

Ethics of DNA research on human remains: five globally applicable guidelines

<https://doi.org/10.1038/s41586-021-04008-x>

Received: 20 March 2021

Accepted: 8 September 2021

Published online: 20 October 2021

 Check for updates

Songül Alpaslan-Roodenberg^{1,2}, David Anthony^{3,4}, Hiba Babiker⁵, Eszter Bánffy⁶, Thomas Booth⁷, Patricia Capone⁸, Arati Deshpande-Mukherjee⁹, Stefanie Eisenmann^{5,10}, Lars Fehren-Schmitz^{11,12}✉, Michael Frachetti¹³, Ricardo Fujita¹⁴, Catherine J. Frieman¹⁵, Qiaomei Fu¹⁶, Victoria Gibbon¹⁷, Wolfgang Haak⁵, Mateja Hajdinjak⁷, Kerstin P. Hofmann⁶, Brian Holguin¹⁸, Takeshi Inomata¹⁹, Hideaki Kanzawa-Kiriyama²⁰, William Keegan²¹, Janet Kelso¹⁰, Johannes Krause¹⁰, Ganesan Kumaresan²², Chapurukha Kusimba²³, Sibel Kusimba²³, Carles Lalueza-Fox²⁴, Bastien Llamas^{25,26}, Scott MacEachern²⁷, Swapan Mallick^{1,28,29}, Hirofumi Matsumura³⁰, Ana Y. Morales-Arce³¹, Giedre Motuzaitė Matuzeviciute³², Veena Mushrif-Tripathy⁹, Nathan Nakatsuka¹, Rodrigo Nores³³, Christine Ogola³⁴, Mercedes Okumura³⁵, Nick Patterson^{4,29}, Ron Pinhasi^{2,36}, Samayamantri P. R. Prasad³⁷, Mary E. Prendergast³⁸✉, Jose Luis Punzo³⁹, David Reich^{1,4,28,29}✉, Rikai Sawafuji⁴⁰, Elizabeth Sawchuk^{41,42}, Stephan Schiffels^{5,10}, Jakob Sedig^{1,4}✉, Svetlana Shnaider⁴³, Kendra Sirak^{1,4}✉, Pontus Skoglund⁷, Viviane Slon^{44,45}, Meradeth Snow⁴⁶, Marie Soressi⁴⁷, Matthew Spriggs^{15,48}, Philipp W. Stockhammer^{10,49}✉, Anna Szécsényi-Nagy⁵⁰, Kumarasamy Thangaraj^{37,51}, Vera Tiesler⁵², Ray Tobler^{23,25}, Chuan-Chao Wang^{53,54}, Christina Warinner^{10,55}, Surangi Yasawardene⁵⁶ & Muhammad Zahir^{5,57}

We are a group of archaeologists, anthropologists, curators and geneticists representing diverse global communities and 31 countries. All of us met in a virtual workshop dedicated to ethics in ancient DNA research held in November 2020. There was widespread agreement that globally applicable ethical guidelines are needed, but that recent recommendations grounded in discussion about research on human remains from North America are not always generalizable worldwide. Here we propose the following globally applicable guidelines, taking into consideration diverse contexts. These hold that: (1) researchers must ensure that all regulations were followed in the places where they work and from which the human remains derived; (2) researchers must prepare a detailed plan prior to beginning any study; (3) researchers must minimize damage to human remains; (4) researchers must ensure that data are made available following publication to allow critical re-examination of scientific findings; and (5) researchers must engage with other stakeholders from the beginning of a study and ensure respect and sensitivity to stakeholder perspectives. We commit to adhering to these guidelines and expect they will promote a high ethical standard in DNA research on human remains going forward.

The analysis of ancient human genomes has emerged as a powerful approach for investigating the relationships of people who lived in the past to each other and to people living today. A consistent theme is that people in any given location across time are usually there as the result of a long history of mobility and interaction. Over the past decade, ancient DNA has provided new evidence—adding to that from other disciplines—refuting myths of the ‘purity’ of any population and falsifying racist and nationalistic narratives. While some have sought to misuse genetics as a tool for determining group belonging, in our opinion it is inappropriate for genetic data to be used as an arbiter of identity¹.

The rapid increase in published genome-wide data from ancient humans—from none in 2009 to more than six thousand individuals today—has been accompanied by growing discussions about how to

conduct ancient DNA research ethically^{2–16}, building on earlier conversations^{17–24}. The ethics of DNA research has a particular urgency because of the rapid growth of the field, the social and political impacts of studying ancestry, and the fact that ancient DNA work analyses once-living people who must be respected.

Institutional or governmental guidelines for obtaining permission to analyse ancient individuals vary and do not always ensure ethical and engaged research. Researchers have an obligation to meet a higher standard than some governing bodies may require, but there is no consensus on what this entails^{11,25–27}. Increasingly, publications on ancient DNA have included statements describing how the research team addressed ethical issues^{28–38}, a development that we support. Professional organizations are also beginning to articulate guidelines^{15,39}, and at least one grant has been awarded to explore these issues in the

A list of affiliations appears at the end of the paper.

Box 1

Five globally applicable guidelines for DNA research on human remains

- (1) Researchers must ensure that all regulations were followed in the places where they work and from which the human remains derived.
- (2) Researchers must prepare a detailed plan prior to beginning any study.
- (3) Researchers must minimize damage to human remains.
- (4) Researchers must ensure that data are made available following publication to allow critical re-examination of scientific findings.
- (5) Researchers must engage with stakeholders from the beginning of a study and ensure respect and sensitivity to other stakeholder perspectives.

context of research on ancient North Americans (<http://www.adnaethics.org/>). Notably lacking has been a statement on ethics co-signed by an internationally diverse and representative group of scholars engaged in ancient DNA research.

We convened more than 60 archaeologists, anthropologists, curators and geneticists representing more than 30 countries and diverse global communities for a virtual workshop on ethics on 4 and 5 November 2020. All participants are committed to carrying out research on DNA from human remains that is ethically responsible and sensitive to diverse perspectives held by stakeholders (people who have a connection to a study, including descendant communities, those responsible for the stewardship of human remains, and researchers). Here we present case studies from a variety of global contexts to illustrate the breadth of issues surrounding community and Indigenous group consultation, highlighting how the relevant issues vary worldwide. We then provide guidelines for DNA research on human remains that apply globally (Box 1).

