I, Brace S, Allentoft ME, et al (2018) The Beaker phenomenon and the genomic transformation of northwest Europe. Nature 555:190-196. https://doi.org/10.1038/Nature25738

Olalde I, Mallick S, Patterson N, et al (2019) The genomic history of the Iberian Peninsula over the past 8000 years. Science 363:1230-1234. https://doi.org/10.1126/science.aav4040

Olalde I, Schroeder H, Sandoval-Velasco M, et al (2015) A common genetic origin for early farmers from Mediterranean Cardial and Central European LBK cultures. Mol Biol Evol 32:3132-3142. https://doi.org/10.1093/molbev/msv181

Oliveira S, Nägele K, Carlhoff S, et al (2022) Ancient genomes from the last three millennia support multiple human dispersals into Wallacea. Nat Ecol Evol 6:1024-1034. https://doi.org/10.1038/s41559-022-01775-2

Omrak A, Günther T, Valdiosera C, et al (2016) Genomic evidence establishes Anatolia as the source of the European Neolithic gene pool. Curr Biol 26:270-275. https://doi.org/10.1016/j.cub.2015.12.019

Orlando L, Allaby R, Skoglund P, et al (2021) Ancient DNA analysis. Nat Rev Methods Primers 1:1-26. https://doi.org/10.1038/s43586-021-00016-3

Orlando L, Ginolhac A, Zhang G, et al (2013) Recalibrating Equus evolution using the genome sequence of an early Middle Pleistocene horse. Nature 499:74-78. https://doi.org/10.1038/Nature12323

Oskam CL, Haile J, McLay E, et al (2010) Fossil avian eggshell preserves ancient DNA. Proc Biol Sci 277:1991-2000. https://doi.org/10.1098/rspb.2009.2019

Pääbo S (1985) Molecular cloning of ancient Egyptian mummy DNA. Nature 314:644-645. https://doi.org/10.1038/314644a0

Pääbo S (1989) Ancient DNA extraction, characterization, molecular cloning, and enzymatic amplification. Proc Natl Acad Sci USA 86:1939-1943. https://doi.org/10.1073/pnas.86.6.1939

Pääbo S, Poinar H, Serre D, et al (2004) Genetic analyses from ancient DNA. Annu Rev Genet 38:645-679. https://doi.org/10.1146/annurev.genet.37.110801.143214

Papac L, Ernée M, Dobeš M, et al (2021) Dynamic changes in genomic and social structures in third millennium BCE central Europe. Sci Adv 7:eabi6941. https://doi.org/10.1126/sciadv.abi6941

Parker C, Rohrlach AB, Friederich S, et al (2020) A systematic investigation of human DNA preservation in medieval skeletons. Sci Rep 10:1-16. https://doi.org/10.1038/s41598-020-75163-w

Patin E, Lopez M, Grollemund R, et al (2017) Dispersals and genetic adaptation of Bantu-speaking populations in Africa and North America. Science 356:543-546. https://doi.org/10.1126/science.aal1988

Patterson N, Isakov M, Booth T, et al (2022) Large-scale migration into Britain during the Middle to Late Bronze Age. Nature 601:588-594. https://doi.org/10.1038/s41586-021-04287-4

Patterson N, Moorjani P, Luo Y, et al (2012) Ancient Admixture in human history. Genetics 192:1065-1093. https://doi.org/10.1534/genetics.112.145037

Patterson N, Price AL, Reich D (2006) Population structure and eigenanalysis. PLoS Genet 2:e190. https://doi.org/10.1371/journal.pgen.0020190

Pedersen MW, Ruter A, Schweger C, et al (2016) Postglacial viability and colonization in North America's ice-free corridor. Nature 537:45-49. https://doi.org/10.1038/Nature19085

Peltzer A, Jager G, Herbig A, et al (2016) EAGER efficient ancient genome reconstruction. Genome Biol 17:60. https://doi.org/10.1186/s13059-016-0918-z

