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Kendra A. Sirak & Jakob W. Sedig

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Balancing analytical goals and anthropological stewardship in the midst of the paleogenomics revolution

Kendra A. Sirak * and Jakob W. Sedig * *

Department of Genetics, Harvard Medical School, Boston, MA, USA

ABSTRACT

Ancient DNA research is on a trajectory of rapid growth and is becoming an increasingly important part of the archaeologist's toolkit. In this paper, we situate the current relationship between ancient DNA and archaeology within the context of how other destructive scientific methods were incorporated into archaeological work. We discuss the need for discipline-wide standards for the destructive sampling of human remains for ancient DNA analysis and propose a set of best practices to aid collaborative teams in the challenging task of balancing the rich information provided by ancient DNA with the damage that sampling will cause to a skeletal specimen. Collaboration between archaeologists and ancient DNA specialists has contributed in new ways to the understanding of the human past, and the relationship between the researchers embedded in these disciplines will continue to develop and mature only through ongoing dialogue and engaged collaboration on topics such as destructive analysis.

KEYWORDS

Ancient DNA analysis; best practices; archaeogenetics

Introduction

Archaeologists and biological anthropologists face a unique challenge: they must weigh the cost of destroying the remains of our human ancestors against the potential benefit of scientific discovery (Scarre 2006). While the incorporation of radiocarbon dating and molecular techniques in archaeology brought this issue into greater focus in recent decades, the unprecedented growth of ancient DNA analyses, particularly within the last several years, has revived discussions surrounding the use of human remains for scientific analysis. Concerns have been articulated about the sustainability and ethics of current practices (Makarewicz, Marom, and Bar-Oz 2017), and pressing issues, including the destruction of cultural heritage, have been identified. The current absence of discipline-wide standards has left a range of stakeholders – from museum curators to archaeologists to potential descendants - to grapple with the intricacies of granting permission for destructive work on a case-by-case basis (Prendergast and Sawchuk 2018).

While many collaborations between archaeologists and ancient DNA specialists have been seen as positive, there is a need to further mature the relationship between these fields through increased dialogue and engaged collaborations (e.g., Bardill et al. 2018; Callaway 2018; Eisenmann et al. 2018; Prendergast and Sawchuk 2018; Veeramah 2018). In this paper, we review the development of ancient



DNA research, examine the relationship between archaeology and scientific techniques (particularly radiocarbon dating), and outline a set of best practices for collaborative ancient DNA analysis that requires the destruction of human skeletal remains. We draw upon our unique perspectives as a biological anthropologist and archaeologist embedded in an ancient DNA laboratory to address some of the concerns that archaeologists have voiced regarding ancient DNA practices, and we explain why these practices often seem foreign to archaeologists.

A brief history of ancient DNA

Ancient DNA research began in 1984 when 229 base pairs (bp) of mitochondrial DNA (mtDNA) were extracted and sequenced from an Equus quagga quagga museum specimen (Higuchi et al. 1984). Reporting their findings, the authors conclude with a prophetic statement: 'If the long-term survival of DNA proves to be a general phenomenon, several fields including palaeontology, evolutionary biology, archaeology, and forensic science may benefit' (Higuchi et al. 1984, 284). Thirty years later, approximately 19.4 Giga-basepairs (Gb) of quagga DNA were sequenced (Jónsson et al. 2014), representing an 85 million-fold increase in data, fulfilling Higuchi's prophecy, and demonstrating the massive advances made in ancient DNA research in only three decades.

The earliest days of ancient DNA research saw the use of plasmid vectors to amplify small DNA sequences (Pääbo 1985; Pääbo, Higuchi, and Wilson 1989), and the challenges that the field would face were soon made clear. Genetic material from ancient specimens was overwhelmingly microbial or fungal in origin, while endogenous DNA was limited to low concentrations of short fragments altered by post-mortem modifications. While the invention of the Polymerase Chain Reaction (PCR) (Mullis et al. 1986) allowed for the amplification of targeted DNA fragments and represented a step forward for ancient DNA research, it also increased sensitivity to contamination from modern DNA, and a number of studies reflected false-positive results (e.g., Golenberg 1991; Zischler et al. 1995). An effort has since been made to expand upon and fine-tune an initial three criteria of authenticity proposed by Pääbo, Higuchi, and Wilson (1989), leading to the development of techniques to detect and minimize contamination and use the characteristic degradation patterns of ancient DNA to assess ancient DNA authenticity (e.g., Cooper and Poinar 2000; Hofreiter et al. 2001; Poinar 2003; Pääbo et al. 2004; Briggs et al. 2007; Sawyer et al. 2012; Skoglund et al. 2014; Llamas et al. 2017).

The last decade of ancient DNA research has been characterized by a shift from sequencing the multicopy mitochondrial genome to the study of genome-wide data from ancient individuals, also known as paleogenomics (Orlando, Gilbert, and Willerslev 2015; Leonardi et al. 2016). This shift was largely driven by the development of next-generation sequencing (NGS) technologies (Margulies et al. 2005), which allow the simultaneous sequencing of millions of DNA fragments, reducing the time, cost, and amount of raw biological material needed to produce genetic data. The ability to generate massive amounts of data has also been the impetus behind a move from identifying a single well-preserved archaeological sample that yields useable DNA and obtaining a partial or complete genome sequence from it (e.g., Rasmussen et al. 2010, which reported the first genomewide data from an ancient human), to an approach that explores genomic identity and change across large reaches of space and time and requires the analysis of ever-larger sample sizes (e.g., Allentoft et al. 2015; Mathieson et al. 2015, 2018; Damgaard et al. 2018a, 2018b; Olalde et al. 2018). This increase in sample size is a transformative one for archaeology; it is a noteworthy move from only a few years back where a single human sample of significant scientific interest was more

often the focus of ancient DNA research. With the technology now available, it is possible to ask and answer much more meaningful questions about the past.

We are now faced with an unprecedented and rapidly-moving situation that is governed by no clear set of rules. As ancient DNA research expands to new regions of the world and attempts to reveal the genetic landscape of the deeper past, more human skeletal material will be used. Adding complexity to this situation is not only the increased emphasis on large sample sizes (some recent publications have included hundreds of ancient individuals) but also that a cortical bone sample with low morphological value is no longer considered to be 'ideal' material for ancient DNA analysis.