Community ethical engagement is context-specific

Much of the literature about ethical DNA research on ancient individuals has focused on the USA^{3,4,13,15}. These discussions have produced recommendations to promote engagement between researchers and Indigenous communities, summarized in the research guidance published by the American Society of Human Genetics, which suggests that all ancient DNA studies should involve formal consultation, address cultural and ethical considerations, engage communities and support capacity building, develop plans for reporting and managing data, and develop plans for long-term responsibility and stewardship¹⁵.

Making Indigenous perspectives central is critical in regions with histories of settler colonialism, expropriation of Indigenous lands and artifacts, and persistent disenfranchisement of Indigenous communities; not consulting with communities can cause harm in such contexts^{5,6}. In the USA, all ancient Native American remains held in federally funded institutions fall under the purview of the Native American Graves Protection and Repatriation Act (NAGPRA), which mandates that institutions consult with and seek to transfer the remains of ancient individuals (culturally identifiable or not) to Indigenous groups. In Australia, analogous laws seek to repatriate human remains, in some cases up to 40,000 years old⁴⁰, that have been removed from Aboriginal and Torres Strait Islander communities^{41,42}. However, when carrying out research on the remains of ancient individuals where there are few (if

any) material or oral links to present-day groups, or where promoting the idea that some groups have more ownership of cultural heritage than others can contribute to social conflict, an Indigenous-centred ethical framework mandating that each ancient individual be associated with a contemporary group does not fit.

Representation of Indigenous perspectives

In many countries in the Americas, Indigenous heritage is embedded in national identity and integrated into governmental cultural institutions. For instance, following Independence in Mexico, mestizos (people of mixed ancestry)—who form the great majority—embraced legacies from the Nahua (Aztec), Maya, Zapotec and other Indigenous groups as an integral part of national identity^{43–45}. In Peru, the Ministry of Culture was created in the context of *indigenismo*, a movement with the goal of promoting Indigenous culture and fighting discrimination^{46–48}. In such contexts, the process of seeking approval from government or heritage organizations for analysis of human remains can be a robust form of engagement, and adopting a US template can be counterproductive. We have had multiple experiences of writing papers about ancient DNA from Central and South America and receiving reviews stating the work did not conform to standards for Indigenous engagement developed in the USA^{3,4}. Those of us who are from Mexico and Central and South America have felt that such reviews have been paternalistic at best and colonialist at worst, especially given that many places have embraced Indigenous heritage and embedded it into government approval processes and cultural institutions to a greater extent than has been done in the USA.

There is wide variation, however, in the nature of relationships between governments and Indigenous communities in the Americas, and researchers must take a case-by-case approach to determining when additional consultation is needed. In Peru and Mexico, groups for whom Indigenous heritage is an important part of identity have variable degrees of representation in the government. In Brazil, Indigenous communities are often disenfranchised, and there is no legal mechanism for Indigenous groups to have a voice in the fate of archaeological materials associated with their ancestors⁴⁹. In Argentina, a legal mandate that community consent must be obtained to carry out any project involving Indigenous heritage is not always followed. In Guatemala, the Maya and other Indigenous groups who form roughly half the population remain marginalized. In such contexts it is the ethical responsibility of members of an ancient DNA research team to carry out additional outreach beyond what is mandated to incorporate Indigenous perspectives.

Global differences in the meaning of Indigeneity

The meaning of Indigeneity varies globally. In Africa, descendants of colonized groups are now overwhelmingly in power, and Indigeneity often refers more to political or social marginalization on the basis of identity than to traditions of how long groups have been established in a region⁵⁰. Many African communities have complex connections to the lands on which they live, including histories of colonial and post-colonial displacement and disruption. In some regions, people do not recognize past local populations as their relatives. This may be owing to contemporary religious or cultural belief systems being different from past ones⁵¹, collective memories of migrations from elsewhere, fear of reprisal for being linked with other groups, and the continuing after-shocks of decisions made during European colonization that fractured socio-political landscapes and still contribute to violence and displacements. In these situations, careful consultation among stakeholders is necessary, from local groups to government representatives, to ensure that vesting decision-making power about cultural heritage does not aggravate social conflict. In such cases, making Indigeneity a central principle for permitting ancient DNA analysis would probably be harmful.

A more pressing issue related to ancient DNA research in Africa (and in many other regions) is confronting the colonial legacies of human remains collected in unethical ways and often sent abroad^{52,53}. Researchers must work with both the curating institution and with scholars from

the country of origin to seek permissions to study the remains of ancient individuals, and engage in discussions about provenance, historical injustices, repatriation and restitution as part of their work^{54–56} (<https://www.globalcodeofconduct.org/affiliated-codes/>). A related challenge is the history of non-equitable and often exploitative research in Africa by predominantly European and North American scientists, with minimal local engagement^{25–27}. Foreign researchers must prioritize establishing equitable collaborations, which may include training and other capacity building that empowers stakeholders to shape research questions and designs⁵⁷.

Potential harm from emphasizing group identity

There are many places in the world where discussions about who is Indigenous have contributed to xenophobic and nationalistic narratives. In these places, using Indigenous identity to determine who can permit ancient DNA research can be harmful, as it can contribute to conflict among groups and to discrimination.

In India, for example, many people avoid asking about caste and religious background because of a long history of abuse based on group identity, and indeed discrimination on the basis of caste is outlawed. The very exercise of trying to determine what groups today have more of a claim to ancient heritage than others has not only contributed to conflict, but is also made almost meaningless in much of South Asia, owing to the fact that the great majority of groups today are mixtures of the same populations whose ancestors have resided in the subcontinent for millennia^{58,59}; however, there are cases in which it is clear who is Indigenous, such as in the Andaman Islands⁶⁰. There are official procedures in many parts of South Asia for protecting cultural heritage, and working within this framework is an important mechanism for protecting communities from harm.

