

Leveraging the power of ancient DNA through archaeology

Niels N. Johannsen,¹ Greger Larson,² David J. Meltzer,³ Marc Vander Linden⁴

Over the past decade, the ability to recover whole genomes from ancient remains (aDNA) has emerged as a powerful tool for understanding the human past. From a strictly biological perspective, the sequencing of ancient genomes has resolved the dispute over our evolutionary relationship with Neanderthals, revealed the extent of gene flow within and between modern and archaic humans, shed light on genetic and health consequences, and uncovered genomic changes in recent human evolution (¹). More generally, these insights have demonstrated that our population history is marked by complex, actively combining and diverging channels, replete with demographic bottlenecks and bursts (²), proving that moving and mating have been more the rule than the exception. For all this, aDNA research has rightly been described as revolutionary, even a ‘celebrity science’ (³).

The possible benefits of aDNA research for archaeology, which is limited in its ability to identify and measure past populations, are in principle enormous. Why, then, have aDNA approaches to archaeological questions occasionally raised eyebrows among archaeologists (^{4,5})?

Most obviously, there is far more to human history than our biology, especially over the last ~100,000 years as culture has played an increasingly dominant role in human evolution. Many of archaeology’s ‘grand challenges’ (⁶) concern our understanding of human cultures and cultural change. Although aDNA can contribute to addressing these challenges, this potential has yet to be fully realized.

The principal obstacles are fourfold: the problem of scale; the challenge of aligning different analytical units; the difficulty of discerning causal connections between population and cultural changes; and, the frequent lack of genuine collaboration between different fields that compounds the first three.

Integration of aDNA and archaeology is arguably least complicated at the smallest spatial scale. aDNA analyses of individuals found at single archaeological sites, bolstered by high-resolution radiocarbon chronologies and careful attention to archaeological context have successfully documented detailed genealogies revealing previously unseen hereditary relationships, and elements of social structure and political hierarchy (⁷).

However, aDNA research has to a significant extent been driven by studies addressing questions at much broader scales. These studies seek to study demographic processes of migration, admixture, and population turnover(⁸), and their effects on culture(s) across regions and through time. aDNA studies revealing ancestral affinities and demographic structure are valuable in ascertaining population origins and movements into continents and regions devoid of people (e.g. Australia, the Americas, islands of the Pacific) (^{9,10,11}) as well as dispersals across already-occupied landscapes (e.g. in the last 10,000 years in Africa and Europe) (^{12,13,14}). But the ability to see broad spatio-temporal patterns in populations is limited by the inability to link those patterns to specific changes seen archaeologically in, for example, economic adaptations or material culture, or to the natural and social environments in which these took place (⁵).

A central problem in this regard is the methodological challenge of aligning very different types of evidence. On the one hand, past populations identified by ancient genomes are biological units whose

¹ Department of Archaeology, Aarhus University, Aarhus, Denmark 8270 Højbjerg

² Palaeogenomics & Bio-Archaeology Research Network, Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, United Kingdom, OX1 3QY

³ Department of Anthropology, Southern Methodist University, Dallas, Texas, USA, 75275

⁴ Institute of Archaeology, University College London, Gordon Square, London, United Kingdom, WC1H 0PY

members were related by degrees that can be precisely measured. That said, those populations can be complex entities cross-cut by differences in class, religion, language and culture that may (or may not) limit mating and gene flow. On the other hand, archaeological cultures are classificatory labels for materially-defined entities, which can vary widely over space and time, and even within cultural units (^{4,5}). We cannot assume individuals who shared material culture traits were part of the same biological population: one can have similar traits without relatedness (owing to convergence or exchange) and relatedness without similarity in traits (divergence). And there is no commonly accepted measure of cultural relatedness, equivalent to the geneticist's composite measure of biological relatedness. The same caution applies to language groups, which are not necessarily isomorphic with biological populations, material assemblages or even social units (¹⁵). Unfortunately, geneticists who venture across disciplinary borders without local guides, too often treat these classificatory units as analytically comparable and coincident in scale. They are not (^{4,5}).

Geneticists are often keen to apply aDNA to understand the causes and mechanisms of demographic and cultural change. But archaeologists long ago abandoned the idea that migrations or encounters between populations are a necessary or sufficient explanation for cultural change (¹⁶). aDNA evidence of admixture, perhaps even migration, is important not because it provides an explanation for cultural change, but because it provokes additional, more significant questions, including: what processes may have triggered movements of people, how did these unfold, and what were the broader social and economic (not just biological) consequences for the populations involved.

Consider the Neolithic of western Eurasia, which has seen the greatest amount of aDNA research to date (⁸). For the 6th millennium BCE in southeastern and central Europe, aDNA evidence has confirmed the occurrence of large-scale population movements involving entire social groups that brought a package of early farming culture, but that only admixed with local foraging populations to a limited extent (^{17,18,19}). In contrast, the introduction of new genes from central Eurasia to Europe during the 3rd millennium BCE unfolded in a markedly different way. This migration, more restricted in time and space, was possibly sex-biased towards males, resulting in high, changing levels of admixture with local populations (^{13,22}). In this case, dispersal happened independently of any general economic transformation, and cultural changes were not homogeneous across regions (⁴).

Here, aDNA evidence has pointed to a previously-unknown diversity and interplay of demographic factors shaping specific episodes of human expansion. Yet, understanding the causes and consequences of these population movements requires a broader investigation of the many factors that may have played a role. These considerations would include the environmental and social contexts in which expansion occurred; the details of its timing and logistics; how new resources and landscapes were managed and cultural knowledge was transmitted. Hence, it requires evidence from archaeology, paleoecology, and other fields to supplement and complement aDNA data – and that entails effective collaboration (²⁰), one that goes beyond archaeologists serving as passive sample providers.