Recent research has shown that the petrous portion of the temporal bone, and specifically the cochlea of the osseous inner ear housed inside the petrous, can provide up to 100x more endogenous human DNA per unit of bone powder than other skeletal elements (Gamba et al. 2014; Pinhasi et al. 2015). While tooth roots, and particularly the layer of cementum covering the roots, have also been shown to be an optimal substrate for ancient DNA analysis – for example, Hansen et al. (2017) identify significantly higher endogenous DNA recovery for teeth than parietal bone - the petrous is still the most targeted skeletal element for ancient DNA analysis. This has troubled some anthropologists who have highlighted the fact that it is also a particularly informative skeletal element for morphological analysis (Ponce de León et al. 2018; Trinkaus 2018). Yet ancient DNA research shows no signs of slowing down, and archaeologists are now faced with another ground-breaking technique that is looking for access to a precious resource in order to investigate humanity's past.

Destructive analysis in archaeology: an example from radiocarbon dating

Archaeologists have conducted destructive analyses of human skeletal material to acquire scientific data since at least the inception of radiocarbon dating almost 70 years ago. As with ancient DNA, some archaeologists were initially hesitant to fully incorporate radiocarbon analyses into their work (Pollard and Bray 2007). While these early analyses provided crucial archaeological data in the form of absolute dates, many archaeologists were uncertain about the value of radiocarbon dating, not because it destroyed samples, but because the technique disrupted how archaeology was practised, from chronology-building to theory-building (Taylor 1997).

Prior to the advent of accelerator mass spectrometry (AMS), bone (human and non-human) was not viewed as an 'ideal' candidate for radiocarbon dating (Taylor 1992, 376). The development of AMS 'revolutionized' radiocarbon dating (Bronk Ramsey 2008) and, along with pre-treatment procedures, made human bone a much more viable candidate for dating. While only 200 mg (or less) of bone material is needed for AMS dating, the success and wide application of the technique have paradoxically increased the amount of human bone damaged for analytical purposes. Archaeologists quickly warmed to the idea of using human bone for dating purposes, possibly because a variety of skeletal elements were shown to be equally successful. For example, small fragments of cortical bone with low morphological value could be selected for radiocarbon dating, leaving skeletal elements with anthropologically important features untouched.

Radiocarbon dating is now unquestionably an essential part of an archaeologist's toolkit. The practice of applying these destructive methods to human bone with the end goal of obtaining radiocarbon dates is now common practice and indeed is seen as essential to many serious publications. Archaeologists, artefact repositories, and government agencies do not automatically approve requests for radiocarbon dating, however, and are careful to balance the benefits that come from this type of destructive analysis against the loss of material, as demonstrated by statements of best practice, such as that promulgated by the United States National Park Service:

Federal collections are subject to provisions under 36 CFR 79, which stipulate that 'The federal agency official shall not allow uses that would alter, damage, or destroy an object in a collection unless... such use is necessary for scientific studies or public interpretation and the potential gain... outweighs the potential loss of the object.'

(https://www.nps.gov/archeology/collections/coll_05.htm).

While many museums, repositories, or governing bodies curating bones have their own criteria for giving permits for destructive analysis (though some do not, further emphasizing the need for a standard set of best practices), the large number of published studies involving radiocarbon dating of human remains demonstrates that archaeologists and repositories frequently decide that the potential value of the information acquired through this analysis outweighs the destructive impact on skeletal assemblages. Increasingly though, and especially in North America (and other places with well-defined legislation surrounding descendance), decisions to pursue destructive analysis may hinge on the cultural affiliation of skeletal remains. While archaeologists and artefact repositories may feel that the data gained far outweigh the loss of 100 mg of bone material, the destruction of even small amounts of bone may still be viewed as a profound loss in communities that see themselves as descended from the population whose remains are being analysed. We therefore advocate that in all ancient DNA studies involving such material, researchers identify whether any associated indigenous, descendent, or guardian communities can be identified, fully consider the impact of their research on these communities, and engage with these communities throughout the course of their research project (e.g. Bardill et al. 2018; Grealy et al. 2016).

Whether or not indigenous communities are involved, researchers are called upon to treat human skeletal material with respect (for details on the behaviours that constitute respectful treatment of human remains, see the 1989 World Archaeological Congress Vermillion Accord), which includes being as minimally impactful as possible. It now seems more necessary than ever to directly address a pressing question: How far are we from a standard framework governing the destruction of human skeletal remains for ancient DNA? There is currently no universally accepted framework, although an effort to develop discipline-wide standards was recently initiated (Prendergast and Sawchuk 2018). These standards are not consistently applied at present, however, and further discussion is needed. Here, in the hope of stimulating dialogue among archaeologists and geneticists, we suggest a set of best practices surrounding destructive sampling techniques for ancient DNA analysis.

Sampling for ancient DNA: best practices

It is the responsibility of all involved stakeholders to balance analytical goals with the damage that sampling for ancient DNA will cause to a skeletal specimen. This should involve determining whether ancient DNA can contribute to the resolution of clearly defined research questions, determining the best method for sampling, and evaluating whether the genomic data obtained justifies the destruction of some part of a skeletal specimen. Prendergast and Sawchuk (2018) provide a comprehensive guide for developing an ancient DNA research program that maximizes success in terms of scientific outcome and collaborative engagement while minimizing loss to institutional collections of human skeletal material. We expand upon several of these ideas



pertaining directly to the selection of skeletal material for analysis and discuss specifically a set of best practices surrounding the use of the petrous for ancient DNA analysis.

1. Identify the research questions that will be addressed with paleogenomic data to determine the number of samples that are needed to meaningfully contribute to the resolution of these questions.

As has been noted elsewhere (Furholt 2018; Johannsen et al. 2017; Klejn et al. 2017; Piscitelli 2019; Sedig 2019), some of the most highly cited and publicized ancient DNA studies focus on reconstructing large-scale human migration events or instances of ancient population interactions and admixture (e.g., Olalde et al. 2018; Posth et al. 2018). In contrast, archaeological studies more often focus on the detailed study of a particular time, place, or group of people of which the archaeologist has intimate knowledge. In this sense, geneticists and archaeologists are occupying different spheres; however, these spheres overlap substantially, and we believe it possible for both parties to achieve a mutual understanding through engaged conversation and the identification of a unified research strategy.