Perego UA, Angerhofer N, Pala M, et al (2010) The initial peopling of the Americas a growing number of founding mitochondrial genomes from Beringia. Genome Res 20:1174-1179. https://doi.org/10.1101/gr.109231.110

Petchey F, Spriggs M, Bedford S, et al (2014) Radiocarbon dating of burials from the Teouma Lapita cemetery, Efate, Vanuatu. J Archeol Sci 50:227-242. https://doi.org/10.1016/j.jas.2014.07.002

Petersen G (2009) Traditional Micronesian societies Adaptation, Integration, and political organization in the central Pacific, University of Hawaii Press. https://doi.org/10.21313/hawaii/9780824832483.001.0001

Petr M, Pääbo S, Kelso J, et al (2019) Limits of long-term selection against Neandertal introgression. Proc Natl Acad Sci USA

116:1639-1644. https://doi.org/10.1073/pnas.1814338116

Pickrell J, Pritchard J (2012) Inference of population splits and mixtures from genome-wide allele frequency data. PLoS Genetics 8:e1002967. https://doi.org/10.1371/journal.pgen.1002967

Pickrell JK, Reich D (2014) Toward a new history and geography of human genes informed by ancient DNA. Trends Genet 30:377-389. https://doi.org/10.1016/j.tig.2014.07.007

Pinhasi R, Fernandes D, Sirak K, et al (2015) Optimal ancient DNA yields from the inner ear part of the human petrous bone. PLoS One 10:e0129102. https://doi.org/10.1371/journal.pone.0129102

Poinar H, Kuch M, McDonald G, et al (2003) Nuclear gene sequences from a late Pleistocene sloth coprolite. Curr Biol 13:1150-1152. https://doi.org/10.1016/s0960-9822(03)00450-0

Pollard AM, Bray P (2007) A bicycle made for two? The integration of scientific techniques into archaeological interpretation. Annu Rev Anthropol 36:245-259. https://doi.org/10.1093/acprof:oso/9780199548262.003.0002

Ponce de León MS, Koesbardiati T, Weissmann JD, et al (2018) Human bony labyrinth is an indicator of population history and dispersal from Africa. Proc Natl Acad Sci USA 115:4128-4133. https://doi.org/10.1073/pnas.1717873115

Posth C, Nägele K, Colleran H, et al (2018) Language continuity despite population replacement in Remote Oceania. Nat Ecol Evol 2:731-740. https://doi.org/10.1038/s41559-018-0498-2

Posth C, Nakatsuka N, Lazaridis I, et al (2018) Reconstructing the Deep Population History of Central and South America. Cell 175:1185-1197 e1122. https://doi.org/10.1016/j.cell.2018.10.027

Posth C, Renaud G, Mittnik A, et al (2016) Pleistocene mitochondrial genomes suggest a single major dispersal of non-Africans and a Late Glacial population turnover in Europe. Curr Biol 26:827-833. https://doi.org/10.1016/j.cub.2016.01.037

Posth C, Zaro V, Spyrou MA, et al (2021) The origin and legacy of the Etruscans through a 2000-year archeogenomic time transect. Sci Adv 7:eabi7673. https://doi.org/10.1126/sciadv.abi7673

Potter BA, Baichtal JF, Beaudoin AB, et al (2018) Current evidence allows multiple models for the peopling of the Americas. Sci Adv 4:eaat5473. https://doi.org/10.1126/sciadv.aat5473

Prates L, Politis GG, Perez SI (2020) Rapid radiation of humans in South America after the last glacial maximum. A radiocarbon-based study. PLoS One 15:e0236023. https://doi.org/10.1371/journal.pone.0236023

Prendergast ME, Lipson M, Sawchuk EA, et al (2019) Ancient DNA reveals a multistep spread of the first herders into sub-Saharan Africa. Science 365:eaaw6275. https://doi.org/10.1126/science.aaw6275

Prüfer K, Posth C, Yu H, et al (2021) A genome sequence from a modern human skull over 45 years old from Zlatý kůň in Czechia. Nat Ecol Evol 5:820-825. https://doi.org/10.1038/s41559-021-01443-x