Fully integrated collaborations have not routinely characterized aDNA studies to date. This situation was perhaps understandable given the dynamics in a comparatively young, competitive, and high-prestige field passing through an inductive, 'golden sample' phase (²⁰) where virtually every specimen revealed facets of heretofore unknown populations. That phase is waning, and simply creating ever more-refined estimates of, say, population admixture (¹⁴), is reaching the point of diminishing returns.

Given the explanatory power of an integrated approach, we believe now is the time for a deeper, more sustained collaboration between geneticists and archaeologists. aDNA is a valuable addition to the interdisciplinary toolbox for studying past human societies, though this research can neither be sample driven nor done in analytical isolation. Instead, an approach that produces hypotheses tested through analyses and comprehensive integration of multiple lines of evidence, including aDNA, will result in far more robust and long-lasting conclusions.

And collaboration goes beyond academia. The archaeological record is a finite, common resource, and we must always aim to maximize information yields when we sample it. In addition, analyses of

ancient human remains are enhanced through systematic collaboration with descendant communities who are stakeholders in the outcome ⁽²¹⁾. Moreover, aDNA research produces data that are easily politicized ⁽²²⁾. Although we cannot control misuse of evidence, it behooves us to make that evidence as robust and comprehensive as possible to minimize the possibility of misappropriation. Not only are the days of the ‘golden sample’ ending, the fact that human history is a story of dispersal and admixture is not revelatory. We have an opportunity to jointly explore human history more deeply, and we should make the most of it.

Acknowledgements: The authors are grateful to C. Gosden, D.K. Grayson, T. O'Connell, R. Nielsen, D. Russell and two anonymous reviewers for comments on an earlier version of this manuscript.

-
- ¹ R. Nielsen *et al.*, Tracing the peopling of the world through genomics. *Nature* **541**, 302-310 (2017)
 - ² M. Haber *et al.*, Ancient DNA and the rewriting of human history: be sparing with Occam's razor. *Genome Biology* **17**, DOI: 10.1186/s13059-015-0866-z (2016).
 - ³ E. Callaway, Ancient DNA and the rise of ‘celebrity science.’ *Nature.com blog*, 4 April 2017 <http://blogs.nature.com/aviewfromthebridge/2017/04/04/celebrity-science/>
 - ⁴ M. Vander Linden, Population history in third-millennium BC Europe: assessing the contribution of genetics. *World Archaeology* DOI: 10.1080/00438243.2016.1209124 (2016).
 - ⁵ S. MacEachern, Genetics and archaeology. In *The Oxford Handbook of African Archaeology*, P. Mitchell and P. Lane editors. Oxford University Press, Oxford, 65-76 (2013).
 - ⁶ K. Kintigh *et al.* Grand challenges for archaeology. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 879–880 (2014).
 - ⁷ D. Kennett *et al.*, Archaeogenomic evidence reveals prehistoric matrilineal dynasty. *Nature Communications* 2017 <http://dx.doi.org/10.1038/ncomms14115>.
 - ⁸ M. Slatkin, F. Racimo, Ancient DNA and human history. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6380-6387 (2016).
 - ⁹ A. Malaspinas *et al.* (2016) A genomic history of Aboriginal Australia. *Nature* **538**, 207-214
 - ¹⁰ M. Raghavan *et al.* Genomic evidence for the Pleistocene and Recent population history of Native Americans. *Science* 349:841, aab3884-1-aab3884-10 (2015)
 - ¹¹ E. Matisoo-Smith, Ancient DNA and the human settlement of the Pacific: a review. *Journal of Human Evolution* **79**, 93-104 (2015)
 - ¹² W. Haak *et al.*, Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207-211 (2015).
 - ¹³ M. Allentoft *et al.*, Population genomics of Bronze Age Eurasia. *Nature* **522**, 167-172 (2015).
 - ¹⁴ I. Lazaridis *et al.*, Genomic insights into the origins of farming in the ancient Near East. *Nature* **536**, 419-424 (2016).
 - ¹⁵ D. Hymes, Linguistic problems in defining the concept of ‘tribe.’ In *Essays on the problem of tribe*, J. Helm, editor. University of Washington Press, Seattle., 23-48 (1968).
 - ¹⁶ L. Binford, Some comments on historical versus processual archaeology. *Southwestern Journal of Anthropology* **24**, 267-275 (1968).
 - ¹⁷ A. Goldberg *et al.*, Ancient X chromosomes reveal contrasting sex bias in Neolithic and Bronze Age Eurasian migrations. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 2657-2662 (2017).
 - ¹⁸ S. Pilaar Birch and M. Vander Linden, A long hard road... Reviewing the evidence for environmental change and population history in the eastern Adriatic and western Balkans during the

Late Pleistocene and Early Holocene. *Quaternary International*. DOI:10.1016/j.quaint.2016.12.035. (2017).

¹⁹ G. Larson et al., Current perspectives and the future of domestication studies. *Proc. Natl. Acad. Sci. U.S.A.* **111**: 6139–6146 (2014).

²⁰ J.D. Pickrell, J. D. Reich, Toward a new history and geography of human genes informed by ancient DNA. *Trends in Genetics* **30**, 377-389 (2014).

²¹ D. Bolnick et al., Native American Genomics and Population Histories. *Annual Review of Anthropology* **45**, 319-340 (2016)

²² S. MacEachern, (2015). African models in global histories. In *Theory in Africa, Africa in history: locating meaning in archaeology*, S. Wynne-Jones S. & Fleisher, J. editors. Routledge, London, 65-76 (2015).