A notable issue in this context is that addressing many of the types of questions of high interest to archaeologists (for example, familial relatedness patterns across cemeteries) often requires larger sample sizes from particular contexts than geneticists typically request. This is because the analysis of genome-wide data effectively allows for the exploration of thousands of an individual's ancestors, making large sample sizes unnecessary for population genetics work. This may be in contrast to a situation with which an archaeologist is more familiar, where many dozens of samples must be studied to recover data pertaining to questions of social organization and concepts of identity for which population-wide genetic data is often not necessary (Piscitelli 2019; Jakob.W 2019). We have witnessed instances where there has been a negotiation between archaeologists wishing to study larger numbers of samples from sites whose ancestry is already well understood, and geneticists who do not need to study more samples from these sites for the purposes of characterizing ancestry. If the combined goals of all participating parties were agreed upon beforehand, these different expectations could be resolved.

We therefore suggest that, before engaging in any destructive sampling, collaborating teams of archaeologists and geneticists have conversations that determine the scale of focus of the proposed analysis (e.g., a site-specific study, a region-specific study, a time-transect), appreciating that all scales of analysis are necessary pieces of a more comprehensive understanding of the past, and recognizing that the actual results of analysis may differ from expectations. This collaborative group should agree upon clearly defined research questions to be investigated with ancient DNA.

A strategy which includes the number of individuals to be sampled from each archaeological context should be developed prior to the commencement of sampling. The number of individuals selected should be large enough to contribute to the resolution of relevant research questions, but not so large that it generates data that does not make a meaningful contribution to the predetermined questions of interest. Relevant (or potentially relevant) geographical and chronological windows should be considered. Most importantly, all members of the collaboration should agree upon the sampling strategy prior to the collection of samples.

To minimize the impact of destructive sampling on collections, analysing the majority of individuals from a single archaeological context should be avoided unless a specific previously defined research question requires this approach or unless the number of individuals from that broad archaeological context is so limited that each sample will make an important contribution to understanding ancestry. In this context, it is crucial to remember that a small subset of samples can often provide profoundly rich information regarding population history. Yet, as

mentioned above, such an approach should be balanced appropriately to meet the research goals of project collaborators and ensure that generated data will relevant to both geneticists and archaeologists.

2. Be realistic about the likelihood of analytical success and consider how results will be disseminated.

While a crude estimate of macroscopic preservation made prior to sampling often correlates with molecular preservation (Hansen et al. 2017), there are currently no objective criteria for determining whether skeletal samples will yield usable genetic data except for genetic analysis itself (Bollongino, Tresset, and Vigne 2008). As such, stakeholders must consider whether the destruction of an irreplaceable skeletal specimen is worth the potential of obtaining paleogenomic data.

The detrimental effects that high temperatures, exposure to humidity or water, and open depositional environments have on ancient DNA preservation are well known; however, methodological and computational developments (e.g., Ginolhac et al. 2011; Dabney et al. 2013; Jónsson et al. 2013; Damgaard et al. 2015; Korlević et al. 2015; Boessenkool et al. 2016; Hajdinjak et al. 2018) have opened the doors to ancient DNA analysis of material from such contexts. Though there are exceptions, ancient DNA analysis using osteological material from low-altitude sites in hot and dry or hot and humid regions such as the Near East (e.g., Broushaki et al. 2016; Lazaridis et al. 2016; Feldman et al. 2018; Harney et al. 2018), Africa (e.g., Schuenemann et al. 2017; Skoglund et al. 2017; Elkamel et al. 2018; Fregel et al. 2018; van de Loosdrecht et al. 2018), Southeast Asia (e.g., Lipson et al. 2018; McColl et al. 2018) and South America (e.g., Lindo et al. 2018; Víctor et al. 2018; Posth et al. 2018) require techniques optimized for the recovery and analysis of damaged DNA present in low quantities. As it becomes increasingly likely that many stakeholders may face the option of sacrificing a small piece of skeletal material to potentially obtain the rich data that can be provided by ancient DNA analysis, we believe it is important that the various possible analytical outcomes are outlined for improved understanding. First, a sample may have little or no preserved endogenous ancient DNA and will not be a candidate for inclusion in any paleogenetic study. Second, a sample may yield a sufficient amount of endogenous ancient DNA (tens to hundreds of thousands of Single Nucleotide Polymorphisms - SNPs) to enable statistical population genetic analyses that depend upon the knowledge of genetic sequence at a large number of positions across the genome. Third, a sample may be so well preserved that genome-wide highquality sequencing is possible as well as economical.

Before agreeing to sampling, all stakeholders should consider the potential impact that each outcome would have on their overall research program. For all outcomes, collaborators should develop a plan for reporting and publishing data. In the ideal case, all samples for which ancient DNA analysis was attempted should be publicly reported, regardless of whether a sample succeeds or fails to produce data. Currently, the dedicated reporting of negative results is not common practice in ancient DNA research, where hundreds of samples may fail to produce data. Although full reporting for all failed samples may be excessive, providing basic information such as sample number, site name, and element sampled in a table or spreadsheet will provide valuable information for researchers who may want to avoid requesting samples from the same specimen. In addition, the creation of a public record of all analyses – especially destructive ones – is an important step toward increased transparency surrounding ancient DNA analysis.

3. Fully assess the chances of generating robust data from the petrous against the selection of other skeletal elements.

When human remains are selected for ancient DNA analysis, it is imperative to maximize the chances of generating as much endogenous DNA as possible. The selection of the petrous as the starting material for ancient DNA analysis and strict adherence to anti-contamination protocols throughout all steps of sample processing are two factors that contribute to analytical success and substantially reduce the amount of destructive analysis that is performed.

We advocate for the use of the petrous as often as possible because of its optimal preservation of DNA; however, prior to the selection of this bone element for destructive analysis, we encourage all parties to discuss the impact of selecting this particular element for analysis. In some cases, for example, when only a single petrous is available, but multiple well-preserved teeth with intact roots are available and loose, a tooth root may instead be the preferred substrate for analysis. While we encourage consideration of this issue on a case-by-case basis, we focus this section on the analysis of the petrous element in ancient DNA analysis.

The emphasis on the petrous as the optimal substrate for ancient DNA analysis (described above) has been critiqued (Trinkaus 2018) in light of its potential use as an indicator of human variation (Ponce de León et al. 2018). An argument has been made that tooth roots provide another optimal substrate for ancient DNA work and may be present in greater number than the petrous (Hansen et al. 2017), meaning that the use of a single tooth root for the purposes of ancient DNA analysis may be interpreted as having less of a destructive effect; however, it has been shown that under various preservation conditions, material from the petrous yields high endogenous DNA content more often than tooth cementum, making the petrous bone the 'safest bet' (Hansen et al. 2017:11). Indeed, sampling of the petrous is a significant reason for the increased recovery of ancient DNA from the environmental contexts mentioned above.