Prüfer K, Racimo F, Patterson N, et al (2014) The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505:43-49. https://doi.org/10.1038/Nature12886

Pugach I, Hubner A, Hung H-C, et al (2021) Ancient DNA from Guam and the Peopling of the Pacific. Proc Natl Acad Sci USA 118:e2022112118. https://doi.org/10.1073/pnas.2022112118

Racimo F, Sikora M, Vander Linden M, et al (2020) Beyond broad strokes sociocultural insights from the study of ancient genomes. Nat Rev Genet 21:355-366. https://doi.org/10.1038/s41576-020-0218-z

Raff J (2022) Origin A genetic history of the Americas, Twelve.

Raghavan M, Skoglund P, Graf KE, et al (2014) Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. Nature 505:87-91. https://doi.org/10.1038/Nature12736

Raghavan M, Steinrücken M, Harris K, et al (2015) Genomic evidence for the Pleistocene and recent population history of Native Americans. Science 349:aab3884. https://doi.org/10.1126/science.aab3884

Ramos-Madrigal J, Iraeta-Orbegozo MJN, et al (forthcomming) Ancient DNA preservation in the Caribbean.

Ramos-Madrigal J, Runge AKW, Bouby L, et al (2019) Palaeogenomic insights into the origins of French grapevine diversity. Nature plants 5:595-603. https://doi.org/10.1038/s41477-019-0437-5

Rasmussen M, Anzick SL, Waters MR, et al (2014) The genome of a Late Pleistocene human from a Clovis burial site in western Montana. Nature 506:225-229. https://doi.org/10.1038/Nature13025

Rasmussen M, Li Y, Lindgreen S, et al (2010) Ancient human genome sequence of an extinct Palaeo-Eskimo. Nature 463:757-762. https://doi.org/10.1038/Nature08835

Reich D, Green RE, Kircher M, et al (2010) Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468:1053. https://doi.org/10.1038/Nature09710

Reich D, Patterson N, Kircher M, et al (2011) Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. Am J Hum Genet 89:516-528. https://doi.org/10.1016/j.ajhg.2011.09.005

Reitsema LJ, Kyle B, Koçi M, et al (2022) Bioarchaeological evidence for ancient human diet and migration at Epidamnus/Dyrrachion and Apollonia in Illyria, Albania. Archaeol Anthropol Sci 14:1-25. https://doi.org/10.1007/s12520-022-01553-y

Rieux A, Balloux F (2016) Inferences from tip-calibrated phylogenies a review and a practical guide. Mol Ecol 25:1911-1924. https://doi.org/10.1111/mec.13586

Ringbauer H, Novembre J, Steinrücken M (2021) Parental relatedness through time revealed by runs of homozygosity in ancient DNA. Nature 12:1-11. https://doi.org/10.1038/s41467-021-25289-w

Rivollat M, Jeong C, Schiffels S, et al (2020) Ancient genome-wide DNA from France highlights the complexity of interactions between Mesolithic hunter-gatherers and Neolithic farmers. Sci Adv 6:eaaz5344. https://doi.org/10.1126/sciadv.aaz5344

Rivollat M, Thomas A, Ghesquière E, et al (2022) Ancient DNA gives new insights into a Norman Neolithic monumental cemetery dedicated to male elites. Proc Natl Acad Sci USA 119:e2120786119. https://doi.org/10.1073/pnas.2120786119

Robbeets M, Bouckaert R, Conte M, et al (2021) Triangulation supports agricultural spread of the Transeurasian languages. Nature 599:616-621. https://doi.org/10.1038/s41586-021-04108-8

Robbeets M, Hudson M, Ning C, et al (2022) Triangulation reduces the polygon of error for the history of Transeurasian. bioRxiv 2022:10.05.510045. https://doi.org/https://doi.org/10.1101/2022.10.05.510045

