Annual Review of Anthropology

The Impact of Ancient Genome Studies in Archaeology

Omer Gokcumen[1] and Michael Frachetti[2]

[1]Department of Biological Sciences, University at Buffalo, State University of New York, Buffalo, New York 14221, USA; email: omergokc@buffalo.edu

[2]Department of Anthropology, Washington University in St. Louis, St. Louis, Missouri 63130, USA; email: frachetti@wustl.edu

Annu. Rev. Anthropol. 2020. 49:277–98

The *Annual Review of Anthropology* is online at anthro.annualreviews.org

https://doi.org/10.1146/annurev-anthro-010220-074353

This article is part of a special theme on Race. For a list of other articles in this theme, see **https://www.annualreviews.org/toc/anthro/49/1**

Keywords

anthropology, human evolution, social structure, migration, culture, nature–nurture

Abstract

The study of ancient genomes has burgeoned at an incredible rate in the last decade. The result is a shift in archaeological narratives, bringing with it a fierce debate on the place of genetics in anthropological research. Archaeogenomics has challenged and scrutinized fundamental themes of anthropological research, including human origins, movement of ancient and modern populations, the role of social organization in shaping material culture, and the relationship between culture, language, and ancestry. Moreover, the discussion has inevitably invoked new debates on indigenous rights, ownership of ancient materials, inclusion in the scientific process, and even the meaning of what it is to be a human. We argue that the broad and seemingly daunting ethical, methodological, and theoretical challenges posed by archaeogenomics, in fact, represent the very cutting edge of social science research. Here, we provide a general review of the field by introducing the contemporary discussion points and summarizing methodological and ethical concerns, while highlighting the exciting possibilities of ancient genome studies in archaeology from an anthropological perspective.

INTRODUCTION

Ancient genomics has irrevocably changed the archaeological narrative (Kristiansen 2014). It is difficult to exaggerate its impact. Dozens of ancient genome articles have amassed thousands of citations from a wide variety of fields, capturing the imagination of nonacademic audiences, while the underpinning research has enjoyed funding beyond the means of most archaeologists (Skoglund & Mathieson 2018). The resulting availability of hundreds of ancient genomes in a matter of a single decade has challenged many long-held theories about cultural complexes, connections between languages and archaeological remains, modern human origins, and processes of cultural change (Callaway 2018), while seemingly settling long-standing debates at the same time.

The criticisms of ancient genomics, mostly from the field of archaeology, have been quick to emerge. Many scholars accused genomicists of being insensitive to subtleties of material culture by pushing for grand narratives of the human past without much attention to the nuances of archaeological data (Heyd 2017). In Heyd's (2017) words, "[A]t a. . .higher level, culture-history and ethnic interpretations are back on the dinner table" (p. 349). Such arguments resonate with a broader criticism that anthropological genomics research offers a misleading quantitative precision regarding present and past human variation (Horsburgh 2015). The genomics community's response to these criticisms has mostly been to portray the critiques to be the old guard who will soon be replaced as genomics comes to define the next phase of the study of the human past (Reich 2018). It is telling that one of the leaders of ancient genomics research, David Reich, responded to this criticism by saying, "We're barbarians coming late to the study of the human past. . . . But it's dangerous to ignore barbarians" (Callaway 2018, p. 576).

There are reasons to think that ancient genomics is the most exciting development in archaeology in the last few decades, one that will reshape our understanding of the human past and, by proxy, the concepts of ethnicities, cultural complexes, and human nature. Genomics deploys a powerful scientific approach to human (and nonhuman) remains that recenters the conversation on culture and biology, yet with all its quantitative might, ancient DNA can explain only one part of this whole (Rutherford 2018). Despite this limitation, we argue that it has been changing how we understand our past and our present in varied ways among archaeologists and the public alike. In addition, we argue that the current trajectory of ancient genomics research, while debatable, fits squarely within an anthropological and archaeological theoretical framework, tackling questions that archaeologists have addressed for decades. In this review, rather than summarizing individual studies in archaeological genomics, we aim to discuss how ancient genome studies revitalize, challenge, and innovate existing anthropological and archaeological questions. In so doing, we hope to alleviate some of the misconceptions within the field with regard to genomics research and terminology, while highlighting the need for adequately contextualizing genetic data with robust anthropological and archaeological explanations.

GENOMIC STUDIES IN ARCHAEOLOGY

Genes are the building blocks of all living organisms, and when arranged together in a complete set they form a species' genome. The human genome contains roughly 20,000 genes. When compared worldwide, human genomes are virtually identical to each other. Only 1 out of 1,000 genetic nucleotide bases ("letters") differ between two human genomes.[1] Yet because our genomes are so large, these minor differences add up to millions of genetic variations, which allow for nuanced differences in regional ancestries to be studied. These differences make up the core analytical unit of anthropological genomics. Archaeogenomics, defined simply as the study of ancient genomes,

[1]Jobling et al. (2013) provides an excellent primer for the field of human evolutionary genomics.

inherently incorporates archaeological explanations derived from more than a century of research documenting the material histories of humankind's technological innovations, economic changes, ideological transformations, and social interconnectedness across space and time. Thus, for archaeogeneticists, biological relationships evident in our DNA are seen as intricately intertwined with millennia of demographic events that reflect our social history. In this section, we give a brief overview of how our increased ability to decode and analyze ancient DNA sequences—from singular genetic regions to entire genomes—has transformed how we interpret our social past and our biology through a shared analytical lens.

The Legacy of Mitochondria

Mitochondrial DNA (mtDNA) serves as a suitable starting point to introduce both the conceptual and the historical frameworks through which anthropological genomics has developed (for more extensive reviews, see Ho & Gilbert 2010, Pakendorf & Stoneking 2005). Mitochondria are organelles that exist in each of our cells and carry their own DNA. Most of the human genome is found in the 2 sets of 23 chromosomes in the nucleus of our cells—one set inherited from the father and the other from the mother. In contrast, mtDNA is housed in each of the dozens to hundreds of mitochondria found in each of our trillions of cells. Thus, the sheer number of mtDNA molecules makes them exceptionally suitable for ancient DNA analysis (Pakendorf & Stoneking 2005). Given that DNA progressively degrades over time, mtDNA was (until fairly recently) the only genetic material that could be reliably extracted from ancient remains because of its sheer abundance.

Because sperm lack mitochondria, all mtDNA is maternally inherited[2] (**Figure 1*a***). With every generation, mothers pass on their mtDNA to their sons and daughters. There is a rare chance for mutations to occur in the mtDNA, such as a change in nucleotide bases (e.g., a "T" for a "C"). These mutations affect only a fraction of mtDNA as a whole, one change out of ∼16,500 nucleotides. However, mutations accumulate over time, passed on from mother to daughter in maternal lineage. Thus, a mutation in the mtDNA of a maternal ancestor is shared by all her descendants, effectively marking that maternal lineage[3].

This relatively simple inheritance of mtDNA and accumulation of mutations along maternal lineages provide a straightforward framework to ask questions about the maternal histories that link ancient remains to extant humans (Fu et al. 2013, Llamas et al. 2016). Perhaps the most famous example is the ancient mtDNA from a European Neanderthal sample discovered 150 years ago. Researchers at the Max Planck Institute managed to extract the mtDNA from this sample, a technical breakthrough at the time (Krings et al. 1997). Moreover, the data from this single sample had the potential to transform our understanding of human history. If the Neanderthal females contributed to the human gene pool, then the Neanderthal-type mtDNA should exist in some extant human samples. However, the mtDNA sequence of this Neanderthal does not carry the variations that mark known human lineages and, as such, falls outside known human mtDNA diversity. The implication was simple. Either there was no Neanderthal genetic admixture with the ancestors of modern humans or, if there was, the mtDNA of those Neanderthals was not represented in the extant human gene pool. Today, we know that the latter explanation is true, thanks to whole-genome sequences from multiple Neanderthals

[2] An interesting debate considers whether there is any paternal leakage during mtDNA transmission (see Luo et al. 2018). Even though this emerging discussion is relevant to biomedical studies, the claimed paternal transmission is negligible when genealogy studies are considered.

[3] In a beautiful, famous study, Cann et al. (1987) traced back all human mtDNA to a single ancestral mtDNA, defining the modern human maternal lineage.