The significant improvement in ancient DNA yield associated with the use of the petrous should be weighed against the much lower yield that will likely result from the use of a less-optimal skeletal element (such as any postcranial bone and possibly tooth roots) and we encourage critical consideration of *pros* and *cons* before the selection of any skeletal element for ancient DNA analysis. It is of utmost importance that best practices (some discussed in greater detail in Prendergast and Sawchuk 2018) are followed when a petrous will be used for ancient DNA analysis. These include:

- In all cases, only one petrous should be sampled for ancient DNA. Whenever possible, we
 recommend restricting sampling for ancient DNA to individuals that have both right and left
 petrous present in acceptable states of preservation so that one is preserved for future
 research. In some circumstances, however, it would be appropriate to sample the only
 petrous that is available for an individual. This would be justifiable, for example, in cases
 where it is the only material available for addressing important archaeological questions.
- All sampling should be done by a trained bioarchaeologist or anthropologist or a geneticist
 with training in human osteology. This person should be able to identify a petrous, determine
 its side, identify the essential landmarks required to ensure the cochlea is present, assess it for
 any morphological abnormalities, and keep clear and informative records of the sampling
 process. Inexpert handling of specimens can result in the destruction of unique skeletal
 material without scientific benefit.
- Whenever possible, a disarticulated petrous that can be processed in an ancient DNA clean room should be selected. Processing the bone in a sterile environment minimizes the chances of introducing additional contamination that may have detrimental downstream effects. If an isolated petrous is not available, we recommend the use of cranial base drilling (CBD) (Sirak et al. 2017) to obtain bone powder directly from the cochlea by approaching it from the base of the skull rather than the use of a sub-optimal postcranial element (see Table 3 from Sirak et al. 2017 for a quantitative comparison of methods). Performing CBD requires specialized training and should only be conducted by someone trained in this method.

- Whenever possible, we highly recommend that all discernible anatomical and morphological data be collected prior to any destructive sampling. In such instances, X-ray computed [micro-] tomography ([µ]CT or micro-CT) scanning should be considered. This may be particularly pertinent in cases of especially unique samples, such as the only representatives of whole ancient archaeological cultures or early modern human or archaic remains.
- 4. Ensure the deposit of raw sequencing data in a publicly accessible repository and fully report all protocols used.

In this sense, the standards in the field of ancient DNA are already excellent. These standards have in multiple instances helped to correct errors in the literature. For example, an error in the first African genome published by Gallego-Llorente et al. (2015) was identified by a researcher in another laboratory; the authors of the original study then went on to publish a corrected analysis.

Indeed, ancient DNA has set a standard in the area of data sharing for archaeological research. A study by Anagnostou et al. (2015) found that ~97.6% of published ancient human DNA data was shared, a rate far higher than physical anthropology, where samples and raw data are often not accessible to independent researchers even after publication. The authors state that 'the case of human paleogenetics tells us that widespread awareness of the importance of Open Science may be important to build reliable scientific practices even in the presence of complex experimental challenges' (Anagnostou et al. 2015, 1).

The unique relationship between geneticists and archaeologists

The ideas presented here describe an ideal scenario, but hope is that these principles will be considered as part of every collaborative project. The importance of active dialogue between archaeologists and geneticists around principles like these is emphasized by contrasting the experience that many archaeologists have with laboratories that provide commercial scientific services with the experience they are likely to have working with ancient DNA.

In a hypothetical scenario, an archaeologist excavated a site and would like to procure radiocarbon dates from multiple burials. Small bone fragments are sent to a laboratory for radiocarbon dating at a cost of \$400-600 per sample. The archaeologist likely had sufficient training to understand the basic data returned with the radiocarbon dates and is now in control of how, when, and where these dates will be published. This template - selecting a sample, paying a fee for analysis, receiving data, and independently developing a publication plan – is not what archaeologists should currently expect with ancient DNA. Instead, a successful ancient DNA project requires the diverse skill sets that both archaeologists and geneticists bring to the table at different points during the project, as well as the intimate and ongoing collaboration between the two groups. Specifically, specialized bioarchaeological training is needed to identify optimal skeletal samples, an ancient DNA laboratory is needed for sample preparation, and sophisticated computational techniques are required to process and analyse raw DNA sequences. Once data are generated, both geneticists and archaeologists should contribute to their interpretation and publication.

The fact that ancient DNA laboratories, mostly staffed by non-archaeologists have been increasingly requesting access to and analysing large numbers of skeletal elements is also a new situation for archaeologists who, along with biological anthropologists, have traditionally led research into ancient skeletal samples. While the trend of ancient DNA laboratories analysing large amounts of skeletal material has been characterized by some as a competition (Callaway 2017), another interpretation is that this perspective reflects unease on the part of archaeologists that the materials of which they have long been the custodians are now being analysed by researchers without traditional archaeological or anthropological training. We believe that active and engaged collaboration between archaeologists and geneticists is therefore essential, as the two communities have far more shared interests, centred upon an interest in understanding the deep human past, than divergent ones.

Finally, methods that aim to increase ancient DNA success rates are continuously under development, which means that some samples will be damaged in order to improve current techniques (although ancient DNA laboratories almost always keep processed samples [bone powder or DNA extracts], making re-analysis with improved future methods a possibility). Most museums or repositories curating human remains have their own criteria for granting permission for destructive analyses, and the fact that ancient DNA analysis is sometimes not successful and that methods are still being refined makes weighing the potential gain against the loss of bone much more challenging than with well-established techniques such as radiocarbon dating. Without discipline-wide standards, these subjective decisions are difficult. Yet the rate of improvement in techniques for ancient DNA analysis is slowing down as the field matures, and current methods are now regularly generating highly useful data.

Conclusion

It has been pointed out that while close collaboration between archaeologists and geneticists is an essential part of informed scientific research on the human past (Halcrow et al. 2018), a truly integrated collaboration 'cannot be defined by just the quantity of joint papers: it comprises discussion, meetings, conferences, and negotiation' (Pollard and Bray 2007, 256). Thus, the primary purposes of this paper were to contribute to the dialogue surrounding the development of quidelines for destructive analysis of human skeletal material for ancient DNA and to situate the current relationship between ancient DNA and archaeology within the context of how other destructive methods were incorporated into the archaeological toolkit. Although any analysis that requires the destruction of human remains should not be taken lightly, ancient DNA analysis has the potential not only to reveal new insights about the past but also help break down barriers between seemingly disparate groups of people.