Rohland N, Harney E, Mallick S, et al (2015) Partial uracil-DNA-glycosylase treatment for screening of ancient DNA. Philos Trans R Soc Lond B Biol Sci 370:20130624. https://doi.org/10.1098/rstb.2013.0624

Rohland N, Hofreiter M (2007) Ancient DNA extraction from bones and teeth. Nat Protoc 2:1756-1762. https://doi.org/10.1038/nprot.2007.247

Rohrlach AB, Papac L, Childebayeva A, et al (2021) Using Y-chromosome capture enrichment to resolve haplogroup H2 shows new evidence for a two-Path Neolithic expansion to Western Europe. BioRxiv 11:15005. https://doi.org/10.1038/s41598-021-94491-z

Saag L, Varul L, Scheib CL, et al (2017) Extensive farming in Estonia started through a sex-biased migration from the Steppe. Curr Biol 27:2185-2193. e2186. https://doi.org/10.1016/j.cub.2017.06.022

Saag L, Vasilyev SV, Varul L, et al (2021) Genetic ancestry changes in Stone to Bronze Age transition in the East European plain. Sci Adv 7:eabd6535. https://doi.org/10.1126/sciadv.abd6535

Sánchez-Quinto F, Malmström H, Fraser M, et al (2019) Megalithic tombs in western and northern Neolithic Europe were linked to a kindred society. Proc Natl Acad Sci USA 116:9469-9474. https://doi.org/10.1073/pnas.1818037116

Sankararaman S, Mallick S, Patterson N, et al (2016) The combined landscape of Denisovan and Neanderthal ancestry in present-day humans. Curr Biol 26:1241-1247. https://doi.org/10.1016/j.cub.2016.03.037

Schablitsky JM, Witt KE, Madrigal JR, et al (2019) Ancient DNA analysis of a nineteenth century tobacco pipe from a Maryland slave quarter. J Archeol Sci 105:11-18. https://doi.org/10.1016/j.jas.2019.02.006

Schiffels S, Haak W, Paajanen P, et al (2016) Iron age and Anglo-Saxon genomes from East England reveal British migration history. Nature 7:1-9. https://doi.org/10.1038/ncomms10408

Schlebusch CM, Malmström H, Günther T, et al (2017) Ancient genomes from southern Africa pushes modern human divergence beyond 260 years ago. bioRxiv:145409. https://doi.org/10.1101/145409

Schroeder H, Margaryan A, Szmyt M, et al (2019) Unraveling ancestry, kinship, and violence in a Late Neolithic mass grave. Proc Natl Acad Sci USA 116:10705-10710. https://doi.org/10.1073/pnas.1820210116

Schuenemann VJ, Peltzer A, Welte B, et al (2017) Ancient Egyptian mummy genomes suggest an increase of Sub-Saharan African ancestry in post-Roman periods. Nature 8:1-11. https://doi.org/10.1038/ncomms15694

Seguin-Orlando A, Donat R, Der Sarkissian C, et al (2021) Heterogeneous hunter-gatherer and steppe-related ancestries in Late Neolithic and Bell Beaker genomes from present-day France. Curr Biol 31:1072-1083.e1010. https://doi.org/10.1016/j.cub.2020.12.015

Seguin-Orlando A, Gamba C, Der Sarkissian C, et al (2015) Pros and cons of methylation-based enrichment methods for ancient DNA. Sci Rep 5:1-15. https://doi.org/10.1038/srep11826

Shinde V, Narasimhan VM, Rohland N, et al (2019) An ancient Harappan genome lacks ancestry from steppe pastoralists or Iranian farmers. Cell 179:729-735.e710. https://doi.org/10.1016/j.cell.2019.08.048

Sikora M, Pitulko VV, Sousa VC, et al (2019) The population history of northeastern Siberia since the Pleistocene. Nature 570:182-188. https://doi.org/10.1038/s41586-019-1279-z

Sirak KA, Fernandes DM, Cheronet O, et al (2017) A minimally-invasive method for sampling human petrous bones from the cranial base for ancient DNA analysis. BioTechniques 62:283-289. https://doi.org/10.2144/000114558