In West Eurasia, the suggestion that groups who claim local origins should have a special status has contributed to xenophobia and genocide. Nationalists promoting the idea of ‘blood and soil’ during the Nazi period twisted archaeological research to legitimize land seizures by claiming that skeletons excavated in eastern Europe had a ‘Germanic’ morphology⁶¹. European archaeologists have worked for decades to deconstruct narratives that claim ownership of cultural heritage by specific groups. Ancient DNA research ethics in a West Eurasian context must follow this movement away from the use of self-identified notions of ancestral connections to certain lands^{61,62}, while simultaneously ensuring respect for the perspectives of national minorities who have been the subject of discrimination. The danger of government leaders citing archaeological and ancient DNA research to support favoured narratives of group identity that can then be used to justify exclusionary policies is not just theoretical, but is an ongoing problem in some countries in West Eurasia today, including in Hungary and Israel^{63–65}.

Five globally applicable guidelines

We present five guidelines to promote robust ethical standards in ancient DNA research that apply across the breadth of research contexts discussed above, as well as other major world regions that we have not discussed owing to space limitations, including Central Asia, Siberia, East Asia, Southeast Asia and Oceania (Box 1). We begin with guidelines that address issues of scientific ethics and then return to the topic of ensuring sensitivity of research to perspectives of communities, including Indigenous groups.

(1) *Researchers must ensure that all regulations were followed in the places where they work and from which the human remains derived.* Researchers must consider whether it is ethical to carry out ancient DNA research given the environment in the place from which they sample human remains. Once engaged in a project, researchers must abide by all local regulations. While this may seem obvious, the experience of some co-authors is that ancient DNA researchers have not always followed all agreements. For example, it may be necessary to obtain multiple levels of permission for scientific analysis or export of biological

material from institutional, local, regional or national bodies, and to provide reports to curating institutions according to agreed timelines. Where local regulations are insufficient⁶⁶, researchers must adhere to a higher standard following the principles below.

(2) *Researchers must prepare a detailed plan prior to beginning any study.* This should include an articulation of research questions; a description of the techniques to be used and expected impact on remains (including skeletal elements to be studied and quantity to be used); a description of the type of DNA data that will be generated; any plan for material sharing with collaborating laboratories; a timeline for the return of unused material and sharing of results; a plan for how, where and by whom results will be disseminated; a plan for capacity building or training in settings where this can be of value; and a plan for data storage and sharing agreed by stakeholders and complying with open data principles⁶⁷. The plan should define the scope of the research and honestly communicate possible outcomes, recognizing that the analysis of genetic data can lead in unanticipated directions. Such a plan creates a record of the intended research that can be referred to later should there be a deviation from it. Adjustments to the study design should occur only with the support of those involved in the original agreement: researchers must acknowledge that when permission is granted to study the remains of ancient individuals, they become the stewards of that material for the purpose for which consent was obtained, but that ‘ownership’ is not transferred⁶⁸. It is the responsibility of the researchers to share their plan with those responsible for the human remains and other groups whose perspectives need to be reflected; as such, it should be written in a way that is accessible to a non-specialist audience. If appropriate and agreed upon by all relevant parties, a pathway toward repatriation of human remains curated outside their area of origin may be outlined in the research plan.

(3) *Researchers must minimize damage to human remains.* Minimizing the impact of research on anthropological collections is especially important given the recent focus on a single skeletal element—the petrous bone—that often yields many-fold more human genetic data than other elements^{69–72}. Researchers should develop a strategy through consultation with other stakeholders to balance concerns about protecting remains with their scientific analysis. Researchers should not collect human remains without training in best practice techniques to minimize damage while maximizing yield of useable data^{11,12,73–76}. Researchers should not sample more material than necessary to be able to address their scientific questions, should provide documentation to those responsible for human remains noting when sampling occurred, and should report negative results to prevent repeated analysis using similar methods on remains with poor DNA preservation. Before sampling, morphology should be documented with high-resolution photography and bioarchaeological assessment. At least for very ancient individuals or those from unique contexts, micro-CT scans or casts should be produced, and there should be discussion about whether analysis of faunal or non-diagnostic remains should take place first to evaluate DNA preservation at a site.

Once sampling has occurred, responsible treatment of remains can also be promoted through the sharing of material as well as derived molecular products such as DNA extracts and libraries, which reduces the need for additional sampling in subsequent studies. Researchers have the responsibility to maintain derived molecular products for the purposes of study replication. We also encourage researchers to seek approval for sharing sampled human remains and derived products between laboratories. This facilitates reappraisal of the questions addressed in the original study, as well as additional analyses beyond the scope of the initial study, as long as such uses are consistent with an approved research plan.

(4) *Researchers must ensure that data are made available following publication to allow critical re-examination of scientific findings.* Ancient DNA data must be published in a timely manner and subsequently made available at least for the purpose of critical reappraisal of results^{77,78}. Scientists cannot ethically participate in a study if there

is not a guarantee that data will be available at least for the purpose of verifying the accuracy of published findings, and this guarantee needs to be incorporated into the original permissions for the study. This is important both to prevent the spread of misinformation, and to enable future analyses that seek to re-examine the same questions.

It is best practice to make data fully available following publication, and indeed nearly all ancient genomic data have been published this way in enduring public data repositories, which has been an ethical strength of the field⁷⁹. Beyond contributing to the advancement of scientific knowledge, making data fully available contributes to responsible stewardship of human remains, in that the ability to reuse data reduces the need for further sampling. However, we can envision scenarios in which discussions among stakeholders reveal that it would be ethical to limit the ways in which ancient DNA data can be reused, such as when reporting results from some types of analyses could harm stakeholders, which could outweigh the benefits of fully open data^{6,10,80}. In these cases—which should be identified during a process of engagement prior to the inception of the study—the limitation of data distribution to qualified researchers who agree to only analyse the data for the purpose of reappraising the study findings should be part of the initial research plan.