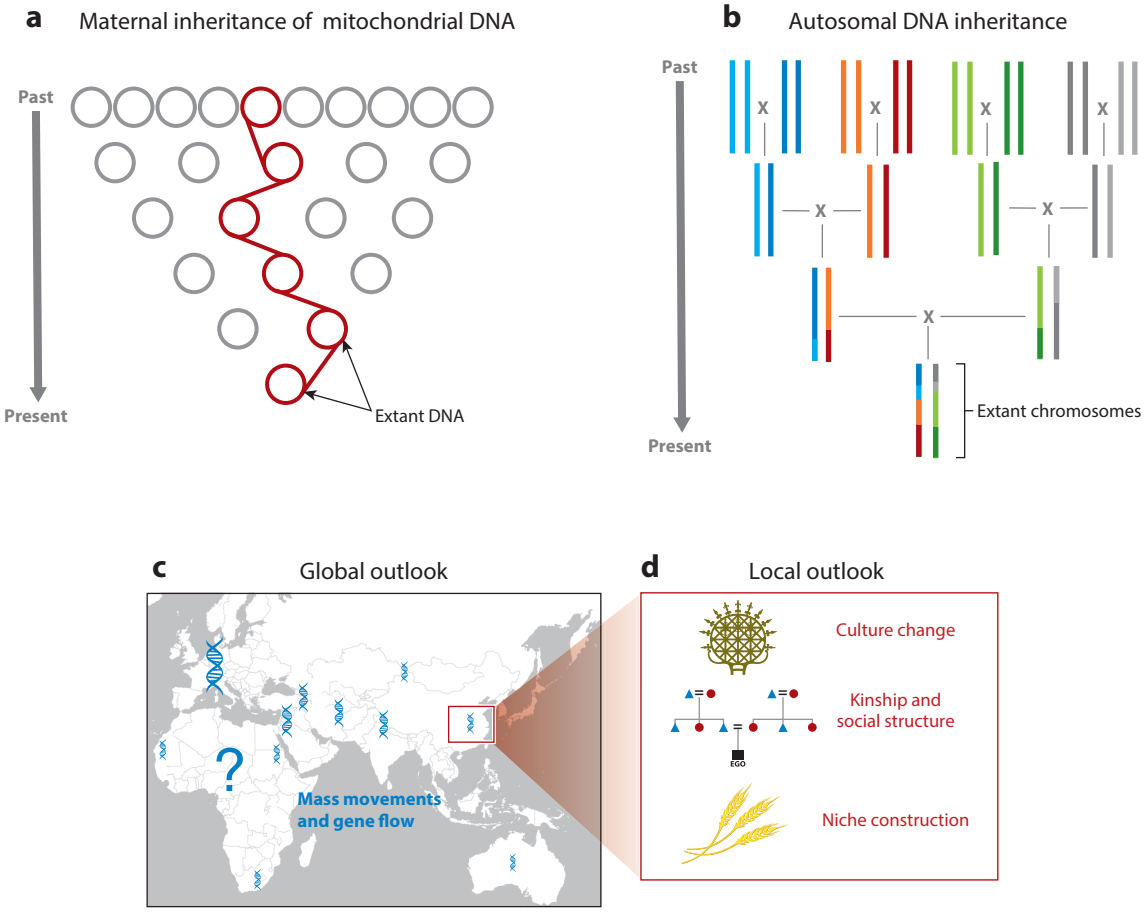

Figure 1

(*a*) The inheritance pattern of mitochondrial DNA (mtDNA). Each circle represents one mtDNA, and inheritance of an extant mtDNA (*red circle at the bottom*) was traced back to a single ancestor in each generation indicated by the red circles. (*b*) The inheritance pattern of autosomal DNA. The extant chromosomes (*colorful chromosome piece at the bottom*) harbor genetic pieces inherited from multiple ancestors from the past. (*c*) A schematic map indicating the European bias of sequenced ancient genomes around the world. The number of ancient genomes available today is indicated by the sizes of the blue DNA helices. Such global analysis of ancient genomes can inform about deep histories of humans as a whole, including evolutionary origins, early migrations, and introgressions with archaic hominins. (*d*) The emerging interest to integrate multiple types of analyses at the local/regional level provides a glimpse into complex issues in anthropology, such as human–environment interactions, cultural change, and social structure.

(Gokcumen 2020, Prüfer et al. 2014, Wolf & Akey 2018). In fact, Neanderthal mtDNA may have been introgressed from an unknown African hominin itself (Posth et al. 2017). Nevertheless, building on the technical advances from the Max Planck team and others, extracting and sequencing ancient mtDNA from samples from different geographies and periods have become relatively commonplace.

Ancient mtDNA research provided a significant step forward in complementing the archaeological record. Broadly, these studies measured the frequencies of particular mitochondrial genetic markers in given archaeological settings and compared them with those documented in other archaeological and extant populations. The results of these studies showed that continuous clines

define human genetic variation without apparent hard borders;[4] allele frequencies of mtDNA variants change gradually across time and geography, shaped by constant gene flow between neighboring populations (Richards et al. 2002, Simoni et al. 2000). Ancient mtDNA data provided a time dimension to this observation as it became clear that mtDNA variation is also clinal across time, changing through drift and gene flow. It further confirms the now decades-old understanding in the field that traditional social categories, e.g., ethnicities, nationalities, races, are not genetically meaningful (Marshall 1998).

More relevant to archaeological questions, analysis of mtDNA has also documented human movement and population expansions geographically. For example, a key success of this approach was the observation that a small subset of mtDNA variants that evolved in Asia was carried to the Americas (Llamas et al. 2016).[5] This observation confirmed earlier interpretations of the archaeological, biological, and linguistic data (e.g., Greenberg et al. 1986), showing that the first humans who arrived in the Americas were from Northern Eurasian ancestral populations (Goebel et al. 2003). Similar conclusions were made regarding initial population movements out of Africa and also demographic changes during the Neolithic transition (Cooper et al. 2001, Haak et al. 2005). Despite the undeniable advances that mtDNA generated in the field, there were notable shortcomings. mtDNA represents a single, haploid locus prone to noise from drift and selection. Thus, mtDNA analysis alone, even when data from ancient remains are available, has proved to be underpowered to conclusively test models of ancient gene flow and population movement.

From mtDNA to Genomes

Genomics, the study of entire genomes, shifted the scale of the investigation of our biological past. The study of ancient genomes is now routine, thanks to the joint effects of next-generation sequencing platforms to generate vast amounts of data, improved computational approaches that allow in silico cleaning of contamination in ancient genomes,[6] and a better understanding of DNA preservation in ancient materials (Millar et al. 2008, Skoglund & Mathieson 2018). With genomic analysis, instead of studying dozens or hundreds of genetic variants that are common in gene-specific analysis, we can now consider millions of genetic markers (Veeramah & Hammer 2014). Unlike the comparatively tiny mtDNA strand with 16,500 base pairs described above, human genomes contain 22 pairs of autosomal chromosomes and 1 pair of sex chromosomes, totaling two sets of 3,000,000,000 nucleotide base pairs. The scale of these data, coupled with the fact that nuclear DNA is inherited from both parents, allows us to reconstruct much more complex ancestral relationships among sampled individuals. Instead of searching for a single maternal ancestor, genome-wide analysis allows us to consider thousands of paternal and maternal ancestors who shaped our genomes.

[4]This idea of gradual geographic distribution of genetic markers was initially discussed as a general rule of population genetics, mostly in nonhuman populations (Avise 2000). Later, similar ideas were applied to human genetic variation, most notably by Cavalli-Sforza (Ammerman & Cavalli-Sforza 2014, Cavalli-Sforza & Bodmer 1999).

[5]Research into extant mtDNA trailblazed several methodological and theoretical advances (Cann et al. 1987; Torroni et al. 1993, 2006), framing the subsequent ancient mtDNA studies.

[6]DNA degradation over time has specific signatures. Ancient DNA is more fragmented and prone to have specific types of DNA damage. For example, "A" and "G" nucleotides are enriched at the ends of ancient sequences because the genome seems to break at these locations over time (Briggs et al. 2007). These degradation signatures, once a major challenge, now allow researchers to identify authentic ancient sequences among vast modern DNA contamination.

The inheritance process for most of our genetic material is not as straightforward as that for mtDNA (**Figure 1*b***).[7] We inherit one copy of a given chromosome from each of our parents, which were, in turn, inherited by our parents from their parents. Moreover, during gamete formation, the maternal and paternal copies of the chromosomes can exchange genetic material through a process called recombination. Therefore, the genome can be imagined as a mosaic. Each mosaic piece can be traced back to a different ancestor. This genome inheritance process enables us to investigate our biological past more realistically: not as a mythical, unbroken lineage of ancestors but as populations of ancestors, each genome with its own story. In this new, exciting era of anthropological genomics, the questions that the field can ask move beyond simple presence or absence of specific genetic markers. It is possible to test archaeological hypotheses within the context of quantitative models for relationships between ancient populations.

A Parenthesis to Acknowledge Some Pitfalls in Interpretation of Genome Data

Anthropological genomics has been one of the most popular and controversial areas of contemporary research. Before we delve into the specific archaeological questions where archaeogenomics provides novel answers, it is important to offer some caveats and address faulty logic that sometimes appears in interpretations of genomic data. The interrelated chemical and biological properties of the DNA, namely its stability and near-perfect inheritance, make it extremely powerful for anthropological research. However, the same features, coupled with complicated data analysis pipelines, can lead to unintended misinterpretation, and on occasion, intended misrepresentation (Furholt 2018, Vander Linden 2016). Here we dissect some potential fallacies in integrating genomics with the archaeological context.

The fallacy of linking genetic markers with specific elements of material culture. The genome is the inheritance molecule. However, oversimplifications can lead to linking certain elements or complexes of material culture with specific genetic markers without proper contextualization.[8] Archaeogenomic analysis can determine the relative ancestral affinities between samples from archaeological sites or cultural complexes to reveal gene flow between the populations of those complexes or sites (e.g., Olalde et al. 2018). It can also identify genetic changes over time, potentially indicating a population replacement or effect of migrant gene flow into a site or region at a given point in history (e.g., Kılınç et al. 2016). These analytical tools can be powerful in detecting subtle changes in allele frequencies over time and space. They do not, however, identify genetic markers that uniquely define populations or cultures, ancient or extant (Gokcumen 2018, Van Arsdale 2019). There are no uniquely diagnostic Viking or Zulu genes; no human population has ever been homogenous.

The fallacy of the definitiveness of DNA results. That we can extract genetic information from specimens that are hundreds of thousands of years old is a testimony to the genome's stability.

[7] An excellent primer on the inheritance of genetic variation within and across a population can be found in Graham Coop's notes on population genetics: **https://github.com/cooplab/popgen-notes/blob/master/popgen_notes.pdf**.

[8] Such oversimplications are especially visible in popular media: for example, "Genetic Tests: Italians Were From Turkey," published in the *Los Angeles Times* (**https://www.latimes.com/archives/la-xpm-2007-jun-18-sci-etruscans18-story.html**). How DNA-based ancestry tests are currently perceived in public further contributes to the perception that cultures and DNA are closely linked, even inseparable. Similarly, commercial ancestry testing can lead to a false sense of immutable biological ancestry, when there is none (Bolnick 2007, Royal 2010).