Sirak K, Fernandes D, Cheronet O, et al (2020) Human auditory ossicles as an alternative optimal source of ancient DNA. Genome Res 30:427-436. https://doi.org/10.1101/gr.260141.119

Sirak KA, Sedig JW (2019) Balancing analytical goals and anthropological stewardship in the midst of the paleogenomics revolution. World Archeol 51:560-573. https://doi.org/10.1080/00438243.2019.1617190

Sjögren K-G, Olalde I, Carver S, et al (2020) Kinship and social organization in Copper Age Europe. A cross-disciplinary analysis of archaeology, DNA, isotopes, and anthropology from two Bell Beaker cemeteries. PLoS One 15:e0241278. https://doi.org/10.1371/journal.pone.0241278

Skoglund P, Mallick S, Bortolini MC, et al (2015) Genetic evidence for two founding populations of the Americas. Nature 525:104-108. https://doi.org/10.1038/Nature14895

Skoglund P, Malmström H, Raghavan M, et al (2012) Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. Science 336:466-469. https://doi.org/10.1126/science.1216304

Skoglund P, Northoff BH, Shunkov MV, et al (2014) Separating endogenous ancient DNA from modern day contamination in a Siberian Neandertal. Proc Natl Acad Sci USA 111:2229-2234. https://doi.org/10.1073/pnas.1318934111

Skoglund P, Posth C, Sirak K, et al (2016) Genomic insights into the peopling of the Southwest Pacific. Nature 538:510-513. https://doi.org/10.1038/Nature19844

Skoglund P, Storå J, Götherström A, et al (2013) Accurate sex identification of ancient human remains using DNA shotgun sequencing. J Archeol Sci 40:4477-4482. https://doi.org/10.1534/g3.119.400833

Skoglund P, Thompson JC, Prendergast ME, et al (2017) Reconstructing prehistoric African population structure. Cell 171:59-71.e21. https://doi.org/10.1016/j.cell.2017.08.049

Skourtanioti E, Erdal YS, Frangipane M, et al (2020) Genomic history of neolithic to bronze age Anatolia, northern Levant, and southern Caucasus. Cell 181:1158-1175.e1128. https://doi.org/10.1016/j.cell.2020.04.044

Slatkin M, Racimo F (2016) Ancient DNA and human history. Proc Natl Acad Sci USA 113:6380-6387. https://doi.org/10.1073/pnas.1524306113

Slon V, Hopfe C, Weiß CL, et al (2017) Neandertal and Denisovan DNA from Pleistocene sediments. Science 356:605-608. https://doi.org/10.1126/science.aam9695

Soares PA, Trejaut JA, Rito T, et al (2016) Resolving the ancestry of Austronesian-speaking populations. Hum Gen 135:309-326. https://doi.org/10.1007/s00439-015-1620-z

Spriggs M, Anderson A (1993) Late colonization of east Polynesia. Antiquity 67:200-217. https://doi.org/10.1017/S0003598X00045324

Squires K, Roberts CA, Márquez-Grant N (2022) Ethical considerations and publishing in human bioarchaeology. Am J Phys Anthropol 177:615-619. https://doi.org/10.1002/ajpa.24467

Stone AC, Milner GR, Pääbo S, et al (1996) Sex determination of ancient human skeletons using DNA. Am J Phys Anthropol 99:231-238. https://doi.org/10.1002/(SICI)1096-8644(199602)99:2<231::AID-AJPA1>3.0.CO;2-1.