When data are not made fully publicly available, management and distribution of data for the purpose of critical re-examination of results should be performed by an organization with expertise to prevent data misuse and without an interest in research outcomes. It has been suggested that stakeholders such as Indigenous groups could be responsible for managing distribution of data after publication to researchers^{10,13,15,81}. However, it is not consistent with professional ethics for researchers to participate in a study where those with a stake in the research findings can deny the sharing of data to qualified researchers whose goal is to critically re-examine the questions covered by the original research agreement. There are established mechanisms for ensuring distribution of non-fully public data to researchers who apply to use it for the purposes of critical re-examination. For example, data could be made available through a repository that shares data only upon formal application and approval from a data access committee that determines whether the applicant's request satisfies the limitations on data use described in the publication. This is sometimes done for modern genomic data to address privacy concerns through mechanisms such as the dbGaP or EGA repositories^{82,83}, although a shortcoming is that the data-acquisition process can be slow⁷⁶. Repositories for data from Indigenous people are also beginning to be established that involve communities in data storage and dissemination^{10,13,79,84,85}. While no stakeholder group—including researchers, community representatives, or curators—should control the distribution of data to researchers who wish to critically re-examine questions covered in the original research agreement, Indigenous data repositories could have an important role in storing and distributing data for purposes beyond those covered by the original research agreement.

(5) *Researchers must engage with other stakeholders from the beginning of a study and ensure respect and sensitivity to stakeholder perspectives.* A project to generate new ancient DNA data may be initiated by diverse stakeholders, including but not limited to local communities, archaeologists, anthropologists, geneticists or curators, any or all of whom may be members of the research team if they contribute in a scholarly way to the work. Other stakeholders who are consulted should be thanked in the Acknowledgments sections of papers if they consent to be named. Stakeholders—ideally including groups from the place of origin of the human remains being studied—should be actively involved in discussions about study design, research questions and whether a scientific project should proceed. Researchers must accept a negative answer if stakeholders are not collectively supportive of the work taking place¹⁵.

Once a consensus to proceed has been reached, professional scientific ethics requires that researchers are able to pursue their work up to the point of publication without requiring further approval. The suggestion

that there should be a requirement for manuscripts to be approved by stakeholder groups who are not members of the research team before publication^{15,81} is not feasible, as researchers cannot ethically participate in a study in which this is mandated. The imperative of scientific independence once a study begins does not mean that researchers should publish results without considering stakeholder perspectives about the implications of the data. It is valuable to invite stakeholders to engage with research results through the addition of their perspectives or by providing critical feedback prior to publication especially when results are surprising and challenge previous assumptions. Continued engagement with other stakeholders after the beginning of a study is an effective mechanism by which researchers can address their professional ethical obligation to understand whether reporting a result in a particular way is likely to cause harm. If these conversations indicate that a result cannot be shared in a way that avoids substantial harm to a stakeholder group, researchers should not publish that result.

Researchers should be available to provide regular updates and must commit to returning results at the culmination of a project. It should be made clear from the outset what the study's potential findings may be, that genetic data may be inconsistent with other forms of knowledge, and that while the results of scientific analyses are reported as scholarly output, they do not discredit, diminish or decrease the importance of traditional expertise and deeply held beliefs. Discrepancies between results from genetic analyses and other lines of evidence should be reported as important elements of the compound nature of understanding the past.

Researchers should commit to working with stakeholders on outreach efforts that create additional outputs accessible to communities. This may involve working with local collaborators to translate the results of papers into local languages^{30,35,36,86,87}, developing children's educational resources^{88–91}, producing brochures and pamphlets for libraries or other community centres, or working with museums to design exhibits. When relevant, researchers should contribute to training and education, especially for members of stakeholder groups and local communities^{4,15}, and should consider ways in which to improve the curatorial state of collections¹¹. This can include supplying the resources needed for participating in the generation, interpretation and dissemination of data, for example training in sampling of human remains or laboratory techniques, and financial support for further training or attending professional meetings. It is important for granting agencies to ensure that adequate funding is allocated to capacity building initiatives.

Promoting ethical DNA research on human remains

As part of their work, scholars also have a broader obligation to correct ideologically motivated distortions of research results. Following the technical presentation of data in academic publications, many studies are summarized by science journalists or educators for communication to broad audiences. There have been instances of journalistic and governmental misrepresentation of study findings for political ends, and scientists have an obligation to work to correct misinterpretation when appropriate⁶⁴. Reaching out to the public can include writing essays and books, and contributing to social media and documentaries^{92–100}.

Given the overwhelming support for these guidelines among the diverse participants in our workshop, we anticipate that the broader community engaged in ancient DNA research will be supportive of these principles as well, and suggest that they could form a basis for official guidelines from journals, professional organizations and granting agencies going forward.

Translation of this article into more than twenty languages. This article was reviewed in English. The authors prepared full translations (which were not peer-reviewed or checked for correctness by Springer Nature) into more than twenty languages they speak, including Afrikaans, Arabic, Catalan, Chinese, Croatian, French, German, Hawaiian, Hebrew, Hindi, Hungarian, Japanese, Portuguese, Punjabi, Russian, Sinhala, Spanish, Swahili, Swedish, Tamil, Turkish, Urdu, and Xhosa, and have made them available at [figshare \(dx.doi.org/10.6084/m9.figshare.16744552\)](https://dx.doi.org/10.6084/m9.figshare.16744552).