Thus, the massive amount of data that remain unchanged across time enables us to design robust comparative studies where we can quantitatively assess human uniqueness (Varki et al. 2008), ancestral connections between populations (Mallick et al. 2016), and genetic bases of biological diversity among us (Frazer et al. 2009). When samples are large, diverse, and anthropologically contextualized, they can provide powerful insights (e.g., Narasimhan et al. 2019). When data are sparse, poorly contextualized, or unevenly sampled, the results can be highly reductive or even misleading.

Even the best of models, which are often supported by impressive probability scores, are neither complete nor definitive. Many models were constructed on the basis of the available historical and archaeological data. However, they all depend on implicit and explicit assumptions of human history informed by available archaeological interpretations and hypotheses. Analysis of ancient DNA is merely a means to test a model that best accounts for the available data; the more data we analyze, the more complex human genetic history appears to be. Therefore, ascertainment bias[9] (**Figure 1*c***), with regard to both known archaeological sites and available ancient genomes, remains a significant burden in the field (Lachance & Tishkoff 2013, Marciniak & Perry 2017). New archaeological sites come to light regularly, generating new models and often making older ones improbable. In parallel, new ancient genomics data often cast doubt on models that had been supported for decades by the previously available genomic data. Archaeogenomics, rather than settling age-old questions with definitive answers, often complicates our understanding of human history, leading to beautiful new puzzles to solve (Reich 2018).

RESURRECTING OLD QUESTIONS

Origins

Ancient genomics has complicated our view of early human history. The fossil record and, later, mtDNA variation among extant human populations both pointed to the African continent as the place of origin of modern humans (Cann et al. 1987, Stringer 2002). In the first decade of the twenty-first century, there was little debate among anthropological geneticists about the origin of modern humans: a single, small population that resided in southern or eastern Africa about 150–200 Kya.

These findings did not necessarily fit well with the archaeological record, however (Scerri et al. 2018). First, archaeological discoveries suggested that by the Middle Stone Age (MSA), which is defined by relatively advanced stone tool technologies including prepared cores, humans had already spread across Africa. This period, roughly 300 Kya, considerably predates the most common ancestor of known extant African genomes. The question becomes, does the MSA archaeological expansion across Africa point to an even earlier date for modern human origins, or do these MSA cultures represent some premodern ancestral populations (Henn et al. 2018)?

Second, archaeologists often placed the emergence of modern human behavior in much more recent times, when more sophisticated use of symbols emerges (Mcbrearty & Brooks 2000). The transition from the MSA to a more "modern" material culture, however, did not occur simultaneously across the region. It was temporally and spatially heterogeneous. Given that this transition coincided with significant increases in regional population densities, it raised questions regarding

[9]Ascertainment bias is a term in population genetics that describes systematic deviations from an expected theoretical result attributable to the sampling processes used to find (ascertain) single-nucleotide polymorphisms and measure (estimate) their population-specific allele frequencies. In a similar fashion, the bias in the archaeological record (e.g., we are just beginning to understand the number and distribution of sites in regions such as Africa and Central Asia) constitutes a second layer of ascertainment bias that affects our model construction.

genetic variation as well. Did some local populations, maybe with the help of new technologies, expand and incorporate smaller neighboring communities, reducing the overall genetic variation in the process (Premo & Hublin 2009)? Were there interactions between groups that used modern archaeological assemblages in different parts of Africa (Blegen 2017)?

The genomic perspective on modern human origins has shifted in the last decade, and it has begun to better align with the archaeological patterns described above. Multiple factors contributed to this shift. First, more powerful ways to analyze whole genome data have emerged, and at the same time, there has been a massive increase in the number of sequenced genomes available for comparison (Nielsen et al. 2017). In parallel, the growing appreciation of the importance of sampling from diverse populations to better represent extant human genetic variation has led to new and informative sampling efforts in understudied areas such as Africa (Campbell & Tishkoff 2008). Last, a growing number of ancient genomes from Africa have become available (Schlebusch et al. 2017, Skoglund et al. 2017).

Collectively, these developments have revealed that a small but considerable number of ancient genomic mosaic pieces from Africa have much greater time depth than previously thought. For example, a recent analysis of ancient genomes that were dated to a mere 2 Kya showed unexpected genetic relationships among extant African populations (Schlebusch et al. 2017), pushing back the times of the most recent common ancestor of modern human genomes to 250–300 Kya. Another study has detailed a complex prehistoric population structure in Africa that is not visible in extant genomes owing to the effects of more recent population events (Skoglund et al. 2017). It revealed that people who were living in Africa even only thousands (as opposed to tens or hundreds of thousands) of years ago had a different population structure than we can observe today. Regardless, it is now clear that ancient hominins contributed to extant human genetic variation at different times and places.[10]

Thus, in agreement with the archaeological record, it is highly plausible that modern human genetic and cultural diversity was the product of interactions among multiple prehistoric African populations, rather than one ancestral population (Henn et al. 2018, Scerri et al. 2018). Major questions remain: What defines a "modern human"? How do African fossil remains, such as *Homo naledi*, fit in the history of modern human origins (Dirks et al. 2017)? What were the defining evolutionary and ecological events that reduced the ancient human genetic variation to result in the contemporary variation we observe today? Nevertheless, the new findings from ancient and modern genomes hold the promise of reconciling genomic and archaeological evidence to construct a more complicated but accurate picture of modern human origins.

Movement

A defining feature of humankind is its mobility: the mobility of culture, the mobility of genes, and the mobility of individuals themselves. In the first half of the twentieth century, scholars assumed that distinct material cultural complexes were associated with distinct ethnic or cultural

[10]First, ancient genome data from multiple Neanderthal specimens have revealed that a small but observable number of the mosaic pieces of extant modern human genomes can be traced back to Neanderthal ancestors (Green et al. 2006, Prüfer et al. 2014). In their migrations out of Africa, ancestors of extant Eurasians met and mated with different populations of Neanderthals (Taskent et al. 2020). A more unexpected finding involved genome sequences retrieved from a ∼50-Kya finger bone from Denisova Cave in Siberia. Initially thought to be a Neanderthal individual, the genome from this Denisovan individual revealed the existence of a previously unknown ancient hominin population. Soon after, it was clear that people in Southeast Asia and Oceania carry in their genomes pieces of Denisovan DNA (Jacobs et al. 2019, Reich et al. 2010, Vernot et al. 2016). Last, the precious few ancient genomes from sub-Saharan Africa show evidence of divergent branches of the human genetic tree that are now lost (Hsieh et al. 2016, Schlebusch et al. 2017, Skoglund et al. 2017, Xu et al. 2017).

groups (Trigger 1989). Within this tradition of "culture history," archaeologists commonly associated population movements with mass migrations of culturally and ethnically homogenous groups (for discussion, see Heyd 2017, Kristiansen et al. 2017). Contemporary archaeology had mostly abandoned, sometimes uncritically, such associations in the wake of new evidence from archaeological and genetics fields (Anthony 1990). Insights from ancient genomes have revived discussions of migrations and increasingly provide more nuanced understanding of how human genes are transferred, whether by population movement or by prolonged interactions. Genomics provides important new data in debates concerning episodic migrations versus systemic mobility and the relationship between concomitant changes in the archaeological record (Frachetti 2011, Nielsen et al. 2017). Rather than imagining a board game of immutable cultural-ethnic complexes, we can now relate the complex interplay between human gene flows and material cultures with increasing detail.

Eurasian genetic variation throughout time serves as a suitable example. Thanks to insights from ancient genomes from different archaeological sites spanning Paleolithic to present-day Eurasia, we now know that at least three phases of population movement seeded European genetic variation (de Barros Damgaard et al. 2018, Lazaridis et al. 2014). First, hunter-gatherer migrants out of Africa populated Europe in relatively isolated and scattered groups roughly 30,000 BP. Then, the Neolithic transformation in the Middle East and Anatolia led to a massive population expansion(s) that spread a new group of alleles first to Southern and later to Northern Europe. Last, the frequency of a distinct set of genetic markers found commonly among Early Bronze Age individuals from the Pontic steppe—related to the so-called Yamnaya archaeological culture—shows marked increase in Bronze Age Central Europe after 5000 BP, suggesting a connection between populations of contemporary Europe and the Eurasian Steppe. This influx of more recent genetic mosaic pieces that arrived in Europe was such that it largely displaced the genomic fabric of pre-Neolithic European hunter-gatherers.

From a broader perspective, the ancient events that shaped the European gene pool—the Paleolithic African immigrants, the arrival of Anatolian farmers, and Bronze Age input from the Pontic Steppe—are all painted over by more recent gene flow events among neighbors. A powerful, albeit mundane force called isolation by distance shapes the distribution of present-day Eurasian genetic diversity (Novembre et al. 2008). The current allele frequency distributions of genetic mosaic pieces in Europe correlate almost perfectly with geography. The allele frequencies that are common in southern France are also common in Northeastern Spain and Northwestern Italy, whereas alleles common in Northern France are also common in Belgium, the Netherlands, and western Germany. These alleles can be used collectively to predict the self-reported geographic origin of 90% of European individuals with a ~700-km margin of error using only the genome information. This trend can be generalized to almost all human populations: Allele frequencies of individual genetic mosaic pieces are not confined to specific geographies but gradually increase or decrease with distance (Manica et al. 2005, Novembre & Peter 2016). Genes flow among proximate social spheres. The result is that, at a given time, human genetic variation "mirrors geography" (Novembre et al. 2008).