Stoneking M, Krause J (2011) Learning about human population history from ancient and modern genomes. Nat Rev Genet 12:603-614. https://doi.org/10.1038/nrg3029

Sullivan AP, Marciniak S, O'Dea A, et al (2021) Modern, archaeological, and paleontological DNA analysis of a human-harvested marine gastropod (*Strombus pugilis*) from Caribbean Panama. Mol Ecol Resour 21:1517-1528. https://doi.org/10.1111/1755-0998.13361

Summerhayes GR, Leavesley M, Fairbairn A, et al (2010) Human adaptation and plant use in highland New Guinea 49 to 44 years ago. Science 330:78-81. https://doi.org/10.1126/science.1193130

Sutter R (2021) The Pre-Columbian peopling and population dispersals of South America. J Archaeol Res 29:93-151. http://doi.org/10.1007/s10814-020-09146-w

Swarts K, Gutaker RM, Benz B, et al (2017) Genomic estimation of complex traits reveals ancient maize adaptation to temperate North America. Science 357:512-515. https://doi.org/10.1126/science.aam9425

Taylor WT, Pruvost M, Posth C, et al (2021) Evidence for early dispersal of domestic sheep into Central Asia. Nature Hum Behav 5:1169-1179. https://doi.org/10.1038/s41562-021-01083-y

Teasdale MD, van Doorn NL Fiddyment S, et al (2015) Paging through history parchment as a reservoir of ancient DNA for next generation sequencing. Philos Trans R Soc Lond B Biol Sci 370:20130379. https://doi.org/10.1098/rstb.2013.0379

Tian Z, Tao Y, Zhu K, et al (2022) Triangulation fails when neither linguistic, genetic, nor archaeological data support the Transeurasian narrative. bioRxiv 2022.06.09.495471 https://doi.org/10.1101/2022.06.09.495471

Tobler R, Rohrlach A, Soubrier J, et al (2017) Aboriginal mitogenomes reveal 50 years of regionalism in Australia. Nature 544:180-184. https://doi.org/10.1038/Nature21416

Vai S, Amorim CEG, Lari M, et al (2020) Kinship determination in archeological contexts through DNA analysis. Am J Phys Anthropol 8:83. https://doi.org/10.1002/ajpa.22738

Van de Loosdrecht M, Bouzouggar A, Humphrey L, et al (2018) Pleistocene North African

genomes link near Eastern and sub-Saharan African human populations. Science 360:548-552. https://doi.org/10.1126/science.aar8380

van der Valk T, Pečnerová P, Díez-del-Molino D, et al (2021) Million-year-old DNA sheds light on the genomic history of mammoths. Nature 591:265–269. https://doi.org/10.1038/s41586-021-03224-9

Veeramah KR, Rott A, Groß M, et al (2018) Population genomic analysis of elongated skulls reveals extensive female-biased immigration in Early Medieval Bavaria. Proc Natl Acad Sci USA 115:3494-3499. https://doi.org/10.1073/pnas.1719880115

Villalba-Mouco V, Oliart C, Rihuete-Herrada C, et al (2021) Genomic transformation and social organization during the Copper Age–Bronze Age transition in southern Iberia. Sci Adv 7:eabi7038. https://doi.org/10.1126/sciadv.abi7038

Villalba-Mouco V, van de Loosdrecht MS, Posth C, et al (2019) Survival of Late Pleistocene hunter-gatherer ancestry in the Iberian Peninsula. Curr Biol 29:1169-1177. e1167. https://doi.org/10.1016/j.cub.2019.02.006

Wagner JK, Colwell C, Claw KG, et al (2020) Fostering responsible research on ancient DNA. Am J Hum Genet 107:183-195. https://doi.org/10.1016/j.ajhg.2020.06.017

Walter R, Sheppard P (2017) Archaeology of the Solomon Islands.

Wang C-C, Reinhold S, Kalmykov A, et al (2019) Ancient human genome-wide data from a 3000-year interval in the Caucasus corresponds with eco-geographic regions. Nature 10:1-13. https://doi.org/10.1038/s41467-018-08220-8

Wang C-C, Yeh H-Y, Popov AN, et al (2021) Genomic insights into the formation of human populations in East Asia. Nature 591:413-419. https://doi.org/10.1038/s41586-021-03336-2

Wang K, Goldstein S, Bleasdale M, et al (2020) Ancient genomes reveal complex patterns of population movement, interaction, and replacement in sub-Saharan Africa. Sci Adv 6:eaaz0183. https://doi.org/10.1126/sciadv.aaz0183