1. Booth, T. J. A stranger in a strange land: a perspective on archaeological responses to the palaeogenetic revolution from an archaeologist working amongst palaeogeneticists. *World Archaeol.* **51**, 586–601 (2019).
An archaeologist's perspective on the challenges to and benefits of integrating palaeogenomic data with archaeological evidence to develop a richer understanding of people in the past.
2. Austin, R. M., Sholts, S. B., Williams, L., Kistler, L. & Hofman, C. A. To curate the molecular past, museums need a carefully considered set of best practices. *Proc. Natl Acad. Sci. USA* **116**, 1471–1474 (2019).
A museum-based perspective on the responsibility of preserving collections and best practices for evaluating proposals for biomolecular research.
3. Bardill, J. et al. Advancing the ethics of paleogenomics. *Science* **360**, 384–385 (2018).
Provides Indigenous perspectives on ethical best practices in ancient DNA research and offers guidance on appropriate engagement with stakeholder communities.
4. Claw, K. G. et al. A framework for enhancing ethical genomic research with Indigenous communities. *Nat. Commun.* **9**, 2957 (2018).
5. Claw, K. G. et al. Chaco Canyon dig unearths ethical concerns. *Hum. Biol.* **89**, 177 (2017).
6. Cortez, A. D., Bolnick, D. A., Nicholas, G., Bardill, J. & Colwell, C. An ethical crisis in ancient DNA research: Insights from the Chaco Canyon controversy as a case study. *J. Soc. Archaeol.* 146960532199160 (2021).
7. Crellin, R. J. & Harris, O. J. T. Beyond binaries. Interrogating ancient DNA. *Archaeol. Dial.* **27**, 37–56 (2020).
8. Eisenmann, S. et al. Reconciling material cultures in archaeology with genetic data: the nomenclature of clusters emerging from archaeogenomic analysis. *Sci. Rep.* **8**, 13003 (2018).
9. Gibbon, V. E. African ancient DNA research requires robust ethics and permission protocols. *Nat. Rev. Genet.* **21**, 645–647 (2020).
A review emphasizing that ethical guidance developed in Africa for genomic research on living people can be applied with modification to ancient DNA studies, highlighting protocols developed through collaboration among South African institutions, agencies and community groups.
10. Hudson, M. et al. Rights, interests and expectations: indigenous perspectives on unrestricted access to genomic data. *Nat. Rev. Genet.* **21**, 377–384 (2020).
11. Prendergast, M. E. & Sawchuk, E. Boots on the ground in Africa's ancient DNA 'revolution': archaeological perspectives on ethics and best practices. *Antiquity* **92**, 803–815 (2018).
Reviews ethical issues particular to African bioarchaeological research contexts and suggests guidelines for best practices for ancient DNA research in institutional collections.
12. Sirak, K. A. & Sedig, J. W. Balancing analytical goals and anthropological stewardship in the midst of the paleogenomics revolution. *World Archaeol.* **51**, 560–573 (2019).
13. Tsosie, K. S., Begay, R. L., Fox, K. & Garrison, N. A. Generations of genomes: advances in paleogenomics technology and engagement for Indigenous people of the Americas. *Curr. Opin. Genet. Dev.* **62**, 91–96 (2020).
14. Hakenbeck, S. E. Genetics, archaeology and the far right: an unholy trinity. *World Archaeol.* **51**, 517–527 (2019).
15. Wagner, J. K. et al. Fostering responsible research on ancient DNA. *Am. J. Human Genet.* **107**, 183–195 (2020).
This guidance to promote ethical engagement between researchers and stakeholder communities involved in ancient DNA research was the first set of recommendations to be approved by a professional organization, the American Society of Human Genetics.
16. *Assessment and Reflection on the Ethical Dimensions of Archaeogenetics Research*, <https://www.eva.mpg.de/archaeogenetics/ethics.html> (Max Planck Institute for Evolutionary Anthropology, 2021).
17. Evison, M. P. Genetics, ethics and archaeology. *Antiquity* **70**, 512–514 (1996).
18. Friedlaender, J. S., Gentz, F., Green, K. & Merriwether, D. A. A cautionary tale on ancient migration detection: mitochondrial DNA variation in Santa Cruz Islands, Solomon Islands. *Hum. Biol.* **74**, 453–471 (2002).
19. Holm, S. The privacy of Tutankhamen—utilising the genetic information in stored tissue samples. *Theor. Med. Bioeth.* **22**, 437–449 (2001).
20. Hublin, J.-J. et al. Suggested guidelines for invasive sampling of hominid remains. *J. Hum. Evol.* **55**, 756–757 (2008).
21. Kaestle, F. A. & Horsburgh, K. A. Ancient DNA in anthropology: methods, applications, and ethics. *Am. J. Phys. Anthropol.* **119**, 92–130 (2002).
22. Lalueza Fox, C. Ancient DNA studies and new bioethical problems. *Hum. Evol.* **12**, 287 (1997).
23. O'Rourke, D. H., Hayes, M. G. & Carlyle, S. W. Ancient DNA studies in physical anthropology. *Annu. Rev. Anthropol.* **29**, 217–242 (2000).
24. Sealy, J. Managing collections of human remains in South African museums and universities: ethical policy-making and scientific value: reviews of current issues and research findings: human origins research in South Africa. *S. Afr. J. Sci.* **99**, 238–239 (2003).
25. Morris, A. Ancient DNA comes of age, but still has some teenage problems. *S. Afr. J. Sci.* **113**, 2 (2017).
26. Schroeder, D. What is ethics dumping? *Biologist* **66**, 22–25 (2019).
27. Bockarie, M. J. We need to end "parachute" research which sidelines the work of African scientists. *Quartz Africa* <https://qz.com/africa/1536355/african-scientists-are-sidelined-by-parachute-research-teams/> (2019).
28. Rasmussen, M. et al. An Aboriginal Australian genome reveals separate human dispersals into Asia. *Science* **334**, 94–98 (2011).
29. Rasmussen, M. et al. The genome of a Late Pleistocene human from a Clovis burial site in western Montana. *Nature* **506**, 225–229 (2014).
30. Posth, C. et al. Reconstructing the deep population history of Central and South America. *Cell* **175**, 1185–1197.e22 (2018).
31. Scheib, C. L. et al. Ancient human parallel lineages within North America contributed to a coastal expansion. *Science* **360**, 1024–1027 (2018).
32. Bongers, J. L. et al. Integration of ancient DNA with transdisciplinary dataset finds strong support for Inca resettlement in the south Peruvian coast. *Proc. Natl Acad. Sci. USA* **117**, 18359–18368 (2020).
33. Fernandes, D. M. et al. A genetic history of the pre-contact Caribbean. *Nature* **590**, 103–110 (2021).
34. Fleskes, R. E. et al. Ancestry, health, and lived experiences of enslaved Africans in 18th century Charleston: an osteobiographical analysis. *Am. J. Phys. Anthropol.* **175**, 3–24 (2021).
35. Nakatsuka, N. et al. A Paleogenomic reconstruction of the deep population history of the Andes. *Cell* **181**, 1131–1145.e21 (2020).
36. Nakatsuka, N. et al. Ancient genomes in South Patagonia reveal population movements associated with technological shifts and geography. *Nat. Commun.* **11**, 3868 (2020).
37. Wang, C.-C. et al. Genomic insights into the formation of human populations in East Asia. *Nature* **591**, 413–419 (2021).
38. Wibowo, M. C. et al. Reconstruction of ancient microbial genomes from the human gut. *Nature* **594**, 234–239 (2021).
39. *Statement Concerning the Treatment of Human Remains* (Society for American Archaeology, 2021).
40. Pickrell, J. Ancient Australian goes home. *Science* **358**, 853–853 (2017).
41. Australian government policy on Indigenous repatriation. *Department of Communications and the Arts* <https://www.arts.gov.au/documents/australian-government-policy-indigenous-repatriation> (2016).
42. Return of cultural heritage. Australian Institute of Aboriginal and Torres Strait Islander Studies <https://aiatsis.gov.au/about/what-we-do/return-cultural-heritage> (2021).
43. Moctezuma, E. M. *Las piedras negadas: De la Coatlicue al Templo Mayor* (Consejo Nacional para la Cultura y las Artes, 1998).
44. Wade, P. Race and Ethnicity in Latin America: *How the East India Company Shaped the Modern Multinational* 2nd edn (Pluto, 2010).
45. Ortega Muñoz, A. & Tiesler, V. in *Colecciones Esqueléticas Humanas en México: Excavación, Catalogación, Conservación y Aspectos Normativos* (eds Márquez Morfín, L. & Ortega Muñoz, A.) 399–413 (Instituto Nacional de Antropología e Historia, 2011).
46. Devine, T. L. Indigenous identity and identification in Peru: Indigenismo, education and contradictions in state discourses. *J. Lat. Am. Stud.* **8**, 63–74 (1999).
47. Herrera, A. in *Indigenous Peoples and Archaeology in Latin America* (eds Gnecco, C. et al.) 67–88 (2011).
48. Silverman, H. Cultural resource management and heritage stewardship in Peru. *J. Heritage Steward.* **3**, 1 (2006).
49. Endere, M. L., Cali, P. & Funari, P. P. A. in *Indigenous Peoples and Archaeology in Latin America* 159–178 (Routledge, 2016).
50. Hodgson, D. L. Becoming Indigenous in Africa. *Afr. Stud. Rev.* **52**, 1–32 (2009).
51. Plackett, B. Arab-World archaeologists must avoid disturbing Islamic graves. *Al-Fanar Media* <https://www.al-fanarmedia.org/2016/05/arab-world-archaeologists-must-avoid-disturbing-islamic-graves/> (2016).
52. Legassick, M. & Rassool, C. *Skeletons in the Cupboard: South African Museums and the Trade in Human Remains 1907–1917* (South African Museum, McGregor Museum, 2000).
53. Redman, S. J. *Bone Rooms: From Scientific Racism to Human Prehistory in Museums* (Harvard University Press, 2016).
54. Gibbon, V. E. & Morris, A. G. UCT Human Skeletal Repository: its stewardship, history, composition and educational use. *J. Compar. Hum. Biol.* **72**, 139–147 (2021).
55. Steyn, M., Morris, A., Mosothwane, M., Nienaber, C. & Maat, G. Opening the cupboard—lessons in biology and history from African skeletons. *S. Afr. Archaeol. Bull.* **11**, 1–6 (2013).
56. Smith, A. B. in *African Memory in Danger* (eds Mayor, A. et al.) 52–60 (2015).
57. Urassa, M. et al. Cross-cultural research must prioritize equitable collaboration. *Nature Human Behaviour* **5**, 668–671 (2021).
58. Nakatsuka, N. et al. The promise of discovering population-specific disease-associated genes in South Asia. *Nat. Genet.* **49**, 1403–1407 (2017).
59. Reich, D., Thangaraj, K., Patterson, N., Price, A. L. & Singh, L. Reconstructing Indian population history. *Nature* **461**, 489–494 (2009).
60. Thangaraj, K. et al. Reconstructing the origin of Andaman Islanders. *Science* **308**, 996–996 (2005).
61. Arnold, B. 'Ariërdämmerung': race and archaeology in Nazi Germany. *World Archaeol.* **38**, 8–31 (2006).
62. Frieman, C. J. & Hofmann, D. Present pasts in the archaeology of genetics, identity, and migration in Europe: a critical essay. *World Archaeol.* **51**, 528–545 (2019).
63. Moody, O. Hungarian royal lineage traced to Afghanistan as Viktor Orban pushes east. *The Times* (17 July 2020).
64. Hasson, N. DNA research holds the keys to human history—but it's being weaponized by politicians. *Haaretz.com* <https://www.haaretz.com/archaeology/premium-magic-or-a-trap-dna-changes-study-of-the-past-1.8009668> (2019).
65. Wolinsky, H. Ancient DNA and contemporary politics. *EMBO Rep.* **20**, e49507 (2019).
66. Ali, J. et al. A scoping review of genetics and genomics research ethics policies and guidelines for Africa. *BMC Med. Ethics* **22**, 39 (2021).
67. Wilkinson, M. D. et al. The FAIR Guiding Principles for scientific data management and stewardship. *Sci. Data* **3**, 160018 (2016).
68. Arbour, L. & Cook, D. DNA on loan: issues to consider when carrying out genetic research with aboriginal families and communities. *Community Genet.* **9**, 153–160 (2006).
69. Gamba, C. et al. Genome flux and stasis in a five millennium transect of European prehistory. *Nat. Commun.* **5**, 5257 (2014).
70. Pinhasi, R. et al. Optimal ancient DNA yields from the inner ear part of the human petrous bone. *PLoS ONE* **10**, e0129102 (2015).
71. Hansen, H. B. et al. Comparing ancient DNA preservation in petrous bone and tooth cementum. *PLoS ONE* **12**, e0170940 (2017).
72. Parker, C. et al. A systematic investigation of human DNA preservation in medieval skeletons. *Sci. Rep.* **10**, 18225 (2020).
73. Sirak, K. A. et al. A minimally-invasive method for sampling human petrous bones from the cranial base for ancient DNA analysis. *BioTechniques* **62**, 283–289 (2017).
74. Sirak, K. A. et al. Human auditory ossicles as an alternative optimal source of ancient DNA. *Genome Res.* **30**, 427–436 (2020).
75. Harney, É. et al. A minimally destructive protocol for DNA extraction from ancient teeth. *Genome Res.* **31**, 472–483 (2021).