Isolation by distance has also shaped distribution of genetic variation in ancient populations, marking geographic paths through which communities interact with each other. Careful consideration of the formation of these allele frequencies across time has painted a multilayered picture: First, at different times, the genetic clines are more visible for specific axes, marking corridors of social interaction between archaeological sites. For example, the early Neolithic was characterized by interaction among distinct farming communities in Southwest Asia, creating a 10,000-year-old cline of mosaic genetic ancestry from Anatolia to the slopes of the Hindu Kush mountains in modern-day Afghanistan (Narasimhan et al. 2019). This cline was later painted over by

subsequent diverse admixture events, representing post-Neolithic movements and interaction corridors connecting the Middle East, North Africa, and Central and South Asia.

Second, geographic barriers such as bodies of water, extensive deserts, and mountain ranges add to the equation by acting as "leaky barriers" that influence the constant flow of genetic variation among human groups (Peter et al. 2020). Over time, the global changes in ecology, technology, and culture led to new corridors of interactions while eliminating previously important ones. The Bering Strait became a frozen bridge for Siberian populations, who peopled the Americas during the last Ice Age (Rasmussen et al. 2010, Scheib et al. 2018, Skoglund et al. 2015). The mountains and deserts of Central Asia at times posed significant barriers between South and East Asia, yet they have also served as important arenas of social and biological interaction throughout various phases of prehistory. Following the rise of mobile pastoralist societies in the Central Asian Bronze Age, new links between populations at the Eurasian peripheries emerged, shaping the extant genetic variation from Europe to South Asia (Narasimhan et al. 2019).

Third, the links between ancient and extant populations are tenuous. The genetic variation of Western European populations is observably different in the Paleolithic, Neolithic, Bronze Age, and modern times (Antonio et al. 2019). For example, the genetic legacy of early farmers of Anatolia can be found in Southern Europe but not in modern-day Turkey (Kılınç et al. 2016). It appears that Anatolian farmers have contributed their genes to cultures to Mediterranean Europe, but their genetic legacy in Anatolia was later diluted by gene flow from the Caucasus, the Near East, and Central Asia. Similarly, the genetic variation of ancient populations of the Old Kingdom of Egypt is observably different from modern genetic variation in Egypt (Schuenemann et al. 2017). Further scrutinization of the changes in genetic variation across time shows a gradual shift in allele frequencies after the Roman period in the region. In other parts of the Middle East, we see deeper genetic connections between extant and ancient populations that occupy the same geographic area. For example, communities that live in Lebanon show a remarkable genetic continuity that can be traced back to the Bronze Age (Haber et al. 2013). In an ironic historical twist, the extant Lebanese population shows recent genetic structuring along religious lines, indicating the strong effect of social groups and religious affiliation on interaction and, consequently, genetic variation within populations.

A recent study sequenced 127 genomes from the inhabitants of what is now known as Rome, from Paleolithic to present day, documenting the genetic change over time in a given locality (Antonio et al. 2019). The Paleolithic residents of Rome were descendants of early migrants from Africa. Their genes were mostly replaced by gene flow from the Neolithic settlers of Anatolia, as farming communities transformed the region's geography, culture, and society. Later, at the peak of its power, Imperial Rome enjoyed unprecedented genetic diversity, representing first- or second-generation immigrants—slaves, immigrants, traders, mercenaries—carrying distinct genetic mosaic pieces from across the Mediterranean. As Rome's power faded, these connections were lost, and the gene flow slackened. Over time, the primordial genetic pieces that once marked differences between Roman genomes through time came to be shared among all Romans. For example, a genetic marker that was found only among Roman citizens who migrated recently from North Africa gradually spread into the rest of the Roman gene pool. Even though the genetic markers found in ancient and modern Rome are similar, their distributions dramatically shifted from their heterogeneous distribution among imperial Roman genomes to more homogenous distribution among extant Roman genomes. Thus while the genetic legacy of imperial Rome's cosmopolitan society still lingers, Rome today is genetically very different from its imperial heyday.

As the above case studies show, genomic studies can reveal the important impact of large-scale population movements such as those of early farmers out of Anatolia. At the same time, the rapidly accumulating ancient and modern genome data also strongly suggest that more localized

gene flow between neighbors is the single most consistent force that shapes human genetic variation across time. Complex and unique interactions between populations, shaped by ecological and cultural factors, influence the scalar movements of people and the magnitude and speed of gene flow. Proper anthropological framing and archaeological contextualization of human strategies and technologies (e.g., economic modes, subsistence strategies and technologies, nature of mobility, geographic and political obstacles to interaction) are essential to understanding genetic and cultural affinities between communities from diverse geographies and sites over time.

Social Structure

One of the most exciting recent developments in archaeogenomics is the investigation of social organization within archaeological sites (**Figure 1*d***). Familial relationships of burials and households, social organization and hierarchical relationships within settlements, and symbolic representations of these social norms have been a staple of archaeology (Ensor 2011, Robb 1998). Now, genomics data lend a hand (e.g., O'Sullivan et al. 2018). In Veeramah's (2018) words, "[I]t will be necessary to focus less on grand narratives over space and time, and instead integrate genomic data with other forms of archaeological information at the level of individual communities to understand the internal social dynamics." Two recent papers highlight the power of integrating archaeological and genomics analyses to understand the cultural complexity of a past society.

The first of these studies, by Amorim et al. (2018), sequenced 63 samples from 2 Longobard cemeteries from Hungary and Italy. These archaeological sites were occupied during a turbulent time when Europe was transitioning from Late Antiquity, culturally defined by the Roman Empire, to the Middle Ages, which are characterized by an influx of non-Romanized people from Central and Northern Europe. Even though the Longobards themselves did not chronicle their histories, other historic accounts placed these people in former East Germany during the height of the Roman Empire (circa first century CE). As the Empire's power shifted east, archaeological and historical evidence indicates that the Longobards expanded southward. By the fifth and sixth centuries CE, archaeological sites (mostly graveyards) associated with Longobard culture had a considerable presence in the archaeological record along the Danube river. The question becomes, then, who were the occupants of these graves. Did they have genetic affinities with individuals found in Northern European archaeological sites? Was there any significance as to how the cemeteries were organized? Were there familial relationships between the occupants of these graves? An integrative approach that combined genetic and archaeological data shed unprecedented light on these questions.

The first clear finding from the genetic perspective was that the burial populations in these two cemeteries were not genetically homogenous. When compared with other ancient genomes from relatively contemporaneous archaeological sites across Europe (mostly Bronze Age), the genomes from the Longobard graves were roughly clustered into two groups, one closer to the genomes from sites in Northern and Central Europe and the other closer to the genomes from sites in Southern Europe. The presence of the genetic mosaic pieces that were clustered with Northern and Central Europe sites supports the general notion that Longobard archaeological culture was partly a product of migration. The leaky barrier effect of the Alps, which slowed interactions for thousands of years between Southern and Northern Europe, was weakening. Strontium isotope analysis showed that at least some of the individuals with genomes similar to Northern/Central European sites were born elsewhere and immigrated into these archaeological sites, further supporting the idea of contemporary population movement. Europe had become more connected than before.

Another remarkable finding of this study was that kinship was the most crucial factor in explaining the organization of the material culture in these cemeteries. Three to five distinct family groups, each composed of parents, children, siblings, and first and second cousins, were buried in these cemeteries. Family members were often placed adjacent to one another. Moreover, the allocation of grave goods depended on the familial connections. For example, one family group in the Szólád graveyard contained the wealthiest burial goods, suggesting an elevated social status. This family also ate more animal protein than did the others in the graveyard, further suggesting their higher social status. The majority of the genomes from this family were most similar to Central and Northern European populations. However, at least one female member had a genome similar to those of Southern European groups, suggesting that she married into this family. Overall, these findings imply that Longabard society was organized around hierarchically ordered kinship groups. Given the female with distinct ancestry in the high-status family, whether immediate kin relationships or perceived ancestry were more important in Longobard society is an open question.

A second notable recent archaeogenomics study focusing on kinship relationships documents genomic variation among 104 individuals from various farmsteads in southern Germany, spanning a period between the Late Neolithic and Bronze Ages (~5 Kya–3 Kya) (Mittnik et al. 2019). The study revealed that each farmstead was occupied by an extended patrilocal kinship group living with lower-status unrelated individuals. One of the key insights from this study is the outstanding stability of this social structure in the same region for more than 700 years, spanning major cultural shifts and inevitable shifts in genetic variation. Investigators also found high-status females unrelated to the core kin group who were from distant areas, according to isotopic and genetic data. The authors suggest these high-status females represent marriage networks connecting distant kinship groups.[11] Furthermore, there is no evidence of the children of these high-status females. The authors suggest that these children may have been sent back to the mother's birthplace, further cementing the genetic connection between two distant locales.

Culture Change

The questions of how material culture emerges and changes over time have occupied the field of archaeology since its beginnings (Trigger 1989). The spread of the Near Eastern Neolithic cultural complex into Europe, for example, was one of the core areas of inquiry for archaeologists of this period (Childe 1936). The spread of specific material culture elements, such as Bell Beaker pottery (Brodie 1997, Vander Linden 2007), has been used as a means to understand interactions and movements between different geographies and cultural complexes in the archaeological record. The reason why this topic has been so crucial in archaeology, spanning periods and geographies, is that it implicitly asks two fundamental questions about human nature: Does culture change necessarily parallel demographic change (e.g., grand migrations), and what (if any) are the biological correlates to archaeological patterns?

Archaeogenomic studies are now revitalizing the study of culture change, revealing unexpected trends in population movement and wide regional admixture that complicate our understanding of the relationship between material culture and demographics. It is impossible to summarize the ocean of new studies here. Instead, we present how the proliferation of archaeogenomics research in Eurasia has impacted an enduring archaeological topic: the spread of Neolithic cultures across Europe (Pinhasi et al. 2005). We hope that this example will offer a glimpse of the potential of genomics to reshape how we investigate culture change.

[11] It is worth noting that similar patterns in modern-day Anatolia, where strong religiously/culturally similar patrilocal communities exchange brides across long distances (Gokcumen et al. 2011).