Earlier in this paper, we asked: *How far are we from a standard framework governing the destruction* of human skeletal remains for ancient DNA? A discipline-wide framework has yet to be achieved, but discussions and forums such as this issue of World Archaeology constitute important steps to developing more comprehensive and refined standards that will govern future work. Yet we also note that standards are likely to vary, due to the different approaches and perspectives towards destructive analysis held by different archaeologists in different parts of the world. Despite these varied approaches, we do feel that some standards should be met, which we have detailed above. While we recognize that adopting these standards may affect the pace at which ancient DNA research proceeds, it is our hope that the practices outlined in this paper are recognized as essential to the continued ethical development of an integrated discipline of archaeogenetics.

While the criteria for other destructive analyses in archaeology developed organically over time, the exponential growth of ancient DNA in just a few years has forced the simultaneous development of methods and standards. The work that has already been done to bridge the gap between archaeologists and geneticists is encouraging. Through further dialogue on the development of a set of criteria that should be met before sampling occurs and the importance of mutually beneficial goals set by both archaeologists and ancient DNA specialists, it should be possible to make further progress toward an integrated field of archaeogenetics.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

Kendra A. Sirak earned a Ph.D. in Anthropology from Emory University in 2018, where she investigated how ancient DNA could provide meaningful insights into specific questions motivated by archaeology using the socially-stratified Early Christian Period site of Kulubnarti in Sudanese Nubia as an example. Her research demonstrated the value of investigating patterns of genetic variation in a context where archaeological research has already revealed much about sociocultural dynamics. Kendra is currently a postdoctoral research fellow for the Reich Laboratory of Medical and Population Genetics at Harvard Medical School.

Jakob W. Sedig earned a Ph.D. in Anthropology from the University of Colorado in 2015 and has spent over a decade studying ancient cultures of the American Southwest. He has worked on archaeological projects at or near Chimney Rock, Mesa Verde, and Casas Grandes, and his work helped define the occupation history of the previously unexcavated site and revealed a distinct form of ephemeral adobe architecture constructed between the Late Pithouse and Classic periods. Jakob is currently a postdoctoral research fellow and Ethics and Outreach Officer for the Reich Laboratory of Medical and Population Genetics at Harvard Medical School. In the Reich Laboratory, Kendra and Jakob occupy the interdisciplinary space between genetics and archaeology and work together to foster the growth of a strong and lasting relationship between the two disciplines.

ORCID

Kendra A. Sirak (i) http://orcid.org/0000-0003-2347-3479 Jakob W. Sedig (i) http://orcid.org/0000-0001-6642-7734

References

Allentoft, M. E., M. Sikora, K.-G. Sjögren, S. Rasmussen, M. Rasmussen, J. Stenderup, P. B. Damgaard, et al. 2015. "Population Genomics of Bronze Age Eurasia." *Nature* 522 (7555): 167–172. doi:10.1038/nature14507.

Anagnostou, P., M. Capocasa, N. Milia, E. Sanna, C. Battaggia, D. Luzi, and G. D. Bisol. 2015. "When Data Sharing Gets Close to 100%: What Human Paleogenetics Can Teach the Open Science Movement." *PloS One* 10 (3): e0121409–e0121409. doi:10.1371/journal.pone.0121409.

Bardill, J., A. C. Bader, N. A. Garrison, D. A. Bolnick, J. A. Raff, A. Walker, and R. S. Malhi, the Summer internship for INdigenous peoples in Genomics (SING) Consortium. 2018. "Advancing the Ethics of Paleogenomics." *Science* 360 (6387): 384–385.doi:10.1126/science.aaq1131.

Boessenkool, S., K. Hanghøj, H. M. Nistelberger, C. Der Sarkissian, A. Gondek, L. Orlando, J. H. Barrett, and B. Star. 2016. "Combining Bleach and Mild Pre-Digestion Improves Ancient DNA Recovery from Bones." *Molecular Ecology Resources* 17 (4): 742–751. doi:10.1111/1755-0998.12623.

Bollongino, R., A. Tresset, and J.-D. Vigne. 2008. "Environment and Excavation: Pre-Lab Impacts on Ancient DNA Analyses." *Comptes Rendus Palevol* 7 (2): 91–98. doi:10.1016/j.crpv.2008.02.002.

Briggs, A. W., U. Stenzel, P. L. F. Johnson, R. E. Green, J. Kelso, K. Prüfer, M. Meyer, et al. 2007. "Patterns of Damage in Genomic DNA Sequences from a Neandertal." *Proceedings of the National Academy of Sciences* 104 (37): 14616–14621. doi:10.1073/pnas.0704665104.