76. Yates, J. A. F. A–Z of ancient DNA protocols for shotgun Illumina Next Generation Sequencing. <https://doi.org/10.17504/protocols.io.bj8nkrve> (2020).
77. The next 20 years of human genomics must be more equitable and more open. *Nature* **590**, 183–184 (2021).
78. Powell, K. The broken promise that undermines human genome research. *Nature* **590**, 198–201 (2021).
79. Anagnostou, P. et al. When data sharing gets close to 100%: what human paleogenetics can teach the open science movement. *PLoS ONE* **10**, e0121409 (2015).
- Discusses the universal practice of fully public data sharing in ancient human DNA research, arguing this is key to establishing reliable and replicable scientific practices.**
80. Prictor, M., Huebner, S., Teare, H. J. A., Burchill, L. & Kaye, J. Australian Aboriginal and Torres Strait Islander collections of genetic heritage: the legal, ethical and practical considerations of a dynamic consent approach to decision making. *J. Law Med. Ethics* **48**, 205–217 (2020).
81. Garrison, N. A. et al. Genomic research through an indigenous lens: understanding the expectations. *Annu. Rev. Genom. Hum. Genet.* **20**, 495–517 (2019).
82. Mailman, M. D. et al. The NCBI dbGaP database of genotypes and phenotypes. *Nat. Genet.* **39**, 1181–1186 (2007).
83. Lappalainen, I. et al. The European Genome–Phenome Archive of human data consented for biomedical research. *Nat. Genet.* **47**, 692–695 (2015).
84. CARE principles of indigenous data governance. *Global Indigenous Data Alliance* <https://www.gida-global.org/care>.
85. Tsoie, K. S., Fox, K. & Yracheta, J. M. Genomics data: the broken promise is to Indigenous people. *Nature* **591**, 529–529 (2021).
86. Jeong, C. et al. A dynamic 6,000-year genetic history of Eurasia's eastern steppe. *Cell* **183**, 890–904.e29 (2020).
87. Wilkin, S. et al. Dairy pastoralism sustained eastern Eurasian steppe populations for 5,000 years. *Nat. Ecol. Evol.* **4**, 346–355 (2020).
88. Stockhammer, P. W., Mittnik, A., Massy, K. & Knipper, C. Mobilität—Die wissenden Frauen vom Lechtal. *Spektrum Wiss. Verl. Ges. Kultur* **4**, 38–41 (2018).
89. Stockhammer, P. W. BRONZEON: learning by gaming. *Archaeologist* **110**, 24–25 (2020).
90. Sirak, K., Keegan, W. F. Where did the first people in the Caribbean come from? *Science Journal for Kids and Teens* <https://sciencejournalforkids.org/articles/where-did-the-first-people-in-the-caribbean-come-from/> (2021).
91. Warinner Group. Adventures in Archaeological Science. <http://christinawarinner.com/outreach/children/adventures-in-archaeological-science/> (2017).
92. Birney, E., Inouye, M., Raff, J., Rutherford, A. & Scally, A. The language of race, ethnicity, and ancestry in human genetic research. Preprint at <https://arxiv.org/abs/2106.10041> (2021).
93. Fischer, M., Krause, J. & Richter, S. *Jena Declaration. The concept of race is the result of racism, not its prerequisite*. Opening joint declaration at the 112th Annual Meeting of the German Zoological Society https://www.uni-jena.de/en/190910_JenaerErklaerung_EN (2019).
94. Gokcumen, O. & Frachetti, M. The impact of ancient genome studies in archaeology. *Annu. Rev. Anthropol.* **49**, 277–298 (2020).
95. Howe, N. 'Stick to the science': when science gets political. *Nature Podcast* <https://doi.org/10.1038/d41586-020-03067-w> (2020).
96. Krause, J. & Trappe, T. *A Short History of Humanity: A New History of Old Europe* (Random House, 2021).
97. Orlando, L. et al. Ancient DNA analysis. *Nat. Rev. Methods Prim.* **1**, 1–26 (2021).
98. Reich, D. *Who We Are and How We Got Here: Ancient DNA and the New Science of the Human Past* (Pantheon, 2018).
99. Reich, D. & Patterson, C. Ancient DNA is changing how we think about the Caribbean. *The New York Times* (23 December 2020).
100. Motti, J. M. B., Luisi, P., Salemme, M., Santiago, F. & Nores, R. 7.000 años de historia en el fin del mundo. *Desde la Patagonia, Difundiendo Saberes* **17**, 12–20 (2020).