The Neolithic transition in Europe is documented as a socioeconomic shift from predominately hunter-gatherer lifestyles in the Mesolithic toward larger sedentary, agricultural communities in the Neolithic from the ninth to the fifth millennia BP across Europe (Bellwood et al. 2007). How this transition unfolded over millennia remains one of the most intriguing questions in archaeology. Early in the twentieth century, scholarly perspectives followed the theories of V. Gordon Childe, who regarded the Neolithic transition as a "revolution." This view has been profoundly influential and informed the studies of early synthesizers of both archaeological and (later) genetic evidence. The relationship between Neolithic farming cultures and their genetic ancestry was one of the first questions to be addressed by archaeogenetics (Cavalli-Sforza & Feldman 1981). In their pioneering study, Cavalli-Sforza and colleagues recognized the clinal pattern of human genetic variation, and they associated these clines in Europe with a staged, demographic expansion of farmers from the Middle East into Europe (Ammerman & Cavalli-Sforza 2014).

Renfrew, offering a more integrative approach, matched Neolithic material culture elements with specific uniparental genetic markers (e.g., mtDNA). He modeled culture change as a process that followed movements and integrations among farmers and in multiple publications noted instances where gene–culture complexes associated with Neolithic technologies spread from the Middle East into Europe (Renfrew 2001). Renfrew put forward the hypothesis that not only material cultural elements and genes, but also Indo-European languages likely spread from Southwest Asia into Europe as part of a Neolithic package (Renfrew 1990). His model was elegant and holds significant merit. Summarized simply, the rise of Neolithic farming in the Fertile Crescent and Anatolia led to a massive increase in population, and thus, Neolithic farmers expanded from the Near East, moving with their culture (and genes) in search of new land, subsequently mixing with or displacing much smaller hunter-gatherer populations in their path.

The recent ancient genome data, however, has lent considerable nuance to debates on the Neolithic transition across Eurasia. Lazaridis et al. (2016) showed that three distinct Neolithic communities in Anatolia, the Levant, and Iran have different genetic features. Furthermore, this study showed a genetic continuity between hunter-gatherer and agriculturalist communities within each region. Local foragers learned how to farm, likely through cultural exchange with neighboring communities. The implication is that the spread of culture, but not genes, defined the Neolithic transition in the Fertile Crescent of Southwest Asia.

However, this trend is not a universal feature of the Neolithic transition (Jones et al. 2017). Subsequent studies showed a spread of the Anatolian Neolithic into Southern Europe, this time with genes moving along with the material culture, supporting earlier models. Yet genomic data served to further complicate the narrative, illustrating that these movements of cultures and genes were more likely a multistep process, with diverse geographic and chronological vectors of transition. It turns out that Anatolian foragers, communities with relatively low genetic variation, adopted agricultural cultural elements, indicating a local, cultural transition (Feldman et al. 2019, Kılınç et al. 2016). These early farmers expanded in population size while constructing new networks with other regional Neolithic settlements (Somel et al. 2016). The result was an increase in Neolithic genetic variation in Anatolia. Only after this population expansion and interregional gene flow did these farmers expand further into Southern Europe, likely in multiple, multidirectional trajectories (Hofmanová et al. 2016, Omrak et al. 2016).

Data from other parts of the world further complicate the story of the Neolithic. The origins of South Asian agriculture have been linked primarily to the Near Eastern Neolithic transition, in part because of the shared Indo-European roots that link the languages of South Asia, Iran, and historic Anatolia (e.g., the Hittites). However, a recent archaeogenomics study provided evidence that Neolithic farmers in South Asia (~9 Kya) likely descended from local foragers, suggesting a cultural but not genetic connection between South Asian and Middle Eastern agriculturalists

(Narasimhan et al. 2019). During the Bronze Age, however, new currents of genetic admixture further diversified South Asian populations, with input from diverse sources including inhabitants of the Indus Valley Civilization (Shinde et al. 2019) and mobile pastoralists of the Central Eurasian steppe, whose ancestry reflected millennia of mixing among herders throughout the steppes and highlands of Inner Asia. This genetic connection, which traces complex vectors of movement and interaction from 5,000 to 3,500 years ago across Eurasia, suggests that a complex and protracted process explains the geographic distribution of Indo-European languages in both Europe and South Asia. However, even in Europe, where we have the most comprehensive representation of ancient genomes, we do not have a full account of how genetic transitions articulate with dynamic semiotic systems such as language. What we realize is that culture change—whether the spread of agriculture, pastoralism, trade, or assimilation—was sometimes driven by demographic movements and sometimes was transmitted through social interaction. Instead of building universal models of culture change, archaeogenomics is helping to reveal alluring intricacies of human nature and diversity, mobility, and interaction.

CONCLUSION

Ethical and Epistemological Considerations

Eurocentrism, both conscious and subconscious, has now been recognized as one of the most challenging obstacles to the study of humans (Wallerstein 1997). Archaeogenomics is not immune to this bias. The majority of ancient genome studies involve samples from Europe, often asking questions about European populations. The studies are led by European and American institutions, thus representing Western perspectives on history, ancestry, and identity. However, there is a growing, healthy debate on these biases in the field—on the part of anthropologists, archaeologists, and geneticists alike—promising a more balanced view of humanity in the near future. To get there, however, it is vital to identify the historical and institutional biases in the field.

The first bias in archaeogenomics is the comparative dearth of genome data from outside Europe. Ancient genomes from Europe led to an impressive array of new questions and provided new methodological advancements. However, the current sampling bias in the field is glaringly unacceptable. Until very recently, we had few ancient genomes from Africa, the birthplace of our species and home to most of our genomic diversity (Scerri et al. 2018). We still have significant gaps in our understanding of the peopling of entire continents, such as Australia and the Americas (but see Malaspinas et al. 2016, Moreno-Mayar et al. 2018, Scheib et al. 2018). For some regions, the ancient genomic record is a practical tabula rasa. Incredible intellectual riches across the world remain hidden, simply because of uneven incentives to look for them. Addressing this bias in the field will require collective action from the archaeologists and geneticists who directly envision future projects, but also from funding agencies, academic institutions, indigenous peoples, and the broader public. The intellectual agenda of the next stage of archaeogenetic research must actively seek the perspectives and voices of indigenous communities and local stakeholders, even if doing so means putting a halt to the research itself. Promoting a simple but powerful idea may help: We are all connected with deep and intermingled roots. Regardless, the quest for archaeogenetic explanations must actively confront colonialist, imperialist, and capitalist agendas.

A second bias is an epistemological one. Archaeogenomics requires a new kind of theoretical and methodological framework outside the traditional training of archaeologists or geneticists. On the one hand, archaeologists struggle to parse the massive genomic data sets, identify compatibility issues, and interpret the results of complicated mathematical and biostatistical analyses. On the other hand, geneticists often overlook or simplify the historical and archaeological issues surrounding sampling, interpretation, and meaning of archaeogenomic research. As is articulated

in a recent opinion piece by Sawchuck & Prendergast (2019), the solution for this epistemological conundrum is training archaeologists in genetics, and geneticists in archaeology and anthropology, while establishing a practical institutional environment for close collaboration.

Indeed, the recent research on social structure and culture change summarized in this review provides examples of productive collaborations between archaeologists and genomicists. However, these studies highlight extremely high-end projects rather than the mainstream. Thus, one potential challenge to the interdisciplinarity from the archaeological perspective is to be able to recognize that the finances, labor distributions, authorship, and ownership in archaeogenomic studies are drastically different from more traditional archaeological research. For example, it is important to accept that ancient genomics work will be funded by agencies that are not anthropologically oriented, will produce papers with dozens of authors, and may require a different mindset concerning promotion, recognition, and regulation of individual researchers in anthropology departments. In spite of these challenges, it is vital to include programs to train anthropologists in the study and interpretation of genomic data. Such programs are sorely missing in most anthropology departments. The inability of anthropologists to analyze and assess genomic data firsthand remains one of the major bottlenecks in proper collaborations in archaeogenomics research and also prevents unique perspectives from archaeology to further the field in novel and exciting directions.

The third bias in archaeogenomics is a broader concern that affects social sciences in general. There is variation in how people view their histories and identities and the degree to which genetic ancestry poses a valid or valuable form of information. The results of archaeogenomics research can be interpreted in various ways, which can be socially and politically charged. The questions that are meaningful for a researcher in a US academic institution may be irrelevant to other perspectives, especially those of indigenous peoples (Guglielmi 2019). The San people of Africa, for example, have long been a population of interest to anthropologists because they represent a group that diverged from other African groups tens (maybe hundreds) of thousands of years before present (Campbell & Tishkoff 2008, Mallick et al. 2016, Tishkoff et al. 2009). However, for many San people themselves, this outgroup status seems absurd.

Similarly, the ancient genomes of Anatolia and the Middle East have been studied often not as a means to understand the history of the region, or even to understand significant cultural changes, such as the Neolithic transition, but to elucidate the peopling of Europe (de Barros Damgaard et al. 2018, Lazaridis et al. 2014). Indigenous peoples have often been sidelined when sweeping narratives about their history were constructed on the basis of data from the very burial sites that they deemed sacred (Garrison et al. 2019). The integration of indigenous voices in archaeogenomics research represents not only ethical but also scientifically more systematic practice, leading to a more comprehensive understanding of human diversity. The future looks bright, and there is now broad recognition of the necessity for better integration of indigenous voices to archaeogenomics research (Bardill et al. 2018, Claw et al. 2018, Guglielmi 2019, Phillips 2019); however, the field remains young with much room for improvement.