- Bronk Ramsey, C. 2008. "Radiocarbon Dating: Revolutions in Understanding." *Archaeometry* 50 (2): 249–275. doi:10.1111/j.1475-4754.2008.00394.x.
- Broushaki, F., M. G. Thomas, V. Link, S. López, L. van Dorp, K. Kirsanow, Z. Hofmanová, Y., et al. 2016. "Early Neolithic Genomes from the Eastern Fertile Crescent." *Science* 353 (6298): 499–503.
- Callaway, E. 2017. "Stop Hoarding Ancient Bones, Plead Archaeologists." *Nature News*. https://www.nature.com/news/stop-hoarding-ancient-bones-plead-archaeologists-1.22445
- Callaway, E. 2018. "The Battle for Common Ground." *Nature* 555: 573–576. doi:10.1038/d41586-018-03773-6. Cooper, A., and H. N. Poinar. 2000. "Ancient DNA: Do It Right or Not at All." *Science* 289 (5482): 1139-1139.
- Dabney, J., M. Knapp, I. Glocke, M.-T. Gansauge, A. Weihmann, B. Nickel, C. Valdiosera, et al. 2013. "Complete Mitochondrial Genome Sequence of a Middle Pleistocene Cave Bear Reconstructed from Ultrashort DNA Fragments." *Proceedings of the National Academy of Sciences* 110 (39): 15758–15763. doi:10.1073/pnas.1314445110.
- Damgaard, P. B., A. Margaryan, H. Schroeder, L. Orlando, E. Willerslev, and M. E. Allentoft. 2015. "Improving Access to Endogenous DNA in Ancient Bones and Teeth." *Scientific Reports* 5: 11184. doi:10.1038/srep11184.
- Damgaard, P. D. B., R. Martiniano, J. Kamm, J. Víctor Moreno-Mayar, G. Kroonen, M. Peyrot, G. Barjamovic, et al. 2018a. "The First Horse Herders and the Impact of Early Bronze Age Steppe Expansions into Asia." *Science* 360 (6396): eaar7711. doi:10.1126/science.aar7711.
- Damgaard, P. B., N. Marchi, S. Rasmussen, M. Peyrot, G. Renaud, T. Korneliussen, J. V. Moreno-Mayar, et al. 2018b. "137 Ancient Human Genomes from across the Eurasian Steppes." *Nature* 557 (7705): 369–374. doi:10.1038/s41586-018-0094-2.
- Eisenmann, S., E. Bánffy, P. van Dommelen, K. P. Hofmann, J. Maran, I. Lazaridis, A. Mittnik, et al. 2018. "Reconciling Material Cultures in Archaeology with Genetic Data: The Nomenclature of Clusters Emerging from Archaeogenomic Analysis." *Scientific Reports* 8 (1): 13003. doi:10.1038/s41598-018-31123-z.
- Elkamel, S., S. Boussetta, H. Khodjet-El-Khil, A. B. Elgaaied, and L. Cherni. 2018. "Ancient and Recent Middle Eastern Maternal Genetic Contribution to North Africa as Viewed by mtDNA Diversity in Tunisian Arab Populations." *American Journal of Human Biology* e23100. doi:10.1002/ajhb.23100.
- Feldman, M., E. Fernández-Domínguez, L. Reynolds, D. Baird, J. Pearson, I. Hershkovitz, H. May, et al. 2018. "Late Pleistocene Human Genome Suggests a Local Origin for the First Farmers of Central Anatolia." *bioRxiv* 422295. doi:10.1101/422295.
- Fregel, R., F. L. Mendez, Y. Bokbot, D. Martin-Socas, M. D. Camalich-Massieu, J. Santana, J. Morales, et al. 2018. "Ancient Genomes from North Africa Evidence Prehistoric Migrations to the Maghreb from Both the Levant and Europe." *Proceedings of the National Academy of Sciences* 201800851. doi:10.1101/191569.
- Furholt, M. 2018. "Massive Migrations? the Impact of Recent aDNA Studies on Our View of Third Millennium Europe." European Journal of Archaeology 21 (2): 159–191. doi:10.1017/eaa.2017.43.
- Gallego-Llorente, M., E. R. Jones, A. Eriksson, V. Siska, K. W. Arthur, J. W. Arthur, M. C. Curtis, et al. 2015. "Ancient Ethiopian Genome Reveals Extensive Eurasian Admixture Throughout the African Continent." Science 350 (6262): 820–822. DOI:10.1126/science.aad2879.
- Gamba, C., E. R. Jones, M. D. Teasdale, R. L. McLaughlin, G. Gonzalez-Fortes, V. Mattiangeli, L. Domboroczki, et al. 2014. "Genome Flux and Stasis in a Five Millennium Transect of European Prehistory". *Nature Communications* 5: 5257. DOI:10.1038/ncomms5972.
- Ginolhac, A., M. Rasmussen, T. P. Gilbert, E. Willerslev, and L. Orlando. 2011. "mapDamage: Testing for Damage Patterns in Ancient DNA Sequences." *Bioinformatics* 27 (15): 2153–2155. doi:10.1093/bioinformatics/btr347.
- Golenberg, E. M. 1991. "Amplification and Analysis of Miocene Plant Fossil DNA." *Philosophical Transactions of the Royal Society B: Biological Sciences* 333 (1268): 419–427. doi:10.1098/rstb.1991.0092.
- Grealy, A., M. E. Amy Macken, N. J. Allentoft, E. R. Rawlence, and M. Bunce. 2016. "An Assessment of Ancient DNA Preservation in Holocene–Pleistocene Fossil Bone Excavated from the World Heritage Naracoorte Caves, South Australia." *Journal of Quaternary Science* 31 (1): 33–45. doi:10.1002/jqs.2830.
- Hajdinjak, M., F. Qiaomei, A. Hübner, M. Petr, F. Mafessoni, S. Grote, P. Skoglund, et al. 2018. "Reconstructing the Genetic History of Late Neanderthals." *Nature* 555 (7698): 652. doi:10.1038/nature26151.
- Halcrow, S. E., K. Killgrove, G. R. Schug, M. Knapp, D. Huffer, B. Arriaza, W. Jungers, and J. Gunter. 2018. "On Engagement with Anthropology: A Critical Evaluation of Skeletal and Developmental Abnormalities in the Atacama Preterm Baby and Issues of Forensic and Bioarchaeological Research Ethics. Response to Bhattacharya Et Al. "Whole-Genome Sequencing of Atacama Skeleton Shows Novel Mutations Linked