Wang T, Wang W, Xie G, et al (2021) Human population history at the crossroads of East and Southeast Asia since 11 years ago. Cell 184:3829-3841.e3821. https://doi.org/10.1016/j.cell.2021.05.018

Warinner C, Hendy J, Speller C, et al (2014) Direct evidence of milk consumption from ancient human dental calculus. Sci Rep 4:1-6. https://doi.org/10.1038/srep07104

Warinner C, Speller C, Collins MJ (2015) A new era in palaeomicrobiology prospects for ancient dental calculus as a long-term record of the human oral microbiome. Philos Trans R Soc Lond B Biol Sci 370:20130376. https://doi.org/10.1098/rstb.2013.0376

Wickler S, Spriggs M (1988) Pleistocene human occupation of the Solomon Islands, Melanesia. Antiquity 62:703-706. https://doi.org/10.1038/331707a0

Willerslev E, Meltzer DJ (2021) Peopling of the Americas as inferred from ancient genomics. Nature 594:356-364. https://doi.org/10.1038/s41586-021-03499-y

Yaka R, Mapelli I, Kaptan D, et al (2021) Variable kinship patterns in Neolithic Anatolia revealed by ancient genomes. Curr Biol 31:2455-2468. e2418. https://doi.org/10.1016/j.cub.2021.03.050

Yang MA, Fan X, Sun B, et al (2020) Ancient DNA indicates human population shifts and admixture in northern and southern China. Science 369:282-288. https://doi.org/10.1126/science.aba0909

Yang MA, Gao X, Theunert C, et al (2017) 40,000-year-old individual from Asia provides insight into early population structure in Eurasia. Curr Biol 27:3202-3208. e3209. https://doi.org/10.1016/j.cub.2017.09.030

Yang X, Wan Z, Perry L, et al (2012) Early millet use in northern China. Proc Natl Acad Sci USA 109:3726-3730. https://doi.org/10.1073/pnas.1115430109

Yu H, Jamieson A, Hulme-Beaman A, et al (2022) Palaeogenomic analysis of black rat (*Rattus rattus*) reveals multiple European introductions associated with human economic history. Nature 13:1-13. https://doi.org/10.1038/s41467-022-30009-z

Yu H, Spyrou MA, Karapetian M, et al (2020) Paleolithic to Bronze Age Siberians Reveal Connections with First Americans and across Eurasia. Cell 181:1232-1245. https://doi.org/10.1016/j.cell.2020.04.037

Žegarac A, Winkelbach L, Blöcher J, et al (2021) Ancient genomes provide insights into family structure and the heredity of social status in the early Bronze Age of southeastern Europe. Sci Rep 11:1-11. https://doi.org/10.1038/s41598-021-89090-x

Zhang F, Ning C, Scott A, et al (2021) The genomic origins of the Bronze Age Tarim Basin mummies. Nature 599:256-261. https://doi.org/10.1038/s41586-021-04052-7

Zhang M, Yan S, Pan W, et al (2019) Phylogenetic evidence for Sino-Tibetan origin in northern China in the Late Neolithic. Nature 569:112-115. https://doi.org/10.1038/s41586-019-1153-z

Zhang P, Zhang X, Zhang X, et al (2022) Denisovans and *Homo sapiens* on the Tibetan Plateau dispersals and adaptations. Trends Ecol Evol 37-3:257-267. https://doi.org/10.1016/j.tree.2021.11.004

Zhang X-L, Ha BB, Wang S-J, et al (2018) The earliest human occupation of the high-altitude Tibetan Plateau was 40 thousand to 30 thousand years ago. Science 362:1049-1051. https://doi.org/10.1126/science.aat8824

Zuo X, Lu H, Jiang L, et al (2017) Dating rice remains through phytolith carbon-14 study reveals domestication at the beginning of the Holocene. Proc Natl Acad Sci USA 114:6486-6491. https://doi.org/10.1073/pnas.1704304114