One overarching issue that runs together with these biases is the ownership and regulation of ancient materials, both before and after sampling and analysis. In certain countries, indigenous peoples have regained some level of ownership over ancient burials with which they are culturally associated (Rasmussen et al. 2015, Wright et al. 2018). In other countries, especially those with less democratic governments, officials have sometimes pushed for research agendas that put forward nationalistic historical narratives rather than promoting the inclusion of diverse voices from minority groups. Even when best practices are employed in sampling decisions, some questions will remain thorny: Which contemporary indigenous community should have ownership of ancient burials? Should some archaeological burials stay outside of the realm of genomic interrogation

because the results may be harmful or offensive to certain groups? Is being left out of the race for genomics analysis for some communities who do not want to participate in genetics research harmful to them in the long term (e.g., they will not be able to access precision medicine)? What is the responsibility of the researchers and participants in the interpretation of genetic continuity and discontinuity within the context of ethnocentric national history narratives? For example, is it acceptable for communities to draw on ancestral connections to claim ownership of specific archaeological remains, places and geographies, and even identities?

These concerns should not discourage the pursuit of archaeogenomics research. Instead, with our awareness of these complex issues, we can enter into wider and important dialogues that resonate with fundamental themes of multiple social science disciplines. Archaeogenomics provides an opportunity to reconcile questions in new and exciting ways. For example, the San people recently wrote an ethics statement, highlighting their requirements for researchers seeking to work with them. These requirements are reasonable and simple: honesty, transparency, respect, and inclusion in the scientific process. Such simple ethical guidelines should be easy to implement as they overlap with the general academic code of ethics in the first place. Indeed, thanks to different groups of scholars that are led by indigenous expert voices and that engage with local communities, an ethical and theoretical framework is emerging (Claw et al. 2018). With such guidance and continued dialogue, we expect the future of archaeogenomics to be fruitful, where multiple interpretations of genetic variation coexist to better understand our intertwined histories.

New Frontiers

It is an exciting time to be studying the relationship between culture and biology: A treasure trove of new archaeological sites, transformative methodologies, and a zeal to integrate previously discrete disciplinary constructs create an unprecedentedly rich intellectual environment for the coming decades. Ancient genomics is a significant part of this richness, and we argue that the next phase of archaeogenomics provides an amazing opportunity to expand our understanding of human diversity, genes and cultures and all, in new and transformative ways.

One of the most exciting frontiers is the emerging role of culture in shaping biological evolution. As we invent new ways of living, we keep changing our environments (Erickson 2003, Erlandson & Rick 2010, Frachetti 2009, Grayson 2001, McGovern et al. 2007). These changes in our environments have affected our genomes in subtle but important ways (Laland & O'Brien 2010). For example, many of us are now adapted to a starch-rich diet, perceiving and liking starchy food much more than our ancestors did (Perry et al. 2007), and lactose tolerance in adulthood is now common (Ingram et al. 2009, Tishkoff et al. 2007). Our genomes evolved to fight off infectious diseases that our recent population density (e.g., tuberculosis) and ecological exploits (e.g., malaria) have encouraged (Bos et al. 2014, Spyrou et al. 2019). Our ecological footprint has been so powerful that the species that live with us have evolved (Pajic et al. 2019). Most notably, the domesticated dog has multiple copies of the *AMY1* gene that codes for the starch-digesting enzyme amylase, whereas its close genetic cousin, the wolf, has only one copy (Axelsson et al. 2013).

A second exciting frontier is the potential to disrupt long-held dogmas about human nature and history. Thanks to the combination of versatile theoretical frameworks in archaeology and the powerful and relatively objective perspective that ancient genomes provide, we are in a position to contribute to thorny debates regarding humanness, race, gender, and ancestry. Anthropological genomics have already shown us that our past was a beautiful mess; different populations carry genetic mosaic pieces from thousands of ancestors, some of them originating from nonhuman populations (Gokcumen 2018). We now know that all human populations, extant and past, are a product of constant gene flow among each other. No population is genetically pure, and we

are all related in deep time. Stereotypical roles of different sexes and genders are now subject to scrutiny from archaeogenetics. A mighty Viking warrior is female (Hedenstierna-Jonson et al. 2017), questioning our biases about gender roles in Viking society. Even in well-established patrilocal communities, researchers found high-status women with no children (Mittnik et al. 2019), undermining simplistic generalizations. The myths of ethnic continuity across millennia and of bounded, biologically homogenous populations have been mostly debunked, replaced by more thoughtful discussions of diversity and intertwined histories, including those of indigenous peoples (Foster & Sharp 2002, Reardon 2009, Reardon & TallBear 2012). As genomics is related to new aspects of our collective histories, new views from archaeogenomics can provide an invaluable perspective from the past for decisions that we will inevitably have to make as a society with regard to identity, race, and what it means to be a human (Racimo et al. 2020).

Archaeogenomics has emerged as one of the most exciting intellectual endeavors of our time. As a field, it has helped spark new perspectives, razed old ones, and ignited ferocious discussions across academia and the public alike. The field itself has been criticized on multiple fronts, and the debates concerning best practice have never been more alive: Sampling strategies, power structures within the field, respect for indigenous rights, and the relationship between archaeologists and genomicists remain subject to heated and ongoing debates. We argue that this is as it should be: Archaeogenomics is the frontier, with all the promise, dangers, and imperfections that this position in academia's scientific mission brings with it.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Drs. Mehmet Somel and Radu Iovita for the discussions and suggestions. We also acknowledge the National Science Foundation (1714867) for letting us push the intellectual boundaries of genomics research in anthropology.

LITERATURE CITED

Ammerman AJ, Cavalli-Sforza LL. 2014. *The Neolithic Transition and the Genetics of Populations in Europe*. Princeton, NJ: Princeton Univ. Press

Amorim CEG, Vai S, Posth C, Modi A, Koncz I, et al. 2018. Understanding 6th-century barbarian social organization and migration through paleogenomics. *Nat. Commun.* 9:3547

Anthony DW. 1990. Migration in archeology: the baby and the bathwater. *Am. Anthropol.* 92(4):895–914

Antonio ML, Gao Z, Moots HM, Lucci M, Candilio F, et al. 2019. Ancient Rome: a genetic crossroads of Europe and the Mediterranean. *Science* 366(6466):708–14

Avise JC. 2000. *Phylogeography: The History and Formation of Species*. Cambridge, MA: Harvard Univ. Press

Axelsson E, Ratnakumar A, Arendt M-L, Maqbool K, Webster MT, et al. 2013. The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature* 495(7441):360–64

Bardill J, Bader AC, Garrison NA, Bolnick DA, Raff JA, et al. 2018. Advancing the ethics of paleogenomics. *Science* 360(6387):384–85

Bellwood P, Gamble C, Le Blanc SA, Pluciennik M, Richards M, Terrell JE. 2007. *First Farmers: the Origins of Agricultural Societies*, by Peter Bellwood. Malden (MA): Blackwell, 2005; ISBN 0-631-20565-9 hardback £60; ISBN 0-631-20566-7 paperback £17.99, xix+360 pp., 59 figs., 3 tables. *Camb. Archaeol. J.* 17(1):87–109

Blegen N. 2017. The earliest long-distance obsidian transport: evidence from the ~200 ka Middle Stone Age Sibilo School Road Site, Baringo, Kenya. *J. Hum. Evol.* 103:1–19

Bolnick DA, Fullwiley D, Duster T, Cooper RS, Fujimura JH, et al. 2007. Genetics. The science and business of genetic ancestry testing. *Science* 318(5849):399–400

Bos KI, Harkins KM, Herbig A, Coscolla M, Weber N, et al. 2014. Pre-Columbian mycobacterial genomes reveal seals as a source of New World human tuberculosis. *Nature* 514(7523):494–97

Briggs AW, Stenzel U, Johnson PLF, Green RE, Kelso J, et al. 2007. Patterns of damage in genomic DNA sequences from a Neandertal. *PNAS* 104(37):14616–21

Brodie N. 1997. New perspectives on the Bell-Beaker culture. *Oxf. J. Archaeol.* 16(3):297–314

Callaway E. 2018. Divided by DNA: the uneasy relationship between archaeology and ancient genomics. *Nature* 555:573–76

Campbell MC, Tishkoff SA. 2008. African genetic diversity: implications for human demographic history, modern human origins, and complex disease mapping. *Annu. Rev. Genomics Hum. Genet.* 9:403–33

Cann RL, Stoneking M, Wilson AC. 1987. Mitochondrial DNA and human evolution. *Nature* 325(6099):31–36

Cavalli-Sforza LL, Bodmer WF. 1999. *The Genetics of Human Populations*. Mineola, NY: Dover

Cavalli-Sforza LL, Feldman MW. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Monogr. Popul. Biol. 16. Princeton, NJ: Princeton Univ. Press

Childe VG. 1936. *Man Makes Himself*. Oxford, UK: Oxford Univ. Press

Claw KG, Anderson MZ, Begay RL, Tsosie KS, Fox K, et al. 2018. A framework for enhancing ethical genomic research with Indigenous communities. *Nat. Commun.* 9(1):2957

Cooper A, Rambaut A, Macaulay V, Willerslev E, Hansen AJ, Stringer C. 2001. Human origins and ancient human DNA. *Science* 292:1655–56

de Barros Damgaard P, Marchi N, Rasmussen S, Peyrot M, Renaud G, et al. 2018. 137 ancient human genomes from across the Eurasian steppes. *Nature* 557(7705):369–74

Dirks PH, Roberts EM, Hilbert-Wolf H, Kramers JD, Hawks J, et al. 2017. The age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa. *eLife* 6:e24231

Ensor BE. 2011. Kinship theory in archaeology: from critiques to the study of transformations. *Am. Antiq.* 76(2):203–27

Erickson C. 2003. Historical ecology and future explorations. In *Amazonian Dark Earths: Origin Properties Management*, ed. J Lehmann, DC Kern, B Glaser, WI Wodos, pp. 455–500. Dordrecht, Neth.: Springer