- with Dysplasia" in Genome Research, 2018, 28: 423–431. Doi: 10.1101/Gr.223693.117." International Journal of Paleopathology 22: 97–100. doi:10.1016/j.ijpp.2018.06.007.
- Hansen, H.B., P.B. Damgaard, A. Margaryan, J. Stenderup, N. Lynnerup, E. Willerslev, and M.E. Allentoft. 2017. "Comparing Ancient Dna Preservation in Petrous Bone and Tooth Cementum." *Plos One* 12 (1): e0170940. doi: 10.1371/journal.pone.0170940.
- Harney, É., H. May, D. Shalem, N. Rohland, S. Mallick, I. Lazaridis, R. Sarig, et al. 2018. "Ancient DNA from Chalcolithic Israel Reveals the Role of Population Mixture in Cultural Transformation." *Nature Communications* 9 (1): 3336. doi:10.1038/s41467-018-05649-9.
- Higuchi, R., B. Bowman, M. Freiberger, O. A. Ryder, and A. C. Wilson. 1984. "DNA Sequences from the Quagga, an Extinct Member of the Horse Family." *Nature* 312: 282–284.
- Hofreiter, M., V. Jaenicke, D. Serre, A. von Haeseler, and S. Pääbo. 2001. "DNA Sequences from Multiple Amplifications Reveal Artifacts Induced by Cytosine Deamination in Ancient DNA." *Nucleic Acids Research* 29 (23): 4793–4799. doi:10.1093/nar/29.23.4793.
- Johannsen, N. N., G. Larson, D. J. Meltzer, and M. Vander Linden. 2017. "A Composite Window into Human History." *Science* 356 (6343): 1118–1120. doi:10.1126/science.aan0737.
- Jónsson, H., A. Ginolhac, M. Schubert, P. L. F. Johnson, and L. Orlando. 2013. "mapDamage2.0: Fast Approximate Bayesian Estimates of Ancient DNA Damage Parameters." *Bioinformatics* 29 (13): 1682–1684. doi:10.1093/bioinformatics/btt193.
- Jónsson, H., M. Schubert, A. Seguin-Orlando, A. Ginolhac, L. Petersen, M. Fumagalli, A. Albrechtsen, et al. 2014. "Speciation with Gene Flow in Equids despite Extensive Chromosomal Plasticity." *Proceedings of the National Academy of Sciences* 111 (52): 18655–18660. doi:10.1073/pnas.1412627111.
- Klejn, L. S., W. Haak, I. Lazaridis, N. Patterson, D. Reich, K. Kristiansen, K.-G. Sjögren, M. Allentoft, M. Sikora, and E. Willserlsev. 2017. "Discussion: Are the Origins of Indo-European Languages Explained by the Migration of the Yamnaya Culture to the West?" *European Journal of Archaeology* 21 (1): 3–17. doi:10.1017/eaa.2017.35.
- Korlević, P., T. Gerber, M.-T. Gansauge, M. Hajdinjak, S. Nagel, A. Aximu-Petri, and M. Meyer. 2015. "Reducing Microbial and Human Contamination in DNA Extractions from Ancient Bones and Teeth." *BioTechniques* 58: 87–93.
- Lazaridis, I., D. Nadel, G. Rollefson, D. C. Merrett, N. Rohland, S. Mallick, D. Fernandes, et al. 2016. "Genomic Insights into the Origin of Farming in the Ancient near East." *Nature* 536 (7617): 419–424. doi:10.1038/nature19310.
- Leonardi, M., P. Librado, C. Der Sarkissian, M. Schubert, A. H. Alfarhan, S. A. Alquraishi, K. A. S. Al-Rasheid, C. Gamba, E. Willerslev, and L. Orlando. 2016. "Evolutionary Patterns and Processes: Lessons from Ancient DNA." Systematic Biology 66.1 (1): e1–e29.
- Lindo, J., R. Haas, C. Hofman, M. Apata, M. Moraga, R. A. Verdugo, J. T. Watson, et al. 2018. "The Genetic Prehistory of the Andean Highlands 7000 Years BP though European Contact." *Science Advances* 4 (11): eaau4921. DOI:10.1126/sciadv.aau4921.
- Lipson, M., O. Cheronet, S. Mallick, N. Rohland, M. Oxenham, M. Pietrusewsky, T. O. Pryce, et al. 2018. "Ancient Genomes Document Multiple Waves of Migration in Southeast Asian Prehistory." *Science* eaat3188. doi:10.1126/science.aat3188.
- Llamas, B., G. Valverde, L. Fehren-Schmitz, L. S. Weyrich, A. Cooper, and W. Haak. 2017. "From the Field to the Laboratory: Controlling DNA Contamination in Human Ancient DNA Research in the High-Throughput Sequencing Era." STAR: Science & Technology of Archaeological Research 3 (1): 1–14. doi:10.1080/20548923.2016.1258824.
- Makarewicz, C., N. Marom, and G. Bar-Oz. 2017. "Palaeobiology: Ensure Equal Access to Ancient DNA." *Nature* 548 (7666): 158. doi:10.1038/nature23004.
- Margulies, M., M. Egholm, W. E. Altman, S. Attiya, J. S. Bader, L. A. Bemben, J. Berka, M. S. Braverman, Y.- J. Chen, and Z. Chen. 2005. "Genome Sequencing in Microfabricated High-Density Picolitre Reactors." *Nature* 437 (7057): 376–380. doi:10.1038/nature03959.
- Mathieson, I., I. Lazaridis, N. Rohland, S. Mallick, N. Patterson, S. A. Roodenberg, E. Harney, et al. 2015. "Genome-Wide Patterns of Selection in 230 Ancient Eurasians." *Nature* 528 (7583): 499–503. doi:10.1038/nature16152.
- Mathieson, I., S. Alpaslan-Roodenberg, C. Posth, A. Szécsényi-Nagy, N. Rohland, S. Mallick, I. Olalde, et al. 2018. "The Genomic History of Southeastern Europe." *Nature* 555 (7695): 197. doi:10.1038/nature25778.
- McColl, H., F. Racimo, L. Vinner, F. Demeter, T. Gakuhari, J. Víctor Moreno-Mayar, G. Van Driem, et al. 2018. "The Prehistoric Peopling of Southeast Asia." *Science* 361 (6397): 88–92. DOI:10.1126/science.aat3628.