Acknowledgements The participants in the workshop on ancient DNA ethics who are authors thank many colleagues who improved this article through discussions and critical comments. To ensure open access, the authors have applied a CC BY licence to any accepted manuscript arising from this submission. C.J.F. acknowledges support from the Australian Research Council Discovery Project DP160100811. V.G. acknowledges support from the National Research Foundation (NRF) South Africa; opinions expressed and conclusions arrived at are those of the authors and are not necessarily attributed to the NRF. M.O. acknowledges support from Conselho Nacional de Desenvolvimento Científico e Tecnológico grant 302163/2017-4 and from Fundação de Amparo à Pesquisa do Estado de São Paulo grant 2018/23282-5. P.S. acknowledges Francis Crick Institute core funding (FC001595) from Cancer Research UK, the UK Medical Research Council and the Wellcome Trust. V.S. acknowledges funding from the Alon Fellowship. M. Soressi acknowledges support from Dutch Research council grant V.I.C.191.070. A.S.-N. acknowledges the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. K.T. was supported by a J. C. Bose Fellowship (JCB/2019/000027). SERB and CSIR, Ministry of Science and Technology, Government of India. C.W. acknowledges support from the European Research Council (ERC-2017-StG 804844- DAIRYCULTURES) and the Werner Siemens Stiftung. The authors from Harvard Medical School acknowledge support from the John Templeton Foundation (6122) and the Howard Hughes Medical Institute. The authors from MPI Leipzig and MPI Jena are funded by the Max Planck Society and the Max Planck Harvard Research Center for the Archaeoscience of the Ancient Mediterranean. R.N., E.S., J.S., K.S., V.T., and J.L.P. acknowledge support from the National Geographic Society.

Author contributions All authors participated in discussions and are listed alphabetically.