Erlandson JM, Rick TC. 2010. Archaeology meets marine ecology: the antiquity of maritime cultures and human impacts on marine fisheries and ecosystems. *Annu. Rev. Mar. Sci.* 2:231–51

Feldman M, Fernández-Domínguez E, Reynolds L, Baird D, Pearson J, et al. 2019. Late Pleistocene human genome suggests a local origin for the first farmers of central Anatolia. *Nat. Commun.* 10(1):1218

Foster MW, Sharp RR. 2002. Race, ethnicity, and genomics: social classifications as proxies of biological heterogeneity. *Genome Res.* 12(6):844–50

Frachetti MD. 2009. *Pastoralist Landscapes and Social Interaction in Bronze Age Eurasia*. Berkeley: Univ. Calif. Press

Frachetti MD. 2011. Migration concepts in Central Eurasian archaeology. *Annu. Rev. Anthropol.* 40:195–212

Frazer KA, Murray SS, Schork NJ, Topol EJ. 2009. Human genetic variation and its contribution to complex traits. *Nat. Rev. Genet.* 10(4):241–51

Fu Q, Mittnik A, Johnson PLF, Bos K, Lari M, et al. 2013. A revised timescale for human evolution based on ancient mitochondrial genomes. *Curr. Biol.* 23(7):553–59

Furholt M. 2018. Massive migrations? The impact of recent aDNA studies on our view of third millennium Europe. *Eur. J. Archaeol.* 21(2):159–91

Garrison NA, Hudson M, Ballantyne LL, Garba I, Martinez A, et al. 2019. Genomic research through an indigenous lens: understanding the expectations. *Annu. Rev. Genomics Hum. Genet.* 20:495–517

Goebel T, Waters MR, Dikova M. 2003. The archaeology of Ushki Lake, Kamchatka, and the Pleistocene peopling of the Americas. *Science* 301(5632):501–5

Gokcumen O. 2018. The year in genetic anthropology: new lands, new technologies, new questions. *Am. Anthropol.* 120(2):266–77

Gokcumen O. 2020. Archaic hominin introgression into modern human genomes. *Am. J. Phys. Anthropol.* 171:60–73

Gokcumen Ö, Gultekin T, Alakoc YD, Tug A, Gulec E, Schurr TG. 2011. Biological ancestries, kinship connections, and projected identities in four central Anatolian settlements: insights from culturally contextualized genetic anthropology. *Am. Anthropol.* 113(1):116–31

Grayson DK. 2001. The archaeological record of human impacts on animal populations. *J. World Prehist.* 15(1):1–68

Green RE, Krause J, Ptak SE, Briggs AW, Ronan MT, et al. 2006. Analysis of one million base pairs of Neanderthal DNA. *Nature* 444(7117):330–36

Greenberg JH, Turner CG II, Zegura SL, Campbell L, Fox JA, et al. 1986. The settlement of the Americas: a comparison of the linguistic, dental, and genetic evidence. *Curr. Anthropol.* 27(5):477–97

Guglielmi G. 2019. Facing up to injustice in genome science. *Nature* 568(7752):290–93

Haak W, Forster P, Bramanti B, Matsumura S, Brandt G, et al. 2005. Ancient DNA from the first European farmers in 7500-year-old Neolithic sites. *Science* 310(5750):1016–18

Haber M, Gauguier D, Youhanna S, Patterson N, Moorjani P, et al. 2013. Genome-wide diversity in the Levant reveals recent structuring by culture. *PLOS Genet.* 9(2):e1003316

Hedenstierna-Jonson C, Kjellström A, Zachrisson T, Krzewińska M, Sobrado V, et al. 2017. A female Viking warrior confirmed by genomics. *Am. J. Phys. Anthropol.* 164(4):853–60

Henn BM, Steele TE, Weaver TD. 2018. Clarifying distinct models of modern human origins in Africa. *Curr. Opin. Genet. Dev.* 53:148–56

Heyd V. 2017. Kossinna's smile. *Antiquity* 91(356):348–59

Ho SYW, Gilbert MTP. 2010. Ancient mitogenomics. *Mitochondrion* 10(1):1–11

Hofmanová Z, Kreutzer S, Hellenthal G, Sell C, Diekmann Y, et al. 2016. Early farmers from across Europe directly descended from Neolithic Aegeans. *PNAS* 113(25):6886–91

Horsburgh KA. 2015. Molecular anthropology: the judicial use of genetic data in archaeology. *J. Archaeol. Sci.* 56:141–45

Hsieh P, Woerner AE, Wall JD, Lachance J, Tishkoff SA, et al. 2016. Model-based analyses of whole-genome data reveal a complex evolutionary history involving archaic introgression in Central African Pygmies. *Genome Res.* 26(3):291–300

Ingram CJE, Mulcare CA, Itan Y, Thomas MG, Swallow DM. 2009. Lactose digestion and the evolutionary genetics of lactase persistence. *Hum. Genet.* 124(6):579–91

Jacobs GS, Hudjashov G, Saag L, Kusuma P, Darusallam CC, et al. 2019. Multiple deeply divergent Denisovan ancestries in Papuans. *Cell* 177(4):1010–21.e32

Jobling M, Hurles M, Tyler-Smith C. 2013. *Human Evolutionary Genetics: Origins, Peoples & Disease*. New York: Garland Sci.

Jones ER, Zarina G, Moiseyev V, Lightfoot E, Nigst PR, et al. 2017. The Neolithic transition in the Baltic was not driven by admixture with early European farmers. *Curr. Biol.* 27(4):576–82

Kılınç GM, Omrak A, Özer F, Günther T, Büyükkarakaya AM, et al. 2016. The demographic development of the first farmers in Anatolia. *Curr. Biol.* 26(19):2659–66

Krings M, Stone A, Schmitz RW, Krainitzki H, Stoneking M, Pääbo S. 1997. Neandertal DNA sequences and the origin of modern humans. *Cell* 90(1):19–30

Kristiansen K. 2014. Towards a new paradigm. The third science revolution and its possible consequences in archaeology. *Curr. Swed. Archaeol.* 22(4):11–34

Kristiansen K, Allentoft ME, Frei KM, Iversen R, Johannsen NN, et al. 2017. Re-theorising mobility and the formation of culture and language among the Corded Ware Culture in Europe. *Antiquity* 91(356):334–47

Lachance J, Tishkoff SA. 2013. SNP ascertainment bias in population genetic analyses: why it is important, and how to correct it. *Bioessays* 35(9):780–86

Laland KN, O'Brien MJ. 2010. Niche construction theory and archaeology. *J. Archaeol. Method Theory* 17(4):303–22

Lazaridis I, Nadel D, Rollefson G, Merrett DC, Rohland N, et al. 2016. Genomic insights into the origin of farming in the ancient Near East. *Nature* 536(7617):419–24

Lazaridis I, Patterson N, Mittnik A, Renaud G, Mallick S, et al. 2014. Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* 513(7518):409–13

Llamas B, Fehren-Schmitz L, Valverde G, Soubrier J, Mallick S, et al. 2016. Ancient mitochondrial DNA provides high-resolution time scale of the peopling of the Americas. *Sci. Adv.* 2(4):e1501385

Luo S, Valencia CA, Zhang J, Lee N-C, Slone J, et al. 2018. Biparental inheritance of mitochondrial DNA in humans. *PNAS* 115(51):13039–44

Malaspinas A-S, Westaway MC, Muller C, Sousa VC, Lao O, et al. 2016. A genomic history of Aboriginal Australia. *Nature* 538(7624):207–14

Mallick S, Li H, Lipson M, Mathieson I, Gymrek M, et al. 2016. The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature* 538(7624):201–6

Manica A, Prugnolle F, Balloux F. 2005. Geography is a better determinant of human genetic differentiation than ethnicity. *Hum. Genet.* 118(3–4):366–71

Marciniak S, Perry GH. 2017. Harnessing ancient genomes to study the history of human adaptation. *Nat. Rev. Genet.* 18(11):659–74

Marshall E. 1998. DNA studies challenge the meaning of race. *Science* 282(5389):654–55

Mcbrearty S, Brooks AS. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39(5):453–563

McGovern TH, Vésteinsson O, Fridriksson A, Church M, Lawson I, et al. 2007. Landscapes of settlement in Northern Iceland: historical ecology of human impact and climate fluctuation on the millennial scale. *Am. Anthropol.* 109(1):27–51

Millar CD, Huynen L, Subramanian S, Mohandesan E, Lambert DM. 2008. New developments in ancient genomics. *Trends Ecol. Evol.* 23(7):386–93

Mittnik A, Massy K, Knipper C, Wittenborn F, Friedrich R, et al. 2019. Kinship-based social inequality in Bronze Age Europe. *Science* 366(6466):731–34

Moreno-Mayar JV, Potter BA, Vinner L, Steinrücken M, Rasmussen S, et al. 2018. Terminal Pleistocene Alaskan genome reveals first founding population of Native Americans. *Nature* 553(7687):203–7

Narasimhan VM, Patterson N, Moorjani P, Rohland N, Bernardos R, et al. 2019. The formation of human populations in South and Central Asia. *Science* 365(6457):eaat7487

Nielsen R, Akey JM, Jakobsson M, Pritchard JK, Tishkoff S, Willerslev E. 2017. Tracing the peopling of the world through genomics. *Nature* 541(7637):302–10

Novembre J, Johnson T, Bryc K, Kutalik Z, Boyko AR, et al. 2008. Genes mirror geography within Europe. *Nature* 456(7218):98–101

Novembre J, Peter BM. 2016. Recent advances in the study of fine-scale population structure in humans. *Curr. Opin. Genet. Dev.* 41:98–105