- Moreno-Mayar, J. V., L. Vinner, P. B. Damgaard, C. de la Fuente, J. Chan, J. P. Spence, M. E. Allentoft, et al. 2018. "Early Human Dispersals within the Americas." *Science* 362 (6419): eaav2621. DOI:10.1126/science.aav2621.
- Mullis, K., F. A. Faloona, S. J. Scharf, R. K. Saiki, G. T. Horn, and H. Erlich. 1986. "Specific Enzymatic Amplification of DNA in Vitro: The Polymerase Chain Reaction." *Cold Spring Harbor Symposia on Quantitative Biology* 51: 263–273.
- National Park Service. Archaeology Program. "Managing Archaeological Collections: Destructive Analysis." https://www.nps.gov/archeology/collections/coll_05.htm
- Olalde, I., S. Brace, M. E. Allentoft, I. Armit, K. Kristiansen, N. Rohland, S. Mallick, et al. 2018. "The Beaker Phenomenon And The Genomic Transformation Of Northwest Europe." *Nature* 555 (7695): 190. doi:10.1101/135962.
- Orlando, L., M. T. Gilbert, and E. Willerslev. 2015. "Reconstructing Ancient Genomes and Epigenomes." *Nature Reviews Genetics* 16 (7): 395–408. doi:10.1038/nrg3935.
- Pääbo, S. 1985. "Molecular Cloning of Ancient Egyptian Mummy DNA." Nature 314 (6012): 644–645.
- Pääbo, S., H. Poinar, D. Serre, V. Jaenicke-Després, J. Hebler, N. Rohland, M. Kuch, J. Krause, L. Vigilant, and M. Hofreiter. 2004. "Genetic Analyses from Ancient DNA." *Annual Review of Genetics* 38: 645–679. doi:10.1146/annurev.genet.37.110801.143214.
- Pääbo, S., R. G. Higuchi, and A. C. Wilson. 1989. "Ancient DNA and the Polymerase Chain Reaction: The Emerging Field of Molecular Archaeology (Minireview)." *The Journal of Biological Chemistry* 264 (17): 9709–9712.
- Pinhasi, R., D. Fernandes, K. Sirak, M. Novak, S. Connell, S. Alpaslan-Roodenberg, F. Gerritsen, et al. 2015. "Optimal Ancient DNA Yields from the Inner Ear Part of the Human Petrous Bone." *PloS One* 10 (6): e0129102. doi:10.1371/journal.pone.0129102.
- Piscitelli, M. 2019. "Bones and Chromosomes: The Ancient Dna Revolution in Archaeology (Part 1)." Saa Archaeological Record 19 (1): 15–17.
- Poinar, H. N. 2003. "The Top 10 List: Criteria of Authenticity for DNA from Ancient and Forensic Samples." *International Congress Series* 1239: 575–579. doi:10.1016/S0531-5131(02)00624-6.
- Pollard, A. M., and P. Bray. 2007. "A Bicycle Made for Two? the Integration of Scientific Techniques into Archaeological Interpretation." *Annual Review of Anthropology* 36 (1): 245–259. doi:10.1146/annurev. anthro.36.081406.094354.
- Ponce de León, M. S., T. Koesbardiati, J. D. Weissmann, M. Milella, C. S. Reyna-Blanco, G. Suwa, O. Kondo, A.-S. Malaspinas, T. D. White, and C. P. E. Zollikofer. 2018. "Human Bony Labyrinth Is an Indicator of Population History and Dispersal from Africa." *Proceedings of the National Academy of Sciences* 115 (16): 4128–4133. doi:10.1073/pnas.1717873115.
- Posth, C., N. Nakatsuka, I. Lazaridis, P. Skoglund, S. Mallick, T. C. Lamnidis, N. Rohland, et al. 2018. "Reconstructing the Deep Population History of Central and South America." *Cell* 175 (5): 1185–1197. doi:10.1016/j.cell.2018.10.027.
- Prendergast, M. E., and E. Sawchuk. 2018. "Boots on the Ground in Africa's Ancient DNA 'Revolution': Archaeological Perspectives on Ethics and Best Practices." *Antiquity* 92 (363): 803–815. doi:10.15184/aqy.2018.70.
- Rasmussen, M., L. Yingrui, S. Lindgreen, J. S. Pedersen, A. Albrechtsen, I. Moltke, M. Metspalu, E. Metspalu, T. Kivisild, and R. Gupta. 2010. "Ancient Human Genome Sequence of an Extinct Palaeo-Eskimo." *Nature* 463 (7282): 757–762. doi:10.1038/nature08835.
- Sawyer, S., J. Krause, K. Guschanski, V. Savolainen, and S. Pääbo. 2012. "Temporal Patterns of Nucleotide Misincorporations and DNA Fragmentation in Ancient DNA." *PloS One* 7 (3): e34131. doi:10.1371/journal. pone.0034131.
- Scarre, G. 2006. "Can Archaeology Harm the Dead?" In *The Ethics of Archaeology: Philosophical Perspectives on Archaeological Practice*, edited by C. Scarre and G. Scarre, p. 181–198. Cambridge: Cambridge University Press.
- Schuenemann, V. J., A. Peltzer, W. Beatrix Welte, P. van Pelt, M. Molak, C.-C. Wang, A. Furtwängler, et al. 2017. "Ancient Egyptian Mummy Genomes Suggest an Increase of Sub-Saharan African Ancestry in post-Roman Periods." *Nature Communications* 8 :15694. doi:10.1038/ncomms15694.
- Sedig, J.W. 2019. "Ancient DNA's Impact on Archaeology: What Has Been Learned and How to Build Stronger Relationships." SAA Archaeological Record 19 (1): 26–32.
- Sirak, K. A., D. M. Fernandes, O. Cheronet, M. Novak, B. Gamarra, T. Balassa, Z. Bernert, et al. 2017. "A Minimally-Invasive Method for Sampling Human Petrous Bones from the Cranial Base for Ancient DNA Analysis". *BioTechniques* 62: 283–289. DOI:10.2144/000114558.



- Skoglund, P., B. H. Northoff, M. V. Shunkov, A. P. Derevianko, S. Pääbo, J. Krause, and M. Jakobsson. 2014. "Separating Endogenous Ancient DNA from Modern Day Contamination in a Siberian Neandertal." Proceedings of the National Academy of Sciences 111 (6): 2229–2234. doi:10.1073/pnas.1318934111.
- Skoglund, P., J. C. Thompson, M. E. Prendergast, A. Mittnik, K. Sirak, M. Hajdinjak, T. Salie, et al. 2017. "Reconstructing Prehistoric African Population Structure." Cell 171 (1): 59-71.e21. doi:10.1016/j. cell.2017.08.049.
- Taylor, R. E. 1992. "Radiocarbon Dating of Bone: To Collagen and Beyond." In Radiocarbon After Four Decades: An Interdisciplinary Perspective, edited by R. E. Taylor, A. Long, and R. S. Kra, p. 375-402. New York, Tucson, AZ: Springer-Verlag.
- Taylor, R. E. 1997. "Radiocarbon Dating." In Chronometric Dating in Archaeology, edited by R. E. Taylor and M. J. Aitken, p. 65–96. New York: Plenum Press.
- Trinkaus, E. 2018. "The Labyrinth of Human Variation." Proceedings of the National Academy of Sciences 115 (16): 3992–3994. doi:10.1073/pnas.1804794115.
- van de Loosdrecht, M., A. Bouzouggar, L. Humphrey, C. Posth, N. Barton, A. Aximu-Petri, B. Nickel, et al. 2018. "Pleistocene North African Genomes Link near Eastern and sub-Saharan African Human Populations." Science eaar8380. doi:10.1126/science.aar8380.
- Veeramah, K. R. 2018. "The Importance of Fine-Scale Studies for Integrating Paleogenomics and Archaeology." Current Opinion in Genetics and Development 53: 83-89. doi:10.1016/j.gde.2018.07.007.
- Zischler, H., M. Hoss, A. Oliva Handt, A. C. Von Haeseler, V. D. Kuyl, and J. Goudsmit. 1995. "Detecting Dinosaur DNA." Science 268 (5214): 1192-1193.