Competing interests The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to Lars Fehren-Schmitz, Mary E. Prendergast, David Reich, Jakob Sedig, Kendra Sirak or Philipp W. Stockhammer.

Peer review information *Nature* thanks Shadreck Chirikure, Emma Kowal, Wibhu Kutanana, Kirsty Squires and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at <http://www.nature.com/reprints>.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© Springer Nature Limited 2021

¹Department of Genetics, Harvard Medical School, Boston, MA, USA. ²Department of Evolutionary Anthropology, University of Vienna, Vienna, Austria. ³Department of Anthropology, Hartwick College, Oneonta, NY, USA. ⁴Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, USA. ⁵Max Planck Institute for the Science of Human History, Jena, Germany. ⁶Romano-Germanic Commission of the German Archaeological Institute, Frankfurt am Main, Germany. ⁷Francis Crick Institute, London, UK. ⁸Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA, USA. ⁹Department of Ancient Indian History Culture and Archaeology, Deccan College Post Graduate and Research Institute, Pune, India. ¹⁰Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. ¹¹Department of Anthropology, University of California, Santa Cruz, CA, USA. ¹²UCSC Genomics Institute, University of California, Santa Cruz, CA, USA. ¹³Department of Anthropology, Washington University in St Louis, St Louis, MO, USA. ¹⁴Centro de Genética y Biología Molecular, Facultad de Medicina, Universidad de San Martín de Porres, Lima, Peru. ¹⁵School of Archaeology and Anthropology, The Australian National University, Canberra, Australian Capital Territory, Australia. ¹⁶Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Beijing, China. ¹⁷Division of Clinical Anatomy and Biological Anthropology, Department of Human Biology, University of Cape Town, Cape Town, South Africa. ¹⁸Department of Anthropology, University of California, Santa Barbara, CA, USA. ¹⁹School of Anthropology, University of Arizona, Tucson, AZ, USA. ²⁰National Museum of Nature and Science, Ibaraki, Japan. ²¹Florida Museum of Natural History, Gainesville, FL, USA. ²²Department of Genetics, School of Biological Sciences, Madurai Kamaraj University, Madurai, India. ²³Department of Anthropology, University of South Florida, Tampa, FL, USA. ²⁴Institute of Evolutionary Biology (CSIC-UPF), Barcelona, Spain. ²⁵Australian Centre for Ancient DNA, School of Biological Sciences and The Environment Institute, University of Adelaide, Adelaide, South Australia, Australia. ²⁶ARC Centre of Excellence for Australian Biodiversity and Heritage, University of Adelaide, Adelaide, South Australia, Australia. ²⁷Office of the Chancellors, Duke Kunshan University, Jiangsu, China. ²⁸Howard Hughes Medical Institute, Boston, MA, USA. ²⁹Broad Institute of MIT and Harvard, Cambridge, MA, USA. ³⁰School of Health Science, Sapporo Medical University, Sapporo, Japan. ³¹Institute of Ecology and Evolution, University of Bern, Bern, Switzerland. ³²Lithuanian Institute of History and Department of Archaeology, History Faculty, Vilnius University, Vilnius, Lithuania. ³³Departamento de Antropología, Facultad de Filosofía y Humanidades, Universidad Nacional de Córdoba, Instituto de Antropología de Córdoba (IDACOR), CONICET, Córdoba, Argentina. ³⁴Earth Sciences Department, National Museums of Kenya, Nairobi, Kenya. ³⁵Department of Genetics and Evolutionary Biology, University of São Paulo, São Paulo, Brazil. ³⁶Human Evolution and Archaeological Sciences, University of Vienna, Vienna, Austria. ³⁷DBT-Centre for DNA Fingerprinting and Diagnostics, Hyderabad, India. ³⁸Department of Anthropology, Rice University, Houston, TX, USA. ³⁹Instituto Nacional de Antropología e Historia, Michoacán, Mexico. ⁴⁰School of Advanced Sciences, The Graduate University for Advanced Studies (SOKENDAI), Kanagawa, Japan. ⁴¹Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada. ⁴²Department of Anthropology, Stony Brook University, Stony Brook, NY, USA. ⁴³ArchaeoZOOlogy in Siberia and Central Asia–ZooSCAN, CNRS–IAET SB RAS International Research Laboratory, Novosibirsk, Russia. ⁴⁴Department of Anatomy and Anthropology and Department of Human Molecular Genetics and Biochemistry, Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv, Israel. ⁴⁵The Dan David Center for Human Evolution and Biohistory Research, Tel Aviv University, Tel Aviv, Israel. ⁴⁶Anthropology Department, University of Montana, Missoula, MO, USA. ⁴⁷Faculty of Archaeology, Leiden University, Leiden, Netherlands. ⁴⁸Vanuatu Cultural Centre, Port Vila, Vanuatu. ⁴⁹Institute for Pre- and Protohistoric Archaeology and Archaeology of the Roman Provinces, Ludwig Maximilian University, Munich, Germany. ⁵⁰Institute of Archaeogenomics, Research Centre for the Humanities, Eötvös Loránd Research Network, Budapest, Hungary. ⁵¹CSIR-Centre for Cellular and Molecular Biology, Hyderabad, India. ⁵²School of Anthropological Sciences, Universidad Autónoma de Yucatán, Mérida, Mexico. ⁵³Department of Anthropology and Ethnology, Institute of Anthropology, School of Sociology and Anthropology, State Key Laboratory of Cellular Stress Biology, School of Life Sciences, Xiamen University, Xiamen, China. ⁵⁴School of Basic Medical Sciences, Zhejiang University School of Medicine, and Institute of Asian Civilizations, Zhejiang University, Hangzhou, China. ⁵⁵Department of Anthropology, Harvard University, Cambridge, MA, USA. ⁵⁶Department of Anatomy, University of Sri Jayewardenepura, Nugegoda, Sri Lanka. ⁵⁷Department of Archaeology, Hazara University, Mansehra, Pakistan. ⁵⁸e-mail: lfehrens@ucsc.edu; mary@rice.edu; reich@genetics.med.harvard.edu; Jakob.Sedig@hms.harvard.edu; Kendra_Sirak@hms.harvard.edu; philipp.stockhammer@lmu.de