Olalde I, Brace S, Allentoft ME, Armit I, Kristiansen K, et al. 2018. The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature* 555(7695):190–96

Omrak A, Günther T, Valdiosera C, Svensson EM, Malmström H, et al. 2016. Genomic evidence establishes Anatolia as the source of the European Neolithic gene pool. *Curr. Biol.* 26(2):270–75

O'Sullivan N, Posth C, Coia V, Schuenemann VJ, Price TD, et al. 2018. Ancient genome-wide analyses infer kinship structure in an Early Medieval Alemannic graveyard. *Sci. Adv.* 4(9):eaao1262

Pajic P, Pavlidis P, Dean K, Neznanova L, Romano R-A, et al. 2019. Independent amylase gene copy number bursts correlate with dietary preferences in mammals. *eLife* 8:e44628

Pakendorf B, Stoneking M. 2005. Mitochondrial DNA and human evolution. *Annu. Rev. Genomics Hum. Genet.* 6:165–83

Perry GH, Dominy NJ, Claw KG, Lee AS, Fiegler H, et al. 2007. Diet and the evolution of human amylase gene copy number variation. *Nat. Genet.* 39(10):1256–60

Peter BM, Petkova D, Novembre J. 2020. Genetic landscapes reveal how human genetic diversity aligns with geography. *Mol. Biol. Evol.* 37:943–51

Phillips N. 2019. Indigenous groups look to ancient DNA to bring their ancestors home. *Nature News* 568:294–97

Pinhasi R, Fort J, Ammerman AJ. 2005. Tracing the origin and spread of agriculture in Europe. *PLOS Biol.* 3(12):e410

Posth C, Wißing C, Kitagawa K, Pagani L, van Holstein L, et al. 2017. Deeply divergent archaic mitochondrial genome provides lower time boundary for African gene flow into Neanderthals. *Nat. Commun.* 8:16046

Premo LS, Hublin J-J. 2009. Culture, population structure, and low genetic diversity in Pleistocene hominins. *PNAS* 106(1):33–37

Prüfer K, Racimo F, Patterson N, Jay F, Sankararaman S, et al. 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* 505(7481):43–49

Racimo F, Sikora M, Vander Linden M, Schroeder H, Lalueza-Fox C. 2020. Beyond broad strokes: sociocultural insights from the study of ancient genomes. *Nat. Rev. Genet.* 21:355–66

Rasmussen M, Li Y, Lindgreen S, Pedersen JS, Albrechtsen A, et al. 2010. Ancient human genome sequence of an extinct Palaeo-Eskimo. *Nature* 463(7282):757–62

Rasmussen M, Sikora M, Albrechtsen A, Korneliussen TS, Moreno-Mayar JV, et al. 2015. The ancestry and affiliations of Kennewick Man. *Nature* 523(7561):455–58

Reardon J. 2009. *Race to the Finish: Identity and Governance in an Age of Genomics*. Princeton, NJ: Princeton Univ. Press

Reardon J, TallBear K. 2012. "Your DNA is *our* history": genomics, anthropology, and the construction of whiteness as property. *Curr. Anthropol.* 53(S5):S233–45

Reich D. 2018. *Who We Are and How We Got Here: Ancient DNA and the New Science of the Human Past*. Oxford, UK: Oxford Univ. Press

Reich D, Green RE, Kircher M, Krause J, Patterson N, et al. 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* 468(7327):1053–60

Renfrew C. 1990. *Archaeology and Language: The Puzzle of Indo-European Origins*. Cambridge, UK: Cambridge Univ. Press Archive

Renfrew C. 2001. From molecular genetics to archaeogenetics. *PNAS* 98:4830–32

Richards M, Macaulay V, Torroni A, Bandelt H-J. 2002. In search of geographical patterns in European mitochondrial DNA. *Am. J. Hum. Genet.* 71(5):1168–74

Robb JE. 1998. The archaeology of symbols. *Annu. Rev. Anthropol.* 27:329–46

Royal CD, Novembre J, Fullerton SM, Goldstein DB, Long JC, et al. 2010. Inferring genetic ancestry: opportunities, challenges, and implications. *Am. J. Hum. Genet.* 86(5):661–73

Rutherford A. 2018. *A Brief History of Everyone Who Ever Lived: The Human Story Retold Through Our Genes*. New York: Experiment

Sawchuk E, Prendergast M. 2019. In the study of ancient DNA, a call for collaboration. *Undark*, March 12. **https://undark.org/2019/03/12/ancient-dna-ethics/**

Scerri EML, Thomas MG, Manica A, Gunz P, Stock JT, et al. 2018. Did our species evolve in subdivided populations across Africa, and why does it matter? *Trends Ecol. Evol.* 33(8):582–94

Scheib CL, Li H, Desai T, Link V, Kendall C, et al. 2018. Ancient human parallel lineages within North America contributed to a coastal expansion. *Science* 360(6392):1024–27

Schlebusch CM, Malmström H, Günther T, Sjödin P, Coutinho A, et al. 2017. Southern African ancient genomes estimate modern human divergence to 350,000 to 260,000 years ago. *Science* 358:652–55

Schuenemann VJ, Peltzer A, Welte B, van Pelt WP, Molak M, et al. 2017. Ancient Egyptian mummy genomes suggest an increase of Sub-Saharan African ancestry in post-Roman periods. *Nat. Commun.* 8:15694

Shinde V, Narasimhan VM, Rohland N, Mallick S, Mah M, et al. 2019. An ancient Harappan genome lacks ancestry from steppe pastoralists or Iranian farmers. *Cell* 179(3):729–35.e10

Simoni L, Calafell F, Pettener D, Bertranpetit J, Barbujani G. 2000. Geographic patterns of mtDNA diversity in Europe. *Am. J. Hum. Genet.* 66(1):262–78

Skoglund P, Mallick S, Bortolini MC, Chennagiri N, Hünemeier T, et al. 2015. Genetic evidence for two founding populations of the Americas. *Nature* 525(7567):104–8

Skoglund P, Mathieson I. 2018. Ancient genomics of modern humans: the first decade. *Annu. Rev. Genomics Hum. Genet.* 19:381–404

Skoglund P, Thompson JC, Prendergast ME, Mittnik A, Sirak K, et al. 2017. Reconstructing prehistoric African population structure. *Cell* 171(1):59–71.e21

Somel M, Kilinc GM, Ozer F, Omrak A, Yaka R, et al. 2016. Archaeogenomic analysis of ancient Anatolians: first genetic indication for Neolithic cultural diffusion in the Near East. *Am. J. Phys. Anthropol.* 159:297–98

Spyrou MA, Bos KI, Herbig A, Krause J. 2019. Ancient pathogen genomics as an emerging tool for infectious disease research. *Nat. Rev. Genet.* 20(6):323–40

Stringer C. 2002. Modern human origins: progress and prospects. *Philos. Trans. R. Soc. B* 357(1420):563–79
Taskent O, Lin YL, Patramanis I, Pavlidis P, Gokcumen O. 2020. Analysis of haplotypic variation and deletion polymorphisms point to multiple archaic introgression events, including from Altai Neanderthal lineage. *Genetics* 215:497–509
Tishkoff SA, Reed FA, Friedlaender FR, Ehret C, Ranciaro A, et al. 2009. The genetic structure and history of Africans and African Americans. *Science* 324(5930):1035–44
Tishkoff SA, Reed FA, Ranciaro A, Voight BF, Babbitt CC, et al. 2007. Convergent adaptation of human lactase persistence in Africa and Europe. *Nat. Genet.* 39(1):31–40
Torroni A, Achilli A, Macaulay V, Richards M, Bandelt H-J. 2006. Harvesting the fruit of the human mtDNA tree. *Trends Genet*. 22(6):339–45
Torroni A, Schurr TG, Cabell MF, Brown MD, Neel JV, et al. 1993. Asian affinities and continental radiation of the four founding Native American mtDNAs. *Am. J. Hum. Genet.* 53(3):563–90
Trigger BG. 1989. *A History of Archaeological Thought*. Cambridge, UK: Cambridge Univ. Press
Van Arsdale AP. 2019. Population demography, ancestry, and the biological concept of race. *Annu. Rev. Anthropol.* 48:227–41
Vander Linden M. 2007. What linked the Bell Beakers in third millennium BC Europe? *Antiquity* 81(312):343–52
Vander Linden M. 2016. Population history in third-millennium-BC Europe: assessing the contribution of genetics. *World Archaeol*. 48(5):714–28
Varki A, Geschwind DH, Eichler EE. 2008. Human uniqueness: genome interactions with environment, behaviour and culture. *Nat. Rev. Genet.* 9(10):749–63
Veeramah KR. 2018. The importance of fine-scale studies for integrating paleogenomics and archaeology. *Curr. Opin. Genet. Dev.* 53:83–89
Veeramah KR, Hammer MF. 2014. The impact of whole-genome sequencing on the reconstruction of human population history. *Nat. Rev. Genet.* 15(3):149–62
Vernot B, Tucci S, Kelso J, Schraiber JG, Wolf AB, et al. 2016. Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals. *Science* 352(6282):235–39
Wallerstein I. 1997. Eurocentrism and its avatars: the dilemmas of social science. *Sociol. Bull.* 46(1):21–39
Wolf AB, Akey JM. 2018. Outstanding questions in the study of archaic hominin admixture. *PLOS Genet*. 14(5):e1007349
Wright JL, Wasef S, Heupink TH, Westaway MC, Rasmussen S, et al. 2018. Ancient nuclear genomes enable repatriation of Indigenous human remains. *Sci. Adv.* 4(12):eaau5064
Xu D, Pavlidis P, Taskent RO, Alachiotis N, Flanagan C, et al. 2017. Archaic hominin introgression in Africa contributes to functional salivary MUC7 genetic variation. *Mol. Biol. Evol.* 34(10):2704–15